Ecophysiology of Crested Wheatgrass: A Comparative Study with Bluebunch Wheatgrass

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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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