Seed and Seedling Relations of Crested Wheatgrass: A Review

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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.

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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

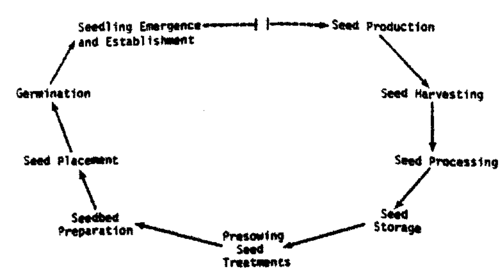

Figure 1.--Factors influencing germination, emergence, and establishment.

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

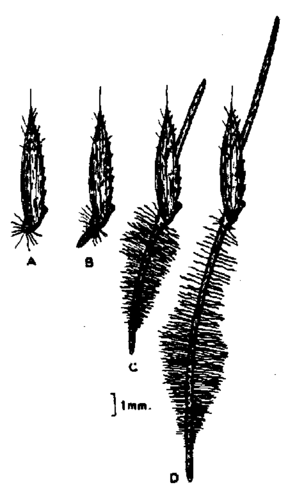

Figure 2.--Morphological changes taking place during the development of a crested wheatgrass seedling: A-24 to 48 hours, B-48 to 72 hours, C-72 to 96 hours, and D-96 to 120 hours (From: Love and Hanson 1932).

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

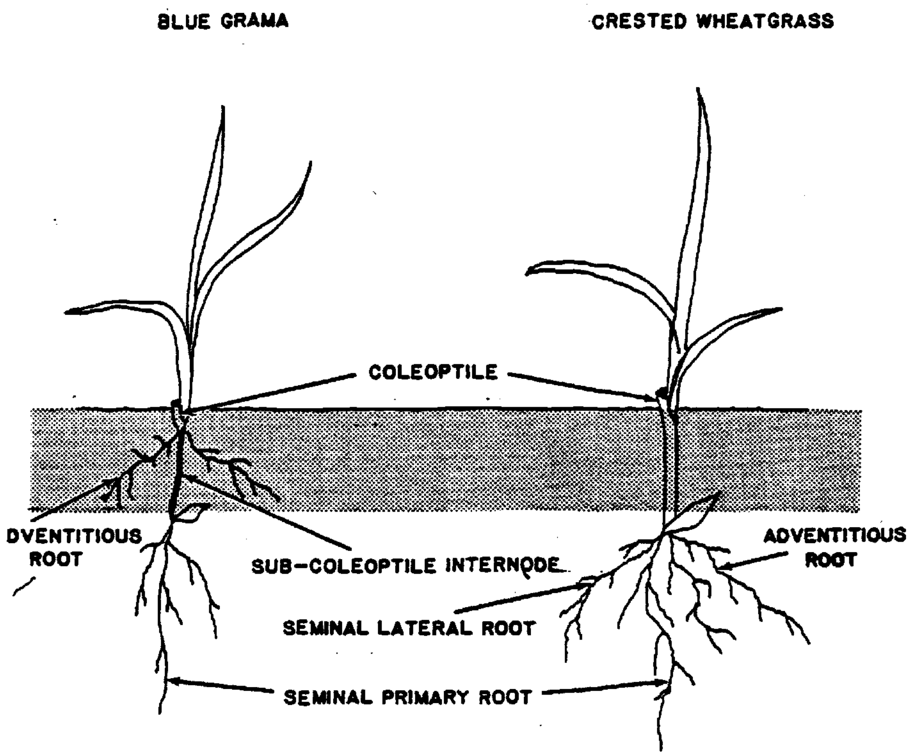

Figure 3.--Two types of grass seedlings. The blue grama type of seedling has an elongated sub-coleoptile internode and a short coleoptile. The crested wheatgrass type of seedling lacks the elongated sub-coleoptile internode but has a long coleoptile. (Adapted from: Hyder 1974).

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

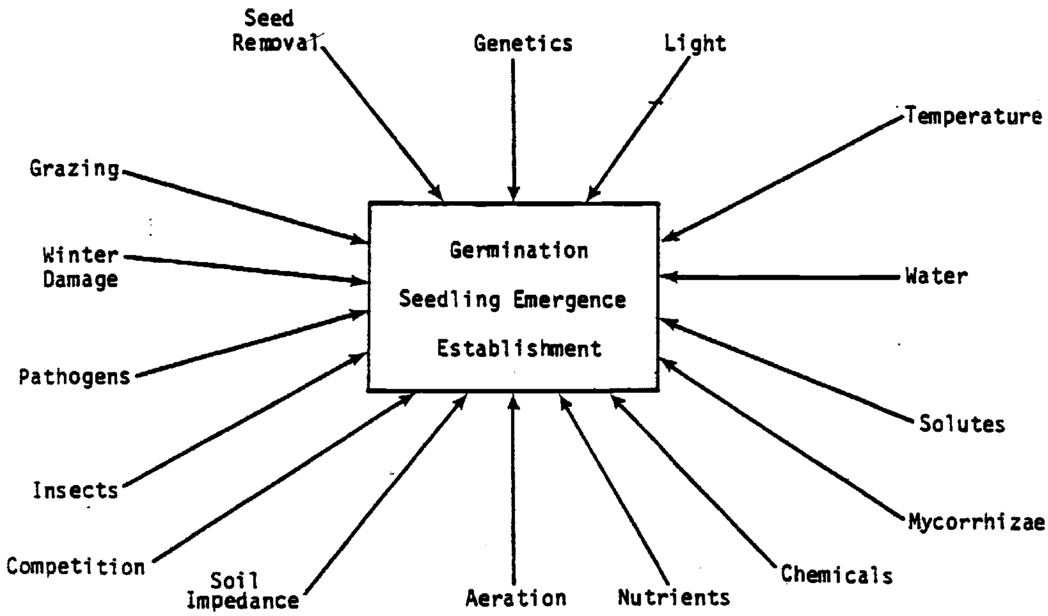

Figure 4.--Environmental factors known to affect germination, emergence, and establishment.

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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