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Changes in Grass Leaf Water Relations Following Bison Urine Deposition

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ABSTRACT.—In a northern, mixed-grass prairie in South Dakota, bison urine deposition leads to patches of vegetation having much higher total aboveground plant biomass, root mass and N concentrations. Although *Schizachyrium scoparium* (C_4) dominated the prairie, these increases in total aboveground plant biomass following urine deposition resulted mainly from the large growth response of *Poa pratensis* (C_3). Field experiments were conducted over 2 growing seasons to investigate the effect of urine deposition on leaf water relations of these two grasses.

Poa on urine patches had higher leaf conductances and lower water potentials than *Poa* off patches. During drought stomatal closure began at lower water potentials in *Poa* on urine patches. Leaf folding was less prevalent in *Poa* on urine patches. Urine deposition had much smaller and usually insignificant effects on leaf water relations of *Schizachyrium*.

INTRODUCTION

In a northern mixed prairie, urine deposition by bison (*Bison bison*) results in increases in above- and belowground plant biomass and foliar N concentrations (Day and Detling, 1990). The increases in aboveground plant biomass are due to large increases in *Poa pratensis* (C_3) biomass, relative to *Schizachyrium scoparium* (C_4) which dominates the prairie. Although the latter study and other studies (Joblin and Keough, 1979; Joblin, 1981; Ledgard *et al.*, 1982; Thomas *et al.*, 1986) have addressed changes in plant biomass, species composition and nutrient concentrations following urine deposition, apparently no studies have investigated changes in plant physiological processes.

Increased soil N availability following urine deposition may have significant effects on plant water relations. However, results from previous studies on N availability and plant water relations have been variable with reports of both lower stomatal sensitivity (Radin and Parker, 1979b; Nagarajah, 1981; Radin and Ackerson, 1981; Radin *et al.*, 1985; Bennett *et al.*, 1986) and higher stomatal sensitivity to drought following increased N availability (Radin and Parker, 1979a; Radin and Boyer, 1982; Morgan, 1984).

In this study we examine the influence of urine deposition of large herbivores on leaf water relations of *Poa pratensis* and *Schizachyrium scoparium*. An objective of this study was to provide further explanation for the large increases in *Poa* production following bison urine deposition (Day and Detling, 1990).

MATERIALS AND METHODS

The study site was a northern mixed-grass prairie in Wind Cave National Park, South Dakota, on the southern edge of the Black Hills. Average annual precipitation at the park is 450 mm, of which over 70% comes between May and September. *Schizachyrium scoparium* and *Poa pratensis* dominate the site in Pringle Valley on the northern edge of the park, with other plant species comprising <1% of the total abtoveground biomass (Day and Detling,

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1990). The dominant large herbivore in this system is the American bison (*Bison bison*). Vegetation, soils and large herbivores are described in Coppock *et al.* (1983a, b).

In July 1986, 32 circular patches of dark green vegetation, created by bison urine deposition were marked along with 32 reference areas within 3 m of each patch. Twenty-four of these on/off patch pairs were split into three groups of eight and were sampled for gravimetric soil moisture at the 5-10 cm depth on 10 and 21 July and 28 August.

The eight remaining urine patches and their reference sites were used to monitor plant water relations. On 12 and 17 July, 28 August and 8 September, midday (1200–1350 h) leaf conductance to water vapor (g) and water potential (ψ) of *Poa* and *Schizachyrium* were measured. Conductance of the adaxial leaf surface was measured with a null-balance porometer (LI-COR 1600). Adaxial surfaces were measured because g of abaxial surfaces are similar (*Schizachyrium*) or near zero (*Poa*). Leaf samples were then wrapped in aluminum foil, cut and placed in a pressure chamber (PMS Model 1000) for measurement of ψ. Leaf conductance measurements were made under full sunlight (photosynthetic photon flux density > 2000 μmol m^{-2} s^{-1}).

In 1987 we used simulated large-bovine urine (Stillwell, 1983) to create patches in order to provide more control over experiments. This simulated urine contains urea and several salts (*see* Day and Detling, 1990) and produces patches of vegetation similar to natural bison urine patches (Day and Detling, 1990). On 9 May eight simulated urine patches were made by applying 2 liters of urine to 0.25 m^2 plots. Nearby reference areas received 2 liters of distilled H_2O. The simulated patches and reference areas were used for midday g and ψ measurements of *Poa* and *Schizachyrium* on two dates in June, July and August. On one of these dates each month diurnal patterns of g and W were measured (13 June, 23 July and 28 August). Measurements of diurnal patterns were made under cloudless conditions.

Twenty-four additional simulated patches and their references were randomly located on 9 May. These areas were divided into three groups of eight pairs, and one group was sampled for gravimetric soil moisture at the 5–10 cm depth on either 10 June, 23 July or 24 August.

Leaf folding was measured on the 24 urine patches and controls before sampling for soil moisture. All leaves within one-quarter of each 0.25 m^2 circular plot were examined for degree of folding between 1300 and 1500 h. *Poa* leaves were noted as being open or completely folded over at their midvein (closed). Leaf folding was more gradual in *Schizachyrium* and the cross-sectional angle of the blade at the midvein was measured. This was done by cutting *Schizachyrium* blades at midlength, quickly touching the cut end to a saturated ink pad, and making a print of the leaf angle on paper which was later measured with a protractor.

Statistical analyses involved paired t-tests to test hypotheses concerning differences between urine patch and reference areas and differences between *Poa* and *Schizachyrium*.

RESULTS

In 1986, midday g was significantly higher and ψ was significantly lower in *Poa* on urine patches compared to off patches (Fig. 1). Results for *Schizachyrium* were not as consistent; urine had a significant effect on g and ψ only in July. *Poa* had significantly higher g and lower ψ than *Schizachyrium* on the same date and location ($P < 0.05$). Soil moisture at the 5–10 cm depth was significantly lower on urine patches (Fig. 1).

In 1987, midday g was significantly higher in *Poa* on simulated urine patches compared with off patch *Poa,* except 23 July when all *Poa* had very low g (Fig. 2). On this date only 0.04 cm of rainfall had fallen in the previous 15 days. On the June and August sampling

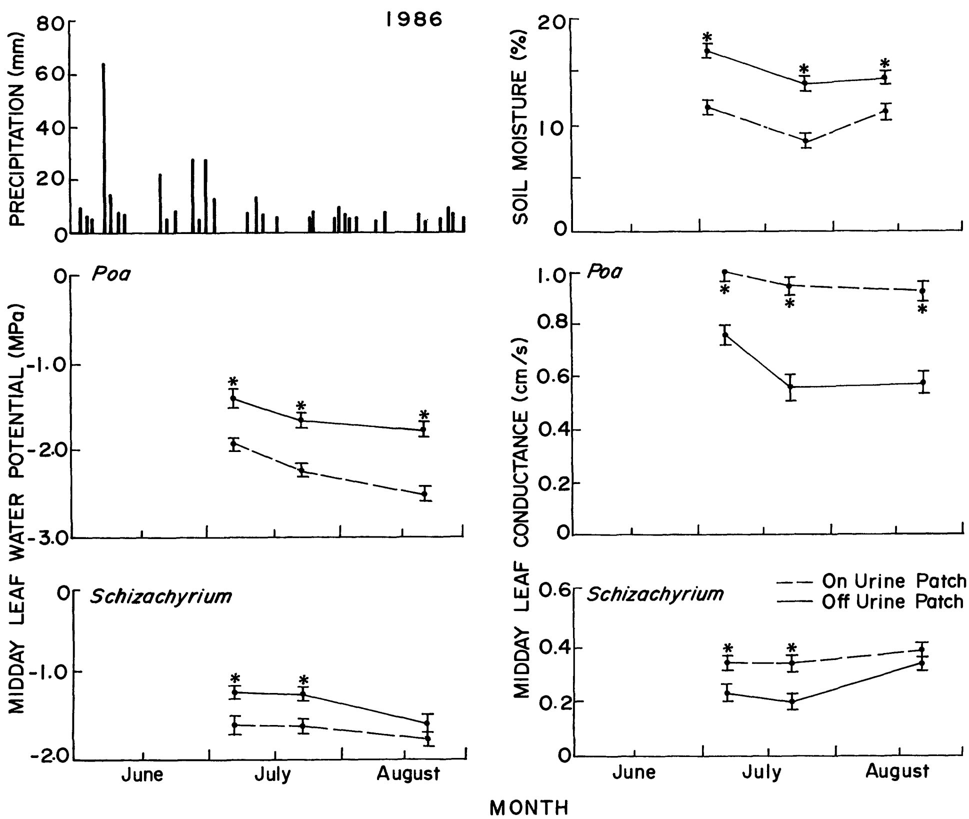

FIG. 1.—Seasonal trends in precipitation, soil moisture content and midday leaf conductance and water potential of *Poa* and *Schizachyrium* on and off urine patches in 1986. Asterisks denote on and off patch means are significantly different ($P < 0.05$). Vertical lines are ± 1 SE ($n = 8$)

dates, when midday g values were relatively high, 4.82 and 2.62 cm of rainfall, respectively, had been received over the preceding 15 days. Midday g of *Schizachyrium* did not differ with treatment on any date. Midday ψ in *Poa* on patches was significantly lower than off patch individuals on all dates, but for *Schizachyrium* only on 23 July. Soil moisture was significantly lower on urine patches in June.

Poa generally had higher g on simulated urine patches than off urine patches throughout the day (Fig. 3). In contrast, no significant differences were found in g between on and off patch individuals of *Schizachyrium.* With the exception of predawn values, leaf water potentials of *Poa* on urine patches were significantly lower than off patch individuals (Fig. 4). Leaf water potentials of *Schizachyrium* were significantly different only on 23 July.

A significantly lower percentage of *Poa* leaves were completely folded on 10 June and 24 August on simulated urine patches (Table 1). On 10 June *Schizachyrium* leaf blades were significantly less folded on urine patches compared to off patches. No significant differences in leaf folding of on and off patch plants were found in either species on 23 July.

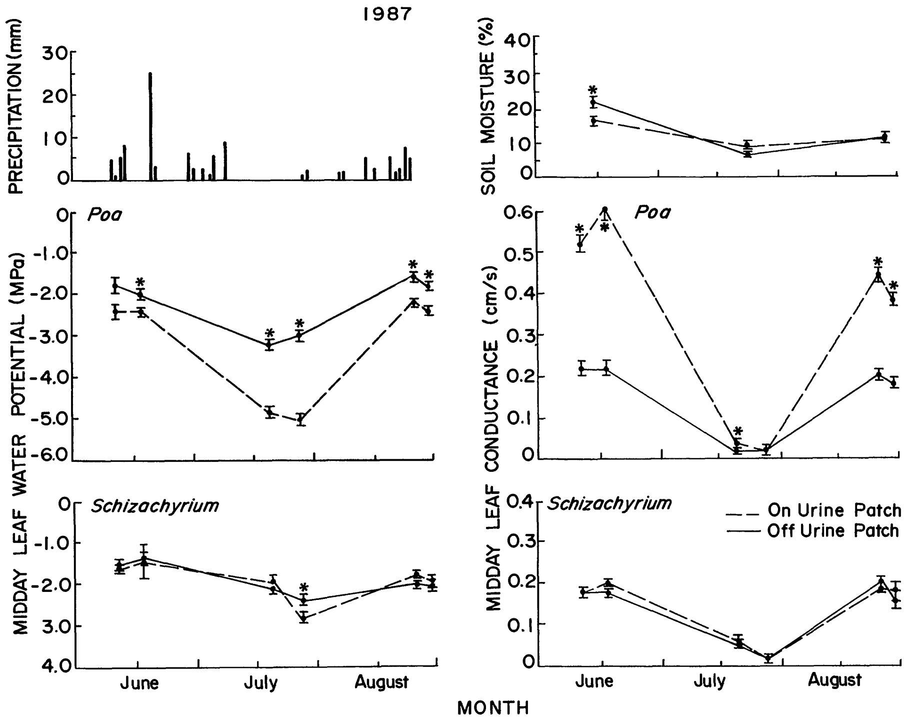

FIG. 2.—Seasonal trends in precipitation, soil moisture content, and midday leaf conductance and water potential of *Poa* and *Pshizachyrium* on and off urine patches in 1987. Asterisks denote on and off patch means are significantly different ($P < 0.05$). Vertical lines are ±1 SE ($n = 8$)

DISCUSSION

Higher aboveground biomass (Day and Detling, 1990) and g of *Poa* on urine patches would likely result in higher transpiration rates per ground surface area on urine patches, which is consistent with lower soil moisture contents found under urine patches in 1986 (Fig. 1). Increased rainfall interception by the greater plant biomass on urine patches may also contribute to lower soil moisture under patches. Soil moisture was lower under urine patches in June 1987, but not in July or August (Fig. 2). Unfortunately, soil moisture content below the 10 cm depth was not measured but may have been lower under urine patches at deeper depths in July and August. Predawn ψ of both species were similar throughout the 1987 growing season (Fig. 4), suggesting that plants were tapping water from deeper depths.

Throughout both field seasons midday g was generally higher in *Poa* than *Schizachyrium* both on and off urine patches. This is not surprising since several researchers have found higher leaf conductance in C_3 than C_4 species (Edwards *et al.*, 1985; Monson *et al.*, 1986; Sage and Pearcy, 1987). Higher g and transpiration rates in *Poa* may result in higher mineral N uptake and thus a greater growth response to urine. Other studies have demonstrated a link between transpiration rate and N uptake in C_3 plants (*e.g.*, Gebauer, Schubert *et al.* 1987; Gebauer, Schuhmaker *et al.* 1987). However, although *Poa* off urine patches usually had higher midday (1986) or peak (1987) g than *Schizachyrium* (Figs. 1, 3), N concentrations were not higher in *Poa* than *Schizachyrium* off urine patches (Day and

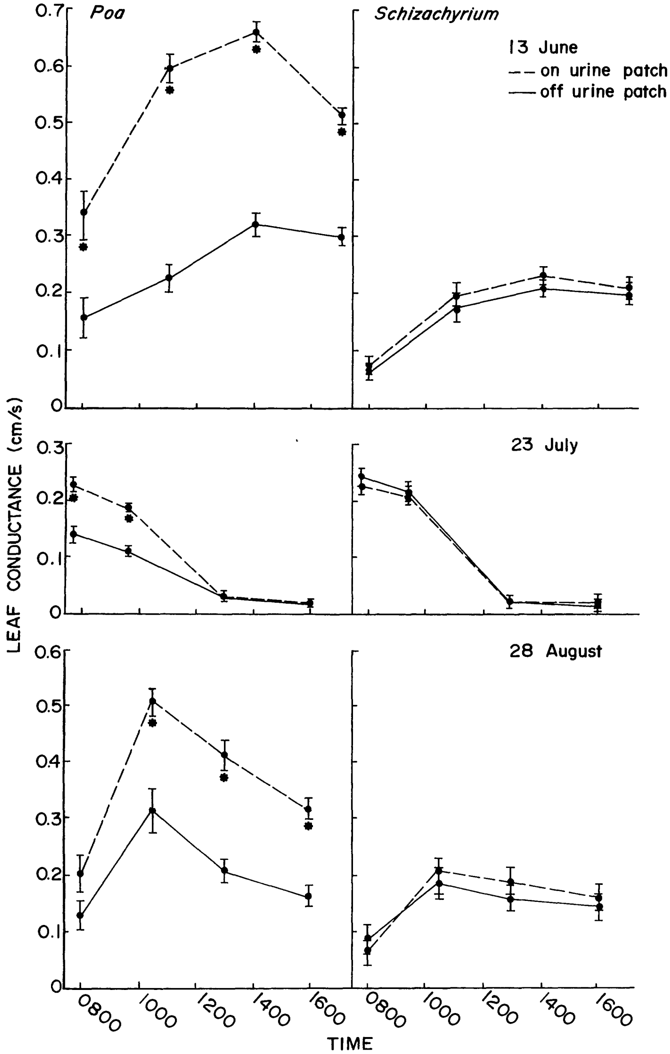

FIG. 3.—Diurnal trends in leaf conductance of *Poa* and *Schizachyrium* on and off urine patches on three dates in 1987. Asterisks denote on and off patch means are significantly different (P < 0.05). Vertical lines are ±1 SE (n = 8)

Detling, 1990), suggesting a weak link between N uptake and g in these species (*also see* Bloom and Schulze, 1984).

Lower stomatal sensitivity to water stress with increased N levels has been found in several studies, although conflicting reports are also common (*see* Introduction). *Poa* exhibited lower stomatal sensitivity to drought under the increased N environment of urine patches as evidenced by its higher g and lower ψ on urine patches. During dry periods *Poa* on urine patches initiated stomatal closure at lower ψ than *Poa* off urine patches. For example, on 28 August 1987 g peaked at 0.52 and 0.29 cm/s on and off urine patches, respectively. This occurred at a ψ of −2.2 on urine patches and −1.7 MPa off patches.

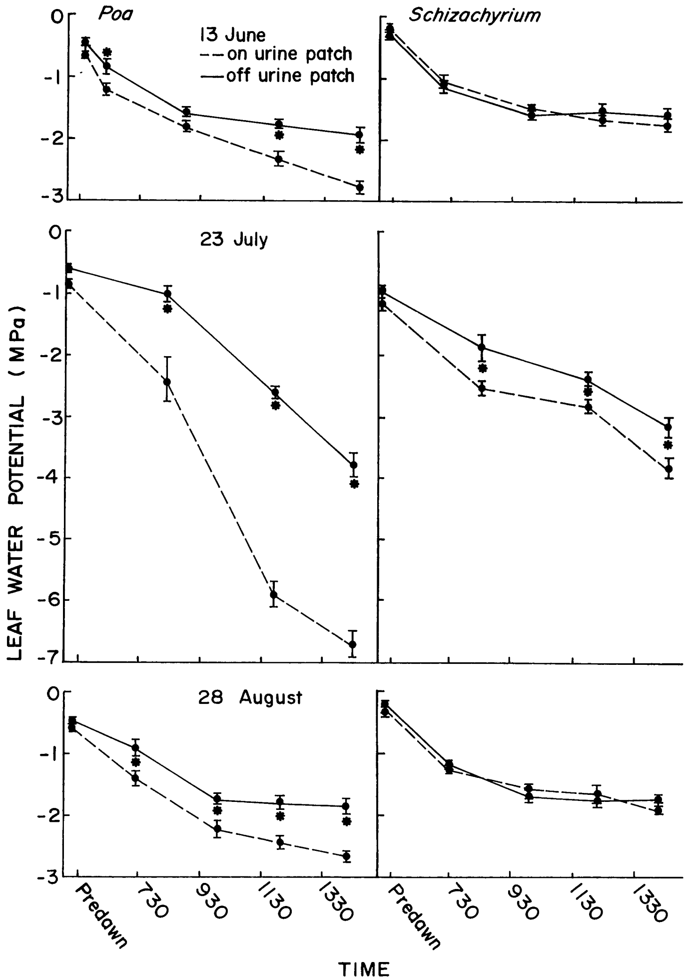

FIG. 4.—Diurnal trends in leaf water potential of *Poa* and *Schizachyrium* on and off urine patches on three dates in 1987. Asterisks denote on and off patch means are significantly different ($P < 0.05$). Vertical lines are ±1 SE ($n = 8$)

Leaf folding is a common response of grasses to water stress (Begg, 1980). Leaf folding was less prevalent in *Poa* on urine patches in June and August (Table 1), which is consistent with its lower sensitivity to drought following urine deposition.

Plant response to increased N availability may partially depend on a plant's photosynthetic pathway type (Brown, 1978, 1985; Schmitt and Edwards, 1981). Since the demand for RUBISCO is greater in C_3 plants we might expect C_3 species such as *Poa* to show a greater growth response due to increased N availability following urine deposition. However, the effects of other environmental factors and plant characteristics may be equally important in predicting plant responses to increased N (Christie and Detling, 1982; Borylawski and Bentley, 1985). In semi-arid areas, plant response to increased N may depend strongly on

TABLE 1.—Leaf folding in *Poa* and *Schizachyrium* on and off urine patches on three dates in 1987. Values are means ± 1 SE (n = 8)

Date	Species/folding character	On urine patch	Off urine patch
10 June	*Poa* (% closed)	11.1 ± 2.1***	87.5 ± 6.7
	Schizachyrium (° angle)	139.5 ± 9.6***	98.8 ± 6.2
23 July	*Poa* (% closed)	79.3 ± 9.0	84.6 ± 8.7
	Schizachyrium (° angle)	53.5 ± 4.6	42.8 ± 6.2
24 August	*Poa* (% closed)	88.1 ± 7.1**	95.8 ± 6.0
	Schizachyrium (° angle)	62.6 ± 6.1	60.3 ± 7.5

Asterisks denote the probability that on and off patch means do not differ
** $P < 0.01$
*** $P < 0.001$

a plant's ability to maintain turgor which is not directly related to its photosynthetic pathway type (Pearcy and Ehleringer, 1984).

The higher g of *Poa* following urine deposition suggests higher photosynthetic rates, since g and photosynthetic rate are generally closely correlated, especially in C_3 species (Nobel, 1983). *Poa*'s ability to maintain higher g and likely continue carbon assimilation at low ψ may partially explain the large growth response of *Poa* following urine deposition (Day and Detling, 1990), as well as N fertilization (Owensby *et al.*, 1970) in semi-arid grasslands. Consistent with this hypothesis, leaf conductance of *Schizachyrium* was usually not higher off patches, and aboveground biomass of this species was generally similar on and off urine patches.

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