Evaluation of Potential Herbivore Mediation of Plant Water Status in a North American Mixed-Grass Prairie
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Xylem water potentials (ψ) were monitored diurnally from June through August 1981 to ascertain the water status of plants of four species growing on a heavily grazed prairie dog (*Cynomys ludovicianus*) colony and an adjacent lightly grazed uncolonized site in southwestern South Dakota. Highest ψ values were observed in June and August after periods of relatively high precipitation. Lowest values occurred in July when soil moisture had been depleted. However, there were no large differences in ψ of grasses (*Agropyron smithii, Andropogon gerardi,* and *A. scoparius*) growing on and off the prairie dog colony, even though root biomass of plants on the colony was substantially lower. While midday leaf conductance was comparable for *A. smithii* tillers on and off the colony, conductance values for *A. gerardi* and *A. scoparius* tillers were generally higher (17 to 60%) on the heavily grazed site. *Artemisia frigida* plants had slightly higher ψ on the prairie dog town during periods of moderate or high water stress. Soil moisture content was slightly but significantly ($P \leqq 0.05$) higher on the heavily grazed prairie dog town, even though afternoon soil temperatures at the 15-cm depth averaged 2.7°C higher.

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Контролировали суточные водные потенциалы (ψ) ксилемы с июня по август 1981 г. для оценки водного статуса в растениях 4-х видов, растущих на сильно выпасаемой территориии прерии, занятой колонией луговой собачки *Cynomys ludovicianus*, а также соседних слабо выпасаемых незаселенных участков на юго-западе южной Дакоты. Максимальные величины ψ наблюдались в июне и августе после периодов выпадения относительно больших количеств осадков. Наименьшие величины наблюдались в июле при недостатке влаги в почве. Однако, не установлено больших различий ψ у злаков (*Agropyron smithii, Andropogon gerardi* и *A. scoparius*) растущих в пределах колонии луговой собачки и вне ее, хотя биомасса корней растений в колонии была значительно ниже. Хотя проводимость листьев в полдень была сравнимой у побегов *A. smithii* внутри и вне колонии, величина проводимости у *A. gerardi* и *A. scoparius* была значительно выше (17-60%) на сильно выпасаемых местах, Растения *Artemisia frigida* имели более высокую ψ на территории колонии луговой собачки в периоды умеренного или высокого водного стресса. Содержание влаги в почве было немного, но достоверно выше ($P \leq 0,05$) на сильно выпасаемых местах колонии, даже когда послеполученные температуры почвы на глубине 15 см были в среднем на 2,7°C выше.

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Introduction

Through a variety of direct and indirect effects, herbivory may alter both the availability of water and its utilization by plants. Thus, plant water status might be expected to vary as a function of grazing pressure. For example, it has been suggested that grazing may conserve soil moisture through the removal of transpiring leaf tissue (White and Brown 1972, Buckhouse and Colthorp 1976, Parton and Risser 1980, McNaughton 1983). This may result in higher water potentials (ψ), which, in turn, may contribute to higher rates of growth in remaining tissues of grazed plants (Hodgkinson 1976, Wolf and Perry 1982). Such positive aspects of herbivory on plant water status may partially offset a variety of negative impacts. For example, defoliation during periods of low soil water availability might accentuate plant water stress by reducing the ability of roots to maintain extension rates high enough to keep ahead of the drying front in the soil profile (White and Brown 1972). Herbivores may also affect plant water status indirectly by altering canopy interception, bulk density, infiltration, runoff of precipitation, and bare soil evaporation (Branson et al. 1981). Grazing and related activities often reduce litter accumulation, resulting in creation of warmer, drier microenvironments (Whitman 1971).

We hypothesized that, as a result of the various positive and negative effects of herbivory on community water status, ψ and stomatal conductance of plants would differ systematically on two areas differentially utilized by herbivores. To evaluate the hypothesis, diurnal patterns of plant ψ and leaf conductance to water vapor of four species were followed through a growing season on a heavily grazed black-tailed prairie dog (*Cynomys ludovicianus*) colony and an adjacent, lightly grazed, uncolonized mixed-grass prairie site.

Materials and methods

The Pringle Valley prairie dog town in Wind Cave National Park, South Dakota was approximately 29 ha in area and had been in existence for 26 yr at the time of this study in 1981. The study was conducted on a portion of the town estimated to have been colonized by prairie dogs for 10 yr (see Coppock et al. 1983a for descriptions of vegetation, soils, climate and herbivores). The uncolonized site, 300 m north, was topographically and edaphically similar to the colonized site and was lightly grazed by free-roaming wildlife. Total live and standing dead vegetation was substantially reduced (51% and 88%, respectively) on the colonized site (Coppock et al. 1983a).

Three grass species, *Andropogon gerardi* (C_4), *A. scoparius* (C_4), and *Agropyron smithii* (C_3), and a dwarf shrub, *Artemisia frigida* (C_3), were monitored (plant nomenclature follows Van Bruggen 1976). Xylem ψ was measured diurnally (predawn, 0800, 1200, 1500, and 1800 hours) at two week intervals during 1981, with a pressure chamber (Scholander et al. 1965). For the grass species, the most recent fully expanded leaf from each of about six tillers was used for ψ determinations. Concurrent measurements of leaf conductance to water vapor were also obtained from each of the grass species using a diffusion porometer (Li-Cor LI-65 Autoporometer) (Kanemasu et al. 1969). Ten tillers of each species were selected on each sample date and the most recent fully expanded leaf on each tiller was followed throughout the day. Because only the adaxial leaf surfaces were read, true conductance was underestimated. The porometer was calibrated under poorly controlled field conditions and absolute values obtained were likely not comparable between dates. For these reasons, conductance results for each date are expressed in relative terms (relative conductance = mean on colony value/mean off colony value). Midday conductance was not measured on two of the six sample dates because of light thundershowers which wetted leaf surfaces.

Soil moisture for each site was determined gravimetrically by extracting 10 soil cores from the 0- to 10-cm and 10- to 20-cm depths, and a rain gauge measured precipitation. Late afternoon (~ 1700 hours) soil temperatures at 15 cm were obtained at five locations from each site. All measurements on the prairie dog colony were obtained from grass-dominated spaces between burrow mounds.

Analysis of variance (Nie et al. 1975) and the Student's t-test was used to test for statistical differences at $P \leqq 0.05$.

Results

Summer rainfall in 1981 (Fig. 1a) was approximately 30% greater than the long-term average (R. Klukas, pers. commun.). Soil moisture at both sites (Fig. 1b,c) was greatest in early June as the result of a series of heavy rains in May, before the study began. A substantial recharge of soil moisture occurred in late July and early August. For soil moisture, the date by location interactions were significant at both depths, with soils on the prairie dog colony having a moisture content higher than or comparable to soils off the colony. Soil temperatures were consistently and significantly higher on the prairie dog colony throughout the growing season (Fig. 1d). On-town soils were, on the average, 2.7°C warmer than off-town soils.

Seasonal trends in daily minimum and maximum plant ψ showed few systematic differences among plants growing on and off the prairie dog colony (Fig. 2). Lowest ψ occurred in early July, when soil moisture was lowest (Fig. 1), while highest ψ occurred in early June, and again in early August, when soil moisture was relatively high. There were, for most species, dates for which plants from one location had ψ which differed significantly from those of plants at the other location. However, because plants having higher ψ on one date at

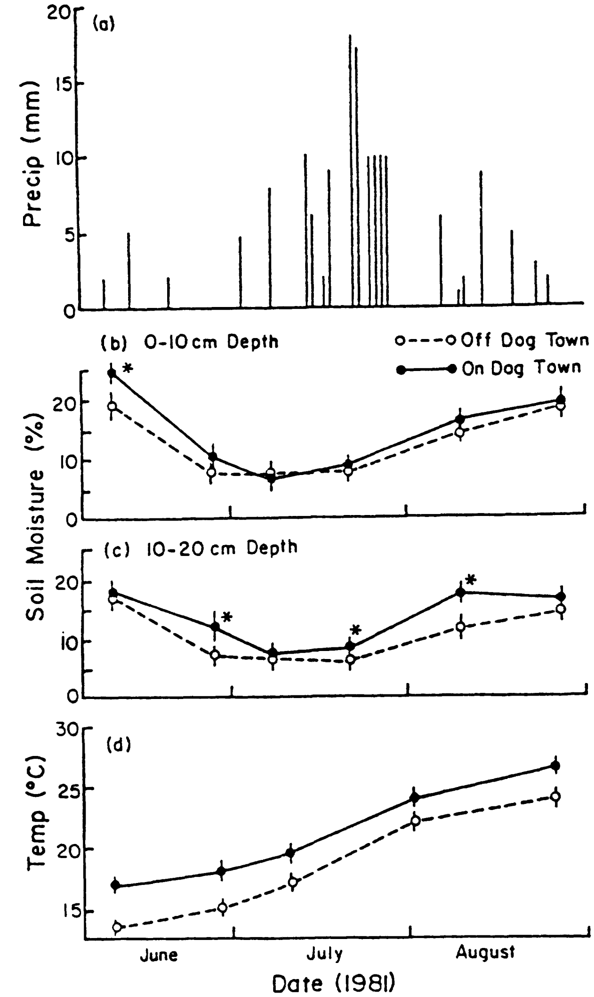

Fig. 1. Seasonal pattern of rainfall at the Pringle Valley site for the summer of 1981 (a) and mean (±SE) percentage soil moisture at the 0–10 (b) and 10–20 cm (c) depths on (●——●) and off (○- - -○) the prairie dog town (n = 10). Starred (*) pairs at each date were significantly different at P ≦ 0.05. Mean (±SE) soil temperatures at 15 cm (n = 5) were significantly (P ≦ 0.05) greater on the colony at each date (d).

one location did not consistently maintain significantly higher ψ on other dates, date by location interactions were usually significant.

For predawn ψ, the date by location interaction term was significant for all species except *A. scoparius*. For this species, the effect of location was significant; plants on the prairie dog town had lower ψ than off-town plants. However, none of the data pairs at any given date differed significantly. In all other species, off-town plants generally had comparable or slightly lower predawn ψ during the first half of the season and comparable or higher predawn ψ during the last half of the season. The main effect of date was significant for all species.

For seasonal minimum (midday) ψ, the date × location interaction term was significant for all species except *A. smithii,* and there were no consistent on town vs. off town patterns apparent among the grasses. However, *A. frigida* usually had lower ψ off the colony. The main effect of location was significant for all species except *A. scoparius,* and the main effect of date was significant for all species, with the lowest overall midday water potentials again occurring on 7 July. *A. smithii* plants exhibited the lowest ψ on this date (ψ = −3.2 MPa), while the other three species each had minimum

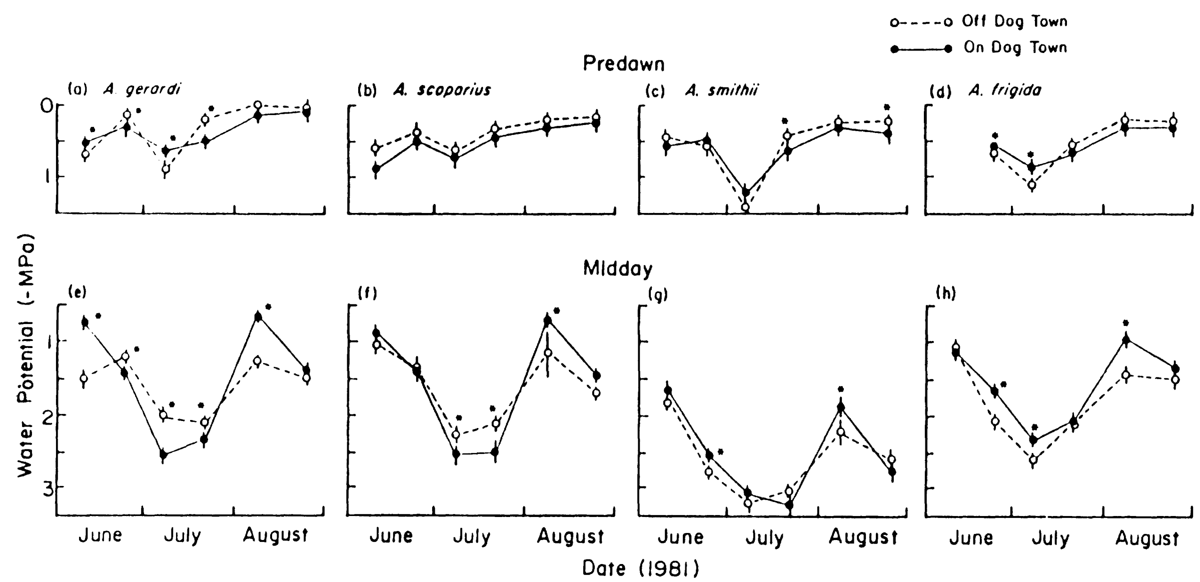

Fig. 2. Seasonal trends of mean (±SE) maximum (predawn) and minimum (midday) xylem water potentials for plants on (●——●) and off (○- - -○) the prairie dog colony. Starred (*) pairs at each date were significantly different at P ≦ 0.05 (n ≅ 6).

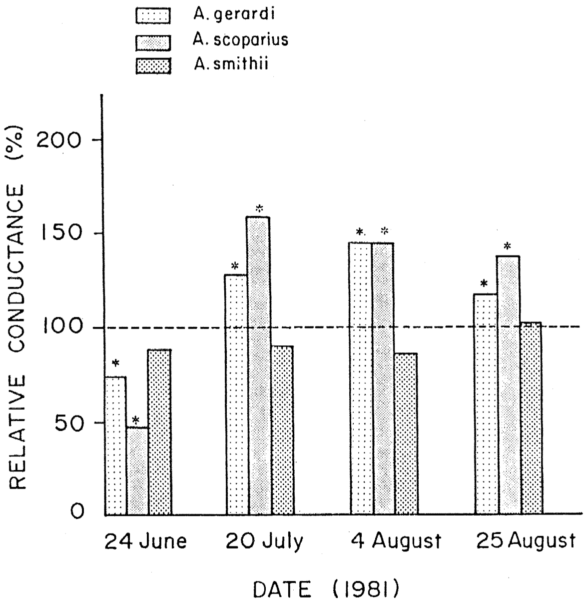

Fig. 3. Mean midday leaf conductance of tillers growing on the Pringle Valley prairie dog colony (vertical bars) relative to mean leaf conductance of tillers occurring off the prairie dog colony (dashed line). Bars with star (*) indicate significant differences between on and off colony leaf conductance on each date.

water potentials of about −2.5 MPa. When all diurnal ψ data were pooled over the growing season and compared, location was significant only for *Artemisia frigida.* At $\psi < -0.8$ MPa *Artemisia* plants on the colony had higher ψ than plants off the colony.

Midday leaf conductance of grasses occurring on the prairie dog colony, relative to off colony tillers, are shown in Fig. 3. Conductance for *A. smithii* tillers was statistically comparable for tillers growing on and off the prairie dog colony on all sample dates. In contrast, conductance values for leaves of both C_4 grasses growing on the colony differed systematically from those of off colony tillers throughout the growing season. Early in the season (June) conductance was 25 to 53% lower for *A. gerardi* and *A. scoparius* plants on the prairie dog colony. Through July and August, however, leaf conductance was 17 to 60% greater for tillers of these species occurring on the prairie dog town.

Discussion

Alteration of plant canopy structure by factors such as fire is known to affect the water balance of component species (Savage 1980). On the prairie dog colony, substantial canopy alterations resulted from heavy, uniform grazing. Although plant standing crop and litter were two to three times greater off the colony (Coppock et al. 1983a), few consistently significant seasonal differences in ψ were observed among grasses (Fig. 2). Similarly, Nowak and Caldwell (1984) experimentally reduced aboveground biomass of two *Agropyron* bunchgrasses by 60% and found no significant differences in midday plant ψ. The various positive and negative effects that herbivores may potentially have on graminoid water status apparently nullified one another on this site. Water potentials of grasses were similar on and off the colonized area, even though (1) soil temperatures were greater on the prairie dog town (Fig. 1), (2) root biomass of *A. smithii* and *A. scoparius* on the prairie dog town was about half that of plants on the uncolonized site (Ingham and Detling 1984), and (3) grazing by large herbivores such as bison (Coppock et al. 1983b) may have increased the bulk density of soils on the prairie dog town and decreased infiltration of precipitation relative to the uncolonized area. However, because growing-season precipitation was regularly distributed and approximately 30% greater than the long-term average during this study, different patterns may occur during years with normal or below-normal rainfall.

The lower live standing crop on the colony (Coppock et al. 1983a) represented a reduction in transpiring leaf surface areas which, in turn, may have facilitated conservation of soil water (Fig. 1), thus enabling these plants to maintain ψ (Fig. 2) at levels comparable to those off the colony. The dwarf growth form (fewer and smaller leaves per tiller) of plants on the colony (Detling and Painter 1983) may also have been conducive to maintenance of leaf ψ if cell sizes of these plants were smaller than those of off-colony plants, since smaller cell sizes facilitate osmotic adjustment and maintenance of turgor (Cutler et al. 1977). In addition, shoot nitrogen concentrations on this prairie dog town have been observed to increase with time since colonization (Coppock et al. 1983a). High shoot nitrogen concentrations in grazed populations may be related to increased drought stress and could be a physiological drought tolerance response (Hsaio 1973) as well as a response to defoliation (Detling and Painter 1983). The possibility for differences in resistance to water transport among plant populations in different environments also exists (e.g., Roy and Mooney 1982), and may have enabled the C_4 grasses on the prairie dog colony to achieve higher conductances while maintaining comparable leaf ψ (Fig. 3).

Soil temperatures (Fig. 1), radiant heat loads and ground level wind speeds are highest on heavily grazed areas (Whitman 1971) and would be expected to contribute to increased rates of transpirational water loss. However, the fact that soil moisture on the colony was comparable to, or slightly greater than, that off the colony (Fig. 1) suggests that transpirational and canopy interception water losses were reduced more than bare soil evaporative or runoff losses were increased. A 60% reduction in shoot biomass of C_4 grasses on the colony (Coppock et al. 1983a) presumably offset the higher rates of transpiration observed for those plants on the colony (Fig. 3).

From this brief review it is apparent that a wide variety of factors interact in various ways to determine plant water status in grazing systems. The complexity and variable magnitude of such interactions, which span several spatial and temporal scales, makes it difficult to generalize about the effects of herbivory on plant water relations in a community context.

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References

Branson, F. A., Gifford, G. F., Renard, K. G. and Hadley, R. F. 1981. Rangeland hydrology. – Range Sci. Series No. 1, 2nd ed., Soc. Range Manage., Denver, CO.

Buckhouse, J. C. and Colthorp, G. B. 1976. Soil moisture response to several levels of foliage removal on two Utah ranges. – J. Range Manage. 29: 313–315.

Coppock, D. L., Detling, J. K., Ellis, J. E. and Dyer, M. I. 1983a. Plant-herbivore interactions in a North American mixed-grass prairie. I. Effects of black-tailed prairie dogs on intraseasonal aboveground plant biomass and nutrient dynamics and plant species diversity. – Oecologia (Berl.) 56: 1–9.

– , Ellis, J. E., Detling, J. K. and Dyer, M. I. 1983b. Plant-herbivore interactions in a North American mixed-grass prairie. II. Responses of bison to modification of vegetation by prairie dogs. – Oecologia (Berl.) 56: 10–15.

Cutler, J. M., Rains, D. W. and Loomis, R. S. 1977. The importance of cell size in the water relations of plants. – Physiol. Plant 40: 253–260.

Detling, J. K. and Painter, E. L. 1983. Defoliation responses of western wheatgrass populations with diverse histories of prairie dog grazing. – Oecologia (Berl.) 57: 65–71.

Hodgkinson, K. C. 1976. The effects of frequency and extent of defoliation, summer irrigation, and fertilizer on the production and survival of the grass *Danthonia caespitosa* (Gaud.). – Aust. J. Agric. Res. 27: 755–767.

Hsaio, T. C. 1973. Plant responses to water stress. – Ann. Rev. Plant Physiol. 24: 519–570.

Ingham, R. E. and Detling, J. K. 1984. Plant-herbivore interactions in a North American mixed-grass prairie. III. Soil nematode population and root biomass dynamics on a black-tailed prairie dog colony and an adjacent uncolonized area. – Oecologia (Berl.) 63: 307–313.

Kanemasu, E. T., Thurtell, G. A. and Tanner, C. B. 1969. Design, calibration and use of a stomatal diffusion porometer. – Plant Physiol. 44: 881–885.

McNaughton, S. J. 1983. Compensatory plant growth as a response to herbivory. – Oikos 40: 329–336.

Nie, N. H., Hull, C. H., Jenkins, J. G. and Bent, D. H. 1975. SPSS: Statistical package for the social sciences. – McGraw Hill, New York.

Nowak, R. S. and Caldwell, M. M. 1984. A test of compensatory photosynthesis in the field: implications for herbivory tolerance. – Oecologia (Berl.) 61: 311–318.

Parton, W. J. and Risser, P. G. 1980. Impact of management practices on the tallgrass prairie. – Oecologia (Berl.) 46: 223–234.

Roy, J. and Mooney, H. A. 1982. Physiological adaptation and plasticity to water stress of coastal and desert populations of *Heliotropium curassavicum* L. – Oecologia (Berl.) 52: 370–375.

Savage, M. J. 1980. The effect of fire on the grassland microclimate. – Herb. Abstr. 50: 589–603.

Scholander, P. R., Hammel, H. T., Bradstreet, E. D. and Hemmingson, E. A. 1965. Sap pressure in vascular plants. – Science 148: 339–346.

Van Bruggen, T. 1976. Vascular plants of South Dakota. – Iowa State Univ. Press, Ames.

White, L. M. and Brown, J. H. 1972. Nitrogen fertilization and clipping effects on green needlegrass (*Stipa viridula* Trin.): II. Evaporation, water use efficiency, and nitrogen recovery. – Agron. J. 64: 487–490.

Whitman, W. C. 1971. Influence of grazing on the microclimate of mixed-grass prairie. – In: Kreitlow, K. M. and Hart, R. H. (eds), Plant morphogenesis as the basis for scientific management of range resources. USDA Misc. Publ. No. 1271, pp. 207–218.

Wolf, D. D. and Perry, D. J. 1982. Short-term growth responses of tall fescue to changes in soil water potential and to defoliation. – Crop Sci. 22: 996–999.