CRESTED WHEATGRASS
ITS VALUES, PROBLEMS, AND MYTHS

Symposium Proceedings

Utah State University
Logan, Utah

CRESTED WHEATGRASS:

Its Values, Problems and Myths;

Symposium Proceedings

Logan, Utah, October 3-7, 1983

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Sponsors: Utah State University
Range Science Department
Cooperative Extension Service
Institute for Land Rehabilitation
Conference and Institute Division

Utah State University
Logan, Utah
1986

Acknowledgements

Appreciation is due personnel of the USU Conference and Institute Division, especially Suzanne Boskoff, for their successful staging of all physical aspects and facilities of the Symposium. The several session chairmen made important contributions to the operation of the Symposium as well, and numerous people helped facilitate the field trips. Particular thanks are due J. C. Smith, Snowville rancher, and Lee A. Sharp of the University of Idaho, who guided the mid-symposium field trip on the ranch and research area, respectively.

Production of the proceedings is heavily in the debt of Roma Henderson, administrative secretary in the Range Science Department, who cheerfully accepted the months-long continuing assignment of preparing copy. Through many drafts, she has patiently worked to produce the proceedings in uncounted hours of editing on the word processor. Except for one major paper, she has personally set every word of the proceedings. The job could not have been done without service such as hers, and this publication is in full measure her accomplishment.

Finally, appreciation is also due Richard Clawson and Kathy Birch of USU Publication Design and Production, who smoothed the way to bringing the proceedings to the light of published day.

To all those who had a hand in this effort, thank you.

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Foreword

Crested wheatgrass has long been the major grass species used in rangeland improvement and rehabilitation projects in western North America. Its many favorable agronomic, forage and ecologic qualities have made it the grass of choice, although reservations about its widespread use have arisen in recent years. In the view of many rangeland managers, scientists and educators, crested wheatgrass may be the most important range grass in North America, having played a larger role in the management of Great Plains and Intermountain rangeland over the last 50 years than any other.

Commensurate with its first-rank status, crested wheatgrass has received a great deal of research and management attention, resulting in a far-reaching, but not well-integrated body of literature. The intent of the symposium was to develop a synthesis of available information to clearly establish the real values, problems and myths of crested wheatgrass. The Crested Wheatgrass Symposium was held at Utah State University in Logan on October 3-7, 1983. Papers were presented by individuals noted for their research or management experience with crested wheatgrass, drawn from livestock producers, western colleges and universities, federal research organizations, and state and federal land management agencies. The Symposium was sponsored by divisions of Utah State University: the Range Science Department, the Cooperative Extension Service, the Institute for Land Rehabilitation and the Conference and Institute Division. It was partially supported by funds provided under the Renewable Resources Extension Act.

The intent of this proceedings is to present the state-of-the art associated with crested wheatgrass, developed at the Symposium, and to provide a reference text to all those concerned with the grass.

Kendall L. Johnson
Editor

Setting the Stage for the Crested Wheatgrass Symposium

Don D. Dwyer

Crested wheatgrass (Agropyron desertorum); good grief--its only a grass! How can an effort such as this full four-day symposium, at such cost to participants and agencies, be justified on just a grass, or even a complex of grasses designated as crested wheatgrass?

There are a number of reasons for having this symposium, but simply stated the authors here are reporting on a singular range species--perhaps the ponderosa pine of the Intermountain range.

First of all, it is an important plant--interesting biologically and economically perhaps the single most important range plant in North America. It was introduced from Siberia with a 5000 year experience in surviving grazing, hard grazing by ungulates, and brought to the Intermountain Region where in historic perspective, grazing by ungulates was light to non-existent. Now it is abundant and widely distributed, although I cannot find a reliable estimate of the number of acres in crested wheatgrass. In addition an enormous number of wild and domestic herbivores depend on it for much of their annual forage ration.

In becoming established in the Intermountain West, crested wheatgrass has replaced a predecessor in many locations that suffers great stress under even relatively light defoliation. Yet that predecessor, bluebunch wheatgrass, (Pseudoroegneria spicata) is generally held in much higher ecological esteem.

Economically and ecologically astounding by most measures, crested wheatgrass produces from 3 to 20 times the grazing capacity of the so-called native plants it has been called on to replace. It sustains surprisingly heavy and long or even continual grazing, much to the surprise of most early range ecologists who predicted it would easily succumb to the pressures of grazing or to its alien environment, or a combination of both. Not only has it not succumbed, but crested wheatgrass has survived three of the century's worst droughts.

Despite these credentials, crested wheatgrass has its detractors. It has been the subject of serious controversy since about 1970 and especially during the "back to nature" period of the mid-70's. The crested wheatgrass detractors have claimed it should not be included in range seedings and especially in energy reclamation seedings because it was an exotic, implying it might be a "short-termer" in such situations.

Although I called it a range plant, many professionals would argue that an exotic is automatically excluded from being classified as a range plant, and must remain an invader, an alien without birthright. Therefore crested wheatgrass continues to confuse those who wish to apply to it range condition criteria and baffle those who wish to monitor its trend. On the one hand we attempt to ignore it or consider it an invader; on the other we arrogantly set utilization standards as though it were just a common, ordinary species of North American range plants. Despite the fact crested wheatgrass is one of our most heavily researched range plants, we have not provided it a place in our neat and simple ecological schemes and explanations; nor in our range management principles and practices.

After 50 years I believe this plant has gained its ecological credentials and is now subject to our vegetation classification schemes. Therefore I am declaring it is a range plant. We have decided here at Utah State University that crested wheatgrass deserves to receive its papers--at least a permanent work visa if we cannot grant it a citizenship based on naturalization.

In such vein, many things have been said both for and against crested wheatgrass and no doubt this symposium will repeat many and maybe even invent more. Personally, I am convinced the grass is too valuable to place on the ecological hold button. There are several million acres, mostly the West's most productive acres, now in crested wheatgrass and waiting for something good to happen to their use

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and management. Will we recognize the grass for the potential productivity it has? or will we continue to allow rangeland now in crested wheatgrass to be managed as though it were no different from the rest of the western range?

Crested wheatgrass has had a lot to do with keeping the western range livestock industry alive since 1935 and can have much more to do with where that industry is going in the future. As well, the role of crested wheatgrass in wildlife habitat improvement will grow in importance.

And finally, I think this grass will be involved in the examination and development of some critically important theories for rangeland management.

The stage has been set for the players who have been called here to deliver their soliloquies. A stage set not by me but by the 50-year history of research and management of crested wheatgrass in the western United States.

Our hope, as the convenors of this symposium, is that it will result in a proceedings of signal value helping us to steer a useful course for rangeland management for the future.

In: Johnson, K. L. (ed.). 1986. Crested wheatgrass: its values, problems and myths; symposium proceedings. Utah State Univ., Logan.

Keynote Address.

Crested Wheatgrass:

Its Values, Problems and Myths

Lee A. Sharp

INTRODUCTION

It is appropriate that a conference commemorating the importance to range management of the grass known as crested wheatgrass be held at this time. Crested wheatgrass was first introduced some 85 years ago and has been of special significance and importance in range revegetation for the past 50 years. The "golden grass of the west", its values, problems and myths is a subject in which I have had a great deal of interest for over 30 years.

BACKGROUND

I would like to spend some time in presenting background material of interest, at least to me, in the evolution of crested wheatgrass to the status of one of the most important forage grasses in the west.

There existed an idea or attitude around the turn of the century that rangeland was of little importance and that it would, except for the parks and forest reserves, pass to private ownership to be used for cropland agriculture. To speed this process along Congress legislated the Carey Act in 1894, the Newlands Act in 1902 and the Enlarged Homestead Act in 1909. The growing of wheat and other cereal crops became a major agricultural activity in the West from 1905 on. No need for a dryland forage crop, such as crested wheatgrass, was apparent.

Although there was no perceived need for a dry-land forage grass, federal and state experiment stations in the West were planting, testing and propagating crested wheatgrass. Were these investigators prophets of the future or only hopeful that their work would someday be useful?

In 1897-1898 Professor N. E. Hansen was sent to Russia as a special agent for the Division of Botany in the U. S. Department of Agriculture. He was charged to secure seeds and plants valuable for a variety of purposes. He "succeeded in collecting 57 varieties of vegetable seed, 289 of melon, 75 of fruit and berry plants, 150 ornamental plants, 70 wheat, 14 barley, 20 oats, 6 rye, 70 forage plants, 5 oil-producing plants, and a large number of miscellaneous seeds of desert plants" (Wilson 1899). Among the 70 forage plants were seeds of crested wheatgrass[1], four accessions identified as *A. desertorum* and one as *A. cristatum* (Dillman 1946).

One can only speculate, but it is probably significant for the western range states that it was Professor Hansen from South Dakota that was sent to Russia rather than a botanist from New York, Alabama or some other eastern state. The western experience undoubtedly gave him an eye for forage grasses adapted to western conditions.

Again in the year 1898, a stirring of concern about rangeland resources was developing. H. L. Bentley (1898), of the U.S. Department of Agriculture, expressed alarm over range injury resulting from over grazing in central Texas. Jared Smith (1899), of the Division of Agrostology, reported on grazing problems in the Southwest and how to meet them. The special Public Lands Commission, appointed by Theodore Roosevelt in October, 1903, reported that 1400 stockmen in 16 states had indicated that, "under present conditions, the greater portion of the public grazing lands is not supporting the number of stock they did formerly" (Potter 1905). Present conditions presumably referred to lack of control and regulation of the rangeland, or the opportunity to homestead, lease or purchase sufficient grazing land to make viable ranching units. In 1898 were the beginnings of the development of scientific range management.

At the turn of the century Griffiths in Arizona (1901), Bentley in Texas (1902), and Cotton in

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[1]Crested wheatgrass refers to both *Agropyron desertorum* [(Fisch. ex Link) Schult.] and *A. cristatum* [(L.) Gaertn.] in this paper.

Washington State (1908) tried artificial seeding as a means of restoring productivity to deteriorated rangelands. Shortly after transfer of the forest reserves from the Department of the Interior to the Department of Agriculture in 1905, the newly created Forest Service initiated seeding trials at a number of locations (Sampson 1913). The success of these seeding trials varied and no pronounced movement to artifically seed rangelands developed. One needs to realize that at the turn of the century, knowledge about how and when to seed was limited, and the equipment for seeding was largely horse drawn. In addition, a scarcity of seed adapted to various rangeland conditions discouraged those that would improve rangelands by artificial seeding techniques.

As one looks at the list of species used in the various seeding trials and experiments, crested wheatgrass does not appear. This is not surprising because seed distributed from the 1898 introduction did not lead to an increase of available seed. Imagine what the agronomists at the experiment stations in Alabama, Indiana and Michigan thought when crested wheatgrass was planted in the kind of environment that exists at those locations. Some seed was sent to Washington and Colorado but there is no record of any seed increase from either location (Dillman 1946).

At about this time (1906), a second introduction of crested wheatgrass from the same area as the first was distributed to various experiment stations. Dillman (1946) indicates that the seed distributed to the Belle Fourche and Mandan experiment stations provided for the distribution and establishment of crested wheatgrass in the northern Great Plains between 1907 and the early 1920's. The first World War increased the conversion of rangeland to wheatland, and the time for crested wheatgrass had not yet arrived.

The depression, drought and dust storms of the 1930's brought home to the nation that renewable natural resources were not inexhaustable. Excessive production of agricultural goods contributed to the economic depression of the 1930's. Advancing technology, along with an increase in the area devoted to crops, increased production and, consequently, depressed farm prices. A severe drought during this period along with depressed farm prices caused a massive abandonment of farm land in the plains and western states. Dust storms were a common occurrence and the fruits of an unwise land policy became evident. The decade of the 30's became a period of transition from a land policy stressing settlement to one conserving the land for the general welfare of society.

Congress and the administration undertook a number of actions to implement the change in land use philosophy that had emerged. Following the national land use conference in Chicago, the Secretary of Agriculture appointed a National Land Use Planning Committee (Gray 1935). An inventory of the nation's land resources was undertaken so that recommendations for correction of the many maladjustments arising from an unwise land use policy and practices could be made (Wooten 1965). The 1930's was the period in which the Civilian Conservation Corps (CCC) was created, the Taylor Grazing Act provided for regulation of the unreserved and unappropriated public domain, the Soil Conservation Act created the Soil Conservation Service, and a massive federal land-purchase program was initiated.

The importance of crested wheatgrass began to be realized when the federally purchased lands (about 7.5 million acres) were put under management. There was a need on these lands to stop soil erosion, restore vegetal cover on abandoned cropland, and provide an example of the benefits that accrue from suitable land use practices. Because much of the potential rangeland was arid or semiarid and existed over a wide range of soil types, a plant species adapted to such conditions was needed to revegetate cropland and deteriorated ranges.

The time had arrived for crested wheatgrass. There probably never has been a grass so right for the time and the conditions that existed in 1933 when the first funds for submarginal land purchases were allotted. It is fortunate that crested wheatgrass was introduced at an earlier period and that some experiment stations were interested in producing seed and testing the species as a forage plant. By the time the drought and depression years of the 1930's had arrived, crested wheatgrass seed was readily available. The seeding of the farmland purchased by the federal government under the Land Utilization program, first by the Agricultural Adjustment Administration and then by the Soil Conservation Service, established the value of crested wheatgrass for range rehabilitation. After 35 years of incubation, crested wheatgrass fulfilled a role of tremendous importance in the western range states. By June 30, 1938, over 100 thousand acres had been seeded (Wooten 1965), mostly to crested wheatgrass, on the Land Utilization project areas and more was to be seeded. Was it fate or manifest destiny that put crested wheatgrass in the right place at the right time?

The second World War slowed the range rehabilitation program that had started in the 1930's. Following the war, range improvement activities quickened. C. L. Forsling (1945), Director of the Grazing Service, commented that, "The forage cover, and hence the grazing capacity can be improved within justifiable economic limits on literally millions of acres of the federal range by mechanical treatment and reseeding." Pearse, Plummer and Savage (1948) estimated that 80 million acres of rangeland had been so badly depleted that artificial seeding would be required if these lands were to be restored in a generation.

Economic and social conditions following the war were more favorable for investment in improvement of natural resources than at any time in our history. Again, it is fortunate that there was a dryland forage grass species available that could be used to improve semiarid rangelands while economic conditions and the mood of the country were favorable. During the 1950's and early 1960's, seeding of crested wheatgrass on deteriorated ranges occurred at an accelerating rate. In Idaho, for example, the federal agencies seeded 36 thousand acres and individual land owners three thousand acres in 1951 to crested wheatgrass. Ten years later in 1961, the federal agencies were seeding 115 thousand acres and individual land owners 55 thousand acres (Sharp 1965). At the present time, in the neighborhood of 2 million acres have been seeded in Idaho. It has been estimated that 12.5

million acres in western North America have been seeded to crested wheatgrass (Gomm 1981).

I have attempted to provide some background on the use of crested wheatgrass as I know it. There is probably more known about crested wheatgrass than any other single western range forage species. Since its second introduction in 1906, information has accumulated on the ecological and physiological characteristics, management strategies, forage production, seed production, seeding methods, nutritive value, wildlife relationships, and economic importance of this plant. Much of this will be covered in the papers that will be presented during this conference. I would now like to comment, briefly and in a general way, on some of the values, problems and myths associated with crested wheatgrass.

VALUES

One cannot underestimate the values of crested wheatgrass to the soil stabilizing and conserving programs of the 1930's. It provided plant cover on abandoned and eroding farm land. It also provided cover for deteriorated rangeland as well as producing tons of forage for grazing animals.

Because crested wheatgrass evolved in an environment where heavy grazing has occurred for centuries, it is well adapted to early and close defoliation. This is not true of most of the native cool season grasses of the West. This characteristic was of special importance in areas where grazing animals had to be removed early in the year from the hay producing lands of the ranch enterprise. Feeding hay is normally more expensive than grazing animals on rangeland. Having range forage available at an earlier date reduced the costs of operation and made ranch enterprises more economically viable.

Good seed production, ease of seed harvesting, high germination rate of the seeds, remarkable establishment rates, drought tolerance and a wide amplitude of adaptability to semi-arid ranges adds greatly to the value of crested wheatgrass. The nutritive value of the plant in the spring of the year has been likened to that of a watered concentrate (Watkins and Kearns 1956). Yearling animal gains of 2.5 pounds a day are not uncommon in the springtime (Sharp 1970).

A value not commonly recognized, and difficult to document, relates to the improvement of adjacent native range. This occurs because the crested wheatgrass seedings often reduce grazing pressure on native range areas, or provide for management programs that are more suitable for improvement of native ranges. The fact that crested wheatgrass is forgiving of management mistakes, provided that they are not continually repeated, also adds to its value in range rehabilitation and management programs.

During the 1940's halogeton (*Halogeton glomeratus*) became a major problem on extensive areas of rangeland in the Intermountain region. Because halogeton is an annual plant and not a good competitor with perennial plants, crested wheatgrass seedings minimized the losses due to halogeton. Crested wheatgrass seedings also reduced the area occupied by host plants of the beet leaf hopper (annual mustards), thus reducing costs of operation to sugar beet growers.

Observations indicate that some species of wildlife benefit directly from crested wheatgrass seedings while others may be adversely affected. Through relieving pressure on other range areas, however, wildlife commonly benefit.

In an area where I have worked for many years, crested wheatgrass seedings have prevented many livestock operators from going out of business. Tax revenue and fee receipts for livestock grazing have been increased over what they would otherwise have been.

Undoubtedly there are additional direct and indirect values associated with crested wheatgrass. Some of these will probably be indicated in the papers that are presented at this conference.

PROBLEMS

Early in the development of the crested wheatgrass seeding program, fear was expressed that range managers would look to artificial seeding of rangeland as an alternative to the application of sound management principles. In my view, this anticipated problem did not materialize. In fact, we find that crested wheatgrass seedings increased the options and flexibility for management of the unseeded rangelands.

Management problems have developed in places where crested wheatgrass has been seeded on areas with adjacent or intermingled native range plants. This is due to the selectivity of animals and the competitive ability of crested wheatgrass. Other plants would often be severely grazed before crested wheatgrass was used to any extent, giving the grass a competitive advantage. Grazing at insufficient levels of utilization causes "wolf" plants to develop in some crested wheatgrass seedings. These plants remain ungrazed year after year while grazed plants may receive excessive defoliation. As a consequence, there is a reduction in carrying capacity and an unpleasing appearance to the stand of grass.

In some areas, where calcium/magnesium imbalances exist, grazing animals may develop grass tetany on crested wheatgrass forage in the spring. This has been particularly troublesome on the loess soils of the Snake River Plains.

Large seedings with rectangular shapes offend the aesthetic sensibilities of some individuals. Others see problems because of a perceived instability of crested wheatgrass "monocultures". The infestation of some stands with the black grass bug (*Labops* spp.) tends to support this concern.

At the present time, the lack of suitable forbs and shrubs that could be seeded with crested wheatgrass over its range of adaptability is a concern of multiple use managers. Attempts are underway to resolve this problem and suitable plants may soon be available (Shaw and Monsen 1983). Reinvasion of stands of crested wheatgrass by species of sagebrush creates problems in some areas.

Some of the problems associated with crested wheatgrass are more imaginary than real. Individual differences in the perceptions of the nature of rangeland, and how and for what purpose it should be used create some problems.

MYTHS

With the knowledge available at the present time, only a few myths persist. Crested wheatgrass was considered to be unpalatable to grazing animals a number of years ago. It is difficult to understand how this myth arose, but one can speculate that seeded stands may have been deferred too long before grazing was permitted. Once the "wolfy" character develops, the palatability of the plant drops dramatically.

The epithet "biological desert" surfaces periodically. This myth appears to be fostered by those who object to livestock grazing on the public lands. As dense sagebrush or annual plant communities are changed to perennial grass communities, the habitat conditions for animal and other plant species also change. The number and kinds of species, plant and animal, that exist in the new habitat may be fewer or more than before modification. When the term "biological desert" is heard, one needs to ask "compared to what"?

CONCLUSIONS

Over the years there have been a number of conferences and symposia focusing on crested wheatgrass. None have been so wide ranging or comprehensive in coverage as this one. A great deal has been learned about crested wheatgrass over the years through research and practical experience. As one looks through the list of speakers and those in the audience, the realization comes that many many years of research and practical experience with crested wheatgrass are represented here. We all stand to gain tremendously in understanding and knowledge from the participants and attendees at this conference. I am very appreciative to have been asked to attend and address this distinguished group.

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SECTION I.

Crested Wheatgrass in North America.

Setting the Stage.

Chairman, Kendall L. Johnson

Introduction and Early Use of Crested Wheatgrass in the Northern Great Plains

Russell J. Lorenz

ABSTRACT: The first introductions of crested wheatgrass [Agropyron cristatum (L.) Gaertn., A. desertorum (Fisch.) Schult., and related taxa] to North America were made by N. E. Hansen in 1898. Additional introduction, intensive early testing and distribution took place primarily in the northern Great Plains of United States and Canada by individuals who recognized the potential of crested wheatgrass for use in this arid and semi-arid climate. The drought years of the 1930's prompted widespread use of this new grass. Government programs in the United States and Canada provided impetus to seeding large acreages to stabilize the land and the economy. Much of these seeded lands remain productive today. Crested wheatgrass has been and will probably continue to be one of the most important forage grasses for the northern Great Plains of the United States and of the Prairie Provinces of Canada.

ACKNOWLEDGEMENTS: I acknowledge Mr. Thomas J. Conlon, Superintendent, Dickinson Branch Station and Dr. Warren C. Whitman, Retired, Botany Department, North Dakota State University; Dr. George A. Rogler, Retired, ARS-USDA; and Mr. Glenn Roloff, USFS-USDA, for their help in finding background information for the paper, and Dr. Robert P. Knowles, Research Scientist, Research Branch-Agriculture Canada; Dr. Reed E. Barker, Research Geneticist, ARS-USDA, and Mr. Thomas J. Conlon for critical and constructive review of the manuscript. I assume reponsibility for any omissions or erroneous interpretation of published and unpublished source materials.

INTRODUCTION

The impact of World War I and of disastrous drought on a newly settled area caused tremendous social and political problems in the northern Great Plains of North America early in the 20th century. Much has been written about a strong people who implemented recovery from what seemed at the time to be a hopeless situation, and about government programs that helped restore the dignity of a people while renewing and preserving the soil, water, and grassland resources.

Some of the major components for making this recovery successful have received less specific attention. Among these was crested wheatgrass. Crested wheatgrass, like the settlers of the plains, was an immigrant. In the beginning, only a small group of dedicated, observant scientists and technicians recognized the great potential crested wheatgrass held for use in the northern Great Plains of United States and Canada. Those individuals saw the potential before the great need arose, so when the problems became greatest, a relatively short time was required to increase, distribute and plant crested wheatgrass on millions of acres of dry, wind blown soil. For much of the land seeded to crested wheatgrass from the late 1920's to the present time, the seeding has become a permanent repair job. I dedicate this historical presentation to those pioneer forage workers and producers who recognized the potential and promoted the use of crested wheatgrass in the northern Great Plains.

SETTLEMENT OF THE NORTHERN GREAT PLAINS

One cannot embark on a history of crested wheatgrass in the northern Great Plains without becoming involved in history of settlement of new lands, demands for wheat production during WWI, rapidly expanding cropland acreage, eventual wheat surpluses, depression, drought and government farm programs. By turns, prosperity and depression, shortage and surplus, success and failure, were encountered by agriculture on both sides of the United States/Canadian border early in this century.

Early history of the agricultural settlement of western Canada included the Selkirk Settlements in Manitoba beginning with the large grant of land to the Fifth Earl of Selkirk in 1811. The slow western movement of these agricultural peoples for the next 60 years was then accelerated by invention of the steel mouldboard plow, barbed wire and the introduction of awnless bromegrass (Bromus inermis).

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In 1879, the last buffalo herd was driven into Montana by prairie fires in Canada. Indians in Canada then hunted the antelope and other grazers to near extinction. During the early 1880's, grass was lightly grazed for a number of years. Good growing conditions and prairie fires contributed to production of a grass cover the likes of which had never before been seen. This situation was short-lived due to the rapid influx of settlers and livestock. An indication of a changing situation appeared in the 1889 annual report from Brandon, Manitoba. S. A. Bedford, the first superintendent of that station wrote:

"Because native hay meadows are becoming exhausted, considerable attention is being paid to experiments with grasses and fodder plants" (Heinrichs 1969).

At this time there was also an influx of cattlemen from United States into southern Saskatchewan and Alberta. By 1919-20, the range was fully stocked. Soon farmers and ranchers were trying to occupy the same area. Much of the land plowed was extremely marginal for cereal crop production. Good growing conditions in the early part of the twentieth century allowed for prosperity. However, the boom was soon to "bust" with the onset of the 10-year drought from 1928 to 1937 in which 7 of the 10 years were below the long-time average precipitation. The drought was accompanied by severe soil drifting, heavy insect infestations, acute shortages of feed for livestock, serious depletion of herds, and other calamities usually associated with severe climatic cycles. Soon there were more than 4 million acres (1.6 million hectares) of abandoned farm lands plus many millions more on which the owners could not survive unless action was taken to help them stabilize the soil and their economy. This acreage (hectarage) included marginal cropland as well as millions of acres (hectares) of severely overgrazed grassland.

Kilcher (1969) described the situation for Canada, but it can be applied equally well to the northern Plains of the United States:

"During the first two decades of this century, very little, if any, attention was devoted to considerations of cultivated forage crops in western Canada. Indeed there was little reason for consideration, since untapped virgin land and the limited livestock population had not yet created a demand for controlled fodder production. The coincidental occurrence of drought, land devastation, and economic depression in the thirties resulted in a rather sudden increased awareness that, among other things, the need for grass and forage crops may have been a costly oversight. These then were the first real set of factors which turned man's attention to forage crop establishment and production in western Canada. Admirable credit must be given to that small handfull of dedicated scientist and producer innovators who accomplished a monumental task of reseeding and stabilizing vast areas of eroded land. Their accomplishments were even more astounding when one considers the limited crop choice, the lack of refinement in available equipment, and the limitation of power commensurate with that time. Much of their seeding was done in late fall and early winter or on frozen ground which allowed shallow seeding. The principle grass used was crested wheatgrass, a species which to this day is the king of tolerance to adversities to establishment."

Dillman (1946) discussed the same situation from the United States side of the border:

"The demand for wheat before and during the First World War brought about a marked change in agriculture of the great plains. Several million acres of native grasslands in the Northern Great Plains area of the United States and Canada were broken up and seeded to wheat during the period of 1905 to 1920. There appeared to be no need for a new dryland grass at that time. Finally the dry years of the middle thirties came on and abandoned wheat lands were in urgent need of grass. One could hardly have foreseen the heroic role that crested wheatgrass was to play in this living drama of the dry plains. It was the only grass available that would adequately fulfill this role. Already it's hardiness, productiveness, and longevity had been proved by experiments of the U. S. Department of Agriculture and state agricultural experiment stations."

EARLY DEVELOPMENT OF CRESTED WHEATGRASS IN UNITED STATES AND CANADA

A. C. Dillman (Fig. 1) presented the early history and documented the Seed and Plant Introduction (SPI) numbers of the first introductions of crested wheatgrass [Agropyron cristatum (L.) Gaertn., A. desertorum (Fisch.) Schult., and related taxa] into the United States (Dillman 1946). I have drawn heavily from these earlier papers and other sources in an attempt to place in one document the pre-1942 history of crested wheatgrass in the northern Great Plains, including the Prairie Provinces of Canada. Most of the post-1942 history is well documented in the

Figure 1.--A.C. Dillman in the 1915 planting of S.P.I. 19538 at Mandan. July 16, 1945.

literature and is at least partially summarized in other papers of this symposium.

United States

The first known introduction of crested wheatgrass into North America was made in 1898 by N. E. Hansen of the South Dakota Agricultural Experiment Station as a result of a plant exploration trip to Russia and Siberia for the U. S. Department of Agriculture (USDA). He observed crested wheatgrass under test at the Valuiki Experiment Station on the Volga River about 150 miles (240 kilometers) north of what is now Volgograd. He obtained a small amount of seed of five accessions, S.P.I. Nos. 835, 837, 838, 1010 and 1012. In 1899, he distributed original seed of one or more of these accessions to one recipient each at experiment stations in Alabama, Indiana, Michigan, Colorado, and Washington. No record has been found as to whether or not the seed was planted at those stations. Hansen apparently supplied seed for a planting at Highmore, South Dakota because Dillman (1946) reported that Johnston T. Sarvis (Fig. 2), then Instructor of Botany, South Dakota State College, saw crested wheatgrass growing in W. A. Wheeler's forage crop nurseries at Highmore in 1906. The Highmore station was placed under new management in 1908 and the grass nurseries were plowed. There is no record of any further distribution of seeds from Hansen's first introduction.

Westover et al. (1932) reported:

"Small samples of seed (crested wheatgrass) received from Sweden in 1905 and from the Royal Botanical Gardens, Dublin, Ireland, were sown at the Arlington Experiment Farm, Rosslyn, Virginia in 1906, but failed to germinate".

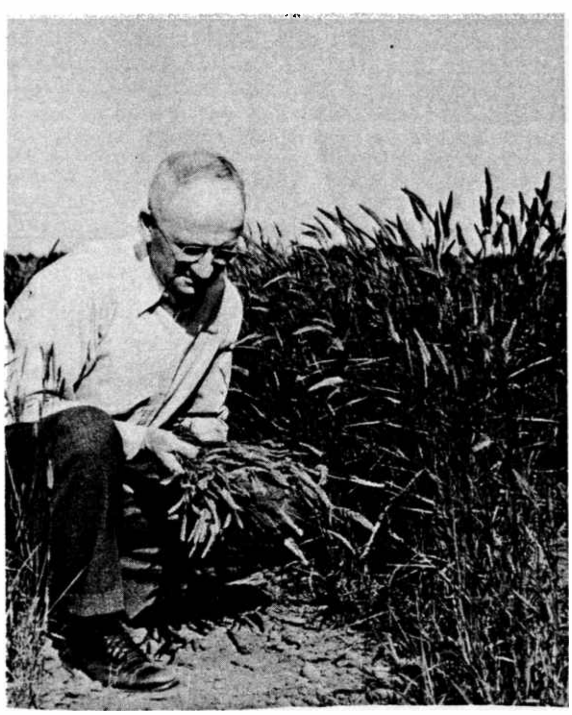


Figure 2.--J. T. Sarvis in the 1915 planting of S.P.I. 19538 at Mandan. June 27, 1941.

No other record of this material has been found.

A second importation of crested wheatgrass by Hansen came from the same source as his original collection, and was sent in 1906 through the Moscow Botanical Gardens by Vasili S. Bogdan, Director of the Kostichev Agricultural Experiment Station, Valuiki, Samara Government, Russia. The shipment contained five lots labeled *Agropyron desertorum* (Fisch.) Schult. (S.P.I. Nos. 19537 through 19541, inclusive) and one lot labeled *Agropyron cristatum* (L.) Gaertn. (S.P.I. No. 19536). Seed of one or more of these four to five pound (1.8 to 2.3 kilogram) lots was distributed to 15 experiment stations from 1907 to 1913.

Early tests.--Dillman (1946) presented a brief account of the early tests of crested wheatgrass at the 15 experiment stations that received seed from Hansen's second importation:

"Crested wheatgrass did not prove to be adapted to conditions at Arlington Farm, Virginia, nor at Chico, California, as noted by R. A. Oakley and Roland McKee, respectively, from plantings made in 1907. The seed sent to W. H. Olin., Fort Collins, Colorado, in 1907 was not planted, as no suitable land was available at the time. According to Professor Alvin Kezer, the first work with crested wheatgrass at Fort Collins was begun about 1925. No records are available as to what happened to the seed supplied T. H. Kearney in 1909; or the seed sent to R. E. Bradley, Lincoln, Nebraska, in 1911; to H. J. Webber, Ithaca, New York, in 1912; or to Samuel Garver, Highmore, South Dakota, in 1913. The planting at Chillicothe, Texas, in 1912 failed to germinate; and 'no stand was obtained' at Burns, Oregon, in 1913. This accounts for about one-half of the distribution of S.P.I. Nos. 19536 to 19541."

Six lots of seed of one pound (0.45 kiligrams) each of Nos. 19536 through 19541, were sent to Akron, Colo. in 1909, but the planting plans for Akron did not include crested wheatgrass that year and there is no record that the planting was made. Dillman (1946) wrote:

"In 1910, W. G. Shelley planted two rows of crested wheatgrass, Nos. 19540 and 19541. In 1911, G. E. Thompson, then in charge of the forage crop work at Akron, reported that these grasses appeared to be promising. He noted, however, that new plantings made in 1911, including S.P.I. Nos. 19536 and 19538 and forage crops Nos. 956-962, 'failed to germinate'. These F.C. numbers were single plant selections of *A. cristatum* obtained by N. E. Hansen from Professor R. W. Williams, Imperial Agricultural College, Moscow. So far as known, no increase or distribution of crested wheatgrass was made from these early experimental tests at the Akron Station."

Some locations had more success in planting seed supplied by Hansen. Rather extensive plantings were made in 1907 by M. W. Evans, Division of Forage Crops and Diseases, USDA, at Pullman, Washington, from several of the S.P.I. numbers included in Hansen's second importation. The original plots were plowed in November of 1908. Other plantings were made and continued until 1910 when M. W. Evans was transferred to another location. Plantings were made at Union, Oregon by Robert Withycombe in 1907 and plants were used in an exhibit in 1911 and in 1913, but there is no record of any increase or distribution of seed from Union. Plantings were made in 1913 at Moro, Oregon. Apparently there was considerable seed distributed from Moro, and definite enthusiasm over the success of the plantings. Dillman (1946) wrote:

"A grass nursery of several species was planted in single 8-rod rows at Moro, May 2, 1913, but only two species germinated. These were A. cristatum, S.P.I. 19540 (A. desertorum or 'Standard' type) and A. imbricatum (Bieb.) R. et S., S.P.I. 24467 (from Manchuria). In his report for 1914, D. E. Stephens, Superintendent, wrote: 'The row of A. cristatum planted in 1913 seeded abundantly, but the row was not harvested until the seed had shattered badly. After autumn rains, the shattered seed germinated and a thick stand of grass was obtained for a distance of 6 feet from the row. This variety which seems to seed freely and spread readily from seed may prove to be of some use as a pasture grass.' In 1916, 15 pounds of seed were harvested from this plot; about 290 pounds per acre. This plot, enlarged by later plantings, is still maintained in production according to M. M. Oveson, the present superintendent of the Moro Station."

Jackman et al. (1936) reported on the research at Moro and Union, Oregon:

"In both the station and field trials, it was apparent at once that crested wheatgrass was an outstanding dry-land grass. In all of the real dry locations other grasses usually died quickly, but wherever stands were obtained the crested wheatgrass survived".

By 1936, there were 3,000 acres (1215 hectares) of crested wheatgrass in small trial plots in eastern Oregon. Jackman et al. continued:

"Cool weather suits it best, and it shows the most promise at elevations above 2,500 feet. So far as the writers know, there are no cases of death of crested wheatgrass plants due to cold. In one high valley where 50 below zero occurred twice during the life of a planting, a stand of crested wheatgrass has taken it and liked it."

Dillman (1946) described the early plantings of crested wheatgrass at Moccasin, Montana:

"The first planting of crested wheatgrass at Moccasin, Montana, was made in 1915 by Leroy Moomaw. This included S.P.I. Nos. 19536, 19537, and 19540. There is some uncertainty as to the source of the seed. In his annual report for 1915, Moomaw noted the source of seed as "Akron, Colo., 1909'. It is possible that seed used at Moccasin was a part of the original seed sent to Akron in 1909. These were one-pound lots of Nos. 19536-19541, inclusive. It is quite certain that the seed was not planted at Akron, and it may have been sent on to Moccasin, with the original address tags stamped 'Akron, 1909'. It is more likely, however, that the seed was grown at the Belle Fourche Station. In the planting plans for 1915 at the Judith Basin Station, Moccasin, prepared by H. N. Vinall, Division of Forage Crops, the following grasses were included: S.P.I. 19536 A. cristatum (D.R. No. 67); S.P.I. 19537 A. desertorum (D.R. No. 68); S.P.I. 19540 A. desertorum (D.R. No. 72); and S.P.I. 25348 A. elongatum (D.R. No. 71)."

The D.R. numbers are Dillman's accession numbers for seed grown at the Belle Fourche Station in 1909 or later. The probability that the seed came from the Belle Fourche Station is substantiated by the fact that the planting at Moccasin included S.P.I. 25348 (D.R. No. 71) which was grown in the Belle Fourche nursery from 1910 to 1915. Cooperative work between Moccasin and Havre, Montana involved plantings at Havre beginning in 1917, but there were no stands established until 1920.

S.P.I. No. 19537 was chosen as the standard for Montana and at that time it was the only crested wheatgrass registered by the Montana Seed Growers Association. Reitz et al. (1936) described it as being tall and vigorous with rather long slender spikes. Twenty-four types of crested wheatgrass were selected from the material growing at Moccasin in 1923, but none were released as commercial varieties.

Although Hansen's second importation of crested wheatgrass was tested in several states, the greatest enthusiasm for its potential use in the United States occurred among scientists at stations in the northern Great Plains, in particular North and South Dakota. During the early years following the second importation by Hansen, plantings made at the Belle Fourche Experiment Station, Newell, South Dakota, the Northern Great Plains Field Station, Mandan, North Dakota, and the Dickinson Substation, Dickinson, North Dakota, were the basis for establishment of seed-increase fields in the northern Great Plains.

The first planting of crested wheatgrass at the Belle Fourche Station (Fig. 3) was made in May of 1908 and included S.P.I. No. 19536 (A. cristatum) and S.P.I. Nos. 19537-19541 (A. desertorum). Another planting was made from the same seed supply in 1909 (Dillman 1910). In 1910 a planting was made using a mixture of seed harvested from the 1909 planting of Nos. 19539 and 19540. In 1913, two 8-rod (40-meter) rows each of five of the original entries from seed produced from the earlier plantings were established. No. 19539 was omitted from the 1913 planting. In 1915, two 8-rod (40 meter) rows each of S.P.I. Nos. 19537 through 19541 were planted. Dillman (1946) reported:

"In 1909 the following notes were recorded: 'The grass nursery, planted in 1908, was continued this season. S.P.I. Nos. 19536-19541, inclusive, came through the winter without any winterkilling, and were very early in beginning growth in the spring. This characteristic might make this species valuable as a pasture grass if it should prove to be valuable otherwise. There has been no effective test of drought resistance so far'. From 10 to 40 pounds of seed were harvested at

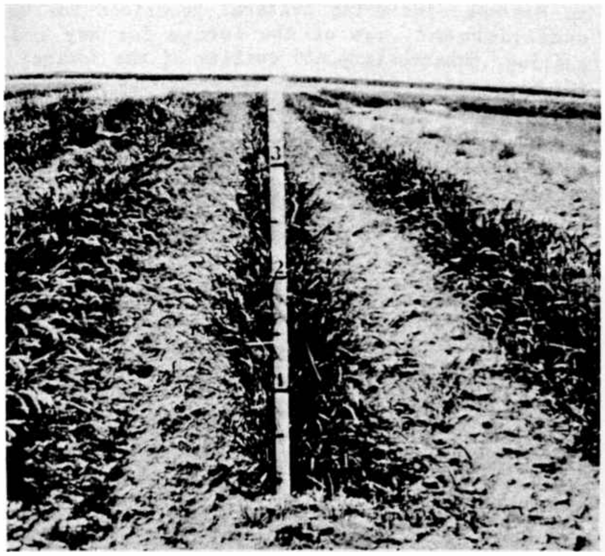


Figure 3.--First known picture of crested wheatgrass grown in North America. Taken at the Belle Fourche Experiment Station, Newell, South Dakota, July 22, 1909. Rows planted in May of 1908. Left to right, S.P.I. Nos. 19541, 19539, 19537.

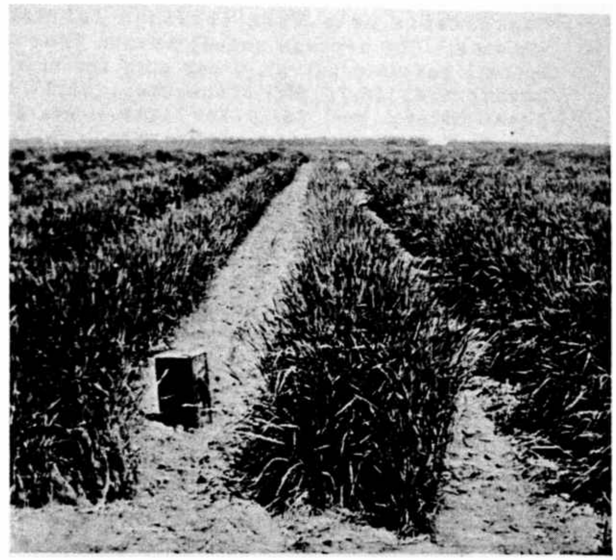


Figure 4.--Planting of S.P.I. 19538 made at Mandan, North Dakota in 1915. June 18, 1919. Size of the planting was reduced in later years, but has been maintained to the present time.

the Belle Fourche Station each year during the period 1909 to 1918. At that time there was little or no demand for the seed except for experimental plantings. Seed of each S.P.I. number (19536 to 19541, inclusive) was forwarded to the Division of Forage Crops as early as 1910 or 1912. Seed was supplied for planting a nursery of about 1/10-acre at the Ardmore (South Dakota) Field Station in 1913, and for two 1/10-acre drilled plots in 1916. In 1915, seed of S.P.I. 19538 was supplied for planting 1/10-acre in rows at the Northern Great Plains Field Station, Mandan, North Dakota, and in 1918, two lots of 27 and 19 pounds were supplied for field plantings at Mandan. These larger lots were composites of S.P.I. Nos. 19537-19541, inclusive. From his first observation of the mature plants in 1909, the writer considered these numbers similar or identical strains of the *A. desertorum* type and distinct from S.P.I. 19536, *A. cristatum*."

The beginning of a forage research program at the new U.S. Northern Great Plains Field Station, Mandan, North Dakota, in 1915 provided an opportunity for another testing location for crested wheatgrass (Fig. 4). The above quotation from Dillman (1946) documented the first plantings at Mandan. The 1915 planting of S.P.I. 19538 has remained productive to the present time, and the long-term plan is to maintain these rows as long as possible. Between 1918 and 1930, 2700 pounds (1225 kilograms) of seed were distributed from the Mandan Station: 1200 pounds (545 kilograms) directly to farmers, 500 pounds (227 kilograms) to farmers through county extension agents, 500 pounds to experiment stations in United States and Canada, and 500 pounds to USDA for further distribution.

Sarvis (1941) reported that in 1917, a small quantity of seed was produced at Mandan, and that in 1918, seed was sent to M. L. Wilson, County Agent Leader in Montana. Wilson distributed the seed to 15 county agents in Montana. Seed harvest continued at Mandan, and in the spring of 1921, seed was sent to A. J. Ogaard, the Extension Agronomist in Montana for distribution to farmers. Within a few years, a farmer in Montana offered seed for sale, which was perhaps the first attempt to sell crested wheatgrass seed in the United States, but no one wanted it, so he gave some to his neighbors. In 1928, he was able to sell seed to Oscar H. Will Seed Company in Bismarck, North Dakota. In 1929 they listed the seed in their catalogue at $28 per 100 pounds (45 kilograms). This was the first offering of crested wheatgrass for sale by a commercial seed firm.

Another early producer of commercial seed in United States was Leroy Moomaw at Dickinson, North Dakota. He became interested in crested wheatgrass while he was working for the USDA at Moccasin, Montana. His interest continued when he transferred to the Dickinson Substation in 1919. In 1926, he started a seed increase field on his land near Dickinson. When the demand for seed came in 1933, he had 200 acres (81 hectares) in production. He erected a grass seed processing plant in 1937 when he had over 400 acres (162 hectares) of crested wheatgrass in rows for seed production.

Forage production and grazing studies.--Forage production tests of crested wheatgrass showed the great promise the species held for the northern Plains. In 1923 the first pasture experiment of record involving crested wheatgrass was begun at the Ardmore Field Station. This experiment was designed to compare the carrying capacity and value of native grasses, crested wheatgrass, bromegrass, and sweet clover using milk production of dairy cows as the measure of production. Dillman (1946) summarized the results of this study:

"Comparable data were obtained for three seasons. The average annual return from the several pastures was $7.70 per acre for crested wheatgrass, $6.75 for bromegrass, $6.63 for sweetclover, and $4.45 for native grasses. Crested wheatgrass provided the earliest pasturage in the spring and somewhat the longest pasturing season."

The field plantings of Nos. 19537-19541 made in 1918 at Mandan were used as a pasture for a few cows beginning in 1920. The first grazing study using crested wheatgrass for beef production was started at Mandan in 1932 (Fig.5). Its success led to a very extensive long-term breeding and evaluation program at Mandan, including continuation of the pasture established in 1932 (Sarvis, 1941). This pasture has been grazed each year, and the long-term plan is to maintain this pasture as a standard for evaluation of other grazing trials at Mandan.

Seed was sent to L. R. Waldron at the Dickinson Experiment Station in 1909. Although Dillman (1946) reported that there was no record that the 1909 plantings were made, Westover et al. (1932) reported that crested wheatgrass was seeded at the Dickinson station in 1909. Other records of the rapid increase of crested wheatgrass plot area and seed production at the Dickinson Station would indicate that these 1909 plantings must have been made and that additional plantings were made through the years[1]. The first well-documented planting of crested wheatgrass at Dickinson was made in 1920 from seed provided by the Division of Forage Crops, USDA, as part of a hay production comparison with other species. In 1922, a field of 2 or 3 acres (0.8 or 1.2 hectares) was planted in rows 42 inches (107 centimeters) apart for seed increase. Part of this seed was of S.P.I. 19538 from the Northern Great Plains Field Station and from the Redfield, South Dakota Field Station. During the period 1922 to 1930, more than 10,000 pounds (4536 kilograms) of crested wheatgrass seed was distributed from the Dickinson Station to 13 states and 4 Canadian Provinces. Through the years, exchange of seed between the Dickinson and Mandan Stations occurred regularly, particularly in relation to the breeding and testing program that led to the release of the cultivar 'Nordan' in 1954. Nordan is a tetraploid, *A. desertorum* type, developed at Mandan from a selection made in 1937 from an old nursery at Dickinson (Rogler 1954) (Fig. 6).

There was extensive testing of the early introductions, especially those of Hansen's second acquisition. Prior to 1942, several reports and bulletins and many journal articles were published describing various aspects of crested wheatgrass. A few examples of these publications are reviewed here. Development and morphology of the seedling and of the mature plant, including information on the seed and the root system, were published by Love and Hanson (1932). Rietz et al. (1936) described early testing and evaluation of crested wheatgrass in Montana, including cultural practices for stand establishment, use of the forage for hay and/or grazing, palatability and quality of the forage, use in regrassing abandoned farm land, insect and disease pests, and seed production. Jackman et al. (1936) published all available information on the culture of crested wheatgrass in eastern Oregon. Their bulletin included 14 testimonial letters which described the procedures used and the experiences of individual farmers in establishing stands. They stated in the foreword to the bulletin that eastern Oregon farmers bought seed and prepared to plant 25,000 acres (10,125 hectares) of crested wheatgrass in the fall of 1936. Westover et al. (1932) also described in detail crested wheatgrass culture and management for hay and pasture. Many more journal articles, bulletins, and reports of research and practical use of crested wheatgrass have been published from 1942 to the present, an indication of the continued interest and use of this species.

Later introductions.--A few other early introductions that may or may not be in the current crested wheatgrass genetic pool are worthy of note. I found no further record of them, but others may know whether or not these have influenced crested wheatgrass development in the United States and Canada. Hansen collected seed identified as S.P.I. Nos. 24466-24468 during a plant collection trip to northern and central Asia in 1908. He classified these as *A. imbricatum*, whose diploid and tetraploid forms cross readily with *A. cristatum* and *A. desertorum*. In his notes, Hansen stated "A grass of very wide distribution in northern Asia and European Russia. Highly recommended as one of the best grasses in the Volga River region, where it was brought into culture by the experiment station at Valuiki near Rowno, south of Saratov". This material was identified in the United States and Canada as S-2284 from Saskatoon (Rogler, 1960). Knowles (1955) described this material.

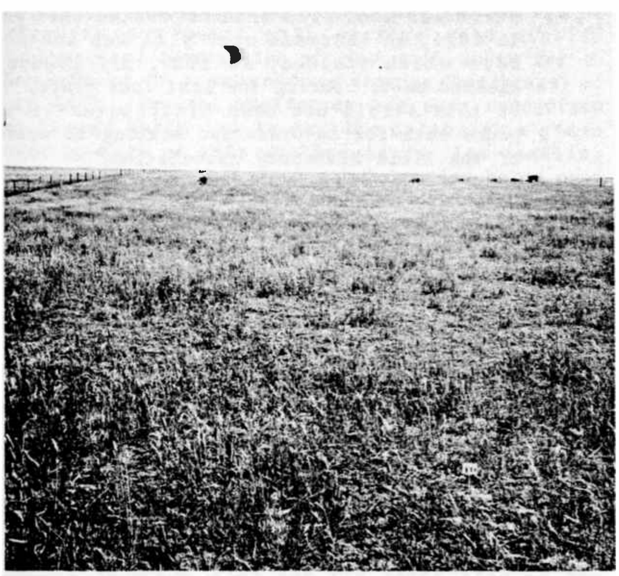
Hansen sent S.P.I. No. 28306 *A. cristatum* from Russia in 1910, and he also sent the first introduction of *A. sibiricum*, as S.P.I. No. 28307, with the note "A native of the dry steppes of eastern European Russia and western Siberia. The present lot is selection No. 1, grown from a single plant, by Prof. R. W. Williams, Imperial Agricultural College, Moscow, Russia". These and other introductions made from 1910 through the 1920's apparently did not receive as wide distribution as did the earlier introductions.

During the 1930's when the real value of crested wheatgrass was being realized for regrassing programs in United States and Canada, several plant exploration expeditions collected crested wheatgrass and related species. The main sources were: The Westover-Enlow expedition to Russia, Turkey, and Turkestan in 1934; the Wellman-Westover expedition to Turkey in 1936; the MacMillan-Stephens expedition to China and Manchuria in 1934; the Roerich expedition to Manchuria in 1934; the Kazakstan Institute of Agriculture in 1935; and the Institute of Plant Industry U.S.S.R. in 1934 and 1935. Seed from these sources was increased and the plant material was evaluated at Mandan, and Pullman,

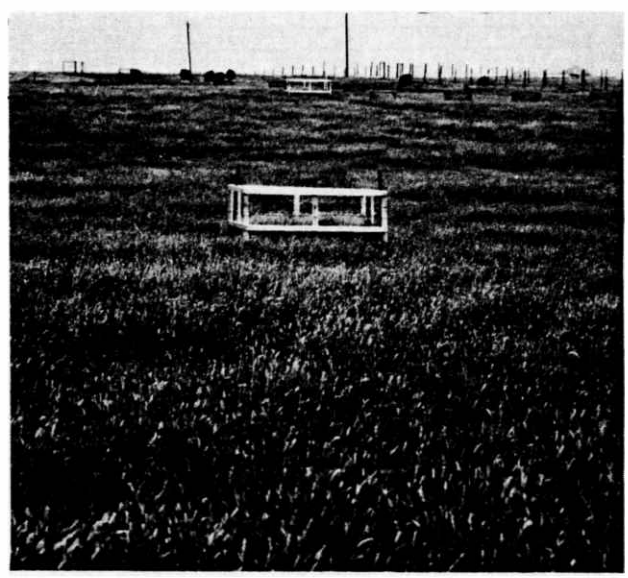
[1] Personal communication with Thomas J. Conlon, Superintendent, Dickinson Branch Station (formerly Substation), Dickinson, North Dakota on August 23, 1983, and Annual Reports of the Dickinson Substation.

a) Not grazed since July 20, but no regrowth due to severe drought, 8 inches of precipitation in 1934. Note uniform stand of grass. October 11, 1934.

c) Fourteen steers on seven acres for 40 days. June 26, 1943.



b) Had been grazed for 46 days, by seven steers on seven acres. Total precipitation was 18.3 inches in 1935. Note vigorous growth and patchy grazing. July 16, 1935.



d) The pasture was more than 30 years old in 1965 and remains very productive after more than 50 years of good grazing management. June 21, 1965.

Figure 5.--First beef cattle grazing study on crested wheatgrass in North America. Seeded at Mandan, North Dakota in 1932.

Figure 6.--G. A. Rogler in the 1915 planting of S.P.I. 19538 at Mandan. June 27, 1970.

Washington[2]. Rogler and others working with this material in the late 1930's were soon aware that many of the introduced accessions were badly mixed and in a number of cases misnamed. It took several years to determine whether the mixtures were mechanical or genetic. Since then, several other expeditions have introduced additional accessions of crested wheatgrass into the United States.

Breeding work with crested wheatgrass was intensified when USDA obtained increased appropriations for grass breeding work in 1936. Mandan, North Dakota and Bozeman, Montana were identified as locations for increased breeding work on crested wheatgrass. The major early program in Canada was at Saskatoon, Saskatchewan, and it was intensified in 1938 when Dr. R. P. Knowles joined the staff. At the present time, Mandan, North Dakota; Saskatoon, Saskatchewan; and Logan, Utah are the primary locations doing breeding work on crested wheatgrass.

Canada

The first official introduction of crested wheatgrass to Canada occurred in 1911. According to S.P.I. card files, seed of No. 19536 (*A. cristatum*) and No. 19540 (*A. desertorum*) was sent to Professor John Bracken of the University of Saskatchewan at Saskatoon (Rogler 1960). L. E. Kirk was a graduate student assistant at the University of Saskatchewan in 1916. He planted the seed obtained by Professor Bracken, and in 1927 the cultivar 'Fairway' came from these nurseries.

The second recorded introduction of crested wheatgrass to Canada occurred in 1915 when a small quantity of seed was obtained from the USDA by the University of Saskatchewan, and planted in experimental plots (Kirk 1932). Establishment and growth of this plant material was encouraging and the Canadian scientists sought additional material. Kirk wrote:

> "In the grass breeding nursery at Saskatoon there are some fifteen strains of crested wheatgrass and about forty-five progenies from single plant selections. The former include eight selections which were sent to us in 1925 by Mr. J. T. Sarvis from the USDA experiment station at Mandan, North Dakota. A few introductions came directly from investigators in Russia, and two strains were developed at Saskatoon."

Kirk (1932) described a disaster in 1925 that delayed development of Fairway:

> "Every lot of crested wheatgrass which we have grown has been exceedingly variable in plant type. Some plants were much more desirable than others. These differences suggested the advisability of doing some selection work, as it was apparent that considerable improvement could be effected by saving seed only from the leafy types and eliminating the coarse and sparsely leaved types. In this way a fine leafy strain was secured, which, by 1925, had produced enough seed for plot tests and for distribution to farmers in small quantities. Unfortunately, all of this seed was lost when the building which housed the Field Husbandry Department burned in the spring of 1925. However, the plants were still in the field, and a fresh start was made from seed harvested that year. In 1926, an increase acre plot was seeded in rows which yielded, in 1927, 517 pounds of cleaned seed. During the last four years, seed of this strain has been distributed in two-pound lots for co-operative testing to members of the Field Husbandry Association."

Rogler (1960) obtained seed of Fairway from the University of Saskatchewan in 1944, and seed of S.P.I. No. 19536 from Moccasin, Montana, the only known original planting of this introduction. When grown side by side at Mandan, these two looked identical. Both were diploid forms and very distinct from S.P.I. Nos. 19537 and 19541 which Dr. Kirk also had in his nurseries at the time Fairway was selected.

In 1927, seed was obtained from Montana by the Dominion Range Experiment Station at Manyberries, Alberta, and planted in test plots (Kirk et al. 1934). Seed produced was used to plant some abandoned fields near the station, and by 1935 all reports were favorable for stand establishment, forage production, and palatability to grazing livestock. These tests demonstrated that a complete grass cover could be obtained by seeding into the weed cover. Crested wheatgrass was the most successful species tested. A desirable degree of conservation could be obtained in a relatively short period of time and during the next few years a considerable acreage of abandoned farm land in the vicinity of the station was restored to grass.

[2]Swallen, Jason R. 1943. Preliminary report of the species of *Agropyron* introduced into the United States. USDA Bureau of Plant Industry Mimeo Report, February 23, 1943. 22 p.

Similar trials were conducted at other experiment Stations throughout the drought area of the Prairie Provinces and all confirmed the results obtained at Manyberries (Stevenson et al. 1937).

Canadian scientists L. E. Kirk, T. M. Stevenson, S. E. Clarke, and D. H. Heinrichs were very active in testing and evaluating crested wheatgrass. Major Canadian Department of Agriculture bulletins were issued by Kirk (1932), Kirk et al. (1934), Stevenson et al. (1937), and Clarke and Heinrichs (1941). These pre-1942 bulletins described in detail all known information on crested wheatgrass culture and use at that time. Much information has been published by Canadian scientists since 1942. Kilcher et al. (1956) included crested wheatgrass in their evaluation of pasture and hay crops for the southern Canadian prairies. Knowles (1955 and 1956), and Knowles and Buglass (1971) presented detailed information on adaptation, culture and use of crested wheatgrass in Canada. As in the past, current literature regularly contains papers from Canadian workers dealing with crested wheatgrass improvement, culture and use.

REGRASSING THE NORTHERN GREAT PLAINS

The introduction of crested wheatgrass to United States and Canada was indeed timely. In both countries, the stage was being set for producing a plant hero, who, like the settlers of the prairie, was an immigrant. The rapid settlement of the northern Great Plains of the United States and the Prairie Provinces of Canada between 1866 and 1920, and the demand for wheat during WWI led to plowing and cropping of much land that was not suited as cropland. Concurrent with this was the series of extremely dry years with serious wind erosion problems, and destruction of good soil which led to abandonment of a tremendous acreage (hectarage) of farm land. Crested wheatgrass was soon recognized for having potential to rapidly establish a grass cover on much of this problem land. Its seedling vigor was better than most other species being used to revegetate lands at that time, and it rapidly developed a solid sod capable of supporting grazing or haying operations. It readily produced a seed crop. All these desirable characteristics contributed to its acceptance as a species for revegetating devastated land.

It was also fortunate that seed increase was started at an early date. Several research stations in North Dakota, South Dakota, and eastern Montana increased seed by careful management of very small quantities of seed and small plots. These stations were responsible for providing seed to other research locations and, in a limited way, to growers prior to 1921. There is early record of 2-pound (0.9 kilogram) seed lots being distributed to growers by L. E. Kirk and his associates at the University of Saskatchewan in Canada. Apparently several of the farmers in Canada were successful in increasing these small quantities of seed to establish seed production fields. When the demand for seed developed in the United States in 1934, the Christianson Seed Co. of Minot, North Dakota bought seed in relatively small lots from many Canadian farmers and sold it to the USDA for use in the regrassing program.

Kirk et al. (1934) discussed seed supply in Canada:

> "In spite of the fact that there is considerable crested wheatgrass seed being produced in western Canada, the supply is still far short of the demand. This is due in part to severe drought which has visited the prairie sections of Saskatchewan and Alberta during the last few years, since crested wheatgrass has had its widest distribution in that area. These conditions have demonstrated its exceptional drought resistance and ability to produce in a dry climate, but while the plants were able to make a substantial growth on available spring moisture and produce heads, the supply of moisture was frequently insufficient to fill the seed. Demand for seed of the Fairway 'strain' is most insistent. Seed distribution of this variety has been quite general so that although both ordinary crested wheat and the Fairway variety have been grown in the semi-arid sections of the south, the latter has been grown almost exclusively in the northern districts and these have been more favorably situated with respect to moisture. Good seed crops have been obtained therefore of Fairway crested wheatgrass and the seed has sold at a considerable premium over ordinary seed. For these reasons it would appear that seed stocks produced in western Canada will soon consist largely of the improved variety. Data are not available on the quantities of crested wheatgrass seed produced in Western Canada in 1933. Several thousand pounds of seed have been sold and the number of farmers who will grow the crop for seed is rapidly increasing. The bulk of the seed which will be sown in 1934 is the 'Fairway' variety, a considerable proportion of which has been inspected by officers of the Dominion Seed Branch and designated 'elite' stock by the Canadian Seed Growers' Association."

It is highly probable that much of the seed imported into the United States during this period was of the Fairway variety grown in northern Canada, and used in the regrassing program particularly in Montana and North Dakota.

By 1937, agriculture in the northern Great Plains was in dire straits. The drought and the depression left no one untouched. There were only two head of cattle reported left in Petroleum County, Montana. All other counties in western North and South Dakota and eastern Montana were also in extremely poor condition. A report by the Great Plains Committee made in 1936 states that 7 million acres (2.8 million hectares) of abandoned or eroding land could not be acquired with the funds available that year. Two million of these acres (0.8 million hectares) were at one time under option, which meant that they had been homesteaded or were in private ownership. The report predicted that 24 million acres (9.7 million hectares) in the Great Plains might well be acquired, that 5 million (2 million hectares) had been acquired and that the mechanism was there for acquiring 6 million acres (2.4 million hectares) per year if funding was available. Actual acreages (hectarages), state by state, were hard to confirm, but small bits of information help describe the situation. A report by C. G. Bates for the U.

S. Forest Service in 1930[3] stated that McHenry County, North Dakota already owned 178 forties (each forty acres or 16 hectares), acquired through abandonment and tax liens. That occurred even before the major drought struck. Much of this land is now in grass, so presumably it was included in some phase of the regrassing program. Trees were planted on some of the sandy areas to help reduce wind erosion. Incomplete records show that county, state, and federal land acquisition of this type amounted to more than 166,000 acres (67,230 hectares) in North Dakota[4].

The Agricultural Adjustment Act (AAA) had been passed by the U. S. Congress in 1933. During the next 10 years, there were several programs administered by the AAA that included purchase and establishment of grass on abandoned farm lands (the regrassing programs). Seeding was begun in 1933 under programs by the Resettlement Administration. For several years, all available seed was harvested from native range and seeded grasslands. But the only species that produced enough seed to have much impact on the seeding program was crested wheatgrass. In spite of the severe drought in 1934, seeding continued, primarily using seed from nothern Canada where the drought was less severe. Favorable growing conditions in 1935 caused many of the acres seeded to become established. This was not only encouraging to those involved in the seeding programs, but it also provided a source of seed for additional seeding. Another drought occurred in 1936, but 1937 was more favorable and by 1938, there was a tremendous seed crop on all the crested wheatgrass acres, including those seeded in 1935 and 1936.

The Bankhead/Jones Tenant Act of 1937 authorized the Secretary of Agriculture to purchase for the Federal Government lands unsuited for cultivation. These became known as the Land Utilization (LU) lands. They were improved and put back into production as rangeland whenever possible. The idea that the Federal Government should buy up homesteaded farms that had failed or were rapidly failing originated in Phillips County, Montana. The Works Progress Administration (WPA) administered the funding while the Soil Conservation Service supervised various projects to improve these lands. The majority of this land was reclaimed by seeding it to crested wheatgrass, often following some other conservation measure such as establishing dams on drainage ways to control water, and/or furrowing or terracing to control runoff. When crested wheatgrass was seeded on these areas, the program was successful. These lands are now administered by Bureau of Land Management and are generally successfully used for livestock grazing.

The Prairie Farm Rehabilitation Act (PFRA) was the Canadian counterpart of the United States AAA. In 1935, the regrassing program became a main function of PFRA. As part of the PFRA program, community pastures were established in Saskatchewan and Manitoba. These pastures were located on the poor soil types and many of them contained large areas of abandoned farm land.

It is difficult to determine the acreage actually seeded to grass under this and other Canadian programs. Knowles (1956) reported that between 1935 and 1954, 190,548 acres (77,172 hectares) of crested wheatgrass were seeded by PFRA on their community pasture system which is a relatively small part of the entire grassland system and of the entire acreage of abandoned farm land. Clarke and Heinrichs (1941) discussed PFRA seeding of 64,000 acres (25,900 hectares) in blocks of from 10 to 30 acres (4 to 12 hectares) in cooperation with each of hundreds of farmers and that a high proportion of good stands had been obtained. These figures represent only a very small part of the several million acres regrassed in Canada.

THE PRESENT AND THE FUTURE

A cursory review of the literature from 1942 to the present shows a continuous flow of research reports on crested wheatgrass. Long-range planning at many research locations specifically includes work on some aspects of crested wheatgrass improvement, management, or use. Crested wheatgrass has become an integral part of the grassland grazing system of the northern Great Plains, and of many other rangeland areas of the West. There is no indication that this will change until a plant superior to crested wheatgrass becomes available.

Sarvis (1941) summed up the crested wheatgrass situation for the northern Great Plains to that date:

> "Crested wheatgrass has progressed from a promising grass in 1917 at the Mandan Station to the leading and outstanding grass for use as hay and pasture in the northern Great Plains. More seed of it is now produced in the northern Plains than of all other grasses of a similar nature. It was the grass available and proved by trial as well adapted for planting on abandoned land and eroded fields, following the severe drought, as protection against wind and water erosion. Many hundreds of acres of it have been planted in western North Dakota, and in one district in Montana over 200,000 acres of it has been planted on abandoned farmland."

Through the years, the desirable characteristics of crested wheatgrass have been proven by research and demonstrated by practice. It has replaced bromegrass (Bromus inermis Leyss.) in many seeding programs in the northern Great Plains of United States and Canada. Following the introduction of bromegrass to the United States in 1884, it was widely used and it became an important part of grassland agriculture in both countries. But there remained a need for a more drought resistant grass for the drier sites. Crested wheatgrass was found to produce as much or more forage than bromegrass on many sites, and it equalled or exceeded bromegrass in seed production, ease and speed of stand establishment, and preference by livestock when grazed or as hay.

The ability to start growth earlier in the spring than other seeded or native species was soon

[3] Bates, C.G. 1930. Forestry in North Dakota. USDA-FS Typed Report in Response to request from Senator Nye (Senate No. 4553) 71st Congress.

[4] Personal communication with Glen Roloff, U. S. Forest Service Office, Bismarck, North Dakota.

recognized as a desirable characteristic of crested wheatgrass (Westover et al. 1932). This led to research on use of crested wheatgrass as the early spring pasture in complementary grazing methods to allow deferment of the native range, which in turn greatly increased the carrying capacity of a given unit of land. The ability of crested wheatgrass to survive under conditions of less than ideal management has also promoted its use.

In Canada, crested wheatgrass has replaced bromegrass in most seeding programs in the southern parts of the Prairie Provinces. For example, community pastures administered by the Provincial Lands Branch required seeding of 21,805 acres (8,830 hectares) in 1982 and 1983. No bromegrass was seeded, but crested wheatgrass was seeded on 7,935 acres (3,214 hectares). Rapid stand establishment and the ability to provide early spring grazing (May 10) were the reasons given for the preference for crested wheatgrass[5].

An informal survey of several county Soil Conservation Service offices in western North Dakota showed that in the early 1980's, crested wheatgrass was seeded alone or in mixture with other species on at least 60% of the acres seeded to grass. Potential longevity of the stand, ease of establishment, and need for early spring grazing were the major reasons for seeding crested wheatgrass.

Crested wheatgrass seed production acreage fluctuates in response to demand, therefore, it is difficult to establish reliable seed production figures. In 1983, certified seed fields in Canada totalled 610 acres (247 hectares) for Fairway, 550 acres (228 hectares) for Nordan, and 261 acres (106 hectares) for all other crested wheatgrass cultivars including Summit and Parkway. The total crested wheatgrass acreage for seed production, certified plus common, was estimated by Knowles[5] to be more than 2800 acres (1134 hectares) in 1983. The cultivar Summit, an A. desertorum type released by Agriculture Canada in 1953 is not extensively used due to poor seed production characteristics. The cultivar Nordan, an A. desertorum type released by USDA in 1954 has taken the place of Summit in Canada due to its good seed production characteristic and to the active seed market in the United States.

It is difficult to determine how many million acres of crested wheatgrass exist in United States and Canada. One of the confounding factors has been that through the years, some lands that were regrassed under the various government programs were again plowed in another attempt to produce cereal crops. Many failed again, and the revegetation process was repeated. Consequently, using total acres seeded does not provide an accurate estimate of the net acres of crested wheatgrass.

Knowles predicts that crested wheatgrass will have a steady future in Canada, and based on past performance, I see no reason for any decrease in usage in the northern Great Plains of United States.

[5] Personal communication from R. P. Knowles, Research Scientist, Research Branch-Agriculture Canada, Saskatoon, Saskatchewan, January 26, 1984.

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History of Crested Wheatgrass in the Intermountain Area

James A. Young and Raymond A. Evans

ABSTRACT: The improvement of degraded sagebrush (Artemisia) rangelands in the Intermountain area was severely restricted during the first part of this century by lack of adapted plant material. Crested wheatgrass (Agropyron cristatum and A. desertorum) became available during the 1930's. Techniques and equipment for seeding were developed during the 1940's. The halogeton (Halogeton glomeratus) control programs gave great impetus to the seeding of crested wheatgrass on public lands during the 1950's. The established stands of crested wheatgrass provide an extremely valuable grazing resource in the Intermountain area.

INTRODUCTION

The need for seeding of depleted big sagebrush (Artemisia tridentata) rangelands was recognized long before the technology for seeding was available. The editor of the Carson City, Nevada, Morning Appeal must have felt especially clairvoyant on an early December day in 1886 as he greeted his readers with a stirring editorial offering an answer to Nevada's declining range productivity. The editor's suggestion was to have the state appropriate funds for research to determine how to reseed grasses on the depleted sagebrush rangelands of Nevada (Young and McKenzie 1982).

By the beginning of the 20th century both P.B. Kennedy of the University of Nevada and David Griffiths of the U.S. Department of Agriculture were calling for seeding to restore the productivity of degraded sagebrush rangelands (Kennedy and Doten 1901, Griffiths 1902). These scientifically trained botanists called for the collection of seeds from native perennial grasses for use in revegetating rangelands. What could be more adapted to the sagebrush environment than grasses that had evolved in that environment?

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Sometime after the turn of the century, there was a dramatic change in many of the sagebrush/grass plant communities of the Intermountain region. A series of alien annual weeds invaded the void in the vegetation created by overutilization of the native herbaceous species. Such weeds as Russian thistle (Salsola iberica), tansy mustard (Descurainia pinnata), tumble mustard (Sisymbrium altissimum) and cheatgrass (Bromus tectorum) spread in successive waves across the Intermountain area. The invasion and establishment of these aliens revolutionized plant succession in the degraded sagebrush/grass communities. Seedings of many of the native perennial herbaceous species could not compete with the alien annuals (Piemeisel 1951, Young et al. 1972, Yenson 1981). Range managers found they did not have plant materials that could be established on the sagebrush rangelands.

Early in the 20th century, the first range scientist working for the U.S. Forest Service, A. W. Sampson, experimented with methods of reseeding depleted rangelands located in the national forests. The early seeding attempts were summarized by Jardine and Anderson (1919): "The results presented in Bulletin 4 (Sampson 1913) as well as the results of investigations since it was issued, indicate that the expense of seeding rangelands to cultivate species is warranted only on mountain meadows and other areas of minor extent 500 feet and more below true timberline and having favorable soil and moisture conditions."

Obviously, the seeding of alpine meadows on national forests was physically and environmentally a long way from rehabilitating vast expanses of degraded sagebrush rangelands in semiarid valleys on the public domain that was open to homesteading. In Nevada, for example, where millions of acres of degraded sagebrush rangeland existed, the vacant public land constituted 71 percent of the state's total land area (Buckman 1938). On June 28, 1934, the Taylor Grazing Act was finally passed by Congress after years of delay. On November 26th of that year, President Franklin D. Roosevelt issued an executive order withdrawing 173 million acres of public lands in 12 western states from homesteading entry.

SEEDING DURING THE 1930'S

The impetus for reseeding degraded sagebrush rangeland came from two sources during the 1930's. First, the long-established research stations of the Forest Service, especially the Intermountain Forest and Range Experiment Station, developed techniques for seeding sagebrush rangelands. Second, the infant Grazing Service of the U. S. Department of the Interior began to instigate range improvement projects.

During the late 1930's, a surplus of manpower was available through such programs as the Civilian Conservation Corps (CCC) for improvement projects on public lands. For the first time the federal government was willing to devote considerable amounts of money toward improving wildlands. The CCC crews were employed on a variety of projects, from building roads and trails to attempting to control the destructive outbreaks of Mormon crickets (*Anabrus simplex*) (Young 1978). Use of labor intensive methods for rehabilitation of degraded rangelands was defeated by the accumulations of woody biomass and the vastness of the sagebrush landscapes. A picture of futility was CCC boys pushing hand garden planters through mature stands of big sagebrush (Anon. 1941). Their efforts were futile because (a) the biological competition from the shrub was not reduced, (b) the physical restrictions of handseeders imposed by the shrubs, and (c) the limited area that could be seeded, even with large crews.

Essentially, the range rehabilitators were faced with the same problems that had plagued homesteaders. The successful homesteader within the sagebrush zone had sometimes overcome the shrub community by developing irrigation systems and flooding potential agronomic fields. The native desert shrubs could not stand prolonged flooding. Thousands of homesteads were cleared by hand grubbing, dragging with rails or timbers, or a combination of several such treatments. The range improvers did not have the option of flooding, and rather than a portion of 160 acres, they had millions of acres of sagebrush-dominated rangeland to clear.

The para-military CCC approached these problems with a militaristic attitude. More troops were futile, but the battle against sagebrush would be more equal if suitable equipment could be substituted for manpower. The logical source of equipment was agriculture, but generally agronomic tillage implements proved too fragile and time consuming to operate on sagebrush rangelands. Borrowing from the techniques used by developers of irrigation tracts, the CCC experimented with dragging heavy railraod rails behind tractors in an attempt to knock down or uproot mature, nonsprouting sagebrush plants.

Several types of rails were developed for knocking down big sagebrush plants. These include the Monte Cristo rail, named for the Monte Cristo Ranger District on the Wasatch National Forest near Ogden, Utah; the Olsen rail, named for a sheep and wheat rancher who developed and extensively used the rail in the Columbia Basin north of Hanford, Washington; and the Supp rail, developed by the Supp Brothers to clear land in the defunct irrigation project at Metropolis, Nevada (Pechanec et al. 1944, Robertson 1944).

First Seedings of Crested Wheatgrass

Standard crested wheatgrass (*Agropyron desertorum*) and Fairway crested wheatgrass (*Agropyron cristatum*) provided the vital ingredient of adapted plant material that brought success to range seeding in the Intermountain area. Crested wheatgrass had undergone a lot of development in Russia and on the Great Plains of the United States and Canada before it was widely used (see Lorenz this volume).

The first known range seeding of crested wheatgrass in the Intermountain area occurred in 1932 on Herman Winter's farm near American Falls, Idaho and at the U.S. Department of Agriculture Sheep Experiment Station near Dubois, Idaho (Hull and Klomp 1966). In 1936, the Rural Resettlement Administration began drilling the first of 57,000 acres of crested wheatgrass on land utilization projects in Curlew and Black Pine Valleys in Oneida County, Idaho. The Crooked River National Grasslands were another center of successful seeding establishment. Crews of local farmers were assembled in 1936 under the Emergency Relief Act, as administered by the Rural Resettlement Administration, to begin seeding abandoned cropland. The farmers brought their own teams and old farm tractors to pull disks, moldboard plows, and grain drills. Various grass species were seeded before crested wheatgrass became more or less the standard species (Young and McKenzie 1982).

Private ranchers also experimented with seeding of sagebrush rangelands. In 1940 there were three successful seedings of crested wheatgrass on rangelands in Nevada and they all were located on private ranches (Young and McKenzie 1982). George Stewart described the first crested wheatgrass seeding as an oasis of perennial herbaceous vegetation in oceans of denuded rangeland (Stewart 1938).

During World War II, pressure was applied to the U.S. Forest Service by wool and meat processors to allow increased numbers of cattle and sheep to graze in national forests. Remembering the disastrous results of such increased allocations during World War I, the Forest Service resisted such efforts, but pointed out that livestock production could be increased if degraded areas were improved through seeding. With the support of the agricultural portions of the War Productions Board, the Forest Service submitted supplemental budget requests for research on range seeding. With the support of livestock producers, funding was greatly increased by Congress (Chapline 1978). The Forest Service seeded about 20,000 acres in this pilot program.

As a part of the Forest Service range improvement program, Joseph Robertson was assigned by the Intermountain Forest and Range Experiment Station during the early 1940's to assess seedable sites on national forests in Nevada and Wyoming. In the Ruby Mountains of Nevada, Robertson suggested that rugged topography, rocky soils, and general condition of the plant communities made seeding unfeasible and undesirable. Robertson suggested that the seeding of degraded sagebrush ranges located off the national forests would benefit the higher ranges by permitting a later turnout date for livestock in the spring. His suggestion was accepted and 820 acres were seeded in the Ruby Valley near Arthur. For many years the seeded area had been a dangerous spring range for cattle because of a poisonous plant, low larkspur (Delphinium bicolor). The area's grazing capacity was rated at 16 acres per animal unit month (AUM). The seeded area was a mixture of private and public lands administered by the USDI Bureau of Land Management. After two years rest the seeding was grazed for three weeks each spring by 400 cows and calves that normally would have been turned out on the national forests. This example of how the seeding money was spent by the Forest Service illustrates the potential of range improvement to alleviate management problems while increasing red meat production. This and other pilot testing projects during the war helped dispel the prevailing attitude that sagebrush ranges could not be seeded (Young and McKenzie 1982).

As a result of the pilot seeding program, the Intermountain Forest and Range Experiment Station issued three landmark bulletins on rangeland seeding. The first concerned seeding of Utah rangelands (Plummer et al. 1943); the second Idaho rangelands (Hull and Pearse 1943); and the third Nevada rangelands (Robertson and Pearse 1943).

PROBLEMS WITH SEEDING EQUIPMENT

The Forest Service claimed 90 percent successful establishment with the pilot seeding program, but equipment breakage was a major problem. A conference was held in Utah in 1945, attended by western Forest Service administrators and researchers, to consider the general subject of range seeding. A lack of effective and suitable equipment was determined to be one of the major stumbling blocks in the way of successful seeding. This led directly to the formation of the Range Seeding Equipment Committee. The first official meeting was held in Portland, Oregon in December 1946. The second meeting followed in Ogden, Utah in 1947. The list of those attending included a blend of old-time range scientists such as George Stewart and W. R. Chapline, and such younger scientists as A. C. Hull, Jr. and Joseph F. Pechanec. Pechanec was elected chairman of the committee. He was beginning his career as a scientist at this time and was to have a great deal to do with the development of special range improvement equipment both as a scientist and a research administrator (Anon. 1974).

Other land management agencies with similar problems eventually joined the Forest Service to form a federal interagency committee for range seeding equipment. The Bureau of Land Management joined the committee in 1949, followed by the USDI Bureau of Indian Affairs, and the USDA Soil Conservation Service. In 1954, after a portion of the range research program was transferred from the Forest Service to the USDA Agricultural Research Service, an ARS scientist joined the committee.

Development of Rangeland Plow

As previously noted, most of the wheatgrass seedings during the 1930's in the Intermountain area were carried out on abandoned cropland. If sagebrush ranges were to successfully be seeded, mechanical means of brush control had to be developed. Among the first projects undertaken by the Range Seeding Equipment Committee was an evaluation of the rail drags and pipe harrows used in brush control. Pipe harrows were self-cleaning harrows for tillage on very rocky sites. Both implements were relatively effective on old growth plants which could be easily uprooted, but neither controlled supple young plants (Anon. 1974).

The implement that did the best job of controlling big sagebrush was the wheatland disk plow. The wheatland plows were subject to a great deal of breakage of castings, disks, and even the frame if they were used on rocky sites. Use of this plow required continued maintenance. But despite its drawbacks, many early seedings including a portion of the Ruby Valley project were established with wheatland plows with seeders attached (Young and Mckenzie 1982).

After his experiment with wheatland plows, J. H. Robertson was interested in the development of a plow for rangelands. He noted in the proceedings of the 1939 World Wheat Congress a report on an Australian stump-jump plow. The plow was designed with each pair of disks independently suspended on spring-loaded arms so that when an obstruction was met the disk rode over the blockage rather than breaking. Robertson called this plow to the attention of his colleagues and a plow known as the Sungeneral or Australian stump-jump plow was imported from H. V. McKay, Massey Harris Ltd. of Sunshine, Australia (Young and McKenzie 1982).

The plow was tested March 17, 1946 on an area south of Boise, Idaho. A portion of this site had lava rocks up to 16 inches in diameter on the soil surface. After the initial test, the plow was taken to an area near Smith Prairie in Boise National Forest where 305 rocky, steep acres were plowed. The site had previously caused excessive breakage of a wheatland plow. Extensive testing in the Pacific Northwest followed. The stump-jump plow proved to be too weak and easily damaged (Pechanec and Hull 1947).

From this prototype plow imported from Australia, the Range Seeding Equipment Committee and the Forest Service Equipment Laboratory at Portland, Oregon in 1947 and 1948 developed the plow which became known as the brushland plow. The engineering work was done by Ted Flynn with assistance from Tom Caldwell and with the approval of J. F. Pechanec (Young and McKenzie 1982).

Land managers now had an implement capable of attacking dense stands of big sagebrush. The plow imported from Australia was relatively inexpensive at a cost of $413 f.o.b. Sunshine, Australia in 1946, and weighed 3,000 pounds (Anon. 1974). The brushland plow produced by the Equipment Committee's efforts was a much more substantial implement weighing 6,000 pounds. The brushland plow was considerably more expensive and the cost has continued to rise, reaching $25,000 in 1979. This underscores the capital requirements for range improvements.

The brushland plow is important in the story of the development of the rangeland drill because a brush control implement had to be developed first, and because the independent suspension of the disks became the pattern for the development of furrow openers on the drill.

Development of Rangeland Drill

Grain drills designed for farms had proven even less adapted to sagebrush ranges than plows. In southern Idaho and central Oregon, there were considerable acreage of abandoned cropland that could be seeded to crested wheatgrass by grain drills with few problems. However, the uneven seedbeds with clumps of woody trash produced by the new brushland plows proved to be particularly hard on grain drills. A major problem was breakage caused by the presence of large rocks on the soil surface.

In early summer 1951 Floyd Iverson, a regional range and wildlife officer for the Forest Service, made a routine trip to the Fremont National Forest in southeastern Oregon. During a discussion of the range seeding program on the forest, the forest, range, and wildlife staff officer, John Kucera, mentioned that during an eight-hour working day they were breaking three or four drill arm assemblies. Mr. Iverson suggested the need for someone to develop a drill for rangelands. Kucera immediately said he would attempt such a development if he had the funds. The regional office contributed $700 toward such a project based on Kucera's cost estimate. The drill conversion eventually cost $1,000 with the Fremont National Forest paying the difference (Young and McKenzie 1982).

Development of the first rangeland drill was started in July 1950. The performance goal for the drill was that it could be used anywhere one could drive a small crawler tractor. Up until 1950 most range seeding was done with John Deere-Van Brunt grain drills. The Fremont Forest happened to have a Minneapolis-Moline drill with a heavy frame, so it became the experimental unit. For clearance, 12-inch spoke extenders were welded around the existing wheels. This prompted taunts that the experimenters were building a mechanical porcupine. A new rim was placed around the outside of the spokes. The designers then developed Y yokes to support the disk openers. These openers made the furrow in the seedbed surface into which the seeds were dropped. Determination of the correct angle of the yokes that permitted them to ride up over obstructions was gained by trial and error (Young and McKenzie 1982).

In the fall of 1951 the modified drill was used to seed 750 acres on the Coffee Pot seeding in the Paisley Ranger District of the Fremont Forest. The openers worked adequately, but the frame and tongue had to be strengthened. In early January the designers loaded what they called "our monstrosity" on a railcar for shipment to the Forest Service Equipment Development Laboratory at Arcadia, California where it was to serve as a model for development of an engineered drill (Young and McKenzie 1982).

SEEDING TO SUPPRESS HALOGETON

During the 1950's there was intense pressure on public land range managers to control the poisonous weed halogeton (Halogeton glomeratus) that had been responsible for the deaths of large numbers of sheep. Several prominent range scientists led by L. A. Stoddart of Utah State University had advocated the biological suppression of halogeton by seeding crested wheatgrass. J. H. Robertson had established experiments near Wells, Nevada during the 1940's on an area burned in a wildfire. These experiments had clearly shown that crested wheatgrass could significantly suppress halogeton (Evans et al. 1984).

Committees were formed in the affected states to develop suppression programs for halogeton. Members of the Idaho committee had visited J. H. Robertson's plots at Wells and extolled the virtues of crested wheatgrass in suppressing the poisonous weed. Extensive plantings were made in the Raft River Valley at Idaho to suppress halogeton. These crested wheatgrass plantings became the center of a concerted research effort on crested wheatgrass under the leadership of Lee Sharp of the University of Idaho.

After federal support was assured by passage of the halogeton control bill by Congress in 1952, the Bureau of Land Management carried out extensive seeding programs with crested wheatgrass. A large portion of the crested wheatgrass on public land in states like Nevada was seeded under the halogeton program.

During the 1960's the public land management agencies came under severe pressure from a variety of environmentally concerned groups (Young et al. 1979). One result of these pressures was the virtual discontinuation of range improvement projects and especially the seeding of crested wheatgrass.

CONCLUSION

The "Golden Age" of seeding crested wheatgrass lasted for barely a decade, from the mid 1950's when the equipment and funds became available to conduct the seedings until the mid 1960's when seeding was largely discontinued. The application of World War II technology in range improvement was startling in its results. Using the sagebrush ranges of Nevada as an example, about 1 million of the 27 million acres of sagebrush rangeland were seeded between 1955 and 1972. This seeded area constitutes only 2% of the total rangeland in Nevada, but produces 10% of the harvestable grazing from the state's rangeland. The crested wheatgrass seedings produced early spring grazing on a sustained basis. Early spring grazing is especially valuable to the livestock industry and it is the period when native forage species are most susceptible to damage by excessive grazing. The successful seeding of crested wheatgrass on degraded sagebrush ranges helps to stabilize the livestock industry and adds a sense of vitality to range management in the Intermountain West (Young and McKenzie 1982).

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In: Johnson, K. L. (ed.). 1986. Crested wheatgrass: its values, problems and myths; symposium proceedings. Utah State Univ., Logan.

Early Use of Crested Wheatgrass Seedings in Halogeton Control

William L. Mathews

ABSTRACT: The first large scale seedings of crested wheatgrass in Idaho were prompted by serious sheep losses to the poisonous plant halogeton. Depleted rangelands were seeded as rapidly as funds would permit to curtail the spread of halogeton. The high adaptability of crested wheatgrass to the soils and climatic conditions of the area, along with its ability to dominate the site to the exclusion of annuals, made it a superior candidate for seeding. The seedings were very successful both from the standpoint of restoring an adequate perennial cover on depleted areas as well as providing substantial relief from grazing use on areas not susceptable to treatment.

INTRODUCTION

Serious sheep losses from poisoning by halogeton (Halogeton glomeratus) during the fall of 1947 led to the first large-scale seedings of crested wheatgrass (Agropyron cristatum and A. desertorum) in Idaho. Prior to this loss most range managers were not aware of the presence of halogeton or of its toxic properties. Suddenly substantial concern was generated over the possible impact of halogeton on the entire rangeland livestock industry in Idaho. Immediate action was taken to determine the location of halogeton infestations, to acquaint range users with the physical characteristics and toxic properties of the plant, and to initiate control actions. With the beginning of the next grazing season action was initiated to contain the spread of this poisonous plant.

Chemical Controls

Halogeton is an annual which moves quickly into disturbed areas, often dominating the site. Most of the initial infestations occurred along roadsides and in small isolated patches where soil disturbance was prevalent. Therefore a chemical program (2,4-D) was initiated in the hope that this would be an effective means of control. But chemical control was complicated by the fact that halogeton produces two types of seed: one type which germinates readily the next growing season, the other with delayed germination over several years. This characteristic required repeated chemical treatment for several years. As the repeat treatments were applied, more and more of the bordering perennial vegetative cover was killed resulting in an enlargement of the disturbed areas. Consequently, it soon became apparent that chemical control was impossible. Attention was then directed to seeding the depleted areas with a perennial plant that would suppress and crowd out halogeton.

Seeding Controls

The search for a perennial plant for seeding purposes was easy. During the late 1930's and early 1940's, A.C. Hull, Jr., working for the Intermountain Forest and Range Experiment Station, installed several trial seeding plots in the Burley District of the Bureau of Land Management. Each plot, as I recall, had 25 species of both native and introduced range plants that were considered to be good candidates for seeding depleted range lands. Several species did very well but the obvious choice was crested wheatgrass (both standard and fairway) from the standpoint of ease of establishment, adaptability to the soil and climatic conditions, and the ability to dominate the site and crowd out annuals. In addition, crested wheatgrass had adequate and cheap seed supplies.

We proceeded to reseed as much depleted rangeland each year as funds would permit. Most of the work was done under contract. Projects varied in size from a few hundred acres to more than 10,000 acres. The areas were plowed to reduce sagebrush and other competition and to prepare a seed bed. Seed (6 lbs/acre) either was drilled or broadcast with fertilizer spreaders depending on the softness of the seed bed at the time of planting. All projects were fenced and protected from livestock use. Grazing was generally permitted during the fall of the second growing season. Plowing cost was

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about $3.25 per acre, seeding cost was around $1.00 per acre, and seed cost about $1.50 per acre. The total cost was around $6.00 per acre without fencing.

We found that crested wheatgrass could be successfully established on all depleted rangelands within the District with the exception of sites having soil with a high content of soluble salts. Even the dry gravel bars eventually produced an adequate stand of grass, although it often took a couple of years longer for the stand to become established.

The seeding program started out in a rather meager manner since we had to scrounge money from our very limited range improvement and soil and watershed funds. With a large acreage of depleted rangeland and very good success with seeding crested wheatgrass, the Burley District was able to obtain a substantial portion of the Bureau's available funding. Increased concern over the possible impacts of halogeton on the livestock industry culminated in the passage of the Halogeton Control Act of 1952, which provided increased funding for an accelerated seeding program beginning in 1953.

AN OVERALL APPRAISAL

Fortunately, crested wheatgrass turned out to be a better forage plant than was earlier suspected. Early crested wheatgrass use in southern Idaho involved small stands that were intermixed with native range. Under these situations crested wheatgrass was lightly used, which generated a feeling that it had low palatability and low forage value. However, with the large seedings it soon became evident that livestock would eat the grass and do well on it. Many questions regarding the value of crested wheatgrass and the best way to manage its use arose. The University of Idaho expressed an interest in evaluating the forage value, economic returns, and management needs of large seedings in the District. Consequently, the Bureau entered into a cooperative agreement in 1955 with the University and the range users involved in the Point Springs seeding. This cooperative project has continued to the present time and has yielded many benefits for all concerned.

The large seedings have provided substantial relief to other range areas that could not be treated because of topography, rockiness, etc. The seedings provided forage early in the season, which permitted a delay in the turnout dates along with an overall reduction in use, on the native range areas. As a result of the seedings, a substantial improvement in the range resource and livestock performance of the area took place.

Areas with soils high in soluble salts as well as some small disturbed areas still support halogeton. However, with improved forage conditions on other areas, decreased sheep use, and knowledge of how to avoid losses, halogeton no longer presents a serious range use problem.

In: Johnson, K. L. (ed.). 1986. Crested wheatgrass: its values, problems and myths; symposium proceedings. Utah State Univ., Logan.

SECTION II.

Systematics and Genetics.

What Crested Wheatgrass is Now and What it Might Become.

Chairman, James H. Richards

Taxonomy of the Crested Wheatgrasses (Agropyron)

Douglas R. Dewey

ABSTRACT: The purposes of this paper are to review the position of the genus Agropyron in the tribe Triticeae and to examine alternative taxonomic treatments within Agropyron. When Agropyron is defined as those species with the P genome, it becomes a small genus with less than 10 species consisting of only the crested wheatgrasses. This narrow definition of Agropyron is now accepted in Europe and Asia; North Americans should accept that same definition. As treated in 1976 by N. N. Tzvelev in Poaceae URSS, Agropyron consists of 10 species and 9 subspecies, but most of those taxa are endemics of little interest to North American users of crested wheatgrass. North Americans need to consider only three species: 1) A. cristatum (L.) Gaertn. sensu lato, 2) A. desertorum (Fisch. ex Link) Schult., and 3) A. fragile (Roth) Candargy [=A. sibiricum (Willd.) Beauv.].

INTRODUCTION

To understand the taxonomy of the crested wheatgrasses, Agropyron cristatum (L.) Gaertn. and related species, it is necessary to view them in the context of the taxonomy of the entire tribe Triticeae (= Hordeeae). Revisions have recently been made in the taxonomy of the Triticeae (Tzvelev 1976, Melderis et al. 1980) and others are being proposed (Dewey 1984, Löve 1984). The significant taxonomic changes involve redefinition of most genera, deletion of a few genera, and establishment of several new genera. The primary catalyst for the current taxonomic activity and controversy in the Triticeae is a movement to bring classification into line with biological relationships.

Traditionally, genera of the Triticeae have been separated on the basis of morphological features of the spikes, such as number of spikelets per node, glume size and shape, and rachis characteristics (Hitchcock 1951). Although these traits lend themselves readily to construction of taxonomic keys, their use often results in placement of closely related species in different genera or distantly related species in the same genus. For example, Agropyron scribneri and Sitanion hystrix are closely related species (Dewey 1967), yet they have been placed in different genera on the basis of one vs. two spikelets per node. On the other hand, Elymus canadensis and Elymus cinereus are distantly related species (Dewey 1966), yet they have been placed in the same genus because they have two or more spikelets per node. To those who subscribe to the philosophy that taxonomy should reflect biological relationships, inconsistencies of this nature are unacceptable.

Over the past 30 to 40 years, cytogeneticists have accumulated a vast amount of information that measures biological relationships in terms of 1) the ability of species to hybridize, 2) the level of chromosome pairing in the interspecific hybrids, and 3) the fertility of the F_1 hybrids. In the Triticeae, a system of classification based on cytogenetic information differs substantially from one based on morphology. Both systems have advantages and disadvantages. The traditional system of classification based on morphology is stable and convenient to use, yet it is somewhat artificial. The system of classification based on cytogenetics will be unstable until all genetic relationships have been determined, and taxonomic keys will always be more difficult to construct and less convenient to use. Nevertheless, I am confident that science will be best served in the long run by a taxonomic system that groups species according to their biological relationships.

Through the process of genome analysis (analysis of chromosome pairing in interspecific hybrids) it has been possible to identify most of the basic chromosome sets (genomes) in the perennial Triticeae. The genomic system of classification as outlined by Löve (1982) is based on the concept that each genome or combination of genomes should be recognized as a different genus. Under this system, Löve recognized 37 genera in the Triticeae, which is almost double the number recognized by more tradi tional taxonomists (Table 1). I agree in principle with Löve's generic concepts; however, some adjustments in generic boundaries must be made as additional cytogenetic data are obtained.

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Löve's (1984) treatment encompasses the entire tribe (annuals and perennials), whereas I have concerned myself largely with the perennials (Dewey 1984). Table 2 presents a summary of the genera, as I view them, that contain perennial grasses. _Critesion_ (= _Hordeum_ pro parte) and _Elymus_ will require further partitioning as genomic relationships become more clearly established. Fortunately, there is little likelihood that the newly defined generic boundaries of _Agropyron_ will be changed.

REDEFINITION OF _AGROPYRON_

Agropyron (wheatgrass) in its traditional and broad sense (sensu lato) has been the largest genus in the Triticeae, encompassing more than 100 species distributed widely in temperate and subarctic regions of both the northern and southern hemispheres. _Agropyron_ sensu lato contained almost all of the perennial species in the Triticeae that had single spiklets per node. North Americans have generally accepted this broad definition, which was advocated by A. S. Hitchcock (1935, 1951) in the United States and W. M. Bowden (1965) in Canada. Until recently, most British and other European agrostologists (Bor 1970, Hubbard 1968, Kerguelen 1975) treated _Agropyron_ in its broad sense.

The Russian agrostologist Nevski (1933) treated _Agropyron_ in a very narrow sense (sensu stricto) by restricting it to 13 species, the crested wheatgrasses. Nevski apparently reconsidered his 1933 decision to be too drastic because in the following year he redefined _Agropyron_ as consisting of two subgenera: _Elytrigia_ and _Eu-Agropyron_ (Nevski 1934). Subgenus _Elytrigia_ consisted of the rhizomatous species of _Agropyron_, e.g., _A. repens_, as well as some of the caespitose species, e.g., _A._

Table 1.-- Genera included in the tribe Triticeae by various authors.[1]

Nevski (1933)	Hitchcock (1951)	Tzvelev (1976)	Melderis et al. (1980)	Löve (1984)
Aegilops	_Aegilops_	_Aegilops_	_Aegilops_	_Aegilemma_
Agropyron	_Agropyron_	_Agropyron_	_Agropyron_	_Aegilonearum_
Aneurolepidium	_Elymus_	_Amblyopyrum_	_Crithopsis_	_Aegilopodes_
Anthosachne	_Hordeum_	_Dasypyrum_	_Dasypyrum_	_Aegilops_
Asperella	_Hystrix_	_Elymus_	_Elymus_	_Agropyron_
Brachypodium	_Lolium_	_Elytrigia_	_Eremopyrum_	_Amblyopyrum_
Clinelymus	_Monerma_	_Eremopyrum_	_Festucopsis_	_Australopyrum_
Critesion	_Parapholis_	_Henrardia_	_Hordelymus_	_Chennapyrum_
Crithopsis	_Scribneria_	_Heteranthelium_	_Hordeum_	_Comopyrum_
Cuviera	_Secale_	_Hordelymus_	_Leymus_	_Critesion_
Elymus	_Sitanion_	_Hordeum_	_Psathyrostachys_	_Crithodium_
Elytrigia	_Triticum_	_Hystrix_	_Secale_	_Crithopsis_
Eremopyrum		_Leymus_	_Taeniatherum_	_Cylindropyrum_
Haynaldia		_Psathyrostachys_	_Triticum_	_Dasypyrum_
Heteranthelium		_Secale_		_Elymus_
Hordeum		_Taeniatherum_		_Elytrigia_
Malacurus		_Triticum_		_Eremopyrum_
Psathyrostachys				_Festucopsis_
Roegneria				_Gigachilon_
Secale				_Gastropyrum_
Sitanion				_Henrardia_
Taeniatherum				_Heteranthelium_
Terrella				_Hordelymus_
Trachynia				_Hordeum_
Triticum				_Kiharapyrum_
				Leymus
				Lophopyrum
				Orrhopygium
				Pascopyrum
				Patropyrum
				Psathyrostachys
				Pseudoroegneria
				Secale
				Sitopsis
				Taeniatherum
				Thinopyrum
				Triticum

[1] The treatments are not necessarily comparable because all do not cover the tribe worldwide and most authors have worked from different geographical and historical perspectives.

Table 2.-- The perennial genera of the Triticeae tribe based on genome content.

Genus	Type species	Basic genome[1]	Approx. no. species	Chromosome no. (2n)
Agropyron	A. cristatum	P	10	14,28,42
Pseudoroegneria	P. strigosa	S	15	14,28
Psathyrostachys	P. lanuginosa	N	10	14
Critesion	C. jubatum	H	30	14,28,42
Thinopyrum	T. junceum	J-E	20	14, 28, 42, 56, 70
Elytrigia	E. repens	SX	5	42,56
Elymus	E. sibiricus	SHY	150	28,42,56
Leymus	L. arenarius	JN	30	28, 42, 56, 70, 84
Pascopyrum	P. smithii	SHJN	1	56

[1]Genome designations are those proposed by Löve (1982).

elongatum. Subgenus Eu-Agropyron consisted of the same crested wheatgrasses that Nevski included in his 1933 definition of Agropyron. Under both the 1933 and 1934 treatments, Nevski treated the large number of self-fertilizing species previously in Agropyron (e.g. A. trachycaulum) as Roegneria. Nevski's treatments did not receive widespread acceptance outside of the U.S.S.R., except in China where a modified version of his 1933 treatment is still in use (Keng 1965).

Tzvelev (1973), another Russian agrostologist, reinstated Nevski's 1933 definition of Agropyron by restricting the genus to 10 species. This treatment was included in Tzvelev's (1976) comprehensive publication, Poaceae URSS, which is now the generally accepted treatment of the grass family in the U.S.S.R. In the recently published Volume 5 of Flora Europaea, British agrostologists (Melderis et al. 1980) have adopted the narrow Nevski (1933) and the Tzvelev (1976) definitions of Agropyron. The treatment in Flora Europaea will almost certainly become accepted throughout Europe and in most of the British Commonwealth.

The narrow definition of Agropyron--now accepted in Europe, China, and the U.S.S.R.--is in complete harmony with the genomic system of classification. In view of the almost worldwide acceptance of the narrow definition of Agropyron by both traditional taxonomists and cytotaxonomists, North Americans should also accept that definition. Considering the facts that all crested wheatgrasses are native to Eurasia (none is native to North America) and that all of the type specimens occur in European or Asian herbaria, it is both illogical and presumptuous for North Americans to define Agropyron in terms drastically different from those accepted in Eurasia.

CYTOGENETICS AND GENOME CONSTITUTION OF AGROPYRON

The crested wheatgrasses occur at three ploidy levels--diploid (2n=14), tetraploid (2n=28), and hexaploid (2n=42) (Jones 1960b). The tetraploids are by far the most common, and they span the entire natural distribution range of crested wheatgrass from Central Europe and the Middle East across Central Asia to Siberia, China, and Mongolia (Tzvelev 1976, Keng 1965). Diploids also occur from Europe to Mongolia; but their distribution is very sporadic, much like scattered islands in an otherwise tetraploid crested wheatgrass sea (Dewey and Asay 1982). Hexaploids are very rare; they apparently occur only in northeastern Turkey and northwestern Iran (Dewey and Asay 1975). Tetraploid strains are the most commonly seeded types in North America, being represented by the so-called "Standard" crested wheatgrass with four varieties— 'Nordan', 'Summit', 'Ephraim', and 'P-27' (Asay & Knowles 1985). Diploid strains are also seeded in North America and include the broadly defined "Fairway" with two varieties, 'Parkway' and 'Ruff', selected from the 'Fairway' germplasm. No hexaploid varieties have been bred.

The genome of diploid crested wheatgrass is represented by the letter "P", as suggested by Löve (1982). I have previously designated this genome as "C" (Dewey 1983), but that letter has also been applied to certain species of Aegilops. To avoid duplication of genome symbols, I suggest following Löve's (1982) system, which accounts for all species of Triticeae worldwide. Chromosome pairing is almost complete in hybrids among various broad-spiked (A. cristatum s. lat.) diploid taxa (Dewey and Asay 1982), showing that they contain the same basic set of chromosomes. Nevertheless, some structural chromosome rearrangements--translocations, inversions, etc.--occur in the genomes of some of the diploid taxa. Structurally or otherwise modified genomes may be represented with subscripts applied to the basic P genome, i.e. P_1, P_2, etc. Recently, a narrow-spiked diploid (A. fragile ssp. mongolicum) has been obtained from China (Dewey 1981) and hybridized with broad-spiked diploid Fairway. Chromosome pairing in these hybrids is very similar to pairing in the broad-spiked hybrids (Dewey and Hsiao 1984). It is now evident that all crested wheatgrass diploids, regardless of spike type, contain the same basic genome.

Tetraploid crested wheatgrasses behave cytologically as strict autoploids or near autoploids (Dewey and Pendse 1968, Dewey 1969), meaning that they contain one basic genome repeated four times. Hybrids between diploid and tetraploid crested wheatgrasses form up to seven trivalent associations per cell at metaphase I (Dewey and Pendse 1967), which shows that the genome in the tetraploids is more or less homologous with the genome in the diploids. The genome constitution of the tetraploids may be represented as PPPP (strict autoploid) or $P_1P_1P_2P_2$ (near autoploid). Doubling of a diploid gives rise to a strict autoploid, PPPP; whereas hybridization between two diploids, $P_1P_1 X P_2P_2$, followed by chromosome doubling gives rise to a near autoploid, $P_1P_1P_2P_2$, or in other words a segmental alloploid (Schulz-Schaeffer et al. 1963).

Hexaploid crested wheatgrasses behave cytologically as strict autoploids or near autoploids by forming frequent hexavalent associations at metaphase I (Dewey and Asay 1975). Chromosome pairing in hybrids of diploids X hexaploids and tetraploids X hexaploids is consistent with the hypothesis that hexaploid crested wheatgrass contains the basic P genome with some structural variations (Dewey 1969, 1973, Asay and Dewey 1979).

CRESTED WHEATGRASS TAXONOMY

The taxonomic history of crested wheatgrass reflects widespread confusion and uncertainty. Any expectation of a simple and neat solution to crested wheatgrass taxonomy is unrealistic because the problem is inherently complex, and subjective judgments must be made. Multiple chromosome races and the ability of crested wheatgrass taxa to hybridize are at the root of the taxonomic problems. All crested wheatgrass taxa can be hybridized with each other, and many taxa hybridize with ease and produce fertile or partially fertile offspring (Knowles 1955). Consequently, a great deal of introgression occurs and a continuum of morphological types covering the full range between the parent taxa results (Fig. 1).

North Americans are at a particular disadvantage in addressing crested wheatgrass taxonomy because: 1) the type specimens are not readily accessible (most are located at the Komarov Botanical Institute in Leningrad), 2) the opportunities to see the taxa in their natural habitats, especially in the U.S.S.R. and China, are limited, and 3) taxa introduced into North America soon lose their taxonomic identity and genetic integrity because of extensive intercrossing that occurs in nursery situations where many accessions are grown in close proximity to each other. Therefore, taxonomic decisions made on introduced materials are often unreliable.

Before undertaking a serious study of crested wheatgrass taxonomy, one must have a clear understanding of the type specimen of _A. cristatum_, which is the type species of _Agropyron_ (Jones 1960a). Some confusion has existed concerning the type specimen of _A. cristatum_ because the original Linnaean description involves a herbarium sheet of _Bromus cristatus_ (= _Agropyron cristatum_) with two specimens, one with glabrous spikelets and one with villous spikelets. After studying the type sheet and Linnaeus' description of _A. cristatum_, Jones (1960a) designated the specimen with villous spikelets as the type. This is in agreement with Nevski's (1934) view of _A. cristatum_ as plants with very dense oblong-ovoid spikes and villous spikelets. Many North Americans have incorrectly assumed that typical _A. cristatum_ consists of plants that look like the variety Fairway, which has glabrous spikelets.

Early Soviet Treatments

Prior to the 1930's, most Soviet agrostologists (Konstantinov 1923) recognized two basic groups of crested wheatgrass: 1) those with broad spikes (_A. cristatum_) and 2) those with narrow spikes (_A. desertorum_). Both groups had many morphological variations, but all were included in the two species (Table 3).

S. A. Nevski's Treatment

Nevski (1934), who has a reputation as a taxonomic splitter, recognized 13 species to accommodate the major morphological variations (Table 3). Nevski emphasized growth habit (rhizomatous vs. caespitose), spike shape (linear, imbricate, and pectinate) and the amount and location of pubescence in separating species. Three taxa--_A. dasyanthum_, _A. tanaiticum_, and _A. cimmericum_--have long rhizomes, and _A. michnoi_ has short rhizomes. I suspect that the three taxa with long rhizomes are rare hybrid derivatives, possibly crested wheatgrass X quackgrass (_Elytrigia repens_) rather than bona fide species. I have never seen plants of this nature in crested wheatgrass introductions, so North Americans need not concern themselves with them. The one taxon with short rhizomes, _A. michnoi_, does not appear to have a hybrid history; it resembles typical _A. cristatum_ very closely. Both taxa are plants of East Asia. The presence of very short rhizomes distinguished _A. michnoi_ from _A. cristatum_, and I do not consider differences of this type sufficient to warrant recognition as separate species.

The remainder of Nevski's (1934) taxa fall into three groups based on spike type: 1) linear spikes (_A. fragile_ and _A. sibiricum_), 2) subcylindrical spikes (_A. desertorum_, _A. badamense_, and _A. ponticum_), and 3) pectinate spikes (_A. cristatum_, _A. pectiniforme_, _A. imbricatum_, and _A. pinifolium_). The two linear-spiked taxa can be distinguished on basis of pubescent (_A. fragile_) vs. glabrous (_A. sibiricum_) leaf sheaths. Separating species on the basis of pubescence on any plant part is a doubtful practice. Genetic studies on hybrids between _A. desertorum_ X _A. fragile_ indicate that leaf-sheath pubescence is controlled by two genes, with pubescence being dominant (D. R. Dewey unpublished). In the group with subcylindrical spikes, swollen culm bases distinguish _A. badamense_ and _A. ponticum_ from _A. desertorum_, whose culm bases are non-swollen. Leaf-sheath pubescence is used to separate

Figure 1.--Variations in spike types of crested wheatgrass (_Agropyron_).

A. badamense (glabrous) from A. ponticum (pubescent). The taxa with pectinate spikes differ from one another with respect to traits such as culm height (A. pinifolium has culms less than 30 cm tall), spike pubescence (A. pectiniforme is glabrous), and spike density (A. cristatum spikes are so dense that no gaps occur between spikelets).

Other morphological characters as well as habitat and distribution differences entered into Nevski's decision to recognize the various crested wheatgrass taxa as species. Nevertheless, several of the key traits, especially pubescence, appear to have little taxonomic value, casting some doubt on Nevski's classification. The Nevski treatment was not widely accepted even in the U.S.S.R. where the tendency was to combine taxa into four species: A. cristatum, A. pectiniforme, A. desertorum, and A. sibiricum. (Kosarev 1949).

K. Jones' Treatment

No new and significant developments occurred in crested wheatgrass taxonomy until Keith Jones, a British cytotaxonomist, published the results of an extensive herbarium study (Jones 1960b). In his classification, Jones placed greatest emphasis on spike shape in combination with spike density, level of spike pubescence, and geographic distribution. Jones was able to recognize only three species (Table 3): 1) a western broad-spiked species (A. pectiniforme), 2) an eastern broad-spiked species (A. cristatum), and 3) a narrow-spiked species (A. sibiricum). Chromosome races were recognized, but Jones did not place much taxonomic significance on chromosome races.

Agropyron pectiniforme sensu Jones is a species located primarily in European Russia (west of the Ural Mountains) and eastern Europe including the Balkan countries, Turkey, and Iran. The spikes of A. pectiniforme are pectinate, generally broad, and spikelets are usually glabrous. This species includes chromosome races of 2n=14, 28, and 42. The Fairway variety of North America is included in Jones' A. pectiniforme. He placed the following taxa in synonymy: A. pectinatum, A. imbricatum, A. dagnae, and A. cristatiforme.

Agropyron cristatum sensu Jones occurs primarily in East Asia. It has broad, compact, imbricated spikes with densely pubescent glumes and lemmas. Plant of this nature agree with Linnaeus' original description of A. cristatum and also with Nevski's (1934) concept. Jones (1960b) placed no other Agropyron species in synonymy with A. cristatum, although he speculated that A. michnoi might be part of the A. cristatum complex.

All crested wheatgrasses with narrow or cylindrical spikes were placed in A. sibiricum, with A. desertorum being considered as part of the complex. Jones pointed out the widespread confusion concerning A. sibiricum (awnless plants) and A. desertorum (short-awned plants) and thought it best simply to combine the two taxa. Numerous head shapes and sizes occur within A. sibiricum as defined by Jones. This species is distributed primarily in Central Asia from the Caspian Sea to Lake Balkhash.

N. N. Tzvelev's Treatment

In 1973, N. N. Tzvelev (Curator of Vascular Plants, Komarov Botanical Institute, Leningrad) published a revision of Agropyron and expanded that revision in his major work, Poaceae URSS (Tzvelev 1976). As might be expected, Tzvelev used Nevski's 1934 treatment as the basis of his own treatment; yet he introduced a number of significant changes (Table 3). Tzvelev promoted the concept of polymorphic species consisting of several subspecies, whereas Nevski did not consider subspecies. Tzvelev relegated several of Nevski's species to the status of subspecies and placed others in synonymy.

Tzvelev treated A. cristatum as a polymorphic species with nine subspecies (Table 3). All are broad-spiked taxa, but they differ with respect to spike details (density, pubescence, etc.), leaf type (flat, convolute, etc.), plant size, geographic distribution, and habitat. Sure recognition of all nine subspecies is very difficult if not impossible. When morphology is coupled with geographic distribution and habitat, Tzvelev may be able to recognize each subspecies; however, anyone with less expertise and lacking the information and herbarium facilities available to Tzvelev would probably be able to distinguish only two or three distinct subspecies. The subspecies cristatum is an East Asian taxon equivalent to Nevski's (1934) and Jones' (1960b) species A. cristatum. The subspecies pectinatum, which consists of 2n=14, 28, and 42 chromosome races, is the same entity as Jones' A. pectiniforme, i.e. the western element of broad-spiked crested wheatgrass (Fig. 2). Most of the other taxa treated by Tzvelev as subspecies are localized endemics that may or may not warrant subspecific status.

Tzvelev treated A. desertorum in the same manner as Nevski (1934). However, he placed A. sibiricum in synonymy with A. fragile, whereas Nevski recognized both taxa as distinct species. Jones took a different course of action and placed A. desertorum in synonymy with A. sibiricum.

The three rather strongly rhizomatous endemic taxa--A. cimmericum, A. tanaiticum, and A. dasyanthum--were recognized as species by Tzvelev, but he suggested that they may have a hybrid history. The last two species under Tzvelev in Table 3, A. pumilum and A. krylovianum, scarcely look like crested wheatgrasses and should not be accepted as such until more convincing evidence is given. Both taxa have very narrow spikes and were at one time included in Elytrigia (Appendix I). Tzvelev suggested that A. krylovianum is a hybrid of Agropyron X Elytrigia.

A. Löve's Treatment

Löve's (1984) treatment of Agropyron differs from all others in that he separated species exclusively on the basis of ploidy level. Inasmuch as the crested wheatgrasses occur at three ploidy levels--2n=14, 28, and 42--Löve recognized only three species--A. pectiniforme (2n=14), A. cristatum (2n=28), and A. deweyi (2n=42). However, he identified four subspecies within diploid A. pectiniforme and 21 subspecies within tetraploid A.

Table 3.--Taxonomic treatments of Agropyron s. str. by authors with broad but different perspectives of the genus.

Konstantinov (1923)	Nevski (1934)	Jones (1960b)	Tzvelev (1976)	Löve (1984)
A. cristatum	A. cristatum	A. cristatum	A. cristatum	A. cristatum
A. desertorum	A. imbricatum	A. sibiricum	ssp. cristatum	ssp. cristatum
	A. pectiniforme	A. pectiniforme	ssp. pectinatum	ssp. imbricatum
	A. pinifolium		ssp. puberulum	ssp. michnoi
	A. michnoi		ssp. tarbagataicum	ssp. nathaliae
	A. ponticum		ssp. kazachstanicum	ssp. puberulum
	A. badamense		ssp. baicalense	ssp. ponticum
	A. desertorum		ssp. sabulosum	ssp. tarbagataicum
	A. sibiricum		ssp. ponticum	ssp. kazachstanicum
	A. fragile		ssp. schlerophyllum	ssp. sclerophyllum
	A. cimmericum		A. michnoi	ssp. stepposum
	A. tanaiticum		ssp. michnoi	ssp. birjutczense
	A. dasyanthum		ssp. nathaliae	ssp. bulbosum
			A. badamense	ssp. eriksonii
			A. desertorum	ssp. badamense
			A. fragile	ssp. desertorum
			A. cimmericum	ssp. sibiricum
			A. tanaiticum	ssp. fragile
			A. dasyanthum	ssp. mongolicum
			A. pumilum	ssp. pumilum
			A. krylovianum	ssp. pachyrrhizum
				ssp. dasyanthum
				A. pectiniforme
				ssp. pectiniforme
				ssp. baicalense
				ssp. brandzae
				ssp. sabulosum
				A. deweyi

cristatum (Table 3). The tetraploid subspecies include narrow-spiked types (ssp. sibiricum), broad-spiked types (ssp. cristatum) and all intermediates.

Löve, who defines species in terms of genetic isolation, defends his position on the basis of putative sterility barriers between crested wheatgrass taxa at different ploidy levels and the general absence of those barriers between taxa within ploidy levels (personal communication with A. Löve, 21 September 1983). Unfortunately, crossing and sterility barriers between and within ploidy levels are not as consistent and distinct as Löve might think. It is true that diploid X tetraploid and diploid X hexaploid crosses are often difficult to make (Knowles 1955, Dewey 1973); however, tetraploids hybridize readily with hexaploids (Dewey 1969).

Sterility is sometimes as high or higher in intraploidy hybrids as in interploidy hybrids. Hybrids among three diploid taxa produced only 5 to 45% stainable pollen (Dewey and Asay 1982), whereas tetraploid X hexaploid hybrids produced 70 to 90% (Dewey 1969), and diploid X hexaploid hybrids produced 35 to 75% stainable pollen (Dewey 1973). In light of this information, I cannot accept Löve's premise that each ploidy level warrants species status.

Taxonomic History of Crested Wheatgrass in North America

The first five accessions of crested wheatgrass (PI's 835, 837, 838, 1010, and 1012)[1] entering the USDA Plant Introduction System came from the U.S.S.R. in 1898 under the name of A. cristatum. Four accessions identified as A. desertorum (PI's 19537-19541) and another accession of A. cristatum (PI 19536) were introduced from the U.S.S.R. in 1906. In that same year, the first accession of A. sibiricum (PI 20223) was introduced from Manchuria. Since those early days, many other accessions of A. cristatum, A. desertorum, and A. sibiricum and a few accessions of other crested wheatgrass taxa have been introduced. Inasmuch as virtually all crested wheatgrass grown in North America (except for that grown in experimental plots) is included in A. cristatum, A. desertorum, or A. sibiricum, the following discussion focuses on these three taxa.

The 1906 introductions of A. cristatum and A. desertorum played an especially important role in

[1] This and other information relative to PI (Plant Inventory) numbers come from USDA Plant Inventories, which contain a record of plant materials entering the National Plant Germplasm System.

crested wheatgrasses history and terminology in North America. The variety Fairway, released in Canada in the early 1930's, was almost certainly selected from PI 19536 (Dillman 1946). The name Fairway has since taken on a broader connotation than just the name of a variety; it now refers to one of the two major groups of crested wheatgrass seeded widely in North America, i.e. "Fairway" and "Standard". Fairway is one of the few diploid (2n=14) crested wheatgrasses and it is more or less morphologically and ecologically distinct. To most users of crested wheatgrass, Fairway includes all plants with broad pectinate spikes that resemble the variety Fairway. Many consider Fairway to be synonymous with A. cristatum, but the point needs to be made that A. cristatum encompasses more than just the variety Fairway or Fairway-like plants.

The name Standard crested wheatgrass has an even broader meaning than Fairway. The term Standard was first applied to an accession of A. desertorum, PI 19537, by the Montana Seed Growers Association, who chose that Plant Introduction as the standard for comparing the performance of various crested wheatgrasses. The meaning of Standard soon expanded to encompass all crested wheatgrasses that were not included in Fairway. Many users now consider Standard crested wheatgrass as being synonymous with A. desertorum. Equating Standard with A. desertorum is not appropriate because some of the variations found in Standard crested wheatgrass do not fall within the description of A. desertorum, which consists of tetraploid (2n=28) plants with cylindrical spikes and imbricated spikelets.

"Siberian" crested wheatgrass is the other common name that needs clarification. This name is usually applied to accessions identified as A. sibiricum. Between 1906 and 1940, about 50 A. sibiricum accessions entered the U.S., which is considerably more than the number of A. desertorum accessions during the same period. Despite this, references to A. sibiricum in crested wheatgrass literature are relatively infrequent. Apparently many of the A. sibiricum accessions fell into the broad category of Standard crested wheatgrass and were treated as A. desertorum. A variety of Siberian crested wheatgrass, 'P-27', was released by the Soil Conservation Service in 1953 from selections made in PI 108434, a 1934 A. sibiricum introduction from the U.S.S.R. (Hanson 1972). Today the names Siberian and A. sibiricum are applied to any crested wheatgrass with very narrow spikes and awnless lemmas.

Taxonomic confusion has surrounded the crested wheatgrasses from the time of their introduction until the present (Table 4). Although the five introductions in 1906 came under two names, A. cristatum and A. desertorum, they were combined under A. cristatum. Dillman (1946) gave the following account of the decision to combine the species: "When they were grown to maturity at the Belle Fouche Station in 1909, it was apparent that the two types were quite distinct. However, editorial changes in the manuscript of the published report referred to both types as A. cristatum. This has caused confusion ever since." This editorial decision set a precedent that continued for many years. Although only one species was recognized, the separation was maintained between Fairway and Standard. Hitchcock (1935) helped perpetuate the one-species concept for crested wheatgrass by including only A. cristatum in the first edition of the Manual of the Grasses of the United States. Swallen and Rogler (1950) reinstated the idea that crested wheatgrass consisted of at least two species, A. cristatum and A. desertorum. The second edition of the Hitchcock Manual recognized three species--A. cristatum, A. desertorum and A. sibiricum (1951). Because of the wide usage of the Hitchcock Manual, this three-species concept of crested wheatgrass is still the most common in North America.

Weintraub (1953) listed the three species recognized by Hitchcock and added a rather obscure taxon, A. michnoi (Table 4). For practical purposes, we can ignore A. michnoi because it probably does not occur in North America outside of experimental plots, and the identity of the A. michnoi spoken of by Weintraub is questionable.

Knowles (1955), a grass breeder at Saskatoon, Canada, accumulated a large collection of crested wheatgrass introductions. He grouped these accessions into six morphological forms, which were equated to six of the species recognized by Nevski (1934) (Table 4). Knowles was aware that Nevski considered Fairway to be A. pectiniforme, yet he put Fairway in A. cristatum to conform to the usage in North America at the time. Knowles demonstrated that most tetraploid crested wheatgrasses hybridize rather easily and produce fully or partially fertile hybrids. Definitive taxonomic conclusions could not be drawn from Knowles' material because most of it had been increased under cultivation and very likely had become genetically mixed by intercrossing between taxa.

Sarkar (1956) recognized six species of crested wheatgrass (Table 4). Sarkar's treatment has not received much acceptance, yet he made an important point that typical A. cristatum is a plant with densely hirsute glumes and lemmas, a fact not widely recognized in North America. He pointed out that Fairway differs from typical A. cristatum in having glabrous spikes; he described a new species, A. cristatiforme, to accommodate Fairway. Sarkar placed tetraploid (2n=28) plants that resembled Fairway into A. pectiniforme. I question the separation of taxa at the species level if they can only be distinguished by a chromosome count.

Bowden (1965) recognized three species of crested wheatgrass (Table 4), but none corresponded fully with those listed by Hitchcock (1951). Bowden viewed A. cristatum in the same fashion as Sarkar, i.e. plants with ovoid spikes, closely imbricated spikelets, and densely villous glumes and lemmas. Plants of this type occur only in experimental plots in North America. Bowden's A. pectiniforme is equivalent to Hitchcock's A. cristatum and includes diploid Fairway as well as broad-spiked tetraploids and hexaploids. Bowden followed Jones' (1960b) recommendation to consolidate A. sibiricum and A. desertorum.

In recent years, the trend has been to place all crested wheatgrasses into one species, A. cristatum (Table 4), thus returning to the course followed between 1910 and 1950. The varied treatments in Table 4 do not foster confidence, so it is tempting for the nonspecialist to accept the broadest definition of A. cristatum at least until some consensus is reached.

Table 4.--Species of crested wheatgrass (*Agropyron*) recognized by North American authors.

Author(s)	*cristatum*	*desertorum*	*sibiricum*	*pectiniforme*	*cristatiforme*	*michnoi*	*imbricatum*	*fragile*
Hitchcock (1935)	X							
Swallen & Rogler (1950)	X	X						
Hitchcock (1951)	X	X	X					
Weintraub (1953)	X	X	X			X		
Knowles (1955)	X	X	X			X	X	X
Sarkar (1956)	X	X	X	X	X	X		
Bowden (1965)	X		X	X				
Holmgren & Holmgren (1977)	X							
Arnow et al. (1980)	X							

SYNTHESIS AND RECOMMENDATIONS

The proposed redefinition of the perennial Triticeae genera on the basis of genome constitution (Table 2) will not gain total or immediate acceptance because it is a drastic departure from taxonomic tradition, especially in North America. However, *Agropyron* in its narrow sense is one of the least controversial genera with respect to its limits. The narrow definition of *Agropyron* as a small genus encompassing only the crested wheatgrasses has already been accepted by agrostologists throughout Europe and Asia.

Those working with crested wheatgrasses are confronted with a difficult choice of treatments. I recommend Tzvelev's (1976) treatment, but with certain modifications. I place confidence in Tzvelev's classification because: 1) it is relatively recent, 2) he considers a combination of morphological, geographical, ecological, and cytological data, and 3) he is curator of the world's most extensive collection of Triticeae grasses and has access to many type specimens. Because Tzvelev's treatment in *Poaceae URSS* is not readily accessible to most North Americans his key to *Agropyron* is reproduced in Appendix II. Reference to this key will give the user an appreciation of the nature and range of variation found in *Agropyron* in Eurasia.

Many North American users of crested wheatgrass may feel overwhelmed by the many taxa (10 species and 9 subspecies) described by Tzvelev. From a practical standpoint, most of us need to be concerned with just three species: 1) *A. cristatum*, 2) *A. desertorum* and 3) *A. fragile*. The remaining "species" are either hybrids or relatively uncommon endemics that have not been introduced into North America. The distinguishing characteristics of the three species are summarized in Table 5.

Classification of crested wheatgrass accessions or individual plants into one of the three species will often be difficult and unsatisfying. Variation is continuous between the morphological extremes of the narrow linear-spiked *A. fragile* to the broad pectinate-spiked *A. cristatum* (Fig. 1). Classification problems are accentuated in North American introductions because many are genetically mixed by hybridization, and single accessions often contain several morphological forms. Some may question the wisdom of attempting to partition a morphological continuum into discrete units. An alternative is to treat all crested wheatgrasses as a single species, *A. cristatum*, and recognize distinctive morphological or ecological types as subspecies. This approach would accomplish very little other than to move the problem to the subspecific level. As imperfect as it may be, I feel that recognition of three species--*A. cristatum*, *A. desertorum*, and *A. fragile*--is the most practical approach to crested wheatgrass taxonomy in North America.

North American crested wheatgrass workers must examine their use of the name *A. cristatum* to insure its correct application. Many users equate *A. cristatum* to the variety Fairway and Fairway-like plants. That perspective is much too narrow because *A. cristatum* is a polymorphic species that encompasses Fairway and a multitude of other broad-spiked taxa. When speaking of Fairway, it is appropriate to use the name *A. cristatum* ssp. *pectinatum*. However, the subspecies *pectinatum* includes tetraploid and hexaploid races in addition to the diploid Fairway (Fig. 2). If one wishes to become even more precise, the name *A. cristatum* ssp. *pectinatum* var. *pectinatum* can be applied to diploid Fairway because Tzvelev (1976) describes the variety *pectinatum* as being $2n=14$. Whenever a particular subspecies cannot be designated, it is best to use the terminology *A. cristatum* sensu lato, meaning that one is unwilling or unable to specify a subspecies.

The correct nomenclature for plants qualifying as *A. desertorum* is simple and straightforward because no subspecies or botanical varieties have been described in this species. The cultivated varieties (cultivars) Nordan and Summit are correctly identified as *A. desertorum*, whose spikes are illustrated in Figure 3.

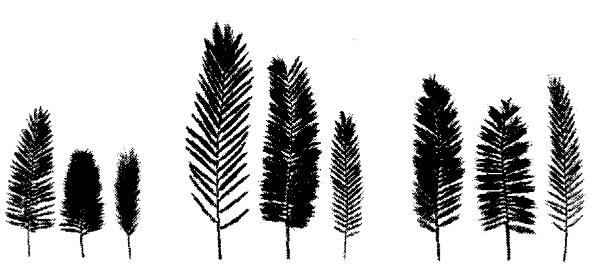
The name *A. fragile*, which is applied to the narrow-spiked crested wheatgrasses, may be new to

Table 5.-- Distinguishing characteristics of the three crested wheatgrass (Agropyron) species grown in North America.

Species and Synonyms	Chromosome No.	Typical Characteristics
A. cristatum sensu lato (A. pectinatum) (A. pectiniforme) (A. cristatiforme) (A. imbricatum) (A. michnoi)	2n=14 (Fairway) 2n=28 (common) 2n=42 (rare)	Spikes broad, pectinate. Spikelets diverging from rachis at angles from 45° to 90°. Glumes not appressed to lemmas, giving the spike a bristly appearance. Lemmas with short, straight awns to 5 mm.
A. desertorum	2n=28 (always)	Spikes subcylindrical, oblong to linear. Spikelets diverging from rachis at angles from 30° to 45°. Glumes appressed to lemmas. Lemmas with short, straight awns to 3 mm.
A. fragile (A. sibiricum) (A. mongolicum)	2n=14 (rare) 2n=28 (common)	Spikes linear. Spikelets diverging from rachis at angles $<30^{\circ}$. Glumes appressed to lemmas. Lemmas mucronate or awnless.

some, because North Americans have traditionally used the name A. sibiricum for these grasses. If one accepts Tzvelev's decision to combine A. sibiricum and A. fragile, the epithet fragile must be chosen because it is the older of the two names. Tzvelev described two botanical varieties: 1) var. fragile (plants with pubescent leaf sheaths and 2) var. sibiricum (plants with glabrous leaf sheaths). Most narrow-spiked crested wheatgrasses in North America, including the cultivated variety, P-27, have glabrous leaf sheaths and fall under A. fragile var. sibiricum.

Narrow-spiked crested wheatgrass from China is identified by Chinese agrostologists as A. monogolicum (Keng 1965). Most, if not all, A. monogolicum is diploid and looks like a diminutive strain of tetraploid A. fragile (Fig. 3). The differences in ploidy levels and geographic distributions of tetraploid A. fragile and diploid A. mongolicum are what I perceive to be differences between subspecies, and I am making the following new combination to reflect those differences: A. fragile ssp. mongolicum (Keng) D. R. Dewey comb. nov., based on Agropyron mongolicum Keng, 1938. J. Wash. Acad. Sci. 28:305.

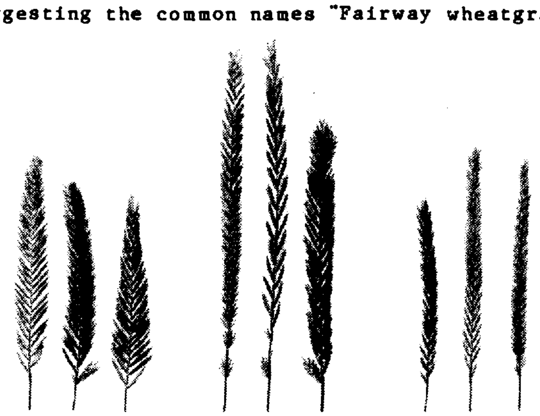


A. cristatum-2X A. cristatum-4X A. cristatum-6X

Figure 2.--Spikes of A. cristatum ssp. pectinatum, consisting of diploid (2n=2x=14), tetraploid (2n=4x=28), and hexaploid (2n=6x=42) chromosome races.

Common names for crested wheatgrass taxa have also been the source of some confusion and disagreement. Early workers spoke of the entire complex as crested wheatgrasses, and most current workers continue that usage. Swallen and Rogler (1950) commented that the common name "crested wheatgrass" was taken from the latin name "cristatus" (meaning crested or comb-like) and such a name is misleading if applied to the narrow-spiked taxa. However, they did not suggest another name. Weintraub (1953) applied the following common names to various crested wheatgrass taxa: A. cristatum = crested wheatgrass, A. desertorum = desert wheatgrass, A. michnoi = transbaikal wheatgrass, A. mongolicum = mongolian wheatgrass, and A. sibiricum = siberian wheatgrass.

Beetle (1961) endorsed Weintraub's common names, but those names have never become widely used except the names crested wheatgrass for A. cristatum and siberian wheatgrass for A. fragile (= A. sibiricum). Only rarely have I heard the name desert wheatgrass applied to A. desertorum. Agropyron michnoi and A. mongolicum are so uncommon that they do not need a common name. Hanson (1972) added some confusion by suggesting the common names "Fairway wheatgrass



A. desertorum-4X A. fragile-4X (=sibiricum) A. fragile-2X (=mongolicum)

Figure 3.--Spikes of A. desertorum, tetraploid A. fragile, and diploid A. fragile ssp. monogolicum.

(also crested wheatgrass)" for A. cristatum and "crested wheatgrass (also standard crested wheatgrass)" for A. desertorum.

I feel strongly that all taxa of Agropyron should be referred to as "crested wheatgrasses" regardless of their spike shape. This designation implies that they are a related group of species and separates them from other wheatgrasses such as tall wheatgrass, intermediate wheatgrass, and western wheatgrass. A descriptive or modifying word may be used in front of the name crested wheatgrass to specify a particular form or type. In North America the following names seem to be appropriate for the three main species groups: A. cristatum = fairway crested wheatgrass, A. desertorum = standard crested wheatgrass, and A. fragile (= sibiricum) = siberian crested wheatgrass. Lower case letters are used with the modifying words--fairway, standard, and siberian--to avoid confusing these names with cultivated variety names. Regardless of one's choice of modifying words, I plead with all to use the general name "crested wheatgrass" for all of the taxa now placed in Agropyron.

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APPENDIX I. Species, subspecies, and synonyms of Agropyron sensu Tzvelev (1976).

Species	Subspecies	Synonyms
A. cristatum (L.) Gaertn.[1]	ssp. cristatum	
	ssp. pectinatum (Bieb.) Tzvel.	A. pectinatum (Bieb.) Beauv. A. imbricatum Bieb. A. pectiniforme Roem. & Schult. A. dagnae Grossh. A. karataviense Pavl. A. litvinovii Prokud.
	ssp. puberulum Boiss. ex. Steud.	A. puberulum (Boiss. ex Steud.) Grossh.
	ssp. tarbagataicum (Plotn.) Tzvel.	A. tarbagataicum Plotn.
	ssp. kazachstanicum Tzvel.	A. badamense auct. non Drob.
	ssp. baicalense Egor. & Sipl.	
	ssp. sabulosum Lavr.	A. lavrenkoanum Prokud.
	ssp. ponticum (Nevski) Tzvel.	A. ponticum Nevski
	ssp. sclerophyllum Novopokr.	A. sclerophyllum Novopokr. A. pinifolium Nevski A. karadaghense Kotov A. ponticum auct. non Nevski
A. michnoi Roshev.	ssp. michnoi	
	ssp. nathaliae (Sipl.) Tzvel.	A. nathaliae Sipl.
A. badamense Drob.		A. desertorum auct. non Schult.
A. desertorum (Fisch. ex Link) Schult.		A. sibiricum var. desertorum (Fisch. ex Link) Boiss.
A. fragile (Roth) Candargy		A. sibiricum (Willd.) Beauv. A. variegatum (Fisch. ex Spreng.) Roem. & Schult. A. angustifolium (Link) Schult.
A. cimmericum Nevski		A. dasyanthum var. birjutczense Lavr. A. dasyanthum ssp. birjutczense (Lavr.) Lavr.
A. tanaiticum Nevski		
A. dasyanthum Lebed.		
A. pumilum Candargy		Elytrigia praetermissa Nevski
A. krylovianum Schischk.		Elytrigia kryloviana (Schischk.) Nevski

[1]Tzvelev cited Palisot de Beauvois as the authority for A. cristatum (L.) Beauvois, but all other authors have cited Gaertner as the authority, i.e. A. cristatum (L.) Gaertn.

APPENDIX II. Description of Agropyron and key to its species and subspecies from Tzvelev (1976). Translation courtesy of U.S. National Herbarium, Washington, D.C. with technical corrections by M. E. Barkworth, Utah State University, Logan, Utah.

Genus 17. Agropyron Gaertner 1770

Inflorescence--Linear, oblongate or ovate spikes (1)1.5-12(16) cm long, with a nondisarticulating rachis; spikelets solitary and arranged in longitudinal rows, sessile, 6-12(15) mm long, with (2)3-8(10) bisexual florets; rachilla scabrous or short-pilose, weakly disarticulating; glumes lanceolate-ovate, unequal, 2.5-5 mm long (excluding awns), glabrous or pilose, more or less asymmetrical, with the mid rib raised to form an obvious keel along the entire length of the glumes and 1-3 less prominent (sometimes not visible) additional ribs, apex acute or with a straight awn to 3 mm long; lemmas 4-8.5 mm long (excluding awns), lanceolate-oblongate, leathery, glabrous or more or less pilose, with 5 veins, the mid rib forming a weak keel, apex acute or with a straight awn to 5(7) mm long; callus very short (to 0.2 mm long), broadly rounded, glabrous or short-pilose; palea almost equal in size to the lemma, more or less scabrous or pilose along the keels, rarely glabrous and smooth; lodicules 2, usually entire, ciliated along the margins; stamens 3, with anthers 2.5-6 mm long. Caryopses 3-5.5 mm long, more or less adnate to the flowering glumes. Perennial plants 15-100(150) cm tall, with or without rhizomes or forming more or less dense tufts; culms erect, sheaths of cauline leaves open over more than 2/3 of their length, auricles (if present) lanceolate, sheaths of innovation leaves almost completely closed, usually with lanceolate auricles; ligules 0.1-1 mm long, leathery-membranous, minutely ciliate along the margins; leaf blades 1.2-8(12) mm wide, flat convolute. Chromosomes large; X=7.

Economic value: All species of the genus are very valuable; they are predominantly pasture-fodder plants, distinguished by their high level of drought tolerance. Of these, the "narrow-spiked wheatgrasses" (A. desertorum and A. fragile) and the "broad-spiked wheatgrasses" (A. cristatum s. lat.) are already under cultivation in the southern regions of the U.S.S.R. The highest hay yields can probably be obtained from such relatively mesophilic subspecies of the broad-spiked wheatgrasses as A. cristatum subsp. pectinatum and subsp. tarbagaticum; however, the narrow-spiked wheatgrasses are more drought tolerant. The sand-adapted species--A. dasyanthum, A. tanaiticum, A. cimmericum, A. michnoi, and A. fragile--can be used successfully for fixing drifting sands.

1. Plants with rhizomes, not forming tufts . 2

\+ Plants without rhizomes, forming fairly dense tufts. 9

2. Keels of palea glabrous and smooth or with a few (up to 10) spinules or cilia; lemmas awnless or with awns to 1.2 mm long; plants from the sands of southern European U.S.S.R. 3

Keels of palea with more than 15 spinules or cilia, rarely about 10 spinules, but in that case the awns of the lemma 2-4 mm long; in European U.S.S.R. restricted to southern coast of Crimea 5

3. Spikes linear, 4-7 mm wide, not pectinate, spikelets relatively distant and appressed to the rachis; lemmas glabrous or more or less pilose, awnless; paleas with 1-10 spinules per keel; plants of the Don Basin . . . . 6 A. tanaiticum

\+ Spikes broadly ovate, 7-18 mm wide, more or less pectinate, but not very densely arranged spiklets 4

4. Spikelets relatively distant on rachis, lower rachis internodes 3-10 mm long; lemmas usually densely pilose, awnless; keels of palea usually smooth, rarely with 1-3 spinules per keel; plants of the lower Dneiper and Molochnaya rivers . . . . 7 A. dasyanthum

\+ Spikelets closer togather on rachis, lower rachis internodes 2-5 mm long; lemmas more or less pilose, apex with a cusp or awn 0.5-1.2 mm long; keels of palea with 1-10 spinules per keel, rarely glabrous; plants of the coastal sands of the Azov Sea. . . . . .8 A. cimmericum

5. Spikes very dense (without spaces between spikelet bases), pectinate (spikelets strongly divergent from the rachis), oblongate or ovate in outline, 2.1-8 cm long and 1-2 cm wide; spikelets villous-pilose; plants of sandy sites in Eastern Siberia, not forming tufts . . . . 9 A. michnoi s. lat. 6

\+ Spikes less dense, not pectinate (spikelets ascending), linear in outline, up to 1 cm wide 7

6. Upper surface of leaf blades densely covered with short hairs; awns of lemma up to 2(3) mm long; plants of Selenga Basin . . . . 9a A. michnoi ssp. michnoi

\+ Upper surface of leaf blades covered with scattered thin spinules or very short hairs; awns of lemmas 2-3.5 mm long; plants of Chara Basin . . . . 9b A. michnoi ssp. nathaliae

7. Awns of lemma 1.5-4 mm long; plants often forming tufts with a few short rhizomes; plants of the Crimea, Transcaucasia, and Kopetdag . . . .
Taxa of the hybrid genus X Agrotrigia

\+ Awns of lemma up to 1(1.5) mm long; plants usually not forming tufts; plants of Altai and Eastern Siberia 8

8. Plants of rocky and aleurite (melkozem) slopes of Altai and Sayan, 40–100 cm tall; leaf blades 1.2–6 mm wide; lemmas usually short-pilose, rarely glabrous, apex with a cusp or awn up to 1.5 mm long . . . . .1 A. krylovianum

\+ Plants of Enisei sands, 12–40 cm tall; leaf blades 1–3 mm wide; lemmas usually glabrous, without cusp or awns; glumes more or less ciliate along the keel . . . . 2 A. pumilum

9. Spikes (1.5)2–12(15) cm long and 0.5–1 cm wide, not pectinate (spikelets appressed to the rachis or barely away from it); glumes usually glabrous, rarely sparsely pilose; leaf blades 1–4(5) mm wide, usually convolute. 10

\+ Spikes (1.5)2–6(8) cm long and 0.8–2.3 cm wide, pectinate (spikelets diverging from rachis at angles of 30–60°); lemmas glabrous or more or less pilose . . . . 10. A. cristatum s. lat. . .12

10. Lemmas awnless or with a cusp up to 1 mm long; spikes linear, 3–15 cm long; plants of sandy sites, 30–100 cm tall. . . . . .5 A. fragile

\+ Lemmas with awns 1–3(4) mm long; plants of the plains or hilly steppes with aleurite or rocky soils. 11

11. Spikes ovate or oblongate in outline, 1.5–3.5 cm long; keels of palea densely covered with spinules, more than 30 spineles . . . . .3 A. badamense

\+ Spikes oblongate or linear in outline, 2–7 cm long; keels of palea with fewer spinules, less than 30 . . 4 A. desertorum

12. Lowest culm internode strongly thickened toward the base; leaf blades usually convolute; plants of southern European U.S.S.R. and surroundings of Novorossiisk 13

\+ Lowest culm internode not thickened . 15

13. Spikes 2–6 cm long, with relatively distant spikelets; lemmas glabrous or mildly pilose; leaf blades glabrous and smooth on the lower side; plants of sandy sites, 25–70 cm tall, without long vegetative shoots . . . . . .10g A. cristatum ssp. sabulosum

\+ Spikes 1.5–4 cm long, with densely arranged spikelets (rarely without space between their bases); lemmas more or less pilose or glabrous; leaf blades covered with sparse hard bristles or spinules on lower surface; plants of gravelly slopes and rocks, 10–40 cm tall, with long vegetative shoots carrying stiff leaf blades horizontally divergent from the culms 14

14. Upper surface of leaf blades densely covered with very short hairs on the ribs; plants primarily of limestone outcrops. . . . . . 10h A. cristatum ssp. ponticum

\+ Upper surface of leaf blades sparsely covered with spinules on the ribs; plants primarily of slate (shale) outcrops . . . . . .10i A. cristatum ssp. sclerophyllum

15. Spikes very dense, with closely compressed spikelets (no spaces between their bases); spikelets usually densely pilose, rarely glabrous; plants of Eastern Siberia, also entering into South Ural, Altai, and mountains of East Asia 16

\+ Spikes less dense, with less crowded spikelets (obvious spaces between their bases); spikelets glabrous or more or less pilose; plants of Eastern Siberia . . 17

16. Plants 50–100 cm tall; leaf blades 2–6 mm wide, usually flat; awns of lemmas 4–7 mm long. . . .10e A. cristatum ssp. baicalense

\+ Plants 20–60 cm tall; leaf blades 1.2–4 mm wide, frequently rolled lengthwise; awns of lemmas 1.5–4 cm long . . . . .10f A. cristatum ssp. cristatum

17. Culms immediately below the spike and below all nodes short-pilose; leaf sheaths and leaf blades frequently short-pilose; leaf blades 1–2.5 mm wide, usually rolled lengthwise; spikelets more or less pilose, rarely glabrous; plants of Transcaucasia . . . .10d A. cristatum ssp. puberulum

\+ Culms immediately below the spike glabrous or more or less pilose, below the nodes glabrous or with a few scattered hairs 18

18. Leaf blades 1–2.5 mm wide, rolled lengthwise and very stiff, usually more or less arcuately bent; tufts very dense, with a relatively large number of vegetative culms; culms with 1–2 nodes, upper node usually located below the middle of the culm; spikelets usually pilose, rarely glabrous; plants of Kazakh hillocky area, 20–40 cm tall . . . . 10c A. cristatum ssp. kazachstanicum

\+ Leaf blades 1.5–8(12) mm wide, flat or rolled lengthwise, less stiff, straight; tufts less dense, usually with only a few vegetative culms; culms with 2–4 nodes, the upper node usually above the middle of the culm 19

19. Plants 50–150 cm tall, with 3–4 culm nodes; leaf blades 4–10(12) mm wide, flat; plants of Eastern Kazakhstan . . . . .10a A. cristatum ssp. tarbagataicum

\+ Plants 25–80 cm tall, with 2–3 culm nodes; leaf blades 1.5–7 mm wide, flat or rolled lengthwise; widely distributed plants . . . . . . .10b. A. cristatum ssp. pectinatum

Plant Materials for Crested Wheatgrass Seedings in the Intermountain West

J. R. Carlson and J. L. Schwendiman

ABSTRACT: Eight cultivars of crested wheatgrass have been released for commercial production and use in the United States and Canada since 1927. Four are fairway types, two are standard types, one a Siberian wheatgrass, and the most recent a cross between fairway and standard. 'Fairway' and 'Nordan' have been produced commercially far more than the other cultivars. Certified seed production has averaged less than 10 percent of the total annual production. Common seed consists primarily of mixed seed from the 1906 introductions including uncertified Fairway and Nordan. Understory grasses should be considered for mixtures with crested wheatgrass, despite the competitiveness of the wheatgrass. 'Hycrest' and 'Ephraim' cultivars offer good potential in the next decade.

INTRODUCTION

Crested wheatgrass is a very popular grass for seeding rangelands, returning abandoned cropland to grass cover, revegetating highway slopes, planting low maintenance turf, seeding burns, and reclaiming a variety of disturbed areas in the Intermountain West. As noted elsewhere in these proceedings, most available seed on the commercial market traces to a relatively few introductions from the USSR during the early part of this century. There currently are eight cultivars of crested wheatgrass that are, or soon will be, available and are adapted in the Intermountain area. This paper will briefly review the genetic makeup, attributes, and seed production of each. The references used in this review include Hanson 1972, Dillman 1946, Swallen and Rogler 1950, Rogler 1954, Knowles 1956, USDA Extension Service 1978, Stevens et al. 1982, and Asay et al. 1985.

As is well known, crested wheatgrasses can be competitive to the point of excluding invading weeds or native plants and suppressing companion species in a mixture. This paper also will review three studies in Oregon and Washington that provide some clues to the role of companion species with crested wheatgrass.

CRESTED WHEATGRASS CULTIVARS

Fairway Crested Wheatgrass (*Agropyron cristatum* (L.) Gaertn.)

'Fairway'.--This was the first cultivar of crested wheatgrass developed in North America, released in 1927 by the Saskatchewan Research Station, with the first seed crop licensed in 1932. 'Fairway' originates from accession PI 19536, introduced in 1906 from the Samara Province of western Siberia. It was the result of a mass selection for fine leafy plants during 1925, followed by direct seed increase. 'Fairway' is more persistent than standard types in Canada where winters are harsher than in the United States. It is shorter and somewhat less productive, but better suited for turf and erosion control.

Certified production of 'Fairway' has averaged about 200,000 pounds (91,000 Kg) in the past five years. Highest production was 1,084,000 pounds (493,000 Kg) in 1939; 676,000 pounds (307,000 Kg) were produced as recently as 1973. Production has been cyclic, influenced by government programs to retire cropland from production or to seed abandoned land. 'Fairway' plantings also are a primary source for harvest of common seed lots that dominate the Canadian commercial market. Most seed production is in Canada.

'Parkway'.--The Saskatchewan station released this cultivar in 1969 as an improvement over 'Fairway'. It is a 16-clone synthetic, derived from the older variety after several cycles of recurrent selection for forage and seed production. 'Parkway' is more vigorous and 2-3 inches (5-8 cm) taller with at least 10 percent more seed and forage production. It is somehwat less leafy than 'Fairway' but more lodging resistant. It is well suited for hay production.

'Parkway' is produced in Canada and 50-100,000 pounds (20-50,000 Kg) of certified seed are

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available annually. Production has leveled off after a high of 183,000 pounds (83,000 Kg) in 1973. As older 'Fairway' fields are plowed out or no longer harvested, 'Parkway' could gradually replace it as the premier variety.

'Ruff'.--This cultivar is the product of three cycles of recurrent selection by the USDA Agricultural Research Service (ARS) and Nebraska Agricultural Experiment Station (AES). Released in 1975, it originates from 'Fairway', or PI 19536. Its forage yield is equal to 'Nordan', and it is a better sod former than 'Fairway'. Certified seed production has varied from 3-15,000 pounds (1.5-7,000 Kg) each year and currently is in limited supply.

'Ephraim'.--This cultivar is the first of the Fairway type with a different germplasm source, originating from PI 109012 collected near Ankara, Turkey by the Westover-Enlow expedition in 1934. 'Ephraim' was released by the USDA Forest Service (USFS), Utah Division of Wildlife Resources, USDA Soil Conservation Service (SCS), and other agencies in 1982. It is a result of mass selection for rhizomatous plants conducted by the USFS Shrub Sciences Laboratory in Utah. Superior rhizome development compared to 'Fairway' is found in seedings on pinyon-juniper and sagebrush-grass sites in the Intermountain area. It was selected primarily for its erosion control potential. The first commercial seed crops were harvested in 1984.

Standard Crested Wheatgrass (Agropyron desertorum (Fisch.) Roem. and Schult.)

'Nordan'.--This first cultivar of the standard type was released in 1953 by ARS, North Dakota AES, and SCS. 'Nordan' consists of selections from an evaluation nursery established in 1937 at Dickinson, North Dakota. It is probable that much of the germplasm traces to PI 19537-41, introduced from the Samara Province of western Siberia in 1906. 'Nordan' was increased from seven superior plants after two cycles of mass selection for more compressed, dense, awnless seedheads, uniformity, and improved forage production over the common type.

'Nordan' currently exceeds all other cultivars in production, ranging from 250-400,000 pounds (115-180,000 Kg) certified seed annually in recent years. Highest production was 1,682,000 pounds (765,000 Kg) in 1972. 'Nordan' plantings also are a large source for uncertified production. With 'Fairway' and common sources of similar parentage, they account for well over 95 percent of the total production. Most 'Nordan' production is in Canada.

Prior to the release of 'Nordan', common standard crested wheatgrass was produced in quantity, as much as 17,000,000 pounds (7,700,000 Kg) in 1944. Much of the seed was used for cropland retirement sponsored by the Agricultural Adjustment Administration in the United States. Nearly all of this seed originated from an increase of PI lines 19537-41 at Dickinson, North Dakota in 1927. The first commercial seed appeared in Bismarck in 1929. Common standard is the most available source of crested wheatgrass today. However, its original identity has been so obscured by uncertified 'Nordan' production that many consider 'Nordan' the source of most supplies. The question is somewhat academic since both germplasm sources are similar if not identical.

'Summit'.--The Saskatchewan Research Station released this cultivar in 1953, selected from an introduction to Canada from the Omsk Experiment Station in western Siberia. This introduction may be similar to PI 63800 and 98524, introduced to the United States from the Omsk Station in 1925 and 1929, respectively. 'Summit' is the result of mass selection for uniformity, higher seed yield and quality. Another round of selection, yielding 40 plants, provided for the increase and release of 'Summit 62' in 1962. However, this new new name was short-lived, and all production since the late sixties has been sold as 'Summit'.

As much as 454,000 pounds (206,000 Kg) were produced in 1960, but production generally has declined since the mid-sixties. Some common seed may have 'Summit' as its source. All production is in Canada.

Siberian Wheatgrass (Agropyron fragile (Roth.) Nevski)

'P-27'.--The only cultivar of Siberian wheatgrass, 'P-27', was released in 1953 by SCS and Idaho AES. It was selected from PI 108434, collected in the mid 1930's by the Westover-Enlow expedition in Kazakhstan, USSR. Selections were for narrow, awnless seedheads, leafiness, and superior performance on coarse textured, droughty soils.

Very limited data in available on the commercial seed production of 'P-27'. Since 1977, production has ranged from 12-35,000 pounds (5-16,000 Kg), with a high of 35,000 pounds (16,000 Kg) in 1982. Production, since release in 1953, has been sporadic, seldom exceeding 50,000 pounds (23,000 Kg) a year. Nevertheless, 'P-27' has filled a need for a crested wheatgrass type on coarse-textured soils.

Fairway x Standard Hybrid

'Hycrest'.--The newest cultivar of crested wheatgrass was released by ARS, SCS, and Utah AES in 1984. Developed by the ARS Crops Research Laboratory at Logan, Utah, 'Hycrest' is described elsewhere in this publication. It represents the most intensively bred line of crested wheatgrass and is a significant step forward. Substantial progress has been made in seedling establishment on arid sites and in forage production.

TREND IN COMMERCIAL SEED SUPPLIES

Although there are some gaps in the data, seed production and marketing reports from Canada and the United States[1] permit a general assessment of supply and demand for crested wheatgrass during the past 50 years. Figures 1a and 1b compare annual total production with certified production. Between 1939-

[1]Association of Seed Certifying Agencies 1955-83, Canadian Seed Growers Association 1932-83, Canadian Seed Growers Association 1965, USDA Bureau of Agricultural Economics 1948, USDA Bureau of Plant Industry 1906-40.

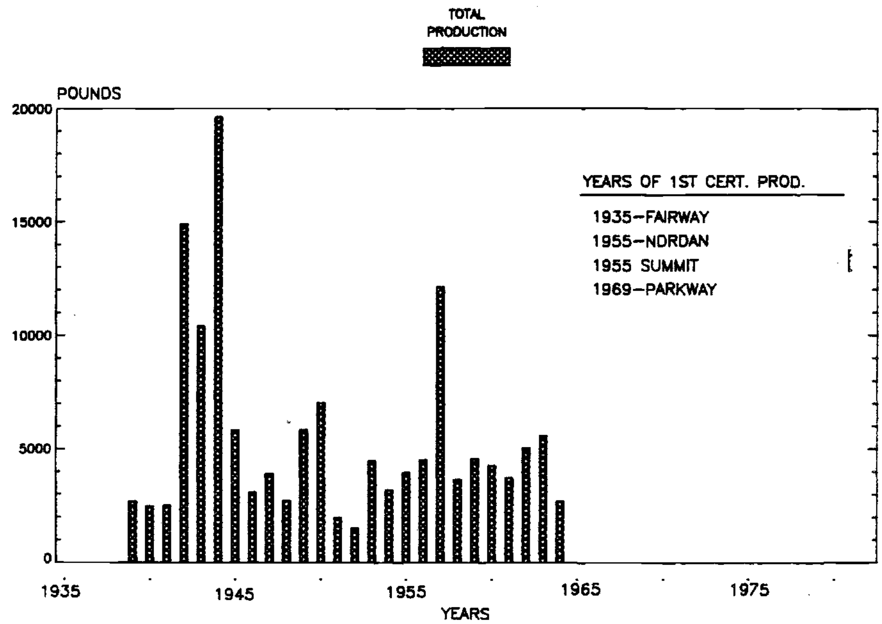

Figure 1a.--Total production of crested wheatgrass: 1935-1964.

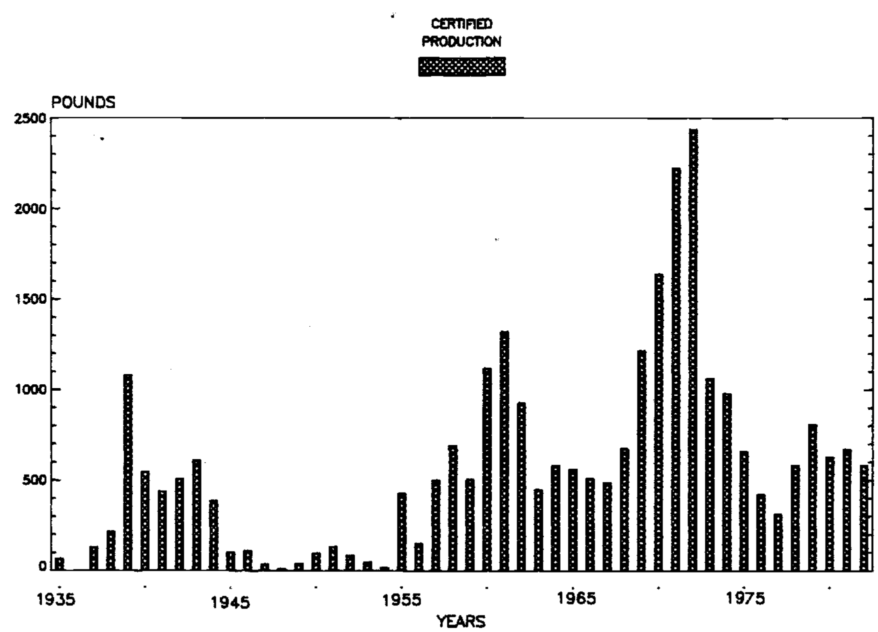

Figure 1b.--Certified production of crested wheatgrass: 1935-1982.

1964, certified seed accounted for 7.7 percent of the total production. Percentages ranged from lows of 0.5 percent in 1948 and 0.6 percent in 1954 to highs of 34.8 percent in 1961 and 39.9 in 1939.

Figure 1b shows that peak production occurs after the release of new cultivars: in the late thirties following 'Fairway', the mid-fifties following 'Nordan' and 'Summit', and a large surge corresponding with the release of 'Parkway'. The sharp increase from 1970-73 probably is incidental to the release of 'Parkway'. It is more likely attributable to higher seed prices, government land retirement programs, and reclamation efforts. However, the two earlier peaks clearly are the result of new releases.

The releases of 'Fairway', 'Nordan', and 'Summit' also appear to have stimulated overall production during 1940-45 and 1955-60. Figure 1a strongly suggests that increased total yield a few years after release come primarily from harvest of plantings made with the new cultivars, particularly in the case of 'Fairway'. Although total yield figures are not available beyond 1964, a large rise in crested wheatgrass imports to the United States from 1972-75 (USDA Agricultural Marketing Service 1956-78) probably reflects a major increase in total production during that time similar to the rise in certified production just a few years before.

Figure 2 shows the relative production of five cultivars of crested wheatgrass for which yield figures are available. As previously discussed, 'Nordan' and 'Fairway' continue to be the cultivars most in demand.

COMPANION SPECIES FOR SEED MIXTURES

Crested wheatgrass forms the backbone of many arid-land seed mixes, because it can be counted on to establish readily and persist under adverse conditions. But it can compete vigorously with other components in the seed mixture, even crowding them out. As a result, is seeded alone, especially for forage, more often than it should be. However, several studies have shown that other species should be considered for inclusion in crested wheatgrass seedings.

A grass mixture study at Squaw Butte, Oregon (11 inches or 29 cm mean annual precipitation) demonstrated the competitiveness of crested wheatgrass (Hedrick et al. 1964). Table 1 shows the relative yields in mixed stands of overstory and understory grasses. Standard crested wheatgrass was much more competitive than bluebunch wheatgrass (*Psuedoroegneria spicata* [Pursh] A. Love) or big bluegrass (*Poa ampla* Merr.) growing with two understory grasses, canby bluegrass (*Poa canbyi* (Scribn.) T. Howell) and streambank wheatgrass (*Elymus lanceolatus* [Scribn. & J. G. Smith) Gould. However, note in Table 2 that the combination of streambank and crested wheatgrasses was more effective than crested alone in suppressing brush invasion.

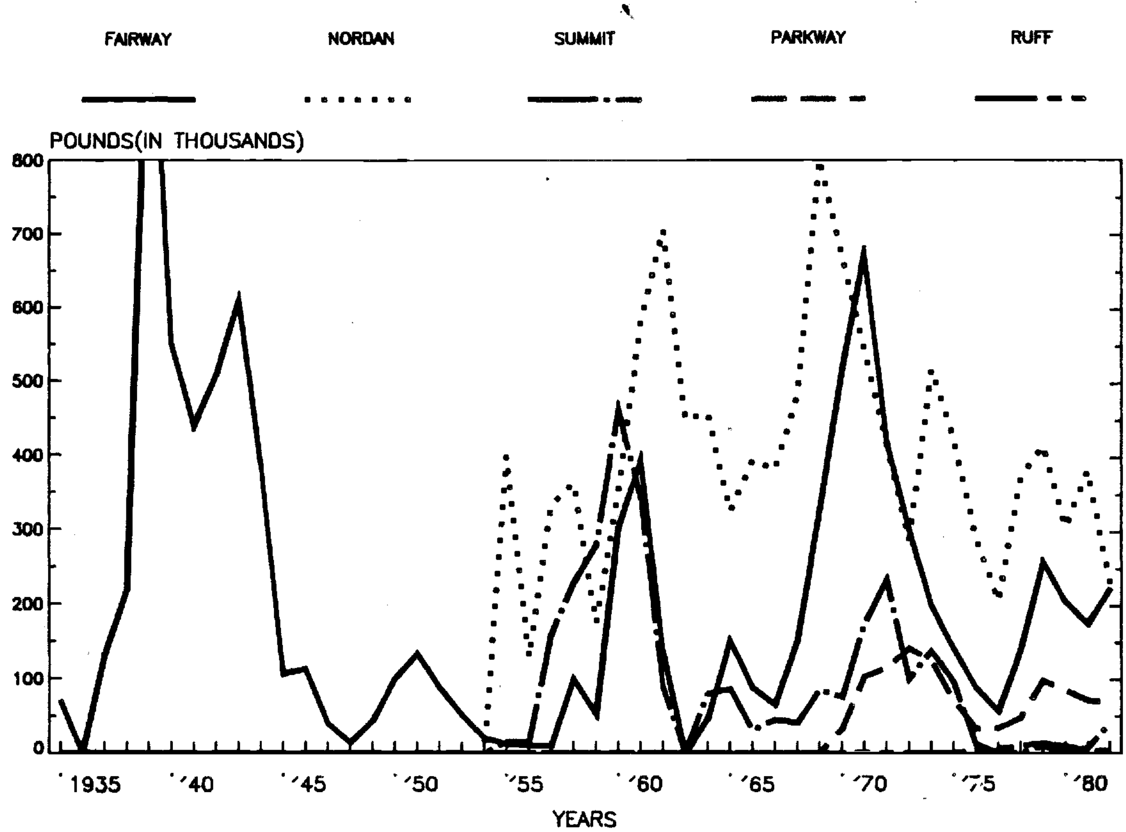

Figure 2.--Certified production of five crested wheatgrasses (1935 thru 1982).

Table 1.--Relative yields of grasses seeded in mixtures at Squaw Butte Agricultural Experiment Station, Harney County, Oregon, from 1956-62.[1]

Seeded species		Relative yields in mixed stands[2]		
Overstory species	Understory species	Overstory grass	Understory grass	Sum
		%		
crested wheatgrass	canby bluegrass	90	10	100
crested wheatgrass	streambank wheatgrass	82	14	96
bluebunch wheatgrass	canby bluegrass	79	41	120
bluebunch wheatgrass	streambank wheatgrass	47	49	96
big bluegrass	canby bluegrass	74	34	108
big bluegrass	streambank wheatgrass	42	51	93
Mean		71	36	107

[1]Excerpt from Hedrick et al. 1964.

[2]Yields by species in mixed stands were expressed in percent of corresponding yields in pure stands. Three years of seeding, each with three replications, two nitrogen fertilization rates, and three consecutive years of harvest are included.

Crested wheatgrass appears to be even more competitive at lower precipitation. In a study by the SCS Pullman Plant Materials Center (Carlson et al. 1978), 'P-27' Siberian wheatgrass maintained excellent stands for six years at Moxee, Washington where precipitation averages 7 inches (18 cm) per year (Table 3). It greatly suppressed its companion species, 'Whitmar' bluebunch wheatgrass, as well as cheatgrass (*Bromus tectorum* L.).

Dryland alfalfa and crested wheatgrass have been successfully planted together at Moro, Oregon with 11 inches (29 cm) mean annual precipitation. In a 4-year test, 'Ladak' alfalfa and 'Fairway' crested wheatgrass produced 3,065 pounds of forage per acre (3465 Kg/ha) and 6,530 pounds (7380 Kg/ha) of roots in the upper 8 inches of a Walla Walla silt loam. Alfalfa alone produced 3,870 pounds (4370 Kg/ha) of hay but only 4,310 pounds (4870 Kg/ha) of roots. Crested wheatgrass contributed 27 percent of the hay mixture but 65 percent of the roots (Hafenrichter et al. 1968).

Also at Moro, Oregon (USDA Soil Conservation Service 1976), 'Fairway' and bluebunch wheatgrass were compared in mixtures with understory grasses in a 15-year study. Throughout the study, 'Fairway' seeded alone produced less ground cover and herbage than the mixtures (Table 4). Furthermore, sheep fescue (*Festuca ovina* L.) and big bluegrass suppressed crested throughout the trial, in contrast to Squaw Butte.

Crested wheatgrass appears to be most competitive in colder, drier areas, below 12 inches (30 cm) precipitation and at plant hardiness zones of 5 (-10° to -20°F or -23° to -29°C) or lower. Harsh winters and dry summers tend to favor early season species such as crested wheatgrass. With milder winters at Moro, (two plant hardiness zones warmer than Squaw Butte), effective moisture is increased and midseason grasses and legumes perform adequately in mixtures with crested wheatgrass. Even in the harsher environments, it is not wise to rely totally on crested wheatgrass, particularly in erosion control seedings. Highway slopes, borrow pits, and even range sites are not uniform but contain microenvironments not conducive to a complete crested wheatgrass establishment. In such cases, it is advisable to include adapted cultivars of other species to improve total cover.

Several species are suitable for seeding in mixtures with crested wheatgrass under appropriate conditions. Following is a partial list:

'Canbar' canby bluegrass(*Poa canbyi* (Scribn.) T. Howell).--A low-growing, early season native bluegrass closely related to Sandberg bluegrass (*Poa sandbergii* (Thurb.) Benth. ex Vasey), and commonly found on shallow soils. Very drought tolerant, it should be considered as an understory component in mixtures with crested wheatgrass, as well as mixtures with other range species.

'Covar' sheep fescue (*Festuca ovina* L.).--The most drought tolerant fine-leaf fescue available. This low-growing and competitive grass should be considered on soils where Idaho fescue (*Festuca idahoensis* Elmer) is adapted.

'Sherman' big bluegrass (*Poa ampla* Merrill).--An early season, native bluegrass similar to canby bluegrass, but much more robust and a good forage producer. It should be seeded only if crested is a relatively minor component of the mixture, or if MAP exceeds 12 inches (30 cm).

'Sodar' streambank wheatgrass (*Elymus lanceolatus* (Scribn. & J. G. Smith) Gould).--A low-growing, rhizomatous mid-season wheatgrass that can form a tight cover with crested, crowding our weeds and resisting brush invasion. 'Sodar' is not very palatable and generally limited to erosion control seedings.

'Critana' thickspike wheatgrass.--Taxonomically similar to 'Sodar', this variety is well adapted throughout the Intermountain West, particularly east of the Continental Divide where summer rainfall is somewhat more prevalent.

'Ladak' alfalfa (*Medicago sativa* L.).--Dryland alfalfa is the best legume to seed with crested wheatgrass, but only where MAP exceeds 12 inches (20 cm).

In addition, where crested wheatgrass is limited to small percentages in a mixture, suitable companion species may include 'Rincon' fourwing saltbush (*Atriplex canescens* (Pursh.) Nutt.), 'Immigrant' forage kochia (*Kochia prostrata* (L.) Schrad.), 'Appar' lewis flax, (*Linum lewisii* Pursh.), 'Delar' small burnet (*Sanguisorba minor* Scop.), among others.

CONCLUSIONS

'Nordan' and 'Fairway' crested wheatgrasses continue to dominate the commercial seed market for the species and likely will do so in the next decade. Common seed usually comes from range or land retirement seedings of common or certified 'Nordan' and 'Fairway'. Both cultivars trace back to early plant introductions at the turn of the century. Their success probably attests to a previous association with agriculture in Russia and purposeful or inadvertant selection of superior types. The new cultivars 'Ephraim' and 'Hycrest' offer good potential, but will have to be considerably better if they are to supplant the established two in the long run. 'Summit', 'Parkway', 'Ruff', and 'P-27' have not, and are relegated to specialized uses. 'Hycrest' is the most intensively bred cultivar, shows considerable improvement for range forage seedings, and may offer the best challenge to the old line varieties. 'Ephraim' is well suited for erosion control because of its rhizomatous nature.

Despite the competitiveness of crested wheatgrasses, companion species should be considered for mixtures in almost all cases. This is especially true for erosion control and reclamation seedings.

Table 2.--Brush established in the first four years after seeding plots to various grasses at Squaw Butte Agricultural Experiment Station, Harney County, Oregon from 1956-62[1].

Species planted	Consecutive Years 1	2	3	4	Grand Mean
	Number of plants per .4 hectare[2]				
none	922	1,162	1,355	2,352	1,470
bluebunch wheatgrass	678	968	1,016	920	895
big bluegrass	411	605	726	750	623
canby bluegrass	169	363	387	774	424
streambank wheatgrass	194	363	363	460	345
crested wheatgrass	387	436	218	242	321
bluebunch wheatgrass-canby bluegrass	218	460	484	508	417
big bluegrass-canby bluegrass	266	508	557	581	478
crested wheatgrass-canby bluegrass	266	629	411	484	448
bluebunch wheatgrass-streambank wheatgrass	436	653	678	678	611
big bluegrass-streambank wheatgrass	290	339	315	315	315
crested wheatgrass-streambank wheatgrass	73	194	145	145	139
Significant ranges[3]	(------------158--------------)				(233)
Grand mean	336	558	556	687	540
Significant ranges	(---------------3---2-----------)				

[1]Excerpt from Hedrick et al. 1964
[2]Includes big sagebrush and rabbitbrush.
[3]Significant ranges at 5 percent were computed by Tukey's method.

Table 3.--Percent stand[1] ratings for understory grasses seeded or occurring with 'Whitmar' bluebunch wheatgrass at Moxee, Washington over a seven-year period.

Associated species	Sampling date[2] 5-58	6-59	7-60	3-61	10-61	6-62	9-64	Cheatgrass[3] 6-62	Whitmar[4] 3-61	6-62
	percent									
Covar sheep fescue	58	13	1	0	0	0	0	83	13	22
Durar hard fescue	95	9	0	0	0	0	0	71	24	25
Sodar streambank wheatgrass	86	65	4	10	5	4	12	87	10	10
Topar pubescent wheatgrass	83	78	28	34	24	33	24	69	9	10
P-27 Siberian wheatgrass	89	86	74	78	91	81	91	13	8	4
P-4874 Bulbous bluegrass	91	71	70	88	96	89	88	49	11	11
Sherman big bluegrass	83	40	5	4	19	21	5	70	10	21
P-851 canby bluegrass	96	65	79	89	82	80	86	23	38	36
P-9012 Russian wildrye	63	25	4	8	5	3	12	84	15	15
Ladak alfalfa	55	16	0	0	0	0	0	86	13	15
Average	80.3	47.0	26.5	31.0	30.0	27.5	31.3			

[1]Percent stand on occular rating comparing the number and condition of plants occurring in the plot to what would be expected where the particular species is successfully established and well adapted. Percent stand for cheatgrass compares number of plants and canopy cover (condition) to what normally occurs in a severe infestation on rangeland in eastern Oregon and Washington (this may be a few robust or numerous less vigorous plants but always providing complete groundcover and severely inhibiting native grasses and forbs).

[2]$LSD_{.01}$ between species = 16.06 (all years); between years (average of all species means) = 6.33; between years for each species = 20.00

[3]$LSD_{.01}$ between understory species = 37.14.

[4]Percent stand ratings do not vary significantly at the 5% probability level (observed F - 2.11, required F = 2.25).

Table 4.--Effect of understory grass mixtures with 'Fairway' crested wheatgrass and bluebunch wheatgrass on groundcover and cheatgrass density at Moro, Oregon, 1938-53.[1]

Understory species	Fifth-sixth year Under-story	Over-story	Cheat-grass	Tenth year Under-story	Over-story	Cheat-grass	Fifteenth year Under-story	Over-story	Cheat-grass
		% cover Fairway			plants/m[2] Fairway			plants/m[2] Fairway	
Bulbous bluegrass (*Poa bulbosa*)	10	33	2	0.1	1.4	none	2.7	2.3	none
Sheep fescue (*Festuca ovina*)	28	19	13	3.9	0.4	0.1	4.2	0.4	0.1
Big bluegrass (*Poa ampla*)	25	22	5	2.1	0.2	0.1	2.5	1.7	0.1
None	--	33	20	--	1.9	0.2	--	2.5	0.2
		Bluebunch			Bluebunch		Bluebunch		
Sandberg bluegrass (*Poa sandbergii*)	9	39	9	1.7	3.4	none	3.2	3.2	none
Idaho fescue (*Festuca idahoensis*)	39	19	4	4.3	0.6	0.1	3.4	2.7	0.1
Big bluegrass (*Poa ampla*)	26	27	7	1.6	1.6	0.1	0.3	3.6	0.1
None	—	38	18	—	3.4	0.3	—	5.2	0.1
	$LSD_{.01}$ (cheatgrass) = 11			$LSD_{.01}$ (total cover) = 1.4			$LSD_{.01}$ (total cover)= 2.3		

[1] Excerpt from USDA Soil Conservation Service 1976.

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Breeding Strategies in Crested Wheatgrass

Kay H. Asay

ABSTRACT: Conventional breeding programs in crested wheatgrass [*Agropyron cristatum* (L.) Gaertn., *A. desertorum* (Fisch. ex Link) Schult., and *A. fragile* (Roth) Candargy] have been confined to selection and hybridizstion within the ploidy levels of the complex, particularly the diploids (Fairway) and tetraploids (Standard and Siberian). Gene flow among the three ploidy levels of the complex has been accelerated by induced polyploidy and hybridization. 'Hycrest', a cultivar developed from hybrids between induced tetraploid Fairway and natural tetraploid Standard types has shown excellent potential on semiarid range sites.

ACKNOWLEDGEMENTS: This work is a cooperative investigation of the USDA Agricultural Research Service and the Utah Agricultural Experiment Station, approved as Utah Agr. Exp. Sta. J. Pap. 2929.

INTRODUCTION

Since its introduction in the early 1900's (Dillman 1946), crested wheatgrass [*Agropyron cristatum* (L.) Gaertn., *A. desertorum* (Fisch. ex Link) Schult., and *A. fragile* (Roth) Candargy] has hsd more impact on the improvement of western rangelands than any other grass. It has been particularly valuable as a source of forage during the early spring.

The crested wheatgrass complex consists of an autoploid series of diploid ($2n=2x=14$), tetraploid ($2n=4x=28$), and hexaploid ($2n=6x=42$) forms. Although some structural differences are evident among the chromosomes of the crested wheatgrass species, Dewey (1974) concluded from several studies that the same basic genome occurs at all three ploidy levels. He advised grass breeders to consider the entire complex as a single gene pool from which selected characteristics could be extracted and combined at a desired ploidy level. Unfortunately, differences in ploidy levels have prevented breeders from exploiting the full range of genetic diversity within the complex. Breeding has been confined largely to selection snd hybridization within ploidy levels, primarily the diploid and tetraploid populations.

The diploids sre represented primarily by the cultivar 'Fairway' developed by Agriculture Canada at Saskatoon, Saskatchewan and released in 1932 (Elliott and Bolton 1970). Fairway, the first crested wheatgrass cultivar to be released in North America, was selected from an introduction from the U.S.S.R. (PI 19536). It is leafier and more procumbent, but less drought tolerant than the major tetraploid Standard cultivars. Fairwsy has been widely used in range reseeding programs and is still an important component of Canadian seed trade (Elliott and Bolton 1970). The diploid cultivar 'Parkway', which was selected from Fairway on the basis of improved vigor, height, and leafiness, was relessed in 1969 by Agriculture Canada at Saskatoon. It is more upright and has been more productive in terms of forage and seed thsn Fairway in Canadian trials. A relatively new cultivar, 'Ruff', was developed from Fairway-type germplasm by the U. S. Department of Agriculture-Agricultural Research Service (USDA-ARS) in cooperation with the Nebraska Agricultural Experiment Station (AES). It has a spresding (brosd-bunch) growth habit and is recommended for grazing and revegetation of problem sites in the low precipitation zones of the Great Plains (Hanson 1972, USDA Extension Service 1978).

The most commonly used tetraploids are the Standard cultivars, 'Nordan' and 'Summit', and the Siberian cultivar 'P-27'. All three cultivars were released in 1953. Nordan, which was released by the USDA-ARS Northern Great Plains Research Center at Mandan, North Dakota, in cooperation with the North Dakota AES, was derived from plant materials obtained from the cold dry plains of the U.S.S.R. It is noted for its upright growth habit, relatively large seeds, and good seedling vigor (Rogler 1954, Wolfe and Morrison 1957). Summit, released by Agriculture Canada at Saskatoon, also wss developed from germplasm obtained from the U.S.S.R. Summit is noted for its abundant forage production, but problems associated with seed processing have

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limited its popularity. The Siberian cultivar 'P-27' was released by the USDA-Soil Conservation Service (SCS). It has narrow, awnless spikes and relatively fine leaves and stems. P-27 is reported to be well adapted on light droughty soils (Hanson 1972) and it matures later and remains green longer than typical Standard types.

Two new tetraploid cultivars, 'Ephraim' and 'Hycrest', were released in 1983 and 1984, respectively. Ephraim was selected from collections made near Ankara, Turkey and released by the USDA-Forest Service (FS), USDA-SCS, Utah Division of Wildlife Resources, and several state experiment Stations. It is reported to be a persistent and drought resistant cultivar; however, it is noted primarily for its sod-forming characteristics. Rhizomes are usually present by the second or third year under semiarid conditions. The cultivar is slightly shorter, but similar to Fairway in biomass production. Hycrest was released in 1984 by the USDA-ARS in cooperation with the Utah AES. It was developed from hybrids between induced tetraploid Fairway and natural tetraploid Standard types (Asay et al. 1985). Hycrest, the first interspecific hybrid of crested wheatgrass to be released, tends to be more productive and vigorous than either of the parental species, particularly during the seedling establishment phase. This cultivar is discussed in more detail under Interploidy Breeding.

BREEDING PROGRAMS

The USDA at Utah State University is actively involved in a research program to develop improved germplasm and cultivars of range grasses, including crested wheatgrass. Breeding populations for this program are obtained from both intra and interploidy hybridization and selection procedures. Even without the added time required to introgress genetic diversity into breeding populations through interploidy crosses, the development of improved, stable cultivars involves a series of time consuming procedures (Fig. 1). Clonal lines selected from genetically broad based source nurseries are often progeny tested in field and laboratory trials. Selection criteria during this phase vary according to the objectives of the breeding program and available resources. They include improved seed and forage yield, better seasonal distribution of growth, leafiness, forage quality, seedling vigor, resistance to plant pests, and resistance to environmental stress.

The grass improvement program at Logan has emphasized evaluation and selection of clonal and progeny lines under range conditions in the field. Laboratory screening procedures are also being refined to evaluate breeding lines for characteristics associated with seedling vigor under environmental stress, and for resistance to insects and diseases. It is encouraging that significant heritable genetic variation has been found among progeny lines in both the field and laboratory. This indicates that selection will result in genuine genetic progress. Superior clones have been selected and isolated in crossing blocks to produce breeders seed of experimental strains, which are evaluated over a range of field environments for possible release as new cultivars.

Interploidy Breeding

The amount of genetic diversity available from a given taxon is limited. Thus, it would be helpful for breeders to investigate the potential benefits of genetic introgression among related taxa. Combining the genetic resources of the three ploidy levels in the crested wheatgrass complex would substantially expand the genetic diversity available at any one level. Barriers, which have restricted crosses among taxa in the complex, have been largely removed by induced polyploidy (Dewey and Pendse 1968). All combinations of crosses have now been made among the diploid, tetraploid, and hexaploid levels (Knowles 1955; Dewey 1969, 1973).

Interploidy breeding at diploid level--Transfer of genes from hexaploid (6x) or tetraploid (4x) crested wheatgrass to diploid forms through (4x-2x) or (6x-2x) X 2x crosses has been difficult to achieve. The necessary crosses and backcrosses are hard to make and the triploids (3x) needed to bridge the transfer are sterile (Asay and Dewey 1979; Dewey 1971). In addition, the triploid hybrids produce a preponderance of functional unreduced (3x) eggs, which results in a one-way gene flow from the diploid to higher ploidy levels. Restriction of genetic transfer to the lower ploidy levels has also been observed in orchardgrass, *Dactylis glomerata* L. (Jones and Borrill 1962, Zohary and Nur 1959).

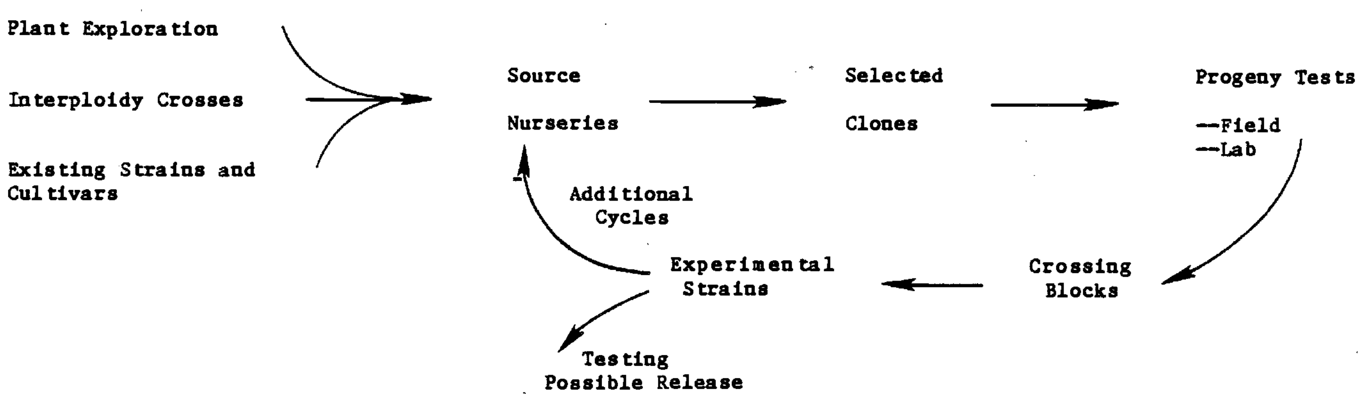

Figure 1.—Sequence of events in crested wheatgrass breeding program.

An infusion of genetic traits from the hexaploids and tetraploids to the diploid level would be particularly valuable to the crested wheatgrass breeder. Although diploid Fairway is leafier and of better forage quality than the Standard forms, it has smaller seeds and tends to be less productive and drought hardy. Moreover, the genetic variability available for selection has been especially limited in the diploid breeding population.

Dewey (1971) found that triploids with a colchicine-induced tetraploid (C4x) in their parentage produced an increased proportion of functional reduced gametes. This made these triploids potentially more useful as a genetic bridge from the natural tetraploid (N4x) to the diploid level. Using triploids from (N4x-C4x) X 2x crosses in a backcrossing sequence, he successfully transferred genes from the tetraploid to the diploid level. This procedure should be extremely useful to breeders working with diploid crested wheatgrass.

Fairway type germplasm has been the only known diploid crested wheatgrass of economic importance. Additional diploid types have recently been reported (Dewey and Asay 1982), and others may yet be found through plant exploration. These diploids may be valuable in the development of improved diploid or tetraploid cultivars or as a source of genetic traits to infuse into Fairway breeding populations. Some proposed schemes for utilizing these diploids are shown in Figure 2. Schemes 1, 2, and 3 illustrate how new tetraploid types could be developed through hybridization and induced polyploidy. Alternative 4 is suggested as a means of combining traits of exotic diploids with Fairway.

Interploidy breeding at tetraploid level--Several procedures could be effectively used to combine germplasm from the three ploidy levels at the tetraploid level (Fig. 3). Fertile tetraploid (C4x) plants have been obtained by treating Fairway diploids with colchicine (Tai and Dewey 1966). Subsequently, Dewey and Pendse (1968) reported that C4x clones crossed readily with N4x selections and

1. C_1C_1 X $C_2C_2 \longrightarrow C_1C_2 \xrightarrow{\text{Colchicine Treatment}} C_1C_1C_2C_2$

2. C_1C_1 Colchicine Treatment $C_1C_1C_1C_1$

X $\longrightarrow C_1C_1C_2C_2$

C_2C_2 Colchicine Treatment $C_2C_2C_2C_2$

3. $C_1C_1C_2C_2$ / $C_1C_1C_1C_1$ X Existing Tetraploids $\longrightarrow$ New Tetraploids

4. Transfer of genetic diversity from diploid taxa to Fairway

C_1C_1 X Fairway $(C_3C_3) \longrightarrow C_1C_3$

C_3C_3 X $C_1C_3 \longrightarrow C_3, C_3,$

Figure 2.--Breeding schemes to combine the genetic resources of diploid taxa of crested wheatgrass. Cn represents a genome of 7 chromosomes and CnCn or CnCnCnCn diploid or tetraploid taxa, respectively.

Induced Tetraploid (C4x) X Natural Tetraploid (N4x) ⟶ 4x

(N4x - 2x) X N4x ⟶ 4x

Hexaploid - Diploid Crosses (6x-2x) ⟶ 4x

(6x-2x) X N4x ⟶ 4x

[(6x - 2x) X C4x] X N4x ⟶ 4x

(6x - 4x) ⟶ 5x ⟶ 4x

(6x-4x) ⟶ 5x X 4x ⟶ 4x

Figure 3.--Interploidy breeding schemes to transfer germplasm to tetraploid (4x) level in crested wheatgrass.

that the fertility of the derived C4x-N4x hybrids compared favorably with that of the parents. Their results also indicated that fertility of the hybrid could be further improved through selection. Furthermore, many of the hybrid plants were substantially more vigorous than the parental species.

The USDA-ARS at Utah State University has included the C4x-N4x hybrid in an intense breeding program. Eighteen clones were selected from an original population of 8,000 hybrid plants on the basis of evaluation in a source nursery and progeny tests on range sites. Selection for vigor of seedlings and mature plants, seed and forage yield, resistance to environmental stress, and resistance to plant pests was stressed. The 18 parental clones were isolated in a crossing block to produce an experimental strain that was evaluated and released as the cultivar, 'Hycrest'. The hybrid has been evaluated on several representative range sites in the Intermountain West. Forage yield data during and immediately after stand establishment at five locations are presented in Table 1. In each of these trials, Hycrest was easier to establish and produced significantly more forage than Nordan or Fairway. The superiority of the hybrid is particularly noteworthy under environmental stress where stands are usually difficult to obtain. This was demonstrated at Location D (Lakeside, UT), where drought, soil salinity, and infestations of cheatgrass and halogeton seriously impeded the establishment of other cultivars (Table 1). Long-term productivity and persistence of Hycrest are being evaluated. Additional crosses are now being made among clones of the parental species to improve the general performance level and broaden the genetic base of the C4x-N4x hybrid breeding population.

Other hybridization schemes offer promise in the interploidy transfer of genetic traits to the tetraploid level (Fig. 3). Although N4x-2x triploids are plagued with sterility problems, Dewey (1971) concluded that fertile 4x plants could be derived from (N4x-2x) X 4x crosses. This would provide an alternative method of transferring germplasm from the diploid to the tetraploid level. Dewey (1969, 1974) also found that stable 4x populations could be derived from 6x-4x crosses. Many of the pentaploid (5x) plants from this cross were more vigorous than either parent and their fertility approached that of natural tetraploids. Dewey proposed that stable 4x populations could be

Table 1.--Forage yield of three crested wheatgrass cultivars on five range sites during stand establishment (Yr-1) and subsequent seasons (Yr-2 and Yr-3).

Cultivar	A	B	C	D		E	
	Yr-1	Yr-1	Yr-2	Yr-2	Yr-3	Yr-2	Yr-3
	lbs/A						
Hycrest	3652	1199	2239	2333	1827	3522	2381
Nordan	3387	431	1556	1380	1338	2174	1743
Fairway	3239	565	----	858	1263	2835	----
$LSD_{(0.05)}$	495	107	449	346	222	743	418

Location A = Decker, MT coal surface mine, 12.5 in average annual precipitation (AP); B = NW Utah, 14.4 in AP; C = near Sublette, ID, 12.8 in AP; D = Lakeside, UT, 6.1 in AP; and E = Thiokol, Wasatch Div., 14.1 in AP.

selected from 5x populations and from progenies of 5x-4x crosses. Crosses between hexaploids and diploids have been proposed as a breeding tool to combine germplasm from all three ploidy levels at the tetraploid level (Asay and Dewey 1979). Although the 6x-2x tetraploids are difficult to obtain and have limited agronomic merit in their own right, they may be crossed with other natural and induced tetraploids to produce genetically diverse breeding populations.

Interploidy breeding at hexaploid level--Selection and hybridization of crested wheatgrass at the hexaploid level is possible but probably is not a productive alternative. Although only a limited number of hexaploid ecotypes have been observed under range conditions in the U.S. and Canada, they appear to be relatively coarse textured and of limited agronomic merit. In addition, the complex inheritance patterns in the hexaploids make them more difficult to manipulate in a breeding program than are the tetraploids or diploids. The rarity of hexaploids under natural range conditions suggests that 2n=42 is above the optimum ploidy level for crested wheatgrass.

Nonetheless, genetic transfer from diploids and tetraploids to the hexaploid level has been achieved (Dewey 1974). Fully fertile 6x plants have been selected from progenies of first generation backcrosses of 6x-C4x or N4x hybrids with the 6x parent. Dewey also produced reasonably fertile 6x plants from crosses among 5x hybrids.

PLANT EXPLORATION

Because crested wheatgrass is indigenous to Asia, plant exploration in this area is essential to provide plant breeders with wider genetic diversity. Most of the early reseeding on western rangeland was done with a relatively few introductions made in the early 1900s, the majority of which were from the U.S.S.R. Plant breeding improved the general performance level of the available plant materials, but the parentage of most cultivars has a relatively narrow genetic base. As the value of crested wheatgrass became more generally accepted, plant exploration efforts were expanded. Introductions from U.S.S.R., Iran, China, and other countries have contributed to the current storehouse of genetic diversity.

Plant materials recently collected from Iran are particularly noteworthy. Significant differences have been found among these accessions for characters such as maturity date, plant height, seed size, seed yield, plant texture, and rhizome development. More than one-half of the plants are rhizomatous (Dewey and Asay 1975). Other accessions recently introduced from Turkey also are rhizomatous. A breeding program is in progress to incorporate selections from these accessions into new rhizomatous cultivars or to transfer the character to existing cultivars. These plant materials will probably be of most utility in special use situations where soil stabilization is a major concern. A low-growing, sod-forming type with a longer green period would be particularly useful for dryland lawns in suburban and rural areas. Newly acquired introductions from the U.S.S.R. and China are also being evaluated. Some of these accessions have shown promise, particularly in terms of aftermath production after clipping or grazing.

SUMMARY

Although crested wheatgrass in its present form has been a valuable source of plant materials for improving western rangelands, it is evident that its potential can be substantially improved through the development of improved cultivars. Plant breeding to date has been restricted largely to selection and hybridization within populations with similar chromosome numbers, primarily diploids (2n = 14) and tetraploids (2n = 28). The noteworthy cultivars released from these intraploidy breeding programs are Fairway, Parkway, Ruff, Nordan, Summit, P-27, and Ephraim.

Several schemes have been devised and tested to transfer genetic traits among the different ploidy levels of crested wheatgrass. The USDA-ARS at Utah State University has successfully combined the germplasm of the diploids and tetraploids by crossing induced tetraploid Fairway with natural tetraploid Standard types. The cultivar 'Hycrest',

released in 1984 from this research program, was developed from this hybrid. Hycrest has been significantly more productive than the most commonly used cultivars, Nordan and Fairway, particularly in terms of stand establishment on harsh range sites. Results from research indicate that additional crosses involving more select parentage will yield even more genetic progress. New diploid populations and rhizomatous forms, obtained from plant collections recently made in Asia, also have made significant contributions to the genetic resources available to geneticists working to improve crested wheatgrass.

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SECTION III.

Ecological Relationships.

Putting Crested Wheatgrass in, Making it Grow and Keeping it There.

Chairman, A.E. (Gene) Gade

Seed and Seedbed Ecology of Crested Wheatgrass

James A. Young and Raymond A. Evans

ABSTRACT: The seeds of crested wheatgrass are not particularly adapted for germination under cold seedbed conditions. Germination in the early spring would be an advantage for successful seedling establishment before soil moisture is exhausted in seedbeds. The development of new plant material with the potential for germination at lower seedbed temperatures should greatly aid in the establishment of adapted grasses on rangelands. Until such grasses are developed, the only alternative is to modify environmental parameters of seedbeds through such practices as seeding in deep furrows. Drilling crested wheatgrass seeds into seedbeds with good soil coverage leads to optimum chances for germination and establishment.

INTRODUCTION

Moisture and temperature conditions needed for germination of seeds of perennial grasses are largely out of phase in the big sagebrush (Artemisia tridentata) environment. When moisture is available, it is too cold for germination and growth, and soon after it warms sufficiently for germination, it often is too dry. Often germination is delayed by cold temperatures in the spring, so grass seedlings are not sufficiently established to survive the summer drought. In an environment without warm season precipitation, the onset of the summer drought is a non-interruptive event. Some of the landscape characterizing native perennial grasses, such as bluebunch wheatgrass (Agropyron spicatum), may only have successful seedling establishment in summers with above average precipitation (Harris and Wilson 1970).

In contrast, in an environment with warm season precipitation in which periodic droughts may limit seedling establishment, there is a definite chance of a moisture event occurring to alleviate the drought. Selective pressure of the warm season precipitation environment could favor characteristics that permit endurance of drought so seedlings can persist until the next moisture event. In an environment with near total cool season precipitation, the successful seedling must avoid the summer drought through dormancy. Earlier germination, even by a few days, may make the difference in successfully enduring inevitable summer drought.

In most wildland situations, it is not possible to add supplemental irrigation water to ensure the establishment of perennial grass seedlings. Lacking the alternative of controlling soil moisture, land managers have two available options: a) they can seed plant material adapted to germinate at low temperatures when soil moisture is available, or 2) they can modify the seedbed to produce environmental conditions conducive to germination.

GERMINATION OF ADAPTED GRASSES IN RELATION TO TEMPERATURE

To ascertain the potential of the first alternative, we recently (Young and Evans 1982) conducted a study on the germination of the commercially available perennial grasses for seeding on rangelands where growth occurs primarily during the cool (moist) season. In all, 71 cultivars, accessions or collections of grasses (with four replications of 25 seeds each) were tested at 55 constant and alternating temperature regimes.

When the data from these germination experiments are segregated into broad groups of species such as wheatgrass, wild ryegrass, fescue, and bluegrass, there is no significant ($P = 0.01$) difference among the germination of the groups (Table 1).

There is one grass that widely occurs on sagebrush rangelands that has markedly better germination than any of the groupings of potential revegetation species. This highly germinable grass is cheatgrass (Bromus tectorum) (Table 1). An alien annual weed, it has invaded many sagebrush range sites in the Intermountain area where it has revolutionized secondary succession (Piemeisel 1951). Cheatgrass provides significant competition to the seedlings of perennial grasses and often

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Table 1.--Comparison of mean germination of broad species groups for 55 constant and alternating temperatures (from Young and Evans 1982).

Species groups	Germination[1]
	percent
Wheatgrass	54 b
Wildrye	53 b
Fescue	40 b
Bluegrass	44 b
Cheatgrass	81 a

[1]Means followed by the same letter are not significantly different at the 0.01 level of probability as determined by Duncan's multiple range test.

closes the community to their establishment (Robertson and Pierce 1945). Not only do the seeds of potential revegetation species have to mesh their germination potential with physical parameters of the seedbed in terms of temperature and moisture, but they must also compete with cheatgrass for sites in the seedbed capable of supporting germination.

Species of the crested wheatgrass group [Fairway (Agropyron cristatum), standard (A. desertorum), and Siberian (A. sibericum)] have very similar germination characteristics (Table 2). Seeds of this group have some germination at virtually all the temperature regimes tested. Optimum germination, defined as mean germination not differing statistically ($P = 0.01$) from the maximum observed and one half its confidence interval (Young and Evans 1982), occurred at 7 to 19 percent of the temperature regimes tested. The mean germination of the optima ranged from 74 to 86 percent. Maximum germination of the Fairway and Siberian sources averaged only 76 and 79 percent respectively, compared to 90 percent for the standard crested wheatgrass group (Table 2).

Another method of evaluating the potential for germination at low seedbed temperatures is to calculate the frequency that a given temperature regime supports optimum germination for seeds of all the plant material tested. For the crested wheatgrass group, only the alternating temperature regime of 20°C for 16 hours and 25°C for 8 hours in each 24 hour period had a hundred percent frequency for supporting optimum germination (Table 3).

When the 20/25°C temperature regime is compared with temperatures recorded in field seedbeds of sagebrush sites in the Intermountain area, a wide discrepancy is apparent (see Evans et al. 1970). During the early spring, seedbed temperatures often included 0°C. This type of comparison can be expanded by making a discriminate breakdown of the 55 temperature regimes used in germination testing into groups of seedbed temperatures based on field monitoring (Young and Evans 1982). In this type of comparison, all of the crested wheatgrass group have significantly ($P = 0.01$) lower germination than that of cheatgrass (Table 4).

It is apparent that existing plant material available for revegetation of sagebrush rangelands has marked variability in its potential for germination at cold seedbed temperatures as would be found in the field in early spring. This underscores the importance of hybridization and selection programs to develop such material. Moreover, the competitive advantages of cheatgrass over available revegetation species extends into the realm of field seedbed temperatures.

Modifying the Existing Environment

Because we lack plant material that can germinate at low seedbed temperatures, modifying the physical seedbed is the practical alternative. McGinnies (1959) demonstrated that deep furrowing aided in the establishment of seedlings of perennial grasses on rangelands. Detailed micro-environmental monitoring studies by Evans et al. (1970) enumerated the environmental parameters that are modified by deep furrowing.

In terms of seedbed temperatures, the influence of deep furrowing is to moderate the temperature extremes, both maximum and minimum. Deep furrowing is not going to bring early spring seedbed temperatures into the high-frequency optimum regimes for crested wheatgrass germination, but it will greatly enhance the potential of the seedbeds to support germination of perennial grasses.

The development of modified arms for the rangeland drill (Asher and Eckert 1973) makes it possible to modify seedbeds, in suitable soils, by deep furrow seeding.

MOISTURE RELATIONS

Temperature relations in germination constitute only a portion of the environmental parameters interacting to control seedling establishment of

Table 2.--Comparison of germination parameters for accessions or cultivar groups of Fairway and standard crested wheatgrass and Siberian wheatgrass. Data generated from quadratic response surfaces based on germination at 55 constant and alternating temperatures.[1]

Germination parameter	Fairway	Standard	Siberian
	percent		
Mean germination	56	59	55
Regimes with some germination	98	99	100
Mean of regimes with some germination	57	59	55
Regimes with optimum germination	19	15	27
Mean of optima	75	86	74
Maximum germination	76	90	79

[1]No significant difference in mean germination among groups.

Table 3.--Frequency of temperature regimes that supported optimum germination for accessions or cultivar groups of Fairway and standard crested wheatgrass and Siberian wheatgrass.

Cold period temperature (°C) 16 hours	Warm period temperature (°C) 8 hours 0	2	5	10	15	20	25	30	35	40
	----Frequency of optima - Percent---									
0						13	13			
2						13	13			
5						13	25			
10					18	63	75	25		
15					25	88	80	50		
20						88	100	50	25	
25							63	38		
30										
35										
40										

crested wheatgrass on rangelands. Available soil moisture and transfer of the moisture from the soil substrate to the seed are highly significant parameters in germination.

Much of the current theory concerning moisture dynamics in seedbeds has been developed by J.L. Harper and his students (Harper et al. 1965, Harper 1977). Harper proposes that seeds must take up moisture from the substrate faster than they lose moisture to the atmosphere. To accomplish this transfer and retention, there must be good contact between the substrate and the seed for hydraulic conductivity. To avoid moisture loss to the atmosphere, the seed must be buried in the soil. Translated to field terms, the best chance of obtaining a stand of crested wheatgrass comes by seeding at the correct depth in a good, firm seedbed.

Not even the seeds of cheatgrass are immune to the dynamics of soil moisture in the seedbed. Cheatgrass seeds require either fortuitous burial in surface microptopography of the seedbed, or litter coverage in order to germinate (Evans and Young 1970 and 1972). Both factors improve seedbed moisture relations for germination.

Germination on the Seedbed Surface

The seeds of grasses generally require soil coverage, litter coverage, or fortuitous placement in relation to seedbed microtopography in order to obtain the required environmental prerequisites for germination. Seeds of other types of plants can germinate on the soil surface, and some of these species are important to the establishment of crested wheatgrass seedlings on sagebrush rangelands.

Seeds of Russian thistle (*Salsola iberica*) follow a high risk germination strategy where a multitude of seeds are produced and a highly evolved dispersal system finds the right seedbeds. The germination of Russian thistle seeds is so rapid and such a simple process that seedling establishment can occur during the course of a single moisture event (see Evans and Young 1983 for discussion of *Salsola* germination). Because of its dispersal and germination systems, Russian thistle can become a summer weed problem on ground being prepared for seeding crested wheatgrass or during the seedling year of the wheatgrass stand.

Table 4.--Comparison of germination of seeds of Fairway and standard crested wheatgrass, Siberian wheatgrass and cheatgrass in relation to a discriminate breakdown of seedbed temperatures.

Seedbed temperatures	Fairway	Standard	Siberian	Cheatgrass
	-------------percent[1]-------------			
Moderate	70 b	78 b	69 b	93 a
Colder than moderate	40 b	33 b	42 b	68 a
Widely fluctuating	54 b	53 b	57 b	84 a
Warmer than moderate	46 b	51 b	38 b	70 a

[1]Means in rows followed by the same letter are not significantly different at the 0.01 level of probability as determined by Duncan's multiple range test.

Several species of mustard can also become weeds during the seedling year of crested wheatgrass. Notable among these is tumble mustard (*Sisymbrium altissimum*). Seeds of this species can germinate on the surface of seedbeds apparently because of mucilaginous seed coats. This mucilage forms when the seed absorbs moisture and apparently retards the loss of moisture to the atmosphere. Unfortunately, it has not been possible to transfer this attribute to seeds of desirable grasses.

PERSPECTIVE IN CRESTED WHEATGRASS SEED ECOLOGY

There is a great need for plant breeders to develop new cultivars of adapted grasses which have the potential for germination and growth at low temperatures. Until such cultivars are developed, it is possible to manipulate environmental parameters in seedbeds through such techniques as deep furrow drilling. The drawbacks and limitations of broadcast seeding of crested wheatgrass seeds are obvious when moisture relations necessary for germination are considered.

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In: Johnson, K. L. (ed.). 1986. Crested wheatgrass: its values, problems and myths; symposium proceedings. Utah State Univ., Logan.

Seed and Seedling Relations of Crested Wheatgrass: A Review

Douglas A. Johnson

ABSTRACT: Considerable literature has accumulated concerning seed and seedling relations of crested wheatgrass. The extensive literature covers a period of more than 40 years and is found in a wide variety of sources. This review is a synthesis of the scattered literature.

ACKNOWLEDGEMENTS: A contribution from the USDA Agricultural Research Service and the Utah Agricultural Experiment Station, approved as Utah Agr. Exp. Sta. J. Pap. 2940. Special thanks go to Howard Skinner and Michelle Mueggler for their capable assistance in reviewing the literature and preparing the bibliography. Appreciation also is extended to Carolyn Lemon and Betty Wood for their secretarial assistance. Manuscript reviews by Drs. K. H. Asay, J. D. Berdahl, R. W. Brown, F. B. Gomm, and A. C. Hull are appreciated. A particularly thorough review by Dr. W. Keller provided numerous helpful suggestions and additional literature sources.

INTRODUCTION

Seeding on rangelands is a very important method of range improvement and is done for a variety of purposes that include: 1) revegetating abandoned croplands, 2) replacing vegetation following fire, 3) extending the grazing season, 4) improving the quantity and quality of forage, 5) reestablishing valuable forage species, and 6) protecting areas from erosion (Stoddart et al. 1975). In addition, rangeland seedings can provide supplemental forage during critical forage periods, thus providing considerable management flexibility to livestock producers (Currie 1969). Rangeland seedings also are necessary in successful mineland reclamation. Nevertheless, seeding is expensive, and not always successful, and as a general rule is used only when ranges are producing substantially below their forage potential and cannot be upgraded to near their potential through management in a reasonable period of time.

Crested wheatgrass has been used successfully for seeding a wide variety of rangeland sites throughout western North America since its introduction in the early 1900s (Rogler and Lorenz 1983). It also has been used in some areas of the Near East (Moghaddam 1976). In this paper, I will refer to crested wheatgrass as proposed by Dewey (1983) and Dewey (this volume), who defined crested wheatgrass as the common name given to a species complex composed of three broad groups or taxa commonly introduced into North America. These are 1) Fairway [Agropyron cristatum (L.) Gaertn. ssp. pectinatum (Bieb.) Tzvel.], 2) Standard [A. desertorum (Fisch. ex Link) Schult.], and 3) Siberian [A. fragile (Roth) Candargy]. Many of the early studies failed to recognize species differences and others confused A. cristatum and A. desertorum. However, the species names used by the authors will be retained in this review. Except where specific comparisons were made between species of crested wheatgrass, data presented for particular species within the crested wheatgrass complex will not be categorized into separate taxon responses. Rather it will be lumped into responses pertaining to crested wheatgrass as a broad, general grouping. However, it should be noted that different species of crested wheatgrass do exhibit differences in at least some characteristics (Stevenson and White 1939, Hafenrichter et al. 1949, Hull 1972, Lodge et al. 1972).

WHY CRESTED WHEATGRASS

The early history concerning the introduction of crested wheatgrass in North America has been reviewed by Dillman (1946), Rogler and Lorenz (1983), and Lorenz (this volume). They described the original native distribution of crested wheatgrass as covering an extensive area from Europe to Central Asia. It is a persistent, drought- and cold-resistant grass in those areas. Consequently, it is not surprising that crested wheatgrass is well adapted to broad expanses of climatically similar areas in the western United States and Canada, primarily the Northern Great Plains and

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Intermountain West. For example, of 90 species seeded in 2,450 range plots in 60 studies on depleted rangelands and abandoned dry farmland in the sagebrush region in southern Idaho, crested wheatgrass was the most successful species on the drier sites (Hull 1974). In southeastern Alberta, crested wheatgrass outyielded forage produced on native range by 1.1 to 1.5 times (Dormaar et al. 1978). Similarly in Oregon, Leckenby and Toweill (1983) reported that crested wheatgrass survived the best of any species tested in juniper/big sagebrush-antelope bitterbrush communities. Reynolds and Springfield (1953) reported that crested wheatgrass is adapted to ponderosa pine rangelands in Arizona and Mexico. They reported that crested wheatgrass gave high forage yields, supplied green forage in both the spring and fall, withstood grazing well, and produced high annual weight gains. Numerous other studies have been conducted concerning the adaptation of crested wheatgrass and have been reviewed by Keller (1979).

Crested wheatgrass also has been well documented as a persistent species across a wide variety of rangeland sites. For example, in southeastern Alberta, stand longevity of crested wheatgrass seedings was reported to be more than 40 years (Dormaar et al. 1978). Similarly, Westover and Rogler (1947), Hull and Klomp (1966), and Judd and Judd (1976) working in central North Dakota, southern Idaho, and northern Arizona, respectively, reported that stand longevities of crested wheatgrass exceeded 30 years. Detailed site and species adaptability reports concerning the success of crested wheatgrass in various environments have been published by Gomm (1974) for the Northern Intermountain Region, McGinnies et al. (1963, 1983) for Colorado, and Lavin and Johnsen (1977) for Arizona. Although crested wheatgrass has been seeded successfully on many rangeland areas, it is not universally adapted to all sites as evidenced by a number of seeding failures or poor stands that occurred when proper cultural practices were used (Halliday 1957, Hull 1963b, Wein and West 1971). Nevertheless, crested wheatgrass has been one of the most successful grasses for seeding semiarid rangelands.

Besides its wide adaptability, crested wheatgrass provides a palatable and nutritious early spring forage (Currie 1969). This is particularly beneficial to ranchers in the Intermountain West where shortage of forage in the spring often may be a limiting constraint to livestock operations. Additionally, it has been well established that crested wheatgrass can withstand relatively heavy spring grazing (Hyder and Sneva 1963), a characteristic probably developed in the early Pleistocene when large ungulates first started grazing the native steppe areas of eastern Europe and central Asia (Mack and Thompson 1982). The basis of this tolerance to herbivory is being investigated by Caldwell et al. (1981, 1983), Caldwell and Richards (1986), and Nowak and Caldwell (1984a, 1984b). Besides being highly productive from a forage standpoint, crested wheatgrass also produces abundant seed that can be easily harvested (Westover and Rogler 1947). This is particularly important because seed can be readily obtained at an economically reasonable price.

Another characteristic that has contributed to the widespread use of crested wheatgrass is its ease of establishment. Because range seedings typically are done on relatively marginal lands that tend to provide suboptimal growth conditions, successful establishment is of critical importance. Consequently, because of their importance in successful establishment, this paper will focus attention on the germination, emergence, and seedling phases of crested wheatgrass.

PREGERMINATION CONSIDERATIONS

A number of pregermination factors can influence subsequent emergence and establishment (Fig. 1). These factors include environmental influences during seed production, seed harvesting, processing, and storage, pre-sowing seed treatments, seedbed preparation, and seed placement.

Seed Production

Crested wheatgrass is a highly productive seed producer under a wide range of conditions. However, the environment does influence the amount of seed produced by crested wheatgrass as evidenced by widely fluctuating seed yields from 1923 to 1943 (Dillman 1946). Drought, high or low temperatures, salinity, plant diseases, insects, frost, and soil nutrient levels can all markedly influence the quantity of seed produced.

In addition, however, the maternal environment influences seed quality or type of seed produced. This has not been documented for crested wheatgrass directly, but evidence for other species suggests that it may be a general phenomenon. For example, abnormal pea (Pisum sativum L.) seedlings result from maternal deficiencies in boron (Leggatt 1948) and manganese (Glasscock and Wain 1940). Gutterman (1973, 1978) examined the influences of daylength and hormones on the germinability of seeds produced and on the performance of the resulting generation of plants of Lactuca scariola L. and Lycopersicum esculentum Mill. He concluded that the external conditions under which the mother plants grow have a far-reaching influence on the germinability of seeds and, therefore, on the progeny of the resulting generation. Position of development of the seed on the mother plant has also been shown to be important in determining subsequent seed and seedling response in various crop species (Thomas et al. 1978). Akpan

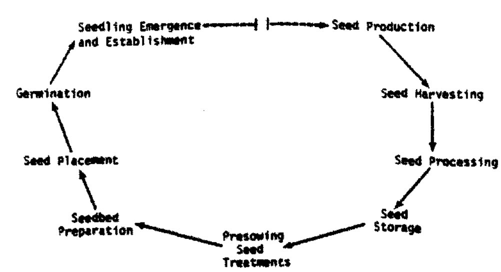

Figure 1.--Factors influencing germination, emergence, and establishment.

and Bean (1977) examined the effect of temperature on the seed development of three forage grasses and concluded that year to year temperature differences do affect both the yield and quality of seed crops. Quality differences within a species were primarily mediated through seed weight and included lower germination percentages as well as slower germination rates. Similar conclusions were reached by Wood et al. (1977) who found that for three crop species large seeds produced larger seedlings and that this difference often persisted to the mature plant stage. They speculated that these differences may be due to greater seed reserves, larger embryo size, and the earlier development of photosynthetic competency.

Seed Harvesting, Processing, and Storage

Seed of crested wheatgrass is relatively easy to harvest with conventional grain-harvesting implements (Westover and Rogler 1947). Because the seed shatters readily, timing of harvest is critical. The stage of maturity at which seed is harvested exhibits a marked influence on germination and subsequent seedling emergence and establishment. At the moment of fertilization a zygote is formed. After development and maturation, this zygote has the potential to become an embryo in a mature seed. Generally, the earlier a seed is harvested before maturity, the lower its germination and longevity. For example, Hermann and Hermann (1939), working with crested wheatgrass seeds ranging across 10 stages of maturity, concluded that vigorous seedlings could not be expected from seed harvested earlier than the hard dough stage. Similarly, McAlister (1943) harvested seed of eight grasses, at the pre-milk, milk, dough, and mature stages of seed development. Results for crested wheatgrass showed that seeds harvested at the pre-milk stage weighed 29% as much as mature seeds. Seeds of crested wheatgrass harvested at the pre-milk stage germinated fairly well shortly after harvest. After being stored for more than 15 months, however, they declined in germination more rapidly than seeds harvested at more mature stages. Even more importantly, percent seedling emergence declined in the field: 46, 33, 10, and 3% for maturity, dough, milk, and pre-milk stages, respectively.

Mechanical damage to the seed is another factor that can influence germination and seedling establishment (Harrington 1972). This may occur during the harvesting, threshing, and cleaning stages of seed processing (Pollock and Roos 1972). Such considerations as the drying process used, types of equipment used, numbers and distances of seed drop, number of handling steps, and the manner in which seeds are passed through each process are important in determining the types and severity of seed damage. Injuries such as split or cracked seed, broken seed, or internal seed fractures from impaction or improper drying can all lead to decreased germination and seed longevity.

Seed storage can affect seed viability, germination, and seedling emergence. The principles and practices of seed storage have been well documented by Harrington (1972), Justice and Bass (1978), and Bass (1979). Storage conditions such as temperature and moisture content of the seed greatly influence seed longevity. Generally, the higher the moisture content, the greater the decline in seed germinability; however, losses in germination may also occur at extremely low moisture contents. Generally, the cooler the storage temperature, the more slowly seed viability declines. However, Hay (1935) reported that two-year-old seed of crested wheatgrass exhibited only a slight loss in germinability whether stored at room temperature in the laboratory or in an unheated granary. Hull (1973) examined the germination of 166 lots of range plant seeds kept in uncontrolled storage environments for 14 to 41 years. He found that seedling emergence percentages of crested wheatgrass were reduced from 83% after two years to 11% after 14 years. However, when storage temperatures of -7 to -18° C were provided, Acikgoz and Knowles (1983) reported that seed viabilities of *A. cristatum* could be maintained at 80 to 90% even after 20 years. Not only can improper storage conditions reduce seed viability, but they can cause genetic change through time (Harrington 1972). This genetic drift was ascribed to seed death so that the few remaining viable seeds may not have the same average genetic composition as the original seedlot. In addition, genetic drift may be due to more mutations occurring as storage time increases.

Presowing Seed Treatments

Seedling establishment can be enhanced through various cultural practices that affect the seed or ameliorate the seed environment. Frequently, periods for favorable germination on rangeland sites are relatively short. Consequently, any seed treatment that shortens the time required for imbibition, germination, and subsequent root and shoot development may increase chances for establishment during the critical period.

Seed pelleting is a treatment in which individual seeds are coated with successive layers of finely powdered material or groups of seed are compressed with a soil mixture to form earthen pellets (Hull et al. 1963). These coatings or mixtures around the seed can contain rodent and insect repellents as well as fertilizer or various growth stimulants (Bleak and Hull 1958). Pelleting was thought to provide seed covering and conditions favorable for germination and seedling growth (Hull 1959). Because pelleted vegetable and flower seeds have been used successfully, pellet seeding by airplane of broad expanses of western U.S. rangeland was proposed. However, a summary of results of pellet seeding done on more than 180,000 acres of rangelands, widespread experimental field tests, and numerous laboratory and greenhouse studies conducted during 1946 to 1961 proved that pelleted crested wheatgrass had no advantage over nonpelleted seed (Hull et al. 1963). Because of the additional cost associated with the pelleting process and the lack of advantage in establishment, seed pelleting cannot be recommended for crested wheatgrass.

Another preplanting treatment to enhance the establishment of crested wheatgrass involves the wetting of seeds for specific lengths of time at specific temperatures. This treatment hastened emergence (Keller and Bleak 1968, Bleak and Keller 1974), quickened root and shoot elongation (Keller and Bleak 1969), and produced better stands in field tests (Bleak and Keller 1970). The best treatment for crested wheatgrass was wetting seeds at 16°C for 60 hours (Bleak and Keller 1972). The advantage of this treatment was enhanced as conditions favoring emergence deteriorated (Bleak and Keller 1970).

Older seeds required more time to produce seedlings, but the advantage derived from seed treatment was not altered by seed age (Bleak and Keller 1969).

Other seed treatments, such as vernalization, have been shown to hasten seedling emergence of crested wheatgrass. Frishknecht (1959) placed seed of four forage grasses in either a snowbank or refrigerator for various lengths of time and compared them with untreated seedlots. Laboratory germination of crested wheatgrass occurred most rapidly for seed that had been stored in a snow bank, but was reduced and greatly slowed for seed stored in the refrigerator. Snowbank-treated seed of crested wheatgrass also exhibited more than double the seedling emergence of untreated seed on a spring-seeded site at Benmore, Utah.

Treatment with fungicides also has enhanced germination and seedling establishment of range forage plants. Ehrenreich (1958) worked with six forage species, three soil-borne pathogens (Fusarium sp., Rhizoctonia solani Kuehn, and Pythium debaryanum Hesse), and three fungicide treatments in the greenhouse and the field. Results with the cool-season grasses Russian wildrye and intermediate wheatgrass [Elymus junceus Fisch. and Agropyron intermedium (Host) Beauv., respectively], showed that in both greenhouse and field trials significantly more seedlings established with treated as compared to untreated seed. Fungicide treatments of crested wheatgrass seeds using Thiram, Captan, and Semesan were examined in northern Utah by Hull and Kreitlow (1971). Thiram and Captan treatments gave significant increases in emergence of 14 and 12%, respectively, whereas no differences were noted in the Semesan treatment.

Apparently, some pretreatments do promote the germination and emergence of crested wheatgrass. Because of the added time and expense, however, none of these treatments are commonly used on crested wheatgrass.

Seedbed Preparation and Seed Placement

Seedbed preparation (which includes the reduction of competing vegetation) and seed placement factors such as methods, times, rates, depths, and row spacings also directly influence germination, emergence, and seedling establishment of crested wheatgrass. Overall considerations of seeding rangeland species are contained in Hull and Holmgren (1964), Plummer et al. (1968), Blaisdell et al. (1982), Laycock (1982), and McLean and Bawtree (1982). Vallentine (1977) reviewed the literature pertaining to range seedings in general, and Keller (1979) reviewed seeding information specifically for crested wheatgrass and summarized the available literature in tabular form. Vallentine (1978) also compiled an extensive bibliography of range management literature that contains numerous references documenting various aspects of range revegetation. These articles also cover a variety of other cultural practices for improving the establishment of crested wheatgrass and other range plants, including furrowing, trenching, terracing, ripping, pitting, and water spreading. Consequently, the detailed mechanics and associated large volume of literature dealing with the various aspects of seedbed preparation and the seeding operation will not be covered here; rather only a few general considerations will be highlighted.

Because of the large expanses of rangeland that could be seeded by airplane, aerial broadcast seeding received considerable research emphasis in the late 1940s and early 1950s (Stewart 1949, Wagner 1949, Killough 1950, Stewart 1950). However, nearly all attempts at aerial seeding of semiarid rangelands have failed (Hull et al. 1963). Nevertheless, where a good seedbed has been prepared and the seed is adequately covered by ground equipment, broadcast seeding has been successful. For example, Cook (1958) reported good stands of crested wheatgrass from broadcast seeding undertaken prior to mechanical eradication of sagebrush.

Generally, however, drilling is more effective in stand establishment than broadcasting as evidenced by the work of Hull and Klomp (1967), who found that drilling produced 10 times more seedlings than broadcasting. In addition, drilled stands reached full production much sooner. Nelson et al. (1970) stated that broadcast seed was subject to depredation by rodents and birds and was exposed to rapidly fluctuating moisture conditions that frequently interrupted the germination process. Conversely, drilled seed remained in relatively constant and favorable soil moisture and carried on metabolic processes rapidly without interruption. Keller (1979) stated that two advantages of drilling over broadcasting were 1) more uniform seed distribution and 2) better uniformity in covering the seed. Also, drilling allows the seed to be pressed firmly into close contact with the soil, an extremely important relationship (Hyder et al. 1955, Hyder and Sneva 1956, McGinnies 1962).

In either broadcast seeding or drilling treatments, it is also important to adequately reduce the competition of the existing vegetation (Robertson and Pearse 1945). Gerity and Harrison (1974) used a drilling method apparently useful for establishing crested wheatgrass in loose, sandy soils dominated by cheatgrass (Bromus tectorum L.). They drilled seed of cereal rye (Secale cereale L.) mixed with crested wheatgrass. The rapidly emerging rye effectively reduced soil movement and cheatgrass competition. Grazing the seeding during the year of establishment thinned the rye stand and allowed crested wheatgrass to germinate and establish. They suggested that this seeding procedure was effective in areas receiving 20 to 35 cm precipitation, and was relatively inexpensive and reliable on sites that were difficult to seed with other methods. However, Stoddart (1946) cautioned that because of the extreme competition for moisture in most semiarid rangeland situations, the use of nurse crops would probably decrease grass establishment except in unusually wet years. In addition, rye has become a major weed on many non-irrigated farming lands in the Intermountain West and probably should not be used as a nurse crop.

In summary, it must be emphasized that to ensure successful seedling establishment of crested wheatgrass or other seeded range species it is essential to 1) reduce competition from existing vegetation, 2) provide a good seedbed, and 3) adequately cover the seed.

GERMINATION AND SEEDLING MORPHOLOGY

The process of seed germination as defined by Berlyn (1972) is the sequential series of morphogenetic events that result in the complex, well-integrated transformation of an embryo into a seedling. Germination involves a large number of physical and chemical processes that result in the transformation of a seed into a seedling and eventually into a mature plant. Torrey (1967) subdivided the germination process into a series of five major events: 1) imbibition or the physical absorption of water, 2) hydration and activation of the chemical constituents of the seed, 3) cell division and cell extension, 4) protrusion or physical emergence of the propagule from the seed, and 5) the establishment of the primary plant body. Numerous treatises have been published on germination (Kozlowski 1972a, 1972b, Heydecker 1973, Rubenstein et al. 1979, Mayer and Poljakoff-Mayber 1982), detailing the process from both physical and chemical standpoints. Consequently, the complexities and details of germination will not be examined extensively in this paper.

A general description of the early germination and seedling development of crested wheatgrass was published by Love and Hanson (1932). They examined the morphological characteristics of the seed, seedling, and mature plant of crested wheatgrass and provided detailed line drawings of the distinguishing features at these various stages. Their work documented the morphological changes that take place in a crested wheatgrass seedling during its first 120 hours (Fig. 2). Twenty-four to 48 hours after placing crested wheatgrass seed in a

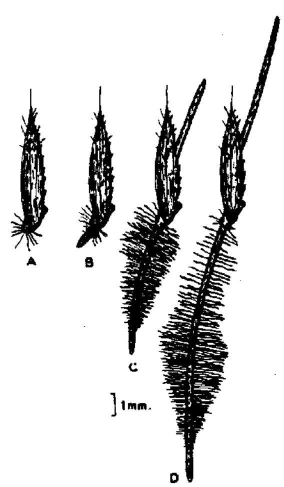

Figure 2.--Morphological changes taking place during the development of a crested wheatgrass seedling: A-24 to 48 hours, B-48 to 72 hours, C-72 to 96 hours, and D-96 to 120 hours (From: Love and Hanson 1932).

moist environment at 25° C, coleorhiza had formed and several distinct root hairs had been initiated. After 48 to 72 hours, the coleoptile began to appear. The primary root had several root hairs by this time and was about twice as long as the coleorhiza. Both the coleoptile and primary root were well developed at 72 to 96 hours, and root hairs were evident on the primary root. From 96 to 120 hours the coleoptile and primary root lengthened to about the same size and twice as long, respectively, as the seed.

Love and Hanson (1932) quantified the lengthening of the shoot and root of crested wheatgrass seedlings during the first 45 days and compared their development with that of smooth brome (Bromus inermis Leyss.). Smooth brome exhibited faster root and shoot development than crested wheatgrass during the first 24 days, but was slightly slower than crested wheatgrass thereafter. Hoshikawa (1969) described similar stages of a number of grasses in more detail.

Hyder (1974) compared the seedling morphology of crested wheatgrass with that of blue grama [Bouteloua gracilis (Willd. ex H.B.K.) Lag. ex. Griffiths]; Figure 3 was adapted from his work. According to Hyder, a major difference between seedlings of the two species is that blue grama has an elongated sub-coleoptile internode with a relatively short coleoptile, whereas crested wheatgrass has a typically long coleoptile with essentially no or very little elongation occurring in the sub-coleoptile internode. The coleoptile is an important structure that protects the underlying meristematic tissue as it pushes upward through the soil. Because crested wheatgrass has a relatively long coleoptile, it can emerge from a relatively deep soil depth. Roots are initiated at the base of the coleoptile, allowing development to occur deeper in the soil where environmental conditions are more favorable. Conversely, blue grama has a short coleoptile and must compensate by elongation of the sub-coleoptile internode. In the process the coleoptile is elevated to near the soil surface where environmental conditions are more extreme. According to Hyder (1974), these conditions can hamper or totally inhibit the initiation of adventitious root development, thereby forcing the blue grama seedling to rely on a single seminal root of short longevity. Consequently, given the suboptimal growing conditions often present on rangelands, seedlings with morphologies similar to that of crested wheatgrass have an advantage in terms of successful establishment.

Root development by seedlings of crested wheatgrass was further examined by Plummer (1943). He quantified total root length, number of roots, root penetration, and root spread for 10 range grasses planted on a site in the mountain brush vegetation type. At approximately 75 days after emergence began, A. cristatum exhibited by far the greatest root length and number of roots of any grass studied. These results suggest that the early seedling root habit of crested wheatgrass is one adaptive attribute that probably contributes to its successful seedling establishment. Apparently, differences in root elongation exist among species within the crested wheatgrass complex, at least for the particular crested wheatgrass accessions examined by Kittock and Patterson (1959). At 49 days after seeding in the greenhouse, depth of root

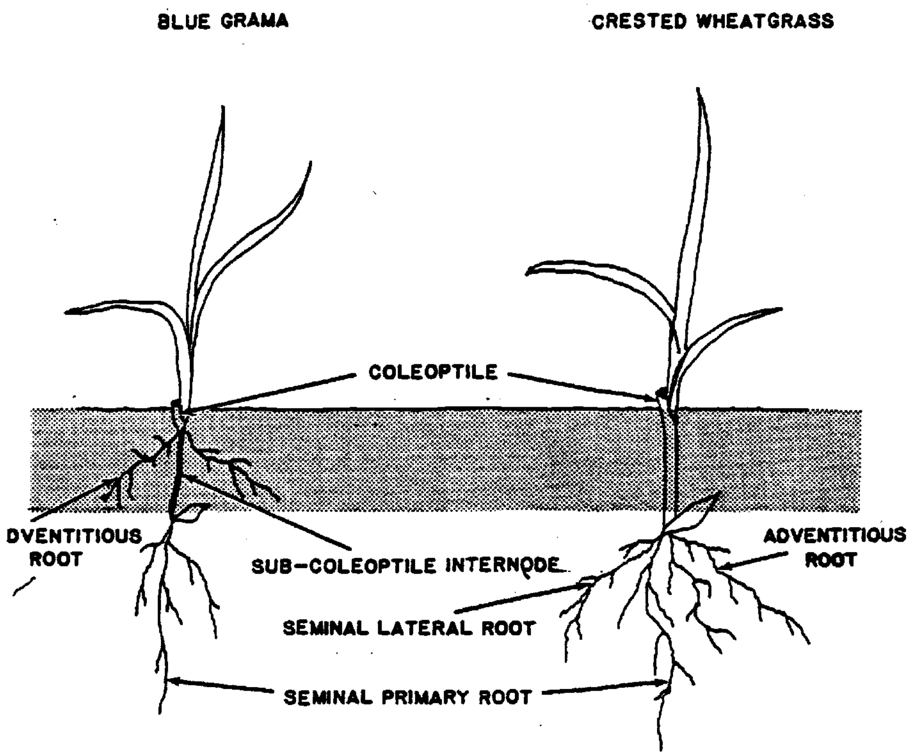

Figure 3.--Two types of grass seedlings. The blue grama type of seedling has an elongated sub-coleoptile internode and a short coleoptile. The crested wheatgrass type of seedling lacks the elongated sub-coleoptile internode but has a long coleoptile. (Adapted from: Hyder 1974).

penetration was significantly greater for A. desertorum and A. sibiricum than for A. cristatum.

EFFECTS OF ENVIRONMENT ON GERMINATION AND SEEDLING DEVELOPMENT

A host of environmental factors directly affect germination (Fig. 4). Because of the importance of this subject area to plant establishment, it has received considerable research emphasis, particularly for agronomically important plants. Consequently, a large amount of literature in the agronomic and ecological fields is devoted to the effects of environment on germination and seedling establishment. General reviews of this subject area are contained in Koller (1972), Heydecker (1973), and Mayer and Poljakoff-Mayber (1982) and for rangeland species in McDonough (1977). Only the literature specifically pertaining to crested wheatgrass will be covered here.

Drought

Aridity or dryness is a common feature of many rangeland areas and is a term referring to a more or less permanent climatic condition characterized by a lack of water (Wallen and Gwynne 1978). Meteorological drought, which also is characterized by a lack of water, is a phenomenon of limited duration that may occur in any climatic zone, caused by anomalies in the normal circulation conditions of the atmosphere that create a lack of precipitation (Wallen and Gwynne 1978). Consequently, when meteorological drought occurs on already relatively arid rangeland, this extreme lack of water can be particularly limiting to plant growth. Although lack of water severely curtails mature plant growth, it is particularly detrimental during seedling development. How well seedlings respond to a lack of water often determines the success or failure of revegetation efforts. Consequently, the effects of lack of water on the germination, emergence, and seedling phases in crested wheatgrass deserve particular emphasis.

Although the total amount of precipitation received is an indicator of the relative aridity of an environment, the timing or seasonal distribution of the precipitation also is important. Other environmental factors such as temperature also must be considered in evaluating the aridity of a particular area. For example, a given amount of precipitation received during active growth in the spring is much more effective in terms of cool season grass production than a similar amount received during the summer, when evaporative water loss is high and cool season grass activity is minimal. Similarly, soil type and other site characteristics can contribute to the effectiveness

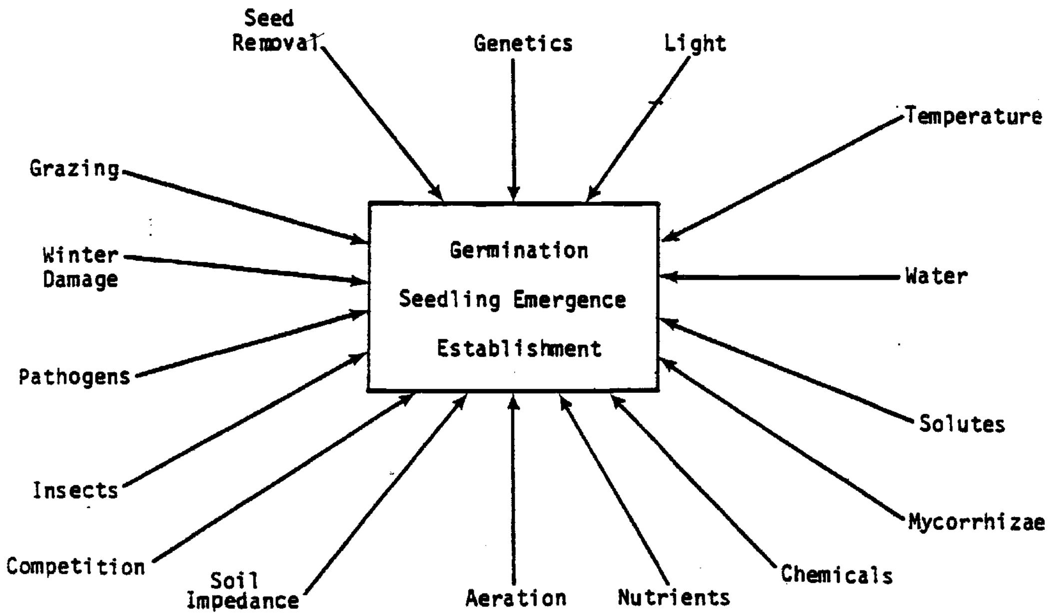

Figure 4.--Environmental factors known to affect germination, emergence, and establishment.

of a given amount of precipitation. All such factors directly influence the intensity and duration of the water deficit, which in turn determines their effects on range plant establishment and survival. The interaction between precipitation and temperature as it relates to seeding rangeland environments was specifically examined by Jordan (1983). He used empirical relationships between temperature and seasonally adjusted precipitation to predict the potential for successful seeding on water-limited rangelands.

The influence of the lack of water on seed germination has been reviewed in general by Heydecker (1977), Hegarty (1978), and Hillel (1972). In addition, Wright (1971), Young et al. (1983), and McDonough (1977) cover this topic area as it relates to rangeland species.

As with most species, germination of crested wheatgrass seed is negatively affected by increasing drought levels in: 1) a reduction in total germination and 2) an increase in the amount of time required for germination (McGinnies 1960). Agropyron desertorum did not exhibit any unique capability in terms of germination under drought imposed by mannitol solutions compared with five other range grasses (McGinnies 1960). Young et al. (1968), using polyethylene glycol to impose various stress levels, showed that percentage germination of A. desertorum, A. cristatum, and A. sibiricum was near average for levels between 0 and -0.8 MPa and better than the average at -1.2 MPa when compared with 16 range species. Johnson and Asay (1978), using a technique that allowed examination of germination response to only matric potential, showed that drought reduced germination of 120 crested wheatgrass progenies to about the same level as reported by McGinnies (1960) and Young et al. (1968). McDonough (1975) made water potential determinations during germination for 11 species of forbs and grasses (including A. cristatum). The effects of low water potentials on specific biochemical processes in germinating seeds of crested wheatgrass have been examined by Wilson (1970, 1971), Wilson and Harris (1966, 1968),and Wilson et al. (1970).

In rangeland plantings seeds of crested wheatgrass can be subjected to alternate cycles of wetting and drying during germination and subsequent seedling growth. The influence of such cycles on the germination of A. desertorum seed was evaluated by Maynard and Gates (1963). Despite large variations, some of the effects they reported were: 1) seeds of crested wheatgrass can tolerate extreme moisture fluctuations, remain viable, and produce vigorous seedlings; 2) when allowed to develop a 2 mm long radicle and then dried for one to four weeks, some seeds still were capable of developing into vigorous seedlings after water subsequently was applied; 3) severe and prolonged wetting-drying treatments reduced vigor of germinating seeds; and 4) in some cases various wetting and drying treatments actually increased seed germination. These trends were corroborated by Wilson (1973). His study indicated that during the interval from planting to germination, several weeks at low water potentials did not seriously injure crested wheatgrass seeds. During exposure to drought, seeds retained much of the advantage they had gained during periods of favorable moisture. After moisture became available again, seeds of crested wheatgrass were able to resume metabolic activity and make rapid gains in hastening of germination.

Hassanyar and Wilson (1979) examined germinating seeds of A. desertorum for tolerance to desiccation at 2 (early), 4 (intermediate), and 6 (advanced) days after the seed had been exposed to favorable germination conditions. After reaching these three stages of germination, seeds were dried in atmospheres ranging in water potential from -10 to -91 MPa. After exposure to these conditions for four days, treated and untreated seeds were placed in a germination or growth test conducted under favorable moisture conditions to evaluate the effects of the temporary drought stress. Seeds were more susceptible to injury in the intermediate and advanced stages of germination than in the early stage. Drought stress delayed and inhibited root growth more than shoot growth.

Hassanyar and Wilson (1978) conducted a similar study that specifically examined the effect of a temporary drought on the development of seminal lateral roots in seedlings of A. desertorum and Russian wildrye at the advanced stage of germination. Their results showed that capacity for seminal lateral root development decreased as severity of the drought treatment increased. However, this capacity was much greater in crested wheatgrass than Russian wildrye, apparently because of differences in the species' latent potentials for growth and in the drought tolerance of their seminal lateral root apices. Hassanyar and Wilson (1978) suggested that capacity for seminal lateral root development after exposure to drought also may be an important selection characteristic allowing more successful seedling establishment under water-limiting conditions. However, genetic variability in crested wheatgrass for this particular seedling characteristic has not been evaluated.

Schultz and Hayes (1938) used a chamber to impose heat and atmospheric drought treatments on 22 forage species for 10 to 26 hour periods. For both 30- and 60-day-old seedlings, "forage" crested wheatgrass (presumably A. desertorum) exhibited less injury than nearly all of the other forages tested. Using six week old A. desertorum plants, Ruf et al. (1963) examined osmotic adjustment of cell sap in response to increases in root medium osmotic stress imposed by various concentrations of Carbowax 1540. As osmotic stress in the root medium increased, total dry matter decreased, with shoot growth being reduced more than root growth. Osmotic potential of the cell sap increased about 0.09 MPa for each 0.1 MPa increase in osmotic potential of the root medium. Even at the greatest stress level (-1.1 MPa), crested wheatgrass did not exhibit any visible signs of wilting.

Seedling response of crested wheatgrass to longer, more gradually developed drought was examined by McAlister (1944). He placed 6- to 8-week old seedlings in a drought chamber and imposed the treatment for 6 to 9 days. After termination of the drought period, plants were allowed to recover under favorable growing conditions and were rated for their recovery. Tests with nine strains of A. cristatum showed wide variability in seedling response to drought and indicated that this procedure might be suitable for selecting seedlings for drought resistance. A similar technique was used by Asay and Johnson (1983b) for examining seedling recovery after drought in 42 breeding lines of crested wheatgrass. Their results showed that significant genetic variation existed for this characteristic and that sufficient variability was present to allow for genetic gain from selection.

Another characteristic related to seedling establishment under drought is seeding depth. Generally, the deeper a seed can be planted in the soil, the less that seed is exposed to the widely fluctuating moisture conditions present at or near the soil surface. However, deep planting of small-seeded forage species such as crested wheatgrass can lead to establishment failures caused by exhaustion of seed reserves during coleoptile penetration through the soil. One way of overcoming this problem is to use cultivars that can emerge from deepar seed placements.

Rogler (1954) examined the effects of various planting depths and seed weights on seedling emergence of crested wheatgrass. He found a highly significant positive correlation between seed weight and ability to emerge from deeper planting depths. Seed weight in crested wheatgrass was also positively associated with forage yields (Schaaf et al. 1962). Specific relationships between seed yield and seed weight in crested wheatgrass have been examined by Dewey and Lu (1959) and Schaaf and Rogler (1963). Recent field studies by Asay and Johnson (1983a) demonstrated a close correlation between seed weight and important seedling establishment parameters. Consequently, breeding and selection for higher seed weight of crested wheatgrass appears promising. Reviews by Asay and Johnson (1983a), Johnson (1980), and Johnson et al. (1981) discuss other aspects of genetic improvement for increased seedling drought resistance.

Temperature

Because of its critical influence in determining metabolic activity, temperature is one of the most important environmental parameters affecting germination and seedling emergence. On sagebrush rangelands, where crested wheatgrass is the most important seeded species, moisture and temperature conditions for germination and seedling growth are largely out of phase (Young and Evans 1982). Generally, in early winter or late spring when moisture availability is greatest, temperatures are too low for optimum germination and growth. Conversely, in early summer when temperatures are optimum for germination and seedling growth, water may not be available long enough to ensure seedling establishment. Rapid germination at low temperatures may be particularly important for the survival of crested wheatgrass seedlings when exposed to drought or competition (Wilson et al. 1974).

Young and Evans (1982) comprehensively examined the influence of 55 constant and alternating temperatures on the germination of a number of cool-season range grasses, including eight seedlots within the crested wheatgrass complex. They compared the temperature profiles for germination of the cool-season range grasses with that of cheatgrass, a weedy annual grass that is a major competitor on many sagebrush rangelands (Klemmedson and Smith 1964). Their results showed that cheatgrass germinated better at cooler seedbed temperatures than did any of the other species examined. Among the major revegetation grasses, the crested wheatgrass group exhibited the highest germination at low seedbed temperatures. These results agree with those of Wilson et al. (1974), who found that after exposure to winter conditions, crested wheatgrass did not germinate as rapidly at 10°C as cheatgrass or medusahead [Taeniatherum asperum (Simonkai) Nevski] but did germinate more quickly than bluebunch wheatgrass [Agropyron spicatum (Pursh) Scribn. & Sm.] or smooth brome. The same patterns apparently carried through to the seedling stage, as reported by Harris and Wilson (1970). After six weeks, average depth of root penetration into soil for the following species was (in order of decreasing penetration): cheatgrass, medusahead, crested wheatgrass, and bluebunch wheatgrass.

Ellern and Tadmor (1966) found that temperatures of 4 to 10°C delayed germination of crested wheatgrass. This delay in germination probably is due to an effect of temperature on imbibition processes involving the physical absorption of water by the seed. This is supported by Keller and Bleak (1970) who reported that water absorption of crested wheatgrass seeds was directly proportional to temperature over a range of 4.5 to 27.8°C. Because crested wheatgrass evolved in the cold steppe regions of East and Central Asia, it is not surprising that its seed is well adapted to cold conditions. This is supported further by Wilson (1973) who found that seeds of crested wheatgrass were not injured after one month in frozen soil. He also reported that subsequent germination was hastened after exposing seeds to favorable moisture conditions at 2°C.

Optimum germination of crested wheatgrass occurs between 15 to 25°C, depending upon the particular combination of constant and alternating conditions (Young and Evans 1982). McGinnies (1960) germinated seeds under different levels of moisture stress at 10, 20, and 30°C. Average germination was greatest at 20°C, although to some extent crested wheatgrass showed a wide tolerance to different temperatures. Hay (1936) reported that for the first few months after harvest, temperatures below 20°C were necessary for part of the germination period. With longer storage this need for a cold period became less marked. He obtained successful germination at temperatures of 14 to 17°C or with a six-day prechilling at 8 to 10°C followed by temperatures of 20 to 22°C. Ellern and Tadmor (1967) reported that germination behavior at alternating high and low temperatures was similar to that at fixed temperatures, and that alternating temperatures did not stimulate germination.

Ellern and Tadmor (1966) found that Nordan crested wheatgrass germinated better than Fairway in the 4 to 10°C range, especially at 4°C. Conversely, Young and Evans (1982) reported that Nordan exhibited lower mean germination over a range of temperatures than did either Fairway or Standard crested wheatgrass. However, considerable variability existed among seedlots of both Fairway and Standard. Consequently, without a broader sampling of seedlots within each of the crested wheatgrass types, these purported germination differences could be due to seed quality differences among seedlots rather than to a genetically fixed characteristic.

Rogler (1943) studied low temperature resistance in seedlings of various warm-season and cool-season species, including both Standard and Fairway varieties of crested wheatgrass. Seedlings of 41 to 72 days old were exposed to freezing temperatures for 6 to 22 hours. After a nine-day recovery period, seedling survival was evaluated. Seedlings of cool-season grasses survived better than those of the warm-season species. Crested wheatgrass seedlings survived better than seedlings of either western wheatgrass (Agropyron smithii Rydb.) or smooth brome under all freezing treatments.

Light

Light is a requirement for germination of some species, while others germinate only in the dark (Koller 1972, Mayer and Poljakoff-Mayber 1982). Not only is light quantity important for light-sensitive species, but also the quality and the periodicity of the light received (Smith 1973). However, light apparently is not a requisite for germination of crested wheatgrass. For example, in the manual entitled "Rules for Testing Seeds" published by the Association of Official Seed Analysts (AOSA 1981), light is optional for testing the germination of crested wheatgrass seed. This implies that crested wheatgrass has no specific light requirement for maximum germination.

Competition

Spatial or temporal competition (or interference) for various plant requirements such as water, light, or nutrients (Evans and Young 1972) can markedly affect seedling establishment of crested wheatgrass. A large body of literature deals with competition for plant resources between crested wheatgrass and various other species. A sampling of this literature for four major plant competitors on western U.S. rangelands is contained in Table 1. Because of the numerous publications concerning competition and the general review of this subject area by Keller (1979), the competition literature pertaining to crested wheatgrass establishment will not be reviewed here. Instead, only the general principles governing the competitive species cheatgrass will be outlined; the same principles should be applicable for other species as well.

Cheatgrass is an introduced winter annual that usually germinates in the fall or winter and produces seed in a relatively short burst of activity in the spring. Mature plants then die and the generation is carried through the summer in the seed stage. For a detailed description of the life history and ecology of cheatgrass see Stewart and Hull (1949) and Klemmedson and Smith (1964).

Keller (1979) indicated that seed production was a major factor in the competitiveness of cheatgrass. Citing data from Stewart and Hull (1949), cheatgrass seed densities on two sites in southwestern Idaho averaged 1,646 seeds/ft^2 (17,717 seeds/m^2). In addition, cheatgrass seeds exhibit high viability after maturity and germinate rapidly and completely within just a few days (Klemmedson and Smith 1964). The rapid emergence and aggressiveness of cheatgrass seedlings were demonstrated by Hull (1964). He compared the emergence of cheatgrass with three wheatgrasses at four seeding depths varying from a surface planting to a 5 cm depth. Cheatgrass seedlings exhibited the most rapid emergence and greatest total emergence of any species at all depths.

Cheatgrass also exhibits remarkable traits during seedling development. For example, Harris (1977) documented rapid development of large numbers

Table 1. Some major plant competitors of crested wheatgrass on western U.S. rangeland with associated literature references.

Competitor	References
Artemisia spp. (Sagebrush, etc.)	Bartolome & Heady (1978)
	Blaisdell (1949)
	Bleak & Miller (1955)
	Bleak & Plummer (1954)
	Brunner (1972)
	Campbell & Harris (1977)
	Cline et al. (1977)
	Cook (1958, 1966)
	Cook & Lewis (1963)
	Cook et al. (1967)
	Daubenmire (1975)
	Fenley (1953)
	Fernandez & Caldwell (1975)
	Frischknecht (1963)
	Frischknecht & Bleak (1957)
	Gifford (1972)
	Gifford & Busby (1974)
	Hull (1941, 1949a)
	Hull & Klomp (1966, 1974)
	Johnson & Payne (1968)
	Pechanec et al. (1954, 1965)
	Rawls et al. (1973)
	Rickard (1967)
	Rittenhouse & Sneva (1976)
	Robertson (1943, 1947)
	Robertson & Pearse (1946)
	Robertson et al. (1966, 1970)
	Shown et al. (1969)
	Stoddart (1946)
	Sturges (1973, 1975, 1977, 1979, 1980)
	Tabler (1964)
	Weldon et al. (1958)
Halogeton glomeratus (Bieb.) C.A. Mey (halogeton)	Bleak & Plummer (1954)
	Cook (1965)
	Cook & Stoddart (1953)
	Cronin & Williams (1966)
	Dayton (1951)
	Frischknecht (1968)
	Haas et al. (1962)
	Hull & Holmgren (1964)
	Robocker (1966)
	Stoddart et al. (1951)
	Tisdale & Zappetini (1953)
Bromus tectorum L. (cheatgrass, downy brome)	Beetle (1954)
	Cline et al. (1977)
	Evans (1961)
	Evans & Young (1977)
	Evans et al. (1967, 1969, 1970)
	Hafenrichter et al. (1968)
	Harris (1967, 1977)
	Harris and Goebel (1976)
	Harris and Wilson (1970)
	Hironaka and Tisdale (1963)
	Hull (1940, 1949b, 1963a, 1964)
	Hull & Hansen (1974)
	Hull & Stewart (1948)
	Klemmedson & Smith (1964)
	Klomp & Hull (1972)
	Piemeisel (1938, 1951)
	Robertson & Pearse (1946)
	Rummel (1946)
	Stewart & Hull (1949)
Taeniatherum asperum (Simonkai) Nevski (Medusahead)	Harris (1977)
	Harris & Goebel (1976)
	Harris & Wilson (1970)
	Lusk et al. (1961)
	Sharp et al. (1957)
	Turner et al. (1963)
	Wilson et al. (1974)
	Young & Evans (1970, 1971 1972)
	Young et al. (1969)

of long primary and adventitious roots. Evans (1961) reported that 15 weeks after germination, cheatgrass developed an extensively branched root system with many finely branched roots. In comparison, the root system of crested wheatgrass was less branched and contained generally coarser roots than cheatgrass. Similar differences were observed by Hull (1963a).

Harris and Wilson (1970) examined root penetration at low temperatures by seedlings of various annual and perennial grasses. Roots of cheatgrass rapidly penetrated to 90 cm and had an even root distribution throughout the entire soil profile. Root penetration and total root mass were somewhat less for Agropyron desertorum than cheatgrass. However, both of these species exhibited considerably faster root development and markedly greater root mass than bluebunch wheatgrass. This ability of cheatgrass to produce considerable root mass was documented on a field site in southcentral Washington by Cline et al. (1977). They examined root mass throughout the soil profile to a depth of 1.6 m for cheatgrass and reported weights of over 450 g/m^2 for the 0 to 10 cm increment. This particular soil layer is extremely important because seed is sown in this layer, and early seedling development hinges on water extraction from this zone.

Cheatgrass densities have been shown to directly affect the growth and survival of crested wheatgrass during germination, emergence, and seedling growth in the greenhouse. For example, Evans (1961) reported that cheatgrass densities of 64 and 256 $plants/ft^2$ (689 and 2,756 $plants/m^2$, respectively) severely curtailed seedling shoot and root growth and greatly increased seedling mortality of Agropyron desertorum. Even cheatgrass densities of 4 and 16 $plants/ft^2$ (43 and 172 $plants/m^2$, respectively) affected seedling growth and survival of crested wheatgrass. A similar pattern of reduced seedling shoot and root growth with increasing cheatgrass densities was also reported by Hull (1963a).

Evans (1961) suggested that two phases of competition occurred at high cheatgrass densities. In the first phase, cheatgrass formed a relatively closed community that purportedly reduced light for crested wheatgrass seedlings. With lower densities this shade factor apparently became effective at a progressively later time, determined by shoot growth for a particular density. The second phase of competitive influence occurred when seedling growth of crested wheatgrass ceased because of soil water depletion. Soil moisture was depleted slowly when crested wheatgrass was grown alone. However, it was depleted much more rapidly at increasing cheatgrass densities.

Consequently, characteristics for cheatgrass that make it a strong competitor with seedlings of crested wheatgrass include: 1) high seed production, resulting in extremely large resident seed banks, 2) highly viable seed that exhibits rapid germination and aggressive emergence capabilities, and 3) rapid root penetration into the soil and extensive root system development. Although these characteristics specifically relate to cheatgrass, various combinations of these factors undoubtedly contribute to the success of other species competing with seedlings of crested wheatgrass.

Soil Characteristics

Soil recommendations for crested wheatgrass seedings usually have been very general. For example, Reynolds and Springfield (1953) recommended that best growth of crested wheatgrass was achieved "on soils that allow rainfall to penetrate, and that have good water-holding capacity, such as those having a heavy-loam texture and good drainage." However, studies such as those by Eckert et al. (1961) have more precisely defined specific soil characteristics that affect seedling establishment of crested wheatgrass. Studying three sagebrush sites in eastern Nevada, they suggested that indicator species and general soil classifications could be used to determine site potentials for the establishment of crested wheatgrass.

Shown et al. (1969) examined the seeding results for crested wheatgrass on 48 study sites across the western United States. Their analysis indicated that success or failure of crested wheatgrass to establish was a complex interaction of climate, soil, treatment methods, and grazing management. Generally, the taller and denser the big sagebrush, the greater the potential for crested wheatgrass establishment. Of the specific soil properties evaluated in their analysis, moisture-holding capacity was the single most important factor. Cluff et al. (1983) examined edaphic factors of four major soil types in a Wyoming big sagebrush (Artemisia tridentata ssp. wyomingensis) grassland community in Nevada and related them to establishment of A. desertorum. Of all the edaphic factors examined, soil texture was best correlated with seedling establishment. They demonstrated that mathematical models based on quantified soil data could allow accurate predictions of site suitability for brush control and subsequent crested wheatgrass establishment.

For a seedling to become successfully established, it must not only germinate, but also penetrate and emerge through the upper soil layer. Mechanical impedance of this upper soil layer can be a barrier to successful seedling emergence and therefore can lead to seedling failure. Rao and Bhardwaj (1976) reviewed the literature concerning soil crusting and stated that the extent of crusting varies with the structural and textural characteristics of the soil. Crusts of varying strength form on soils of almost any textural condition except on coarse sands that have extremely low silt and clay contents. They also reported that soils containing large amounts of fine sand or silt promote crusting. Lateritic, calcareous, and saline soils form crusts most readily. In addition, the amount, intensity, and duration of rainfall, as well as the rate of drying, organic matter content, and soil moisture content both at the beginning of the rainfall event and at the time of crust-breaking, all influence crust strength.

Several studies have demonstrated that soil crusting inhibits seedling emergence. For example, Taylor et al. (1966), working in the laboratory with six plant species, measured soil strength using a penetrometer and found that emergence of Gramineae seedlings decreased slightly at strengths of 6 to 9 bars. As soil strengths further increased, emergence decreased to zero above the range of 12 to 18 bars (1.2 to 1.8 MPa) strength. Stout et al. (1961), working in the laboratory with a different soil and three row crop species, prepared seedbeds that were compacted differentially at the surface and seed level. Pressures above 0.5 psi (3,450 Pa) at the surface usually suppressed seedling emergence, whereas pressures of 5 to 10 psi (34,500 to 69,000 Pa) at seed level improved emergence. Hyder and Sneva (1956) also found that a firm seedbed improved seedling emergence and growth, while heavy rolling above the seed mechanically restricted emergence.

Frishknecht (1951) reported that soil crusting on a sagebrush site in central Utah greatly limited the emergence of 14 grasses (including crested wheatgrass) from a late-fall planting. This soil crust formed soon after snowmelt in the spring and became about 5 cm thick in places. Seedlings that emerged were limited mainly to cracks in the crust. Early emerging species were less affected than later emergers. Apparently puddling occurred on the surface during snowmelt because of slow water infiltration into the frozen subsoil. Subsequent rapid drying aided in forming the soil crust. Emergence of crested wheatgrass species was less affected than that of most other species. Wood et al. (1982), also working on rangelands of the Intermountain West, reported that crusting occurred more readily in big sagebrush interspaces than underneath big sagebrush plants. They suggested that generally a dense stand of large sagebrush indicates a site with texture, structure, and moisture holding characteristics of the soil favorable for seedling emergence and establishment. Their work also showed that crested wheatgrass emerged better than squirreltail [Sitanion hystrix (Nutt.) J. G. Sm.] or fourwing saltbush [Atriplex canescens (Pursh) Nutt.] in crusted soils.

Salinity

Salinity is a soil factor affecting germination and seedling emergence of crested wheatgrass which deserves special emphasis. High salt content is characteristic of many arid and semiarid rangelands, and leaching of these accumulated salts from the upper soil layers is limited due to low precipitation (Poljakoff-Mayber and Gale 1975). As desert soils dry in the spring, salt is carried upward which, combined with the decrease in soil water potential, produces a harsh environment for mature plant growth and particularly so for seed germination (Roundy 1984, Roundy et al. 1984). A general discussion of salinity stress and its effects on specific plant processes is contained in Levitt (1980), and a comprehensive bibliography on the subject has been assembled by Francois and Maas (1978).

Salinity adversely affects germination by 1) decreasing the ease of water uptake and thereby reducing the rate of water entry into the seed, and 2) facilitating the intake of ions in sufficient quantities to be toxic (Ayers and Hayward 1948). These physio-chemical effects upon the seed result both in a slower rate of emergence as well as a lowered percentage of seeds which germinate. Under field conditions a slow rate of germination could be accompanied by an appreciable drying of the soil, thereby accentuating the stress upon the seedling.

For many agronomically important species, resistance to salinity is often expressed as reduction of commercial crop yield, based on performance of the mature plant. Salinity resistance at the seedling stage is not considered particularly important in intensively managed crop species because field cultural practices to ameliorate the effects of salinity can be employed at the seedling stage. On rangelands, where such intensive management is not feasible, resistance to salinity at the seedling stage is an important characteristic (McElgunn and Lawrence 1973). In addition, because plant performance at later phenological stages critically hinges on successful germination and seedling establishment, salinity resistance at both the seedling and mature plant stages should be considered when evaluating plant growth on saline rangelands.

On the basis of mature plant yields, Maas and Hoffman (1977) reviewed the salt resistance of a number of forage and crop species. In general, they found that yields did not decrease until a threshold salinity level was reached. Agropyron cristatum was considered salt resistant with a threshold conductivity of 7.5 mmho/cm, whereas A. desertorum had moderate salinity resistance with a threshold value of 3.5 mmho/cm. Dewey (1960) examined vegetative yields of various species of Agropyron including one strain of A. cristatum and three strains of A. desertorum. The A. cristatum strain gave greater yields than the average of the three strains of A. desertorum.

That salinity limits seedling establishment of crested wheatgrass in rangeland soils has been documented in a number of studies. For example, Hull (1962) used shadscale soils from northern Utah in greenhouse studies which showed that no crested wheatgrass plants emerged and that all transplants died in soils taken below depths of 15.3 cm, even when amendments were added to the soil. He attributed these results to salinity and sodium toxicities in the shadscale soils. Hull (1963b) seeded 14 species on 18 salt-desert shrub areas in Wyoming and noted poor stands due to a combination of aridity, salinity, and alkalinity of the soils. A. desertorum and Russian wildrye did the best of the species examined. Haas et al. (1962) examined the establishment of crested wheatgrass in the field in artificially salinized soils in Idaho. During the establishment years, more than twice as many crested wheatgrass plants were present on the non-saline plots as on the high salinity plots. Ludwig and McGinnies (1978), working in a saltgrass [Distichlis stricta (Torr.) Rydb.] meadow in Colorado, reported that A. desertorum with its combined high seedling vigor and good drought tolerance, produced significantly better stands than three other forage species. However, in greenhouse tests using the same Natrustoll soils, A. desertorum failed to establish in C horizon soils because of their saline-alkali nature (McGinnies and Ludwig 1978).

Other studies in the greenhouse and laboratory also have shown the effects of salinity on germination, emergence, and seedling establishment. Dewey (1962b) observed that germination percentage decreased and germination time increased with increasing salinity for four strains of A. desertorum. Forsberg (1953) examined the response of various forage crops to saline soils in the greenhouse. He reported that vigor of seedlings at seven weeks after seeding was greater for A. cristatum than for A. desertorum. Of the species examined in his study, A. desertorum exhibited near-average seedling response to salinity, while A. cristatum was below average. However, species rankings varied with the particular test and length of evaluation. In a greenhouse study of relative seedling survival under four salinity levels conducted by Hughes et al. (1975), A. cristatum ranked about average in comparison to five other grasses being examined. Dewey (1960) examined germination in salinized soil of 25 strains of Agropyron representing 14 species and found that average germination over three salinity levels was better for the three strains of A. desertorum than the one strain of A. cristatum tested. Additionally, results for another species of crested wheatgrass, A. sibiricum, showed that one strain exhibited the second best average germination of all strains tested. Species averages indicated that A. sibiricum and A. desertorum germinated better than tall wheatgrass [A. elongatum (Host) Beauv.], a species highly regarded for its salt resistance.

Dewey (1962b) showed that sufficient genetic variation existed among strains of A. desertorum to permit effective selection for improved germinability under saline conditions. His work showed that progenies previously selected under conditions of high salinity produced seed that germinated better under high salinity than did seed from progenies selected under nonsaline conditions. Work by Dewey (1962a) further evaluated the breeding potential of A. desertorum for response to effects of salinity on both germination and vegetative growth. His work with 60 clones of A. desertorum showed that selection on the basis of germination under salinity in the laboratory was not in itself a promising method for improving salt resistance in subsequent growth stages. Instead, Dewey (1962a) recommended a plant selection approach utilizing germination tests as well as field evaluations of vegetative growth in salinized soil basins.

Grazing

The general recommendation and practice after seeding rangelands is to protect the seeded stand from grazing (Vallentine et al. 1963, Reynolds and Martin 1968, Blaisdell et al. 1982, Laycock 1982). Typically, grazing is not recommended until after the second full growing season following seeding. For difficult sites or during particularly dry years, it is generally recommended that this grazing restriction should be extended an additional year or more. This nonuse period supposedly allows the seeded plants to become firmly rooted so that uprooting by grazing is minimized. In addition, this protection purportedly enhances plant "vigor" and allows for increased seed production by the seeded species.

However, when grazing is deferred, operating costs involved in feeding livestock will increase the longer grazing is restricted in newly seeded areas. The cost to purchase or lease additional forage during this period and to provide transportation to and from these leased areas must be considered in economically analyzing the rate of return from seeding projects (Nielsen 1977). If attempts are made to carry the livestock on existing ranch land and overgrazing results in a permanent reduction in forage production, nonuse costs could be extremely high. Consequently, from an economic viewpoint it would be advantageous to minimize the deferred grazing period for newly established seedings.

Only a few studies are available that quantitatively document the effects of grazing on newly seeded crested wheatgrass stands. Hull (1944) reported work conducted on newly established crested wheatgrass seedings in southern Idaho, which compared herbage yields, average height, and number of plants in grazed versus protected areas of the seeding. Protected plants produced more herbage and were taller than grazed plants, but total numbers of plants were equal in the two areas. Factors that apparently favored plant establishment in spite of grazing were: 1) level topography with a firm surface that was seldom cut up under trampling, 2) above-average precipitation during the year of establishment, 3) seed depth of approximately 1.3 cm so that seedlings were less susceptible to uprooting or trampling by grazing, and 4) opportunity for seedlings to grow and recover after defoliation. Based upon results from these studies and field observations from stockmen throughout southern Idaho, Hull (1944) suggested that fully established stands of crested wheatgrass can be achieved, even under grazing during seedling establishment. However, he cautioned that vigor of grazed plants may be low.

Further experimentation on grazing seeded range during the first year of establishment was not published until nearly 30 years later. McGinnies (1973), working in northern Colorado, clipped crested wheatgrass seedlings to a 1.3 cm stubble height and to ground level, and compared survival of these to unclipped seedlings. His results showed that crested wheatgrass seedlings can withstand clipping to 1.3 cm with little or no seedling mortality. However, seedlings clipped to ground level were killed depending on the individual year and date of clipping. Apparently the severity of defoliation can markedly affect seedling mortality. McGinnies (1973) cautioned against extrapolating clipping results to actual grazing responses because of 1) soil disturbance commonly associated with grazing and 2) uprooting of seedlings by grazing animals. As a result, the effect of grazing on the seedling establishment of crested wheatgrass awaits further experimentation.

Insects

Another form of grazing that directly affects plant growth and productivity is insect herbivory. An annotated checklist of grass feeding insects for rangelands in Arizona, New Mexico, Nevada, Colorado, and Utah has been prepared by Thomas and Werner (1981). It probably is applicable to other western rangelands as well. Overviews of rangeland entomology are contained in Hewitt et al. (1974) and Watts et al. (1982). A general introduction to rangeland insects of western U.S. was prepared by Haws (1982).

Hewitt and Burleson (1975) surveyed two crested wheatgrass pastures in central Montana and on the basis of abundance and aboveground biomass reported that important groups of arthropods included grasshoppers (Subfamily: Acrididae), ants (Formicinae), leafhoppers (Cicadellidae), thrips (Thysanoptera), and mites (Acarina). They reported that ants probably have a minimum effect on the growth of crested wheatgrass, but that any of the other four groups could drastically affect either forage production or seed yield. Similarly, Tingey et al. (1972), working in a sagebrush-grass community in westcentral Utah, indicated that of the four plant species studied, crested wheatgrass had the most diverse fauna with 12 potentially damaging thrips species. They suggested that thrips may decrease plant grazing potential by limiting seed production required for natural reseeding.

Hewitt (1977) and Capinera and Sechrist (1982) reviewed forage losses caused by rangeland grasshoppers. Losses were documented for crested wheatgrass in Idaho, Wyoming, Colorado, and North Dakota. Although larvae of the bluegrass billbug damaged a number of bunchgrass species in field studies in Montana, both A. cristatum and A. desertorum exhibited a relatively high degree of resistance to the insect (Asay et al. 1983). Forage losses have been reported for black grass bugs [Labops hesperius Uhler and Irbisia pacifica Uhler] for established stands of crested wheatgrass (Bohning and Currier 1967, Hewitt 1980, Ansley and McKell 1982). Infestations of black grass bugs cause irregular yellow or white spots on the grass leaves (Dickerson 1978), presumably due to feeding removal of cellular contents (Haws 1978). They also have been reported to generally reduce plant vigor and adversely affect leaf length, seedhead height, as well as root and crown carbohydrate reserves (Ansley and McKell 1982). They tend to accelerate phenological development and lead to increased auxillary tillering (Hewitt 1980). Studies concerning management practices and control measures for black grass bugs in stands of crested wheatgrass have been reported by Todd and Kamm (1974), Kamm and Fuxa (1977), Dickerson (1978), and Hagen (1982). Recent work with 16 grasses including crested wheatgrass indicates that variation in feeding preference of black grass bugs may allow selection of germplasm with resistance to black grass bug feeding (J. D. Hansen, unpublished data). However, most of the research on the influence of insects on crested wheatgrass to date has been done with mature plants.

Hansen et al. (1984) evaluated feeding damage to seedlings of five range grasses in greenhouse experiments using two species of caged black grass bugs. Except for the smallest plants, the rate of insect attack decreased with increasing leaf size. Seedlings of crested wheatgrass and its closely related hybrids were more susceptible to bug damage than the other range grasses. However, resistant individual seedlings were identified within each grass population. Clones of crested wheatgrass selected as individual seedlings maintained their resistance in subsequent feeding trials. These results indicated that sufficient genetic variation was present within crested wheatgrass germplasm to breed plant materials that would resist black grass bug damage at the seedling stage.

It should also be mentioned that increasing the diversity of plant species within a seeding may reduce the likelihood of infestations of damaging insects compared to monoculture stands of crested wheatgrass. Literature reviewed by Bach (1980) indicated that simple plant communities have greater population densities, colonization rates, and reproduction than more diverse plant communities. Bach (1980) reviewed possible reasons for this including 1) difficulty of specialist insect herbivores to locate their host plants in diverse habitats, and 2) greater numbers and effectiveness of insect predators and parasitoids in diverse habitats as compared to simple, less diverse communities of plants. Consequently, inclusion of additional plant species into seedings of crested wheatgrass may aid in minimizing severe infestations of damaging insects.

Pathogens

Parasitism by plant pathogens undoubtedly contributes to poor seedling establishment and seedling mortality in some rangeland seedings. Buchholtz (1949) isolated various fungal pathogens from crested wheatgrass seedlings grown in the field, including species of Pythium, Helminthosporium, and Fusarium. He indicated that Pythium gramnicola was the primary causal agent for seedling blight in crested wheatgrass and that Pythium debaryanum was the principal cause of seed rotting. According to Andrews (1943) and Buchholtz (1949), Helminthosporium sativum also may be a factor in both seed rotting and blighting of crested wheatgrass seedlings. The pathogenecity of H. sativum on crested wheatgrass probably is expected because of its common association with numerous grass genera, its world-wide distribution in the temperate zone, and its extensive presence in arid and semiarid areas of the western United States (Sprague 1950). The influence of various Fusarium fungal species on stands of crested wheatgrass seedlings was reported by Slykhuis (1947). Fusarium isolates caused wilting and death of crested wheatgrass seedlings, and frequently produced a brownish discoloration of seedling stem bases.

Other studies by Bleak and Keller (1973) indicated that crested wheatgrass exhibited a certain amount of susceptibility to snow mold. They measured the mortality of one-year-old plants caused by snow mold under prolonged spring snow cover. Large variability existed among Fairway crested wheatgrass accessions with mortality ranging from 2.7 to 29.4%. Nordan averaged 4.9% mortality, while five other sources of crested wheatgrass had less mortality than Nordan.

A soil-borne pathogen (Podosporiella verticillata) was reported by Kreitlow and Bleak (1964) to infect 10 Gramineae species including crested wheatgrass. This pathogen reduced seed emergence and vigor. Field observations suggested that incidence of infection varied with location and season. Most infection occurred at lower elevations on sagebrush sites, while none occurred on aspen-fir sites. Percentage of seed infection decreased with later fall planting. In comparison with the 10 other species, crested wheatgrass was moderately infected by this soil-borne fungus.

Fischer (1939) reported that crested wheatgrass was susceptible to wheat bunt, primarily a seed-borne pathogen, but that its susceptibility depended on both the species and race of fungus. Tilletia levis was 35% more virulent than T. tritici. Within both species some races were several times as virulent as others. Average percent infection of A. cristatum by T. levis was 24 to 32%. None of the selections were completely immune to T. levis, although a few were highly resistant. One selection appeared immune to T. tritici. The mycelium of the fungus was perennial but not indefinitely so. Of 90 plants showing smut in 1935, 39 were free of infection, 2 died, and 44 retained the disease in 1937.

Winter Damage

Winter damage is an environmental factor which is probably a combination of other environmental factors such as temperature, pathogens, or soil impedance. Nevertheless, because of the potential importance that winter damage can have in determining successful stand establishment in crested wheatgrass, it will be examined as a separate environmental factor.

The ability of crested wheatgrass seedlings to withstand winter damage apparently is related directly to their stage of development or size going into the winter period. White and Horner (1943) found that only 18.7% of the unemerged seedlings of crested wheatgrass survived the winter, whereas 93.7% of the plants with three or more leaves survived. White and Currie (1980) also found that as plant size increased, injury decreased. This relationship was most easily quantified by counting the number of leaves, although plant height, seedling weight, and plant leaf area were all inversely related to winter injury. In their study only slight damage occurred over winter when seedlings had three or more leaves. Winter damage increased with later planting dates due to reduced growth before the onset of winter. Winter severity apparently has little effect on the survival of plants in the more advanced stages of seedling development (White and Horner 1943).

Frishknecht (1951) seeded 14 species of range grasses in early fall and followed their emergence and survival or mortality at regular intervals. Little seedling mortality occurred under the snow; however, considerable mortality took place immediately following snowmelt in early spring. This mortality was associated with three factors: 1) heaving of the seedling by alternate freezing and thawing of the saturated soil surface, 2) latent frost injury to young seedlings, and 3) seedling breakage at or near ground level. Frishknecht speculated that breakage of the seedlings may have been caused by the weight of melting snow or weight of the seedling itself upon the frozen plant tissue. However, he stated that it was not known if seedling breakage caused mortality or whether breakage resulted from earlier frost damage.

Chemicals

Herbicides have been applied frequently on rangelands to eliminate or reduce competition from undesirable range species. However, some herbicides may persist in the soil and adversely affect subsequent germination and emergence of desirable range plants. Seedling susceptibility usually depends on the particular herbicide, its residue duration time in the soil, plant species and stage of phenological development, as well as rate and timing of herbicide application.

The residues of 16 herbicides used to control cheatgrass were examined in the greenhouse for effects on crested wheatgrass seedlings by Klomp and Hull (1968b). Seedling dry weights for crested wheatgrass were reduced by only two herbicides at low application rates. However, at the high application rates six herbicides significantly reduced seedling weights, and some even resulted in total death loss. In addition, even though weights of crested wheatgrass seedlings may not have been affected, some herbicides caused epinasty, onion-leaf, and other malformations. The researchers recommended that careful choices of herbicides and application rates used to control weedy species must precede seeding of crested wheatgrass.

Klomp and Hull (1968a) examined the effect of 2,4-D used to control tarweed (Madia glomerata Hook.) on spring- and fall-sown crested wheatgrass. Simulated fall seeding in the greenhouse showed that injury to crested wheatgrass was greatest with high rates of 2,4-D application at the earliest stage of seedling development. Spraying when grass seed was not covered by soil reduced seedling numbers and yields greater than did spraying of covered seed. Where spring seeding of tarweed-infested lands is feasible, the best procedure is to drill early and follow by spraying at low application rates of 2,4-D.

Eckert (1979) evaluated atrazine and simazine applications for renovating sparse crested wheatgrass stands. Both herbicides effectively reduced cheatgrass and tumble mustard (Sisymbrium altissimum L.). Atrazine residues in the soil in the spring of the seeding year were below the toxic level for seedlings of crested wheatgrass, but simazine residues were above the toxic level. However, crested wheatgrass density at the end of the seedling year was sufficient to give a fully stocked stand of crested wheatgrass with both herbicide treatments.

Besides their effects as herbicides, chemicals may influence germination and emergence of crested wheatgrass through allelopathic effects. Many rangelands which have been or can be seeded to crested wheatgrass were or are occupied by big sagebrush and other Artemisia species. These species are known to produce a variety of phototoxic, volatile and soluble secondary compounds (Kelsey et al. 1978), which have been implicated as potential allelochemic substances. Aqueous extracts and volatile substances from big sagebrush inhibited shoot and radical growth of several grass and herbaceous species (including crested wheatgrass) in the laboratory (Klarich and Weaver 1973). Groves and Anderson (1981) reported that uncrushed and crushed leaves of big sagebrush and aqueous extracts from the latter significantly inhibited the germination of crested wheatgrass seeds in the laboratory. In addition, crushed leaves of big sagebrush significantly reduced shoot and radicle growth of crested wheatgrass seedlings. However, to date these allochemic relationships have not been quantitatively documented as being operational in field environments.

Mycorrhizae

Mycorrhizal associations are important for a vast number of plant species. The nature and extent of mycorrhizal associations for plants on arid and semiarid rangelands have been reviewed by Trappe (1981). Similar to plants from other ecosystems, mycorrhizal associations for plants from arid and semiarid rangelands are generally of the vesicular-arbuscular (VA) type. Despite the apparent wide-spread presence of these mycorrhizal associations, only limited information is available concerning the specific mycorrhizae-host plant-environment interactions that occur in rangeland habitats (Trappe 1981).

Associations between plants and mycorrhizae can be classified as symbiotic because both organisms are mutually beneficial to each other (Trappe 1981). Mycorrhizal fungi grow between or into cortical cells of host rootlets and out into the surrounding soil. Fungal hyphae from the mycorrhizae extend into the soil, and nutrients and water absorbed by the fungus are translocated to the plant, increasing the effective absorption area of the plant roots. In turn the host plant provides carbon products derived from photosynthesis for mycorrhizal growth and function. Trappe (1981) cites numerous studies confirming that mycorrhizae aid in translocating nitrogen, phosphorus, potassium, calcium, sulphur, zinc, and copper to the host plant. Apparently, minerals as far as 4 cm away from plant roots can be absorbed by the fungal hyphae and translocated to the plant root. Mycorrhizae also may facilitate water uptake in host plants (Allen and Boosalis 1983). Although research specifically examining mycorrhizal relationships in crested wheatgrass is limited, information from related rangeland species suggests the potential role that these associations might play in crested wheatgrass establishment.

One of the few studies that examined mycorrhizal associations in crested wheatgrass was reported by Allen and Boosalis (1983). They showed that Agropyron desertorum exhibited arbuscule formation as well as internal and external vesicle formation. However, total infection in crested wheatgrass was less than in needle and thread grass (Stipa comata Trin. & Rupr.). Stahl and Christenson (1982), working in four sagebrush- grassland sites in Wyoming, showed that at least six species of VA mycorrhizal fungi were associated with western wheatgrass and blue grama grass. Each of the four soils sampled had unique spore populations that differed in total spore numbers, species, and relative and absolute densities. Composition of VA fungal communities apparently was affected mostly by environmental factors, but to some extent by the host plant as well.

Reeves et al. (1979) compared mycorrhizal relationships on an undisturbed mid-elevation sagebrush community and a severely disturbed old roadbed in western Colorado. Although their species designation of Agropyron smithii is confused with their common name designation of "crested wheatgrass," their study suggested that colonizing species on disturbed land were often nonmycorrhizal and that climax species were predominantly (99%) mycorrhizal. They hypothesized that nonmycorrhizal species may hinder succession in ecosystem development, and that advancement towards the climax stage may require inoculation and manipulation of essential mycorrhizal fungi.

In establishing stands of crested wheatgrass, various land treatments often are used to reduce competition from non-desirable plants and prepare a desirable seedbed. Such practices as plowing, chaining, and burning probably would cause a decrease in mycorrhizal spores because the major plant component would be removed or at least reduced in abundance (E. Allen, personal communication). This spore reduction probably would not be enough to negatively affect seedling establishment of crested wheatgrass (E. Allen, personal communication). However, because various herbicides are known to affect the development and efficacy of some mycorrhizal fungi and their colonization of seedling roots (e.g., Pope and Holt 1978, 1981), range improvement using herbicide treatments may be deleterious to VA mycorrhizal associations. Research addressing this topic is currently underway (E. Allen, personal communication).

VA mycorrhizae may be particularly critical to plant establishment on mined land soils where spore populations may be extremely low or non-existent (Allen and Allen 1980). Zak and Parkinson (1982) showed that different organic and inorganic soil amendments on two mine spoils in Alberta produced very different rates of mycorrhizal development on slender wheatgrass [Agropyron trachycaulum (Link) Malte.] during the first 10 weeks after seeding. Three years after seeding, these amendments exhibited significant effects on the occurrence of particular mycorrhizal species and spore numbers (Zak et al. 1982). Even after four years, the effects of these soil amendments were still evident on the development of the VA mycorrhizae with slender wheatgrass (Zak and Parkinson 1983). These studies showed that initial application of an amendment to a mine spoil may have significant long-term effects on the development of VA mycorrhizae and the ultimate success of the particular revegetation program.

Miscellaneous

Dasberg et al. (1966) examined the influence of various concentrations of oxygen and carbon dioxide on the germination of range grasses, including Agropyron desertorum and A. cristatum. In the absence of carbon dioxide over the range of oxygen concentrations tested, both crested wheatgrass species exhibited decreases in rate of germination and final germination percentage with declining oxygen. The imbibition stage of water uptake was not affected by oxygen concentration, whereas respiration decreased at low oxygen. Carbon dioxide concentration (0 to 15%) only slightly affected germination compared to the oxygen effect.

CONCLUSIONS

Crested wheatgrass has been used widely for rangeland revegetation in North America. One characteristic that has contributed to its widespread use is its ease of establishment. Because of the importance of this characteristic, considerable research has been undertaken concerning seed and seedling relationships in crested wheatgrass. A review of this literature indicated that early seedling root development and seedling ability to tolerate widely fluctuating moisture and temperature conditions undoubtedly contribute to the ease of establishment of crested wheatgrass. Genetic variability for these responses among genotypes of crested wheatgrass suggests that this already valuable species complex can be improved through plant breeding and selection.

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High Technology Weed Control--

Revegetation Systems for Establishment

and Maintenance of Crested Wheatgrass

Raymond A. Evans, Richard E. Eckert, Jr. and James A. Young

ABSTRACT: Large areas of sagebrush-grass rangelands are brush dominated and are producing 50 percent or less of their forage potential. Conversion of these rangelands to crested wheatgrass for increased forage production involves brush and weed control and seeding. Application of herbicides, either by air or ground sprayer, controls brush and weeds effectively and economically. Systems that combine herbicide spraying for brush and weed control with seeding by rangeland drills of crested wheatgrass and other forage species have been developed and shown to be effective for improvement of degraded sagebrush rangelands. Periodic spraying of brush may be necessary to maintain high forage productivity of the established crested wheatgrass.

INTRODUCTION

Development of equipment and techniques for seeding large areas of western rangelands to crested wheatgrass (Agropyron cristatum and A. desertorum) has been discussed (see Young and Evans in this proceedings). Our intent in this paper is to present the most modern technology in plant control and revegetation systems now available to range managers. From the historical basis of mechanical brush control we will emphasize development and use of herbicides and spraying technologies.

The Problem

The sagebrush-grass ecosystem is the largest rangeland type in the western United States. In the Great Basin and Northwest subregion, which includes most of northern Nevada and parts of Utah, Idaho, Oregon, and Washington, there are almost 85 million acres (35 million ha) of sagebrush-grass rangeland (Evans et al. 1981). Of these rangelands, 88 percent or almost 75 million acres (30 million ha) are degraded to the point that they are producing 50 percent or less of their forage potential (Forest Service 1972). Only 1 percent of the over 4 million acres in the Humboldt River Basin of northeastern Nevada are in the high forage production class (Anonymous 1966). Low forage production on these rangelands has been caused by overgrazing and other past land abuses (Young et al. 1979), resulting in a severe depletion of native perennial grasses, a dominance of brush, and in many instances an annual alien weed dominance in the understory.

Once big sagebrush (Artemisia tridentata) becomes established as the dominant species of degraded sagebrush-grass rangelands, it is persistent enough to stabilize succession in these communities for long periods. The tenure of dominance has not been determined, but the life expectancy of big sagebrush may exceed 150 years (Ferguson 1964). Degraded rangelands dominated by big sagebrush can remain static, producing virtually no forage for decades regardless of grazing management or even without livestock grazing.

By far the most abundant brush species of the sagebrush-grass rangelands is big sagebrush with its three subspecies: basin (A. t. ssp. tridentata), Wyoming (A. t. ssp. wyomingensis), and mountain (A. t. ssp. vaseyana). On specific sites other species of sagebrush dominate, e.g., low sagebrush (A. arbuscula) and early sagebrush (A. longiloba) usually occur on shallow soils with an argillic horizon, black sagebrush (A. nova) usually is associated with carbonate soils, and silver sagebrush (A. cana) is found primarily on sites with impounded drainage.

Representing seral stages after disturbances, and on many sites occurring as either codominant or subdominant with big sagebrush, are green and gray rabbitbrush (Chrysothamnus viscidiflorus and C. nauseosus) and horsebrush Tedradymia canescens). Other brush species occurring in some stands are species of Ribes, Ephedra, and Prunus.

The Solution

To improve these brush-dominated rangelands for increased livestock production, the first consideration is the control of brush. The second is, on some sites, the control of herbaceous weeds, and the third is replacement of brush and weeds by

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forage species. Historically and at the present time, the most widely adapted forage species for seeding on sagebrush rangelands is crested wheatgrass. Development of other grasses, broad-leaved plants, palatable shrubs, and seeding mixtures of forage and browse broadens the spectrum of available replacement vegetation. An array of plant species not only increases environmental adaptability of replacement vegetation, but widens their use by domestic livestock and wildlife. The latter consideration is becoming increasingly important as society puts more and more demands on the multiple use of rangelands.

BRUSH CONTROL WITH HERBICIDES

What to Spray

The discovery of 2,4-D [(2,4-dichlorophenoxy) acetic acid] as a plant growth regulator in 1942 began the development of synthetic hormones for weed control (Bovey 1971). After World War II, several scientists independently recognized the potential of 2,4-D in controlling sagebrush for the release of perennial grasses. This herbicide is currently registered by the Environmental Protection Agency (EPA) for use on sagebrush-grass rangelands.

Among the first to demonstrate the effectiveness of 2,4-D for controlling big sagebrush were Elwell and Cox (1950), Cornelius and Graham (1951), and Hull and Vaughn (1951). Later, the usefulness of 2,4-D was demonstrated by Hyder (1953) in eastern Oregon, and by Hull et al. (1952) and Bohmont (1954) in Wyoming.

Gradually, guidelines were developed to help ensure the success of spray application. As the brush control program with 2,4-D became widespread, there were a few failures, almost all of which can be traced to violations of the initial guidelines. Additional research is warranted on improving the efficacy of 2,4-D for brush control. Improved application technology is needed for equipment modifications; use of different total volumes of spray and improved surfactants, additives and carriers; and the use of remote sensing to more accurately predict the periods of optimum susceptibility.

Although 2,4-D effectively controls sagebrush, other brush species either occurring alone or in mixed stands with sagebrush are more resistant to this herbicide. Effective control of green rabbitbrush by 2,4-D requires careful timing of application in relation to its phenology and to air temperature and available soil moisture. In some years, 2,4-D does not adequately control green rabbitbrush or the period of susceptibility is so short that only small areas can be treated. These problems have been lessened by the use of more recently developed herbicides that translocate better.

The most effective and widely tested of the alternative herbercides has been picloram (4-amino-3,5,6-trichloropicolinic acid). Relatively low rates of picloram have been shown to be extremely effective for control of green rabbitbrush (Cook et al. 1965, Tueller and Evans 1969). Picloram does not control big sagebrush at these rates, so 2,4-D must be applied with the picloram for control of both species. Picloram has not been marketed as a mixture with low-volatile esters of 2,4-D. Tank mixtures of potassium salts of picloram and low-volatile esters of 2,4-D have been effective in aerial applications to mixed stands of green rabbitbrush and big sagebrush (Evans and Young 1975). Picloram has been registered by EPA for application either alone or in tank mixtures with 2,4-D for control of rabbitbrush and other brush species on rangelands with a Special Local Needs Label for Idaho, Nevada, Oregon, Utah, and Washington. A Supplemental Use Label has been issued for control of weed and brush species, including rabbitbrush, in Wyoming.

Tebuthiuron [N-[5-1,1-dimethylethyl-1,3,4-thiadiazol-2-yl]-N,N'-dimethylurea] and dicamba (3,6-dichloro-anisic acid) are both registered for brush control on rangelands by EPA but there are very few publications verifying their efficacy on sagebrush-grass rangelands. Britton and Sneva (1981) indicated that frequency of occurrence of sagebrush was severely reduced with 1.8 lb/A (2 kg/ha) of tebuthiuron (20 percent a.i. pellets). Big sagebrush was virtually eliminated by 3.6 lb/A (4 kg/ha). At these rates, associated perennial grasses were also damaged.

Further studies in Oregon with tebuthiuron at lower rates indicate 80 percent control of big sagebrush with 0.87 lb/A (1 kg/ha), 58 percent with 0.75 lb/A (0.8 kg/ha), and 35 percent with 0.5 lb/A (0.6 kg/ha) of the 20 percent a.i. pellets, respectively (unpublished data, R. Miller, USDA-ARS, Burns, OR). No significant damage was seen on perennial grasses when tebuthiuron was applied at these rates. Cooperative studies among Elanco (chemical company marketing tebuthiuron), the Bureau of Land Management, and ranchers are being conducted in many areas to evaluate the efficiency of tebuthiuron for brush control.

It must be kept in mind that tebuthiuron is a wide-spectrum, soil-active herbicide which will persist over several years, so its use for brush control preparatory to seeding of crested wheatgrass cannot be considered. Its best use will be control of sagebrush in established stands of crested wheatgrass and other perennial grasses.

At this time, 2,4-D is the most practical herbicide for brush control on sagebrush-grass rangelands. Big sagebrush is usually controlled by 2 lb/A (2.2 kg/ha) of low-volatile esters of 2,4-D. With mixed stands of sagebrush and green rabbitbrush, control can be effective with either 3 lb/A (3.4 kg/ha) of 2,4-D or a mixture of 1/2 lb/A (0.6 kg/ha) of picloram and 2 lb/A (2.2 kg/ha) of 2,4-D.

When to Spray

Big sagebrush is most susceptible to 2,4-D when it is growing rapidly in the spring. Because big sagebrush has persistent leaves, however, its phenology is difficult to measure. Hyder (1954) used the phenology of a native perennial grass, Sandberg bluegrass (*Poa secunda*), to estimate the correct time for applying 2,4-D. He concluded that the best time for spraying in eastern Oregon extended from the heading of Sandberg bluegrass until one-half of the green color was gone. Measurements of soil moisture have been found to be important in estimating the correct time for herbicide application, generally in the month of May. However, on shallow soils or south slopes, the correct application time may be earlier and of much shorter duration; in wet years it may be later and of much longer duration. In Wyoming, a more reliable way of estimating the correct timing of herbicide application is based on the phenology of big sagebrush itself (personal communication from H. P. Alley).

As previously noted, species of rabbitbrush are more difficult to control with 2,4-D than big sagebrush. Hyder et al. (1958) and Hyder and Sneva (1962) determined that application must be carefully timed for adequate control of rabbitbrush. Current annual growth of shoots must reach 3 inches (7.6 cm) and soil moisture must be available for effective herbicidal action. The length of time that green rabbitbrush is susceptible to 2,4-D varies greatly among years and locations. The period of susceptibility may equal that of big sagebrush or it may not occur at all.

In mixed stands of big sagebrush and rabbitbrush, herbicide application should be timed with the phenology of rabbitbrush because of its usually shorter period of susceptibility. When determining date of spray of both big sagebrush and rabbitbrush, measurements of available soil water are important. Roundy et al (1983) recently published methods of measuring soil water on rangelands which should prove useful to the range manager.

Prediction of the optimum date for application of 2,4-D to green rabbitbrush is essential because herbicide-mixing facilities, aircraft, and flagging crews must be prepared in advance if they are to be ready by the chosen date at the often remote sites. Prediction is complicated by the phenology pattern of growth for green rabbitbrush, in which 40 percent of the current year's growth can occur within 2 weeks before the optimum application date (Young and Evans 1974). Prediction is further complicated by the interaction of age and competition on the growth rate and phenology of green rabbitbrush. Young stands grow faster than old stands that are competing with big sagebrush plants.

Color infrared photographs can be used to predict the optimum spray date for green rabbitbrush (Evans et al. 1973, Young et al. 1976). This method has the advantage of enabling the collection of large, statistically precise samples from remote areas in a very short time. A single trained interpreter can predict the optimum application date from photographs and return a recommendation within 24 hours.

How to Spray

Aerial applications of 2,4-D are the most practical to control big sagebrush over large areas. Prevailing recommendations are to use 5 gal/A (47 L/ha) of water as a carrier for the 2,4-D. In the past, some range managers preferred diesel oil to water as a carrier, but the increase in efficiency of weed control seldom justified the increase in cost and associated environmental hazards. In an assessment of spraying for control of big sagebrush on the Vale project in southeastern Oregon, Heady and Bartolome (1977) concluded that no clear-cut advantage was gained by the use of oil as a carrier. However, many land managers and some scientists (personal communication from H. P. Alley) strongly believe that oil is a better carrier than water.

Errors made in spraying for big sagebrush control include improper mixing of the herbicide and carrier, flying too high or too fast, and improper marking of sites to be sprayed during herbicide application (Pechanec et al. 1965). Such errors are probably less important than errors in the timing of spraying (personal communication from F. A. Sneva). A ground sprayer may be more practical to spray small areas, or to treat places remote from agricultural areas where aerial applicators may be difficult to obtain. Young et al. (1979) have modified readily available power-ground sprayers to permit their use on sagebrush rangelands

HERBACEOUS WEED CONTROL

On sagebrush rangelands, control of herbaceous weeds to allow the establishment of seedlings of desirable perennials is predominantly the control of alien annuals. The secondary successional role of native herbaceous species has been almost entirely preempted by downy brome (Bromus tectorum) and associated alien species (Piemeisel 1938).

Sites that have burned or otherwise had brush removed and are dominated by downy brome are largely closed to the establishment of perennial grass seedlings (Robertson and Pearce 1945). Attempts to introduce wheatgrasses on such sites by seeding generally have failed unless the sites were first fallowed by mechanical methods (Hull and Holmgren 1964).

The alien annual grass, medusahead (Taeniatherum asperum) has invaded portions of Oregon, California, Washington, and Idaho (Young and Evans 1970). Medusahead invasion on sagebrush rangelands is largely restricted to low sagebrush sites (Young and Evans 1971).

Paraquat

The herbicide paraquat (1,1'dimethyl-4-4'-bipyridinium ion) was evaluated for downy brome control because of its relatively unique characteristic of being deactivated upon adsorption to soil particles. This characteristic permits the spraying of paraquat at 0.5 to 1 lb/A (0.6 to 1.1 kg/ha) and the immediate seeding of wheatgrass (Evans et al. 1967). Paraquat is registered by EPA for downy brome control on sagebrush rangelands, but is a restricted-use herbicide because of its high mammalian toxicity. Proper care must be exercised in its use.

If the annual community being treated with paraquat contains tumble mustard (Sisymbrium altissimum), it is necessary to add 2,4-D at 0.5 lb/A (0.6 kg/ha) for control of this species. Paraquat, a contact herbicide, must be applied after the downy brome has emerged. On sagebrush rangelands, when fall emergence has occurred, spraying and seeding can be done. Otherwise, it is necessary to delay these operations until spring.

Under the environmental conditions of sagebrush rangelands, it is difficult to consistently control downy brome with aerially applied paraquat even though ground applications are always effective. The addition of proper surfactants enhances the effectiveness of ground applications (Evans and Eckert 1965).

Atrazine Fallow

After evaluating large numbers of soil-active herbicides, Evans et al. (1969) determined that atrazine [2-chloro-4-(ethylamino)-6-(isopropylamino)-s-triazine] was the best candidate for creating herbicidal fallows. The characteristics evaluated were the spectrum of weed control, consistency of performance among years, and amount of herbicide residue 1 year after application.

The atrazine-fallow technique was developed (Eckert and Evans 1967) and tested extensively (Eckert et al. 1974). Atrazine is registered by EPA for specific uses on sagebrush rangelands. It is applied at 1 lb/A (1.1 kg/ha) in the fall, creating a fallow field during the next growing season. The area is seeded to wheatgrasses 1 year after the herbicide is applied. The amount of herbicide residue that is present at the time of seeding is critical in the success of seedling establishment (Eckert et al. 1972, Eckert 1974). The atrazine-fallow technique controls medusahead as well as downy brome (Young and Evans 1971).

SEEDING OF CRESTED WHEATGRASS

The rangeland drill and its modifications make possible seeding of crested wheatgrass through standing dead sagebrush and on rocky uneven sites. Historical accounts of seeding technology on rangelands outline the evolution of equipment that has culminated in the present rangeland drill (see Young and Evans in this proceedings and Young and McKenzie 1982). A modified rangeland drill that makes deep furrows while drilling is discussed by Asher and Eckert (1973) and Young and McKenzie (1982).

While the use of a grain drill is practical on a few plowed or burned sites, the rangeland drill is almost synonymous with seeding crested wheatgrass. The use of herbicides for control of sagebrush as part of an economical technology for replacement of brush with grass is a reality only with the use of the specifically designed, heavy duty rangeland drill (Kay and Street 1961). On many sites, seedling success is enhanced by seeding in the bottom of furrows made with the modified rangeland drill which provides a favorable microenvironment (McGinnies 1959 and Evans et al. 1970). In the atrazine-fallow method for downy brome control, furrowing removes herbicide residues in the surface soil in the immediate vicinity of the growing seedlings (Eckert 1974).

Standard rangeland drills in tandem can be pulled by a 40-horsepower tractor in a non-brushy situation. A 60-horsepower tracklaying tractor is required to pull standard rangeland drills in tandem through standing dead brush. Less power is required to pull modified rangeland drills through brush than standard drills because of fewer, wide-spaced arms.

Weed Control-Revegetation Systems

For big sagebrush communities in which perennial grasses are depleted and downy brome has invaded the shrub understory, it is possible to combine in sequence 2,4-D and atrazine-fallow treatments, and seeding of crested wheatgrass (Evans and Young 1977). This system approach allows for control of brush and herbaceous weeds and seeding to obtain successful stands of a forage species in place of degraded plant communities. The system can be used by (a) applying atrazine in the fall and 2,4-D the next spring; (b) applying 2,4-D in the spring and atrazine the following fall; or (c) applying a mixture of both herbicides in the spring at an optimum date for brush control.

Atrazine fallows make excellent weed-free seedbeds for transplanting seedlings of desirable browse species (Christensen et al. 1974). Shrub transplanting can also be adapted to weed control systems of atrazine and 2,4-D, or integrated with seedings of perennial grasses for establishment of forage-browse combinations (Evans and Young 1977).

MAINTENANCE OF GRASS STANDS

Many crested wheatgrass seedings become infested with sagebrush and rabbitbrush within 5 to 10 years following establishment. Brush infestation, which may be as heavy as 20 to 25 percent crown cover, drastically reduces forage productivity of crested wheatgrass. Data are limited, but one estimate of reduction is that each 1 percent increase of sagebrush crown cover was equivalent to a decrease of 4.5 percent in forge production when crown cover varied from 0 to 22 percent (Rittenhouse and Sneva 1976).

Control of sagebrush and rabbitbrush in established crested wheatgrass stands constitutes a cost-effective range improvement technology because the established stand of forage plants will respond to a relatively inexpensive treatment.

In a 1981 economic study of range improvement costs from Nevada, Sonnemann et al. (1981) determined an aerial application cost of $9.00 per acre for 2,4-D brush control. The study contrasted this with a cost of $21.50 per acre for spray and drill and $41.80 per acre for plow and drill to establish crested wheatgrass on similar rangelands.

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Probabilities of Seedling Recruitment and the Stability of Crested Wheatgrass Stands

Jay E. Anderson and Guy M. Marlette

ABSTRACT: Crested wheatgrass seedings in the western United States have persisted as virtual monocultures for over 50 years following their establishment. Such stability typically is attributed to superior competition by crested wheatgrass, but this explanation assumes that native propagules are available for recruitment. Data on seedling emergence from undisturbed topsoil samples show that there is a paucity of native propagules within crested wheatgrass stands. For two stands that were near monocultures, the probability of a seedling being crested wheatgrass was over 85%. Recruitment probabilities favor the maintenance of a monoculture rather than its successional replacement.

ACKNOWLEDGEMENTS: This paper is a contribution from the Idaho National Engineering Laboratory Ecological Studies Program, supported by the Office of Health and Environmental Research, U.S. Department of Energy. We thank Nancy Cole, David Humphrey, Amy Marlette, and Diane Pavek for assisting with data collection and O. D. Markham for his support and suggestions.

INTRODUCTION

Crested wheatgrass (*Agropyron cristatum* (L.) Gaertn. and *A. desertorum* (Fisch.) Schult.) often has been seeded and managed in North America under the assumption that without continued intervention by man the stand will eventually revert to a native climax community (Lewis 1969). Implicit in the assumption is the concept of only one stable climax for any particular site, and that succession will follow a directional, predictable course toward that stabilized community. Clements (1935) wrote, "the grasses of a particular climax are the best adapted to its climate and have a distinct advantage in terms of competition over the introduced ones. ... Crested wheatgrass (*Agropyron cristatum*) has often been cited as a warrant for such a procedure (introduction), but all evidence available indicates that it can persist in the face of the competition of the indigenous grasses only when man aids it by cultivation or otherwise." The life expectancy of crested wheatgrass seedings is usually placed at 20 years or less (Bartolome and Heady 1978), although some investigators consider that to be a conservative estimate (Sonnermann et al. 1981).

Contrary to these views of crested wheatgrass forming unstable, temporary stands, it is now generally recognized that the species spreads quickly by seed and is capable of invading native, undisturbed habitat (Hull and Klomp 1967, Hull 1971). When sown in a mixture with native species, crested wheatgrass frequently becomes the dominant species in the stand (Heinrichs and Bolton 1950, Hull 1971, Holechek et al. 1981). Several investigators considered crested wheatgrass to be competitively superior to dominant native species (Hubbard 1957, Eckert et al. 1961, Robertson et al. 1966, Robertson 1972, Holechek et al. 1981). Recent studies by Caldwell et al. (1981, 1983) have elucidated some physiological and morphological attributes that contribute to the superior competitive ability and greater grazing tolerance of crested wheatgrass in comparison to bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) Love).[1]

Crested wheatgrass seedings in the western United States have resisted invasion by native species for as long as 30 to 50 years (Hull and Klomp 1966, Looman and Heinrichs 1973, Sonnermann et al. 1981), which simply indicates the length of time for which data are available rather than the

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[1]Nomenclature follows Hitchcock and Cronquist (1973) except for grasses of the Triticeae tribe. For bluebunch wheatgrass, we have used the taxonomic revision proposed by Love (1980); nomenclature for other members of the Triticeae follows Dewey (1983).

longevity of the stands. Soils beneath some seedings are not converging to their original condition even after 50 years and may be evolving toward a different equilibrium point than undisturbed soils (Dormaar et al. 1980). In its native habitat, crested wheatgrass is known for its ability to establish on disturbed sites and persist in virtual monocultures (Looman and Heinrichs 1973). Thus, rather than crested wheatgrass eventually being replaced by native species, it may inhibit or even preclude the recovery of native vegetation. It is, therefore, desirable to understand the factors responsible for the stability of crested wheatgrass stands.

Succession ultimately depends on whether a species replaces itself on a given site or is replaced by members of other species (Grubb 1977, McIntosh 1980). This replacement process is a function of two factors (Gleason 1926, Poore 1964, Harper 1977, Whipple 1978): 1) the availability of propagules on the site, and 2) whether those propagules find a suitable environment for germination, growth, and ultimately, survival.

Dispersal of native propagules into crested wheatgrass seedings is usually assumed to occur. Shepherd (1937 cited by Weldon et al. 1959) concluded that "a supply of viable seed is probably never a limiting factor for the aggression of sagebrush." Looman and Heinrichs (1973) surmised that "Over the years, a considerable reservoir of seeds of native and introduced species has built up, and the chances that a given crested wheatgrass plant will be replaced by its own kind after death are lessened with increasing age." Thus, it is typically assumed that the stability of a crested wheatgrass seeding is a function of the superior competitive ability of crested wheatgrass which renders the site unsuitable for the establishment of other species.

Competition can be responsible for the stability of crested wheatgrass stands only if propagules of native species are dispersed into the stands. The purpose of this investigation was to test the assumption that there is sufficient dispersal of native species into crested wheatgrass seedings to result in a store of native propagules available for recruitment. In essence we asked, "If a safe site (sensu Harper 1977) becomes available, what is the probability that it will be colonized by crested wheatgrass as opposed to one of its potential competitors?" Our results suggest that there is a paucity of native propagules available for recruitment within crested wheatgrass stands.

METHODS

This study was conducted on the Idaho National Engineering Laboratory (INEL), which occupied some 2300 km^2 of sagebrush steppe rangeland on the upper Snake River Plain. Vegetation of the area is dominated by big sagebrush (*Artemisia tridentata* Nutt.). Other common shrubs include green rabbitbrush (*Chrysothamnus viscidiflorus* (Hook.) Nutt.), prickly phlox (*Leptodactylon pungens* (Torr.) Nutt.), horsebrush (*Tetradymia canescens* DC.), and spiny hopsage (*Atriplex spinosa* (Hook.) Collotzi. The most important grasses are bottlebrush squirreltail (*Elymus elymoides* (Raf.) Swezey), thick-spike wheatgrass (*Elymus lanceolatus* (Scribn. & Smith) Gould), bluebunch wheatgrass, needle-and-thread (*Stipa comata* Trin. & Rupt.), and Indian ricegrass (*Oryzopsis hymenoides* (R. & S.) Ricker).

Average annual precipitation for the INEL is about 21 cm, with 40% typically falling during April, May and June (Anderson and Holte 1981). Mean annual temperature is about 5.5°C; the frost free period averages 91 days. The topography is flat to gently rolling, with occasional lava outcrops. The soils are primarily shallow, calcic aridisols of aeolian origin lying over basalt.

Four crested wheatgrass stands and adjacent native communities were studied during the summers of 1978 and 1979. Three stands, located on a remote section of the INEL known as Tractor Flat, were established following plowing and seeding in the fall of 1956. They are referred to as TFA, TFB, and TFC. They have been grazed by sheep, primarily in the spring, since 1959. The fourth stand (PBF), located near the INEL Power Burst Facility, was seeded in 1960 and has never been grazed by domestic livestock. This stand and TFB were near monocultures; the other two areas were selected because re-establishment of native species (primarily big sagebrush) within the seeding was evident. All study areas were selected so that the main interface between the native community and the adjacent seeding was approximately perpendicular to the prevailing wind direction. At PBF, TFA, and TFB, the seedings were downwind from the native communities, which was assumed to represent the maximum potential for wind dispersal of propagules from the native communities.

At each study area, crown cover of shrubs and basal cover of grasses and forbs were estimated using a 0.5 m^2 sampling frame that was subdivided into dm^2 grids (Floyd and Anderson 1982). The frame was systematically placed at 2- to 4-m intervals along three parallel transects that extended from the native stand into or across the adjacent crested wheatgrass seeding. Transects were 23 m apart; their lengths varied from 115 to over 500 m, depending on the layout of the seeding and adjacent native community. Seed reserves were sampled in March of 1979 by driving cylinders cut from #10 cans into the soil to a depth of 6 cm and removing the intact soil core by passing a trowel under the cylinder. Paired samples from bare and littered areas were taken at systematic intervals along the vegetation transects, sampling both the crested wheatgrass stands and the native community. Between 130 and 180 samples from each study area were placed in a greenhouse or environmental chamber where they were watered regularly with distilled water. Emerging seedlings were identified, counted, and removed. We refer to these counts as seed reserves, but it should be noted that the data actually represent seedling emergence from undisturbed topsoil, except where natural disturbances occurring in the field were sampled. Further details about the study areas and sampling regimes can be found in Marlette (1982).

RESULTS

Vegetal Cover

Native communities at all four study areas were dominated by big sagebrush; green rabbitbrush was also common at the Tractor Flat study areas (Tables 1-4). Crested wheatgrass contributed from 2% (Table 2) to over 17% (Table 4) of the plant cover in the native communities, showing that it had indeed moved from the original seedings into the native communities.

Total plant cover was generally higher in the native communities than the crested wheatgrass stands at Tractor Flat (Tables 2-4), but not at PBF (Table 1). Total cover was remarkably similar (about 36%) among the four crested wheatgrass stands (Tables 1-4).

Relative cover of crested wheatgrass was 95% and 93% in the two "monocultural" stands (Tables 1 and 3). A rhizomatous grass, beardless wildrye (Leymus triticoides (Buckl.) Pilger), was the only other species contributing over 1% relative cover in the crested wheatgrass seeding at the PBF study area (Table 1). Big sagebrush and green rabbitbrush, with 2.7% and 1.1% relative cover respectively, were the next most important species at TFB (Table 3). Thirty species were identified on the vegetation transects in the PBF native community compared to only 14 within the crested wheatgrass seeding. At TFB, species richness was 20 in the native community and 17 in the crested wheatgrass seeding.

The TFA and TFC study areas were chosen because there appeared to be considerable re-establishment of native species within the seedings. Relative cover of crested wheatgrass in both cases was 73% (Tables 2 and 4). Big sagebrush, threetip sagebrush (Artemisia tripartita Rydb.), and green rabbitbrush contributed the bulk of the remaining cover within the seeding at TFA (Table 2). Big sagebrush green rabbitbrush and two annuals also having relative cover greater than 1% (Table 4).

Table 1.--Cover of the more important plant species in the native community and adjacent crested wheatgrass stand at the PBF study area.

Species	Relative Cover[1]: Native Community	Relative Cover[1]: Wheatgrass Stand
	percent	
Artemisia tridentata	52.1	0.05
Agropyron cristatum	15.7	95.2
Elymus elymoides	8.4	
Elymus lanceolatus	6.9	0.05
Stipa comata	3.3	
Opuntia polyacantha	1.8	0.05
Descurainia pinnata	1.6	0.03
Leymus triticoides	1.4	3.5
Poa sp.	1.4	
Lappula redowskii	0.9	
Astragalus filipes	0.7	0.6
Carex douglasii	0.1	0.3
Other species	6.6 (n=18)	0.2 (n=6)
Total absolute cover	27.1	36.7

[1]Relative cover is the cover of species i divided by the total cover of all vascular plants, expressed as a percentage. The absolute cover for a species equals relative cover for species i times total absolute cover divided by 100.

Table 2.--Cover of the more important plant species in the native community and adjacent crested wheatgrass stand the the TFA study area.

Species	Relative Cover[1]: Native Community	Relative Cover[1]: Wheatgrass Stand
	percent	
Artemisia tridentata	48.9	9.6
Pseudoroegneria spicata	14.9	
Chrysothamnus viscidiflorus	14.0	8.1
Phlox hoodii	12.9	0.5
Elymus elymoides	4.2	0.03
Agropyron cristatum	2.4	72.7
Poa sp.	0.6	0.2
Eriogonum microthecum	0.5	0.2
Oryzopsis hymenoides	0.5	
Halogeton glomeratus	0.3	
Artemisia tripartita		8.0
Astragalus filipes		0.4
Gilia congesta		0.1
Leptodactylon pungens		0.1
Other species	0.8 (n=7)	0.5 (n=4)
Total Absolute Cover	39.0	35.9

[1]See Table 1 for definition.

Species richness was 15 and 18 in the native and crested wheatgrass communities respectively at TFC, and 17 vs. 15 at TFA. Despite the similarities in richness, there were large differences in structure between the native and crested wheatgrass stands. Simpson's index of dominance concentration, a measure of the probability that two individuals drawn at random from a community will belong to the same species (Poole 1974), was 0.30 for the TFA and TFC native communities, but 0.55 and 0.56 for the TFA and TFC seedings respectively.

Seed Reserves

Over 17,000 seedlings representing some 46 taxa emerged from the 612 topsoil samples taken from the four study areas. On the average, three to four times as many seedlings emerged from samples of littered areas than from those of bare areas (Marlette 1982). Crested wheatgrass and big sagebrush each contributed about 6500 seedlings to the total count. Bottlebrush squirreltail, with 680 seedlings, was the next most abundant perennial species. Lappula redowskii (Hornem.) Greene was the most common annual, with over 1160 seedlings; halogeton (Halogeton glomeratus Meyer.) and tansymustard (Descurainia pinnata (Walt.) Britt.) were also common, having 457 and 446 emergent seedlings respectively. Ten of the taxa identified among the emerging seedlings were not found in the vegetal cover samples. Likewise, ten of the 46 taxa identified along the cover transects were not represented in the seedling emergence data. Thus, 64% of the taxa were common to both data sets.

Crested wheatgrass contributed from 84% to 99% of the total seedling density within the crested wheatgrass stand at the PBF study area (Fig. 1). For seed reserve samples from the seeded area as a whole, 92% of the seedlings were crested wheatgrass, 3% were big sagebrush, and the remaining 5% represented 11 species, of which nine were annuals or biennials. For samples taken at the interface, 51% of the seedlings were crested wheatgrass, whereas only from 2% to 18% of the seedlings in the PBF native community were crested wheatgrass. From 12% to 35% of the seedlings emerging from samples from the PBF native community were big sagebrush; the remaining 50% to 80% represented a variety of native species. Seedlings of 29 species emerged from samples of the PBF native community; only 13 species were represented among seedlings from samples of the crested wheatgrass stand.

At TFB, the second study area where the seeding ~~appeared to be essentially a pure~~ stand of crested wheatgrass, from 1% to 34% of the seedlings in the native community and from 67% to 96% of those in the seeding were crested wheatgrass (Fig. 2). In the native community, big sagebrush contributed from 26% to 76% of the total seedling count, but sagebrush seedlings were virtually absent in samples from the crested wheatgrass seeding (Fig. 2). Seedlings of 17 species emerged from samples from the native community, but only 11 species were recorded for samples from the seeding. Of 1778 seedlings that emerged from topsoil samples from the TFB seeding, over 1500 (84.7%) were crested wheatgrass; 10% of the seedlings were Lappula redowskii and 3% were halogeton. None of the other eight species contributed over 1% to the seedling total.

Table 3.--Cover of the more important plant species in the native community and adjacent crested wheatgrass stand at the TFB study area.

Species	Relative Cover[1] Native Community	Relative Cover[1] Wheatgrass Stand
	------percent------	
Artemisia tridentata	41.5	2.7
Pseudoroegneria spicata	12.9	
Chrysothamnus viscidiflorus	11.7	1.1
Agropyron cristatum	10.7	93.4
Phlox hoodii	7.6	0.3
Elymus elymoides	5.3	
Artemisia tripartita	4.1	0.3
Oryzopsis hymenoides	2.1	0.4
Eriogonum microthecum	1.8	0.3
Poa sp.	0.8	0.5
Halogeton glomeratus	0.1	0.5
Tetradymia canescens		0.3
Other species	1.4 (n=9)	0.2 (n=7)
Total Absolute Cover	38.4	36.0

[1]See Table 1 for definition.

Table 4.--Cover of the more important plant species in the native community and adjacent crested wheatgrass stand at the TFC study area.

Species	Relative Cover[1] Native Community	Relative Cover[1] Wheatgrass Stand
	-----percent-----	
Artemisia tridentata	48.2	16.3
Chrysothamnus viscidiflorus	18.6	2.3
Agropyron cristatum	17.6	73.1
Elymus elymoides	9.5	
Phlox hoodii	2.4	
Halogeton glomeratus	1.9	3.1
Poa sp.	0.8	
Lappula redowskii	0.5	4.1
Descurainia pinnata	0.3	
Oryzopsis hymenoides	0.2	0.3
Leymus cinereus		0.6
Salsola kali		0.1
Opuntia polyacantha		0.1
Other species	trace (n=7)	0.05 (n=9)
Total Absolute Cover	34.5	34.1

[1]See Table 1 for definition.

At TFA, one of two areas where significant numbers of native species appeared to be re-established, crested wheatgrass seedlings were rare in samples from the native community but made up from 40% to 95% of the totals from the seeding (Fig. 3). Sagebrush seedlings dominated samples from the native community, and were common in samples from the center of the crested wheatgrass seeding. Two additional points should be emphasized concernig the data in Figure 3. First, sagebrush seedlings were uncommon at the interface between the native community and the crested wheatgrass seeding. Thus, the re-establishment of big sagebrush within the seeding was not taking place as a sort of wave out from the native community. The second point is that within the crested wheatgrass seeding, species other than crested wheatgrass and big sagebrush (n = 11) contributed only about 4% to the total seedling pool. The area was essentially a biculture of crested wheatgrass and big sagebrush.

The same general patterns were found at the second sagebrush re-establishment area, except that there were few seedlings of either crested wheatgrass or big sagebrush in samples from the native community (Fig. 4). Again, crested wheatgrass seedlings strongly dominated samples from the interface, and sagebrush seedlings became most numerous in the middle of the crested wheatgrass stand. We believe that the most probable explanation of this pattern is that some big sagebrush plants survived the original revegetation treatment and that they provided the original seed source for re-establishment within the seeded area. At TFC, from the interface to 360 m into the seeding, less than 2% of the seedlings were species other than crested wheatgrass and big sagebrush (Fig. 4). Thus, succession on this area, like the

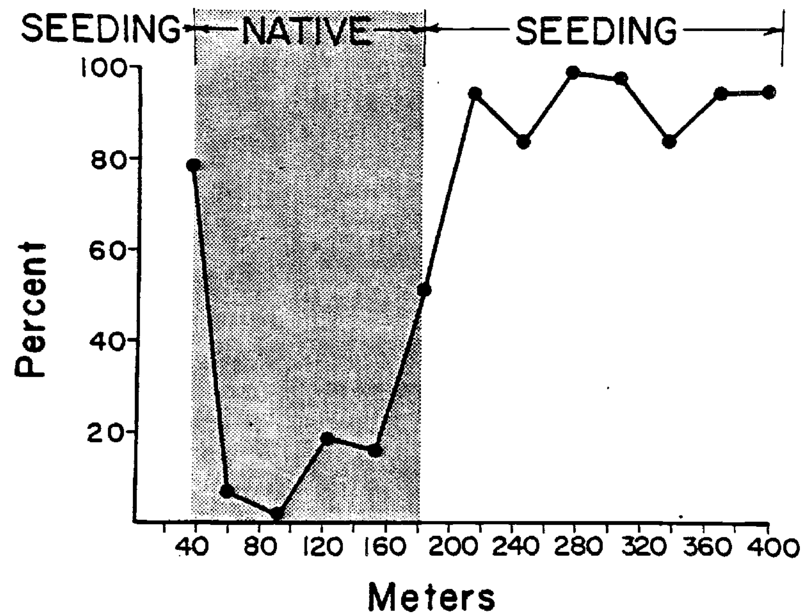

Figure 1.--Percentage of total seedlings emerging from topsoil samples from the PBF study area that were crested wheatgrass vs. distance along the sampling transects.

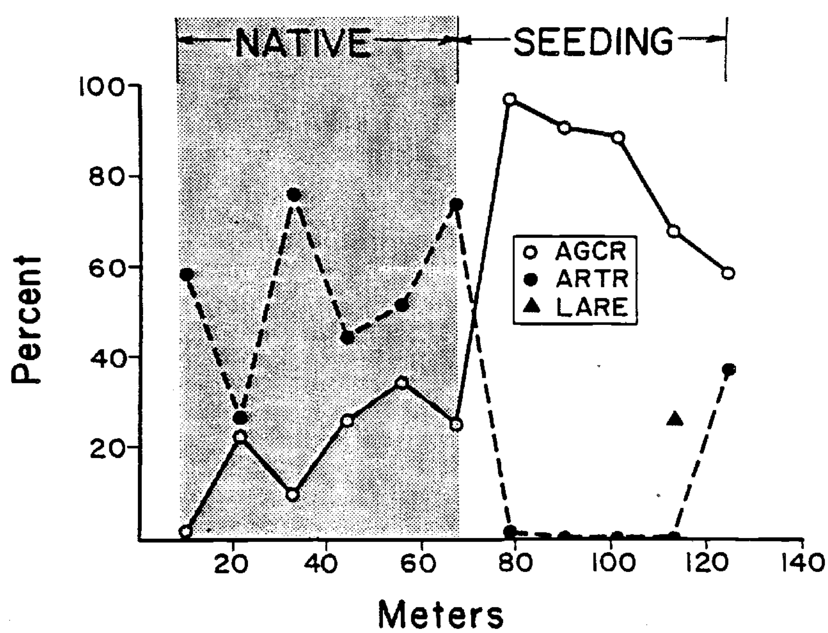

Figure 2.--Percentage of total seedlings emerging from topsoil samples from the TFB study area that were crested wheatgrass (AGCR) or big sagebrush (ARTR) vs. distance along the sampling transects. LARE = Lappula redowskii.

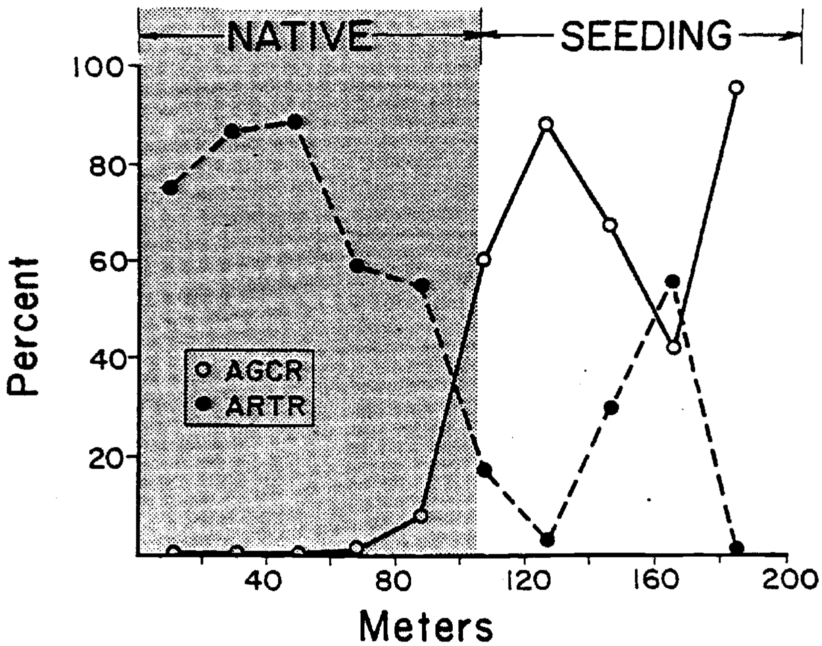

Figure 3.--Percentage of total seedlings emerging from topsoil samples from the TFA study area that were crested wheatgrass (AGCR) or big sagebrush (ARTR) vs. distance along the sampling transects.

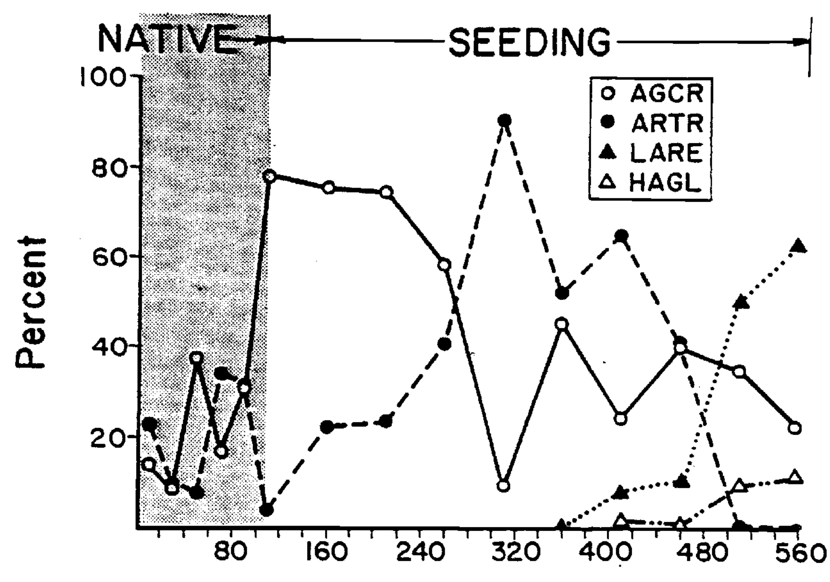

Figure 4.--Percentage of total seedlings emerging from topsoil samples from the TFC study area that were crested wheatgrass (AGCR), big sagebrush (ARTR), Lappula redowskii (LARE), or halogeton (HAGL) vs. distance along the sampling transects.

previous one, was producing a crested wheatgrass-big sagebrush biculture, not a diverse native community. Our seed reserve samples from distances beyond 360 m from the interface produced sizeable numbers of two annuals, Lappula redowskii and halogeton (Fig. 4).

In general, we found a close positive correlation between the cover of a dominant species and its potential for recruitment as estimated by seedling emergence from topsoil samples (Marlette 1982). There was little evidence to suggest any significant dispersal of propagules from the native communities into the adjacent crested wheatgrass stands.

DISCUSSION

These results show that there may be little opportunity for recruitment of native species, especially perennials, within crested wheatgrass seedings. We found no rich store of native propagules within the crested wheatgrass stands. In the four areas examined, the seed bank, as evidenced by seedling emergence from undisturbed topsoil samples, was heavily dominated by crested wheatgrass, or crested wheatgrass and big sagebrush. In the two monocultural areas, the probability of a seedling being crested wheatgrass was between 85 and 92%. Seed reserves on the other two areas reflected the composition of the vegetation; crested wheatgrass and big sagebrush comprised the bulk of emergent seedlings. The only other species contributing sizeable numbers of seedlings were two annuals.

Our results do not support the assumption that competition is the primary factor responsible for the persistence of relatively pure stands of crested wheatgrass. This does not mean that competition doesn't occur between plants within the stand. Competition may well be a factor in the survival of any seedlings that do emerge within a seeding; our data simply indicate that such cases involving native species will be relatively rare occurrences.

The results of numerous studies (Robertson and Pearse 1945, Blaisdell 1949, Hubbard 1957, Cook and Lewis 1963, Frischknecht 1963, 1968, Harris and Wilson 1970, Robertson 1972, Rittenhouse and Sneva 1976, Harris 1977), as well as the observation that native grasses often fail to persist when sown in mixtures with crested wheatgrass (Hull 1971, Holechek et al. 1981), attest to the strong competitive ability of crested wheatgrass. In addition to competing effectively for space and soil resources, crested wheatgrass has an advantage over many of the native grasses in terms of seed production (Frischknecht and Bleak 1957, Harlan 1960). In fact, Cook et al. (1958) found that if the vigor of a crested wheatgrass plant is sufficient for seed production at all, the seed produced is likely to be viable. Thus, crested wheatgrass seems to have an advantage over native grasses in both vegetative and reproductive attributes. Both its competitive ability and the limited availability of native propagules would contribute to the persistence of a crested wheatgrass monoculture.

Our results suggest that adjacent native communities do not serve as significant sources of propagules for the colonization of crested wheatgrass seedings by native species. It is well known that the number of seeds deposited at increasing distance from a parent plant generally falls off exponentially (Cook 1980), and long-range dispersal is rare in semiarid regions (Ellner and Shmida 1981). Even the achene-pappus dispersal of many composites is local and ineffective over long distances (Cook 1980). Frischknecht (1978) reported that 90% of the total progeny of big sagebrush plants were within 9 m of the parents. Johnson and Payne (1968) concluded that sagebrush plants adjacent to seedings were of no practical importance as a seed source for re-establishment.

Succession in crested wheatgrass seedings is consistent with the initial floristics model proposed by Egler (1954) and with the inhibition model of Connell and Slatyer (1977). Succession is primarily a function of what species survive a disturbance (or treatment) and what species become established immediately following the disturbance. Once established, the vegetation tends to inhibit further recruitment of other species. Chance plays an important role in such models because the initial colonization and establishment are dependent upon a number of random factors. Recruitment as the stand ages also depends largely upon probabilistic events associated with the relative abundances of propagules. Our data show that chance favors the maintenance of the monoculture rather than its successional replacement.

These results have several important implications for management. The nature of a disturbance and the differential survival of species on the disturbed area are important factors in determining subsequent species composition on the site. Plants surviving a revegetation treatment are the primary seed source for the re-establishment of their populations. Our results suggest that crested wheatgrass monocultures could be maintained with minimum effort if the existing vegetation (including rhizomes, sprouting roots, and seed reserves) was eliminated from the area prior to seeding. Such a treatment could hardly be recommended except in cases where the native vegetation had been destroyed previously. On the other hand, if the goal is to re-establish a diverse native flora on a site, seeding initially with crested wheatgrass may preclude, or at least delay, the recovery of native vegetation.

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SECTION IV.

Ecological Relationships.

Looking at Crested Wheatgrass Stands from Several Angles.

Chairman, Fred D. Provenza

The Role of Shrubs in Diversifying a Crested Wheatgrass Monoculture
Cyrus M. McKell

Hydrology of Crested Wheatgrass Seedings
Gerald F. Gifford

Black Grass Bugs *Labops hesperius* Uhler (Hemiptera: Miridae) and Other Insects in Relation to Crested Wheatgrass
B. Austin Haws

Value of Crested Wheatgrass for Big Game
Philip J. Urness

Nongame Bird Responses to Type Conversion of Sagebrush Communities
J. Kent McAdoo, Raymond A. Evans and William S. Longland

The Role of Shrubs in Diversifying a Crested Wheatgrass Monoculture

Cyrus M. McKell

ABSTRACT: Vegetation diversity and productivity of western rangelands have been reduced by selective grazing. Range improvement research in the late 1930's and 1940's suggested that controlling shrubs and seeding crested wheatgrass was a suitable answer to restoring range productivity. However, range ecosystems that resulted from widespread seeding with crested wheatgrass lack diversity in many important aspects. This paper discusses the nature of diversity and the role of shrubs in relation to the effective use of common-pool resources in range ecosystems. Shrubs can fill an ecological need in diversifying monocultures of crested wheatgrass and thus increase the spectrum of opportunity for multiple use management of public rangelands. Suitable methods for establishment and availability of seeds now make it possible to utilize superior species of shrubs in range improvement and land reclamation programs.

INTRODUCTION

Suggesting that shrubs can be used to diversify a crested wheatgrass monoculture may seem to be a great step backwards to those who consider shrubs undesirable and their control to be the first step in range improvement. However, shrubs possess many valuable characteristics useful to the productivity and stability of a rangeland ecosystem and have been described as an overlooked resource of arid lands (McKell 1975). Many shrub species, under appropriate management, can be useful components of rangeland vegetation, especially as an interplanting with crested wheatgrass (Agropyron desertorum (Fisch. ex Link) Schult.).

The purpose of this paper is to briefly look at the diversity problem in crested wheatgrass monocultures, review the nature of community diversity, examine how shrubs can contribute to grassland community stability, suggest how shrubs can enhance rangelands for multiple uses and finally, to describe ways of establishing shrubs in an existing crested wheatgrass stand.

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THE DIVERSITY PROBLEM IN CRESTED WHEATGRASS PLANTINGS

Before discussing the role of shrubs in diversifying a crested wheatgrass monoculture, I believe it would be helpful to provide a brief historical perspective to the vegetation diversity question. In the 1930's there was widespread recognition that because of intense and unregulated grazing, the western rangelands were in a deteriorated condition and getting worse. Observers at that time reasoned that overgrazing had caused sagebrush (Artemisia tridentata Nutt.) and other shrubs to invade the depleted grasslands (Cottam and Stewart 1940). Later, Ellison (1960) showed that the vegetation diversity of sagebrush-bunchgrass range had been lost through livestock grazing that selectively reduced the grasses and palatable forbs, leaving sagebrush as the dominant. This conclusion has been validated by several studies in the sagebrush region (Eggler 1941, Vale 1975, Tisdale and Hironaka 1981). These studies have established that the sagebrush-grass region is ecologically stable and that sagebrush is an integral part of the regional climax vegetation.

Remedial action appeared to be necessary in the late 1930's and 1940's as mountain ranges serving a dual purpose as watersheds and grazing lands failed to hold intense summer rains and rapid spring runoff. The result was mud and rock flows into small communities along the Wasatch Front and other mountain west towns. The report of the Secretary of Agriculture to the U. S. Senate (1936) called for research "to develop low cost methods and suitable species for 'seeding or transplanting' on 38 million acres of rangelands now so badly depleted that reasonably rapid natural revegetation appears improbable." Research efforts to find appropriate species and methods for range improvement resulted in the highly successful formula of brush control and drill-seeding with crested wheatgrass. As early as the mid-1930's, crested wheatgrass was suggested as a possible choice for seeding rangelands drier than the Wasatch Plateau, location of the Great Basin Experiment Station (Keck 1972).

Brush control, vegetation type conversions, range improvement projects and watershed protection projects sponsored by the U. S. Forest Service and the Bureau of Land Management resulted in over 4 million acres (1,600,000 ha) of foothill and desert rangeland in the 10-16 inch rainfall zone being seeded to crested wheatgrass as a principal species (Valentine et al. 1963, Robertson 1947). In some locations other *Agropyron* species were seeded because they were better suited for site conditions (Plummer et al. 1968). Mixtures of a few species or single-species stands were observed to be easier to manage under grazing use than diverse, multiple-species stands (Cook 1966).

Reinvasion of sagebrush and other shrubs into a crested wheatgrass seeding may be a function of its relative openness (Cook and Lewis 1963, Rittenhouse and Sneva 1976). Blaisdell (1949) observed that the degree of competition between sagebrush and crested wheatgrass seedlings depended largely on their relative ages. According to Frischknecht and Bleak (1957), new crested wheatgrass stands are more vulnerable to invasion of shrub seedlings than old ones. Goodwin (1956) observed sagebrush reinvasion by seed dispersal and seedling establishment from the perimeter of crested wheatgrass plantings on several seeding projects in the Great Basin. The greatest incidence of sagebrush seedlings was near the perimeter of the seeded area and in places where the crested wheatgrass stand was thin. Wasser (1982) noted that greater stand longevity occurred when species used in seeding were of similar palatability and phenology. He did not place shrub reinvasion in context with this observation, however.

Good management of seeded stands of crested wheatgrass to minimize sagebrush reinvasion is necessary to keep the stand intact long enough for grazing to pay for seeding costs. Hubbard (1956) in his work with *Purshia tridentata* seedlings concluded that wheatgrass is as severe a competitor as native vegetation. The gradual increase in sagebrush canopy cover is a prime factor in reducing stand productivity (Frischknecht 1963, Rittenhouse and Sneva 1976). From an evaluation of forty-eight study sites, Shown et al. (1969) concluded that the most stable seedings of crested wheatgrass are those located on sites where annual precipitation exceeded 10 inches (250 mm) and soils were medium in moisture holding capacity. Site unsuitability was a large factor in reinvasion by various species of sagebrush, rabbitbrush (*Chrysothamnus*), and halophytes.

Whether a closed community (Robertson and Pearse 1945) exists or not in a crested wheatgrass monoculture has an important bearing on its long term stability and longevity. Unless a stand of crested wheatgrass effectively utilizes all factors of the environment at its various phenological stages, it cannot be considered closed. Another way of stating the case is to say that the stand should have sufficient resistance to change to prevent gradual reinvasion by forbs and shrubs as well as to make optimum use of abiotic resources. An examination of the nature of community diversity would therefore help in understanding the concept as applied to a monoculture.

NATURE OF COMMUNITY DIVERSITY

According to Harper (1977), community diversity is derived from five sources:

1) Somatic polymorphism within the genotype of a species provides for different expressions of root, stem, leaf, and flower sizes and their display according to the space available. Plants in a monoculture tend to emphasize diversity within the same morphological features. West and Rea (1979) working in native sagebrush-grass communities observed that community stability is achieved more by plant plasticity than by shifts in age class distribution, although pulses of establishment occur in favorable years.

2) Age distribution grouping occurs in response to cyclic temporal periods of suitable conditions for germination and establishment. Early seedlings may have a greater opportunity for growth than later ones of the same or different species, although a few may be found in an even-aged stand. Distribution of ages within a stand may be one of the elements of diversity that permit or deny recovery after stress. In the case of a crested wheatgrass monoculture, age distribution exhibits very little diversity once full stand establishment has occurred because new seedlings are denied the opportunity for survival (Cook and Lewis 1963).

3) Genetic variants within a species provide plants that can respond to the range of conditions within sites as well as those found over a spectrum of geographic locations. Species with great genetic diversity may be expected to include genetic combinations capable of resisting stresses as well as those responding to favorable conditions in given habitats. Continued natural selection under such conditions leads to ecotype development. Crested wheatgrass is an example of a genetic complex possessing wide variability as well as extensive stress tolerance. Dewey (1983) pointed out that crested wheatgrass taxonomy is complicated because the species and subspecies can hybridize with each other. However, *A. desertorum* is always tetraploid (2n=28) and less variable than the diverse materials referred to as *A. cristatum* (L.) Gaertn. Even so, this diversity is not as wide as the sum of all plant diversities in a mixed community.

4) Diversity of microsites within the habitat is a non-plant function that is important to community diversity and provides an opportunity for a range of genetic and somatic variants to establish and persist. The safe-site concept described by Harper (1977) and elaborated for rangeland conditions by Eckert et al. (1978) is a recognition that micro-site variability provides an opportunity for seedling establishment. Once a crested wheatgrass stand is established, further seedling recruitment is very limited. Within a fully stocked stand (Hyder and Sneva 1956), most if not all safe sites have been taken or modified. Competition from mature plants is extreme during critical stress periods when growth of new seedlings is most critical.

5) Diversity of growth form, consisting of generic and family diversity in morphology and community composition, provides for a stratification of the vegetal cover as well as distribution of roots. With such diversity, many different plant

species can be accommodated in their use of light, nutrients, water, heat, etc. for optimum growth over the maximum seasonal periods of favorability. A crested wheatgrass monoculture lacks the height, distribution of leaves and roots, and phenological range that a mixed plant community of shrubs, forbs, and grasses can display. However, physiological efficiency and concentration of biomass productivity in a short favorable season help compensate for the deficiency in life-form diversity.

To cope with the above elements or sources of diversity, various species maintain their place (to avoid a losing battle of competition) by specializing. Inasmuch as the resources needed by plants are distributed in space as well as time, various specializations are possible for plants to compete or survive.

Several papers in this conference provide information about crested wheatgrass that help to evaluate its characteristics as a unique biological entity and as an excellent range forage plant. This information should be evaluated in relation to those elements discussed by Harper (1977) as ways in which a species or a group of species can attain a sufficient diversity to effectively use common-pool resources:

1) Diversity in relation to the use of different resources. Some species become specialized in their use of pool resources such as development of exclusive mycorrhizal relationships to increase phosphorus uptake. Call and McKell (1982) reported that differences in mycorrhizal inoculation response among various shrub species were an indication of their ability to colonize new sites. Many rangeland species vary in their requirements for soil nutrients, and as Harris and Wilson (1970) showed, an annual species such as *Taeniatherum caput-medusae* (L.) Nevski, with a high capacity to respond to nitrogen, can dominate a perennial species such as *Agropyron spicatum* (Pursh.) Scribn. and Smith. Field observations indicate that seedlings of the annual species grow considerably faster than the perennial seedlings. Shrubs show less response to nitrogen than grasses.

2) Use of lateral heterogeneity of microsites. The observation of clumped plant distribution in arid and semi-arid ecosystems suggests a favorability created by one species for others associated with it. Rumbaugh et al. (1981) reported that fourwing saltbush (*Atriplex canescens* (Pursh.) Nutt.) created a more favorable habitat for production of forage by crested wheatgrass than when the crested wheatgrass was grown alone. Garcia-Moya and McKell (1972) used the term "islands of fertility" to describe the more favorable soil nitrogen status under shrubs in a desert environment than in the open spaces between shrubs. Charley (1972) also noted this soil fertility phenomenon in his work in the Great Basin.

3) Use of vertical heterogenity of environments. The canopy of shrubs offers considerable protection for understory species that lack stature. Such protection may be against intense grazing or cold temperature but also carries with it the risks of competition for soil moisture and sunlight, and possibly production of allelopathic substances. Rumbaugh et al. (1981) described a favorable influence of the fourwing saltbush canopy on crested wheatgrass and concluded that a synergistic condition was created for the grass by the shrub.

4) Use of resources temporally. A group of species with diverse phenological schedules can make greater use of common pool resources than a monoculture which concentrates its demands for resources according to a single schedule. For example, Fernandez and Caldwell (1975) pointed out that considerable difference exists in the time that maximum demands are made by the root systems of the three main subspecies of *Artemisia tridentata*. The continued root activity of these shrubs at a time when crested wheatgrass is dormant suggests that a stratification of activity exists which involves but minimal shrub-grass competition during fall months. Mohammad's (1979) work with responses of crested wheatgrass and fourwing saltbush to typical fall temperatures indicates a higher level of root activity of the shrub than the grass at a day-night alternating temperature of 11-7°C.

In each of the sources of community diversity described above, as well as the various ways that species use to survive in a diverse community, it seems clear that a monospecific community lacks sufficient diversity to achieve long-term stability or to exploit all environmental resources effectively. There is ample evidence that crested wheatgrass is well-adapted to many rangeland sites, especially those that were originally dominated by big sagebrush (Shown et al. 1969). Although crested wheatgrass has been a recommended choice for inclusion in rangeland seedings, extra management inputs may be necessary to make up for the diversity normally present in a multiple-species community. In some cases the usefulness of a crested wheatgrass monoculture may be less than that possible from a diverse community. The importance of shrubs to community diversity can be argued on the basis that they broaden the sources of productivity, increase opportunities for utilization, and extend ecological stability. Because community diversity is derived from various sources, each of these factors provide a degree of stability to the plant community. However, there is no satisfactory determinant of the amount of each diversity source needed to assure community stability or to allow additional species to enter the community.

NEED FOR DIVERSITY IN CRESTED WHEATGRASS STANDS

The need for diversity in crested wheatgrass seedings may not be perceived with equal understanding among range managers. The reason for this is their perception of the role shrubs play in the use of rangelands. If a range area is used principally for spring and summer grazing of livestock, a crested wheatgrass monoculture may be a suitable vegetal cover. However, a combination of grass and shrubs would be the best for wildlife habitat.

Even though management of rangelands is mandated to be on a multiple use basis (Public Land Law Review Commission 1970), some vegetation types may be more advantageously managed for a particular use than another because of the type of vegetation, topography, and other factors. The composition of the vegetation in a management unit is a big factor in determining optimum use(s). In general, a diverse vegetation composition is more amenable to multiple uses. Rumbaugh et al. (1981) concluded that combinations of shrubs and forbs with crested wheatgrass could extend the grazing season and provide a forage resource less susceptible to attacks by various insects and diseases than monocultures of crested wheatgrass.

Extensive areas seeded in the past to crested wheatgrass as a monoculture, or areas appropriate for a range improvement or reclamation project involving seeding, should be carefully considered in relation to the place that shrubs could fill in enhancing their future uses. The major uses of rangelands are grazing, wildlife, watershed, and recreation, and each has a particular requirement for shrubs.

SHRUBS INCREASE OPPORTUNITIES FOR MULTIPLE USE

Livestock Grazing

Five main feed criteria must be considered in evaluating species suitability for rangeland grazing. They are nutritional quality, palatability, digestibility, quantity, and seasonal availability.

Crested wheatgrass does an excellent job of meeting the first four conditions, but in the fifth criteria its nutritional quality is low in the post-maturity stage (Otsyina et al. 1982, Cook 1972). The best time for grazing use of crested wheatgrass is in the spring and early summer. Normally this is when livestock are in transition from winter grazing on the desert to summer grazing in the mountains.

Including shrubs as a protein source in crested wheatgrass monocultures has been suggested as a way to improve their use for fall and winter grazing (Monson 1980, Otsyina et al. 1982). Rumbaugh et al. (1981) reported the production of crude protein in August to be over ten times greater in plots containing fourwing saltbush and crested wheatgrass as compared with crested wheatgrass alone. In an October-November study grazing with fistulated sheep at the Nephi Field Station in central Utah, Otsyina (1983) found that diet of sheep on a grass/shrub pasture was adequate in digestible protein to sustain gestation while those on a grass alone pasture were deficient. The conclusion reached from these studies is that shrubs interplanted into crested wheatgrass monoculture plantings could provide adequate feed quality as well as extend the grazing season. Concern for the effect of grazing on regrowth of the shrub must be registered. Inasmuch as many shrubs are not fully dormant in the winter, intensive grazing must be approached carefully until further research is done. Observations of the shrubs following the grazing study at the Nephi Field Station indicated that shrubs are variable in their regrowth. In other studies spring and summer clipping appears to be more damaging than at any other season.

Wildlife Habitat

Because shrubs are used by wildlife for feed, escape cover, and thermal protection, they are a critical component of wildlife habitat. Each species of wildlife has its own set of habitat requirements (Institute for Land Rehabilitation 1978) for nourishment, survival, and reproduction. Wildlife habitat requirements often overlap as would be expected where many animal species are present. Thus, diversity is the main element of habitat quality to meet as many animal species needs as possible. Areas of sagebrush converted to crested wheatgrass can still be suitable sage grouse habitat if areas of sagebrush are left or if some brush reinvasion occurs. In an analysis of quality sage grouse habitat Phillips (1972) reported that sagebrush density of 2000 plants per acre was optimum for food and cover. Sagebrush stands of between 5 and 10 percent canopy cover afford the best conditions for growth of understory grasses and forbs. Deer habitat can be enhanced by open spaces seeded to crested wheatgrass as long as the openings are not any larger than 0.4 to 0.8 km wide (Institute for Land Rehabilitation 1978). Welch and McArthur (1979) identified several sagebrush accessions that meet protein requirements for winter deer feed. They pointed to the feasibility of using sagebrush and other shrubs for game range improvement. This follows earlier advice by Plummer et al. (1968).

Thus, shrubs are an essential part of most all wildlife habitats. Areas cleared of shrubby vegetation and seeded to crested wheatgrass should include selected shrub species in the seeding. If shrubs are not included in the seeding, eventually some shrubs will reinvade to provide diversity needed by wildlife.

Watershed

Adequate vegetal cover of the soil is one of the most critical aspects of a functioning watershed. Watershed condition can be measured in terms of minimal sediment yield and optimal water infiltration and yield. Loss of understory vegetation will increase soil erosion (Branson et al. 1973). Because deep percolation enhances watershed yield, any means to control shrubs might be construed as a means to increase waterflow. However, another force comes into play -- the overall stability of the soil mantle. Experience in 1983 and 1984 with accelerated spring runoff along the Wasatch Front of central Utah bears out the need for deep soil stability that is assisted by shrub roots permeating the saturated soil to the geologic parent material. A diverse cover of both deep rooted shrubs and relatively shallow-rooted grasses seems to be the best answer.

Surface Mining

Surface mining is only a temporary land use which by law (U. S. Congress 1977) must be ameliorated by replacement of spoil and topsoil, and seeding to a diverse and productive plant cover. Prevention of erosion and restoration of productivity are two key functions that justify reclamation costs that often range upwards to $2,500 per acre. Although regulations give priority to native species in the seeding mix, crested wheatgrass is frequently included with western wheatgrass (Agropyron smithii Rydb.), fourwing saltbush and sagebrush in seed mixtures (Hansen 1982). Stringent rules promulgated by the Office of Surface Mining require careful monitoring of species diversity to ensure that a broad spectrum of species and their attendant ecological stability results from seeding operations.

Recreational Use

Recreational use of rangelands includes many different activities as well as value judgements concerning environmental quality. How much a diverse vegetation adds to the recreation experience is not known. Questionnaires on attitudes tend to show that pristine-looking landscape rates higher in environmental quality than disturbed areas, and the greater the disturbance the lower the recreational experience. Whether shrubs growing in a seeded crested wheatgrass stand would raise the quality of experience of recreation visitors to the rangelands is doubtful, but if a shrub planting attracts a herd of antlered deer during the third week in October in Utah, there would be no question about a heightened recreational experience for a hunter with a loaded rifle!

WAYS TO ESTABLISH SHRUBS IN A RANGELAND SEEDED TO CRESTED WHEATGRASS

Inclusion of shrub seeds in a seeding mix is the best way to assure their presence in the resulting stand (Plummer et al. 1968). Large numbers of shrub seeds are being planted in the Intermountain West today as contrasted with ten years ago. Fourwing saltbush is especially favored as a species for seeding areas to be reclaimed from surface mining. Rangeland seedings for grazing are also now including palatable shrubs. Dependable seed supplies and improvement of techniques may be given credit for this.[1]

Shrubs seeded directly into existing crested wheatgrass stands face extreme odds for establishment (Hyder and Sneva 1956). The dense concentration of roots near the surface precludes shrub seedling root growth into moist soil. Van Epps and McKell (1977) reported success in shrub establishment by discing out three rows of crested wheatgrass and seeding in the open space thus created. No shrub seedlings were found in the space adjacent to the crested wheatgrass--thus indicating an area of high risk. Transplanting container-grown plantlets provides a means for establishing shrubs in an existing grass stand. Thousands of shrub seedlings were hand planted to diversify crested wheatgrass pastures at the Nephi Station in readiness for a grazing study (Otsyina 1983). This same technique has been used to establish shrubs in reclamation study sites in the Uinta basin of eastern Utah where rainfall averages below 7.0 inches (175 mm) (Institute for Land Rehabilitation 1979). Millions of container-grown shrubs have been transplanted to reclamation sites on a routine basis, thus providing assurance of the success available by following recommended procedures (Hansen 1982).

SUMMARY

By their very nature, crested wheatgrass monocultures lack diversity in many aspects. The uniformity obtained with this outstanding species overcomes some of the deficiencies that would otherwise occur with a species that is less vigorous, less productive and only moderately adapted to stress. The choice of crested wheatgrass for seeding western rangelands was indeed wise, but selected shrubs can help diversify the plant community to make it more stable, improve the use efficiency of environmental factors, and enhance the management of seeded rangelands for multiple uses. Establishment of shrubs by direct seeding or transplanting can be done with success.

[1]Roger Stewart. 1983. Personal communication from the Manager of NPI seed collections and seed processing facility, Ephriam, Utah.

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Hydrology of Crested Wheatgrass Seedings

Gerald F. Gifford

ABSTRACT: Ungrazed crested wheatgrass seedings may intercept from 7 to 22 percent of the annual precipitation. Infiltration rates following seeding are not particularly impacted on coarse-textured soils characteristic of pinyon-juniper sites but on medium-textured soils (and especially if plowing is involved) a reduction in infiltration rates may occur. Seeded sites exhibit large variability in both time and space in terms of measured infiltration rates. Soil water is usually increased through seeding former pinyon-juniper and sagebrush sites. Sediment is the primary water quality problem on seeded areas; chemical water quality is usually good.

INTRODUCTION

During the past several decades many thousands of acres of crested wheatgrass (Agropyron cristatum or A. desertorum) have been seeded on western rangelands. The hydrologic impacts of these seedings have not been well documented, but changes in infiltration, soil water recharge, evapotranspiration and perhaps even groundwater recharge might be expected, with the absolute magnitude of such changes being a function of specific site characteristics. The objective of this paper is to briefly review hydrologic studies which relate to crested wheatgrass seedings as a starting point for those who may want to explore the topic in greater detail.

HYDROLOGY OF CRESTED WHEATGRASS SEEDINGS

Interception

Interception involves wetting of various segments of a plant community (live vegetal material, litter, rock) and the eventual loss of that water through evaporation. Precipitation that eventually reaches the mineral soil surface is called throughfall. Though interception studies on crested wheatgrass seedings are lacking, interception values for several grass species have been tabulated by Branson et al. (1981), with values ranging from .01 to .51 cm on a per-storm basis. Interception characteristics of pinyon (Pinus spp.), juniper (Juniperus spp.), and sagebrush (Artemisia spp.), plants commonly occurring in crested wheatgrass seedings, have been outlined by Gifford (1975a) and Sturges (1979).

Calculations by Gifford (1975b) for an ungrazed seeding in southeastern Utah indicate that from 12 to 22 percent of the annual precipitation may be lost to interception, depending on pinyon-juniper debris disposal techniques. Similar calculations for a site in southwestern Utah indicated a potential loss of from 7 to 18 percent of the annual precipitation.

Infiltration

Infiltration studies on crested wheatgrass seedings have been reported by several researchers. Blackburn and Skau (1974) and Blackburn (1973) found little change in infiltration rates several years after seeding on several sites in Nevada.

Rather extensive studies have been made in Utah regarding surface soil infiltration rates on seeded pinyon-juniper sites (Williams et al. 1969 and 1972, Gifford et al. 1970, Loope and Gifford 1972, Buckhouse and Gifford 1976b, Busby and Gifford 1981). In essence, these studies have shown that infiltration and interrill erosion rates on chained and seeded sites were not particularly affected by the treatment practice. If impacts occur they are most pronounced on sites where debris has been windrowed (lots of mechanical disturbance), and the impact is probably slightly negative.

Near Blanding in southeastern Utah, part of an observed reduction in infiltration rates on a chained (windrowed) and seeded treatment appeared related to destruction of cryptogamic soil crusts (Loope and Gifford 1972). However, the reduction apparently is not permanent, because total

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protection (no grazing by domestic livestock) of the same windrowed and seeded site for a period of six years was sufficient for recovery of infiltration rates (but not the cryptogamic cover) (Buckhouse and Gifford 1976b).

Infiltration studies on a plowed and seeded silty loam big sagebrush (Artemisia tridentata) site in southern Idaho have shown that there was a significant decline in infiltration rates over a 2- or 3-year period (Gifford 1972, Gifford and Busby 1974, Gifford 1982a). Grazing did not cause a further reduction in infiltration rates beyond that caused by the plowing, but did appear to eliminate seasonal trends and recovery to pre-plowing rates appeared impossible as long as grazing continued. Gifford and Skau (1967) also found that plowing prior to seeding reduced infiltration rates on two sites in Eastgate Basin, Nevada.

Little is known regarding seasonal and yearly infiltration rate trends on seeded sites, but rather dramatic changes with time were reported for an ungrazed site in southeastern Utah (Gifford 1979). Grazing appears to reduce the temporal variability of infiltration. Springer and Gifford (1980) discuss the use of a normal or log-normal distribution for describing measured infiltration rates on a seeded site in southern Idaho.

Spatial variability studies of infiltration rates as a function of three seasons, two different instruments (sprinkling rainfall simulator and double-ring infiltrometer), and two grazing intensities were conducted by Achouri and Gifford (1984) and Merzougui and Gifford (manuscript submitted) on a seeded site near Eureka, Utah. Use of autocorrelograms and semi-variograms on a two-meter grid spacing showed a complete lack of variance structure among measured infiltration rates regardless of treatment. Spring infiltration rates were significantly higher than summer or fall rates; moderate grazing reduced infiltration rates by a factor of three over an ungrazed area protected for over 20 years; and the rainfall simulator gave significantly lower infiltration rates (by a factor of 2 to 3) than rates measured with a double-ring infiltrometer.

Coefficients for use in Philip's infiltration equation have been derived for a number of seeded sites in the western U.S. by Jaynes and Gifford (1981). Applicability of Kostiakov's, Horton's and Philip's infiltration equations to the representation of plant community infiltration rates has been examined by Gifford (1976). Relationships between steady-state infiltration velocities as measured with double-ring and rainfall simulation devices, along with the influence of antecedent plot moisture ("wet" vs "dry") have been presented by Aboulabbes et al. (1985).

Factors influencing infiltration.--Williams et al. (1972), Gifford (1972), Blackburn (1973), Gifford and Skau (1967), Gifford and Busby (1974), and Busby and Gifford (1981) have all studied various site factors which influence infiltration rates. Busby and Gifford (1981) found 21 different variables that explained significant amounts of variation in infiltration rates on seeded sites. However, none of the variables proved consistently useful for explaining variation in infiltration on all vegetation-conversion/grazing-condition combinations studied. Their results are typical of results obtained in the other studies.

Results presented by Blackburn (1973) in Nevada are similar in that the importance of measured site factors in predicting infiltration rates varied from one watershed to another. In general the rate at which water entered the soil profile was governed mainly by the extent and morphology of the surface soil horizon in interspace areas between plants. The influence of cover on infiltration was highly variable. Hessary and Gifford (1979) point out that seeding does not guarantee an increase in plant cover over that originally present.

The relationship of selected rangeland vegetation characteristics and soil physical properties to various infiltration coefficients in Kostiakov's, Horton's, and Philip's infiltration equations was studied on 13 seeded pinyon-juniper sites in Utah (Gifford 1978). Based on an analysis of data pooled over 12 of the 13 sites, it appeared that coefficients in Kostiakov's equation were related more to vegetation factors, while coefficients in Philip's equation were more related to soil factors. The single coefficient in Horton's equation was somewhat intermediate, representing both vegetation and soil influences. It was concluded that perhaps changes in use or intensities of use could be detected through changes encountered in infiltration coefficients, with emphasis on either vegetation or soil factors or both, depending on the equation or model used.

Published literature (Gifford 1982a, Busby and Gifford 1981, Buckhouse and Gifford 1976b) has indicated that grazing does affect infiltration rates on seeded sites. Impact of burning on infiltration rates is apparently related to site characteristics (Roundy et al. 1978, Buckhouse and Gifford 1976b). The effects of incremental surface soil depths on infiltration rates, erosion, chemical water quality, plant production, transpiration ratios, and nitrogen mineralization rates have been studied on a seeded area in southeastern Utah (Lyons and Gifford 1980a,b).

Soil Water Studies

Soil water studies described by Gifford and Shaw (1973) and Gifford (1982b) indicate that pinyon-juniper sites cleared and seeded to crested wheatgrass almost always develop greater soil water contents. The same is often true on big sagebrush sites (Hull and Klomp 1974). Grazing had little impact on soil water patterns on a seeded site in southeastern Utah, but burning of pinyon-juniper debris on another seeded area increased soil water beginning the second year (Gifford 1982b).

Seeding of crested wheatgrass in conjunction with contour furrowing has been very successful in Montana. This treatment combination increased total water infiltration and soil water content (Branson et al. 1962, Soiseth et al. 1979). Similar treatments on marine shales in Utah were less successful (Wein and West 1971).

Bleak and Keller (1973) found that water requirements of several Agropyrons and Elymus junceus averaged from 429 to 823 ml water/g dry matter, depending on harvest date. Black (1968), Power and Alessi (1970) and Williams et al. (1979)

have all shown that water use efficiencies of crested wheatgrass can be improved through application of nitrogen fertilizer.

WATER BUDGETS

Even though evapotranspiration approximates precipitation on many crested wheatgrass seedings, the only published approximate annual water budgets are those of Gifford (1975b) for two sites in southern Utah. His calculations indicated that most of the 250 mm annual precipitation falling on each treatment was lost through evapotranspiration, with much of the balance lost through interception.

Runoff

Other than rainfall simulator studies already described there has been only one runoff study utilizing natural rainfall on seeded crested wheatgrass ranges. In Utah, Gifford (1973) found during a five-year study that runoff from .04-hectare runoff plots on seeded pinyon-juniper sites (chained-with-windrowing) yielded 1.2 to 5 times more water during a runoff event than similar woodland plots. Runoff from seeded debris-in-place plots was equal to or less than that measured from natural woodland for all storms. On these particular sites (perhaps 250 mm annual precipitation) all runoff results from high intensity convectional thunderstorms during the approximate period June 15 to September 15. Results from this study indicate strongly that debris-disposal techniques are the key to minimizing runoff from seeded pinyon-juniper sites. Because infiltration rates are only slightly affected by chaining and seeding activities (at least on sites in Utah and perhaps also in Nevada), the runoff differences are apparently the result of debris and depressions left from uprooting trees which simply hold water on site until it has the opportunity to infiltrate.

Water Quality

Sediment is the most important water quality parameter associated with seeded crested wheatgrass stands. Studies of 28 seeded sites throughout central and southern Utah have shown that point measures of interrill erosion are, for the most part, not increased by chaining and seeding activities (Williams et al. 1969, Gifford et al. 1970, Buckhouse and Gifford 1976b, Busby and Gifford 1981). Based on a smaller sample, the same appears true in Nevada (Blackburn 1973).

Data from .04-hectare runoff plots in Utah are in agreement with the above with regard to seedings on chained pinyon-juniper sites (debris-in-place treatments). But on debris-windrowed treatments, 1.6 to 6 times more sediment can be expected from the windrowed areas than from the adjacent woodland when runoff exceeds about 0.1 cm (Gifford 1973).

Gifford and Busby (1974) noted an increased potential for interrill erosion following plowing and seeding on a site in southern Idaho.

Factors Influencing Erosion.--Factors influencing erosion on seeded crested wheatgrass sites have been identified in a very general way. Though numerous sites have been studied (Gifford and Skau 1967, Williams et al. 1972, Blackburn 1973, Gifford and Busby 1974, Busby and Gifford 1981), factors that influence interrill erosion are so variable from one geographic location to another that no consistent relation has been found. No studies have been published that deal with both rill and interrill erosion.

Other Water Quality Parameters.--Buckhouse and Gifford (1976a) collected baseline water quality data from three treatments (including two seeded areas) during one field season on a pinyon-juniper study site in southeastern Utah. This was followed by another season of sampling where secondary treatments were imposed, consisting of controlled burning of a seeded debris-in-place site and livestock grazing of a seeded debris-windrowed site. A Rocky Mountain infiltrometer was used to create simulated, high intensity rainstorms on the area. Results of the study indicated that potential public health hazards of livestock grazing of seeded crested wheatgrass range on gentle slopes are minimal. As for nutrient release following burning, significantly increased amounts of phosphorus and potassium were measured season long in overland flow on the chained and seeded with debris-left-in-place site. No significant changes were detected in calcium, sodium, or nitrate-nitrogen contents in the runoff due to differences in land treatment.

Lyons and Gifford (1980a) found that as surface soils were removed on a seeded site in both southeastern and southwestern Utah that potassium concentrations in runoff waters decreased with soil depth, but phosphorus concentrations did not.

SUMMARY

Hydrologic features of crested wheatgrass seedings have been briefly reviewed with respect to interception, infiltration, soil water, runoff, and water quality. Most of the available literature concentrates on the impacts of seeding on infiltration rates and interrill erosion. In this regard, it would appear that hydrology of former pinyon-juniper sites has been only slightly affected by seeding, the main effect being an increase in soil water. The same is probably true on former big sagebrush sites. Plowing with seeding may significantly reduce infiltration rates on medium textured soils.

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Black Grass Bugs (Labops hesperius) Uhler (Hemiptera: Miridae) and Other Insects in Relation to Crested Wheatgrass

B. Austin Haws and George E. Bohart

ABSTRACT: The history and present status of entomological observations and research in Utah and other states as related to crested wheatgrass is reviewed. The black grass bug Labops hesperius Uhler is the principal insect discussed but a few other major insects and grasses involved in resistance studies are considered. Research methods and six strategies using Integrated Interdisciplinary Pest Management (IIPM) procedures of insect control are presented. Approximately 160 insects collected from crested wheatgrass are classified as to their beneficial or injurious impacts. Grasses along highways as sources of problems with insects and their weed hosts are described. Reasons that insect-free plants are needed for standardization of range grass research are explained.

ACKNOWLEDGMENTS: The authors are indebted to numerous individuals and institutions who have helped in many ways in the planning, execution, and the financial or human resource support of some of the projects reported in this paper. Recognition is given to them through the citation of their written contributions.

Special thanks are given to those who provided photographs: E. J. Araya, P. S. Brewer, W. F. Campbell, E. M. Coombs, W. P. Nye, and J. Spillett. The assistance of A. H. Roe in use of his computer talents and the editorial expertise of G. H. Haws have greatly facilitated revisions of the manuscript.

INTRODUCTION

This paper will briefly overview studies conducted at Utah State University (USU) of range insects in relation to crested wheatgrass, mainly Fairway [Agropyron cristatum (L.) Gaert.] and standard [A. desertorum (Fisch. ex Link) Schult.], and review the reports of others. The present status of the studies and needs for future research are discussed. Our research aim is to improve the quality, quantity, and longevity of crested wheatgrass (and other grasses) by devéloping range management practices to control injurious insects and protect beneficial ones.

During the past 14 to 15 years, many new details of the biology of several insects directly or indirectly affecting crested wheatgrass have been learned in Utah and other western states, including Arizona, Colorado, Nevada, New Mexico, Montana, Oregon, and Wyoming.

We understood at the start of our studies in Utah that a major aspect of the insect problem would be the black grass bug Labops hesperius Uhler. We got this impression from some of the literature, such as Denning (1948), who referred to this insect as the crested wheatgrass bug. Markgraff (1974) stated that Labops hesperius was first described in 1872 from specimens collected in Colorado and Montana and that only four or five studies of the insect had been conducted to that time. We now know that wherever Labops hesperius is present nearly all introduced and native grasses are hosts to some degree. Several black grass bugs of similar appearance occur in crested wheatgrass, notably Irbisia species (Hansen 1986), but unless otherwise indicated we refer to Labops (Fig. 1).

The most acceptable solutions to rangeland problems will require interdisciplinary consideration of all major components of rangeland ecosystems and the effects of manipulating any components on the rest of the system. Our rangeland insect research has been guided by these principles. Researchers have developed insect pest control strategies known as Integrated Pest Management (IPM) (Metcalf and Luckmann 1982, Huffaker 1980). To clarify this statement of methodology, we have added "Interdisciplinary" (IIPM). In IIPM, a pest is considered to be any agent that decreases the quantity, quality, or longevity of target plants (i.e., insects, mites, nematodes, diseases, weeds, rodents or larger animals). IIPM specialists (such as those in soils, plant science, entomology, plant

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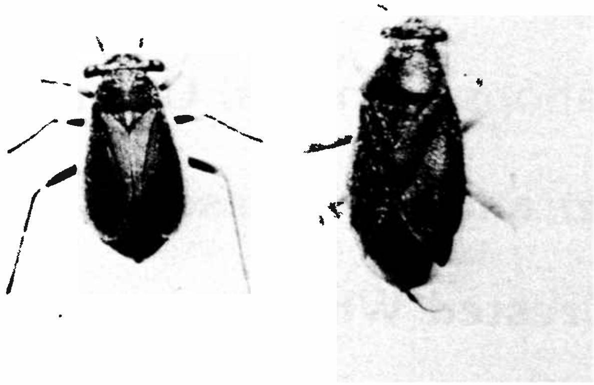


Figure 1.--Black grass bug adults: Irbisia brachycera (right) with completely black wings is often mistaken for Labops hesperius (left), distinguished by buff-colored margins around the borders of its wings.

pathology, economics, climatology, ranching, etc.) try to integrate their knowledge and experience into effective pest control strategies that are economically and environmentally acceptable. Potential benefits of the IIPM approach are discussed by Haws (1979).

Because the taxonomic classification of certain grasses has recently been changed, the authors have faced a problem of consistency in using the new nomenclature. It was decided that generally names written in earlier publications will not be changed, with few exceptions. Where possible the new names are used. The recent publications of Dewey (1983) and Barkworth et al. (1983) contain the new terminology.

RANGE GRASS INSECTS IN GENERAL

For this symposium the authors have examined their collections and records of crested wheatgrass insects. It has not been possible to sort and list all of the insects now on record, but those collected by G. E. Bohart in 1973-4 from Curlew Valley, Utah near the north shore of Great Salt Lake have been identified as far as possible (Appendix). These insects were collected by regular sweepings with an insect net throughout the season. Moths were generally so damaged by sweeping that they could not be identified and are therefore poorly represented in the collection. Fast flying insects, such as mature grasshoppers, usually evaded capture. For unknown reasons some of the major insects found in crested wheatgrass elsewhere have not been found in the Curlew Valley, e.g. Labops spp. Only a few specimens of Irbisia spp. were collected.

The collection illustrates four important facts about grassland insects: (1) It demonstrates the number and variety of insects that occur on range grasses and indicates briefly the possible role of each insect or group. (2) It presents an overview of the present status of knowledge about insects in rangeland ecosystems. (3) It underlines the rather primitive state of taxonomic work relating to insects of crested wheatgrass and many other rangeland plants. (4) It shows the practical and scientific limits of utility of the information available. The following notes provide some knowledge about the insects listed in the Appendix.

1. Many specimens can only be identified to genus at best and some of these names may not be acceptable to all taxonomists. It will take years to obtain reliable taxonomic names for many rangeland insects because often the specimens must be sent to specialists for identification. This list of insects does not represent the insects found everywhere in crested wheatgrass. To help solve problems relating to insects, specific collections are needed for each problem area.

2. Even when a species is positively identified, biological information concerning it often is lacking, scarce, or incomplete. Impacts of the insects listed are often based on generalized "common knowledge" of a particular group of insects. For example we may know that a species belongs to a group which is parasitic, phytophagous, or predaceous. Much of the information is drawn from annotations in exiting catalogues.

3. The behaviors and impacts of immature and adult forms of a species may differ completely. A given insect life stage may have more than one ecological role. Some insects may exhibit both injurious and beneficial roles. The impact column indicates the role of the most "important" stage of the insect as we understand it. The assessment of impacts is also partially based on the number of insects collected and the frequency of their capture during sampling. Insect species captured only once or twice were generally considered to be accidental visitors, although such an assessment is obviously subject to error.

4. Approximately 70 percent of the species listed could be considered neutral or beneficial (from the human point of view) to crested wheatgrass, that is, they are decomposers of organic matter, parasites, predators, helpful in soil genesis or in penetration of water and air into the soil, etc. However, some parasites would have to be considered harmful when they are hyperparasitic on primary beneficial parasites.

5. The majority of plant feeding insects were not found in sufficient numbers to suggest they were having a detrimental influence on the plants, but, as is noted, others have at least the potential of being substantial pests of crested wheatgrass. Several well known grass-infesting members of the family Miridae, such as Leptoterna, Litomiris, and Trigonotylus, were present in populations sufficient to damage the grass.

Several other individuals or groups have studied (or are now studying) rangeland grass-inhabiting insects. Knight (1982) listed 1,095 insect species collected during 1978-1979 from crested wheatgrass and other grasses in the Great Basin Experimental Range in Ephraim Canyon, Utah. This study was USU's first attempt to compile a list of insects found in grassland communities. Knight selected the following insect groups for future biological studies because of their apparent importance: leafhoppers, scale insects, click beetles (wireworms), thrips, ground beetles (mostly beneficial--26 species found), and snout beetles (weevils). Knight indicated that most of the injurious insects he observed appeared to feed indiscriminately on all the grasses. In Nevada, Knight and Lauderdale (1982) reported that Irbisia brachycera preferred feeding on squirreltail [Elymus elymoides (Raf.) Swezey], crested wheatgrass and intermediate wheatgrass [Elytrigia intermedia (Host) Nevski], but also fed on most other grasses. Thomas and Werner (1981) have published a list of grass feeding insects of western ranges.

The kinds and numbers of nematodes present in crested wheatgrass and other range grasses are largely unknown. Examination of soil samples (220 grams) from crested wheatgrass enclosures in Diamond Fork Canyon, Utah showed 8 Tylenchorhynchus spp. from a plot treated with a nematacide, and 80 Tylenchorhynchus spp. and Pratylenchus neglectus from an untreated plot. Research with nematodes associated with range grasses has been expanded. This work will be important in the grass breeding programs of the USDA Agricultural Research Service (ARS) in the search for pest-resistant grasses.

Through the years spittlebugs [Philaronia bilineata (Say)] have been collected on crested wheatgrass in Salina Canyon and from many other places in Utah. Severe damage by these insects has been observed, but little is known concerning their biology or economic impacts. These observations are of concern because one of the most destructive pests of grass reported by entomologists in Monterrey, Mexico are the spittlebugs commonly called "mosca pinta" (pinkfly). These insects are not flies, but belong to the Order Homoptera, (Aeneolamia spp. and Prosapia spp.). Spittlebugs are able to destroy or severely damage even the tough semitropical grasses (Enkerlin and Velarde 1973).

Hewitt and Onsager (1982) state that grasshoppers are considered to be the most important invertebrate pests on western rangelands. They report that one grasshopper per square yard is estimated to consume 12 pounds of forage per acre (this represents a generalization because grasshoppers vary considerably in size and food preferences). There are approximately 120 species of grasshoppers listed for Colorado (Capinera and Sechrist 1982).

The average number of grasshoppers per square yard in the United States from 1936-1969 was calculated to be 3.84 per square yard. Grasshoppers are reported to destroy 21-23 percent of western rangeland forage each year. In 1984, grasshoppers were estimated to be 50-100 per yard on some ranges in central Utah. Generally, eight grasshoppers per square yard is considered to be the approximate level of abundance justifying control with insecticides. Those who doubt the capacity of insects to consume vegetation had a demonstration in 1984-5. The grasshoppers consumed all of the grass on some ranges, then the sagebrush, rabbitbrush, musk thistle, and finally pinyon and juniper trees.

The economic benefits of chemical control of grasshoppers depend on the value of the forage being destroyed, costs of control, and other factors such as the weight losses of livestock, costs of relocating livestock, additional costs for feed, and forced sales of livestock. Even though many of approximately 600 grasshopper species found in the United States have different host preferences, they all contribute to reducing available forage.

DISTRIBUTION, ABUNDANCE, HOSTS, AND BEHAVIORS OF BLACK GRASS BUGS

The distribution of L. hesperius appears to be related to cool or cold temperatures. First instar nymphs have often been seen feeding a few yards from melting snow banks. We have observed feeding on crested wheatgrass when the air temperature was 22°F (-5.5°C), but at the same time the temperature in the crowns of the crested wheatgrass was 45°F (7.2°C). Evidently, the microhabitats where the insects live need to be considered in calculating correlations of insect behavior with temperatures. This early development of the bugs puts them out of phase with many other animals (including beneficial insects) and provides a period when the insects may be controlled without endangering other organisms. In the northwest, Todd and Kamm (1974) found grass bugs from the native sagebrush communities to the high deserts of the mountain parks near the timber line. Bugs were sparse in native vegetation and plentiful in modified, reseeded wheatgrasses.

Knowlton (1967) indicated that in the higher mountainous areas of Utah 95-99 percent of the infestations of grass bugs were on crested wheatgreass. Irbisia spp. were more commonly found at lower elevations and were often the dominant grass bugs in highway grasses.

Thirty-six native and introduced grasses are reported to have been fed upon by L. hesperius (Haws 1978). In 1972 Haws reported collecting 900 bugs per sweep (L. hesperius) from crested wheatgrass growing in Diamond Fork Canyon, Utah. Much lower populations are reported in some areas of Utah: 45-90 at Sterling Ranch in the same canyon in 1977; an average of 38 bugs per sweep in Cedar Breaks (Haws 1978).

Labops hesperius has not been found in crested wheatgrass in several areas of Utah such as certain ranges in Duchesne County and western Box Elder County. There is no verifiable evidence to explain this lack of infestation, inasmuch as the bugs infest grasses in 18 western states and Canada (Ostlie 1979). We have speculated that isolation from sources of bug infestation (such as bug-infested freeways) or unfavorable winter conditions may not permit the bugs to become established or the eggs to survive in some areas.

UTAH STUDIES ON BLACK GRASS BUGS (LABOPS AND IRBISIA)

Historical Background and Overview

Although crested wheatgrass and other introduced grasses were established in Utah as early as 1942, and acreages had increased substantially by 1966, Cook (1966, 1967) did not mention problems with insects even though black grass bugs were already of much concern to state and federal agencies, ranchers, and entomologists.

In Utah, Knowlton (1945, 1967) and Lindsay (1970) reported damage to thousands of acres of rangeland grasses by black grass bugs. The Federal Plant Pest Control Division, now known as the Animal and Plant Health Inspection Service (APHIS), had detected widespread grass bug damage in its surveys. APHIS had attempted to solve the problem in several areas by applying insecticides to infested ranges, especially in the East Fork of the Sevier River, Utah. A series of letters and reports from Thornley[1] provide valuable information about the range grass/insect situation in 1967. Thornley wrote that:

1. Problems with the black grass bug had been observed periodically for the past 25 years (approximately since 1942), but infestations had been "spotty" and irregular. (The USU insect collection has specimens of Labops hesperius collected at least as early as 1939).

2. The bugs seemed to thrive best at elevations between 6,000-9,000 feet (1829-2743 m).

3. Crested wheatgrass and intermediate wheatgrass appeared to be the favorite host plants, but native grasses were acceptable if there were many bugs.

4. Populations of bugs in excess of 1,000 per square foot (0.093 m^2) were observed (Fig. 2). Feeding by the bugs resulted in removal of the green color from grasses, and left the grass straw colored. Severely damaged plants failed to produce seed.

5. Scant information was available about where or when the insects laid their eggs, or about other details concerning the life cycle and the seasonal history of black grass bugs.

6. Ninety-five percent malathion applied at 8 oz per acre by fixed-wing aircraft reduced the populations of bugs from more than 1,000 to about one per square foot (0.093m^2). Results were variable, partly because there was little biological information upon which to base control programs. Sometimes control was ineffective because the insecticide was applied after the female bugs had laid their eggs. Young nymphs and the adult bugs sometimes were not found early enough to implement successful control programs.

Studies by USU entomologists and others have since confirmed most observations reported by Thornley.

An administrative report from New Mexico (Brandt)[2] stated that Labops hesperius infested about a quarter of an acre (0.618 ha) of crested wheatgrass in the Laguna Seca Allotment in 1962. By 1963 an infestation of 500 acres (1,235.5 ha) was discovered and control was attempted by applying malathion with a mist blower. An estimated 10,000 acres (24,710 ha) were reported infested in 1966. Chemical controls were tried with variable success. Some unanswered questions Brandt pointed out were:

Figure 2.--Nymphs of Labops hesperius on the ground and leaves of crested wheatgrass on Whiteman Bench, Garfield County, Utah. There are about 800 bugs per square foot in this photograph.

Where are the insect eggs laid? How can outbreaks of the pest be forecast? What factors influence the infestation patterns? What are the sources of infestation? What are the preferred plant hosts and why are they preferred? How many generations of the bugs are there per year? What are effective methods of control? Some, but not all, of these questions can now be answered.

Dewey[3] has conducted genetic and breeding research with grasses since 1956. He has traveled extensively, collecting and examining grasses in the United States, Iran, Russia, and China. He indicates that he and other scientists had a general lack of awareness of range grass insects until about 1972, when the USDA/ARS Crops Laboratory staff at Logan, Utah began cooperative studies with USU entomologists. Grass bugs have not been a problem in the ARS experimental plots (they usually are kept too clean--free of dead stems and debris--and they are harvested frequently) but billbugs (Coleoptera: Curculionidae) have been a problem (Haws 1982a).

Details of these historical beginnings in Utah and subsequent interstate cooperative research are given in various publications and reports (Haws 1972, 1975, 1978, 1982a, 1982b; Haws et al. 1973). A detailed review of the history, distribution, hosts and status of research on Labops has been written by Ostlie (1979). The Society for Range Management commissioned a publication concerning range insects (Hewitt et al. 1974). A review of rangeland entomology has been published (Watts et al. 1982).

Tasks undertaken by entomologists, and their associates from other disciplines, concerning black

[1] Thornley, H. F. 1967. Letter to Jim R. Dutton, Regional Supervisor. In Range Insect Literature File R-56, Utah State Univ., Logan. Other valuable letters: R-55, 57, 59, 88, and 89.

[2] Brandt, C. J. 1966. Administrative study of Labops hesperius. Santa Fe National Forest. In Range Insect Literature File R-4, Utah State Univ., Logan.

[3] D. R. Dewey, USDA/ARS, Logan, Utah, personal communication, 22 Feb. 1984.

grass bugs include: (1) finding out where the bugs lay their eggs, (2) determining where and how fast the eggs and immature forms (nymphs) develop, (3) learning what the impacts of all life forms of the bugs are and when, where, and how each might be most vulnerable to strategies for interrupting the life cycle, (4) developing basic principles and practical methods of control (cultural, biological, plant resistance, or chemical).

Our main objective in Utah has been to develop strategies for controlling black grass bugs infesting all rangeland grasses--not only crested wheatgrass. This symposium has influenced the authors to review their observations and research as specifically related to crested wheatgrass. However, many of the observations and principles presented here apply to other grasses as well. Our present research also includes studies of insects of rangeland forbs and shrubs as related to range improvement and management, and rehabilitation of perturbed sites such as surface mines.

Black Grass Bug Development--Eggs, Nymphs, Adults

To formulate management strategies for Labops control, it was necessary first to understand their biology. Haws et al. (1973) removed eggs from the ovaries of female Labops to determine their shape and size, and observed that their ovipositors were designed for injecting eggs. Kamm and Ritcher (1972) reported a technique for removing eggs from Labops females. Entomologists in Oregon (Markgraff 1974; Fuxa 1975; Kamm 1974; Fuxa and Kamm 1976a; Todd 1974) and Utah (Haws 1972, 1975; Higgins 1975) studied the seasonal and life cycles of Labops. It was found that the insects laid their eggs mostly in dry grass culms (Fig. 3), that there were five nymphal instars (Fig. 4), and that there was only one generation of the bugs per year.

Early reports related bug development to calendar days. Later studies related growth and development to growing degree hours (GDH) (Coombs 1985). Because GDH is becoming so widely used, and has such general applicability, mostly GDH data are reported here. Methods for calculating GDH are available in several publications (Haws 1982a; Richardson et al. 1975, 1983; Richardson 1985).

Grass bug eggs were gathered in the fall of 1971 for greenhouse studies of bug development through the winter. When the eggs would not hatch, cooperative efforts resulted in the development of growing degree hour models useful in predicting the development of black grass bugs in the laboratory and in the field:

	GDH (^{o}C)
Hatch	4,800
1st Instar	5,560
2nd Instar	6,500
3rd Instar	7,940
4th Instar	9,426
5th Instar	11,357
Adult	13,666
Mature adult	15,257

Growing degree hours are likewise quite accurate in predicting the developmental stages of crested wheatgrass (Table 1). Models similar to that shown in Figure 5 have been developed for crested wheatgrass and several other grasses (Richardson et al. 1983). Development of growth models for other insects and range plants, including other growth factors besides GDH, are continuing. When the impacts of factors such as moisture, soil nutrients, diseases, and plant competition are known and incorporated into growth formulae, the precision of predictive models is expected to increase substantially.

In 1971, after black grass bug eggs were found in intermediate wheatgrass culms (Haws 1972), they were sought in crested wheatgrass. Despite lengthy searches in Utah, only a few eggs have been found in either green or dry crested wheatgrass culms. Later, it was discovered that bulbous bluegrass (Poa bulbosa L.), in a bug-infested crested wheatgrass pasture, contained large numbers of black grass bug

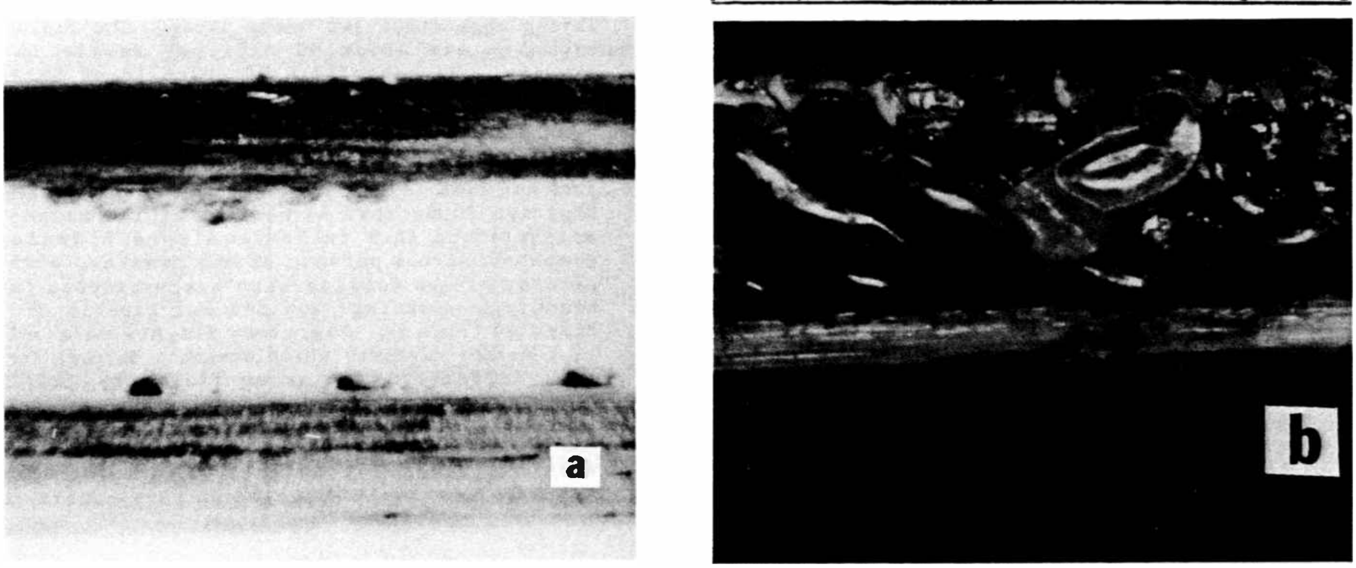


Figure 3.--Caps of Labops eggs protruding from a grass stem (a, top); caps of insect predator eggs (damsel bug or nabid) below. Nymphs (b) emerge from the overwintered eggs very early in the spring, often as the snow melts.

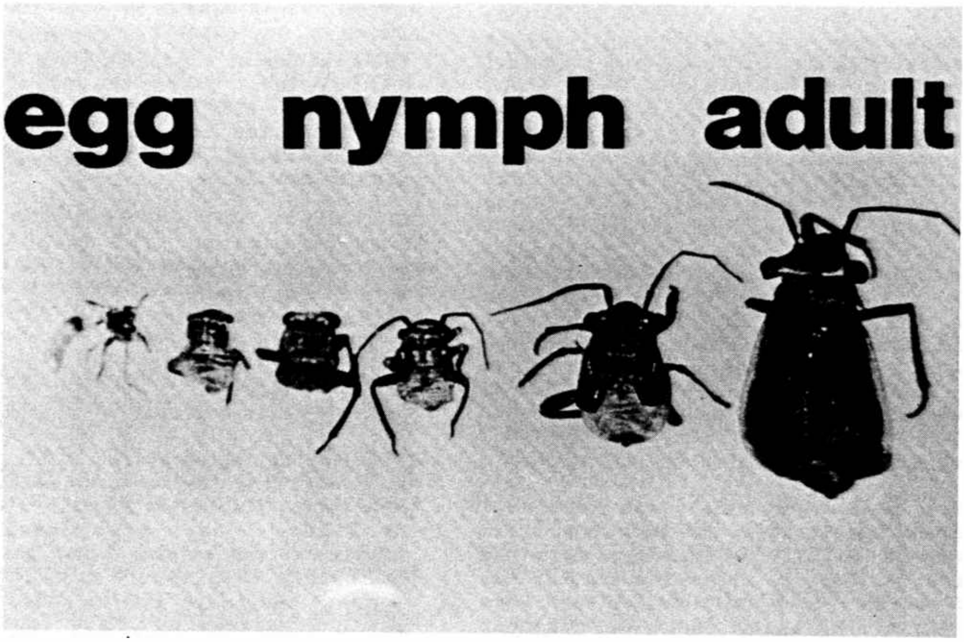


Figure 4.--Life cycle of Labops hesperius: egg, five nymphal instars, and the adult.

eggs. Subsequently, this grass has been the basic source of the eggs gathered for laboratory research. Todd and Kamm (1974) found Labops eggs in crested wheatgrass, blue bunch wheatgrass [Pseudoroegneria spicata (Pursh) Love], and especially in bulbous bluegrass. They found few eggs in green culms or broken stubble. In Utah, eggs have been found on other range plants such as dandelion, asters, clovers, and yarrow. Black grass bugs belong to the family Miridae, the same family as lygus bugs, one of the most destructive pests of alfalfa. Inasmuch as alfalfa is being planted with range grasses in some areas to improve the quality of the feed and of the soil, we decided to see if black grass bugs feed on alfalfa. Grass bugs were caged on Nomad and Ranger alfalfa in the greenhouse. The bugs fed at once on the alfalfas, and almost immediately oviposited eggs in the alfalfa stems. It was too late in the season to obtain bugs for longer term studies, so we were unable to determine if the bugs survived and reproduced when fed alfalfa. We have not observed the bugs feeding on alfalfa in the field when they have a choice between it and grasses.

Caged black grass bugs laid their eggs in many places if ideal sites (seed-bearing stems) were not available. Eggs laid by caged female bugs were inserted in cracks of paper greenhouse pots, through leaf blades or into cut-off stems, and wrapped in grass leaves without being inserted.

Paraqueima (1977) and Coombs (1985) have reared Labops in the laboratory with varying degrees of success. Control of diseases and relative humidity sometimes are problems. It is now possible to rear substantial numbers of bugs (from eggs gathered from the field) for use in winter studies. Coombs has continued previous studies at USU and has an accurate method of identifying grass bug nymphal instars by the measurement of head capsuls. He reports that nymphs of Labops and Irbisia brachycera (Uhler) can be distinguished by the presence of a broad white line bisecting the dorsal thorax of Irbisia nymphs.

Coombs (1985) observed grass bugs mating about one week after they became adults. They began laying eggs about two weeks later. The biological capacity was about 48 eggs per female in his studies. He reported a 60-40 ratio of males to females at the start of the season, but only 5 percent of the population were males toward the end of the life cycle. Todd and Kamm (1974) found eggs in adults about two weeks after the adults emerged. Fuxa and Kamm (1976b) examined the wing condition of bugs and found that 43 percent of the males were macropterous (had fully developed hindwings), compared with 4 percent of the females, while 53 percent of the females were brachypterous (short hindwings--meaning they are not capable of long flights) (Fig. 6). Migratory flights were only up to 2 meters distance which accounts in part for the slow infestation of grass fields by the bugs. Ovaries of the macropterous females appeared delayed in development until approximately three weeks after the "flight period." In one field Coombs found that the bugs lived for 80 days (egg through adult stages), but the life cycle can vary considerably depending on various conditions.

Coombs found a 0.982 correlation between nymphal development and GDH. Our knowledge of lethal cold temperature for bug eggs helps explain some of the

Table 1.--Comparison of predicted and observed dates of occurrence of selected phenological stages and heights of crested wheatgrass based on known GDH values associated with phenological developmental stages of crested wheatgrass (Richardson et al. 1974).

Phenology stage	Predicted date	Observed date	Height of culm	Predicted date	Observed date
	-------GDH-------		cm	-------GDH-------	
3 Leaf	232	230	10	240	233
4 Leaf	246	250	15	258	249
5 Leaf	273	279	20	273	267
Boot	291	292	25	286	281
Full flower	310	306	30	300	290
Seed ripe	341	347			

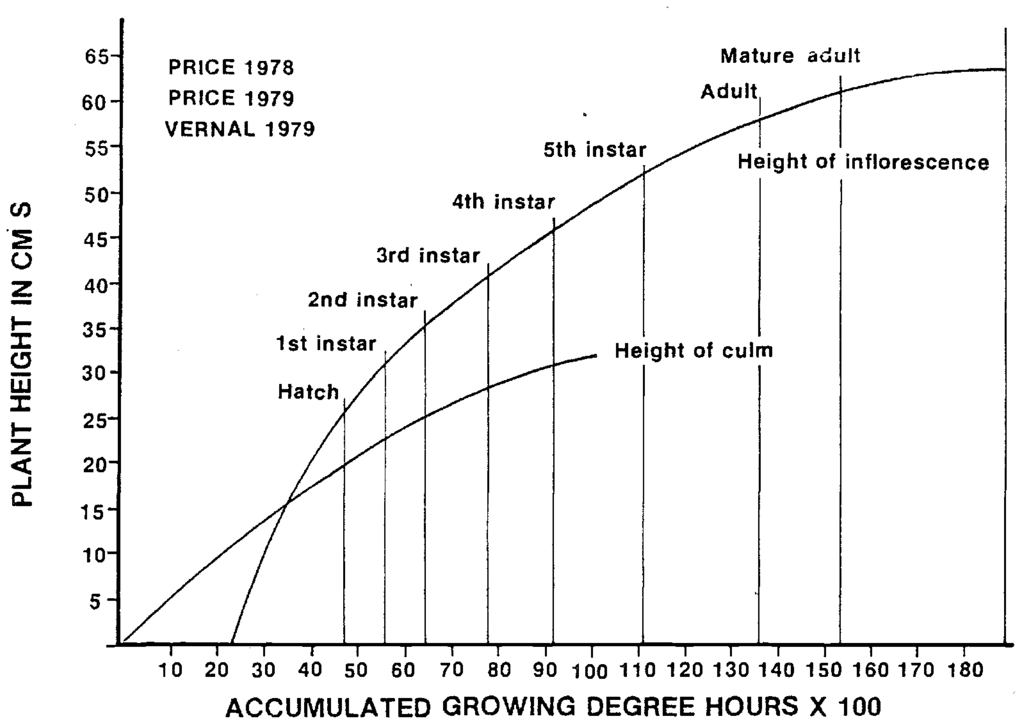


Figure 5.--Development of Labops hesperius and height of culm and inflorescence of crested wheatgrass related to growing degree hours. Adapted from Richardson et al. 1983.

Figure 6.--Labops hesperius adults: the female (left) has brachypterous wings lying over the thorax suggesting it cannot fly; the male (right) has two pairs of fully developed wings.

tremendous variations in bug populations from year to year. For example, Ostlie (1979) estimated that the grass bug population in a crested wheatgrass study area was reduced from approximately 2,256,000 bugs per acre in 1977 to 35,000 in 1978, presumably due to a lack of snow cover that allowed the eggs to freeze.

Biological and Economic Impacts of Black Grass Bugs on Grasses

Staff members and students in several colleges and departments at USU have studied the impacts of black grass bugs on range grasses, including plant physiology, seed production, photosynthesis, root reserves, consumption of grass forage by insects as compared with that of livestock, and certain impacts of insects as related to range economics. These studies have laid a foundation for our present and future research.

Physiology.--Wiebe et al. (1978) studied the physiological impacts of grass bug feeding. The studies included the effects of bug feeding on stomatal openings, chlorophyll content, photosynthesis, and forage yield. They also studied the attractiveness of water-stressed and nonwater-stressed plants. In these studies the impacts of three species of black grass bugs [Labops hirtus, Labops hesperius, and Irbisia pacifica (Uhler)] were compared. Because these were our first physiological studies and much had to be learned about methods, the authors considered the results as tentative and in need of follow-up research.

Plants damaged by the bugs appeared to transpire at rates comparable to those of healthy plants, which resulted in a degradation of water-use efficiency. Extremely high feeding intensities may have resulted in reduced leaf conductance, with consequent water conservation, for at least a period during and soon after feeding. Leaf chlorophyll concentration was correlated loosely with visual bug damage estimates. Feeding intensity predicted relative chlorophyll loss better than it did absolute loss. Some photosynthesis occurred in areas that did not appear green to the human eye. Visual estimates of insect damage were higher than were reflected in lowered rates of photosynthesis. Damage to wheat by I. pacifica (where the bugs had migrated into the wheatfield from roadside grass) resulted in a decrease in the number of grains per head. Bug incidence (BI=percentage of all bugs in an area that were on all plants) and damage to wheat were greatest on dry plants fed on by L. hesperius. The influence of soil moisture on plant attractiveness and on insect feeding merits further investigation.

Growth.--Ansley et al. (1978), Ansley (1979), and Ansley and McKell (1982) studied the effects of "grazing" by insects and livestock on some growth characteristics of crested wheatgrass. Tabulation of the yearly cycle of changes in carbohydrate root reserves as related to development of L. hesperius are shown in Figure 7. The data suggest that the early impact of bug feeding came when the root reserves were already being depleted by the spring growth of the plants. Production of crested wheatgrass protected from all feeding by enclosures and a systemic insecticide (aldicarb), was compared to that produced inside an enclosure where only insects were allowed to feed, and to that fed on by insects and cattle in a customary grazing regime outside the enclosures. Seedhead height was greatest in the aldicarb plots, but seedhead frequency was greatest in the grass outside the enclosures, (aldicarb=420; insect-grazed=880; outside the enclosures=1810). The percentage of plants developing inflorescenses was greatest outside the enclosures, and least in the aldicarb plots. Ansley theorized that perhaps the grass required some grazing or clipping to stimulate seedhead production.

The information we have concerning the impacts of grass bugs on longevity of crested wheatgrass and other grasses is mostly empirical. Long term, replicated longevity data are needed. In 1972, well-established drilled rows of crested wheatgrass were heavily infested with L. hesperius along Red Canyon and on Whiteman Bench, near the East Fork of the Sevier River. By the spring of 1984, only scattered plants of crested wheatgrass remained. Native vegetation is invading the areas along the sides of Red Canyon Road where thousands of black grass bugs have been collected from crested wheatgrass for experimental purposes during a 12 year period. On Whiteman Bench, smooth bromegrass (shown to be significantly less damaged by grass bugs than wheatgrasses in essentially all of our experimental tests) appeared to be the dominating grass. Our yearly observations since 1971, as well as reports of numerous bugs and severe damage since at least 1966, suggest that these insects have been a major influence in decreasing longevity of crested wheatgrass along the East Fork of the Sevier River. Jensen (1971) observed stands of grass damaged by the bugs, but none were killed.

Forage Yield.--In their studies of the impacts of grass bugs on the forage yields and nutrition of mature grass plants, Malechek et al. (1977) were not able to measure significant differences in herbage yields of grasses with moderate bug infestations compared with noninfested plants. Because the grass bugs are sucking insects, their damage is less obvious than that of chewing insects such as

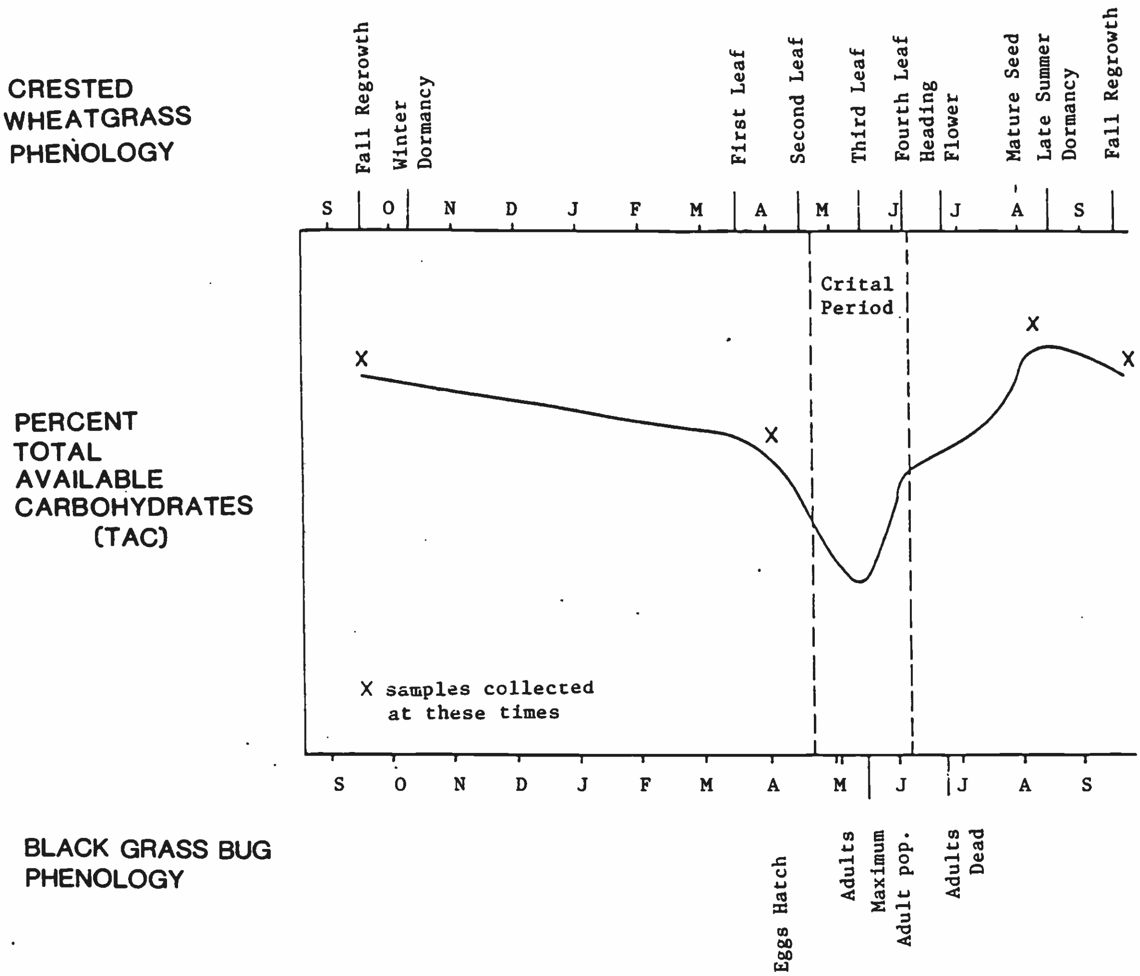


Figure 7.--Corresponding phenology and seasonal development of crested wheatgrass and Labops hesperius, observed in Diamond Fork Canyon, Utah, 1976-1977.

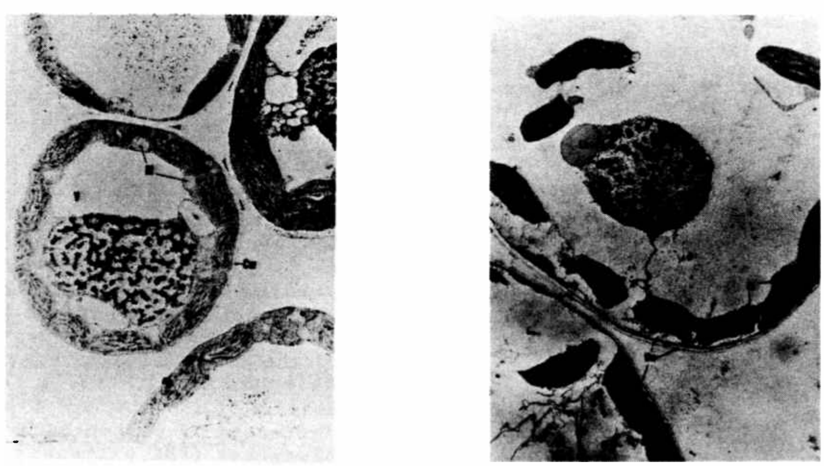


Figure 8.--Grass plant cells that have not been fed on by grass bugs at left. Right disintegration of grass plant cells 60 minutes after being fed on by black grass bugs. This may be caused by mechanical removal of plant substances or by the injection of substances not yet identified.

grasshoppers whose feeding partly or completely removes plant structures. Sucking insects insert small stylets into the grass tissues and remove plant fluids (Fig. 8), but the major external structures of the leaves remain. Thus, unless the bug populations are so numerous that the vegetative growth of the plants are reduced, measurements of damage to mature plants may not show great differences in forage weights. It would be easy to draw a wrong conclusion about bug impacts from these kinds of data if one were to conclude from laboratory studies that the feeding of the bugs was not detrimental to forage production.

A major problem is loss of early growing grasses in the field during the spring. Damage to crested wheatgrass and other introduced grasses occurs very early in the season (April and May--depending on the elevation) when livestock producers are eager to get their animals out of feed lots and onto early spring grass. But often, stockmen found the grasses were heavily damaged or destroyed by the bugs. This substantial loss of spring feed has been the major problem with black grass bugs in drier areas such as Utah. These early losses seem less of a problem in areas of greater moisture and where bug populations are smaller.

According to Bohning and Currier (1967) and Knowlton (1967), the bugs may reduce yields 50 to 60 percent. Todd and Kamm (1974) found no significant differences in forage yields of grass treated with insecticide compared with a nontreated control. Under conditions in Oregon (bug density averaging 120 per 0.97 ft^2), the total loss to mature grass was only two percent. The impact of feeding varied with time of utilization, annual rainfall, and drought. Even severely damaged grass recovers after the bugs complete their life cycle and die, if adequate moisture for growth is available to the plants. If the growing season remains dry after grass has been severely damaged, vegetative growth and seed production continue to be inhibited (Fig. 9).

Nutrition.--Traditional chemical methods of evaluating nutritional qualities of grasses as related to grass bug damage have been inconclusive and have not shown the detrimental effects that might be expected from the devastated appearance of the damaged grasses (Higgins et al. 1977, Malechek et al. 1977, Markgraff 1974). Todd and Kamm (1974) found a reduced combined value of yield reduction and loss of cell contents of 18 percent midway through the growing season (at the bug density indicated above). Both Malechek et al. and Todd and Kamm found that bug-damaged grass showed a slight increase in crude protein. In Utah, studies of chemical profiling (Windig et al. 1983) have belatedly suggested that grass bug feces covering infested grasses may be confounding the results of chemical analyses. As the bugs feed, they deposit large quantities of liquid feces on leaves and stems. After the liquid dries, it appears as a black deposit. We have not yet tested or determined the chemical content of the feces, or tried to physically or chemically remove the material from leaves being compared for nutritional quality. This must be done to obtain valid data on the impacts of grass bugs on nutritional quality of grasses.

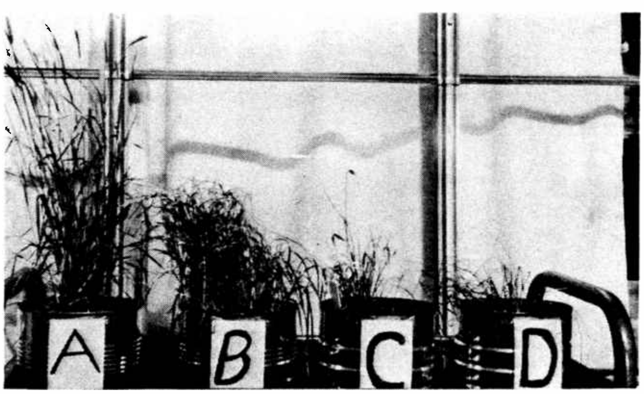


Figure 9.--Clones of crested wheatgrass heavily infested with Labops hesperius in a greenhouse did not produce seed. Bug-free plants (container A) produced seed, while containers with different levels of bug infestations (B,C,D) did not produce seed.

In the field, we have observed that substantial rains remove all or most of the fecal material from the grasses. The nutritional value of the grass contaminated with bug feces may be near that of nondamaged grass because of the chemical contents of the feces. If the feces are washed off, the nutritional value may be considerably less. But ranchers and researchers have reported that even when spring grasses have not been totally destroyed by the bugs, some infested fields appear to be repugnant to cattle. The Green Lake Pasture near Cedar City, Utah had a population of approximately 100 grass bugs per sweep in 1975. Cattle in this pasture ate only a little of the damaged grass, then sought other feed. The basis for this repellence has not been determined. Apparently the black grass bugs inject chemicals into the grasses to liquify some of the plant materials. The bugs also cover the plants with feces as they feed. It is possible that the infested plants, or the bugs themselves, are unpalatable or have characteristics repellent to the livestock. The nutritional value of such repugnant forage is zero if the livestock will not eat it! Just how extensive this problem is or the level of bug damage when it occurs has not been determined.

Seed Production.--It is common to see insects feeding on seed heads of grasses (Bowers 1976). USU has attempted a few studies of the impacts of insects on seed production of plants such as alfalfa (Haws 1982b, p. 13, 35, 36). The damage causes seed to be shriveled, discolored and nonviable. Similar damage can be expected on grasses. To investigate the impacts of insects on seed production in the USDA/ARS grass breeding nurseries, insects were collected from grasses and caged on developing seed. The results indicated that bugs of the genus Labops survived well when caged on the seed while 100 percent of those of the genus Irbisia died (suggesting they did not feed on the seed) (Table 2). Unfortunately elk destroyed the cages and some of the seed in these tests before it was examined. Malechek et al. (1977) found that at an average density of 156 bugs per m^2, seedhead production was depressed 56 percent. In studies of two grasses, bluegrass (Poa pratensis L. cv. Merion) and fine fescue (Festuca rubra L. cv. Cascade), Kamm (1979) found that the plant bugs Leptoterna ferrugata (Fallen) and Megaloceroea recticornis (Geoffrey) reduced seed set and destroyed seed viability when

Table 2.--Percent survival of five insect species caged on green growing seed of Agropyron cristatum for two days.

Insect	No. of insects per cage	Average percent survival
Irbisia pacifica	6	0 a[1]
Irbisia brachycera	6	0 a
Labops hesperius	6	55 b
Melyrid spp.	10	75 b
Stink bugs (Pentatomidae)	5	76 b
Leptoterna spp.	6	77 b

[1]Analysis based on arcsin square root transformation of percentage data. C.V. 0.43. Means followed by the same letter are significantly different at P>0.01. Five replications.

the bugs fed directly on the developing seed. Burning the straw reduced the incidence of feeding injury. At USU, thrips (Chirothrips aculeatus Bagnall) destroyed valuable grass breeding crosses (Haws 1978, p. 102). The impacts of various insects on grass seed should be investigated when both the insects and seed are in different stages of development. Control of insects affecting grass seed production needs to be determined.

Economic Impacts.--Glover (1978) has reviewed some economic impacts of black grass bugs on range grasses. He has outlined two economic methods for analyzing the feasibility of pest control on rangelands [Bayesian (benefit-cost) analysis and an optimizing algorithm approach]. Glover calculated some cost/profit economics of rangeland via insect control (Glover 1982). Using 1979 as the base year, he estimated losses associated with L. hesperius in Utah, New Mexico and Nevada during 1980-1981. He concluded that if the benefits of grass bug control were to continue to accrue one year beyond the first year of control, based on the average internal rate of return, the chemical control investment can be shown to be a highly productive investment. Practical field experiences and experimental studies cited elsewhere in this paper have shown that economical control of black grass bugs by application of chemicals has been achieved. Several years of control have resulted from one proper application of ULV malathion in Morgan County, Utah (Haws 1982a, p. 185), and recently in Beaver County, Utah.

IIPM STRATEGIES FOR CONTROLLING GRASS BUGS

Range Management: Mixed Vegetation vs Monocultures

The consensus of the Utah research team was that the origin of problems with Labops probably was related to range grass management (planting monocultures, undergrazing etc.). Possible changes in management of ranges and livestock were among the first strategies investigated. Logic supporting the strategy of planting heterocultures instead of monocultures is based partly on data suggesting fewer grass bugs have been found in mixed communities of forbs, shrubs, and grasses than in adjacent monocultures of crested wheatgrass. The different insect population of native ranges, together with common knowledge and experiences with insects in other crops, suggest that the beneficial impacts of these insects can be increased by providing proper food and habitat for them.

Greater insect diversity in mixed plant communities is one feasible strategy for insect control. One way of promoting insect diversity, and thus developing a biological balance, is to include those plants in range renovation that will provide continuous food and favorable habitat for beneficial insects. Parasites and predators are particularly important components of an undisturbed ecosystem (Spangler 1984), keeping many injurious insects in check. Promoting beneficial insects usually requires plants which provide pollen and nectar and protection from the elements. One of the ultimate goals for rangeland management is to set up a self-regulating system that would limit the ability of pest insects (such as black grass bugs) to compete with livestock for forage. We do not know enough yet about insect/plant relationships to recommend these favorable combination of plants. After his experiences with grass bugs, Jensen (1971) concluded that the best insurance against heavy Labops infestations is a balance of plants in reseeded range communities.

In 1980 and 1981, Spangler (1984) studied sap-feeding and predatory insects in pure stands of manipulated grass densities compared with mixtures of native plants, including sagebrush. His data suggest that in comparing pure stands of crested wheatgrass with those mixed with sagebrush, the shrubs were more important than density of the grass in determining faunal structure. Fewer sap-feeding insects were found where the grass was interplanted with plants that were taxonomically unrelated. Lower levels of insect predators were found in the reseeded areas. There was a shift from a homopteran-dominated fauna, in a mixed range, to a mirid-dominated one in a monoculture.

Debris-in-place management (in which large plants such as juniper trees or sagebrush are removed, but some grasses, forbs, and shrubs remain) provides habitat and food for many insectivorous animals (birds, lizards, parasites, and insect predators). The studies of Ostlie (1979) (Fig. 10), in which the numbers and behaviors of L. hesperius in a monoculture of crested wheatgrass were compared with those in a native range, suggest that a mix of range plants might also include plants that are repugnant to insects (perhaps sagebrush) or that are otherwise unfavorable to them.

Society has learned to manage and increase the productivity of many crops by growing them as monocultures (corn, wheat, potatoes etc.). Inasmuch as there are millions of acres of monocultural grasslands, we need to learn how to manage them for pest control. But in the future, some problems with range insects probably can be avoided if the steady state of ecological balances existing in some native rangelands can be imitated. Our hypothesis is that a combination of plants that will help attain a favorable ecological balance of injurious and

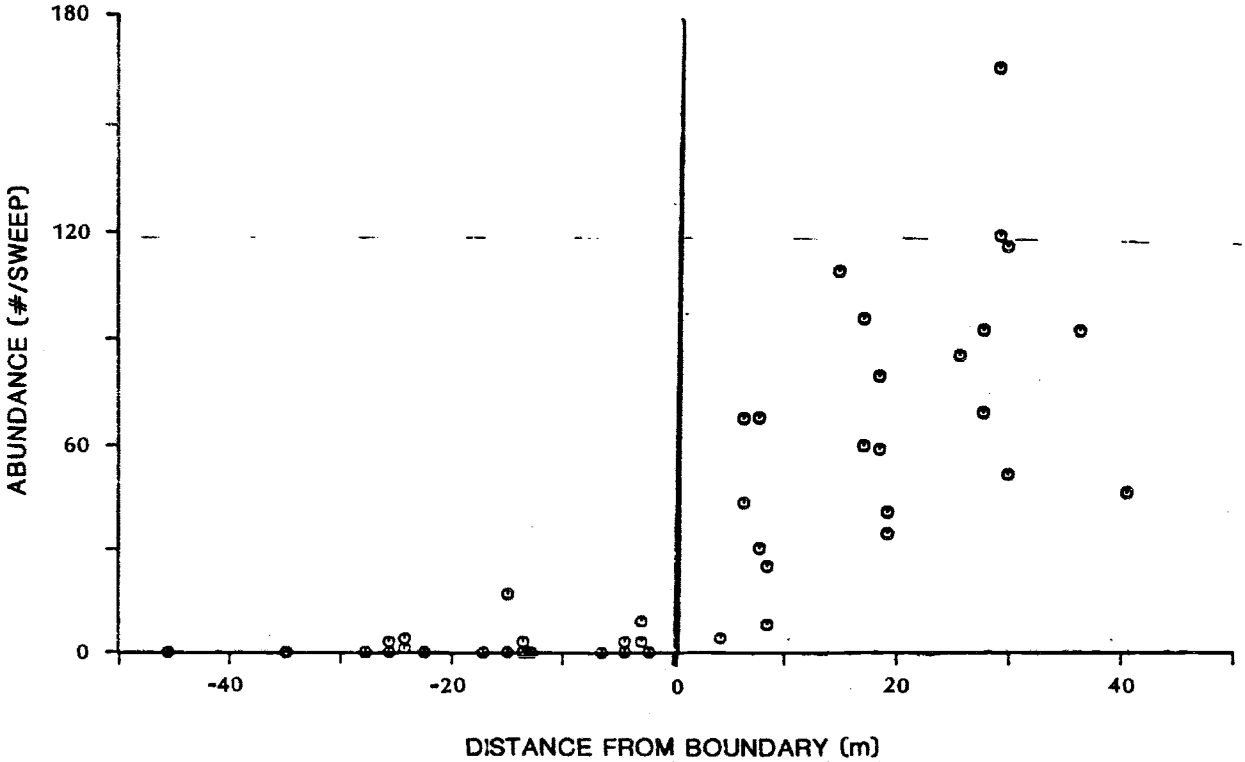


Figure 10.--Abundance of Labops hesperius as a function of sample distance from the boundary of reseeded range (right of midline) with unimproved range (left of midline) Ostlie 1979).

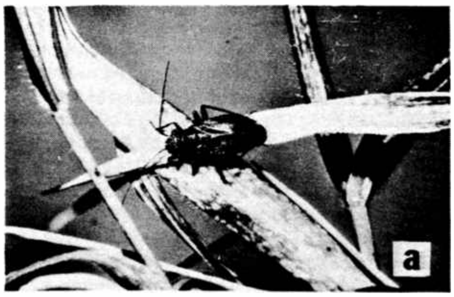
beneficial insects can be realized without resorting to the outright reestablishment of all the original elements of the native range. The strategies proposed for control of black grass bugs are simplified by the fact that the bugs have only one generation per year.

Egg destruction: burning and grazing--Inasmuch as black grass bug eggs usually are inserted in grass stems, they can be destroyed by burning or grazing before they hatch, thus interrupting the life cycle. Grass bugs of the species I. brachycera (Fig. 11) present a different problem than Labops because Irbisia appears to be more mobile.

Information obtained from studies of accidental and controlled burns (Haws 1978 p. 59; Haws 1982a p. 186-193; Huddleston and Smith 1982) suggests that burning lowers grass bug populations for several years. Because grass bugs migrate and reinfest fields slowly, thorough burning of pastures in the fall, when there was enough fuel to support a uniform burn, destroyed most eggs. In Utah, many Labops nymphs survived a spring burn by hiding in cracks in the soil while the fire passed over them. Todd and Kamm (1974) also proposed that removal of straw (where the bugs lay their eggs) by burning or grazing were feasible control strategies. They found an average of 7 nymphs in a burned area compared with 92 in a nonburned one. Their conclusion, after several studies of grass litter, was that reduction of straw preferred by the bugs for oviposition may reduce the densities of the bugs the following year. Hagen (1982) concluded after an eight-year study that L. hesperius populations can be reduced significantly by harvesting crested wheatgrass each year.

The principle of controlling bugs by grazing is the same as that for burning--destruction of the eggs in the fall, and its effectiveness also depends on the thoroughness of egg destruction (Kamm and Fuxa 1977). Undergrazing sometimes permits eggs to remain in the grass stems and develop their biological potential. Substantial reduction of bug populations has been successful where intense grazing by one or more species of livestock was applied, controlled with permanent or electrical fences. Some ranchers remove range litter containing eggs by allowing short periods of intense grazing in the fall and again in the spring. Management by grazing should not violate known principles of protecting the grass. Both in burning and grazing, islands of eggs in grasses that are not removed often provide enough eggs to reinfest an area. The most effective use of grazing that we have observed has been short periods of intense grazing by several kinds of animals at the same time (horses, cows, and sheep).

Insecticides.--Tests of chemicals in small plots and in practical field applications have resulted in effective, economical control and an understanding of certain aspects of the toxicology of black grass bugs (Brindley and Osman 1978; Haws 1979, 1982a; Huddleston and Smith 1982). The present control recommendation is 8 ounces (AI) ultra low volume (ULV) malathion per acre (.4 ha) at temperatures above 65° F (18°C) after all eggs have hatched (3-4 instar, approximately 28,000 GDH) and before the



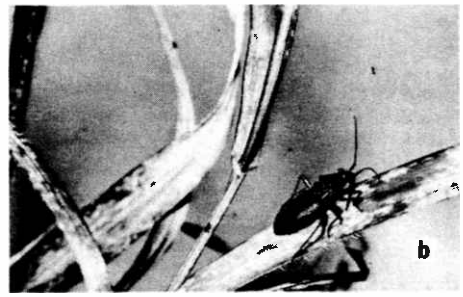
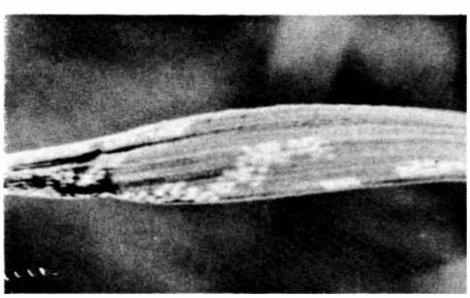


Figure 11.--Irbisia brachycera (a) and Irbisia pacifica (b) are being recognized as serious pests of crested wheatgrass and other grasses. Their damage is similar to that of Labops hesperius but they appear to be more mobile and less delicate.

females have laid their eggs. If more than one year of control can be gained from a single application of malathion, control is usually economically feasible (Glover 1982). Application of the ULV formulation by helicopter or fixed-wing aircraft (if terrain is not too irregular or difficult to permit thorough application of the insecticide) has proven effective in distribution of the toxicant. Our ground sprayer applications of emulsifiable malathion have also resulted in good control. If chemical control is necessary a second year because of poorly timed application of pesticide the previous year, the cost of control may be excessive. When the bugs are effectively controlled before the females lay their eggs, practical experience indicates that because the bugs reinfest or migrate into fields slowly, retreatment may not be necessary for several years. Todd and Kamm (1974) concluded that under their conditions losses attributed to Labops feeding usually didn't justify the use of insecticides.

Early identification of an infestation and proper application of a pesticide are essential elements for successful chemical control. The eggs hatch as snow melts and the nymphs begin to feed as soon as they hatch. This means very early inspection (look for bug damage or sweep fields with a net) of rangeland grasses is necessary (late March or early April and May, depending on the elevation and GDH). Fortunately, the total infestation intensity can be determined early because the bug population will not increase during the year. The eggs present in the spring represent the total potential infestation for that particular year. Close examination of the grasses may reveal the presence of bugs by their damage--whitish or yellowish feeding spots on the leaves. Young nymphs are difficult to see or capture but later instars (3-5), and their damage, are easier to see and are useful in determining the intensity of an infestation (Fig. 12). The general tendency is for range managers to wait until there is too much



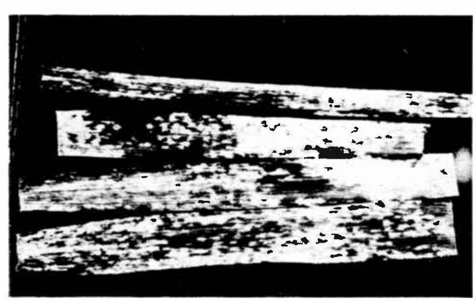


Figure 12.--When grass bug nymphs first hatch, and as the early instars develop, they are difficult to find; however, their damage to grasses is easier to find and utilize as an evidence of the intensity of an infestation. A light infestation (left) and a severe infestation (right).

damage to the grasses and until after the females have laid their eggs, before attempting control with chemicals or other strategies.

Grass bug eggs hatch and nymphs develop fairly uniformly in flat rangelands with a similar exposure to the sun, but have substantially different rates where land contours, elevations and exposures to sunlight influence the accumulation of growing degree hours. Both nymphal stages and adults may be found in clumps of crested wheatgrass (especially "wolf plants"--ungrazed grass containing tall dry stems) because the insects are exposed to various temperatures.

Varying conditions during the winter may also result in anomolous development of grass bugs. By the time the snow melts in the spring, late instars and extensive damage to grasses may already be present. This condition apparently results from winter thaws and temperatures above 40°F (4.4°C) in the microhabitat of the bugs. After the chill requirements of the bugs have been fulfilled, the eggs can hatch and nymphs continue their development on and off as temperature and weather conditions vary during the winter. Where the conditions result in uneven hatching, chemical control should be delayed until all the eggs have hatched.

Plant resistance.--Staff members of the USDA/ARS Crops Laboratory in Logan, Utah, have cooperated with USU entomologists and plant scientists since 1972 in studies of resistance of grasses to *Labops*. Differences among and within genera of grasses, and among clones and their crosses (Fig. 13) have been demonstrated by Asay et al. (1983), Hansen et al. 1985a, 1985b), Haws (1979, 1982a), Hewitt (1980), and Windig et al. (1983). Fields of intermediate wheatgrass frequently have more *Labops* than crested wheatgrass and sustain substantial damage (Todd and Kamm 1974; Higgins et al. 1977). Crested wheatgrass and its hybrids along with intermediate wheatgrass were the most susceptible; western wheatgrass was the least preferred. They note that reports of host plant preferences by different persons often are confusing and conflicting. For example, Hewitt (1980) concluded that intermediate wheatgrass was more resistant to *Labops* than western wheatgrass or bluebunch wheatgrass. Orchardgrass (*Dactylis glomerata* L.) and reed canarygrass (*Phalaris*

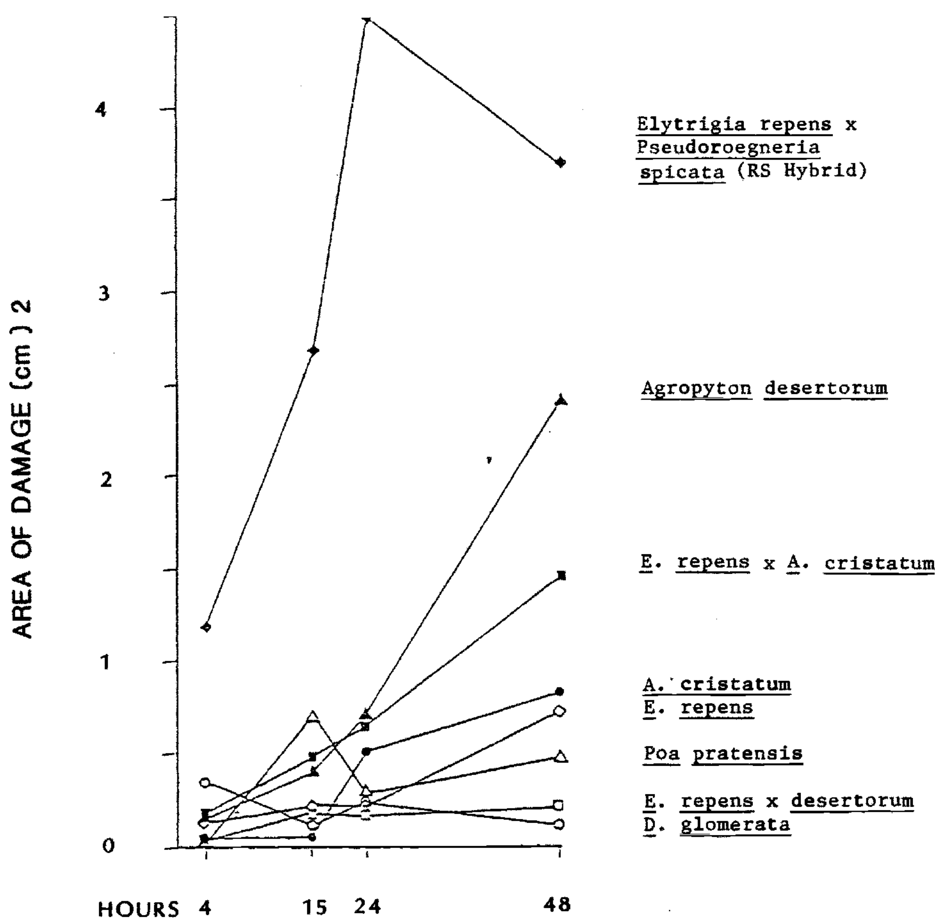


Figure 13.--Average amount of damage to eight grasses by *Labops hesperius* after 48 hours of feeding. Note that differences in damage become more distinct after 48 hours (Haws et al. 1982a).

arundinacea L.) have usually sustained little damage by black grass bugs in Utah tests (Hansen et al. 1985a; Windig et al. 1983), but Todd and Kamm (1974) list orchardgrass as a host. Campbell et al. (1984) have reviewed the literature concerning grass resistance to Labops.

It can be concluded that the relatively few grasses that have been compared for possible use in resistance as a management strategy show definite differences that might be incorporated into new resistant varieties (Fig. 14), such as intermediate wheatgrass and smooth brome (Bromus inermis Leyss.). There are many more species available for testing in grass breeding institutions and perhaps others to be found elsewhere. There is little doubt where grass is expected to be established for long periods of time that new resistant grasses offer one of the best management alternatives. There remains much to be done before resistant grasses can be expected to be available for practical use, even though the technical skills, germ plasm, and facilities to do most of the needed research are available. Asay (1986) has recently discussed the potential of using resistant grasses as a management strategy to lessen range pest damage.

In most breeding programs, plant characteristics imparting resistance to major pests are sought. To date, studies of only a few insects have been included in the development of resistant grasses. Resistance to other important insects, as well as to plant diseases and nematodes, must be investigated. The plants selected then have to be combined with plants having other desirable characteristics. Finally the new varieties should be fed to livestock to be sure that they are acceptable as forage.

Biological control: insect predators and parasites.--Studies of rangeland insect predators and parasites are few. Research by Araya (1982) indicates that spiders and damsel bugs (Hemiptera: Nabidae) (Fig. 15) are important predators of some range grass insects, including black grass bugs. Parasites of the hymenopterous family Scelionidae have been seen emerging from grass bug eggs reared in the laboratory (Haws 1978, p. 59, 60, 129). Female Labops were found parasitized by dipterous larvae and myrmenthid worms (Coombs 1985). The parasites appeared to render the infested females incapable of producing viable eggs. Our observations of predators feeding on captured hosts in the laboratory and in the field have indicated there is little doubt that large populations of damsel bugs, together with other predators and parasites, reduce grass bug populations. Many details concerning insect predators and parasites and methods of increasing their populations and utilizing them in management strategies are yet to be discovered. Biological controls are common, successful strategies in the solutions of some pest problems in crops and animals. It is reasonable to expect similar solutions can be developed for rangeland pests.

MYTHS ABOUT INSECTS AND CRESTED WHEATGRASS

It was suggested that contributors to the crested wheatgrass symposium call attention to "myths" related to this grass in view of our present status of knowledge. There are a few "myths" related to insects and crested wheatgrass.

Myth 1. Crested wheatgrass is the major host of L. hesperius.

For many years a general impression in the literature has been that crested wheatgrass is the major host of L. hesperius. Denning (1948) referred to L. hesperius as the crested wheatgrass bug. There is no doubt that L. hesperius damages crested wheatgrass severely, but there is substantial evidence that the species prefers at least one grass more than crested wheatgrass. Thomson[4] reported that intermediate wheatgrass was heavily infested with grass bugs, whereas adjacent crested wheatgrass was only lightly infested. Samples of L. hesperius from crested wheatgrass and intermediate wheatgrass in Salina Canyon, Utah, before a chemical control study began, showed there were more bugs in the intermediate wheatgrass (Table 3). This observation is verified in many of our resistance studies.

Myth 2. Labops hesperius is the major range grass pest.

Knowlton (1967) recognized there were various species of insects other than L. hesperius infesting range grasses, but there seemed to be a general use of the term "Labops" among many ranchers and other range specialists when they talked about injury to grasses by almost any black bugs. Pure populations of I. brachycera or mixtures of the two species have been found. I. brachycera may prove to be a more serious pest than Labops in some areas because the females of I. brachycera have functional flight wings while most Labops females do not. This difference in wing development allows I. brachycera to be more mobile than Labops. Other insect pests of crested wheatgrass, such as leafhoppers and click beetles (wireworms), and grub worms (larvae of beetles) may be important under some circumstances (Knight 1982).

Samples of range insects in the past few years suggest that leafhoppers are among the most abundant insects generally found. Studies of leafhoppers on other crops have shown that some of them carry viruses or microplasmas and infect plants with disastrous epidemics of diseases. The substances some sucking insects inject into plants are toxicogenic, and they may substantially change the phenology of plants (Sorenson 1946, Carlson 1940). Grasses are reported to be carriers of disease agents but generally they are immune to pathogenic impacts of viruses (Nielson).[5] Relatively little is known about the impacts of most leafhoppers found on rangeland grasses.

Billbugs are serious pests of crested wheatgrass and some other range grasses (Haws 1982a, p. 123, 136, 138; Nielson 1985). Studies of the biologies, impacts, and control of billbugs and other rangeland insects are underway.

[4] Thomson, R.R. 1969. Report on Labops hesperius. A reconnaissance survey on Labops populations on portions of the Dixie National Forest. In Range Insect Literature File R-8, Utah State Univ., Logan.

[5] M. W. Nielson, USDA/ARS (Ret.); Personal communication, October, 1984.

Figure 14.--Grasses evidently have genetic differences in their susceptibility to black grass bugs as shown by the amount of damage sustained by intermediate wheatgrass (left) compared with smooth brome (right), growing together in an area infested by Irbisia pacifica.

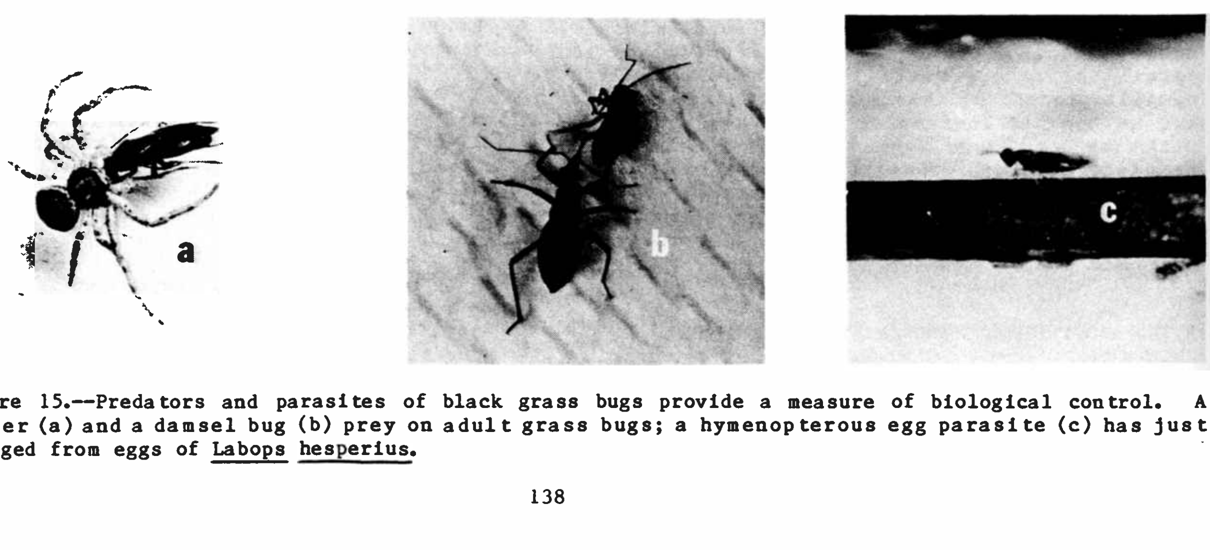


Figure 15.--Predators and parasites of black grass bugs provide a measure of biological control. A spider (a) and a damsel bug (b) prey on adult grass bugs; a hymenopterous egg parasite (c) has just emerged from eggs of Labops hesperius.

Table 3.--Black grass bug (Labops hesperius) concentrations on crested wheatgrass and intermediate wheatgrass during a study of malathion as a chemical control.

Plot[1]	Crested Wheatgrass[2]	Plot	Intermediate Wheatgrass[2]
1	42	26	139
2	45	27	61
3	37	32	203
4	183	33	543
5	66	36	59
7	95	38	144
8	50	39	57
	Mean = 65	40	171
		41	121
		42	226
		43	109
			Mean = 167

[1]Plots of 1/2 acre (.2 ha) each.
[2]Number of bugs per 6 sweeps

Myth 3. Long term rest rotation benefits range grasses.

Benefits of long term rest rotation are not likely if a range is heavily infested by certain insects. The insects continue to "graze" and multiply even if the larger livestock are removed.

A commonly described problem in grasslands is overgrazing, but from the entomological point of view, many of the problems associated with insects have resulted from undergrazing. The problem of undergrazing is that plant litter provides a place for some insects to lay eggs and be protected from unfavorable weather. Range managers can effectively control grass bugs by grazing early to remove eggs inserted in the grass stems. Some of the intensive, short term grazing regimes implemented by certain managers (before bug eggs have hatched) provide an economical, effective control strategy, if the grazing is done in accord with proper range management practices (i.e. not overgrazing at critical periods of grass growth and development).

The oft proposed rule of thumb about grazing, "take half and leave half," nullifies its possibility of controlling grass bugs because most eggs are found in the lower parts of the plants. Empirical studies suggest that eggs of L. hesperius do not survive a trip through the digestive tract of grazing animals. We have observed heavily grazed fields to be practically free of grass bugs while nearby ungrazed fields may be infested. Long-term rest rotations, like inadequate grazing, often allow the majority of black grass bug eggs to hatch unmolested.

SUMMARY AND CONCLUSIONS

1. USU range grass insect research concentrated on the black grass bug, Labops hesperius. This emphasis has been a response to requests for help from state, federal, and private owners and users of range grasses. We have worked with a number of introduced grasses, including pure stands of crested wheatgrass, but for this symposium we have sorted through our data and insect collections to find out what we know specifically about crested wheatgrass.

2. Reports of insect damage to crested wheatgrass by black grass bugs date back to at least the late 1930s in various western states. Cooperative efforts to gather information about insects in grasses of Utah and attempts to apply chemical controls were documented in the 1960s. Using the combined knowledge and experience of scientists and ranchers, six management strategies have been explored in varying degrees. These strategies involve planting (monocultures vs mixes), grazing, burning, development of resistant varieties, biological control, and chemical control. The status of each strategy is discussed.

3. Approximately 160 species of insects were collected from crested wheatgrass. Other insects have also been reported from grasses and these reports are summarized and discussed. The total number of insect species found on crested wheatgrass and their impacts are unknown and under only preliminary investigation. Insects are part of the range grass ecosystem, and they should be put on our check list when we are looking for ways to improve or manage ranges, plan research, or diagnose problems with range grasses.

4. Many of the serious problems with insects in crested wheatgrasses and other range grasses appear to be related to traditional methods of range management, such as planting monocultures, grazing at the wrong times and intensities, planting susceptible varieties, etc. We have learned to cope with problems of many crops grown as monocultures, and we can do the same with grasslands.

5. Range researchers need to include insect-free grass plots as checks or controls in studies of physiology, nutrition, establishment, quality and quantity of forage and seed yields, longevity of stands, soil genesis, penetration of water and air into soils, soil erosion, hydrology, economics, and most other aspects of range improvement and management.

6. A major gap in our information regarding crested wheatgrass and other grasses is the effects of various pests (insects, nematodes, diseases, etc.) on grass phenology. Normal as compared to anomolous phenology, brought about by these pests or by other stresses, must be known in order to select resistant varieties, and to diagnose other problems with range grasses.

7. The main principles of management strategies proposed for controlling insects that inhabit grasses are: (1) break the insect cycles in the egg stage; (b) implement chemical controls after all insects are hatched in the spring, but before they mature and lay their eggs; (c) inspect ranges on a regular basis to detect infestations before critical damage occurs and it is too late to apply effective control; (d) obtain information about the different grazing behavior of sheep, cattle, goats, horses, and perhaps exotic animals (such as llamas), and integrate this with control strategies. Each range may require specific kinds of management based

on information that is unique to a particular area (e.g. a collection of insects or information about growing degree hours, average precipitation, contours of terrain, etc.).

8. The essential biological information required to implement IIPM principles for improvement and management of ranges is available for only a few insects. Little is known about underground pests of grasslands, e.g. cutworms, white grubs, wireworms, etc. Chemical and physical plant characteristics associated with the attraction or repugnance of grasses to animals must be identified for use by plant breeders and range managers. The comparative palatability of grasses to livestock and insects should be determined. Critical information about the most important injurious and beneficial insects needs to be obtained.

9. Little is known about the interrelationships of insects and mixtures of plants in grassland ranges, e.g. the impacts of mixing alfalfa with grasses. Will it increase problems with insects or decrease them? Which mixtures of grasses, forbs, or shrubs favor or retard insect development? Which plants need to be included to provide food and habitat for beneficial insects? Which mixtures provide a balanced, steady state condition requiring the least expense and monitoring? Interdisciplinary research groups have much to contribute to answering these questions.

10. Problems of biological pollution of our ranges by insects and weeds that develop in the thousands of acres of grasses and other plants growing along our freeways, should be investigated. Cursory studies and observations suggest that the freeways (largely unmanaged) may be a main source of contamination of many rangelands. Our observations indicate more than ten times as many grasshoppers can be found in weedy crested wheatgrass than in weed-free grass nearby.

11. Apparent conflicts in the range literature about densities of insect populations, extent and intensity of insect damage, and impacts on forage, seed and longevity of grasses, may stem from true differences in climatic factors, methods of management, and other conditions. Differences such as those found in various states concerning the impacts of *Labops* on host grasses, emphasize the importance of repeating research in different ecological conditions.

12. Range economists and climatologists can increase the precision of their economic predictive models if they have additional, accurate biological information about factors that influence variations in yields, nutritional values, cost/benefits, etc. Biologists and range specialists need to help provide this information.

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APPENDIX

Insects of crested wheatgrass collected from Curlew Valley, Box Elder County, Utah by G. E. Bohart, June-August, 1973-74.

Order/Family	Genus & Species	Apparent significance as a visitor of crested wheatgrass*	Nature of insect impact on host
Coleoptera			
Anthicidae	Notoxus serratus	1	chews fruit (?)
Chrysomelidae	Psylliodes sp.	2	skeletonizes leaves
Coccinellidae	Hippodamia convergens	3	preys on aphids
	Hyperaspis fastidiosus	2	preys on aphids
Melyridae	Listrus sp.	2	feeds on pollen
	Listrus interruptus	3	feeds on pollen
Histeridae	Saprinus desertorum	1	preys on scavengers
Leiodidae	undetermined sp.	1	feeds on fungi
Melyridae	Collops utahensis	2	preys on aphids
Staphylinidae	undetermined sp.	2	preys on soil
Collembola			
Sminthuridae	undetermined sp.	2	chews shoot epidermis
Diptera			
Agromyzidae	Agromyza albertensis	3	mines leaves
	Liriomyza sp.	3	mines leaves
	Melanomyza virens	2	mines leaves
	Phytomyza sp.	3	mines leaves
Anthomyiidae	Hylemya cinerella	2	feeds on roots
	Hylemya platura	3	feeds on roots
Bibionidae	Bibio albipennis	1	feeds on decayed veg.
Bombyliidae	Exoprosopa calyptera	2	feeds on grasshopper eggs
	Geron sp.	2	parasitizes insects
	Mythicomyia sp.	2	parasitizes small insects
Cecidomyiidae	undetermined sp. #1	2	makes galls or bores stems
	undetermined sp. #2	2	makes galls or bores stems
	undetermined sp. #3	2	makes galls or bores stem
	undetermined sp. #4	3	makes galls or bores stem
	undetermined sp. #5	2	makes galls or bores stems
Ceratopogonidae	undetermined sp. #1	1	feeds on decayed veg.
	undetermined sp. #2	1	feeds on decayed veg.
	Dasyhelea sp.	1	feeds on decayed veg.
	Forcipomyia sp.	1	feeds on decayed veg.
	Leptoconops sp.	1	feeds on decayed veg.
Chamaemyiidae	Leucopis sp.	3	preys on psyllids
Chironomidae	Chironomus sp.	1	feeds on dead aquatic veg.
	Conioscinella sp.	3	feeds on plants
	Olcella sp.	3	feeds on plants
	Oscinella sp.	2	feeds on plants
	Siphonella sp. #1	2	feeds on plants
	Siphonella sp. #2	3	feeds on plants
	Thaumatomyia apropinqua	3	preys on root aphids
Culicidae	Aedes dorsalis	1	feeds on dead aquatic veg.
Empididae	Drapetis sp.	2	preys on insects
Ephydridae	Hydrellia sp.	1	feeds on equatic plants
	Philygria debilis	3	bores in stems
Muscidae	Haematobia irritans	1	feeds on fresh manure
	Schoenomyza dorsalis	2	bores in stems(?)
Phoridae	undetermined sp.	1	various for family
Pipunculidae	Pipunculus	3	parasitizes leafhoppers
	Prothecus sp.	2	parasitizes leafhoppers
Sarcophagidae	Senotainia rubriventris	1	parasitizes aculeate Hymenoptera
Scenopinidae	Scenopinus albifasciatus	2	
Sciaridae	undetermined sp. #1	3	feeds on decayed veg.
	undetermined sp. #2	3	feeds on decayed veg.
	undetermined sp. #3	2	feeds on decayed veg.
Syrphidae	Eupeodes volucris	1	preys on aphids
	Scaeva pyrastri	1	preys on aphids
Tachinidae	Hyalomyia aldrichii	2	parasitizes true bugs

Tephritidae	Paroxyna clathrata	2	makes galls (?)
	Trupanea jonesi	2	makes galls in comp. heads
	Trupanea bisetosa	2	makes galls in comp. heads
Tethinidae	Pelomyia coronata	3	feeds on decayed veg.
Therevidae	Psilocephala costalis	1	preys on soil insects
Hemiptera			
Anthocoridae	Orius tristicolor	3	preys on thrips
Lygaeidae	Nyssius minutus	3	sucks sap
	Peritrechus saskatchewanensis		preys on insects
Miridae	Clivinema sp.	2	sucks sap
	Coquillettia sp.	2	sucks sap
	Irbisia brachycera	3	sucks sap
	Leptoterna ferrugata	3	sucks sap
	Litomiris sp.	3	sucks sap
	Orthotylus sp.	3	sucks sap
	Stenodyma virens	3	sucks sap
	Trigonotylus ruficornis	3	sucks sap
Nabidae	Nabis alternatus	3	preys on mirid bugs
Pentatomidae	Aelia americana	3	sucks sap
	Thyanta pallidovirens	2	sucks sap
Rhopalidae	Liorrhyssus hyalinus	2	sucks sap
Homoptera			
Aphididae	Acyrthosiphon dirhodum	3	sucks sap
	Acyrthosiphon sp.	2	sucks sap
Cicadellidae	Aplanus albida	3	sucks sap
	Athysanella sp.	3	sucks sap
	Auridius sp.	3	sucks sap
	Balclutha neglecta	3	sucks sap
	Ballana sp.	2	sucks sap
	Commellus sp.	3	sucks sap
	Dikraneura carneola	3	sucks sap
	Empoasca alboneura	2	sucks sap
	Hebecephalus sp.	2	sucks sap
	Parabolocratus sp.	3	sucks sap
	Psammotettix sp.	3	sucks sap
Delphacidae	Delphacodes campestris	2	sucks sap
Issidae	Aphalonema sp.	3	sucks sap
Psyllidae	Aphalara sp.	2	sucks sap
Hymenoptera			
Braconidae	Adialytus sp.	3	parasitizes aphids
	Apanteles sp.	2	parasitizes Lepidoptera
	Apanteles bedelliae	3	parasitizes Lepidoptera
	Bracon sp.	2	probably parasitizes Lepidoptera
	Bracon gelechiae	3	parasitizes Lepidoptera
	Chelonus sericeus	2	parasitizes Lepidoptera
	Hormius sp.	2	parasitizes Lepidoptera
	Lysiphlebus utahensis	2	parasitizes aphids
	Microctonus sp.	2	parasitizes beetles
	Microplitis sp.	2	parasitizes Lepidoptera
	Opius nr. chewaucanus	3	parasitizes Diptera
Chalcididae	Spilochalcis side	2	parasitizes Lepidoptera, Hymenoptera
Encyrtidae	Copidosoma sp.	3	parasitizes Lepidoptera
	Psuedoencyrtus sp.	3	parasitizes scale insects
Eucoilidae	Hexacola sp.	2	parasitizes insects
Eulophidae	Chrysocharini sp. #1	2	parasitizes Diptera
	Chrysocharini sp. #2	3	parasitizes Diptera
	Diaulinopsis callichroma	2	parasitizes leaf mining Diptera
	Diglyphus begini	2	parasitizes leaf mining Diptera
	Diglyphus intermedia	2	parasitizes leaf mining Diptera
	Diglyphus websteri	3	parasitizes leaf mining Diptera
	Hemiptarsenus americanus	2	parasitizes insects
	Necremnus sp.	2	parasitizes snout beetles
	Notanisomorpha sp.	2	parasitizes leaf mining Diptera
	Sympiesis sp.	2	parasitizes leaf miners, rollers (Lepidoptera)
	Tetrastichus sp. #1	3	parasitizes insects

	Tetrastichus sp. #2	2	parasitizes insects
	Tetrastichus sp. #3	2	parasitizes insects
	Zagrammosoma sp. #1	2	parasitizes acalyptera Diptera
	Zagrammosoma sp. #2	3	parasitizes acalypterate Diptera
Eurytomidae	Harmoleta sp. #1	2	bores grass stems
	Harmoleta sp. #2	3	bores grass stems
Formicidae	Formica rufa	2	feeds on honeydew
	undetermined sp.	2	feeds on honeydew
Ichneumonidae	Gelis sp.	2	feeds on honeydew parasitizes insects
	Diadegma insulare	2	parasitizes insects
	Temelucha sp.	3	parasitizesmicro Lepidoptera
Mymaridae	undetermined sp. #1	2	parasitizes insects
	undetermined sp. #2	3	parasitizes insect eggs
Platygasteridae	Platygaster sp.	2	parasitizes insect eggs
Pteromalidae	undetermined sp. #1	2	parasitizes insect eggs
	undetermined sp. #2	2	parasitizes insects
	undetermined sp. #3	2	parasitizes insects
	undetermined sp. #4	2	parasitizes insects
	Habrocytus sp. #1	2	parasitizes insects
	Habrocytus sp. #2	3	parasitizes insects
	Homoporus sp.	2	parasitizes insects
	Neocatolaccus sp.	2	parasitizes beetles
	Pachyneuron allograpta	2	Parasitizes parasitic Hymenoptera
	Sphegigastrini sp. #1	2	parasitizes insects, their parasites
	Sphegigastrini sp. #2	2	parasitizes mostly Diptera
	Sphegigastrini sp. #3	3	parasitizes mostly Diptera
	Sphegigastrini sp. #4	4	parasitizes mostly Diptera
	Sphegigastrini sp. #5	3	parasitizes mostly Diptera
Scelionidae	Scelio opacus	2	parasitizes mostly Diptera
	Trimorus sp.	2	parasitizes grasshopper eggs
	Trissolcus utahensis	2	parasitizes pentatomid eggs
Torymidae	Torymus thalassinus	2	parasitizes eurytomids (stem borers)
Trichogrammatidae	undetermined sp. #1	2	parasitizes insect eggs
	undetermined sp. #2	2	parasitizes insect eggs
Lepidoptera			
Lyonetiidae	Bucculatrix sp.	2	chews leaves
Plutellidae	Plutella xylostella	2	skeletonizes leaves
Neuroptera			
Chrysopidae	Chrysopa sp.	2	preys on aphids
Hemerobiidae	Micromus variolosus	2	preys on small, soft insects
Orthoptera			
Acrididae	Amphitornus coloradus	2	chews on leaves, stems
	Aulocara elipti	3	chews on leaves, stems
	Melanoplus sp.	2	chews on leaves, stems
Strepsiptera			
Halictophagidae	undetermined sp.	3	parasitizes leafhoppers
Thysanoptera			
Thripidae	Frankliniella sp. #1	2	rasps plant epidermis
	Frankliniella sp. #2	3	rasps plant epidermis
	Frankliniella sp. #3	3	rasps plant epidermis
	Scolothrips sexmaculatus	2	preys on mites

*Explanation of code numbers for apparent significance:
1. accidental
2. scarce, possibly accidental
3. abundant, probably not accidental

In: Johnson, K. L. (ed.). 1986. Crested wheatgrass: its values, problems and myths; symposium proceedings. Utah State Univ., Logan.

Value of Crested Wheatgrass for Big Game

Philip J. Urness

ABSTRACT: Crested wheatgrass (Agropyron desertorum, Agde "Standard," A. cristatum, Agcr "Fairway") have had great impact on western North America rangeland habitats of mule deer (Odocoileus hemionus) and pronghorn antelope (Antilocapra americana). The contribution of crested wheatgrass to seasonal diets and nutrition of deer is controversial and appears to vary widely by region and location. Nevertheless, green growth of these exotic grasses has been shown in some cases to be very important from fall to mid-spring, supplementing browse diets of frequently modest or low value until new forb growth in spring. A major general benefit of these exotic grasses has been a reduction of conflicts between deer and livestock on foothill ranges via extensive seedings in broad valley floors that tend to separate ungulate species during critical periods. Antelope have received less direct value from crested wheatgrass than deer. Forbs associated with grass seedings (some themselves seeded) are avidly sought by and of considerable value to antelope. Comparatively few areas of elk (Cervus elaphus) and bighorn sheep (Ovis canadensis) habitat have been seeded to crested wheatgrass, but where available they are used by these strongly graminivorous species. Any serious assessment of the pros and cons of seeding on big game ranges must be more comprehensive than a mere examination of diet composition. Moreover, trends away from grass monocultures toward simple grass-forb mixes or complexes of all three forage classes are commendable, albeit more difficult to establish and manage.

INTRODUCTION

Concerns that crested wheatgrass seedings could be detrimental to big game winter range values were expressed as early as the 1950's when large projects on burned, plowed, chained or sprayed areas began to reduce shrub forages in the sagebrush-grass and juniper-pinyon zones (Wagner 1983). However, little effort to assess impacts occurred until the early 1960's (Urness 1966). Since then a large number of studies have been published on various aspects of the problem. This paper attempts a synthesis of the overall topic and, by inference, points to the gaps in our knowledge at present.

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MULE DEER

The myth that mule deer are obligate browsers on winter range dies hard despite many literature sources, citing importance of green grass and forbs to their diets, over a period of at least 50 years (Dasmann 1949, Dietz et al. 1962, Dixon 1934, Edwards 1961, Kufeld et al. 1973, Leach 1956, Leckenby 1969, McLean and Willms 1982, Plummer et al. 1968, Robinette et al. 1973, Skovlin and Vavra 1979, Willms et al. 1979, and many others). Granted that browse is an indispensible component of deer winter diets when snow depths prevent access to short forb and grass forages, the fact remains that on many deer wintering areas snow cover is often alternated with snow-free periods on south and west-facing slopes. Consequently, green growth initiated in fall by perennial and annual grasses is periodically available. Where snow cover is deep and continuous, or in drought years when fall regrowth is sparse or absent, herbaceous forages obviously have minimal importance to wintering deer. Adequacy of shrub resources then becomes critical.

These contrasts between years, regions and locations within regions have developed conflicting viewpoints regarding the value to deer of grass in general and crested wheatgrass in particular. For instance, Vavra et al. (1982) found very low spring use of green Agde on the Keating unit near Baker, Oregon. Although total grass consumption exceeded browse use, Sandberg bluegrass (Poa sandbergii) was the preferred species. Tausch (1973) studied sagebrush and juniper-pinyon chainings in Nevada; those seeded to Agcr had low deer use compared to treated areas where native grasses such as squirreltail (Sitanion hystrix) and Sandberg bluegrass dominated the understory. Cole (1968) discussed the potential for deer of monotypic Agde seedings as generally developed in Nevada in the 1950's and 1960's; he found no extension of deer range due to seedings, at best peripheral use, and lowest use levels where Agde was most abundant. Providing herbaceous forages on seedings when prolonged winter conditions kept deer at lower elevations was considered one of the limited benefits.

Terrel and Spillett (1975), investigating seeded juniper-pinyon conversion areas in Utah, found grass use by deer in winter to be less than expected on the basis of its contribution to the total forage resource; however, grasses were first and third in dietary importance over the two years of the study. They were vague in identifying species, but indicated that Agcr dominated the conversions, so one can infer that it also dominated use. The authors implied that Agcr is less desirable or less attractive to deer than bluegrasses (*Poa* spp.), Russian wildrye (*Elymus junceus*), and cheatgrass (*Bromus tectorum*). Terrel (1973) made a rough calculation of the amount of grass needed for deer on winter range based on (1) green grass comprising 25% of deer diets, (2) an average consumption of 1 pound (0.45 kg) air-dry grass per day, (3) a 180-day season, (4) an effective availability of 200 pounds per acre (200 kg/ha), and (5) the number of deer using a wintering area. He concluded that grass need could be satisfied with far fewer seeded acres (ha) than were present on his study area. While one might quarrel about some of the assumptions, his calculation probably is reasonable except that no parallel calculation was made of shrub needs of deer. If those resources again exceeded need, such an exercise might have revealed that the larger seedings, while not contributing to deer, also did not limit them.

Vale (1974) speculated that large seedings of crested wheatgrass would decrease carrying capacity of deer winter ranges and discounted any real benefits except during the late spring fawning period. The latter point seems odd since few large seedings are located at intermediate elevations where deer fawns are born. Moreover, it is the very broad Intermountain Region valleys he emphasized that were seeded in large tracts and that tend to have minimal values as winter range for deer under any conditions. Commonly, a narrow belt of steeper lands along mountain toe slopes or bajadas are typically deer concentration areas. Indeed, Vale (1974) stated that valley-bottom seedings have improved foothill areas by concentrating livestock on seedings so that native ranges could recover from excessive past use. Heady and Bartolome (1977) made essentially the same point relative to the Vale Program in southeastern Oregon.

Conversely, a number of studies have shown that green crested wheatgrass can provide valuable nutrients to otherwise browse-dominated diets on many deer winter ranges throughout the western United States and Canada. For example, Austin and Urness (1983) found green Agde percentages in seasonal deer diets of 51 (Nov.), 2 (Dec.), 3 (Jan.-Feb.), 38 (Mar. 1-20), 90 (Mar. 21-Apr. 10), and 57 (Apr. 11-30). The low levels from December through February reflected snow depths that limited access to green leaves near ground level. Leckenby (1969) reported Agde as constituting 35 (Feb.), 45 (Mar.), and 30 (Apr.) percent of feeding observations of mule deer in central Oregon. Over the entire winter 1968-69 (Dec.-May), Agde comprised 34 percent of total feeding observations; green grass of all species totaled 72 percent. In British Columbia, green Agcr was second in importance to Sandberg bluegrass in deer diets from a seeded habitat during the period 6 March to 5 May; Agcr was most important from 6-31 May (Willms and McLean 1978).

Nutritional value of green Agde to mule deer is quite important when consumed in dietary percentages as high as noted above. Urness et al. (1983) showed that digestibilities of pure Agde diets in April averaged 62 percent over 20-day *in vivo* feeding trials with four deer, a figure generally much higher than those for available browse forages in late winter and early spring. Similarly, *in vitro* trials showed dry matter disappearance percentages for green Agde of 58 (fall), 51 (winter), 58 (at greenup in late March to early April), and 76 (spring). Crude protein levels for the same periods were 23, 15, 23, and 30 percent. The two primary browse plants, mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) and Douglas rabbitbrush (*Chrysothamnus viscidiflorus*), ranged from 14-19 and 6-8 percent crude protein, respectively. The contribution of green Agde to deer diets was compared by weighting dietary crude protein and digestibility levels with and without grass. Fall (Nov.-Dec.) and greenup (Mar. 21-Apr. 10) diets showed significantly higher values with grass added, whereas mid-winter and spring diets were not different. Moen (1978) emphasized the critical importance of the greenup period to deer reproduction and overwinter survival.

Koehler and Leckenby (1970) conducted a preliminary analysis of the costs and benefits of chaining and seeding vs. artificial feeding of a commercial pelleted ration, based on estimated costs per pound of total digestible nutrients (TDN) and projected TDN needs of wintering mule deer. They concluded it was less costly to artificially feed deer (both approaches were expensive in terms of the revenues generated under existing management systems), but entire costs of seedings were charged to deer as though that were the only benefit. Inclusion of other values (e.g. livestock forage, soil stability) and greater-than- estimated future costs of the artificial ration could easily reverse the ranking. Nevertheless, it was a useful attempt to sort out various aspects of the value of seeded grass to wild ungulates. The authors made an important additional point: rehabilitation efforts, when placed in optimal pattern with native vegetation types, appear to increase efficiency of use of native range. Therefore, they provided greater value than just the available AUMs of seeded forage by improving the balance of dietary nutrients.

A number of investigators (Koehler and Leckenby 1970, Leckenby 1968, Leckenby et al. 1982, Lamb 1966, Willms and McLean 1978, Willms et al. 1979) have mentioned the greater accessibility to wintering deer of green grasses when standing dead straw has been removed or reduced by prior grazing of livestock. While this is generally true for snow-free periods, Austin et al. (1983) showed that ungrazed straw can significantly increase the amount of green Agde in deer diets under certain snow-cover conditions via a black-body effect. Thus basal green leaves on previously ungrazed plants become available through differential snowmelt whereas those on heavily grazed plants do not. Moreover, they found that the production of basal green leaves was usually as great or greater on plants ungrazed by livestock, especially in years when conditions favored abundant fall growth. This is, perhaps, the only solid evidence in support of a rest-rotation management system for Agde and, even then, it means that only about 1/3 of seeded areas where deer concentrate in winter need be rested. Preferably this would be in many scattered small units, rather than a few large ones.

Recent emphasis on smaller seeded areas and mixtures of seeded species may reduce the objections of many wildlife biologists to crested wheatgrass, especially if interseeding of shrubs and forbs are successfully achieved on existing monoculture stands (Rumbaugh et al. 1982). However, despite the advantages of mixed seedings, the fact remains (Leckenby and Toweill 1983 a and b) that exotic wheatgrasses are the primary species that establish on the drier end of the seeding range. Costs of other less-commercially-available species are often too high, and examples of successful establishment too few, to justify risking scarce range-and habitat-development capital. Therefore, in my opinion, one can expect to see a very important role for crested wheatgrass on semi-arid shrublands used by deer far into the future. Research has shown that grass can be a positive element if management is keyed to optimizing the benefits of seedings.

PRONGHORN ANTELOPE

Pronghorn consume even less grass on an annual basis than deer, therefore they have benefited directly to a lesser extent from crested wheatgrass seedings. Actual use of crested wheatgrass is quite low, only a few percent, even when pronghorn winter on seedings (Kindschy et al. 1982, Spalinger 1979); use is a bit more on spring range perhaps. Early-growth leaves appear most attractive (Heady and Bartolome 1977).

Moreover, the patterns of antelope range use on the broad valley-bottoms of the Great Basin, typically seeded in large tracts, indicate a greater potential for negative impacts on important forb and browse forage resources. This appears especially true where herbicides constituted the pretreatment (brush control) in advance of drill seeding.

There are two general viewpoints regarding required habitat for antelope. One is that pronghorns need strongly shrub-dominated ranges, especially species of sagebrush, because their diets are mostly browse (Pyrah 1971, Sundstrom et al. 1973, Vale 1974). In this view, loss of shrub dominance via herbicidal, pyric, and mechanical treatments is a major cause of low antelope densities in some areas. The other school of thought emphasizes the importance of grasslands as historic antelope range, and the fact that their greatest densities were attained on the prairies east of the Rocky Mountains, not on the shrublands of the Intermountain West (Kindschy et al. 1982, Leopold 1959, Yoakum 1978, 1983). In the latter view, increased height and density of sagebrush resulting from (1) reduced perennial grasses and forbs with heavy continuous livestock grazing and (2) reduced fire frequency (active fire suppression) was not a boon to antelope.

On the contrary, it was Leopold's (1959) conclusion that loss of valley grasslands where antelope once thrived was the cause of their low numbers in present-day Nevada. He predicted that increased range seeding of perennial grasses after removal of some dense shrub stands would lead to gradual increases in antelope numbers with proper management. Leopold gave as evidence citations of early explorations in the Great Basin. Bryant (1848) saw hundreds of pronghorns along the Humboldt River in 1846. However, Simpson's 1859 expedition for the US Army across the central Great Basin, from Salt Lake City to Genoa (in Carson Valley), recorded few pronghorn except in Antelope Valley, where they were abundant. Sightings by his party were also sparse on the return trip via a more southern route (Simpson 1876). The reader must conclude that antelope were strongly aggregated and abundant only in the most favorable habitats composed of the more open grassy valleys, especially on well-watered lowlands. The interminable stretches of sagebrush across the wide valleys of the eastern Great Basin, cited *ad nauseum* by Simpson, yielded few or no sightings of antelope despite the fact that indigenous peoples could not effectively capture the few that were there.

Thus, it appears that presence of abundant sagebrush did not assure more than scattered populations of antelope in the pristine Great Basin, nor did absence of sagebrush prevent their existing in hordes on the prairies of the Great Plains. If sagebrush and grass are not the key to antelope abundance, what is? The common thread through this apparent conflict of views resolves to the relative availability and importance of the forb class of forage, and the variety and adequacy of shrubs (not the superabundance of one). While many studies indicate the dominance of big sagebrush in antelope diets at the present time (extensively reviewed by Sundstrom et al. 1973), this may reflect only great availability and the depletion of "something" that once occurred (i.e. a sagebrush disclimax induced by heavy long-term livestock grazing). Deming (1963) hypothesized that that "something" was forbs and shrubs more palatable to livestock than big sagebrush.

The importance of forbs to pronghorn during the growing season, and therefore to satisfying the high nutritional demands of late gestation and lactation, appears generally accepted by biologists. The association of forbs with seeded grasses make crested wheatgrass projects valuable to antelope. This association may be relatively short-lived unless forbs are part of the seeding mixture (Heady and Bartolome 1977, Reeher 1969, Yoakum 1980 and 1983). Native and adventive forbs can be lost rather quickly where grasses establish at levels most range managers term successful; for pronghorn marginal seedings may be the most used (Reeher 1969). For example, the Chicken Creek project on the Vale Program in southeast Oregon showed a ground cover of only 35% grass, 20% forbs and 2% shrubs; 43% was bare ground. Antelope pellet groups were over three times more numerous on the seeding than on the adjacent sagebrush area that served as the control.

While most seeded mixtures on pronghorn ranges in the Great Basin have been simple Agde and dryland Nomad alfalfa (*Medicago sativa*), it is Yoakum's (1983) opinion that more complex mixtures should receive greater research effort. This is based on the greater availability of a wider variety of forb seeds today than when most monoculture grass seedings were established 20-30 years ago. The potential for more complex seedings is, however, most likely better at the higher end of the precipitation spectrum (Leckenby and Toweill 1983 a and b). Interseedings of forbs and shrubs show some promise, but are expensive (Rumbaugh et al. 1982).

Structure of managed rangelands, including Agde seedings, has recently been suggested to be as important to antelope as composition (Kindschy et al. 1982, Yoakum 1980, 1983). Their guidelines give very specific characterizations of optimal height (averaging 38-61 cm, 15-24 inches), composition (40-60% grasses, 10-30% forbs, 5-20% shrubs), variety (5-10 species of grasses, 20-40 forbs, 5-10 shrubs), ground cover (averaging 50% live vegetation), and other habitat factors. Biologists in the drier regions of antelope range would no doubt agree but they hardly can expect such luxury except, perhaps, in the wettest cycles. Their options, while limited, should still focus on forb and shrub variety to the extent possible. Weedy annual forbs, the bane of the "true-believer" range conservationist, may be quite satisfactory for antelope. Indeed, the extent to which introduced exotic weeds contribute seasonally to pronghorn diets and nutrition is a poorly researched topic.

The value for antelope of many seeded ranges in summer has been the provision of dependable water sources in otherwise dry valleys (Heady and Bartolome 1977, Kindschy et al. 1982, Yoakum 1980). The distribution of seasonal use may have more to do with water availability than forage kind or amount in the arid Great Basin. Development of large numbers of watering points likely benefits antelope by allowing them to disperse over a greater area. Conversely, limited water points can concentrate use, restrict expression of selective forage preferences (and thus nutritional intake), and possibly influence predation on fawns.

Improved range conditions resulting from a combination of better livestock management, a series of wet years, and rangeland seedings have generally resulted in expanding antelope populations in the US (82% increase aided by transplanting populations into new or former habitats) in the past two decades. Increases have been even greater in the northwestern states except Oregon where the population has remained unchanged (Table 1). The Vale Program population in southeastern Oregon showed an approximately 3-fold increase from 1961 to 1976 (Heady and Bartolome 1977). Thus, it appears that at worst extensive seedings in the Great Basin have had little negative impact. They may have been, as predicted by Leopold (1959), an important factor in gradual population increases. There seems no reason to doubt that, with greater attention to management with antelope needs as an integral element, population levels will continue to increase. The complementarity between pronghorn and cattle diets, and the steady decline in the range sheep industry, indicates a reduction of conflict despite expanded antelope populations.

Table 1.—Antelope population levels in four western states (data supplied by Don Klebenow, University of Nevada—Reno).

	Oregon	Idaho	Nevada	Utah
1964	8,950	4,700	4,500	970
1982	8,900	17,500	9,000	5,000

ELK, BIGHORN SHEEP, and BISON

Little information is extant on use of crested wheatgrass by elk. Kirsch (1962) indicated Agcr use was greater than bluebunch wheatgrass (*Agropyron spicatum*) in a ponderosa pine-grassland type in Montana, despite the greater abundance of the latter species. Agcr was seeded with smooth brome (*Bromus inermis*) on abandoned farmland and brome was much preferred. However, since the majority of total grass items in the diet analysis was unidentified, the relative usage stated may have limited utility. Kufeld (1968) reported various conversion of extensive areas of juniper-pinyon and sagebrush-grass types in Colorado. Of those seeded, 84% were seeded to Agcr, and nearly half to sweetclover (*Melilotus* spp.). Thirty-eight percent of the treated lands in Colorado was elk range, with two-thirds used by elk from fall through spring. Effects on elk were not evaluated except on sagebrush spraying treatments and most of those were not seeded.

Brooks and Urness (1984) fed crested wheatgrass at two phenological stages to tractable elk. Organic matter digestibilities were 74% for the late vegetative stage and 53% for the late bloom stage. This indicates a very high value of green leaves and a moderately high value for nearly mature forage. Voluntary intakes of forage in the late vegetative stage were as high as good quality alfalfa hay, thus elk seemed to relish crested wheatgrass in hay form. Observation of elk feeding on crested wheatgrass seedings in early spring at several locations in Utah (James Bates, Utah Division of Wildlife Resources) supports the view that elk find Agde palatable. A seeding on a 10-year-old, juniper-pinyon burn at Boulder Mountain was especially heavily used by elk in winter and early spring, as was a seeding at Johns Valley. Although relatively few areas of elk range have been seeded to crested wheatgrass, it appears they will eat it readily when available and derive adequate or better nutrition when it is green. Obviously elk can also utilize mature crested wheatgrass much better than either mule deer or antelope.

Even less information was found regarding bighorn sheep use of crested wheatgrass. A recent book on desert bighorn sheep (*Ovis canadensis mexicana*) ecology (Browning and Monson 1980) gave no data on foods eaten in the Great Basin, nor mentioned crested wheatgrass elsewhere. They emphasized the importance of grass and browse to yearlong sheep diets, so it is likely if sheep encounter seedings they would use them. A radio-telemetry study of desert bighorn on Dark Canyon Plateau and Horse Flats in Glen Canyon National Recreation Area showed sheep traversing seeded stands, but it was not known if they actually used seeded grass (Michael King, Utah State University). King also said Bureau of Land Management personnel reported bighorns using seeded ranges near the Colorado River rim across the river from Canyonlands National Park. James Bates believes heavy cattle grazing limits bighorn sheep use of seedings in this area.

McQuivey (1978) gave a brief summary of desert bighorn sheep diets in Nevada but only discussed forage classes rather than species. Grasses predominated (65%) in all rumens analyzed and it is therefore likely that crested wheatgrass would be used if available. The very rocky and arid locations that desert bighorns generally occupy restricts opportunities for seeding any significant area.

No reference to use of crested wheatgrass by mountain sheep (Ovis canadensis canadensis) was found. Heady and Bartolome (1977) mentioned an introduction in 1965 in the vicinity of the Vale Rehabilitation Program area in southeastern Oregon, but no use of seedings by the expanding population had been observed by 1975. It was their opinion that improved native ranges resulting from reduced livestock pressure were a derived benefit from seeding at lower elevations.

Finally, a study by Van Vuren and Bray (1983) of bison (Bison bison) and cattle diets on seeded range in the Henry Mountains of southcentral Utah, showed diets of both animal species were dominated (over 80%) by Agropyron spp., presumably mostly crested wheatgrass.

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Nongame Bird Responses to Type Conversion of Sagebrush Communities

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ABSTRACT: When degraded sagebrush communities are converted to grasslands to improve forage production for livestock, impacts on nongame birds occur. Removal of sagebrush results in displacement of the shrub-nesting species which are dominant in degraded sagebrush habitat. However, seeding with perennial grasses results in habitat more suitable for some ground-nesting species which may increase accordingly. When successional invasion by sagebrush reaches the point where a "sagebrush-grass" community is established, relative abundance of bird species may change, resulting in a well-balanced mixture of both shrub and ground-nesting species. This diverse bird community in a shrub-invaded seeding is a result of the more diverse vegetation structure compared to the single-layered stands of either grasses or shrubs. The time required to reach this point depends on several factors, including extent of sagebrush control, success of seeding establishment, and livestock management.

ACKNOWLEDGEMENTS: A contribution of the Nevada Agricultural Experiment Station, University of Nevada, Reno, and the USDA Agricultural Research Service. The senior author also acknowledges support from the Bureau of Land Management during the writing of this paper.

INTRODUCTION

Beginning in the 1930's, vast acreages of sagebrush-dominated rangelands in the West were treated to increase forage production for domestic livestock, and to improve range condition and prevent erosion. Sagebrush "control" efforts peaked in the late 1950's and 1960's, resulting in the conversion of thousands of acres to grass and croplands. Approximately 10% of the sagebrush rangelands have been converted to cropland or altered to increase livestock production (Braun et al. 1976). Many of the sites where sagebrush cover was removed or reduced were seeded with desirable livestock forage, primarily perennial grasses. Because little success was obtained with native grasses, introduced species were used. Varieties of the alien crested wheatgrass (Agropyron cristatum, A. desertorum) were among the most successfully seeded grasses in the Intermountain West (Blaisdell et al. 1982), and are recognized by range managers and livestockmen as being good livestock forage.

Concern for the effects of sagebrush community alteration on nongame birds was expressed in the 1950's by Carhart (1954), and concern has intensified in recent years (Braun et al. 1976). There have been few studies on the response of nongame birds to sagebrush control (Scott et al. 1966, Best 1972, Pyrah and Jorgensen 1974, Schroeder and Sturges 1975, Castrale 1982). Still fewer have been conducted on the combined effects of sagebrush control and single-species seeding of crested wheatgrass. In this paper we attempt to draw from available literature and our own research experience to show the sequence of bird responses to sagebrush habitat changes: from the pristine sagebrush-grass habitat through eventual degradation by overgrazing, to conversion to grassland and eventual sagebrush reinvasion.

BIRD COMMUNITIES IN PRISTINE SAGEBRUSH-GRASSLAND

It has been estimated that sagebrush covers up to 109 million ha (270 million acres) of western rangeland, with big sagebrush (Artemisia tridentata) comprising more than half of this area (Beetle 1960). It is not possible to know the exact composition of bird communities during presettlement times. Even today bird communities in sagebrush habitats are highly variable by location (Wiens and Rotenberry 1981). However, we can speculate on historical conditions based on descriptions of sagebrush communities by early explorers and settlers.

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According to Vale (1975), the early travelers in the Intermountain West encountered a landscape that was largely shrub dominated, with sagebrush being particularly common. There are indications that although grass coverage was variable, much of the sagebrush range had a vigorous understory of perennial grass and forbs (Harniss and Murray 1973).

Over 100 species of birds are known to forage and nest in sagebrush communities (Brown et al. 1976). The pristine sagebrush-grassland community probably had a diverse mixture of both shrub-nesting and ground-nesting birds. Shrub-nesters such as Brewer's sparrows (Spizella breweri), sage sparrows (Amphispiza belli), sage thrashers (Oreoscoptes montanus), gray fly-catchers (Empidonax wrightii), and loggerhead shrikes (Lanius ludovicianus) are among those common today in sagebrush communities (Braun et al. 1976, Reynolds and Trost 1980, Wiens and Rotenberry 1981, Castrale 1982). These species were probably abundant in pristine vegetation with its reported shrub component. Ground-nesters in sagebrush communities include horned larks (Eremophilus alpestris), western meadowlarks (Sturnella neglecta), vesper sparrows (Poecetes gramineus), and lark sparrows (Chondestes grammacus). Densities of ground-nesting birds, especially the latter three species, were probably higher in presettlement vegetation because of the greater herbaceous cover available. Wiens and Rotenberry (1981) refer to these birds as "grassland" species, and mention particularly that western meadowlarks and lark sparrows are more abundant where perennial grass cover is greater. Castrale (1982) pointed out that vesper sparrows nest both under sagebrush and at the base of grass tussocks.

BIRD COMMUNITIES IN DEGRADED "MONOTYPIC" SAGEBRUSH HABITATS

Sagebrush-grass communities on rangelands were severely overgrazed by livestock near the beginning of this century. This overgrazing destroyed much of the understory vegetation and, combined with fire suppression, resulted in heavy overstory dominance by sagebrush (Stewart 1941). The present condition of sagebrush rangelands probably bears minimal resemblance to the pristine potential (Young et al. 1979). Assuming the sequence of understory degradation followed by shrub dominance, bird populations in today's near-monoculture sagebrush habitats should not be considered as "natural" or "pristine" bird communities, especially in terms of species composition. On the other hand, since the rangelands in question were apparently sagebrush dominated (although with a better herbaceous understory), type conversion of these areas to pure stands of grass (e.g., crested wheatgrass) cannot be justified in terms of reestablishing "natural" plant cover (Vale 1975). Rather, the primary justification for such conversions has been (and remains) to increase forage production for livestock.

Bird communities in today's degraded sagebrush habitats probably include most if not all of the species present in the pristine environment. However, the relative abundance of many species may be markedly different. In a Nevada study, Page et al. (1978) found that grass-nesting species such as vesper sparrows and western meadowlarks decreased when livestock grazing reduced herbaceous vegetation cover in sagebrush habitat. If indeed livestock grazing has also resulted in an increase in shrub (e.g., sagebrush) density over the years in some areas, then some of the shrub-nesting bird species might have increased accordingly. Grassland studies under the International Biological Program have shown that where grazing produced marked changes in vegetation, there were accompanying major shifts in the avian community (Wiens and Dyer 1975). We would therefore like to reemphasize that the bird communities in today's degraded sagebrush stands are probably very different (in terms of relative abundance) than those in presettlement vegetation.

EFFECTS OF SAGEBRUSH HABITAT CONVERSION ON PASSERINE BIRDS

Sagebrush Control

Big sagebrush rangelands with depleted understory vegetation are those which are typically chosen for sagebrush control and seeding (Evans et al. 1979). The most immediate effects on the avifauna of the treated areas are brought about by this removal or reduction of shrub cover (Rotenberry and Wiens 1978). Sagebrush is most often removed by burning, spraying, or mechanical means. Basically, all of these methods result in the elimination of the necessary stratum for shrub-nesting species, and an increse in openness of the habitat. Food habitats of passerine birds (perching songbirds) in sagebrush habitats may also be affected by changes in plant and animal (insect) abundance and composition brought about by sagebrush control, and the accompanying damage to herbaceous vegetation (Best 1972). According to Rotenberry and Wiens (1978), there is a real lack of information on how the food base of birds is affected by habitat manipulation.

Burning.--Fire is a natural component of many sagebrush-grass rangelands, and any site with vegetation dense enough to carry a fire has probably burned many times in its history. The use of fire as a management tool in sagebrush communities has been thoroughly reviewed by Britton and Ralphs (1979). In a Utah study, Castrale (1982) found that the effects of burning were much more pronounced four years after treatment than the effects of mechanical control (chaining). He also stated that, compared to herbicide spraying and chaining, burning causes the most immediate and persistent changes in sagebrush habitat because whole shrubs are consumed by fire and ground litter is reduced. However, intensity of the burn may affect the outcome as well. When fires burn in a mosaic pattern, some sagebrush plants which are left unburned provide suitable nesting cover for birds (Castrale 1982). Also, Harniss and Murray (1973) stated that sagebrush will sometimes invade an area immediately following a burn.

Studying bird communities in rangelands of the Pacific Northwest, Rotenberry and Wiens (1978) found no change in total density and biomass of birds during the first year after fire removed nearly all shrubs (primarily sagebrush) on a study plot. However, they did note some significant changes in relative abundance of species. In particular, horned larks (ground-nesters) replaced the shrub-nesting sage sparrows as the dominant breeding species. The authors concluded that this phenomenon reflected the differing relationships of these species to the presence of shrub cover. Although there was a reduction in biomass diversity, species composition remained unchanged.

Mechanical shrub removal.--The most commonly employed mechanical shrub removal methods are plowing or disking, beating or shredding, railing, and chaining (Blaisdell et al. 1982). These methods differ somewhat in their effectiveness as sagebrush control measures and in the extent to which understory vegetation is harmed. Beating and railing produce only light kills of sagebrush and sprouting shrubs, and damage to understory vegetation is minimal. Plowing (or disking) and modified chaining result in more thorough shrub removal and also prepare a good seedbed where revegetation is planned. Shrub removal by mechanical methods is considered by some to be less permanent than that achieved by other methods (Parker 1979).

Plummer et al. (1968) recognized that chaining did not completely kill sagebrush and that native grasses and forbs were retained in the treated area. However, plow and seed treatments account for most of the crested wheatgrass seedings in the Great Basin and Northwest (Heady and Bartolome 1977). Urness (1979) suggested that crested wheatgrass seedings would not differ materially whether done on a burned, sprayed, or plowed seedbed. However, he pointed out that a big advantage of mechanical control methods was their potential for partial control and interspersion of native range.

Castrale (1982) studied bird populations in sagebrush habitats that were mechanically controlled (by plowing and chaining). Basically, he concluded that the more thorough removal of sagebrush and accompanying understory damage by plowing are more detrimental to bird populations the first few years after control than are the vegetation changes which result from chaining.

Spraying with herbicides.--The use of herbicides in sagebrush control became common in the 1950's with the use of 2,4-D (Evans et al. 1979). Other chemicals have also been used successfully since then, but 2,4-D has received the most widespread use because of its effectiveness, low cost, low toxicity to humans and animals, and degradability (Blaisdell et al. 1982).

In addition to killing shrubs, 2,4-D kills some species of forbs as well, but seldom damages perennial grasses. The loss of some forb species in the understory may be of consequence to birds because of a resulting loss of food items such as seeds and insects (Best 1972). However, this forb loss through spraying is partially offset by the more gradual loss of shrub cover (compared to other control methods). Schroeder and Sturges (1975) reported that, during the year of herbicide application, nesting success of Brewer's sparrows was not affected by spraying with 2,4-D. However, they found that use of sagebrush decreased greatly after the leaves had dropped from the plants. Bird densities were 67% lower one year after spraying and 99% lower 2 years afterward. Best (1972) reported a 54% decrease in breeding pairs of Brewer's sparrows one year after spraying. Vesper sparrow pairs on his study area were not affected because of their ground-nesting habits.

In comparing sagebrush control methods, Castrale (1982) suggested that effective control by herbicide application continues to offer cover and suitable nest sites for a few years after treatment. The dead shrubs then eventually deteriorate, leaving the habitat unsuitable for shrub-nesters until sagebrush becomes reestablished. Kindschy (1978) also mentions the same phenomenon. Rotenberry and Wiens (1978) suggest that this adaptability of sagebrush dependent birds shows they are at least moderately resistant to small scale habitat alteration (i.e., if the basic vegetation structure is not altered markedly).

Seeding Stages After Brush Control

After shrubs have been controlled by one of the methods mentioned above, the treated area is then usually seeded with perennial grass (typically some variety of crested wheatgrass) or some mixture of grasses, forbs, and possibly even important forage shrubs (Keller 1979). Sometimes, in habitats where remnant understory vegetation is sufficient, sagebrush is controlled for the purpose of "releasing" the existent understory by reducing competition with shrubs (Braun et al. 1976). However, since crested wheatgrass is the focus of this symposium, we will primarily address conversion to crested wheatgrass seedings. There are many parallels between bird response to seedings and bird response to understory release, and these will be pointed out. We will consider seedings as having four basic stages, though obviously seedings change slowly and continually as secondary succession proceeds.

Stage one-immediately after seeding.--The initial effects of the seeding will be variable, related primarily to the method and effectiveness of brush control, and the resulting extent of damage to the understory vegetation. Another influence on bird populations in the early stages of the seeding is the relative "barrenness" of the area until crested wheatgrass becomes established. This stage is often compounded by the invasion of alien weeds. On some sites, cheatgrass (Bromus tectorum) can be a serious deterrent to successful range seeding (Harris 1967). In southern Idaho, Rickard (1981) reported that horned larks and western meadowlarks were common in cheatgrass monocultures, while other species resident in adjacent sagebrush-grass habitat were seldom observed. Horned larks nest on the ground or in open areas, and are most common in disturbed grassland habitats in the West (Kendeigh 1941). Because western meadowlarks are considered closely tied to perennial grass cover, their utilization of annual cheatgrass is apparently a suboptimal situation.

Stage two-established seeding.--Degree of seeding establishment depends on a variety of factors, including site potential, weather (especially precipitation), reduction of plant competition (e.g., with cheatgrass), method and timing of seeding, and adequate early protection from grazing (Keller 1979). Most seedings are left ungrazed until at least the latter part of the second growing season, and up to two or more years later.

Braun et al. (1976) and Kindschy (1978) acknowledged that reduction of sagebrush cover can benefit such bird species as horned larks, western meadowlarks, vesper sparrows, lark sparrows, and mourning doves. Wildlife response to such understory "release" is widely accepted by wildlife managers as being positive (Buttery and Shields 1975, Urness 1979). When areas require seeding due to lack of an understory, a mixed species seeding (as opposed to single species seeding) would undoubtedly be more beneficial to a variety of wildlife. In particular, a rangeland seeding with native grasses and forbs is largely beneficial to bird habitat (Buttery and Shields 1975). However, single-species seeding of crested wheatgrass was the usual practice in past habitat conversions. Fortunately, the ecological distribution of nesting birds is controlled by life form of vegetation rather than species composition (Johnsgaard and Rickard 1957, MacArthur and MacArthur 1961). This being the case, "grassland" bird species may be expected to respond favorably when an introduced grass such as crested wheatgrass becomes well established.

There have been few studies which specifically dealt with bird populations in older, well established crested wheatgrass seedings. Reynolds and Trost (1980) reported on breeding bird populations in 21- to 22-year-old crested wheatgrass seedings in southern Idaho. They found nests of horned larks, western meadowlarks, and vesper sparrows in an ungrazed seeding, but horned larks were the only nesting species in a seeding grazed by sheep. No nests of shrub-nesting species were discovered in either of the seedings. They also reported that total bird density, species diversity, and species richness were lower in both the grazed and ungrazed seedings than in either grazed or ungrazed sagebrush habitats. However, nesting densities of both horned larks and meadowlarks were higher in the ungrazed crested wheatgrass than in either the grazed or ungrazed sagebrush communities, and ungrazed seeding habitat was the only area where a vesper sparrow nest was located. Similarly, both meadowlarks and vesper sparrows have been observed to be more abundant where native perennial grass cover is greater (Wiens and Rotenberry 1981), and where a mixture of native grass/crested wheatgrass cover is greater (Castrale 1982).

Rickard (1981) investigated bird populations on established crested wheatgrass seedings in southern Idaho and found likewise that vesper sparrows, western meadowlarks, and horned larks nested in these man-made communities. He stated that crested wheatgrass seedings were suitable habitat for the latter two species. Although horned larks were most abundant in the seedings, communities with sagebrush harbored more meadowlarks. Once again, the missing component in crested wheatgrass seedings was shrub-nesting species.

In an ongoing study in central Nevada[1], ground-nesting species (primarily horned larks and meadowlarks) comprised 91% of the nesting avifauna in a 26-year-old crested wheatgrass seeding. Comparatively, in unconverted sagebrush habitat with 21% shrub cover, only 30% of the birds were ground-nesters. Both the seeding and surrounding sagebrush habitat were grazed by cattle. Although total number of bird species nesting in the seeding was lower than that in the untreated sagebrush, total abundance was nearly the same. This finding conflicts with what Reynolds and Trost (1980) reported for total bird abundance on both grazed and ungrazed seedings in Idaho. Variables which might explain this difference include livestock class, season and intensity of grazing, and success of original seeding establishment in terms of perennial grass cover. Where brush control for understory release is practiced there may or may not be changes in total abundance, although those species closely tied to shrub cover may be nearly eliminated (Rotenberry and Wiens 1978).

<u>Stage three-reinvasion by sagebrush</u>.--Little mention has been made in the literature of passerine bird population responses to the reinvasion of sagebrush into areas of sagebrush control. Sneva (1972) recognized that shrub invasion of treated range in the Intermountain area was to be expected. Fifteen years after chemical control of sagebrush on his study area, the number of sagebrush plants 6 in (15 cm) or less in height on the treated area was similar to the number of mature sagebrush on untreated areas. He also maintained that even when treated areas are managed for minimal ecological impact, shrubs will return.

Harniss and Murray (1973) reported a similar occurrence for burned sagebrush range. According to Pechanec and Stewart (1944), good grazing management will not prevent sagebrush invasion, but heavy grazing and poor brush control will accelerate such invasion. Frischnecht (1968) observed that in wet years sagebrush will invade grazed or ungrazed stands of crested wheatgrass. Time lapse before invasion is highly variable (Urness 1979). According to Evans et al. (1979), some seedings are invaded almost immediately after establishment, while others remain shrub-free for years. Unkilled mature sagebrush in the seeding is a source of reinvasion (Parker 1979).

According to Urness (1979), wildlife research has tended toward all-or-none comparisons (i.e., intact sagebrush stands vs. crested wheatgrass monocultures). He also suggests that there has been a tendency to deny stand dynamism and what it means to specific wildlife forms. Black and Thomas (1978) noted in general that type conversions without maintenance tended to revert to the original plant community.

Best (1972) pointed out that the duration of changes in bird food habits resulting from chemical control of sagebrush would depend upon future grazing practices, the return of forb species, and <u>reinvasion of sagebrush</u>. He also mentioned that the <u>duration of compensatory</u> cover (for birds) provided by dead sagebrush would depend on the rate of deterioration of these dead plants and the rapidity and <u>extent of sagebrush reinvasion</u> (our emphases).

Castrale (1982) studied a 17-year-old seeding in Utah which had been plowed and seeded with a mixture of perennial grasses, including crested wheatgrass as well as native species. He found that this site had greater sagebrush density (apparently form

[1] McAdoo, J.K. Data obtained from research at the Gund Research and Demonstration Ranch and presently being analyzed for publication.

reinvasion) than 4-year-old sites in the same area which had been either chained or burned. However, size of the shrubs was considerably less than those in islands of the burned site and the remaining sagebrush in the chained area. Brewer's sparrow densities varied directly with percent cover and density of sagebrush, being highest on the oldest (chained) site and lowest on the burned site. Sage thrasher densities were low on all sites, but were highest on islands in the burn, due to the larger size of the shrubs there. Thrashers apparently require larger shrubs for nesting (Reynolds 1981), and therefore might be expected to respond more slowly to sagebrush reestablishment in seedings. Ground-nesting western meadowlarks were slightly more abundant on the younger treatments where grass cover was the greatest.

In our ongoing study in central Nevada[1], we have been sampling breeding bird populations of seedings in various successional stages of sagebrush reinvasion, as well as of degraded sagebrush communities. The seedings vary in age from 17 to 27 years. All sites were originally plowed to control sagebrush and seeded with crested wheatgrass. Preliminary results of first year data indicate that sagebrush reinvasion of seedings results in some obvious changes in the bird community.

We found that shrub-nesters (especially sage sparrows and Brewer's sparrows) were more abundant on seedings with the greatest extent of sagebrush invasion (as measured by percent canopy cover). Similarly, Rotenberry and Wiens (1978) reported a strong correlation between sage sparrow density and shrub cover in unseeded sagebrush habitat. The dependence of sage sparrows and Brewer's sparrows on shrubs (especially sagebrush) for nesting has been widely reported (Best 1972, Schroeder and Sturges 1975, Wiens and Rotenberry 1981, Castrale 1982). Other shrub-nesting passerine birds (e.g., gray flycatchers, loggerhead shrikes, and sage thrashers) could also conceivably be benefited by sagebrush reinvasion of seedings.

The most obvious ground-nesting responder in the central Nevada study was the horned lark. Abundance of this species varied inversely with sagebrush canopy cover in seedings. Horned larks were most abundant in near-monoculture seedings ($\leq$ 5% shrub cover) and least abundant in unconverted sagebrush habitat ($\geq$20% shrub cover). Rotenberry and Wiens (1978) also found that horned lark abundance was inversely correlated with percent shrub cover in unconverted sagebrush habitat.

For the western meadowlark, another ground-nesting species, total cover seems to be an important factor influencing abundance. In central Nevada, meadowlarks were abundant in near-monoculture seedings with high grass cover, but also in invaded seedings which had moderate grass cover, and in unconverted sagebrush habitat with only 1% herbaceous cover. On a depleted 17-year-old seeding which had both low herbaceous cover (3%) and low shrub cover (5%), nesting western meadowlarks were not found. In unconverted native sagebrush communities, Wiens and Rotenberry (1981) found that meadowlark densities varied directly with grass and litter cover, total cover, and some measures of vertical vegetation structure.

Probably the most interesting response to sagebrush invasion of crested wheatgrass seedings in central Nevada was that of lark sparrows. This ground-nesting species was either absent or present in very low numbers in both unconverted sagebrush habitat and near-monoculture seedings. However, it was found regularly in moderate abundance in invaded seedings with approximately 10 to 12% shrub cover. At this point in our analysis, the most important variable influencing lark sparrow abundance appears to be the interaction between herbaceous cover and shrub cover. Similarly, Wiens and Rotenberry (1981) found that lark sparrows were correlated with both grass and shrub cover.

The combination of shrub-nesting and ground-nesting species which nested in invaded seedings (10-12% shrub cover) in central Nevada resulted in greater species richness than in either near-monoculture seedings or unconverted sagebrush habitat. Birds were also more evenly distributed (by nesting guild) in terms of relative abundance in the invaded seedings, with 60% ground-nesters and 40% shrub-nesters (compared to 91% ground-nesters in near-monoculture seedings and 30% ground-nesters in unconverted sagebrush). Total abundance (all species combined) was nearly the same among uninvaded seedings with good grass cover, areas of unconverted sagebrush, and seedings with 10 to 12% sagebrush cover.

Stage-four-sagebrush-dominance.--As secondary succession proceeds, sagebrush may eventually outcompete crested wheatgrass to the point where perennial grass cover is minimal once again as it was in the degraded sagebrush community before seeding. Vale (1975) stressed that shrubs were an integral component of presettlement sagebrush-grass communities. Their competitive advantage over grasses under livestock grazing is obvious from the history of understory depletion and shrub dominance in the sagebrush ecosystem (Young et al. 1979). Therefore improper grazing management of livestock could accelerate the occurrence of this sagebrush dominance "stage". In a review of the literature, Keller (1979) noted that sagebrush invasion of seedings is inversely proportional to the density of grass cover, and that sagebrush increases more slowly under light grazing use.

We found no available information concerning the effects of this stage on nongame bird populations. However, it seems reasonable to assume that the avifauna in a grass depleted, shrub-dominated seeding would be very similar to that in a degraded sagebrush stand before seeding, i.e., dominated by shrub-nesting species.

EFFECTS OF SAGEBRUSH HABITAT CONVERSION ON RAPTORS

Use of Sagebrush Rangelands by Raptors

Sagebrush habitat is used by a wide variety of raptorial bird species (birds of prey). These include the golden eagle (Aquila chrysaetos), red-tailed hawk (Buteo jamaicensis), rough-legged hawk (B. lagopus), ferruginous hawk (B. regalis), Swainson's hawk (B. swainsoni), marsh hawk (Circus cyaneus), prairie falcon (Falco mexicanus), American kestrel (F. sparverius), short-eared owl (Asio flammeus), long-eared owl (A. otus), great horned owl (Bubo virginianus), and burrowing owl (Speotyto cunicularia). Although many of these species nest in habitats other than sagebrush, their large hunting territories often include portions of sagebrush range.

Direct Effects of Habitat Conversion

Occasionally, sagebrush control may result in the loss of nesting habitat for some raptors. For example, ferruginous hawks in parts of their range nest primarily in juniper trees (Howard and Wolfe 1976), with lone or peripheral trees being preferred (Woffinden 1975). Type conversion of sagebrush habitat adjacent to juniper stands where lone trees might be destroyed could thus have potential for nest-site elimination. Swainson's hawks occasionally nest in tall sagebrush plants, and could also suffer directly from shrub control. However, some ground-nesting species may utilize the open areas created by brush removal and seeding. Reynolds and Trost (1980) discovered evidence of short-eared owls nesting in crested wheatgrass seedings in Idaho, and we have seen burrowing owls nesting in recently burned sagebrush habitat in central Nevada.

Indirect Effects of Habitat Conversion

The indirect effects of sagebrush habitat conversion on raptors are potentially of more consequence than the direct effects. Several authors have mentioned that raptors can be affected by habitat conversion (Snyder and Snyder 1975, Call 1979, McAdoo and Klebeneow 1979, Olendorff et al. 1980, and Craighead and Mindell 1981), primarily through changes in prey base. This potential change in prey base can affect not only distribution of raptors, but also their breeding density and productivity (Howard and Wolfe 1976).

Some examples of differing prey base responses to habitat alteration of sagebrush communities are available from the literature. Baker and Frischknecht (1973) reported in Utah that chaining to remove juniper from sagebrush-grass habitats, followed by reseeding, resulted in higher rodent populations during the first two years following treatment. Larrison and Johnson (1973) found that certain grass-adapted rodent species in Idaho were more numerous in crested wheatgrass seedings, but total rodent abundance was about the same as in depleted sagebrush sites. In a northern Nevada study, Jenkins (1978) concluded that although there was no significant difference in densities of Richardson's ground squirrel (Spermophilus richardsonii) between sagebrush habitat and a crested wheatgrass seeding, the seeding provided comparatively more food for the squirrels.

Negative responses of prey species to alteration of sagebrush communities have also been recorded. In Idaho, Reynolds and Trost (1980) found lower total rodent and reptile densities in crested wheatgrass seedings, compared to sagebrush-dominated areas. Working in Colorado, Johnson and Hansen (1969) found that the density of least chipmunks (Eutamias minimus) was lower after shrub reduction. Chipmunks are dependent on shrubs for food and cover.

The literature also contains conflicting information concerning the effects of type conversion on lagomorphs. According to Call (1979), conversion of brushland to grass can be disruptive to production of both jackrabbits (Lepus spp.) and cottontails (Sylvilagus spp.) that survive best in shrub-grass mixtures. But Westoby and Wagner (1973) reported that abundance of jackrabbits (L. californicus) in shrub habitat adjacent to a crested wheatgrass seeding was much the same as that in similar habitat 900 m away. Use of open areas (like seedings) by prey species makes them more vulnerable to predation (Olendorff et al. 1980).

Whether the initial result of a crested wheatgrass seeding is an increase or decrease in prey abundance, or an increase in prey vulnerability, the successional reinvasion of sagebrush into these areas results in further change. According to Howard and Wolfe (1976), the presence of crested wheatgrass seedings in various stages of "reversion" to original vegetation (reinvasion by sagebrush) may increase the probability that ferruginous hawks will produce young in years of low jackrabbit densities, due to greater vulnerability of prey in these areas than elsewhere. They also concluded that past crested wheatgrass seedings did not adversely affect reproduction of the hawks. The authors stated that reversion to native vegetation in these seedings created suitable prey base habitat within 6 to 8 years following treatment.

SUMMARY

Passerine bird populations in pristine sagebrush-grass communities probably consisted of more ground-nesting species, in addition to shrub-nesters, than we see in degraded sagebrush habitats today. Overgrazing by livestock at the turn of the century apparently resulted in depletion of the herbaceous understory which these birds require. However, most attempts to revegetate "degraded" sagebrush habitat are aimed at conversion to grassland rather than restoration to sagebrush-grassland.

It is generally assumed, and correctly so, that passerine birds in sagebrush habitats would be more benefitted by improvement of native understory vegetation or by mixed species seeding than by shrub removal and seeding to crested wheatgrass. However, type conversion of sagebrush habitat is typically justified by the goal of increased forage for livestock production, and derived wildlife responses are often coincidental.

Wildlife trade-offs occur when sagebrush cover is removed or greatly reduced and crested wheatgrass is planted. Specifically, shrub-dependent species are displaced or reduced dramatically, and some ground-nesting species may then increase on the seeding in response to improved herbaceous cover. Although crested wheatgrass is non-native, ground nesting birds are adapted to its life form or structure and therefore can live in this man-made habitat successfully. Total bird abundance in the seeding may be similar to that of unconverted sagebrush habitat, but total number of species is lower and relative abundance of species is much different in the monoculture seeding.

After several years, sagebrush invasion of a crested wheatgrass seeding may reach the point where a well-balanced mixture of both ground-nesting species and shrub-nesting species is present. If and when this stage occurs depends upon several variables, including grazing management and effectiveness of original sagebrush control and grass seeding. (Indeed, some seedings may never accomodate abundant and diverse bird-life if, for example, low herbaceous cover results from poor grass establishment or overgrazing). As secondary succession continues, the seeding may become sagebrush dominated at the expense of the perennial grass. Good livestock grazing management should help postpone this stage.

Birds of prey are affected primarily in an indirect manner by type conversion of sagebrush communities to grassland. Specifically, the changes in prey species populations (i.e., total abundance, relative abundance of species, and vulnerability) that are brought about by changes in shrub and herbaceous cover may in turn affect raptor distribution, nesting success, etc. In some cases, prey abundance and vulnerability increases after habitat conversion, thus benefitting raptors. Sagebrush-invaded seedings with their diverse vegetation structure may be of even more indirect benefit to some raptors because of the combination of food and cover these areas provide for prey species (especially rabbits and rodents).

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SECTION V.

Ecophysiology.

How Crested Wheatgrass Works.

Chairman, A. E. (Gene) Gade

Ecophysiology of Crested Wheatgrass: A Comparative Study with Bluebunch Wheatgrass

Martyn M. Caldwell and James H. Richards

INTRODUCTION

Despite the widespread success of crested wheatgrass (Agropyron cristatum and A. desertorum) as a seeded species for rangeland improvement and rehabilitation, the ecophysiology of the plant has received only sporadic attention. In 1979, we initiated a field study to intensively investigate physiological and morphological characteristics of crested wheatgrass that could be responsible for its success. Although the mission of these studies was to answer basic questions, what has been learned in this work has both implications and applications for applied research and potentially for management.

Scientific studies that are based on comparisons can often enjoy more resolution than descriptive research of only a single species or phenomenon. Thus, we have chosen for comparison a grass species, bluebunch wheatgrass (Agropyron spicatum)[1] that is in many respects very similar to crested wheatgrass but differs greatly in its ability to tolerate grazing and to hold its competitive place in rangeland communities. We have conducted these studies primarily in the field and have taken an integrated approach, where we measured many characteristics of these plants under similar conditions. This is the basis of a quantitative evaluation of how differences in characteristics might be important for the success of crested wheatgrass and places individual findings in better perspective.

On the study site, the two grass species have been interplanted with mountain big sagebrush, (Artemisia tridentata ssp. vaseyana), because the competitive environment in which a plant exists has a large bearing on how well it will recover from grazing (Mueggler 1972, 1975). All of the field experiments have been conducted on grasses with sagebrush growing as neighbors.

This comparative study of crested and bluebunch wheatgrass is an ongoing project and the published articles appended to this contribution describe only certain aspects of the work. Highlights of the papers are included in this summary and continuing facets of the study are outlined. The financial support for this intensive work has come primarily from the National Science Foundation and the Utah Agricultural Experiment Station.

GRAZING TOLERANCE

It is well known that crested wheatgrass recovers better from grazing than does bluebunch wheatgrass. We also found this to be the case in our controlled experiments. The difference in recovery was particularly large when the growing tips (apical meristems) were removed when the plants were clipped (Caldwell et al. 1981). (In most of our experiments clipping has been used as a grazing simulation. While clipping has often been criticized as unrealistic, it has been the most feasible approach in this intensive work. Currently, we have experiments under way to specifically compare defoliation effected by clipping, cattle grazing, and grasshoppers under field conditions.)

Photosynthetic Capacity

Even though the two grasses differ greatly in their ability to regrow following clipping, other attributes are very similar. For example, many aspects of their photosynthetic performance are surprisingly similar as are growth and phenological development. Photosynthetic capacity of fall regrowth, overwintering of a portion of this autumn-grown foliage, its activity in the next spring, the development of tussocks in the spring, the timing of stem elongation, and the importance of stems as major photosynthetic plant parts in the summer are all remarkably similar (Caldwell et al. 1981, Caldwell et al. 1983, Nowak and Caldwell 1984b). Another similarity is in the photosynthetic response of foliage on plants that have been partially

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[1]Recent taxonomic revisions make A. spicatum synonymous with Pseudoroegneria spicata (Löve 1980, Dewey 1984).

defoliated. Known as compensatory photosynthesis, the response involves an increase in photosynthesis of remaining foliage on partially defoliated plants relative to foliage of similar age on plants where no defoliation has taken place. This phenomenon has been shown in many laboratory experiments. We have documented its occurrence in the field for certain leaves of both wheatgrass species. The magnitude of increased photosynthesis is similarly small for the two species (Nowak and Caldwell 1984a). Thus, it does not appear to be a key characteristic explaining the grazing tolerance of crested wheatgrass.

Photosynthesis/Transpiration

Although virtually every aspect of the photosynthetic characteristics of these species is the same, questions can be raised concerning how much water is lost during photosynthesis. (Because the stomates of leaves need to be open during periods of photosynthesis, water must inevitably be lost. The degree to which different plants regulate this balance can have obvious consequences). The ratio of photosynthesis/transpiration (P/T) is about the same in both species for individual leaves and stems (Caldwell et al. 1981). A more complicated question concerns P/T of whole tussocks because the microenvironment, especially light relations, can greatly influence this ratio. For example, if some foliage is shaded it may be conducting less photosynthesis relative to the amount of water being lost. An analysis of tussock structure, light interception, and photosynthesis and transpiration of whole tussocks revealed that crested and bluebunch wheatgrasses were very similar in their performance (Caldwell et al. 1983). The increased P/T that might be expected to occur with partial defoliation (due to reduced self-shading) did not occur for either species in the tests conducted; in fact, the opposite occurred. Thus, the concept that grasses will increase P/T following defoliation does not appear to be valid at least under the conditions existing in these experiments. However, further work is underway to learn if other patterns of defoliation lead to an increase of this important ratio.

Stored Carbon

The capacity of both wheatgrasses to gain carbon is remarkably similar, but the capacity to regrow following defoliation is very different. It has often been assumed that grazing-tolerant species have higher concentrations of stored carbon reserves, such as starch, fructosans and sugars, resulting in faster regrowth. However, the manner in which the two species of wheatgrass allocate their acquired carbon to different plant structures and the size of the stored carbon pools (soluble carbohydrate concentrations in different organs multiplied by the mass of each organ) are very similar (Caldwell et al. 1981). These studies, as well as more intensive research on carbohydrate dynamics, suggest there is no direct correlation between the size of the soluble carbohydrate pools and the capacity to regrow following grazing (Richards and Caldwell 1985). Analogous to the situation with soluble carbon pools, there is no immediate indication that nitrogen pools are correlated with regrowth capacity (Caldwell et al. 1981). While the importance of carbohydrates as a stored energy source cannot be denied, we believe the quantitative significance of these reserves has not been properly taken into account. The importance of photosynthesis as a carbon source for further regrowth has also not been appreciated.

New Growth and Carbon Allocation

The key difference between the species controlling their capacity to regrow is the difference in their abilities to activate basal buds to produce new tiller growth. This is important when other growing tips, such as apical meristems, have been removed by defoliation. Crested wheatgrass has a much greater capacity to quickly produce new tillers under these circumstances (Caldwell et al. 1981, Richards and Caldwell 1985).

The rapid regrowth of foliage afforded by new tiller production is of key importance because there is the immediate positive feedback of new carbon gained by the regrowing foliage. We believe the new carbon gained in photosynthesis of the regrowing foliage is quantitatively more important than the reserve carbon *per se* (Richards and Caldwell 1985). Yet when the plant is just initiating new growth, the allocation of the limited stored reserves is central to regrowth capacity. If the reserves are channeled into new foliage rather than other organs, such as root systems, the plant will benefit enormously. Observations of root growth after defoliation have revealed that crested wheatgrass curtails root development considerably while bluebunch wheatgrass does not (Richards 1984). This flexibility to allocate additional carbon reserves to shoots for a period of time until the plant has reestablished its carbon balance is of critical importance. Once reestablished, new root growth can proceed so that the plant can compete for resources with its neighbors. Although root growth was curtailed in crested wheatgrass in the few months immediately following severe defoliation, in the following year crested wheatgrass exhibited greater root growth than bluebunch wheatgrass which had been subject to the same defoliation (Richards 1984). Thus, short-term curtailment of root growth is a phenomenon that pays definite dividends later.

CONCLUSIONS

Certainly the key differences between bluebunch wheatgrass and crested wheatgrass in their capacities to recover from defoliation lie first in the ability to activate buds and initiate new tillers and second in the flexibility to allocate limited carbon reserves to regrowing foliage. These differences between the species are vivid whereas differences in quantities of carbon reserves, photosynthetic capacity of foliage, the balance between photosynthesis and transpiration, phenological development and other morphological traits are not so apparent.

Still many questions remain. These concern how effectively the carbon reserves are mobilized, how large the carbon reserves are with respect to the carbon balance of the entire plant, how long individual tillers live with and without grazing, how the response to clipping actually compares with response to grazing, how water stress and grazing interact, and which environmental and plant factors induce new tiller formation in these plants. Most of these questions are being addressed by ongoing research.

Another set of questions surrounds the phenomenon of competitive effectiveness. Even in the absence of defoliation, crested wheatgrass can compete with other plants such as sagebrush much more effectively than bluebunch wheatgrass. How well a plant persists in the range community likely depends on its innate competitive effectiveness, as well as its capacity to regrow foliage when grazed. Most of the competition takes place belowground. Thus, a set of questions emerges concerning why crested wheatgrass is more competitive in acquiring soil resources. Several new facets of this continuing research address the qualities of competitive effectiveness.

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Oecologia (Berl) (1981) 50:14–24

Coping with Herbivory: Photosynthetic Capacity and Resource Allocation in Two Semiarid *Agropyron* bunchgrasses *

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Summary. *Agropyron desertorum*, a grazing-tolerant bunchgrass introduced to the western U.S. from Eurasia, and *Agropyron spicatum*, a grazing-sensitive bunchgrass native to North America, were examined in the field for photosynthetic capacity, growth, resource allocation, and tiller dynamics. These observations allowed identification of physiological characteristics that may contribute to grazing tolerance in semiarid environments. A uniform matrix of sagebrush, *Artemisia tridentata*, provided an ecologically relevant competitive environment for both bunchgrass species. Physiological activity, growth, and allocation were also followed during recovery from a severe defoliation treatment and were correlated with tiller dynamics.

Potential photosynthetic carbon uptake of both species was dominated by stems and leaf sheaths during June, when maximum uptake rates occurred. For both species, water use efficiency of stems and sheaths was similar to that of leaf blades, but nitrogen investment per photosynthetic surface area was less than in blades. In addition, soluble carbohydrates in stems and sheaths of both species constituted the major labile carbon pools in control plants. Contrary to current theory, these findings suggest that culms from which leaf blades have been removed should be of considerable value to defoliated bunchgrasses, and in the case of partial defoliation could provide important supplies of organic nutrients for regrowth. These interpretations, based on total pool sizes, differ markedly from previous interpretations based on carbohydrate concentrations alone, which suggested that crowns contain large carbohydrate reserves. In this study, crowns of both species contained a minor component of the total plant carbohydrate pool.

Following defoliation, *A. desertorum* plants rapidly reestablished a canopy with 3 to 5 times the photosynthetic surface of *A. spicatum* plants. This difference was primarily due to the greater number of quickly growing new tillers produced following defoliation. *Agropyron spicatum* produced few new tillers following defoliation despite adequate moisture, and carbohydrate pools that were equivalent to those in *A. desertorum*.

Leaf blades of regrowing tillers had higher photosynthetic capacity than blades on unclipped plants of both species, but the relative increase, considered on a unit mass, area, or nitrogen basis, was greater for *A. desertorum* than for *A. spicatum*. *Agropyron desertorum* also had lower investment of nitrogen and biomass per unit area of photosynthetic tissues, more tillers and leaves per bunch, and shorter lived stems, all of which can contribute to greater tolerance of partial defoliation.

Greater flexibility of resource allocation following defoliation was demonstrated by *A. desertorum* for both nitrogen and carbohydrates. Relatively more allocation to the shoot system and curtailed root growth in *A. desertorum* resulted in more rapid approach to the preclipping balance between the root and shoot systems, whereas root growth in *A. spicatum* continued unabated following defoliation. Nitrogen required for regrowth in both species was apparently supplied by uptake rather than reserve depletion. Carbohydrate pools in the shoot system of both species remained very low following severe defoliation and were approximately equivalent to carbon fixed in one day by photosynthesis of the whole canopy.

Introduction

Chemical, mechanical and phenological mechanisms by which plants avoid or minimize herbivory have received considerable attention in the last decade (e.g. Janzen 1969; Rosenthal 1977; Cates and Orians 1975; Janzen et al. 1976; Stiles 1977). Much less work has been directed towards an understanding of how plants tolerate heavy herbivore pressure.

Plants of different life form often differ in tolerance to defoliation. Plant growth form influences the capacity to reestablish foliage following defoliation, such as by the protection or redundancy of apical meristems, or possession of active basal intercalary meristems (Dahl and Hyder 1977). Life forms that are tolerant of herbivory also possess characteristics such as higher photosynthetic rates, reduced foliage longevity, a low proportion of reproductive shoots, and faster rates of leaf replacement (Branson 1953; Archer and Tieszen 1980).

Striking differences in tolerance of herbivory by species of the same growth form and similar phenological characteristics seem less explicable. Therefore, we undertook the comparative study of two *Agropyron* bunchgrasses *A. spicatum* (Pursh) Scribn. and Smith and *A. desertorum* (Fisch. ex Link) Schult. which differ markedly in their tolerance of grazing. *Agropryon spicatum* is an important component of the Great Basin Desert of North America; however, when subjected to heavy spring-season grazing it cannot compete effectively in this community. Extensive livestock grazing in the Great Basin Desert has generally been credited with the greatly reduced presence of *A. spicatum* and other grasses that are relatively intolerant of herbivory, such as *Poa secunda* and *Festuca idahoensis* (Young 1943; Christensen 1963; Daubenmire 1940, 1975; Laycock 1967). Between Pleistocene extinctions of many large herbivores some 10,000 years ago

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and the relatively recent arrival of domestic livestock in the Intermountain West, large herbivores were not a significant component of the Great Basin fauna (Cronquist 1978).

The crested wheatgrasses, which include *A. desertorum*, were introduced into North America from Eurasia at the turn of the century (Dillman 1946). Because of their popularity among stockmen, the crested wheatgrasses have been established on approximately four million hectares of the North American West (Rogler, unpublished). The ability of these wheatgrasses to establish and compete in semiarid habitats, to better tolerate grazing during the spring season and to provide an important forage resource are now well recognized characteristics. Presumably, the past and continuing history of large herbivore pressure on these wheatgrasses in the steppe environments of Eurasia (Kowalski 1967; Vereshchagin 1967; Frenzel 1968; Hoffmann 1974) has led to the selection for characteristics which confer greater grazing tolerance.

Although *A. spicatum* and *A. desertorum* exhibit differences in grazing tolerance, they are remarkably similar in many traits. Both species are upright bunchgrasses that exhibit culmed growth during much of the growing season; both have a reasonably high proportion of reproductive shoots and a similar phenological progression; and both are most sensitive to grazing during the period of maximum vegetative growth because subsequent regrowth of foliage is usually greatly constrained by moisture limitation in early summer (Stoddart 1946; Blaisdell and Pechanec 1949; Hyder 1972, 1974; Hyder and Sneva 1963; Cook et al. 1958; McIlvanie 1942).

Since the growth form and phenological timing of these plants are so similar, differences in grazing tolerance may be explained by quantitative differences in physiological characteristics of these two species. Investment of carbon and nitrogen in foliage susceptible to removal by the grazing animal, photosynthetic rates and water use efficiency of foliage, rate of replacement of photosynthetic tissues following defoliation – often with tissues that are more photosynthetically active, amount of soluble carbon and nitrogen reserves, degree of flexibility in allocation of plant resources in the event of severe defoliation, and degree of flexibility in provision of meristematic tissues for regrowth of foliage are some of the characteristics investigated in this study. This paper addresses aspects of the photosynthetic potential of these species, their growth and photosynthetic response following severe defoliation, and their general pattern of resource allocation during a year of particularly abundant precipitation.

In addition to physiological recovery from herbivory, plants in the field must at the same time continue to compete for resources with neighboring vegetation, some of which may not be subject to the burden of defoliation. Mueggler (1972) vividly demonstrated that even *A. spicatum* could tolerate extreme defoliation if competing vegetation was removed or substantially reduced. Thus, the present study was conducted in a competitive field environment.

Study Area

This research was conducted 4 km northeast of Logan, Utah (41° 45′N, 111° 48′W, 1,460 m a.s.l.) on a site formerly occupied by *Agropyron spicatum* and *Artemisia tridentata*. This area is also characteristic of Intermountain rangelands where *Agropyron desertorum* has been established. A matrix of about 7,000 regularly distributed transplants was established two years before this study. In addition to the two species of *Agropyron*, *Artemisia tridentata* Nutt. ssp. *tridentata* was established in the matrix so that each individual bunchgrass was surrounded by *Artemisia* plants to form a uniform competitive environment. *Artemisia tridentata* was used since it is a major competitor with *Agropyron spicatum* in the Great Basin and is subject to much less grazing pressure (Laycock 1967). *Artemisia tridentata* is also a species with which *Agropyron desertorum* must compete in many of the Intermountain rangelands where it has been established (Hull and Klomp 1974). *Agropyron spicatum* and *Artemisia tridentata* were transplanted from adjacent, ecologically similar areas where both species still occur and *Agropyron desertorum* was transplanted from a pasture in central Utah which had been established in 1953.

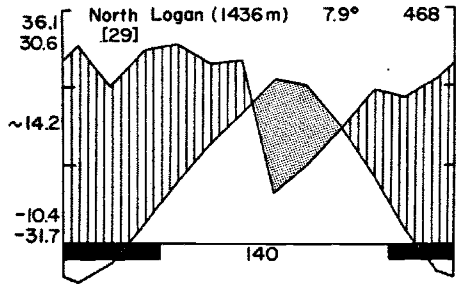

Fig. 1. Climate diagram compiled from weather stations within 2 km of the study site using the format of Walter and Lieth (1960). The abscissa represents the 12 months of the year beginning in January. The blackened bar along the abscissa indicates months of the year when the daily minimum is below 0° C. The number below the center of the abscissa indicates the mean duration of the freeze-free period in days. One division on the ordinate represents either 10° C or 20 mm precipitation. Numbers to the left of the ordinate beginning at the top represent the highest temperature recorded at this site, the mean daily maximum temperature of the warmest month, mean daily temperature variation, mean daily minimum temperature of the coldest month, and the lowest temperature recorded at this site. At the top of the diagram the site elevation, mean annual temperature, and mean annual precipitation are indicated from left to right and the number of years of observations for this compilation is given in brackets

Soils are rocky Mollisols (Typic Haploxerolls) which have been formed on alluvial fan material (Southard et al. 1978). Salient features of the climate are given in Fig. 1. The precipitation for the year of this study from October, 1979 to September, 1980 was 682 mm, substantially above the 468 mm average.

Methods

Net photosynthesis and transpiration of individual leaf blades, leaf sheaths, stems and inflorescences were measured in the field on intact plants with a carbon dioxide and water vapor exchange porometer (Bingham and Coyne 1977). Carbon dioxide and water vapor exchange of entire bunchgrass plants in the field were measured with a modified Siemens Co. gas exchange chamber (Koch et al. 1971). Modifications included an enlarged chamber lid, which accommodated an entire bunchgrass, chamber walls which penetrated the upper 2 cm of the soil surface, and positive pressure (4-cm water column) which was maintained to minimize gas exchange with the soil surface (Leafe 1972). Water vapor concentrations were measured with thin-film capacitance sensors (Vaisala Co.) and flow rates were determined with a pneumotachometer (Hans Rudolph Co.) and a pressure transducer (Validyne Co.). Photosynthetically active radiation was measured as quantum flux between 400 and 700 nm (Li-Cor Co.), leaf temperatures with fine-wire thermocouples, and projected area of plant parts with a leaf area meter (Li-Cor Co.). Whole-plant gas exchange measurements were conducted with the large cuvette programmed to track ambient environmental conditions. Gas exchange measurements of individual plant parts were conducted between 21 and 27° C, which is within the mid- and late-season temperature optimum for net photosynthesis of both bunchgrass species, and at light saturation for photosynthesis.

Plant xylem pressure potentials were determined with a pressure bomb (Waring and Cleary 1967). Plant parts were enclosed in small polyethylene bags prior to their excision and during the pressure potential determination in order to minimize tissue water loss (Turner and Long 1980). Soil moisture content was determined with a neutron soil moisture probe (Campbell Pacific Nuclear, Inc.).

Inclined point quadrats (Warren Wilson 1960) were used to nondestructively determine canopy geometry and leaf blade and projected stem and leaf sheath areas of bunchgrasses in the field. Projected areas of cylindrical plant parts were corrected to surface area of one half of the cylinder. A series of destructive harvests at approximately 3-week intervals was also conducted to determine biomass of plant components. Sampled plants were randomly selected from a population of individuals of median size class. Plants were meticulously separated into apparently live or dead fractions for each plant part. The root system was assessed by extraction of a 12-l soil monolith directly beneath the crown of the plants, and by soil cores from an enlarged soil volume included in a 60-cm diameter cylinder of 80-cm depth. Roots in subsamples of the soil monolith and in the soil cores were removed by washing and wet sieving (No. 45 with 0.35 mm pores). The roots were stained (0.25% Congo red for 15 min) to more effectively separate intact roots from organic debris (Ward et al. 1978). Following oven-drying both weight and then ash-free weight, following incineration at 500° C, were determined for the roots.

Subsamples of all plant part materials were lyophilized and ground. Nitrogen concentrations of tissues were determined by standard Kjeldahl analysis. Tissues were also analyzed for total nonstructural carbohydrates which are considered the carbon that can be stored and subsequently mobilized as an energy source in the plants. Sugars were extracted with boiling water, and the concentration of the filtrate determined using the phenol-sulfuric acid method of Dubois et al. (1956) with glucose as a standard. Starch in the residue was determined using the enzyme digestion technique of Haissig and Dickson (1979) except that the enzyme used was an amyloglucosidase (Sigma Chemical Co.) and glucose was measured by the phenol-sulfuric acid method.

As a severe defoliation treatment, both species were clipped at approximately 5-cm height when in the four to five-leaf stage. There was no appreciable culm elongation at this time (April 30). This first clipping resulted in removal of 80% of the photosynthetic tissue that was present at that time. The same individuals were clipped again at the same height two weeks later (May 13). This second clipping resulted in a removal of 90% of the leaf material that had regrown since the first clipping.

To follow tiller demography, four tillers (two in the center and two in the periphery of individual plants) were marked on six bunches of each species within both control and defoliated treatments. These four populations of 24 tillers and their daughter tillers were followed throughout the season.

Results

Winter and early spring precipitation had recharged the upper 1.5 m of soil profile to a water content of 30% by volume and spring and early summer precipitation maintained a favorable moisture status. Predawn xylem pressure potential measurements (Fig. 2) indicated little change in soil moisture stress until late June. Thus, this year provided the opportunity to assess potential photosynthetic activity, response following severe defoliation, and growth and resource allocation under quite favorable moisture conditions in the field.

Photosynthetic Capacity, Water Use Efficiency, and Canopy Reestablishment

Potential contribution of different plant parts to photosynthetic carbon gain is shown for the two species at five times during the season (Fig. 3). Light-saturated photosynthetic rates of different plant parts were multipled by the biomass components of

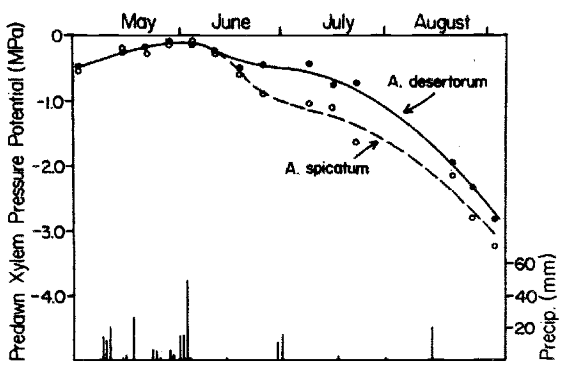

Fig. 2. Predawn xylem pressure potential measurements of the two bunchgrass species during 1980. Individual precipitation events are indicated by the vertical bars. Each point is the mean of 4 samples

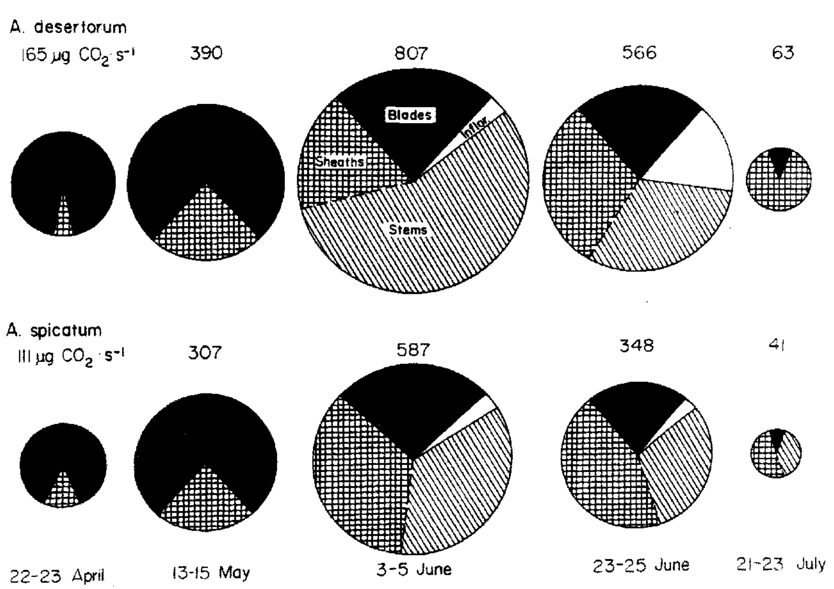

Fig. 3. Potential photosynthetic contribution of different plant parts for *A. desertorum* and *A. spicatum*. These values were derived from the product of light-saturated photosynthetic rates at the optimum temperature for photosynthesis (21–23° C) (300 to 330 ppm CO_2 concentration) and biomass of different aboveground plant components. The numbers indicate potential photosynthesis of entire bunchgrasses and are proportional to the area of the circles. The pie segments indicate fractional contribution of different plant parts to potential carbon gain

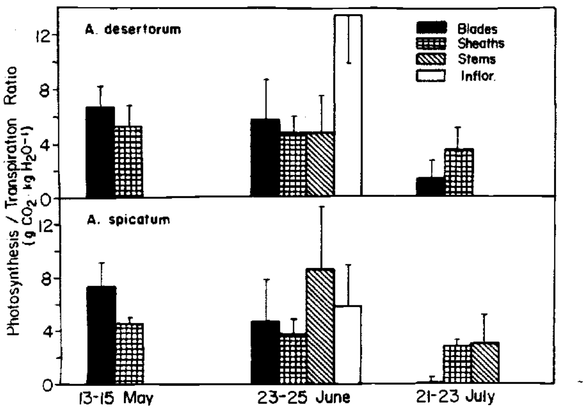

Fig. 4. Photosynthesis/transpiration ratios for different plant parts for *A. desertorum* and *A. spicatum* at three different times during the year. These ratios were determined at: light saturation for photosynthesis, tissue temperatures of 21 to 23° C, CO_2 concentrations of 300–330 ppm and 2.5 to 2.7 kPa vapor pressure difference between plant parts and the atmosphere. Vertical bars indicate standard deviations. Sample size average was 8 and ranged from 3 to 21

unclipped plants to estimate the potential photosynthetic contribution. Blades refer to leaf blades only, stems to segments of stems not covered by leaf sheaths, and sheaths are leaf sheaths and the segments of stem enclosed by the sheaths. The dramatic increase in the contribution of stems and sheath-covered stems during the period of maximum photosynthesis in early June was similar for both species. Only in the spring period did leaf blades constitute the primary organs of potential photosynthetic contribution. The greater total potential photosynthesis of *A. desertorum* reflected primarily a greater biomass of photosynthetic organs, especially stems, rather than higher photosynthetic rates. In late July, photosynthetic capacity had declined considerably for both species. Photosynthesis/transpiration ratios of different plant parts did not differ significantly, nor were there significant differences between the two species at most times (Fig. 4). Water-use efficiency declined in the summer. For *A. spicatum*, leaf blades showed a greater decline by July than stems or sheaths.

Investment of biomass and nitrogen in photosynthetic tissues for the two species is portrayed in Fig. 5. Leaf blades of *A. desertorum* were consistently thinner than those of *A. spicatum*. The area/weight ratios for stems and sheaths of *A. desertorum* were also consistently greater than *A. spicatum* but the magnitude of difference between the species was not as great as for leaf blades. Nitrogen concentrations of photosynthetic tissues on a unit mass basis were about the same for both species during much of the growing season. Nitrogen concentrations in the spring were quite high, especially for *A. desertorum*. Nevertheless, *A. spicatum* invested more biomass and nitrogen per unit of photosynthetic surface area for both leaf blades and stems and sheaths.

Leaf blades regrowing following the defoliation treatments exhibited higher photosynthetic rates than foliage on control plants at the same time of year for both species. However, the relative difference in photosynthetic rates between regrowing and control leaf blades was greater for *A. desertorum* than *A. spicatum*, especially during the period of most active photosynthesis in May and June (Fig. 6). The greater photosynthetic capacity of regrown leaf blades could be due partly to greater photosynthetic capacity of younger foliage. These regrowing leaf blades had higher nitrogen concentrations, which is often associated with greater photosynthetic capacity (Bolton and Brown 1980). For example, early June samples of regrowing foliage of both species had nitrogen concentrations as great as samples collected

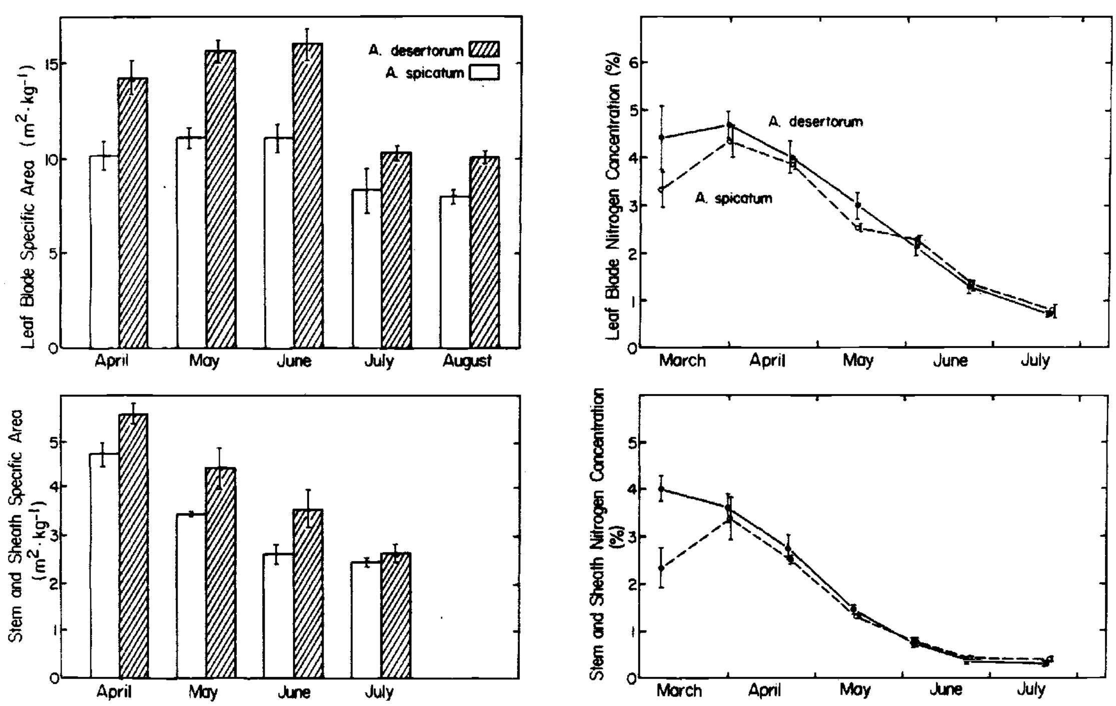

Fig. 5. Surface area/dry weight ratios for leaf blades and stems and sheaths of *A. spicatum* and *A. desertorum* at different times during the year. Leaf blades were those in the upper part of the canopy. Sample size, N, ranged from 7 to 38 with the exception of samples in mid-July where $N=3$. Nitrogen concentrations per unit mass for the two species are also presented. These are based on the average tissue nitrogen concentration from three entire plants harvested at different times of the year. Vertical bars indicate standard error of the mean

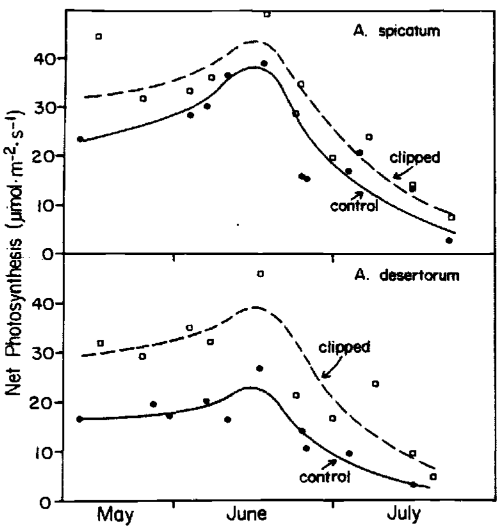

Fig. 6. Photosynthetic capacity of control and regrowth *A. spicatum* and *A. desertorum* leaf blades determined at light saturation, temperature optimum for photosynthesis (21–27° C) and cuvette CO_2 concentration of 300–330 ppm. Each point is the mean of 1 to 6 measurements

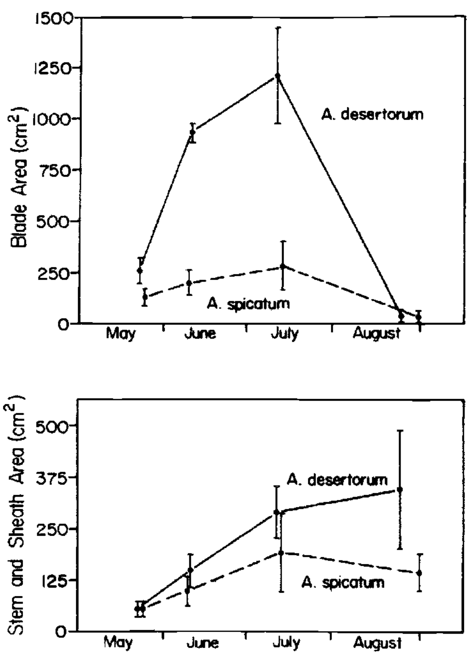

Fig. 7. Development of photosynthetic tissue area, leaf blades and stems and sheaths, for plants following severe defoliation. Three individual bunches of both species were repeatedly sampled nondestructively using inclined point quadrats. Vertical bars indicate standard error of the mean

one month earlier from control plants (Fig. 5). Though photosynthetic capacity of *A. spicatum* was greater when expressed on a leaf blade area basis, as shown in Fig. 6, when leaf area/weight ratios are considered, photosynthetic capacity of leaf blades on control *A. desertorum* and *A. spicatum* plants was about the same when expressed on a leaf mass basis. For regrown leaf blades, however, photosynthetic capacity of *A. desertorum* on a leaf blade mass basis was 20 to 90% greater than *A. spicatum* in May and early June.

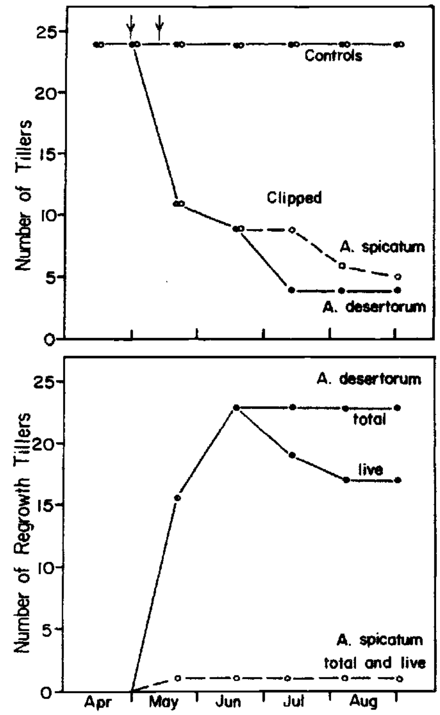

Fig. 8. Survivorship of marked populations of tillers on control and severely defoliated *A. desertorum* and *A. spicatum* plants. The times of clipping are shown by arrows. Regrowth tillers are tillers produced by the marked population of parent tillers following defoliation. Sample size for each population was 24

In addition to proportionately greater photosynthetic capacity of regrowing leaf blades following severe defoliation, replacement of photosynthetic tissues, especially leaf blades, was more rapid for *A. desertorum* (Fig. 7). This difference resulted from the marked difference in production of regrowth tillers following defoliation (Fig. 8). Both species eventually reestablished canopies, and total green surface area continued to increase until mid-July (Fig. 9), when leaf blade senescence (Fig. 7) began to reduce the total photosynthetic surface.

Survivorship of tillers on defoliated plants of both species was similar, as was the timing of mortality (Fig. 8). Mortality occurred immediately following clipping, or after the development of substantial water stress in late June and July (Fig. 9). In both species new tillers were not produced by tillers which survived clipping. Tillers that died produced from zero to two new tillers in *A. desertorum*. Only one new tiller was produced by the 24 marked *A. spicatum* tillers.

Daily photosynthetic carbon gain of these previously-defoliated plants is portrayed in Fig. 9. Individual bunches of the two species were alternately sampled for one to two day periods with the gas exchange chamber programmed to track ambient environmental conditions. The total green blade and sheath and stem areas (one side) of the plants sampled in this gas exchange series are also given. The surface area of photosynthetic tissues of *A. desertorum* was substantially greater than that of *A. spicatum*, because of greater allocation of biomass to foliage (Fig. 10), coupled with more surface area per mass (Fig. 5). Although average photosynthetic rates per unit area of photosynthetic tissues in the bunches were greater in *A. spicatum*, daily carbon gain of entire *A. desertorum* bunchgrasses was usually larger. The greater variability in carbon gain from day to day of *A. desertorum* was probably due to the greater depression of photosyn-

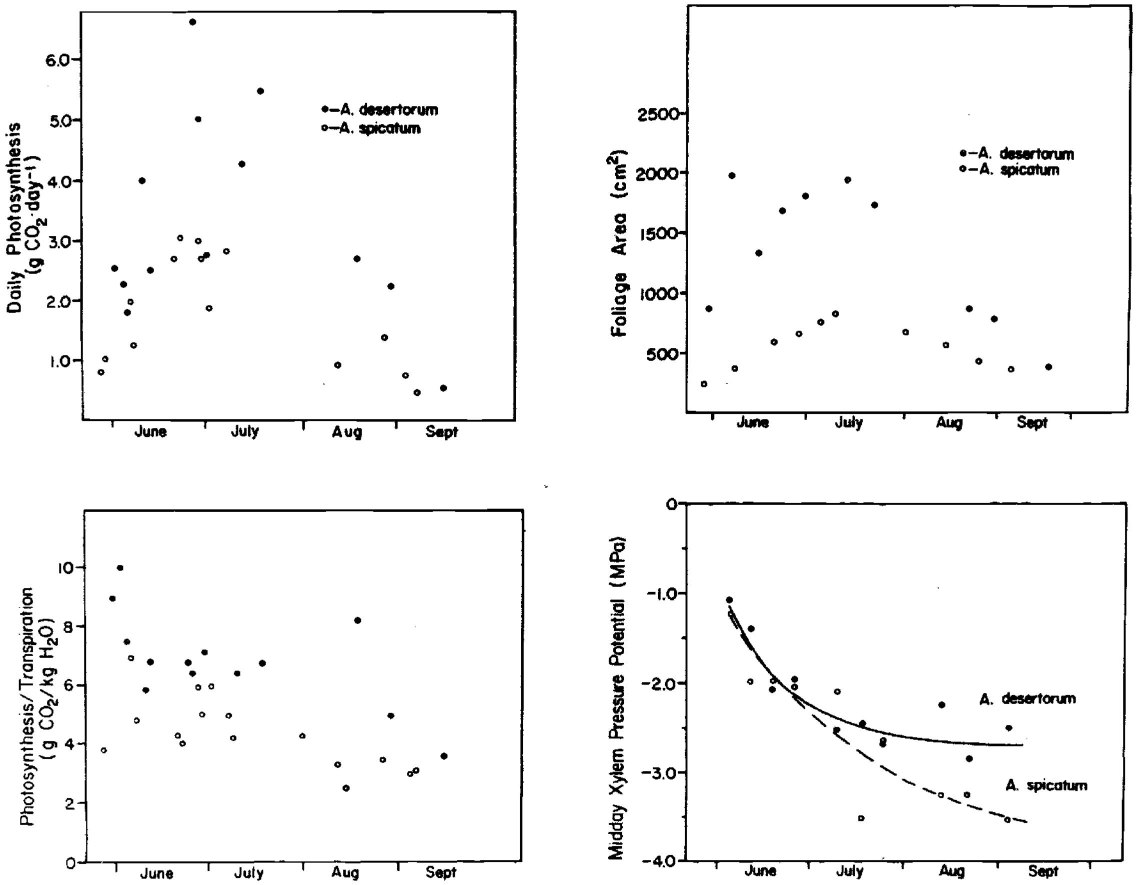

Fig. 9. Daily net photosynthesis and photosynthesis/transpiration ratios of individual bunchgrass plants of *A. desertorum* and *A. spicatum* sampled between late May and September. Total daily photosynthesis is represented for the period of the day when net photosynthetic rates were positive. Total green surface area (one side) of the sampled bunchgrasses and midday xylem pressure potentials are also represented. All data pertain to foliage regrown after the plants were subjected to defoliation treatments in the spring

thesis on cloudy days since the canopy of this species was more compact and dense.

Water-use efficiency, expressed as photosynthesis/transpiration ratios, was also usually greater for *A. desertorum* throughout the season (Fig. 9). Plant water stress of the two species, as indicated by midday xylem pressure potentials, was comparable except in late summer when *A. spicatum* was more highly stressed. Although winter, spring, and early summer moisture conditions had been very favorable, depletion of soil moisture as indicated by predawn xylem pressure potentials (Fig. 2) and high atmospheric demands led to the development of substantial midday water stress in both species by early July. Correspondingly, both photosynthesis and water-use efficiency declined.

Growth and Resource Allocation

Biomass of different plant parts for control and defoliated plants is shown for both species in Fig. 10. The biomass of roots is represented as ash-free weight while biomass for other plant parts is expressed on a dry weight basis. Ash-free weight was employed for the root system because it was not possible to completely remove all the soil mineral material from the diffuse root system. Also, roots at depths greater than 80 cm could not be sampled due to the rocky nature of the soil profile. Thus, root system biomass presented here is a conservative estimate.

During most of the season, total biomass of control plants as well as of defoliated plants, was essentially the same for the two species. *Agroypyron desertorum*, however, had greater aboveground biomass, and often less belowground biomass than control *A. spicatum* plants. For defoliated plants, more biomass was allocated to aboveground parts for *A. desertorum*. As was reported by Hyder and Sneva (1963), *A. desertorum* initiated foliage growth earlier in the season than *A. spicatum*. Earlier canopy development of *A. desertorum* was also quite apparent in our studies and associated with this was an earlier increase in root biomass accrual. Nevertheless, the major shoot and root system growth for both species occurred in late April and May. The timing and rate of total plant growth was remarkably similar for the two species. Following severe defoliation, root and shoot mass of both species continued to increase, but the rate of root biomass increase was greater than that of aboveground plant parts. Eventually, root system mass for *A. desertorum* declined, but biomass of the *A. spicatum* root system continued to increase even during the midsummer.

Total nitrogen in different plant components except for inflorescences is represented in Fig. 11 for the two species. Total nitrogen pools in *A. desertorum* were somewhat greater than those in *A. spicatum*. However, the most significant difference was in the early season which was associated with the earlier growth initiation of *A. desertorum*. In *A. desertorum*, a greater proportion of the nitrogen was allocated to photosynthetic tis-

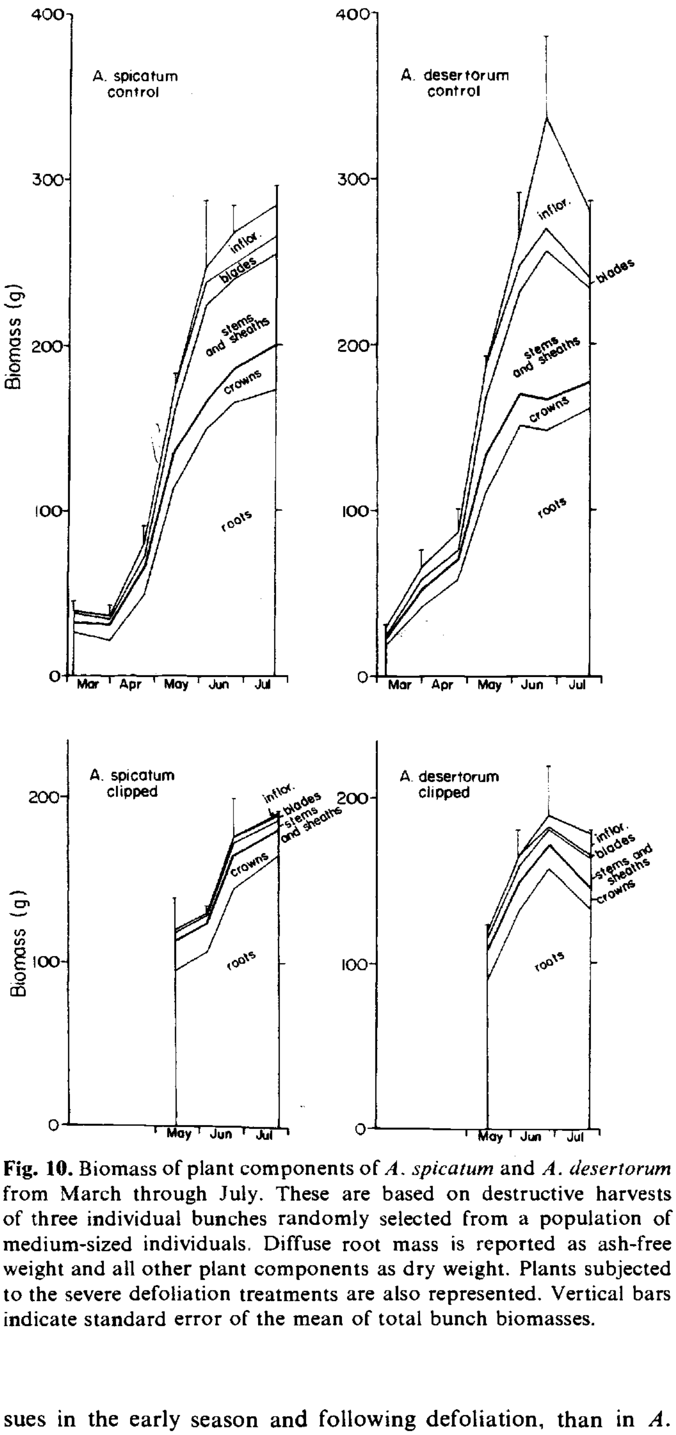

Fig. 10. Biomass of plant components of *A. spicatum* and *A. desertorum* from March through July. These are based on destructive harvests of three individual bunches randomly selected from a population of medium-sized individuals. Diffuse root mass is reported as ash-free weight and all other plant components as dry weight. Plants subjected to the severe defoliation treatments are also represented. Vertical bars indicate standard error of the mean of total bunch biomasses.

sues in the early season and following defoliation, than in *A. spicatum.*

Nonstructural carbohydrate reserves of plants are commonly represented as concentrations of sugars and starches in various plant parts (White 1973). However, biomass components of grasses can change much more rapidly than carbohydrate concentrations and, thus, the total soluble carbon pools may be poorly represented by carbohydrate concentrations. Total soluble carbon pools of the two bunchgrass species are presented in Fig. 12 with the exception of soluble carbon in inflorescences. Though *A. desertorum* exhibited somewhat higher carbohydrate pools in the early season the major increase of soluble carbon in both species took place through late April and during the month of May. For control plants, the total quantity of soluble carbon was greater in *A. spicatum* than in *A. desertorum*. A major soluble carbon pool for both species was in the stems and sheaths. Replenishment of carbon pools following severe defoliation was very limited in both species relative to the increases shown by control plants.

Discussion

Many morphological features of caespitose grasses contribute to their grazing sensitivity as compared to rhizomatous grasses (Branson 1953; Hyder 1972). Caespitose grasses generally have been associated with geographical areas that have not had a history of strong selective pressure from large herbivores (Mark 1969; Klotzli 1977; Baker 1978; Mack and Thompson, unpublished manuscript). Recent introductions of livestock have led to greatly reduced presence of these species (e.g. Laycock 1967).

The bunchgrasses of the arid and semiarid steppes of Central Asia constitute a notable exception (Mack and Thompson, unpublished manuscript). In addition to the crested wheatgrasses, several other caespitose grasses are prominent components of these communities and, yet, this region has a long history of grazing pressure from many species of Artiodactyla and a few Proboscidea and Perissodactyla (Vereshchagin 1967; Kurtén 1968). Although large herbivore pressure in the native environments of *A. desertorum* has apparently resulted in the selection of characteristics which contribute to evolution of grazing tolerance, this species is still a distinctly caespitose bunchgrass possessing many of the characteristics traditionally associated with grazing sensitivity. Once culm elongation is initiated (in late April for 1980), the apical meristem and culm leaves are elevated and susceptible to removal by the grazing animal. Without apical meristems or protected intercalary meristems, replacement of the photosynthetic surface in caespitose grasses following grazing is dependent on activation of axillary buds and production of new tillers, a comparatively slow process (Hyder 1972). *Agropyron desertorum* also has a relatively high proportion of reproductive culms, another characteristic which has been associated with grazing sensitivity (Branson 1953). In all of these characteristics *A. desertorum* is essentially identical to the grazing-sensitive *A. spicatum* (Hyder and Sneva 1963). The seasonal timing and rate of growth of these two species is also remarkably similar (Fig. 10).

The differences in herbivory tolerance of these two species must result from quantitative differences in a suite of characteristics rather than distinct qualitative differences in traits or growth patterns. This discussion addresses a few of the attributes that may contribute to differences in grazing tolerance between *A. desertorum* and *A. spicatum.*

Investment in Foliage

Species that invest less biomass and fewer nutrients in individual foliage elements, but produce more foliage surface, may better cope with partial defoliation, which is the most frequent type of grazing event (Norton and Johnson, unpublished manuscript), than species that invest heavily in a few long-lived foliage elements. Foliage element, as used in this discussion refers to any photosynthetically active plant part, including leaf blades, sheaths, stems and inflorescences. *Agropyron desertorum* produced leaves, and to a lesser degree stems and sheaths, with a greater surface area per unit biomass than *A. spicatum* (Fig. 5). Except in early March, *A. desertorum* also invested less nitrogen per surface area of foliage, although the nitrogen concentrations by weight were about the same for the two species.

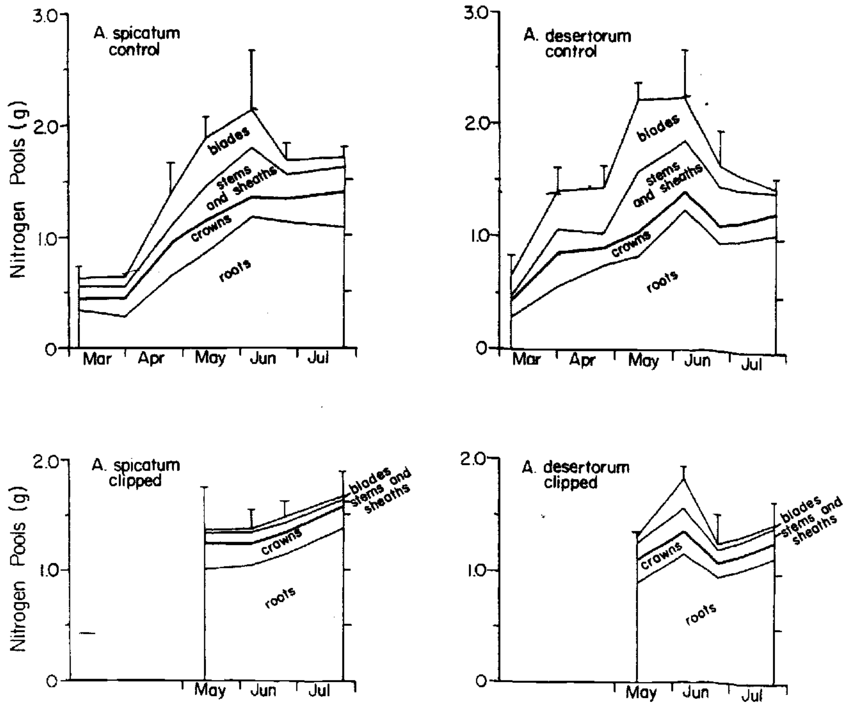

Fig. 11. Total nitrogen in different plant parts of *A. spicatum* and *A. desertorum*. These are from analyses of the same plants represented in Fig. 10. Vertical bars indicate standard error of the mean of total bunch nitrogen

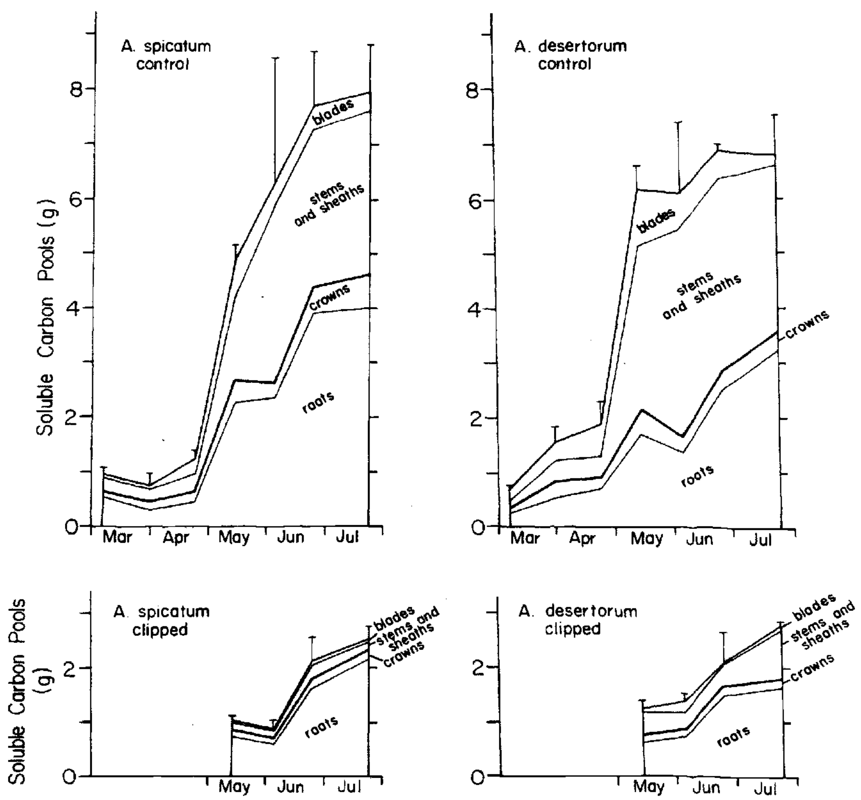

Fig. 12. Total quantity of nonstructural carbohydrates in different plant parts of *A. spicatum* and *A. desertorum*. These are from analyses of the same plants represented in Figs. 10 and 11. Vertical bars indicate standard error of the mean of total bunch soluble carbon

Consistent with expectations, *A. desertorum* produced a greater number of foliage elements. For control plants of the same total biomass (Fig. 10), the average number of tillers per bunch was 187 for *A. desertorum* and only 113 for *A. spicatum* during most of the growing season. Since the number of leaves per tiller was approximately the same for the two species, *A. desertorum* also had more leaves per bunch than *A. spicatum*. While longevity of leaf blades was about the same for two species, stems stayed green longer in *A. spicatum*. *Agropryon desertorum* produced a greater number of foliage elements than *A. spicatum* plants of the same size, invested less nitrogen and biomass in each element, and longevity of the photosynthetically important stems was less. Thus, partial defoliation would be of less consequence for *A. desertorum* than *A. spicatum*.

In the absence of defoliation, the very compact, dense canopies of *A. desertorum* resulted in considerable self-shading of the foliage. While specific aspects of canopy microenvironments are not being addressed in this paper, measurements of photosynthetically active radiation in the canopy have revealed that much of the foliage in the lower part of the canopy for *A. desertorum* was light limited. In contrast, the less dense canopy of *A. spicatum* and the tendency for a more splayed arrangement of tillers results in much better display of the foliage to sunlight. Thus, *A. desertorum* may actually produce more foliage than can be efficiently displayed in the canopy. Much of the foliage in the lower part of the canopy may not be sufficiently well illuminated and, in the absence of partial defoliation, may exhibit early senescence.

Photosynthetic Capacity and Reestablishment of Photosynthetic Surfaces

The greater investment of biomass and nutrients in leaf blades and stems and sheaths of *A. spicatum* resulted in greater photosynthetic capacity per unit surface area (Fig. 6). However, when calculated on a unit mass or unit of nitrogen basis, photosynthetic capacity of leaf blades on unclipped plants–was about the same for both species. Following severe defoliation, regrown leaf blades of both species exhibited higher photosynthetic rates than control leaf blades. When computed on surface area, mass, or nitrogen bases, the relative increase of photosynthetic capacity for regrowing leaf blades compared to leaf blades of unclipped plants was greater for *A. desertorum* than for *A. spicatum*.

The considerably more rapid regrowth of *A. desertorum* foliage following severe defoliation when compared to *A. spicatum* (Fig. 7) is attributable to several factors. In addition to the high photosynthetic capacity of regrowing *A. desertorum* leaf blades, there was both greater absolute and greater relative allocation of plant biomass to photosynthetic organs rather than to crowns or roots (Fig. 10). Of key importance, however, was the proclivity for new tiller production, which was considerably greater for *A. desertorum* than for of *A. spicatum* (Fig. 8). Because shoot apices were nearly all removed by the second defoliation, foliage regrowth was dependent on new tiller formation in both bunchgrass species. The ability of *A. desertorum* to quickly activate axillary buds, mobilize stored reserves and allocate them to maintenance of the new tillers, and produce rapidly growing new tillers compensates to some degree for the lack of active, protected apical and intercalary meristems that confer grazing tolerance in culmless graminoids.

The potential contribution of stems and sheaths for photosynthetic carbon gain of both species is notably large (Fig. 3). The seasonal progression of potential photosynthetic contribution of leaf blades and stems and sheaths was quite similar for the two species. With culm elongation, intercalary meristems of individual culm leaves cease to be active and certain grazing patterns can result in leafless culms which continue to elongate (Cook and Stoddart 1953; Hyder 1972). Such leafless culms have traditionally been portrayed as being of little value to the plant (Dahl and Hyder 1977). However, results from our study document that the photosynthetic potential of these stems and sheaths is considerable. Photosynthesis/transpiration ratios of stems and sheaths are of the same magnitude as those of leaf blades; thus, carbon gain from these organs would not be at the expense of excessive water use when compared to leaf blades.

With respect to nitrogen investment, stems and sheaths yielded a greater potential carbon gain for the plant than leaf blades. In early June when unclipped plants of both species had the maximum potential whole-bunch photosynthetic capacity (Fig. 3), leaf blades of both species represented a potential contribution of only 25% while stems and sheaths contributed in excess of 70%. Yet, total nitrogen in stems and sheaths was only 30% greater than the total quantity of nitrogen contained in leaf blades (Fig. 11).

A high proportion of reproductive shoots has traditionally been associated with grazing sensitivity (Branson 1953; Hyder 1972). This concept should be reexamined in view of the potential photosynthetic contribution of stems, sheaths, and inflorescences. In 1980, more than 90% of the culms of *A. desertorum* and 75% of the culms of *A. spicatum* were reproductive. Furthermore, a particularly sizable fraction of the shoot biomass was allocated to inflorescences of *A. desertorum* (Fig. 10). While a comparison of the carbon balance of reproductive and vegetative culms has yet to be undertaken, the potential photosynthetic carbon gain of stems, sheaths, and inflorescences of *A. desertorum* suggests that reproductive culms may not be a liability for these grasses, even under the duress of grazing. Additionally, a high proportion of stem tissue, whether supporting vegetative or reproductive culms, may help deter excessive consumption of individual plants by large herbivores (Stoddart et al. 1975; Willms et al. 1980).

In the canopies that were reestablished following defoliation, average photosynthetic rates per unit area of foliage were lower for *A. desertorum* than *A. spicatum* (Fig. 9). This was due in part to the lower photosynthetic capacity of foliage elements of *A. desertorum* when expressed on a foliage surface area basis (Fig. 6), but was also likely the result of greater self-shading in the canopies of *A. desertorum*. Despite this self-shading, the substantially greater foliage surface area of the reestablished canopies of *A. desertorum* resulted in greater photosynthesis and even somewhat greater photosynthesis/transpiration ratios for whole bunches when compared to *A. spicatum* during the summer months (Fig. 9).

Allocation of Resources and Reserves

After removal of plant photosynthetic tissue, regrowth of foliage and continued maintenance of the remainder of the plant depends initially on stored carbon. In grasses, carbohydrates constitute the primary form of carbon reserve and are traditionally considered as stored primarily in crowns and stem bases (White 1973). Hyder and Sneva (1963) reported that carbohydrate concentrations in stem bases of *A. desertorum* increased earlier in the spring and were maintained at higher levels throughout the growing season than in *A. spicatum*. Similar patterns in carbohydrate concentrations were found for the crown plus 1-cm stem base tissues of both species in our study. Concentrations in crowns were 50 to 60% greater for *A. desertorum*. Yet, because *A. spicatum* had a somewhat greater proportion of its biomass in crown tissues, the total quantity of carbohydrates in crowns of whole bunches of the two species was about the same (Fig. 12). Furthermore, soluble carbohydrate pools in the crowns of both species constituted usually less than 15% of the total plant carbon pool, except in early spring when this proportion approached 20%. Thus, examination of total carbohydrate pools rather than carbohydrate concentrations in specific organs rendered a significantly different view of these reserves.

For both species, carbohydrates in stems represented the major carbohydrate pool apart from that of the diffuse root system. Leaf and stem soluble carbon pools were almost completely removed by the severe defoliation imposed in this study. However, if plants are only partially defoliated, stem soluble carbon may be quite important for recovery. In any case, the two species did not differ to a large degree in the magnitude of soluble carbon pools, seasonal changes or their apportionment among plant organs.

Although carbohydrate concentrations in the diffuse root system of both species were quite low (less than 50 mg/g), the total soluble carbon pools were sizable because of the proportionally large root biomass (Figs. 10, 12). If a plant is defoliated, carbohydrate pools in the diffuse root system could be deployed for root system activity when the supply of photosynthates from the shoot system is curtailed. Even if root growth were greatly slowed following defoliation, however, maintenance respiration of a large root mass would require a significant carbon supply.

Following the severe defoliation treatment, soluble carbon pools of both species were greatly depressed. A majority of the soluble carbon was in the diffuse root systems of both species following defoliation. Soluble carbon pools of the shoot system and crowns, which would be the most likely source of energy for shoot regrowth following an additional defoliation event, remained quite small, despite the reestablished canopies following defoliation (Figs. 7, 10, 12). Total soluble carbon in the shoot system and crowns was equivalent to or less than the photosynthetic carbon gain of entire bunchgrasses for a single day in June or July. Thus, both species apparently had only a small soluble carbon buffer.

Curtailment of root growth has often been observed following defoliation (Crider 1955; Jameson 1963). This constitutes a mechanism for conserving plant resources and aids in reestablishing a balance between root and shoot systems. Following severe defoliation, root biomass accrual in *A. spicatum* continued, perhaps some with abatement immediately following dipping (Fig. 10). In contrast, *A. desertorum* eventually curtailed root growth, thus allocating more resources to reestablishment of photosynthetic surfaces. Although a net decrease in root biomass was not observed for *A. desertorum* until July (Fig. 10), root growth observations indicated a substantial decrease in growth of new roots by early June (Richards, unpublished). This net decrease in root biomass reflected root death which likely lagged behind the curtailment of new root production. In contrast, new root production in severely defoliated *A. spicatum* plants continued at a rate similar to that of control plants (Richards, unpublished).

Plants coping with severe defoliation must compensate for loss of photosynthetic tissues by a combination of stored carbon reserves, rapid replacement of photosynthetic tissues and appropriate allocation of carbon. However, plant mineral nutrient status may also be important for tolerance to herbivory (Chapin 1980). Nitrogen has been chosen as a key nutrient for study because fertilization experiments have shown this element to be a limiting factor for crested wheatgrass productivity even in the absence of defoliation (Sneva and Rittenhouse 1976; James and Jurinak 1978).

Total nitrogen in the two *Agropyron* species was similar except in late March and early April when total plant nitrogen of *A. desertorum* was twice that of *A. spicatum* (Fig. 11). This is associated with the earlier root and total biomass growth and canopy development of *A. desertorum*. At this time, nitrogen pools of leaves and stems were threefold greater than those in *A. spicatum*. In the spring and early summer, nitrogen concentrations of photosynthetic tissues of both species were two to three times greater than in the diffuse root system. Nevertheless, because of the large root system biomass, nitrogen pools in the root system still represented about half of the total plant nitrogen for both species.

Because of the high concentrations of nitrogen in photosynthetic tissues, in excess of a third of the total nitrogen capital of both species was removed in the severe defoliations imposed (Fig. 11). Yet, demands for nitrogen in regrowing foliage were apparently met by absorption from the soil as there was no evidence of a net withdrawal of nitrogen from the crowns or diffuse root system in either species.

Conclusions

Of the several characteristics investigated in this study, the most important attributes of *A. desertorum* that permit better recovery from severe defoliation appear to be the capactiy for new tiller formation, the rapid and successful regrowth of these new tillers to prevent depletion of the limited soluble carbon buffer, and flexibility in allocation of plant resources which includes supply to regrowing tillers and curtailment of root system growth. Secondary characteristics include increased photosynthetic capacity of regrowing foliage, which occurs in both species, but to a greater degree in *A. desertorum*. Since *A. desertorum* invests less biomass and nitrogen per surface area of photosynthetic tissues, partial defoliation should be less detrimental to this species. A greater allocation of total plant biomass to photosynthetic tissues, particularly following defoliation, also results in greater carbon gain for whole *A. desertorum* bunches and somewhat greater photosynthesis/transpiration ratios.

Stems and sheaths of both species are the principal photosynthetic surfaces during much of the late spring and summer season and these organs also constitute a major soluble carbon reservoir for these bunchgrasses. Thus, culms lacking leaf blades can hardly be considered disadvantageous for the plant. Crowns of these grasses represent a minor proportion of the total soluble carbon.

Acknowledgements. This research was supported by the National Science Foundation (DEB 7907323) and the Utah Agricultural Experiment Station. Development of procedures and thoughtful technical assistance provided by L.A. Price and G. Harris were instrumental in this research. Assistance of L. Bodily, L. Camp, C. Nowak, and M. Menconi are also gratefully acknowledged.

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Received April 15, 1981

Oecologia (Berlin) (1983) 59:178–184

Oecologia

Bunchgrass architecture, light interception, and water-use efficiency: assessment by fiber optic point quadrats and gas exchange

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Summary. The bunchgrass growth form, which is very prominent in water-limited environments, can result in considerable self-shading of photosynthetically active foliage. The consequences of this growth form for light interception and water-use efficiency (photosynthesis/transpiration, P/T) were investigated for two *Agropyron* species which differ in tussock density and degree of self-shading. During the period of most active gas exchange, the tussocks were very compact and photosynthesis of shaded foliage was markedly light-limited. Stomatal control of older shaded foliage was poorly attuned for water-use efficiency. At low light, P/T decreased and intercellular CO_2 concentrations increased. Despite differences in architecture and amount of shaded foliage, P/T of whole tussocks under ambient field conditions did not differ between these species. Partial defoliation decreased, rather than increased, P/T, primarily as a result of the poor photosynthetic light harvesting by the remaining foliage. Despite self-shading, the architecture of widely-spaced bunchgrasses provides for interception of as much direct beam solar radiation as is calculated for a rhizomatous grass occupying an area six-fold greater than the ground area underneath the canopy of these bunchgrasses.

Introduction

Grasses with a bunched or tussock growth form are prominent in steppe and desert regions of North America, Asia, Australia, Africa and South America (Schimper 1898; Moore 1964; Mack and Thompson 1982). The tillers of bunchgrasses are tightly clustered which can result in a very compact tussock and considerable self-shading of foliage. In contrast, rhizomatous grasses, such as in the water-limited short grass prairie, are considered to experience rather little self-shading (Knight 1973; Detling et al. 1978).

This paper explores the consequences of the bunched growth habit for light interception and the relationship between photosynthesis and transpiration, denoted as water-use efficiency. We compared two C_3 *Agroprryon* bunchgrass species which differ in foliage density and arrangement, but whose leaf photosynthetic and stomatal conductance characteristics are similar (Caldwell et al. 1981). This assessment concentrates on the time of year when these grasses had developed substantial new foliage but before extensive internode elongation had taken place and the grass tussocks were still in a very compact growth form (mid-April to end of May at this northern Utah site in western USA). The plants are most active in photosynthesis at this time since the foliage is still young and possesses high nitrogen concentrations. In addition, soil moisture is more abundant than later in the growing season and photosynthesis is not limited by excessive leaf temperatures or large vapor pressure differences between the foliage and air (Caldwell et al. 1981). Indeed, light may be the primary limiting factor for photosynthesis during this period.

Although removal of green foliage, such as by grazing animals, would generally be expected to decrease the photosynthetic capacity of the plant, it could result in a more favorable ratio between photosynthesis and transpiration, P/T, if photosynthesis of a significant portion of the tussock is light-limited due to shading.

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Methods

Unlike a grass sward, bunchgrasses intercept solar radiation on the sides as well as top of the tussock. Interception of solar radiation by green foliage is a function of solar angle, foliage inclination and dispersion patterns and the arrangement of green and standing dead foliage of the tussock. The problem can be approached empirically by use of inclined point quadrats. Warren Wilson (1960, 1963, 1965 and 1967) has developed the theoretical basis for determination of canopy architecture and light penetration into vegetation. This theory can be extended to the question of light interception by isolated plants. Fiber optic point quadrats were employed in this study to increase accuracy and sampling speed (Caldwell et al. 1983). Foliage area of different plant parts of 11 bunchgrasses was determined by quadrats, inclined at 32°, during the period of 23 April to 24 May in 1981 and 1982 (Warren Wilson 1960, 1963, 1965). Projected areas of cylindrical parts were corrected to 1/2 the surface area of the cylinder. Two individuals of each species were intensively sampled both in 1981 and 1982 to determine foliage inclination at different heights in the tussocks by a combination of near vertical and horizontal quadrat samples. The variance in foliage angles was estimated independently from protractor measurements. These plants were also sampled to determine projected sunlit foliage at different solar angles corresponding to the position of the sun on May 20 for each hour of the day (List 1968). The projected sunlit green foliage was taken as the frequency of first contacts with green foliage. Although the geometry of these tussocks is assumed to be symmetrical with respect to azimuth angle, the intensive quadrat sampling was conducted at azimuth angles corresponding to the position of the sun at appropriate times of day.

Global (direct beam plus diffuse) solar photon flux density in the 400–700 nm waveband (termed photosynthetic photon flux density, PPFD) was measured by horizontally-mounted quantum sensors (Li-Cor Co. Lincoln, Nebraska) above and at the center of the base of bunchgrasses to assess light penetration into these tussocks. These sensors were interrogated every 10 s by a computerized data acquisition system and 1/2-h averages were calculated. Direct PPFD striking a plane normal to the solar beam was computed from ratios of global PPFD/total shortwave irradiation striking a horizontal plane as measured by a Stern pyranometer, and the calculated normally-incident direct beam total shortwave radiation. This normally-incident flux was derived using a pair of Stern pyranometers, one of which was equipped with a shadow ring. With corrections for the portion of the sky radiation blocked by the shadow ring, this pyranometer provided a measure of diffuse total shortwave radiation. Direct beam reaching a horizontal plane was derived by subtraction (Coulson 1975). Direct beam flux normal to the solar beam was then calculated from cosine law corrections. The ratio of direct beam to diffuse total shortwave radiation was assumed to apply to PPFD. Diffuse PPFD striking a plane normal to the solar beam was calculated from diffuse PPFD striking a horizontal plane assuming an isotropic hemisphere (Burt and Luther 1979). Shortwave and PPFD measurements were taken for several clear days in May of 1982 and calculations are appropriate to solar angles as would occur on May 20.

Simultaneous measurements of CO_2 and water vapor flux of individual leaf blades were made in situ on several dates from mid-April to the end of May. The dependency of net photosynthesis on PPFD for leaf blades near the bottom and the top of the tussock canopies was determined at a leaf temperature of 21° C, vapor pressure difference between leaf and air of 2.3 ± 0.3 kPa and near ambient air CO_2 concentrations. From the gas exchange data, leaf diffusive conductances and leaf intercellular CO_2 concentrations were also calculated. Carbon dioxide and water vapor exchange of individual foliage elements was measured on intact plants in the field with a CO_2 and H_2O vapor exchange porometer (Bingham and Coyne 1977). For the PPFD dependency relationships, either neutral density filters with solar radiation or an incandescent light source was employed.

Carbon dioxide and water vapor gas exchange of whole plants was also determined on several dates during this period with a large cuvette system programmed to track ambient conditions of temperature and vapor pressure deficit as the plants were exposed to solar radiation on primarily cloudless days. A measurement series was also conducted following partial defoliation of bunchgrass plants. The semi-cylindrical configuration of the chamber allowed solar radiation to impinge on the plants from all azimuth angles except from the north, where the Peltier heat exchanger was located. The heat exchanger and electronic control system were modified from an original Sirigor (Siemens Co., Erlangen, West Germany) chamber (Koch et al. 1971). Regulated flow rates up to 100 l min^{-1} can be accommodated in this chamber. Incoming air was partially dehumidified using a heatless dryer (Puregas Co.) so that outgoing vapor concentrations approximated those of the ambient air. In all but three dates in 1981, air flow from the cuvette to the infrared gas analyzer was transported in stainless steel tubing to minimize water vapor and CO_2 adsorption. Further details of this system are contained in Caldwell et al. (1981).

Gas exchange calculations for both the $CO_2 - H_2O$ porometer and the whole-tussock cuvette systems included correction factors recommended by von Caemmerer and Farquhar (1981) to take into account dilution of the air stream by transpiration and interactions of gasses in calculation of conductances.

A description of the *Agropyron* bunchgrass species, the study area and climate in northern Utah is contained in Caldwell et al. (1981).

Results

The architecture of the two *Agropyron* bunchgrasses for the period of the growing season when these tussocks are most compact is shown in Fig. 1. This is a composite diagram of the 11 bunchgrass plants sampled during a 31-day period (23 April–24 May) in 1981 and 1982. Individual plant size varied and the plants were rapidly growing during this period of active photosynthesis. The average total green foliage area of *Agropyron desertorum* (Fisch. ex Link) Schult. was 1,920 cm^2 (standard error, S.E., 410 cm^2) and 1,240 cm^2 (S. E., 135 cm^2) for *Agropyron spicatum* (Pursh) Scribn. and Smith. (A proposed taxonomic revision (Dewey 1983) will change this name to *Elytrigia spicata* (Pursh) D.R. Dewey.) The green stem area accounted for only 2% of the total green foliage area of *A. spicatum* and less than 0.5% for *A. desertorum*. The primary differences between these species were that *A. desertorum* had greater foliage area and canopy denseness while *A. spicatum* had greater variance of foliage angle distribution. Destructive harvests

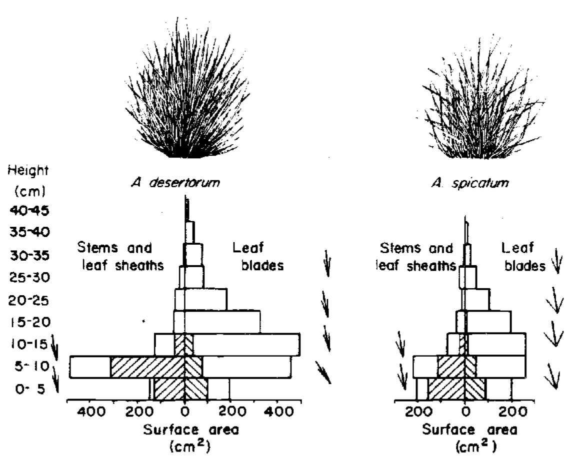

Fig. 1. Composite depictions of leaf blade, leaf sheath and stem area distributions with height for bunchgrasses of *A. desertorum* and *A. spicatum* during the season when these grasses are most compact. This composite is based on 6 *A. desertorum* and 5 *A. spicatum* plants intensively sampled between April 23–May 24 in 1981 and 1982. The hatched portion of the histograms indicates dead or senescent foliage. Average foliage inclination angles and their standard deviations are indicated for different heights of the tussocks for both leaf blades and sheaths

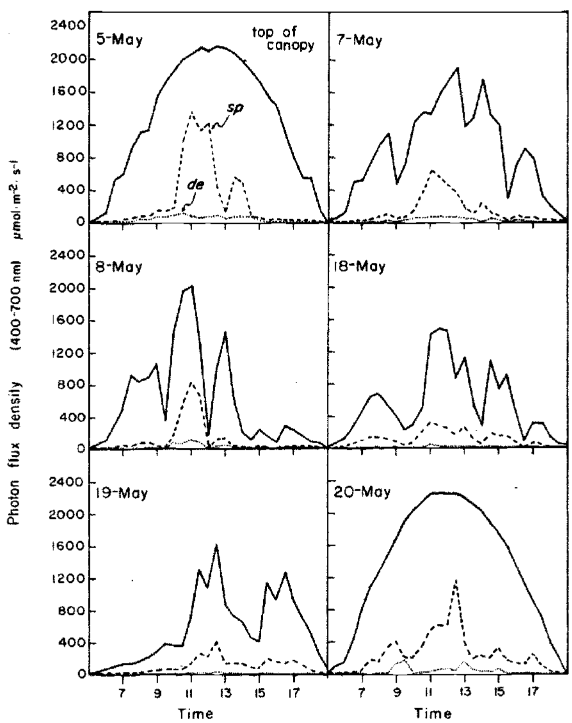

Fig. 2. Measurements of photon flux density (400–700 nm) at the top and at the base of tussocks of *A. desertorum* (de) and *A. spicatum* (sp) on several days in 1982. The quantum sensors were horizontally mounted. The irradiance is plotted as 1/2-h averages as a function of true solar time

of other plants in this study have also indicated that *A. spicatum* tends to have about 20% more green foliage area per tiller than *A. desertorum*. Therefore, the total green foliage area in tussocks of *A. spicatum* is distributed on fewer tillers than in *A. desertorum*. These differences result in a more open-structured tussock for *A. spicatum*.

The differences in these two species are also indicated by measurements of PPFD at the tussock base (Fig. 2). Even on cloudless days, PPFD at the base of the *A. desertorum* tussock exceeded only 50 μmol quanta$\cdot m^{-2} \cdot s^{-1}$ for 4 to 5 h per day and usually did not exceed 100 μmol quanta$\cdot m^{-2} \cdot s^{-1}$ for more than a 1/2-h period. In contrast, PPFD at the base of the *A. spicatum* tussock on cloudless days could exceed 1,000 μmol quanta$\cdot m^{-2} \cdot s^{-1}$ and was always greater than in *A. desertorum* under all conditions. The quantum sensors at the base of the tussocks were adjacent to green, photosynthetically-active foliage. Because the values shown in Fig. 2 are averages over 1/2-h periods, short-duration sun flecks would be integrated into these 1/2-h values. On a daily basis, total photon flux reaching green foliage at the bottom of *A. spicatum* tussocks ranged from 17 to 22% of that at the top of the tussock for the days depicted in Fig. 2, while in the *A. desertorum* tussock total daily photon flux was always less than 5% of that reaching the top of the tussock. While it is evident from these measurements that considerable self-shading of foliage in the tussocks occurs, a quantitative depiction of light interception by whole tussocks is better represented by the point quadrat sampling.

The projected area of green foliage in the direction of the solar beam during the course of a cloudless day is given

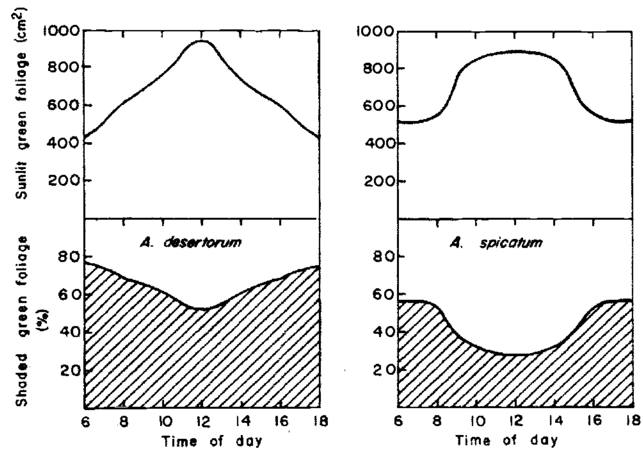

Fig. 3. Projected area of green foliage intercepting direct beam solar radiation for the plants depicted in Fig. 1 for solar angles as would occur on May 20 at latitude 42° N. The percentage of green foliage area in shade is also shown. Time of day is true solar time

in Fig. 3 for solar angles appropriate to May 20 at this location. This is calculated for the composite plant architectures depicted in Fig. 1 and based on the intensive point quadrat sampling at angles corresponding to the solar beam at each hour of the day. Although the total green foliage area of *A. desertorum* is 50% greater than for *A. spicatum*, the projected sunlit foliage area during much of the day is about the same for the two species. The percentage of shaded foliage, calculated as the difference between total green foliage area and projected sunlit foliage area, is greater for *A. desertorum*. This calculation of shaded foliage corresponds in magnitude with that calculated from total and initial contact frequencies at three different quadrat angles. However, due to light scattering and penumbral effects, there is not always a sharp distinction between sunlit and shaded foliage as depicted here, especially in the interior of the tussock. Nevertheless, *A. desertorum* has a greater proportion of foliage that is not receiving direct beam radiation.

For widely-spaced bunchgrass plants, the direct beam irradiance from all angles impinging on sides and top of the tussock should be considered. Normally-incident solar direct photon flux density (400–700 nm), PPFD, is presented in Fig. 4 (top) for solar angles appropriate to May 20. The diffuse PPFD incident on a similarly-inclined surface is also presented for perspective. The total direct beam photon flux intercepted by green foliage of the plants portrayed in Figs. 1 and 3 is also depicted in Fig. 4 (bottom). This is the product of normally-incident PPFD and projected sunlit green foliage area for solar angles appropriate to May 20. The total direct beam and diffuse photon flux received on a level plane equivalent in area to the ground beneath the canopy crown of an average tussock (27 cm diam.) is also shown for perspective.

Net photosynthesis, diffusive leaf conductance for water vapor, g_w, and leaf intercellular CO_2 concentration, c_i, are presented as a function of PPFD for individual leaf blades in Fig. 5. These are taken from a series of field measurements on intact leaves conducted throughout April and May in 1980 and 1981, and represent leaf blades near the base and near the top of the tussocks. Leaf blades at the base of the tillers were older and normally well shaded.

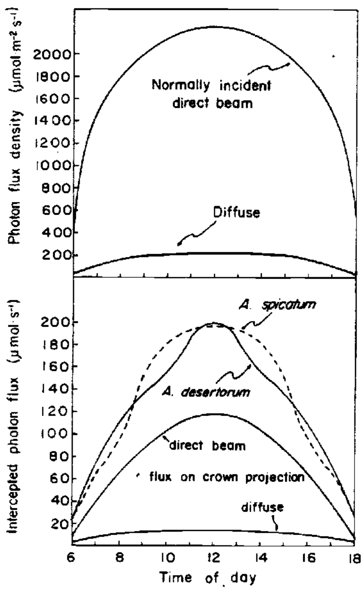

Fig. 4. Normally-incident solar direct beam photon flux density (400–700 nm) and diffuse photon flux density incident on a similarly-inclined surface for solar angles appropriate to May 20 at this site (top). Total direct beam photon flux intercepted by green foliage of the plants depicted in Figs. 1 and 3 and the direct beam and diffuse photon flux intercepted by level ground equivalent in area to the average canopy crown projection of these tussocks as a function of true solar time

Although the gas exchange behaviour of individual leaf blades of different tillers varied somewhat, older leaves at the base of the tillers had consistently lower photosynthetic rates and usually exhibited light saturation at much lower PPFD than blades near the top of the tussock. Leaf conductance, g_w, of older foliage was often, though not always, lower than that of young foliage. Conductance generally decreased with declining PPFD but not as rapidly as the decrease of photosynthesis. Consequently, c_i increased for almost all leaf blades at PPFD less than 800 μmol quanta $\cdot$ $m^{-2} \cdot s^{-1}$. Thus, the photosynthesis/transpiration ratio, P/T, of shaded foliage would probably be much lower than for sunlit foliage, especially since shaded foliage is usually the older foliage on the tiller and g_w of older foliage is less responsive to PPFD changes than is g_w of younger foliage. The gas exchange characteristics of these two species were generally similar except that maximum photosynthetic rates of *A. spicatum* leaves at the top of the canopy were often greater and g_w of this species differed more between upper and lower leaves than in *A. desertorum*. Photosynthesis and transpiration of individual leaf blades taken under prevailing ambient conditions of PPFD, leaf temperature and vapor pressure difference between leaf and air showed that P/T ratios of shaded foliage were considerably lower than those of sunlit foliage (Fig. 6).

Because *A. desertorum* has a smaller proportion of its foliage directly exposed to the solar beam and foliage lying in deep shade exhibits very low P/T, tussocks of *A. desertorum* might be expected to have lower water-use efficiency

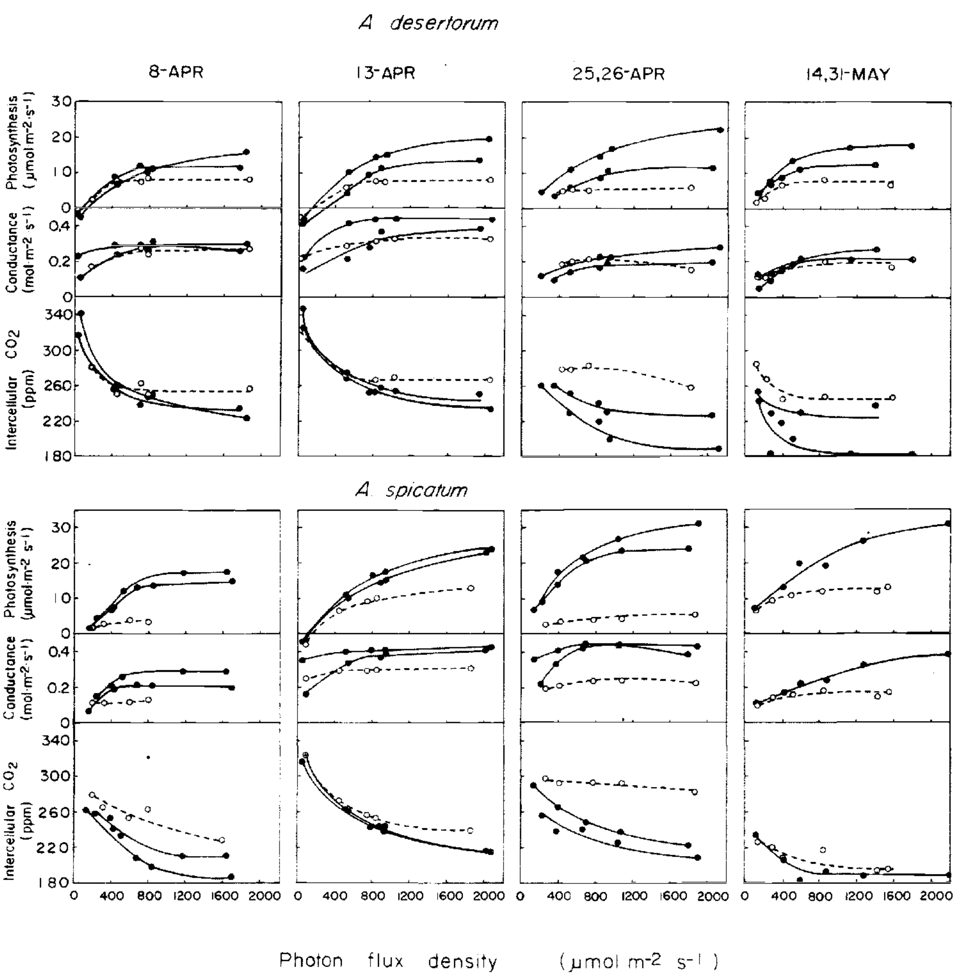

Fig. 5. Net photosynthesis, diffusive leaf conductance for water vapor and leaf intercellular CO_2 concentrations as a function of photon flux density for leaves of individual bunchgrass tillers on different dates in 1980 and 1981. The dashed lines and open circles represent older leaf blades near the base of the tussocks while the solid lines and closed circles are for the two leaves of the same tillers near the top of the tussocks

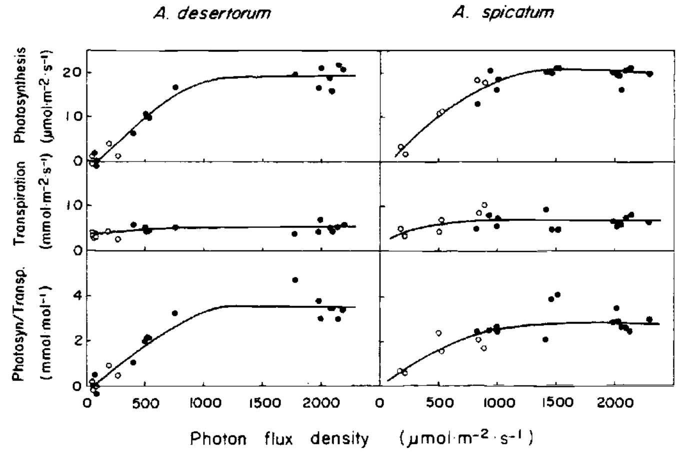

Fig. 6. Net photosynthesis and transpiration of individual leaf blades measured under prevailing ambient conditions of leaf temperature, vapor pressure difference between leaf and air, and photon flux density. These measurements were collected for leaves at different heights in the tussock. Open circles represent the oldest green leaf blades on individual tillers at the base of the tussock and the other data points represent younger leaf blades at higher locations in the tussocks. These measurements were taken during the middle 5-h of the day on May 13, 20 in 1982. Leaf temperatures ranged between 12 and 24° and vapor pressure difference between leaf and air was in the range of 1.0 to 2.6 kPa

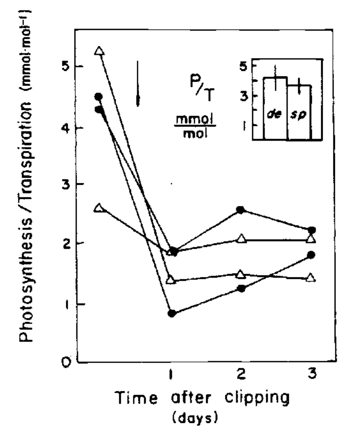

Fig. 7. Daily integrated ratios of photosynthesis/transpiration measured for whole bunchgrasses with the large gas exchange cuvette system tracking ambient environmental conditions during the period from mid-April to mid-June in 1981 and 1982. All measurements were taken during days of minimum cloud cover. The arrow indicates the time of partial defoliation of 4 plants (open triangles, *A. spicatum*, closed circles, *A. desertorum*) and the time following partial defoliation represents measurements of daily gas exchange during primarily cloudless days. In the inset are average and standard deviations of daily P/T ratios of 11 tussocks not subjected to defoliation during this period of time

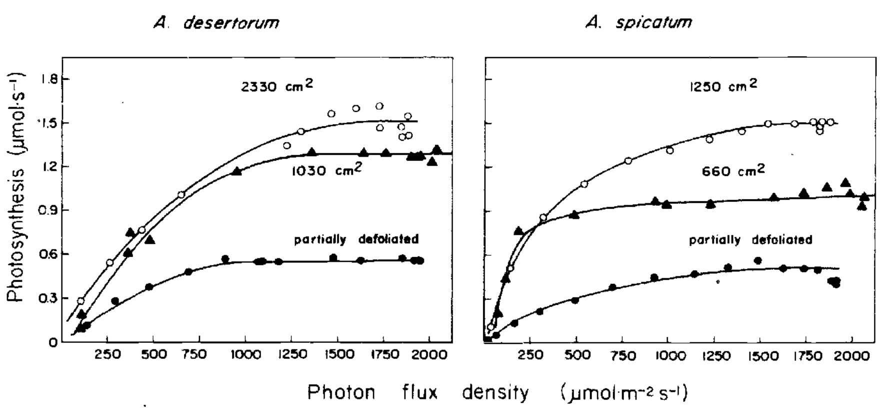

Fig. 8. The relationship between daily net photosynthesis of entire bunchgrasses as a function of photon flux density for bunchgrasses of different size. These data were collected during the afternoon periods (April 29–May 4, 1981 and 1982) on cloudless days when the large cuvette system was tracking ambient environmental conditions. The green foliage area of each plant is indicated. Also shown are the same relationships for the second cloudless day following partial defoliation of tussocks in mid-May, 1982. Foliage temperatures were between 17 to 27° C which is within the optimal range for photosynthesis at this time of year

over the course of a day than *A. spicatum*. It might also be expected from these individual leaf measurements that partial defoliation of either species could improve water-use efficiency because of reduced self-shading. However, it should be emphasized that water-use efficiency of entire tussocks depends on the quantitative contribution of foliage of different physiological states in different microenvironments in the tussock. Much of the sunlit foliage is younger, more photosynthetically-active tissue and gas exchange of this foliage may overwhelm that of older, shaded foliage. This is borne out by gas exchange measurements of whole bunchgrasses over several days in the late April–May period when the large cuvette system was tracking ambient environmental conditions (Fig. 7). These measurements indicated that the two species did not differ in water-use efficiency and further showed that partial defoliation of either species always resulted in decreased water-use efficiency. Approximately 60 to 85% of the green foliage area was removed in these partial defoliations.

An indication of photosynthetic light harvesting by these bunchgrasses under ambient conditions can be gleaned from the relationship between photosynthesis of the whole tussock and PPFD. Such relationships are plotted for tussocks of quite different size and also for partially defoliated tussocks in Fig. 8 (these are from the measurement series included in Fig. 7). Smaller tussocks underwent apparent light saturation at lower PPFD, whereas, larger bunchgrasses exhibited increasing tussock photosynthetic rates at higher PPFD. In this case, however, an *A. spicatum* of 1,250 cm^2 foliage area apparently can harvest as much light as an *A. desertorum* with 2,330 cm^2 foliage area. The partially defoliated plants exhibited very little increase of photosynthesis above a PPFD of 750 µmol quanta·m^{-2}·s^{-1}. At this time of year, the partially defoliated bunchgrasses would be essentially light saturated for the middle 9 h of the day. This apparent light saturation was not the result of excessive leaf temperature because foliage temperatures were in the range of 17–27°, which are in the optimal range for photosynthesis of these species at this time of year (Nowak, unpublished data).

Discussion

Photosynthetic light harvesting by these *Agropyron* bunchgrasses is dependent on size of tussock as well as environmental conditions; however, it appears that at least under certain conditions an *A. spicatum* tussock is able to harvest the same amount of light as an *A. desertorum* tussock which has 80% more green foliage area (Fig. 8). This may be attributed both to the architecture and photosynthetic characteristics of these species. The green foliage of an *A. spicatum* tussock can intercept as much direct beam light as that of an *A. desertorum* tussock which has approximately 50% more total green foliage area (Fig. 4). In addition, the most photosynthetically active leaves of *A. spicatum* often have higher photosynthetic rates per unit foliage area than those of *A. desertorum* (Fig. 5, Caldwell et al. 1981). Each species likely has an optimal tussock size for light harvesting under particular conditions; however, more data would be required to test this proposition.

The differences in these species may reflect the different herbivory pressures received during their evolutionary history. *Agropyron desertorum* is a Eurasian species which has been naturalized in North America and in its native environment evolved in the presence of large populations of ungulates. Thus, it likely encountered a greater probability of defoliation than *A. spicatum* which is native to the Intermountain West of North America where few large herbivorous mammals have existed, at least since the Pleistocene (Mack and Thompson 1982; Caldwell et al. 1981). In its native environment, the *A. desertorum* tussocks may have been typically grazed and thus at least partially defoliated. Consequently, without herbivory, *A. desertorum* has a greater proportion of shaded green foliage than *A. spicatum* (Fig. 3) and some of this foliage can be in a very low light envionment even on cloudless days (Fig. 2).

The question can be raised as to whether *A. desertorum* without some foliage removal may have tussocks which are too dense, especially for efficient use of water. The P/T of light-limited foliage depends on the stomatal behavior of shaded foliage elements. Until photosynthesis becomes severely light-limited, a reduction of g_w in response to decreasing light that is proportional to the decline of photosynthesis can reduce transpiration and yet maintain a constant c_i. Thus, if these shaded leaves maintain a positive carbon balance and P/T similar to those of other foliage on the plant, this shaded foliage would still be an asset to the tussock. The very shaded foliage elements of both bunchgrass species are primarily the older leaves which exhibit reduced photosynthetic capacity and saturation of photosynthesis at low PPFD. These photosynthetic characteristics may in part be the result of a shade adaptation and in part simply the result of advanced leaf age (Field 1981). These older leaves did not, however, exhibit efficient curtailment of g_w at low PPFD (Figs. 5 and 6). Instead, under light-limiting conditions, c_i increased and P/T tended to decrease. Although, this may be a general characteristic of older foliage (Turner 1974) it has not been well documented in the literature.

Extrapolation of information on canopy architecture, the light environment within tussocks, and individual leaf gas exchange behavior (Figs. 2, 3, 5 and 6) to gas exchange of whole tussocks would suggest that *A. desertorum* should exhibit lower water-use efficiency than *A. spicatum* under field conditions when photosynthesis is not otherwise limited by environmental factors such as excessive leaf temperatures or water stress. However, such differences were not apparent in the series of gas exchange measurements of whole tussocks in the field (Fig. 7 inset). Under these conditions, the proportional contribution of the more physiologically active, well-illuminated foliage to gas exchange of the entire tussock outweighed differences between these species in the proportion of shaded foliage with reduced P/T. Although it is common in ecophysiological studies to extrapolate from individual leaf gas exchange activity to behavior of the whole plant, such extrapolations present a formidable sampling problem (e.g., Leverenz et al. 1982). This underscores the importance of gas exchange measurements of whole plants or larger subunits of plants under field conditions whenever feasible.

Partial defoliation of compact bunchgrasses with a significant amount of light-limited foliage hypothetically could result in increased P/T even though total tussock photosynthesis would be reduced. However, gas exchange measurements of whole tussocks in the field clearly did not support this proposition (Fig. 7). Photosynthesis/transpiration ratios sharply declined following partial defoliation and though total tussock photosynthesis slowly increased in succeeding days, P/T remained low. The tussocks in these experiments were defoliated to the extent that there was practically no self-shading within the tussock. The majority of foliage removed from these bunchgrasses was in the category of young, upper leaf blades and leaf sheaths which were the most photosynthetically active foliage elements (Fig. 5). This type of foliage is preferentially eaten by livestock when these plants are in this growth stage (P. Johnson, personal communication). Consequently, the remaining foliage is older, less photosynthetically active material. The net result was that the P/T of the tussock was reduced.

Photosynthetic harvesting of solar radiation by these partially defoliated tussocks was not efficient. Only a slight increase of photosynthesis occurred when PPFD increased above 750 μmol quanta $\cdot m^{-2} \cdot s^{-1}$ (Fig. 8). Thus, for clear days at this time of year, the tussocks were effectively light-saturated for the middle 9 h of the day. Although partial defoliation clearly did not result in increased P/T, it is plausible that a different pattern of defoliation could result in an increase of water-use efficiency. For example, insect herbivores might remove foliage on the plant in a pattern which could reduce the amount of shaded foliage without a disproportionate loss of the most productive foliage elements.

Even if water-use efficiency were increased by a particular pattern of partial defoliation, the benefits might be questionable. In this environment, soil moisture, and likely mineral nutrient resources, are most dependably available to the plants at this time of year (mid-April to end of May) (Caldwell et al. 1981). Vapor pressure differences between foliage and the atmosphere in these experiments seldom exceeded 2 kPa and, thus, would be very conducive to high P/T. Leaf temperatures seldom exceeded 25° and were generally in the optimum range for photosynthesis (Nowak, unpublished data). Indeed, total day P/T values are as high as have been reported for plants in arid environments (Lange et al. 1969, Hellmuth 1971; Caldwell et al. 1977). If partial defoliation did improve water use efficiency, the rate of water use by these tussocks also would be reduced because of less transpiring foliage. Postponement of this moisture resource use to later in the year when the higher atmospheric stress is much less conducive to high P/T could more than offset the improved P/T earlier in the season due to partial defoliation. Furthermore, postponement of resource use could result in surrendering some of this resource to neighboring plants.

Widely-spaced bunchgrasses in water-limited environments constitute islands of compact foliage. When calculated on the basis of ground area beneath the canopy of these grasses, the composite plants depicted in Fig. 1 would have green foliage area indices (foliage area/ground area) of 3.4 and 2.2 for *A. desertorum* and *A. spicatum*, respectively (assuming an average canopy crown projection of 27 cm diameter). In contrast, in the short grass prairie, an environment of similar annual precipitation and evaporative demand, the maximum green foliage area index is 0.5 (Knight 1973). Though considerable self-shading occurs in these bunchgrass islands, the total daily interception of photon flux by green foliage of these tussocks may not be so much different than that received by a rhizomatous grass with little self-shading. Because the tussocks receive solar radiation on the sides as well as the top of the tussock, the total direct beam photon flux received during the course of a day could be equivalent to that received on a level ground area some 70% greater than the canopy crown projection of these tussocks (Fig. 4).

It is possible to compute the total intercepted direct beam photon flux that would impinge on a rhizomatous grass assuming a foliage area index of 0.5, foliage inclination angles the same as those of the bunchgrasses, and randomly distributed foliage elements from the theory developed by Warren Wilson (1967). If this is done for solar angles and radiation conditions as depicted in Fig. 4, a rhizomatous grass of these characteristics would need to occupy an area 6.4 times that of the ground area under the canopy crown projection of these bunchgrasses in order to intercept the same total direct beam flux. However, the diurnal course of intercepted direct beam photon flux would be different for the rhizomatous and tussock grasses with proportionately more radiation being intercepted in the mid-portion of the day by the bunchgrasses. Interestingly, if the green foliage area of these bunchgrasses as portrayed in Fig. 1 were dispersed as randomly arranged foliage over this 6.4-fold greater ground area, they would have foliage area indices of 0.53 and 0.34 for *A. desertorum* and *A. spicatum*, respectively.

The selective advantages of the bunchgrass growth habit probably lie with factors other than display of foliage to solar radiation. These may involve fire tolerance, reduction of the extent of grazing, competitive position and space occupation, etc. These factors are presently, however, largely a matter of speculation. While the bunchgrass growth habit may not necessarily represent optimal architecture for light interception, photosynthetic light harvesting and water use efficiency, this analysis suggests that these bunchgrasses are not so inefficient in this regard. Furthermore, for partial defoliation to improve water use efficiency, it would need to be executed very selectively with respect to age and position of foliage elements within the tussock.

Acknowledgements. This research was supported by the National Science Foundation (DEB 7907323 and DEB 8207171) and the Utah Agricultural Experiment Station. Pyranometer data were provided by L.E. Hipps and L.F. Hall. Assistance in the field by J. Warenski, J. Whitehouse and J. Erickson are gratefully acknowledged. Review of this paper by D.A. Johnson led to many improvements.

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Received April 27, 1983

Oecologia (Berlin) (1984) 61:311–318

Oecologia

A test of compensatory photosynthesis in the field: implications for herbivory tolerance

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Summary. The occurrence of compensatory photosynthesis was examined in the field for all foliage elements on two *Agropyron* bunchgrass species that differ in their evolutionary history of grazing pressure. This is the first reported field study of compensatory photosynthesis in individual foliage elements of graminoids. Compensatory photosynthesis was defined as an increase in the photosynthetic rates of foliage on partially defoliated plants relative to foliage *of the same age* on undefoliated plants. Compensatory photosynthesis did occur in many individual foliage elements during at least part of their ontogeny. For both species, compensatory photosynthesis was related primarily to delayed leaf senescence and increased soluble protein concentrations, but not to an improvement in the water status of clipped plants. Soluble protein concentration increased in all foliage elements. A delay in senescence on clipped plants was documented for the two oldest, fully-expanded leaves that were present when the plants were initially clipped, but the initiation and senescence of all other foliage elements were not affected by the clipping treatments. Photosynthetic water use efficiency and photosynthetic rates per unit soluble protein of foliage on partially defoliated plants were not increased following the clipping treatments. Although *A. desertorum* and *A. spicatum* were exposed to different levels of grazing pressure during their evolutionary history, the phenology, water status, and gas exchange rates of foliage were very similar both for undefoliated as well as partially defoliated plants. Thus, we conclude that compensatory photosynthesis does not appear to be an important ecological component of herbivory tolerance for these species.

Introduction

An increase in photosynthetic rates of foliage on partially defoliated plants may be a mechanism to partially compensate for herbivory (McNaughton 1979, 1983, Dyer et al. 1982). This enhanced photosynthesis following partial foliage removal may be due to either an increase in the photosynthetic rates of foliage on these plants relative to *similar-aged* foliage on undefoliated plants, which we define as "compensatory photosynthesis", or a change in the age composition of foliage from predominantly older tissue on undefoliated plants to younger regrowing tissue on partially defoliated plants. Following severe defoliation of two *Agrópyron* species, Caldwell et al. (1981) found that the younger regrowing foliage on defoliated plants had higher net photosynthetic rates than the relatively older foliage on undefoliated plants. This increase in photosynthesis that accompanies a change in age composition is to be expected because younger foliage usually exhibits greater photosynthetic capability. However, the phenomenon of compensatory photosynthesis is more impressive, especially since photosynthetic rates of leaves that remain after partial defoliation may in some cases be more than twice the rates of leaves of similar age on undefoliated plants (Gifford and Marshall 1973, Hodgkinson et al. 1972, Hodgkinson 1974). Photosynthetic rates of leaves that regrow after partial defoliation can also be greater than photosynthetic rates measured on leaves of the same age on undefoliated plants (Woledge 1977, Heichel and Turner 1983).

Although compensatory photosynthesis after partial defoliation is well documented in many plant species, not all species exhibit this phenomenon (Ryle and Powell 1975). Also, changes in photosynthetic rates after partial defoliation may be influenced by the method of defoliation, leaf age, light conditions, and probably other factors as well. For example, in experiments with *Agropyron smithii*, leaves damaged by simulated insect herbivory exhibited a depression of net photosynthesis (Detling et al. 1979), whereas compensatory photosynthesis occurred in undamaged leaves when 75% of the tillers on a plant were clipped (Detling and Painter 1983). Continuous or severe defoliation can sometimes yield different results than a single, moderate one (Alderfer and Eagles 1976, Hodgkinson 1974), but the severity of defoliation is not always influential (Painter and Detling 1981). Leaf age and the light environment may also influence the degree of change in photosynthetic rates following partial defoliation (Hodgkinson 1974, Woledge 1977). Finally, compensatory photosynthesis in growth chamber and greenhouse studies may be exaggerated when compared to field conditions because of the optimal growing conditions. Because most of the studies cited above were conducted under greenhouse or growth chamber conditions and usually limited to investigations of short-term photosynthetic changes of one or two cohorts of leaves following a single defoliation, the application of these results to plant responses following herbivory in nature is questionable.

The purpose of our experiment was twofold. First, we wanted to determine the magnitude and extent to which

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compensatory photosynthesis occurs in the field on mature plants that were clipped in a manner that simulated the defoliation behavior of cattle in a rangeland pasture. Therefore, the life histories of individual foliage elements were examined, and the photosynthetic rates of all foliage elements were measured during their ontogeny. The second goal was to determine if photosynthetic water use efficiency (photosynthesis/transpiration) or photosynthetic rates per unit soluble protein were altered concurrently with photosynthesis following clipping. For these experiments, we selected two species that are morphologically and phenologically very similar, but likely have had different levels of grazing pressure during their evolutionary history (see Caldwell et al. 1981).

Materials and methods

Two bunchgrass species, *Agropyron desertorum* (Fisch. ex Link) Schult. and *A. spicatum* (Pursh) Scribn. and Smith[1], were used in our experiment. Mature plants of both bunchgrass species and a shrub, *Artemisia tridentata* ssp. *vaseyana* (Rybd.) Beetle, were transplanted in 1978 in a regular matrix such that the nearest neighbors of each individual bunchgrass plant were four *Artemisia* plants located in orthogonal directions from the bunchgrass plant. The northern Utah, U.S.A., study area is representative of semiarid, North American Great Basin rangelands where *A. spicatum* and *Artemisia tridentata* are native and where *A. desertorum* has been seeded. Further descriptions of the three species and the study site are found in Caldwell et al. (1981).

Individual plants of each bunchgrass species were paired on the basis of aboveground biomass in mid-April, 1981, and one member of each pair was randomly selected for the clipping treatments. Plants were manually clipped on April 16, 1981, and the same plants were clipped two more times at two-week intervals. With each clipping treatment, approximately 50% of the standing crop was removed with a cut that was above the majority of the apical meristems and also parallel to the ground surface. This frequency, intensity, and horizontal method of defoliation simulated the cattle grazing behavior that has been observed to occur on similar-sized *A. desertorum* plants in rangeland pastures (P.A. Johnson, personal communication). In 1982, control (undefoliated) plants from 1981 were paired, and one member of each pair was randomly selected for clipping treatments. The intensity, frequency, and horizontal method of defoliation in 1982 was identical to 1981, but the first clipping treatment in 1982 was delayed until April 27, 1982, because a cold, snowy winter and spring delayed plant growth.

Net photosynthesis and transpiration were determined in the field with a steady-state gas exchange system (Bingham and Coyne 1977). All gas exchange measurements were at saturating light intensity (a photosynthetic photon flux density greater than 1.7 mmol quanta m^{-2} s^{-1}), and a cuvette CO_2 concentration near 335 $\mu l\ l^{-1}$ (range: 320–365 $\mu l\ l^{-1}$). Leaf temperatures for photosynthetic measurements were between 21 and 24 C, which is within the optimal temperature range of photosynthesis for these two species (Nowak 1984), and the water vapor mole fraction gradient from leaf to air was near 0.027 mol mol^{-1} (range: 0.023–0.030). Net photosynthesis and transpiration were calculated as outlined in von Caemmerer and Farquhar (1981). The photosynthetic rates of all green leaf blades, leaf sheaths, stems, and inflorescences were sampled from April through July, 1981, and in mid-June, 1982. Three or four gas exchange measurements usually could be obtained each week for each foliage element. Photosynthesis and transpiration are expressed on a comparable area basis for the different plant parts: a "one-side" unit of reference for blades, one half the actual surface area for the sheaths and stems, and the projected (one-side) area for inflorescences. The projected area of a plant part that was enclosed by the gas exchange cuvette was determined nondestructively by measuring its image projected on blueprint paper. In addition to the gas exchange data, the developmental stage, length, and canopy position of the individual foliage elements were also recorded.

Plant water potential was estimated by the pressure chamber technique (Waring and Cleary 1967). Predawn xylem pressure potentials were estimated near sunrise on plants that had been covered by buckets to exclude the early sunlight. Recent research with these two species shows that predawn water potential measurements of covered plants are more than those of uncovered plants, but the difference between predawn water potential of covered plants and that of uncovered plants is the same for both species (D.A. Johnson and J.H. Richards, personal communications). Therefore, the term "covered" will be used to indicate predawn water potential measurements of covered plants. Midday values were measured on the same plants shortly after solar noon. Leaves were enclosed in small plastic bags in order to minimize water loss during measurement of xylem pressure potential (Turner and Long 1980). Because the water potential measurements constituted an additional clipping treatment, an individual plant was sampled only once during the growing season.

Specific mass and soluble protein concentration of foliage were obtained from 11 destructive tiller harvests that were spaced approximately 10 days apart from mid-April to mid-July, 1981, and one harvest that occurred in mid-June, 1982. On each harvest date, a total of 6 to 20 tillers, which were randomly selected from both the edge and the center of each tussock, were harvested from one to three plants of each species-treatment group. The developmental stage, length, and canopy position of each green foliage element were recorded, and then the tillers were separated into the individual foliage elements. The projected area of individual foliage elements was measured with a LiCor (Lincoln, NB) leaf area meter. Foliage was either oven-dried (70–80 C) or freeze-dried, and the dry mass of each foliage element was divided by the surface area to calculate specific mass. Soluble proteins of individual foliage elements were extracted and digested to amino acids (Dickson 1979), and the soluble protein concentration was determined with ninhydrin (see Nowak and Caldwell 1984). As with the water potential determinations, no other measurements were taken from plants after they had been destructively harvested.

In mid-April, 1981, 5 tillers on each of 8 plants that had been paired for the clipping treatments were marked

[1] Two taxonomic revisions of *A. spicatum* have recently been proposed: *Elytrigia spicata* (Pursh) D.R. Dewey (Dewey 1983) and *Pseudoroegneria spicata* (Pursh) Löve (Löve 1980). Although the genomic evidence indicates that this species is not an *Agropyron*, not enough data is available to clearly finalize its phylogeny. Therefore, we will use *A. spicatum* in this paper

with colored wire tags. There were 2 pairs of plants from each species. Three days before the first clipping treatment, the developmental stage, length, and canopy position of each individual leaf were recorded. These measurements, which were repeated at approximately seven-day intervals, provided known cohorts of leaves to cross-reference similar leaves from the photosynthetic and destructive harvest samples.

A three-way analysis of variance (ANOVA) that had species, treatment, and day as the main effects and incorporated all possible two- and three-way interactions was used for most of the statistical analyses. A mixed model analysis was used, where the species and treatment main effects were fixed and the day main effect was random. A separate ANOVA was conducted for each cohort of foliage elements to avoid confounding the results of one foliage element by the results of another, different-aged foliage element. However, if the results from one cohort were identical to another, then the data from these cohorts were combined. For all statistical tests, $P < 0.05$ was considered significant. Data are reported as mean ± 1 standard error.

Results

Phenology

The physiognomy of reproductive and vegetative (nonreproductive) tillers on control (undefoliated) plants during 1981 are shown in Fig. 1. The 5 dates correspond to when the partially defoliated plants were initially clipped (April 16), when the partially defoliated plants were reclipped a second (April 30) and third (May 14) time, and when the growth of foliage on reproductive (June 22) and vegetative (July 20) tillers was curtailed. Length, developmental stage, and canopy position data from our marked and destructive harvest tillers and foliage angle data from Caldwell et al. (1983) were used to depict these tillers. The developmental stages (inset, Fig. 1) and canopy position of foliage elements on *A. desertorum* plants were nearly identical to those on *A. spicatum* plants. Sheath and stem lengths were also the same for the two species, but the length of leaf blades on *A. spicatum* plants was generally greater than the length of similar leaves on *A. desertorum* plants. The dimensions and phenology of foliage elements in Fig. 1 are averages from control plants of both species.

Although the tillers drawn in Fig. 1 are representative of control plants, some attributes of foliage on clipped plants can also be observed. The clipping, which was parallel to the ground surface, did not uniformly damage a cohort of leaves because the foliage angles varied (e.g., the F-3 leaves on April 16). Also, a particular leaf may have been reclipped during successive clipping treatments (e.g., F-2 leaves on April 16 and 30).

The initiation of new leaves was not affected by the clipping treatments, but the senescence of the 2 oldest, fully-expanded leaves that were present at the time of the first clipping treatment was delayed (inset, Fig. 1). Senescence of these two leaves on partially defoliated *A. desertorum* plants was delayed approximately one month later than the marked leaves on control plants. Senescence of marked F-4 leaves on partially defoliated *A. spicatum* plants was delayed approximately 2 weeks relative to similar leaves on control plants. However, senescence of F-3 leaves on clipped *A. spicatum* plants was only marginally delayed.

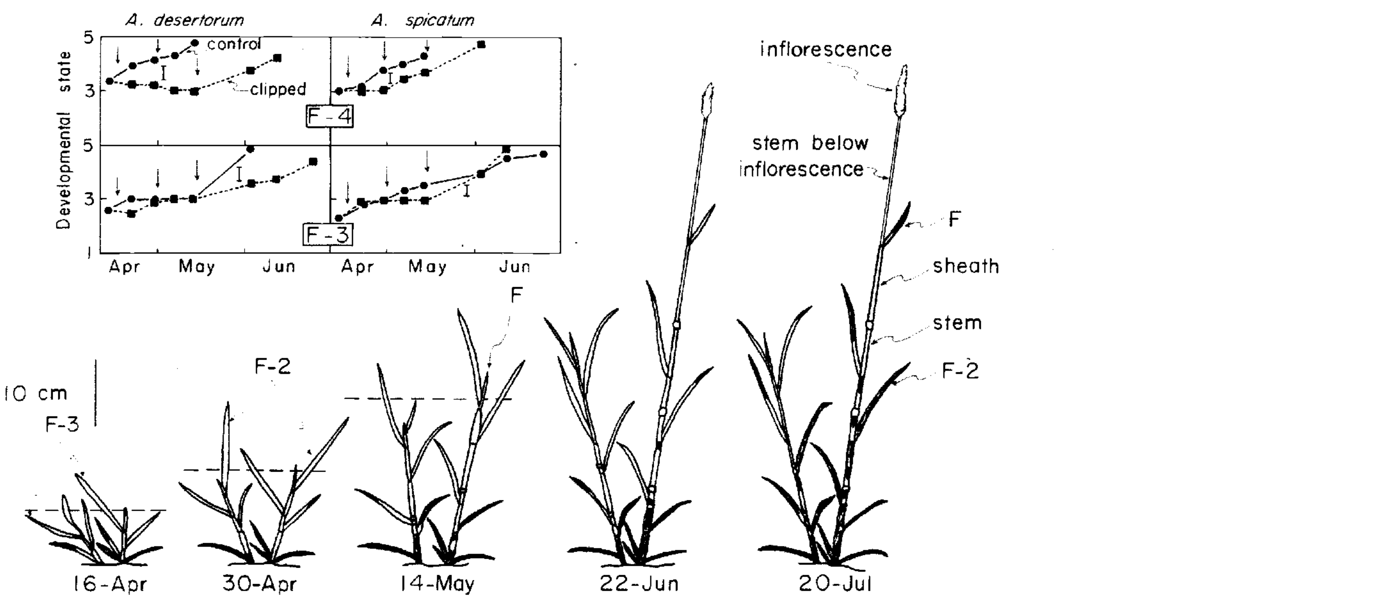

Fig. 1. Scale drawings of foliage elements on a reproductive and a vegetative tiller during 1981. Phenology, length, canopy position, and foliage inclination data from control plants of both bunchgrass species were used to depict these tillers. Individual leaves are indicated by: F, blade of flag leaf; F-1, blade of first leaf below the flag leaf; etc. The senesced portions of foliage elements are shaded. The horizontal, dashed lines indicate the height at which partially defoliated plants were clipped. *Inset:* Developmental stages of F-4 and F-3 leaves on marked tillers from control (circles, solid lines) and clipped (squares, dashed lines) plants of *A. desertorum* and *A. spicatum*. Developmental stages of individual leaves were rated as: 1, a newly expanded leaf that was still completely rolled; 2, an expanding leaf with a flattened distal area; 3, a fully-expanded leaf; 4, a leaf that had senesced 20 mm or more at the tip; 5, a completely senesced leaf. Each point is the mean of ten leaves, and the standard error is shown. Arrows correspond to when partially defoliated plants were clipped in 1981

Data for the F-2, F-1, and F leaves did not show any differences in leaf senescence between control and clipped plants within each species.

The photosynthetic behavior of leaves following clipping may differ between leaves that were fully expanded at the time of clipping and those that were initiated or continued to grow following the clipping. Thus, 2 categories of foliage will be considered: fully-expanded foliage at the time of clipping that remained on the plants, designated as "remaining foliage"; and the newer, expanding foliage at the time of clipping, or "regrowth foliage". Because the timing of new leaf initiation was not significantly different between control and clipped plants, Fig. 1 would indicate the developmental stages of cohorts of leaves on clipped plants at the time of each clipping treatment. For example, the cohort of F-2 leaves were expanding when the plants were initially clipped, and therefore F-2 leaves are designated as "regrowth foliage" after this initial clip. However, F-2 leaves were fully expanded before the second clipping treatment, and would be classed as remaining foliage after the last two clipping treatments.

Before late May, reproductive and vegetative tillers had the same appearance (Fig. 1). Therefore, all data collected before late May were arbitrarily considered as representing reproductive tillers because most of the marked tillers became reproductive. In mid- or late-May, reproductive tillers were in the boot stage, and both reproductive and vegetative culms were elongating. Therefore, the inflorescence and most of the sheath and stem foliage elements were regrowth foliage. In addition, vegetative tillers continued to produce new leaves during the remainder of the growing season. Vegetative tillers generally had 4 green, fully-expanded leaves per tiller: 2 younger leaves that were regrowth leaves after the third clipping treatment and two older leaves that were remaining foliage.

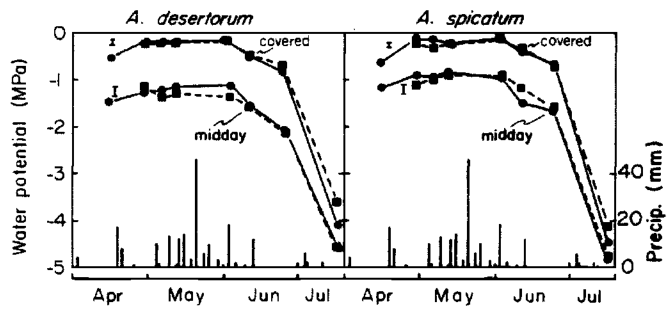

Fig. 2. Covered and midday xylem pressure potential during 1981 of foliage on control (circles, solid lines) and clipped (squares, dashed lines) plants of *A. desertorum* and *A. spicatum*. Each point is the mean of 4–8 pressure chamber determinations, and the standard error is shown. Precipitation at the field site during the same time period are indicated by the vertical lines at the bottom of the graphs

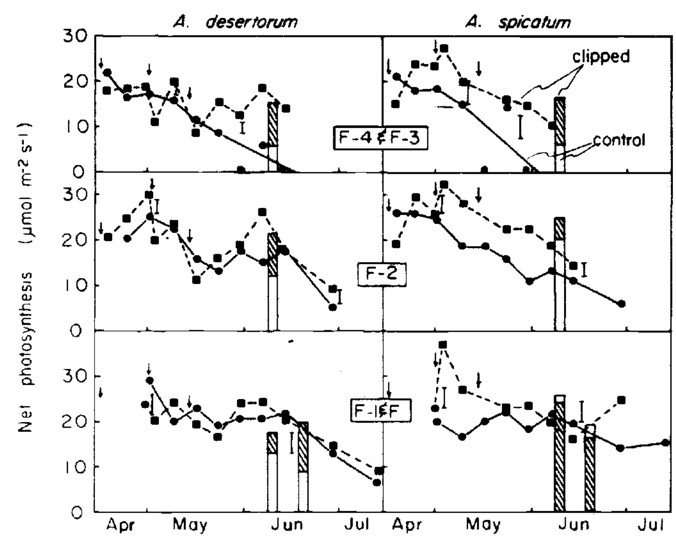

Fig. 3. Photosynthetic rates during 1981 of leaf blades on reproductive tillers from control (circles, solid lines) and clipped (squares, dashed lines) plants. The results from a different set of bunchgrass plants in 1982 are shown by bar graphs (control = open bars; clipped = shaded bars). Arrows mark when partially defoliated plants were clipped in 1981. Each point and bar graph is the mean of 2–22 measurements of net photosynthesis, and the standard error is shown. Analyses of variance for individual cohorts of leaves were conducted, but the data from cohorts that had similar results were combined

Water status and gas exchange of foliage: Effects of clipping

Clipping did not enhance the water status of clipped plants relative to control plants (Fig. 2), even though the aboveground biomass on clipped plants was only 40% of that on control plants. For both bunchgrass species, neither covered nor midday plant water potential of foliage on clipped plants was significantly different from the water potential of foliage on control plants during 1981. Although air temperatures were relatively cool in April, plant water potential was low, probably because of the low rainfall for that month (32 mm). In May, near-record precipitation was received (119 mm) and all plant water potentials were relatively high and constant. Both covered and midday water potential dropped by more than 3 MPa during the summer drought period in June and July.

The significant clipping treatment effects on the net photosynthetic rates of leaves on reproductive tillers (Fig. 3) showed that compensatory photosynthesis occurred in the field. The results for net photosynthetic rates of individual leaf blades measured in 1981 are presented as 3 groups of leaves that had similar photosynthetic rates within each group. The oldest remaining foliage on partially defoliated plants (F-4 and F-3 leaves) of both species had significantly higher photosynthetic rates than similar foliage on control plants by the second week after each clipping treatment. Net photosynthesis of the F-2 leaves on partially defoliated plants, which was remaining foliage after the second and third clipping treatments, was also significantly greater than similar foliage on control plants following the second and third clipping treatments for *A. spicatum*, but only following the third clipping treatment for *A. desertorum*. Some regrowth foliage, the F-2 leaves of *A. desertorum* after the first clipping treatment and the F-1 leaves of *A. spicatum* after the second clip, had photosynthetic rates that were significantly greater than similar foliage on control plants. However, the photosynthetic rates of other regrowth leaves and the youngest remaining leaves (the F-1 leaves) on reproductive tillers were not greater than that of corresponding leaves on control plants. A temporary period of reduced photosynthesis occurred after each clipping treatment for leaves on partially defoliated *A. desertorum* plants. In *A.*

spicatum, a similar pattern occurred following the first clipping treatment, but not following the second or third clipping treatments. The photosynthetic behavior in June, 1982, of leaves on reproductive tillers was very similar to that in June, 1981.

Compensatory photosynthesis for leaves on vegetative tillers was evident in *A. spicatum*, but not in *A. desertorum*. For *A. desertorum*, net photosynthesis of leaves on clipped plants (15.0 ± 0.7 μmol m^{-2} s^{-1}) was not significantly different from control plants (14.0 ± 1.0). However, net photosynthesis of leaves on vegetative tillers from partially defoliated *A. spicatum* plants (18.0 ± 1.2) was significantly greater than similar leaves on control plants (14.3 ± 1.0). These means are the combined results of data collected from remaining and regrowing leaves during the last half of June, 1981 and 1982. Photosynthetic rates were very similar among the different leaves and did not change during this time period.

The level of damage sustained by an individual leaf on clipped plants did not affect its photosynthetic rate. Each cohort of leaves on partially defoliated plants consisted of 2 leaf populations, one population of damaged leaves and another of leaves that were undamaged. This variability in leaf damage occurred because of the natural variation in leaf and stem inclination and the horizontal clipping treatment (Fig. 1). Photosynthetic rates of these 2 populations were not significantly different. For example, the mean net photosynthetic rate of F-4 and F-3 leaves on clipped *A. desertorum* plants after the third clipping treatment was 13.8 ± 1.1 μmol m^{-2} s^{-1} for undamaged leaves and 14.0 ± 1.3 for damaged leaves; and for clipped *A. spicatum* plants, the mean was 15.1 ± 0.4 for undamaged leaves and 16.1 ± 1.5 for damaged leaves.

Green leaf sheath, stem, and inflorescence foliage elements were also photosynthetically active, and some of these plant parts exhibited compensatory photosynthesis after partial defoliation (Fig. 4). For both species, regrowth leaf sheaths and stems on partially defoliated plants initially had greater photosynthetic rates than similar foliage elements on control plants. Although this difference did not persist in either species, net photosynthesis of sheaths and stems on partially defoliated *A. desertorum* plants was again significantly greater than control plants in early July. Net photosynthesis of the inflorescence and the stem that subtends the inflorescence on clipped *A. desertorum* plants was significantly greater than similar reproductive tissue on control plants. However, partial defoliation had no effect on the photosynthetic rates of reproductive foliage on *A. spicatum* plants. These effects of partial defoliation on photosynthetic rates of nonblade foliage were the same in 1981 and 1982.

Photosynthetic water use efficiency, or P/T ratio, was not significantly affected by the clipping treatment for all foliage elements of both species. For example, the P/T ratio of F-2 leaves on clipped *A. spicatum* plants averaged 2.4 ± 0.1 mmol CO_2 mol H_2O^{-1} following the second clipping treatment and 1.4 ± 0.1 following the third. The mean P/T ratio of similar foliage on control plants of this species was 2.2 ± 0.1 after the second clipping treatment and 1.4 ± 0.1 after the third.

Specific mass of most foliage elements also was not affected by the clipping treatments, but soluble protein concentration was increased in all foliage elements (Table 1). The specific mass of all leaf blades on partially defoliated

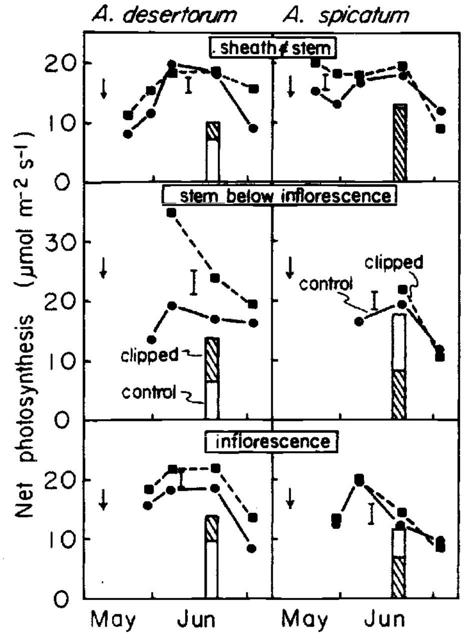

Fig. 4. Photosynthetic rates of leaf sheaths and stems, the stems that subtend the inflorescences, and the inflorescences on both bunchgrass species. Measurements from control plants are shown by circles and solid lines (1981) and open bar graphs (1982); from clipped plants, by squares and dashed lines (1981) and shaded bar graphs (1982). Each point and bar graph is the mean of 2–19 measurements, and the standard error is shown. The arrows mark when the partially defoliated plants were clipped the third time in 1981

Table 1. Mean and standard error of specific mass and of soluble protein concentration for groups of foliage. Measurements were collected from April through July, 1981, and in June, 1982. The groups of foliage represent individual cohorts of foliage elements that had statistically similar results. The means represent 60–162 measurements for specific mass and 28–151 determinations for soluble protein concentration

	A. desertorum		*A. spicatum*	
	Control	Clipped	Control	Clipped
Specific mass (g m^{-2})				
F-4 and F-3 leaf blades	81 ± 4	77 ± 2	83 ± 5	75 ± 5
F-2, F-1 and F leaf blades	88 ± 2	86 ± 3	99 ± 3	102 ± 5
Vegetative leaf blades	92 ± 3	91 ± 3	108 ± 4	107 ± 3
Sheaths and stems	287 ± 8	212 ± 7	284 ± 8	207 ± 6
Soluble protein concentration (% dry mass)				
F-4 and F-3 leaf blades	5.2 ± 0.2	7.0 ± 0.2	6.4 ± 0.4	6.9 ± 0.2
F-2, F-1 and F leaf blades	6.4 ± 0.3	8.6 ± 0.2	5.7 ± 0.2	7.6 ± 0.3
Vegetative leaf blades	4.5 ± 0.3	5.7 ± 0.3	3.8 ± 0.2	4.7 ± 0.2
Sheaths and stems	3.2 ± 0.2	4.9 ± 0.2	2.8 ± 0.2	4.1 ± 0.2

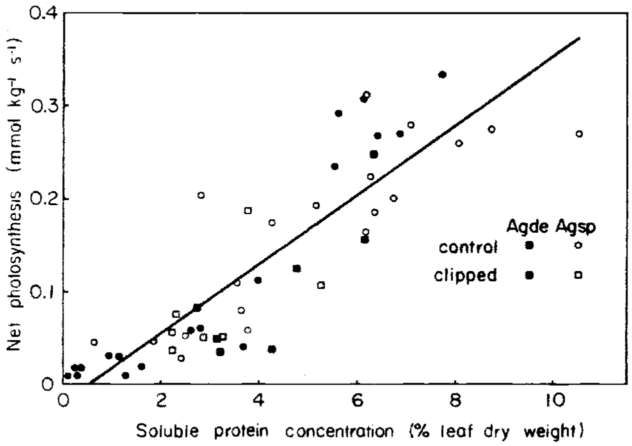

Fig. 5. Photosynthetic rate per unit dry mass for leaf blade and nonblade plant parts plotted against soluble protein concentration. Each point is a measurement from an individual foliage element. Data for *A. desertorum* plants are indicated by closed symbols; for *A. spicatum*, by open symbols. Measurements from control plants are represented by circles; from clipped plants, by squares. The linear correlation coefficient (r) for all data points is 0.87

plants was not significantly different from similar blades on control plants. However, specific mass of regrowth sheaths and stems on partially defoliated plants was significantly less than those on control plants. Soluble protein concentrations of both remaining and regrowth foliage elements on clipped plants were significantly greater than similar elements on control plants.

Photosynthetic rates expressed on a unit dry mass basis were linearly correlated with soluble protein concentrations (Fig. 5). The data in Fig. 5 is for foliage from control and partially defoliated plants of both species, and includes measurements of blade, sheath, and stem foliage. The linear correlation of data from control plants ($r=0.89$) was not significantly different from the linear correlation of data from clipped plants ($r=0.71$).

Water status and gas exchange of foliage: Species differences

The water status and gas exchange rates of foliage on control and clipped *A. desertorum* plants were not significantly different from similar foliage on *A. spicatum* plants. Covered and midday water potential of *A. desertorum* were the same as those of *A. spicatum* (Fig. 2). A few foliage elements on partially defoliated *A. desertorum* plants had higher photosynthetic rates than similar foliage on *A. spicatum* plants (e.g., reproductive foliage, Fig. 4), but photosynthetic rates of some other foliage elements on clipped *A. spicatum* plants were greater (e.g., leaves on vegetative tillers). However, the photosynthetic rates of most foliage elements on clipped plants were not significantly different between species. Finally, water use efficiency of *A. desertorum* foliage was not significantly different from similar foliage on *A. spicatum* plants. For example, the mean P/T ratio of leaves on vegetative tillers from partially defoliated *A. spicatum* plants was 1.4 ± 0.1 mmol CO_2 mol H_2O^{-1}; for similar foliage on clipped *A. desertorum* plants, 1.6 ± 0.1.

The specific mass of many foliage elements was not significantly different between the two species (Table 1). The specific masses of F-2, F-1, and F leaves on reproductive tillers and of leaves on vegetative tillers in *A. spicatum* plants were greater than similar leaves in *A. desertorum* plants, but no significant differences were found between species for the specific masses of F-4 and F-3 leaves and all sheaths and stems. Also, the soluble protein concentrations of all foliage elements on both control and clipped *A. desertorum* plants were not significantly different from similar foliage on the respective *A. spicatum* plants. Finally, the linear correlation between photosynthetic rates per unit dry mass and soluble protein concentrations for *A. desertorum* ($r=0.89$) was not significantly different from the linear correlation of data from *A. spicatum* ($r=0.83$) (Fig. 5).

Discussion

Compensatory photosynthesis

The average increase in photosynthetic rates following partial defoliation in our field study was generally less than that reported in previous laboratory studies. For comparison, mean daily differences in photosynthetic rates between foliage on clipped plants and similar-aged foliage on control plants were calculated for the duration of each study. In our study, the photosynthetic rates of foliage on partially defoliated plants averaged 27% higher than similar foliage of the same age on control plants for both *Agropyron* species. This magnitude of compensatory photosynthesis is similar to that reported for *Agropyron smithii* grown in growth chambers (Painter and Detling 1981, Detling and Painter 1983), but less than one half the magnitude found for *Lolium multiflorum* (Gifford and Marshall 1973) and *Medicago sativa* (Hodgkinson et al. 1972) grown in glasshouses. In the only other known field study of compensatory photosynthesis in individual foliage elements, the average increase in net photosynthetic rates of two deciduous tree species following defoliation was generally greater than that in our study (Heichel and Turner 1983).

To place compensatory photosynthesis in a proper ecological perspective, it is necessary to assess the degree of change in photosynthesis in conjunction with the amount of photosynthetic biomass. For example, the greatest increase in compensatory photosynthesis was in the oldest foliage elements remaining after clipping, the F-4 and F-3 leaves (Fig. 3). Even though the photosynthetic contribution of these leaves relative to similar leaves on control plants would be further enhanced by a delay in leaf senescence (Fig. 1), they constituted less than 10% of the total aboveground biomass on clipped plants after June 1. Secondly, the average magnitude of the increase in photosynthetic rates following clipping was about one half the magnitude of the 60% decrease in aboveground biomass, relative to control plants.

Compensatory photosynthesis was not accompanied by an increase in photosynthetic water use efficiency or photosynthetic rates per unit soluble protein. Photosynthetic rates per unit soluble protein for foliage on clipped plants would be similar to those on control plants because the relative increases in soluble protein concentrations (Table 1) and in photosynthetic rates (Figs. 3 and 4) were similar. Furthermore, photosynthetic water use efficiency and photosynthetic rates per unit protein were very similar between species.

In our earlier study of these *Agropyron* species (Caldwell et al. 1981), we defoliated plants in a manner that resulted in a younger average age of foliage on clipped plants. The regrowth leaves on these clipped plants had consistently higher photosynthetic rates than leaves on control plants and the relative increase of photosynthetic rates for *A. desertorum* foliage following clipping was greater than *A. spicatum* foliage (Caldwell et al. 1981). These earlier results represent a valid comparison of foliage that was present on plants at the same point in time. When foliage elements of the same age are compared, as we have done in this paper, the increase in photosynthetic rates following clipping was not as pronounced as in our earlier study, and there was no significant difference in the degree of increased photosynthesis between species.

An increase in photosynthetic rates of foliage following partial defoliation would be beneficial to a plant, but it is difficult to establish a clear relationship between this phenomenon and the ability to regrow following clipping or to tolerate grazing. Current photosynthetic carbon assimilation is the major source of carbon for foliage regrowth in grass plants (Ryle and Powell 1975, Caldwell et al. 1981, Richards and Caldwell submitted). In our study, we chose 2 bunchgrass species that are known to have different levels of grazing tolerance (Hyder 1974), but regrowth and compensatory photosynthesis of the 2 species were almost identical following three moderate clipping treatments. In an earlier study, we did find relatively greater regrowth in *A. desertorum* plants following 2 severe clipping treatments, but the greater regrowth was attributed primarily to the ability to reallocate resources and activate meristems, and only secondarily to photosynthetic characteristics (Caldwell et al. 1981). Also, a difference in the ability to regrow following partial defoliation between an *Agropyron smithii* genotype collected from an area open to grazing and one from a grazing exclosure was not accompanied by a difference in compensatory photosynthesis (Detling and Painter 1983).

Factors which may influence compensatory photosynthesis

The occurrence of compensatory photosynthesis in the field cannot be attributed to a more favorable water status of clipped plants. McNaughton (1983) has suggested that a large decrease in transpirational surface area by grazing may conserve soil moisture, which may improve the water status of clipped plants. In our study, the clipping treatments resulted in a 60% reduction of aboveground biomass on these 2 bunchgrass species, but no significant differences existed between species or between treatments for covered and midday plant water potential in 1980 (Nowak 1984) and 1981 (Fig. 2). The root systems of *Artemisia tridentata* and the 2 bunchgrass species overlap in the field (Caldwell and Richards 1984). Soil water that was not used by clipped bunchgrass plants was probably utilized by neighboring, unclipped *Artemisia* plants. The *Artemisia* plants were not clipped in this study because they are usually not grazed in Great Basin rangelands. However, in experiments or ecosystems where all plants are uniformly grazed, a decrease in soil water depletion after grazing may improve the water status of grazed plants.

Within both species, the oldest remaining leaves had the largest difference in photosynthetic rates between control and clipped plants (Fig. 3), which is similar to Hodgkinson's (1974) results. Also, the large differences in photosynthetic rates of F-4 and F-3 leaves between clipped and control plants were related to a delay in senescence of these leaves (inset, Fig. 1). This same phenomenon also occurred in clipped alfalfa (Hodgkinson et al. 1972) and Italian ryegrass (Gifford and Marshall 1973) plants. Field (1981) and Mooney et al. (1981) have suggested that leaf aging may be accelerated for shaded leaves. In our experiments, clipping removed overtopping foliage and allowed more light to penetrate into the bunchgrass canopy. Thus, the senescence of older remaining foliage in the lower portion of the canopy, which normally would become densely shaded (Caldwell et al. 1983), may have been delayed by the increased light intensity resulting from partial defoliation.

Increased soluble protein levels may have stimulated compensatory photosynthesis. Soluble protein concentrations of all foliage elements on partially defoliated bunchgrass plants were significantly higher than similar foliage of the same age on control plants (Table 1). Many of those foliage elements also had greater photosynthetic rates (Figs. 3 and 4). There was also a high correlation between photosynthetic rates and protein concentration for all plant parts of these two species (Fig. 5). Ribulose bisphosphate carboxylase constitutes a sizeable proportion of the leaf soluble protein pool (Jensen 1977), and activity of this enzyme is often directly related to photosynthesis (Björkman 1981, Friedrich and Huffaker 1980, Joseph et al. 1981).

Unlike the situation with older remaining foliage elements, the light environment of regrowth foliage was not an important factor that influenced the occurrence of compensatory photosynthesis in our study. Woledge (1977) found that compensatory photosynthesis in regrowth foliage after partial defoliation of perennial ryegrass plants only occurred if there was a concomitant increase in light intensity. The light environment for regrowth foliage in our field study was uniformly high because regrowth foliage was at the top of the canopy. Therefore, the lack of compensatory photosynthesis in some regrowth foliage elements in our study was not caused by relatively low light intensities.

Two other factors, specific mass and damage to individual leaves, also did not influence the occurrence of compensatory photosynthesis in our experiments. Regrowth sheaths and stems were the only plant parts whose specific mass was affected by the clipping treatments (Table 1). However, the lower specific mass of sheaths and stems is probably related to their structural and vascular functions rather than to their photosynthetic capability. Dyer et al. (1982) suggested that net photosynthetic rates of undamaged leaves are frequently enhanced following clipping, but photosynthetic rates of damaged leaves are almost always reduced. In our study, photosynthetic rates of undamaged leaves on clipped plants were not significantly different from that of damaged leaves for both bunchgrass species.

Conclusions

Compensatory photosynthesis did occur in the field for many foliage elements of *A. desertorum* and *A. spicatum*. However, the average increase in photosynthetic rates of foliage in this study were generally lower than the increases in photosynthesis noted in laboratory studies. The magnitude of compensatory photosynthesis was largest in the 2 oldest, fully-expanded leaves that were present when the plants were initially clipped, but the contribution of these leaves to total carbon assimilation would be small after

June 1 because they represented only a small proportion of the total aboveground biomass. Even though current photosynthetic carbon assimilation is essential for foliage regrowth after partial defoliation, the magnitude and extent of compensatory photosynthesis does not appear to be related to the ability to tolerate herbivory.

Acknowledgements. The National Science Foundation (DEB 7907323 and DEB 8207171) and the Utah Agricultural Experiment Station provided support for this research. We gratefully acknowledge C. Nowak, K. Dustin, S. Vaniman, and K. Ziemke for their technical assistance, and C. Warner for drafting the figures. We also thank D. Johnson for the generous use of his gas exchange system, and he and J. Richards for profitable discussions during the initial stages of this research and for their reviews of this manuscript.

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Received October 4, 1983

Oecologia (Berlin) (1984) 64:21–25

Oecologia

Root growth response to defoliation in two *Agropyron* bunchgrasses: field observations with an improved root periscope

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Summary. Root growth responses to defoliation were observed in the field with an improved root periscope technique, which is described. The grazing tolerant, Eurasian bunchgrass, *Agropyron desertorum*, was compared with the very similar but grazing sensitive, North American bunchgrass, *A. spicatum*. Root length growth of clipped *A. desertorum* was about 50% of that of intact plants, while root elongation of clipped *A. spicatum* continued relatively unabated during ninety days of regrowth following severe defoliation. The reduced root growth in *A. desertorum* was correlated with the allocation of relatively more resources to aboveground regrowth, thus aiding reestablishment of the root:shoot balance. This balance was apparent in similar root mortality patterns of clipped and control *A. desertorum* plants in the season following defoliation. In clipped *A. spicatum*, however, root mortality increased in the winter following the season in which the clipping was done and continued into the subsequent growing season. Reduction of root growth following defoliation appears to be an effective mechanism to aid reestablishment of the photosynthetic canopy and the root:shoot balance. As such it contributes to both herbivory tolerance and maintenance of competitive ability.

Introduction

Root growth is an important process for water and nutrient uptake (Caldwell 1976, 1979), especially at low soil water potentials (Cowan 1965; Gardner 1960) and in the case of immobile soil nutrients, such as phosphorus (Bhat and Nye 1973, 1974). Defoliation usually results in immediate reductions in root growth (Crider 1955; Jameson 1963; Davidson and Milthorpe 1966), which might reduce the ability of a defoliated plant to regrow since both nutrient and water uptake would be reduced. Differences between species in amount or duration of root growth inhibition might thus be an important mechanism by which defoliation affects the competitive balance in natural communities and pastures. Alternatively, root growth reductions might be a mechanism to reduce belowground carbon demand in defoliated plants and would thus allow greater allocation of carbon to the shoot resulting in more rapid reestablishment of the canopy and return to root:shoot equilibrium. In this paper results of experiments designed to test the hypothesis that following defoliation root growth in the grazing-sensitive *Agropyron spicatum* (Pursh) Scribn. and Smith[1] is reduced to the same extent as in the grazing-tolerant *A. desertorum* (Fisch. ex Link) Schult. are reported and discussed. These two species were chosen for study because of their morphological and phenological similarity, their importance on nutrient poor, semiarid rangelands, and their large difference in tolerance of defoliation (Caldwell et al. 1981).

Study of root growth under natural conditions is extremely difficult. Most techniques are either destructive, preventing study of the same root or root system through time, or introduce largely artificial conditions or constraints on roots (Böhm 1979). Some of the observations reported in this paper were made possible by improvements in a root observation technique proposed by Bates (1937), Waddington (1971) and Böhm (1974). These improvements allow rapid, quantitative observation of root length growth of relatively undisturbed plants growing under field conditions. In this study additional plants were excavated and root system biomass determined to verify the observations made with the improved root periscope.

Materials and methods

Ten plants each of crested wheatgrass (*A. desertorum*) and bluebunch wheatgrass (*A. spicatum*) were chosen randomly from stands of these species which had been established two years previously at an experimental site 4 km northeast of Logan, Utah (41° 45′ N, 111° 48′ W, 1460 m a.s.l.). Sagebrush (*Artemisia tridentata* ssp. *vaseyana* Rydb.) Beetle had also been planted in the experimental plots to provide a uniform competitive background. Further description of the site, soils, climate and planted stands is given in Caldwell et al. (1981). Plants chosen for root growth study were randomly assigned to control (5 each species) or treatment (5 each species). The treatment was a severe defoliation (85% foliage removal) repeated twice, on April 30 and on May 13, during the 1980 growing season. This simulated the pattern and timing of defoliation commonly experienced by these bunchgrasses (Norton and Johnson 1983).

[1] Recent taxonomic revisions make *Pseudoroegneria spicata* (Pursh) Löve (Löve 1980) and *Elytrigia spicata* (Pursh) D.R. Dewey (Dewey 1983) synonymous with *A. spicatum*

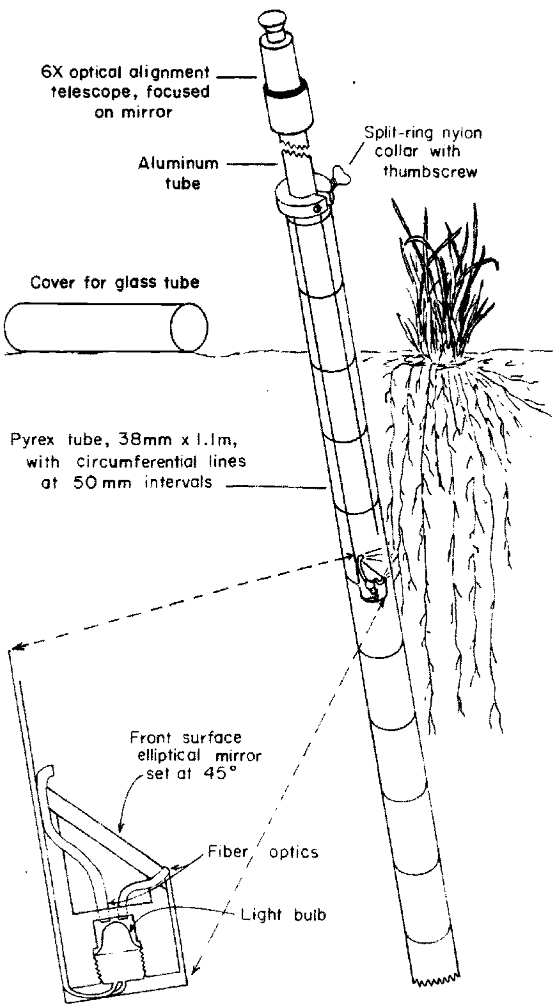

Fig. 1. Schematic illustration of the root periscope developed for observing roots through the wall of a glass root observation tube installed in the soil beneath a bunchgrass plant. Roots intersecting lines scribed at 5 cm depth increments on the tube were counted at intervals to determine net root growth. The glass tubes were kept covered to exclude light and prevent overheating when observations were not being made. Each observation, to 1 m depth, required approximately 20 min

In April 1980 a 4 cm diameter hole was augered into the soil to a depth of 1 m directly beneath each bunchgrass. The soil extracted was sieved to remove stones and used as backfill when the root observation tubes were installed in the holes. Glass tubes (38 mm O.D. × 1.1 m, Pyrex) were scribed with circumferential lines at 5 cm intervals and a rubber stopper was placed in one end before installation. During installation the backfill soil was mixed with water to form a thick slurry and poured into the holes to completely fill the spaces (~7 mm) around the tube. Aluminum covers, painted white to minimize heating, were placed over the portion of the tubes (~15 cm) which extended above the soil surface to exclude light, precipitation, and small animals. The relationship of an installed root observation tube and a bunchgrass plant is shown in Fig. 1.

Observations of root growth were made with a periscope which is also shown schematically in Fig. 1. The periscope consisted of a 1.6-m aluminum tube (27 mm O.D.) machined to accept an illumination source and mirror at one end and an optical alignment telescope (6 ×, Edmund Scientific) on the other. The telescope was focused on a front-surface, eliptical mirror (Edmund Scientific) which was mounted at 45° at the base of the periscope (see Fig. 1). A 10W 6V quartz halogen lamp (Gilway Technical Lamps, Inc.; No. L8017) provided light which was directed at the plane viewed by the mirror by two glass fiber optics (American Optical). Oblique illumination by one of the fiber optics provided better resolution of small translucent roots. A small voltage regulated power supply (not shown in Fig. 1) was mounted on the upper end of the aluminum tube and power was supplied to the bulb by wires set in narrow grooves machined along the outside of the aluminum tube. A rechargeable 12V Ni-Cd battery was used as a power source. The periscope was fitted with an adjustable nylon collar (Fig. 1), which, when resting on the top of the glass tube, allowed the periscope to be held firmly at any depth.

Observations were made by counting the number of roots intersecting each circumferential line of each tube. The medium to dark brown sagebrush roots were distinguishable from the light tan to white bunchgrass roots and were not counted. Most bunchgrass roots grow verticaly; thus they crossed the circumferential lines at angles near the perpendicular. In cases where roots are growing horizontally, vertical lines should be scribed on the glass tubes and roots intersecting them counted. Counts were made at intervals starting in early June 1980, 38 days following the first defoliation, until the end of the next growing season (1981). The number of intersections was converted to root length visible per unit depth using an equation adapted from Newman (1966) and Tennant (1975).

In this paper, root length visible per unit depth was averaged over the 1 m depth profile and is presented as relative root length. Gregory (1979), Köpke (1981) and Bragg et al. (1983) have compared the tube method, similar to that described here, with other methods for measuring root growth. They found that this technique is good for comparative purposes, and for long-term root growth studies, although it underestimates root density at shallow depths. This may be due to more horizontal root growth near the surface, or to localized modification of the soil temperature, water or nutrient regime.

The root periscope described here has a number of advantages over previously described tube observation devices. Small diameter glass tubes (38 mm in contrast to 70–100 mm tubes used by Köpke (1981) and Gregory (1979), respectively) can be used, thus causing minimal disturbance during installation, which is of particular importance with perennial species. Small diameter glass tubes also avoid problems of accumulation of roots at the soil tube interface (see Böhm et al. 1977), and avoid problems of plastic effects on root growth (Taylor and Böhm 1976; Voorhees 1976). The telescope and improved illumination source allow consistent viewing (resolution of 0.1 mm) at all depths to >1 m (see Böhm 1974), and the periscope system is less expensive (~$500) than several described previously (Waddington 1971; Sanders and Brown 1978; Gregory 1979; Upchurch and Ritchie 1983).

Results and discussion

Severe defoliation caused a reduction of about 50% in root length visible and significantly reduced root length growth

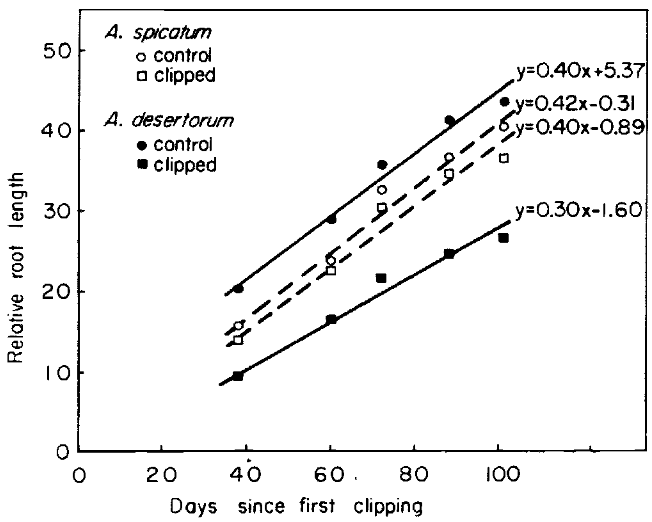

Fig. 2. Relative root length growth of control and clipped *A. desertorum* and *A. spicatum* for the first 100 days following severe defoliation. Clipped plants were defoliated on day 0 (April 30) and on day 13. Each point represents the mean of five plants. Lines are weighted least squares fits and all are significant at $p<0.029$, $0.44<r<0.84$; the fitted line for clipped *A. desertorum* has significantly lower slope ($p<0.005$) than the other three lines, which are not significantly different from each other

rate in *A. desertorum*, whereas severely defoliated *A. spicatum* plants had root length growth parallel that of controls (Fig. 2). The grazing-tolerant, more competitive species, *A. desertorum*, showed greater root growth reduction than the grazing-sensitive, less competitive species, *A. spicatum*. Reduced root growth in *A. desertorum* is probably related to that species' ability to preferentially allocate carbon resources to aboveground growth following defoliation, while the continued root growth of *A. spicatum* utilizes resources that might otherwise allow more rapid shoot replacement following defoliation. Thus aboveground recovery, i.e. foliage replacement, and reestablishment of the root:shoot balance (Drew and Ledig 1980; Richards 1978; Richards et al. 1979) is prevented.

Root length visible was slightly greater in *A. desertorum* control plants than in *A. spicatum* control plants at all sampling dates (Fig. 2). These relative data agree with the greater rooting density of *A. desertorum* determined by direct measurement of roots washed from known volumes of soil (Caldwell and Richards 1984). In both species root growth was rapid through June and July (days 28–88), a time when aboveground growth rate was declining (Caldwell et al. 1981), and continued in both species into late August when shoot xylem water potentials were below −2.5 MPa (Caldwell et al. 1981). Rapid root growth corresponded with the time of rapid water extraction (Richards et al., unpublished). Root growth observations were not made before June since adequate time had not elapsed for the backfilled soil to become permeated with roots (see Gregory 1979). Previous observations of root biomass changes showed that root growth also occurs in both species in late April and in May, when aboveground growth is most rapid (Caldwell et al. 1981).

Sequential destructive harvests of plants to determine root and shoot biomass also detected different postclipping allocation patterns in the two bunchgrass species (Table 1).

Table 1. Proportion of biomass belowground for control and defoliated (clipped) bunchgrasses harvested immediately following defoliation (13 May 1980, 18 May 1981) and at the end of the growing season (23 July 1980, 22 July 1981). Each value is the mean of three destructively harvested plants and within years those followed by different letters are significantly different at $p<0.05$. Analysis of variance utilized arcsine-square root transformed data and between cell differences were determined with a LSD test. Values for 1980 were calculated from data given by Caldwell et al. (1981).

Species	Treatment	Date	
		1980 13 May	23 July
Agropyron desertorum	control	0.70 cd	0.63 d
	severely clipped	0.92 a	0.81 b
Agropyron spicatum	control	0.77 bc	0.70 cd
	severely clipped	0.95 a	0.95 a
		1981 18 May	22 July
Agropyron desertorum	control	0.88 ab	0.73 c
	moderately clipped	0.94 a	0.86 b
Agropyron spicatum	control	0.87 ab	0.70 c
	moderately clipped	0.94 a	0.91 ab

After two and one-half months of regrowth the proportion of biomass belowground of clipped *A. spicatum* was not significantly reduced from the proportion immediately following defoliation. Clipped *A. desertorum* plants, however, allocated relatively more carbon aboveground causing the proportion of biomass belowground to be significantly reduced during regrowth. This occurred in 1980, following severe defoliation, and also in 1981 for a different set of plants subjected to moderate defoliation (50% foliage removal on 16 and 30 April and 15 May, 1981) and harvested in a manner similar to that described by Caldwell et al. (1981) (Table 1). Control plants of both species were similar in relative aboveground-belowground allocation in both years. These destructive harvest data corroborate the root periscope observations. *Agropyron spicatum* appears to inflexibly allocate carbon belowground, maintaining root growth, even when defoliation has caused a major imbalance in root:shoot biomass proportions. This inflexible allocation reduces carbon available for canopy reestablishment and contrasts sharply with the allocation pattern exhibited by defoliated *A. desertorum*.

Carbohydrates necessary for continued root growth in both species were primarily supplied by photosynthesis during regrowth rather than by carbohydrates synthesized before defoliation. Following severe defoliation total soluble carbohydrate pools in roots, crowns and regrowing shoots of both bunchgrass species were less than or equivalent to those produced during two to four days of photosynthesis during regrowth (Caldwell et al. 1981). Therefore, during the two and one-half month regrowth period most of the carbon utilized was derived from photosynthesis. Greater

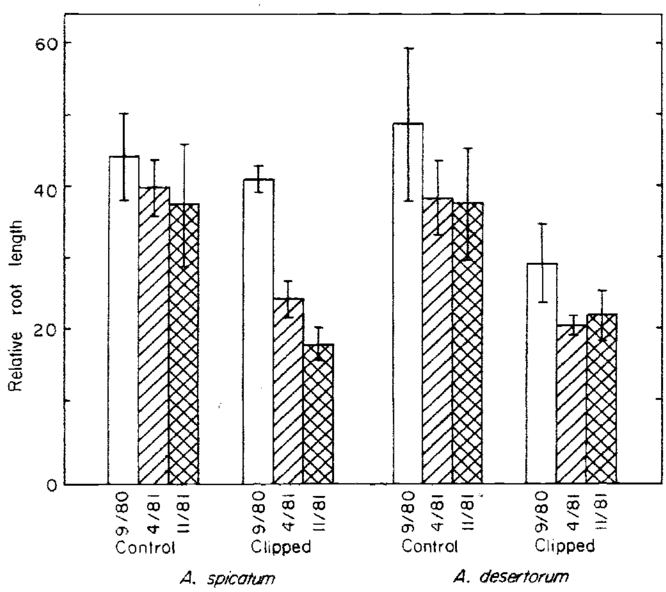

Fig. 3. Relative root length changes from the peak values reached during the 1980 season (September), in which two severe defoliations occurred, to values at the beginning of the following season (April 1981). Minimum values in November following the 1981 growing season are also shown. Mean ± 1 SE, $n=5$

relative allocation of current photosynthate to the shoot in *A. desertorum* resulted in more rapid increases in foliage area and whole-plant net assimilation rate in that species than in *A. spicatum* (Caldwell et al. 1981; Richards and Caldwell, unpublished).

If continued root growth in clipped *A. spicatum* prevents accumulation of adequate carbohydrates by the end of the growing season, the roots would be expected to suffer greater mortality in the following seasons. There was a greater decline in visible root length during the winter of 1980–1981 in clipped *A. spicatum* when compared with either control plants of the same species or with clipped plants of *A. desertorum* (Fig. 3). In the growing season following the clipping treatments root length continued to decline in *A. spicatum*, but began to recover in *A. desertorum*.

Immediately following defoliation root growth stops or is radically reduced (Crider 1955; Davidson and Milthorpe 1966). While root growth resumes after several days or weeks it may do so at a reduced rate, as in *A. desertorum*. Both immediate and continued reduction in root growth and productivity are usually considered to be detrimental to the survival and competitive ability of defoliated plants (Crider 1955; Jameson 1963). Reduced root growth during regrowth of *A. desertorum*, however, appears to be a mechanism contributing to more rapid reestablishment of the photosynthetic canopy and the balance between root and shoot. The similar but less grazing-tolerant and less competitive species, *A. spicatum*, suffered more long-term root mortality than *A. desertorum*, perhaps as a consequence of maintaining high root growth rates during regrowth. Root growth reductions thus may be an important component of the ability of *A. desertorum* to tolerate herbivory and maintain its competitive position in the rangeland plant community.

Acknowledgements. This research was supported by the National Science Foundation (DEB 7907323 and DEB 8207171) and the Utah Agricultural Experiment Station. M.M. Caldwell provided helpful discussion and review of the manuscript. G.W. Harris aided in design and construction of the periscope, and L. Bodily provided much appreciated field assistance.

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Received January 5, 1984

Journal of Applied Ecology (1985) **22**, 907–920

SOLUBLE CARBOHYDRATES, CONCURRENT PHOTOSYNTHESIS AND EFFICIENCY IN REGROWTH FOLLOWING DEFOLIATION: A FIELD STUDY WITH *AGROPYRON* SPECIES

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SUMMARY

(1) The contribution of stored carbon to plant regrowth following defoliation is commonly thought to be large. This study quantitatively compared the amount of carbon supplied to regrowth from storage with photosynthesis of regrowth in the field.

(2) Two bunchgrass species were selected for comparison because of markedly different abilities to regrow following defoliation despite very similar photosynthetic, morphologic and phenologic characteristics.

(3) The more grazing-tolerant *Agropyron desertorum* (Fisch. ex Link) Schult. consistently produced more regrowth in the absence of photosynthesis than *A. spicatum* (Pursch) Scribn. & Smith, but a severe preclipping treatment (which has been shown to reduce carbohydrate reserves by more than 40%) did not significantly reduce etiolated regrowth in either species.

(4) Differences in regrowth between and within species were not correlated with crown non-structural carbohydrate concentrations, total pools, or amounts utilized during regrowth.

(5) The daily contribution of carbon from reserves exceeded measured daily photosynthetically-fixed carbon for only 2·5 days following defoliation when regrowth rate was maximal. However, when apical meristems were removed and regrowth was much slower, photosynthesis during regrowth immediately outweighed stored reserves as a source of carbon. The latter is the usual case when these grasses are subjected to managed grazing.

(6) In both species, apical meristem removal was followed by sharply reduced regrowth efficiency due to a delay in and reduced rate of regrowth production. There was, however, no increase in respiration rate.

(7) Meristematic limitations appear to be the dominant control on the amount of etiolated regrowth produced. These limitations also appear to be of prime importance in determining regrowth in the light and for grazing tolerance of plants.

INTRODUCTION

Soluble carbohydrate reserves are often considered the primary source of carbon for regrowth following defoliation (Cook 1966; White 1973; Trlica 1977; Trlica & Singh 1979; Deregibus, Trlica & Jameson 1982). However, in several species there is little, if any, mobilization of reserves from roots to shoots following defoliation (Marshall & Sagar 1965; Davidson & Milthorpe 1966) and correlations between soluble carbohydrates and regrowth have frequently been unsuccessful (May 1960; Ward & Blaser 1961; Jameson 1963; Stoddart, Smith & Box 1975; Caldwell *et al.* 1981).

Possible causes for the lack of correlation between carbohydrate pools or concentrations and regrowth are: (i) the contribution of concurrent photosynthesis to regrowth is large; (ii) morphological or meristematic features limit regrowth; or (iii) carbohydrate pools are inadequately assessed by common procedures. The importance of each of these factors was examined in field experiments utilizing two species that were selected because they differ greatly in tolerance of herbivory. These species, *Agropyron desertorum* (Fisch. ex Link) Schult. and *Agropyron spicatum* (Pursh) Scribn. & Smith,* have similar photosynthetic characteristics, the same growth form, and nearly identical phenology (Caldwell *et al.* 1981, 1983).

In addition to the confounding effects of concurrent photosynthesis and meristematic limitations on the relationship between regrowth and stored carbohydrates, there may be inherent differences in the efficiency with which the plant utilizes carbon for shoot regrowth. Following severe defoliation, *A. desertorum* allocates relatively more carbon to the shoot system and curtails root growth more than does *A. spicatum* (Caldwell *et al.* 1981; Richards 1984). *Agropyron desertorum* thus should have higher efficiency of carbon utilization for regrowth.

To examine the relationship between regrowth and soluble carbohydrates without confoundment by current photosynthesis, it was necessary to prevent photosynthesis since regrowing *A. desertorum* plants, which rapidly produce a large canopy, can fix up to twice as much carbon on a daily basis as regrowing *A. spicatum* plants (Caldwell *et al.* 1981). Thus, the etiolated regrowth technique (e.g. McKendrick & Sharp 1970; Christiansen, Ruelke & Lynch 1981) was used to provide a measure of the ability of the two grasses to mobilize stored reserves and synthesize new above-ground tissues.

Net CO_2 exchange measurements of severely defoliated bunchgrasses were conducted under field conditions to determine if the above-ground portion of severely defoliated plants could maintain a positive carbon balance, and to assess the potential contribution of photosynthesis to regrowth immediately following defoliation. Comparison of results of experiments in which active meristems were or were not removed allowed evaluation of morphological or meristematic limitations to regrowth.

MATERIALS AND METHODS

Plants of the widely utilized Eurasian *A. desertorum* and the North American *A. spicatum* had been established in 1978 in experimental plots 4 km north-east of Logan, Utah (41°45'N, 111°48'W, 1460 m a.s.l.) in an area formerly dominated by *A. spicatum* and *Artemisia tridentata* ssp. *vaseyana* (Rydb.) Beetle. The *Agropyron* species are commonly defoliated heavily by large grazing mammals in semi-arid rangelands. Since grass response to defoliation is strongly influenced by competitors (Mueggler 1972), both species of grass were planted alternately within a uniform matrix of the *Artemisia* which provided a natural competitive background. Further site details are provided by Caldwell *et al.* (1981).

Etiolated regrowth experiments

Fifty plants of each grass species were used for the etiolated regrowth experiments. Plants were randomly assigned to control or preclipping treatments and to date of initiation of etiolated regrowth. The preclipping treatment removed approximately 85% of the photosynthetic surface (5–7 cm stubble) on 30 April and 14 May 1981. This treatment caused a large reduction in the amount of stored carbohydrate. Crown carbohydrate

* Recent taxonomic revisions make *A. spicatum* synonymous with *Pseudoroegneria spicata* (Pursh) Löve (Löve 1980; Dewey 1984).

concentrations and pools were reduced 40–50% in *A. desertorum* and 55–65% in *A. spicatum* for the entire growing season by a similar severe defoliation treatment in 1980 (Caldwell *et al.* 1981) and comparable reductions in stored cabohydrate following defoliation have been reported by many other authors (e.g. Hanson & Stoddart 1940; Blaisdell & Pechanec 1949; Cook, Stoddart & Kinsinger 1958; Menke & Trlica 1983). Etiolated regrowth was initiated for five control plants of each species on 16 March and 16 April, and for five control and five preclipped plants of each species on 27 May, 18 June, 30 July and 27 October 1981. Etiolated regrowth was initiated by severely defoliating the plant and covering the tussock with an opaque plastic container.

Because both *Agropyron* species exhibit rapid internode elongation in early May, active apical and intercalary meristems were elevated and were removed in the defoliation at the initiation of the May, June and July etiolated regrowth experiments. When these active meristems were removed regrowth could only proceed after activation of basal (axillary) meristems. In the March, April and October experiments active meristems were not elevated and remained on the plants. Thus, these two groups of experiments represent different meristematic potential for regrowth.

The covers used in the etiolated regrowth experiments were painted white to prevent overheating. Crown temperatures of covered plants were not significantly different than those of uncovered plants in March–July or October, when most regrowth occurred. Soil water potential was at or above $-0{\cdot}1$ MPa in the lower rooting zone of these plants until early July, and October rains recharged the upper profile. Thus, no significant water or heat stress occurred during periods when regrowth was proceeding in the dark.

Etiolated foliage produced in the dark was removed at frequent intervals, oven dried (80 °C, 24 h) and weighed. When regrowth ceased the plant was excavated, the crowns were washed free of soil, freeze-dried and weighed. Regrown foliage and crowns were each ground in a Wiley mill to pass a 40-mesh screen. Subsamples (50 mg) were then used for crown total non-structural carbohydrate (TNC) analyses and crown and foliage carbon content determinations.

At 2–3-week intervals during the 1981 growing season, other plants similar to the etiolated regrowth control plants were harvested to provide estimates of crown biomass, TNC concentration and pool size, and crude protein concentration and pool size at the beginning of each dark regrowth experiment. Shoots and crowns were freeze-dried, weighed and ground for analysis of TNC and Kjeldahl nitrogen. Crowns were also analysed for carbon content.

Although the diffuse root systems of both *Agropyron* species contain carbohydrates, there is no indication from studies with these and other grasses that root carbohydrates are mobilized for shoot growth (Marshall & Sagar 1965; Davidson & Milthorpe 1966; White 1973; Caldwell *et al.* 1981). In this study, carbohydrates available for shoot growth were considered to reside in the crowns, which included the lowest 1 cm of stem base and 1 cm of attached roots.

Carbohydrate and total carbon analyses

Numerous extraction techniques have been used for determination of TNC. Each provides a different estimate of the amount of carbohydrate that can be mobilized easily for metabolism or translocation (Smith 1981). Two standard extraction techniques were used in this study; one (boiling water extraction) provided a conservative estimate of soluble carbohydrates and the other (boiling $0{\cdot}2$ N H_2SO_4 extraction) an overestimate of TNC (Smith 1981). Starch in the residue was digested using amyloglucosidase (Sigma

Chemical Co.) in the enzyme digestion technique of Haissig & Dickson (1979). Sugar concentration in all fractions was determined by the phenol-sulphuric acid method (Dubois *et al.* 1956). In these grasses the majority of TNC is fructosan (Smith 1968). Thus, fructose was used as standard. Starch concentrations were consistently very low (<0·5%) and were often not significantly different from zero. Thus, TNC concentrations (dry weight basis) given here include only the carbohydrate in the water or acid extract. TNC pools were calculated by multiplying plant part biomass by TNC concentration.

The carbon content of crowns and regrown foliage was determined by combustion in oxygen at 900 °C in the furnace of a carbon train (Lingberg, Sola Basic Industries). Water vapour was removed from the furnace exhaust by passing it through a column of Drierite (W. A. Hammond Drierite Co.). Carbon dioxide in the exhaust was then determined by absorption in a preweighed column of Ascarite (Arthur Thomas Co.). Carbon content, rather than biomass, was the basic unit for comparison of regrowth, respiration and photosynthesis.

CO_2 efflux during etiolated regrowth

Relative CO_2 efflux rates during regrowth in the dark were determined on ten control plants of each species from May through July 1982. Carbon dioxide evolved beneath aluminium foil-covered metal containers was trapped by 40 g of soda lime following the procedure described by Minderman & Vulto (1973) and etiolated regrowth produced by these plants was harvested at frequent intervals, dried and weighed. The metal containers were pressed into the soil 2·5 cm and sealed around the perimeter with a saturated soil paste. The rate of CO_2 evolution was corrected by subtracting the amount of CO_2 evolved under nearby identical containers over bare soil. This soil component averaged 27% of the total CO_2 efflux. The daily plant CO_2 efflux rates determined by soda line trapping were of the same magnitude as rates determined by gas exchange measurements (see below) in the dark. Although the magnitudes of CO_2 efflux determined by soda line trapping were reasonable, only comparative CO_2 efflux values are reported, as suggested by Minderman & Vulto (1973).

Daily net assimilation following defoliation

Carbon dioxide exchange of whole bunchgrass plants following severe defoliation was measured with a large cuvette system programmed to track ambient conditions of temperature and vapour pressure deficit as plants were exposed to normal solar radiation in May 1982. The heat exchanger and electronic control system were modified from an original Sirigor (Siemens Co.) chamber (Koch, Lange & Schulze 1971). Further details of this system are contained in Caldwell *et al.* (1981). Plants used for gas exchange measurements were severely defoliated by removing all foliage above 8-cm height and removing all remaining leaf blades. Thus, the only remaining photosynthetic tissue was leaf sheath material on the stubble. The plants were then subjected to continuous gas exchange measurement for 4 days.

RESULTS

Regrowth produced from stored reserves

Contrary to conventional expectation, the total amount of etiolated regrowth produced was not significantly affected by the severe preclipping treatment ($F < 0.93$, $P > 0.41$) (Fig. 1, inset). Because of this, further analyses were performed on the data for control

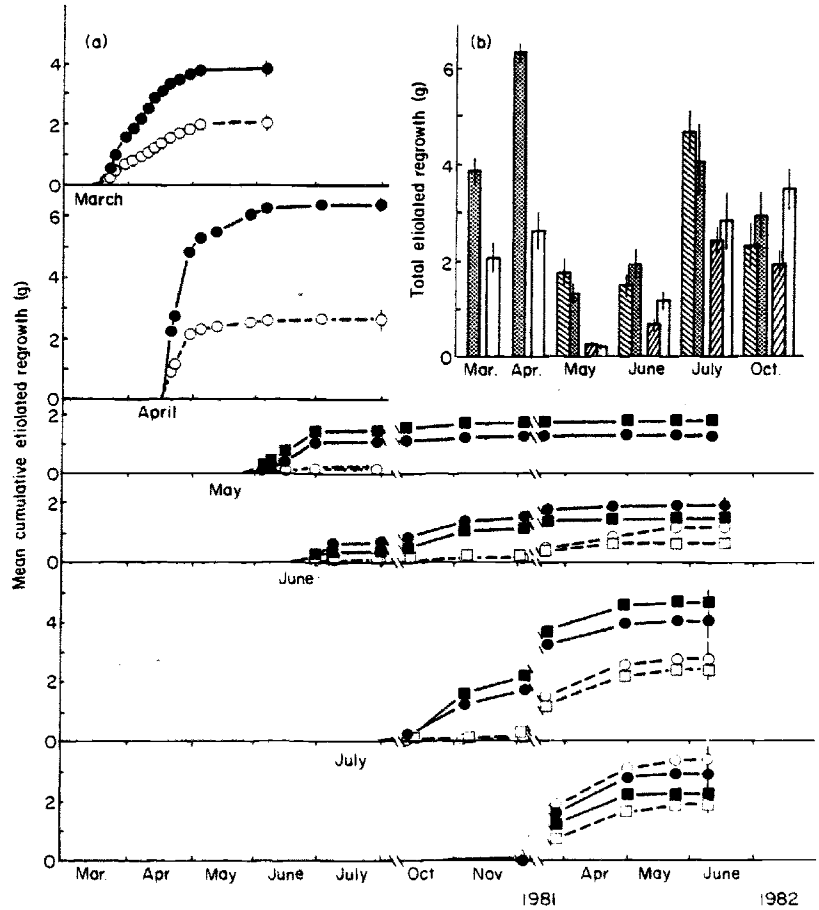

FIG. 1. (a) Time course of etiolated regrowth production in each of the six field experiments conducted in 1981 for control (●, ○) and preclipped (■, □) *Agropyron desertorum* (●, ■) and *A. spicatum* (○, □) plants. (b) Seasonal comparison of total etiolated regrowth (inset) for control (▦, □) and preclipped (■, ■) *A. desertorum* (▦, ■) and *A. spicatum* (□, ■) plants. Each point or bar represents the mean cumulative or mean total etiolated regrowth of five plants and ±S.E. is shown for the totals.

plants alone or as an unbalanced design, by combining the data for the preclipped and control plants for each species and date. These analyses gave similar results (Table 1).

The more grazing tolerant *A. desertorum* consistently produced more etiolated regrowth than *A. spicatum* except in October (Fig. 1, inset; Table 1). Etiolated regrowth production was lowest in both species in May and June and higher both earlier and later. In early spring, March and April, initial regrowth occurred rapidly in both species, but in the May and June experiments initial regrowth was much slower (Fig. 1). In these two experiments the rate of regrowth of *A. desertorum* increased after 2–3 weeks, whereas *A. spicatum* continued to regrow slowly. Coincident with the increased growth rate of *A. desertorum*, we observed the appearance of daughter tillers which arose from basal axillary buds. In other studies where tiller numbers were intensively monitored following defoliation, *A. desertorum* always produced daughter tillers more rapidly and in greater numbers than *A.*

spicatum (e.g. 0·71 and 0·04 daughter tillers per defoliated tiller, respectively, 2 weeks following a May defoliation (Caldwell *et al.* 1981)).

When etiolated regrowth was initiated in May or June, some regrowth occurred in the following fall and spring growing periods, and in the July and October experiments the majority of regrowth was produced in the following spring (1982) growing period (Fig. 1). This spring etiolated regrowth exhibited a time course similar to that seen in the March and April (1981) experiments. The normal seasonal growth pattern for both of these species is characterized by production of small tillers in the fall followed by rapid spring growth of those tillers. Regrowth produced in each season was correlated with the initial rate of regrowth in that season (Fig. 1).

Reserve availability and utilization

Crown biomass and soluble carbohydrate availability at the beginning of each dark regrowth experiment were estimated by harvesting and analysing plants which were similar in size and age to the dark regrowth control plants. The harvested plants were growing in adjacent field plots of identical density, treatment history and with the same competitive environment of *Artemisia*. In both species crown biomass increased significantly through the growing season and declined during the summer drought period from July to October (Table 1). Crown carbohydrate pools followed a similar pattern; however, when weak acid was used as the extractant the pools appeared 2–3 times larger than when boiling water was used as the extractant. There were no significant differences between species in crown biomass or carbohydrate pools regardless of extraction technique used (Table 1). Crown carbohydrate concentrations exhibited seasonal patterns not dissimilar to the patterns exhibited by crown biomass and carbohydrate pools (Table 1). Concentrations, however, were significantly higher in *A. desertorum* than in *A. spicatum*.

As expected, crown biomass and crown carbohydrate pools were severely reduced during all dark regrowth experiments (Table 1). After regrowth ceased *A. spicatum* generally had smaller remaining carbohydrate pools, by both extraction methods, than did *A. desertorum*, but species comparisons within dates were statistically significant ($P < 0{\cdot}05$) in only two of twelve comparisons (i.e., water-extracted pools in April and June).

Initial, water-extracted carbohydrate pools (and the change in these pools during regrowth) were often not large enough to account for the amount of regrowth produced. For example, in the March experiment, 3·81 and 2·06 g of regrowth were produced in the dark by *A. desertorum* and *A. spicatum*, respectively, but initial water-soluble carbohydrate pools were only 1·70 and 1·46 g, respectively (Table 1). However, the initial, acid-extracted carbohydrate pools (5·62 and 5·14 g, respectively) were large enough to account for the etiolated regrowth produced in all but one case (*A. desertorum*, April). Yet, compounds other than acid-extracted carbohydrates may have been mobilized because the change in crown biomass, which averaged 45% of the original biomass, was generally greater than the initial, acid-extracted carbohydrate pool, which averaged 35% of original crown biomass.

Nitrogenous compounds may have been one important constituent of the net carbon loss from the crowns that were not included in acid-extracted carbohydrates. The carbon content of the crude protein in the crowns was similar in both species and was equivalent to 11–15% of the carbon in acid-extracted carbohydrates in July and 26–34% in March (crude protein was calculated as 6·25 times Kjeldahl nitrogen and assumed to contain 53% carbon—Maynard & Loosli 1969).

TABLE 1. Crown carbohydrate and biomass parameters and shoot regrowth production† for control plants of *Agropyron desertorum* (Agde) and *Agropyron spicatum* (Agsp) in six 1981 etiolated regrowth experiments. Within columns, numbers followed by the same letter are not significantly different at $P = 0\cdot05$ by Duncan's multiple range test.

		Initial conditions					Conditions after cessation of regrowth								
			Crown soluble carbohydrates					Crown soluble carbohydrates				Change in soluble carbohydrate pool			
			Water extract		Acid extract			Water extract		Acid extract					
Date of regrowth initiation 1981		Crown biomass (g)	Conc. (mg g⁻¹)	Pool (g)	Conc. (mg g⁻¹)	Pool (g)	Crown biomass (g)	Conc. (mg g⁻¹)	Pool (g)	Conc. (mg g⁻¹)	Pool (g)	Water extract (g)	Acid extract (g)	Change in crown biomass (g)	Shoot regrowth produced‡ (g)
16 March	Agde	14·7a	114·5abc	1·70a	381·3bcde	5·62ab	8·0ab	41·6cde	0·34abc	227·4ab	1·83ab	1·35	3·79	6·7	3·81de
	Agsp	14·6a	100·4ab	1·46a	353·0abcd	5·14a	6·0a	41·9cde	0·24ab	251·8abcd	1·51a	1·22	3·63	8.6	2·06bc
16 April	Agde	16·8a	114·5abc	1·93ab	314·6abc	5·27a	12·5abc	55·7e	0·69e	271·1bcd	3·39abcd	1·25	1·88	4·3	6·33f
	Agsp	25·6bcd	81·6a	2·09ab	316·4abc	8·11abc	9·0ab	46·6de	0·42abcd	196·4ab	1·78a	1·67	6·33	16·6	2·61cd
27 May	Agde	25·5bcd	122·2bc	3·13b	336·8abc	8·59bc	13·2bc	45·3cde	0·61cde	243·5abc	3·21abcd	2·52	5·38	12·3	1·29ab
	Agsp	22·2abc	95·4ab	2·12ab	285·7a	6·33ab	9·2ab	58·6e	0·53cde	254·1bcd	2·33abc	1·59	4·00	13·0	0·15a
18 June	Agde	25·8bcd	176·2e	4·56c	386·1cde	9·96cd	17·1c	36·6bcd	0·64de	294·7cd	5·04d	3·92	4·93	8·7	1·92bc
	Agsp	21·7abc	155·8de	3·39bc	346·9abc	7·53abc	9·8ab	20·4ab	0·21a	298·1cd	2·92abcd	3·18	4·61	11·9	1·18ab
30 July	Agde	32·7d	139·1cd	4·56c	443·4e	14·50e	14·2bc	17·8a	0·27ab	305·8d	4·35cd	4·29	10·15	18·5	4·06e
	Agsp	28·9cd	159·0de	4·58c	422·2de	12·90de	14·0bc	18·8ab	0·27ab	260·2bcd	3·63abcd	4·32	8·56	14·9	2·81cde
27 October	Agde	18·5ab	118·7bc	2·20ab	376·8bcde	6·97abc	14·9bc	35·5abcd	0·53bcde	234·3ab	3·50abcd	1·67	3·47	3·6	2·93cde
	Agsp	21·6abc	115·5abc	2·49ab	302·9abc	6·55ab	17·4c	28·1abc	0·48abcd	232·1ab	4·03bcd	2·01	2·52	4·2	3·46de
								F values							
da		8·73***	12·54***	14·26***	8·03***	16·71***	4·36**	11·06***	5·39***	4·90***	3·75**				21·56***
sp		0·01	4·34*	1·83	7·46**	2·29	3·76	0·85	7·88**	1·96	4·66*				31·61***
da × sp		1·99	1·59	0·93	0·67	2·28	1·25	1·62	3·16*	2·39	0·87				5·70***

Significance: $^{*}P < 0\cdot05$, $^{**}P < 0\cdot01$, $^{***}P < 0\cdot001$ for data (da), species (sp), and date–species interaction (da × sp) effects.

† Soluble carbohydrates were extracted by boiling water or boiling 0·2 N H_2SO_4 and are expressed as concentrations (mg fructose equivalent per g dry weight of crown tissue) or pools (g fructose equivalent); crown biomass and shoot regrowth production are dry weights.

‡ Increasing sample size by combining control and preclipped plants of each species (see Results) caused all F values to increase and species means were significantly different at all dates except October.

Efficiency of regrowth

Carbon content of regrowth and of crown tissue (average for all dates: 37·5 and 37·7%, respectively) was determined for each date and used to calculate total carbon in regrowth biomass and change in carbon of crowns. One index of the efficiency with which a plant utilizes carbon for shoot regrowth is the ratio of carbon in regrowth to the loss of carbon from the crown of the plant during regrowth. This ratio was relativized to the highest value and is shown for each of the six 1981 experiments (Fig. 2). This carbon utilization efficiency was generally much greater for *A. desertorum* than for *A. spicatum*. In the three experiments, May, June and July, where all active apical and intercalary meristems were removed, *A. desertorum* had reduced carbon utilization efficiency, but such reduction was apparent for *A. spicatum* only in May and June. In the October experiment *A. spicatum* regrew as efficienctly as *A. desertorum*.

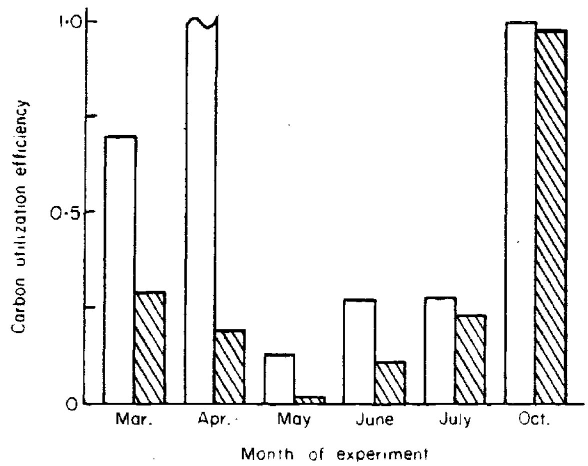

FIG. 2. Carbon utilization efficiency (carbon in regrown foliage divided by carbon lost from crowns) over the whole regrowth period, for experiments initiated in 1981 in the months indicated for *Agropyron desertorum* (□) and *A. spicatum* (■). In the April experiment *A. desertorum* regrowth carbon was greater than carbon lost from crowns (see Table 1), a result of necessarily using one set of plants to determine initial crown biomass and another set to determine regrowth and final crown biomass. Thus, carbon utilization efficiency, which was obviously high, was set = 1·0 in this case.

Another index of the efficiency of regrowth, shoot regrowth efficiency, is the ratio:

$$\frac{\text{regrowth C}}{\text{C efflux (as } CO_2\text{)} + \text{regrowth C}}$$

and is reported relative to the highest value. Carbon dioxide efflux was determined by 24-h sampling periods each week and interpolated for the total regrowth period (Fig. 3). When dark regrowth was initiated on 24 May 1982 active apical and intercalary meristems were not removed. After 1 week of regrowth these meristems were removed (Fig. 3) so that all further regrowth was from newly activated basal meristems. *Agropyron desertorum* had a higher CO_2 efflux rate than *A. spicatum* ($P < 0.001$), but still was able to produce regrowth more efficiently. Removal of active meristems decreased CO_2 efflux rates of both species and caused a severe drop in shoot regrowth efficiency. Shoot regrowth efficiency

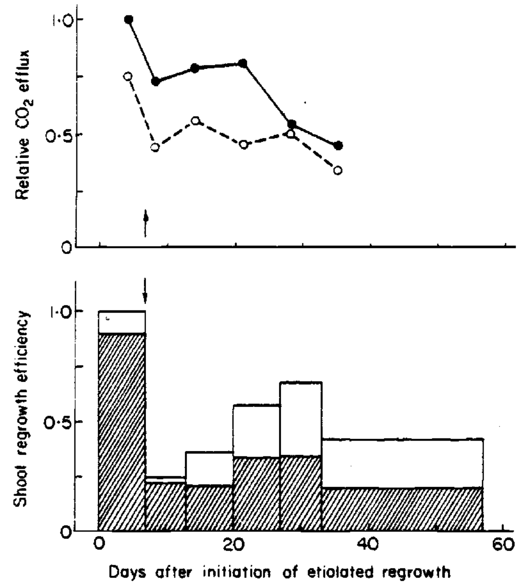

FIG. 3. Relative CO_2 efflux rates during single 24-h periods and calculated shoot regrowth efficiency (see text) for the same plants over approximately weekly intervals for *Agropyron desertorum* (●, □) and *A. spicatum* (○, ■). Etiolated regrowth was initiated on 24 May 1982 by removing all leaf blades and expanded leaf sheaths and covering the plants ($n = 10$). Arrows indicate the time of apical and active intercalary meristem removal.

recovered more rapidly in *A. desertorum* in parallel with greater production of new tillers from basal meristems. Thus, apical meristem removal caused reduced shoot regrowth efficiency not by increasing respiration losses but by causing a delay in the plant's ability to utilize available reserves for new regrowth. This result agrees with the seasonal pattern of carbon utilization efficiency shown in Fig. 2.

Photosynthesis following defoliation

The maximum etiolated regrowth rate for both species occurred in the first few days of the experiment initiated in April (Fig. 1). This represents a situation where the carbon flux from stored reserves to shoot regrowth is maximal. In Fig. 4 this contribution from stored reserves is compared with the photosynthetic carbon gain of very severely defoliated plants during the first few days following a defoliation event. Daily net photosynthetic rates are based on field gas-exchange measurements of severely defoliated tussocks and are scaled to correspond with the average plant size of those in the etiolated regrowth experiment. The running mean of daily regrowth from the April etiolated regrowth experiment, expressed as carbon, plus the carbon utilized in nocturnal respiration of the above-ground plant parts (based on the gas-exchange measurements shown) is the maximum potential daily contribution of stored reserves to above-ground regrowth. This is represented in Fig. 4 by the hatched bars. They are, of course, conservative estimates of total stored carbon use since they do not include any growth or respiration of the root system. For perspective, the daily photosynthetic carbon gain and the carbon involved in daily growth of the above-ground portion of tussocks in the light are shown for the sixteenth day following severe defoliation (data from Caldwell *et al.* 1981).

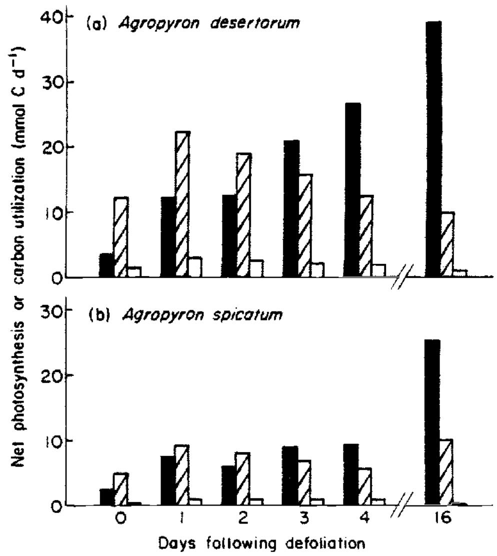

FIG. 4. Daytime net photosynthetic carbon uptake (■) of (a) *Agropyron desertorum* and (b) *A. spicatum* tussocks in the field following severe defoliation at midday on day 0, compared with daily carbon utilization (regrowth plus nocturnal respiration). (▨) represents stored carbon utilization when daily regrowth of severely defoliated tussocks in the field in the absence of photosynthesis (i.e. etiolated regrowth) was maximal (April experiments). (□) represents carbon utilization when etiolated regrowth rate paralleled regrowth rates more typically encountered following grazing. Daytime net photosynthesis and nocturnal respiration of the above-ground portion of defoliated plants is based on field CO_2-exchange measurements of entire tussocks. The gas exchange rates were scaled to correspond to plants of the same size as those used in the etiolated regrowth experiments.

If there are no meristematic limitations to regrowth and other conditions are conducive to rapid shoot growth, as in the April etiolated regrowth experiment, the potential contribution of carbon from reserves to shoot regrowth can exceed the photosynthetically fixed carbon of a very severely defoliated plant for a few days. This appears, however, to be an extreme case. When the carbon utilization for daily etiolated regrowth was plotted (Fig. 4) from experiments initiated at other times, a very different picture emerged. For example, in the experiment initiated in May, the carbon required for etiolated regrowth was less than 0·2 mmol carbon per day for both species, and the majority of carbon utilization was for nocturnal respiration. In this case, which is a more realistic simulation of the defoliation these species normally receive, total carbon utilized for regrowth plus dark shoot respiration was much less than the carbon provided by photosynthesis even on the day of defoliation for both species.

DISCUSSION

Contribution of concurrent photosynthesis to regrowth

While both *A. spicatum* and *A. desertorum* were able to produce substantial amounts of etiolated regrowth, up to 3 or 6 g per plant, respectively, these amounts represent only a small portion of the amount of regrowth produced in the light. For both species, regrowth in the light following clipping at various times through the growing season follows a seasonal pattern similar to the pattern found in this study for dark regrowth (Blaisdell &

Pechanec 1949; Cook, Stoddart & Kinsinger 1958) (Fig. 1, inset). When comparisons between dark regrowth and light regrowth following defoliation in different months (March–October) were made, dark regrowth ranged from 4 to 11% of light regrowth for *A. desertorum* and 1 to 9% of light regrowth for *A. spicatum*. Light regrowth amounts were obtained from severely defoliated plants used for another experiment at the same field site in 1981. If it is assumed that the amount of dark regrowth produced represents the maximum possible contribution of stored carbon to normal regrowth in the light, then it must be concluded that a least 89–99% of the carbon in regrown tissues of these species, under normal conditions, is derived from current photosynthate.

Under certain conditions, as following mid-April defoliation, the carbon contribution by stored reserves to shoot regrowth and respiration can exceed photosynthetic carbon gain of a tussock during the first few days following severe defoliation (Fig. 4). However, we consider this condition to be an unusual case. The plants used for gas exchange measurements were very severely defoliated as they possessed only sheath leaves on the remaining stubble, and no leaf blades. Furthermore, in this case, photosynthetic rates of these severely defoliated plants have been compared with short-term etiolated regrowth rates which were unusually high (Fig. 1). Therefore, under most field situations when less severe defoliation by grazing removes apical meristems, photosynthesis during regrowth would far outweigh stored reserves as a source of carbon, as also indicated in Fig. 4. It is commonly accepted that stored reserves are the major source of carbon for regrowth in these and other grasses (e.g. Hyder & Sneva 1959, 1963; Bokhari 1977; Daer & Willard 1981; Deregibus, Trlica & Jameson 1982). Our results contrast with this view, contribute to an explanation of why attempts to correlate soluble carbohydrates and regrowth have often been unsuccessful, and are in agreement with the laboratory studies of Marshall & Sagar (1965), Davidson & Milthorpe (1966) and the review of May (1960).

Soluble storage compounds

Non-structural carbohydrates, which have been considered the most important carbon storage compounds (Cook 1966; White 1973; Deregibus, Trlica & Jameson 1982), are only a portion of the stored carbon which was utilized during dark regrowth in our experiments. The liberal estimates of change in soluble carbohydrate pool provided by the acid extraction procedure, which extracts some structural materials (Smith 1973), average only 52% (range: 31–96%) of changes in crown biomass (Table 1). Thus, compounds other than carbohydrates were probably utilized for regrowth, as has also been reported by Davidson & Milthorpe (1966), Chung & Trlica (1980), and Dewald & Sims (1981). The identity of these compounds remains unclear, but proteins, hemicelluloses, organic acids, etc., have been suggested. In this study, even if crude protein was completely utilized, it would not account for the discrepancy between the loss of carbon in acid-extracted carbohydrates and the loss of total carbon from the crowns. The participation of compounds apart from TNC as a source of regrowth carbon is apparent and could be one reason for previous difficulties in attempts to correlate TNC and regrowth (May 1960; Stoddart, Smith & Box 1975; Caldwell *et al.* 1981).

Relationship of soluble carbohydrates and etiolated regrowth

Concentrations and pools of TNC found in *A. desertorum* and *A. spicatum* in this study are comparable to those reported in many previous studies of these and other perennial grasses in both absolute magnitude and in seasonal changes (Hanson & Stoddart 1940; Hyder & Sneva 1959, 1963; Daer & Willard 1981; Caldwell *et al.* 1981; Menke & Trlica

1981, 1983). Nevertheless, these values are poor indicators of etiolated regrowth production.

The amount of etiolated regrowth produced by *A. desertorum* and *A. spicatum* was not correlated with any measure of TNC pool or concentration in the plant at the beginning of the dark regrowth period or TNC or biomass lost during regrowth ($r < 0{\cdot}46$ and always N.S.) (Table 1). These two species are similar in amount and location of total carbohydrate pools; yet, the amount of etiolated regrowth produced was consistently greater in *A. desertorum* (Fig. 1, Table 1). This species also produces more foliage when regrowing in in the light than does *A. spicatum* (Hanson & Stoddart 1940; Cook, Stoddart & Kinsinger 1958; Caldwell *et al.* 1981). Furthermore, total carbohydrate pools and TNC concentrations were high when etiolated regrowth of these species was low (e.g. May and June, Table 1) and when TNC concentrations and pools were reduced due to preclipping, the production of etiolated regrowth was not reduced (Fig. 1).

Regrowth efficiency and meristematic limitations to regrowth

Meristematic limitations to etiolated regrowth may provide the best explanation for the differences in regrowth between *A. desertorum* and *A. spicatum.* Nevertheless, even in the March and April experiments when regrowth was immediate and rapid from active apical and intercalary meristems in both species, more etiolated regrowth was produced by *A. desertorum.* This species utilized stored reserves more efficiently to produce new foliage or directed a larger proportion of the mobilized compounds to foliage-producing meristems (Fig. 2), perhaps at the expense of root growth (Richards 1984). The greater efficiency of *A. desertorum* was not due to lower CO_2 efflux rates of whole plants (Fig. 3).

Meristematic limitations, or limited flexibility for reallocation of resources (Watson & Casper 1984), appear to be much more important than the amount of stored or photosynthetically fixed carbon in determining the ability of these grasses to regrow following defoliation. Much past research has considered only one species or time of defoliation, or has compared species with different growth form or phenology. This may have obscured the importance of developmental constraints on allocation of carbon resources. Study focused on the characteristics which allow grazing-tolerant species, such as *A. desertorum,* to rapidly adjust carbon allocation in favour of shoot regrowth following apical meristem or canopy removal, is needed. This field study showed clearly that photosynthesis of regrowth was quantitatively the most important, and, under most conditions, nearly the sole source of carbon for shoot regrowth. The efficiency with which a species directs available carbon to above-ground growing points and utilizes it for synthesis of new foliage may be a key physiological feature which determines that species' ability to tolerate defoliation by large grazing animals.

ACKNOWLEDGMENTS

This research was supported by the National Science Foundation (DEB-7907323 and DEB-8207171) and the Utah Agricultural Experiment Station. We gratefully acknowledge the laboratory analyses and testing of carbohydrate extraction procedures by L. Jordan and J. Daie, the field gas exchange measurements by T. Dean, field assistance by J. Whitehouse, J. Erickson and M. Mazurski, drafting by C. Warner and statistical consultation by H. Thorgeirsson. Discussions with R. Wyse and D. Doney also contributed much to this paper.

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(Received 29 January 1985; revision received 7 June 1985)

SECTION VI.

Productivity and Nutrition.

The Effects of Crested Wheatgrass for Domestic Livestock.

Chairman, A. E. (Gene) Gade

Factors Affecting Yield and Nutritional Quality of Crested Wheatgrass

H. F. Mayland

ABSTRACT: This paper reviews the literature on factors affecting the yield and nutritional value of crested wheatgrass (Agropyron cristatum, A. desertorum or A. fragile). The Agropyrons are cool-season perennial bunch grasses that are grown in the western United States and Canada where annual precipitation ranges from 9 to 18 inches (230 to 460 mm) and forage yield ranges from 400 to 3000 pounds of dry matter per acre (450 to 3360 kg/ha). Forage production in the northern Great Plains is best correlated with April to June precipitation whereas in the area west of the Rocky Mountains production is best correlated with total autumn to spring precipitation.

Yields are responsive to applications of 20 to 30 pounds of nitrogen per acre (22 to 34 kg/ha) in areas receiving at least 12 inches of precipitation (300 mm). Early forage growth is stimulated by fertilizer nitrogen, thereby advancing the grazing period by as much as two weeks. Yield responses to phosphorus fertilization are frequently measured when soil moisture and nitrogen are adequate. Sulfur deficiencies occur in some soils in the Pacific Northwest and yield responses to sulfur fertilization may be obtained under conditions where nitrogen and moisture are adequate for additional plant growth.

Digestible nutrients in the forage are high and adequate for growing yearlings, cow-calf, and ewe-lamb pairs during the green feed period, but decline rapidly as the forage matures. Chemical curing at flowering time, interseeding with legumes, or supplementing the protein-energy requirements of grazing livestock have been used to counter the forage quality deficiencies in maturing crested wheatgrass. Grazing systems that utilize crested wheatgrass in spring, native range in summer, and Russian wildrye grass (Psathyrostachys juncea) in late summer and autumn have been successful in maintaining high daily gains for beef production in the northern Great Plains. Animal health problems that are associated with, but not limited to grazing crested wheatgrass include silicosis, white muscle disease, grass tetany, and marginal zinc deficiency.

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ACKNOWLEDGMENTS: The author recognizes the valuable services of Jean Sanborn and Aartje Smith for typing the text; Jeanne Earl for preparing the figures; and Don C. Adams, Raymond F. Angell, Verle R. Bohman, Kenneth D. Sanders, and S. Smoliak for their helpful suggestions upon reviewing the manuscript.

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INTRODUCTION

Crested wheatgrass is composed of several cool-season, perennial, bunchgrass species taxonomically identified as Agropyron cristatum, A. desertorum or A. fragile (Dewey 1983). It was successfully introduced into North America in 1906 from Eurasia (Westover et al. 1932, Dillman 1946, Richardson et al. 1980 and Rogler and Lorenz 1983). It has since been seeded on millions of acres in the northern Great Plains, Intermountain, Great Basin, Snake River, and Columbia Plateau regions of the United States and the prairie provinces of Canada (Reynolds and Springfield 1953). Smoliak et al. (1981a) estimated that crested wheatgrass had been seeded on 2.5 million acres in Canada and Dewey and Asay (1975) estimated 12 million acres of seedings in the western United States.

There are a number of reasons why crested wheatgrass was planted so extensively. Land managers discovered that the grass was an excellent competitor with weeds when planted properly (Pavlychenko 1942). For example, crested wheatgrass was seeded in many areas to displace halogeton (Halogeton glomeratus), a weed poisonous to sheep (Frischknecht 1968a), and Russian thistle (Salsola kali), an alternate host to the sugar beet leafhopper (Circulifer tenellus). This insect is a carrier of the curly top virus that reduced production of susceptible varieties of bean (Phaseolus vulgaris), tomato (Lycopersicon esculentum) and sugar beet (Beta vulgaris) (Douglass and Cook 1954). Crested wheatgrass was also planted as an alternative to cheatgrass (Bromus tectorum), a winter annual that provides a very short green-feed period and is very flammable when mature (Hull and Stewart 1948). Crested wheatgrass was seeded in areas denuded by fire (Piemeisel et al. 1951) to protect the soil from wind and water erosion. In fact, many acres of farmland in the United States and Canada were abandoned because of drought during the 1930's and were later seeded with crested wheatgrass to increase soil stability (Hubbard 1949).

First and foremost, however, crested wheatgrass was seeded to increase the forage resources available to grazing livestock. This review examines the factors affecting the yield and nutritional quality of crested wheatgrass for domestic livestock. The taxonomic classification by Dewey (1983) is used here. The genus Agropyron is confined to crested wheatgrass. Most of the other former Agropyrons are now classified in the Elytrigia, Elymus, or Pascopyrum genera. The common names of plants used in this review and their Latin binomials are listed in the appendix. Values of annual precipitation are drawn from the referenced sources, the 1941 Yearbook of Agriculture (Kincer 1941), or World Weather Records (U.S. Department of Commerce 1965).

FACTORS AFFECTING DRY MATTER YIELDS OF CRESTED WHEATGRASS

Productivity Studies

Forage yield trials began within a few years after crested wheatgrass was introduced to North America. Results of early studies conducted on the USDA Great Plains stations were summarized by Westover et al. (1932) as listed in Table 1.

Table 1.--Average air dry forage yields of crested wheatgrass for given number of years and precipitation at seven locations in the northern Great Plains (Westover et al. 1932).

Location	Years	Rainfall	Yield
		Inches	Pounds per acre
Havre, MT	10	13.1	1600
Moccasin, MT	9	15.5	1900
Sheridan, WY	6	15.1	1917
Mandan, ND	15	15.2	1940
Archer, WY	13	15.9	1460
Redfield, SD	6	18.7	2140
Ardmore, SD	10	15.8	1910

In the prairie region of western Canada, Hubbard (1949) measured an average dry matter yield of 352 pounds per acre near Manyberries, Alberta, with an average annual precipitation of only 11.3 inches. On areas receiving run-on water, dry matter yields were 1660 pounds per acre. Areas in Alberta and Saskatchewan with greater precipitation have yields similar to the latter amount. Agropyron cristatum is better adapted to more moist conditions, while A. desertorum grows best in drier areas (Smoliak and Bjorge 1981).

Much farther south Reynolds and Springfield (1953) reported that crested wheatgrass was adapted to moderately moist sites in the big sagebrush, pinyon-juniper, and ponderosa pine vegetational types of northern New Mexico and Arizona, where it produced 500 to 800 pounds per acre in pinyon juniper, 900 to 1500 in big sagebrush, and 1100 to 1200 in the ponderosa pine type. After 1950, the production potential of crested wheatgrass was evaluated in many areas of the western United States and Canada and some of these results are shown in Table 2. Average annual yields ranged from 400 up to nearly 1900 pounds per acre in experiments that were 3 to 13 years in length; the 13-year mean yield in southeastern Idaho was 500 pounds.

The dry matter yields of crested wheatgrass are related to rate of growth, which is dependent upon soil and climate parameters. Williams and Post (1941) reported that crested wheatgrass was a valuable grass in the northern Great Plains because it furnished two to three weeks earlier grazing than did either native or bromegrass pastures. Sharp (1970) reported the daily rate of growth (air dry pounds per acre per day) during 1967 at Point Springs, Idaho as follows:

Late March - Mid-April	3.6
Mid-April - Late April	6.8
Late April - Mid-May	7.1
Mid-May - Late May	19.1
Late May - Mid-June	25.5

These rates when multiplied by 15 days per interval give a mid-June dry matter yield of 930 pounds per acre, almost twice the 13-year mean yield (Table 2) of 500 pounds. Precipitation during the November through June period in 1967 was greater than normal, 10.27 vs. 8.82 inches, explaining the difference.

Five reports (Table 3) compared yields of various cultivars within the *Agropyron* genus. With either Nordan or Standard used as a reference, yields for the other cultivars ranged from 85 to 144% of the reference varieties. The wide range in yield within the genus could be exploited to produce high yielding or high quality forage plants. Others (Coulman and Knowles 1974, Murphy 1942, and Schaff et al. 1962) have arrived at similar conclusions. Lamb et al. (1984) and Vogel et al. (1984) screened 50 strains including 38 accessions (PI lines). They were ranked for yield and *in vitro* dry matter digestibility (IVDMD) using the Nebraska Index (NI):

$$NI = \frac{Yield - \bar{X}(yield)}{s(yield)} + \frac{IVDMD - \bar{X}(IVDMD)}{s(IVDMD)}$$

where $\bar{X}$ was the mean and s was the square root of the error mean square in the F test for the appropriate trait. Values of NI ranged from -4.0 to +2.8, with the varieties Ruff (*A. cristatum*) and Nordan (*A. desertorum*) scoring 2.49 and 2.08, respectively. This indicates that good material is already in use, but some opportunity may exist for improvement.

Comparisons of crested wheatgrass yields with smooth brome (*Bromus inermis*) and slender wheatgrass (*Elymus trachycaulus*) were made by Reitz et al. (1936) at Moccasin and Havre, Montana, with annual precipitation of 15.5 and 13.1 inches, respectively. Average yields over the 15 years at Moccasin (14 years at Havre) in pounds of air-dry forage per acre were:

	Moccasin	Havre
Crested wheatgrass	1860	1660
Smooth brome	1780	1190
Slender wheatgrass	1770	1740

The ability of crested wheatgrass to maintain a productive stand throughout the 14-year period encouraged these investigators and others to further evaluate this promising forage resource. Hyder and Sneva (1963b) compared the forage-yielding potential of grasses grown in eastern Oregon in pounds of dry matter per acre:

Standard crested wheatgrass	1650
P-27 Siberian wheatgrass	1450
Whitmar beardless wheatgrass	1350
Alkar tall wheatgrass	1260
Topar pubescent wheatgrass	1190
Sherman big bluegrass	1110

Hull and Johnson (1955) summarized forage production data from 28 studies conducted at 20 locations in the Ponderosa pine zone of Colorado. Crested wheatgrass was the best adapted species and Russian wildrye (*Psathyrostachys juncea*) also did well. Average yields at six locations were 1060 pounds per acre for crested wheatgrass and 634 pounds per acre for Russian wildrye.

Cooper and Hyder (1958) reported the mean yields (12% moisture) of 11 grasses grown in a 5-year study at Squaw Butte, Oregon. These forage yields are for eight crested wheatgrass cultivars reported in pounds per acre.

A. fragile	1310
A. cristatum	
Commercial	800
A-1770	793
A. desertorum	
Commercial	910
Mandan 571	950
Nebraska-10	970
Utah 42-1	900
5% LSD	360

Hull (1972) reported that in southern Idaho Fairway produced only 79 percent as much forage as Standard. However, Fairway spread 112 percent further and was grazed more uniformly than Standard. He reported forage yields of *Agropyron desertorum* and *A. cristatum* for 15 sites.

Row Spacing

The effect of row spacing on forage yield of crested wheatgrass was studied in southern Idaho by Hull (1948) and Hull and Holmgren (1964). Row spacings of 6, 12, 18, and 24 inches produced similar forage yields, but the 6- and 12-inch spacings gave better protection against soil erosion and weed invasion, and produced a more palatable forage.

Reitz et al. (1936) reported that 12-year average forage yields were 1770 pounds per acre from rows spaced 36 inches apart, but only 1300 pounds per acre from drilled rows 7 to 9 inches apart. The 36-inch rows were periodically cultivated which may have stimulated production. During a 5-year study at Squaw Butte, however, Hyder and Sneva (1963b) did not measure any difference in yields when crested wheatgrass was planted in rows spaced 6, 12, 24, 36, 48, or 60 inches apart. It is probable that these plots were not tilled. Hubbard (1949) also found that after 12 years different row spacings (6, 12, or 24 inches) had no effect on plant density or yield.

McGinnies (1970) seeded crested wheatgrass during each of three years at 10, 20, or 30 seeds/foot in rows spaced 6, 12, 18, 24, and 30 inches apart. Stand survival after 6 years was best at the highest seeding rate. Forage yield was not affected by seeding rate, but was highest in rows spaced 12 to 18 inches apart and lowest in 30-inch rows. Invasion by other perennial grasses was also greatest at the widest spacing. Forage yields in pounds per acre were:

Spacing	
6	850
12	1010
18	1000
24	900
30	760

The effect of row spacing on forage yield was also studied in southwestern Saskatchewan (Leyshon et al. 1981). "Mayak" Russian wildrye, "Summit" crested wheatgrass, and "Drylander," a creeping

Table 2.--Dry matter yield responses of crested wheatgrass to fertilizer nitrogen and mixtures with legumes at 19 locations in Canada and the United States.

Location		Reference[8]		Expt. years	Annual ppt.	Total dry matter yields for given levels of annually applied N fertilizer, lb/a: 0	20	30	40-60	Alfalfa + crested wheatgrass
					Inches	Pounds per acre				
Pincher	ALB	Lutwick	77	3	[1]17.6	1870	-	-	[2]2510	3520
Mandan	ND	Rogler	69	10	[3]15.4	1680	-	-	2760	2440
Mandan	ND	Power	80	6	16.8	1000	-	1790	-	-
Mandan	ND	Smika	60	7	16.8	470	-	1370	1890	-
Mandan	ND	Lorenz	62	12	16.8	530	-	1320	1990	1270
Alliance	NE	Schultz	82	2	16.5	-	-	-	-	1771
Holbrook	ID	Hull	74	6	[3]16.0	1220	-	-	-	-
Manitou	CO	McGinnies	68	6	15.7	630	1070	-	1280	-
Moccasin	MT	Stitt	58	8	15.5	1620	-	-	-	1860
Gillette	WY	Rauzi	82	8	15.1	1870	-	-	-	1930
Sidney	MT	Black	68	4	14.9	970	-	-	1440	-
Archer	WY	Rauzi	75	3	14.7	800	-	-	-	-
Red Bluff	MT	Gomm	64	3	[3]14.1	1330	-	-	-	[5]2580
Swift Current	SAS	Kilcher	58	4	14.0	700	1200	1400	2200	-
Goodwell	OK	Huffine	59	3	[3]13.4	740	-	-	-	-
Tintic	UT	Havstad	83	[4]3	13.0	680	-	-	-	-
Point Springs[7]	ID	Sharp	70	13	[3]12.5	500	-	-	-	-
Glorieta	NM	Reynolds	53	5	[3]12.3	420	-	-	-	-
W. Central	NV	Eckert	61	4	12	490	-	-	550	-
Squaw Butte	OR	Sneva	76	[6]10	11.3	810	1200	1190	1280	-
Twin Falls	ID	Hull	74	6	9.3	670	-	-	-	-
N. Central	NV	Eckert	61	4	9	620	-	-	840	-

1 Exclusive of August precipitation.
2 Fertilizer applied only once.
3 Mean annual precipitation during the study.
4 Includes data from D.L. Scarnecchia.
5 Yellow sweet clover plus crested wheatgrass.
6 May 15 yield plus regrowth harvested August 1.
7 Now the Lee A. Sharp Experimental Area.
8 Senior author and year of publication.

Table 3.--Forage yields (12% moisture) of *Agropyron* cultivars grown at different locations.

Cultivar	Susanville, CA[1]	Perkins, OK[2]	Burns, OR: A[3]	Burns, OR: B[4]	Sheridan and Gillette, WY[5]
	Pounds per acre				
Agropyron desertorum					
Standard	-	[6]670	910	750(1980)	2500
Nordan	1140	1070	-	-	2530
Nebraska -10	1290	-	970	1000(1710)	-
Mandan 571	-	910	950	870(1810)	-
Summit	-	-	-	-	2480(2420)
Agropyron cristatum					
Fairway	1080	740	800	780(1930)	2220
A-1770	-	[6]820	790	760(1630)	-
Parkway	-	-	-	-	2340(1960)
Agropyron fragile					
P-27 Siberian	1060	930	1310	850(2220)	-

1 Mean yields for 3 years at Black Mountain Experimental Station, 18.6 inches annual precipitation (Cornelius and Williams 1961).
2 Mean yields for 2 years, 34.1 inches annual precipitation (Huffine et al. 1959).
3 Mean yields for 5 years at Squaw Butte Experiment Station, 11.3 inches annual precipitation (Cooper and Hyder 1958).
4 Mean yields for 4 years at Squaw Butte. Values in parentheses are forage yields achieved with 30 pounds nitrogen per acre applied annually (Hyder and Sneva 1961).
5 Mean yields for 5 years at Sheridan and 4 years at Gillette, 15.1 and 14.4 inches annual precipitation, respectively (values in parentheses are for a second experiment (Richardson et al. 1980).
6 Mean yields for 2 years at Goodwell, OK, 17.0 inches annual precipitation (Huffine et al. 1959). The value shown here for Standard was identified as Commercial by this reference.

Table 4.--Mean annual forage yields over five years and three row spacings (Leyshon et al. 1981).

Forage	Yield for spacing, inches 12	24	36
	------ Pounds per acre ------		
Summit	1250	1330	1480
Mayak	570	1030	1640
Drylander	2250	2070	2180

Table 5.--Mean forage yield during year four at three row spacings (Leyshon et al. 1981).

Forage	Yield for spacing, inches 12	24	36
	------ Pounds per acre -------		
Summit	410	460	890
Mayak	140	460	1280
Drylander	560	870	1430

alfalfa, were seeded at 12-, 24-, and 36-inch row spacings. Dry matter yields were generally greater for the 12-inch spacing the first year. By the second year, both grasses had greater production on the wider spacings. By the fifth year, the yield advantage had shifted to the 36-inch rows (Table 4). In the fourth year, which received below normal precipitation, the dry matter yields were much greater for the 36-inch spacing (Table 5). To explain the benefit of the wider spacing, the authors argued that "there is only enough moisture and nutrients available for a limited amount of dry matter production by a limited number of plants." Apparently soil water is used more efficiently under the 36-inch row than under closer spacing (Kilcher 1961).

This concept is supported by spacing and seeding rate studies at Fort Valley in northern Arizona (Lavin and Springfield 1955). The highest forage yields were produced in the narrower spacings during wet years and the wider spacings in dry years.

Springfield (1965) conducted similar rate and spacing studies near Tres Piedras, New Mexico. The site was a medium textured, rocky, shallow soil at 8500 feet elevation having 13 inches annual precipitation. The plots were seeded at 3 rates and 3 row spacings in 1951, and grazed from 1953 until 1956. The forage yields are shown in Table 6. These yields reflect a period of low rainfall from October 1955 to May 1956 dry enough to restrict growth at all row spacings. Thus, the 12- to 18-inch row spacing still seems best.

Forage yield responses to wider row spacings have been noted in the northern Great Plains, but not in the Great Basin, Snake River, or Columbia Plateau regions (Sneva and Rittenhouse 1976, Sims 1969). Perhaps the summer rainfall pattern and somewhat higher precipitation amounts in the northern Great Plains develop the spacing response.

Sims (1969) examined the effect of stand density on characteristics of wheatgrasses in Utah. He found that dense stands of crested wheatgrass, tall wheatgrass (*Elytrigia pontica*), intermediate wheatgrass *Elytrigia intermedia*), and pubescent wheatgrass (*E. intermedia* ssp. *barbulata*) produced more herbage per acre, had fewer and shorter seed stalks, fewer viable seeds, narrower and shorter leaves, and a lower stem/leaf ratio than open stands. More research is needed to identify the contrasting results of plant or row spacing between the northern Great Plains and the Intermountain and Snake River Plains.

Stand Age

Crested wheatgrass has been frequently seeded in fields that have been fallowed one or more seasons. The accumulation of mineralized soil nitrogen and soil water may have boosted forage production the first couple of years after seeding. After the plants adjusted to current precipitation and available nitrogen levels, yields often declined with age.

Some researchers in the northern Great Plains found that yields of old stands could be increased by land scarification or renovation (Black 1968, Houston 1957, Lorenz and Rogler 1962, Lodge 1960, and Stitt 1958) and nitrogen application. Smoliak et al. (1967) examined 29- to 38-year old stands of *A. cristatum* and found that they consistently outyielded native mixed prairie vegetation by a ratio ranging from 12.4 to 1.1. Soil analyses showed that exhaustion of nitrogen was not a factor in the persistence of stands. Crested wheatgrass had become a permanent part of the vegetation and forage yield was dependent mainly on current rainfall.

Lodge (1960) measured the effects of burning, cultivation, and mowing on the yield of crested wheatgrass grown near Swift Current, Saskatchewan. He noted that all treatments reduced yields the first year and spring burning even longer. In the long run, however, basal area was not affected by any of the treatments. Rauzi et al. (1971) measured yields for 5 years after light discing or chiseling on 16- or 24-inch centers at Archer and Gillette. Forage yields were depressed the first year after renovation and were not different from untreated plots after that.

Table 6.--Mean annual forage yields of crested wheatgrass planted in three row spacings (Lavin and Springfield 1955).

Year	October-May precipitation	Yield for spacing, inches 6	12	18
		---- Pounds per acre ----		
1956	33% of normal	50	55	53
1957	110% of normal	1090	1180	1210
1959	90% of normal	432	455	468
Mean		525	564	578

Hull and Klomp (1966) reported that crested wheatgrass was well adapted to southern Idaho, and that during 7 to 14 years of production, it could maintain itself and even spread. Smoliak et al. (1981b) reported that a stand seeded in 1928 at the Manyberries Research Station was still productive after 50 years. Many of the seedings in the prairie region of Canada remained as monocultures for 15 to 20 years. Native plants then began to invade, but seldom made up more than 10 percent of the plant density, and yield loss was negligible (Looman and Heinrichs 1973). Dormaar et al. (1978) reported that forage yields on 40 to 59 year-old stands still out-yielded native range by 1.1 to 1.5 times.

Hubbard (1949) noted an average yield of 1675 pounds air-dry hay for 30 consecutive years at Mandan. Because of experiences there and at Havre and Swift Current, he suggested that most stands would yield well for 20 to 30 years. Others have felt that crested wheatgrass stands would become decadent with age and encroaching shrubs and weeds would further reduce productivity. Scarifying the soil surface has been used to stimulate wheatgrass stands, but little evidence exists that a net improvement in forage yield is produced by this treatment (Black 1968, Stitt 1958, Lorenz and Rogler 1962, Smika et al. 1963). Weed and shrub control may be necessary and nitrogen fertilizer application may be helpful in stimulating forage production (Stauber et al. 1974). Forage yield response to nitrogen fertilizer may be greater for new stands than for old stands. Sneva (1973b) found that 16 pounds of forage were produced per pound of nitrogen on new stands, but only 8 pounds on old stands. These findings might explain why Seamands and Lang (1960) found that the most efficient yield per unit of nitrogen applied to an old stand was 7 pounds of forage per pound of nitrogen.

Precipitation

Crested wheatgrass is grown in semiarid areas of the United States and Canada. It is, therefore, logical to assume that precipitation is the primary factor limiting forage production (Sneva and Hyder 1962), and that production increases with additional precipitation. However, the forage production data for the 19 experimental sites of Table 2 are not well correlated with precipitation (r^2 = .2). This is probably due to large differences in the seasonal distribution or "quality" of precipitation, in addition to variability in soil fertility, temperature, etc.

Figure 1 illustrates the relative amount of annual precipitation occurring in any month, expressed as a percentage of total precipitation, for a number of locations where crested wheatgrass is grown. Areas east of the Rocky Mountains such as Mandan, North Dakota, receive a majority of their rainfall as summer storms. This rainfall pattern tends to extend the green-feed period compared to areas west of the Rocky Mountains. It also may increase the yield response to nitrogen fertilizer. Precipitation in the Great Basin, Snake River Plateau, and Columbia Plateau primarily occurs during winter and spring followed by a relatively dry summer and fall season. The subfigures for Ritzville, Washington and Austin, Nevada are examples of this seasonal pattern. Precipitation in the Intermountain area may be evenly distributed throughout the year as shown for the Benmore, Utah site.

Experimental seedings of crested wheatgrass and other grass and legume forages have been made at Susanville, California (Cornelius and Talbot 1955, Cornelius and Williams 1961). Although at the extreme western periphery of the Great Basin, this area has a mediterranean type climate with very dry, warm summers. Long-term studies in this and similar regions indicate that rhizomatous wheatgrass types (pubescent and intermediate wheatgrass) out-spread and out-persist the bunch-type wheatgrasses (*A. cristatum/desertorum* and other non-rhizomatous wheatgrass species now identified in the *Elytrigia* and *Elymus* genera). The dry summers apparently limit seed formation and establishment of new crested wheatgrass plants (Graves et al. 1984).

Experimental seedings of crested wheatgrass have also been made at Perkins, Oklahoma (Huffine et al. 1959). Forage yields were satisfactory the first two years, but few plants remained in the third and fourth year after establishment. The area receives 34.1 inches of annual precipitation, but average January (37°F, 3°C) and July (81°F, 27°C) temperatures are about 10 Fahrenheit degrees higher than areas where the *Agropyrons* persist. Warm season grasses are more adapted to sites like this and can outcompete the *Agropyrons*.

Forage yields of crested wheatgrass have been predicted from soil moisture values or from precipitation and temperature data. June forage production in New Mexico averaged 980 pounds per acre over four years, and was best predicted as:

$$Y = 203X - 368, \ (r^2 = .99)$$

where X was the January through May precipitation in inches (Gray and Springfield 1962). The wheatgrass yield of 980 pounds per acre compared with a yield of only 114 pounds on native range.

Sharp (1970) reported that 70 to 80 percent of the variability in annual production of crested wheatgrass at Point Springs, in south central Idaho, could be attributed to variation in the April to June precipitation. In eastern Oregon, Sneva (1977) found that spring yields were best predicted from mean February temperature and March precipitation (r^2 = .83). The best combination for predicting mature yield was July (of the previous year) through May precipitation plus mean March through May temperature (r^2 = .64).

Sneva and Hyder (1961, 1962) used an indexing system to predict yield. They defined the yield index (YI) for a given year as the actual yield divided by the mean yield expressed as a percentage. The precipitation index (PI) was defined in the same way for the crop year (September 1 to June 30). Regressing the YI values against the PI values produced the prediction equation (r^2 = .77; $s_{y.x}$ = 18.4 pounds per acre).

$$YI = 1.11PI - 10.6$$

Sneva and Britton (1983) reassessed the yield relationship within the sagebrush-bunchgrass zone in Washington, Oregon, Idaho, Utah, Nevada, and

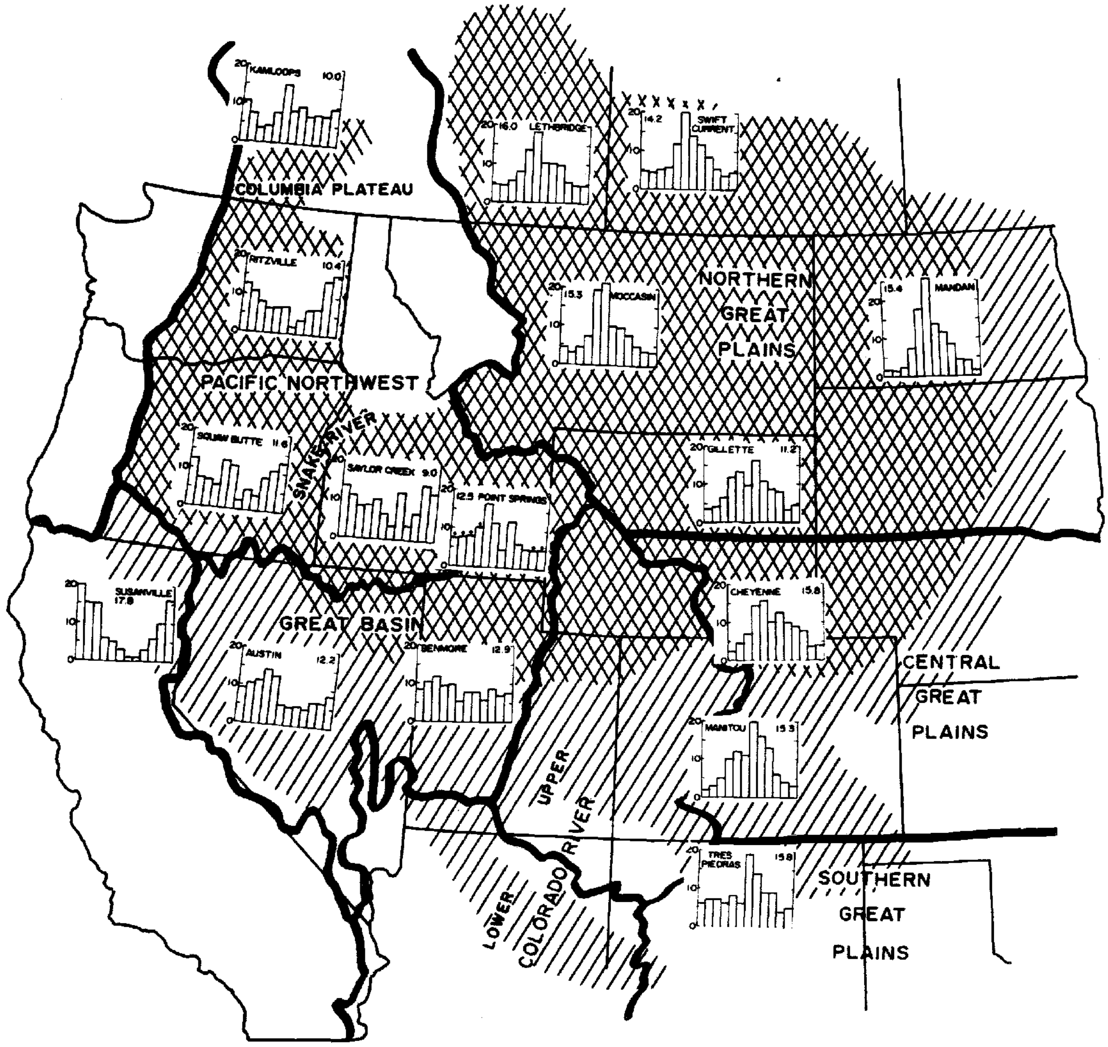

Figure 1.--The quantity (inches/year) and distribution of precipitation for areas where crested wheatgrass is grown. The bars from left to right represent relative January through December precipitation, as a percentage of the total. Major watersheds and primary (cross hatched) and secondary (diagonal lines) areas of crested wheatgrass distribution are illustrated.

California. This report increased the length of record and extended the use of the precipitation index (PI) and yield index (YI) to additional sites.

A more direct approach was used by Power (1970) and Power and Alessi (1970) who reported that the growth of crested wheatgrass at Mandan was linearly related to available soil water (Fig. 2). The yield was described (r^2 = .98) as:

$$Y = 190X - 990$$

where Y was yield in pounds per acre and X was inches of available soil water. A threefold increase in yield occurred as available soil water increased from 8 to 14 inches.

Love and Hanson (1932) reported that most roots of crested wheatgrass were above 3 feet, but that some extended to 8 feet (Fig. 3).

However, Brown et al. (1982) reported that crested wheatgrass used water from a 13-foot soil depth compared with an average 20-foot depth for 10 alfalfa varieties. Soil conditions, plant competition in mixed stands, and time when soil water is being extracted are all factors that may control water use and growth. Nevertheless, 2200 to 2500 pounds of dry matter per acre may be the yield potential for the presently available lines of crested wheatgrass.

Increasing soil water by snow-trapping or run-on techniques has been used to increase forage production. In the northern Great Plains, snow moves laterally or horizontally, losing some of its moisture by sublimation until it is finally trapped in depressions, in standing vegetation, or on the leeward side of snow barriers. Rauzi and Landers (1982) evaluated 13 and 26-foot wide level benches as snow catchment devices at Gillette, Wyoming. The benches trapped more snow and increased soil water

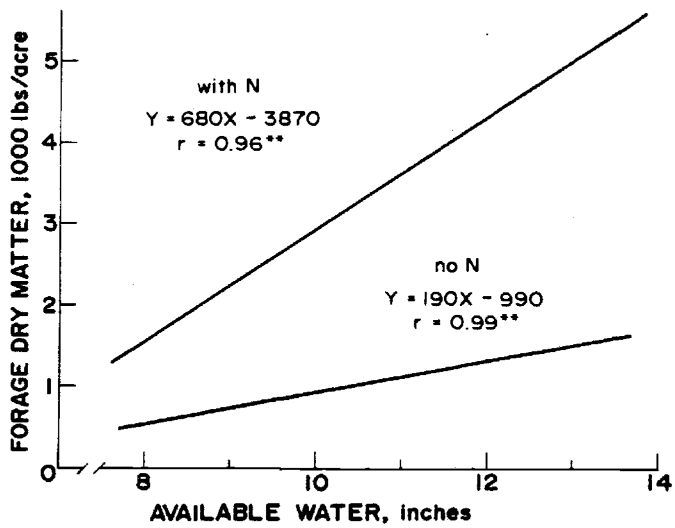

Figure 2.--Forage yields of control- and nitrogen-fertilized crested wheatgrass grown at Mandan, North Dakota, as related to available soil water (Power 1970).

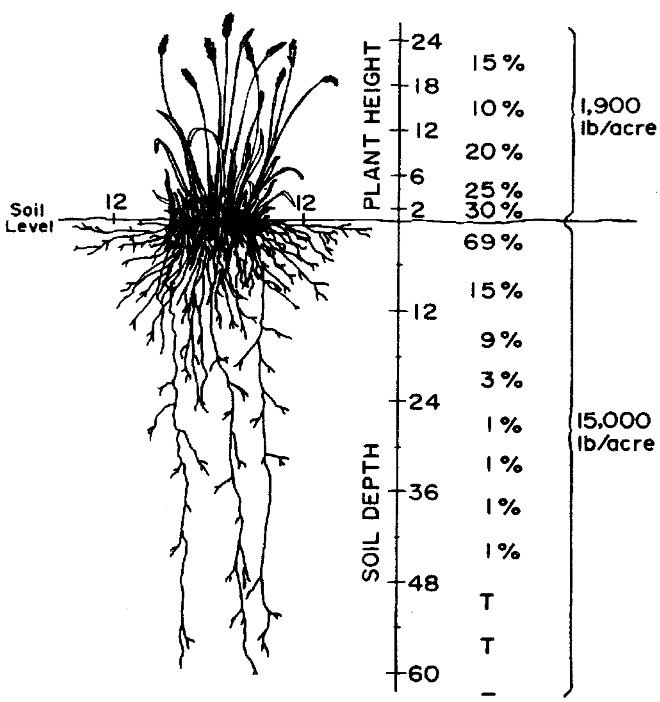

Figure 3.--The distribution of above and below ground biomass of a flowering crested wheatgrass plant growing on a deep friable silt loam soil with 16 inches annual precipitation. Data are primarily drawn from Hull and Klomp (1974) with additional information from Caldwell et al. (1981), Richards (1984), and the author. The length and depth increments are in inches.

by 12 to 20 inches when compared to control areas. It is possible that this extra water percolated below the root zone of crested wheatgrass plants where it was available only to the deeply rooted alfalfa. The average yields of the crops grown on the two different benches were compared to those on the control in pounds per acre:

	Control	Level Bench
Alfalfa	2590	3230
Crested wheatgrass	2300	2240
Alfalfa plus crested wheatgrass	2470	3310

Increasing the effectiveness of precipitation is another way to improve forage production. Rauzi (1968) compared yields on native undisturbed rangeland with areas that had been pitted, and with a third area that was pitted and seeded. The areas were grazed by sheep with the results shown in Table 7.

The review to this point has discussed the relationship of dry matter yields of crested wheatgrass to precipitation or soil moisture. Robertson et al. (1970a) extended the value of precipitation regressions by relating steer-weight gains to precipitation and temperature parameters of an area in northeastern Nevada where annual precipitation was 16 inches. Animal gains were best predicted by the November through June precipitation ($r^2 = .53$). Other precipitation periods or temperature data reduced the correlation values.

Nitrogen Fertilization

Forage yield responses to fertilizer nitrogen are limited to a large extent by available soil water. Power (1980a, 1980b) showed that the forage yield of crested wheatgrass grown at Mandan, North Dakota was linearly related to available soil water

Table 7.--Forage and lamp production on shortgrass native range (control), pitted or pitted plus interseeded with crested wheatgrass (Rauzi 1968).[1]

Parameter	Parameter response for given treatment: Control	Pitted	Pitted and interseeded
1955-60			
Forage production, lbs/acre	410	630	1050
Sheep days/acre	42	59	72
Lamb gain, lbs/head	52	49	52
Lamb gain, lbs/acre	28	36	45
1961-65			
Forage production, lbs/acre	720	1070	1350
Sheep days/acre	46	61	66
Lamb gain, lbs/head	56	52	51
Lamb gain, lbs/acre	31	36	40

[1]Pitting removed a piece of soil 4 inches deep, 7 inches wide, and 5.5 feet long in every 8 feet.

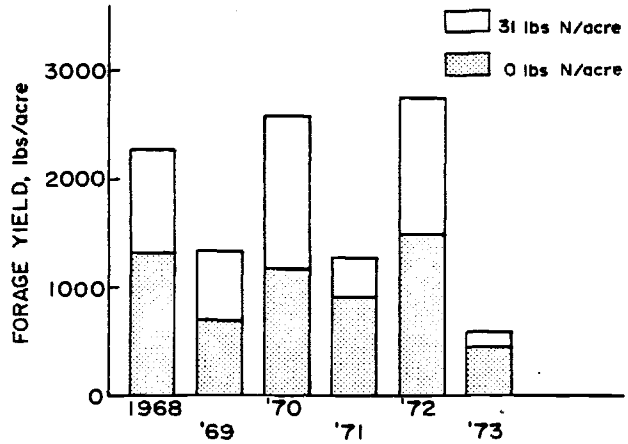

Figure 4.--Forage production of crested wheatgrass with annual applications of ammonium nitrate at Mandan, North Dakota (adapted from Power 1980a).

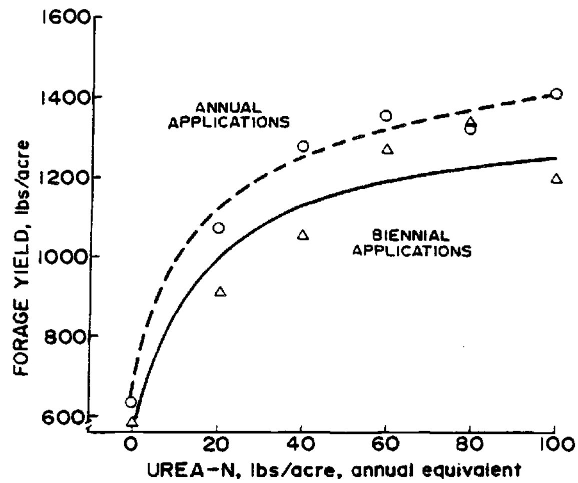

Figure 5.--The forage yield of crested wheatgrass on the Manitou Forest in Colorado in relation to annual application of urea-nitrogen (adapted from McGinnies 1968).

(Fig. 2), and that the yield response per increment of water between 7 and 14 inches was greater when nitrogen fertilizer was applied. Conversely, the yield response per increment of nitrogen fertilizer was greater at above-normal levels of soil water as indicated by the yield of unfertilized plots (Fig. 4).

The magnitude of the response to nitrogen fertilizer on perennial grasslands was site specific, integrated over the capacity of the soil to immobilize nitrogen, the capacity of plants to take up nitrogen, the nitrogen transformations active at the site and, of course, the amount of available soil water. These conclusions were supported by cumulative yield responses of bromegrass, crested wheatgrass, and native grasses to cumulative nitrogen applications over a 5- to 6-year period on several sites (Power 1980a). The order of response was least for native grasses, intermediate for crested wheatgrass and greatest for bromegrass at Mandan. The yield responses of crested wheatgrass at two sites were predicted by:

$$Y = 12.95X - 0.0037X^2 + 833 \ (r^2 = .90) \text{ and}$$
$$Y = 11.79X - 0.0037X^2 + 544 \ (r^2 = .72)$$

where Y was cumulative dry matter yield and X was cumulative fertilizer nitrogen applied.

McGinnies (1968) reported yield data for the Manitou Experimental Forest in Colorado, in response to urea-nitrogen applied annually or biennially (Fig. 5). The latter was twice the annual rate, but was treated as an annual equivalent for the regression analysis. The regressions were:

$$Y = 598 + 402 \log N \ (r^2 = .98)$$
$$Y = 532 + 367 \log N \ (r^2 = .89)$$

for annual and biennial treatments, respectively. About 80 percent of maximum forage production was achieved by applying 20 pounds of nitrogen per acre. Biennial application of nitrogen at twice the amount was less efficient than the annual application (slopes are not equal, P = .12), even though the same amount of nitrogen was applied in both treatments.

Lang and Landers (1968) summarized 10 years of Wyoming data and concluded that 20 pounds of nitrogen per acre was the most efficient level for increasing crested wheatgrass forage production. However, Fairbourn and Rauzi (1982) reported that 20 to 30 pounds of nitrogen per acre appeared too low to effectively increase crested wheatgrass yields at their site, and concluded that nitrogen was immobilized in litter and soil.

Power and Legg (1984) followed nitrogen-15 recovery for five years after application as ammonium nitrate to crested wheatgrass. Annual forage yields varied as a function of available soil water, and the nitrogen content was about 25 percent greater than unfertilized plants. Cumulative recovery of nitrogen-15 in tops increased with time; 12 to 52 percent being recovered the first year after application. After four seasons about 75 percent of the total initially applied nitrogen was recovered. About 70 to 95 percent of the total was accounted for in tops, roots, and soil.

Wight (1976) noted that water use efficiency was increased by nitrogen fertilization and that annual applications of 30 to 50 pounds of nitrogen per acre doubled forage production and subsequent beef production in the northern Great Plains. These findings are supported by those of Williams et al. (1979) in Kamloops. Rogler and Lorenz (1969) reported that over a 10-year period, crested wheatgrass forage production was increased by annual applications of 40 and 80 pounds of nitrogen per acre (Fig. 6). Beef production was increased with the application of 40 pounds, but was not further increased with the 80-pound rate. A mixed planting of crested wheatgrass and alfalfa produced as much forage and beef as crested wheatgrass fertilized with about 15 pounds of nitrogen per acre.

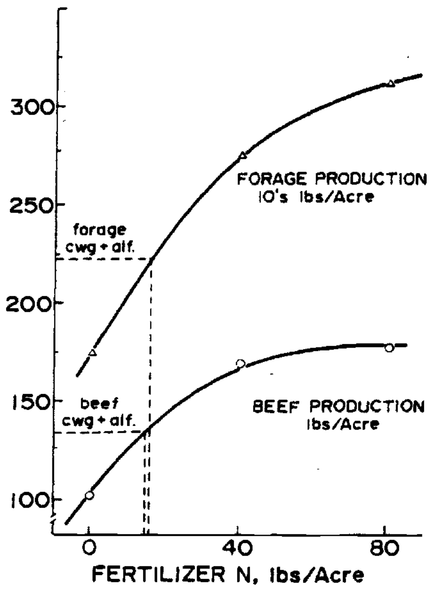

Figure 6.--Ten-year mean production of forage and beef on crested wheatgrass fertilized annually with nitrogen compared with a mixed seeding of crested wheatgrass and Ladak alfalfa at Mandan, North Dakota (adapted from Rogler and Lorenz 1969).

Bleak and Keller (1974) reported that the benefit of applying nitrogen fertilizer to crested wheatgrass grown near Logan, Utah was nil. Sneva et al. (1958), however, reported that 20 pounds of nitrogen per acre returned 25 pounds of forage for each pound of nitrogen applied at Squaw Butte, Oregon. Perhaps more importantly, they found that nitrogen-fertilized crested wheatgrass initiated growth earlier in the season and that the relative amount of growth occurring prior to June 1 (as percent of total yield at maturity) was nitrogen - rate (given in pounds per acre) dependent:

Fertilizer N	Yield
0	44
10	53
20	63
30	69
40	66

Miller (1960) reported that nitrogen-fertilized plots near Fort Collins, Colorado were ready for grazing 10 to 14 days sooner the first year, but that there was no difference the second year. Forage moisture concentrations were significantly increased by nitrogen fertilizer at vegetative and boot stages, but were unaffected at the dough stage. Forage, seed yield, and crude protein concentration were increased by nitrogen fertilization, but dates of flowering and seed maturation were not affected.

In another fertilizer study near Fort Collins, Hull et al. (1958) measured forage production fertilized with 0 or 33 pounds per acre of nitrogen. Air dry forage yields in pounds per acre were:

	0N	33N
Crested wheatgrass	2160	3050
Fairway wheatgrass	1700	3100
Pubescent wheatgrass	1400	2680
Tall wheatgrass	3360	4280
Smooth brome, northern strain	960	1840
Smooth brome, southern strain	1700	2400

McCormick and Workman (1975) conducted an economic analysis of the early range readiness of crested wheatgrass produced by 25 to 30 pounds per acre of nitrogen fertilizer. The study was based on the Curlew National Grassland located north of Snowville, Utah, and on the Benmore seedings located south of Vernon, Utah. Annual precipitation was 11 and 13 inches, respectively. They calculated that in 1973 ranchers could have profitably substituted nitrogen fertilizer for purchased hay. Their costs included $0.12 per pound of nitrogen and $1.50 per acre for application.

Sneva (1973a) showed that 30 pounds of nitrogen per acre increased yields 375 pounds (583 lbs/acre on control and 958 on fertilized). Costs were $8.00 and expected returns were $8.40. This was a very simple analysis and did not consider proportion of increased feed that might be lost to trampling, or nutrient availability, or increased risk of grass tetany. In 1984-1985, fertilizer nitrogen costs are about $0.30 per pound and application costs are also higher. Purchased feed costs are not greatly different. Expected profitability should be calculated for each situation using figures appropriate for that time and place.

Another economic analysis was conducted at Hooper, Washington with applications of 0 to 80 pounds of nitrogen per acre (Patterson and Youngman, 1960). They found that at this 13-inch precipitation site the 5-year mean yields in pounds per acre and nitrogen use efficiency (lbs/lb) were:

Fertilizer N	Yield	Efficiency
0	1220	
20	1490	13.5
40	2300	40.5
60	2730	21.5
80	2960	11.5

The most efficient yield response came with the 40 pound rate where 40.5 pounds of forage were produced for each pound of nitrogen applied. However, most of this extra herbage was cheatgrass, an early competitor for nutrients and water, particularly in the Snake River and Columbia River Plateau regions where normal precipitation is often less than 13 inches and winters are relatively mild (Eckert and Evans 1963).

Hyder and Sneva (1961) reported 4-year mean yield responses of various *Agropyron* cultivars to nitrogen fertilizer at 30 pounds per acre (Table 8). *Agropyron fragile* (Siberian wheatgrass) produced more dry matter per pound of nitrogen fertilizer than the other *Agropyrons*. This may be a genetically controlled trait or simply a site-specific response.

Schlatterer (1974) reviewed the use of fertilizers to increase production on rangelands. For the Great Basin and Snake River Plateau he concluded that:

1. Nitrogen consistently increased production, but only in areas receiving more than 13 inches annual precipitation.
2. Introduced grasses responded more to nitrogen than did native species.
3. Residual fertilizer effects are usually limited to less than three years on grazed ranges.
4. Cheatgrass responds more quickly than perennial grasses to nitrogen fertilizer.
5. The high costs of nitrogen and of application, lack of consistent year-to-year production increases, and lack of long term residual effects under grazed conditions raise serious questions as to the economic practicality of using nitrogen fertilizer.

Crested wheatgrass is grown extensively in the northern and central Great Plains where summer-type precipitation occurs (Fig. 1), and most areas receive in excess of 13 inches precipitation. Under these conditions, nitrogen fertilization to increase forage production is a viable management option.

Phosphorus, Sulfur, and Trace Element Fertilization

As noted before, available water is the factor most limiting production. Available nitrogen may be the second most limiting factor and phosphorus may be the third (Thomas and Osenbrug 1964). Available soil phosphorus is generally adequate to support the growth of crested wheatgrass in the absence of fertilizer nitrogen. Power and Alessi (1970) annually applied a series of nitrogen fertilizer rates with and without fertilizer phosphorus to crested wheatgrass grown at Mandan, North Dakota. Over the 5-year period, dry matter yields averaged 380 pounds per acre for each inch of precipitation in excess of 5 inches. A greater response, 490 pounds, was measured when phosphorus was also applied.

Table 8.--Forage yield and nitrogen use efficiency for seven Agropyron cultivars (Hyder and Sneva 1961).

Cultivar	Yield when fertilized at level of ON	Yield when fertilized at level of 30N	Nitrogen use efficiency
	Pounds per acre		
Agropyron fragile	852	2223	46
Agropyron desertorum			
Standard	752	1982	41
Mandan 571	873	1806	31
Nebraska 10	1002	1708	24
Utah 42.1	874	1792	31
Agropyron cristatum			
Fairway	780	1927	38
A-1770	756	1634	29

Table 9.--Spring and regrowth forage yields of crested wheatgrass when fertilized with nitrogen or nitrogen plus phosphorus (Segura 1962).[1]

Fertilizer	Spring growth	Regrowth	Total
	-------- Pounds per acre ---------		
ON + OP	1470	590	2060
45N + OP	2390	1360	3750
90N + OP	2200	1250	3450
90N + 18P	2390	1780	4170

[1]Nitrogen applied as ammonium nitrate and phosphorus as treble superphosphate.

Phosphorus fertilizer has generally been drilled into the soil. Yield increases of 340 pounds per acre have been attributed to the scarifying action of the disc openers on the drill (Black 1968, Smika et al. 1963). Nitrogen fertilizers are more water soluble than phosphorus sources and readily move into the rooting zone. Thus maximum yield responses to nitrogen often occur the first year after application and decrease in subsequent years as fertilizer N is immobilized. Maximum yield responses to phosphorus, in the presence of adequate moisture and nitrogen, however, may not occur until the second or third year after application because of the delay in movement of phosphorus into the root zone (Stitt et al. 1955).

In a Colorado study, Segura (1962) reported that surface applications of nitrogen and phosphorus increased yields of crested wheatgrass (Table 9). Some of these values greatly exceed those reported elsewhere in this review. Nevertheless they illustrate that crested wheatgrass responded to the first increment of nitrogen fertilizer (45 lbs), but not to the second (90 lbs) unless accompanied by phosphorus.

Smoliak et al. (1981) summarized crested wheatgrass production for a 5-year period after a single application of nitrogen or phosphorus at Manyberries, Alberta. Yields were not affected by phosphorus. Nitrogen increased yields the first year and less with each succeeding year (Table 10).

Table 10.--Forage yields of crested wheatgrass following a single application of fertilizer (Smoliak et al. 1981).

Fertilizer	First year	Second Year	Five year total
	-------- Pounds per acre ---------		
Check	240	240	1410
30P	240	250	1490
30N	510	310	1890
30N + 30P	510	320	1910
60N	650	380	2180
60N + 30P	640	390	2100

At some sites crested wheatgrass yields did not respond to phosphorus even when nitrogen was applied. This suggests that resident soil phosphorus was adequate to sustain growth under the soil water and nitrogen levels present at these sites (Kilcher 1958, Read and Winkleman 1982).

Soil moisture, nitrogen, and phosphorus may affect forage quality in addition to yield. Thomas and Osenbrug (1964) reported that forage nitrogen concentrations increased with nitrogen fertilization and decreased with precipitation. Smika et al. (1960) demonstrated in a 7-year study how the availability of soil nitrogen and phosphorus affected quantity and quality of crested wheatgrass (Fig. 7). Dry matter yields were increased with each increase in fertilizer nitrogen up to the 90 pound per acre rate. Yields were only slightly responsive to phosphorus fertilizer, but were greater at the higher nitrogen rates. Crude protein values increased with increasing fertilizer nitrogen rates, but were not affected by fertilizer phosphorus levels. On the other hand, nitrogen promoted growth, but not phosphorus uptake, thus diluting the phosphorus concentration in the forage from a level of .20 to .13 percent, which is low for some classes of livestock. Phosphorus fertilization, while not greatly affecting yield, did maintain the concentration of phosphorus in the forage.

Many of the rangeland soils in the Pacific Northwest were derived from volcanic materials. Because selenium and sulfur are easily volatilized it is common to encounter low concentrations of these two elements in area forage crops, especially legumes. Only sulfur is required by plants in significant quantities and it is not unusual to find sulfur responses in crops grown in this area, especially when fertilized with non-sulfur nitrogen sources (Westermann and Robbins 1974). Sneva and Rittenhouse (1976) reported that adding sulfur to nitrogen fertilizer caused spring yields of crested wheatgrass to double when compared with yields from unfertilized plots. Crested wheatgrass yields were increased on some but not all sites, only in some years, and only when accompanied by nitrogen (Sneva 1978). The growth rate of crested wheatgrass is dependent on soil factors, including the levels of nitrogen and sulfur that must be mineralized from

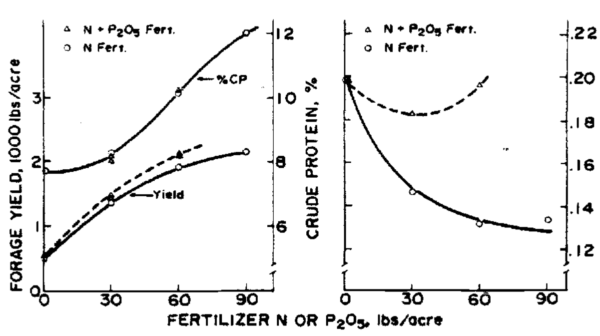

Figure 7.--Seven-year mean forage production and concentration of crude protein and phosphorus in crested wheatgrass fertilized annually with ammonium nitrate (N) or N plus treble superphosphate (P_2O_5) at Mandan, North Dakota (adapted from Smika et al. 1960).

organic forms. Activity in these transformations is site dependent and may explain why forage yields are only sometimes responsive to nitrogen, phosphorus, and sulfur fertilization.

Crested wheatgrass is grown in semiarid areas where soils are largely calcisols which means that they have a high proportion of exchangeable calcium and perhaps even free lime, and an alkaline to neutral pH. These soils generally have adequate potassium and magnesium for plant growth. Trace mineral levels in these soils are generally adequate (Eckert et al. 1961) and no trace element deficiencies have been identified with the exception of sulfur. There are many discussions of appropriate plant tissue tests that can be conducted to determine the adequacy of trace elements. Mayland (1983) is only one of many that presents information on critical nutrient ranges. Little directed progress will be made in the evaluation of fertilizer responses until investigators utilize soil and tissue testing to determine the status of nutrient availability in crested wheatgrass.

Forage Mixtures

In 1938, Stitt (1958) seeded 14 grasses and two forage mixtures at the Central Montana Branch Station at Moccasin. The seed mixtures contained the following species and seed weights as pounds per acre:

No. 1	
Crested wheatgrass	2
Russian wildrye	3
Smooth brome	3
Ladak alfalfa	4
No. 2	
Crested wheatgrass	2
Slender wheatgrass	2
Western wheatgrass	1
Smooth brome	1
Big bluestem	1
Side-oats grama	1
Switchgrass	1
Ladak alfalfa	1

These were planted in 7-inch rows and the next year about half of the plants in alternate rows were cultivated out. Good stands of blue grama, side-oats grama, Sandberg bluegrass and western wheatgrass were obtained the first year, but by 1941 these stands had been invaded by crested wheatgrass. Indian ricegrass was seeded, but not harvested, because of thin stands. By 1941, the forage resulting from the first mixture contained 15 percent alfalfa and 85 percent crested wheatgrass; while that from the second mixture contained 45 percent alfalfa and 55 percent crested wheatgrass. Mean forage yields in pounds per acre for the eight-year period were:

Crested wheatgrass	1620
" " M24-3	1580
" " M24-17	1480
Fairway wheatgrass	1420
Beardless wheatgrass	1520
Smooth brome	1260
Russian wildrye	860
Big bluegrass	1600
Green needlegrass	1220
Mixture No. 1	1680
Mixture No. 2	2040
LSD 5 %	160

Table 11.--Total forage yield and percent composition of Nordan crested wheatgrass (cwg) when seeded with native grasses in a 25:75 mixture (cwg:other) of pure live seed (Schuman et al. 1982).

Year	Slender + cwg		Thickspike + cwg		Western + cwg		Green needlegrass + cwg		4-natives + cwg	
	Yield	cwg	Yield	cwg	Yield	cwg	Yield	cwg	Yield	cwg
	Pounds per acre	Percent	Pounds per acre	Percent	Pounds per acre	Percent	Pounds per acre	Percent	Pounds per acre	Percent
1977	1260	30	1230	58	1000	78	880	78	980	38
1978	2090	61	2170	55	2360	74	1640	67	2000	69
1979	3560	96	2830	91	3310	89	3540	77	2890	79
1980	3420	97	1590	85	2130	85	3640	64	2150	96

Only the number 2 mixture produced more than crested wheatgrass. Ladak alfalfa made up a larger portion of the forage in mixture 2 than in mixture 1, even though seeded at one-fourth the rate.

In 1976, Schuman et al. (1982) seeded crested wheatgrass with several other grasses at Cheyenne where annual rainfall is nearly 16 inches. Crested wheatgrass became a strong dominant in all mixtures by 1980, even though seeded at one-fourth the rate. When seeded with slender wheatgrass, the stand became essentially a pure stand of crested wheatgrass (Table 11). This was attributed to the competitive nature of crested wheatgrass and the short-lived nature of slender, even though the latter is easily established and initially quite productive.

Johnson and Nichols (1969) planted 11 grasses in monoculture stands with 0 or 100 pounds of nitrogen applied annually or as a 50:50 mixture with alfalfa. The studies were conducted at Newell, South Dakota where annual precipitation was 15.5 inches. Forage was harvested at anthesis of the grasses during the fourth and fifth year after establishment. Crude protein concentrations in the grass (Table 12) were least in the unfertilized stands, and were not different in the grass fertilized with nitrogen or grown with alfalfa ($P < .05$). Forage yields of crested wheatgrass in pounds per acre were:

Crested wheatgrass	2300
Crested + 100 lb N A	6200
Crested + alfalfa	6350

Kilcher and Heinrichs (1958) evaluated the productivity of Fairway crested wheatgrass grown alone in pure stands with 30 pounds of nitrogen per acre and in a mixture or in alternate rows with alfalfa. Dry matter yields (lbs/acre) of these combinations when averaged over four years were:

Fairway + 30N	3120
Mixed Fairway + alfalfa	3720
Rowed Fairway + alfalfa	4000

The increased yield of alternate row versus mixed stand was attributed to a greater legume yield.

Schultz and Stubbendieck (1982) studied grass-legume mixtures in a 16.5-inch precipitation area of western Nebraska. Mixtures of Ruff crested wheatgrass (Agropyron cristatum) and either alfalfa or cicer milkvetch (Astragalus cicer) were fertilized with various combinations of nitrogen and phosphorus. Yields at the June 26 harvest were averaged across two years and all fertilizer treatments in pounds per acre:

Alfalfa	1650
Cicer	1510
Alfalfa + Ruff	2250
Cicer + Ruff	1950

The grass-legume mixtures out-yielded the legumes when the latter were grown alone.

Legume persistence is often limiting under some rangeland conditions. McGinnies and Townsend (1983) measured the persistence of sicklepod milkvetch, Ladak 65 alfalfa, Eski sainfoin, and Penngift crownvetch when seeded in alternate 12-inch rows with either Nordan crested wheatgrass, Vinall Russian wildrye, or Topar pubescent wheatgrass. The study was conducted near Fort Collins over a 7-year period. Long term annual precipitation was 14.4 inches, but two droughty years occurred in the middle of the study period. Crownvetch did not survive the first winter and pubescent wheatgrass gradually thinned out. Sainfoin declined and disappeared by the sixth year. The authors anticipated that pubescent wheatgrass would be marginal, and concluded that sainfoin was probably a

Table 12.--Crude protein concentrations in grass fertilized with two levels of nitrogen or grown with alfalfa at Newell, South Dakota (Johnson and Nichols, 1969).[1]

Forage	0N	100N	Alfalfa + grass
	Percent		
Wheatgrass			
Crested	10.8 cd	13.9 f	12.8 ef
Tall	7.5 a	8.3 a	9.0 a
Intermediate	8.2 ab	10.0 bcd	8.9 a
Slender	8.2 ab	8.5 ab	9.3 ab
Pubescent	8.7 ab	9.0 bc	9.4 ab
Smooth brome	9.5 bc	11.0 de	10.7 bcd
Orchard grass	9.6 bc	11.8 e	10.3 abc
Russian wildrye	11.2 d	16.5 g	14.0 f
Tall fescue	8.2 ab	11.1 de	10.7 bcd
Meadow fescue	9.7 c	12.1 e	12.0 de
Reed canarygrass	11.0 cd	10.4 cde	11.8 cde

[1]Means within the same column not followed by the same letter are different ($P < .05$).

short-lived species under rangeland conditions. Alfalfa also declined because of drought and depredation by pocket gophers except in the pubescent wheatgrass stand, where it was able to compete more effectively for available soil water.

The alternate-row planting of crested wheatgrass and sicklepod milkvetch yielded well, as did the Russian wildrye and sicklepod milkvetch (Table 13).

Canadian researchers at Lethbridge compared the productivity and persistence of Eski sainfoin and Ladak alfalfa in pure and mixed stands subjected to frequent clipping over five years (Hanna et al. 1977). The legumes were grown alone or in mixed- and alternate-row seedings with Nordan crested wheatgrass, Sawki Russian wildrye, or Greenleaf pubescent wheatgrass. Mixed-row seedings out-yielded alternate-row seedings in sainfoin-Russian wildrye, alfalfa-crested wheatgrass, and alfalfa-pubescent wheatgrass associations as shown in Table 14. Hanna and coworkers concluded that sainfoin was a suitable alternative to alfalfa in parts of the Canadian prairie region, but that particular attention should be given to the selection of companion species. Sainfoin longevity there, in contrast to Fort Collins, must be satisfactory.

Phosphorus fertilization often stimulates legume yields while nitrogen fertilization stimulates grass yields. However, fertilizer effects may be different as shown below where a 450 pound per acre yield response resulted when alfalfa was fertilized with either 40 pounds of nitrogen or 20 pounds of phosphorus per acre (Schultz and Stubbendieck 1982).

	Alfalfa	Alfalfa + Ruff
0N + 0P	1380	1770
40N + 20P	1570	2660
0N + 20P	1840	1980
40N + 0P	1820	2610

Table 13.--Relative leguee composition and yields of grass and grass: legume mixtures grown at Ft. Collins (McGinnies and Townsend 1983).

Grass/legume	Legume in stand 1972	Legume in stand 1980	Forage yield 1972	Forage yield 1980
	--- Percent ---		Pounds per acre	
Crested wheatgrass				
Sicklepod milkvetch	13	19	2290	3850
Alfalfa	47	0	1630	2800
Sainfoin	46	0	1520	2920
Grass only, 60-cm rows			2350	2390
Grass only, 30-cm rows			2150	2150
Russian wildrye				
Sicklepod milkvetch	34	18	1580	3140
Alfalfa	72	0	1730	3050
Sainfoin	77	0	1300	2300
Grase only, 60-cm rows			1210	1540
Grase only, 30-cm rows			1340	1470
Pubescent wheatgrass				
Sicklepod milkvetch	12	35	1950	1290
Alfalfa	48	53	1620	2330
Sainfoin	51	0	1440	1200
Grass only, 60-cm rows			2200	1380
Grase only, 30-cm rows			1660	70

Table 14.--Forage yields of legume and legume grass forages grown in mixtures or alternate rows (Hanna et al. 1977).

Forage	Yield Mixed	Yield Alternate Row
	-- Pounds per acre --	
Sainfoin with:		
Crested wheatgrass	4650	4710
Russian wildrye	5160	4770
Pubescent wheatgrass	4320	4710
Sainfoin alone	5630	
Alfalfa with:		
Crested wheatgrass	6160	5740
Russian wildrye	5690	5540
Pubescent wheatgrass	5950	5540
Alfalfa alone	6330	

Applying nitrogen to grass-alfalfa mixtures often favors the grass component with subsequent reduction in the legume portion. Maximum forage yield was obtained with the grass-legume mixture fertilized with 40 pounds of nitrogen and 20 pounds of phosphorus per acre. Yield for the 40N + 0P treatment was not much different (2610 vs. 2660 lb/a). Because the proportion of grass and legume in each treatment was not reported, it is not possible to determine the net effect of fertilization on each component.

Another legume frequently seen with crested wheatgrass, especially along roadsides, is sweet clover. This legume will grow on calcareous soils of low fertility, and is more tolerant of soil salinity than alfalfa (U.S. Salinity Laboratory Staff 1954). However, it is a biennial and may be lost from the plant community during the third growing season unless soil moisture is adequate for reseeding. Even under good moisture conditions it is difficult to get satisfactory stands.

Gomm (1964) grew sweet clover, alfalfa, and crested wheatgrass singly, in mixture and in alternate rows at the Red Bluff Ranch west of Bozeman, Montana. The annual precipitation was 14.5 inches during the study. The two sweet clover varieties produced 3000 to 4700 pounds the second year, but none the third year (Table 15). Alternate rows of Nordan crested wheatgrass and sweet clover also produced well the first year, but yield was composed primarily of crested wheatgrass the second year. As expected, crude protein concentrations were much higher in the legumes than in the grass. The crude protein was also higher in the Nordan component when grown in the grass-legume mixture than when grown alone. This provides evidence that some biologically fixed nitrogen from the legume was available to the wheatgrass.

McWilliams and Van Cleave (1960) examined several pastures in southeastern Montana 17 years after they were seeded with a mixture containing crested wheatgrass (1 lb), western wheatgrass (1 lb), green needlegrass (1 lb), blue grama (1/2 lb), and sandberg bluegrass (1/2 lb) per acre. Crested wheatgrass was also planted singly at the 4-pound rate. The area was abandoned cropland receiving 12 to 13 inches rainfall. A 40-acre block was seeded to the crested wheatgrass alone and an adjacent

30-acre block was seeded to the mixture. These seedings were moderately grazed season-long from 15 April to 15 December. In a nearby pasture 24-foot wide strips of crested wheatgrass were alternated with similar strips of the mixture. It was moderately grazed during May and in winter.

Other forage species encroached upon both the monoculture and mixed seedings reducing the proportion of crested wheatgrass forage from its place in the initial seeding mixture (Table 16). Season-long grazing increased the presence of needle-and-thread, while spring and winter grazing increased green needlegrass in the strips of crested wheatgrass and mixed seedings alike. Seed mixtures resulted in higher yields. Crested wheatgrass provided early green feed and other species provided quality feed later in the season.

Cultivating strips 6 to 18 inches wide in native range and planting in the tilled area has been evaluated in a number of areas. This practice removes competition from low-producing native species and increases the opportunity for establishment of the seeded species. Early attempts at interseeding met with varying success (Heinrichs and Bolton 1950). In southern Saskatchewan, Fairway wheatgrass was seeded into existing native range, and made very large gains in basal cover especially where the original cover was low.

Lutwick and Smith (1977) measured the yield and composition of Ladak alfalfa and Fairway crested wheatgrass, grown singly and in a mixture. The study was conducted near Pincher Creek in southern Alberta where September through July precipitation averaged 17.6 inches. Nitrogen at 0, 40, 80, and 160 and phosphorus at 0 and 71 pounds per acre were surface broadcast as single applications during early spring in each of three years. Plots were harvested when alfalfa was in midbloom. Yields of alfalfa and crested wheatgrass were not affected by phosphorus fertilization. Grass yields are seldom affected by phosphorus fertilization, but the non-response by alfalfa in this study was a puzzlement even to the authors.

Table 15.--Forage yield and crude protein concentration (1959 only) of two legumes and Nordan crested wheatgrass grown singly, in mixture, and in alternate rows at Red Bluff, Montana (adapted from Goss 1964).[1]

Species or mixture	Forage yield 1959[2]	1960[2]	1960[3]	Crude protein 1959[2]
	------ Pounds per acre ------			percent
Sweet clover				
Madrid	4730 a	0	960 a	17.9 a
PI-L57	2950 c	0	660 a	17.7 a
Ladak alfalfa	2700 cd	310 b	--	14.1 c
Nordan crested wheatgrass	1730 e	1300 a	980 a	6.5 e
Mixtures				
Madrid + Nordan	--	--	1280 a	15.0 bc
PI-L57 + Nordan	--	--	720 a	16.9 ab
Ladak + Nordan	--	--	--	13.7 c
Alternate rows				
Madrid & Nordan	4880 a	1610 e	1260 a	--
PI-L57 & Nordan	3580 b	1480 c	940 a	--
Ladak & Nordan	2250 e	1420 a	--	--
Nordan from Madrid + Nordan mixture				9.3 d
Nordan from PI-L57 + Nordan mixture				8.9 de
Nordan from Ladak + Nordan mixture				7.1 de

[1] Means in any column followed by a similar letter are not different as determined by Duncan's Multiple Range test at P = .05.
[2] Seeded in 1958.
[3] Seeded in 1959.

Table 16.--Herbage production in 1957 on areas seeded in 1940 to crested wheatgrass or a grass mixture (adapted from McWilliams and Van Cleave 1960).

Forage	Block Planting Crested	Block Planting Mixture	Strip Planting Crested	Strip Planting Mixture
	---------- Percent ----------			
Crested wheatgrass				
Proportion in 1940 seed mixture	100	25	100	25
Proportion in 1957 herbage	83	11	86	18
1957 yield	---------- Pounds per acre ----------			
Crested wheatgrass	780	170	1010	290
Green needlegrass	0	420	110	1020
Needleandthread grass	20	580	0	10
Total[1]	940	1510	1170	1640

[1] Total yield includes miscellaneous grasses and forbs.

Mayland (1983) reported that the critical range for phosphorus concentration in the upper 6-inch portion of legumes was between .20 and .25 percent P when in the bud to first bloom stage. Alfalfa sampled in the Pincher Creek study contained an average of .19 percent P, but this represented entire top growth from more mature plants and could therefore have been adequate. This is especially true because the legume yield was not increased by phosphorus fertilization. Phosphorus percentages in the fertilized forage (71 lbs/acre) were:

	0P	71P
Alfalfa	.19	.23
Alfalfa in mixture	.17	.20
Crested in mixture	.16	.19
Crested	.16	.23

Thus, forage phosphorus concentration, but not yields, was increased when phosphorus fertilizer was applied to the grass, legume, or grass-legume mixture in this study.

Dry matter yields (lbs/acre) of crested wheatgrass and the grass-legume mixture, but not of alfalfa, were increased by the 40 pound nitrogen treatment the first year after fertilization (Lutwick and Smith 1977):

	0N	40N
Alfalfa	3830	3870
Fairway	1260	2630
Alfalfa plus Fairway	3400	3930

The application of nitrogen to a grass-legume mix, though not determined in this study, frequently results in a reduction of the legume component. The data from the Pincher Creek study, at first glance, appears to follow this observation. The proportion of alfalfa herbage in the alfalfa-crested wheatgrass mixtures for each of three nitrogen fertilizer levels is shown as a percentage of total yield.

	0N	40N	160N
Year 1	75	45	41
Year 2	73	65	61
Year 3	53	50	46

Alfalfa was obviously dying out in the unfertilized plots over the three-year period. Perhaps nitrogen fertilizer promoted grass growth at an earlier period, indirectly reducing soil water available to the alfalfa. That does not, however, explain the decline in alfalfa composition of the nonfertilized plots.

Forage yield and quality of grasses are often increased by nitrogen fertilization (Anonymous 1957). Growing the grass in a legume mixture may achieve similar results as shown in Table 17. Crude protein concentrations in crested wheatgrass grown in the grass-legume mixture were about three percent higher under both fertilized and unfertilized treatments.

Growth Regulators

The forage quality of immature grasses and forbs is often quite high, but as growth continues nutrient quality and digestibility decline as cell wall, fiber and other non-digestible components increase. The dry matter yield may continue to increase up to flowering time, and then decline as leaves fall off and seeds are shattered (Hyder and Sneva 1963a).

Miller et al. (1984) observed that older leaves of crested wheatgrass died and broke off from the plant as new leaves formed (Fig. 8). Crested wheatgrass plants seldom had more than three or four photosynthetically active green leaves. As the fourth leaf developed, the first died; and as the fifth began to elongate, the second died. The dead leaves lay on the ground and were unavailable to grazing animals. When plants were in the boot stage, the upper three leaves were green, but the lower three were dead and unavailable. When the plant reached full maturity, it consisted of a reproductive stem with only two or three attached leaves. More than 25 percent of the total material produced was not available in the standing crop.

Preventing the leaf loss and even the development of the reproductive tillers would produce a higher quality forage. Researchers have applied several growth regulator chemicals to grass, hoping to improve forage quality. Sneva (1967,

Table 17.--Crude protein concentrations in alfalfa and crested wheatgrass grown singly and in mixed stands that were not fertilized, or fertilized once with 180 pounds of nitrogen per acre 1, 2, or 3 years prior to harvest (adapted from Lutwick and Smith 1977).

Forage component	0N	180N 1st yr	180N 2nd yr	180N 3rd yr
	Percent			
Alfalfa	18.4	18.8	18.0	18.7
Alfalfa from mix	17.3	17.5	17.4	19.4
Crested wheatgrass from mix	11.3	16.1	11.2	10.8
Crested wheatgrass	8.0	13.6	8.4	7.6

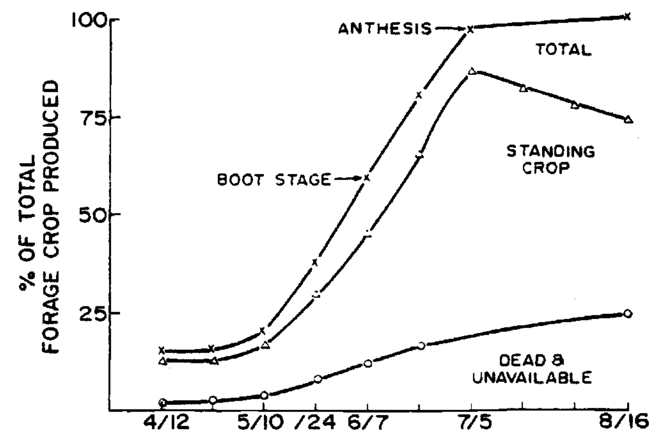

Figure 8.--The percent of standing, dead and unavailable, and total crested wheatgrass crop in relation to total current biomass at Squaw Butte, Oregon (adapted from Miller et al. 1984).

1973c) reported that the application of paraquat (1, 1'-dimethyl-4, 4'-bipyridinium di(methylsulphate)) on range grasses arrested growth and retained the nutrient quality. This procedure allowed "curing on the stump" for later grazing. The effect of 0.2 pounds paraquat and 20 pounds nitrogen applied singly or together on crested wheatgrass was measured at flowering time (Table 18). Paraquat reduced the standing dry matter but combined with nitrogen increased the yield and crude protein concentration.

Rainfall often reduces forage quality by leaching soluble nutrients from the plant and possibly hastening leaf senescence. Forage treated with paraquat retains its quality (Fig. 9) under those conditions, but yields in subsequent years may be reduced. The effectiveness of chemical curing was also shown by the results of a 3-year grazing experiment (Sneva et al. 1973), that showed the average daily gain of yearling steers grazing Paraquat-treated wheatgrass was 0.6 pounds per head higher than that of animals grazing naturally cured wheatgrass.

Table 18.--Forage yield and crude protein concentration in crested wheatgrass as affected by nitrogen and paraquat (Sneva 1967, 1973c).

Treatment	Yield	Crude protein[1]	
	Pounds per acre		Percent
Control	3270b	38a	3.8a
Paraquat	2530a	61b	7.6a
Nitrogen	5880d	68b	3.6a
Paraquat + N	4590c	94c	6.4b

[1]Data within a given column not followed by the same letter are different at the 5% probability level.

Table 19.--Effect of clipping date on forage regrowth production and characteristics at Archer, Wyoming. April to August precipitation was normal at 10.4 inches (adapted from Bedell 1973).

Initial clipping 1972		Regrowth		CP conc. in regrowth		CP yield in regrowth		DMD conc. in regrowth		DMD yield in regrowth	
Date	DM yield	June 29	Sept 7	June 29	Sept 7	June 29	Sept 7	June 29	Sept 7	June 29	Sept 7
	---- Pounds per acre	-----		--- Percent ---		Pounds per acre		--- Percent --		Pounds per acre	
None	-	[1](1970)	[1](1460)	11	11	217	161	64	52	1260	760
May 16	255	1370a	1315a	13(24)[1]	12	178(61)[1]	158	62(79)[1]	50	849(201)[1]	658
May 26	645	885b	955b	16(20)	12	148(129)	115	70(75)	60	620(484)	573
June 2	663	610a	920b	17(18)	14	104(120)	129	68(72)	55	415(479)	506
June 9	945	255d	575c	20(16)	17	51(151)	98	69(71)	58	176(670)	334

[1]Characteristic of initially clipped forage.

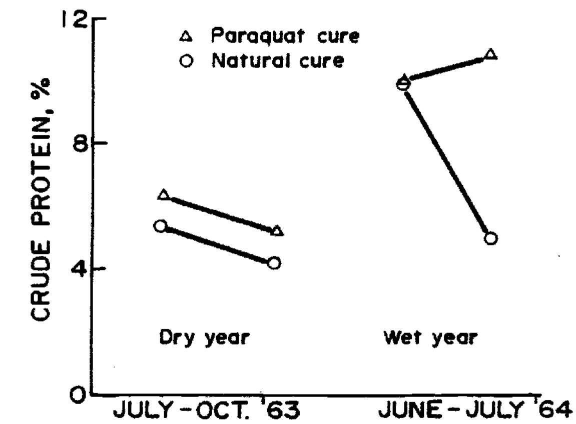

Figure 9.--Crude protein concentration in crested wheatgrass naturally or chemically cured with Paraquat during a dry and wet season at Squaw Butte, Oregon (adapted from Sneva 1967).

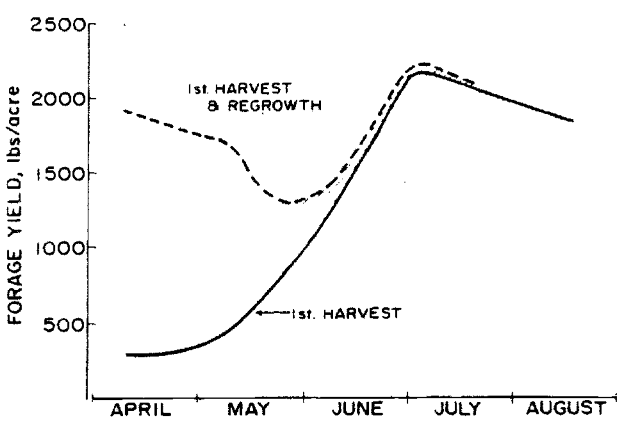

Figure 10.--Standing crop yields of crested wheatgrass, harvested at different dates, and cumulative first harvest plus the regrowth. The shaded area represents regrowth from new tillers at Squaw Butte, Oregon (adapted from Miller et al. 1984).

Forage quality decreases as plants mature. The appearance of reproductive tillers or stems initiates the decline in quality. Bedell (1973) reported that as long as soil moisture was available and the growing point was removed, then growth of crested wheatgrass remained vegetative and highly nutritious (Table 19). Removal of the growing point can be accomplished by high-intensity, short-duration grazing, but timing is very important. Various clipping treatments imposed in 1971 influenced the yield (lbs/acre) in 1972:

1971 Clipping	1972 Yield
May 4	885
May 21	815
June 3	640
June 13	615
July 9	435
Sept 7	1030

The research team at the Squaw Butte Experiment Station examined these relationships (Miller et al. 1984 and Angell et al. 1984), and reported that defoliating crested wheatgrass prior to mid-May had little effect on total forage produced (Fig. 10). Defoliating between mid-May and early June removed the reproductive stems, causing the plant to produce a second group of vegetative tillers. More than 90 percent of the 1200 to 1400 pounds per are of forage produced was leaf material. The reduction in total forage produced was caused by the absence of reproductive stems. Plants that were defoliated prior to mid-May developed reproductive stems just like those that were not clipped and contained less than 30 percent leaf material. Defoliating the plants during the mid-May to early-June period maximizes the amount of leaf material available for later grazing. The quality of this regrowth is also higher because of the larger proportion of leaves in the regrowth (Table 20).

White (1984) searched for means to reduce heading in foxtail barley. Several growth regulators and a desiccant were applied to the grass when floral primordia first appeared, reducing heading and dry matter yields that year and the year following. The *in vivo* dry matter digestibility and crude protein concentrations were increased when compared to the untreated grass. Moisture stress, however, limited the effectiveness of the growth regulators.

Table 20.--Crude protein concentration and digestible organic matter for crested wheatgrass first harvested on given dates, or for regrowth (adapted from Angell et al. 1984).[1]

Date	Crude protein 1st harvest	Crude protein Regrowth	Digestible organic matter 1st harvest	Digestible organic matter Regrowth
	---------- Percent ----------			
4-12-83	-	3.3	-	58
4-26-83	14.7	3.4	77	59
5-10-83	13.6	3.4	80	58
5-24-83	11.0	5.4	73	63
6-7-83	7.8	7.8	71	62
6-20-83	6.4	9.1	72	58
7-5-83	4.9	8.9	65	58
7-18-83	3.6	NR[2]	61	NR
8-2-83	3.3	NR	58	NR
8-16-83	3.1	NR	53	NR

[1] All regrowth data are for samples harvested 8-16-83.
[2] NR is no regrowth.

Haferkamp et al. (1984) reported that the growth regulator Mefluidide [N-(2,4-dimethyl-5-[[(trifluoromethyl)- sulfonyl]amino]-phenyl) acetamide] inhibited reproductive shoot development in crested wheatgrass when applied before or during floral initiation. Mefluidide was applied at rates of 0, .12, and .25 pounds per acre and July dry matter yields were 890 and 700 pounds per acre for the control and treated plots, respectively. The treated forage had higher crude protein and detergent fiber, and reproductive shoot numbers were reduced by 64 to 90 percent. The use of growth regulators to maintain highly nutritious vegetative growth in grasses appears useful, but more research needs to be conducted.

Seed Yield

Most of the immediate concern with crested wheatgrass has centered on its yield of forage. However, seed production is another aspect that is of interest. During the mid-1930's, general information on seeding, forage utilization, and seed production of crested wheatgrass was made available through state and federal publications (Westover 1934, Westover and Rogler 1947, and Jackman et al. 1936).

The earliest document on crested wheatgrass available to this reviewer was an English translation of a Russian language report by Konstantinov (1923). It was a summary of data and observations, made during the period 1910 to 1920 on the wide-spiked "Zitniak" (A. cristatum) and the narrow-spiked "Zitniak" (A. desertorum). He reported 7 year-mean seed yields per plant as 17.7 and 22.7 g and 8 year-mean seed yields per acre of 248 and 364 pounds, respectively. Westover et al.(1932) noted that seed yields at the various experiment stations in the northern Great Plains ranged from a total failure in dry seasons to 600 to 800 pounds per acre in favorable years. The best seed yields were obtained under conditions that also produced the best forage yields. A good average yield would be about 250 to 300 pounds per acre. Double rows have yielded better than single rows, which in turn have generally produced better than rows spaced less than 12 inches apart. Birch and Lang (1961) reported that the application of 50 or 100 pounds of nitrogen per acre in each of four years increased Nordan seed yields in pounds per acre only slightly:

Fertilizer	Seed yields
Check	143
50N	153
100N	150

These yields were obtained from the Archer substation in southeastern Wyoming on the western edge of the central Great Plains. Precipitation averaged 14.4 inches during the 4-year period.

Reynolds and Springfield (1953) reported that about 100 pounds of seed per acre were produced normally by crested wheatgrass in northern New Mexico, with a maximum of 350 pounds per acre in some years.

Windle et al. (1966) measured seed yield at Tetonia, Idaho (elevation 6000 feet and annual precipitation 11.3 inches) in 36-inch rows (Table 21). Seed yields declined with increasing age of stand even though annual precipitation was greatest during the fourth and fifth years. During this same 5-year period, crested wheatgrass seed yields were reduced an average of 35 percent when planted in 6-inch rows compared with 36-inch rows.

Buglass (1964) also noted that crested wheatgrass initially produced several good crops of seed, but then yields declined to a uniformly low level, especially in close-row spacings. Ammonium nitrate fertilizer applied in the fall or spring increased seed yields in an established Fairway sod. Four-year average mean seed yields in pounds per acre were as follows:

N rate	Fall fertilized	Spring fertilized
0	40	40
20	180	100
40	320	170
60	350	140
80	510	260

This illustrated the benefits of nitrogen, especially when applied in the fall. Results of a similar 3-year study at Indian Head, Saskatchewan (8.4 inches annual precipitation) were reported for Summit crested wheatgrass planted in 12-inch rows and fertilized with ammonium nitrate (Fig. 11). There was no seed yield response to phosphorus treatments that included nitrogen (Buglass 1964).

Table 21.--Seed yields of three Agropyron species grown at Tetonia, Idaho (Windle et al. 1966).

Year after seeding	Precipitation	Fairway	Nordan	Siberian P-27
	Inches	----- Pounds per acre -----		
1st	12.9	630	740	690
2nd	12.2	360	440	500
3rd	11.5	130	250	280
4th	18.6	80	200	330
5th	17.0	70	120	210
Mean	13.9	250	350	400

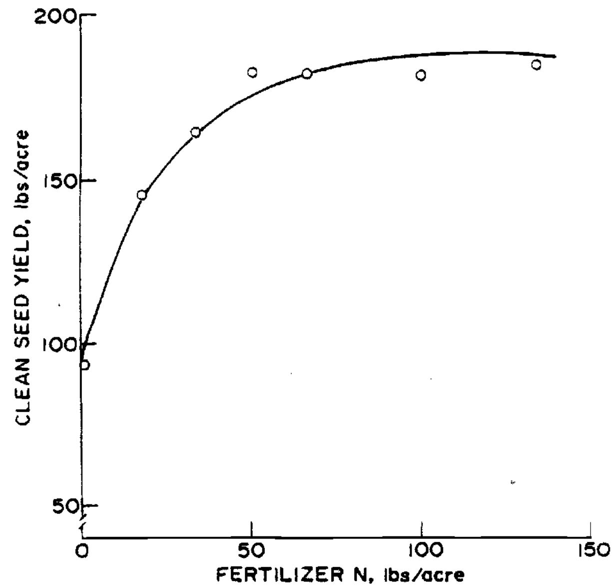

Figure 11.--Annual mean clean seed yield of Summit crested wheatgrass planted in 12-inch rows, fertilized annually and harvested during the third through the sixth year after seeding at Indian Head, Saskatchewan (adapted from Buglass 1964).

The effects of row spacing and nitrogen fertilizer on seed yields were evaluated in another 4-year experiment using Summit crested wheatgrass grown at Indian Head, Saskatchewan (Buglass 1964). Rows were spaced 6, 12, and 36 inches apart, or 12 inches apart and grouped by 2, 3, or 4 rows with 36 inches between groups. Seed yields (lbs/acre) obtained for plots receiving 0 or 68 pounds N per acre were:

Row spacing	ON	68N
6	90	210
12	120	230
36	220	220
2 x 12	140	190
3 x 12	130	180
4 x 12	120	190

Bennett et al. (1954) reported 4-year mean clean-seed yields of crested wheatgrass grown at Nephi, Utah were 50, 56, and 53 pounds per acre when grown at solid, 30-inch or 48-inch row spacings. The application of nitrogen fertilizer did not change these yields (annual rainfall was 12.7 inches). Yields as threshed were 313, 571, and 279 pounds per acre during 1937, 1938, and 1940, respectively.

Schaff et al. (1962) measured seed yields for 8 to 42 entries (including a wide range of crested wheatgrass genetic materials) established annually over an 11-year period. Seed yields were 513, 420, and 308 pounds per acre during the first, second, and third years, respectively. Seed weights were 0.56, 0.53, and 0.53 g/200 seeds, respectively.

McGinnies (1971) published the only information available on components of crested wheatgrass seed yield in relation to row spacing. This study was conducted over a 5-year period west of Fort Collins when the average rainfall was 14.7 inches. The mean data values found for clean seed are given in Table 22. During years of average precipitation, only plants of the 18- and 24-inch spacings produced enough to warrant harvesting. Seed yields ranged from 1 to 266 pounds per acre, with the highest yields at wider spacings in dry years and closer spacings in wet years. McGinnies opted for an 18-inch spacing and recommended that fields be cultivated.

Table 22.--Seed yield components for crested wheatgrass (McGinnies 1971).

	Yield for spacing, inches			
Parameter	6	12	18	24
Clean seed, lbs/acre	107	131	146	181
Seedheads/ft of row	13	27	37	51
Seedheads/ft	25	27	24	25
Weight, g/100 seedheads	4.5	5.7	7.1	8.5
Weight, g/200 seeds	.32	.34	.34	.36

Klages and Stark (1949) reported crested wheatgrass seed production at Moscow and Aberdeen, Idaho. They noted that 4-year mean yields were on the order of solid stand < solid stand + N < cultivated rows < cultivated rows + N. Seed yield in relation to age of seeding was year 2 > year 3 > year 4 = year 5. The fertility of culms in relation to age of seeding was on the order of year 2 > year 3 > year 4 > year 5. Fertility of culms in relation to row spacing was solid stand < solid stand + N < cultivated row < cultivated row + N.

Knowles and Kilcher (1983) reported relative seed yields (lbs/acre) of four varieties of crested wheatgrass grown in western Canada during 1976 to 1979:

Variety	Relative seed yield	Relative hay yield
Fairway	100	100
Parkway	124	104
Summit	98	110
Nordan	102	102

In general, the maximum yields of clean seed having a high germination will be obtained in young stands that are planted on 12- to 18-inch row spacings, fertilized with about 40 pounds N per acre, and cultivated.

Shrub Competition

Seeding of crested wheatgrass has continued for the past five decades on western rangelands. Historically, few seedings have remained free of shrub invasion for an extended period of time (Blaisdell 1949). Competition between big sagebrush and crested wheatgrass depressed yields of grass (Frischknecht 1963, Robertson 1947). The decision on when to control sagebrush depends largely on the rate of reinvasion by the shrub and the level of suppressed forage production.

Rittenhouse and Sneva (1976) summarized data from several locations. They reported that the production (lbs/acre) of crested wheatgrass declined 3 to 5 percent of its potential with each 1 percent increase in sagebrush crown cover from 0 to 22 percent. The average grass yield was related to crown cover in the relation:

Yield = 1030 - 42 (% crown cover of sagebrush)

The standard error of the estimate was 128 pounds per acre. These data are in general agreement with those of Gobena (1984) in Utah (Table 23). Assuming 30-inch diameter crown cover for the shrubs, the regression of forage yield on cover was:

$$Y = 1230 - 73 \ (\%\ \text{cover}),\ r = -.95$$

This equation predicts a 6 percent reduction in forage yields for each 1 percent increase in sagebrush canopy cover.

Frischknecht (1963) contrasted the effects of big sagebrush and rubber rabbitbrush on the production of crested wheatgrass grown at Benmore. Active growth periods of big sagebrush and crested wheatgrass coincide, whereas the growth of rabbitbrush occurs later. The depressed yields of grass around big sagebrush plants were associated with highly developed lateral brush roots in the grass-root zone. In contrast, relatively few lateral roots of rubber rabbitbrush occur in this zone.

Caldwell and Richards (1986) have studied the greater competitiveness of crested wheatgrass compared with bluebunch wheatgrass when growing with big sagebrush. They reported that while the root biomass of crested wheatgrass was similar to that of bluebunch (6.9 vs 7.0 oz or 196 vs. 199 g on the average), crested wheatgrass had more fine roots and greater length (11.3 vs 7.33 miles/plant or 18.2 vs 11.8 km/plant). These characteristics, together with a greater rooting depth by crested wheatgrass (> 40 vs 35 inches or 100 vs 90 cm for conditions at Green Canyon near Logan), undoubtedly made crested wheatgrass a better scavenger of nutrients and soil water. They provided a very interesting diagram illustrating root distributions of the two grasses and one shrub.

Table 23.--Herbage production for four densities of big sagebrush in central Utah (adapted from Gobena 1984).

Sagebrush Plants Acre^{-1}	Square Feet Plant^{-1}	Feet Between Plants	New Production, lbs/acre: Sagebrush	New Production, lbs/acre: Crested Wheatgrass	Percent Cover[1]
0	-	-	0	1180	0
40.5	1076	35	12	1160	0.5
724	60	8	200	860	8.2
1242	33	6	376	90	14

[1]Cover is calculated on an assumed 30-inch diameter shrub.

Other papers presenting similar information on the effect of competition between big sagebrush and crested wheatgrass include those of Frischknecht and Bleak (1957), Hull and Klomp (1974), Johnson and Payne (1968), and Robertson (1969, 1972).

FACTORS AFFECTING QUALITY OF CRESTED WHEATGRASS

The first requirement in developing a range livestock management program is a quantitative and qualitative inventory of forage resources (Raleigh 1970). Many of the factors affecting the quantitative production of crested wheatgrass have already been discussed. This section reviews factors affecting the quality of crested wheatgrass.

Forage quality is a many-faceted term. It includes digestible organic matter, crude protein, readily fermentable carbohydrates, and available vitamins and minerals. Quality may also relate to the esthetic appearance, smell, taste, or touch of the forage to the grazing animal. This discussion deals primarily with _in vitro_ and laboratory assessment of quality, even when used to explain grazing-animal behavior.

Site Effects

Some quality characteristics of field-grown materials may vary more between sites than between cultivars. This was true for the two _A. cristatum_ and three _A. desertorum_ cultivars tested by Junk and Austenson (1971) in western Canada. Location differences were found for all characteristics measured except iron and molybdenum. Varietal differences were _in vitro_ dry matter digestibility (IVDMD), fat, crude fiber (CF), and stem diameter. The organic quality constituents, phosphorus and potassium, were associated with leafiness.

Rangeland sites may be described by climatic characteristics including temperature, solar radiation and precipitation, and by edaphic characteristics including soil structure, fertility, waterholding capacity, salinity, and alkalinity. These factors may also affect forage quality. Cook (1959) noted that cattle had a high preference for crested wheatgrass and several other grasses growing on unfavorable sites, located on low productive knobs previously dominated by juniper. No further description was provided, but the soils on these knobs may have been slightly hydrophobic, increasing the runoff and making them more droughty. Utilization on the unfavorable site was approximately twice that on the favorable site (Table 24). The preferred plants were more leafy and had lower stem/leaf ratios than the undesirable plants. Forage from the unfavorable site had slightly higher concentrations of crude protein and ash, but lower concentrations of lignin, cellulose, and ether extract (Table 25).

Droughty spots may occur because of gravelly subsoils or on knolls having low water holding capacity. This phenomenon also occurs where solodized-solenetz soils (Natra argid soils), commonly called slick-spots, are intermingled with normal soils. The slick spot has a sodium saturated B-horizon with very low water infiltration characteristics, making it a droughty soil. This soil complex occurs throughout the northern Great

Plains, on the lower end of the Snake River Plateau, and elsewhere. Observations of animal preference for plants growing in 10- to 50-foot diameter areas have been noted,[1] but not well documented. Soil conditions like the above result in a patterned droughtiness and subsequent patterned grazing behavior by animals.

Wurster et al. (1971b) described the quality of four grasses grown on a silty clay loam interspersed with areas of droughty soil in South Dakota. Forage samples were taken from smooth bromegrass and intermediate, crested, and Siberian wheatgrass at 6-day intervals from 23 May to 15 August. The forage grown on the droughty soils had higher digestibility and acid detergent fiber (ADF) values than did forage grown on moister soils. The higher digestibility of forage grown on the droughty soil was most pronounced in the early maturing crested wheatgrass, and may be related to slower development of structural material under suboptimum conditions. Dry matter yields were significantly lower on the droughty area for all species except intermediate wheatgrass.

Seasonal Effects

The morphological development of a grass progresses from the appearance of vegetative tillers and succulent leaves to leaf maturation and senescence. Reproductive tillers will develop and the plant will flower, set seed, and upon further curing will shed seed. This process is genetically controlled and carried out under restraints of the environment. Hyder and Sneva (1963a) noted that crested wheatgrass, like other grasses, continues to accumulate dry matter until flowering time when dry matter yields will level off for a while and then decline as leaves are lost and seed is shed (Fig. 7).

Table 24.--Plant characteristics and animal utilization of three wheatgrasses at the end of the spring grazing season on adjacent favorable and unfavorable sites in Utah (Cook 1959).

Site and species	Stem/leaf ratio	Height of seed culm	Utilization
		Inches	Percent
Favorable			
Crested wheatgrass	2.46	24	35
Intermediate wheatgrass	1.15	27	63
Tall wheatgrass	1.12	33	31
Unfavorable			
Crested wheatgrass	1.67	20	80
Intermediate wheatgrass	.71	24	96
Tall wheatgrass	.45	28	66

Table 25.--Mean chemical characteristics of three wheatgrasses grown on adjacent favorable and unfavorable sites in Utah (Cook 1959, Cook et al. 1958).

Site conditions	Plant part	Ether extract	Protein	Ash	Lignin	Cellulose
		Percent				
Favorable	Leaves	4.7	12.1	13.5	5.8	27.4
	Stems	1.6	8.1	7.4	6.9	33.6
	Whole plant	2.8	9.6	9.7	6.5	31.2
Unfavorable	Leaves	3.8	12.5	14.3	5.5	25.9
	Stems	1.5	8.9	7.5	6.5	32.2
	Whole plant	2.6	10.8	11.0	6.0	28.7

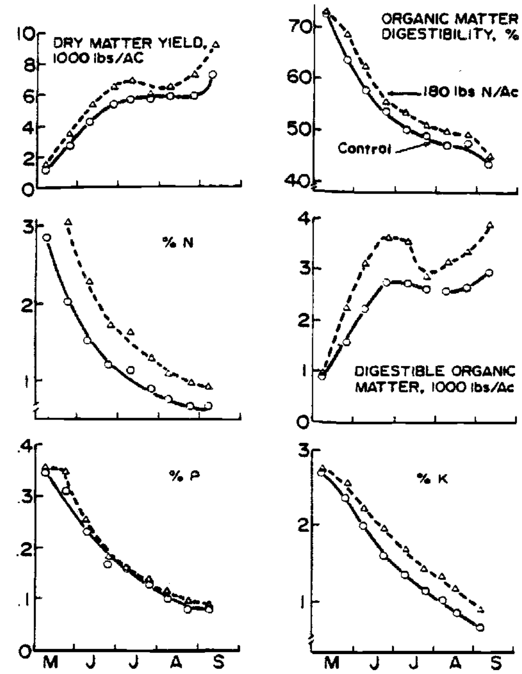

Figure 12.--Two-year mean yield and nutritional component values of crested wheatgrass grown at Swift Current, Saskatchewan with zero or 180 lbs N per acre (200 kg N/ha) and irrigated with 10 inches (26 cm) of supplemental water annually (adapted from Lawrence and Knipfel 1981).

If fall regrowth occurs then dry matter yields may continue to increase as shown in Figure 12.

During morphological development photosynthetic products are cycled through soluble sugars having a highly digestible organic matter (DOM) to other materials having low solubility and low DOM (Cook et al. 1958). Crested wheatgrass forage that has 70 percent DOM in early spring may decline to 50 to 55 percent DOM at flowering and even less by midsummer (Fig. 12). The amount of DOM increses up to flowering time. It may then decrease if either percent DOM or yield decreases, or may increase if fall regrowth occurs. Fertilizer nitrogen increased the amount of DOM by 35 percent when compared with the control. Crude protein concentration, shown as percent nitrogen, was elevated about three percentage units (0.5 percent N x 6.24). Even though nitrogen may change the amplitude of these response curves, the shape of the curve is not greatly different from that of the control response.

Seasonal changes in forage quality parameters are also available for a 9-inch precipitation area in south central Idaho (Murray et al. 1978). Like the results from Swift Current (Fig. 12), data from the Idaho location show curvilinear decreases in total digestible dry matter (TDDM), crude protein (shown as % N) and digestible cell wall (DCW) presented on an organic matter basis (Fig. 13).

[1]R.B. Murray, Dubois, Idaho, personal communication.

Willms et al. (1980) used polynomial regression analyses to describe the change in chemical constituent concentrations in A. desertorum and four other grasses sampled between 14 February and 31 May 1974 in south central British Columbia. Forage quality was high initially, but declined as the grasses matured. There were few differences in quality when new growth on fall-grazed pastures was compared with new growth on fall-deferred pastures.

Forage quality may have various definitions to researchers and producers. As a consequence, there is a variety of information in the literature. Rauzi (1975) reported the yield, crude protein and levels of several minerals in crested wheatgrass grown at Archer, Wyoming (Table 26). Dry matter yield continued to increase up to the time of anthesis or flowering. The quality parameters, however, declined as the plants matured.

Patton and Gieseker (1942) monitored changes on two quality parameters in Agropyron cristatum and A. desertorum grown in central Montana (Table 27). A general increase in cellulose and lignin occurred in both species as the plants matured. The A. desertorum plants were of lower forage quality than A. cristatum at the seed-ripe and seed-shed stages, because of higher cellulose and lignin contents.

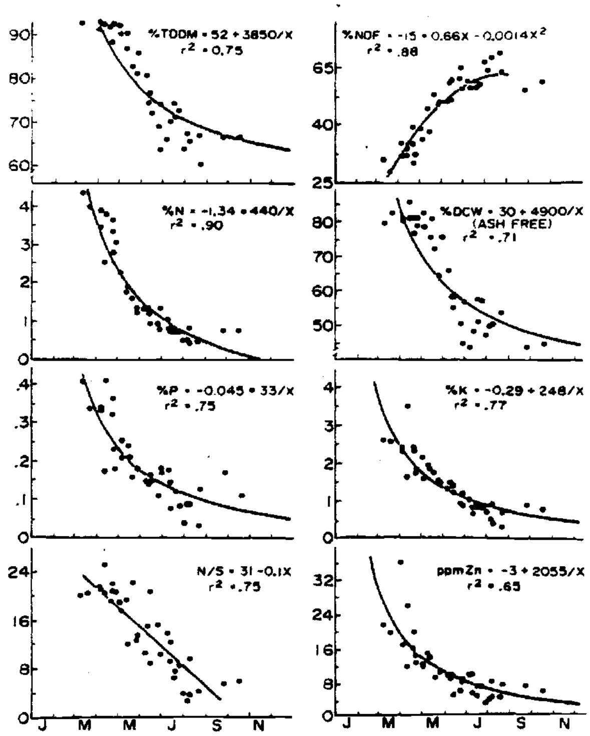

Figure 13.--Seven-years of forage quality data regressed against Julian date (x-axis) for crested wheatgrass grown at Saylor Creek in south central Idaho. Abbreviations are total digestible dry matter (TDDM), total nitrogen (N), phosphorus (P), nitrogen/sulfur ratio (N/S), neutral detergent fiber (NDF), digestible cell wall on an organic matter basis (DCW), potassium (K) and zinc (Zn) (adapted from Murray et al. 1978).

Table 26.--Three-year-mean of chemical constituents in crested wheatgrass for five phenological stages of growth in southeastern Wyoming (Rauzi 1975).[1]

Component	Stage of maturity				
	Early veg.	Late veg.	Boot	Seed head emerged	Early-full bloom
	Percent				
Crude protein	23a	20b	16c	13d	10e
Calcium	.37a	.35ab	.31c	.29c	.23d
Phosphorous	.26a	.22b	.23b	.22b	.19c
Potassium	2.07a	1.95b	1.76d	1.79c	1.35e

[1]Values for given component with the same letter are not different at P <.05.

Table 27.--Mean cellulose and lignin concentration in Agropyron desertorum and A. cristatum at five maturity stages (adapted from Patton and Gieseker 1942).

Stage of Maturity	Sampling date	Cellulose		Lignin	
		A. de.	A. cr.	A. de.	A. cr.
		Percent			
Vegetative	5/16	20.2	22.5	5.3	5.7
Heading	5/31	25.2	25.5	7.2	7.5
Flowering	6/12	27.6	27.9	8.9	9.3
Seed ripe	6/26	32.4	29.1	13.2	11.6
Seed shed	9/4	40.4	36.9	15.6	14.1

In another study (Sotola 1940), crested wheatgrass forage samples were taken at two week intervals during the May through September period. Ash, crude fiber, and nitrogen free extract (NFE) increased with maturity. Crude protein decreased markedly at first and then changed very little after early summer.

Knowledge of the seasonal quality differences is helpful in prescribing grazing programs. Heinrichs and Carson (1956) harvested forage from nine grasses, including Fairway and Summit crested wheatgrass, at six stages of maturity. The samples were analyzed for proximate constituents, crude protein, crude fiber, calcium, phosphorus and ash. Nitrogen free extract was calculated. After they had examined the data, they recommended that crested and intermediate wheatgrass be used for spring and early summer grazing, smooth brome and green needlegrass for summer, and Russian wildrye and streambank wheatgrass for fall and possibly winter grazing.

Wight et al. (1983) reported that crested wheatgrass and Russian wildrye were more resistant to damage from early spring grazing than were most native species in the northern Great Plains. They also noted that Russian wildrye remained quite palatable after dormancy, making it particularly valuable for late summer and fall grazing.

A similar set of quality factors in A. cristatum was monitored over a 13-year period at Manyberries and Swift Current (Clarke and Tisdale 1945). These factors also demonstrated a reduction in forage quality as the wheatgrass matured (Table 28).

Table 28.--Mean chemical composition of Agropyron cristatum plants sampled at various stages of maturity from 1927 to 1940 at Manyberries and Swift Current, Alberta (adapted from Clarke and Tisdale 1945).

Stage of Maturity	Sampling date	Crude protein	Crude fiber	Ether extract	Nitrogen free extract	Total ash	Calcium	Phosphorus
		Percent						
Vegetative	5/10	22.7	19.9	2.7	45.8	8.85	.42	.27
Heading	6/8	13.9	29.2	1.6	48.0	7.45	.29	.24
Flowering	6/29	11.7	33.1	1.8	46.3	7.12	.32	.19
Seed ripe	7/30	8.5	32.5	1.9	51.1	5.92	.33	.14
Seed shed	10/21	4.5	34.7	1.9	52.1	6.85	.30	.05

The Canadians harvest mature crested wheatgrass for winter feeding programs. *Agropyron cristatum* harvested in late August was hammermilled through a .25 screen and pelleted. It was then compared with other sheep diets composed of wheat straw and hay processed in a similar way (Knipfel 1977). The straw-alfalfa mixtures were adequate for the pregnant ewe, but the wheatgrass diet was deficient in crude protein. A previous study (Beacon et al. 1973) reported that pelleting of various ratios of crested wheatgrass to concentrate mixtures increased dry matter intake, weight gain, and feed efficiency by 15, 47, and 23 percent, respectively, when fed to growing lambs. The crested wheatgrass served as a good roughage in this diet.

Plant Parts

Leaves have higher concentrations of crude protein, ash and ether extract than stems, and lower concentrations of lignin and cellulose (Table 25). Leaves initially make up most of the standing biomass of crested wheatgrass. As the plant matures, however, this proportion declines to almost zero as first the sheath and then the stem makes up an important part of the above ground biomass (Wurster et al. 1971a). Figure 14 illustrates the portions of leaf, sheath, and stem inflorescence, and the IVDMD of the plant parts of two *Agropyrons* grown in the field at Brookings, South Dakota. The IVDMD of each part, including the leaves, declines because of the formation of strongly bonded structural materials that are used for enlarging cells and thickening cell walls.

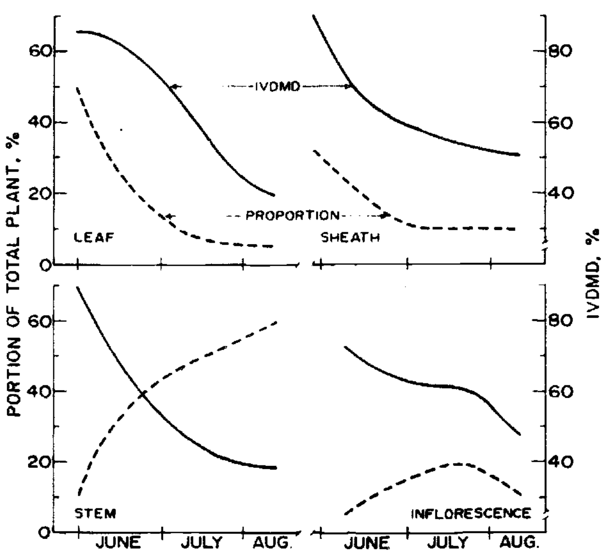

Figure 14.--Mean seasonal trends in the relative dry matter proportions (dotted lines) and *in vitro* dry matter digestibility (IVDMD) of those plant parts (solid lines) for P27 and Nordan crested wheatgrass grown at Brookings, South Dakota (adapted from Wurster et al. 1971a).

Seven wheatgrasses including three *Agropyrons* (Fairway, Nordan and Siberian) were grown on a calciorthid soil near Kimberly, Idaho. Whole plant samples were harvested at anthesis and separated into leaf, stem, and head components. The chemical composition of each is shown in Table 29. Of the three plant parts, stems had the highest dry matter and highest nitrate nitrogen, as expected. The heads had the highest soluble nitrogen, phosphorus, copper, and zinc concentrations, also as expected. Additional data on the nitrogen content of reproductive organs of crested wheatgrass are given by Sneva (1983). These mineral data illustrate the differences that occur in the composition of plant parts. The availability of these nutrients to grazing animals, however, may be different from their concentration in the plant part.

Table 29.--Mean chemical composition of seven wheatgrasses grown at Kimberly, Idaho, and harvested at anthesis. (Mayland unpublished).

	Leaves	Stems	Heads
	Percent		
Dry matter	42 ± 18	45 ± 10	19 ± 9
K	2.50 ± .43	2.10 ± .21	1.60 ± .15
Mg	.18 ± .01	.07 ± .01	.09 ± .01
Ca	.50 ± .12	.16 ± .03	.16 ± .05
P	.15 ± .01	.13 ± .03	.27 ± .03
Cl	.77 ± .17	.82 ± .12	.29 ± .06
N	3.40 ± .31	1.80 ± .33	2.70 ± .35
H_2O Sol. N	.96 ± .18	.67 ± .15	1.43 ± .26
t-aconitate	1.80 ± .5	.26 ± .32	.20 ± .16
	Parts per million		
NO_3 - N	300 ± 110	760 ± 120	380 ± 100
Na	310 ± 130	450 ± 250	300 ± 180
Fe	130 ± 50	60 ± 50	76 ± 15
Mn	70 ± 30	30 ± 9	30 ± 10
Zn	14 ± 2	12 ± 2	24 ± 2
Cu	5 ± 1	6 ± 3	9 ± 1
	Parts per billion		
Se	83 ± 24	98 ± 19	120 ± 60
Co	80 ± 20	80 ± 20	100 ± 90
Mo	870 ± 450	330 ± 260	630 ± 340
	milliequivalents per kilogram		
Ash alk.	700 ± 80	440 ± 50	330 ± 15
HFA	72 ± 11	31 ± 4	56 ± 4

Mineral Concentrations

Only a few studies on minerals in forages deal specifically with crested wheatgrass. Such reports may be categorized under one of two headings: those that discuss mineral concentrations in relation to animal health, and those that provide baseline data on mineral concentrations in relation to geochemistry of top soil or spoil material. Allway (1975) and Kubota and Allaway (1972) discuss the elements essential to animals and their role in the soil-plant-animal cycle.

Forage minerals and animal health.--Crested wheatgrass samples from various areas in northern Nevada (Dye 1962, Blincoe and Lambert 1972) contained the following mineral concentrations in parts per million:

	Range	Mean
Cobalt	0.56 to 23	12
Copper	0.84 to 5.4	2
Iron	180 to 802	117
Manganese	19 to 59	29
Molybdenum	0.8 to 3.4	2.4
Zinc	8 to 24	13

The cobalt concentrations were unusually high when compared with values from other plants (Lambert and Blincoe 1971), but the findings were verified by several different analytical procedures. The authors concluded that crested wheatgrass was a potential accumulator of cobalt. It is possible that their samples were contaminated with cobalt during collection, transportation, or processing. Analysis of separate samples taken from the San Jacinto seeding (an area also sampled by Blincoe and Lambert 1972), produced values of about 0.1 part per million (H. F. Mayland, unpublished), comparable with data from other sources.

Murray et al. (1978, 1979) sampled crested wheatgrass forage for mineral concentrations between March and December over a period of seven years (Fig. 13). The elements in crested wheatgrass in order of their being or becoming deficient for animals during the grazing season are as follows: Nitrogen (crude protein) > phosphorus > zinc > potassium. Magnesium deficiency often occurs in animals grazing crested wheatgrass. However, this occurs because of other factors that reduce its availability to ruminants.

Forage minerals and geochemistry.--Crested wheatgrass is common to many areas of the Western Energy Belt where spoils from coal and uranium mines are revegetated. Crested wheatgrass is used as a biological indicator of the solubility or availability of minerals in top soil and spoil. A mineral profile of the forage sample provides information about the elements that are entering the food chain.

Contamination of the forage by dust or soil splash must be considered in determining the selection, forage sampling, and chemical analysis of forages (Mayland and Sneva 1983). High iron concentrations (greater than 100 µg/g) are often associated with soil contamination, but some effects may be explained by differences in soil pH.

Ebens and Shacklette (1982) provided summary statistics for 59 elements contained in mineral and biological materials from 25 study areas. Cultivated cereals and native grasses and shrubs are among the biological materials included in the study. Crested wheatgrass is identified for some sites. This reference is a useful source of elemental-concentrations expected in soils and plant materials and the natural error associated with such values.

Fairway crested wheatgrass was selected as the biological subject to monitor mineral solubilities in a topsoil and spoil area in east-central Wyoming (Erdman and Ebens 1979). The concentration of 26 elements is reported for forage samples obtained at the seed ripe stage from a reclaimed-coal spoil and a topsoiled area (Table 30). Forage grown on the spoil contained higher concentrations of cadmium, cobalt, fluorine, manganese, uranium, vanadium, and zinc, but a lower concentration of phosphorus than forage grown on the topsoiled area. The data provide a valuable reference for those wishing to compare elemental-concentration data.

In another study, forage samples were collected in June and August from three reclaimed mine sites and adjacent undisturbed native sites in south central Montana and eastern Wyoming (Stanley et al. 1982). The plant material was analyzed for 14 elements by ICP (inductively coupled plasma atomic emission spectrometry) which, along with possible soil contamination of samples, may explain some of the variations. Selenium and crude protein concentrations were also determined. Nitrogen and nickel were the only elements not also reported by

Table 30.--Geometric mean concentrations and observed ranges of elements in crested wheatgrass from topsoil borrow areas and from reclaimed spoil areas in eastern Wyoming (Erdman and Ebens 1979).[1]

Element	Topsoil borrow areas Mean	Topsoil borrow areas Range	Reclaimed spoil areas Mean	Reclaimed spoil areas Range
	Parts per thousand			
Al	.69	.30-2.7	1.1	.41-3.7
Ca	2.6	2.2-3.0	2.3	1.6-3.5
K	11	9-14	12	7.2-16
Mg	1.2	.8-1.7	1.1	.8-1.7
[3]P	1.3	.9-1.9	.84	.41-1.7
S, total	1.7	1.0-2.7	1.8	.9-3.3
Si	12	7-19	9.8	4.4-19
	Parts per million			
B	15	11-28	17	11-48
Ba	12	6-22	10	6-22
[2]Cd	.054	.016-.15	.082	.034-.15
[3]Co	.069	<.05-.13	.099	<.06-.44
Cr	.27	11-.60	.40	.16-1.1
Cu	2.8	1.6-6.0	3.2	1.6-5.9
[2]F	4.5	3-6	6.2	3-10
Fe	190	81-350	270	120-740
Hg	.011	.01-.02	.011	.01-.02
Li	.82	.29-1.8	1.3	.58-4.0
[3]Mn	16	5.6-36	39	23-140
Mo	.39	<.4-.58	.43	<.4-.84
Na	8.4	3.6-22	11	3.5-21
Se	.23	.10-.60	.27	.10-.70
Sr	25	16-39	25	14-41
Ti	16	3-50	26	11-74
[2]U	.021	<0.2-.067	.062	<.03-.55
[2]V	.63	<.5-.98	.82	<.7-1.5
[3]Zn	20	13-28	26	18-32

[1]Data are based on 10 samples and their analytical duplicates from each area; concentrations are expressed on a dry basis.
[2]Means are significantly different at the P<0.05 level.
[3]Means are significantly different at the P<0.01 level.

Table 31.--Chemical composition and apparent digestibility of crested wheatgrass tissue eaten by sheep during spring and summer (after Cook and Harris 1968).

Growth stage	Chemical composition					Apparent digestibility		
	Ether extract	Total protein	Lignin	Cellulose	Phos-phorus	Protein	Total nutrients	Metabolizable energy
	Percent							Kcal/lb
Fifth leaf 5-9-53	3.3	20	3.3	19	.27	16.2	76	1325
Early head 6-8-53	2.3	13	7.4	31	.23	6.6	51	683
Anthesis 6-16-54	2.4	11	7.3	31	.18	5.9	52	751
Hard seed 7-10-54	3.6	9	7.3	28	.14	5.5	57	914

Erdman and Ebens (1979). Stanley et al. (1982) reported that copper values ranged from 20 to 40 ppm which seems high by a factor of 10X when compared with other data. Zinc values ranged from 30 to 50 parts ppm and seem high by a factor of 2X.

Element profiles for plants growing on the reclaimed areas provide baseline data for the long term studies. In addition, these profiles are useful in determining the forage quality and suitability for animal consumption, and in determining the success of top-soiling the reclaimed areas.

Nielson and Peterson (1973) evaluated the ability of 54 species including grasses and legumes to grow on copper mine tailings. Nothing grew on untreated tailings. Agropyron species were among the 16 that were established on leached tailings fertilized with nitrogen, phosphorus, and trace minerals. Grasses were more tolerant of salinity and high copper than were legumes.

Digestible Nutrients

Forage quality can be defined in many ways, but usually is related to some animal response, such as feed intake, weight gain, reproduction, or production of milk or wool (Murray et al. 1978). Sometimes forages are fed directly to animals to determine apparent or true digestibility and these values may be compared with information obtained through indirect methods. Cook and Harris (1968) using sheep examined both the chemical composition and the apparent digestibility of crested wheatgrass at four different growth stages (Table 31). Parameters like ether extract, crude protein (CP = %N x 6.24), phosphorus, metabolizable energy, and total nutrients are factors that relate positively to quality. Parameters like lignin and cellulose may contribute negatively to overall quality.

Sosulski et al. (1960) reported the lignin concentrations in five Agropyron species grown in the field in southeastern Washington. The lignin percentages at five growth stages were:

Early vegetative	4.0
Boot	4.7
Preheading	6.3
Heading	7.1
Flowering	7.7

These values were consistently higher than the concentrations in bromegrass and orchardgrass. Differences in lignin concentrations between Agropyron cultivars were as great or greater at flowering than earlier. The lignin percentages for whole plants sampled at the flowering stage of maturity were:

Fairway	7.6
Siberian	7.6
A 1770	8.0
Nordan	8.3
Commercial	8.3
Nebraska 10	8.4

Sims and Cook (1970) evaluated the digestibility of four wheatgrasses harvested between 20 June and 22 July, and reported that cellulose digestibility was higher in plants grown in dense stands, perhaps relating to the retarding of plant maturation. Cellulose digestibility was also higher in leaves than in stems. Dry matter digestibility (%) was not affected by stand density, but was related to cultivars:

	DMD
A. cristatum	52
Intermediate	50
Pubescent	49
Tall	47

The forage quality of seven grasses was determined at anthesis in a 7-year study conducted in eastern Montana (Table 32).

Forage quality generally declines as crude protein values decline with plant progression from vegetative to seed-ripe stages. The levels can also be affected by cultural practices. For example, crested wheatgrass can be fertilized (Fig. 7), treated with growth regulators (Fig. 9) or planted in mixtures with a legume. Schultz and Stubbendieck (1983) showed the effect of fertilizer nitrogen and phosphorus on the crude protein percentages of alfalfa or a mixture of alfalfa and A. cristatum:

	Alfalfa	Alfalfa + *A. cristatum*
ON + OP	15.6	10.3
45N + OP	13.9	10.8
45N + 22P	14.3	11.2
ON + 22P	15.0	11.0

In the same study a small difference in IVDMD between alfalfa and the alfalfa-grass mix was reported, but no difference relating to fertilizer treatment.

	Alfalfa	Alfalfa + *A. cristatum*
ON + OP	63	61
45N + OP	64	62
45N + 22P	65	61
ON + 22P	64	61

Some of the older studies on forage quality reported data for parameters like ether extract (Tables 25 and 28) and digestible organic matter (Fig. 10, Table 16). Data on the negative aspects of forage quality are provided by nitrogen free extract (NFE), crude fiber (CF), cellulose and lignin (Tables 25, 27, and 28). Each of these parameters provides evidence that as the plant develops morphologically it becomes increasingly less nutritious for the grazing animal.

A newer method of measuring forage quality determines cell wall residues (total of lignin, cellulose and hemicellulose) and replaces crude fiber analysis (Van Soest 1966). The residues are considered to be chemical components that cannot be completely digested, separated into components that are (1) insoluble in a neutral detergent solution (NDF), (2) soluble in an acid detergent solution (hemicellulose), and (3) insoluble in the same solution (acid detergent fiber (ADF) including cellulose, lignin, lignified nitrogen compounds, and silica). The cell contents are soluble in neutral detergent solution. The method separates the highly digestible from the partially digestible and indigestible components of forage.

Table 32.--Forage yields, estimated in vivo dry matter digestibility (IVDMD), and crude protein (CP) concentrations in grasses grown at Sidney, Montana (White and Wight 1984).

Species	Yield	IVDMD	CP
	Pounds per acre	--- Percent ---	
Altai wildrye	3000	62	12
Russian wildrye	2900	61	10
Crested wheatgrass	2900	60	9
Green needlegrass	2700	60	10
Pubescent wheatgrass	2700	60	8
Meadow bromegrass	2100	63	9
Reed canarygrass	1600	65	15

The method of Van Soest (Goering and Van Soest 1970) was used to estimate the dry matter digestibility of seven grasses grown in south central Idaho over a seven-year period (Murray et al. 1978). The NDF (a measure of total fiber) data for crested wheatgrass are given in Figure 11. The values begin at about 25 percent in early March and increase to about 60 percent by early July, reflecting the maturation of the plants. The digestible cell wall (Fig. 13) is given on an ash free basis and as such is not exactly the inverse of the NDF curve, but it does have the inverse shape. The true dry matter digestibility (TDMD) corrected for ash is also shown in Figure 13. On an ash-free basis, the TDMD values decline from 90 percent early in the season to 60 to 65 percent during midsummer.

White and Wight (1981) using another approach estimated the *in vivo* digestibility of seven grasses plus alfalfa and cicer milkvetch grown in eastern Montana. The samples were subjected to a modified Tilley and Terry two-stage procedure as were three forage samples whose true dry matter digestibility was known from previous animal studies. Regression analyses were employed to calculate the estimated *in vivo* digestible values for crested wheatgrass and two wildrye species (Fig. 15). Digestibility of all species declined with increasing maturity. The wildrye species were more digestible during late summer and autumn than crested wheatgrass. This relationship was also verified by animal response data and leads to the recommendation that crested wheatgrass be used in early spring and wildrye in late summer and autumn.

Coulman and Knowles (1974) reported significant differences in IVDMD between plants of the diploid *A. cristatum* and those of the tetraploid *A. desertorum* strains. The values were highly correlated with proportion of leaves in the sample. The *A. cristatum* strains were more palatable and superior in IVDMD. Like others, Coulman and Knowles measured a sharp decline in IVDMD between heading and the end of anthesis with little subsequent change thereafter.

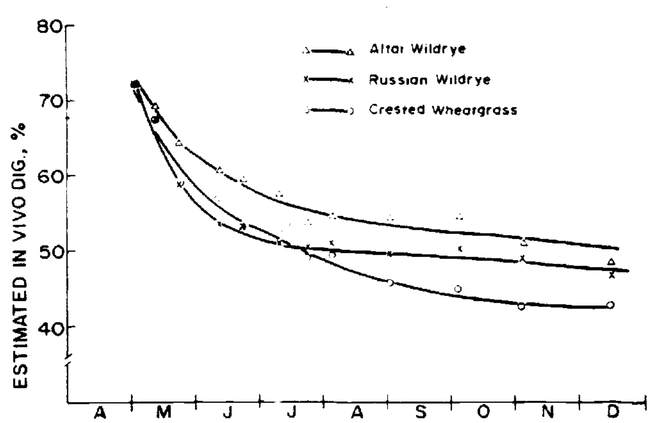

Figure 15.--Estimated *in vivo* digestibility of three grasses grown at Sidney, Montana (adapted from White and Wight 1981).

Lawrence (1978) published an evaluation of the yield and quality characteristics of thirty grasses grown in southwestern Saskatchewan. Data on forage yield, nitrogen, phosphorus, and digestible organic matter were provided for samples taken during spring, summer, late summer, fall, and late winter. The favorable and unfavorable characteristics were shown by an alpha-code in a summary table. A more quantitative approach would have been desirable.

Index values are often used in programs involving selection for two or more traits. Vogel et al. (1984) calculated an index (NI) based on forage yield and IVDMD for 38 crested wheatgrass introductions and experimental strains. Strains with high positive NI values usually had both high yield and high IVDMD values. The opposite was true for strains with negative NI values. The index, when calculated for two years and two locations in Nebraska, ranged from -4.00 to 2.80. The varieties Ruff (A. cristatum) and Nordon (A. desertorum) were among the top six selections. Strains with the highest first-cut yields also had high second-cut yields and were taller but earlier in maturity than the low yielding strains. Later maturing strains tended to be higher in IVDMD. Most of the differences were probably due to factors other than maturity, because most of the strains headed within the same week.

Using the above approach, the four Agropyrons described by Lawrence (1978) were indexed for yield and digestibility traits:

A. desertorum	1.18
A. cr. x A. de.	.42
A. cristatum	- .25
A. sibericum	- 1.34

The above indices were based equally on yield and digestibility. If desired, factors can be differentially weighted and more than two factors can be used. The index is a simple tool by which entries can be numerically ranked, remembering that some quality factors are not easily quantified.

Smoliak and Bezeau (1967) determined the chemical composition and in vitro digestibility of crested wheatgrass, Russian wildrye and pubescent wheatgrass relative to a standard of early-cut, chopped, dehydrated legume hay (Fig. 16). The nutritive value of crested wheatgrass was between that of the other grasses prior to the soft dough stage while Russian wildrye was superior to the other grasses after curing.

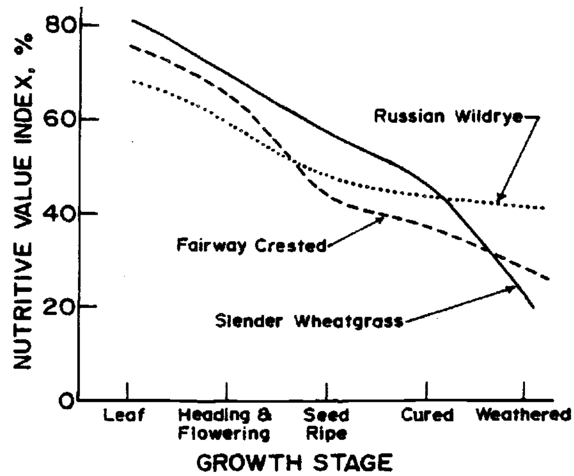

Figure 16.--Nutritive value index for three grasses compared to legume hay at Manyberries, Alberta (Smoliak and Bezeau 1967).

Feeding studies and chemical analyses are the two most common methods used to estimate quality. Feeding studies are labor intensive and costly, therefore not frequently used. Laboratory methods that predict forage value based on chemical composition and in vitro digestibility are also expensive and time consuming. An alternative may be the infrared reflectance (IR) technique that has potential for rapid, routine analyses and prediction of a wide variety of forage quality characteristics and animal responses to forages.

Park et al. (1983) evaluated the IR technique on forage samples of A. cristatum, A. desertorum, A. sibericum, and A. cristatum x A. desertorum. The instrument responses to each of 80 samples were regressed against forage quality data for several nitrogen and fibrous fractions in the laboratory. Values for these fractions were next predicted by the IR technique for 30 additional samples. The predicted values were then compared with laboratory results (Table 33). The IR technique can be used to predict some chemical values with accuracy and precision similar to conventional wet-chemistry methods. However, the IR technique requires a large number of representative samples upon which to develop and test the predictive equations.

Table 33.--Actual values of nitrogen and fiber fractions determined by wet chemistry compared with those values determined by IR for 30 samples of Agropyron cristatum, A. desertorum, A. sibiricum, and A. cristatum x A. desertorum (adapted from Park et al. 1983).

Component	Mean Actual	Mean Predicted	Standard Deviation Actual	Standard Deviation Predicted	Std. error of difference	r^2
	Percent					
Total nitrogen (N)	1.01	1.00	.18	.16	.04	.96
N soluble in NaCl	.43	.40	.08	.07	.04	.76
Neutral detergent fiber	64.1	64.0	2.6	2.5	.96	.86
Acid detergent fiber	36.2	36.0	2.2	1.8	1.01	.83
Acid detergent lignin	5.24	5.19	.66	.53	.53	.38

The methods of forage chemical analyses are chosen to provide estimates of animal response in terms of preference, intake, digestibility, etc. Handl and Rittenhouse (1975) compared three methods of estimating digestibility for the purpose of predicting dry matter intake by cattle grazing crested wheatgrass range. Digestibility was determined by (a) the _in vitro_ method of Tilley and Terry using a 48-hour pepsin digestion, (b) the lignin ratio, and (c) the method of Van Soest for soluble cell wall constituents. Forage digestibility averaged 61, 63, and 72 percent for the three methods, respectively. Because the forage was highly digestible, variation among methods was small and each responded similarly within dates. Estimates of dry matter intake derived from (a) and (b) did not differ significantly, but both were greater than estimates derived from (c), which were lower than expected, perhaps because of the difficulty in estimating cell wall constituents in fecal samples.

Troelsen (1971) estimated the consumption of digestible energy by sheep from the concentrations of _in vitro_ digestible energy, cell wall constituents, and crude fiber in coarse roughage. Four grasses, including _A. cristatum_ and alfalfa were harvested annually at four to seven growth stages over a period of four years and fed to sheep. The concentration of _in vitro_ digestible energy, cell wall and crude fiber were each related to intake of digestible energy. For grass hays, _in vitro_ digestible energy gave the best prediction of consumed digestible energy with a coefficient of variation of 18 percent compared with 24 percent for other fiber measures.

Biological factors affecting forage quality include disease and insects. Karn and Krupinsky (1983) found field grown intermediate wheatgrass plants naturally infested with stem rust had lower IVDOM and higher NDF, ADF and lignin than smut-free plants. Intermediate wheatgrass plants infected with leaf spot diseases had lower IVDOM and higher NDF than healthy plants.

Clipping and Sampling

Factors affecting the proportion of leaves on the plant will have a major impact on forage quality. Cook et al. (1958) found that frequent clipping of crested wheatgrass increased forage quality. This was probably a result of increased vegetative growth and higher leaf to stem ratios. The frequent clipping, however, resulted in decreased dry matter yields. More recent research at Squaw Butte has shown that clipping crested wheatgrass during late May removed the apical meristem, increased regrowth and increased the proportion of leaf tissue (Miller et al. 1984). Clipping at that time, however, decreased the overall yield because reproductive tillers were not formed.

Sheep, and perhaps cattle also, will discriminate against plants having reproductive tillers and will be attracted to those having only vegetative tillers (Murray 1984). Because animals graze quite selectively, choosing some plants and plant parts while refusing others, it may be very important that herbage sampling mimic the same selectivity exhibited by the animals.

Hart et al. (1983a) checked their ability to manually sample crested wheatgrass forage against esophageal collections at Cheyenne, Wyoming. Crested wheatgrass samples were collected over the 15 May to 30 June period and analyzed for crude protein, lignin, ADF and IVDMD (Fig. 17). They found that as the season advanced there were linear increases in lignin and ADF fractions and linear decreases in crude protein and IVDMD. Quality data for the manually-collected samples did not mimic well the data from the esophageal-collected samples. Agreement can be achieved only after careful observations of grazing selectivity followed by careful sampling. Another source of error is that differences between grazing animals may be as great as differences between collection techniques.

FACTORS AFFECTING THE ANIMAL RESPONSE TO CRESTED WHEATGRASS

Many interacting factors influence animal response to grazing crested wheatgrass. These include not only what they eat, but the quantity and quality of the ingested forage.

Grazing Preferences

It is probable that animals ingest greater quantities of a preferred species, increasing their performance in terms of milk or wool production, or live weight gain. The less-preferred plants may have lower protein, magnesium, moisture, or carbohydrate concentrations, or higher silica levels.

Smoliak (1968) made daily observations of the grazing habits of yearling ewes having daily access to crested wheatgrass, Russian wildrye and native range at Manyberries, Alberta. Ewes preferred crested wheatgrass from initiation of grazing (late April - early May) until the third week of June. They then grazed Russian wildrye for about three

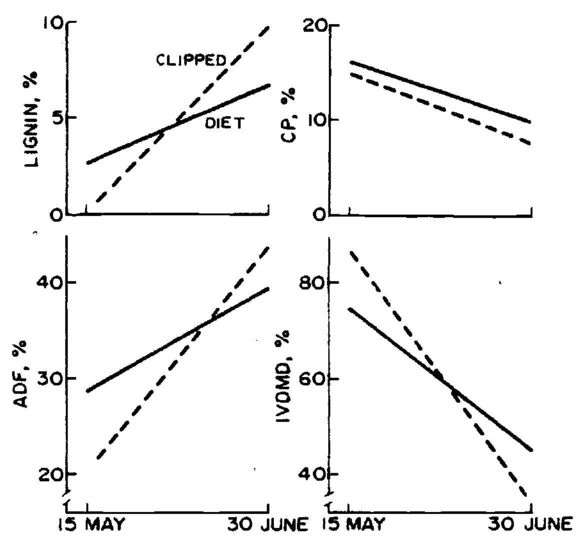

Figure 17.--Lignin, crude protein (CP), acid detergent fiber (ADF) and _in vitro_ dry matter disappearance (IVDMD) values for clipped or esophageal (diet) samples for one season at Cheyenne, Wyoming (adapted from Hart et al. 1983a).

Table 34.—Forage production and relative animal preference for six grasses at three growth stages (adapted from Gesshe and Walton 1980, 1981).

Forage	Production			Preference Rating[1]		
	Vegetative	Heading or flowering	Seed ripe	Vegetative	Heading or flowering	Seed ripe
	--------- Pounds per acre ---------					
Bromegrass	2070	5080	5480	1.2	1.0	1.2
Creeping red fescue	2590	4580	4630	1.1	.6	.0
Crested wheatgrass	1380	2800	3720	.8	.2	.0
Intermediate wheatgrass	2560	5490	5140	1.2	.2	.0
Red top	1120	3640	5650	.9	1.1	1.5
Russian wildrye	580	700	1410	1.2	1.9	1.7

[1] Values greater than 1.0 indicated preference, values less than 1.0 indicated avoidance.

weeks, shifted to native range from mid-July until mid-August, and then grazed the Russian wildrye again until late October. Toward the end of the grazing season ewes preferred crested wheatgrass during periods of deep snow and cold weather. The preference for a certain type of herbage was influenced not only by its palatability, but also its seasonal availability and accessibility. (See section on 'Winter Use').

A study evaluating cattle preference for several forages, including crested wheatgrass, was conducted at Kinsella, Alberta (annual rainfall 16.0 inches)(Gesshe and Walton 1980, 1981). Six grasses, three legumes and a forage mixture were seeded into three sets of pastures, each having four replications of each forage. The forages were grazed at three stages of maturity and grazing preferences were assigned (Table 34). Values greater than 1.0 indicated preference, less than 1.0 avoidance. Russian wildrye had the highest overall rating, but lowest dry matter yield of the grasses, attributed to wide row spacing (14 inches), and slow establishment. Crested wheatgrass had the lowest preference rating of the six grasses. The rating was highest at the vegetative stage, decreasing with advancing maturity to zero at the seed ripe stage.

Gesshe and Walton (1980) noted that each of the forages tested on the University of Alberta farm were all common pasture species, any one of which would be readily utilized by cattle if no alternatives were offered. The relatively high quality of all species in the early vegetative stage encouraged more random grazing. During later grazing periods forage quality differences became much greater and the multiple regression equation accounted for 94 percent of the variation in the animal preference ratings.

$$Y = -4.2 + .04X_2 + .07X_8 + .12X_9 - .07X_4 - .12X_7$$

where Y = Animal preference rating
X_1 = % moisture
X_2 = % leaves (W/W)
X_4 = % crude protein in leaves
X_7 = % crude protein in stem
X_8 = % crude fiber in stem
X_9 = % acid pepsin DM disappearance in stem

The moisture content of the forage was the major positive influence on the preference rating (R^2 = .77) in the seed-ripe stage where

$$Y = 2.42 + .16X_1 - .15X_8 + .01X_2$$

Many ranchers on semiarid rangeland know the value of moisture to 'soften up' mature forage and increase its palatability. It is also not surprising that crude protein, digestibility and crude fiber components appear in the regression equations indicating their importance in determining animal preference ratings.

Preference rankings are increased by some characteristics and decreased by others as shown below.

<u>Positive factors</u>
- Succulent forage
- High leaf:stem ratio
- High crude protein
- High digestibility

<u>Negative factors</u>
- Seed stalks present
- High lignin concentration
- High dry matter concentration
- Low leaf:stem ratio

Preference rankings of crested wheatgrass depend upon stage of growth. The Agropyrons are 'at their best' in early spring, but lose quality with advancing maturity. The dry matter intake of cattle restricted to mature crested wheatgrass will average 1.25 percent of body weight (Havstad et al. 1983) even when the organic matter digestibility averages only 33 to 43 percent. This level is not sufficient to maintain weight gains achieved earlier in the grazing season (Fig. 18). Under such circumstances cattle, if given a choice, would graze other species that were more palatable and nutritious.

Palatability of crested wheatgrass can be manipulated to some extent by applying nitrogen fertilizer. Thomas et al. (1964) applied nitrogen to a crested wheatgrass pasture in the Black Hills. The nitrogen increased yields, crude protein, phosphorus and calcium concentrations. Deer preferred the nitrogen-fertilized grass because of its increased nutritional value and succulence.

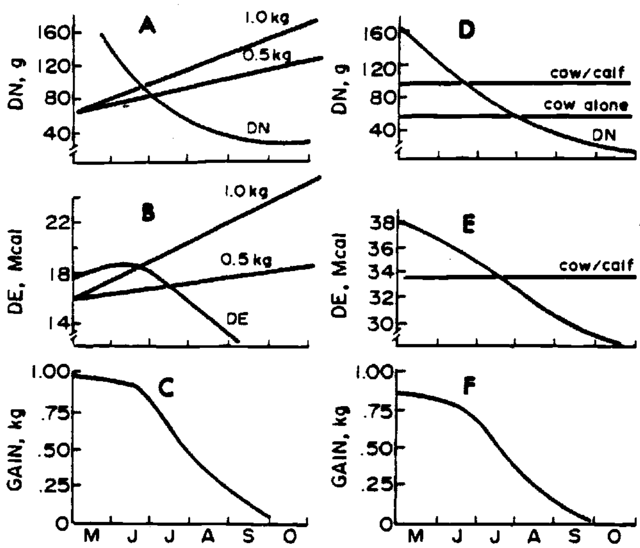

Figure 18.--Digestible nitrogen (DN, Fig. a) and digestible energy (DE, Fig. b) required for maintenance plus 0.5 or 1.0 kg (1.1 or 2.2 lb) daily gain by 250 kg (550 lb) yearling steers, the amount of DN (Fig. a) and DE (Fig. b) they will get from the range forage at Squaw Butte, Oregon, and the average daily gain (Fig. c). The DN (Fig. d) required by a cow-calf pair or cow alone, the DE (Fig. e) required by the cow-calf pair, the amount of DN (Fig. d) and DE (Fig. e) they will get from the range forage at Squaw Butte, and the average daily gain (Fig. f) by the suckling calf (adapted from Raleigh 1970).

Roberts (1977) noted cattle preference for nitrogen fertilized crested wheatgrass when they broke into an exclosure at Benmore, Utah and selectively grazed the fertilized plots.

There may be other factors that affect animal preferences for given forages. Chewing insects may have amino acid receptors that help select their host plants. Grasshoppers and locusts detected and preferentially fed on grasses treated with the amino acids proline and valine (Haglund 1980). These amino acids commonly increase in plants during drought stress. This may explain why chewing insects seek out drought-stressed plants, or it may be simply the higher leaf/stem ratio (Table 24) in the stressed plants. Cattle may also select forage that may be slightly water stressed[2].

Springfield and Reynolds (1951) also evaluated the grazing preferences of cattle for certain grasses. The grasses had been seeded into one-quarter acre plots, in three replications. Four years later it was grazed during the period 21 August through 12 September by 24 cows, 6 calves and 1 bull. This experiment was conducted in the Ponderosa pine type near Vallecitos, New Mexico where the annual precipitation averaged 22 inches. Utilization was determined by clipping the forage at the beginning, midpoint, and end of study.

Utilization percentage at the end of the first week of grazing was:

Orchardgrass	26
Smooth brome	24
Slender wheatgrass	21
Crested wheatgrass	9
Kentucky bluegrass	9
Tall oatgrass	9
Western wheatgrass	1
Big bluegrass	1

As grazing continued and removed the more palatable forage the less palatable species became more important. By the second week dry matter intake of big bluegrass was 43 percent and that of orchardgrass was only 1 percent. Succulence strongly influenced preference and dietary composition was related to forage moisture concentration ($r = .69$). There was less discrimination when mature forage was wet from rain or heavy dew.

Cattle preferences for cured herbage of six grasses grown at Squaw Butte were evaluated by Hyder and Sneva (1963b). Relative palatability or cattle preference was evaluated in the first two weeks during August 1959-1961. Percent utilization of the cured forage was:

Big bluegrass	69
Tall oatgrass	65
Beardless wheatgrass	44
Pubescent wheatgrass	42
Siberian wheatgrass	17
Crested wheatgrass	15

Sheep at Swift Current (Heinrichs 1959) ranked the palatability of grasses in the following order: Russian wildrye > Summit crested wheatgrass > bromegrass = Fairway crested wheatgrass. In September and October cattle and sheep gained weight on Russian wildrye, but not on the other species. It should be noted that _A. desertorum_ ranked over _A. cristatum_ when indexed for yield and digestibility traits (see section Digestible Nutrients).

Fourteen grass accessions, including nine _Agropyrons_, were evaluated for yield, nutrient quality and palatability to sheep at Dubois, Idaho (Murray 1984). The results show a strong preference for the Russian wildrye cultivars and a low preference for the _Agropyrons_, especially in midsummer (Table 35). Murray noted that when preference was considered in the absence of seed stalks, then all cultivars were similarly preferred by sheep. Preference decreased as numbers of seed stalks increased.

Animal Performance

Crested wheatgrass initiates growth in early spring. Dry matter continues to increase until anthesis and then may remain static for several weeks prior to decreasing (Fig. 8). Throughout this period the leaf/stem ratio and forage quality decline until late summer or fall when standing forage is mainly stems and seed heads. An exception to this decline occurs when fall moisture is adequate for regrowth. A second exception occurs when early grazing removes the reproductive point

[2] R.B. Murray, Dubois, Idaho, personal communication.

Table 35.--Nutrient quality and palatability characteristics of 14 grasses at the Dubois, Idaho Sheep Experiment Station (adapted from Murray 1984).

Accession	Relative value: Leafiness[1]	Relative value: Crude Protein[2]	K (Ca+Mg)[3]	Sheep use[4]: 5/14	Sheep use[4]: 7/14	Sheep use[4]: 9/15	Index[5]	Rank
	----- Percent -----							
Russian wildrye								
Bozoisky	100	100	1.99	7.0	7.9	9.6	295	1
RWR-V13	99	85	1.81	7.5	8.7	9.6	284	2
RWR-128	98	82	1.65	7.2	8.7	9.7	279	3
Tall fescue	93	72	2.23	5.1	8.3	9.1	252	4
Bluebunch X _quackgrass_	50	61	2.46	4.6	5.7	6.2	175	5
Agropyron cristatum								
Fairway-128	33	74	1.67	2.7	1.3	3.0	134	6
CWG-163	36	71	1.40	1.8	1.8	2.9	132	8
Fairway	38	72	1.17	1.9	1.1	1.7	128	9
CWG-R	30	75	1.09	2.2	1.6	1.4	125	10
Agropyron desertorum								
Nordan	32	79	1.35	4.3	.5	1.2	134	7
CWG(M34-38)	36	71	1.32	2.0	.9	1.8	125	11
CWG (V6-7)	22	79	1.38	2.2	.3	1.6	117	13
Agropyron fragile	33	67	1.25	2.2	.9	1.5	118	12
A. cristatum X _A. desertorum_	28	66	1.58	2.1	.8	1.1	110	14

[1] Leafiness, as percent of biomass during late August, relative to Bozoisky Russian wildrye.
[2] The sum of crude protein values for biomass relative to Bozoisky Russian wildrye.
[3] Expressed on a chemical equivalency basis.
[4] This is on a scale of 0 to 10 with 10 being maximum use.
[5] The index is the sum of the leafiness on 3 July relative to maximum plus the sum of crude protein concentrations on 30 June and 15 September relative to maximum, plus the sum of the sheep use values on the three dates relative to maximum. All values were initially expressed on a percentage basis for a possible 300 point maximum.

(apical meristem) and the plant produces mostly leaves and few seed stalks.

Nutrient levels during the green-feed period are adequate for grazing livestock (Springfield 1963, Watkins and Kearns 1956, and Woolfolk 1951). There may be some exceptions to this, because heavily lactating cows can lose weight on green crested wheatgrass[3]. Perhaps these animals were not able to eat enough dry matter because high moisture limited dry matter in the vegetative material. After anthesis, weight gains of yearlings and calves begin to decline.

Raleigh (1970) showed that the decline in animal performance was associated with a decline in digestible nitrogen and digestible energy in the forage at Squaw Butte. Forage quality of crested wheatgrass may be maintained for longer periods on higher elevation ranges or where summer precipitation encourages continued growth or regrowth in the fall.

[3] D.C. Adams, Miles City, Montana, personal communication.

Cattle and sheep have been used to assess the nutritive value of crested wheatgrass and other grasses and legumes on Utah foothill ranges (Cook and Stoddart 1961, Cook and Harris 1968, Houston and Urick 1972). Weight gains produced by ewes, lambs, cows, and calves during early spring grazing are given in Table 36. Weight gains during late spring began to decline as forage progressed toward anthesis.

Table 36.—Weight gains by sheep and cattle grazing crested wheatgrass on Utah foothills during early and late spring (after Cook and Harris 1968).

Period	Daily gain: Ewes	Lambs	Cows	Calves
	---------- Pounds	----------		
Early spring	.37	.56	1.5	2.3
Late spring	-.25	.39	.3	1.6

Hart et al. (1983b) measured animal-grazing performance on crested wheatgrass grown at Cheyenne. The pastures were grazed by steers during three spring periods and calves during two autumn periods at each of two stocking intensities (Table 37). Steers grazing the highly nutritious spring growth gained about 2.4 pounds per animal-day. Calves grazing much lower quality forage during the autumn period gained only about 20 percent of the steer rate. In addition, calves gained only 12 pounds per 1000 pounds of forage, while steers gained 4 to 5 times more efficiently.

In a 12-year study conducted on seeded pastures in central Colorado (Currie and Smith 1970), yearling heifers grazed four forage grasses plus a mixture of crested wheatgrass, yellow sweet clover, smooth brome and intermediate wheatgrass. Weight gains per acre and on a daily animal basis were:

	Gain/acre	Gain/day
Smooth brome	40.2	1.52
Crested wheatgrass	59.2	1.67
Intermediate wheatgrass	52.3	1.92
Mixture	71.6	1.81
Russian wildrye	48.8	1.53

The forage mixture produced the greatest gains over the entire period even though it tended to become dominated by crested wheatgrass. Perhaps the resulting mixture maintained a quality green-feed period longer than the monocultures. Or perhaps the heifers had a high preference for some of the feed, ate more, and performed better. The possible animal preference for species other than crested wheatgrass might explain why it began to dominate the stand.

Stocking Intensity

Harris et al. (1958) measured the effects of light (50%), moderate (65%), and heavy (80% utilization) stocking rates with cattle on _A. cristatum_ in a Utah study. Spring grazing at the moderate rate produced significantly greater individual gains than grazing at the heavy rate. Yields of rabbitbrush declined 53, 40, and 23 percent under light, moderate, and heavy grazing while yields of big sagebrush increased 6, 32, and 79 percent, respectively.

Table 37.--Beef production in spring by steers and autumn by calves at two stocking rates on crested wheatgrass at Cheyenne, Wyoming (Hart et al. 1983b).

Parameter	590 lb steers		425 lb calves	
Stocking rate				
Animals/acre	.46	.64	.96	1.26
Days/acre	22	30	54	60
Days/1000 lbs forage	23	32	24	31
Animal gain				
Lbs/day	2.38	2.44	.58	.41
Lbs/acre	45	74	28	26
Lbs/1000 lbs forage	48	68	12	12

The longterm animal response to stocking intensity will depend in part on the effect such stocking rates have on plant vigor. Horton and Weissert (1970) studied plant vigor on three sites in the oakbrush-sagebrush type of central Utah that had been grazed at 15 to 25, 60 to 70, and 85 to 90 percent utilization for eight years. At the end of that time vigor was mesured by average height of the tallest seed stalk, dry weight per square inch of basal cover, number of seed stalks per square foot, and percentage ground cover. Vigor was highest with the 60 to 70 percent utilization level.

Reynolds and Springfield (1953) measured weight gains by cattle in northern New Mexico stocked at light (15 to 35%), moderate (36 to 55%), heavy (56 to 75%), and very heavy (75% utilization). Daily weight gains were 1.7, 1.8, 1.5, and 1.1 pounds per animal with the 36 to 55 percent utilization rate producing the most gain.

Weight gain responses were measured in another New Mexico study for 1-month periods in early spring (Springfield and Reid 1967). Cow-calf pairs in an 8-year study and yearlings in a 4-year study were grazed on both crested wheatgrass and native range. Average daily gains (lbs/day) were:

	Crested Wheatgrass	Native Range
Cows	3.23	1.21
Calves	2.18	1.16
Yearlings	1.98	1.50

Weight gain by cows was largely compensatory gain, but nevertheless the data illustrate the availability and nutrition of the crested wheatgrass. The poorer performance on native range may have resulted from inadequate dry matter intake.

Grazing studies on crested wheatgrass were conducted as early as 1933 at Mandan, North Dakota (Sarvis 1941). Two-year old steers grazed crested wheatgrass at an average intensity of 52 animal days per acre (range of 14 to 86) for eight years. Grazing occurred from mid-May through July and occasionally in August. Daily weight gains in pounds were:

15 days in May	3.92
30 days in June	2.24
27 days in July	1.63
18 days in August	1.30

Johnson (1959) reported the results of a grazing intensity study on crested wheatgrass, smooth brome, intermediate wheatgrass, Russian wildrye, and a sweet clover-crested wheatgrass-smooth brome mixture in central Colorado. Grazing occurred from April or May to October on a put-and-take approach. Cattle expressed a higher preference for smooth brome than crested wheatgrass in the mixture by grazing it to a shorter stubble height. The mixture produced significantly more herbage than either species alone (Table 38) largely because of the presence of sweet clover. The biennial life cycle of this clover was not discussed. Yields decreased under all intensities of grazing, perhaps due to decreased rainfall. Grazing smooth brome and intermediate wheatgrass to 2-inch stubble height reduced the stand, but grazing Russian wildrye to 1.5-inch stubble had little effect on forage yield. Animal gains per day were greatest on the intermediate wheatgrass. Gains per

Table 38.--Mean annual forage and yearling heifer production under a five-pasture grazing system of four grasses and a mixture (adapted from Johnson 1959).

	Crested wheatgrass			Smooth Brome			Sweet clover, Crested + Brome			Intermediate wheatgrass			Russian Wildrye		
	L	M	H	L	M	H	L	M	H	L	M	H	L	M	H [1]
Forage production, lb/acre	1200	820	990	730	730	580	1320	1310	1040	910	1090	650	910	840	790
Utilization, percent	31	46	67	31	41	61	35	46	65	33	47	63	11	20	41
Yearling, days/acre	27	32	46	19	24	29	31	37	47	29	34	32	31	34	46
Yearling gains, lbs/day		1.70			1.70			1.90			2.05			1.62	
Yearling gains, lbs/head		60			46			70			56			50	
Yearling gains, lbs/acre		51			37			60			51			50	

[1] Grazing intensities: Light (L), Moderate (M), and Heavy (H) corresponding to stubble heights of 6, 4, and 2 inches, respectively. Stubble heights for Russian wildrye were 4.5, 3, and 1.5 inches, respectively.

animal and gains per acre, however, were greatest for the forage mixture.

Grazing intensity studies were also conducted on a crested wheatgrass stand in central Colorado (Currie and Smith 1970). The intensity was judged by a stubble height of 6, 4, 2, and 1 inch which corresponded to a utilization of 31, 46, 67, and 81 percent, respectively. Forage production over the 13-year study averaged 1300, 1300, and 1200 pounds per acre for the 31, 46, and 67 percent utilization treatments. The authors concluded that the 2-inch stubble height appeared to be an optimum intensity of grazing.

Intensity data were also obtained from a study conducted in a northeastern Nevada area of about 16 inches annual precipitation (Robertson et al. 1970b). The 480-acre area was cleared of big sagebrush and seeded with a mixture containing Fairway, Standard and western wheatgrass, and bulbous bluegrass in 1944. Crested wheatgrass soon became the dominant species with small amounts of Sandberg bluegrass, bulbous bluegrass, and streambank wheatgrass (ranked in decreasing frequency). Forage yield during a 3-year period averaged 1130 pounds per acre. Responses measured on moderate and heavy intensity treatments were:

	Moderate	Heavy
Forage utilization, %	54	74
Steer gains, lbs/day	2.2	2.1
Steer gains, lbs/ acre	23.5	30.8

Gray and Springfield (1962) studied the performance of ewe-lamb pairs at four stocking rates on crested wheatgrass in northern New Mexico. The 3-year study provided the following results for May and June use:

	Light	Heavy
Forage utilization, %	39	84
Sheep days per acre	75	150
Lamb gains, lbs	76	73

Crested wheatgrass on these pastures produced 980 pounds dry matter per acre compared with only 110 pounds per acre on native range.

Another grazing intensity study on crested wheatgrass was conducted on foothill range in central Utah at 5600 feet elevation (Bleak and Plummer 1954). Ewe-lamb pairs were stocked at three intensity levels (light, moderate, and heavy) for seven years (Table 39). Sheep were placed on the pasture again in the fall at an intensity that provided a total of 151, 158, and 167 sheep days per acre for spring and fall on the light, moderate, and heavy use treatments, respectively. Crested wheatgrass maintained equally good production under light (59%) and moderate (71%) use during the 7-year period, but declined on the heavy use pasture because many of the plants died and those that were alive were small. The rate of lamb gains was slightly higher on the light versus moderate use

Table 39.--Sheep responses to grazing crested wheatgrass at three intensities for seven years in central Utah (Bleak and Plummer 1954).

Parameter	Utilization intensity Light	Moderate	Heavy
Utilization, percent	59	71	88
Spring grazing			
Sheep days/acre	117	134	149
Lamb gains, lbs/acre [1]	28.2	32.0	35.41
Ewe gains, lbs/acre [1]	8.2	15.7	5.6
Lamb gains, lbs/day [1]	.64	.58	.58
Ewe gains, lbs/day [1]	.18	.30	.08
Autumn grazing [2]			
Sheep days/acre	34	34	18
Sheep gain, lbs/acre	10.7	7.5	2.4
Sheep gain, lbs/day	.32	.17	.16

[1] Large year to year variation.
[2] These same pastures were grazed in the spring.

pasture, but gains per acre were higher on the moderate pasture. There were no differences in vegetation production between light and moderate use pastures. However, during the last year of the study Russian thistle produced 80, 67, and 364 pounds dry matter per acre on the light, moderate, and heavy use pastures.

Grazing experiments have been conducted at the Lee A. Sharp Experimental Area in southcentral Idaho since 1957. Stocking rate and animal performance data were available for 1960 through 1965 (Sharp 1970) and are given in Table 40. Utilization rates were 50, 65, and 80 percent at stocking rates of 12, 12.5, and 14.3 animal days per acre, which does not provide a very wide spread. It does illustrate the reduced performance by individual animals with a net increase in overall production at the higher stocking rates during spring and fall. Animals gained 125 pounds in spring and 32 pounds in fall while the weight gains per acre were 40 and 8 pounds, respectively. Weight gains by yearling cattle averaged 2.05, .95, and .56 pounds per animal-day during spring (May-June), summer (July-August) and fall (September-October), respectively.

Sharp (1970) concluded that 15 years of heavy spring grazing had not destroyed the stand of grass, but forage production and stand density had declined. Plant vigor and production of the heavily grazed pastures were restored by two years of deferred grazing during the green-feed period.

A grazing system and intensity study was conducted by Frischknecht and Harris (1968) and Frischknecht et al. (1953) on the Benmore Experimental Area in northern Utah, at an elevation of 5800 feet and annual precipitation of 12 to 13 inches. They determined cow and calf weight-gain responses to four grazing methods, each at three grazing intensities for four years (Table 41). They concluded that the moderate grazing rate was the best for long term productivity of forage and beef.

Table 40.--Yearling cattle responses to grazing crested wheatgrass at three intensities for six years in southern Idaho (adapted from Sharp 1970).

Parameter	Utilization intensity		
	Light	Moderate	Heavy
Utilization, percent	50	65	80
Stocking rate			
Acres (AUM)	2.5	2.4	2.1
Animal days/acre	12	12.5	14.3
Spring grazing[1]			
Gain per animal, lbs.	122	117	111
Gain per acre, lbs.	48	50	53
Fall grazing[2]			
Gain per animal, lbs.	26	25	25
Gain per acre, lbs.	9	10	14

[1] Spring grazing was primarily May and June.
[2] Fall grazing was primarily September and October.

Table 41.--Crested wheatgrass utilization and animal performance (Frischknecht and Harris 1968)

Variable	Light	Moderate	Heavy
Utilization, percent	50	65	80
Cow days/acre	10	13	17
Weight gain, lbs/day[1]			
Cows	3.03a	2.90a	2.21b
Calves	1.87a	1.87a	1.74b
Weight gain, lbs/acre			
Cows	29b	36a	35a

[1] Data within a given row not followed by the same letter are different at the 5% probability level.

Grazing Systems

Currie (1970) examined the influence of spring, fall, and spring-fall grazing on crested wheatgrass grown on the Manitou Experimental Forest. He reported that grazing crested wheatgrass to a 1-inch stubble height for 10 years had little effect on the vegetative characteristics of the stand. Invasion by other species was greatest under spring and spring-fall use. Spring-fall use was most productive (177 lbs beef/acre) and fall grazing least for yearling heifer gains (lbs/day):

Spring	1.10
Spring-fall	0.80
Fall	0.10

Animal performance on crested wheatgrass utilized at 60 to 70 percent reflects both the palatability and quality of the forage. Harris et al. (1968) measured substantial weight gains by yearlings during all seasons except late fall on the Benmore Experimental Area. Weight gains by yearlings, cows and calves for the various grazing periods in pounds per day averaged:

25 April to 24 May	2.75
24 May to 21 June	1.48
21 June to 8 August	.99
8 August to 16 September	.49
16 September to 31 October	.59
31 October to 7 December	-1.08

Lang and Landers (1960) evaluated a grazing system on crested wheatgrass in the early season (Period I), intermediate wheatgrass during mid season (Period II) and Russian wildrye during late season (Period III) in southeastern Wyoming. These gains were compared with those on native shortgrass vegetation. The 5-year means in pounds per day were:

	Seeded	Native
I	2.22	2.13
II	1.90	1.91
III	1.03	1.18

Table 42.--Mean annual forage and animal production for three grazing systems evaluated at Manyberries, Alberta (Smoliak 1968, Smoliak and Slen 1974).

	Continuous			Rotation			Free choice		
Parameter	Crested wheat-grass	Native	Russian wildrye[1]	Crested wheat-grass	Native	Russian wildrye[1]	Crested wheat-grass	Native	Russian wildrye[1]
Yearling sheep study, 10 years									
Forage production, lbs/acre	832	393	646	813	453	677	821	359	600
Utilization, percent	40	47	63	46	49	65	32	52	63
Sheep days/acre	118	39	118	118	42	116		79	
Sheep gains, lbs/day	.18	.21	.23		.21			.23	
Spring, 58 days	.38	.35	.35	.35				.38	
Summer, 53 days	.19	.26	.26		.18			.24	
Fall, 86 days	.05	.08	.13			.13		.13	
Sheep gains, lbs/head	36.0	41.7	45.6		41.4			46.1	
Sheep gains, lbs/acre	21.7	8.3	26.3		16.5			18.5	
Lbs forage/lb gain	15.3	22.3	15.5		63			45	
Yearling steer study, 6 years									
Forage production, lbs/acre		310	1120	705	300	515	800	305	450
Utilization, percent		66	81	74	64	82	60	72	81
Steer days/acre		9	52	27	8	25		17	
Steer gains, lbs/day		1.74	1.85		1.45			1.56	
Spring, 65 days		2.21	2.41	2.02				2.18	
Summer, 41 days		2.01	2.05		1.86			2.06	
Fall, 65 days		1.10	1.18			0.63		0.62	
Steer gains, lbs/head		298ab	317a		249c			267bc	
Steer gains, lbs/acre		16.0b	96.2a		24.8b			26.6b	
Lbs forage/lb gain		19	12		46			40	

[1]Russian wildrye was seeded on 18-inch row spacing in the pasture continuously grazed by yearling steers, and on 6-inch row spacing in all others.

Stocking intensity was 4 times greater on seeded pastures. Beef gains per acre were 60 lbs on seeded pastures, but only 20 lbs on native range.

Crested wheatgrass on three dissimilar sites in Nevada was grazed by cattle on seven schedules over a 10-year study (Robertson et al. 1970). Quick utilization was achieved by heavy stocking. Alternate year or continuous protection from grazing favored pocket gophers. Early grazing generally resulted in an upward trend measured by most indicators. Time of grazing exerted major effects. Forage yields were not measured.

Smoliak (1968) evaluated weight gains of yearling ewes on three different grazing systems (continuous, rotation, free choice) at Manyberries, Alberta. Each involved crested wheatgrass, Russian wildrye and native range. For the rotational system ewes started on crested wheatgrass in spring, moved to native in summer and then finished on Russian wildrye in fall. Forage production, utilization and ewe performance for the 10-year study are shown in Table 42. The grazing period lasted about six months beginning in late April or early May and continuing through October. Ewe live weight gains were highest on the free choice pasture (46.1 lb) and continuously grazed Russian wildrye (45.6 lb) and lowest on the continuously grazed crested wheatgrass (36.0 lb). Daily gains declined with advancing season of use which was attributed to decreasing nutritive value of all forage species. Seasonal gains during spring were greatest on continuous crested wheatgrass and free choice pastures. During summer lowest gains were on continuously grazed crested wheatgrass and the native pasture grazed in rotation. For fall grazing, systems containing Russian wildrye produced the greatest weight gain. Gains per acre were highest on the continuously grazed Russian wildrye and lowest on the native range.

After completion of the 10-year sheep study, the grazing systems were reevaluated using yearling steers (Smoliak and Slen 1974), except that the continuously- grazed crested wheatgrass treatment was omitted. Steer gains were greatest with continuous grazing on Russian wildrye, but this may be due to its increased production when seeded in 18-inch row spacings (1120 lb/a) compared to 6-inch spacings (480 lb/a). Sheep and steers on the free choice system utilized Russian wildrye most and crested wheatgrass least. It was unfortunate that steer performance on continuously grazed crested wheatgrass was not included in the study. Results may be biased because of the difference in row spacing and yield of Russian wildrye. The basal area of the grasses on the three systems did not vary greatly between 1966 and 1973, except on the rotation crested wheatgrass where a 30 percent reduction occurred. These results led Smoliak and Bjorge (1981) to recommend a grazing calendar illustrating the best use of various pasture types in the Northern Great Plains (Fig. 19).

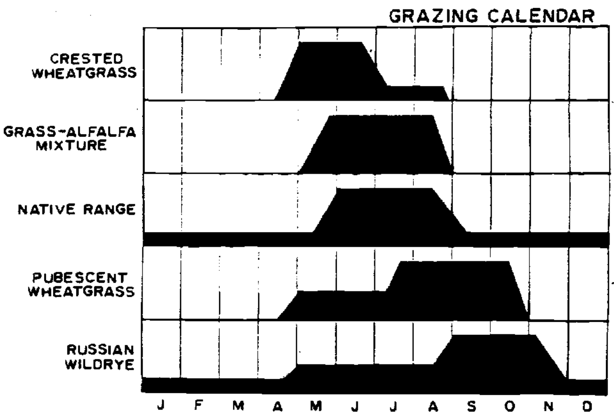

Figure 19.--Grazing calendar showing periods of high and low forage availability for pasture or rangeland forage types in Alberta (adapted from Smoliak and Bjorge 1981).

Lodge (1963) measured steer response to four grazing systems on the sandhills of the northern Great Plains. The systems were:

1. Rotation - crested wheatgrass from May to mid-June followed by native range until September.
2. Free choice - free access to equal areas of crested wheatgrass and native range from mid-June until September.
3. Complimentary - crested wheatgrass from May to mid-June followed by access to an equal sized area of native range until September.
4. Native - native range from May until September.

The grazing season averaged 137 days and produced the results shown in Table 43.

A three-pasture system was evaluated using yearling steers in a five year study at Dickenson, North Dakota (Nyren et al. 1983). It compared spring grazing of crested wheatgrass, summer grazing of native rangeland, and fall grazing of Russian wildrye (Table 44). One set of the crested and native pastures was fertilized with nitrogen that increased forage production by 42 and 50 percent and beef production by 70 and 52 percent, respectively. Utilization of Russian wildrye was similar to that shown in Table 37 (79 vs. 81%), but the daily weight gain was considerably less (.77 vs. 1.76 lb/day).

Table 43.--Steer performance on four grazing systems in northern Great Plains (Lodge 1963).

	System			
	1	2	3	4
Gain, lbs/head	211	233	243	185
Gain, lbs/acre	34.7	38.7	34.9	20.1
Animal days/acre	22.5	22.8	19.7	14.9

Table 44.--Mean annual forage and animal production from a three pasture system involving crested wheatgrass, native range, and Russian wildrye in North Dakota (adapted from Myren et al. 1983).

Parameter	Crested wheat-grass	Native	Russian wild-rye
Unfertilized			
Forage production, lbs/acre	2110	2680	-
Utilization, percent	54	40	-
Animal days/acre	41	38	-
Beef gains, lbs/day	1.63	1.63	-
Beef gains, lbs/acre	67	63	-
Lbs forage/lb beef	17	17	-
Fertilized annually with 50 lbs N/a[1]			
Forage production, lbs/a	3000	4010	1740
Utilization, percent	61	45	79
Animal days/acre	83	57	46
Beef gains, lbs/day	1.39	1.65	.73
Beef gains, lbs/acre	112	96	34
Lbs forage/lb beef	16	19	40

[1] All Russian wildrye pastures were fertilized with 50 to 150 lbs N/acre plus 13 lbs P/acre.

Whitman et al. (1963) compared weight gains of steers grazing alfalfa plus crested wheatgrass with those grazing crested wheatgrass alone. Two of four crested wheatgrass pastures were seeded with 4 pounds of Ladak alfalfa and later grazed for 7 years during May and June. Forage and beef productivity at the Dickinson, North Dakota study were:

	Crested	Crested + Alfalfa
Forage yield, lbs/acre	920	1170
Utilization, percent	81	82
Steer days/acre	43	56
Steer gain, lbs/day	2.07	2.08
Steer gain, lbs/acre	88	117
Lb forage/lb gain	8.5	8.2

The grass-legume forage contained about 15 percent alfalfa with a higher yield and crude protein concentration which allowed a higher stocking intensity. Feed conversion ratios of 8 pounds of forage per pound of gain are often one-half or less than those calculated in Table 37, 42 or 44.

Another study conducted in the Northern Great Plains evaluated the benefits of fertilizing crested wheatgrass or growing it in a grass-legume mixture (Rogler and Lorenz 1969). Forage yield, stocking rate and beef production per acre were increased when nitrogen was applied to crested wheatgrass (Table 45). Forage yield and beef production from the grass-legume mixture were each increased about 30 percent compared with the unfertilized grass.

Yearling steers were used to compare continuous versus short duration grazing on crested wheatgrass at Squaw Butte (Daugherty et al. 1982). On short duration grazing, animals were moved to new pasture when 30 percent of the forage was utilized. The study was conducted for two seasons and illustrated a small increased weight gain by steers on the short

Table 45.--Mean annual forage and beef production on crested wheatgrass fertilized or grown in mixture with Ladak alfalfa at Mandan, North Dakota (Rogler and Lorenz 1969).[1]

Parameter	Responses on pastures treated with ON	40N	80N	Mixture
Forage yield,lbs/acre	1740a	2760c	3120d	2240b
Utilization, percent	52	60	60	63
Steer days/acre	38	66	71	48
Steer gains, lbs/day	2.66	2.63	2.53	2.82
Steer gains,lbs/acre	101a	169c	176c	135b
Lbs forage/lb beef	9.1	9.8	10.4	10.3

[1]Means on a given line followed by the same letter do not differ at P=.05.

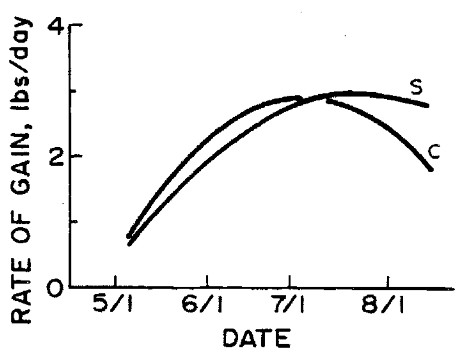

Figure 20.--Daily weight gains by steers grazing crested wheatgrass on short duration (s) or continuous (c) systems in eastern Oregon (adapted from Daugherty et al. 1982).

duration pasture when compared with continuous grazing (Fig. 20). This 'cream' type grazing (30% utilization) would use the more nutritious plant parts for maintenance and weight gain whereas the remaining forage might be used by livestock where only maintenance was required (Raleigh 1970). This would work best under a fall-calving program.

Sheep were used by Campbell (1961) at Swift Current to evaluate continuous and rotation grazed grass-legume mixtures (Table 46). Forage yields, utilization and stocking rates were higher here than reported for the sheep study in Table 42. Continuously grazed Russian wildrye with or without alfalfa outperformed crested wheatgrass (Tables 42 and 46).

Frischknecht et al. (1953) measured cow/calf performance over four years on crested wheatgrass at Benmore. Animals were stocked at light (50%), moderate (65%), and heavy (80% utilization) intensity. Superimposed on stocking rates were four methods of spring grazing. The treatments included (1) rotation, with cattle shifted periodically among three sections of the pasture so as to graze each section twice during a 60-day season; (2) continuous; (3) 10-day deferred where grazing started 10 days late; (4) 10-day short where grazing terminated 10 days early. Pastures in the first two groups were grazed for about 60 days in the spring while those in the latter two groups were grazed for about 50 days. The animal gains in pounds were as shown in Table 47. The four methods had little influence on calf gains and trends did not follow those of the cows. Early removal resulted in higher weight gains by cows because of higher forage quality early in the spring.

Animal Grazing with Supplementation

Reproduction, weight gain, and milk or wool production are traits controlled by genetics and influenced by environment. The latter includes temperature and availability and quality of both drinking water and forage. When the forage diet is inadequate for a desired level of production, it may be supplemented to correct the deficiency (Raleigh 1970). Supplements include salt (NaCl), crude protein, energy, and other minerals and vitamins. Supplementation may be provided orally via inorganic sources such as sodium chloride, biuret (nonprotein

Table 46.--Mean annual forage and yearling ewe production for continuous and rotation grazing systems on three grasses plus alfalfa at Swift Current, Saskatchewan (adapted from Campbell 1961).

Parameter	Continuous			Rotation			
	Crested +alfalfa	Intermediate +alfalfa	Wildrye +alfalfa	Crested +alfalfa 6/5-7/7	Itermediate +alfalfa 7/8-8/20	Wildrye +alfalfa 8/21-10/15	Season Long
Forage production, lbs/acre	1160	1120	1210	1560	1340	1145	1350
Utilization, percent	86	79	90	85	79	82	82
Sheep days/acre	358	325	361	400	398	322	373
Sheep gains, lbs/day	.10	.11	.14	.14	.08	.12	.11
Sheep gains, lbs/head	14	14	24	5	3	6	14
Sheep gains, lbs/acre	35	36	50	55	32	40	42
Lbs forage per lb gain	26	24	21	24	33	23	26

Table 47.--The effect of four systems on gains of animals, grazing spring growth of crested wheatgrass, (Frischknecht et al. 1953).

	Gain/day		Gain/acre
	Cows[1]	Calves	cows
	---------- Pounds ----------		
Rotation	2.53a	1.79	34
Continuous	2.70a	1.87	33
10-Day deferred	2.68a	1.82	34
10-Day short	2.95b	1.83	33

[1]Means not followed by similar letters are different at P <.05.

nitrogen), monosodium phosphate, magnesium oxide, and various iodine salts. Injectable forms of copper and selenium are used to meet animal requirements or pellets, bullets, or wires composed of cobalt, copper, magnesium, or selenium can be placed in the rumen-reticulum to supplement dietary availability of these elements. The latter method has had varying degrees of success.

Protein may be provided as alfalfa hay or as meal from soybean, cottonseed, rape, or other high nitrogen seeds. Energy is often provided as barley or corn. Energy supplementation can sometimes be detrimental to performance of cattle grazing poor quality forage (Harris et al. 1968 and Kartchner 1981). To make the most profitable decisions it is important to know what the animal needs for a desired level of production, what the animal is presently getting in the diet, and then what supplement is needed to make up the deficiency if one occurs (Raleigh 1970).

Wallace et al. (1963) measured the weight gain response of yearling cattle on crested wheatgrass at Squaw Butte to energy (barley), protein (cottonseed meal), and salt (NaCl) supplements. Cattle grazed a common pasture from mid-May through August and were penned to receive their assigned supplement. The barley was fed at two pounds per animal day and cottonseed meal at a rate to assure that overall protein intake was about 10 percent of the diet. The least-squares mean values for daily weight gain (P<.05) were combined for simplification:

1. Energy-supplemented animals gained more (1.83 vs 1.70 lb/day) than controls.
2. Protein-supplemented animals gained more (1.83 vs 1.69 lb/day) than controls.
3. Salt-supplemented animals gained the same (1.78 lbs/day) as controls.

The effects of additional energy appeared more favorable when forage was limited or when dry matter concentrations were low. The benefit of protein supplementation occurred during the latter part of the season when protein levels in the forage were low.

Another approach to supplementation is to increase the diversity of the forage base that is inherent in native rangelands and to some extent in grass-legume mixtures. In both cases succulent forage having a relatively high feed value is available for a longer period of time than in monoculture grass, especially crested wheatgrass.

Another approach is the interseeding of grass stands with palatable shrubs. Springfield (1960) observed sheep making comparatively heavy use of big sagebrush, silver sagebrush, rubber rabbitbrush, and Douglas rabbitbrush in northern New Mexico. Otsyina et al. (1982) reported that shrubs were consistently higher in both total and digestible protein than crested wheatgrass. Pregnant ewes grazing mature crested wheatgrass and supplementing their diets with shrubs would have to consume 56 percent fourwing saltbush or 69 percent winterfat to meet their requirements. Mountain big sagebrush and rubber rabbitbruah were lower in digestible protein and therefore could not be used alone or with crested wheatgrass if the pregnant ewe was to receive adequate protein.

Winter Use

Williams et al. (1942) determined the performance of long-yearling steers when wintered on crested wheatgrass either as hay or standing grass at Judith Basin. Steers receiving average quality crested wheatgrass hay plus 1 lb/day of a supplement containing cottonseed, molasses and beet pulp gained 1 lb/day while those receiving 3 lbs of supplement gained 1.2 lb/day. Similar steers pastured on cured crested wheatgrass gained 0 lbs if given 1 lb of supplement or 0.34 lbs if given 3 lbs of supplement. Steers fed prebloom Fairway plus 3 lbs of supplement gained 1.52 lb/day. The authors noted that grazing steers preferred Fairway to Standard when not covered with snow.

Sheep were used to compare diet selection from a stand of crested wheatgrass or a mixed shrub-crested wheatgrass field during early, mid and late January (Gade and Provenza, In Press). Sheep grazing grass pasture consumed diets that were about 55 percent mature grass and 45 percent green vegetative growth during the first two periods. In late January green feed was no longer available because of trampling and snow cover and sheep consumed diets containing 93 percent mature grass. Sheep grazing the grass-shrub pastures consumed about 50 percent shrub and 50 percent grass during all three periods. Sheep on the mixed pastures consumed diets that were higher in crude protein than those grazing only grass during the early (9.0 vs. 5.8% CP), mid (7.3 vs. 6.6% CP) and late period (7.9 vs. 4.6% CP). The <u>in vitro</u> organic matter digestibilities of the diets were higher on the mixed pasture during the early (48 vs. 45%), mid (46 vs. 29%) and late period (32 vs. 24%). Utilization of shrubs was winterfat (100%) fourwing saltbush (79%), bitterbrush (52%), forage Kochia (34%), sagebrush (29%) and rubber rabbitbrush (17%).

Antiquality Factors

Some forbs and shrubs contain organic or inorganic compounds that pose health hazards to grazing livestock. Even some grasses contain toxins produced either by their own metabolism or that of endophytic organisms associated with the plant. Crested wheatgrass does not contain significant amounts of any of these toxic compounds, except for occasionally high levels of certain elements, nitrates, or trans-aconitic acid. The latter may reduce magnesium availability to livestock.

The literature contains some information on the accumulation of mineral elements in crested wheatgrass. It is not uncommon for spring and well water in semiarid areas to be high in fluorine (F). For example, high levels of fluorine are present in thermal springs throughout the Great Basin and Snake River Plains; concentrations frequently range from 2 to 17 ppm while the concentration in plants ranges from 0.1 to over 220 ppm depending on the species and soils. Fluorosis of animals is attributed to the fluorine in forage and drinking water. Kubota et al. (1982) collected over 300 plant samples in the Great Basin and identified the following fluorine levels (ppm):

	Median	Range
Grasses	2.3	.1 - 70
Sedges	7.0	.4 - 42
Rushes	4.7	.2 - 224
Desert shrub		
Leaves	1.3	.1 - 12
Stems	1.1	.4 - 7

Fluorine concentrations decreased with increasing distance to the fluorine source or spring.

Fallout from ore smelters may be a source of large amounts of fluorine. Severson and Gough (1976) published data on elements in soil and plant material in relation to distance from the phosphorus smelter at Pocatello, Idaho. Fluorosis was observed in a dairy herd located several miles downwind from the smelter (Mayland, unpublished). In general, however, high-fluorine levels will not be found in crested wheatgrass.

Rauzi and Landers (1979) evaluated crested wheatgrass forage production along Interstate Highway 90 in northeastern Wyoming. They concluded that grass grown in the medians and borrow areas was a valuable source of quality hay. The areas received run-on water and forage generally contained adequate crude protein, calcium, phosphorus and magnesium for maintenance. The lead content ranged from 3.9 to 4.3 ppm which was not toxic.

Both sulfur (S) and selenium (Se) are required for animal health. High sulfur levels might occur as fallout from ore smelters and power-generating plants that burn coal. Another, but fortunately infrequent, source was the ash fallout from the Mt. St. Helen eruption (Mahler 1984, Sneva et al. 1982). Sulfur may not occur in toxic concentrations in itself, but may reduce the availability of selenium to plants and animals (Milchunas et al. 1983). In other situations, agronomic practices that suddenly increase crop yields may reduce or dilute the selenium concentrations in forage (Westermann and Robbins 1974). If this occurs where forage selenium concentrations are marginal, then selenium deficiencies may appear in livestock, indicated by the occurrence of "White Muscle Disease" in calves, lambs, and other young animals. This problem has occurred many times in the Snake River and Columbia Plateau regions and is of great importance to livestock producers. However, the sulfur:selenium interaction occurs most often on irrigated lands and therefore is not a problem associated with crested wheatgrass.

Soils derived from sedimentary materials may have high selenium levels. Crops grown on these soils will contain corresponding levels of selenium. Crested wheatgrass grown in Lyman County, South Dakota, had 2 ppm Se in forage and 7 ppm Se in the heads (Williams et al. 1941). These values are probably similar to those of other grasses grown on the same soils. Such concentrations of selenium are marginally toxic to animals.

Lambert and Blincoe (1971) collected crested wheatgrass from 11 sites in northern Nevada and found them to contain 0.6 to 23 ppm cobalt with a mean of 6.9. They were able to confirm these unusually high concentrations in the wheatgrass samples by several analytical methods. While these cobalt concentrations may not be high enough to be toxic to livestock, they could interact with other elements. The authors suggested that the *Agropyrons* may accumulate cobalt. Mayland (unpublished) sampled crested wheatgrass from two of the 11 sites and measured concentrations of less than .2 ppm, which appear normal compared with other forages. Perhaps the 1971 samples were contaminated sometime between harvest and analysis.

Interactions between elements may greatly affect the availability of each. For example molybdenum, sulfur, and possibly manganese reduce copper availability to the grazing animal. Yearling heifers were fed tall fescue or quackgrass with the following elemental profile in ppm (Stoszek et al. 1979)

	Tall fescue	Quackgrass
Copper	6.6	4.6
Molybdenum	2.3	1.2
Sulfur	340.0	160.0
Manganese	91.0	38.0

The animals on the tall fescue had rapidly declining levels of liver and plasma copper, whereas those on the quackgrass maintained normal copper levels.

High nitrate levels in herbage can be found in rapidly growing, nitrogen-fertilized grass or in plants that become droughty while growing on fertile soil. Forage containing 1000 to 2200 ppm NO_3-N (0.5 to 1.0% nitrate) is safe for most animals, but higher levels of nitrate may produce haemoglobinuria and death in livestock. Lawrence et al. (1981) were able to increase nitrate nitrogen levels to more than 2000 ppm in crested wheatgrass by irrigation and fertilizing with 350 pounds of nitrogen, but levels declined with increasing maturity. Nitrate toxicity is not a likely problem in crested wheatgrass grown without irrigation and only modest amounts of nitrogen fertilizer.

Grasses contain silica (SiO_2) in concentrations approaching 10 percent on a dry matter basis (Mayland, unpublished), but forbs seldom have greater than .5 percent SiO_2. Some of the silica in grass is distributed as opaline silica bodies in the leaves. Their shape and color are unique for genera and can be used to identify the grassland type of a site even thousands of years after its disappearance (Blackman 1971).

Silica reduces the digestibility of herbage by about three percentage units for each unit of silica (Mayland, unpublished). The mechanism is not known, but may relate to the silica acting as a varnish on the cell wall, or to its precipitation with some trace mineral, limiting its availability to rumen flora. Another mechanism may entail the inactivation of some enzymatic reaction during rumination.

Silica is also responsible for the development of silica urolithiasis (water belly) in livestock, especially castrated males (Bailey 1981). The problem is particularly acute in the northern Great Plains. An eight-year survey was conducted in two areas, one with a low incidence and the other with a high incidence of urolithiasis in grazing animals (Bezeau et al. 1966). Silica concentrations were not different between the two areas, but were higher in grasses and sedges than in forbs and shrubs. It was apparent that reduced water intake by the livestock was as much of a problem as silica in the forage in inducing urolithiasis. A combination of low water intake with a forage silica content greater than two percent could be expected to induce the condition.

Soil ingestion can also affect animal health. The soil might be a source of small amounts of some trace elements. On the other hand, soils might absorb some elements. For example, some soils have the capacity to absorb phosphorus and ingestion by the animal could increase the dietary requirement. Mayland et al. (1977) measured soil ingestion of 1.6 to 2.2 pounds per day by heifers grazing crested wheatgrass during June and August in southcentral Idaho. Soil impaction of the gastrointestinal tract can be fatal, especially in lambs and horses. Most importantly, soil ingestion can increase the rate of tooth wear and reduce productive lifetime of breeding animals. The author is aware of eight-year old cows from one area that have worn teeth resembling those of 12-year old cows from another area. Local cattle buyers are known to take this into consideration.

Grass Tetany

Grass tetany (hypomagnesemia) is probably the most important antiquality factor associated with crested wheatgrass. Magnesium deficiency has produced large numbers of deaths and production losses in cattle and sheep. Mayland (unpublished) estimated that in the United States 30 percent of these losses occurred on crested wheatgrass, 40 percent on tall fescue, and the remaining 30 percent on perennial ryegrass, cereal grain forages, other cool season grasses, fodders, and hays (including alfalfa, Bohman et al. 1977).

Grass tetany is a deficiency of magnesium to the ruminant. The problem can result from a simple deficiency of magnesium in the diet, but more often from reduced availability of forage magnesium to the grazing animal. This reduction is attributed to a number of factors (Fig. 21).

Spring tetany occurs most often in older, lactating cows recently turned onto crested wheatgrass seedings. Forage growth preceding the occurrence of grass tetany is limited by cool or dry conditions. Rapid changes in weather conditions resulting in a flush of growth and the development of "washy" feed (low dry matter content) are often followed by grass tetany (Mayland and Grunes 1974b). The rapidly growing crested wheatgrass forage will contain high concentrations of trans-aconitic acid (Stout et al. 1967, Stuart et al. 1973, Mayland and Grunes 1979). It has been assumed that trans-aconitic and other organic acids are in some way associated with a reduction in magnesium availability. The field observations made by Mayland and coworkers were conducted on seedings of standard crested wheatgrass. Nordan and standard accumulate aconitic acid whereas Fairway crested wheatgrass accumulates malic acid as shown in the percentages below (Prior et al. 1973).

	Nordan	Fairway
Fumarate	T	T
Formate	1	1
Acetate	3	4
Aconitate	26	5
Malate	64	82
Citrate	6	8

It is not known whether there is a greater risk to tetany from grazing Nordan than Fairway.

Russell and Van Soest (1984) reported that an *in vitro* fermentation of trans-aconitic acid by mixed rumen bacteria led to the formation of tricarballylic acid that appears as an end product of aconitic acid metabolism. Evidence exists[4] that it may block portions of the citric acid cycle. Obviously, much is yet to be learned about the role of organic acids in magnesium tetany.

Elevated concentrations of higher fatty acids (HFA) occur in crested wheatgrass coincident to the tetany (Stuart et al. 1973). Unsaturated HFA forms water-insoluble soaps with magnesium and calcium which are then excreted in the feces (Mayland and Grunes 1979). Nitrogen fertilization of grass pastures increases the tetany hazard and was shown by Mayland et al. (1976) to increase the HFA concentration in crested wheatgrass (Fig. 22).

Nitrogen concentrations in crested wheatgrass parallel the concentrations of total inorganic acids, aconitic acid, and HFA. Thus, forage nitrogen values are elevated when grass tetany occurs. Much of this nitrogen exists as non-protein nitrogen (NPN), which after ingestion is readily

[4] J. B. Russel, Ithaca, New York, personal communication.

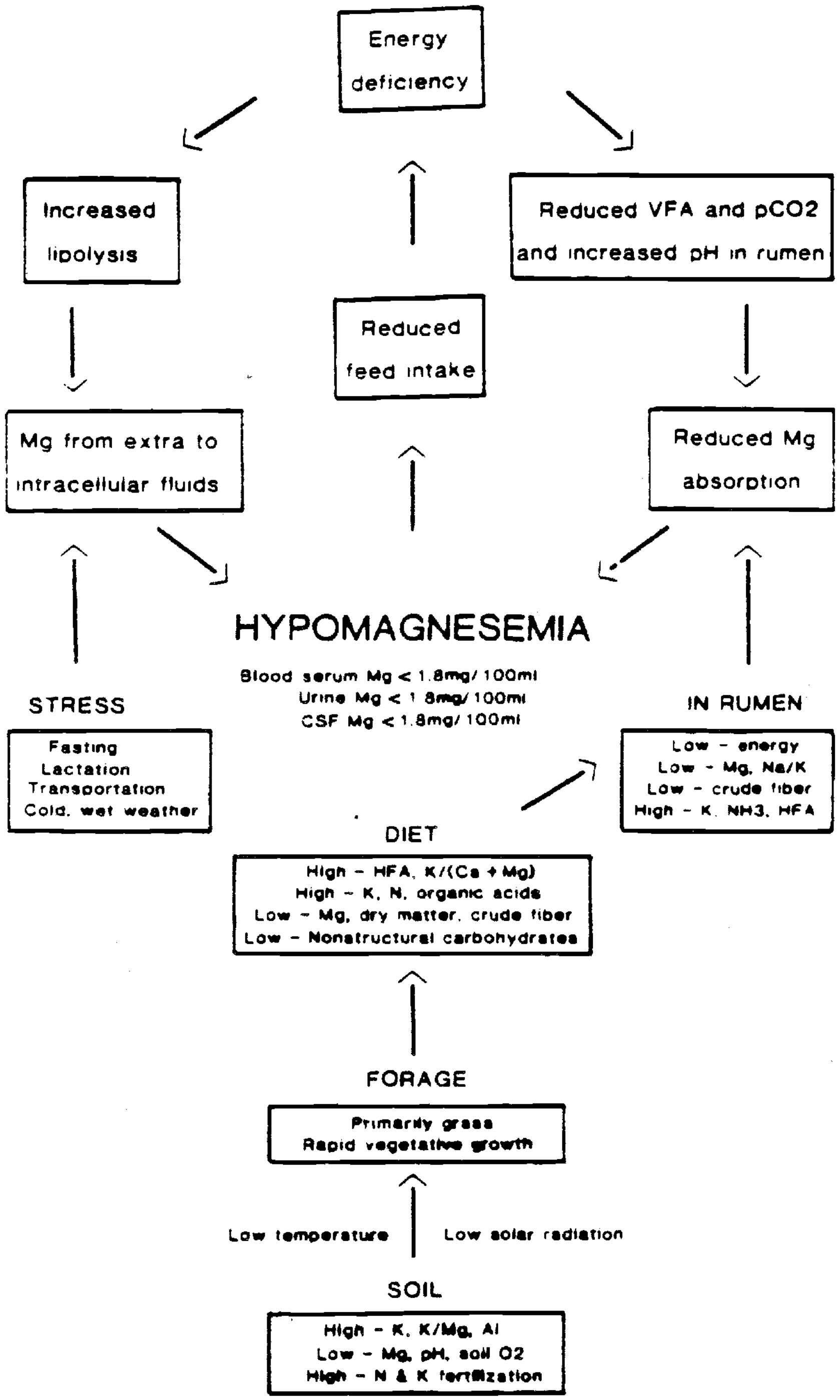

Figure 21.--Etiology of grass tetany.

available to the rumen flora. Total water soluble carbohydrate (TWSC) concentrations in the wheatgrass are particularly low at this time, because the plant used this energy source for rapid growth. Mayland et al. (1974c, 1975) reported that the N/TWSC values in crested wheatgrass peaked with the occurrence of grass tetany on the San Jacinto seedings south of Jackpot, Nevada (Fig. 23). The authors hypothesized that high NPN and low TWSC resulted in excess ammonia (NH_3), increased pH, and reduced magnesium availability. Later work by House and Mayland (1976) and Madsen et al. (1976) verified the hypothesis that elevated N/TWSC in the diet resulted in reduced magnesium availability.

The elemental cation concentrations in the forage also relate to the tetany hazard. Increased levels of potassium in the forage reduce the amount of magnesium absorbed by the animal (Fontenot 1979). Researchers related the chemical equivalency ratio of potassium (magnesium and calcium) in forage to the incidence of grass tetany (Mayland and Grunes 1979, Thill and George 1975). Animal death loss increases exponentially with an increase in the ratio and, at a value of 2.2, may reach 3 percent. At a ratio of 3.0, losses may exceed 10 percent.

A second approach, now identified as the Dutch nomograph (Mayland and Grunes 1979), uses information on forage nitrogen, magnesium, and potassium to predict the potential tetany hazard of the forage.

Fertilizing pastures or dusting forage with various magnesium salts has helped to reduce the incidence of grass tetany on acid soils in humid regions (Wilkinson and Stuedemann 1979). Crested wheatgrass is grown in the semiarid areas of the western United States and Canada where soils are generally calcareous and contain abundant levels of calcium and magnesium. Under these conditions, the application of magnesium is not a practical method of increasing magnesium in forage (Mayland and Grunes 1974a).

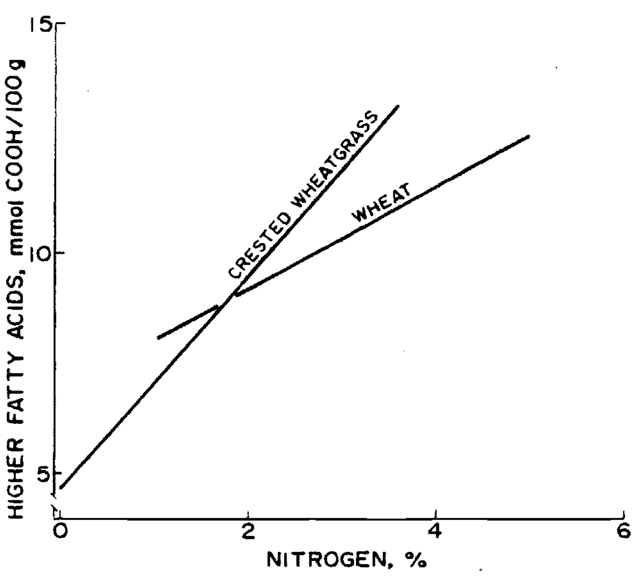

Figure 22.--Higher fatty acid concentrations in relation to the total herbage nitrogen in Nordan crested wheatgrass and cereal wheat (adapted from Mayland et al. 1976).

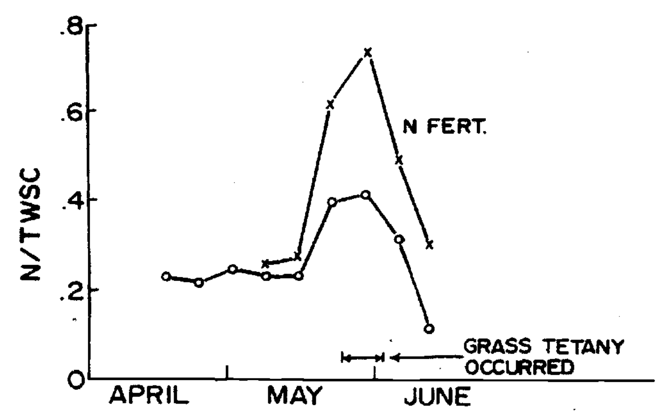

Figure 23.--The ratio of total nitrogen to total water soluble carbohydrates (N/TWSC) in crested wheatgrass as affected by N fertilization and its relation to the occurrence of grass tetany in northeastern Nevada (Mayland et al. 1975).

Controlling grass tetany on large pastures of crested wheatgrass can be accomplished by one or more of the following practices (Grunes and Mayland 1975).

1. Feed a supplement that will provide 1/2 oz of Magnesium per animal each day.

2. Magnesium sulfate as Epsom salt can be given in the drinking water if animals water only from closed water systems.

3. Animals that incur grass tetany may be given injections of magnesium sulfate or calcium-magnesium gluconate.

4. Use of native pastures or deferred seeded pastures is somewhat helpful, but animals are able to selectively graze the new growth which is the cause of the problem.

CONCLUSIONS

Crested wheatgrass is a valuable forage resource on semiarid rangeland in the western United States and Canada. It is tolerant of occasional drought or overgrazing. It provides feed several weeks earlier in the spring than native range, and yields are consistently greater than on native range. Forage yields within given areas are generally proportional to annual precipitation. The generally higher amounts and summer frequencies of rainfall in the Northern Great Plains compared with the Great Basin, Snake River, and Columbia Plateau regions favors higher forage yields. Overall yield and forage quality of the wheatgrass grown in the Northern Great Plains are often increased by planting alternate rows of creeping-rooted alfalfas with the grass. Wider row spacings, up to 24 inches apart, favor long-term yields of crested wheatgrass in the Northern Great Plains. However, information from areas west of the Rocky Mountains does not confirm this relationship.

The use of chemicals to prevent the development of reproductive florets or clipping and grazing management that removes the floret will result in a larger proportion of leaves. Dry matter yield reductions attributed to the absence of seed stalks can be accepted periodically in favor of the high quality leafy material. More research on these relationships is desirable.

Yield evaluations generally show similar productivity ranges for _A. desertorum_ and _A. cristatum_, but lower ranges for _A. fragile_. Breeding and selection programs indicate that a broad base of genetic material is available through which progress can be made for improved stand establishment, forage yield, and forage quality. Animal responses to these new materials must be carefully evaluated.

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APPENDIX

COMMON AND SCIENTIFIC NAMES OF PLANTS MENTIONED

Wheatgrasses

Beardless wheatgrass	Elytrigia spicata (Pursh) R. D. Dewey, previously Agropyron inerme (Scribn and Smith) Rydb.
Bluebunch wheatgrass	Elytrigia spicata previously A. spicata.
Crested wheatgrass	Agropyron desertorum (Fisch. ex Link) Schult. A. cristatum (L.) Gaertn.
Intermediate wheatgrass	Elytrigia intermedia (Host) Nevski, previously A. intermedium (Host) Beauv.
Pubescent wheatgrass	Elytrigia intermedia subsp. barbulato (Schur) A. Löve, previously A. trichophorum (Link) Richt.
Quackgrass	Elytrigia repens (L.) Nevski, previously A. repens. (L.) Beauv.
Siberian wheatgrass	A. fragile (Roth) Candargy, previously A. sibiricum (Willd.) Beauv.
Slender wheatgrass	Elymus trachycaulus (Link) Gould ex Shinners subsp. trachycaulus, previously A. tracycaulum (Link) Malte.

Streambank wheatgrass	*Elymus lanceolatus*, previously *A. riparium* Scribn. and Smith.
Tall wheatgrass	*Elytrigia pontica* (Podp.) Holub, previously *A. elongatum* (Host) Beauv.
Thickspike wheatgrass	*Elymus lanceolatus* (Scribn. and Smith) Gould, previously *A. dasystachyum* (Hook.) Scribn.
Western wheatgrass	*Pascopyrum smithii* (Rydb.) A. Löve, previously *A. smithii* Rydb.

Other Grasses

Altai wildrye	*Leymus angustus* (Trin.) Pilger, previously *Elymus angustus* Trin. not native to North America.
Big bluegrass	*Poa ampla* Merr.
Big bluestem	*Andropogon gerardi* (Vitman).
Blue grama	*Boutelova gracilis* (H.B.K.) Lag. ex Steud.
Bromegrass	*Bromus inermis* Leyss.
Bulbous bluegrass	*Poa bulbosa* L.
Cheatgrass	*Bromus tectorum* L.
Creeping red fescue	*Festuca rubra* L. subsp. rubra.
Foxtail barley	*Hordeum jubatum* L.
Green needlegrass	*Stipa viridula* Trin.
Green stipagrass	*Stipa viridula* Trin.
Indian ricegrass	*Oryzopsis hymenoides* (Roem. and Schult.) Ricker.
Kentucky bluegrass	*Poa pratensis*.
Orchard grass	*Dactylis glomerata*.
Red top	*Agrostis alba* L.
Russian wildrye	*Psathyrostachys juncea*, previously *Elymus junceus* Fisch.
Sandberg bluegrass	*Poa secunda* Presl.
Side-oats grama	*Bouteloua curtipendula* (Michx.) Torr.
Switchgrass	*Panicum virgatum* L.
Tall oatgrass	*Arrhenatherum elatus*.

Others

Alfalfa	*Medicago sativa* L. *Medicago media* Pers. "Drylander" also *M sativa* subsp. varia (Martyn) Arc.
Bean, dry cultivated	*Phaseolus vulgaris*.
Big sagebrush	*Artemisia tridentata* Nutt.
Bitterbrush	*Purshia tridentata*.
Cicer milkvetch	*Astragalus cicer* L.
Cotton	*Gossypium hirsutum*.
Crownvetch	*Coronilla varia*.
Douglas rabbitbrush	*Chrysothamnus visidiflorus*.
Forage kochia	*Kochia prostrata*.
Fourwing saltbrush	*Atriplex canescens*.
Halogeton	*Halogeton glomeratus*.
Pinyon-juniper	*Pinus edulis* Engelm., also *P. monophylla*; *Juniperus monosperma* (Engelm.) Sarg., also *J. osteosperma*.
Ponderosa pine	*Pinus ponderosa* Lawson.
Rubber rabbitbrush	*Chrysothamnus nauseosus*.
Russian thistle	*Salsola kali*.
Sainfoin	*Onobrychis viciaefolia* Scop.
Sicklepod milkvetch	*Astragalus falcatus*.
Soybean	*Glycine max*.
Sugar beet	*Beta vulgaris* (L.).
Sweet clover	*Melilotus officinalis* (L.) Lam.
Tomato	*Lycopersicon esculentum*.
Saltbrush	*Atriplex canescens* (Pursh Nutt.).
Silver sagebrush	*Artemisia cana*.
Winterfat	*Ceratoides lanata* (Pursh, Howell).

In: Johnson, K. L. (ed.). 1986. Crested wheatgrass: its values, problems and myths; symposium proceedings. Utah State Univ., Logan.

Nutritional Limits of Crested Wheatgrass for Range Livestock Production

John C. Malechek

ABSTRACT: Crested wheatgrass has been remarkably successful in fulfilling its purpose of providing productive, nutritious livestock forage during the spring. Livestock production per are has been increased from 5- to 10- fold by establishing crested wheatgrass on degraded Intermountain area ranges. While forage quality is characteristically high during May and June, it declines rapidly as plants enter the flowering and seed stages of growth. By early July, it typically fails to meet nutritional requirements of lactating animals. This rapid decline can be delayed by droughty growing conditions that delay or prevent plants from reaching full maturity. Potential for better realizing the full forage value of crested wheatgrass include winter grazing in some areas and more intensive spring grazing in other areas.

INTRODUCTION

Crested wheatgrass (Agropyron cristatum and A. desertorum) has been planted on public and private rangelands of the western U.S. and Canada for the express purpose of providing productive, palatable, and nutritious forage for the livestock industry. It has been remarkably successful in fulfilling this need. Its main contribution in the Intermountian region has been in helping to alleviate the so-called spring forage "bottleneck" that generally exists on most ranches from late April (when winter hay supplies are normally exhausted) until early July (when abundant summer range forage is available). However, like most good things and ideas, crested wheatgrass is not without limitations. Thus, the purpose of this paper is to briefly review what is known about the productive potential of the species and to specifically discuss some of its limitations. This could lead to changes in management approaches where information is available but is not being applied, and can point to areas of ignorance where research should be directed.

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The underlying hypothesis of this paper is that there are ways to more efficiently utilize established crested wheatgrass stands. These avenues should be pursued completely and all possibilities exhausted, considering that the economic costs and environmental constraints of establishing new seedings (particularly on public lands) are now almost prohibitive.

LIVESTOCK PRODUCTION POTENTIAL

Based on a broad but not exhaustive review of published literature, cattle weight gains of about 2 lbs per head per day can be expected on crested wheatgrass range during May and June (Table 1). In terms of production per unit area of land, this translates to about 45 lbs of beef per acre (Table 1). These data are based largely on yearling animals (typically used for the sake of experimental simplicity), not on the growing, nursing calves that are of primary interest to most Intermountain-area ranchers. Close scrutiny of Table 1 indicates more variation around the mean per-acre value than around the mean per-head value. This probably reflects inherent differences in grazing capacities and stocking rates over the broad geographic range from which these data were compiled (central Oregon, Utah and central Colorado).

When animal production on crested wheatgrass range is compared to that of typical, unimproved native range, the margins are indeed impressive (Table 2). While results in terms of gains per head were mixed, production on a per-area basis was greatly improved in all cases by utilizing crested wheatgrass. The two studies from the Intermountain area (Lesperance et al. 1983 and Frischknecht 1978) showed 5- to 10-fold increases while one study from the Northern Great Plains in Canada (Smoliak and Slen 1974) revealed a smaller but nevertheless significant advantage to crested wheatgrass range (Table 2). The smaller improvement over native range noted by the Canadian researchers might be attributed to the rather unique features of their native shortgrass prairie vegetation. It is generally quite resistant to degradation from overgrazing, while the opposite is true of

Table 1.--Animal production on crested wheatgrass range grazed during spring.

	Stocking rate	Kind/class of animals	Animal production Per head	Per acre	Reference
	(acres/AUM)		(lbs)	(lbs)	
(1)	2.5	Yearlings	2.0	47	Sharp 1970
	2.4	Yearlings	1.9	50	
	2.1	Yearlings	1.8	51	
(2)	Variable (put & take)	Yearlings	1.7	59	Currie & Smith
(3)	2.2	Yearlings	2.6	37	Frischknecht & Harris (1968)
	1.8	Yearlings	2.6	43	
	1.5	Yearlings	2.3	39	
(4)	2.1	Calves	2.1	67	Jefferies et al. 1967
(5)		Calves:			
	---	Early spr.	2.3	--	Cook & Harris 1968
	---	Late spr.	1.6	--	
(6)	---	Yearlings	1.6	--	Wallace et al. 1963
(7)	4	Yearlings	1.5	22	Hedrick et al. 1963
		Average (yearlings only)	2.0	44	

bunchgrass vegetation in the Great Basin. Under a history of overgrazing, shortgrass prairie in southern Saskatchewan would probably maintain a relatively vigorous cover of native grass and a reasonably good grazing capacity for cattle. In contrast, overgrazing in Nevada and Utah where the Lesperance et al. and Frischknecht studies were done has typically led to replacement of native bunchgrasses by shrubs of low palatability e.g. sagebrush (Artemisia spp.), rabbitbrush (Chrysothamnus spp.), broom snakeweed (Xanthocephalum sarothrae). Hence, grazing capacity for cattle has been severely reduced. Conversion of these ranges back to a productive grass stand, i.e. crested wheatgrass, generates a phenomenal improvement in grazing capacity and, in turn, an increase in livestock production on a per-area basis.

While these data are few, they are consistent with conventional wisdom among livestock producers using Intermountain area rangelands. There should be little wonder as to why ranchers are ardent supporters of converting native sagebrush ranges to crested wheatgrass seedings.

FORAGE QUALITY LIMITATIONS

A highly desirable trait of crested wheatgrass is its ability to supply nutritious forage early in the spring, often several weeks before its native counterparts. From the standpoint of efficient livestock production, this is a critical period in the annual management cycle. Cows giving birth in March are at the peak of their lactation period at this time, and nutrient demands are high if the calf is to receive the quantity of milk necessary for rapid growth. Additionally, an elevated plane of nutrition during this period is highly desirable in order to ensure that the female is cycling normally with respect to estrus so that she is physiologically prepared for re-breeding in June or July.

Nutritional values of crested wheatgrass are often exceptionally high during April and May, but decline rapidly thereafter. Figures 1 and 2 illustrate the decline of crude protein content (CP) and in vitro digestibility coefficients (IVD). The latter is considered a good indicator of digestible organic matter (DOM) content of grass forages (Tilley and Terry 1963) and DOM is, in turn, closely related to the digestibile energy content of forages (Rittenhouse et al. 1971).

Crude protein

Crude protein values (Figure 1) are presented from a variety of geographic locations, and dry years are compared to normal years for two locations. First, note the steep and predictable decline from over 20% CP in March and April to less than 5% in September. A similar relationship, using other data, is demonstrated by Mayland (1985), in another paper in this symposium. By early July, CP content of crested wheatgrass has typically fallen below the recommended allowances (National Academy of Science 1976) for both cows and ewes nursing young. This is supported by animal performance data from central Utah (Cook and Harris 1968), showing that lactating cows grazing crested wheatgrass lost weight after June 29. However, young nursing animals, buffered by milk supplied by their dams, continued to gain although at reduced rates. During early May, calves and lambs gained 2.3 and 0.56 lbs

Table 2.--Cattle production on crested wheatgrass as compared to native ranges.

Grazing period	Gain per head Native	Wheatgrass	Prod. per acre Native	Wheatgrass	Reference
	lbs/da.		lbs		
(1) May 12 June 9	1.6	3.3	4	33	Lesperance et al. 1983
June 9 June 30	1.8	2.1	4	21	
(2) Apr-June	1.5	3.0	3.6[a]	36[a]	Frischknecht 1978
(3) May-Oct	2.0[a]	1.8[a]	16	25	Smoliak & Slen 1974

[a]Values calculated from initial data

per head per day, while in late June these rates had declined to 1.6 and 0.39 lbs per head, respectively.

Data points depicted by 4's and 7's (Fig. 1) illustrate how current growing conditions can radically alter the typical seasonal decay pattern of CP levels. These data points are from analyses conducted during years of sub-normal rainfall when crested wheatgrass was forced into drought-induced dormancy before entering the reproductive stage. In effect, the forage was "cured" in its highly-nutritious immature stage and it maintained this high level of CP well into late summer. Sneva (1967) demonstrated a similar effect by artificially "curing" crested wheatgrass by application of the herbicide paraquat. Of course, there is a trade-off of high quality forage for reduced quantities of forage biomass under such circumstances.

Digestibility

Not as many researchers have reported data on digestibility as CP content. However, from the information available, a curve was constructed showing a steep decline over time for in vitro digestion coefficients (Figure 2). A drought-related effect similar to that for CP is apparent here also (compare data points represented by 7's and 8's).

Digestibility is an especially important measure of forage quality because it plays a dual role in ruminant nutrition. The digestibility of a forage determines the proportion of nutrients liberated in the gastro-intestinal tract for assimilation by the animal. It also plays a major controlling role in the amount of forage dry matter (hence, energy) an animal can consume per unit of time. As a general rule, when dry matter digestibility of forage declines below about 50%, restrictions in intake rate can be expected due to longer residence time of material in the rumen and a slower rate of passage through the digestive tract. This digestibility level corresponds roughly to forage digestible energy (DE) content of about 2.5 kcal per gram of forage. From data shown in Table 3, crested wheatgrass has declined to this level of DE by the time flowering occurs. Thus, the relatively poor animal performance generally observed once seedheads appear is related both to its reduced level of CP and, perhaps more importantly, to its reduced contribution to the animal's energy needs. Havstad et al. (1983) reported that heifers grazing crested wheatgrass from late June to late August were virtually unaffected by the amount of forage available (from 920 down to 140 kg/ha), because they could consume only about 1.2% of their body weight in forage dry matter due to quality limitations. In contrast, Handl and Rittenhouse (1972) found that cattle were affected during early spring by the quantity of forage on-offer, and daily intake ranged from 1.9 to 2.1% of body weight.

In central Utah, flowering in crested wheatgrass typically occurs from early to mid-June. Thus, the plant may be generally characterized as extremely nutritious and productive during vegetative stages of growth, but marginally adequate to inadequate soon after flowering.

PALATABILITY

Crested wheatgrass is generally a palatable species. However, it typically occurs as monospecific stands or as the dominant species in relatively simple mixed stands with sagebrush, rabbitbrush, and cheatgrass (Bromus tectorum). Thus palatability often does not play the same role in grazing management of crested wheatgrass as it might in more complex mixed stands where several palatable species are usually represented.

On the basis of a single study, there are indications that crested wheatgrass may not be as palatable as generally believed. Gesshe and Walton (1980) reported that cattle showed the lowest relative preference for crested wheatgrass of four species tested. Results of their study are shown in Table 4. After flowering, both crested wheagrass and intermediate wheatgrass (A. intermedium) were distinctly lower in relative preference than either alfalfa (Medicago sativa) or Russian wildrye (Elymus junceus). The latter tends to retain green leaves well after flowering while those of crested wheatgrass soon senesce and become dormant.

POSSIBILITIES FOR IMPROVED MANAGEMENT AND CORRESPONDING RESEARCH NEEDS

Readdressing the original assumption of this paper that better ways of utilizing established seedings are available, one potential is winter grazing. Considering the prevailing high cost of wintering beef cows on either purchased or home-grown hay, the incentive for finding alternative,

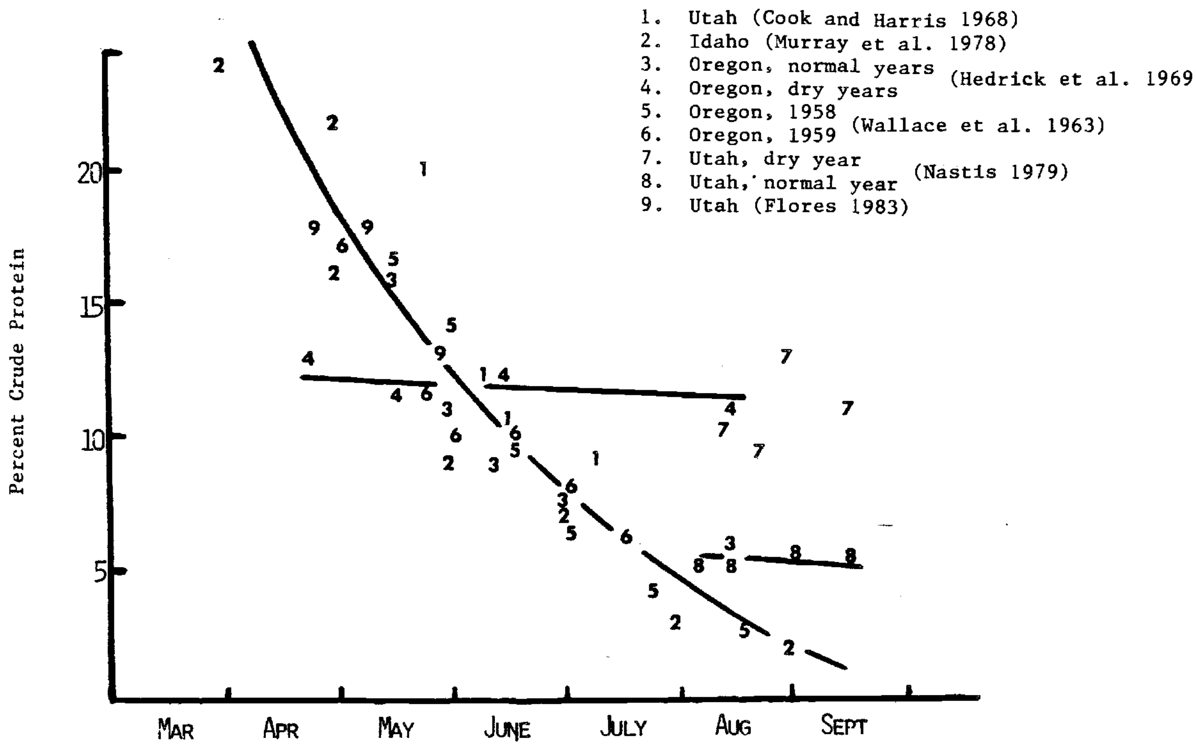

Figure 1.--Seasonal trends in crude protein content of crested wheatgrass, Great Basin area locations.

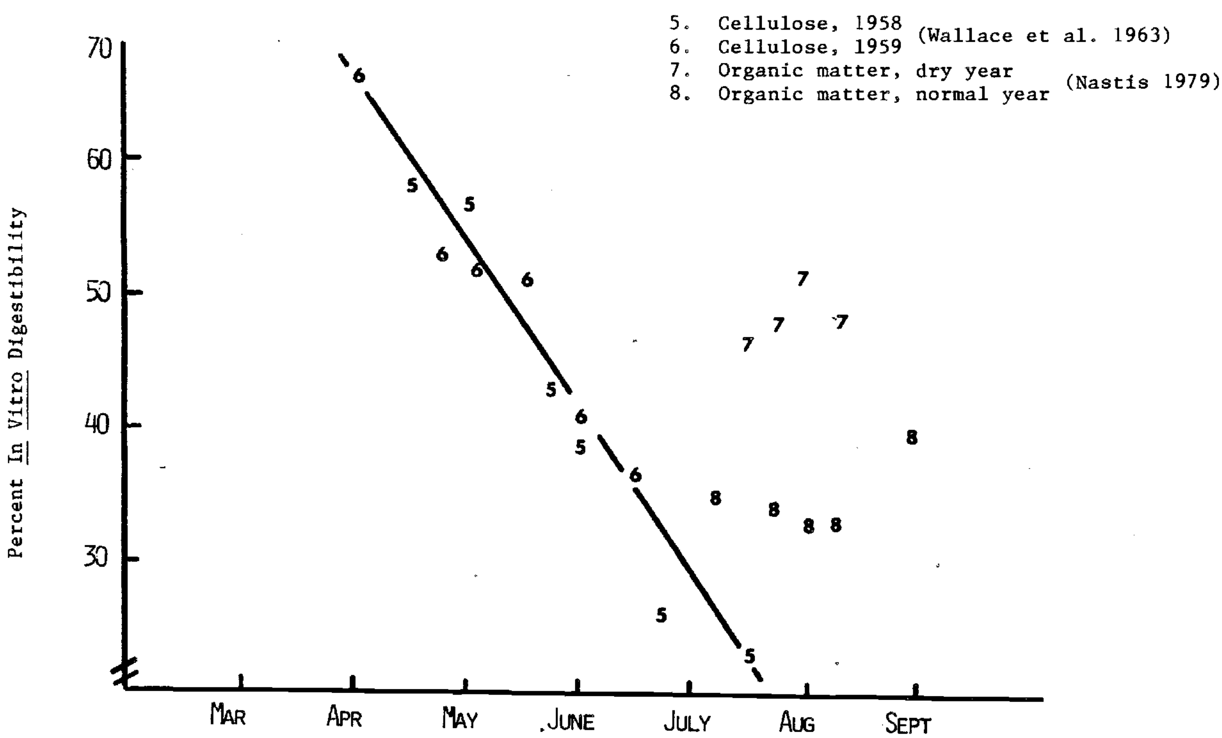

Figure 2.--Seasonal trends in *in vitro* digestibility of crested wheatgrass, Great Basin area locations.

Table 3.--Digestibile energy content of crested wheatgrass at four stages of maturity (Cook and Harris 1968).

Date	Stage	DE
		(kcal·gm^{-1})
5/9	5th leaf	3.5
6/8	early head	2.2
6/16	anthesis	2.2
7/7	hard seed	1.8

cheaper forage is high. Although research information on this question is extremely scarce, limited practical experience as well as preliminary research suggests some possibilities. Rancher J. C. Smith of Snowville, in northwestern Utah, has successfully wintered cows on range supporting a mixture of crested wheatgrass and native bluebunch wheatgrass (A. spicatum) for some 17 years. Hay feeding has been necessary only in three winters when deeper-than-normal snow prevented access to the standing grass foliage. Smith typically weans a 93% calf crop of calves weighing between 450 and 500 lbs per head based on a year-round grazing program (Utah State Extension Service 1982).

In a nearby area, animal weight response was measured during a single winter for a 900-cow herd grazing crested wheatgrass range from mid-November to late January (Malechek and Smith 1976). The range was stocked at the rate of 5 acres per animal unit per month. These cows sustained an average daily weight loss of about 0.3 lbs. per head, or about 2.5% of their initial weight during the 65-day period. Considering that mature cows in good condition can lose up to 20% of their body weight over winter without measurable losses of productivity (Corah 1980), the bodyweight losses observed in this study were small. Also, these losses were under conditions of no supplemental feeding.

Winter grazing on crested wheatgrass presents several questions needing research. Further documentation of cow herd performance (body weight change, calf crop, cow longevity) is needed under a variety of conditions. The influence of supplements, particularly protein, needs clarification particularly under variable weather and snow conditions. Cow behavior and feed requirements in response to different snow conditions needs to be determined so standards can be established for provision of feed during adverse weather conditions. Above all, the economics of winter grazing needs to be better understood.

Another possibility for improved use of seeded crested wheatgrass stands is earlier use in spring. Economic studies show that major returns per dollar invested can be achieved by getting cows on the range earlier in the spring. Traditionally, range managers have been reluctant to push the date of range entry too early for fear of compromising the principle of range readiness. While this principle was developed for native rangeland, it has been extended to seeded range in many situations. Thus, major economic gains may be passing unrealized by this conservative approach to grazing management.

From the standpoint of plant welfare, this concern may not be justified. Sharp's (1970) long-term studies at Point Springs in southern Idaho indicated that early grazing was more detrimental to animal production (presumably because of insufficient forage) than to plant production and plant vigor. However, specific amounts of standing spring forage necessary to meet animal demand were not established in the study and are still largely unknown, although Handl and Rittenhouse (1972) indicated that intake limitations were likely when available forage fell below 176 kg/ha.

Another aspect of Sharp's (1970) study relating to early grazing use was that too light grazing led to production of coarse, stemmy plants ("wolf plants") while heavy continuous grazing in the spring led to plant fragmentation and a reduction in stand density. These findings suggest that some form of rotational grazing at reasonably heavy stocking rates may be desirable for early spring management of crested wheatgrass stands. However, as Sharp (1970) cautioned, neither rigid rotation schemes nor general utilization guidelines are sufficient for gaining the most effective use of the species. Rather, attention should be given to specific characteristics of annual plant growth and environmental limitations in view of animal nutritional requirements and management goals. The particular characteristics and tolerances of crested wheatgrass give the appearance that the species might be well suited to management under the so-called short-duration grazing management schema where great flexibility in livestock management is possible and practical.

Crested wheatgrass is the kind of grass species that seems admirably suited to much greater intensity of grazing management than it has received. However, for this to be realized, a number of questions must first be answered. These include both animal- and plant-related aspects, such as the quantity of standing biomass of early spring forage necessary to meet animal requirements; effects of dead carry-over plant material on animal forage selection and subsequent plant growth; proper timing of grazing to stimulate daughter tiller production; how early grazing and trampling affects soil surface properties and site water budgets; and how various combinations of rest and graze periods affect carrying capacity and long-term site productivity. This list is, by no means, comprehensive but highlights some of the important issues.

Meanwhile, until the new research is done, range managers should accept the challenge of performing better management on crested wheatgrass stands than

Table 4.--Relative preference by cattle for crested wheatgrass and other forage species at three stages of maturity (Gesshe and Walton 1980).

Forage Species	Vegetative	Flowering	Seedset
Crested wheatgrass	0.8	0.2	0
Intermediate wheatgrass	1.2	0.2	0
Russian wildrye	1.2	1.9	1.7
Alfalfa	1.3	1.5	1.3

is currently being done. For a species with such great biological potential and the key economic need it can serve, a stronger attempt to apply state-of-the-art management is certainly warranted. Application of practical guidelines such as those presented by Sharp (1970) can yield major returns next year.

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SECTION VII.

Practical Management of Crested Wheatgrass.

Management Programs, How Early, How Long, How Much.

Chairman, Thomas E. Bedell

Impact of Grazing on Crested Wheatgrass in Relation to Plant Size

B. E. Norton and Patricia S. Johnson

ABSTRACT: Utilization of crested wheatgrass on a plant-by-plant basis was studied using heifers for a six-week grazing period on foothill rangeland in Utah seeded almost 30 years previously. The cattle preferred medium-sized plants with basal areas ranging from 11 to 200 cm^2. Smaller plants seemed more likely to be damaged by trampling than by defoliation. Larger plants contributed relatively less to forage harvested, receiving some protection from grazing due to the physical impediment of standing stalks from old inflorescences. Many plants were not grazed at all (20 percent of plants with basal area larger than 10 cm^2). The probability of regrazing was low (less than 17 percent) and most of it occurred after the first two weeks of grazing. Regrazing was concentrated on plants lightly grazed at first and on portions not previously utilized. There was an observable change in the character of grazing impacts during the grazing season. The number of small plants defoliated in a two-day period increased steadily for the first two weeks and then rapidly declined, reflecting an apparent shift in grazing behavior.

INTRODUCTION

Converting native range vegetation to crested wheatgrass pastures has been the major success story of range improvement on the Great Plains and Intermountain regions of North America (Holochek 1981). Many indigenous forage species, especially bunchgrasses, have a low tolerance of livestock grazing and give way to less palatable woody species and exotic weedy annuals.

Introduced from Eurasia, crested wheatgrass by comparison exhibits remarkable persistence under grazing pressure and is adapted to a cold continental climate with dry summers. It begins spring growth early, reaches maturity in June, enters a post-reproductive dormancy and then resumes growth following fall rains. This growth pattern supplies highly nutritious forage at a critical period for ranchers who need to move their livestock off costly winter supplements onto spring pastures, awaiting access to mountain ranges (Cook and Harris 1952, Frischnecht and Harris 1968). The stock can return to wheatgrass pastures in the fall and continue grazing them into December if snow depth permits (Harris et al. 1968).

Crested wheatgrass pastures require a substantial investment for site preparation and stand establishment, but they can be maintained for decades under proper management. In order to make the best use of the abundant but expensive grass grown in a crested wheatgrass pasture it is important to know how forage removal impacts the forage resource. Even in an almost monotypic stand, as crested wheatgrass pastures often are, livestock appear to exercise selectivity in defoliation, leaving some portions of the pasture more heavily used than others. This is most apparent when pastures are grazed continuously to a moderate level of utilization for the entire grazing season, and when there is a relatively large number of "wolf" plants present -- large plants that retain the old stalks of flowering culms from year to year. The character of grazing impacts may change during the grazing season as the forage on offer is depleted of the more preferred material and as the livestock are presented with an opportunity to consume regrowth on previously defoliated plants. Estimates of gross utilization do not provide sufficient detail. We are interested in answering questions like: Is grazing random or uniform? Is there a grazing preference for certain kinds of plants within the same species and, if so, what plant or pasture characteristics are correlated with apparent preferences? What is the probability that plants will be regrazed during the grazing season? How often will they be regrazed? Is regrazing likely to occur on parts of the plant that were previously defoliated?

In order to describe defoliation at this level of specificity it is necessary to observe individual plants in a grazed pasture on a regular basis. Not surprisingly, given the effort required to collect such data and the difficulties of analysis, the

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available information on this subject is very limited. More studies have been reported on patterns of defoliation by sheep (e.g., Hodgson and Ollerenshaw 1969, Greenwood and Arnold 1968, Hodgkinson 1980) than cattle (e.g., Gammon and Roberts 1978), and nothing at the detail addressed here has been attempted with cattle grazing crested wheatgrass, apart from work done by the authors (Norton and Johnson 1983). The present paper is concerned with the plant component at the plant-animal interface in grazing of crested wheatgrass by cattle.

RESEARCH AREA AND TECHNIQUES

Crested wheatgrass pastures at the Tintic Range Research Station near Eureka, Utah, were seeded in the early 1950's. Several of them, including pastures 8 and 19 where our grazig study was conducted, retain an almost pure stand of crested wheatgrass (*Agropyron desertorum*) with the rhizomatous native western wheatgrass (*Agropyron smithii*) contributing the minor grass component. Scattered remnants of juniper occur in pasture 8. Basin big sagebrush (*Artemisia tridentata* ssp. *tridentata*) covered these foothill ranges prior to clearing the vegetation in preparation for seeding. It is now reappearing, but not yet in sufficient quantity in pastures 8 and 19 to substantially influence crested wheatgrass production.

The Tintic research pastures provide spring and summer forage for Angus heifers. Traditional management has been to graze each 28-ha pasture for six to eight weeks with 30 heifers and two bulls to achieve at least 50 percent forage utilization, usually more. Under a rotational grazing system, such as short-duration grazing being tested in a companion study, it may be possible to improve efficiency of forage utilization and increase livestock production. But in order to describe changes in pasture utilization due to rotational grazing one must first understand the nature of defoliation under continuous grazing, in this case continuous grazing for a six to eight-week period. The information on grazing reported here was developed as part of a baseline study of traditional pasture management to serve as a reference in the evaluation of rotational grazing schemes.

Nearly 300 permanent plots (0.5 m^2) in the two pastures were inspected every second day for six weeks beginning May 31, 1979 when the heifers were introduced. Evidence of grazing was recorded on a plant-by-plant basis noting the stubble height of the grazed portion and the area of defoliated crown cover. Initial plant heights were marked on basal outlines of perennial grass plants drawn on plot maps; ungrazed plant heights were remeasured halfway through the study. The total number of plants sampled was 4,566.

RESULTS

Size Class Utilization

A breakdown of the plant population by nine arbitrary size classes appears in Figure 1. The smallest plants were somewhat neglected by the cattle. Only 40 percent of plants less than 0.5 cm^2 basal area, and 59 percent of plants with basal area between 0.5 and 10 cm^2, were grazed to any degree. These two smallest size classes contained 42 percent of the number of plants sampled but together represented only 1.5 percent of the available forage, calculated on a volume basis, and contributed only 2.0 percent of harvested forage. The average plant was nibbled down from a height of 15 cm to 9 cm. The very smallness of these crested wheatgrass plants, their obscurity in the foraging environment of grazing cattle, appears to confer a degree of protection from defoliation. Such small plants are probably damaged more by livestock trampling than by defoliation.

Plants larger than 10 cm^2 basal area were more likely to be grazed, an 80 percent probability over the six-week period. It is perhaps surprising that one fifth of all plants of 11 cm^2 basal area or larger failed to experience observable defoliation while 32 cattle spent six weeks roaming a pasture of 28 ha! Severity of grazing impact was inversely related to plant size. Grazed plants with a basal area from 11 to 50 cm, the major group among these larger size classes, were reduced from an average height of 18 cm to 10 cm, and an average 83% of the crown cover was defoliated.

In contrast, grazed plants in the largest class of >500 cm^2 basal area, which included the wolf plants, retained a 21 cm stubble from an initial average height of 33 cm, and only an average 31 percent of the crown area was grazed. These largest plants, although making up only 1 percent of the total plant population, comprised 20 percent of the total available forage and contributed 16 percent of the forage harvested.

An additional measure of selective grazing was calculated by comparing the percent of available forage in each size class with the relative contribution to harvested forage, all on a forage volume basis. The results in Figure 2 indicate that livestock were placing the greatest grazing pressure

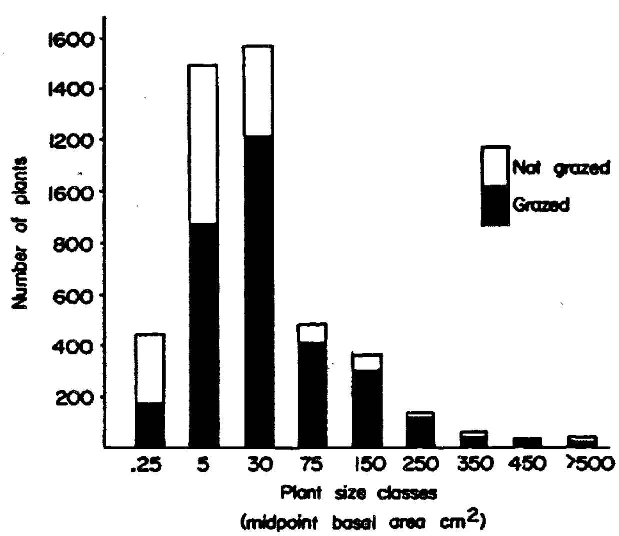

Figure 1.--Distribution of plants sampled according to size classes. The solid portion of each bar represents the number of plants that were grazed to any degree during the six-week grazing period.

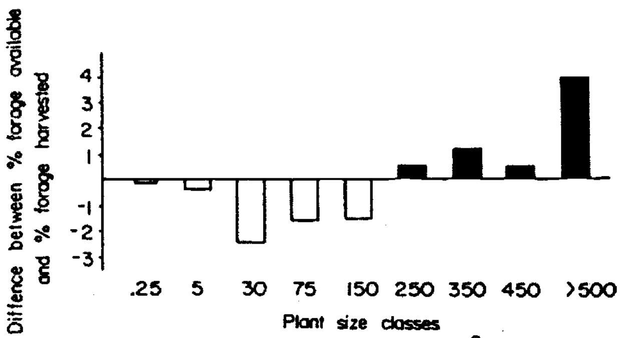

Figure 2.--Percent of available forage in each size class relative to percent of forage consumed from the size class. Forage amounts were calculated in terms of volume.

on medium-sized crested wheatgrass plants, those with basal areas from 11 to 200 cm^2. For example, plants in the 11-50 cm^2 basal area class contained 11.75 percent of the total available forage, but the heifers took from these plants 14.25 percent of what they harvested overall. Altogether the plants in this medium-sized group contributed 49 percent of the forage consumed from an offering of 43 percent of the forage available.

Wolf Plants

The relative neglect of the largest plants requires explanation. Wolf plants carry a substantial amount of standing stalks left over from the culms of old inflorescences. This residual straw could constitute a physical impediment to livestock grazing (Willms et al. 1980) and deter herbivory. This hypothesis was tested by comparing grazing impact on plants with and without over-winter stalks. Prior to spring grazing a number of matched pairs of plants with heavy over-winter stalk accumulations were identified and from a randomly chosen member of each pair the stalks were removed by hand. As previously reported by Norton et al. (1983) plants without standing straw were grazed more. The impediment of stalks increased with increasing plant size, and the influence of old culms on grazing was most pronounced in early spring and declined with the rising growth of new foliage (Johnson and Norton, manuscript submitted). We conclude that wherever there is moderate utilization of crested wheatgrass under continuous season-long use, nonuniform grazing will allow a residue of flowering stalks to be carried into the winter and initiate or exacerbate the self-perpetuating problem of wolf plants. Large plants neglected one year will tend to be neglected the next, and so on.

Regrazing

The data on incidence of regrazing were unexpected. Of all plants that were grazed during the study, only 16.6 percent were regrazed. Of all those that were regrazed, 86.5 percent were grazed twice and 11.4 percent were grazed three times. Only 11 plants in the whole study were grazed more than three times. If continuous season-long grazing has a detrimental impact it is not likely to be caused by repeated grazing on preferred plants, at least within the same grazing season. Analysis of data from the same plots from subsequent years, still incomplete at this time, will enable us to address the proposition that any danger of pasture deterioration from continuous grazing is more likely due to repeated defoliation of the same plants or patches of plants year after year or season after season, rather than the result of repeated grazing over the short term.

The following analysis of regrazing was confined to plants of at least 101 cm^2 basal area, large enough for a heifer to discriminate between the ungrazed and previously grazed portions. Evidence of regrazing was not apparent until the cattle had been in the pastures for 8 days. Over 90 percent of regrazing occurred after the first 14 days of use. The cattle did not prefer to regraze plants that were more extensively defoliated at the first grazing. Plants grazed just once had on average 66 percent of their crown cover defoliated and were reduced to a stubble of 16 cm. Regrazed plants had on average 48 percent of their crown cover affected at the first grazing event with a remaining stubble of 15 cm. The second grazing event defoliated 49 percent of crown cover on average with stubble height again at 15 cm. The second grazing overlapped the first only 32 percent of the time, and where overlap occurred only 44 percent of the crown cover was subjected to two defoliations. When these data are related to the low probability of a plant being regrazed, there was obviously only light grazing pressure on regrowth. On the other hand, the study was conducted in early summer when rate of regrowth after defoliation was much slower than in spring, so that there may have been less growth on grazed portions than if the grazing had occurred in late April or May. It is also probable that repeated grazing and defoliation of previously grazed portions would have been more severe if the overall utilization of the two pastures at the end of the study had been greater than the moderate 50 percent level achieved.

Plant Use Through Time

As the grazing season progressed, the total number of plants defoliated (to any degree) in a two-day period steadily rose to a maximum of almost 450 (about 10 percent of the sample population) at 16 days of grazing and then declined as steeply for the next 8 days, finally levelling out at around 200 plants per two days of grazing (Figure 3). The shape of this curve is due almost entirely to the pattern of utilization of the smaller plants, up to 100 cm^2 basal area. Medium-sized plants, 100-300 cm^2 basal area, exhibit a faint echo of the trend, but at the peak only 50 of these plants were being grazed every two days. These patterns could reflect an exploratory phase of grazing behavior lasting for two weeks, during which time the larger and more readily accessible members of the small size class were selected. These data do not provide a self-evident behavioral explanation. It is clear from Figure 3, however, that for the first 16 days of grazing the herbage consumed was coming from an increasingly larger number of plants, almost all of them plants not previously grazed.

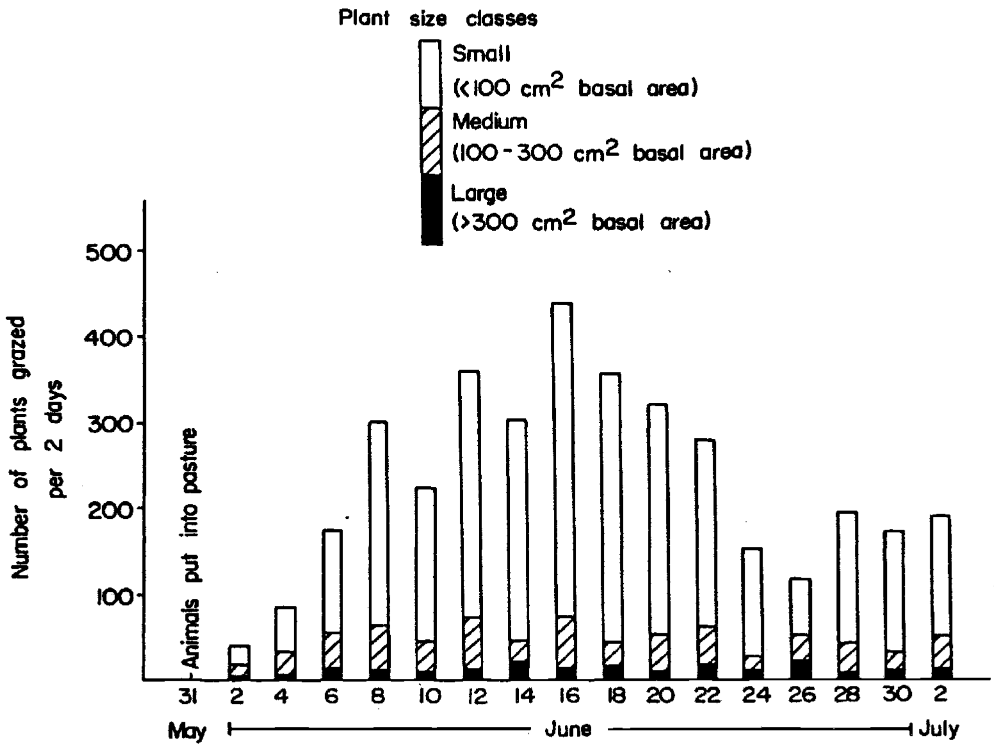

Figure 3.--Number of plants, in 3 size classes, grazed to any degree in 2-day grazing periods.

DISCUSSION

This rather superficial, single-season investigation of defoliation set out to answer questions about the dynamics of cattle grazing crested wheatgrass under traditional management on Utah's foothill ranges. We discovered that grazing is not a random process and that utilization is far from uniform. Medium-sized plants were preferred over either small or large plants; the proportion of forage they contributed to consumption was in excess of their proportion of total forage on offer. The cattle appeared to seek out small plants for the first 16 days of the grazing season, however.

The probability of a plant being grazed at all in six weeks was only 69.3 percent; this increased to 80 percent for plants which had a basal area of at least 11 cm^2. The probability of a grazed plant being defoliated again, to any degree, was only 16.6 percent, and nearly nine out of ten of these repeated grazings stopped there. A very small proportion of grazed plants, 2.2 percent, was defoliated three or more times. We found no evidence that regrazing was concentrated on parts of the plant that had been grazed before, although we must note that the study was conducted after the spring period when rapid and substantial regrowth would be expected. Perhaps the most provocative portion of the data revealed changes through time in the grazing behavior of cattle on the pastures, which raises a fresh set of questions and underscores the limitations of the information we have gathered so far.

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The Optimum Retreatment Schedule for Established Crested Wheatgrass Stands

L. Allen Torell and E. Bruce Godfrey

ABSTRACT: This paper outlines and describes research conducted at Utah State University on the optimum length of time before invading brush and timber species should be removed from established crested wheatgrass stands. The primary purposes are to 1) analyze the economically optimal frequency of long-term improvements of crested wheatgrass stands, and 2) include the interaction of grazing in the dynamic pasture and range investment decision.

INTRODUCTION

Crested wheatgrass (Agropyron cristatum, Agropyron desertorum) seedings have come to provide a significant amount of the grazing resource for the western livestock industry. In Nevada, as an example, about 1 million of the 27 million acres (10.9 million ha) of sagebrush rangeland in the state have been seeded. The seeded area constitutes only 2 percent of the total rangeland in the state but produces 10 percent of the harvestable animal unit months (AUM's) of grazing (Young and McKenzie 1982). A similar contribution of crested wheatgrass is also found in other western states. Given the importance of crested wheatgrass as a source of forage to the western livestock industry, the management of these stands will continue to be a vital concern.

At least three interrelated management decisions concerning crested wheatgrass stands are of primary importance. First, the optimal stocking rate and second, the best season of use of the stand must be determined. Taken together, these management decisions relate to optimal use of the grazing resource. A third management decision that must be considered deals with optimal timing of stand improvement and rejuvenation. As stand productivity declines over time, the manager has the following alternative management options. First, the stand can be allowed to deteriorate with no additional range improvements, or second, stand productivity can be rejuvenated by clearing invading brush and nonforage species. If the second option is followed, then the question as to when to retreat the stand must also be considered.

There are two primary purposes of this research. First, the retreatment problem (e.g., choosing optimal frequencies of long-term improvements) is extended to an analysis of crested wheatgrass growth and production over time. Second, the interaction and impact of grazing on the dynamic pasture and range investment decision is considered. The following discussion will 1) outline the nature of the problem, 2) discuss the basic economic theory underlying the optimal decision rule for making long-term improvements in natural resource problems, and 3) outline the proposed procedure which will be used to define and formulate the various functional relationships needed to address the retreatment problem. The approach is developed fully in Torell (1984).

NATURE OF THE PROBLEM

Complete control of big sagebrush (Artemisia tridentata), e.g., 100 percent brush eradication, is seldom achieved at the time of seeding. In southwestern Montana, Johnson and Payne (1968) estimated that from 0.1 to 0.7 sagebrush plants/m^2 survived eradication treatments. Johnson (1969) estimated that initial sagebrush kill of a spray project in central Wyoming ranged from 45 to 87 percent. Given a general inability to completely eradicate the brush canopy, brush surviving the treatment provides an important seed source for reestablishing species.[1]

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[1] The economically optimum rate of control at the time of stand rejuvenation was studied by Tanaka (1985), reported in a companion paper in this volume.

Other environmental factors affecting the rate of brush encroachment onto crested wheatgrass stands include soil and topography, precipitation, time of treatment in relation to sagebrush seed maturity, and grazing practices (Johnson and Payne 1968). The effects of grazing have been documented with conclusive but still inadequate quantitative definition to allow economic analysis.

Bleak and Plummer (1954) reported on crested wheatgrass pastures in central Utah that had been grazed by sheep in the spring for seven consecutive years. In this study, the heavily utilized pastures (88 percent use) showed a decrease in grass production with most grass clumps having died in the middle. Crested wheatgrass plants were small, and there was a marked increase in growth of Russian thistle (Salsola kali). Light (59 percent) and moderate (71 percent) uses resulted in maintenance of "good" production, with some decline with age of the stand noted.

Similar results were reported by Currie and Smith (1970), Sharp (1970), Springfield (1963), Frischknecht and Bleak (1957), Frishknecht and Harris (1968), and Robertson and others (1970). While the impact of grazing intensity on forage production and brush invasion was variable, the general conclusions were that heavy grazing reduced both crown cover and vigor of crested wheatgrass while encouraging return of sagebrush.

The literature generally indicates that production of crested wheatgrass will likely decline over time. This is due to brush canopy increasing with establishment of new plants and increase in size of surviving shrubs. However, the rate of brush encroachment will likely be affected by environmental influences as well as grazing management.

Stand longevity can be extended by light to moderate grazing use (Currie and Smith 1970, Sharp 1970). Therefore, the economic question of concern is the tradeoff between extended stand life resulting from light to moderate use and the additional returns which could be realized by heavier stocking. If heavy stocking is practiced, the grass stand will eventually be damaged, herbage production will be reduced, and beef production and annual profits will decline (Springfield 1963). However, the range manager generally has the option of undertaking range improvements which will rejuvenate stand productivity, and thus, mitigate detrimental impacts from heavy use.[2] The goal of the profit-seeking range planner comes down to determining the grazing-use pattern and stand-retreatment schedule that will maximize the net present value (NPV) of future net returns from use of the crested wheatgrass stand. To address the question properly, dynamic aspects of grazing impact on the rate of brush encroachment must be explicitly considered, as well as the time aspect of rejuvenating stand productivity.

[2]This may not be true on public rangelands because Federal and State regulations may limit the use of some improvement practices.

OPTIMAL DECISION RULE FOR LONG-TERM INVESTMENTS

Techniques for determinig the optimum replacement pattern for long-lived assets have been studied, debated, and improved upon by agricultural economists for a number of years. Pioneer work in the area was published in 1960 by Faris. This was followed by Winder and Trant (1961), Cotner (1963), Chisholm (1966), Burt (1971), and Perrin (1972).

The general premise is that selection of the particular production period yielding the maximum NPV of future net returns over a specified planning horizon is the central aim (Chisholm 1966). One must compare the gains from keeping the current asset for another time interval with the opportunity gains which could be realized from replacement of the asset during the same period.

The problem of choosing the optimal frequency for rangeland improvements has an added dimension compared to the classical replacement problem, wherein the age of an asset has no affect on the value of its replacement (e.g., the age of a tractor when replaced has no effect on the value that can be derived from the replacement tractor). For the dynamic rangeland and pasture improvement problem this is not necessarily the case. The longer the time interval before brush and timber removal the greater the amount of pasture deterioration and the more likely that forage values will be reduced in at least the next renewal cycle. If economic and biological conditions are such that pasture renewal implies complete reseeding with destruction of the old stand, then the lagged effect is completely wiped out, and the problem is the same as that of the classical replacement problem. This lagged effect of the last renewal cycle on recovery rate of the stand was discussed in detail by Burt (1971) using an example of pinyon-juniper encroachment onto native rangeland in the southwestern United States.

For native rangeland invaded by pinyon-juniper, the recovery to full potential can vary from just a few years with control at the 15th year of depletion to over 15 years if control is postponed until the 45th year of depletion (Cotner 1963). Control of small trees at the 15th year of encroachment provided benefits mostly in the form of protection against future forage loss. Conversely, control at a date late in the renewal cycle primarily benefited increased forage production in the present.

While the lagged effect is important for range improvement decisions on native rangeland, its importance for improvement decisions of crested wheatgrass stands is not so clear. Robertson (1969) estimated that aerial spraying of sagebrush within a crested wheatgrass stand in Nevada, which formed a 12 percent canopy cover before the spray, resulted in production levels of 1,163 pounds (527 kg) per acre within four years, as compared with only 600 pounds (272 kg) per acre for the control area. The fourth-year production was regarded as peak production or full recovery[3].

[3] Personal communication with J.H. Robertson, Range Scientist, University of Nevada - Reno; October 26, 1983.

Hull and Klomp (1974) estimated that, with normal precipitation, approximately two years of moderate use after brush control should bring a stand of crested wheatgrass to full productivity. This conclusion was reached for one study site which had a big sagebrush canopy cover of nearly 34 percent.

It appears that the age of the brush when controlled does not significantly affect the rate of crested wheatgrass stand recovery--given that an adequate grass understory exists. If this is the case, the dynamic investment problem is greatly simplified. Similar to the classical replacement problem, the problem becomes one of deciding how long the renewal cycle should be so as to maximize the net present value of future net returns from the land. It is not complicated by the problem discussed by Burt (1971), whereby replacement age (i.e., age of stand at rejuvenation) enters into the revenue function of following renewal cycles. While a dynamic analysis is still needed, it is not nearly so dynamic as an analysis of native rangeland.

THE "NO DATA" PROBLEM

Economic analysis of range improvements requires that physical and biological relationships be quantified. It is not enough to just assert or determine that heavy stocking rates shorten the life of crested wheatgrass stands or that increasing brush density reduces grass yields. Yet these are the conclusions reached through the design of most biological studies. Multiple rate treatments and long-term studies, which would allow one to quantify biological relationships in a functional form, are generally not conducted. While the researcher may conclude "beyond a reasonable doubt" that action A impacts desired production of B, the question of by how much has generally not been answered. While the literature indicates the direction of impact for most of the relationships discussed, functional specification is generally not available. Rigorous mathematical specificiation of the investment problem from on-the-ground studies in the literature is not possible.

Given this limitation, a second best alternative must be used, such as the use of simulation models. One of these models SPUR (standing for Simulation of Production and Utilization of Rangelands[4]) was used in this study to simulate the multiple rate long-term data needed to address the investment question. Using these simulated data, an economic model was developed to analyze optimal timing of control of sagebrush invading crested wheatgrass stands.

Multiple simulations of crested wheatgrass production under alternative stocking rates and brush densities provide what has been called "pseudo data" by Griffin (1977). These points on a simulated production surface are used to estimate the functional form of equations depicting 1) the relationship between brush density and crested wheatgrass production, 2) the relationship between livestock grazing and brush invasion into a crested wheatgrass stand, and 3) other relationships which may be deemed important to the problem.

[4]For a complete description of SPUR see Wight (1983).

The obvious problem with this pseudo data approach is that the results ultimately rest on the quality and completeness of the underlying process model (SPUR in this case). The results of these simulations are also typically difficult to validate. However, the pseudo data approach also offers some important advantages relative to conventional time series and cross sectional data. First, data can be generated as needed for economic analysis. That is, relationships undefined in the literature but crucial to the economic analysis can be defined through simulation modeling. Second, as discussed by Griffin (1977), generated pseudo data is generally free of problems with multicollinearity and limited sample range.

While this approach may not be totally acceptable, depending upon the validity of SPUR simulation results, it appears to be the only approach which can be followed at this time. The challenge to researchers studying optimal management of crested wheatgrass stands is to design long-term studies with multiple rate applications which can be used to quantify the various relationships needed for making sound economic decisions. In the meantime, computer modeling provides a second best solution to the no data problem. Furthermore, given the expense of conducting long-term range studies, simulation modeling may provide answers of adequate resolution. That is, long-term on-the-ground studies may not be justified from a benefit/cost perspective.

RESULTS

Figure 1 provides an example of the type of information that can be obtained through simulation modeling. In this application, peak crested wheatgrass production over time as affected by stocking rate was simulated using SPUR. Simulation results indicate that the long-run trend of grass production will be downwards at all three stocking rates considered, but grass production is estimated to decrease the fastest at the heavier rates. However, it should be noted that the stand is estimated to be very long lived and able to withstand even heavy grazing pressure.

Testing of the SPUR model, as with other simulation models, has been a major problem. Field data are generally not available. However, one test of SPUR model results was made with data available from Harris and others (1968) for crested wheatgrass grazing trials conducted at Benmore, Utah. The trial considered the weight gain of yearlings grazing season-long (April 25 through December 7) on crested wheatgrass seedings. Both supplemented and non-supplemented options were considered.

For comparison purposes, this same grazing scheme was simulated using SPUR, on the assumption of no supplement being fed. Model results were amazingly close with no significant difference in accumulated weight gain until late in the grazing season (Fig. 2). While more model validation and testing is needed, these results are encouraging. Other tests of the SPUR model have been conducted and more are planned (Wight 1983).

The economic model developed using SPUR-simulated data indicates that crested wheatgrass is persistent and long-lived, and the optimal

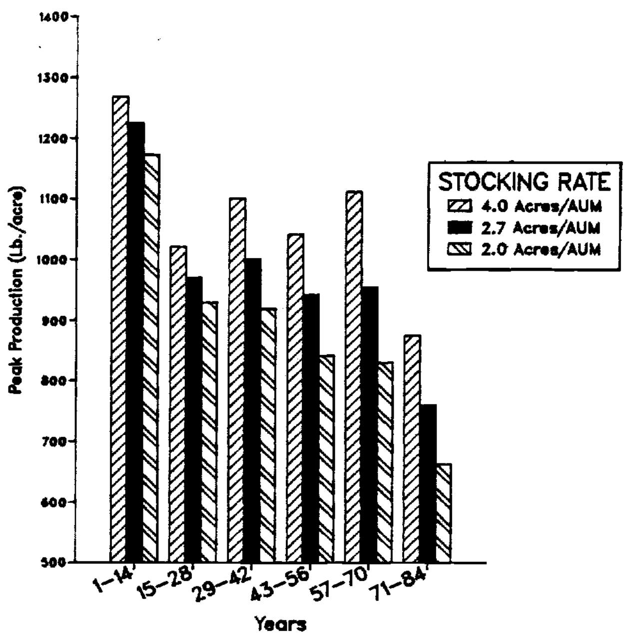

Figure 1. SPUR simulated crested wheatgrass production as affected by stocking rate.

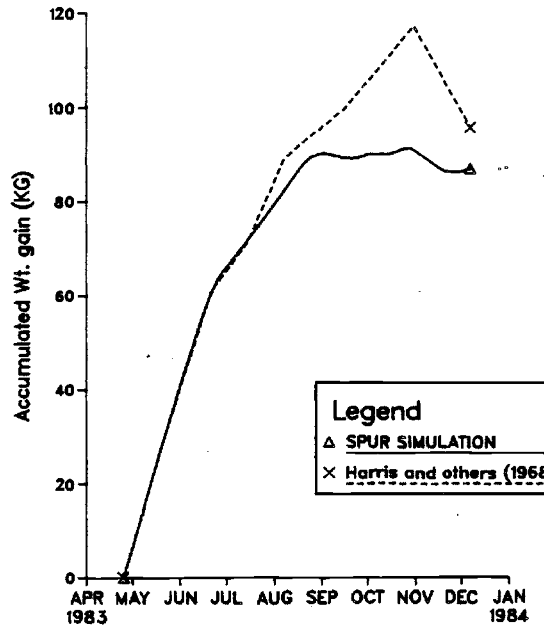

Figure 2.--SPUR simulated livestock gains as compared with Harris and others (1968).

retreatment schedule is at least 35 years long. NPV of the income stream derived from the seeding was increased greatly by extending the retreatment cycle to 35 years and beyond.

Optimal forage utilization rates were found to be slightly over 70 percent. This is not significantly different from the 65-70 percent rate recommended in the literature (Currie and Smith 1970, Springfield 1963, Sharp 1970, Smoliak et al. 1981, Frischknecht and Harris 1968, and Springfield and Reid 1967.

While the results of computer simulation analysis may always be suspect, simulation models such as SPUR do provide a tool for addressing relevant research and management questions. In some cases, it is the only option available and will provide useful information for managers who are trying to determine when to rejuvenate a stand of crested wheatgrass.

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Nitrogen - Sulfur Relations in Nordan Crested Wheatgrass (Agropyron desertorum) and its Response to Nitrogen and Sulfur Fertilizer

Forrest A. Sneva

ABSTRACT: The response to a sulfur (S) application of 28.5 pounds per acre in combination with 25, 50, and 75 pounds per acre (28, 56, 84 kg/ha) nitrogen (N) applied annually to an established stand of Nordan crested wheatgrass was compared with that receiving the same rates of N only. In the first growing season mean herbage N:S ratios of 8:1 were maintained under all levels of N fertilization with S present; however, in its absence, N:S ratios ranged from 9:1 in the controls to 15:1 in plants fertilized with 75 pounds per acre (84 kg/ha) N. Yield of herbage, herbage N, and herbage S was increased with N fertilization in the subsequent six years but with S also present further and significant ($P<0.05$) increases were measured during the second, third, and fourth growing seasons following the initial application. Soil S increases in the upper 10 inches (25 cm) due to S additions were evident only in the first growing season. These results suggest that crested wheatgrass under N fertilization programs may suffer from S deficiencies which can be corrected with periodic applications of S.

ACKNOWLEDGEMENTS: The research is a cooperative investigation of the USDA Agricultural Research Service and the Oregon Agricultural Experiment Station, Burns, Ore. Oregon Agr. Exp. Sta. Tech. Pap. 7028.

INTRODUCTION

Nitrogen (N) is recognized as a limiting factor to the production of crested wheatgrass (Agropyron ssp.) growing on semiarid soils. As such, nitrogen fertilization research within the Intermountain sagebrush province has been extensive over the past three decades. Schmisseur and Miller (1978) cite 18 papers presenting nitrogen response data applicable to their economic analysis of fertilization on seeded sagebrush lands.

Sulfur (S) deficiencies in the Pacific Northwest were recognized by Cheney and others in 1956, and clarified further by Woodhouse in 1964. Wheatgrass response to sulfur fertilization was examined by Hyder and Sneva in eastern Oregon in 1952-53 (unpublished data - Squaw Butte Experiment Station); by Eckert and others (1961) in northern Nevada; and by Kay and Evans (1965) in northeastern California. In all three studies there was little or no response to sulfur alone or in combination with other elements considered. However, in all three locations stands of the seeded grass were three years or less in age. Subsequently, Sneva and Rittenhouse (1976) reported strong response to sulfur in combination with nitrogen in some years on aged stands or those on soils that had been growing improved species for several decades. Elsewhere in the Pacific Northwest, Pumphrey and Hart (1973) and Geist (1976) reported positive production response from both nitrogen and sulfur additions to soils derived from volcanic ash at higher elevations in northeastern Oregon.

This study is a phase of research conducted to examine the N:S relations within native and introduced vegetation of the big sagebrush (Artemisia tridentata) ecosystem in eastern Oregon. Specifically I examined the N:S relations in crested wheatgrass in the first year following N fertilization with and without S. In the following six years I monitored herbage yield, N, and S concentrations in the herbage when nitrogen treatments were annually repeated but with no additional sulfur applied.

Locale

The study site was in a 5 acre (2 ha) nursery on the Squaw Butte Experiment Station approximately 39 miles (65 km) west of Burns in eastern Oregon. The site, originally dominated by big sagebrush and bunchgrasses, was seeded to an unknown crested wheatgrass selection in the mid-1940's. The area was subsequently plowed and seeded to Nordan crested wheatgrass (A. desertorum [Link] Schultes) in 1966. The stand was in good condition, had previously received no irrigation or fertilization, and had been grazed or mowed annually after maturity.

The soil has been described by Eckert (1957). These residual or alluvial soils developed from basalt or rhyolite parent material. Textures range from loam or sandy loam in the surface layer to

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sandy clay loams in the sub-surface layers. An indurated restrictive layer cemented by silica or calcium is present between the 18 to 30 inch (46 to 76 cm) depth. Surface layers normally contain less than 1 percent organic matter and the pH ranges from 6.4 to 7.0.

Procedures

Plots 6 X 18 feet (1.8 x 5.5 m) were established in the fall of 1970 and fertilizer treatments applied on 28 January 1971. Treatments were no fertilizer, ammonium nitrate and ammonium sulphate alone and in combination to provide levels of 25, 50, and 75 pounds per acre (28, 56, and 84 kg/ha) of actual N only, and those same N levels plus 28.5 pounds per acre (32 kg/ha) S. Sulfur was applied only to N treated plots in the first year. Plots were subsequently fertilized annually with ammonium nitrate commencing in the fall of 1971 through 1976. Rates of N fertilizer were randomly allocated to subplots within randomly assigned main plots (N vs N plus S) with 3 replicates of treatments.

In 1971, herbage from 13 linear feet (3.7 m) of drill row within each subplot was harvested on 30 April, 14 May, 2 June, 11 June, and 14 July. These samples were oven dried and prepared for N and S analyses. Soil samples (three 0.75 inch diameter (1.9 cm) cores per sub-plot) of the surface 10 inches (25 cm) were obtained on 15 July and similarily handled and prepared for analyses. Nitrogen and sulfur analysis followed that of Association of Official Agricultural Chemists (1965).

In subsequent years herbage yield was estimated by harvesting 24 feet^2 (2.2 m^2) within each plot. Following oven drying and weighing this sample was prepared for nitrogen and sulfur analysis. Yield sample dates were 12 July 1972, 14 May 1973, 29 July 1974, 8 August 1975, 27 August 1976 and 12 July 1977. The surface 10 inches (25 cm) of subplot soils were sampled as previously described above on 14 July 1972 and 10 July 1973, and analyzed for nitrogen and sulfur.

Data analyses were for a split-split plot over years with treatment mean differences tested with Duncan's multiple range test. Nitrogen-sulfur ratios were transformed by angles prior to analysis.

RESULTS AND DISCUSSION

First Year Response

Crop-year precipitation (Sept.-June, inc.) for 1971 was 107 percent of the long term median amount. Temperature during April, May, and June was slightly below the long term mean with average monthly maximum temperatures of 12, 18 and 19° C, respectively. Thus, responses measured in that year are inferred to be relatively free of strong climatic influences.

All main effects, and first and second order interactions (except the latter for N:S ratios) were significant ($P<0.05$) sources of variation in the analyses for N and S concentrations and their ratios. These relations are presented in Figures 1 to 3.

Mean N concentrations ranged from 1.5 in the controls to about 2.5 percent when fertilized with 75 pounds per acre (84 kg/ha) N, with highest concentrations associated with N only treatments (Fig. 1a). Mean concentrations decreased in the controls from about 2 to less than 1 percent from 30 April to 14 July, as compared with a more rapid decline (3.5 to 1.5 percent) for the same period in grass fertilized with 75 pounds N per acre (84 kg/ha). Concentrations of N in grasses receiving inbetween fertilizer rates showed proportional rates of decline (Fig. 1b). Mean N concentrations on 30 April were the same in grasses fertilized with N or N plus S, but as the grasses matured the N declined most rapidly in grasses fertilized with N plus S (Fig. 1c). This difference is shown more clearly in Figure 1d which also shows a greater consistency in linear trend with rate of N in those plants fertilized with N only as they matured.

Mean S concentrations in herbage were increased with S fertilization; however, it also increased slightly with an increase in the N level of fertilization (Fig. 2a). Sulfur concentrations ranged from about 0.15 to about 0.3 percent. Like N concentration, S declined as the plants matured, the rate influenced by the level of N fertilization (Fig. 2b). Sulfur decline differed from that of N in that the rate of decline was most rapid up to 2 June; thereafter the rate slowed (Fig. 2c). In the presence of S, the two highest levels of N consistently caused high levels of S concentrations in plants, but the lowest level of N fertilization was inconsistent in that effect as the grasses matured (Fig. 2d). Also, when fertilized with N only, the response of S concentrations to level of N was extremely inconsistent as plants matured.

Nitrogen-Sulfur ratios in plants fertilized with S remained at 8:1, but ratios in grasses receiving no S increased from 9:1 to 15:1 as N rate increased (Fig. 3a). The N:S ratios generally declined as plants matured but this was influenced by nitrogen level (Fig. 3b). The decline in N and S ratios was similar in plants fertilized with N or with N plus S, but the ratios of plants fertilized with S were three to six units lower than those fertilized with only N (Fig. 3c).

Residual Response

The residual years (1972 to 1977) were dry with crop-year precipitation ranging from 64 to 94 percent of the long term median amount of 10 inches (25 cm), averaging 81 percent. Temperature in April was cooler than the long term mean in all years but 1977. May temperature was above its normal in 1972, 1973 and 1976 while in June temperature exceeded its normal in all years but 1976. The yield results obtained in those years reflect responses associated with years of below normal precipitation but with a non-consistent temperature pattern during the growing season months.

In the six residual years the mean yield of crested wheatgrass averaged 165 gm per 24 feet^2 (2.2 m^2) with N alone. It was further increased ($P>0.05$) by 10 percent on plots initially fertilized with S. A typical response to N occurred with 25 pounds per acre (28 kg/ha) of N causing a 68 percent increase in yield above the control, with increasing N rates causing no further increases. Crested wheatgrass response to 25 pounds per acre (28 kg/ha) of N was

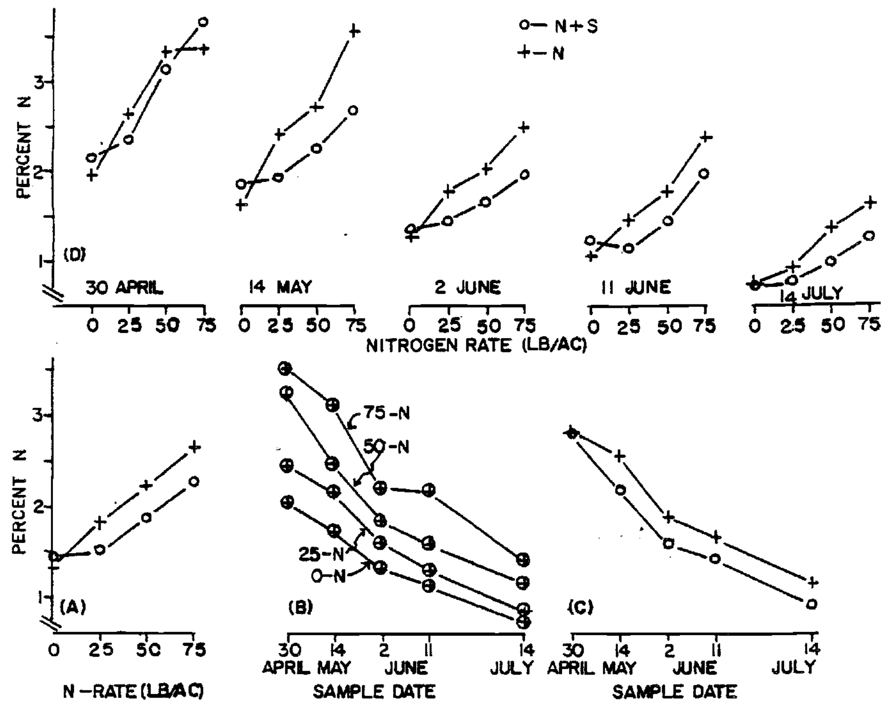

Figure 1.--Mean concentrations of N in crested wheatgrass in the first growing season following S fertilization of 28.5 pounds per acre (32 kg/ha) and N at rates indicated.

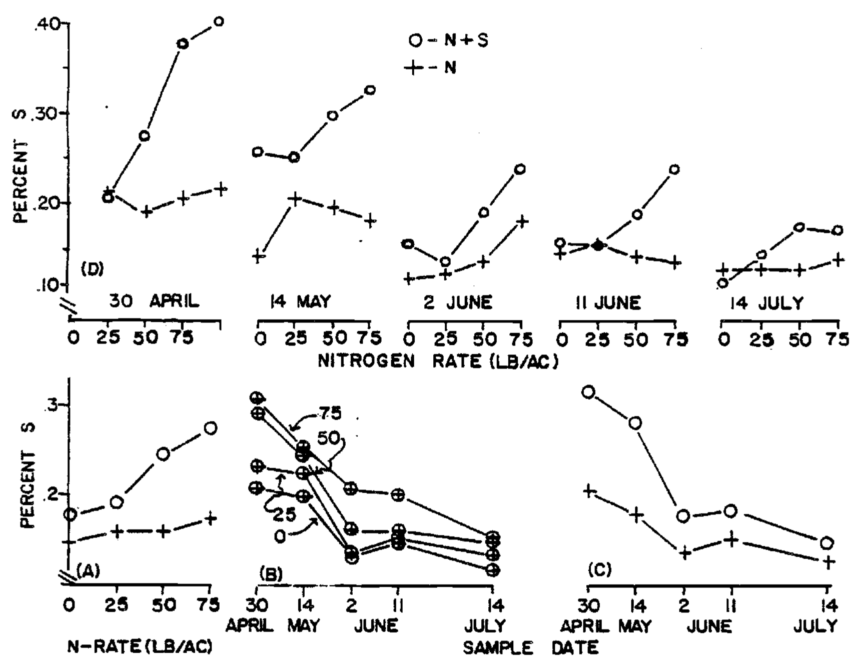

Figure 2.--Mean concentrations of S in crested wheatgrass in the first growing season following S fertilization of 28.5 pounds per acre (32 kg/ha) and N at rates indicated.

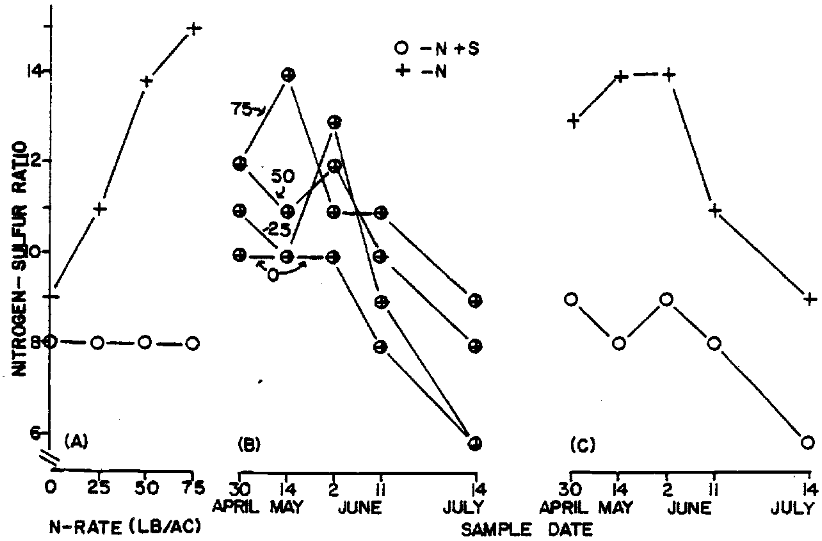

Figure 3.--Mean N:S ratios in the first growing season following S fertilization of 28.5 pounds per acre)32 kg/ha) and N at rates indicated.

consistent, relative to year variation, whereas yields declined across years at the two highest levels of N (Fig. 4a), causing a significant interaction. Similarily, in the presence of S, yields of crested wheatgrass were increased in the first three years above that fertilized with N alone. In the last three years there was no difference in yield from plots fertilized with N alone compared to that initially fertilized with N and S and thereafter only with N (Fig. 4b). The results suggest that the effects of the single application of S in the first year may have diminished by the fourth growing season.

The six year mean herbage yield increase of 10 percent induced by the addition of S, while statistically non-significant, is believed to be real and underestimates S response. Nitrogen additions to crested wheatgrass results in greater production in the spring and advances the depletion of available soil moisture (Sneva and Rittenhouse, 1976). In the present study crested wheatgrass growth in the presence of both N and S was so great that grasses receiving both elements rarely completed phenological development due to early soil moisture exhaustion. Thus, herbage loss due to decomposition and leaf shatter prior to harvest was high on plots receiving both fertilizers. The early harvest date in 1973 on 14 May, which was in error, severely damaged plants in the sampled area on plots receiving both N and S fertilizer, requiring subsequent sampling of those plots to eliminate that area. Also yields in 1973 from the N and S fertilized plots on 14 May were equal to that of mature yields of nearby plots harvested on August 1.

Mean N concentrations in crested wheatgrass were not influenced significantly by S, but increased ($P<0.05$) from 1.5 in the control to 2.2 percent in grasses fertilized with 25 pounds per acre (28 kg/ha N. Concentrations were further increased about 23 percent ($P<0.05$) with 50 or 75 pounds per acre (56 or 85 kg/ha) N. The year effect was strong with mean concentrations significantly different ($P<0.05$), ranging from 1.3 to 3.4 percent. The kind of fertilizer and the rate of N fertilizer interacted with years and these interactions are presented in figures 4c and 4d. Though significant these interactions are not particularly meaningful.

Nitrogen yield in the harvested herbage was similarily influenced by N level and years, with the year x N level and the year x kind of fertilizer interactions also significant ($P<0.05$). Nitrogen yield more than doubled with 25 pounds per acre (28 kg/ha) N (1.7 vs 3.8 gm per 24 feet^2 (2.2 m^2), and increased an additional 28 percent with N additions of 50 and 75 pounds per acre (56 and 84 kg/ha). Nitrogen yield ranged from 3.0 to 5.3 gm per 24 feet^2 (2.2 m^2) with the latter occurring in 1973. The significant interactions (Fig. 5a and 5b) of both concentration and yield of N are in part due to the early harvesting in 1973, because N concentrations are much higher at that time as compared with concentrations at maturity. However, there is still evidence of differences particularly as one compares the responses in the first three years with those of the last three years.

Mean S concentration in crested wheatgrass over the six years significantly ($P<0.05$) increased about 13 percent from the initial application of S. Interestingly, herbage S concentrations increased from plots fertilized with or without S although the increase was not as great from plots receiving no sulfur. Years interacted significantly with level of N (Fig. 5c) and with kind of fertilizer (Fig. 5d), but as with N concentrations these interactions

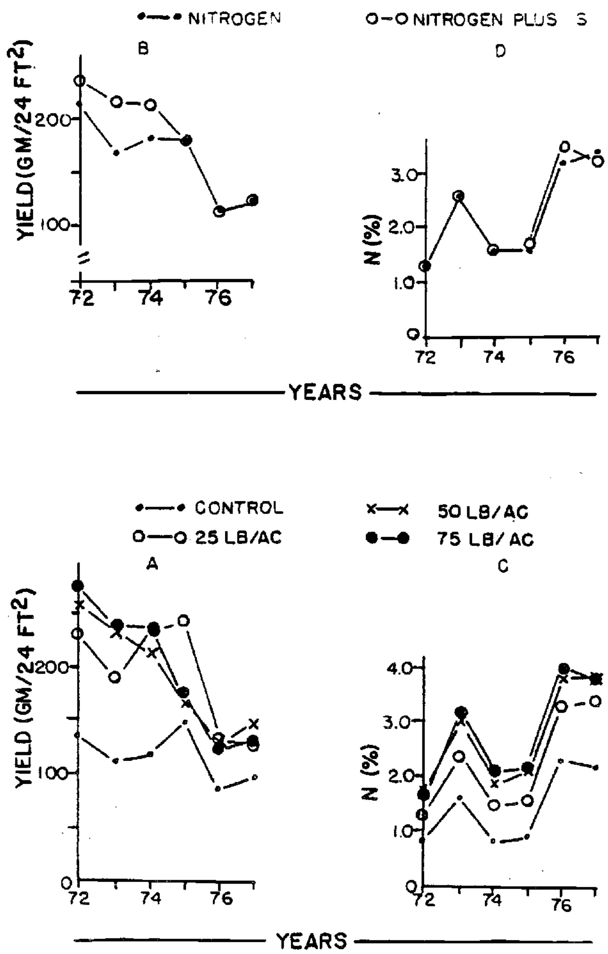

Figure 4.--Mean herbage yield and N concentrations in crested wheatgrass fertilized with 28.5 pounds per acre (32 kg/ha) S in the winter of 1971 only, with N levels as indicated applied annually.

were not strong and no particular significance is attached to them.

Sulfur yield in the herbage of crested wheatgrass fertilized with N more than doubled ($P<0.05$), but differences between mean S concentrations in plants receiving S or no S (0.354 vs 0.444 percent) were non-significant. Sulfur concentrations varied significantly ($P<0.05$) among years from 0.286 to 0.464 percent with all first and second order interactions involving years significant ($P<0.05$). Sulfur yield in herbage from plots fertilized at the 25 pounds per acre (28 kg/ha) N fluctuated similarily across years as did S yields in herbage from the controls (Fig. 5e). However, at the two highest levels of N fertilization the relative year response diminished in time. The year x kind of fertilizer interaction (Fig. 5f) occurred because yield in plants initially fertilized with S was higher than yield in plants not fertilized, but in the last three years those differences diminished. Comparing figure 5f with 5d and 4b, it seems clear that herbage yield response (rather than S concentrations) is primarily responsible for the results obtained.

The initial application of 28.5 pounds per acre (32 kg/ha) S on 27 January 1971 significantly increased the level of sulfur in the upper 10 inches (25 cm) of soil from 3.4 to 7.5 ppm when sampled on 15 July 1971. Subsequent samplings in July 1972 and 1973 revealed no differences in soil S between plots fertilized with S or those receiving no S.

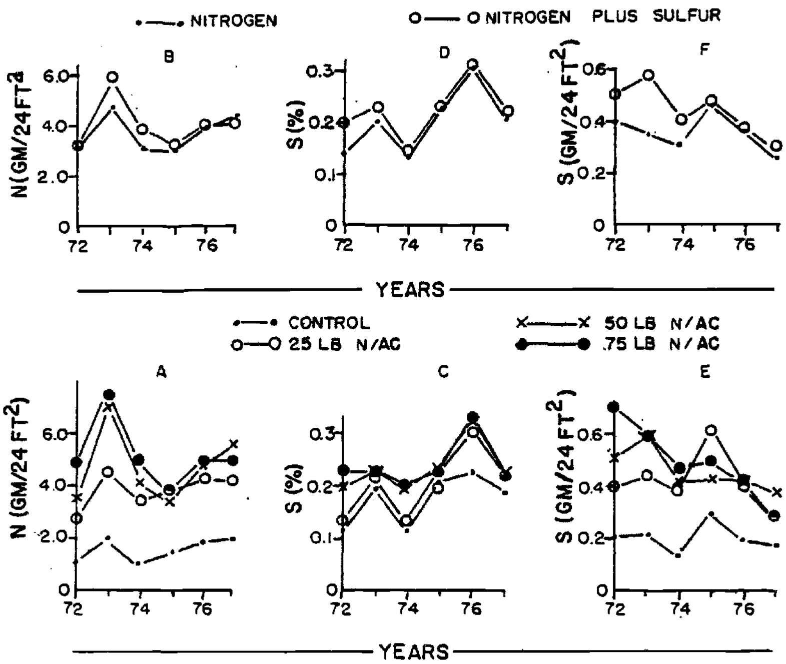

Figure 5.—Mean N and S concentrations in crested wheatgrass fertilized with 28.5 pounds per acre (32 kg/ha) S in the winter of 1971 only, with N levels as indicated applied annually.

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SECTION VIII.

Economic Considerations.

Is Crested Wheatgrass Seeding Worth it?

Chairman, Stephen B. Monsen

Increasing Grass Production by Reducing Overstory Competition -- An Optimization Procedure

John A. Tanaka

ABSTRACT: The purpose of this paper is to investigate an optimization procedure for estimating the intensity of overstory reduction when the biological goal is to increase forage production and the economic goal is to maximize ranch profits. The procedure is based on the decision-maker's ability to accurately estimate production, cost, and benefit functions for specific range improvements.

INTRODUCTION

Research on the use of crested wheatgrass (Agropyron desertorum and A. cristatum) for rangeland seeding has focused primarily on biological and economic feasibility. The success of this research, however informal, can be judged in terms of the acreages and diversity of locales in which crested wheatgrass has been seeded. In many situations these seeded ranges have overstory species such as big sagebrush (Artemisia tridentata), pinyon pine (Pinus edulis) or juniper (Juniperus spp.) becoming re-established. The purpose of this project is to develop a procedure for estimating the optimal rate of overstory control for increasing understory forage production.

The procedure will be developed in conjunction with work by Allen Torell in the Department of Economics at Utah State University (Torell and Godfrey 1986). The goal of our research is to answer on-the-ground management questions for investment decisions. Our projects will form a package to provide range managers with an analytical framework for decision-making. In general, the manager should be able to decide (1) if a forage stand is depleted enough to warrent control of the re-establishing overstory species, (2) the optimal kill rate target (with implications as to the selected improvement methods), and (3) how long before recontrol would be needed--which completes the decision cycle. This paper will describe the rationale and principal components of the proposed procedure. Implications for research and management will also be discussed.

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Range Economics and Decision-making

Range economics has been defined as the application of "the principles of economics and range management simultaneously to determine the economic consequences of decisions involving the use, development, and/or preservation of rangelands" (Workman 1986). Economics deals with the allocation of scarce resources among competing uses.

In this context, decisions to allocate limited investment capital among alternative choices need to be made within the context of a given decision-making unit (e.g. an individual ranch). Many of the problems associated with the valuation of range improvement benefits can be avoided by using the ranch as the decision-making unit of analysis for range improvement decisions (Workman 1986).

If the individual rancher is the decision-maker, the procedure should provide useful information for ranch investment decisions when the biological goal is to increase desirable forage production by reducing the competing overstory, and the economic goal is to maximize profits. Specifically, the results should indicate how much capital to invest in order to obtain an optimal target kill rate of the overstory species. The initial investment will help determine which of the alternative methods and intensities of treatment are economically feasible. Each feasible method must then be analyzed under other decision criteria (e.g. political, sociological, biological, risk). The economically optimal kill rate will result in maximum expected net returns (profits) to the ranching operation.

In a multiple use decision-making context, if the target kill rate is less than that determined to be optimal for the ranch, then the resource manager will have information on what is being given up in terms of economic efficiency. Any kill rate other than the optimal rate will result in lower profit levels and is, therefore, a less efficient use of capital.

The procedure is not designed to indicate what should be the socially optimal decision on public lands. The usefulness of this marginal evaluation procedure to public land managers will depend on their need for additional information. Maximizing profit on a ranch is rarely a goal of the public land manager. Therefore, the procedure probably will not be useful for deciding the intensity of a given range improvement practice, but it will, nevertheless, provide useful information for the decision-making process. It identifies the trade-off between the loss of economic efficiency of a non-optimal policy decision vs. the economically efficient improvement policy. Through its application, the effects of a given decision on an individual permittee's economic well-being can be assessed.

Rationale for the Proposed Analytical Procedure

What to do with established stands of crested wheatgrass is a central issue from a business management and investment viewpoint. In other words, once an investment is in the rancher's portfolio, the relevant decision is what to do with it. In terms of a crested wheatgrass stand subject to an increasing population of an overstory species such as big sagebrush, at least three options are available from a ranch perspective: (1) to allow the overstory species to mature resulting in less usable forage through time, (2) to reduce the overstory species by investing more capital and thereby increasing forage production, and (3) to sell, lease, or otherwise divest in the seeding and use the released capital in alternative uses. For an operating ranch the second alternative is only desirable if additional forage is needed to balance yearlong forage supply and demand, increase herd size, or replace more expensive feed (Plath 1954, Workman 1986). Otherwise, investment to maintain an unnecessary seeding (for livestock production) will result in no economic benefit to the investor.

Once the decision is made that additional investment (i.e. overstory reduction) is necessary, the procedure being developed will indicate the optimal kill rate for a given set of relative prices. Examples of overstory reductions resulting in an increase in understory production are abundant in the literature. These examples span vegetation types as well as improvement methods within a vegetation type. However, most of this type of research has focused on finding a significant difference between the treatment and a control. In order to develop a functional relationship between overstory control and understory production, multi-rate experimental designs are required. The estimated function could then be used in deciding how intensively similar stands should be treated in order to benefit both the understory species and the ranch business enterprise.

BASIS FOR THE PROPOSED ANALYTICAL PROCEDURE

The baseline information necessary for the analytical procedure is derived from published research results and the concepts of economics and range management. For example, the underlying production function must accurately predict forage responses for given levels of overstory kill. If the predicted response is accurate, then the economic model will supply useful information for decision-making provided that all economic relationships can be estimated. Therefore, the procedure must be based on known and proven biological and economic relationships. The procedure will be developed using crested wheatgrass/big sagebrush interactions as an example, but the technique will be applicable to other vegetation types where overstory competition limits desirable understory production.

Crested Wheatgrass/Big Sagebrush Relationships

Controlling woody overstory species to increase production of desirable forage and browse plants has been a guiding principle of range management since its beginnings. Robertson (1947) concluded that if sagebrush stands of forty percent cover could "...be reduced to spacing of more than a meter apart, a release from competition will occur which will be progressively better for growth of grasses as more brush is eradicated." Results from a southern Idaho study designed to evaluate crested wheatgrass production when sagebrush was controlled at various rates indicated that the last remaining sagebrush plant suppressed grass production the most, and that each preceeding sagebrush plant suppressed relatively less production (Hull and Klomp 1974).

The general crested wheatgrass/big sagebrush relationship will be discussed in terms of both static and dynamic interactions. The static model views crested wheatgrass production as an average yearly amount in relation to the amount of big sagebrush killed. The dynamic model views crested wheatgrass production as a yearly average that changes as a result of changes in big sagebrush parameters (e.g. density, age structure, canopy cover). In each case, the average production can be associated with a range of values indicative of yearly or seasonal variations in production.

The two model formulations provide the framework for determining the significant variables to be included in the production function. While the dynamic model formulation is more meaningful, the procedure will be developed in this project as a static model because of data limitations. The discussion of dynamic relationships is included to provide the link to the procedure being developed by Torell and Godfrey (1986).

Static Crested Wheatgrass/Big Sagebrush Relationships.--The static production function will relate crested wheatgrass production to any of several variables (e.g. big sagebrush characters, climatic parameters). The relationship between crested wheatgrass production and big sagebrush canopy cover has been estimated as a linear function (Rittenhouse and Sneva 1976). The form of the production function has been estimated for different vegetation types as curvilinear (Pase 1958, Halls and Schuster 1965, Jameson 1967, Clary 1971, Scifres et al. 1982). Several authors have also estimated curvilinear functions relating understory production to overstory basal area (Halls and Schuster 1965, Woods et al. 1982, Wolters et al. 1982). Bartolome and Heady (1978) concluded that the hypothesis of a negative correlation of big sagebrush density and grass production should be rejected. These approaches yield estimates of production either for an average year or for a year similar to the data collection year.

Yearly variations in herbage production were accounted for based on monthly precipitation and temperature by Sneva (1977). He found that mature yields of a given crested wheatgrass stand were correlated best with monthly precipitation for eight consecutive months beginning in July, August, or September of the previous year. This approach allowed for prediction of current mature yields based on information obtainable prior to the start of the growing season. Clary and Jensen (1981) related herbage production potential to annual precipitation and tree cover. This model provided the type of production surface expected in the crested wheatgrass/big sagebrush production function. It predicted the expected response from overstory control as well as the range of responses that were expected based on yearly fluctuation.

Research designed to specifically estimate the relationship between crested wheatgrass production and such factors as big sagebrush canopy cover, density, or age structure are relatively rare. Hull et al. (1952) and Alley (1956) measured the response of native grasses to big sagebrush control. Their data indicated that grass production increased relatively faster as more big sagebrush was killed. Hull and Klomp (1974) found that killing the last twenty-five percent of a big sagebrush stand was at least as effective as killing the first seventy-five percent in terms of increased crested wheatgrass production.

Dynamic Crested Wheatgrass/Big Sagebrush Relationships.--The dynamic relationship determines project life and the production time stream. Economic feasibility analyses that use constant production values over the life of the project discount the effects of dynamic factors which affect overstory re-establishment (e.g. stocking rate). Initial kill may have the greatest impact on sagebrush re-establishment (Johnson 1958, Johnson and Payne 1968). In Nevada, Frischknecht and Bleak (1957) found that most of the sagebrush in a seeding became established within two years following control. In Oregon, Bartolome and Heady (1978) found that sagebrush re-establishment was highest in the first year after treatment. Big sagebrush reached pre-treatment densities, at some point in time, regardless of initial kill rate (Johnson 1969, Bartolome and Heady 1978).

As with initial kill rate results, the literature indicates that estimated project life varies widely. In Wyoming, Johnson (1969) found that increased native herbage from big sagebrush control was nullified within six years. Thilenius and Brown (1974), also in Wyoming, found that native herbage production was below pre-treatment levels after ten to eleven years. In southern Idaho, Hull and Klomp (1966) found that crested wheatgrass stands remained productive after thirty years. Crested wheatgrass stands were also found to have thickened and spread because of a lack of competing vegetation, rough soil surface, and soil movement (Hull and Klomp 1967). Harniss and Murray (1973) supported the conclusion that sagebrush control evaluations should be done on a subspecies basis. Variation in the results may be alleviated by using a homogeneous site for model development.

A dynamic relationship between overstory and understory has been formulated for the pinyon/juniper vegetation type. The biological effects of recovery rate after control and the forage depletion rate have been used in economic models designed to estimate the optimal time between control actions (Cotner 1963a, Jameson 1971, Burt 1971).

Biological Case Study.--Research conducted in southern Idaho by Hull and Klomp (1974) was selected for development of the big sagebrush/crested wheatgrass production function. This study was conducted in two different sagebrush communities -- basin big sagebrush (*Artemisia tridentata* ssp. *tridentata*) near Holbrook and Wyoming big sagebrush (*A. tridentata* ssp. *wyomingensis*) near Twin Falls. Annual precipitation for the Holbrook and Twin Falls sites averaged sixteen and nine inches, respectively. Complete site descriptions can be found in Hull and Klomp (1974).

The study design was to reduce big sagebrush stands, with an initial density of twenty plants per 100 sq ft, by 0, 50, 75, and 100-percent in each age class. Crested wheatgrass production response to big sagebrush kill rate is shown in Table 1. Because no significant difference in production response was found among burning, spraying, and hand-grubbing treatments within each kill rate, data shown in Table 1 represent yearly averages for 1965-1970. The shape of the production relationship (averaged over 1967 through 1970 data) is shown to be a curve increasing at an increasing rate (Fig. 1). The shape of this production relationship is one crucial factor for accurate determination of the optimal kill rate of big sagebrush. The convex shape is also consistent with the curve hypothesized by Clary and Jensen (1981) for the pinyon/juniper vegetation type.

Economic Analysis of Overstory Reduction Projects

The use of economic theory in the process of natural resource decision-making has been of

Table 1.--Pounds of air-dry crested wheatgrass production at four intensities of big sagebrush control at Holbrook and Twin Falls, Idaho. Adapted from Hull and Klomp (1974).

Location and control rate	1965	1966	1967	1968	1969	1970
percent	-------pounds of yield[1]-------					
Holbrook:						
0	627	397	555	503	400	502
50	638	395	850	705	511	668
75	672	505	1042	954	757	961
100	642	581	1593	1468	1152	1874
Twin Falls:						
0	498	210	415	250	452	652
50	446	188	535	315	551	827
75	499	201	589	389	597	977
100	458	231	777	531	763	1250

[1]Yields are expressed as an average of burning, spraying and handgrubbing.

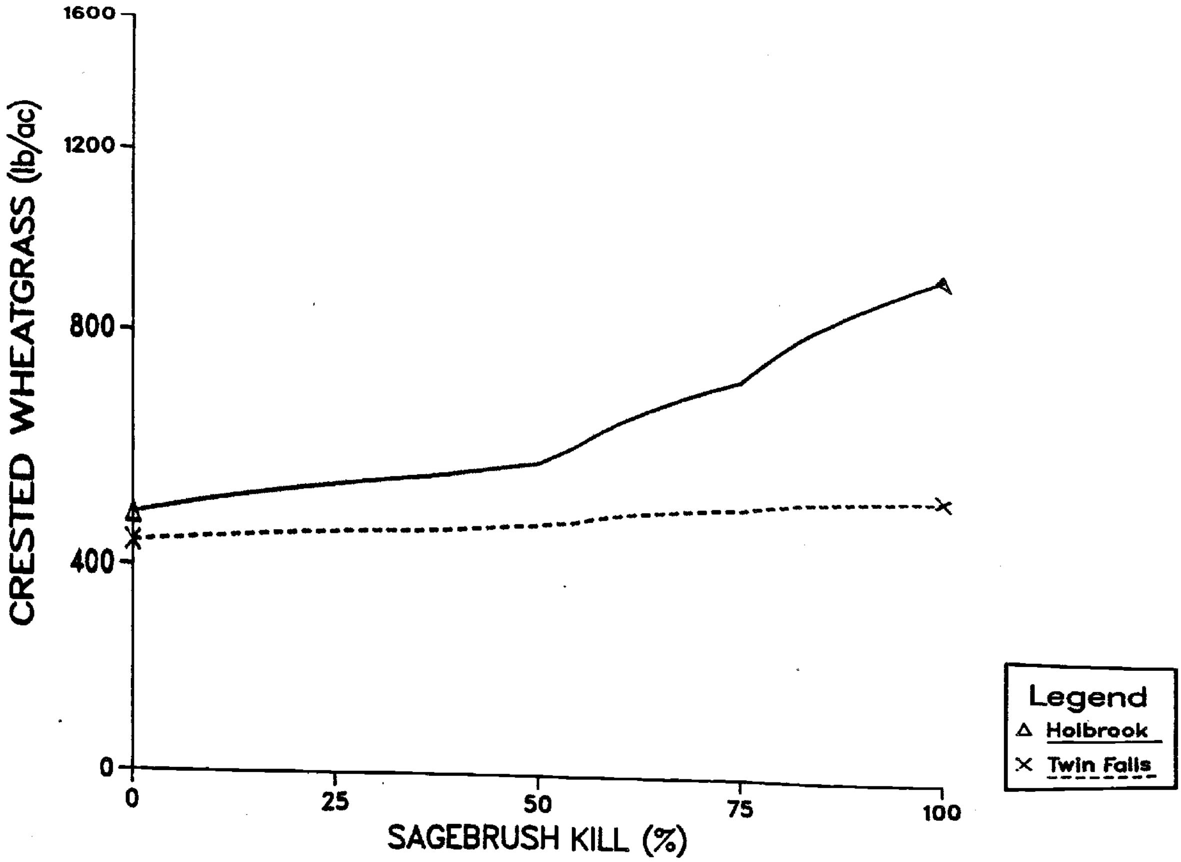

Figure 1.--Yields of crested wheatgrass under 0, 50, 75, and 100 percent big sagebrush reductions; average of four years (1976-1970). Adapted from Hull and Klomp (1974).

interest to researchers. Although the theory underlying economic research may not be of interest to resource managers, results from such studies will be useful. In the present model, determination of an economically optimal intensity of a range improvement must be based on this theory.

Static and dynamic procedures have been developed to economically analyze range improvements. All such methodologies have been concerned with estimating biological responses and associated benefits and costs attributed to the project. Economic analyses have been conducted for individual projects (Caton and Beringer 1960, Gardner 1961, Krenz 1962, Sassaman and Fight 1975, Godfrey 1979, Godfrey et al. 1979); optimal combinations of animal species (Upchurch 1954, Hopkin 1954); optimal grazing intensity (Hooper and Heady 1970, Pearson 1973); and optimal timing for recontrol of woody plants (Krenz 1962, Cotner 1963b, Jameson 1971, Burt 1971, Perrin 1972, Stevens and Godfrey 1972, Dixon and Howitt 1980). Analytical methods used to evaluate individual projects have led to the development of techniques for estimation of average (i.e. typical) control costs and expected benefits.

Economic analyses of crested wheatgrass seedings have been largely based on individual project analysis, focused on obtaining costs and benefits of the practice (Lloyd 1959, Caton and Beringer 1960). The analysis usually proceeds by discounting future net benefits to present value (less initial investment) in order to determine economic feasibility (Workman 1986). Costs have been reported in terms of physical units (e.g. labor, materials) for specific practices (McCorkle et al. 1964, Ralphs and Busby 1979, Sonnemann et al. 1981, Young et al. 1982). The cost approach will be useful for conducting (<u>ex ante</u>) analyses of proposed projects on similar <u>sites</u>. Forage benefits have been estimated as the value of substitute products (e.g. hay, private leased land), capitalization of permit values, and the value of additional livestock produced (Workman 1986, Wagstaff 1983). Care must be used in estimating benefit values by any of these methods because their validity will depend on what the additional forage does for the year-round ranching operation (Workman 1986). In any event, once the benefit and cost data have been estimated, there are three basic methods of determining economic feasibility (Workman 1986): (1) internal rate of return (IRR), (2) benefit/cost ratio (B/C), and (3) present net worth (PNW). Economic feasibility has been determined using IRR by Krenz (1962), Gray (1965), Nielsen et al. (1966), Sassaman (1972), and Sassaman and Fight (1975). The IRR method identifies the discount rate that forces the present value of all costs to equal the present value of all benefits (Workman 1981, 1986). The IRR can then be compared to the investor's opportunity cost and the economic feasibility (IRR greater than required rate of return in this case) determined on an individual basis. Lloyd and Cook (1960), Gray (1965), Gray et al. (1965), and Sassaman (1972) used the IRR method to determine net returns necessary to cover project costs at different required rates of return.

On the other hand, both B/C and PNW methods require an interest rate to be specified prior to analysis. That is, an analysis using a given interest rate will only be meaningful to another decision-maker with a similar opportunity cost. From a specific decision-making perspective, however, these criteria may provide more useful information than the IRR criterion. The B/C ratio determines the present value of net benefits per $1.00 of the present value of costs. PNW is merely the present value difference between benefits and costs; in effect, a measure of profit. In general, the case can be made that PNW should be the economic criterion used to select alternatives for investment when capital is limiting (Workman 1981, 1986).

Although these three economic criteria indicate economic feasibility of specific range improvements, none of them indicate an optimal intensity of project implementation. The economic principle of marginality provides the basis for finding the optimal level of input use for producing an output (Workman 1986). This principle indicates that the optimal sagebrush kill rate is the point where the marginal cost (MC) of obtaining one more unit of crested wheatgrass is equal to the marginal return (MR) to the ranch resulting from that unit of crested wheatgrass.

For a profit maximizer, the optimal level of crested wheatgrass production should be the management objective. Figure 2 shows, with hypothetical curves, how profit is maximized when MC equals MR.[1] As crested wheatgrass production increases from 500 to 1000 lb/ac, each additional pound of grass returns more to the ranch than it costs to produce. At 1000 lb/ac the point is reached where no further profit can be made. In fact, the next (and each succeeding) pound of crested wheatgrass actually decreases profit. The shape and position of the MC curve will be determined by the underlying production function and the relationship of input costs to percent sagebrush kill. The MR curve is assumed to be equal to the price per pound of crested wheatgrass. This value will vary from ranch to ranch depending on seasonal forage needs. In a ranching situation, this curve may be nonlinear (i.e. forage has a non-constant value).

The optimal kill rate will vary based on the relative values of inputs and outputs. As the output price increases relative to the cost of producing that output, the optimal kill rate will also increase (Workman 1986). That is, it will now be more profitable to invest more money in killing sagebrush since these marginal funds invested will be offset by the higher marginal revenue. Thus, the procedure needs to be used each time a decision is to be made. Although the production function would be expected to remain constant, results from a study conducted at a given point in time under a given relative price set will not necessarily be applicable in another situation.

DISCUSSION: THE PROPOSED OPTIMIZATION PROCEDURE

Based on the objective of profit maximization, the level of investment will be determined such that the maximum net returns (project benefits minus project costs) are realized. In the crested wheatgrass/big sagebrush model, the value of additional forage production will depend on the specific needs of a given ranch. These benefits must be maximized relative to the project costs (e.g. initial investment, annual costs, deferment costs). The purpose of this section is to: (1) outline the steps required to develop the proposed optimization procedure, (2) examine some relevant implications of different model formulations for making investment decisions, and (3) discuss data requirements for on-the-ground application of the model.

Steps in Development of the Model

The true value in developing an economic model lies in being able to apply it in a variety of situations. The procedure is merely an analytical framework for interpreting relevant data; a usable model will need to be developed for each ranch unit. Once developed, however, the procedure will provide useful information even if profit maximization is not the goal of the decision-maker. If another goal is relevant to the decision-maker, and a non-optimal kill rate is chosen, the model will indicate the trade-off involved. In general, model development should consist of estimating (1) a site specific production function, (2) project benefits, and (3) project costs. This order is based on the premise that if the biological relationship can not be estimated then the remainder of the model will not be useful. Next, estimation of project benefits requires the decision-maker to consider if, how, and when the additional forage will be used within the present operation. Finally, costs are estimated based on the least cost methods of attaining expected overstory kill rates. All information will be combined to determine the optimal intensity of overstory kill.

Overstory/Understory Production Functions.--The production function can be estimated in several ways. Percent kill of the overstory species can be estimated as either a deterministic or a stochastic value. The deterministic version is the percent kill based on the least cost improvement method for a given initial vegetation parameter (e.g. density, canopy cover, age structure). The stochastic version also includes random variables (e.g. precipitation, temperature). Forage production, also deterministic or stochastic, will then be a function of the estimated kill rate.

The shape of the production function can be estimated as linear, strictly concave, strictly convex, or sigmoidal. Results such as those shown in Figure 1 indicate that the production function will be strictly convex.

The time aspect of the overstory/understory relationship can be formulated either as a static or dynamic function. The static analysis uses an average production response as if it could be maintained over the life of the project (i.e. even flow). The dynamic analysis incorporates parameters that cause changes in understory production through time (e.g. rate of overstory re-establishment, grazing, fire). The dynamic aspect will not be directly addressed by this project except as it relates to the work being completed by Allen Torell (Torell and Godfrey 1986).

[1] See Doll and Orazem (1978), Chiang (1974), or Workman (1986).

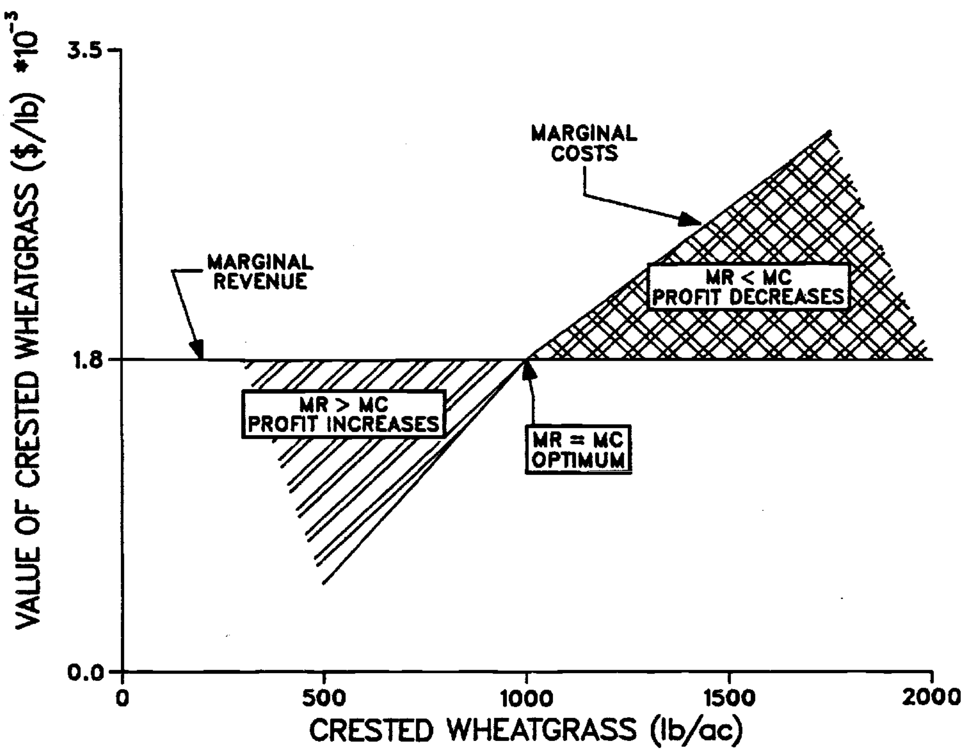

Figure 2.--Profit maximization occurs at the point where marginal revenue equals marginal cost as production output increases.

Estimated Project Benefits.--Project benefits to a specific ranch will vary among operations as well as for a given operation at different times. Additional crested wheatgrass production will only have value for a ranch if it balances seasonal forage production with seasonal forage requirements or replaces more expensive feeds (e.g. hay, grain) with less expensive forage.

Once it is determined that additional forage is needed, the value of that forage to the ranch can either be estimated as a constant value or as a value that changes with the level of production. In the former case, once it is shown that the forage can replace hay during winter, the value of an animal unit month (AUM) of forage may be assumed to be equal to the price of an AUM of hay. However, if more forage is produced than there is hay to replace, the extra amount will be valueless from a livestock production perspective unless other uses for the extra production of grass can be found. In the latter case, the marginal benefits from each additional unit of forage would likely decline from some relatively high value for the first forage unit down to zero value for the last useful unit of forage.

Total revenue derived from reduction of the overstory population will then be a function of estimated project values ($/unit) multiplied by the appropriate production response. The marginal revenue function can then be calculated from the total revenue function. As shown in Figure 2, the MR function is one piece of information required to find the optimal level of crested wheatgrass production.

Estimated Project Costs.--Project costs may be divided into initial investment, annual maintenance, deferment, and future stock costs. The model assumes that each range improvement alternative is applied in a technically efficient manner, and that this will result in an average overstory kill rate. In other words, some methods are better suited to flat topography on a large project than to rough topography on a small project.

For estimating initial investment, the cost of killing the overstory species is assumed to be a function of the selected method, initial density and age structure of the target population, project size, and other variables. Initial investment includes the cost of control in addition to any structural improvements (e.g. fences, water developments) needed to properly manage the site.

Because project benefits are calculated on a per year basis, it is necessary to convert the initial investment (a stock value) into an annual cost (a flow value) in order that the benefits and costs be comparable. The annual investment is determined through a procedure of amortization.[2] This process spreads the initial investment costs over the life of the project and adds the amount of interest payment necessary to compensate the investor for use of the capital.

[2] The interested reader is referred to Workman (1986) or any textbook on finance.

The total annual cost can then be computed by adding estimated annual maintenance costs to the amortized initial investment cost. The total costs result in a cost equation (i.e. costs are expressed based on the amount of inputs used). However, to be comparable to the MR function estimated earlier, the total cost curve needs to be estimated using a cost function (i.e. one that relates costs to the production output). Once the cost function is estimated, the MC curve can be derived through the calculus. The MR and MC functions can then be equalized to find the production level where maximum profit occurs, assuming that the second order conditions for a maximum are satisfied.[3] This optimal production level can then be related to percent overstory kill required, relative to an optimal investment level.

Implications of Different Model Formulations

Determination of the optimal overstory kill rate by use of the theoretically correct model (equating marginal costs and marginal revenues) involves use of the calculus. The mathematical derivations make the method somewhat unwieldy from a management perspective. Nevertheless, it is important to understand how the theoretical model can be interpreted in terms of range improvement practices designed to reduce the specific overstory species to favor the desirable understory forage.

The principle of marginality determines the optimal level of production by finding the point where the slopes of the total revenue and total cost curves (as defined) are equal. Mathematically this is the same as finding the point where the first derivatives of each function are equal (i.e. MC = MR). Through mathematical manipulation of the MC and MR functions, the model can be reformulated into a more useful procedure. That is, a useful model should be relatively easy to manipulate in order to respond to changing economic conditions.

One modification of the MR equals MC procedure is a graphical procedure described by Workman (1986). This method involves plotting the production relationship between one input bundle and one output. If long-term carrying capacity of the site remains constant, this average production relationship will be useful for decision-making on a given site. However, if factors such as brush encroachment or stocking rate affect site productivity, this production relationship will be dynamic in nature and the decision criteria become more complex. For the simple model, assuming an average production function, there are implications for management based on how forage production, variable cost, and output price functions are estimated.

Once the production function is graphed it is a relatively easy procedure to find the optimal production level. The next step is to plot the ratio of input costs to output price as an iso-budget line. This line represents the combination of inputs and outputs that will exhaust a given budget. Conceptually, this assumes that both inputs and outputs are costs to the firm. Once the price ratio curve is estimated the object is to find the point where the price ratio curve becomes tangent to the production curve. This point is the optimum.

There are four cases of the one input and one output situation, each with its own implications for management. The four cases are displayed in Figures 3 and 4. A hypothesized linear production function (Fig. 3) will lead to recommendations different than a strictly convex production function (Fig. 4). By the same token, the linear and nonlinear price ratios each have different implications when combined with the appropriate production function form.

The first case is the linear production function-linear price ratio (Fig. 3a). As depicted, Price Ratio 1 indicates that the price of overstory kill is relatively high compared to the price of the forage. In this case, the management decision should be to not invest in this site. On the other hand, as the price of forage increases relative to the cost of control (Price Ratio 2), it becomes economically feasible to kill 100 percent of the overstory stand. With this model formulation, it is mathematically possible for the price ratio to lie exactly on top of the production function (i.e. it becomes tangent everywhere). In this case, the decision-maker should be indifferent as to the overstory kill rate.

The second case is a linear production function with a nonlinear price ratio (Fig. 3b). In this example the price of sagebrush control is expected to increase relative to the price of crested wheatgrass. This can be caused by a cost function that increases at an increasing rate, and because the value of the forage declines as more is produced. If either costs or benefits are assumed to be linear and the other one nonlinear as described above, the shape of the price ratio will be as shown in Figure 3b. The management implication is that the optimal kill rate will likely be somewhere between 0 and 100 percent. Thus, instead of an either/or situation, as depicted in the first case, the optimal kill rate can occur at any point along the production function, depending on relative prices.

The third case is a nonlinear production function with a linear price ratio (Fig. 4a). This example is similar to that depicted in Figure 3a except that the only possibilities are 0 or 100 percent kill. It would never be economically efficient to have a target kill rate other than at the end points.

The fourth case is a nonlinear production function with a nonlinear price ratio (Fig. 4b). This example probably represents the theoretically correct model and would be the most useful for making management decisions. In essence, the optimal control rate could occur at any point depending on the shape of the two curves. This model should provide the most realistic expected response.

Data Requirements for Model Application

As with any predictive model, the results are only as good as the data base. Three data sets, of equal importance, are required to drive this model. In the absence of an adequate data base, certain restrictive assumptions must be made. The data sets

3 See Chiang (1974).

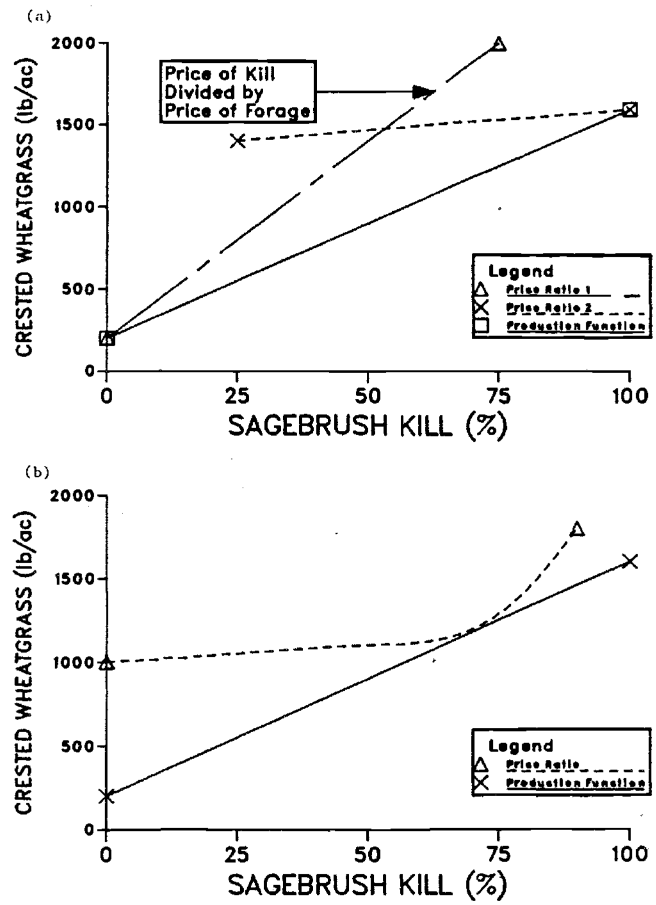

Figure 3.--Linear production function with linear (a) and nonlinear (b) cost functions.

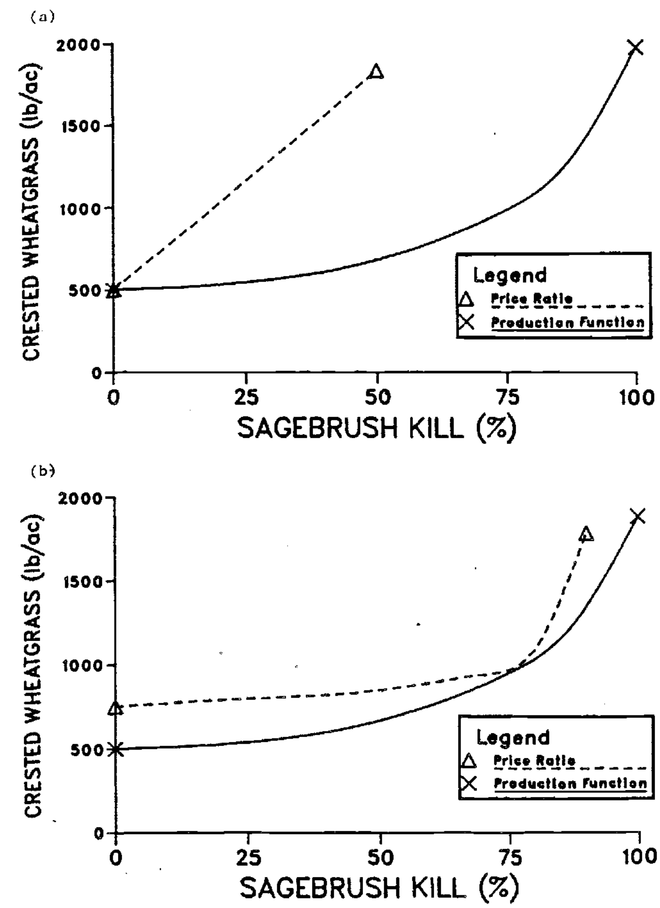

Figure 4.--Nonlinear production function with linear (a) and nonlinear (b) cost functions.

relate to the estimation of the production function, the input cost function, and the output revenue function.

Obviously, these three data sets are intricately interrelated. The greatest need for better data is related to the estimation of the production function. Ideally, the data set should be from a multi-rate experiment conducted for the life of the project. Impacts on forage production from the initial kill, as well as initial kill effects on overstory re-establishment, with and without grazing through time, are crucial factors in determining an optimum.

Range improvement research has primarily focused on determining whether or not there is a significant impact on understory production from control of the overstory population. These experiments typically involve up to five replications of sampling sites for the treatment and a control. It is possible to use the same number of samples (i.e. replications times treatments) and collect more useful information by rearranging the experimental design in order to provide data for function estimation. One such experimental design would be to have two replications and five treatment levels.

Input and output price data are relatively easy to obtain compared to the overstory/understory data. Input costs for a given range improvement should be tracked by physical units (e.g. labor, materials) rather than in total dollars spent. Further, these physical costs need to be related to initial stand parameters and post-treatment reponses if they are to be useful for estimating the cost function.

Output values will be the most variable because of differing specific needs of individual ranch operations. Based on these different values, economic feasibilty of the same range improvement practice will vary widely among operations. Therefore, even though the analysis may show a certain control rate to be the optimum for one ranch, extrapolations to other ranches must be made within the context of differences between operations. Thus, the need is for ranch-specific data both in terms of forage requirement and forage production/availability, on a seasonal basis, in order to determine the value to the ranch of additional forage in a given season.

CONCLUSION

The purpose of this project is to develop a usable analytical procedure to determine the economically optimal kill rate of an overstory species competing with desirable understory forage. Although the procedure is being developed within the crested wheatgrass/big sagebrush community, it should be widely applicable to other vegetation types.

An individual ranch unit is assumed to be the relevant decision-making unit. The investor is also assumed to be a profit maximizer for purposes of this analysis. In this framework, the procedure integrates biological relationships with costs and benefits of production, and the results are interpreted through range management principles. The final product should help in determining what is best from the ranch owner's perspective. It should also provide useful information to the public land manager by demonstrating the economic impacts of a range improvement decision on a public grazing allotment.

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Economic Value of Crested Wheatgrass: A Case Study

L. Allen Torell

ABSTRACT: The purposes of this paper are to define as a case study the economics of crested wheatgrass seedings when grazed under traditional spring/fall grazing patterns, and to contrast this with seeding economics when the stand is an integral part of a deferred/rest rotation grazing system. The major conclusion is that crested wheatgrass seedings will not always be profitable. The seeding must "fit-in" and alleviate seasonal forage constraints on the ranch.

ACKNOWLEDGEMENTS: This publication is contribution number 5 of the Saval Ranch Research and Evaluation Project: Bureau of Land Management; Agricultural Research Service; Saval Ranch; College of Agriculture, University of Nevada-Reno; Forest Service; and Soil Conservation Service cooperating.

INTRODUCTION

This study is a part of the Saval Ranch Research and Evaluation Project. In May 1978, the Saval Ranch, Bureau of Land Management (BLM), Soil Conservation Service (SCS), United States Forest Service (USFS), University of Nevada-Reno and the Agricultural Research Service (ARS) entered a cooperative agreement to evaluate the effects of livestock grazing management systems on livestock production, vegetation, fish and wildlife and their habitat, watershed hydrology, water quality, economic factors, and other resource values.

This paper concentrates on the economics of developing a crested wheatgrass (*Agropyron desertorum*) seeding as part of a proposed grazing system to be implemented on the Saval Ranch in 1985. The analysis considers expected benefits and costs and as such reflects an ex ante analysis. Only livestock benefits are considered.

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STUDY AREA

The Saval Ranch is located approximately 45 miles (72 km) north of Elko in northeastern Nevada (Figure 1). The ranch operation contains approximately 49,105 acres (19,873 ha), including lands owned and managed privately (7,557 acres; 3,058 ha), and lands managed by the Bureau of Land Management (25,908 acres; 10,485 ha), and the Forest Service (15,640 acres; 6,330 ha). Nearly 4,200 acres (1,700 ha) of existing crested wheatgrass stands are included.

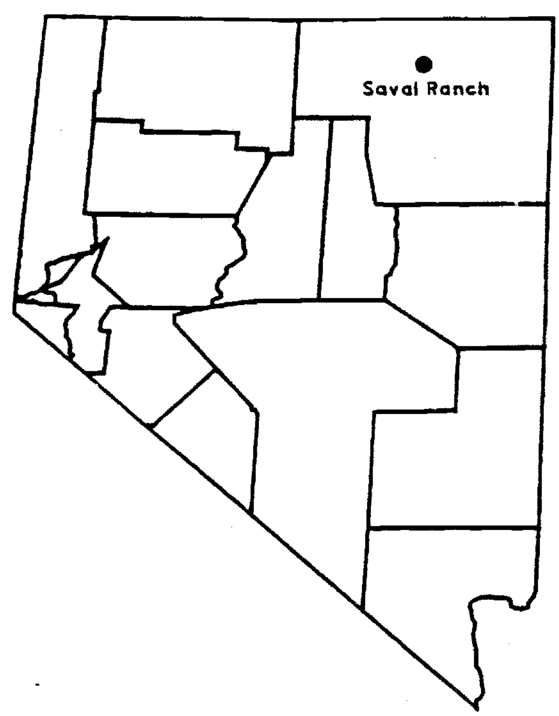

Figure 1.—Location of the Saval Ranch.

The ranch has operated as a cow/calf operation. On January 1, 1983, 713 brood cows were maintained on the ranch (including first-calf heifers). For a more complete description of forage resources, livestock production levels, and costs of production see Torell et al. (1985).

PROCEDURES

Two alternative grazing patterns are considered. First, the economics of the seeding is considered when it is grazed every year under traditional spring/fall use. Second, the economics of the proposed Saval grazing system is outlined, which includes the crested wheatgrass seedings evaluated in this study.

Production costs, grazing/hay resources, "typical" livestock production practices, and production levels were obtained for the Saval Ranch (Torell et al. 1985) and were used to develop a profit maximizing linear programming (LP) model. The model allocates resources (e.g. hay, grazing forage) to livestock so as to maximize ranch income (returns over variable costs). It captures the interrelationship between classes of resources, seasonal livestock forage requirements, and seasonal forage availability. Total seasonal grazing resources are considered in relation to the "optimal" (profit maximizing) management strategy. Beef prices, costs of production, and "typical" livestock production levels are considered explicitly. As a result, the model is a tool for estimating how range improvements and implementation of the proposed grazing management system would affect optimal livestock production and net ranch income.

To determine the benefits and costs of developing the new crested wheatgrass seeding on the Saval Ranch, several alternative management scenarios were considered. First a management alternative (e.g. LP run) was established which reflected optimal (profit maximizing) production without the new 2,430 acre (983 ha) seeding under season-long grazing. This established a benchmark against which other management strategies reflecting optimal livestock production with the new seeding could be compared. The resulting difference reflected the estimated net annual livestock benefit from adding the seeding when traditional grazing patterns are followed. This net annual benefit was assumed to accrue every year over a 50 year planning period. After discounting this flow of returns to present value, the cost of the seeding and the cost of the purchased livestock were subtracted, and the present net worth of the seeding was estimated.

Two management options were considered for traditional season-long grazing patterns. First, the economics of the new seeding was considered when winter feed (hay) was the limiting factor of production. This reflects the existing situation on the ranch. As a second option, fertilizing hayland on the ranch was considered. It was estimated that one-third of available hayland (564 acres; 228 ha) on the ranch could be fertilized (Torell et al. 1985). Hay yields on fertilized acres would be expected to increase by 1.25 tons/acre (2.8 MT/ha). The cost of the fertilization program was estimated to be $40/acre ($98.89/ha).[1]

The economics of the Saval Ranch grazing system was considered using procedures similar to those used for traditional season-long grazing patterns. That is, a benchmark was established which reflected optimal production without the grazing system. Selected years of the grazing system were then simulated to estimate optimal livestock production under the proposed system. For the grazing system analysis, it was assumed that 1/3 of available hayland was already being fertilized (as outlined above), and range forage was the limiting factor of production.

Range Improvement Costs

Range improvements amounting to an estimated $149,381 have been implemented on the Saval Ranch since 1981 (Torell et al. 1985). Over half of this expense ($78,204) was for implementation of the new 2,430 acre (983 ha) crested wheatgrass seeding. Other improvements include new fence construction, fence reconstruction, and water developments[2]. In addition, it was estimated that an additional $43,545 of water developments may need to be implemented as a part of the proposed Saval grazing system, bringing total expenditures for range improvements to an estimated $192,926 (Torell et al. 1985). Maintenance costs of these improvements were estimated to be about $2,400 per year.

The costs incurred in plowing and seeding the new crested wheatgrass seeding on the ranch are outlined in Table 1. The total cost is estimated to be $32.18 per acre ($13.02/ha). Seed cost of $10.70 per acre ($4.33/ha) accounts for one-third of this expense, considerably higher than if a monoculture of crested wheatgrass had been planted.

As outlined in Table 1, in addition to crested wheatgrass (<u>Agropyron desertorum</u>), pubescent wheatgrass (<u>Agropyron trichophorum</u>), Russian wildrye (<u>Elymus junceus</u>), ladak alfalfa (<u>Medicago sativa</u>), small burnet (<u>Sanquisorba minor</u>), and sweet clover (<u>Melilotus officinalis</u>) were also planted.[3] Planting these additional species increased seed cost by $7.30 per acre ($2.95/ha). This means that the cost of the seeding was increased by 29 percent to avoid planting a crested wheatgrass monoculture.

Saval Ranch Grazing System

Under the proposed management plan for the Saval Ranch, crested wheatgrass seedings will be grazed under a 3-pasture, deferred-rotation system with one pasture grazed only in the fall every year. BLM native range will be grazed under a 3-pasture, rest-rotation pattern with one pasture rested every year. USFS range will be grazed as a 2-pasture, deferred-rotation system with grazing starting on the early pasture on July 1 and on the late pasture on August 16.

[1]For an economic analysis of this fertilization scheme, see Torell et al. (1985).

[2]A complete listing of specific range improvements implemented is provided by Torell et al. (1985).

[3]Even though several forage species were planted I will follow tradition and refer to the seeding as a "crested wheatgrass seeding."

Table 1.--Plowing and seeding costs for the implemented crested wheatgrass seeding on the Saval Ranch.

Expense Category	Total Cost for 2,430 Acres			Cost Per Acre		
Plowing						
Contract Plowing	$30,254			$12.45		
Repair	6,318			2.60		
Subtotal		$36,572			15.05	
Seeding						
Contract Seeding	12,150			5.00		
Seeder Repair	875			0.36		
Seed[1]	26,000			10.70		
Subtotal		39,025			16.06	
General Expenses						
Transport of Plow and Seeder	840			0.35		
Non-Use of Range for 1 year (310 AUMs x $5.70)	1,767			0.73		
Subtotal		2,607			1.08	
Total			$78,204			$32.18

[1]Per acre seeding costs: 5 lbs. crested wheatgrass @ $.68; 2 lbs. pubescent wheatgrass @ $1.47; 2 lbs. Russian wildrye @ $ 0.85; 0.5 lbs. ladak alfalfa @ $1.14; 0.5 lbs. small burnet @ $3.55; 1 lb. sweet clover @ $0.30

The objectives and rationale of the Saval Ranch grazing system as outlined in the Saval Coordinated Management Plan (USDI Bureau of Land Management 1981) are as follows:

A. Improve livestock distribution on all pastures by 1) implementing grazing systems with proper fencing, 2) providing water developments away from major creek bottoms, 3) having the permittee provide at least one range rider, and 4) having the permittee place salt a minimum of one-quarter mile from waters, with subsequent salting on the same location.

B. Improve range condition from poor to good and increase production to 60 percent of potential within 15 years after implementation of the grazing system on 3,639 acres (1,473 ha). Improve range condition from fair to good and increase production to 70 percent of potential within 15 years after implementation on 30,948 acres (12,530 ha)

C. Increase hayland production from the current 1600-1800 tons (1,455-1,636 MT) to 3000-3400 tons (2,727-3,090 MT) within 6 years.

D. Eliminate active headcutting of streams directly affecting or threatening Lahontan Cutthroat Trout habitat within 3 years after implementation.

E. Minimize forced moves of cattle for management or distribution so as to maximize weight gain.

F. Increase calf crop from 70 to 80 percent (based on number of calves weaned as a percentage of total cows exposed) within 10 years after implementation of the grazing system.

G. Increase weaning weights from 350 to 450 pounds and increase yearling weights from 650 to 750 pounds within 20 years after implementation.

In the economic analysis of the grazing system, the expected benefit is assumed to differ slightly from the objectives of the grazing system as outlined above. Calf crop was assumed to increase from 80 percent to 85 percent seven years after implementation of the grazing system. This adjustment was made because the Saval Ranch should be able to achieve an 80 percent calf crop (the average calf crop in Elko County as reported by Myer and Hackett [1981]) through improved breeding management without the grazing system. An 80 percent calf crop has been assumed in the seeding economics analysis under traditional grazing patterns, and as the starting point under the grazing system.

After the grazing system has been in place for seven years, selling weights of livestock sold are expected to reflect levels similar to those outlined under objective G of the grazing management plan. Average selling weight of heifer calves was assumed to be 398 pounds (181 kg) and yearling steers were expected to weigh 728 pounds at sale (331 kg).

A major expected livestock benefit of the grazing system will be increased livestock forage availability and grazing capacity due to better livestock distribution, water developments, seedings, and herding. In the economic analysis of the grazing system, it was assumed that grazing capacity on all Federal and private rangelands (native rangeland and seeded areas) would increase by 25 percent, including the additional forage from the new seeding. This level of increase is based upon objective B of the Saval Grazing Management Plan. The assumed pattern of forage increase is outlined as Figure 2.[4]

RESULTS

The additional species were planted to improve wildlife habitat. While wildlife benefits/impacts are not considered explicitly in this study, the extra seed cost has apparently not produced positive economic benefits. A July 1982 evaluation of the success of the seeding rated stands of Russian wildrye, sweet clover, alfalfa, and small burnet as "failures," based upon a success rating scale developed by Hyder and Sneva (1954). It was estimated that stands of forbs were very sparse—0-5 percent stocked (Stager et al. 1983). This means that the stand had, on average, only one forb plant/25 ft^2 (one plant/7.6 m^2)—a very sparse plant density. The stand of crested wheatgrass and pubescent wheatgrass was considered a "success."

Traditional Grazing Pattern—Hay Limiting

When hay acreages are not fertilized, such that winter feed supplies limit livestock production, optimal herd size would be 670 brood cows (Torell et al. 1985). With the addition of an estimated 972 AUMs from the seeding, with all other grazing resources held constant, optimal herd size was estimated as 734 brood cows. Management as a cow-calf/yearling operation with all steer calves carried over for sale as yearlings was estimated to maximize profit.

Gross benefits from the seeding were estimated to be $22,991 (Table 2). Annual production costs were estimated to increase by $16,047. The resulting net annual livestock benefit is then $6,944. Thus, the net annual benefit to the ranch is positive. However, this does not consider the costs of the seeding or of additional brood stock purchased in order to utilize the additional forage. After discounting the $6,944 annual flow of returns to present value, the cost of the seeding and purchased livestock were subtracted. The resulting net present value was estimated to be minus $20,167 (Table 2). The internal rate of return was then 6.26 percent and the benefit/cost (B/C) ratio was less than one. If the only livestock benefits were additional early spring or fall forage, and additional forage for herd expansion, then the seeding cannot be considered beneficial. Based on the B/C ratio, benefits were estimated to be only 93 percent of costs. There are at least three reasons why this is the case. First, the Saval Ranch has a considerable number of acres of existing crested wheatgrass (4,200 acres; 1,700 ha). These stands are generally adequate for spring forage requirements. Second, winter feed is the most limiting forage resource on the ranch. Developing additional grazing resources does not solve the more important need for winter feed. Without developing or improving existing hayland production on the ranch, additional grazing forage will only add to the existing forage balance problem. While hay could be purchased from off the ranch, this is not a profitable alternative on a large scale basis as shown by linear programming analyses. The third reason why the seeding would not yield positive economic returns is the diverse seed mixture. As mentioned earlier, the policy of "not planting a monoculture of crested wheatgrass" increased seed cost by $7.30 per acre ($2.95/ha) or by $17,738 for the 2,430 acre seeding. Had this expense not been incurred, the present net worth of the seeding would

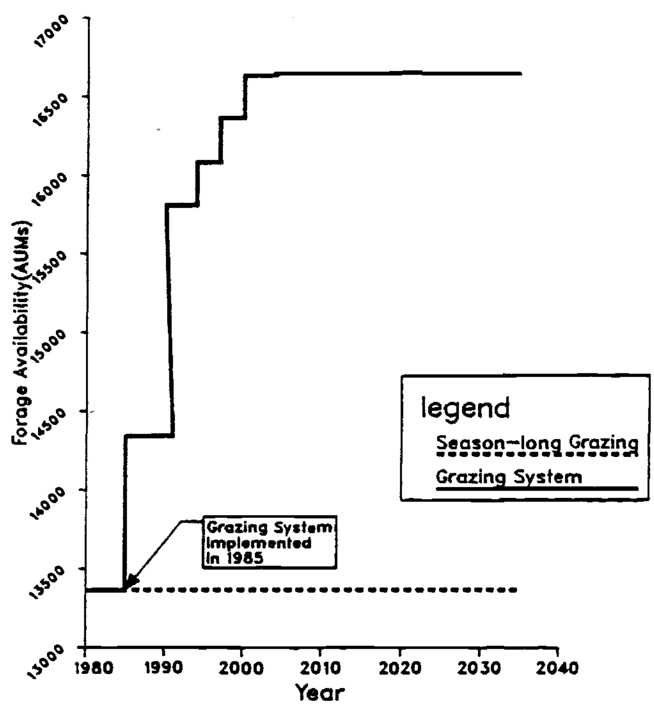

Figure 2.—Total annual forage availability under "traditional" grazing and under the Saval Ranch grazing system.

[4]For an additional discussion of the rationale used, the interested reader is referred to Torell et al. (1985).

Table 2.--Benefit/cost analysis of the implemented seeding under traditional grazing patterns when winter feed is the limiting resource.

Annual Benefits				
Increased livestock sales	$21,028			
Increased grazing fees (972 AUM's @ $2.02)[1]	1,963			
Total annual benefits		$ 22,991		
Annual Costs				
Increased production	15,265			
Seeding maintenance	782			
Total annual costs		16,047		
Net annual benefit			$6,944	
Present Values				
Present value of $6,944 (50 years @ 7-7/8%)	86,186			
Present value of $28,800 worth of breeding stock from year 50[2]	651			
Required range improvement investment	-78,204			
Purchase of 64 additional cows and 4 bulls	-28,800			
Present net worth				-20,167
Internal rate of return (IRR)				6.26%
Benefit/Cost Ratio				.93

[1]Although grazing fees reflect out-of-pocket costs for the Saval Ranch, they are merely transfer payments from the point of view of society. Therefore, grazing fees should be excluded from the calculation of the change in net income when deriving the marginal value of forage to society (Brown 1982). Because the additional grazing fees are included in the $15,265 increase in livestock production costs for the Saval Ranch, an equivalent amount, ($2.02 X 972 AUM's = $1,963) is added as a benefit. The $2.02 fee used in the analysis reflects the 1979-81 average of federal lands grazing fees.

[2]In order for the Saval to fully utilize the additional grazing resource, herd size must be expanded by 64 cows and 4 bulls. At the end of the 50 year planning horizon the investment in additional livestock is added back as a benefit. Mature cows were valued at $400 per head, and additional purchased bulls were valued at $800 per head and discounted to present value.

be minus $2,429 as compared to minus $20,167. Thus, had these additional costs not been incurred, the seeding would have been basically a break-even investment under a hay limiting option.

Traditional Grazing Pattern--Hay Not Limiting

Assuming that the Saval Ranch was initially fertilizing 1/3 of available hayland on the ranch (increasing hay production by an estimated 705 tons), then optimal herd size would be 762 brood cows. After adding the seeding, optimal herd size would increase to 816 brood cows (Torell et al. 1985). With sufficient winter feed, the economics of the seeding is positive (Table 3). Range forage now limits livestock production. The switch to positive present net worth when hay is not limiting indicates the importance of considering seasonal forage balance when assessing the need and worth of a crested wheatgrass seeding.

Grazing System--Hay not Limiting

Present net worth of range improvements and the grazing management system was estimated to be $68,090. The internal rate of return was estimated to be 9.54 percent, and the calculated B/C ratio was 1.15:1.[5]

The grazing system, which includes an estimated $192,926 in range improvements, is estimated to be cost effective with benefits exceeding costs based solely on benefits to livestock. Additional expected wildlife and watershed benefits, which were not included in the B/C analysis, would further improve the economics of the grazing system.

It should be pointed out that the analysis presented here does not provide a direct comparison of the economics of crested wheatgrass when grazed under traditional grazing patterns with results obtained under a grazing system. The Saval grazing system includes nearly $115,000 worth of range

[5]The interested reader is referred to Torell et al. (1985) for detail of considerations used in calculating these parameters.

Table 3.--Benefit/cost analysis of the implemented seeding under traditional grazing patterns when range forage is the limiting resource.

Annual Benefits				
Increased livestock sales	$17,742			
Increased grazing fees (972 AUM's @ $2.02)	1,963			
Total annual benefits		$19,705		
Annual Costs				
Increased production	10,251			
Seeding maintenance	782			
Total annual costs		11,033		
Net Annual Benefit			$ 8,672	
Present Values				
Present value of $8,672 (50 years @ 7-7/8%)	107,633			
Present value of $24,000 worth of breeding stock from year 50	542			
Required range improvement investment	-78,204			
Purchase of 54 additional cows and 3 bulls	-24,000			
Present net worth				$5,971
Internal rate of return (IRR)				8.36%
Benefit/Cost Ratio				1.03

improvements in addition to the crested wheatgrass seeding under consideration. Ideally, one would analyze the value of each range improvement individually with specific consideration of benefits and costs. This would allow determination of the contribution of just the seeding to the economics of the grazing system. A direct comparison of economic returns following either traditional grazing patterns or a grazing system would then be possible. However, in practice, it is very difficult to project the contribution of a cross-fence, a water development, or other specific range improvements to forage production and availability. For this reason only an estimate of total benefits of the grazing system was made.

CONCLUSIONS

Crested wheatgrass seedings will not always be profitable. It depends upon the seasonal forage demands of the ranch and how a crested wheatgrass seeding would alleviate any seasonal forage limitations. In fact, the major economic benefit of a seeding is the potential to meet a forage requirement in a limiting forage season. Implementation of a seeding not providing that benefit may be uneconomical.

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The Economics of Seeding Crested Wheatgrass : A Synthesis and Evaluation

E. Bruce Godfrey

ABSTRACT: Various types of range improvements such as seedings of crested wheatgrass were extensively used during the period 1955-1970. Since 1970 the number of improvements implemented has declined dramatically. Reasons for this decline are suggested. Studies that have estimated the benefits and costs of seeding an area to crested wheatgrass indicate that the economic value of this range improvement practice is variable, ranging from very profitable to very costly. Reasons why the "payoff" for seedings are variable are reviewed and evaluated.

INTRODUCTION

The deterioration and remedial treatment of America's rangelands have been issues for nearly a century. Various measures have been taken to increase their productivity, including several types of range improvements after World War II. Data are not available that can be used to show results of improvements implemented before the early 1960s, but insight can be gained from the data available since that time. For example, data in Figures 1 through 5 show that the number of range improvements (seedings, brush control, reservoirs, springs, and fencing) on lands administered by the Bureau of Land Management (BLM) reached a maximum in the late 1960s. The implementation of such improvements declined thereafter, and are nearly nonexistent at the present time. The limited amount of data available for the Forest Service (Figures 6 through 9) show a similar pattern. Data are generally not available for improvements on private or state-owned lands but it is believed that a similar pattern exists (Godfrey 1972). This raises the question concerning why this pattern has occurred and represents the focus of the remaining discussion.

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REASONS FOR REDUCED USE OF IMPROVEMENTS

Although numerous reasons could be given why range improvement practices have been reduced over time, they can generally be classified into one or more of the following: 1) no potential, 2) insufficient funding, or 3) they don't "pay". Let us therefore briefly evaluate each of these reasons.

No Potential

The suggestion that all of the sites having improvement potential have already been treated would be rejected by any range scientist familiar with western rangelands. Agency documents are replete with examples of potential range improvements, especially EIS statements that have been prepared during the last five years (Schuster 1979). Some would argue that the best sites have been improved and that viable (profitable) alternatives no longer exist, but this opinion is not accepted by most range managers. One would, therefore, have to reject this as a viable reason for the above trends.

Insufficient Funding

It is generally conceded that agencies administering most of the federal rangeland do not have sufficient budgets. However, the data in Fig. 10 and 11 suggest that the amount of money available for range improvements on federal lands has increased in real terms over time. This increase in funds has occurred at the same time that the number of range improvements has declined. This indicates that agencies have spent these funds for nonstructural items instead of for "on-the-ground" improvements. While this practice or policy could be questioned, these data indicate that budget constraints cannot be used as a primary reason for the reduction in improvements that has occurred over time.

They Don't Pay

If potential sites still exist and if funding is not a problem, then one must assume that other investments have a higher "payoff". While every suggested improvement must be evaluated on its own merits, some insight into the possible benefits and costs of seeding an area to crested wheatgrass can be obtained by reviewing the studies that have been conducted in the past. Table 1 lists a number of studies that have estimated the benefits and costs of seeding crested wheatgrass and indicates the general conclusions reached by the author(s). The conclusions outlined in Table 1 suggest that the returns from seeding are generally variable and depend on several interrelated factors.

REASONS FOR VARIABILITY IN RETURNS

The variability in returns reported by several of the authors shown in Table 1 can be attributed to the factors discussed below.

Response

Some seedings did not pay simply because the seeding failed--i.e., a viable stand was not established. In many cases, the increased production was not sufficient to offset the costs incurred. One of the reasons for this result stems from the fact that areas of low production were seeded before areas having high potential but relatively high current production—a "worst first" site selection criterion. For example, a site with a current capacity of 33 acres per AUM with a potential of 5 ac/AUM would be seeded before an area having a current capacity of 7 ac/AUM with a potential increase to 3 ac/AUM. The second has the greatest potential increase in forage production even if the percent increase is smaller. This suggests that greater attention needs to be paid to the expected response and to put funds where they yield the largest return. A fixed investment must result in a difference in use and not just improve the condition of a site if the investment is to pay.

Intensity

One of the most common reasons why a seeding may not pay stems from the fact that too much is spent for the response obtained. For example, Kearl and Brannan (1967) reported that seeding costs varied more than three fold depending on the brush removal method used. As a result, some seedings paid while others did not. This may also occur when the overstory is difficult to control. For example, few studies indicate that the removal of juniper trees

Table 1.—Synoptic review of selected studies on the economics of seeding crested wheatgrass.[1]

Author(s)	Year study published	Location of area studied	Net returns positive?
Pearce and Hull	1943	Intermountain West	Yes
Short	1943	Montana	Unknown
Meik	1950	Bitter Root/Montana	Yes
Caton, McCorkle, and Upchurch	1955	Intermountain West	Yes
Pingree and Dortignac	1959	Northern New Mexico	Questionable
Caton and Beringer	1960	Southern Idaho	Unknown
Lloyd and Cook	1960	Utah	Variable
Gardner	1961	Colorado	Yes
Gray and Springfield	1962	New Mexico	Unknown
Gray, Stubblefield, and Roberts	1965	Southwest	Variable
Kearl	1965	Central Wyoming	Yes
Rader	1965	Intermountain West	No
Nielsen, Brown, Gates, and Bunch	1966	Eastern Oregon	Variable
Kearl and Brannan	1967	Central Wyoming	Variable
McCarthur, Nielsen, and Andersen	1971	Southeastern Utah	Yes
Araji and Godfrey	1972	Southern Idaho	Variable
Brown, O'Connell, and Hilbert	1974	Northern Arizona	Variable
Daley, Olsen, and McAfee	1974	Wyoming	Yes
Cordingly and Kearl[2]	1975	Central Wyoming	Yes
Workman and Kienast	1975	Central Utah	Variable
Stevens and Godfrey	1976	Eastern Oregon	Variable
Heady and Bartholome	1977	Eastern Oregon	Variable
Godfrey, Sharp, and Sellasie	1978	Southern Idaho	Yes
Kearl	1979	Wyoming	Variable

[1]This list is not intended to be inclusive of all studies that have estimated the benefits/costs of seeding an area to crested wheatgrass but it does include most of the studies that have been conducted. The reader should also recognize that these studies are based on the principles of benefit/cost analysis. Readers interested in this methodology should review Nielsen (1977), Gittinger (1972), Prest and Turvey (1965) or one of the many other texts that are available.

[2]Also Kearl and Cordingly (1975).

and subsequent seedings pay because juniper is more costly to control than is sagebrush.

A related, but all too common problem involves the installation of other improvements (e.g., fencing, water developments) with a seeding--a practice the author has called "including a silk purse with a sows ear"--that have few, if any, benefits.[1] For example, the BLM Wells District EIS[2] suggested that $2.3 million dollars be spent to obtain approximately 5,000 AUM's of forage, an expenditure of about $485 per AUM or nearly $29,500 per operator. This suggests that too much can be spent on range improvements. It also suggests that each of the suggested parts of an "improvement package" should pay, and that each should be evaluated to determine if it is a worthwhile practice.

Grazing Use

There is probably no factor that has a greater impact on the "payoff" associated with a seeding than how it is used. For example, Godfrey (1979) has shown that the returns from a crested wheatgrass seeding are highest if it is used at relatively heavy rates during the spring. Some have suggested that light grazing will make the stand last longer but this additional life would probably not be worth the loss of benefits foregone as long as society has any positive rate of time preference (see Baumol 1968 for a discussion of this issue). Furthermore, a serious question can be raised concerning the need for long periods of deferment, and their associated costs, while seedings become "established". Research is also needed on the use of crested wheatgrass seedings during the winter as a substitute for expensive hay.

Associated Uses

One of the major reasons why seedings have not recently been implemented stems from a belief that they are detrimental to wildlife. This belief has been questioned by some writers (Recher 1969, Heady and Bartolome 1977). The major reason for these differences of opinion arises from the lack of quantitative evidence of the positive or negative impact of a seeding on wildlife populations. The effects of seedings on wildlife are only one of several impacts that have not been quantitatively measured. For example, some evidence indicates that livestock gains on crested wheatgrass seedings used in the spring are greater than they are on native pastures. Some workers view seedings as a major source of erosion and resultant siltation, but these impacts have not been quantified. Furthermore, the economic evaluation of seedings for environmentally related uses will await further study because no methods are available to either value or assess damages to wildlife species or watershed considerations such as siltation and riparian habitat (Nielsen and Hinckley 1975, Godfrey 1983, Schuster and Jones 1983). As a result, seedings are not implemented because values are viewed as too high--or damages too large--as subjectively evaluated by range land decisionmakers.

Social Values

One of the most controversial issues associated with the establishment of seedings concerns their "social acceptability". Some interest groups view them as a "biological desert" while livestock operators generally view them very favorably. There may be biological reasons why the establishment of a monoculture[3] may be undesireable but there has been no quantitative evaluation of the social acceptance of seedings from an aesthetic point of view--except in the view of particular individuals. Evaluation of questions such as, 'Who objects to seedings and why?' needs to be carefully done.

Measurement of Benefits and Costs

Unfortunately, one reason for the variability in the reported results from seedings stems from the improper use of economic methodology (Godfrey and Torell 1984). For example, Gardner (1963) reviewed four of the early studies and concluded that much of the reported variability was due to the use of improper methods of economic analysis.

It must be remembered however, that seedings are only one of many types of forage used by wild and domestic animals and that the need for other types of forage may be greater. This suggests that any economic evaluation of the payoff from seeding an area must be done within a framework that considers the need for this type of forage as opposed to other types (see Torell et al. [1985] for an example of this issue).

CONCLUSIONS

The economic studies that have evaluated the benefits and costs of seeding an area to crested wheatgrass indicate there is considerable variation in the "payoff" that could be expected from a seeding, and that some of the information for a complete analysis has been and remains unknown. Most studies do indicate however, that the benefits are greater than the costs if seedings are used in a manner that captures their comparative advantages.

While crested wheatgrass seedings should not be viewed as a panacea, they tend to be relatively profitable investments.

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[2]This is only one of many cases that could be cited and should not be interpreted as a particular criticism of the managers of the Wells, Nevada District.

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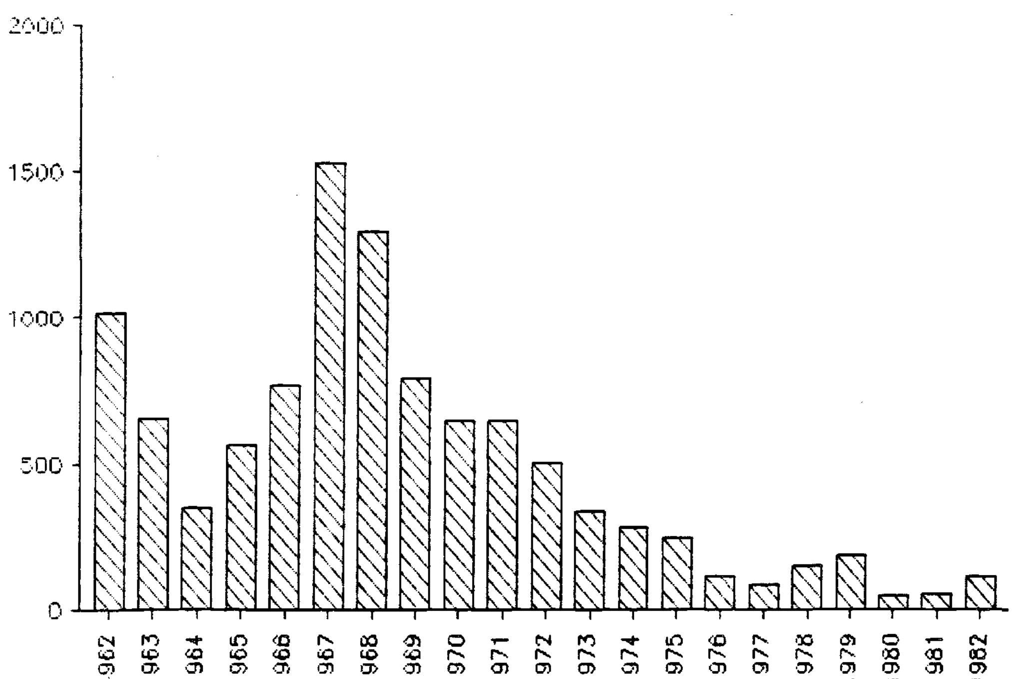

Figure 1.--Number of reservoirs on BLM lands, 1962-1982 (USDI Bureau of Land Management 1962-82).

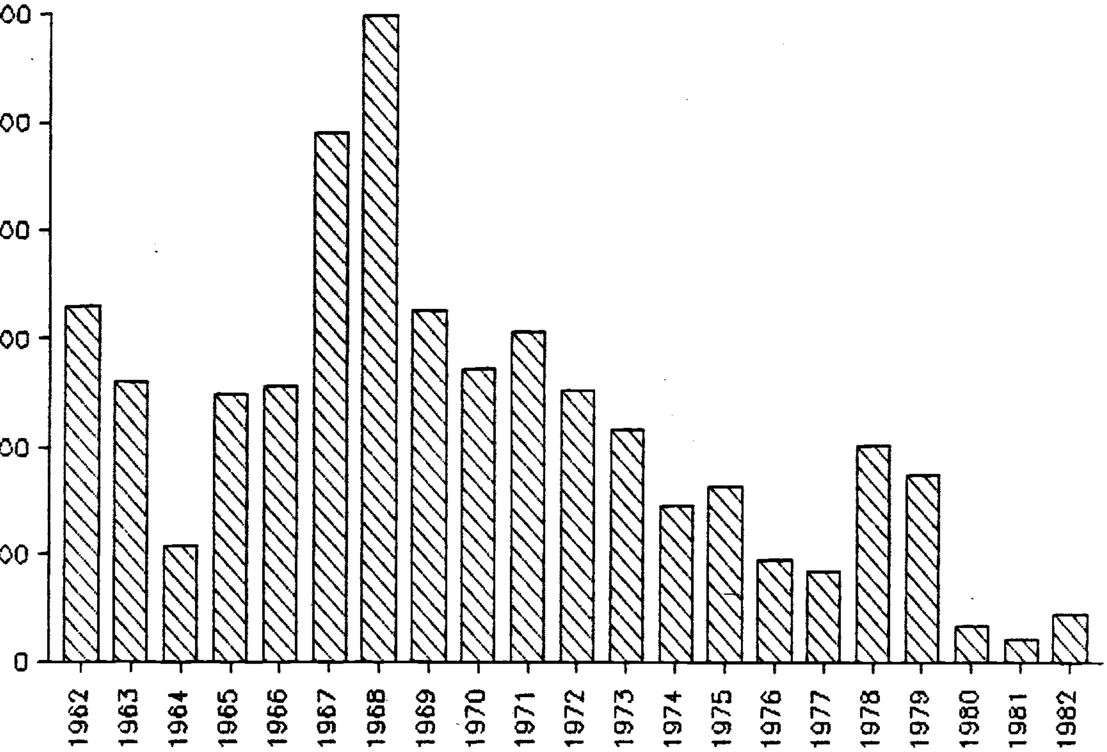

Figure 2.—Number of springs on BLM lands, 1962-1982 (USDI Bureau of Land Management 1962-82).

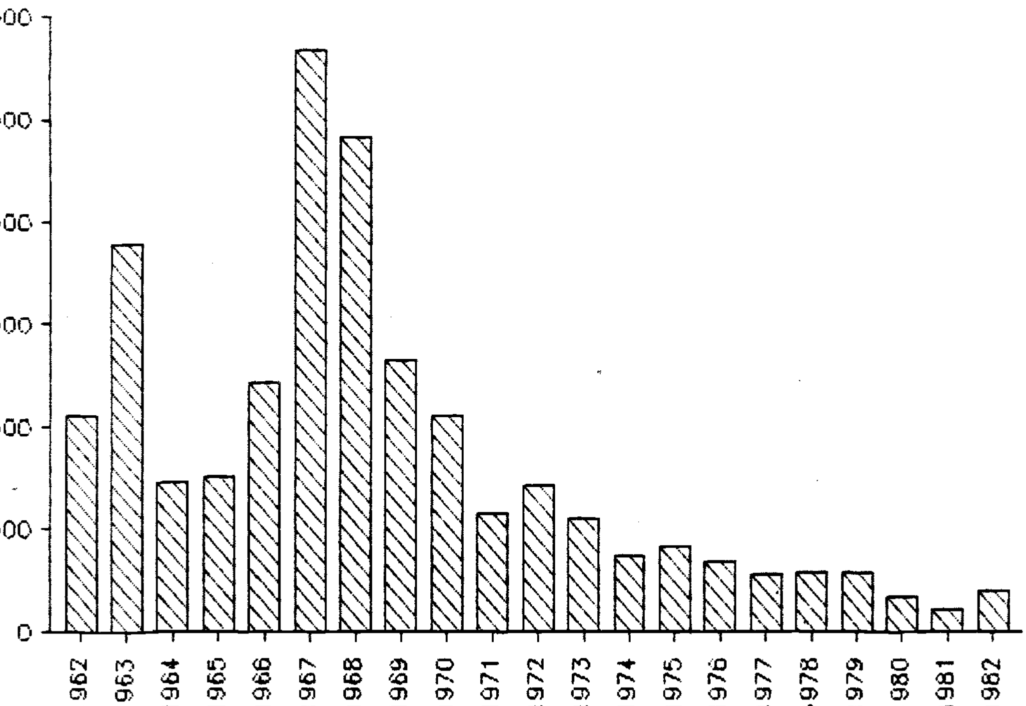

Figure 3.—Miles of fencing on BLM lands, 1962-1982 (USDI Bureau of Land Management 1962-82).

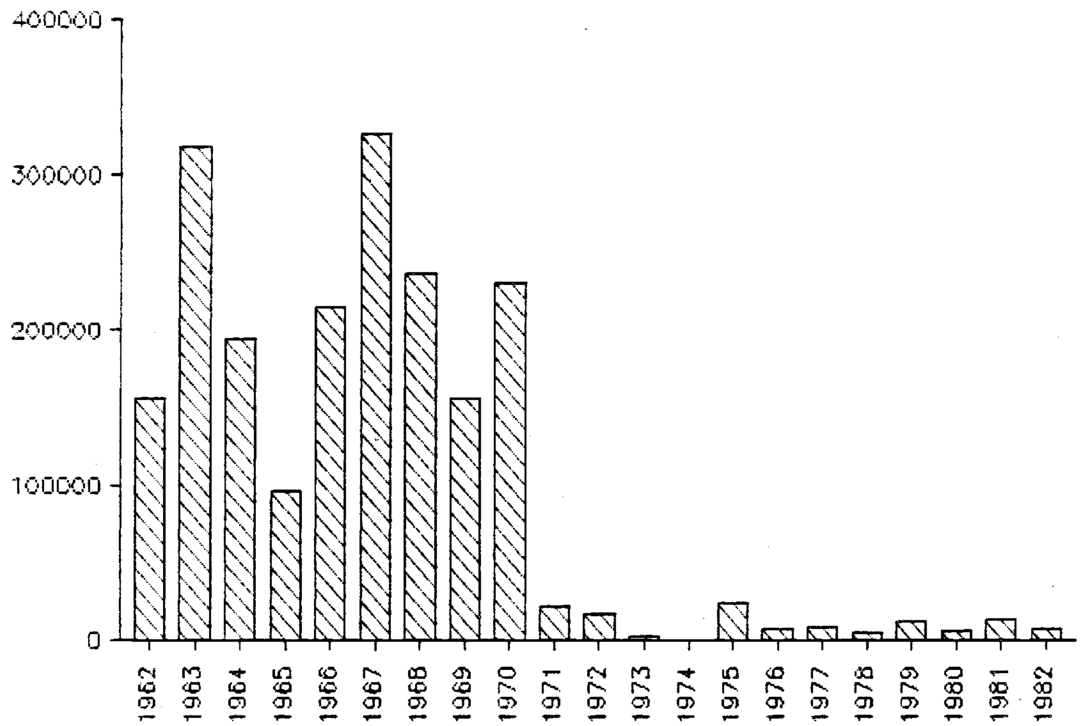

Figure 4.--Acres of brush control on BLM lands, 1962-1982 (USDI Bureau of Land Management 1962-82). Data not available for 1974.

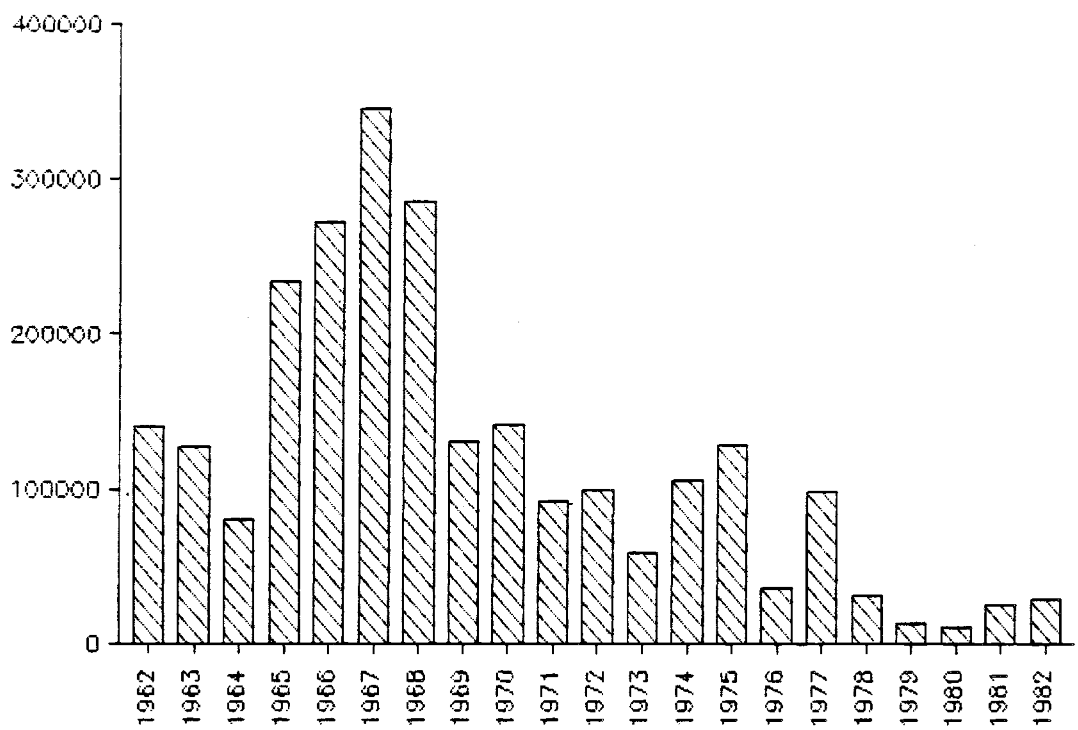

Figure 5.--Acres of seeding on BLM lands, 1962-1982 (USDI Bureau of Land Management 1962-82).

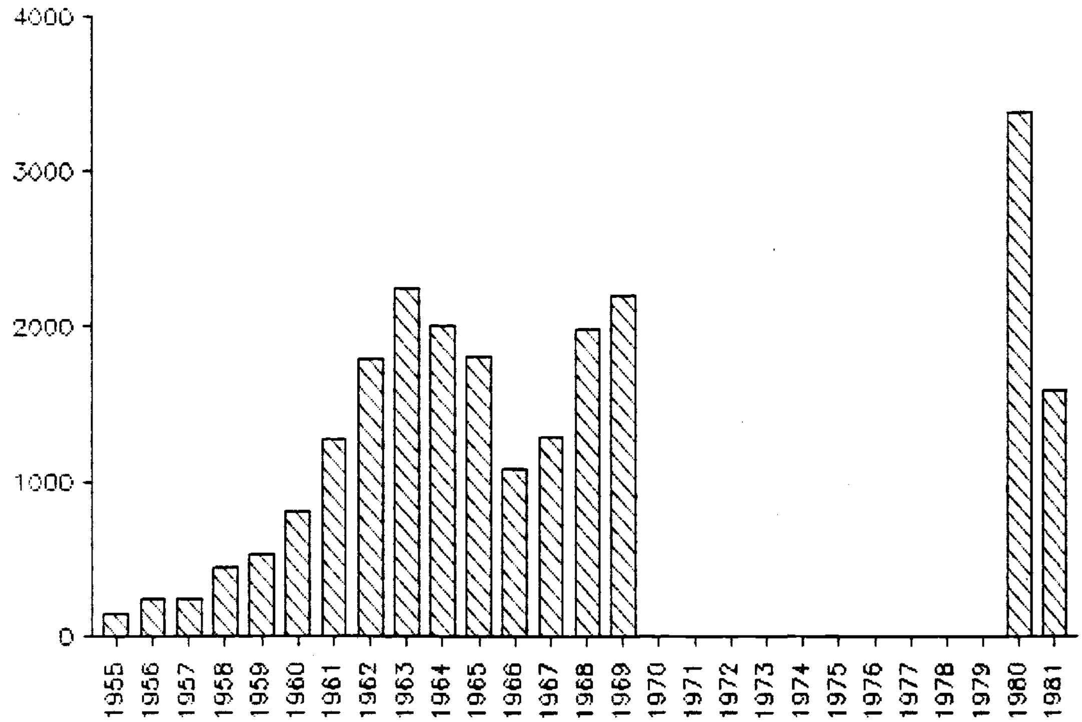

Figure 6.—Miles of fencing on Forest Service lands, 1955-1981. (USDA Forest Service 1955-81). Data not available for 1970-79.

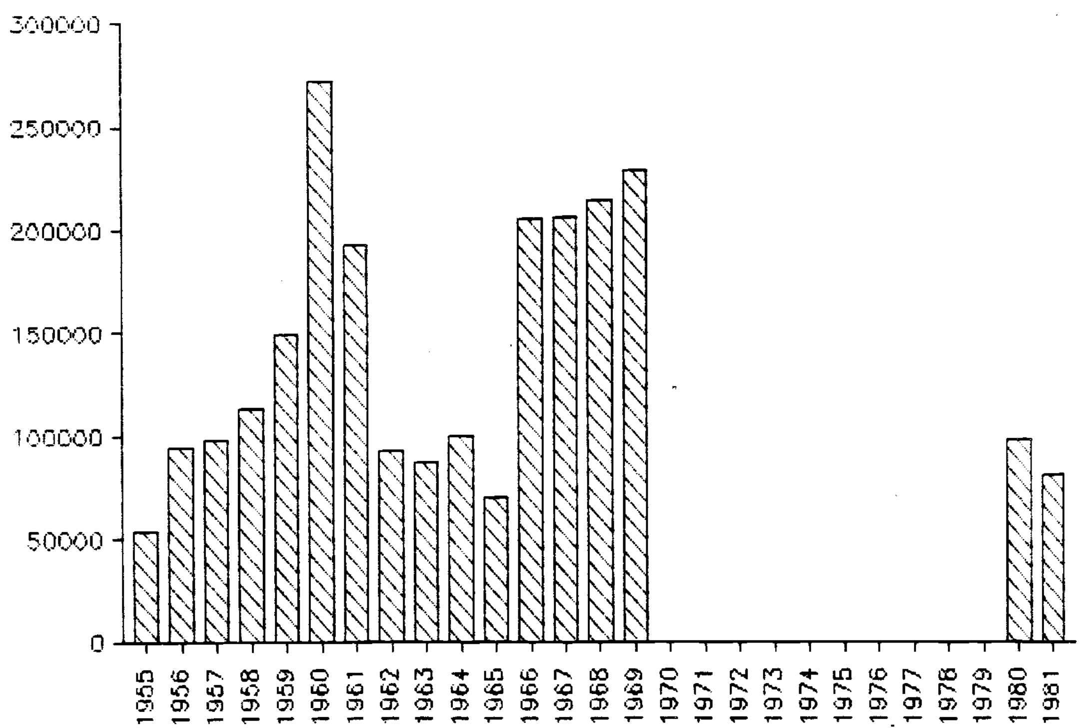

Figure 7.--Acres of cover manipulation on Forest Service lands, 1955-1981. (USDA Forest Service 1955-81). Data not available for 1970-79.

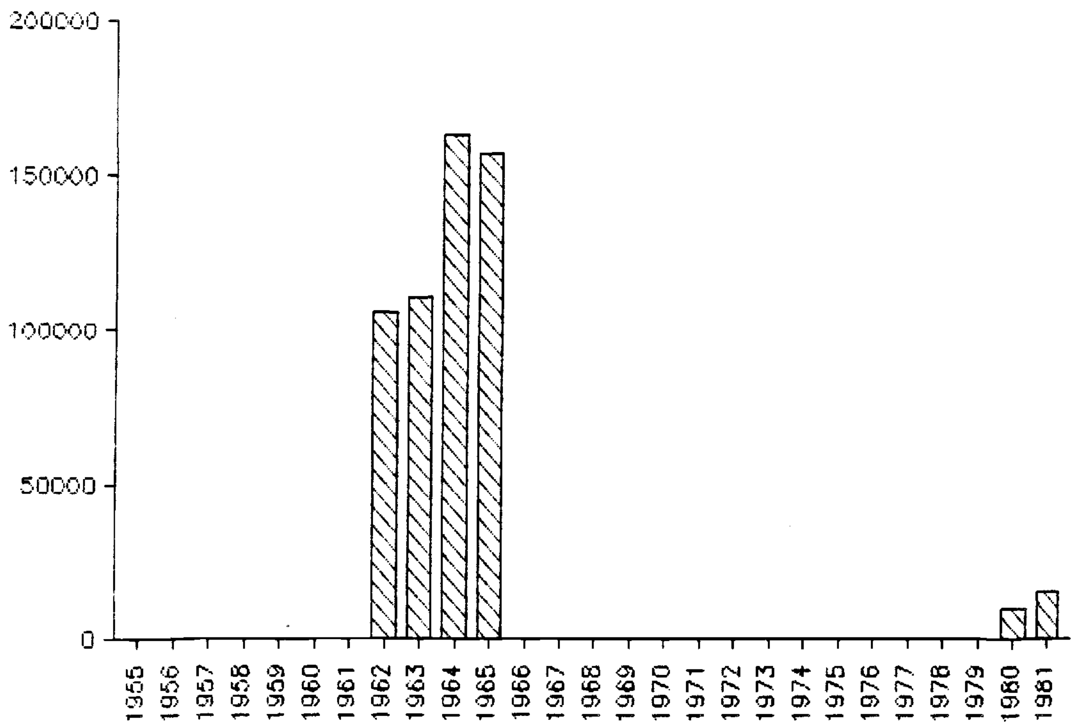

Figure 8.--Acres of range plant control on Forest Service lands, 1955-1981. (USDA Forest Service 1955-81). Data not available for most years.

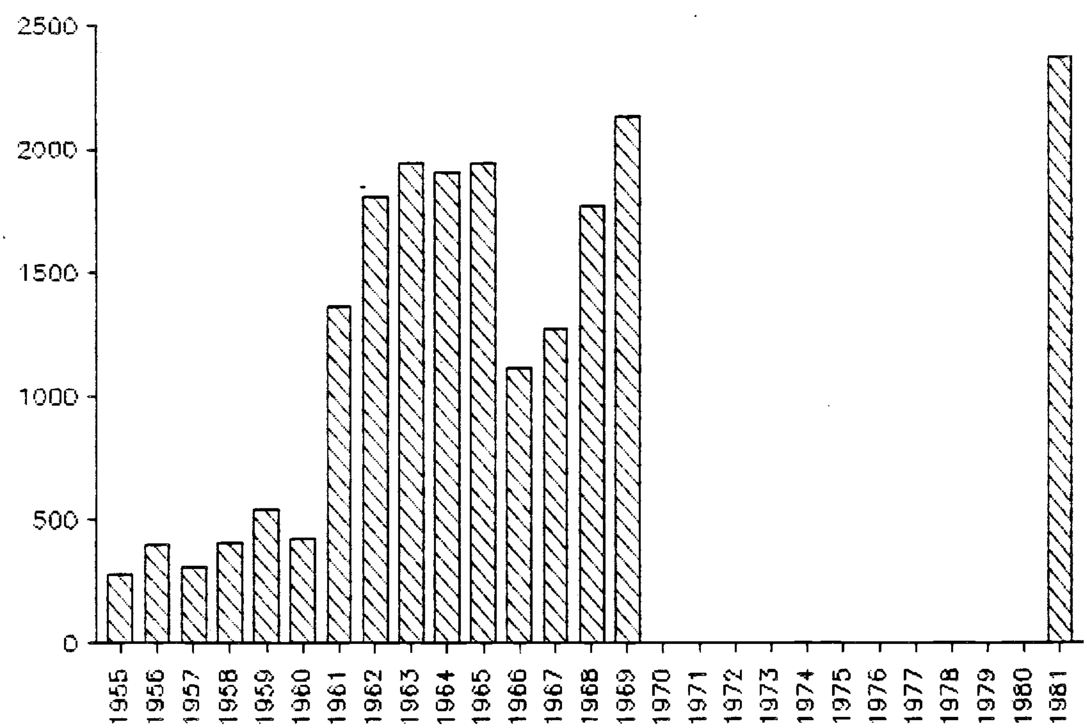

Figure 9.--Number of water developments on Forest Service lands, 1955-1981. (USDA Forest Service 1955-81). Data not available for 1970-80.

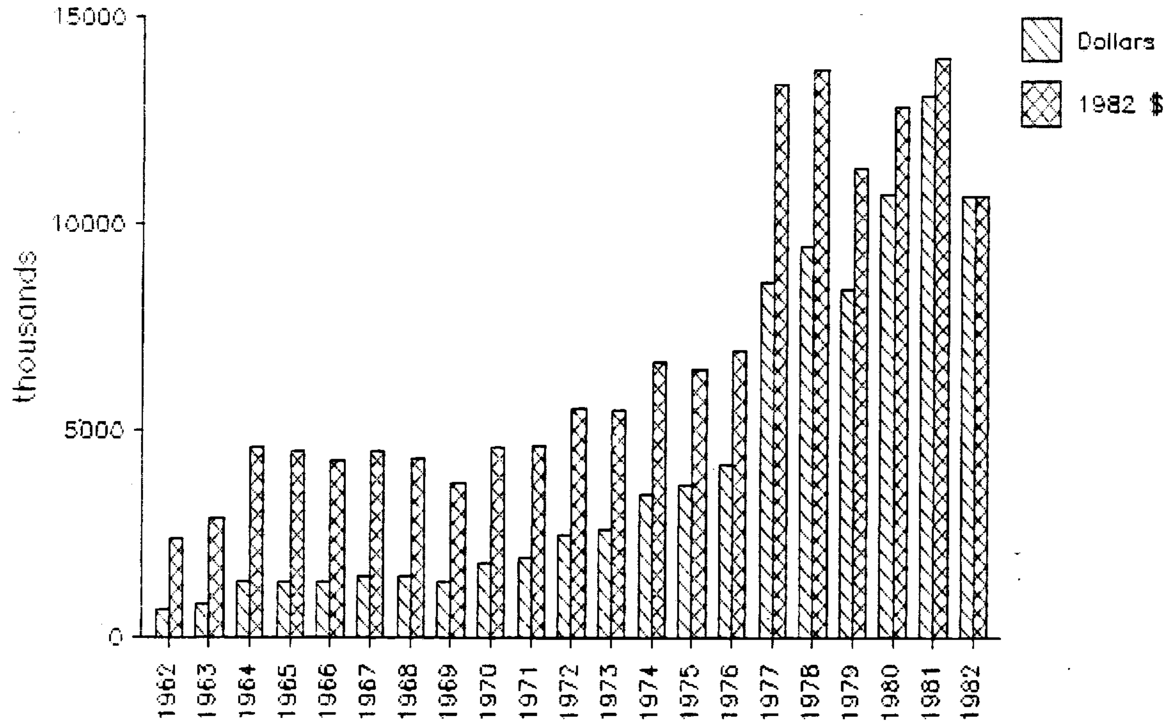

Figure 10.--Appropriations for range improvements on BLM lands (USDI Bureau of Land Management 1962-82).

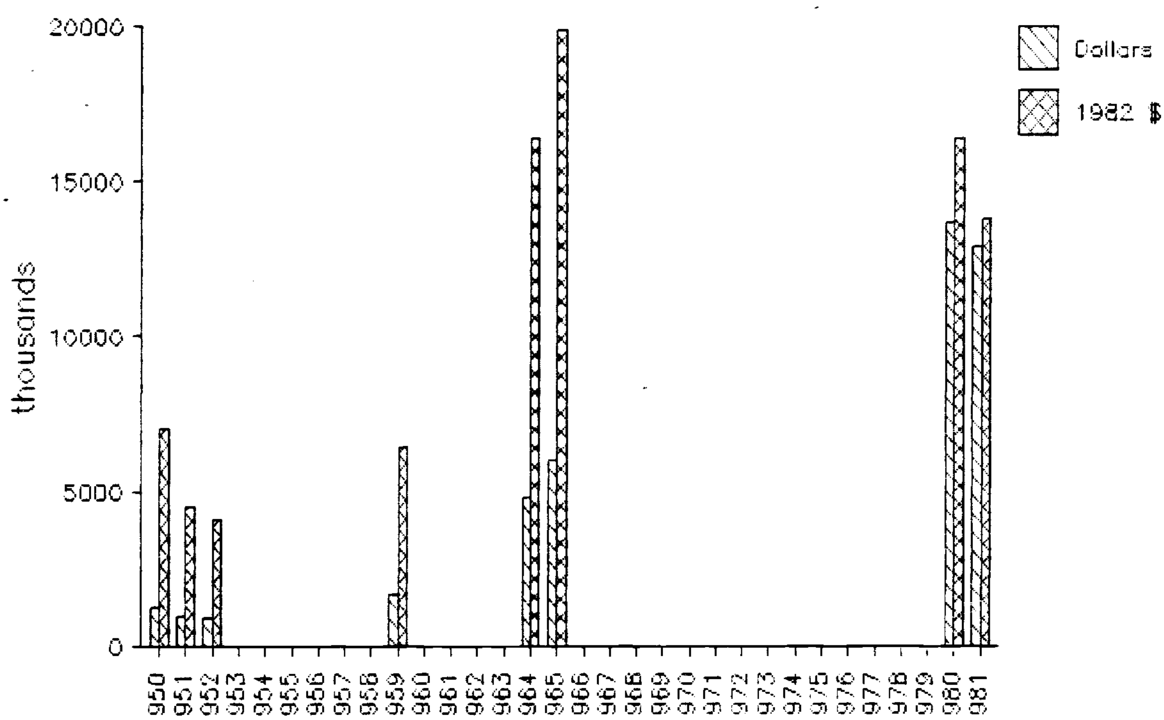

Figure 11.--Appropriations for range improvements on Forest Service lands (USDA Forest Service 1950-81). Data not available for most years.

SECTION IX.

Environmental and Social Issues.

Should We Use Crested Wheatgrass and if so, Where?

Chairman, Stephen B. Monsen

The Role of Crested Wheatgrass in Reclamation of Drastically Disturbed Lands

Edward J. DePuit

ABSTRACT: Rangelands of the western United States are subjected to a variety of drastic disturbances which necessitate reclamation for impact mitigation. Crested wheatgrass may play an important role in the revegetation phase of the reclamation process. Characteristics of the species governing its use in revegetation are discussed, and its past and present performance on drastically disturbed lands is reviewed. Conclusions and recommendations are drawn on the proper future role of crested wheatgrass in disturbed land reclamation.

INTRODUCTION

In response to expanding needs for energy, services, and essential raw materials, rangelands in the West are being devoted to an increasing variety of non-agricultural uses. Many involve drastic land disturbances which completely destroy existing ecosystems and land uses. Mining activity is perhaps the most recognized example of such drastic land disturbance, and certainly has produced major environmental impacts in many parts of the West. However, other types of disturbance such as oil and gas development; construction of pipelines, powerlines, highways, and railroads; and cropland reversion are numerous and in aggregate very important. If not reclaimed such disturbances will remove hundreds of thousands of acres of western rangelands from productive uses for indefinite periods of time.

The Significance and Nature of Reclamation

Reclamation comprises one obvious solution to the environmental trade-off dilemma of drastic land disturbances. As noted by the National Academy of Sciences (1981), the goal of reclamation is to insure that society does not lose the actual or potential land use opportunities available prior to disturbance. Reclamation has been recognized for some time as ethically, ecologically and agriculturally important (Box 1978); for many types of disturbance it is now legally mandated as well.

As reviewed by Box (1978), numerous concepts and definitions of reclamation exist. These range from complete restoration of prior conditions to rehabilitation on pre-designated criteria. For purposes of this paper, reclamation will be considered the process of returning a drastically disturbed site to conditions approximately equal to or greater than those prior to disturbance in terms of sustained support of functional physical processes, biological organisms and land uses. This definition is similar to that recently proposed by Narten et al. (1983).

Because reclamation essentially strives to re-establish entire, functional ecosystems on disturbed lands, the necessity of properly integrated, "entire-system" approaches has become widely recognized (Wali 1975). Reclamation thus becomes a complex endeavor with numerous facets, involving a multiplicity of scientific disciplines. Revegetation is one important aspect of the reclamation process, because its nature will obviously be a major determinant of the function and use of re-established ecosystems.

Revegetation Goals and Principles

In broad terms, revegetation objectives on disturbed rangelands usually call for establishment of permanent, self-sustaining vegetation to stabilize the soil and provide habitat and forage for livestock and wildlife (Narten et al. 1983). In a narrower sense, the specific nature of "successful" revegetation is controversial. Diverse, predominantly native vegetation on reclaimed lands is propounded by many (Blake 1981), and is the type of vegetation stressed in current reclamation regulations (Imes and Wali 1978). However, the feasibility or desirability of such objectives has frequently been challenged by those favoring a more flexible, utilitarian approach including the use of introduced species (Laycock 1980, Currie 1981, Hofmann et al. 1981).

Ries and DePuit (1984) felt the nature of successful revegetation largely depended upon

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proposed land uses, and its achievement rested on proper plant materials selection and revegetation methods. While great progress in revegetation methods has been made (Packer and Aldon 1978), selection of proper plant species often remains problematic or controversial.

DePuit (1982) proposed five criteria for selection of plant species in disturbed land reclamation:

1) adaptational and other autecological characteristics,
2) initial establishment characteristics,
3) synecological characteristics,
4) functional utility,
and 5) practical availability.

It was postulated that if a given species properly met these criteria, it should be acceptable for revegetation use, irrespective of its origin. Therefore, depending upon specific reclamation goals, environmental conditions and plant species characteristics, there should be a role for both native and introduced species in disturbed land reclamation (DePuit 1982, Thornburg and Fuchs 1978).

Objectives of Paper

Crested wheatgrass (i.e., the Agropyron cristatum, A. desertorum, A. sibericum complex) has been widely used in disturbed land revegetation in the Northern Great Plains, Rocky Mountain and Intermountain regions. For a number of reasons, this use has prompted more controversy than any other single species utilized in revegetation. This paper will analyze the characteristics of crested wheatgrass pertinent to species selection criteria, review the past and present use of the grass on disturbed lands, and then draw conclusions on the proper future utilization of this species in revegetation.

CRESTED WHEATGRASS FOR DISTURBED SITE REVEGETATION

Characteristics Pertinent to Revegation

Adaptational and autecological characteristics.--To be considered for revegetation use, a plant species must be adaptated to prevailing climatic, physiographic and edaphic conditions of the site. Such conditions are usually more severe (i.e., less conducive to plant growth) on disturbed than on non-disturbed sites. The autecological characteristics of the species also must be conducive to the desired functions and uses of the re-established ecosystem.

Crested wheatgrass is a perennial, cool-season bunchgrass first introduced into the United States in 1896 (Holechek 1981). Crested wheatgrass exhibits one of the widest adaptational amplitudes of any grass species (native or introduced) in the western United States (Rogler and Lorenz 1983). As summarized below much information is available on the specific adaptational nature of crested wheatgrass (Holechek 1981, Rogler and Lorenz 1983, Thornburg 1982, Wasser 1982, Keller 1979).

Climatically, crested wheatgrass is a cold-tolerant xerophyte best adapted to areas of 9 to 15 inches (23 to 38 cm) annual precipitation and cool to cold winters. These conditions typify a significant portion of the Northern Great Plains and Intermountain regions. Its drouth tolerance is very high, an important adaptational characteristic in light of the overriding importance of moisture availability as a limiting factor for western revegetation (May 1975).

Edaphically, crested wheatgrass can establish and persist on a wide variety of soils, but is best adapted to moderately deep, well-drained, loamy soils. While certainly responsive to increased fertility (DePuit and Coenenberg 1979), the species can establish on soils with relatively low inherent fertility (Holechek et al. 1982). Such tolerance of infertility is a physiological asset on drastically disturbed soils, which commonly are low in certain essential plant nutrients (Bauer et al. 1978). Soil salinity or sodicity are edaphic constraints to revegetation on many arid and semiarid disturbed lands (Sandoval and Gould 1978). Although not adapted to highly salty (especially sodic) soils, crested wheatgrass has often established well on moderately saline disturbed soils in the West (Holechek 1981).

In addition to its adaptational traits, crested wheatgrass possesses a number of other autecological characteristics pertinent to its role in revegetation. As reviewed by Rogler and Lorenz (1983), crested wheatgrass is a long-lived species under proper management, is capable of self-regeneration, is tolerant of fire (in the dormant stage), and has relatively few disease problems. These characteristics enhance the desirability of the species for disturbed land revegetation in terms of providing permanent, self-sustaining vegetation.

The relatively good forage production potential of crested wheatgrass is also an asset. It is a cool-season species exhibiting maximum growth and forage quality during the spring. This attribute carries a number of implications for the functional utility of crested wheatgrass on reclaimed lands.

Initial establishment characteristics.--In addition to adaptation when mature, rapid initial establishment is a requisite of plant species used in revegetation. As noted by DePuit (1982), mature plant adaptation and ease of initial establishment are not always positively correlated on disturbed lands. Weak or slow initial establishment may detrimentally affect revegetation through accelerated soil erosion or weed infestation. Poor initial establishment of a seeded species also may increase chances of its competitive inhibition or exclusion by more rapidly establishing species.

A great amount of accumulated information is available on the seed and seedling ecology and physiology of this species (Johnson this volume, Wasser 1982, Fulbright et al. 1982). Although exceptions have occurred, research and practice have demonstrated that crested wheatgrass is a rapidly establishing grass on sites where it is adapted within the Northern Great Plains and Intermountain regions (Plummer 1977, Hafenrichter et al. 1968, Thornburg 1982). Germinative capacity of seeds is typically high (Wasser 1982). Further, crested wheatgrass germinates and initiates active growth very early in the spring, contributing to relatively good seedling vigor.

Initial establishment of crested wheatgrass can usually be achieved using known and available cultivation, direct seeding and subsequent management practices (Keller 1979, Wasser 1982, Fulbright et al. 1982). Crested wheatgrass has often responded well to cultural practices applied to promote plant establishment on disturbed lands, most notably fertilization (DePuit and Coenenberg 1979).

Therefore, crested wheatgrass meets the initial establishment criterion for species selection quite well, adding to its credibility as a disturbed site revegetation species.

Synecological characteristics.--As noted previously, current regulations strongly emphasize species diversity in revegetation of many types of land disturbance, especially surface mining. Logical arguments have been propounded both for (Monsen 1975, Plummer 1977) and against (Laycock 1980, Currie 1981) this regulatory predisposition, with respect to feasibility, ecological desirability and utility. Despite the ongoing controversy, the fact remains that revegetation goals for many, if not most, disturbances involve re-establishment of mixtures of plants rather than single species. It is therefore important that species included in seeded mixtures be synecologically compatible. As noted by Power (1978), the area of interspecific competition and compatibility within mixed plant communities on disturbed lands is one of the least understood aspects of revegetation.

Crested wheatgrass is an exceptionally vigorous, competitive species on sites where it is adapted due to its specific physiology, phenology and morphology (Caldwell et al. 1981, Richards and Caldwell 1982, Harris 1977). Because of its competitive nature, crested wheatgrass coexists variably with other species in mixed stands. Persistent and useful mixtures of crested wheatgrass with certain shrubs, introduced legumes and grasses have sometimes been established on improved pastures, rangelands and disturbed lands (Dubbs 1975, Rumbaugh et al. 1982, DePuit and Coenenberg 1978). However such mixed communities are often floristically simple--particularly on disturbed lands (DePuit et al. 1978).

Considerable evidence exists of the synecological incompatibility of crested wheatgrass with many native grasses, forbs and shrubs whose presence in reclaimed plant communities is sometimes desirable. The competitive superiority of crested wheatgrass over many native grasses has been long recognized in rangeland seedings (Heinrichs and Bolten 1950). In a recent Wyoming study, Schuman et al. (1982) seeded crested wheatgrass with both single species and mixtures of native grasses. While crested wheatgrass comprised only 25% of the initial seed mix in all cases, after four years it comprised an average (across all treatments) of 85% of the ultimate stand. Similar results were reported from Montana mined land studies (DePuit et al. 1978, Sindelar 1978), in which crested wheatgrass and other seeded introduced species competitively excluded concurrently seeded native species. DePuit et al. (1980) concluded that it may be necessary to exclude crested wheatgrass and other exceptionally vigorous species from seed mixtures to enable establishment of diverse plant communities on Northern Great Plains mined lands.

These results on Northern Great Plains disturbed lands have major implications for use of crested wheatgrass relative to revegetation goals. If a relatively simple plant community dominated or co-dominated by crested wheatgrass is acceptale, seeding of the species may be justified. Conversely, if a more diverse community is required for land use or regulatory goals, inclusion of crested wheatgrass in seed mixtures may be inadvisable.

These general relationships for the Northern Great Plains region may require qualification for specific sites or for other regions. However, synecological incompatibility between crested wheatgrass and certain other species does exist, indicating that relationships between crested wheatgrass and other desired plant species must be considered in designing species mixtures.

Functional utility.--Selection of any plant species for disturbed land revegetation must be based in part upon its functional utility, in terms of both the processes associated with reclamation and the projected land use goals. Such functional utility depends upon many of the autecological and synecological characteristics already discussed.

In terms of reclamation processes, the rapid initial establishment, vigor and hardiness of crested wheatgrass provide considerable potential for the soil stabilization mandatory on drastically disturbed lands. However, because of its bunchgrass morphology, crested wheatgrass may not be as effective in longterm erosion control as certain rhizomatous species, and for this reason should often be seeded in conjunction with the latter for maximum site stabilization (Cook et al. 1970). The relatively high production potential of crested wheatgrass on adverse sites is also an asset in reclamation processes. Higher organic matter production will promote soil development and carbon/nutrient cycling (Schafer and Nielson 1978). However, if accelerated plant community development (i.e. succession) toward a "native" condition is desired, establishment of crested wheatgrass may be inappropriate due to its competitiveness and persistence.

The functional utility of crested wheatgrass on disturbed lands also depends upon its suitability for the type or types of land use goals established. For livestock land use, results of mined land grazing studies in Montana and North Dakota (Hofmann et al. 1981, DePuit and Coenenberg 1978, DePuit 1983) have indicated crested wheatgrass has high utility for early season grazing, in terms of forage quality and quantity, animal production and vegetation responses. These results conform to those of many rangeland studies. However, the forage value of crested wheatgrass during other seasons is often inferior to other species currently available for revegetation, both on mined lands (DePuit 1983) and elsewhere (White and Wight 1981, Rumbaugh et al. 1982). Therefore, the functional utility of crested wheatgrass for livestock grazing on disturbed lands is linked to its management:

1) as a component of complementary grazing systems involving other seasonal forages in other pastures (DePuit 1983, Currie 1981); or

2) as a part of mixed stands with other species of different seasonal forage values (Rumbaugh et al. 1982).

As previously discussed, the latter approach may not always be possible due to the synecological incompatibility of crested wheatgrass with certain other species. If neither of the above approaches prove possible or practical, species other than crested wheatgrass may be more appropriate for revegetation.

In addition to livestock, reclamation goals for many disturbed sites in the West include support of wildlife. Considerable controversy has surrounded the value of crested wheatgrass for wildlife on disturbed lands (Harju 1980). Crested wheatgrass, contrary to the impressions of many, does have specific value to some wildlife species at certain times of the year (Urness et al. 1983, Holechek 1975). However, these benefits can be outweighed by the negative effects of crested wheatgrass on vegetation diversity, which is recognized as a prerequisite for both diversified wildlife populations and adequate season-long support of many individual wildlife species. The detrimental effects of large-scale crested wheatgrass plantings on many wildlife species have been recognized (Value 1974).

Practical availability. In addition to acceptability in terms of autecological, synecological and utilitarian characteristics, any plant species used in disturbed land revegetation must have seeds or propagules available in sufficient quantities. Due to its ample seed production and ease of harvest and treatment (Hafenrichter et al. 1978), adequate commercial seed availability is usually not a problem with crested wheatgrass. Several species and species cultivars within the crested wheatgrass complex have been evaluated and released for use, such as Nordan, Fairway, Ruff, Parkway and Siberian. Each of these selections exhibit somewhat different autecological, synecological and utilitarian characteristics (Thornburg 1982, Wasser 1982).

Past Use and Performance on Disturbed Lands

Crested wheatgrass has been one of the most commonly used grass species for general range reseeding in the western United States (Holechek 1975). Because of its history of use on rangelands, crested wheatgrass early became a prime species in disturbed land revegetation efforts when reclamation of such lands became a major concern in the 1960's. The species found an early place in roadside revegetation and stabilization (Cook et al. 1970, Hodder 1970, Jensen and Sindelar 1979). Crested wheatgrass was also a common component of early seed mixtures for mined lands in North Dakota, Montana, Wyoming, Colorado and Utah. This use was generally vindicated by adequate initial establishment, site stabilization, vigor, productivity and persistance (Frischknecht and Fergusen 1979, Ries et al. 1978, DePuit et al. 1978, May et al. 1971, Sims and Redente 1974).

Although crested wheatgrass proved useful in revegetating disturbed lands in the region, certain problems were associated with its usage. The paramount problem involved the competitive aggressiveness of crested wheatgrass, which has often eliminated or reduced other concurrently seeded and desired species (Sindelar 1978, Ries et al. 1978). DePuit et al. (1978) also suggested that without proper management (i.e., grazing or maintenance of fertility), vigor of crested wheatgrass would decline over time on disurbed lands. In addition, the high responsiveness of crested wheatgrass to fertilization (DePuit and Coenenberg 1979, Redente et al. 1982) has sometimes created soil C:N imbalance problems (Schafer and Nielsen 1978, Sindelar 1978) and declines in vegetation diversity (DePuit and Coenenberg 1979, Doerr et al. 1983). Clearly, proper management of crested wheatgrass is as essential on disturbed lands as elsewhere, and such management on disturbed lands involves some rather unusual problems.

Grazing studies on reclaimed pastures containing crested wheatgrass have demonstrated the species to be either tolerant of or stimulated by livestock utilization if well-established (Hofmann et al. 1981, DePuit 1983). Animal performance during spring grazing periods was excellent. DePuit (1983) found that lower forage quality during summer and fall was associated with reduced animal gains relative to native rangeland pastures.

Present Use on Disturbed Lands

Because of its early successful establishment on disturbed lands in the West, crested wheatgrass was perhaps over-utilized -- that is, used in many situations where other plant species could have been established and were better suited to projected land uses. This "overuse" has led to a current public and regulatory reaction against crested wheatgrass in reclamation and a reduction in use. Another reason for reduced utilization of crested wheatgrass in reclamation arises from the development of other plant species with high revegetation potential, including many native species (Thornburg 1982). A third reason for reduced crested wheatgrass use involves a current prejudice against introduced species in general within environmentalist and regulatory sectors, which some observers feel to be highly unjustified (Laycock 1980, Currie 1981).

Consequently, and in contrast to earlier years, crested wheatgrass is presently being "under-used" in disturbed land revegetation. Nowhere is this more evident than in mined land reclamation. In response to regulatory mandates and other considerations, many mine companies in the region have completely eliminated crested wheatgrass from seed mixtures (e.g., Coenenberg 1982). In some cases, this elimination may be justified on ecological or utilitarian grounds. But in other cases it may be unfortunate, because crested wheatgrass, if properly utilized in appropriate situations, has a role to play in reclamation.

SUMMARY

The characteristics of crested wheatgrass pertinent to disturbed land revegetation are those relating to its adaptation and autecology, initial establishment, synecology, utility, and availability. Autecologically, the species has many desirable attributes, including wide climatic and edaphic adaptation, tolerance of poor quality soils, long life, capability for self-regeneration, vigor, good production potential and tolerance of grazing.

Due to certain of its seed and seedling characteristics, crested wheatgrass can be established readily on disturbed lands with conventional seeding methods, and is generally responsive to cultural practices applied to promote initial plant growth. The availability of crested wheatgrass seed is not a practical problem, and several species/species cultivars have been developed for use in specific situations. These attributes suggest that crested wheatgrass is an excellent species for revegetation.

The major limitations of crested wheatgrass for disturbed land revegetation derive from its synecological and utilitarian nature. Its vigor, hardiness, aggressiveness and persistence enable crested wheatgrass to inhibit certain other plant species whose presence may be desirable in mixed communities. There often appears to be an inverse relationship between crested wheatgrass dominance and plant community diversity, which limits its value where floristic diversity is an important reclamation goal.

In a utilitarian sense, crested wheatgrass has a number of attributes which are beneficial to the reclamation process itself, such as capability for rapid soil stabilization and increasing organic matter accumulation. However, its persistence and competitiveness may retard community succession toward a "native" condition, an obviously undesirable effect if such a progression is a goal. Optimal maintenance of crested wheatgrass on disturbed lands may be dependent upon somewhat more specialized or intensive management practices than those required for other species. The land-use capabilities of crested wheatgrass tend to be more specific than general. For instance, the phenology of crested wheatgrass makes it valuable for spring grazing. During other seasons, however, it may be inferior to other plant species currently available for revegetation.

Crested wheatgrass has been widely, perhaps over-widely, used in disturbed land revegetation programs. The species generally performed well in terms of initial establishment, productivity and persistence over a wide range of environmental conditions. Nonetheless, the use of crested wheatgrass on disturbed lands has recently been greatly curtailed. This is partly a result of a public and regulatory reaction to the earlier over-use of the species. In some cases, this reaction may be justified; in other cases, the reduced use of crested wheatgrass is neither objective nor logical.

CONCLUSIONS: THE PROPER FUTURE USE OF CRESTED WHEATGRASS ON DISTURBED LANDS

In the past, crested wheatgrass was perceived by many as a "panacea" species for range seeding and disturbed land revegetation over much of the West. Recent recognition of the fact that crested wheatgrass - like any species - has ecological and utilitarian limitations has negated this perception. Crested wheatgrass, as noted by Keller (1978), indeed does not have universal utility. Conversely, neither does the species have universal inutility. Any plant species with desirable characteristics may prove valuable in disturbed land revegetation if used properly (DePuit 1982, Currie 1981), and crested wheatgrass is certainly no exception. The proper role of crested wheatgrass on disturbed lands depends on an integration of environmental conditions and reclamation goals. This yields a number of general recommendations for use of crested wheatgrass in reclamation:

1) Extensive, monotypic seedings of crested wheatgrass on disturbed lands should be avoided, for both ecological and utilitarian reasons.

2) Crested wheatgrass use should be limited or eliminated on sites where relatively high floristic diversity or accelerated succession toward native conditions are reclamation goals. The research basis for this recommendation is strongest within the Northern Great Plains, but the principle may apply (with some modification) to the Intermountain region as well.

3) If its dominance is expected or desired, crested wheatgrass may be profitably used to support livestock in separate pastures managed in a complementary grazing system with pastures dominated by other species. The inter-pasture community (i.e., "habitat") diversity engendered by such management may also provide benefits to wildlife.

4) If non-complementary, season-long grazing is a land-use goal but high floristic diversity is not, crested wheatgrass may be used in relatively simple mixtures with other species that are synecologically compatible and which have differing phenologies or morphologies. A number of other species (grasses, legumes and shrubs) meet these criteria. Without such concurrently established species, optimum season-long forage benefits probably cannot be attained.

5) Crested wheatgrass may have particular value as a primary revegetation species in situations where its autecological attributes outweigh any synecological or utilitarian limitations. Examples of such situations include sites with edaphic or climatic conditions sufficiently adverse to preclude establishment of other species, and sites where the limitations of crested wheatgrass are not relevant to reclamation goals.

The above recommendations are generalizations, and specific exceptions may occur. They nonetheless outline broad considerations related to the appropriate use of crested wheatgrass in reclamation. The future use and evaluation of crested wheatgrass on disturbed lands should be based on its characteristics in relation to the criteria, principles and goals of reclamation, rather than on polarized positive or negative opinion. Only in this manner will the true value of this controversial species in disturbed land reclamation be recognized and achieved.

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The Social Values of Crested Wheatgrass: Pros, Cons and Tradeoffs

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ABSTRACT: The social values of crested wheatgrass are based on the biological characteristics that make it perhaps the most valuable plant available for range revegetation. Negative social aspects of crested wheatgrass arise from its foreign origin, in a general distaste for exotic species. A balance between these points can be developed under management programs that emphasize species diversity and reduction of monoculture size and extent. Most importantly, the introduced label on crested wheatgrass should be replaced by the recognition that it is now a North American range plant, proven by 90 years of testing and use. The grass should now be included in range management criteria and continue to be used in revegetation programs whereever it can best meet management objectives.

INTRODUCTION

Crested wheatgrass first gained wide attention in the drought-ravaged Great Plains of the 1930's. In the search for ways to stabilize the blowing, eroding, abandoned wheatfields of the region, it was crested wheatgrass that appeared to offer the best chance to quickly re-establish grassland. After the successful reseeding program, Dillman (1946) wrote:

> "The demand for wheat before and during the First World War brought about a marked change in agriculture of the great plains. Several million acres of native grasslands in the Northern Great Plains area of the United States and Canada were broken up and seeded to wheat during the period of 1905 to 1920. There appeared to be no need for a new dryland grass at that time. Finally the dry years of the middle thirties came on and abandoned wheat lands were in urgent need of grass. One could hardly have foreseen the heroic role that crested wheatgrass was to play in this living drama of the dry plains. It was the only grass available that would adequately fulfill this role. Already it's hardiness, productiveness, and longevity had been proved by experiments of the U. S. Department of Agriculture and state agricultural experiment stations."

Forty years later, however, Abbey (1986) in a general diatribe against livestock and ranchers was writing:

> "They (cattle) are a pest and a plague. They pollute our springs and streams and rivers. They infest our canyons, valleys, meadows, and forests. They graze off the native bluestem and grama and bunch grasses, leaving behind jungles of prickly pear. They trample down the native forbs and shrubs and cactus. They spread the exotic cheat grass, the Russian thistle and the crested wheat grass. Weeds."

It is clear that in the intervening period, a more complex and mutually opposed set of attitudes about crested wheatgrass had developed. The change was not linear, that is, the 1946 appraisal of crested wheatgrass did not evolve into the 1986 expression, but rather the latter joined the former. Today numbers of people entertain a general disdain of the grass; numerous other remain its apologists and, inevitably, an even larger group adopt intermediate positions.

The disagreement is a social rather than biological or technical problem, because crested wheatgrass and its main uses remain the same. Like all biological organisms, it has a set of characteristics that equip it to survive within a certain environment or, turned the other way round, crested wheatgrass has fitted itself to a certain environment through the process of selective change. Biologists speak of the environmental niche of an organism. In the case of crested wheatgrass, the niche is rather broad and extensive: the high, seasonally cold, semiarid, and often somewhat salty rangelands that occupy considerable portions of the Eurasian and North American landmasses. The general area of adaptation in North America is the Intermountain and Northern Great Plains regions of the United States and Canada. All or major parts of 11 states (Washington, Oregon, Nevada, Idaho, Utah, Montana, Wyoming, Colorado, North Dakota, South

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Dakota, Nebraska) and 3 provinces (British Columbia, Alberta, Saskatchewan) form its general distribution (Rogler 1960). The total acreage of crested wheatgrass is unknown, although Holechek (1981) suggests there may be 20 million acres in the United States and another 6 million in Canada.

The biological characteristics that enable it to prosper in that environment have long been known and, indeed, lie at the core of its widespread acceptance and support as a plant material suited to the reclamation of ravaged rangeland. The papers of this symposium and those found elsewhere in a very extensive body of literature bear ample witness of its characteristics. Today it is fair to say that crested wheatgrass is perhaps the most important range grass in North America and that we know more about it than any other grass of the western rangeland.

BIOLOGICAL CHARACTERISTICS AS SOCIAL VALUES

The Pros

Briefly, what makes crested wheatgrass what it is? Put another way, what gave it the social values associated with it in this century? As pointed out by Dewey (this volume) and many others, it is first of all not just a species, but rather a species complex of related varieties or cultivars commonly referred to as crested wheatgrass. The center points of the intraspecific variation are usually standard or Nordan (*Agropyron desertorum*), Fairway (*Agropyron cristatum*), and to a lesser extent Siberian (*Agropyron fragile*). Between them is found an unusually flexible biological entity, adapted to a wide variety of soil and climatic conditions within its zone of distribution.

Crested wheatgrass is a prolific producer of relatively large, viable seeds that germinate readily under a fairly wide range of moisture and temperature conditions (Young and Evans this volume). Once germinated, the seedlings display a strong vigor (Johnson this volume) that allows crested wheatgrass to rapidly establish in most seeded areas. Unlike many other grasses, crested wheatgrass is an agronomically forgiving species. Its requirements for proper seeding are less rigid, allowing it some prospect of establishment even when the seeding process is conducted improperly. Once established, the grass is tolerant of extremes in cold and drought, and remains productive under a wide range of growing conditions. Normally, crested wheatgrass outproduces the native grasses in its area of adaptation. Moreover, it is long-lived, persisting for many years in seeded stands (Rogler and Lorenz 1983).

Because of its germination, establishment and growth characteristics, crested wheatgrass offers a potential for providing early ground cover and site stabilization of reseeded lands. Like any biological organism, it has its environmental limits. But those limits are broad enough to allow it to be seeded on some very harsh sites with a reasonable prospect of success. Sometimes an assist in the planting year — in the form of an unusually wet spring or a bit of irrigation -- will allow it to establish on sites otherwise hostile to revegetation. Thus its initial role of the 1930's continues today. It is often the only plant material available to revegetate some sites, at least to some degree. And it continues to offer the immense social value of relatively rapid, easy establishment on dryland plantings for early control of the site.

As forage for livestock and to a lesser extent for big game, crested wheatgrass has several valuable characteristics, among them the capacity for early spring greenup. Far earlier than the native grasses, it develops green growth, sometimes carrying over the winter green foliage developed under favorable conditions of the previous fall. This makes the grass of particular value for a livestock operation, equalled only by Russian wildrye (*Psathyrostachys juncea*).[1] It offers much-needed early spring forage for livestock and big game (Urness this volume), and enables vital early-spring deferment of native grasses in grazing systems of management. Later in the summer and fall, crested wheatgrass becomes dry and rank, especially if not grazed earlier, but retains the capacity for greenup again under fall rains. But it is as spring forage that crested wheatgrass is most useful.

Another forage characteristic of great value is the exceptional ability of crested wheatgrass to tolerate grazing, far more than any native grass of similar adaptation. This feature probably arises from having evolved over the centuries with large grazing animals on the Eurasian steppe. Its ability to withstand grazing endows it with exceptional value in grazing operations. It literally can open the spring forage bottleneck so common to Intermountain area livestock operations.

Far more than other valuable perennial grasses like smooth brome (*Bromus inermis*), timothy (*Phleum pratense*) and orchardgrass (*Dactylis glomerata*), crested wheatgrass is remarkably well behaved. Unlike many other introduced plant species, it stays where it is seeded and only sparingly volunteers into nearby areas. Indeed, many observers have commented on its occurrence in drillrows long after seeding. It shows little capacity to invade undisturbed rangeland; only scattered plants appear. On the other hand, crested wheatgrass is remarkably persistent in seeded stands. Many seedings established in the 1930's remain productive; some are even older.

Because of its wide use and productivity, a great deal of crested wheatgrass seed is produced annually. This in turn makes it relatively cheap in comparison to the seed of most other grasses. This is a characteristic of no mean consequence, because together with its easy agronomic utility, low price has been the determining factor in its selection by highway departments to stabilize roadsides, often creating strips of crested wheatgrass tens and even hundreds of miles long.

These biological characteristics endow crested wheatgrass with its social utility — the 'pros' of its appraisal. On them has been based over a half-

[1]Nomenclature of the Triticeae grasses follows Dewey (1983).

century of widespread application in reseeding disturbed areas and improving forage production of western rangeland.

The Cons

At first glance it might appear that a grass with such obvious biological and social utility would have no characteristics that might imply a degree of disutility. But crested wheatgrass has a few, arising from the same characters producing its desirable features. Prominent among these are its high competitive ability that has allowed it to maintain seedings indefinitely. Many studies (DePuit this volume) have shown that even when seeded in mixtures as a minor component crested wheatgrass can assume dominance within a few years. That same competitive ability often forestalls secondary succession in seeded stands, essentially excluding major entry and establishment of native herbaceous species and most shrubs except big sagebrush (*Artemisia tridentata*). Indeed, Anderson and Marlette (this volume) have shown a lack of seed supplies of competing species in established sagebrush/wheatgrass stands, implying a successional stagnation. These results are by no means universal. There are many instances where crested wheatgrass has become a member of a vigorous seeded community with other introduced and native plants, or is found with many resident native species. There are even a few instances where crested wheatgrass has lost a competitive battle, notably with Russian wildrye. Nonetheless, reclamation of areas where the goal is reestablishment of native plant communities perhaps should not start with crested wheatgrass.

There is also objection to the frequent use of the grass in large seedings that form monocultures. Not only may successional change be blunted, but near-ideal conditions are created for epidemic outbreaks of insect pests such as black grass bugs (*Labops* and *Irbisia* spp.) as noted by Haws (this volume). And the large seedings are sometimes esthetically objectionable to many people.

While these negative aspects of crested wheatgrass culture are biologically well-founded, a much larger but less clear objection seems to issue from the fact that crested wheatgrass is not native to North America. As a general biological rule, there is good reason to prefer the use of natives instead of exotics because the gene pool of native vegetation is by definition adapted to the environmental conditions where it occurs. The adaptation of an exotic to those conditions is problematic, pending a long period of screening and study, and indiscriminate use could create new environmental problems (Black 1981). This statement is true over the whole range of adaptability. Plant species with insufficient adaptation to the environment in which they are introduced will not become established, or may not persist after initial establishment. The first category has of course no long term ecological consequences, but the latter could create problems if the introduced species are found unable to withstand subsequent environmental conditions.

At the other extreme, some plant species are all too well adapted, as the inadvertent release and subsequent distributional explosion of some species have shown. The alien annual cheatgrass (*Bromus tectorum*) is a prominent example, as are several noxious weeds such as leafy spurge (*Euphorbia esula*) and several knapweeds (*Centaurea* spp.). Avoiding these kinds of problems is almost an imperative, and fully justifies an extensive period of testing. On the other hand, some species equally well adapted but with inherent agronomic value, such as Kentucky bluegrass (*Poa pratensis*), are also widespread but for the most part have created no problems. This is also true of species widely used in a more agronomic sense, such as alfalfa (*Medicago sativa*) and, to a lesser extent, yellow sweet clover (*Melilotus officinale*).

Because crested wheatgrass was introduced to North America at the turn of the century, underwent extensive screening and testing until about 1920, and has been seeded on millions of acres since, it is clear that both the adaptation and agronomic utility of the grass have been established beyond question (Table 1). Hence it seems that objections to its use based solely on its not being a native species are simply prejudice, a form of 'botanical bigotry' as described by DePuit (this volume). Nonetheless, such perceptions do form a social 'con' of particular strength, now reflected in laws that mandate only native species be used to reclaim mined lands.

THE TRADEOFFS

A mature view of the social utility of crested wheatgrass in the late years of the twentieth century could well be based on the following observations:

First, the adaptation potential and agronomic qualities of the grass have been established through extensive testing and even wider practical use over many decades. The grass is exactly as it has been described: an introduced, cold-tolerant, drought-tolerant, highly productive and stable bunchgrass adapted to seeding rangelands throughout the Intermountain and Northern Great Plains regions of the United States and Canada. As such, it should continue to find many applications in reclaiming disturbed areas and reseeding rangeland to improve stability and production.

Second, it is equally clear that crested wheatgrass, just like any other biological resource, does not fit every situation, area or purpose. It is not, and never has been, a panacea. Its best uses must be defined by land managers and technicians able and willing to assess the ecological characteristics of a given site, evaluate that profile within an established set of management objectives, and then develop a treatment and management prescription. In this kind of an approach, crested wheatgrass will sometimes be useful, sometimes not. For example, an area whose ecological characters fit the adaptational profile of crested wheatgrass, but where management objectives call for the reestablishment of a diverse native community without particular reference to grazing use, should probably not be seeded to crested wheatgrass at all. In such case, the greater expense, difficulty, and problematic establishment of native species are worth their use.

Conversely, where the primary management objective is to develop an early spring grazing

Table 1.--An event chronology of crested wheatgrass since its introduction to North America.[1]

Year	Location	Event
1898	South Dakota	first introduction
1906	South Dakota	second introduction
1907-13	15 experiment stations	early testing
1915	North Dakota	forage research program
1921 (circa)	Montana	first general seeding in Great Plains
1923	South Dakota	first pasture experiment
1929	North Dakota	first offering of commercial seed
1932	North Dakota	first grazing study
1932	Saskatchewan	release of cultivar Fairway
1932	Idaho	first general seeding in Intermountain area
1937	west-wide	land utilization act seedings
1940's	Intermountain area	reseeding following big sagebrush control
1950's	Intermountain area	halogeton control seedings
1953	North Dakota	release of cultivar Nordan
1970's	west-wide	environmental concern
1984	Utah	release of cultivar Hycrest

[1]Compiled from Asay, Lorenz, and Young and Evans (this volume).

capability, or where a perennial ground cover must be immediately established, or where expense and ease of seeding are important, crested wheatgrass should be considered for its unquestioned values in those areas of concern.

Third, too-retrictive guidelines on use of crested wheatgrass, such as state regulations excluding use of all introduced species, are not helpful and often reflect ignorance of ecological understanding. Such regulations should be replaced by an ecological approach allowing maximum appropriate use of all available biological resources.

Fourth, many of the objections to the use of crested wheatgrass can probably be satisfied by management programs that emphasize species diversity and reduction of monoculture size and extent. For example, in many areas the introduced Russian wildrye and the rhizomatous native wheatgrasses western (Pascopyrum smithii) and thickspike (Elymus lanceolatus) have competed satisfactorily with crested. Where appropriate, these could be seeded with crested wheatgrass, or the planting area broken up along natural boundaries to reduce the extent of single-species monocultures. Special provisions can be taken as well to introduce adapted shrubs into a seeding, thereby increasing diversity and improving the overall grazing resource.

Fifth, and most important, the introduced label on crested wheatgrass, while historically true, has ceased to have meaning in ecological terms. The presence of crested wheatgrass in North America, like that of any other well-established introduced species, is impossible to reverse. In a continent full of human emigrants, crested wheatgrass and all of the other introduced plant species are their vegetative analogs; like them they are here to stay. The future ecological relationships of the Intermountain and Great Plains regions will necessarily contain crested wheatgrass. Hence, no useful biological purpose is served by continuing the distinction. The plant should now be included in vegetation classification schemes, contribute to range condition criteria, and be an indicator of range trend. It is in fact a North American range plant, and a particularly important and valuable one at that.

Equally, no important social purpose, save that of history, is served by continuing to label crested wheatgrass an exotic --a word that imputes a degree of instability and an ephemeral nature arising from its foreign origin. By any standard, crested wheatgrass has disproved those allegations by its performance over the past 90 years. Hence it is high time that crested wheatgrass receives its citizenship papers and takes its place among the most productive, useful range plants in North America.

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SECTION X.

Field Trip.

Crested Wheatgrass on the Ground.

Chairman, Kendall L. Johnson

Beefing Up the Winter Range.

The J. C. Smith Ranch:

A Demonstration of a Year-Round Grazing System

A. E. (Gene) Gade and Kendall L. Johnson

TO FEED OR NOT TO FEED...

Winters in the Intermountain West are often long and severe, and present real problems to most livestock ranchers. Both operating costs and livestock losses during this period can be very high while incomes are low or non-existent. How to efficiently sustain the herd through this difficult period is one of the central problems of cattle ranching in this region.

In order to maintain their cattle most ranchers rely on production of hay on their own lands in summer and the feeding of this hay in the winter. These practices usually entail irrigation, large expenditures for machines and energy, and much labor in both summer and winter. At present, crop production accounts for up to 65% of total beef production costs. And the costs of water, energy, labor, and machines are likely to increase in the future.

J. C. Smith, a northern Utah rancher, has demonstrated an effective method of dealing with these problems. He has freed himself from much of the high cost of haying and feeding by developing a year-round grazing system for his herd.

The features of Smith's operation which will be emphasized here are:

a. the effective use of two major seasonal grazing units,

b. the efforts to improve and maintain high quality winter forage for cattle, and

c. the resulting success in minimizing the haying and feeding aspects of cattle ranching while remaining economically competitive.

J. C. SMITH

The son of a dairy farmer from Beaver, Utah, J. C. Smith got his start in the beef cattle business with an FHA loan in 1942. In the fall of 1948, he moved to a ranch at Grays Lake, Idaho. He began purchase of the Snowville unit in the mid-1960's.

Smith's philosophy of "let the cows do everything they can for themselves" has led directly to the innovative and successful grazing scheme detailed here. He notes with a twinkle that his style of ranching also gives him time to pursue other activities such as his hobby of collecting Indian artifacts.

Though he is not formally trained in range or animal science, years of astute observation, asking questions and listening to answers, reading and thinking have made him an outstanding manager. He was honored as Utah Rancher of the Year in 1978 by the Utah Section of the Society for Range Management.

THE J. C. SMITH RANCH

During the summer and autumn, J. C. Smith's ranching activities are centered in the Grays Lake area of Idaho (Fig. 1) where he owns 2,000 acres of meadow land and utilizes two small grazing permits. The Grays Lake unit is located in high country (6,400 feet) where the winters are too long, cold and snowy to permit grazing during winter and spring. For nearly twenty years, Smith struggled with the requisite haying and feeding demanded by that beautiful but rigorous environment.

In 1966, Smith began purchasing a second unit to serve as winter range for his cow-calf and yearling operation. This unit is composed of 6,650 acres of private land located about 15 miles west of Snowville, in Box Elder County, Utah.

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[1] This information is also published under the same title as a brochure available from the Cooperative Extension Service, Utah State University, Logan.

The Snowville Unit

The Snowville unit is ideal for winter range. Elevation ranges from 4,800 to 5,200 feet. Annual precipitation is 9-11 inches, with snow cover averaging 6-8 inches. The winters on the unit are cold, but not usually beyond the tolerances of cattle. About 5,862 acres of this land are classified by the Soil Conservation Service as a semi-desert loam site, characterized by low, rolling hills, gullies and benches, with slopes of less than 10%. The remaining 844 acres of the unit are classified as a mixed semi-desert and alkali mixed range site. The terrain there is nearly flat with fine textured soils.

Range Improvements

J. C. Smith has made a very successful effort to improve forage production for cattle on his winter rangelands.

About half of the total acreage has been seeded to a nearly pure stand of crested wheatgrass (Fig. 2). Most of this portion was marginal cropland which had been in the soil bank before Smith bought it. Now it has a carrying capacity of about 0.45 animal unit months per acre in most years.

Another fourth of the land supports native vegetation, but has been improved as grazing land by a combination of railing, chaining, and spraying to control sagebrush (Fig. 3). Some seeding of native species has been done. Bluebunch wheatgrass is by far the most abundant forage species on these sites. Bottlebrush squirreltail is locally abundant. The carrying capacity on this improved native vegetation averages 0.30 aums per acre.

The remaining land, slightly over one fourth of the total, has been left unimproved, with native vegetation intact. This land is about half sagebrush semi-desert (mainly basin big sagebrush, bluebunch wheatgrass, and Indian ricegrass) and half alkali flats where Great Basin wildrye, greasewood, and shadscale are the plant dominants. The grazing capacity on this land varies from 0.35 aums to 0.47 aums per acre, depending upon the vegetative mix.

Smith has purposely left these areas unimproved and interspersed with the improved types because they provide shelter and food during severe storms, and good calving grounds. In addition, some of the native forb and shrub species provide protein, vitamins, and minerals which are not as available in the dormant grasses.

THE MANAGEMENT PROGRAM

Contingency plans for weather conditions prohibiting grazing are a part of Smith's management program. Prior to each grazing season at Snowville, emergency hay is stored on the unit or firm arrangements are made to purchase hay. Initially Smith stored hay, but found it so little used that he changed his contingency plan to as-needed purchases.

All of Smith's cows and first calf heifers are trucked from the Idaho summer range to spend the period between December 1 and June 1 on the Snowville unit. The area is divided into fenced sub-units with salt and water located to control livestock distribution (Figs. 4 and 5).

These cattle are grazed all winter except under exceptionally severe weather conditions. By 1983, had had been fed only twice in the preceding 16 years, in the severe winters of 1974 and 1982. The total amount of time the livestock were fed amounted to only 12 weeks during the entire period.[2] Occasionally, alfalfa pellets containing chlorotetracycline are used to combat anaplasmosis problems if ticks are abundant. Also, a salt-mineral mix containing phosphorus and magnesium oxide is used to control grass tetany where cattle are grazing young, growing grasses.

Only the weaner calves (about 280 head) and 13 Angus bulls are fed hay during the winter. This limited feeding is contracted out to ranches near Snowville from November 20 to April 10. The animals are then turned out on leased pasture until June 10.

All of the native range types are rated as being in excellent condition. One of the probable reasons

[2] In the severe winter of 1983, Smith chose to sell the herd rather than feed. He was not forced to do so, but simply chose another management alternative under the contingency plan.

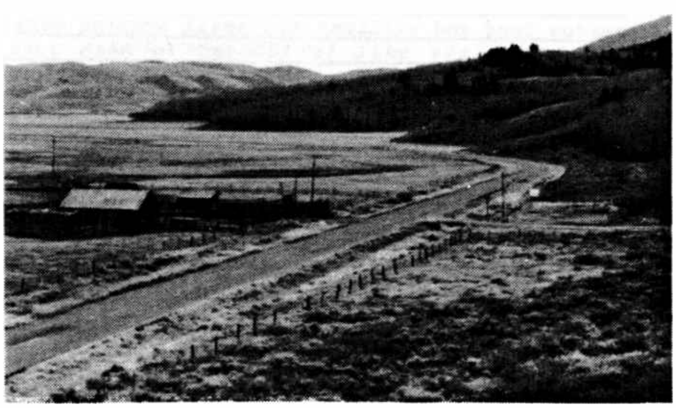

Figure 1.--Grays Lake summer range.

Figure 2.--Snowville range, crested wheatgrass.

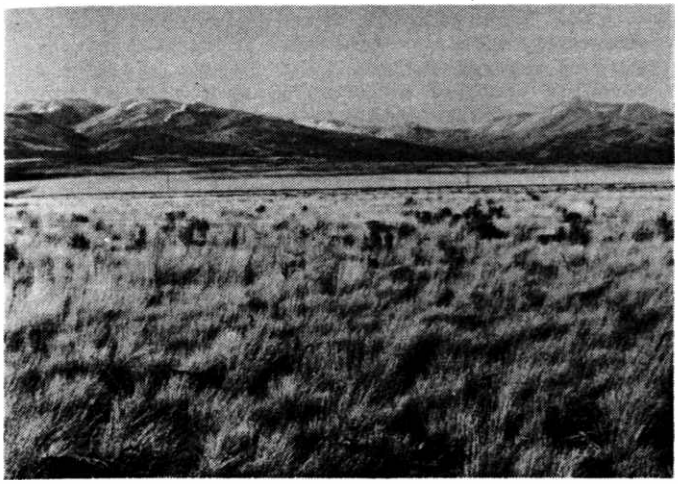

Figure 3.--Snowville, improved native range.

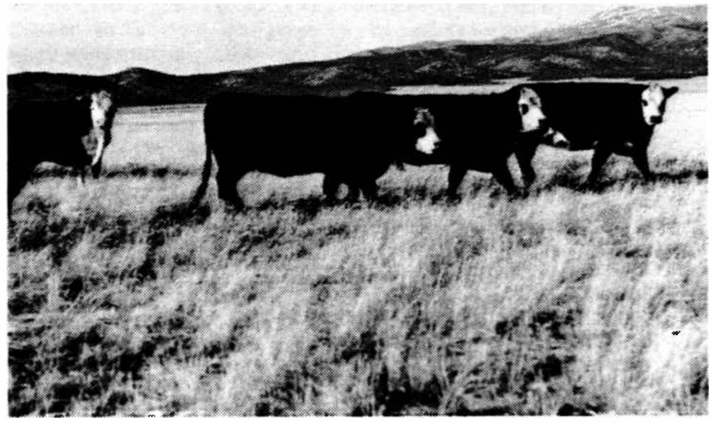

Figure 4.--Arrival at winter range.

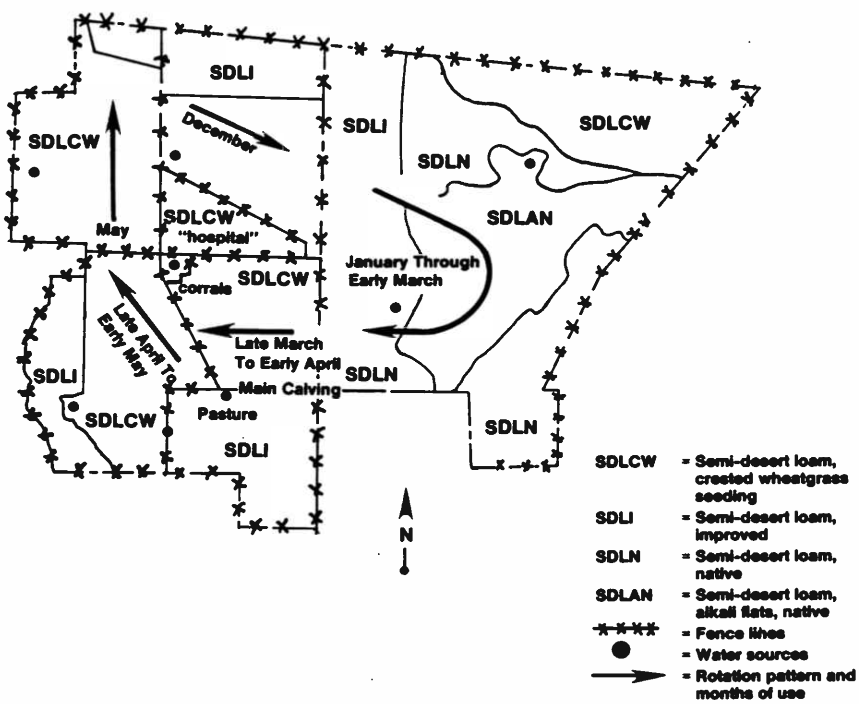

Figure 5.--Land types, fencing, water developments and use patterns.

for this is that rancher Smith is very conservative in his stocking rates. For example, he stocks about 340 animal units on land which normally produces enough forage to support about 440 animals. His rationale is that variability in precipitation and forage production on a semi-desert site can be extreme in different years. Such stocking rates should provide stability (in terms of economics and numbers of animals) during drought years and still insure the health and vigor of the valuable forage plants (Fig. 6).

The milder winter at Snowville and the dispersal of animals on dry range also means that there is much better sanitation than existed in the spring snows at Grays Lake. Smith now adjusts his breeding program so that calves will be born after March 15, which allows them to avoid most spring storms. In short, this means less medication, less work and fewer losses.

THE PAYOFF

The management practices outlined here eventually translate into some impressive statistics and, of course, dollars. For example, Smith's ranch normally produces about a 93% calf crop at weaning time. His calves usually weigh 450-500 pounds when they are weaned, about November 15. Non-replacement heifers weigh an average of 780 pounds when they are sold in August. Yearling steers are marketed in October when they average over 900 pounds. Smith normally sells about 140 steers and 80 heifers each year. About 60 mature cows are culled and marketed either at calving or weaning time.

J. C. Smith has developed a year-round grazing system which clearly works for him. It accomplishes the goal of minimizing haying and feeding and the high costs and labor that attend them. It is a system which could and probably should be adapted to work for other ranchers in the Intermountain region. In it may lie much of the means to profitable livestock ranching in the late years of the twentieth century.

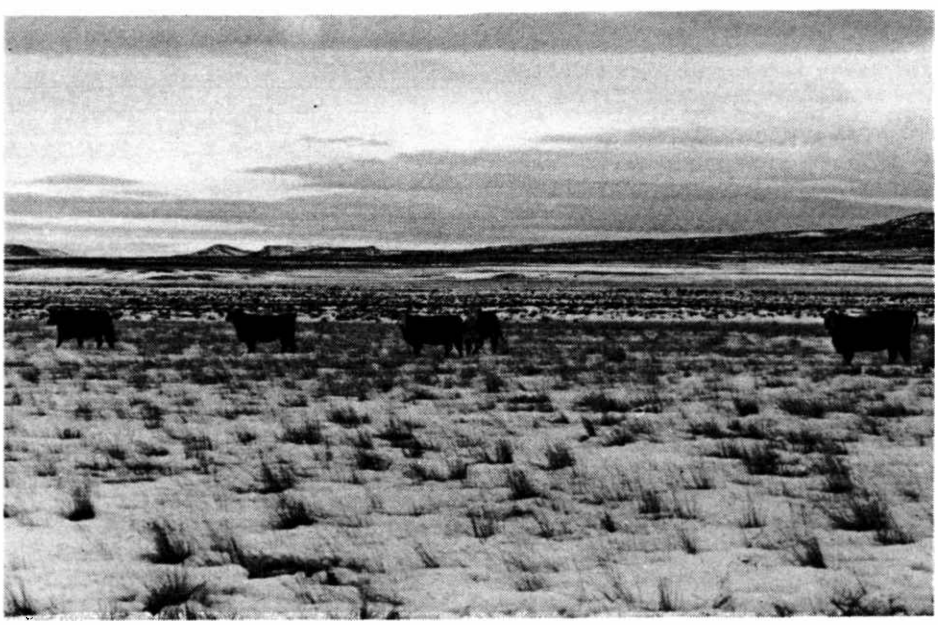

Figure 6.--Snowville, a successful winter grazing scheme.

In: Johnson, K. L. (ed.). 1986. Crested wheatgrass: its values, problems and myths; symposium proceedings. Utah State Univ., Logan.

Capstone Address.

Crested Wheatgrass:

Its Values, Problems and Myths; Where Now?

Thadis W. Box

INTRODUCTION

After three days of many fine papers examining crested wheatgrass from every angle, it would seem there is little left to say on the subject. However, my task is to summarize the papers and speculate on what may be done with crested wheatgrass in the future. It is a task I approach with pleasure.

Crested wheatgrass is, according to this conference, a truly great grass. Its performance record is indeed impressive. First introduced some 85 years ago from Russia and planted in a few nurseries, it spent some thirty years in relative obscurity waiting for its big chance to help reestablish productivity of the deteriorated western ranges. Between 1930 and World War II it was seeded throughout the northern Great Plains, the prairie provinces of Canada, and the Intermountain region in the United States. Today it continues to be one of the major grasses used for the rehabilitation of deteriorated lands in the drier portions of western North America.

Biologically, crested wheatgrass is an aristocrat. It is the type species of its genus and retains the name Agropyron while its cousins in the Triticeae are forced to use such foreign-sounding names as Pseudoroegneria and Pascopyrum and other tongue-twisters.

Crested wheatgrass has three ploidy levels. The commonly-known varieties of Fairway, Parkway, and Ruff are diploids. Nordan, Summit, P-27, and Ephraim are tetraploids. Both the diploid and tetraploid level offer opportunities for breeding improved plants. Some gain in forage production can be expected through conventional breeding within the diploid or tetraploid level. However, Asay in this conference predicted that even better cultivars may be developed by putting all ploidy levels in a common gene pool and developing breeds from that pool. One new cultivar, Hycrest, combines many of the desirable characteristics of Agropyron cristatum and Agropyron desertorum.

SOME VALUES

Crested wheatgrass has many outstanding characteristics. It is a good seeder. The seeds are easily harvested and easy to establish in other locations provided a good seed bed is prepared. It is tolerant of a wide range of environmental conditions, especially those toward the drier end of the spectrum. Seeds are generally viable and produce vigorous young plants that can grow into maturity. Once established, crested wheatgrass competes well with other plant species and is especially good in retarding the reinvasion of brush. It produces high yields and responds well to nitrogen fertilization. It is of high nutritive value for livestock and provides needed green forage at critical periods of the year for large ungulates. It covers drastically disturbed sites such as roadsides and stripmines. Most of all, as Lee Sharp observed in this conference, it is a forgiving grass. It allows range managers to make mistakes and responds even after abusive treatment.

SOME PROBLEMS

The attributes discussed at this conference form a long list of impressive credentials for crested wheatgrass as a seeded forage grass. Most of the negative attributes discussed here are in areas other than that of producing livestock forage. There appears to be a botanical bigotry, a term coined by Ed DePuit, in the reaction of many people to crested wheatgrass. Because it is an exotic, it is excluded from seed mixes and seedings in many areas where it could perform effectively. There are some adverse reactions because it has been closely aligned with the livestock industry. In many cases it has been oversold as a wonder grass for nearly all range uses and problems.

A major concern is loss of wildlife habitat in areas seeded to crested wheatgrass. While it has been shown in Urness's paper that crested wheatgrass is indeed a valuable forage species for big game

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animals during the early growing season, little has been said about other forms of wildlife. McAdoo, Evans, and Longland reported that conversion of shrub land to crested wheatgrass diminished the number of bird species and changed the avian species composition. Although no other papers were presented on wildlife, it can generally be assumed that conversion to a single-species stand will reduce diversity and eliminate many of the species of small mammals, reptiles, and birds that live in shrub lands. Some of these adverse effects may be mitigated, as for instance, by proper design of seedings to increase edge effect, but no papers were presented to show ways that wildlife habitat could be maintained.

Many people find stands of wheatgrass aesthetically displeasing. Comments have been made that the drill rows in many seeded stands persist after 50 years. There is fear that the Iowa farm has moved to the West. This is symptomatic of a major societal concern today: reduction in diversity. As resource managers, I believe we have grossly underestimated the public concern for diversity. We have been lulled into thinking that the quest for diversity was simply an attack on monocultures or a battle to save a few endangered species. It is not. It is part of a much deeper desire for diversity of thought, of communities, and of gene pools.

KNOWNS AND UNKNOWNS

It is clear to me that the positive attributes presented at this congress far outweigh the negative, showing that crested wheatgrass is indeed a valuable forage grass. But the status of crested wheatgrass is as dependent on what has not been said as on what has been said in this symposium. There are many questions that are still unanswered. For instance, where does crested wheatgrass fit in the synecology of rangelands? It has been pointed out several times that crested wheatgrass crowds out invaders once it is established. The species has been seeded throughout the Great Plains and Intermountain West, yet it does not invade stands of native grass but remains only where it was seeded. The ecophysiological data being gathered by Caldwell and Richards go a long way toward explaining why crested wheatgrass is resistant to grazing and why it is such an excellent competitor once it is seeded. However, there are not equivalent studies in synecology that would help to explain why it is not acting like a native.

Nothing was said here on how the effects of crested wheatgrass can be measured and evaluated for management. Where does it fit into range condition and trend studies? In many cases we have done a better job of making an economic evaluation of crested wheatgrass than we have a biological evaluation. Can this grass be fitted into successional schemes and evaluated like a native? Or must it continue to be treated as an introduced, seeded species, with separate rules for its behavior from those of a native wheatgrass?

Little was said at this conference about where crested wheatgrass fits into livestock management schemes. A. K. Majors discussed the need for flexibility in management and documented a number of successful schemes in the Pacific Northwest. In the end Majors maintained that crested wheatgrass would succeed only through flexible management schemes that depended on the experience of the manager. Peter Markgraf and Tom Bunch advocated heavy, "shock grazing" of crested wheatgrass to "clean up the mess." Their experience showed that crested wheatgrass could withstand extremely heavy grazing. Jack Pierce outlined the use of the species on his ranch in southern Idaho, where it fills a valuable niche in the year-round grazing scheme. Even with these fine papers, much was left unsaid about the value of crested wheatgrass in livestock management operations. Is it only a spring-fall species? Where does it fit in winter grazing? How will it respond to yearlong grazing?

There is a current fad for short-duration high-intensity grazing management schemes. Little is known about how crested wheatgrass will respond to such management systems. Can mixed species-stands, including crested wheatgrass, be maintained under intensive management?

Not enough was said about the place of crested wheatgrass in multiple-use management. DePuit's paper on its use in rehabilitating drastically disturbed lands covered a role other than forage; but here, too, the discussion was about a specific use, and not in a multiple-use context.

WHERE NOW?

What does the future hold for crested wheatgrass? This conference has reaffirmed that crested wheatgrass is a proven performer in the field of providing livestock forage. It is especially good for spring-fall ranges and areas where rainfall is limited. Any land manager, on either private or public range, can proceed with confidence to design seedings and management schemes based on what is known about crested wheatgrass.

Crested wheatgrass is a good grass. Much can be done without any new research. However, we must be careful to stick to what is known and recognize the limitations of the species. Don Dwyer, in his introductory paper at this conference, stated that the Russians have made three major contributions to the western United States--vodka, ballet, and crested wheatgrass. A trip to any bar will substantiate that vodka is making its own dubious contribution to the western way of life.

Although ballet may not be as widely accepted, Mikhail Baryshnikov is one of the greatest athletes in America today. His body is in almost perfect physical condition. His every move shows grace and power. We do not expect, however, for him to turn his athletic prowess to winning the decathlon. I do not think he could play point guard on the Philadelphia Seventy-sixers. He would probably make a poor tight end for the Dallas Cowboys. He might not even be able to fill the role long reserved for foreigners and kick a field goal for any NFL team. He is a great athlete, but he does his best when he sticks to his chosen field, ballet. Similarly, we cannot expect crested wheatgrass to play in a game for which it is not suited. We have a proven seeded forage species. We must use it appropriately.

There is much new knowledge that needs to be developed. Crested wheatgrass is an almost ideal species for at least two areas of research. The first is the development of ecological theories and principles for management. The work by Richards and Caldwell is a good example of using the proven grass species to develop ecological theory from the internal workings of the plant. Unfortunately, similar synecological data are not available. There is a need for a number of specific studies to determine where crested wheatgrass fits in successional schemes. Why has this species not become naturalized or become a pest? Crested wheatgrass could be a test species for determining a number of theories on introduction and adaptation of an exotic species to a native successional sere. It could be used to test many hypotheses in synecology and diversity theory.

Crested wheatgrass is also an ideal species for research on special grazing systems. The fact that it is a very forgiving species would allow researchers to test radical grazing management theories that might otherwise destroy valuable stands. Not only would more information on management of the species be developed, but some generalizations and principles should emerge from studies of special management schemes on crested wheatgrass.

In conclusion, crested wheatgrass is a good but limited species. Its positive attributes far outweigh its drawbacks. It does some things extremely well, but like Baryshnikov, it is a specialist. It is not the wonder grass that will save the western ranges from deterioration. What it can do is fill a niche as a badly needed producer of reseeded range forage.

There are many areas where present knowledge can be implemented immediately. My recommendation would be to continue to use crested wheatgrass as a seeded forage species. There are many areas of new research that could add to our understanding. These range from basic biological questions to those of perception and acceptance. This conference has done a good job of summarizing what is known about crested wheatgrass. It is up to us now to apply that knowledge and to fill in the gaps with new studies.

In: Johnson, K. L. (ed.). 1986. Crested wheatgrass: its values, problems and myths; symposium proceedings. Utah State Univ., Logan.

Crested Wheatgrass Symposium

October 3-7, 1983

Utah State University
Logan, Utah

Issued in furtherance of Cooperative Extension work, Acts of May 8 and June 30, 1914, in cooperation with the U. S. Department of Agriculture. R. Paul Larsen, Vice President and Director, Cooperative Extension Service, Utah State University.

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