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 (Woleadge 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, Woleadge 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...
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, were used in our experiment. Mature plants of both bunchgrass species and a shrub, *Artemisia tridentata* ssp. easeyana (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 μl l$^{-1}$ (range: 320-365 μl 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.