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# A test of compensatory photosynthesis in the field: implications for herbivory tolerance

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**Summary.** The occurrence of compensatory photosynthesis was examined in the field for all foliage elements on two *Agropyron* bunchgrass species that differ in their evolutionary history of grazing pressure. This is the first reported field study of compensatory photosynthesis in individual foliage elements of graminoids. Compensatory photosynthesis was defined as an increase in the photosynthetic rates of foliage on partially defoliated plants relative to foliage *of the same age* on undefoliated plants. Compensatory photosynthesis did occur in many individual foliage elements during at least part of their ontogeny. For both species, compensatory photosynthesis was related primarily to delayed leaf senescence and increased soluble protein concentrations, but not to an improvement in the water status of clipped plants. Soluble protein concentration increased in all foliage elements. A delay in senescence on clipped plants was documented for the two oldest, fully-expanded leaves that were present when the plants were initially clipped, but the initiation and senescence of all other foliage elements were not affected by the clipping treatments. Photosynthetic water use efficiency and photosynthetic rates per unit soluble protein of foliage on partially defoliated plants were not increased following the clipping treatments. Although *A. desertorum* and *A. spicatum* were exposed to different levels of grazing pressure during their evolutionary history, the phenology, water status, and gas exchange rates of foliage were very similar both for undefoliated as well as partially defoliated plants. Thus, we conclude that compensatory photosynthesis does not appear to be an important ecological component of herbivory tolerance for these species.

## Introduction

An increase in photosynthetic rates of foliage on partially defoliated plants may be a mechanism to partially compensate for herbivory (McNaughton 1979, 1983, Dyer et al. 1982). This enhanced photosynthesis following partial foliage removal may be due to either an increase in the photosynthetic rates of foliage on these plants relative to *similar-aged* foliage on undefoliated plants, which we define as "compensatory photosynthesis", or a change in the age composition of foliage from predominantly older tissue on undefoliated plants to younger regrowing tissue on partially defoliated plants. Following severe defoliation of two *Agropyron* species, Caldwell et al. (1981) found that the younger regrowing foliage on defoliated plants had higher net photosynthetic rates than the relatively older foliage on undefoliated plants. This increase in photosynthesis that accompanies a change in age composition is to be expected because younger foliage usually exhibits greater photosynthetic capability. However, the phenomenon of compensatory photosynthesis is more impressive, especially since photosynthetic rates of leaves that remain after partial defoliation may in some cases be more than twice the rates of leaves of similar age on undefoliated plants (Gifford and Marshall 1973, Hodgkinson et al. 1972, Hodgkinson 1974). Photosynthetic rates of leaves that regrow after partial defoliation can also be greater than photosynthetic rates measured on leaves of the same age on undefoliated plants (Woledge 1977, Heichel and Turner 1983).

Although compensatory photosynthesis after partial defoliation is well documented in many plant species, not all species exhibit this phenomenon (Ryle and Powell 1975). Also, changes in photosynthetic rates after partial defoliation may be influenced by the method of defoliation, leaf age, light conditions, and probably other factors as well. For example, in experiments with *Agropyron smithii*, leaves damaged by simulated insect herbivory exhibited a depression of net photosynthesis (Detling et al. 1979), whereas compensatory photosynthesis occurred in undamaged leaves when 75% of the tillers on a plant were clipped (Detling and Painter 1983). Continuous or severe defoliation can sometimes yield different results than a single, moderate one (Alderfer and Eagles 1976, Hodgkinson 1974), but the severity of defoliation is not always influential (Painter and Detling 1981). Leaf age and the light environment may also influence the degree of change in photosynthetic rates following partial defoliation (Hodgkinson 1974, Woledge 1977). Finally, compensatory photosynthesis in growth chamber and greenhouse studies may be exaggerated when compared to field conditions because of the optimal growing conditions. Because most of the studies cited above were conducted under greenhouse or growth chamber conditions and usually limited to investigations of short-term photosynthetic changes of one or two cohorts of leaves following a single defoliation, the application of these results to plant responses following herbivory in nature is questionable.

The purpose of our experiment was twofold. First, we wanted to determine the magnitude and extent to which

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*Offprint requests to:* Martyn M. Caldwell compensatory photosynthesis occurs in the field on mature plants that were clipped in a manner that simulated the defoliation behavior of cattle in a rangeland pasture. Therefore, the life histories of individual foliage elements were examined, and the photosynthetic rates of all foliage elements were measured during their ontogeny. The second goal was to determine if photosynthetic water use efficiency (photosynthesis/transpiration) or photosynthetic rates per unit soluble protein were altered concurrently with photosynthesis following clipping. For these experiments, we selected two species that are morphologically and phenologically very similar, but likely have had different levels of grazing pressure during their evolutionary history (see Caldwell et al. 1981).

## Materials and methods

Two bunchgrass species, *Agropyron desertorum* (Fisch. ex Link) Schult. and *A. spicatum* (Pursh) Scribn. and Smith[1], were used in our experiment. Mature plants of both bunchgrass species and a shrub, *Artemisia tridentata* ssp. *vaseyana* (Rybd.) Beetle, were transplanted in 1978 in a regular matrix such that the nearest neighbors of each individual bunchgrass plant were four *Artemisia* plants located in orthogonal directions from the bunchgrass plant. The northern Utah, U.S.A., study area is representative of semiarid, North American Great Basin rangelands where *A. spicatum* and *Artemisia tridentata* are native and where *A. desertorum* has been seeded. Further descriptions of the three species and the study site are found in Caldwell et al. (1981).

Individual plants of each bunchgrass species were paired on the basis of aboveground biomass in mid-April, 1981, and one member of each pair was randomly selected for the clipping treatments. Plants were manually clipped on April 16, 1981, and the same plants were clipped two more times at two-week intervals. With each clipping treatment, approximately 50% of the standing crop was removed with a cut that was above the majority of the apical meristems and also parallel to the ground surface. This frequency, intensity, and horizontal method of defoliation simulated the cattle grazing behavior that has been observed to occur on similar-sized *A. desertorum* plants in rangeland pastures (P.A. Johnson, personal communication). In 1982, control (undefoliated) plants from 1981 were paired, and one member of each pair was randomly selected for clipping treatments. The intensity, frequency, and horizontal method of defoliation in 1982 was identical to 1981, but the first clipping treatment in 1982 was delayed until April 27, 1982, because a cold, snowy winter and spring delayed plant growth.

Net photosynthesis and transpiration were determined in the field with a steady-state gas exchange system (Bingham and Coyne 1977). All gas exchange measurements were at saturating light intensity (a photosynthetic photon flux density greater than 1.7 mmol quanta $m^{-2} s^{-1}$), and a cuvette $CO_2$ concentration near 335 $\mu l\, l^{-1}$ (range: 320–365 $\mu l\, l^{-1}$). Leaf temperatures for photosynthetic measurements were between 21 and 24 C, which is within the optimal temperature range of photosynthesis for these two species (Nowak 1984), and the water vapor mole fraction gradient from leaf to air was near 0.027 mol $mol^{-1}$ (range: 0.023–0.030). Net photosynthesis and transpiration were calculated as outlined in von Caemmerer and Farquhar (1981). The photosynthetic rates of all green leaf blades, leaf sheaths, stems, and inflorescences were sampled from April through July, 1981, and in mid-June, 1982. Three or four gas exchange measurements usually could be obtained each week for each foliage element. Photosynthesis and transpiration are expressed on a comparable area basis for the different plant parts: a "one-side" unit of reference for blades, one half the actual surface area for the sheaths and stems, and the projected (one-side) area for inflorescences. The projected area of a plant part that was enclosed by the gas exchange cuvette was determined nondestructively by measuring its image projected on blueprint paper. In addition to the gas exchange data, the developmental stage, length, and canopy position of the individual foliage elements were also recorded.

Plant water potential was estimated by the pressure chamber technique (Waring and Cleary 1967). Predawn xylem pressure potentials were estimated near sunrise on plants that had been covered by buckets to exclude the early sunlight. Recent research with these two species shows that predawn water potential measurements of covered plants are more than those of uncovered plants, but the difference between predawn water potential of covered plants and that of uncovered plants is the same for both species (D.A. Johnson and J.H. Richards, personal communications). Therefore, the term "covered" will be used to indicate predawn water potential measurements of covered plants. Midday values were measured on the same plants shortly after solar noon. Leaves were enclosed in small plastic bags in order to minimize water loss during measurement of xylem pressure potential (Turner and Long 1980). Because the water potential measurements constituted an additional clipping treatment, an individual plant was sampled only once during the growing season.

Specific mass and soluble protein concentration of foliage were obtained from 11 destructive tiller harvests that were spaced approximately 10 days apart from mid-April to mid-July, 1981, and one harvest that occurred in mid-June, 1982. On each harvest date, a total of 6 to 20 tillers, which were randomly selected from both the edge and the center of each tussock, were harvested from one to three plants of each species-treatment group. The developmental stage, length, and canopy position of each green foliage element were recorded, and then the tillers were separated into the individual foliage elements. The projected area of individual foliage elements was measured with a LiCor (Lincoln, NB) leaf area meter. Foliage was either oven-dried (70–80 C) or freeze-dried, and the dry mass of each foliage element was divided by the surface area to calculate specific mass. Soluble proteins of individual foliage elements were extracted and digested to amino acids (Dickson 1979), and the soluble protein concentration was determined with ninhydrin (see Nowak and Caldwell 1984). As with the water potential determinations, no other measurements were taken from plants after they had been destructively harvested.

In mid-April, 1981, 5 tillers on each of 8 plants that had been paired for the clipping treatments were marked

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[1] Two taxonomic revisions of *A. spicatum* have recently been proposed: *Elytrigia spicata* (Pursh) D.R. Dewey (Dewey 1983) and *Pseudoroegneria spicata* (Pursh) Löve (Löve 1980). Although the genomic evidence indicates that this species is not an *Agropyron*, not enough data is available to clearly finalize its phylogeny. Therefore, we will use *A. spicatum* in this paper

with colored wire tags. There were 2 pairs of plants from each species. Three days before the first clipping treatment, the developmental stage, length, and canopy position of each individual leaf were recorded. These measurements, which were repeated at approximately seven-day intervals, provided known cohorts of leaves to cross-reference similar leaves from the photosynthetic and destructive harvest samples.

A three-way analysis of variance (ANOVA) that had species, treatment, and day as the main effects and incorporated all possible two- and three-way interactions was used for most of the statistical analyses. A mixed model analysis was used, where the species and treatment main effects were fixed and the day main effect was random. A separate ANOVA was conducted for each cohort of foliage elements to avoid confounding the results of one foliage element by the results of another, different-aged foliage element. However, if the results from one cohort were identical to another, then the data from these cohorts were combined. For all statistical tests, $P < 0.05$ was considered significant. Data are reported as mean ±1 standard error.

## Results

### Phenology

The physiognomy of reproductive and vegetative (nonreproductive) tillers on control (undefoliated) plants during 1981 are shown in Fig. 1. The 5 dates correspond to when the partially defoliated plants were initially clipped (April 16), when the partially defoliated plants were reclipped a second (April 30) and third (May 14) time, and when the growth of foliage on reproductive (June 22) and vegetative (July 20) tillers was curtailed. Length, developmental stage, and canopy position data from our marked and destructive harvest tillers and foliage angle data from Caldwell et al. (1983) were used to depict these tillers. The developmental stages (inset, Fig. 1) and canopy position of foliage elements on *A. desertorum* plants were nearly identical to those on *A. spicatum* plants. Sheath and stem lengths were also the same for the two species, but the length of leaf blades on *A. spicatum* plants was generally greater than the length of similar leaves on *A. desertorum* plants. The dimensions and phenology of foliage elements in Fig. 1 are averages from control plants of both species.

Although the tillers drawn in Fig. 1 are representative of control plants, some attributes of foliage on clipped plants can also be observed. The clipping, which was parallel to the ground surface, did not uniformly damage a cohort of leaves because the foliage angles varied (e.g., the F-3 leaves on April 16). Also, a particular leaf may have been reclipped during successive clipping treatments (e.g., F-2 leaves on April 16 and 30).

The initiation of new leaves was not affected by the clipping treatments, but the senescence of the 2 oldest, fully-expanded leaves that were present at the time of the first clipping treatment was delayed (inset, Fig. 1). Senescence of these two leaves on partially defoliated *A. desertorum* plants was delayed approximately one month later than the marked leaves on control plants. Senescence of marked F-4 leaves on partially defoliated *A. spicatum* plants was delayed approximately 2 weeks relative to similar leaves on control plants. However, senescence of F-3 leaves on clipped *A. spicatum* plants was only marginally delayed.

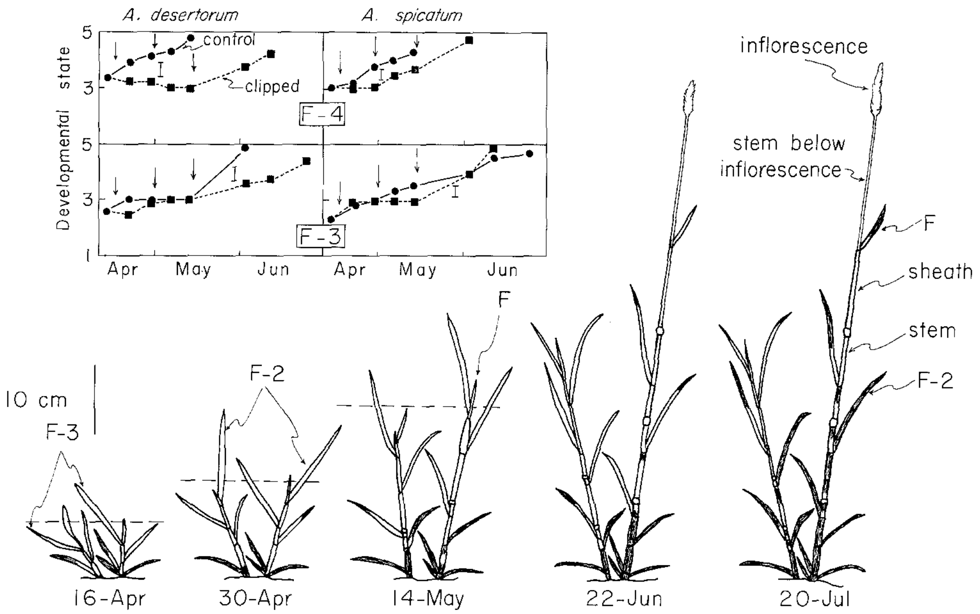

**Fig. 1.** Scale drawings of foliage elements on a reproductive and a vegetative tiller during 1981. Phenology, length, canopy position, and foliage inclination data from control plants of both bunchgrass species were used to depict these tillers. Individual leaves are indicated by: F, blade of flag leaf; F-1, blade of first leaf below the flag leaf; etc. The senesced portions of foliage elements are shaded. The horizontal, dashed lines indicate the height at which partially defoliated plants were clipped. *Inset:* Developmental stages of F-4 and F-3 leaves on marked tillers from control (circles, solid lines) and clipped (squares, dashed lines) plants of *A. desertorum* and *A. spicatum*. Developmental stages of individual leaves were rated as: 1, a newly expanded leaf that was still completely rolled; 2, an expanding leaf with a flattened distal area; 3, a fully-expanded leaf; 4, a leaf that had senesced 20 mm or more at the tip; 5, a completely senesced leaf. Each point is the mean of ten leaves, and the standard error is shown. Arrows correspond to when partially defoliated plants were clipped in 1981

Data for the F-2, F-1, and F leaves did not show any differences in leaf senescence between control and clipped plants within each species.

The photosynthetic behavior of leaves following clipping may differ between leaves that were fully expanded at the time of clipping and those that were initiated or continued to grow following the clipping. Thus, 2 categories of foliage will be considered: fully-expanded foliage at the time of clipping that remained on the plants, designated as "remaining foliage"; and the newer, expanding foliage at the time of clipping, or "regrowth foliage". Because the timing of new leaf initiation was not significantly different between control and clipped plants, Fig. 1 would indicate the developmental stages of cohorts of leaves on clipped plants at the time of each clipping treatment. For example, the cohort of F-2 leaves were expanding when the plants were initially clipped, and therefore F-2 leaves are designated as "regrowth foliage" after this initial clip. However, F-2 leaves were fully expanded before the second clipping treatment, and would be classed as remaining foliage after the last two clipping treatments.

Before late May, reproductive and vegetative tillers had the same appearance (Fig. 1). Therefore, all data collected before late May were arbitrarily considered as representing reproductive tillers because most of the marked tillers became reproductive. In mid- or late-May, reproductive tillers were in the boot stage, and both reproductive and vegetative culms were elongating. Therefore, the inflorescence and most of the sheath and stem foliage elements were regrowth foliage. In addition, vegetative tillers continued to produce new leaves during the remainder of the growing season. Vegetative tillers generally had 4 green, fully-expanded leaves per tiller: 2 younger leaves that were regrowth leaves after the third clipping treatment and two older leaves that were remaining foliage.

### *Water status and gas exchange of foliage: Effects of clipping*

Clipping did not enhance the water status of clipped plants relative to control plants (Fig. 2), even though the aboveground biomass on clipped plants was only 40% of that on control plants. For both bunchgrass species, neither covered nor midday plant water potential of foliage on clipped plants was significantly different from the water potential of foliage on control plants during 1981. Although air temperatures were relatively cool in April, plant water potential was low, probably because of the low rainfall for that month (32 mm). In May, near-record precipitation was received (119 mm) and all plant water potentials were relatively high and constant. Both covered and midday water potential dropped by more than 3 MPa during the summer drought period in June and July.

The significant clipping treatment effects on the net photosynthetic rates of leaves on reproductive tillers (Fig. 3) showed that compensatory photosynthesis occurred in the field. The results for net photosynthetic rates of individual leaf blades measured in 1981 are presented as 3 groups of leaves that had similar photosynthetic rates within each group. The oldest remaining foliage on partially defoliated plants (F-4 and F-3 leaves) of both species had significantly higher photosynthetic rates than similar foliage on control plants by the second week after each clipping treatment. Net photosynthesis of the F-2 leaves on partially defoliated plants, which was remaining foliage after the second and third clipping treatments, was also significantly greater than similar foliage on control plants following the second and third clipping treatments for *A. spicatum*, but only following the third clipping treatment for *A. desertorum*. Some regrowth foliage, the F-2 leaves of *A. desertorum* after the first clipping treatment and the F-1 leaves of *A. spicatum* after the second clip, had photosynthetic rates that were significantly greater than similar foliage on control plants. However, the photosynthetic rates of other regrowth leaves and the youngest remaining leaves (the F-1 leaves) on reproductive tillers were not greater than that of corresponding leaves on control plants. A temporary period of reduced photosynthesis occurred after each clipping treatment for leaves on partially defoliated *A. desertorum* plants. In *A.*

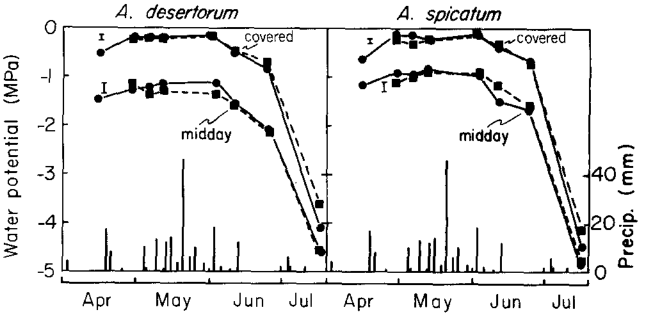

**Fig. 2.** Covered and midday xylem pressure potential during 1981 of foliage on control (circles, solid lines) and clipped (squares, dashed lines) plants of *A. desertorum* and *A. spicatum*. Each point is the mean of 4–8 pressure chamber determinations, and the standard error is shown. Precipitation at the field site during the same time period are indicated by the vertical lines at the bottom of the graphs

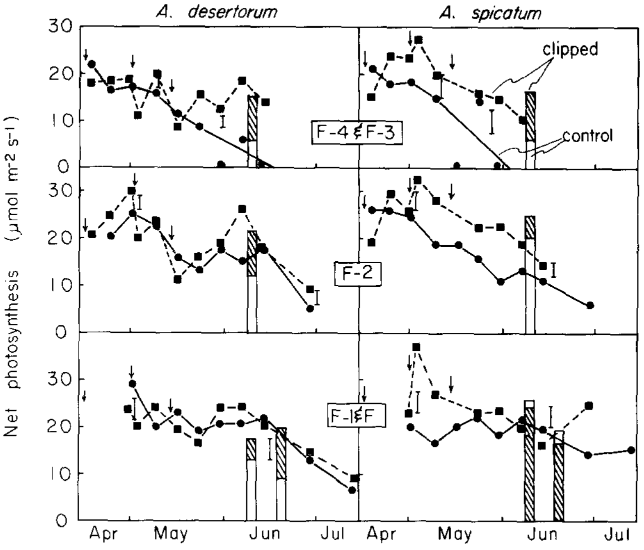

**Fig. 3.** Photosynthetic rates during 1981 of leaf blades on reproductive tillers from control (circles, solid lines) and clipped (squares, dashed lines) plants. The results from a different set of bunchgrass plants in 1982 are shown by bar graphs (control = open bars; clipped = shaded bars). Arrows mark when partially defoliated plants were clipped in 1981. Each point and bar graph is the mean of 2–22 measurements of net photosynthesis, and the standard error is shown. Analyses of variance for individual cohorts of leaves were conducted, but the data from cohorts that had similar results were combined

*spicatum*, a similar pattern occurred following the first clipping treatment, but not following the second or third clipping treatments. The photosynthetic behavior in June, 1982, of leaves on reproductive tillers was very similar to that in June, 1981.

Compensatory photosynthesis for leaves on vegetative tillers was evident in *A. spicatum*, but not in *A. desertorum*. For *A. desertorum*, net photosynthesis of leaves on clipped plants (15.0±0.7 μmol $m^{-2}$ $s^{-1}$) was not significantly different from control plants (14.0±1.0). However, net photosynthesis of leaves on vegetative tillers from partially defoliated *A. spicatum* plants (18.0±1.2) was significantly greater than similar leaves on control plants (14.3±1.0). These means are the combined results of data collected from remaining and regrowing leaves during the last half of June, 1981 and 1982. Photosynthetic rates were very similar among the different leaves and did not change during this time period.

The level of damage sustained by an individual leaf on clipped plants did not affect its photosynthetic rate. Each cohort of leaves on partially defoliated plants consisted of 2 leaf populations, one population of damaged leaves and another of leaves that were undamaged. This variability in leaf damage occurred because of the natural variation in leaf and stem inclination and the horizontal clipping treatment (Fig. 1). Photosynthetic rates of these 2 populations were not significantly different. For example, the mean net photosynthetic rate of F-4 and F-3 leaves on clipped *A. desertorum* plants after the third clipping treatment was 13.8±1.1 μmol $m^{-2}$ $s^{-1}$ for undamaged leaves and 14.0±1.3 for damaged leaves; and for clipped *A. spicatum* plants, the mean was 15.1±0.4 for undamaged leaves and 16.1±1.5 for damaged leaves.

Green leaf sheath, stem, and inflorescence foliage elements were also photosynthetically active, and some of these plant parts exhibited compensatory photosynthesis after partial defoliation (Fig. 4). For both species, regrowth leaf sheaths and stems on partially defoliated plants initially had greater photosynthetic rates than similar foliage elements on control plants. Although this difference did not persist in either species, net photosynthesis of sheaths and stems on partially defoliated *A. desertorum* plants was again significantly greater than control plants in early July. Net photosynthesis of the inflorescence and the stem that subtends the inflorescence on clipped *A. desertorum* plants was significantly greater than similar reproductive tissue on control plants. However, partial defoliation had no effect on the photosynthetic rates of reproductive foliage on *A. spicatum* plants. These effects of partial defoliation on photosynthetic rates of nonblade foliage were the same in 1981 and 1982.

Photosynthetic water use efficiency, or P/T ratio, was not significantly affected by the clipping treatment for all foliage elements of both species. For example, the P/T ratio of F-2 leaves on clipped *A. spicatum* plants averaged 2.4±0.1 mmol $CO_2$ mol $H_2O^{-1}$ following the second clipping treatment and 1.4±0.1 following the third. The mean P/T ratio of similar foliage on control plants of this species was 2.2±0.1 after the second clipping treatment and 1.4±0.1 after the third.

Specific mass of most foliage elements also was not affected by the clipping treatments, but soluble protein concentration was increased in all foliage elements (Table 1). The specific mass of all leaf blades on partially defoliated

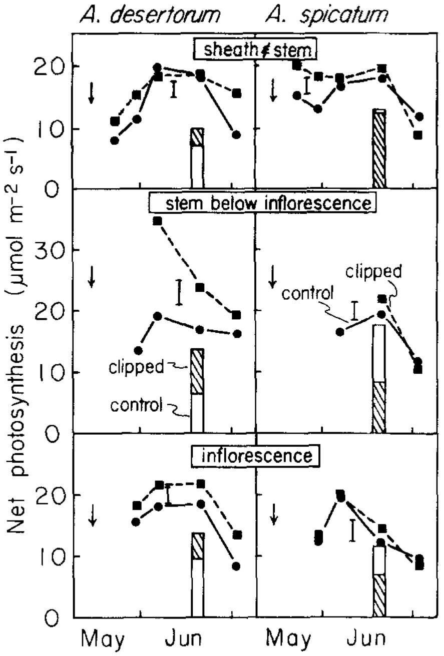

**Fig. 4.** Photosynthetic rates of leaf sheaths and stems, the stems that subtend the inflorescences, and the inflorescences on both bunchgrass species. Measurements from control plants are shown by circles and solid lines (1981) and open bar graphs (1982); from clipped plants, by squares and dashed lines (1981) and shaded bar graphs (1982). Each point and bar graph is the mean of 2–19 measurements, and the standard error is shown. The arrows mark when the partially defoliated plants were clipped the third time in 1981

**Table 1.** Mean and standard error of specific mass and of soluble protein concentration for groups of foliage. Measurements were collected from April through July, 1981, and in June, 1982. The groups of foliage represent individual cohorts of foliage elements that had statistically similar results. The means represent 60–162 measurements for specific mass and 28–151 determinations for soluble protein concentration

| | *A. desertorum* | | *A. spicatum* | |
|---|---|---|---|---|
| | Control | Clipped | Control | Clipped |
| Specific mass (g $m^{-2}$) | | | | |
| F-4 and F-3 leaf blades | 81±4 | 77±2 | 83±5 | 75±5 |
| F-2, F-1 and F leaf blades | 88±2 | 86±3 | 99±3 | 102±5 |
| Vegetative leaf blades | 92±3 | 91±3 | 108±4 | 107±3 |
| Sheaths and stems | 287±8 | 212±7 | 284±8 | 207±6 |
| Soluble protein concentration (% dry mass) | | | | |
| F-4 and F-3 leaf blades | 5.2±0.2 | 7.0±0.2 | 6.4±0.4 | 6.9±0.2 |
| F-2, F-1 and F leaf blades | 6.4±0.3 | 8.6±0.2 | 5.7±0.2 | 7.6±0.3 |
| Vegetative leaf blades | 4.5±0.3 | 5.7±0.3 | 3.8±0.2 | 4.7±0.2 |
| Sheaths and stems | 3.2±0.2 | 4.9±0.2 | 2.8±0.2 | 4.1±0.2 |

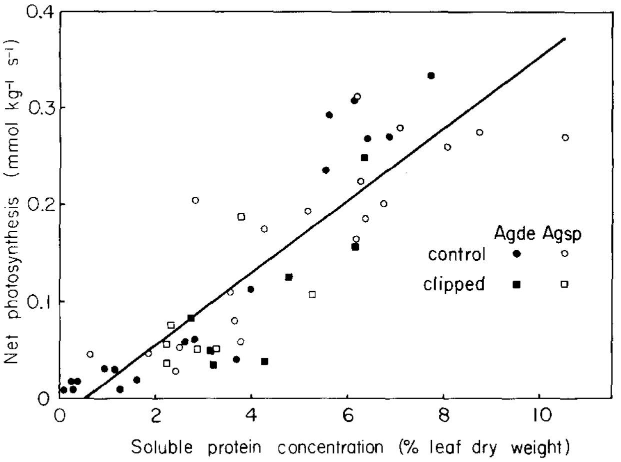

**Fig. 5.** Photosynthetic rate per unit dry mass for leaf blade and nonblade plant parts plotted against soluble protein concentration. Each point is a measurement from an individual foliage element. Data for *A. desertorum* plants are indicated by closed symbols; for *A. spicatum*, by open symbols. Measurements from control plants are represented by circles; from clipped plants, by squares. The linear correlation coefficient ($r$) for all data points is 0.87

plants was not significantly different from similar blades on control plants. However, specific mass of regrowth sheaths and stems on partially defoliated plants was significantly less than those on control plants. Soluble protein concentrations of both remaining and regrowth foliage elements on clipped plants were significantly greater than similar elements on control plants.

Photosynthetic rates expressed on a unit dry mass basis were linearly correlated with soluble protein concentrations (Fig. 5). The data in Fig. 5 is for foliage from control and partially defoliated plants of both species, and includes measurements of blade, sheath, and stem foliage. The linear correlation of data from control plants ($r = 0.89$) was not significantly different from the linear correlation of data from clipped plants ($r = 0.71$).

### *Water status and gas exchange of foliage: Species differences*

The water status and gas exchange rates of foliage on control and clipped *A. desertorum* plants were not significantly different from similar foliage on *A. spicatum* plants. Covered and midday water potential of *A. desertorum* were the same as those of *A. spicatum* (Fig. 2). A few foliage elements on partially defoliated *A. desertorum* plants had higher photosynthetic rates than similar foliage on *A. spicatum* plants (e.g., reproductive foliage, Fig. 4), but photosynthetic rates of some other foliage elements on clipped *A. spicatum* plants were greater (e.g., leaves on vegetative tillers). However, the photosynthetic rates of most foliage elements on clipped plants were not significantly different between species. Finally, water use efficiency of *A. desertorum* foliage was not significantly different from similar foliage on *A. spicatum* plants. For example, the mean P/T ratio of leaves on vegetative tillers from partially defoliated *A. spicatum* plants was $1.4 \pm 0.1$ mmol $CO_2$ mol $H_2O^{-1}$; for similar foliage on clipped *A. desertorum* plants, $1.6 \pm 0.1$.

The specific mass of many foliage elements was not significantly different between the two species (Table 1). The specific masses of F-2, F-1, and F leaves on reproductive tillers and of leaves on vegetative tillers in *A. spicatum* plants were greater than similar leaves in *A. desertorum* plants, but no significant differences were found between species for the specific masses of F-4 and F-3 leaves and all sheaths and stems. Also, the soluble protein concentrations of all foliage elements on both control and clipped *A. desertorum* plants were not significantly different from similar foliage on the respective *A. spicatum* plants. Finally, the linear correlation between photosynthetic rates per unit dry mass and soluble protein concentrations for *A. desertorum* ($r = 0.89$) was not significantly different from the linear correlation of data from *A. spicatum* ($r = 0.83$) (Fig. 5).

## Discussion

### *Compensatory photosynthesis*

The average increase in photosynthetic rates following partial defoliation in our field study was generally less than that reported in previous laboratory studies. For comparison, mean daily differences in photosynthetic rates between foliage on clipped plants and similar-aged foliage on control plants were calculated for the duration of each study. In our study, the photosynthetic rates of foliage on partially defoliated plants averaged 27% higher than similar foliage of the same age on control plants for both *Agropyron* species. This magnitude of compensatory photosynthesis is similar to that reported for *Agropyron smithii* grown in growth chambers (Painter and Detling 1981, Detling and Painter 1983), but less than one half the magnitude found for *Lolium multiflorum* (Gifford and Marshall 1973) and *Medicago sativa* (Hodgkinson et al. 1972) grown in glasshouses. In the only other known field study of compensatory photosynthesis in individual foliage elements, the average increase in net photosynthetic rates of two deciduous tree species following defoliation was generally greater than that in our study (Heichel and Turner 1983).

To place compensatory photosynthesis in a proper ecological perspective, it is necessary to assess the degree of change in photosynthesis in conjunction with the amount of photosynthetic biomass. For example, the greatest increase in compensatory photosynthesis was in the oldest foliage elements remaining after clipping, the F-4 and F-3 leaves (Fig. 3). Even though the photosynthetic contribution of these leaves relative to similar leaves on control plants would be further enhanced by a delay in leaf senescence (Fig. 1), they constituted less than 10% of the total aboveground biomass on clipped plants after June 1. Secondly, the average magnitude of the increase in photosynthetic rates following clipping was about one half the magnitude of the 60% decrease in aboveground biomass, relative to control plants.

Compensatory photosynthesis was not accompanied by an increase in photosynthetic water use efficiency or photosynthetic rates per unit soluble protein. Photosynthetic rates per unit soluble protein for foliage on clipped plants would be similar to those on control plants because the relative increases in soluble protein concentrations (Table 1) and in photosynthetic rates (Figs. 3 and 4) were similar. Furthermore, photosynthetic water use efficiency and photosynthetic rates per unit protein were very similar between species.

In our earlier study of these *Agropyron* species (Caldwell et al. 1981), we defoliated plants in a manner that resulted in a younger average age of foliage on clipped plants. The regrowth leaves on these clipped plants had consistently higher photosynthetic rates than leaves on control plants and the relative increase of photosynthetic rates for *A. desertorum* foliage following clipping was greater than *A. spicatum* foliage (Caldwell et al. 1981). These earlier results represent a valid comparison of foliage that was present on plants at the same point in time. When foliage elements of the same age are compared, as we have done in this paper, the increase in photosynthetic rates following clipping was not as pronounced as in our earlier study, and there was no significant difference in the degree of increased photosynthesis between species.

An increase in photosynthetic rates of foliage following partial defoliation would be beneficial to a plant, but it is difficult to establish a clear relationship between this phenomenon and the ability to regrow following clipping or to tolerate grazing. Current photosynthetic carbon assimilation is the major source of carbon for foliage regrowth in grass plants (Ryle and Powell 1975, Caldwell et al. 1981, Richards and Caldwell submitted). In our study, we chose 2 bunchgrass species that are known to have different levels of grazing tolerance (Hyder 1974), but regrowth and compensatory photosynthesis of the 2 species were almost identical following three moderate clipping treatments. In an earlier study, we did find relatively greater regrowth in *A. desertorum* plants following 2 severe clipping treatments, but the greater regrowth was attributed primarily to the ability to reallocate resources and activate meristems, and only secondarily to photosynthetic characteristics (Caldwell et al. 1981). Also, a difference in the ability to regrow following partial defoliation between an *Agropyron smithii* genotype collected from an area open to grazing and one from a grazing exclosure was not accompanied by a difference in compensatory photosynthesis (Detling and Painter 1983).

### *Factors which may influence compensatory photosynthesis*

The occurrence of compensatory photosynthesis in the field cannot be attributed to a more favorable water status of clipped plants. McNaughton (1983) has suggested that a large decrease in transpirational surface area by grazing may conserve soil moisture, which may improve the water status of clipped plants. In our study, the clipping treatments resulted in a 60% reduction of aboveground biomass on these 2 bunchgrass species, but no significant differences existed between species or between treatments for covered and midday plant water potential in 1980 (Nowak 1984) and 1981 (Fig. 2). The root systems of *Artemisia tridentata* and the 2 bunchgrass species overlap in the field (Caldwell and Richards 1984). Soil water that was not used by clipped bunchgrass plants was probably utilized by neighboring, unclipped *Artemisia* plants. The *Artemisia* plants were not clipped in this study because they are usually not grazed in Great Basin rangelands. However, in experiments or ecosystems where all plants are uniformly grazed, a decrease in soil water depletion after grazing may improve the water status of grazed plants.

Within both species, the oldest remaining leaves had the largest difference in photosynthetic rates between control and clipped plants (Fig. 3), which is similar to Hodgkinson's (1974) results. Also, the large differences in photosynthetic rates of F-4 and F-3 leaves between clipped and control plants were related to a delay in senescence of these leaves (inset, Fig. 1). This same phenomenon also occurred in clipped alfalfa (Hodgkinson et al. 1972) and Italian ryegrass (Gifford and Marshall 1973) plants. Field (1981) and Mooney et al. (1981) have suggested that leaf aging may be accelerated for shaded leaves. In our experiments, clipping removed overtopping foliage and allowed more light to penetrate into the bunchgrass canopy. Thus, the senescence of older remaining foliage in the lower portion of the canopy, which normally would become densely shaded (Caldwell et al. 1983), may have been delayed by the increased light intensity resulting from partial defoliation.

Increased soluble protein levels may have stimulated compensatory photosynthesis. Soluble protein concentrations of all foliage elements on partially defoliated bunchgrass plants were significantly higher than similar foliage of the same age on control plants (Table 1). Many of those foliage elements also had greater photosynthetic rates (Figs. 3 and 4). There was also a high correlation between photosynthetic rates and protein concentration for all plant parts of these two species (Fig. 5). Ribulose bisphosphate carboxylase constitutes a sizeable proportion of the leaf soluble protein pool (Jensen 1977), and activity of this enzyme is often directly related to photosynthesis (Björkman 1981, Friedrich and Huffaker 1980, Joseph et al. 1981).

Unlike the situation with older remaining foliage elements, the light environment of regrowth foliage was not an important factor that influenced the occurrence of compensatory photosynthesis in our study. Woledge (1977) found that compensatory photosynthesis in regrowth foliage after partial defoliation of perennial ryegrass plants only occurred if there was a concomitant increase in light intensity. The light environment for regrowth foliage in our field study was uniformly high because regrowth foliage was at the top of the canopy. Therefore, the lack of compensatory photosynthesis in some regrowth foliage elements in our study was not caused by relatively low light intensities.

Two other factors, specific mass and damage to individual leaves, also did not influence the occurrence of compensatory photosynthesis in our experiments. Regrowth sheaths and stems were the only plant parts whose specific mass was affected by the clipping treatments (Table 1). However, the lower specific mass of sheaths and stems is probably related to their structural and vascular functions rather than to their photosynthetic capability. Dyer et al. (1982) suggested that net photosynthetic rates of undamaged leaves are frequently enhanced following clipping, but photosynthetic rates of damaged leaves are almost always reduced. In our study, photosynthetic rates of undamaged leaves on clipped plants were not significantly different from that of damaged leaves for both bunchgrass species.

## Conclusions

Compensatory photosynthesis did occur in the field for many foliage elements of *A. desertorum* and *A. spicatum*. However, the average increase in photosynthetic rates of foliage in this study were generally lower than the increases in photosynthesis noted in laboratory studies. The magnitude of compensatory photosynthesis was largest in the 2 oldest, fully-expanded leaves that were present when the plants were initially clipped, but the contribution of these leaves to total carbon assimilation would be small after

June 1 because they represented only a small proportion of the total aboveground biomass. Even though current photosynthetic carbon assimilation is essential for foliage regrowth after partial defoliation, the magnitude and extent of compensatory photosynthesis does not appear to be related to the ability to tolerate herbivory.

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