# Variation in response to defoliation between populations of *Bouteloua curtipendula* var. *caespitosa* (Poaceae) with different livestock grazing histories[1]

## Steven E. Smith

Department of Plant Sciences, University of Arizona, Tucson, Arizona 85721

Distinctive plant growth and development have been associated with resistance to defoliation by herbivores. Descriptions of resistance (tolerance/avoidance) strategies are common, although little is known about genetic variation affecting their expression in natural plant communities. This research compared response to three frequencies of defoliation in populations of *Bouteloua curtipendula* var. *caespitosa* from Arizona with different histories of exposure to domestic herbivores. One population occurs on a site that has likely been unaffected by large herbivores including cattle, while the other has been regularly grazed by cattle. Mixed-model analysis of variance was used to examine variation in traits associated with defoliation resistance. Data were collected in a 168-d greenhouse experiment using ramets of 15 genets from each population. Mortality was lower in the cattle-impacted population, suggesting improved defoliation resistance. This was associated with increased production of tillers with lower mass following defoliation. Plasticity was observed for all traits in response to different defoliation frequencies. The cattle-free population exhibited significant genetic variation for plasticity affecting leaf blade angle, while little variation was noted for this trait in the cattle-impacted population. Evidence of reduced genetic variation within the cattle-impacted population was noted for traits associated with defoliation resistance. In general, these observations are consistent with expectations following selection for resistance to defoliation.

**Key words:** *Bouteloua*; defoliation resistance; genetic variation; grazing; phenotypic plasticity; Poaceae; sideoats grama.

Plants repeatedly exposed to intense defoliation may exhibit distinctive morphological and physiological characteristics thought to be adaptive under these conditions (Carmen and Briske, 1985; Briske, 1996). In caespitose grasses, defoliation resistance, involving either tolerance or avoidance (Briske, 1991, 1996), is typically associated with changes in plant architecture including an increased number of tillers, a shorter and less upright growth form, and fewer and smaller leaves (McNaughton, 1979; Painter, Detling, and Steingraeber, 1989, 1993; Briske and Richards, 1994). Other presumably adaptive responses have been noted in populations exposed to frequent defoliation including more horizontal display of leaf blades (Detling and Painter, 1983), reduced relative carbon allocation to leaves (Carmen and Briske, 1985), changes in nutrient allocation (Polley and Detling, 1988; Jaramillo and Detling, 1988), and increases in photosynthetic rate (Detling, Dyer, and Winn, 1979) and blade:sheath ratio (Detling and Painter, 1983). Expression of these traits in response to defoliation may reflect genetic changes within populations or plastic responses of existing genotypes.

Grazing by livestock, especially during the period 1870–1930, is associated with significant changes in the composition of vegetation in the desert grasslands of North America (Bahre, 1995). (Herein, grazing is assumed to include defoliation of aboveground herbaceous plant tissues by an animal as well as fouling, trampling, uprooting, and root feeding [Valentine, 1990].) Historical evidence suggests that the sizes of native grass populations were drastically reduced by intensive livestock grazing, and this was often exacerbated by drought (Hastings and Turner, 1965). Local extinction of perennial grasses (O'Connor, 1991) may have been common as this occurred (Humphrey, 1958). Historical photographs (Hastings and Turner, 1965) show that recolonization by native plants occurred at many grassland sites following reductions in grazing intensity. Little is known of the possible genetic consequences of the period of overgrazing on populations of recolonizing plants. The sequence of events described could have resulted in significant genetic changes. For example, extreme declines in effective population size could have resulted in inbreeding or reductions in levels of genetic variation due to random genetic drift in recolonizing populations (Polans and Allard, 1989; Barrett and Kohn, 1991). Genetic variation may have been further affected by selection for colonizing ability (Barrett and Husband, 1990) or resistance to the stresses of herbivory or the grazing-modified environment (Aarssen and Turkington, 1985). Alternatively, there may have been little lasting genetic effect of extended exposure to frequent defoliation or changes in local population size if plants responded plastically to defoliation and the postgrazing environment.

Comparison of the responses to defoliation in conspecific populations with different grazing histories represents a common experimental strategy for studying de-

foliation resistance. Numerous studies of this sort have taken place in the Great Plains of North America (Detling and Painter, 1983; Aarssen and Turkington, 1985; Carmen and Briske, 1985; Painter, Detling, and Steingraeber, 1989, 1993). Fewer comparable studies have been done with species from the more arid grasslands of North America where large native ungulates were less common than in the relatively mesic Great Plains (Parmenter and Van Devender, 1995). Trlica and Orodho (1989) compared heavily grazed and protected populations of *Oryzopis hymenoides* [Roem. & Schult] Ricker from a Great Basin grassland biotic community (Brown, 1994) in northwestern New Mexico. When grown in a common garden, no differences were observed in height or aboveground biomass between plants from a population that was heavily grazed and one that had been protected from livestock for >50 yr. These authors found no evidence for differential selection for defoliation resistance in the protected and grazed populations.

The research described here involved a comparison of the responses of two populations of a perennial nonrhizomatous grass *Bouteloua curtipendula* var. *caespitosa* (sideoats grama) (Gould and Kapadia, 1964) from southern Arizona to increasing frequencies of defoliation. The populations exist on desert grassland sites that differ in their history of exposure to domestic grazers. One site has natural physical barriers that effectively prevent access by these grazers. The other site has been regularly grazed by cattle for nearly 100 yr. Traits thought to be associated with defoliation resistance (Briske, 1996) were evaluated in ramets from both populations. The experimental design used permitted distinguishing that proportion of the total phenotypic variation over different frequencies of defoliation that was attributable to genetic differences within and between the populations. In addition to differentiating the two populations, this approach permitted estimates of the relative magnitudes of genetic variation and phenotypic plasticity for traits related to response to defoliation.

## MATERIALS AND METHODS

***Population sampling and plant propagation***—Genets (individuals arising from seed that may become fragmented through clonal growth) from two populations of *B. curtipendula* var. *caespitosa* Gould & Kapadia from the semidesert grassland biotic community (Brown, 1994) were used in this research. One population occupies a 41-ha site (1655 m asl) near Mammoth, Arizona. Because it occurs atop a steep-walled butte (Sombrero Butte), it probably has never been grazed by large (>100 kg) herbivores, including most domestic livestock (Hadley, Warshall, and Bufkin, 1991). This site and the population present there are referred to here as "cattle-free." The other population (cattle-impacted) occurs 4.8 km from the cattle-free population on a site (1338 m asl) that has been regularly grazed by cattle since before 1900 (V. Mercer, Mammoth, Arizona, personal communication). Soils at both sites are shallow Haplargids (D. Robinette, USDA-NRCS, Tucson, Arizona, personal communication) on 20–35% slopes with numerous rock outcrops. Vegetation at both sites is dominated by warm-season perennial grasses including most prominently (in decreasing order of density) *B. curtipendula* var. *caespitosa*, *Eragrostis intermedia* Hitchc., *Bouteloua hirsuta* Lag., *Leptochloa dubia* (Kunth) Nees, and *Panicum obtusum* Kunth. *Digitaria californica* (Benth.) Henrad is more frequent at the cattle-impacted than the cattle-free site and *Muhlenbergia emersleyi* Vasey is present only at the cattle-impacted site. Other perennial plants common at both sites are *Dasylirion wheeleri* S. Wats. and *Fouquieria splendens* Engelm. *Acacia constricta* Benth. and *Opuntia phaeacantha* var. *discata* (Griffiths) occur only at the cattle-impacted site. Aggregate cover for all species ranges from 15 to 30% at both sites. Evidence was observed that deer (*Odocoileus* spp.) and small mammalian herbivores are able to reach both sites and may graze on *B. curtipendula* (Krausman et al., 1997). Until the late 1930s, prairie dogs (*Cynomys* spp.) occurred in southeastern Arizona (Hoffmeister, 1986) and may have also grazed on both sites. No description of fire history is available for either site.

Fifteen randomly selected mature *B. curtipendula* plants (basal area >15 cm) were dug from both populations in 1994. Plants from both populations are high polyploids with $2n = 75$–$92$ (D. D. Showalter, University of Arizona, unpublished data). The plants dug were separated by at least 3 m along a 400-m transect at each site. Since *B. curtipendula* var. *caespitosa* is strongly caespitose (Gould and Kapadia, 1964), each of these plants was assumed to represent a unique genet. These genets were grown in 4-L pots in 1:1 (by volume) soil:potting mix in a shadehouse in Tucson, Arizona, for 6 mo. A minimum of 12 ramets was then established for each genet from single rooted tillers. These ramets were grown in 4-L pots in a greenhouse and treated uniformly for an additional 7.5 mo until differential defoliation treatments were imposed. This was done to reduce the possibility that any differences between the populations reflected transient effects associated with the original site of collection (Quinn and Miller, 1967). To insure equal opportunity for induction of any defoliation-induced responses in both populations, ramets were clipped 5 cm above the soil surface (removing all leaf blades) every 6 wk during the 13.5-mo acclimatization period, and the herbage was discarded. This clipping height, which represents ~70% removal of aboveground biomass (Schmutz, 1978), was used because it corresponds to the average defoliation observed on grazed plants on the cattle-impacted site when plants were dug.

***Experimental design and treatments***—Fourteen days following the final clipping of the acclimatization period, three defoliation treatments (frequencies) were imposed on the 15 genets from each population using a split-plot arrangement with four replications. Defoliation treatment (every 14, 28, or 56 d) was the main plot factor and population was the sub plot factor. Defoliation treatments continued for 168 d (14 d, $N = 12$; 28 d, $N = 6$; 56 d, $N = 3$). Preliminary experiments (S. E. Smith, unpublished data) showed that fresh and dry shoot biomasses were closely correlated across the range of developmental stages of tillers produced in the three defoliation treatments. Fresh biomass was found to be ~16% dry matter in these experiments and this value was used to calculate dry biomass, which is reported throughout.

Mean daily temperature in the greenhouse during the experiment was 25.7°C (mean low of 13.2°C, mean high of 38.0°C). Ramets were irrigated individually when leaf curling and color indicated drought stress. Soil moisture content was ~20–30% of field capacity at this point. Additional ramets grown in 4-L pots bordered the experimental ramets. Border ramets were defoliated on the same schedule as the experimental ramets they adjoined.

I measured traits associated with defoliation resistance (Briske and Richards, 1994) rather than focusing on traits likely to be selectively neutral, such as most molecular genetic markers (Eckert, Manicacci, and Barrett, 1996). This approach permitted evaluation of developmental plasticity and the likelihood and effects of selection on ecologically relevant genetic variation. Only vegetative tillers were produced by ramets in all treatments of this experiment. The number of newly produced or regrowing tillers not previously defoliated and the amount of fresh biomass removed was recorded after each defoliation. Morphological measurements were taken on each ramet before defoliation on day 112. Traits measured included the length, maximum width, specific mass of a 3-cm section, and angle of divergence from the vertical of a fully expanded leaf blade, length of the leaf sheath on the longest single tiller, and height (measured as soil surface to tip of tallest extended leaf

TABLE 1. Ramet mortality and least-squares mean values (±1 SE) for traits related to growth and development of ramets from two populations of *B. curtipendula* with different grazing histories exposed to three frequencies of defoliation.

| Trait | Population | Defoliation frequency[a] | | | | | | Population mean |
|---|---|---|---|---|---|---|---|---|
| | | 56 d | | 28 d | | 14 d | | |
| Cumulative aboveground biomass (g/ramet) | Cattle-free | 7.49 ± 0.78 | > | 4.80 ± 0.78 | > | 3.01 ± 0.78 | | 5.10 ± 0.72 |
| | Cattle-impacted | 6.48 ± 0.78 | > | 4.46 ± 0.78 | > | 2.42 ± 0.78 | | 4.45 ± 0.72 |
| Root biomass (g/ramet) | Cattle-free | 7.05 ± 0.76 | > | 3.73 ± 0.76 | = | 3.12 ± 0.76 | | 4.63 ± 0.66 |
| | Cattle-impacted | 7.12 ± 0.76 | > | 4.62 ± 0.76 | = | 3.10 ± 0.76 | | 4.95 ± 0.66 |
| Mass/tiller (g) | Cattle-free | 0.31 ± 0.02 | > | 0.27 ± 0.02 | > | 0.21 ± 0.02 | | 0.26 ± 0.02 |
| | Cattle-impacted | 0.28 ± 0.02 | = | 0.26 ± 0.02 | > | 0.18 ± 0.02 | | 0.24 ± 0.02 |
| Tillers/ramet | Cattle-free | 24.0 ± 1.9 | > | 17.5 ± 1.9 | = | 14.3 ± 1.9 | | 18.6 ± 1.8 |
| | Cattle-impacted | 22.9 ± 1.9 | > | 17.4 ± 1.9 | = | 13.7 ± 1.9 | | 18.0 ± 1.8 |
| Relative tiller number (%)[b] | Cattle-free | 122.5 ± 13.8* | > | 32.0 ± 13.9* | = | 25.1 ± 13.9 | | 59.9 ± 8.8* |
| | Cattle-impacted | 153.2 ± 13.8* | > | 64.4 ± 13.8* | = | 38.6 ± 14.0 | | 85.4 ± 8.7* |
| Ramet mortality (%)[b] | Cattle-free | 17.8 | < | 33.3* | < | 48.9* | | 33.3 |
| | Cattle-impacted | 17.8 | = | 17.8* | < | 35.6* | | 23.7 |

[a] Significant differences in values between populations within a defoliation treatment or over all treatments are denoted by *. Significant differences between treatments within a population are denoted by ">" ($P \leq 0.05$).

[b] Number of live tillers at final defoliation as percentage of that at the defoliation immediately before treatments were imposed.

since plants defoliated most frequently produced exclusively leaf blades). Relative tiller number was evaluated as the number of live tillers per ramet at the final defoliation of the experiment as a percentage of that in the defoliation immediately before treatments were imposed. Increases in this trait may reflect increased production of tillers and/or reduced tiller mortality. Ramets that failed to regrow 3 wk after the final defoliation were considered dead. The validity of this mortality assessment is supported by the observation that all border ramets that had failed to regrow 3 wk after the final defoliation also had not regrown >8 mo later (data not shown) under environmental conditions that would favor rapid growth in *B. curtipendula*. Three weeks after the final defoliation, soil was washed from roots, which were then dried at 60°C and weighed. Analyses for all traits other than ramet mortality were conducted only on ramets that survived until the final defoliation.

***Statistical analyses and their interpretation***—A mixed-model analysis of variance was used to examine the sources of variation in response to defoliation treatments (Miller and Fowler, 1993). In analyses containing data from both populations (combined analyses), populations and defoliation treatments were considered fixed effects and approximate significance of these effects and their interactions was determined by likelihood ratio Type III *F* tests using restricted maximum-likelihood estimation in the procedure MIXED of SAS (SAS, 1992). Using this procedure, variation within populations was also estimated and its significance evaluated by determining whether the component divided by the standard error (*Z* value) was different from zero. Three-way interactions were not significant and are not reported. A mixed-model analysis of variance was conducted for each population separately for traits when a significant population effect or population × treatment interaction was observed in the combined analysis, or when a significant variance component for genets was observed for at least one population in the separate analysis. Before analysis, normality was evaluated using the method of Shapiro and Wilk (1965) and homogeneity of variances tested using the $F_{max}$ test (Sokal and Rohlf, 1981). Accordingly, total aboveground biomass and plant height were log transformed, and the number of tillers per ramet was square-root transformed. Least-squares means and their associated SEs are reported. Significance of differences in ramet mortality between populations for each treatment and between treatments within a population were determined by constructing 2 × 2 contingency tables (mortality/survival vs. populations or treatments). Significance of any differences in mortality was determined by log likelihood ratio tests (Sokal and Rohlf, 1981). In all cases, statistical significance was assigned at $P \leq 0.05$.

With this analysis, genetic differentiation between the populations for a given trait is indicated by a significant population effect. Total genetic variation is estimated by the variance component for genets within populations. Because the genets examined could not be considered a random sample of the genetic variation within *B. curtipendula* var. *caespitosa*, estimates of genetic variance based on this analysis should be viewed conservatively. Evidence for phenotypic plasticity is provided by significant effects for defoliation treatment or the interaction between populations or genets and defoliation treatment. Significant variation in phenotypic plasticity (i.e., differences in slope of the reaction norm) is manifested in a significant population × defoliation treatment interaction (Miller and Fowler, 1993).

Variation in tiller number per ramet was observed among single-tiller-derived ramets at the time defoliation treatments were imposed. However, this trait was not significantly correlated with any other trait measured. Variation in this trait was also insignificant when included as a covariate in analysis of variance with each of the other traits analyzed. Therefore, no adjustment for initial tiller number per ramet was done.

## RESULTS

More frequent defoliation resulted in a significant and progressive decline in cumulative aboveground biomass produced by ramets from both populations (Table 1). Aboveground biomass produced by each ramet did not differ significantly between populations at either the beginning or the end of the experiment within each treatment (data not shown). However, significantly lower ramet mortality was observed in the cattle-impacted population than in the cattle-free population following defoliation every 14 or 28 d (Table 1). Ramet mortality in the cattle-free population also increased significantly as the frequency of defoliation increased. A different pattern was seen in the cattle-impacted population where defoliation every 28 or 56 d resulted in equivalent mortality. Significantly greater ramet mortality was observed only with defoliation every 14 d in this population.

Among ramets that survived until the final defoliation, there were fewer tillers per ramet in the cattle-impacted population than in the cattle-free population over all treatments at the start of the defoliation treatments (14.3 ± 1.0 [least-squares mean ± SE] vs. 16.5 ± 1.0 tillers per ramet), although at the final defoliation this difference was reversed. There were more tillers per ramet in the cattle-impacted (11.2 ± 1.1) than the cattle-free population (9.0 ± 1.1). Relative tiller number, which reflects the
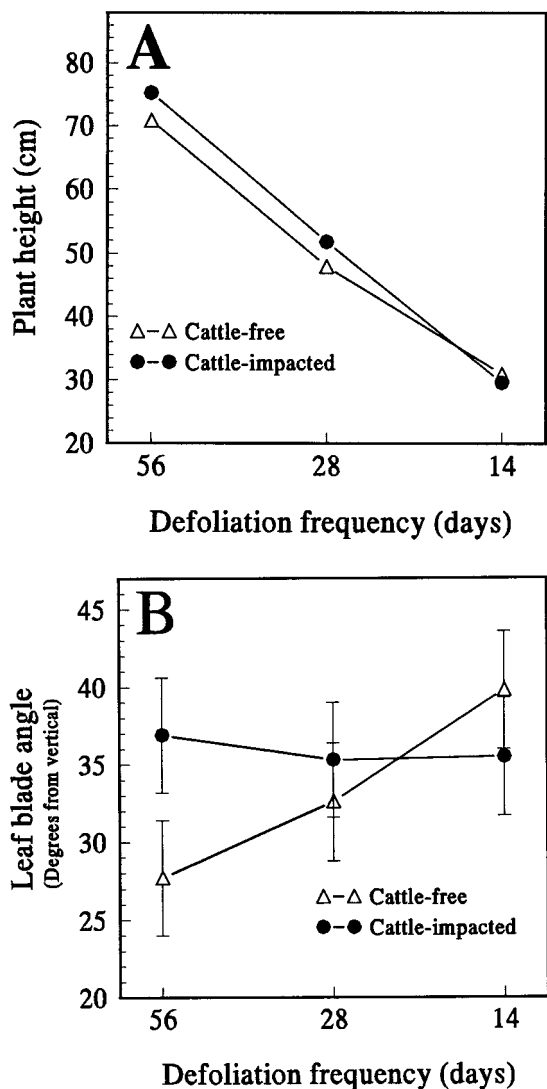
Fig. 1. Reaction norms for plant height (A) and leaf blade angle (B) for cattle-free and cattle-impacted populations of *Bouteloua curtipendula* exposed to three frequencies of defoliation. Values are least-squares means ± 1 SE from the combined mixed-model analysis of variance as described in the text. SE values are contained within symbols in (A).

proportional change in tiller number throughout the experiment, was also significantly higher in ramets from the cattle-impacted population than in those from the cattle-free population with defoliation every 28 or 56 d. The two populations did not differ in this trait with defoliation every 14 d (Table 1). No significant differences were observed between populations within a defoliation treatment for all other traits related to plant size including aboveground and root biomasses, tiller mass and number per ramet (Table 1), height (Fig. 1), whole-plant biomass, root:aboveground biomass ratio, leaf sheath length, and leaf blade length × width (data not shown).

Traits closely associated with the production of aboveground biomass exhibited significant plasticity in response to more frequent defoliation (Tables 1, 2). This was also observed for specific leaf mass and width, and blade and sheath length, root and whole-plant biomass,

TABLE 2. Type III *F* tests for fixed effects from mixed-model analysis of effects of defoliation frequency (56, 28, 14 d) on growth and development of ramets from two populations of *Bouteloua curtipendula* (cattle-free, cattle-impacted). Cumulative aboveground biomass, and plant height were log transformed; tillers per ramet was square-root transformed.

| Source | Cumulative above-ground biomass | Root biomass | Mass/ tiller | Tillers/ ramet | Plant height | Relative tiller number | Leaf blade angle[a] |
|---|---|---|---|---|---|---|---|
| Population | 4.2 | 4.1 | 2.1 | 0.3 | 1.5 | 20.3* | 0.5 |
| Treatment | 134.1* | 38.8* | 102.8* | 41.3* | 87.2* | 21.2* | 1.2 |
| Population × treatment | 2.7 | 2.2 | 1.8 | 0.3 | 3.4* | 1.4 | 4.5* |

\* *P* ≥ 0.05.
[a] Degrees from vertical.

and root:aboveground biomass and leaf blade:sheath length ratios (data not shown). Nevertheless, evidence for population-level differences in plasticity was observed only for plant height and the angle of leaf blade divergence from vertical (Table 2, Fig. 1). A significant genet × treatment interaction indicates that the populations differed in plasticity for plant height in response to defoliation (Table 3). The cattle-impacted population also exhibited significantly more plasticity in this trait than did the cattle-free population (Fig. 1).

The two populations could be considered genetically differentiated, independent of environmental factors, only for relative tiller number (Tables 1, 2). However, significant genetic variation existed within populations for all traits except plant height and relative tiller number (Table 3). Comparing results of separate analyses of each population, similar genetic variation was noted in each population for cumulative aboveground biomass and tillers per ramet (Table 4). These analyses also indicated that the cattle-impacted population was more variable genetically for tiller mass than the cattle-free population. For

TABLE 3. Percentage of total phenotypic variance in various traits that was accounted for by defoliation frequency (14, 28, 56 d), population, and genets within two populations of *Bouteloua curtipendula* (cattle-free, cattle-impacted). Variance components for three-way interactions were nonsignificant and are not shown.

| Source | Cumulative above-ground biomass | Root biomass | Mass/ tiller | Tillers/ ramet | Plant height | Relative tiller number | Leaf blade angle[a] |
|---|---|---|---|---|---|---|---|
| Genet (population) | 19.0* | 17.0* | 23.6* | 30.4* | 4.9 | 3.1 | 27.8* |
| Genet (population) × treatment | 0 | 0 | 5.0 | 2.6 | 19.8* | 11.1 | 3.4 |
| Genet (population) × replication | 1.2 | 0 | 0 | 3.4 | 0 | 0 | 0 |
| Replication | 39.8 | 27.0 | 26.6 | 22.4 | 1.1 | 2.7 | 0 |
| Replication × treatment | 1.7 | 11.8 | 0.4 | 4.1 | 24.7 | 23.9 | 3.9 |
| Replication × population | 0 | 0.3 | 3.1 | 1.0 | 0.9 | 0 | 0 |
| Residual | 38.3* | 33.9* | 41.3* | 36.1* | 48.6* | 59.2* | 64.9* |

\* Variance components significant (*P* ≤ 0.05) if the component ÷ SE (*Z* value) is greater than zero.
[a] Degrees from vertical.

TABLE 4. Type III *F* tests for the fixed effect (defoliation treatment) and variance components (presented as percentage of total phenotypic variance) for random effects from mixed-model analysis of variance conducted separately for data from two populations of *Bouteloua curtipendula*. Variance components for three-way interactions were nonsignificant and are not shown.

| Source | Cumulative aboveground biomass | | Root biomass | | Mass/tiller | | Tillers/ramet | | Plant height | | Relative tiller number | | Leaf blade angle[a] | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Cattle-free | Cattle-impacted | Cattle-free | Cattle-impacted | Cattle-free | Cattle-impacted | Cattle-free | Cattle-impacted | Cattle-free | Cattle-impacted | Cattle-free | Cattle-impacted | Cattle-free | Cattle-impacted |
| Treatment | 106.7* | 57.6* | | | 65.3* | 43.2* | 39.7* | 20.5* | 52.14* | 125.16* | 23.49* | 18.12* | 5.30 | 0.12 |
| Genet | 22.7* | 15.7* | 28.2 | 12.1 | 14.4 | 32.9* | 28.7* | 30.8* | 7.8 | 0.9 | 0 | 5.8 | 41.3* | 11.6 |
| Genet × treatment | 0 | 0 | 11.8 | 0.1 | 2.8 | 7.4 | 0 | 6.4 | 18.9* | 20.9 | 20.5* | 4.1 | 0.1 | 6.9 |
| Genet × replication | 4.0 | 0.8 | 0 | 0.5 | 3.0 | 0 | 5.9 | 3.5 | 0 | 0 | 0 | 0 | 3.2 | 0 |
| Replication | 36.7 | 40.7 | 0 | 30.3 | 43.0 | 15.2 | 15.8 | 26.9 | 1.8 | 2.6 | 4.0 | 2.2 | 0 | 0 |
| Replication × treatment | 0.9 | 5.4 | 10.4 | 4.7 | 0 | 2.2 | 4.1 | 6.2 | 29.9 | 17.5 | 21.0 | 23.5 | 3.2 | 1.0 |
| Residual | 35.4* | 37.4* | 49.6* | 52.3* | 36.8* | 42.3* | 45.5* | 26.2* | 41.6* | 58.1* | 54.5* | 64.4* | 52.1* | 80.5* |

* *F* tests significant (for treatment effect) or variance components significant (all other sources) if the component ÷ SE (Z value) is > 0. $P \leq 0.05$ in both cases.

[a] Degrees from vertical.

plant height and relative tiller number, separate analysis demonstrated evidence of a significant genetic basis for plasticity (i.e., a significant genet × treatment interaction), but only within the cattle-free population (Table 4).

The most pronounced differential response to defoliation between the populations was seen in leaf blade angle. Blade angle did not change significantly among treatments within the cattle-impacted population but increased significantly with increasing frequency of defoliation in the cattle-free population (Fig. 1). Separate analyses of each population also showed significant genetic variation for this trait only within the cattle-free population (Table 4). At least some of the variation in this trait in this population could be explained by its relationship with leaf blade length ($r = -0.291$, $N = 120$). This relationship was not as pronounced in the cattle-impacted population ($r = -0.091$, $N = 127$). A nonsignificant genet × treatment interaction for leaf blade angle demonstrated that individual genets within both populations responded similarly to defoliation treatments relative to each other (Tables 3, 4).

## DISCUSSION

Differences observed in growth and development of ramets that survived defoliation from the two populations were relatively slight and did not involve significant changes in biomass allocation between roots and shoots. However, dissimilar ramet mortality between the populations indicates that, on average, plants from the cattle-impacted population are more resistant than those from the cattle-free population to defoliation similar to that of the 14- and 28-d defoliation treatments. Improved resistance to these defoliation frequencies may be based primarily on increased relative tiller number coupled with the production of slightly smaller tillers. This may reflect lower tiller mortality, an increased propensity to produce new tillers, and/or more successful tiller regrowth following defoliation. These are typical tolerance strategies used by caespitose grasses when repeatedly defoliated (Briske and Richards, 1994). While these traits may be directly associated with response to grazing either by cattle or

native herbivores, it is also possible they are ultimately the direct result of selection for resistance to other stresses such as fire (Belsky, 1986). The extremely low aboveground biomass produced by all ramets under the most frequent defoliation treatment may also suggest that this level of defoliation may be beyond the range of resistance of even the cattle-impacted population.

It has been demonstrated that frequently defoliated plants will be more productive if additional available carbohydrates are invested in rebuilding photosynthetic area, or if such plants exhibit higher photosynthetic rates following defoliation (Briske, 1996). Duncan et al. (1967) proposed that at leaf area indices less than ~3.5, photosynthesis across a community will be maximized when leaves are more horizontal. Therefore, producing more horizontally displayed leaves may be one way to increase carbon fixation following defoliation. Additionally, increased leaf angles may be associated with defoliation avoidance in grasses by placing more leaf biomass low to the ground where it would be less accessible to large herbivores (Painter, Detling, and Steingraeber, 1989). Differences in leaf blade angle of this sort were observed among populations of *Andropogon gerardii* Vitman, *Pascopyrum smithii* (Rydb.) Löve, *Schizachyrium scoparium* (Michx.) Nash, and *Bouteloua gracilis* (H.B.K.) Griffiths that had either been exposed to or protected from defoliation by prairie dogs and associated ungulates (Detling and Painter, 1983; Painter, Detling, and Steingraeber, 1989, 1993). In my experiment, the highest leaf angles (closest to horizontal) were exhibited with defoliation every 14 d in the cattle-free population (Fig. 1). These angles were uniformly high in this population in all treatments. The possible importance of this trait in affecting response to defoliation is also indicated by the apparent lack of genetic variation in this trait within the cattle-impacted population (Table 4). This would imply that strong selection toward more horizontal leaf blade display has occurred in this population. However, this result could also be due to selection acting on other traits that are strongly genetically correlated with the expression of leaf blade angle. Since high leaf blade angles would in-

crease access to light by leaves in a closed canopy, differences in this trait between populations could also have been affected by differences in interplant competition at the two sites (Caldwell and Richards, 1986). This seems unlikely, however, given the low vegetative cover at the two sites and the associated reduced probability for aboveground competition among genets.

In addition to leaf blade angle, my results suggest that exposure to cattle may have resulted in reduced plasticity in plant height and relative tiller number in response to variation in defoliation frequency in the cattle-impacted population (Table 4, Fig. 1). Little difference in mean height between the populations indicates that reductions in variability in this trait within the cattle-impacted population may simply reflect the effects of selection for traits more closely related to defoliation resistance. Given the generally greater differences in relative tiller number between the populations and the association of relative tiller number with defoliation resistance (Briske and Richards, 1994), it appears reasonable to assume that selection for defoliation resistance is responsible for the reduction in genetic variation in this trait within the cattle-impacted population. Nevertheless, reductions in genetic variation within this population cannot be attributed entirely to the effects of selection. Random genetic drift could be at least partially responsible, although it is not possible to separate the individual effects of selection and random genetic drift with these data. The cattle-impacted population did exhibit significant genetic variation in tiller mass while the cattle-free population did not. Comparable findings were reported by Polley and Detling (1988) in studies with *Pascopyrum smithii*, although any adaptive significance of variation in this trait has not been explained.

My research shows that plants from two *Bouteloua curtipendula* populations from southern Arizona show remarkable developmental plasticity in many traits in response to different frequencies of defoliation. It also suggests that long-term exposure to cattle or other environmental differences between the sites the two populations occupy may have resulted in selection for traits associated with defoliation resistance. However, inadequate sampling when collecting genets for this study, random genetic drift, or selection for traits genetically correlated with those associated with defoliation resistance cannot be entirely excluded as factors leading to reduced genetic variation. It is also possible that uncharacterized environmental differences between the two sites are at least partially responsible for the differences between the two populations.

Reductions in genetic variation in the cattle-impacted population could negatively affect its evolutionary potential both in the presence and absence of domestic herbivores. The exact consequences of these reductions in genetic variation are difficult to predict, although it is likely that the potential for rapid adaptation to changing environments has been reduced as a result of exposure to domestic herbivores (Bazzaz, 1996). Moreover, my findings agree with Painter, Detling, and Steingraeber (1989) who suggested that caution should be used when interpreting research using artificial exclosure areas where domestic herbivores have been excluded for varying lengths of time. While the species composition within these areas

may resemble the assumed pre-exclosure conditions, the genetic constitution of the populations may differ considerably between ones impacted by an exotic environmental force, such as domestic livestock, from those of native, naturally disturbed environments.

## LITERATURE CITED

Aarssen, L. W., and R. Turkington. 1985. Within-species diversity in natural populations of *Holcus lanatus*, *Lolium perenne* and *Trifolium repens* from four different-aged pastures. *Journal of Ecology* 73: 869–886.

Bahre, C. J. 1995. Human impacts on the grasslands of southeastern Arizona. *In* M. P. McClaren and T. R. Van Devender [eds.], The desert grassland, 230–264. University of Arizona Press, Tucson, AZ.

Barrett, S. C. H., and B. C. Husband. 1990. The genetics of plant migration and colonization. *In* A. H. D. Brown, M. T. Clegg, A. L. Kahler, and B. S. Weir [eds.], Plant population genetics, breeding and genetic resources, 254–277. Sinauer, Sunderland, MA.

———, and J. R. Kohn. 1991. Genetic and evolutionary consequences of small population size in plants: implications for conservation. *In* D. A. Falk and K. E. Holsinger [eds.], Genetics and conservation of rare plants, 3–30. Oxford University Press, New York, NY.

Bazzaz, F. A. 1996. Plants in changing environments: linking physiological, population and community ecology. Cambridge University Press, New York, NY.

Belsky, A. J. 1986. Does herbivory benefit plants: a review of the evidence. *American Naturalist* 127: 870–892.

Briske, D. D. 1991. Developmental morphology and physiology of grasses. *In* R. K. Heitschmidt and J. W. Stuth [eds.], Grazing management: an ecological perspective, 85–108. Timber Press, Portland, OR.

———. 1996. Strategies of plant survival in grazed systems: a functional interpretation. *In* J. Hodgson [ed.], The ecology and management of grazing systems, 37–67. Oxford University Press, New York, NY.

———, and J. H. Richards. 1994. Physiological responses of individual plants to grazing: current status and ecological significance. *In* M. Vavra, W. A. Laycock, and R. D. Pieper [eds.], Ecological implications of livestock herbivory in the west, 147–176. Society for Range Management, Denver, CO.

Brown, D. E. 1994. Semidesert grasslands. *In* D. E. Brown [ed.], Biotic communities: southwestern United States and northwestern Mexico, 123–135. University of Utah Press, Salt Lake City, UT.

Caldwell, M. M., and J. H. Richards. 1986. Competitive position of species in respect to grazing tolerance: some perspective on ecophysiological processes. *In* P. J. Joss, P. W. Lynch, and O. B. Williams [eds.], Rangelands: a resource under siege. Proceedings of the Second International Rangelands Congress, 447–449. Australian Academy of Science, Canberra.

Carmen, J. G., and D. D. Briske. 1985. Morphologic and allozymic variation between long-term grazed and non-grazed populations of the bunchgrass *Schizachyrium scoparium* var. *frequens*. *Oecologia* 66: 332–337.

Detling, J. K., M. I. Dyer, and D. T. Winn. 1979. Net photosynthesis, root respiration, and regrowth of *Bouteloua gracilis* following simulated grazing. *Oecologia* 41: 127–134.

———, and E. L. Painter. 1983. Defoliation responses of western wheatgrass populations with diverse histories of prairie dog grazing. *Oecologia* 57: 65–71.

Duncan, W.G., R. S. Loomis, W. A. Williams, and R. Hanau. 1967. A model for simulating photosynthesis in plant communities. *Hilgardia* 38: 181–205.

Eckert, C. G., D. Manicacci, and S. C. H. Barrett. 1996. Genetic drift and founder effect in native versus introduced populations of an invading plant, *Lythrum salicaria* (Lythraceae). *Evolution* 50: 1512–1519.

Gould, F. W., and Z. J. Kapadia. 1964. Biosystematic studies in the *Bouteloua curtipendula* complex II. Taxonomy. *Brittonia* 16: 182–207.

Hadley, D., P. Warshall, and D. Bufkin. 1991. Environmental

change in Aravaipa, 1870–1970: an ethnoecological survey. Cultural Resource Series 7, Arizona Bureau of Land Management, Phoenix, AZ.

HASTINGS, J. R., AND R. M. TURNER. 1965. The changing mile: an ecological study of vegetation change with time in the lower mile of an arid and semiarid region. University of Arizona Press, Tucson, AZ.

HOFFMEISTER, D. F. 1986. Mammals of Arizona. University of Arizona Press, Tucson, AZ.

HUMPHREY, R. R. 1958. The desert grassland: a history of vegetational change and an analysis of causes. *Botanical Review* 24: 193–252.

JARAMILLO, V. J., AND J. K. DETLING. 1988. Grazing history, defoliation, and competition: effects on shortgrass production and nitrogen accumulation. *Ecology* 69: 1599–1608.

KRAUSMAN, P. R., A. J. KUENZI, R. C. ETCHBERGER, J. R. RAUTENSTRAUCH, L. L. ORDWAY, AND J. J. HERVERT. 1997. Diets of desert mule deer. *Journal of Range Management* 50: 513–522.

MCNAUGHTON, S. J. 1979. Grazing as an optimization process: grass-ungulate relationships in the Serengeti. *American Midlands Naturalist* 113: 691–703.

MILLER, R. E., AND N. L. FOWLER. 1993. Variation in reaction norms among populations of the grass *Bouteloua rigidiseta*. *Evolution* 47: 1446–1455.

O'CONNOR, T. G. 1991. Local extinction in perennial grasslands: a life-history approach. *American Naturalist* 137: 753–773.

PAINTER, E. L., J. K. DETLING, AND D. A. STEINGRAEBER. 1989. Grazing history, defoliation, and frequency-dependent competition: effects on two North American grasses. *American Journal of Botany* 76: 1368–1379.

———, ———, AND ———. 1993. Plant morphology and grazing history: relationships between native grasses and herbivores. *Vegetatio* 106: 37–62.

PARMENTER, R. R., AND T. R. VAN DEVENDER. 1995. Diversity, spatial variability, and functional roles of vertebrates in the desert grassland. *In* M. P. McClaren and T. R. Van Devender [eds.], The desert grassland, 196–229. University of Arizona Press, Tucson, AZ.

POLANS, N. O., AND R. W. ALLARD. 1989. An experimental evaluation of the recovery potential of ryegrass populations from genetic stress resulting from restriction of population size. *Evolution* 43: 1320–1324.

POLLEY, H. W., AND J. K. DETLING. 1988. Herbivory tolerance of *Agropyron smithii* populations with different grazing histories. *Oecologia* 77: 261–267.

QUINN, J. A., AND R. V. MILLER. 1967. A biotic selection study utilizing *Muhlenbergia montana*. *Bulletin of the Torrey Botanical Club* 94: 423–432.

SAS. 1992. SAS technical report P-229. SAS/STAT Software: changes and enhancements, Release 6.07. SAS Institute, Cary, NC.

SCHMUTZ, E. M. 1978. Estimating range use with grazed-class photo guides. Bulletin A-73, Cooperative Extension Service, University of Arizona, Tucson, AZ.

SHAPIRO, S. S., AND M. B. WILK. 1965. An analysis of variance test for normality (complete samples). *Biometrika* 52: 591–611.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry, the principles and practices of statistics in biological research, 2d ed. W. H. Freeman, New York, NY.

TRLICA, M. J., AND A. B. ORODHO. 1989. Effects of protection from grazing on morphological and chemical characteristics of Indian ricegrass, *Oryzopsis hymenoides*. *Oikos* 56: 299–308.

VALENTINE, J. F. 1990. Grazing management. Academic Press, San Diego, CA.