

Coping with Herbivory: Photosynthetic Capacity and Resource Allocation in Two Semiarid *Agropyron* bunchgrasses*

M.M. Caldwell¹, J.H. Richards¹, D.A. Johnson², R.S. Nowak¹, and R.S. Dzurec¹

¹ Department of Range Science and the Ecology Center, UMC 52, Utah State University, Logan, Utah 84322

² USDA-SEA-AR, Crops Research Laboratory, Utah State University UMC 63, Logan, Utah 84322, USA

Summary. *Agropyron desertorum*, a grazing-tolerant bunchgrass introduced to the western U.S. from Eurasia, and *Agropyron spicatum*, a grazing-sensitive bunchgrass native to North America, were examined in the field for photosynthetic capacity, growth, resource allocation, and tiller dynamics. These observations allowed identification of physiological characteristics that may contribute to grazing tolerance in semiarid environments. A uniform matrix of sagebrush, *Artemisia tridentata*, provided an ecologically relevant competitive environment for both bunchgrass species. Physiological activity, growth, and allocation were also followed during recovery from a severe defoliation treatment and were correlated with tiller dynamics.

Potential photosynthetic carbon uptake of both species was dominated by stems and leaf sheaths during June, when maximum uptake rates occurred. For both species, water use efficiency of stems and sheaths was similar to that of leaf blades, but nitrogen investment per photosynthetic surface area was less than in blades. In addition, soluble carbohydrates in stems and sheaths of both species constituted the major labile carbon pools in control plants. Contrary to current theory, these findings suggest that culms from which leaf blades have been removed should be of considerable value to defoliated bunchgrasses, and in the case of partial defoliation could provide important supplies of organic nutrients for regrowth. These interpretations, based on total pool sizes, differ markedly from previous interpretations based on carbohydrate concentrations alone, which suggested that crowns contain large carbohydrate reserves. In this study, crowns of both species contained a minor component of the total plant carbohydrate pool.

Following defoliation, *A. desertorum* plants rapidly reestablished a canopy with 3 to 5 times the photosynthetic surface of *A. spicatum* plants. This difference was primarily due to the greater number of quickly growing new tillers produced following defoliation. *Agropyron spicatum* produced few new tillers following defoliation despite adequate moisture, and carbohydrate pools that were equivalent to those in *A. desertorum*.

Leaf blades of regrowing tillers had higher photosynthetic capacity than blades on unclipped plants of both species, but the relative increase, considered on a unit mass, area, or nitrogen basis, was greater for *A. desertorum* than for *A. spicatum*. *Agropyron desertorum* also had lower investment of nitrogen and biomass per unit area of photosynthetic tissues, more tillers and leaves per bunch, and shorter lived stems, all of which can contribute to greater tolerance of partial defoliation.

Greater flexibility of resource allocation following defoliation was demonstrated by *A. desertorum* for both nitrogen and carbohydrates. Relatively more allocation to the shoot system and curtailed root growth in *A. desertorum* resulted in more rapid approach to the preclipping balance between the root and shoot systems, whereas root growth in *A. spicatum* continued unabated following defoliation. Nitrogen required for regrowth in both species was apparently supplied by uptake rather than reserve depletion. Carbohydrate pools in the shoot system of both species remained very low following severe defoliation and were approximately equivalent to carbon fixed in one day by photosynthesis of the whole canopy.

Introduction

Chemical, mechanical and phenological mechanisms by which plants avoid or minimize herbivory have received considerable attention in the last decade (e.g. Janzen 1969; Rosenthal 1977; Cates and Orians 1975; Janzen et al. 1976; Stiles 1977). Much less work has been directed towards an understanding of how plants tolerate heavy herbivore pressure.

Plants of different life form often differ in tolerance to defoliation. Plant growth form influences the capacity to reestablish foliage following defoliation, such as by the protection or redundancy of apical meristems, or possession of active basal intercalary meristems (Dahl and Hyder 1977). Life forms that are tolerant of herbivory also possess characteristics such as higher photosynthetic rates, reduced foliage longevity, a low proportion of reproductive shoots, and faster rates of leaf replacement (Branson 1953; Archer and Tieszen 1980).

Striking differences in tolerance of herbivory by species of the same growth form and similar phenological characteristics seem less explicable. Therefore, we undertook the comparative study of two *Agropyron* bunchgrasses *A. spicatum* (Pursh) Scribn. and Smith and *A. desertorum* (Fisch. ex Link) Schult. which differ markedly in their tolerance of grazing. *Agropyron spicatum* is an important component of the Great Basin Desert of North America; however, when subjected to heavy spring-season grazing it cannot compete effectively in this community. Extensive livestock grazing in the Great Basin Desert has generally been credited with the greatly reduced presence of *A. spicatum* and other grasses that are relatively intolerant of herbivory, such as *Poa secunda* and *Festuca idahoensis* (Young 1943; Christensen 1963; Daubenmire 1940, 1975; Laycock 1967). Between Pleistocene extinctions of many large herbivores some 10,000 years ago

Offprint requests to: M. Caldwell

* Dedicated to Drs. Michael Evenari and Konrad Springer

and the relatively recent arrival of domestic livestock in the Intermountain West, large herbivores were not a significant component of the Great Basin fauna (Cronquist 1978).

The crested wheatgrasses, which include *A. desertorum*, were introduced into North America from Eurasia at the turn of the century (Dillman 1946). Because of their popularity among stockmen, the crested wheatgrasses have been established on approximately four million hectares of the North American West (Rogler, unpublished). The ability of these wheatgrasses to establish and compete in semiarid habitats, to better tolerate grazing during the spring season and to provide an important forage resource are now well recognized characteristics. Presumably, the past and continuing history of large herbivore pressure on these wheatgrasses in the steppe environments of Eurasia (Kowalski 1967; Vereshchagin 1967; Frenzel 1968; Hoffmann 1974) has led to the selection for characteristics which confer greater grazing tolerance.

Although *A. spicatum* and *A. desertorum* exhibit differences in grazing tolerance, they are remarkably similar in many traits. Both species are upright bunchgrasses that exhibit culmed growth during much of the growing season; both have a reasonably high proportion of reproductive shoots and a similar phenological progression; and both are most sensitive to grazing during the period of maximum vegetative growth because subsequent regrowth of foliage is usually greatly constrained by moisture limitation in early summer (Stoddart 1946; Blaisdell and Pechanec 1949; Hyder 1972, 1974; Hyder and Sneva 1963; Cook et al. 1958; McIlvanie 1942).

Since the growth form and phenological timing of these plants are so similar, differences in grazing tolerance may be explained by quantitative differences in physiological characteristics of these two species. Investment of carbon and nitrogen in foliage susceptible to removal by the grazing animal, photosynthetic rates and water use efficiency of foliage, rate of replacement of photosynthetic tissues following defoliation – often with tissues that are more photosynthetically active, amount of soluble carbon and nitrogen reserves, degree of flexibility in allocation of plant resources in the event of severe defoliation, and degree of flexibility in provision of meristematic tissues for regrowth of foliage are some of the characteristics investigated in this study. This paper addresses aspects of the photosynthetic potential of these species, their growth and photosynthetic response following severe defoliation, and their general pattern of resource allocation during a year of particularly abundant precipitation.

In addition to physiological recovery from herbivory, plants in the field must at the same time continue to compete for resources with neighboring vegetation, some of which may not be subject to the burden of defoliation. Mueggler (1972) vividly demonstrated that even *A. spicatum* could tolerate extreme defoliation if competing vegetation was removed or substantially reduced. Thus, the present study was conducted in a competitive field environment.

Study Area

This research was conducted 4 km northeast of Logan, Utah (41° 45'N, 111° 48'W, 1,460 m a.s.l.) on a site formerly occupied by *Agropyron spicatum* and *Artemisia tridentata*. This area is also characteristic of Intermountain rangelands where *Agropyron desertorum* has been established. A matrix of about 7,000 regularly distributed transplants was established two years before this study. In addition to the two species of *Agropyron*, *Artemisia tridentata* Nutt. ssp. *tridentata* was established in the matrix so that each individual bunchgrass was surrounded by *Artemisia*

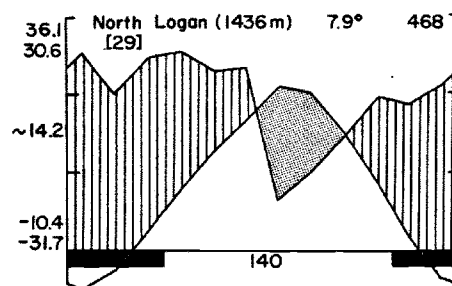


Fig. 1. Climate diagram compiled from weather stations within 2 km of the study site using the format of Walter and Lieth (1960). The abscissa represents the 12 months of the year beginning in January. The blackened bar along the abscissa indicates months of the year when the daily minimum is below 0° C. The number below the center of the abscissa indicates the mean duration of the freeze-free period in days. One division on the ordinate represents either 10° C or 20 mm precipitation. Numbers to the left of the ordinate beginning at the top represent the highest temperature recorded at this site, the mean daily maximum temperature of the warmest month, mean daily temperature variation, mean daily minimum temperature of the coldest month, and the lowest temperature recorded at this site. At the top of the diagram the site elevation, mean annual temperature, and mean annual precipitation are indicated from left to right and the number of years of observations for this compilation is given in brackets

plants to form a uniform competitive environment. *Artemisia tridentata* was used since it is a major competitor with *Agropyron spicatum* in the Great Basin and is subject to much less grazing pressure (Laycock 1967). *Artemisia tridentata* is also a species with which *Agropyron desertorum* must compete in many of the Intermountain rangelands where it has been established (Hull and Klomp 1974). *Agropyron spicatum* and *Artemisia tridentata* were transplanted from adjacent, ecologically similar areas where both species still occur and *Agropyron desertorum* was transplanted from a pasture in central Utah which had been established in 1953.

Soils are rocky Mollisols (Typic Haploxerolls) which have been formed on alluvial fan material (Southard et al. 1978). Salient features of the climate are given in Fig. 1. The precipitation for the year of this study from October, 1979 to September, 1980 was 682 mm, substantially above the 468 mm average.

Methods

Net photosynthesis and transpiration of individual leaf blades, leaf sheaths, stems and inflorescences were measured in the field on intact plants with a carbon dioxide and water vapor exchange porometer (Bingham and Coyne 1977). Carbon dioxide and water vapor exchange of entire bunchgrass plants in the field were measured with a modified Siemens Co. gas exchange chamber (Koch et al. 1971). Modifications included an enlarged chamber lid, which accommodated an entire bunchgrass, chamber walls which penetrated the upper 2 cm of the soil surface, and positive pressure (4-cm water column) which was maintained to minimize gas exchange with the soil surface (Leafe 1972). Water vapor concentrations were measured with thin-film capacitance sensors (Vaisala Co.) and flow rates were determined with a pneumotachometer (Hans Rudolph Co.) and a pressure transducer (Validyne Co.). Photosynthetically active radiation was measured as quantum flux between 400 and 700 nm (Li-Cor Co.), leaf temperatures with fine-wire thermocouples, and projected area of plant parts with a leaf area meter (Li-Cor Co.). Whole-plant gas exchange measurements were conducted with the large cuvette programmed to track ambient environmental conditions. Gas exchange measurements of individual plant parts were conducted between 21 and 27° C, which is within the mid- and late-season temperature optimum for net photo-

synthesis of both bunchgrass species, and at light saturation for photosynthesis.

Plant xylem pressure potentials were determined with a pressure bomb (Waring and Cleary 1967). Plant parts were enclosed in small polyethylene bags prior to their excision and during the pressure potential determination in order to minimize tissue water loss (Turner and Long 1980). Soil moisture content was determined with a neutron soil moisture probe (Campbell Pacific Nuclear, Inc.).

Inclined point quadrats (Warren Wilson 1960) were used to non-destructively determine canopy geometry and leaf blade and projected stem and leaf sheath areas of bunchgrasses in the field. Projected areas of cylindrical plant parts were corrected to surface area of one half of the cylinder. A series of destructive harvests at approximately 3-week intervals was also conducted to determine biomass of plant components. Sampled plants were randomly selected from a population of individuals of median size class. Plants were meticulously separated into apparently live or dead fractions for each plant part. The root system was assessed by extraction of a 12-l soil monolith directly beneath the crown of the plants, and by soil cores from an enlarged soil volume included in a 60-cm diameter cylinder of 80-cm depth. Roots in subsamples of the soil monolith and in the soil cores were removed by washing and wet sieving (No. 45 with 0.35 mm pores). The roots were stained (0.25% Congo red for 15 min) to more effectively separate intact roots from organic debris (Ward et al. 1978). Following oven-drying both weight and then ash-free weight, following incineration at 500° C, were determined for the roots.

Subsamples of all plant part materials were lyophilized and ground. Nitrogen concentrations of tissues were determined by standard Kjeldahl analysis. Tissues were also analyzed for total nonstructural carbohydrates which are considered the carbon that can be stored and subsequently mobilized as an energy source in the plants. Sugars were extracted with boiling water, and the concentration of the filtrate determined using the phenol-sulfuric acid method of Dubois et al. (1956) with glucose as a standard. Starch in the residue was determined using the enzyme digestion technique of Haissig and Dickson (1979) except that the enzyme used was an amyloglucosidase (Sigma Chemical Co.) and glucose was measured by the phenol-sulfuric acid method.

As a severe defoliation treatment, both species were clipped at approximately 5-cm height when in the four to five-leaf stage. There was no appreciable culm elongation at this time (April 30). This first clipping resulted in removal of 80% of the photosynthetic tissue that was present at that time. The same individuals were clipped again at the same height two weeks later (May 13). This second clipping resulted in a removal of 90% of the leaf material that had regrown since the first clipping.

To follow tiller demography, four tillers (two in the center and two in the periphery of individual plants) were marked on six bunches of each species within both control and defoliated treatments. These four populations of 24 tillers and their daughter tillers were followed throughout the season.

Results

Winter and early spring precipitation had recharged the upper 1.5 m of soil profile to a water content of 30% by volume and spring and early summer precipitation maintained a favorable moisture status. Predawn xylem pressure potential measurements (Fig. 2) indicated little change in soil moisture stress until late June. Thus, this year provided the opportunity to assess potential photosynthetic activity, response following severe defoliation, and growth and resource allocation under quite favorable moisture conditions in the field.

Photosynthetic Capacity, Water Use Efficiency, and Canopy Reestablishment

Potential contribution of different plant parts to photosynthetic carbon gain is shown for the two species at five times during the season (Fig. 3). Light-saturated photosynthetic rates of different plant parts were multiplied by the biomass components of

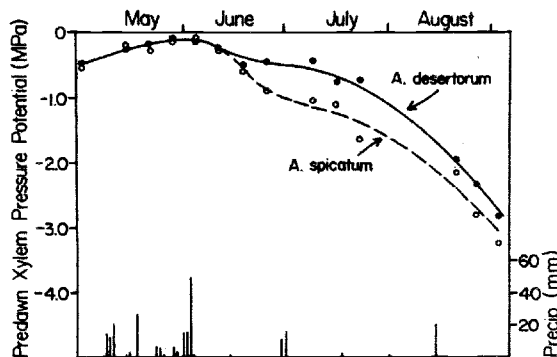


Fig. 2. Predawn xylem pressure potential measurements of the two bunchgrass species during 1980. Individual precipitation events are indicated by the vertical bars. Each point is the mean of 4 samples

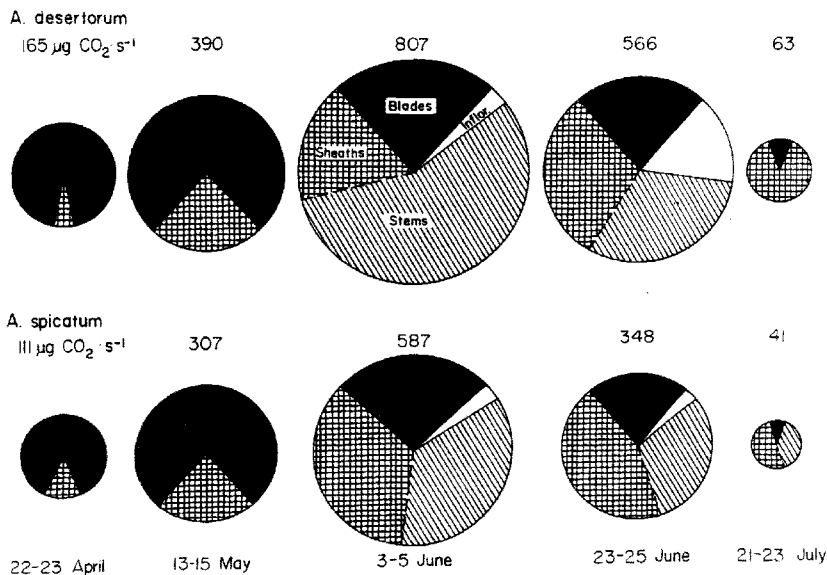


Fig. 3. Potential photosynthetic contribution of different plant parts for *A. desertorum* and *A. spicatum*. These values were derived from the product of light-saturated photosynthetic rates at the optimum temperature for photosynthesis (21–23° C) (300 to 330 ppm CO₂ concentration) and biomass of different aboveground plant components. The numbers indicate potential photosynthesis of entire bunchgrasses and are proportional to the area of the circles. The pie segments indicate fractional contribution of different plant parts to potential carbon gain

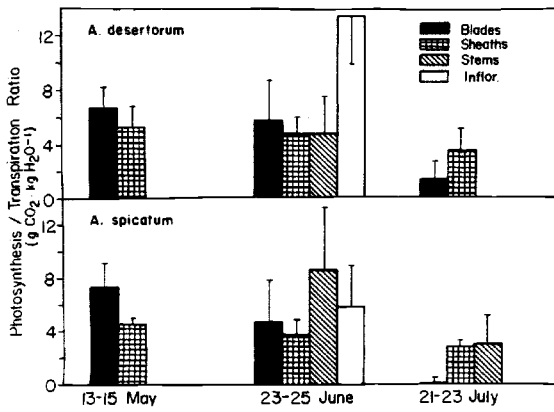


Fig. 4. Photosynthesis/transpiration ratios for different plant parts for *A. desertorum* and *A. spicatum* at three different times during the year. These ratios were determined at: light saturation for photosynthesis, tissue temperatures of 21 to 23° C, CO₂ concentrations of 300–330 ppm and 2.5 to 2.7 kPa vapor pressure difference between plant parts and the atmosphere. Vertical bars indicate standard deviations. Sample size average was 8 and ranged from 3 to 21

unclipped plants to estimate the potential photosynthetic contribution. Blades refer to leaf blades only, stems to segments of stems not covered by leaf sheaths, and sheaths are leaf sheaths and the segments of stem enclosed by the sheaths. The dramatic increase in the contribution of stems and sheath-covered stems during the period of maximum photosynthesis in early June was similar for both species. Only in the spring period did leaf blades constitute the primary organs of potential photosynthetic contribution. The greater total potential photosynthesis of *A. desertorum* reflected primarily a greater biomass of photosynthetic

organs, especially stems, rather than higher photosynthetic rates. In late July, photosynthetic capacity had declined considerably for both species. Photosynthesis/transpiration ratios of different plant parts did not differ significantly, nor were there significant differences between the two species at most times (Fig. 4). Water-use efficiency declined in the summer. For *A. spicatum*, leaf blades showed a greater decline by July than stems or sheaths.

Investment of biomass and nitrogen in photosynthetic tissues for the two species is portrayed in Fig. 5. Leaf blades of *A. desertorum* were consistently thinner than those of *A. spicatum*. The area/weight ratios for stems and sheaths of *A. desertorum* were also consistently greater than *A. spicatum* but the magnitude of difference between the species was not as great as for leaf blades. Nitrogen concentrations of photosynthetic tissues on a unit mass basis were about the same for both species during much of the growing season. Nitrogen concentrations in the spring were quite high, especially for *A. desertorum*. Nevertheless, *A. spicatum* invested more biomass and nitrogen per unit of photosynthetic surface area for both leaf blades and stems and sheaths.

Leaf blades regrowing following the defoliation treatments exhibited higher photosynthetic rates than foliage on control plants at the same time of year for both species. However, the relative difference in photosynthetic rates between regrowing and control leaf blades was greater for *A. desertorum* than *A. spicatum*, especially during the period of most active photosynthesis in May and June (Fig. 6). The greater photosynthetic capacity of regrown leaf blades could be due partly to greater photosynthetic capacity of younger foliage. These regrowing leaf blades had higher nitrogen concentrations, which is often associated with greater photosynthetic capacity (Bolton and Brown 1980). For example, early June samples of regrowing foliage of both species had nitrogen concentrations as great as samples collected

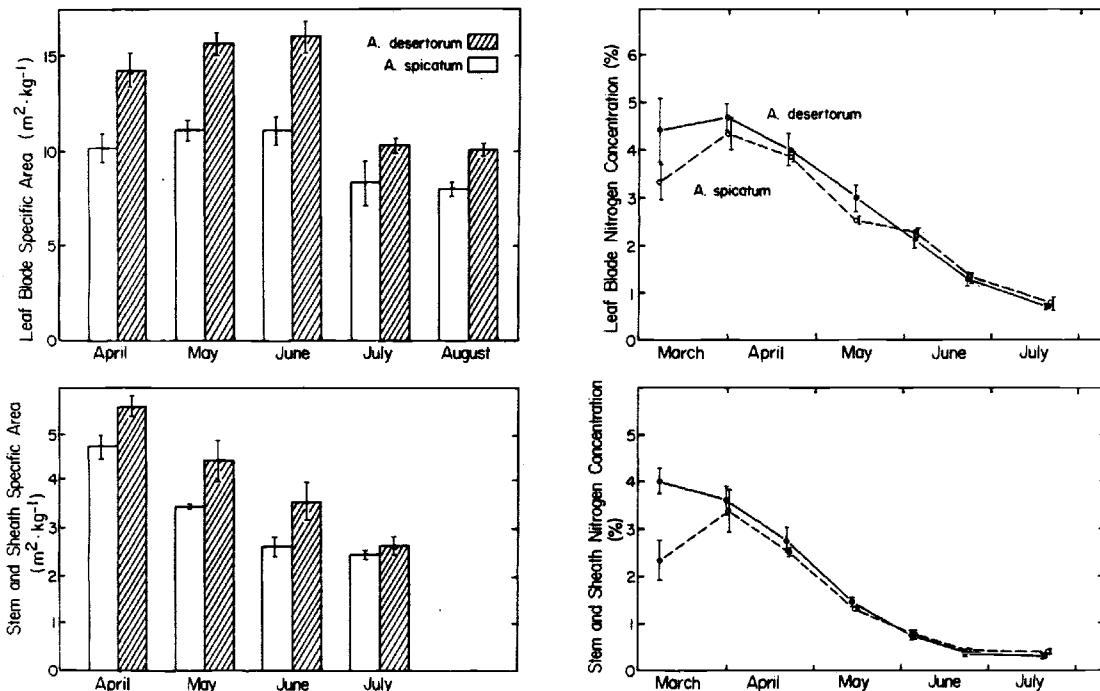


Fig. 5. Surface area/dry weight ratios for leaf blades and stems and sheaths of *A. spicatum* and *A. desertorum* at different times during the year. Leaf blades were those in the upper part of the canopy. Sample size, *N*, ranged from 7 to 38 with the exception of samples in mid-July where *N*=3. Nitrogen concentrations per unit mass for the two species are also presented. These are based on the average tissue nitrogen concentration from three entire plants harvested at different times of the year. Vertical bars indicate standard error of the mean

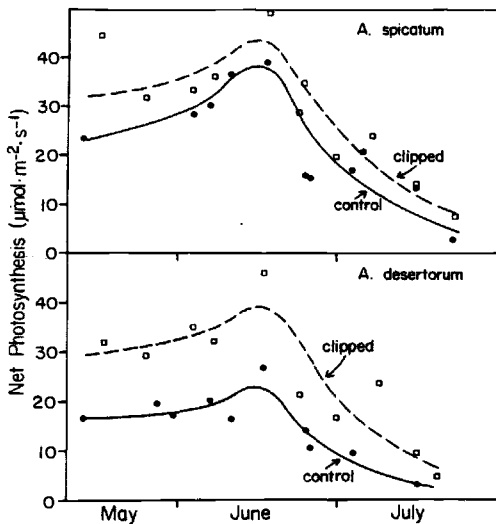


Fig. 6. Photosynthetic capacity of control and regrowth *A. spicatum* and *A. desertorum* leaf blades determined at light saturation, temperature optimum for photosynthesis (21–27° C) and cuvette CO₂ concentration of 300–330 ppm. Each point is the mean of 1 to 6 measurements

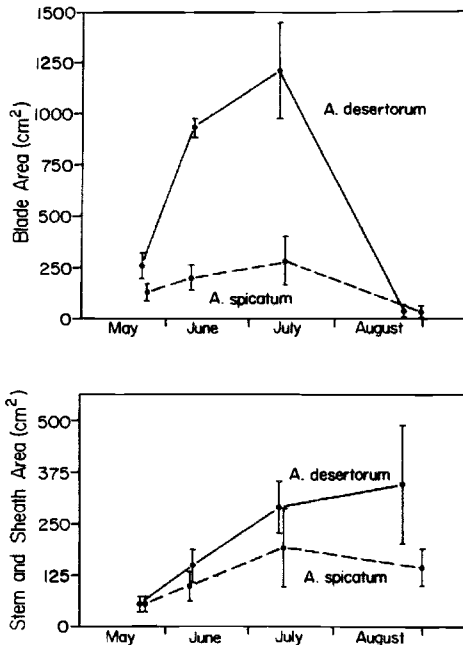


Fig. 7. Development of photosynthetic tissue area, leaf blades and stems and sheaths, for plants following severe defoliation. Three individual bunches of both species were repeatedly sampled nondestructively using inclined point quadrats. Vertical bars indicate standard error of the mean

one month earlier from control plants (Fig. 5). Though photosynthetic capacity of *A. spicatum* was greater when expressed on a leaf blade area basis, as shown in Fig. 6, when leaf area/weight ratios are considered, photosynthetic capacity of leaf blades on control *A. desertorum* and *A. spicatum* plants was about the same when expressed on a leaf mass basis. For regrown leaf blades, however, photosynthetic capacity of *A. desertorum* on a leaf blade mass basis was 20 to 90% greater than *A. spicatum* in May and early June.

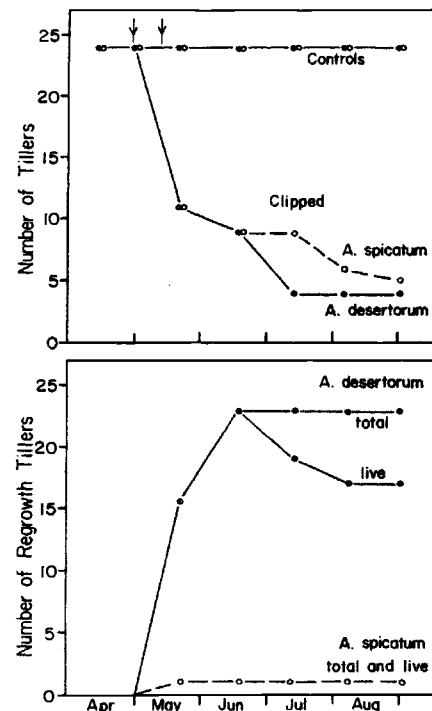


Fig. 8. Survivorship of marked populations of tillers on control and severely defoliated *A. desertorum* and *A. spicatum* plants. The times of clipping are shown by arrows. Regrowth tillers are tillers produced by the marked population of parent tillers following defoliation. Sample size for each population was 24

In addition to proportionately greater photosynthetic capacity of regrowing leaf blades following severe defoliation, replacement of photosynthetic tissues, especially leaf blades, was more rapid for *A. desertorum* (Fig. 7). This difference resulted from the marked difference in production of regrowth tillers following defoliation (Fig. 8). Both species eventually reestablished canopies, and total green surface area continued to increase until mid-July (Fig. 9), when leaf blade senescence (Fig. 7) began to reduce the total photosynthetic surface.

Survivorship of tillers on defoliated plants of both species was similar, as was the timing of mortality (Fig. 8). Mortality occurred immediately following clipping, or after the development of substantial water stress in late June and July (Fig. 9). In both species new tillers were not produced by tillers which survived clipping. Tillers that died produced from zero to two new tillers in *A. desertorum*. Only one new tiller was produced by the 24 marked *A. spicatum* tillers.

Daily photosynthetic carbon gain of these previously-defoliated plants is portrayed in Fig. 9. Individual bunches of the two species were alternately sampled for one to two day periods with the gas exchange chamber programmed to track ambient environmental conditions. The total green blade and sheath and stem areas (one side) of the plants sampled in this gas exchange series are also given. The surface area of photosynthetic tissues of *A. desertorum* was substantially greater than that of *A. spicatum*, because of greater allocation of biomass to foliage (Fig. 10), coupled with more surface area per mass (Fig. 5). Although average photosynthetic rates per unit area of photosynthetic tissues in the bunches were greater in *A. spicatum*, daily carbon gain of entire *A. desertorum* bunchgrasses was usually larger. The greater variability in carbon gain from day to day of *A. desertorum* was probably due to the greater depression of photosyn-

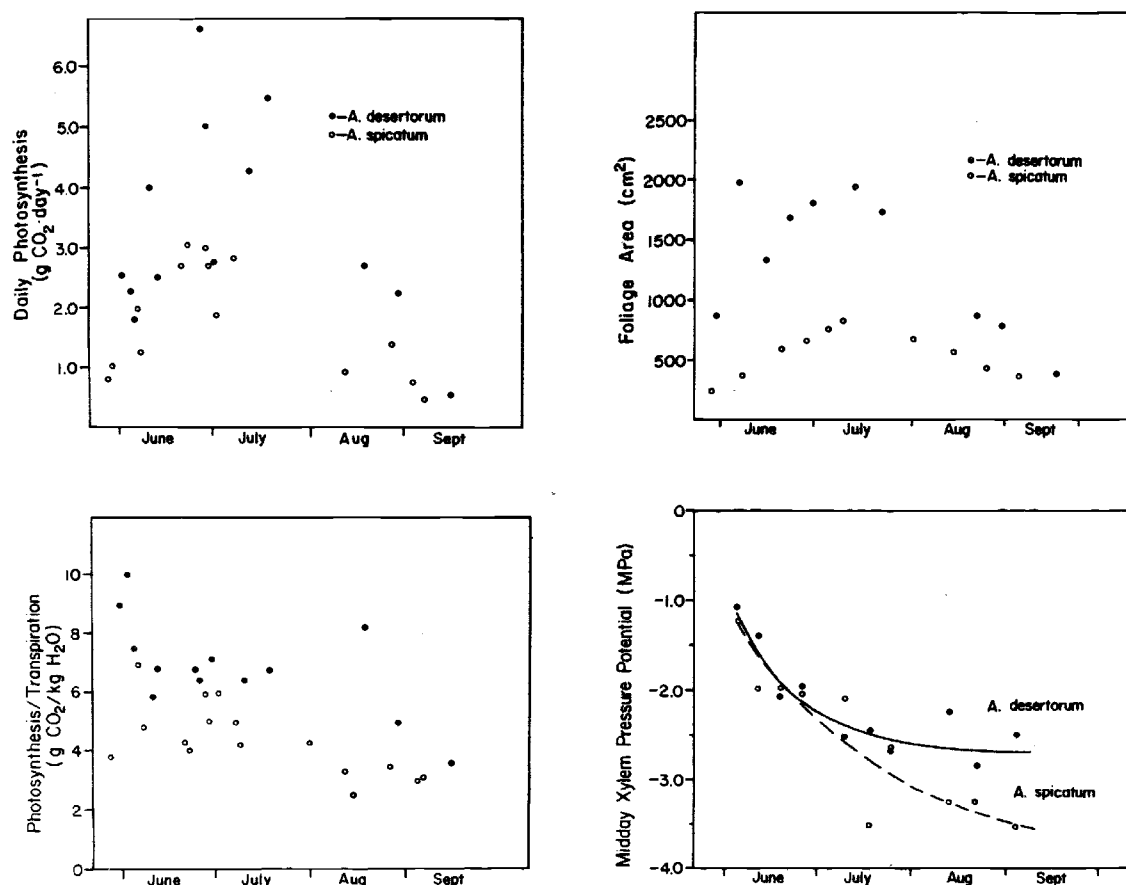


Fig. 9. Daily net photosynthesis and photosynthesis/transpiration ratios of individual bunchgrass plants of *A. desertorum* and *A. spicatum* sampled between late May and September. Total daily photosynthesis is represented for the period of the day when net photosynthetic rates were positive. Total green surface area (one side) of the sampled bunchgrasses and midday xylem pressure potentials are also represented. All data pertain to foliage regrown after the plants were subjected to defoliation treatments in the spring

thesis on cloudy days since the canopy of this species was more compact and dense.

Water-use efficiency, expressed as photosynthesis/transpiration ratios, was also usually greater for *A. desertorum* throughout the season (Fig. 9). Plant water stress of the two species, as indicated by midday xylem pressure potentials, was comparable except in late summer when *A. spicatum* was more highly stressed. Although winter, spring, and early summer moisture conditions had been very favorable, depletion of soil moisture as indicated by predawn xylem pressure potentials (Fig. 2) and high atmospheric demands led to the development of substantial midday water stress in both species by early July. Correspondingly, both photosynthesis and water-use efficiency declined.

Growth and Resource Allocation

Biomass of different plant parts for control and defoliated plants is shown for both species in Fig. 10. The biomass of roots is represented as ash-free weight while biomass for other plant parts is expressed on a dry weight basis. Ash-free weight was employed for the root system because it was not possible to completely remove all the soil mineral material from the diffuse root system. Also, roots at depths greater than 80 cm could not be sampled due to the rocky nature of the soil profile. Thus, root system biomass presented here is a conservative estimate.

During most of the season, total biomass of control plants as well as of defoliated plants, was essentially the same for the two species. *Agropyron desertorum*, however, had greater aboveground biomass, and often less belowground biomass than control *A. spicatum* plants. For defoliated plants, more biomass was allocated to aboveground parts for *A. desertorum*. As was reported by Hyder and Sneva (1963), *A. desertorum* initiated foliage growth earlier in the season than *A. spicatum*. Earlier canopy development of *A. desertorum* was also quite apparent in our studies and associated with this was an earlier increase in root biomass accrual. Nevertheless, the major shoot and root system growth for both species occurred in late April and May. The timing and rate of total plant growth was remarkably similar for the two species. Following severe defoliation, root and shoot mass of both species continued to increase, but the rate of root biomass increase was greater than that of aboveground plant parts. Eventually, root system mass for *A. desertorum* declined, but biomass of the *A. spicatum* root system continued to increase even during the midsummer.

Total nitrogen in different plant components except for inflorescences is represented in Fig. 11 for the two species. Total nitrogen pools in *A. desertorum* were somewhat greater than those in *A. spicatum*. However, the most significant difference was in the early season which was associated with the earlier growth initiation of *A. desertorum*. In *A. desertorum*, a greater proportion of the nitrogen was allocated to photosynthetic tis-

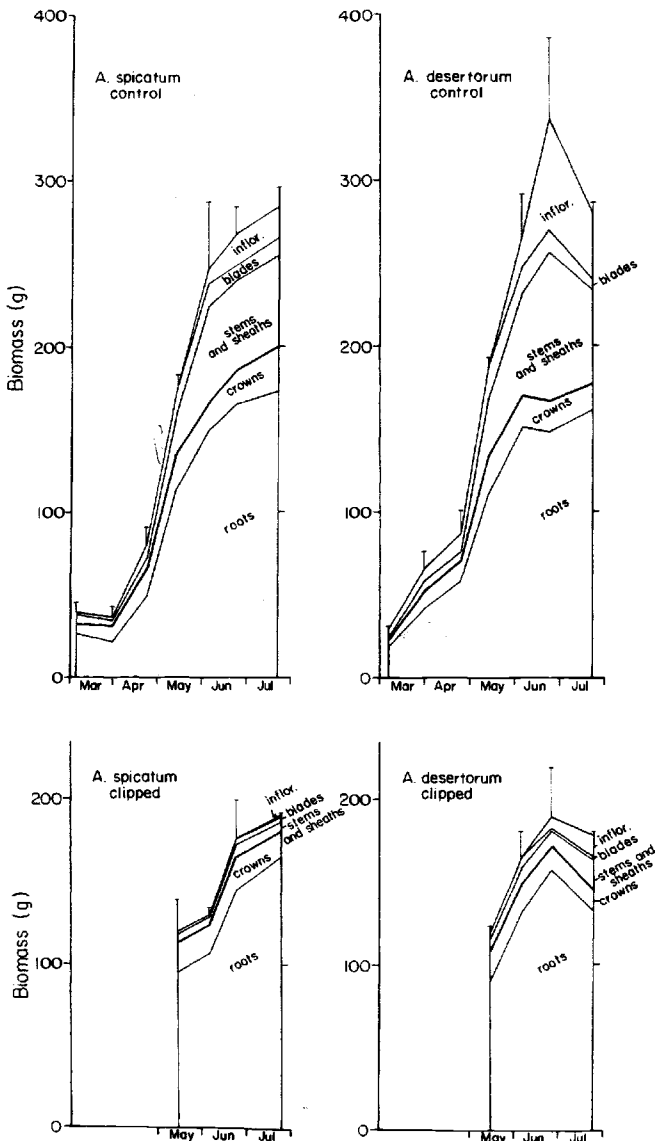


Fig. 10. Biomass of plant components of *A. spicatum* and *A. desertorum* from March through July. These are based on destructive harvests of three individual bunches randomly selected from a population of medium-sized individuals. Diffuse root mass is reported as ash-free weight and all other plant components as dry weight. Plants subjected to the severe defoliation treatments are also represented. Vertical bars indicate standard error of the mean of total bunch biomasses.

sues in the early season and following defoliation, than in *A. spicatum*.

Nonstructural carbohydrate reserves of plants are commonly represented as concentrations of sugars and starches in various plant parts (White 1973). However, biomass components of grasses can change much more rapidly than carbohydrate concentrations and, thus, the total soluble carbon pools may be poorly represented by carbohydrate concentrations. Total soluble carbon pools of the two bunchgrass species are presented in Fig. 12 with the exception of soluble carbon in inflorescences. Though *A. desertorum* exhibited somewhat higher carbohydrate pools in the early season the major increase of soluble carbon in both species took place through late April and during the month of May. For control plants, the total quantity of soluble

carbon was greater in *A. spicatum* than in *A. desertorum*. A major soluble carbon pool for both species was in the stems and sheaths. Replenishment of carbon pools following severe defoliation was very limited in both species relative to the increases shown by control plants.

Discussion

Many morphological features of caespitose grasses contribute to their grazing sensitivity as compared to rhizomatous grasses (Branson 1953; Hyder 1972). Caespitose grasses generally have been associated with geographical areas that have not had a history of strong selective pressure from large herbivores (Mark 1969; Klotzli 1977; Baker 1978; Mack and Thompson, unpublished manuscript). Recent introductions of livestock have led to greatly reduced presence of these species (e.g. Laycock 1967).

The bunchgrasses of the arid and semiarid steppes of Central Asia constitute a notable exception (Mack and Thompson, unpublished manuscript). In addition to the crested wheatgrasses, several other caespitose grasses are prominent components of these communities and, yet, this region has a long history of grazing pressure from many species of Artiodactyla and a few Proboscidea and Perissodactyla (Vereshchagin 1967; Kurtén 1968). Although large herbivore pressure in the native environments of *A. desertorum* has apparently resulted in the selection of characteristics which contribute to evolution of grazing tolerance, this species is still a distinctly caespitose bunchgrass possessing many of the characteristics traditionally associated with grazing sensitivity. Once culm elongation is initiated (in late April for 1980), the apical meristem and culm leaves are elevated and susceptible to removal by the grazing animal. Without apical meristems or protected intercalary meristems, replacement of the photosynthetic surface in caespitose grasses following grazing is dependent on activation of axillary buds and production of new tillers, a comparatively slow process (Hyder 1972). *Agropyron desertorum* also has a relatively high proportion of reproductive culms, another characteristic which has been associated with grazing sensitivity (Branson 1953). In all of these characteristics *A. desertorum* is essentially identical to the grazing-sensitive *A. spicatum* (Hyder and Sneva 1963). The seasonal timing and rate of growth of these two species is also remarkably similar (Fig. 10).

The differences in herbivory tolerance of these two species must result from quantitative differences in a suite of characteristics rather than distinct qualitative differences in traits or growth patterns. This discussion addresses a few of the attributes that may contribute to differences in grazing tolerance between *A. desertorum* and *A. spicatum*.

Investment in Foliage

Species that invest less biomass and fewer nutrients in individual foliage elements, but produce more foliage surface, may better cope with partial defoliation, which is the most frequent type of grazing event (Norton and Johnson, unpublished manuscript), than species that invest heavily in a few long-lived foliage elements. Foliage element, as used in this discussion refers to any photosynthetically active plant part, including leaf blades, sheaths, stems and inflorescences. *Agropyron desertorum* produced leaves, and to a lesser degree stems and sheaths, with a greater surface area per unit biomass than *A. spicatum* (Fig. 5). Except in early March, *A. desertorum* also invested less nitrogen per surface area of foliage, although the nitrogen concentrations by weight were about the same for the two species.

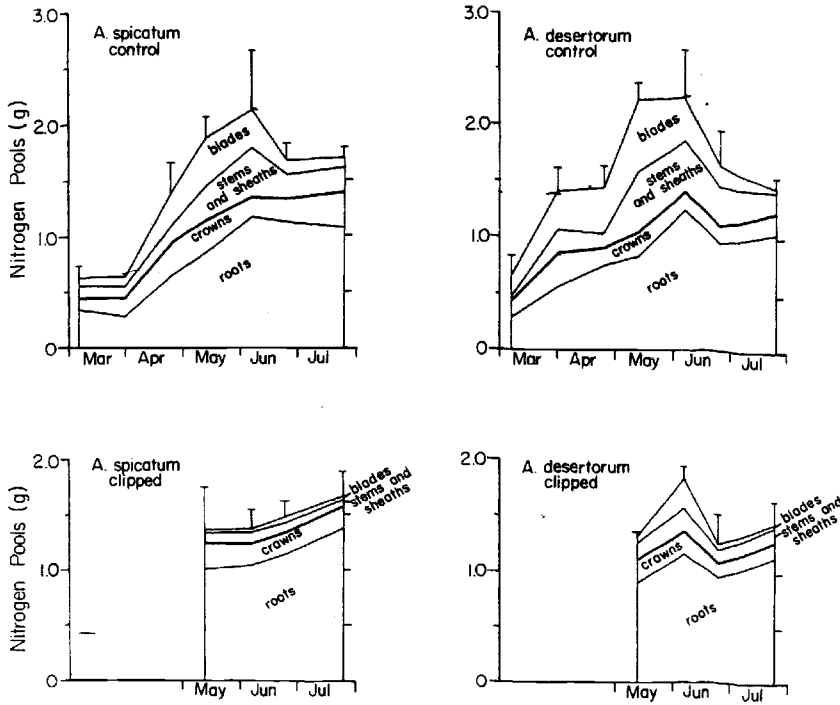


Fig. 11. Total nitrogen in different plant parts of *A. spicatum* and *A. desertorum*. These are from analyses of the same plants represented in Fig. 10. Vertical bars indicate standard error of the mean of total bunch nitrogen

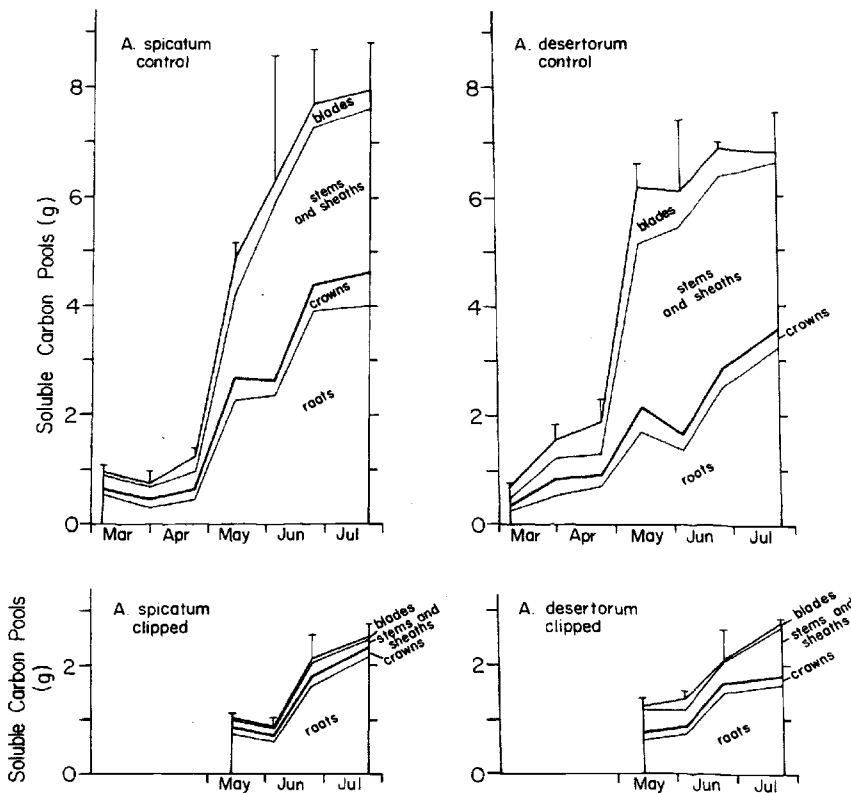


Fig. 12. Total quantity of nonstructural carbohydrates in different plant parts of *A. spicatum* and *A. desertorum*. These are from analyses of the same plants represented in Figs. 10 and 11. Vertical bars indicate standard error of the mean of total bunch soluble carbon

Consistent with expectations, *A. desertorum* produced a greater number of foliage elements. For control plants of the same total biomass (Fig. 10), the average number of tillers per bunch was 187 for *A. desertorum* and only 113 for *A. spicatum* during most of the growing season. Since the number of leaves per tiller was approximately the same for the two species, *A. desertorum* also had more leaves per bunch than *A. spicatum*. While

longevity of leaf blades was about the same for two species, stems stayed green longer in *A. spicatum*. *Agropyron desertorum* produced a greater number of foliage elements than *A. spicatum* plants of the same size, invested less nitrogen and biomass in each element, and longevity of the photosynthetically important stems was less. Thus, partial defoliation would be of less consequence for *A. desertorum* than *A. spicatum*.

In the absence of defoliation, the very compact, dense canopies of *A. desertorum* resulted in considerable self-shading of the foliage. While specific aspects of canopy microenvironments are not being addressed in this paper, measurements of photosynthetically active radiation in the canopy have revealed that much of the foliage in the lower part of the canopy for *A. desertorum* was light limited. In contrast, the less dense canopy of *A. spicatum* and the tendency for a more splayed arrangement of tillers results in much better display of the foliage to sunlight. Thus, *A. desertorum* may actually produce more foliage than can be efficiently displayed in the canopy. Much of the foliage in the lower part of the canopy may not be sufficiently well illuminated and, in the absence of partial defoliation, may exhibit early senescence.

Photosynthetic Capacity and Reestablishment of Photosynthetic Surfaces

The greater investment of biomass and nutrients in leaf blades and stems and sheaths of *A. spicatum* resulted in greater photosynthetic capacity per unit surface area (Fig. 6). However, when calculated on a unit mass or unit of nitrogen basis, photosynthetic capacity of leaf blades on unclipped plants was about the same for both species. Following severe defoliation, regrown leaf blades of both species exhibited higher photosynthetic rates than control leaf blades. When computed on surface area, mass, or nitrogen bases, the relative increase of photosynthetic capacity for regrowing leaf blades compared to leaf blades of unclipped plants was greater for *A. desertorum* than for *A. spicatum*.

The considerably more rapid regrowth of *A. desertorum* foliage following severe defoliation when compared to *A. spicatum* (Fig. 7) is attributable to several factors. In addition to the high photosynthetic capacity of regrowing *A. desertorum* leaf blades, there was both greater absolute and greater relative allocation of plant biomass to photosynthetic organs rather than to crowns or roots (Fig. 10). Of key importance, however, was the proclivity for new tiller production, which was considerably greater for *A. desertorum* than for *A. spicatum* (Fig. 8). Because shoot apices were nearly all removed by the second defoliation, foliage regrowth was dependent on new tiller formation in both bunchgrass species. The ability of *A. desertorum* to quickly activate axillary buds, mobilize stored reserves and allocate them to maintenance of the new tillers, and produce rapidly growing new tillers compensates to some degree for the lack of active, protected apical and intercalary meristems that confer grazing tolerance in culmless graminoids.

The potential contribution of stems and sheaths for photosynthetic carbon gain of both species is notably large (Fig. 3). The seasonal progression of potential photosynthetic contribution of leaf blades and stems and sheaths was quite similar for the two species. With culm elongation, intercalary meristems of individual culm leaves cease to be active and certain grazing patterns can result in leafless culms which continue to elongate (Cook and Stoddart 1953; Hyder 1972). Such leafless culms have traditionally been portrayed as being of little value to the plant (Dahl and Hyder 1977). However, results from our study document that the photosynthetic potential of these stems and sheaths is considerable. Photosynthesis/transpiration ratios of stems and sheaths are of the same magnitude as those of leaf blades; thus, carbon gain from these organs would not be at the expense of excessive water use when compared to leaf blades.

With respect to nitrogen investment, stems and sheaths yielded a greater potential carbon gain for the plant than leaf blades. In early June when unclipped plants of both species

had the maximum potential whole-bunch photosynthetic capacity (Fig. 3), leaf blades of both species represented a potential contribution of only 25% while stems and sheaths contributed in excess of 70%. Yet, total nitrogen in stems and sheaths was only 30% greater than the total quantity of nitrogen contained in leaf blades (Fig. 11).

A high proportion of reproductive shoots has traditionally been associated with grazing sensitivity (Branson 1953; Hyder 1972). This concept should be reexamined in view of the potential photosynthetic contribution of stems, sheaths, and inflorescences. In 1980, more than 90% of the culms of *A. desertorum* and 75% of the culms of *A. spicatum* were reproductive. Furthermore, a particularly sizable fraction of the shoot biomass was allocated to inflorescences of *A. desertorum* (Fig. 10). While a comparison of the carbon balance of reproductive and vegetative culms has yet to be undertaken, the potential photosynthetic carbon gain of stems, sheaths, and inflorescences of *A. desertorum* suggests that reproductive culms may not be a liability for these grasses, even under the duress of grazing. Additionally, a high proportion of stem tissue, whether supporting vegetative or reproductive culms, may help deter excessive consumption of individual plants by large herbivores (Stoddart et al. 1975; Willms et al. 1980).

In the canopies that were reestablished following defoliation, average photosynthetic rates per unit area of foliage were lower for *A. desertorum* than *A. spicatum* (Fig. 9). This was due in part to the lower photosynthetic capacity of foliage elements of *A. desertorum* when expressed on a foliage surface area basis (Fig. 6), but was also likely the result of greater self-shading in the canopies of *A. desertorum*. Despite this self-shading, the substantially greater foliage surface area of the reestablished canopies of *A. desertorum* resulted in greater photosynthesis and even somewhat greater photosynthesis/transpiration ratios for whole bunches when compared to *A. spicatum* during the summer months (Fig. 9).

Allocation of Resources and Reserves

After removal of plant photosynthetic tissue, regrowth of foliage and continued maintenance of the remainder of the plant depends initially on stored carbon. In grasses, carbohydrates constitute the primary form of carbon reserve and are traditionally considered as stored primarily in crowns and stem bases (White 1973). Hyder and Sneva (1963) reported that carbohydrate concentrations in stem bases of *A. desertorum* increased earlier in the spring and were maintained at higher levels throughout the growing season than in *A. spicatum*. Similar patterns in carbohydrate concentrations were found for the crown plus 1-cm stem base tissues of both species in our study. Concentrations in crowns were 50 to 60% greater for *A. desertorum*. Yet, because *A. spicatum* had a somewhat greater proportion of its biomass in crown tissues, the total quantity of carbohydrates in crowns of whole bunches of the two species was about the same (Fig. 12). Furthermore, soluble carbohydrate pools in the crowns of both species constituted usually less than 15% of the total plant carbon pool, except in early spring when this proportion approached 20%. Thus, examination of total carbohydrate pools rather than carbohydrate concentrations in specific organs rendered a significantly different view of these reserves.

For both species, carbohydrates in stems represented the major carbohydrate pool apart from that of the diffuse root system. Leaf and stem soluble carbon pools were almost completely removed by the severe defoliation imposed in this study. However, if plants are only partially defoliated, stem soluble carbon

may be quite important for recovery. In any case, the two species did not differ to a large degree in the magnitude of soluble carbon pools, seasonal changes or their apportionment among plant organs.

Although carbohydrate concentrations in the diffuse root system of both species were quite low (less than 50 mg/g), the total soluble carbon pools were sizable because of the proportionally large root biomass (Figs. 10, 12). If a plant is defoliated, carbohydrate pools in the diffuse root system could be deployed for root system activity when the supply of photosynthates from the shoot system is curtailed. Even if root growth were greatly slowed following defoliation, however, maintenance respiration of a large root mass would require a significant carbon supply.

Following the severe defoliation treatment, soluble carbon pools of both species were greatly depressed. A majority of the soluble carbon was in the diffuse root systems of both species following defoliation. Soluble carbon pools of the shoot system and crowns, which would be the most likely source of energy for shoot regrowth following an additional defoliation event, remained quite small, despite the reestablished canopies following defoliation (Figs. 7, 10, 12). Total soluble carbon in the shoot system and crowns was equivalent to or less than the photosynthetic carbon gain of entire bunchgrasses for a single day in June or July. Thus, both species apparently had only a small soluble carbon buffer.

Curtailment of root growth has often been observed following defoliation (Crider 1955; Jameson 1963). This constitutes a mechanism for conserving plant resources and aids in reestablishing a balance between root and shoot systems. Following severe defoliation, root biomass accrual in *A. spicatum* continued, perhaps some with abatement immediately following dipping (Fig. 10). In contrast, *A. desertorum* eventually curtailed root growth, thus allocating more resources to reestablishment of photosynthetic surfaces. Although a net decrease in root biomass was not observed for *A. desertorum* until July (Fig. 10), root growth observations indicated a substantial decrease in growth of new roots by early June (Richards, unpublished). This net decrease in root biomass reflected root death which likely lagged behind the curtailment of new root production. In contrast, new root production in severely defoliated *A. spicatum* plants continued at a rate similar to that of control plants (Richards, unpublished).

Plants coping with severe defoliation must compensate for loss of photosynthetic tissues by a combination of stored carbon reserves, rapid replacement of photosynthetic tissues and appropriate allocation of carbon. However, plant mineral nutrient status may also be important for tolerance to herbivory (Chapin 1980). Nitrogen has been chosen as a key nutrient for study because fertilization experiments have shown this element to be a limiting factor for crested wheatgrass productivity even in the absence of defoliation (Sneva and Rittenhouse 1976; James and Jurinak 1978).

Total nitrogen in the two *Agropyron* species was similar except in late March and early April when total plant nitrogen of *A. desertorum* was twice that of *A. spicatum* (Fig. 11). This is associated with the earlier root and total biomass growth and canopy development of *A. desertorum*. At this time, nitrogen pools of leaves and stems were threefold greater than those in *A. spicatum*. In the spring and early summer, nitrogen concentrations of photosynthetic tissues of both species were two to three times greater than in the diffuse root system. Nevertheless, because of the large root system biomass, nitrogen pools in the root system still represented about half of the total plant nitrogen for both species.

Because of the high concentrations of nitrogen in photosynthetic tissues, in excess of a third of the total nitrogen capital of both species was removed in the severe defoliations imposed (Fig. 11). Yet, demands for nitrogen in regrowing foliage were apparently met by absorption from the soil as there was no evidence of a net withdrawal of nitrogen from the crowns or diffuse root system in either species.

Conclusions

Of the several characteristics investigated in this study, the most important attributes of *A. desertorum* that permit better recovery from severe defoliation appear to be the capacity for new tiller formation, the rapid and successful regrowth of these new tillers to prevent depletion of the limited soluble carbon buffer, and flexibility in allocation of plant resources which includes supply to regrowing tillers and curtailment of root system growth. Secondary characteristics include increased photosynthetic capacity of regrowing foliage, which occurs in both species, but to a greater degree in *A. desertorum*. Since *A. desertorum* invests less biomass and nitrogen per surface area of photosynthetic tissues, partial defoliation should be less detrimental to this species. A greater allocation of total plant biomass to photosynthetic tissues, particularly following defoliation, also results in greater carbon gain for whole *A. desertorum* bunches and somewhat greater photosynthesis/transpiration ratios.

Stems and sheaths of both species are the principal photosynthetic surfaces during much of the late spring and summer season and these organs also constitute a major soluble carbon reservoir for these bunchgrasses. Thus, culms lacking leaf blades can hardly be considered disadvantageous for the plant. Crowns of these grasses represent a minor proportion of the total soluble carbon.

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