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Source: *Journal of Applied Ecology*, Vol. 29, No. 1 (1992), pp. 1-8

Published by: [British Ecological Society](#)

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Small-scale heterogeneity in a semi-arid North American grassland. I. Tillering, N uptake and retranslocation in simulated urine patches

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Summary

1. We examined the response of two grass species differing in growth form and photosynthetic pathway to simulated cattle urine deposition in a native semi-arid grassland. The species were *Agropyron smithii*, a spreading, rhizomatous C₃ grass, and *Bouteloua gracilis*, a cespitose C₄ grass. They are codominants in this grassland and *A. smithii* is the most important forage species in the study site.

2. Simulated urine increased tiller density of both species, with *B. gracilis* increasing in the first growing season while *A. smithii* was not increased until the second year. Both species had increased tiller densities and above-ground N concentrations in a ring outside the area wetted by urine. The percentage of retranslocated leaf N decreased, and standing dead litter N concentration increased in both species after urine deposition.

3. Above-ground biomass, N yield, and tiller height of *A. smithii* increased in urine patches. Leaf production was not affected by treatment. Both the increase in the live:dead biomass ratio and the higher number of live leaves at the end of the first growing season suggested urine deposition delayed senescence of *A. smithii*.

4. The implications of plant growth form in the spread of urine, the potential duration of urine effects in semi-arid grasslands, and the role of herbivore urine deposition in promoting grassland structural and functional heterogeneity are discussed.

Key-words: urine, grassland, tiller, uptake, heterogeneity.

Journal of Applied Ecology (1992) 29, 1–8

Introduction

Environments can be regarded as mosaics of patches at any scale of resolution (Wiens 1976). Large grazing animals generate patchiness in terrestrial vegetation through activities such as defoliation, trampling and excretion (Harper 1977). Dung and urine patches may thus be regarded as grazer-induced factors that promote variation in grasslands, both in space and time (Snaydon 1985).

Urine deposition by grazers is an important contributor to the fertility of pastures (Watkin 1957) and is considered a key pathway for fast nitrogen cycling in grasslands (Woodmansee 1978; Floate 1981). Because of rapid chemical transformations of urea in the soil (Stillwell & Woodmansee 1981),

the input of nutrients in urine is analogous to the addition of inorganic fertilizer N (Wolton 1979), thus providing a pulse of N potentially available for plant uptake.

Although considerable research has addressed the effects of urine deposition in pastures and grasslands, little has been done in native semi-arid grasslands of North America (e.g. Stillwell 1983), where species with both contrasting growth forms and photosynthetic pathways coexist. Urine deposition may have a variety of potential consequences in these ecosystems. For example, rhizomatous species may be able to spatially spread the effect of urine pulses more effectively than cespitose ones. Also, C₃ and C₄ plants may exhibit different temporal responses because of different temperature effects on phenology, nutrient uptake, and nitrogen use efficiency (Christie & Detling 1982). Moreover, C₃ and C₄ species respond differently to high N availability,

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although the kind of response is still controversial (Brown 1978; Sage & Pearcy 1987a).

The objectives of this field study were twofold. First, we determined how simulated urine deposition affected changes in tiller number, N uptake, and N retranslocation of two grass species with contrasting growth forms and photosynthetic pathways. The species were *Agropyron smithii* Rydb., a spreading, rhizomatous, C₃ grass, and *Bouteloua gracilis* (H.B.K.) Griffiths, a cespitose, C₄ species. We predicted that the rhizomatous species would transport N away from the urine patch, increasing the size of the response area, while the cespitose species would respond only in the area wetted by urine. Second, we examined above-ground biomass, N-yield and allocation, and leaf production of *A. smithii*, the most important forage species at the study site (Samuel & Howard 1982), in response to the same urine deposition event.

Study area

The study area (Hart *et al.* 1988), was located at the High Plains Grasslands Research Station (HPGRS) 7 km NW of Cheyenne, Wyoming, USA. The vegetation is native semi-arid mixed grass prairie dominated by *A. smithii*, *Stipa comata* Trin. & Rupr., and *B. gracilis*. The topography consists of rolling hills at 1910–1950 m altitude. Mean annual precipitation is 338 mm, with a maximum in May and early June, and about 70% occurring during April–September. The growing season averages 127 days. The area is grazed by Hereford and Hereford cross-bred cattle.

The experiment was done during the 1986 and 1987 growing seasons in a nearly level enclosure, 70 × 30 m, to avoid confounding problems of cattle grazing, trampling, urination and defecation. It was established in 1983 in a lightly grazed pasture. The soil is an Ascalon loam, Aridic Argiustoll. Precipitation in 1986 (376 mm) was near normal, but in 1987 (492 mm) it was considerably above the long-term average.

Methods

Sixteen randomly located plots were paired according to tiller density of both species. One member of each of the eight pairs was randomly assigned to receive a urine treatment or to remain untreated. The urine treatment consisted of a single application of 2 litres of artificial urine (formula in Stillwell 1983; Day & Detling 1990) to a circular plot 28 cm in radius (0.25 m²) on 13 June 1986, 2 weeks after steers were introduced to adjacent pastures. The volume added and the area covered were within the normal range for cattle urine patches (Doak 1952; Wilkinson & Lowrey 1973; Betteridge, Andrewes & Sedcole 1986) and were equivalent to a fertilization of

51 g N m⁻². Two concentric rings were established around each plot by adding 14 and 28 cm to the radius. These three areas are referred to as rings 1, 2 and 3, ring 1 being the innermost 0.25 m² circle.

Tillers were counted every 15 days from mid-June to August in 1986 and at the end of each month from May to August in 1987. Total number of live tillers in each of the three rings was recorded for *Agropyron*. Because they were smaller and far more numerous, live tillers of *Bouteloua* were counted in only two randomly located, permanent 10 × 10 cm quadrats in each of the three rings. Sample size for *Bouteloua* was reduced to six pairs because of difficulty in distinguishing its vegetative tillers from those of *Buchloe dactyloides* (Nutt.) Engelm. in two plots. Additionally, individual tillers of *Agropyron* (two per ring in 1986, three per ring in 1987) were marked with coloured bird bands and the number of live and dead leaves was recorded at each sampling date.

In early September 1986 and 1987, all above-ground material of *Agropyron* was harvested, separated into live and current year's dead material, dried for at least 24 h at 60 °C, and weighed. Material collected in ring 1 was further separated into blades and sheaths plus culms. For *Bouteloua*, enough material for N determinations was harvested, including both 10 × 10 cm tiller-density quadrats, and it was also separated into live and current year's dead components. Dead material of both species from previous years was discarded. Samples of both species were also collected from ring 1 in June 1987, the period of peak tiller densities in 1986 (see Results). Plant N concentration was determined by a micro-Kjeldahl procedure.

Prior to flowering, in June 1987, the height of all *Agropyron* tillers was measured in contiguous 10 × 10 cm quadrats along a 120-cm transect across all three rings of urine and control patches. The number of flowering tillers in each ring was recorded at the end of June and July.

As N is withdrawn from leaves prior to senescence, a relatively immobile nutrient like Ca may be used to estimate its retranslocation (Vitousek & Sanford 1986). Nitrogen retranslocation was thus estimated (for ring 1 only) by dividing the N/Ca ratio in standing dead litter by the N/Ca ratio in the live plant tissue (at harvest both years and June 1987) and subtracting it from 1 (Vitousek & Sanford 1986). The results were expressed as percentages. This method, however, may overestimate retranslocation measured on a leaf area basis (P.M. Vitousek, unpublished). Ca concentration of plant samples was determined by atomic absorption spectrophotometry.

Tiller density was analysed with a repeated measures analysis of variance (ANOVA), with urine as the between-plots treatment and ring and date as the within-plots treatments. Because the pair (block) × treatment interactions were not assumed to be zero,

they were used as the error terms. The ANOVA was done for each individual date and on the overall means. The means were compared only when the urine \times ring interaction was significant ($P \leq 0.05$) in the ANOVA. The Satterthwaite procedure (Milliken & Johnson 1984) was used to calculate degrees of freedom for mean comparisons at each individual date. The statistical model allowed comparisons of (a) means of urine and control patches at the same level of ring, and (b) means of the three rings within the urine and control patches. To correct for initial differences in tiller density, the ratio of each measured density over the initial was used. This ratio and both the total above-ground biomass and N-yield data were log-transformed to satisfy ANOVA assumptions.

Variables measured only once were analysed with the same model, omitting the date factor. Data collected only for ring 1 were compared with *t*-tests. Standard errors of data analysed after transformation are omitted since results are presented in the original scale of measurement (Steel & Torrie 1980).

Results

Both species responded to artificial urine deposition but there was a temporal displacement in their response (Fig. 1). *Bouteloua* had significant increases in tiller density in 1986, both averaged

over time and at individual dates. Tiller density averaged over date in ring 1 of urine patches (4497 tillers m^{-2}) was significantly higher ($P < 0.01$) than in ring 1 of controls (2877 tillers m^{-2}). However, it did not differ among rings 2 and 3 of treated and untreated patches ($P > 0.1$). Within the urine patches, tiller density in ring 1 was higher than in rings 2 and 3 (3373 and 2618, respectively). The seasonal decrease in tiller density after June in 1986 (Fig. 1) was significant ($P < 0.001$) for both urine and control patches. By the end of July and August, ring 1 in urine patches had a higher tiller density than rings 2 and 3 (Fig. 1). The individual date comparisons also showed that, in late August, tiller densities in rings 1 and 2 of urine patches were significantly higher ($P < 0.05$) than in rings 1 and 2 of controls. In 1987 there was no significant treatment effect for *Bouteloua*, and tiller density was generally lower than in 1986 in both treated and control patches.

In contrast to *Bouteloua*, tiller density of *Agropyron* in urine patches did not differ from controls in 1986, but it increased greatly in 1987 (Fig. 1). Tiller densities of rings 1 and 2 of urine patches, averaged over the 1987 season (438 and 248 respectively), were significantly greater than their respective controls (217 and 193). The individual date comparisons showed that significant differences within urine patches developed early in the 1987 growing season (Fig. 1). Furthermore, by May, tiller densities in

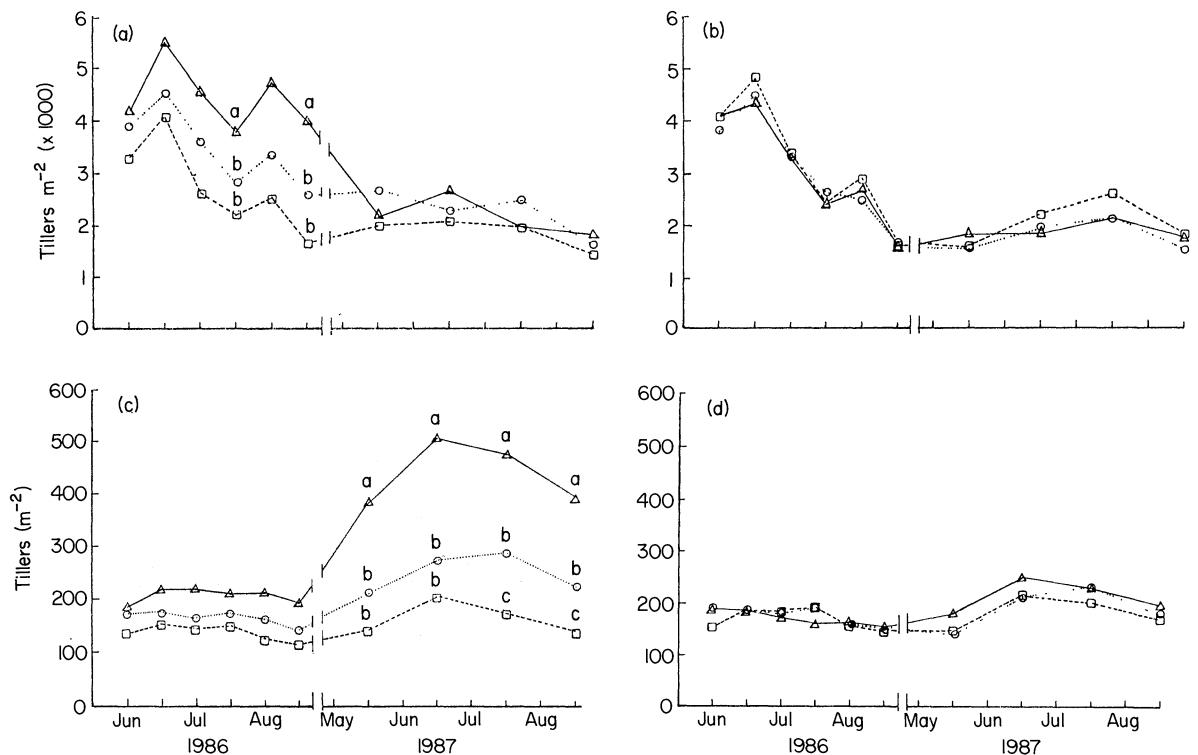


Fig. 1. Seasonal trend of live tiller densities of *Bouteloua gracilis* (a,b) and *Agropyron smithii* (c,d) in three concentric rings (ring 1 is the innermost) of simulated urine patches and controls. Each point is the mean of six (a,b) or eight (c,d) replicates. Means within the same date with different letters are significantly different at $P < 0.05$. Only significant differences are indicated. Between-treatment comparisons are described in the Results. Δ , ring 1; \circ , ring 2; \square , ring 3.

rings 1 and 2 of urine patches were already significantly higher than in their respective controls. These differences were maintained until the end of the experiment.

Shoots of both species had higher N concentrations in rings 1 and 2 of simulated urine patches than in the controls in 1986, and within urine patches, N concentrations decreased from the inner to the outermost ring (Fig. 2a, b). In 1987, the average N concentration of *Bouteloua* across all three rings in urine patches was still significantly higher ($P < 0.01$) than in the controls, but for *Agropyron* the urine effect was not significant ($P = 0.075$). The samples of both species collected from ring 1 in June 1987 however, had significantly higher N concentrations in treated patches than in the controls (Tables 1 and 2). Similarly, standing dead litter of both species in ring 1 of simulated urine patches had higher N concentrations than the controls in both years (Tables 1 and 2).

In 1987, flowering of *Agropyron* was stimulated by artificial urine in rings 1 and 2. The mean percentage

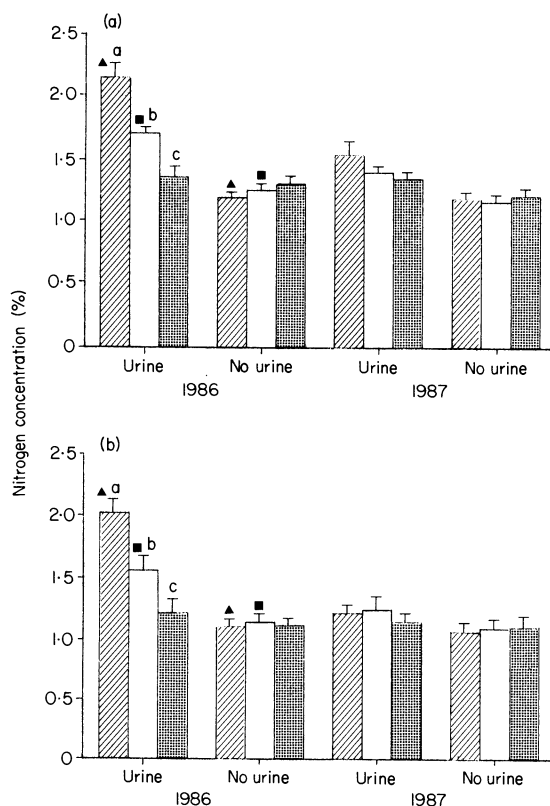


Fig. 2. Above-ground N concentration at harvest of (a) *Bouteloua gracilis*, and (b) *Agropyron smithii* in three concentric rings (ring 1 is the innermost) of simulated urine patches and controls. Each bar represents the mean of six (a) or eight (b) replicates. Symbols indicate between-treatment and letters within-treatment comparisons. Rings with the same symbol in different treatments and with different letters within the same treatment are significantly different at $P < 0.05$. Only significant differences are indicated. Standard errors are shown. ▲, ring 1; □, ring 2; ■, ring 3.

(\pm SE) of flowering tillers in these rings (13.5 ± 2.0 and 8.6 ± 1.8 , respectively) was significantly higher ($P < 0.01$) than in their controls (1.8 ± 0.7 and 0.8 ± 0.4). Flowering in 1986 was negligible in both treated and control plots. Total above-ground biomass at harvest also increased in rings 1 and 2 of urine patches in 1987 (Fig. 3a). In 1987, blade and individual tiller biomass were both greater in urine patches than in the controls, and the blade:sheath+culm ratio decreased (Table 1), while the mean tiller height differed ($P < 0.001$) between urine patches (24.5 ± 0.4 cm) and the controls (18.8 ± 0.3).

Above-ground N yield of *Agropyron* was greater in ring 1 of simulated urine patches than in the controls in both years (Fig. 3b). Also, there was a significant decrease in N yield from ring 1 to ring 3 of the urine patches (Fig. 3b). Blade N yield and N concentration of *Agropyron* were higher in ring 1 of treated patches than controls both years, but above-ground N allocation (blade:sheath + culm ratio) changed significantly only in 1987 (Table 1).

The live:dead biomass ratio of *Agropyron* was higher in ring 1 of urine patches than in controls in September 1986, but not in 1987 (Table 1). This is consistent with the greater number of live leaves per tiller in ring 1 of urine patches (3.4 ± 0.3) than in controls (2.4 ± 0.2 ; $P \leq 0.05$) in August 1986.

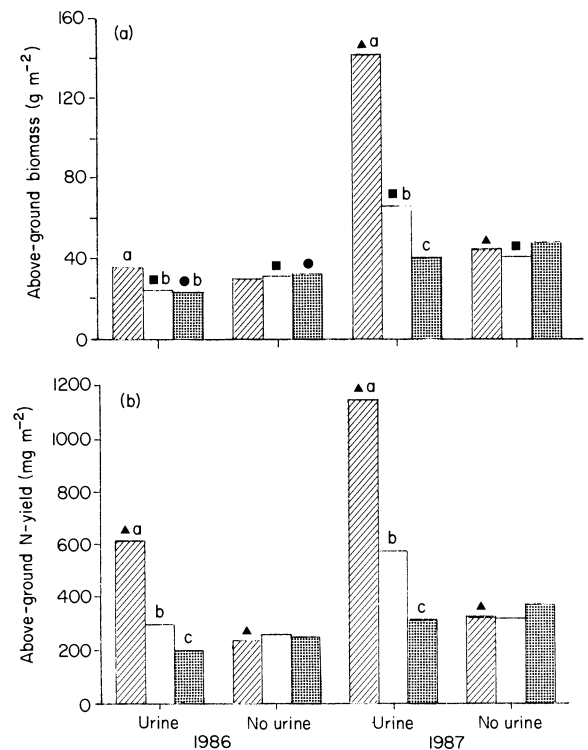


Fig. 3. Above-ground biomass at harvest (a) and above-ground N-yield (b) of *Agropyron smithii* in simulated urine patches and controls. Each bar represents the mean of eight replicates. Symbols, letters, and significance levels as in Fig. 2. Comparisons are for each individual year.

Table 1. The effect of simulated urine deposition on biomass and N of plant parts of *Agropyron smithii*; data for ring 1 only ($\bar{x} \pm SE$, $n = 8$ except litter and June 1987 data where $n = 4$)

	Urine	No urine	P
(a) Biomass			
1986			
Blade (g m^{-2})	19.5 \pm 4.7	12.3 \pm 2.2	NS
Blade:sheath+culm ratio	1.8 \pm 0.5	2.2 \pm 0.3	NS
Biomass per tiller (mg)	151 \pm 17	149 \pm 14	NS
Live/dead ratio	5.7 \pm 1.0	2.4 \pm 0.2	**
1987			
Blade (g m^{-2})	36.0 \pm 9.7	17.4 \pm 3.3	*
Blade:sheath+culm ratio	0.6 \pm 0.1	1.6 \pm 0.3	**
Biomass per tiller (mg)	235 \pm 27	148 \pm 9	*
Live/dead ratio	1.9 \pm 0.3	2.1 \pm 0.3	NS
(b) Nitrogen			
1986			
Blade N-yield (mg m^{-2})	471 \pm 124	163 \pm 30	*
Blade:sheath+culm N ratio	3.4 \pm 0.4	2.6 \pm 0.5	NS
Blade (%)	2.34 \pm 0.10	1.32 \pm 0.05	***
Standing dead litter (%) [†]	1.04 \pm 0.09	0.51 \pm 0.02	*
1987			
Blade N-yield (mg m^{-2})	608 \pm 158	233 \pm 47	*
Blade:sheath+culm N ratio	1.1 \pm 0.2	2.2 \pm 0.3	**
Blade N concentration (%)	1.74 \pm 0.06	1.31 \pm 0.06	**
Standing dead litter (%)	0.77 \pm 0.06	0.55 \pm 0.03	*
Shoot N in June (%)	2.59 \pm 0.18	1.64 \pm 0.07	*

* $P \leq 0.05$, ** $P < 0.01$, *** $P < 0.001$, NS = not significant ($P > 0.05$), by paired t -tests.

[†] For the determination of standing dead litter and June shoot N concentrations, material was pooled and the pairing criterion was lost, so independent t -tests were employed.

Table 2. The effect of the simulated urine deposition on standing dead litter and June live shoot N concentrations (%) of *Bouteloua gracilis*; data for ring 1 only ($\bar{x} \pm SE$; $n = 4$)

	Urine	No urine	P
(a) 1986			
Standing dead litter	1.22 \pm 0.10	0.59 \pm 0.02	*
(b) 1987			
Standing dead litter	1.07 \pm 0.04	0.56 \pm 0.02	*
Live shoot	2.59 \pm 0.14	1.53 \pm 0.04	**

* $P < 0.05$, ** $P \pm 0.01$, by independent t -tests.

The total number of leaves produced per tiller in treated and control patches did not differ however. Averaged over both patch types, tillers produced 4.4 \pm 0.1 leaves in 1986 and 5.0 \pm 0.1 in 1987 ($\bar{x} \pm SE$).

Nitrogen retranslocation was estimated from live material harvested in September both years and in June of 1987 only (Table 3). Estimates based on September data are conservative because, by then, some N probably had been translocated out of the leaves. Thus, June estimates may better reflect the percentage of N actually retranslocated. Plants of both species growing in simulated urine patches generally retranslocated a smaller proportion of N below-ground than did control plants (Table 3).

Table 3. Percentage shoot-N retranslocation to below-ground structures ($\bar{x} \pm SE$, with sample sizes in parentheses) of *Agropyron smithii* and *Bouteloua gracilis*; data for ring 1 only.

	Urine	No urine	P
(a) 1986 (Sep) [†]			
<i>Agropyron</i>	59 \pm 2 (3)	68 \pm 2 (4)	*
<i>Bouteloua</i>	51 \pm 7 (4)	63 \pm 2 (4)	+
(b) 1987 (Sep)			
<i>Agropyron</i>	59 \pm 2 (5)	60 \pm 3 (5)	NS
<i>Bouteloua</i>	54 \pm 6 (3)	65 \pm 1 (3)	+
1987 (Jun)			
<i>Agropyron</i>	69 \pm 1 (4)	74 \pm 1 (4)	*
<i>Bouteloua</i>	63 \pm 2 (3)	79 \pm 1 (3)	*

+ $P < 0.1$, * $P < 0.05$, NS = not significant ($P > 0.01$), by one-tailed independent t -tests.

[†] Retranslocation was estimated from material harvested in early September each year and in June 1987.

Discussion

TILLERING DYNAMICS AND SPATIAL RESPONSE

Although urine return has been regarded as beneficial because it increases dry matter production and nutrient yield of grasses (Watkin 1957), few

other studies have investigated its effects on tiller numbers. Marriott, Smith & Baird (1987) reported poor tiller production of a mixture of *Lolium perenne* and *Poa* spp. in response to urine addition, while Curll & Wilkins (1983) found increased numbers of *L. perenne* tillers which they attributed to the readily available N in urine. Our results are more similar to the latter and suggest that increases in dry matter production of grass following urine return (Watkin & Clements 1978) may result partly from N stimulation of tiller production and partly from increased tiller size.

The temporal differences in the species' responses to simulated urine may have resulted from their contrasting photosynthetic pathways and phenologies. A greater photosynthetic N use efficiency (PNUE) and a higher growth rate per unit N under high N conditions might allow C_4 species to allocate a greater proportion of available N to production of roots or leaves, as less N would be invested in photosynthetic enzymes (Sage & Pearcy 1987a, b). This implies that *Bouteloua* could have used such available N for tiller production. Furthermore, since some grasses resume tillering after flowering (Langer 1979) and *Bouteloua* flowers in mid- to late July (Dickinson & Dodd 1976), well after the simulated urine addition, tiller production could be higher in N-rich patches. In contrast, by the time of urine addition *Agropyron* would have nearly completed its 'developmental programme', thus not allowing the release of buds involved in tiller development. In other studies in which C_3 species failed to increase tillering or production after urine addition, treatment was applied in mid- or late June and the studies were concluded after the first growing season (Day & Detling 1990; Marriott, Smith & Baird 1987). As an alternative hypothesis, possible differences in root:shoot allocation patterns of the species may have resulted in *Agropyron* storing some available N below ground initially while *Bouteloua* was able to utilize it more readily above ground.

Contrary to expectations, both species showed tillering responses and higher above-ground N concentrations in rings 1 and 2 of urine patches. These results partially agree with those of Stillwell (1983), who reported biomass increases in urine patches for 2 years in *B. gracilis*-dominated shortgrass steppe, and higher above-ground N concentration in areas larger than those wetted by urine in the first year. We suggest that older parts of a rhizomatous or stoloniferous clone affected by urine deposition may translocate nutrients to growing points located beyond the urine patch. Available evidence indicates this is the prevalent mode of nutrient movement in such clonal plants (Noble & Marshall 1983; Slade & Hutchings 1987). The increase in *Bouteloua* shoot N concentration in ring 2 may have resulted from intra- or interspecific nutrient transfer through mycorrhizae (Haystead, Malacjzuk & Grove 1988)

as both species are facultatively mycorrhizal (Allen, Allen & Stahl 1984).

BIOMASS PRODUCTION AND N YIELD OF *AGROPYRON*

Differences in above-ground biomass in 1986 were probably a function of initial tiller densities. However, the higher number of tillers and their greater mass, but not a higher number of leaves, were responsible for the increase in above-ground biomass of *Agropyron* in urine patches in 1987. Increases in tiller number and size after fertilization have been reported for other graminoids (Shaver, Chapin & Gartner 1986), and the constancy of leaf number per tiller, despite variation in nutrient supply, seems a general feature of grasses (Langer 1966, but see Polley 1987).

Simulated urine deposition apparently delayed senescence only in the first growing season when the live:dead biomass ratio and the number of live leaves per tiller were greater in urine patches. Similar results have been obtained with grasses (Day & Detling 1990), and in fertilization studies with conifers (Miller, Cooper & Miller 1976; Turner 1977), the herb *Glechoma hederacea* L. (Slade & Hutchings 1987), and with an evergreen arctic tundra shrub which showed short-term increases but long-term decreases in leaf longevity (Shaver 1983).

Delayed leaf senescence and increases in N uptake and yield, and in biomass production (only in 1987) suggest urine deposition in this semi-arid grassland may result in patches consisting of better quality and greater quantity of forage for grazing animals, particularly at times when the surrounding vegetation is senescing or not actively growing.

NITROGEN RETRANSLLOCATION

The proportional decrease in N retranslocation with increased N availability in urine patches is generally consistent with results of other research (Turner 1977; Shaver & Melillo 1984; Vitousek & Sanford 1986; but see Birk & Vitousek 1986; Lajtha 1987). Despite a decrease in nutrient recovery efficiency, our conservative estimates indicated that even after very heavy fertilization both species still retranslocated more than 50% of their above-ground N to crowns, rhizomes and roots. Utilizing ^{15}N , Clark (1977) estimated that 33–50% of *Bouteloua*'s above-ground N in any one year could be recycled internally and used in the following season. Our estimates for control plants indicated that more than 60% of above-ground plant N may be retranslocated. This may be an important mechanism for nutrient conservation in clonal plants (Cook 1985; Jónsdóttir & Callaghan 1988).

Results of this and Stillwell's (1983) study indicate that the potential effects of urinary N on plant production and on N concentration and yield in semi-arid grasslands may last longer than the maximum 9.5 months (production) and 3 months (N concentration and yield) reported by others (Loter, Woodhouse & Petersen 1966; Watkin & Clements 1978; Wolton 1979). Tiller and biomass accumulation of *Agropyron* were significantly higher in urine patches 15 months after treatment, and N concentrations of both species in urine patches were higher for at least 12 months after simulated urine addition. Long-term effects of a single application of fertilizer in a native semi-arid grassland were reported by Black & Wight (1979), whose N fertilization rates of 336 kg N ha⁻¹ and 1008 kg N ha⁻¹ increased N concentration of plants even after 8 years of application and when dry matter yield responses had ceased.

Conclusions

The effects of urine deposition in this semi-arid grassland may be viewed at two different temporal scales. A short-term effect resulting from increased nutrient availability leads to greater plant N uptake and consequently to higher leaf N concentrations. In the longer term, plant N retranslocation apparently allows re-utilization of assimilated N, and the changes in litter quality may affect N release through the decomposition pathway. Clearly, the actual N dynamics at the level of the urine patch will strongly depend on the grazing pressure experienced by plants in these sites.

Increases in tiller density (a measure of plant spatial concentration), plant biomass and tiller height in simulated urine patches indicate grazing animals may promote local structural patchiness of the vegetation. Similarly, increases in N uptake and yield and litter N concentration, and the decrease in relative N retranslocation indicate that functional properties of the vegetation are also affected. Thus, urine return by grazing animals, mediated by plant morphological and ecophysiological processes, may produce a mosaic of patches or 'microecosystems' not only structurally, but functionally, different from the surrounding grassland matrix.

Acknowledgments

We thank Drs April Whicker, David Steingraeber, David Swift, and Richard Hart for their comments on the manuscript, Dr F.S. Chapin III for a discussion of the results, Dr Phillip L. Chapman for statistical advice and for developing the formulas for mean comparisons, Ernie Taylor of the High Plains Grasslands Research Station (HPGRS) for the calcium analyses, Dr R. Hart for the field facili-

ties, and Mariana A. de Jaramillo for help in the field. The work was supported by a postgraduate scholarship from the Universidad Nacional Autónoma de México to V.J.J., by the HPGRS, and by NSF Grant BSR-8406660 to J.K.D.

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Received 14 December 1989; revision received 7 December 1990