

Peter M. Kotanen · Joy Bergelson

Effects of simulated grazing on different genotypes of *Bouteloua gracilis*: how important is morphology?

Received: 22 March 1999 / Accepted: 26 October 1999

Abstract Populations of grasses exposed to grazing by vertebrates often exhibit reduced stature, increased tillering, reduced flowering, and other morphological differences which distinguish them from ungrazed populations. These differences frequently are interpreted as an adaptive response that reduces grazing damage; however, there are few experimental tests of this hypothesis. This paper describes a field experiment designed to determine whether morphological variation among genotypes of the grass *Bouteloua gracilis* is related to variation in their responses to grazing. Eleven genotypes differing in morphological and reproductive characters were transplanted into a shortgrass steppe community near Fort Collins, Colorado. Replicates of each genotype were subjected to clipping treatments intended to realistically simulate three grazing intensities. After two growing seasons, different genotypes still maintained significant differences in a wide range of morphological and demographic characters. However, there were few significant effects of grazing treatment, and no significant genotype × treatment interactions. These results suggest that for *B. gracilis* clipped in simulation of natural grazing, defoliation has few short-term effects on fitness components, and intrapopulation morphological variation has few consequences for defoliation resistance.

Key words *Bouteloua gracilis* · Grazing · Morphology · Resistance · Shortgrass steppe · Tolerance

Introduction

Grazing by vertebrate herbivores can have strong negative impacts on plant growth and reproduction (e.g., Harper 1977; Crawley 1983, 1997; Hendrix 1988; Lindroth 1989; Louda et al. 1990; Marquis 1992). Chronic grazing also frequently leads to changes in plant morphology and development (e.g., Jameson 1963; Crawley 1983, 1997; McNaughton 1984; Lindroth 1989; Louda et al. 1990; Vallentine 1990; Huntly 1991; Mopper et al. 1991). In grasses, these changes typically comprise a syndrome including decreased stature, reduced flowering, more prostrate growth form, increased turf formation, and increased tillering (e.g., Gregor and Sansome 1927; Kemp 1937; Hickey 1961; Peterson 1962; Jameson 1963; Crawley 1983; McNaughton 1984; Aarssen and Turkington 1985; Carman and Briske 1985; Coughenour 1985; Milchunas et al. 1988; Oosterheld and McNaughton 1988; Vallentine 1990). Such morphological shifts may reflect genetic changes in grazed populations in addition to the plastic responses of grazed individuals, as has been best demonstrated for grasses exposed to grazing by prairie dogs (Detling and Painter 1983; Detling et al. 1986; Jaramillo and Detling 1988; Polley and Detling 1988, 1990; Whicker and Detling 1988a, 1988b; Painter et al. 1989, 1993).

Even in taxa able to survive intense grazing pressure, selection generally should favour grazing-resistant genotypes (Dawkins 1986, p. 182; Westoby 1989). Morphological changes in grazed grass populations frequently are explained in this manner (e.g., Kemp 1937; Jameson 1963; McNaughton 1984; Carman and Briske 1985; Detling et al. 1986). Grazing resistance includes at least two distinct components: herbivore avoidance, or strategies which decrease losses to herbivores, and tolerance, or strategies which decrease the fitness costs of these losses (Belsky et al. 1993; Rosenthal and Kotanen 1994; Strauss and Agrawal 1999). Avoidance can be further subdivided into defense, or strategies which actively deter herbivores, and escape, or the reduction of herbivory by making tissues inaccessible. (Fritz and Simms 1992;

P.M. Kotanen¹ (✉) · J. Bergelson
Department of Ecology and Evolution, The University of Chicago,
1101 East 57th St., Chicago, IL 60637, USA

Present address:

¹ Department of Botany, University of Toronto at Mississauga,
3359 Mississauga Road North,
Mississauga, Ontario, L5L 1C6, Canada

Belsky et al. 1993; Rosenthal and Kotanen 1994; Strauss and Agrawal 1999). In plants lacking spines or other physical defences, morphology is likely to most directly influence tolerance and the escape component of avoidance. Shorter stature, prostrate morphology, and turf formation may make a plant less exposed to damage by grazing animals, while reduced flowering may reflect an allocation of resources away from vulnerable inflorescences and toward vegetative growth. Increased tillering and the production of smaller structures may allow rapid replacement of lost photosynthetic tissue, and increase the ability of plants to flexibly capitalize on the nutrient pulses provided by herbivore feces and urine. Many of these responses may carry costs in ungrazed habitats; for example, smaller plants risk being outcompeted for light, nutrients, or space by larger competitors (e.g., Grime 1979; Tilman 1982, 1988; Grace and Tilman 1990).

Comparative studies of heavily versus lightly-grazed populations risk confounding the effects of grazing *per se* with the effects of other differences between grazed and ungrazed habitats (e.g., competitive regime, fire frequency, soil characteristics). This is especially troublesome since small stature and other features believed to confer resistance to grazing also confer resistance to other environmental stresses, such as fire and drought, and may in fact have originated in response to these stresses (Coughenour 1985; Belsky et al. 1993; Rosenthal and Kotanen 1994). For example, smaller plants in grazed populations actually may be a consequence of decreased competition for light, increased surface wind, increased drying of soil, or other physical differences between sites. Common garden and greenhouse clipping experiments provide a partial solution. These allow the performance of different morphs to be compared in a uniform environment; while such experiments do not eliminate the possibility that differences between morphs evolved in response to a stress other than grazing, they do demonstrate whether differences between morphs currently confer grazing resistance.

Such experimental studies are scarce, and the results are mixed. A few deal with plants other than grasses; to cite two examples, Solbrig and Simpson (1974, 1977) found that taller genotypes of *Taraxacum officinale* dominated in frequently-mowed sites, but performed less well when clipped than shorter genotypes from infrequently-mowed sites; Warwick and Briggs (1980) found that prostrate genotypes of *Plantago major* from lawn populations did better when clipped than erect plants from roadsides. However, most studies focus on mammalian grazing of graminoids. Carman and Briske (1985) reported that smaller *Schizachyrium scoparium* from livestock-grazed populations were more grazing-resistant than taller plants from ungrazed populations. In a series of studies of *Agropyron smithii* and *Bouteloua gracilis*, Detling and Painter (1983), Detling et al. (1986), and Painter et al. (1989) also found that smaller plants from heavily grazed prairie dog towns grew better following defoliation than larger plants from lightly-grazed areas, but in other studies of this system, Polley and Detling

(1988, 1990) and Jaramillo and Detling (1988) found practically no population \times defoliation interactions for these same grasses. Jaendl et al. (1994) found a history of livestock grazing had no effects on defoliation responses of *Festuca idahoensis*, though it did reduce plant height; conversely, Smith (1998) found plants from livestock-grazed populations of *B. curtipendula* survived clipping better than plants from ungrazed populations, though there were few morphological differences between populations. Finally, Oesterheld and McNaughton (1988) found that, given sufficient time following clipping, tall plants of *Themeda triandra* from sites lightly grazed by African ungulates overcompensated in terms of biomass, while short plants from heavily grazed areas performed relatively less well. One potential problem with these studies is that all have been conducted in pots, growth chambers, greenhouses, or common gardens; these artificial environments are likely to produce unnatural responses which can mask the effects of experimental treatments. Conversely, effects detected in a highly controlled growth chamber environment may be lost in the “noise” of real field conditions. The solution to these problems is to experimentally compare the performance of genotypes which are known to differ stably with respect to morphological characters, and are transplanted into a common field environment. This is the approach that we have taken.

In this paper, we describe the results of a field experiment designed to determine whether morphological variation within a grazed population of *B. gracilis* leads to variation in the resistance of this grass to grazing. This morphological variability might be maintained in part by variation in soil properties and other microenvironmental characteristics (Coughenour 1985; McGinnies et al. 1988; Belsky et al. 1993; Rosenthal and Kotanen 1994); however, it has the potential to affect the ability of these plants to tolerate or escape grazing. Experimentally separating tolerance and escape requires designs that remove constant fractions of tissue from different genotypes (Oesterheld and McNaughton 1991; also Strauss and Agrawal 1999). Instead, we chose to study morphological influences on overall resistance under more realistic grazing regimes. Our approach was to select genotypes which were known to differ with respect to stature and reproductive characters, and expose them to different defoliation treatments, within an otherwise shared environment. We predicted that if morphology affects the ability of *B. gracilis* to resist grazing, we should detect morphology \times grazing interactions with respect to important fitness components: when clipped, smaller and less fecund genotypes should perform better than other genotypes; when unclipped, this advantage should diminish or be reversed. Unlike most studies, we compared genotypes originating in the same area, rather than populations with different histories; as such, we were attempting to see whether local variation provides the scope for a selective response to grazing pressure. This paper is one of the first to compare grazing responses of morphologically different genotypes in a field setting.

Methods

Study site

This study was conducted at the Central Plains Experimental Range (CPER) (40°49'N, 107°47'W, 1660 m above sea level), c. 60 km northeast of Fort Collins, Colorado, United States. This 6280-ha area, a research site since 1937, is set within the much larger Shortgrass Steppe Long-Term Ecological Research site (Shortgrass Steppe LTER Home Page <<http://sgs.cnr.colostate.edu/>>). This site once supported bison, currently supports numerous pronghorn, and is used for grazing by cattle (Lauenroth et al. 1994a). Much of this site is dominated by *Bouteloua gracilis* (H.B.K.) Lag. ex Griffiths=*Chondrosium gracile* Humboldt, Bonpland & Knuth, a native drought- and grazing-tolerant caespitose C₄ perennial grass (Milchunas et al. 1989, 1990; Kotanen et al. 1998). At this location, growth of *B. gracilis* (blue grama) occurs approximately between April and October (Dickinson and Dodd 1976). Culms are frequent, and are taller than vegetative shoots. Successful establishment from seed is rare in shortgrass steppe (though not in wetter regions: Fair et al. 1999), probably occurring only in suitable sites in wet years; in most years, plants exclusively spread by clonal expansion (Lauenroth et al. 1994b; Aguilera and Lauenroth 1995). Like many grasses, *B. gracilis* has a small and variable seed bank (Coffin and Lauenroth 1989b).

Sources of material

The genotypes used in this experiment originally were collected in 1981 for the study of McGinnies et al. (1988). Samples were gathered from a 7 ha area within a single 2.5-km² section of the CPER (Section 17). This area has never been ploughed (McGinnies et al. 1988), and has been subject to variable but moderate levels of cattle grazing for many years; on an evolutionary timescale, it is small enough that all plants presumably shared similar grazing histories. Plants were chosen to maximize variation in a range of morphological characters, including culm height, number of culms, leaf length, leaf colour, "bunchiness", and "general plant appearance" (McGinnies et al. 1988). Each was subdivided into replicate clones, which were placed in a common garden at the CPER in 1982. Different genotypes maintained significantly different morphologies under these common garden conditions, suggesting a genetic basis (McGinnies et al. 1988).

This common garden was maintained subsequently by CPER staff. In October 1995, we revisited it, and collected plug samples from multiple replicates of 15 genotypes. These plugs were transported to a greenhouse at the University of Chicago, where they were grown and subdivided over the winter. Survivorship and growth of most genotypes was good, but 4 were discarded because of poor survival or contamination by other grasses, leaving a set of 11 genotypes. In May 1996, replicates of each of these genotypes were transplanted into experimental plots set in a moderately-grazed *B. gracilis*-*Buchloe dactyloides* community at the CPER (section 21N), a few kilometers from their original collection site. Grazing of this community is managed by the CPER so that approximately 40% of unprotected above-ground biomass is removed annually by cattle.

Forty-one 1 m×0.5 m experimental plots were established in two staggered lines along a 100 m×5 m transect. Each plot received one replicate of each genotype (mean size=7.12 shoots; SEM=0.16 shoots), planted into a small (5 cm) hole dug into the surrounding vegetation. This resulted in a total of 41 replicates/genotype, or 451 plants in total. Plants were marked with wire rings and watered once immediately following transplantation. All plots were protected by wire cages (length=1.0 m; width=0.5 m; height=0.5 m; 25 cm mesh). These cages restricted grazing by cattle, while subjecting experimental plants to essentially the same physical environment as the surrounding grazed community, including exposure to cattle urine and faeces.

Grazing treatments

All plants within each plot were subjected to one of three treatments: clipping to 1.5 cm above the crown (similar to cattle grazing), clipping to 3.0 cm above the crown (milder than cattle grazing), and unclipped. Clipping treatments were applied twice: once in May 1996 (coincident with the annual start of cattle grazing), and once in July 1996 (mid-summer). By the end of the experiment, the ratio of (total above-ground biomass removed):(above-ground standing crop of unclipped plants) was 0.65 for the severe clipping treatment, 0.46 for the moderate treatment, and 0 for the unclipped treatment. Though these numbers are very crude estimates of treatment intensity, they are close to the percentage of above-ground production consumed annually by cattle (40% in the surrounding pasture; up to 60% in nearby sites: Lauenroth et al. 1994a). This clipping regime imitates the pattern of defoliation typical of moderately-grazed areas at this site: most plants are grazed only once or twice per year, either because they are simply missed (Varnamkhasti et al. 1995), or because they temporarily occur in refuges such as areas near cattle faeces (Harper 1977; Vallentine 1990).

Data collection

Between May and September 1996, plants were examined at regular intervals to determine survivorship, reproductive status, and the number of living and dead shoots taller than 1 cm. A few plants escaped detection at some of these samplings. The live-tissue traits measured were chosen as examples of the type of growth and reproductive characters frequently affected by grazing, as measures of performance, and because they could be sampled nondestructively; dead shoots were included because they may reflect production and losses of biomass missed between periodic censuses of living shoots. After nearly two complete growing seasons, all plants were destructively harvested in August of 1997, allowing accurate final measurements and the determination of standing crop biomass; this allowed plants time to recover from any greenhouse effects or transplant shock, and to respond to the previous season's clipping, but did not represent an unrealistically long time between grazing events. Previously harvested clippings were not added to this final standing crop, which therefore represents performance a year after the final treatment, rather than cumulative yield. Unbiased estimates of yield would have required repeated destructive sampling, demanding unacceptable losses of experimental plants.

Statistical analyses

Continuous data were analyzed using standard ANOVA designs. Initial genotypic differences were assessed with one-way tests, while experimental results were analyzed using a split-plot design, with one between-plot factor (treatment) and one within-plot factor (genotype) (SPF 3.11 design: Kirk 1982). Grazing treatment was treated as fixed because clipping intensities were chosen arbitrarily. Genotype was treated as fixed because these genotypes were not originally selected randomly; instead, they were selected to capture large amounts of morphological variation. Blocks were treated as random representatives of the surrounding community. Square root transformations were most effective at controlling heterogeneity of variance (generally $P>0.05$; $P>0.01$ in the remainder: Cochran's C), and were used throughout. Categorical data (survivorship and proportion of plants flowering) were pooled across plots and analyzed with hierarchical loglinear models (full model=genotype×treatment×response) (Feinberg 1977). The significance of each source of variation was assessed by partitioning G^2 values and testing the component associated with each factor against the corresponding χ^2 distribution.

Table 1 Initial values of measured variables for plants in the common garden. Data are means±SEM; sample sizes are given in *parentheses*. 1995 data are based on each entire clone; 1996 data are derived from a 12-cm² subsample

Geno- type	Number of live culms (1995)	Longest live culm length (1995)	Longest live leaf length (1995)	Proportion surviving length (1995)	Proportion reproductive (1995)	Number of live shoots(1996)
3	20.800±3.030 (15)	36.667±1.814 (15)	17.600±1.530 (15)	1.000±0.000 (15)	1.000±0.000 (15)	16.143±1.818 (7)
22	36.125±9.915 (8)	40.714±1.128 (7)	24.625±2.771 (8)	1.000±0.000 (8)	0.875±0.125 (8)	13.833±2.496 (6)
26	6.400±3.076 (5)	39.333±3.333 (3)	14.800±1.319 (5)	0.833±0.167 (6)	0.600±0.245 (5)	14.000±1.000 (2)
27	26.875±5.146 (8)	38.375±1.742 (8)	24.875±1.695 (8)	1.000±0.000 (8)	1.000±0.000 (8)	16.571±1.556 (7)
32	8.556±2.944 (9)	25.778±2.253 (9)	19.000±2.034 (9)	1.000±0.000 (9)	1.000±0.000 (9)	11.000±1.949 (6)
36	17.600±4.762 (15)	32.867±1.696 (15)	17.714±1.238 (14)	1.000±0.000 (15)	1.000±0.000 (15)	15.167±2.272 (6)
54	6.875±.915 (8)	27.500±2.330 (8)	24.375±1.426 (8)	1.000±0.000 (8)	1.000±0.000 (8)	13.125±1.407 (8)
56	20.600±5.080 (10)	34.900±3.053 (10)	20.100±2.791 (10)	1.000±0.000 (10)	1.000±0.000 (10)	10.500±1.803 (6)
57	13.900±3.647 (10)	36.900±2.964 (10)	20.000±1.726 (10)	1.000±0.000 (10)	1.000±0.000 (10)	16.750±1.065 (8)
62	35.700±7.737 (10)	42.100±1.785 (10)	23.000±2.534 (10)	0.909±0.091 (11)	1.000±0.000 (10)	12.875±1.202 (8)
67	24.889±9.417 (9)	39.286±2.974 (7)	20.444±1.994 (9)	0.643±0.133 (14)	0.778±0.147 (9)	12.333±1.563 (6)

Table 2 Initial relationships among measured variables for plants in the common garden. Values are Spearman correlation coefficients (r_s) of the mean values for each genotype; $n=11$ for all com-parisons. 1995 data are based on each entire clone; 1996 data are derived from a 12-cm² subplot

	Number of culms (1995)	Longest culm length (1995)	Longest leaf length (1995)
Longest culm length (1995)	0.591 ^a		
Longest leaf length (1995)	0.591 ^a	0.264	
Number of shoots (1996)	0.000	0.145	-0.091

^a $P<0.10$ **Table 3** Results of split-plot factorial ANOVAs at the interim sampling (September 1996). Data were square-root-transformed prior to analysis. Degrees of freedom vary according to the number of plants located and scored

Source of variation	Live shoots		Dead shoots	
	<i>F</i>	<i>df</i>	<i>F</i>	<i>df</i>
Treatment	0.206	2,26	0.415	2,21
Genotype	4.606***	10,260	0.608	10,210
Genotype×Treatment	0.932	20,260	0.929	20,210

* $P<0.05$, ** $P<0.01$, *** $P<0.001$

Results

Initial variation

In October of 1995, prior to their collection from the common garden, significant genotypic variation still existed among surviving plants for the number of culms produced ($F_{10,96}=2.765$; $P<0.01$; genotypic variance component=72%), culm height ($F_{10,91}=4.431$; $P<0.0001$; genotypic variance component=16%), and leaf height ($F_{10,95}=2.435$; $P<0.05$; genotypic variance component=7%). These measurements varied 1.5–6 fold among genotypes (Table 1). Survival and reproduction generally were good; still, the fraction of plants still alive and the proportion of plants with flowers also varied among genotypes ($\chi^2_{10}=27.995$ and $\chi^2_{10}=41.969$ respectively; $P<0.01$ in both cases) (Table 1). Numbers of living

shoots in a subsample totalling 12 cm² in area did not differ among genotypes, based on an additional sampling in May of 1996; ($F_{10,59}=1.643$; $P>0.05$); however, differences probably were obscured by the very high shoot density in these long-established clones (Table 1). Correlations between genotypic means generally were weak and nonsignificant, but stature-related characters (leaf height, culm height, culm production) tended to positively co-vary (Table 2). Because of weed invasion, the environment experienced by each replicate was not uniform, probably reducing both correlations and estimates of genotypic variance (Falconer 1989).

These differences were maintained despite growth under greenhouse conditions. When the experimental genotypes were transplanted back into the field, they still differed with respect to mean leaf length (genotypic means: 26–37 cm; $F_{10,380}=11.895$), mean number of live shoots (genotypic means: 6.0–8.4 per plant; $F_{10,380}=3.017$), and mean number of dead shoots (genotypic means: 4.6–7.8 per plant; $F_{10,380}=2.800$) ($P<0.01$ in all cases). As expected, these variables initially did not differ among grazing treatments ($F_{2,38}<0.3$; $P>0.7$) and there were no genotype×treatment interactions ($F_{20,380}<1.2$; $P>0.3$).

Experimental results

At the end of the 1996 field season, the number of living shoots per plant differed significantly among genotypes (genotypic means: 2.7–5.8) (Fig. 1; Table 3). With this exception, ANOVAs revealed no significant main effects, indicating no further effects of genotype or grazing

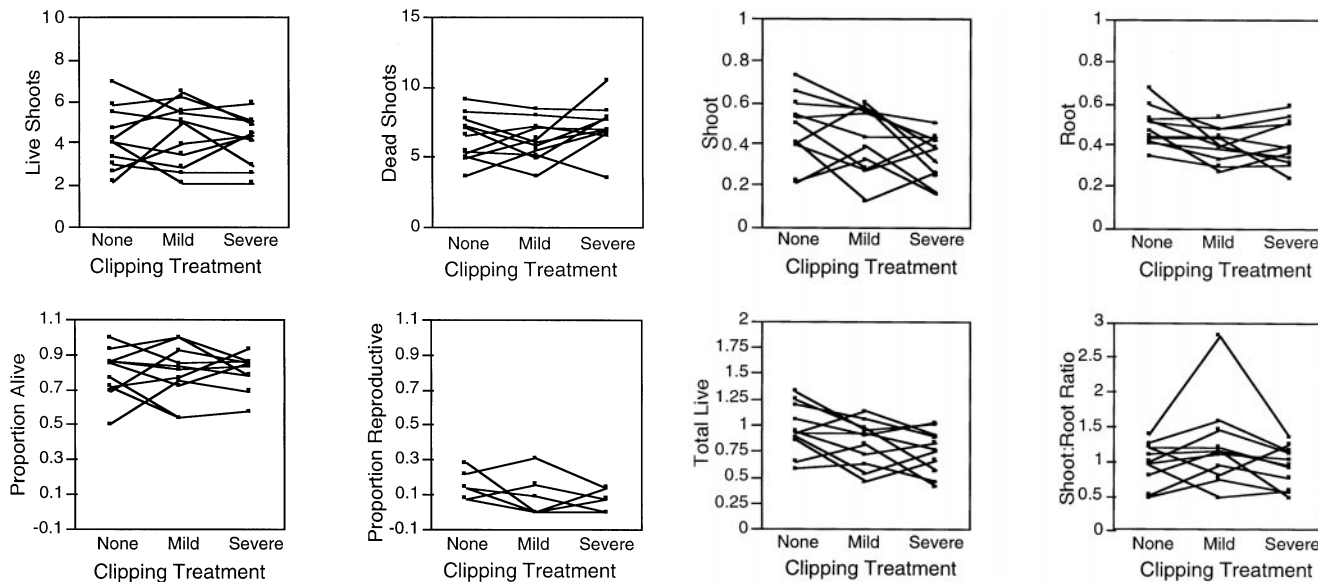


Fig. 1 Effects of clipping treatment (*None, Mild, Severe*) on interim (September 1996) numbers of live and dead shoots, and on the proportion of surviving and reproductive plants. *Points* indicate means; each *line* represents 1 of the 11 experimental genotypes. Significance tests are reported in Tables 3, 4

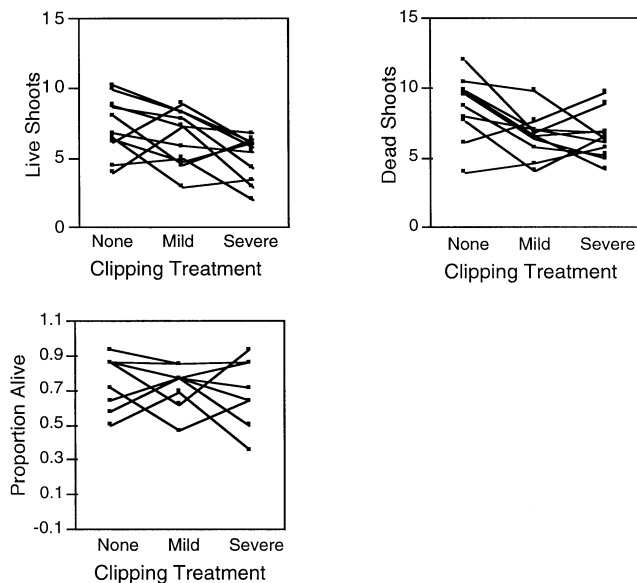


Fig. 2 Effects of clipping treatment (*None, Mild, Severe*) on final (August 1997) numbers of live and dead shoots, and on the proportion of surviving plants. *Points* indicate means; each *line* represents 1 of the 11 experimental genotypes. Significance tests are reported in Tables 4, 5

treatment on shoot numbers. Responses varied among genotypes, but ANOVAs detected no significant genotype \times treatment interactions, indicating that different genotypes responded similarly to grazing (Fig. 1; Table 3). Loglinear models also detected no significant genotype \times treatment interaction with respect either to survival or to the probability of flowering, but survivorship did

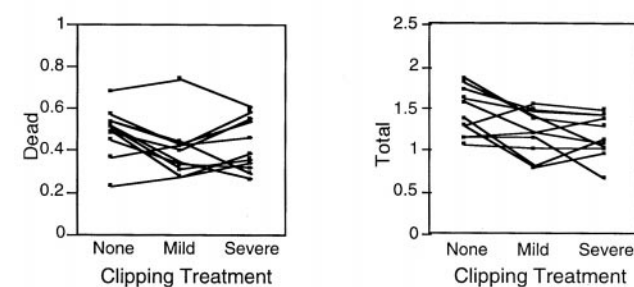


Fig. 3 Effects of clipping treatment (*None, Mild, Severe*) on components of final (August 1997) biomass. *Points* indicate mean weights (g); each *line* represents 1 of the 11 experimental genotypes. $Total\ live = Live\ shoot + Reproductive\ structures + Root$; $Shoot:Root\ Ratio = (Live\ shoot + Reproductive\ structures) / Root$; $Total = Total\ live + Dead$. Significance tests are reported in Table 6

differ significantly among genotypes (genotypic means: probability of survival=0.61 to 0.90) (Fig. 1; Table 4). Flowering also varied significantly among defoliation treatments (treatment means: probability of flowering=0.13 unclipped, 0.05 mild, 0.04 severe) (Fig. 1; Table 4); this effect probably reflected the removal of developing flowers during clipping.

At the final sampling in 1997, ANOVAs detected significant genotypic effects on all variables (genotypic means: number of live shoots=3.7 to 8.0; number of dead shoots=4.7 to 9.2; vegetative shoot dry weight=0.23 g to 0.57 g; root dry weight=0.31 g to 0.55 g; total live dry weight=0.55 g to 1.1 g; dead dry weight=0.28 g to 0.68 g; total dry weight=0.99 g to 1.5 g; shoot:root ratio=0.58 to 1.8) (Figs. 2, 3; Tables 5, 6). One significant treatment effect also was detected (total dry weight: treatment means=1.4 g unclipped, 1.2 g mild, 1.2 g severe), as well as several marginally non-significant effects (Figs. 2, 3; Tables 5, 6). There was a marginally non-significant ($P=0.08$) genotype \times treatment interaction with respect to the number of dead shoots, but with this exception no other genotype \times treatment interaction approached signifi-

Table 4 Results of loglinear analyses of plant survivorship and reproduction. Too few shoots flowered in August 1997 to permit statistical testing

Source of variation	Survival (September 1996)		Survival (August 1997)		Reproduction (September 1996)	
	G^2	df	G^2	df	G^2	df
Treatment	0.15	2	1.82	2	10.71**	2
Genotype	28.73**	10	28.12**	10	17.23	10
Genotype×Treatment	21.23	20	15.00	20	22.03	20

* $P<0.05$, ** $P<0.01$, *** $P<0.001$

Table 5 Results of split-plot factorial ANOVAs of shoot numbers at the final sampling (August 1997). Data were square-root-transformed prior to analysis

Source of variation	Live shoots		Dead shoots	
	F	df	F	df
Treatment	2.111	2,38	3.183	2,38
Genotype	3.659***	10,380	2.127*	10,380
Genotype×Treatment	0.838	20,380	1.503	20,380

* $P<0.05$, ** $P<0.01$, *** $P<0.001$

Table 6 Results of split-plot factorial ANOVAs of dry biomass at the final sampling (August 1997). Data were square-root-transformed prior to analysis. Degrees of freedom vary because of undefined values (0/0)

Source of variation	Live shoot		Root		Total live ^a		Shoot:root ratio ^b		Dead		Total ^c	
	F	df	F	df	F	df	F	df	F	df	F	df
Treatment	2.717	2,38	2.849	2,38	1.642	2,38	0.726	2,22	1.939	2,38	3.318*	2,38
Genotype	3.861***	10,380	3.478***	10,380	4.266***	10,380	4.103***	10,220	3.027**	10,380	2.978**	10,380
Genotype ×Treatment	0.912	20,380	0.868	20,380	1.000	20,380	0.993	20,220	1.072	20,380	0.985	20,380

* $P<0.05$, ** $P<0.01$, *** $P<0.001$

^aTotal live=Live shoot+Reproductive structures+Root

^bShoot:Root Ratio=(Live shoot+Reproductive structures)/Root

^cTotal=Total live+Dead

cance ($P>0.3$ in all cases). Loglinear models found no significant genotype×treatment interaction with respect to survival, but did indicate a significant effect of genotype on survivorship (genotypic means: probability of survival=0.51 to 0.88) (Fig. 2; Table 4). Too few plants ($n=8$) produced culms to allow the statistical evaluation of sexual reproduction. At the individual plant level, most measures of performance were positively correlated; for example, Spearman correlations of the number of live shoots versus total live dry weight ($r_s=0.840$), number of live shoots versus proportion surviving ($r_s=0.769$), and total live dry weight versus proportion surviving ($r_s=0.648$) all were highly significant ($P<0.001$; $n=451$); this indicates that larger plants tended to be larger in all measures.

On average, plant size was stable over the course of the experiment (mean final live shoots per initial live shoot=0.956; SEM=0.047). There were significant positive correlations between initial and final plant size in all treatments: the numbers of live shoots at the end of the 1996 and 1997 seasons were correlated with initial shoot number ($r_s=0.28$, $n=434$ and $r_s=0.22$, $n=451$ respectively; $P<0.001$ for both). Therefore, final differences among genotypes may in part reflect initial differences in size or

vigour among transplanted individuals. However, since plant size did not initially differ among treatments or treatment×genotype combinations, final results for tests of these factors are not simply products of initial differences. For example, on each sampling date, neither analyses of live shoots nor analyses of live shoots per initial shoot detected significant treatment or treatment×genotype effects ($P>0.05$).

Discussion

When we designed this experiment, we expected to find that genotypes with shorter stature, less frequent flowering, and other “grazing syndrome” characters would perform better when clipped than other genotypes, and hence might be selectively favoured by grazing pressure. Instead, we found little evidence that clipping reduced fitness, and practically no evidence of genotype×clipping interactions. Grazing-syndrome morphologies can confer resistance to drought, fire, and other physical and disturbance factors, and may have originated for these reasons; however, regardless of their origins, such characters generally are believed to confer grazing resistance as well

(Coughenour 1985; Belsky et al. 1993; Rosenthal and Kotanen 1994). Why could we detect no evidence of this?

We believe our results are real because our design was both biologically and statistically reasonable. We used plants which differed genetically with respect to potentially important morphological characters. Initial differences among our genotypes were significant and often large (1.5–6 fold); in their original study of the set of clones from which ours were drawn, McGinnies et al. (1988) reported similar magnitudes of variation for numbers of culms (54–287 per plant), culm height (26–48 cm), plant weight (9–54 g), and basal diameter (8–17 cm). Though all grazing syndrome characters need not occur in the same plant, we found characters relating to plant stature (leaf height, culm height, culm number) tended to co-vary among genotypes; these are likely to be the characters that most directly influence tissue losses to grazing. We transplanted our experimental plants into a grazed background only a few kilometers from their point of origin, we adopted treatments that were realistic but more severe than grazing in many natural and managed systems (Cyr and Pace 1993), and sampled over a timescale much longer than *B. gracilis* required to respond to clipping in greenhouse experiments (Jaramillo and Detling 1988; Painter et al. 1989). It is possible that our treatments failed to simulate some aspects of cattle grazing; for example, we may have underestimated the importance of prostrateness by clipping all plants, upright or not; however, this should have amplified, rather than obviated, differences between clipped and unclipped plants. Finally, our statistical approach was adequate for the detection of reasonably strong interactions. Our design was blocked by plot to reduce “nuisance” variation (Kirk 1982), our degrees of freedom for treatment effects were respectable ($F_{2,38}$), and our degrees of freedom ($F_{20,380}$) for interactions were high, both absolutely and relative to numerous highly significant tests of genotypic effects ($F_{10,380}$).

Although our field experimental approach had considerable advantages over greenhouse or correlational field studies, it had costs as well. The greater variability of field conditions may have obscured treatment effects. The transition from greenhouse conditions to field conditions may have entailed transplant shock, which may have differed among genotypes, as suggested by the significant genotypic effect on survival at the end of the first growing season. Finally, because of difficulties in precisely matching the ramets available for transplantation, there were initial size differences among transplanted genotypes that tended to increase over time. As with any uncontrolled variation, it is possible that factors such as these may have obscured treatment effects, but we believe they are unlikely to have seriously confounded the factor of primary interest: genotype × treatment variation. Differences in transplant shock or size and growth of genotypes may have been among the many factors contributing to significant genotypic effects, but should not have confounded the results of primary interest: whether performance of each genotype varied with clipping treat-

ment. Our lack of significant genotype × treatment interactions does not prove such interactions did not exist; however, it does suggest such interactions, if they did occur, were weak compared to genotypic differences.

If genotypic differences among our *B. gracilis* clones arose under a more intense grazing regime than they currently experience, it may be that their importance would only be evident if they were even more severely clipped. Consistently heavy grazing, such as that associated with prairie dog towns, can select for changes in the growth and morphology of *B. gracilis* (e.g., Painter et al. 1989, 1993). However, we are not convinced that such a defoliation regime would have been appropriate. First, we were primarily interested in whether morphology currently is important, rather than whether it was historically important. Livestock are currently the primary large grazers in most of the Great Plains, and have been so for more than 100 years; consequently, we attempted to simulate pressures locally exerted by modern range cattle. Second, while the local impact of modern cattle and pre-settlement bison probably differed, the extent of this difference is unclear, and depends upon the management regime adopted. The foraging ecology of these species does differ in many details; for example, bison have a stronger preference for grasses, while their migratory patterns may have made their impacts even more sporadic than those of either modern cattle grazing or our experimental treatments (Schwartz and Ellis 1981; Peden et al. 1974; Plumb and Dodd 1993; Lauenroth et al. 1994a; Hartnett et al. 1997). However, broadly considered, cattle and bison both are large, primarily gramivorous ruminants with substantial dietary overlap, and their potential impacts on vegetation are thought to be broadly similar as a result (Schwartz and Ellis 1981; Plumb and Dodd 1993; Hartnett et al. 1997; Knapp et al. 1999). We feel that our results are relevant to variation in modern rangeland populations of *B. gracilis*; in absence of firmer evidence, we also believe they represent a first approximation to the responses expected prior to the introduction of range cattle.

Why did clipping have such weak effects? Part of the explanation simply may be that, even for a grass, *B. gracilis* is highly resistant to defoliation by ungulates. Like other shortgrass steppe species, *B. gracilis* has evolved for millennia in the presence of widespread grazing by bison, and for more than a century with grazing by cattle (Larson 1940; Stebbins 1981; Mack and Thompson 1982; Coughenour 1985; Milchunas et al. 1988; Hartnett et al. 1997). As a result, modern shortgrass steppe is highly resistant to damage by domestic livestock (Stebbins 1981; Mack and Thompson 1982; Milchunas et al. 1988; Sims 1988; Mack 1989). *B. gracilis* tends to increase in cattle-grazed areas; in contrast, the cessation of grazing tends to result in invasions by grazing-sensitive species (Milchunas et al. 1989, 1990, 1992; Kotanen et al. 1998; Schuman et al. 1999). The mild effects of our clipping treatments on *B. gracilis* probably reflected the highly grazing-resistant response of this grass to the simulated grazing regime we adopted. Since

morphological differences among genotypes did not translate to performance differences in clipped plants, there apparently is little scope for the current cattle grazing regime to select for different genotypes of this grass, though cattle still may produce plastic responses. This contrasts with the impacts of prairie dog grazing, which are more localized, but perhaps more likely to select for smaller morphologies (e.g., Painter et al. 1989, 1993). As hypothesized by MacGinnies et al. (1988), genetic variation in the morphology of *B. gracilis* at our site may principally reflect and respond to spatiotemporal variation in environmental factors other than grazing, such as soil characteristics, plant cover, and rainfall (e.g., Coffin and Lauenroth 1988, 1989a, 1992; Hook et al. 1991; Milchunas et al. 1989, 1990, 1994).

Acknowledgements This is a contribution of the Shortgrass Steppe Long-Term Ecological Research Program (NSF BSR-8114822). Research was supported in part by NSF DEB-9496331 and a Packard Fellowship (J.B.), and by NSERC and the University of Toronto (P.M.K.). We also would like to thank the Rangeland Resources Research Unit of the USDA Agricultural Research Service, which administers the CPER, and which allowed us to use the common garden as a source of material. Indy Burke, Bill Lauenroth, and Daniel Milchunas supplied invaluable advice at all stages of this project, and Mark Lindquist and the LTER field crew supplied much of the labour. Bob Jefferies and two anonymous reviewers helpfully commented on the manuscript.

References

- Aarssen LW, Turkington R (1985) Within-species diversity in natural populations of *Holcus lanatus*, *Lolium perenne* and *Trifolium repens* from four different-aged pastures. *J Ecol* 73: 869–886
- Aguilera MO, Lauenroth WK (1995) Influence of gap disturbances and type of microsites on seedling establishment in *Bouteloua gracilis*. *J Ecol* 83:87–97
- Belsky AJ, Carson WP, Jensen CL, Fox GA (1993) Overcompensation by plants: herbivore optimization or red herring? *Evol Ecol* 7:109–121
- Carman JG, Briske DD (1985) Morphologic and allozymic variation between long-term grazed and non-grazed populations of the bunchgrass *Schizachyrium scoparium* var. *frequens*. *Oecologia* 66:332–337
- Coffin DP, Lauenroth WK (1988) The effects of disturbance size and frequency on a shortgrass plant community. *Ecology* 69: 1609–1617
- Coffin DP, Lauenroth WK (1989a) Small scale disturbances and successional dynamics in a shortgrass plant community: interactions of disturbance characteristics. *Phytologia* 67:258–286
- Coffin DP, Lauenroth WK (1989b) Spatial and temporal variation in the seed bank of a semiarid grassland. *Am J Bot* 76:53–58
- Coffin DP, Lauenroth WK (1992) Spatial variability in seed production of the perennial bunchgrass *Bouteloua gracilis* (Gramineae). *Am J Bot* 79:347–353
- Coughenour MB (1985) Graminoid responses to grazing by larger herbivores: adaptations, exaptations, and interacting processes. *Ann Mo Bot Gard* 72:852–863
- Crawley M (1983) *Herbivory: the dynamics of animal-plant interactions*. University of California Press, Berkeley
- Crawley M (1997) Plant-herbivore dynamics. In: Crawley M (ed) *Plant ecology*, 2nd edn. Blackwell, Oxford, pp 401–474
- Cyr H, Pace ML (1993) Magnitude and patterns of herbivory in aquatic and terrestrial ecosystems. *Nature* 361:148–150
- Dawkins R (1986) *The blind watchmaker*. Norton, New York
- Detling JK, Painter EL (1983) Defoliation responses of western wheatgrass populations with diverse histories of prairie dog grazing. *Oecologia* 57:65–71
- Detling JK, Painter EL, Coppock DL (1986) Ecotypic differentiation resulting from grazing pressure: evidence for a likely phenomenon. In: Joss PJ, Lynch PW, Williams OB (eds) *Rangelands: a resource under siege*. Cambridge University Press, Cambridge, pp 431–433
- Dickinson CE, Dodd JL (1976) Phenological pattern in the shortgrass prairie. *Am Midl Nat* 96:367–378
- Fair J, Lauenroth WK, Coffin DP (1999) Demography of *Bouteloua gracilis* in a mixed prairie: analysis of genets and individuals. *J Ecol* 87: 233–243
- Falconer DS (1989) *Introduction to quantitative genetics*, 3rd edn. Longman, Harlow
- Feinberg SE (1977) *The analysis of cross-classified categorical data*. MIT, Cambridge
- Fritz RS, Simms EL (eds) (1992) *Plant resistance to herbivores and pathogens: ecology, evolution, and genetics*. University of Chicago Press, Chicago
- Grace JB, Tilman D (1990) *Perspectives on plant competition*. Academic Press, San Diego
- Gregor JW, Sansome FW (1927) Experiments on the genetics of wild populations. Part I. Grasses. *J Genet* 17:349–364
- Grime JP (1979) *Plant strategies and vegetation processes*. Wiley, Chichester
- Harper J (1977) *Population biology of plants*. Academic Press, London
- Hartnett DC, Steuter AA, Hickman KR (1997) Comparative ecology of native and introduced ungulates. In: Knopf FL, Samson FB (eds) *Ecology and conservation of Great Plains vertebrates*. Springer, Berlin Heidelberg New York, pp 72–101
- Hendrix SD (1988) Herbivory and its impacts on plant reproduction. In: Lovett Doust J, Lovett Doust L (eds) *Plant reproductive processes: patterns and strategies*. Oxford University Press, New York, pp 246–263
- Hickey WC Jr (1961) Growth form of crested wheatgrass as affected by site and grazing. *Ecology* 42:173–176
- Hook PB, Burke IC, Lauenroth WK (1991) Heterogeneity of soil N and C associated with individual plants and openings in North American shortgrass steppe. *Plant Soil* 138:247–256
- Huntly N (1991) Herbivores and the dynamics of communities and ecosystems. *Annu Rev Ecol Syst* 22:477–503
- Jaindl RG, Doescher P, Miller RF, Eddleman LE (1994) Persistence of Idaho fescue on degraded rangelands: adaptation to defoliation or tolerance. *J Range Manage* 47:54–59
- Jameson DA (1963) Responses of individual plants to harvesting. *Bot Rev* 29:532–594
- Jaramillo VJ, Detling JK (1988) Grazing history, defoliation, and competition: effects on shortgrass production and nitrogen accumulation. *Ecology* 69:1599–1608
- Kemp WB (1937) Natural selection within plant species as exemplified in a permanent pasture. *J Hered* 28:329–333
- Kirk RE (1982) *Experimental design: procedures for the behavioral sciences*, 2nd edn. Brooks/Cole, Monterey
- Knapp AK, Blair JM, Briggs JM, Collins SL, Harnett DC, Johnson LC, Towne EG (1999) The keystone role of bison in North American tallgrass prairie. *Bioscience* 49:39–50
- Kotani PM, Bergelson J, Hazlett DL (1998) Habitats of native and exotic plants in Colorado shortgrass steppe: a comparative approach. *Can J Bot* 76:664–672
- Larson F (1940) The role of bison in maintaining the short grass plains. *Ecology* 21:113–121
- Lauenroth WK, Milchunas DG, Dodd JL, Hart RH, Heitschmidt RK, Rittenhouse LR (1994a) Effects of grazing on ecosystems of the Great Plains. In: Vaura M, Laycock WA, Pieper RD (eds) *Ecological implications of livestock herbivory in the west*. Society for Range Management, Denver, pp 69–100
- Lauenroth WK, Sala OE, Coffin DP, Kirchner TB (1994b) The importance of soil water in the recruitment of *Bouteloua gracilis* in the shortgrass steppe. *Ecol Appl* 4:741–749

- Lindroth RL (1989) Mammalian plant-herbivore interactions. In: Abrahamson WG (ed) Plant-animal interactions. McGraw-Hill, New York, pp 163–206
- Louda SM, Keeler KH, Holt RD (1990) Herbivore influences on plant performance and competitive interactions. In: Grace JB, Tilman D (eds) Perspectives on plant competition. Academic Press, San Diego, pp 413–444
- Mack RN (1989) Temperate grasslands vulnerable to plant invasions: characteristics and consequences. In: Drake JA, Mooney HA, Castri F di, Groves RH, Kruger FJ, Rejmánek M, Williamson M (eds) Biological invasions: a global perspective (SCOPE 37). Wiley, Chichester, pp 155–179
- Mack RN, Thompson JN (1982) Evolution in steppe with few large, hooved mammals. *Am Nat* 119:757–773
- Marquis RJ (1992) The selective impact of herbivores. In: Fritz RS, Simms EL (eds) Plant resistance to herbivores and pathogens: ecology, evolution, and genetics. University of Chicago Press, Chicago, pp 301–325
- McGinnies WJ, Laycock WA, Tsuchiya T, Edmunds DA (1988) Variability within a native stand of blue grama. *J Range Manage* 41:391–395
- McNaughton SJ (1984) Grazing lawns: animals in herds, plant form, and coevolution. *Am Nat* 124:863–886
- Milchunas DG, Sala OE, Lauenroth WK (1988) A generalized model of grazing by large herbivores on grassland community structure. *Am Nat* 132:87–106
- Milchunas DG, Lauenroth WK, Chapman PL, Kazempour MK (1989) Effects of grazing, topography, and precipitation on the structure of a semiarid grassland. *Vegetatio* 80:11–23
- Milchunas DG, Lauenroth WK, Chapman PL, Kazempour MK (1990) Community attributes along a perturbation gradient in a shortgrass steppe. *J Veg Sci* 1:375–384
- Milchunas DG, Lauenroth WK, Chapman PL (1992) Plant competition, abiotic, and long- and short-term effects of large herbivores on demography of opportunistic species in a semiarid grassland. *Oecologia* 92:520–531
- Milchunas DG, Forwood JR, Lauenroth WK (1994) Productivity of long-term grazing treatments in response to seasonal precipitation. *J Range Manage* 47:133–139
- Mopper S, Maschinski J, Cobb N, Whitham TG (1991) A new look at habitat structure: consequences of herbivore-modified plant architecture. In: Bell S, McCoy E, Mushinsky H (eds) Habitat structure: the physical arrangement of objects in space. Chapman Hall, London, pp 260–280
- Oosterheld M, McNaughton SJ (1988) Intraspecific variation in the response of *Themeda triandra* to defoliation: the effect of time of recovery and growth rates on compensatory growth. *Oecologia* 77:181–186
- Oosterheld M, McNaughton SJ (1991) Effect of stress and time for recovery on the amount of compensatory growth after grazing. *Oecologia* 85:305–313
- Painter EL, Detling JK, Steingraeber DA (1989) Grazing history, defoliation, and frequency-dependent competition: effects on two North American grasses. *Am J Bot* 76:1368–1379
- Painter EL, Detling JK, Steingraeber DA (1993) Plant morphology and grazing history: relationships between native grasses and herbivores. *Vegetatio* 106:37–62
- Peden DG, Van Dyne GM, Rice RW, Hansen RM (1974) The trophic ecology of *Bison bison* L. on shortgrass plains. *J Appl Ecol* 11:489–498
- Peterson RA (1962) Factors affecting resistance to heavy grazing in needle-and-thread grass. *J Range Manage* 15:183–189
- Plumb GE, Dodd JL (1993) Foraging ecology of bison and cattle on a mixed prairie: implications for natural area management. *Ecol Appl* 3:631–643
- Polley HW, Detling JK (1988) Herbivory tolerance of *Agropyron smithii* populations with different grazing histories. *Oecologia* 77:261–267
- Polley HW, Detling JK (1990) Grazing-mediated differentiation in *Agropyron smithii*: evidence from populations with different grazing histories. *Oikos* 57:326–332
- Rosenthal J, Kotanen PM (1994) Terrestrial plant tolerance to herbivory. *Trends Ecol Evol* 9:117–157
- Schuman GE, Reeder JD, Manley JT, Hart RH, Manley WA (1999) Impact of grazing management on the carbon and nitrogen balance of a mixed-grass rangeland. *Ecol Appl* 9:65–71
- Schwartz CC, Ellis JE (1981) Feeding ecology and niche separation in some native and domestic ungulates on the shortgrass prairie. *J Appl Ecol* 18:343–353
- Sims PL (1988) Grasslands. In: Barbour MG, Billings WD (eds) North American terrestrial vegetation. Cambridge University Press, Cambridge, pp 265–286
- Smith SE (1998) Variation in response to defoliation between populations of *Bouteloua curtipendula* var. *caespitosa* (Poaceae) with different livestock grazing histories. *Am J Bot* 85:1266–1272
- Solbrig O, Simpson BB (1974) Components of regulation of a population of dandelions in Michigan. *J Ecol* 62:473–486
- Solbrig O, Simpson BB (1977) A garden experiment on competition between biotypes of the common dandelion (*Taraxacum officinale*). *J Ecol* 65:427–430
- Stebbins GL (1981) Coevolution of grasses and herbivores. *Ann Mo Bot Gard* 68:75–86
- Strauss SY, Agrawal AA (1999) The ecology and evolution of plant tolerance to herbivory. *Trends Ecol Evol* 14:179–185
- Tilman D (1982) Resource competition and community structure. Princeton University Press, Princeton
- Tilman D (1988) Dynamics and structure of plant communities. Princeton University Press, Princeton
- Vallentine JF (1990) Grazing management. Academic Press, San Diego
- Varnamkhasti AS, Milchunas DG, Lauenroth WK, Goetz H (1995) Production and rain use efficiency in short-grass steppe: grazing history, defoliation and water resource. *J Veg Sci* 6:787–796
- Warwick SI, Briggs D (1980) The genecology of lawn weeds. V. The adaptive significance of different growth habit in lawn and roadside populations of *Plantago major* L. *New Phytol* 85: 289–300
- Westoby M (1989) Selective forces exerted by vertebrate herbivores on plants. *Trends Ecol Evol* 4:115–117
- Whicker AD, Detling JK (1988a) Ecological consequences of prairie dog disturbances. *Bioscience* 38:778–795
- Whicker AD, Detling JK (1988b) Modification of vegetation structure and ecosystem processes by North American grassland mammals. In: Werger MJA, Aart PJM van der, During HJ, Verhoeven JTA (eds) Plant form and vegetation structure. SPB Academic, The Hague, pp 301–316