



Gender-related differences of shrubs in stands of *Atriplex canescens* with different histories of grazing by cattle

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Atriplex canescens is a relatively common dioecious shrub in western North America. It is considered a valuable forage resource for both wild and domestic herbivores. Sex ratios and shrub dimensions were recorded in stands of tetraploid *A. canescens* that had been either protected from cattle grazing or summer- or winter-grazed by cattle for at least 20 years. Stem diameter and crown shape were used as surrogates for shrub age which could not be estimated by counting growth rings. Shrub sex ratios in exclosures were significantly more female biased than the empirically derived ratio for tetraploid *A. canescens* (55 female : 35 male : 10 monocious). Conversely, shrub sex ratios in grazed pastures were not significantly different from the empirical ratio. Proportion of female shrubs in exclosures was significantly higher than in grazed pastures. Proportion of male shrubs, on the other hand, was similar in exclosures and grazed pastures. Winter-grazed shrub stands were apparently younger than both summer-grazed and protected shrubs. Protected shrubs appeared to be the oldest. Grazed female shrubs were apparently younger than grazed males, however, shrub ages of protected male and female shrubs were apparently not different. Cattle-grazing may have affected female shrubs more negatively at this site, causing gender-based differential mortality, and/or sex-shifting. Such processes could account for the differences in sex ratios, and for the apparent gender-related differences in shrub age that were observed.

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Introduction

Atriplex canescens (Pursh) Nut. (Chenopodiaceae) is a dioecious wind-pollinated shrub that is widespread across rangelands of western North America (Brown, 1956). *A. canescens* is an important component of winter diets of cattle on the shortgrass steppe (Shoop *et al.*, 1985) and due to its chemical attributes (Welch & Monsen, 1981)

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presumably also contributes significantly to winter diets of native herbivores. Tetraploid *A. canescens* (the most common of the known cytotypes) is sub-dioecious, with female, male, and monoecious individuals (McArthur, 1977). Sex ratios of these shrub populations are female-biased exhibiting fairly constant proportions of sexes across a wide variety of environments (McArthur & Freeman, 1982). Very few studies addressing shrub-gender-herbivore interactions have been conducted in *A. canescens* (Maywald *et al.*, 1998) as compared to the amount of research focusing on aspects of its genetics (Stutz & Sanderson, 1979; Sanderson & Stutz, 1994), breeding system (McArthur, 1977; Freeman *et al.*, 1984; Barrow, 1987), chemical attributes (Rumbaugh *et al.*, 1982; Garza & Fullbright, 1988), and responses to defoliation (Pieper & Donart, 1978; Price *et al.*, 1989; Benjamin *et al.*, 1995).

Herbivores that consume dioecious plants often exhibit gender-related preferences that frequently result in male-biased herbivory (Watson, 1995, and references therein). A few cases of female-biased herbivory, however, have also been reported (Lovett Doust & Lovett Doust, 1985; Maywald, 1998). The relationship between sex-biased herbivory and plant sex ratios has seldom been formally addressed. However, most of the studies on sex-biased herbivory reviewed by Boecklen & Hoffman (1993) report plant sex ratios with biases opposite to the herbivory bias observed (i.e. female-biased sex ratios in plant species subjected to male-biased herbivory, or *vice versa*). Variations in the proportion of sexes in stands of *Atriplex canescens* have never been studied in the context of history of use by grazers. Such variations have been studied in other species of *Atriplex*, such as *A. vesicaria* Heward ex. Benth., a dominant saltbush of the Australian chenopod shrublands, where alterations in the proportions of male and female shrubs in relation to sheep herbivory have been known for a long time (Osborn *et al.*, 1932). Under grazing, sex ratios of *A. vesicaria* tend to be less female biased than in exclosures due to the fact that sheep consume female shrubs preferentially and apparently promote gender-biased mortality (Williams *et al.*, 1978; Maywald, 1998).

Herbivores can affect plant morphological traits both by present levels of use, and by historical patterns of herbivory (Painter *et al.*, 1993; Singer *et al.*, 1994). Whereas crown dimensions in *Atriplex canescens* have been studied in relation to ploidy level (Stutz *et al.*, 1975), shrub accession (McArthur *et al.*, 1983), shrub gender (Pendelton *et al.*, 1992), topographic position (Freeman *et al.*, 1993), and biomass production (Ruess, 1980), they have never been studied (to our knowledge) in relation to herbivory. Herbivores can potentially alter crown dimensions in *A. canescens* by affecting shrub growth and development, by favouring the proliferation of less palatable genotypes, or, more importantly, by promoting changes in the population age structure. Heavy browsing promotes increases in shrub mortality rates in *A. canescens* (Benjamin *et al.*, 1995), and appears to increase population turnover rates (Cibils *et al.*, 1997). Therefore, browsed shrub stands can be expected to be younger than protected ones. Such browsing-induced age differences should translate into measurable differences in crown and stem dimensions. Furthermore, in situations where browsing promotes gender-biased shrub mortality (as in the case of *A. vesicaria*), differences in mean ages of male and female individuals should also translate into gender-biased differences in shrub dimensions.

Shrub sex counts and crown and stem dimension measurements of female and male shrubs of tetraploid *Atriplex canescens* were analysed in relation to history of grazing by cattle, at a site on the shortgrass steppe in north-eastern Colorado. At this site *A. canescens* can be heavily used by cattle; in January and August heifer diets can include high percentages of this shrub (55 and 42%, respectively; Shoop *et al.*, 1985). The objectives of this study were to determine (1) whether stands that had been subjected to contrasting grazing regimes exhibited differences in shrub sex ratios, and (2) whether such stands exhibited both overall and shrub gender-related differences in crown and stem morphometric relations. It was hypothesized that if shrubs of *A. canescens* at the study site had been subjected to different levels of cattle herbivory

on the basis of gender, differences in shrub sex ratios between stands with contrasting histories of grazing by cattle would be found. It was predicted that shrub stands in exclosures would exhibit a larger proportion of female shrubs than adjacent browsed stands. It was also hypothesized that either seasonal, or gender-related differences in levels of cattle herbivory would cause differences in crown and stem dimensions of shrub populations subjected to contrasting grazing regimes. It was predicted that the smallest shrubs would be found in winter-grazed stands (that are browsed the most; Shoop *et al.*, 1985) and largest shrubs would be found in exclosures. It was also predicted that under grazing female shrubs would be smaller than males.

Methods

Study area

The field study site was located within the USDA-ARS Central Plains Experimental Range (CPER), approximately 60 km north-east of Fort Collins, Colorado (40°49'N; 107°47'W) at 1650 m elevation. The study was conducted at a shrub-dominated site on the Owl Creek floodplain. Soils of this site have been described as loamy to sandy loams; *Atriplex canescens*, *Bouteloua gracilis* (H.B.K.) Lag. ex Griffiths. and *Agropyron smithii* Rydb. are the dominant plant species at the site (Liang *et al.*, 1989). Mean annual precipitation is 320 mm. Most of the rainfall occurs between April and September.

Data collection

Two distinct areas with important amounts of *Atriplex canescens* have been described at the CPER, namely: (1) creek flood plains also characterized as 'sandy plains' with dense stands of larger saltbush shrubs; and (2) (higher) creek terraces described as 'loamy plains' with sparser stands of shorter saltbush shrubs (Shoop *et al.*, 1985). Six 50-m transects were placed within the 'sandy plains' areas in exclosures and in adjacent summer- and winter-grazed pastures. All transects were placed in N-S direction, parallel to the creek within a range of approximately 70–100 m from the creek bed. The pastures (64 ha) had been moderately grazed by cattle (at approximately 5.3 ha AUM⁻¹ per 6 months) either in winter or summer for at least 20 years. The summer- and winter-grazed pastures studied were adjacent, so the transects were placed about 15 m from the fences dividing pastures to minimize soil-related influences on overall shrub density. The exclosures (0.4–0.8 ha rectangular plots) had been protected from cattle grazing for at least 25 years, and were placed within the pastures we studied. Rabbits, other rodents, and possibly pronghorn antelope had access to the exclosures. Stems browsed by rabbits exhibit a characteristic 45° (approximately) angle tip. Evidence of rabbit browsing was only found on thin stems of young shrubs in grazed pastures. It was assumed that any hypothetical impact of rabbits on shrubs in exclosures (with almost exclusively large (adult) individuals) would be minimal. Pronghorn, on the other hand, were only seen twice in a 3.5-year period by the authors in the general study area.

Therefore, two transects were laid out in winter-grazed stands, two in summer-grazed stands, and two in exclosures. The closest shrub to each 1-m interval point along the transect was selected. In a few cases where the closest individual to a point had already been recorded and measured, the second closest individual was taken at the point in order to avoid recording the same shrub twice. A total of 100 shrubs per history of grazing class were examined (total = 300 observations).

Sex phenotype of each shrub was determined by ocular inspection, classifying them as either 'females', 'males', 'monecious', or 'zeros' depending on whether they exhibited utricles, staminate flower remnants, both staminate flower remnants and utricles, or neither of them, respectively. Individuals with no sexual expression classified as 'zeros' were small (young) shrubs in almost all cases. On each shrub the largest crown diameter (D1) and the diameter perpendicular to it (D2) were measured to the nearest centimeter. Shrub height of the tallest stem was also measured to the closest centimeter. Percentage of dead crown was estimated by subjectively assessing the relative amount of dead stems. Stem D1 and D2 were measured on the thickest stem of each individual at ground level, using a 6-inch dial caliper, following the same criteria as with the crown measurements. Crown dimension measurements were used to calculate crown volume, assuming an elliptical cylindrical shape. Stem diameter measurements were used to calculate stem cross-section area, again assuming an elliptical shape.

Data analysis

Student's *t*-tests were performed to detect differences in mean percentage of females, males and monecious shrubs between exclosures and grazed pastures (grazing season was not considered in this case). Percentages were arcsin transformed in order to meet normality assumptions. χ^2 goodness-of-fit tests were also performed with the shrub sex phenotype counts, comparing the measured sex ratios to the empirically determined 35 male : 55 female : 10 monecious ratio (McArthur, 1977). All adult shrubs were included in this analysis and count data for each history of grazing class were pooled.

The analysis of crown and stem morphometric variables was performed using a subset of the data including only male and female shrubs ($n = 202$). Means and standard errors were calculated for each measured variable, as well as Pearson correlation coefficients between all pairs of stem and crown measurements.

Multivariate techniques were applied to analyse crown and stem dimensions. Such techniques had been previously applied by Dunford (1985) to the study of leaf morphology of *Atriplex canescens* individuals of different ploidy levels. Crown D1, crown D2, crown height, crown volume, stem D1, stem D2, stem cross-section area, and percentage of dead crown were the variables used in the analysis. The data was assumed to be unstructured; discriminant analysis, stepwise discriminant analysis, and canonical analysis were performed in a sequential manner on the data set, following a procedure proposed by Horton *et al.* (1968). In this way, morphometric variables used to discriminate individuals were reduced (from the initial eight to two canonical variates) allowing a clearer interpretation of the results.

Shrubs were grouped *a priori* into three classes on the basis of grazing regime, namely: shrubs grazed in winter (W), shrubs grazed in summer (S), and shrubs in exclosures (X). Once the discriminant functions were developed and individual observations were discriminated into the *a priori* groups, multivariate analysis of variance and Wilk's Lambda were used to test for significant differences among groups. A stepwise discriminant analysis was then performed in order to select a subset of the original set of eight variables including only the ones that contributed significantly to the discrimination of groups. The significance level to enter a variable in the selection iterations of this procedure was set at $p = 0.05$, while the level of significance for a variable to remain in the reduced model was set at $p = 0.10$. The number of variables was finally reduced even further by developing canonical variates, new orthogonal variables resulting from linear combinations of the original *p*-variates (Horton *et al.*, 1968; Seal, 1994). The means of the canonical variables for each group with their corresponding confidence interval (95%), calculated as z/\sqrt{n} (n = number of

individuals in each group; Seal 1964), were then plotted on two canonical axes allowing the separation of significantly different canonical score means. Exploratory correlation analyses between canonical variates and the original crown and stem morphometric variables (or ratios of these variables), and plots of all individual observations on the canonical axes were performed in order to determine the biological meaning of the first and second canonical variate.

Finally, a second situation was considered with a different *a priori* grouping of the data. In this case shrub gender was taken into account and six groups were defined: female shrubs in exclosures (FX), male shrubs in exclosures (MX), winter-grazed female shrubs (FW), winter-grazed male shrubs (MW), summer-grazed female shrubs (FS), and summer-grazed male shrubs (MS). The full analysis described above was then carried out. SAS (1996) procs TTEST, REG, CORR, DISCRIM, STEPDISC, and CANDISC were used to perform the statistical analyses. Statgraphics (1995) was used to perform the χ^2 goodness-of-fit tests.

Additional measurements

Factors other than level of herbivory (competition, resource availability, and resultant ecophysiological interactions) can affect shrub growth and mortality rates and sex ratios. Therefore, additional data were collected which would help in determining if any differences found should be attributed to herbivory or to other factors.

Staminate flower buds were collected (in the following spring) from five male plants on each of three transects representing all three grazing regimes at the site. The material collected was fixed in 5% acetic acid and sent to the U.S. Forest Service Shrub Sciences Laboratory in Provo, Utah, to have chromosome counts performed in order to confirm previous identification of ploidy level of this population.

Since woody plants are more abundant on coarser-textured soils on the shortgrass steppe (Dodd & Lauenroth, 1997, and references therein), and because soil texture variations can affect moisture availability to plants (Noy Meir, 1973) and can ultimately alter shrub sex ratios (Freeman *et al.*, 1976), total shrub density and soil texture was also determined on each transect. Shrub density was estimated using the closest individual method (Cottam & Curtis, 1956). Soil texture was measured on three composite samples collected on each transect. Composite samples included three 30-cm-deep cores collected at 10 m intervals along the transect. Soil texture analysis was performed at the USDA ARS High Plains Grasslands Research Station soils laboratory, following procedures proposed by Bouyoucos (1962). Pearson correlation coefficients were calculated between soil texture (per cent sand) and shrub-related variables of interest (shrub density, crown volume, and per cent male and female plants). Pearson correlation coefficients were also calculated between pairs of the shrub-related variables of interest in order to detect significant associations between shrub density and relative numbers of male and female shrubs. All variables expressed as percentages were arcsin transformed in order to meet normality assumptions.

Results

Additional measurements

Chromosome counts performed on the staminate flower buds indicated that all individuals examined were tetraploid, confirming earlier identifications of plant material from the site. It is possible, however, that tetraploid *Atriplex canescens* populations may occasionally include a small number of hexaploid individuals (E. D. McArthur & S. Sanderson, pers. comm.).

Correlation analyses between soil texture and shrub-related variables indicated that neither shrub crown volume nor relative numbers of females and males were significantly related to soil texture. Shrub density was the only variable significantly correlated with soil texture ($r = -0.82$, $p = 0.046$). As soils became coarser, shrub density tended to decrease. Per cent male shrubs was not significantly correlated with shrub density. Conversely, relative number of female shrubs showed a positive and significant association with shrub density ($r = 0.81$, $p = 0.05$). Thus, denser stands tended to have an increasing proportion of female shrubs (Table 1).

Tests of predictions

With regards to the first prediction, it was found that exclosures exhibited a significantly greater proportion of females than did the grazed pastures ($t = 2.67$; $p = 0.04$). The proportion of male and monocious shrubs was similar in exclosures and grazed pastures (males: $t = -1.76$, $p = 0.128$; monocious: $t = -1.18$, $p = 0.284$). Sex ratios of shrubs in stands that had been grazed either in winter or summer did not differ significantly from the empirically derived 55 female:35 male:10 monocious sex ratio (summer-grazed = 62 female:32 male:6 monocious, $p = 0.273$; winter-grazed = 59 female:28 male:13 monocious, $p = 0.253$). Conversely, shrub sex ratios in exclosures were significantly more female biased (70 female:25 male:5 monocious, $p = 0.009$).

The multivariate analysis of the shrub dimensions addressed the second and third prediction. Almost all crown and stem morphometric variables were positively and significantly correlated with each other (Table 2). Hence, bivariate analysis between each single predictor and either shrub grazing regime or shrub gender would have been difficult to interpret, and would have overlooked the effect of covariance among variables.

Shrubs discriminated on the basis of all eight crown and stem morphometric variables into the *a priori* defined classes (both by history of grazing alone, and by history of grazing + shrub gender) produced groupings with at least one class significantly different from the others (Table 3(a)). The stepwise discriminant analysis procedure

Table 1. Means and standard errors for the eight variables measured on female and male shrubs with different histories of cattle grazing

	Summer grazed		Winter grazed		Exclosures	
	Female ($n = 44$) \bar{x} $S_{\bar{x}}$	Male ($n = 23$) \bar{x} $S_{\bar{x}}$	Female ($n = 38$) \bar{x} $S_{\bar{x}}$	Male ($n = 17$) \bar{x} $S_{\bar{x}}$	Female ($n = 60$) \bar{x} $S_{\bar{x}}$	Male ($n = 20$) \bar{x} $S_{\bar{x}}$
Crown D1 (cm)	83 ± 3.9	79 ± 5.8	78 ± 3.2	84 ± 6.3	92 ± 4.9	96 ± 6.3
Crown D2 (cm)	60 ± 3.5	59 ± 5.8	61 ± 3.7	64 ± 6.1	70 ± 4.0	77 ± 6.0
Crown height (cm)	67 ± 1.8	71 ± 3.3	65 ± 1.8	66 ± 3.2	71 ± 2.5	73 ± 6.0
Crown vol. (dm ³)	310 ± 39	340 ± 71	280 ± 31	320 ± 68	460 ± 58	460 ± 78
Stem D1 (cm)	4.1 ± 0.2	4.8 ± 0.4	3.46 ± 0.3	4.1 ± 0.2	5.3 ± 0.3	5.0 ± 0.2
Stem D2 (cm)	3.1 ± 0.2	3.5 ± 0.2	2.5 ± 0.2	2.9 ± 0.2	3.6 ± 0.1	3.8 ± 0.2
Stem c. sect. (dm ²)	10.8 ± 0.1	14.8 ± 0.2	7.6 ± 0.1	10 ± 0.1	15.8 ± 0.1	15.8 ± 0.2
Dead crown (%)	29 ± 2.6	32 ± 4.6	24 ± 3.2	27 ± 3.2	55 ± 3.0	58 ± 4.7
	\bar{x} $S_{\bar{x}}$		\bar{x} $S_{\bar{x}}$		\bar{x} $S_{\bar{x}}$	
Shrub density (shrubs ha ⁻¹)	4853 ± 416		3540 ± 110		7496 ± 896	

Table 2. Pearson correlation coefficients significant at $p < 0.01$

	Crown D1	Crown D2	Crown height	Crown volume	% dead	Stem D1	Stem D2	Stem C. sect.
Crown D2	0.87	—	—	—	—	—	—	—
Crown height	0.47	0.50	—	—	—	—	—	—
Crown vol.	0.85	0.88	0.66	—	—	—	—	—
% dead	0.18	—	—	—	—	—	—	—
Stem D1	0.56	0.56	0.42	0.55	0.36	—	—	—
Stem D2	0.54	0.57	0.50	0.59	0.31	0.76	—	—
Stem C. sect.	0.57	0.60	0.48	0.62	0.31	0.90	0.93	—

selected four significant crown and stem morphometric variables for the classes defined by history of grazing alone. The reduced set of variables was able to discriminate observations into significantly different groups (Table 3(b)). For the six classes defined by history of grazing + shrub gender, the stepwise discriminant procedure selected three significant crown and stem morphometric variables that were also able to produce a significant discrimination of observations into the *a priori* defined classes (Table 3(b)).

The canonical analysis performed on the reduced set of crown and stem morphometric variables indicated that mean canonical scores for the classes defined by history of grazing alone were significantly ($p < 0.05$) different from each other (Fig. 1(a)).

Table 3. Tests of significance of differences among means of observations discriminated into the different groups. (a) Discriminant analysis; (b) stepwise discriminant analysis

(a) Discriminant analysis					
Grouping criterion	No. Groups	No. Variables	Wilk's Lambda	<i>F</i>	<i>p</i>
History of grazing	3	8	0.5466	8.46	0.001
History of grazing + gender	6	8	0.4558	4.08	0.001
(b) Stepwise discriminant analysis					
Grouping criterion	Variables selected				
History of grazing	% dead crown, crown height, crown D2, stem D2				
History of grazing + gender	% dead crown, crown height, stem D1				
	No. Groups	No. Variables	Wilk's Lambda	<i>F</i>	<i>p</i>
History of grazing	3	4	0.5831	15.16	0.001
History of grazing + gender	6	3	0.5567	8.44	0.001

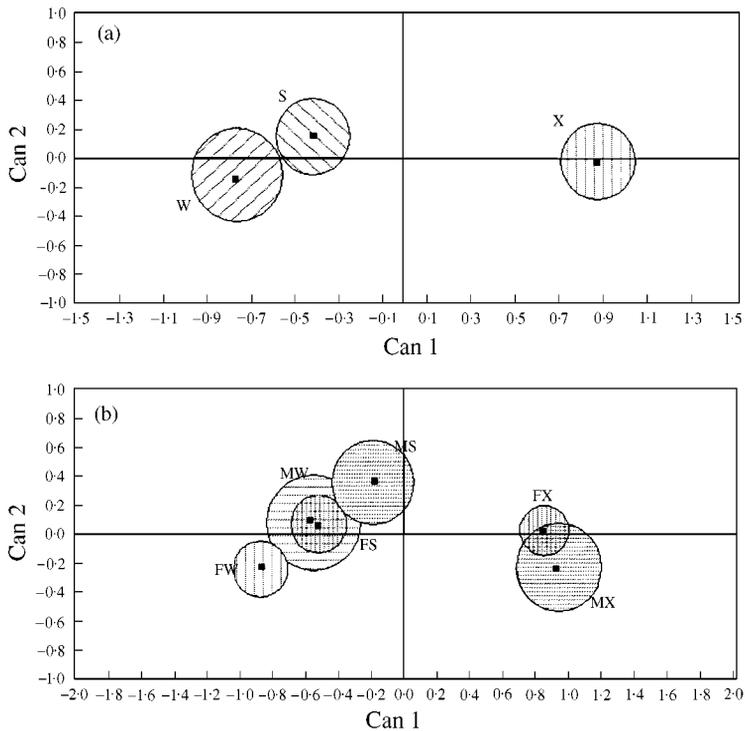


Figure 1. (a) Mean canonical scores with 95% confidence intervals for winter-grazed shrubs (W), summer-grazed shrubs (S), and protected shrubs (X). (b) Mean canonical scores with 95% confidence intervals for winter-grazed females (FW), winter-grazed males (MW), summer-grazed females (FS), summer-grazed males (MS), protected females (FX), and protected males (MX).

The same analysis for the classes defined by history of grazing + shrub gender showed significant differences (in some instances) between males and females subjected to the same history of grazing. Such differences were not evident in exclosures (Fig. 1(b)). Both the plot of individual scores (not shown), and the correlation analyses between canonical variates and the original crown morphometric variables (or ratios between them) indicated that the first canonical variate was related to shrub size (as indicated by stem D1) ($r = 0.90$, $p = 0.01$; Fig. 2(a)), and that the second canonical variate was related to crown shape (ratio of Crown D1 to Crown D2) ($r = 0.85$, $p = 0.03$; Fig. 2(b)). Thus, increasing values on the first canonical axis indicated an increase in shrub size, while increases in values along the second canonical axis indicated transitions from circular to elliptical crown shapes.

It seemed puzzling that, according to the analysis, with increasing shrub size, crown shapes changed from circular (in small shrubs), to elliptical (in medium-sized shrubs), and back to circular (in the largest shrubs) (Fig. 1(a, b)). Knowing that woody plants may exhibit characteristic changes in crown shape throughout their life-span (Horn, 1971), crown shape *vs.* stem D1 (our best surrogate for shrub age) were plotted. It was found that crown shapes changed from circular to elliptical, and back to circular with increasing stem D1 (Fig. 3). Because *Atriplex canescens* (as most woody chenopods; Fahn & Zimmerman, 1982) exhibits anomalous secondary thickening, it is impossible to assess shrub age by performing vascular ring counts (Schweingruber, 1992). Malik *et al.* (1976) used crown dimensions as surrogates for age in *Atriplex*, however, stem diameter was used in this study because it is assumed to be less influenced by the direct

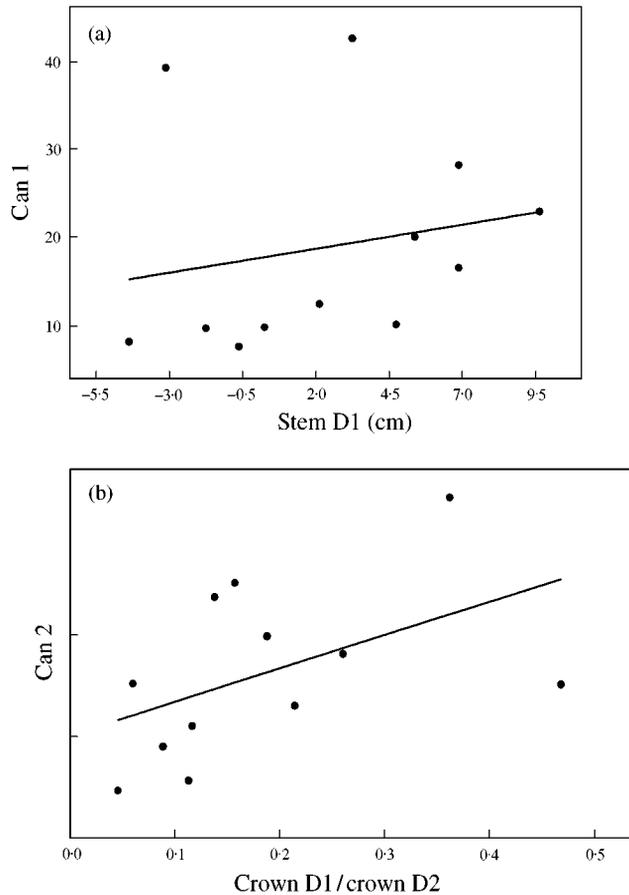


Figure 2. (a) Relation between first canonical variate and stem D1. (b) Relation between second canonical variate and the ratio of crown D1: crown D2.

effects of cattle browsing. Although secondary thickening of stems can potentially be affected by herbivory (Swetnam *et al.*, 1988), age-related differences (within the range of stem diameters that were examined) would certainly override such effects.

Whereas the difficulty in corroborating this analysis by vascular ring counts calls for caution in the interpretation of the data, it was considered (given the evidence discussed above) reasonable to assume that the shrub-size/crown-shape relations were indicators of shrub age. It was postulated that separation of group means in the multivariate space was basically age-related. Consequently, with regards to the second prediction, it was found that winter-grazed shrubs were the smallest class, with nearly circular-shaped crowns, whereas shrubs in exclosures were the largest, also with nearly circular-shaped crowns. Summer-grazed shrubs were intermediate sized with elliptical crowns (Fig. 1(a)). Hence, shrubs in exclosures were apparently the oldest, winter-grazed stands were apparently the youngest, and summer-grazed stands had intermediate ages. In relation to the third prediction, it was found that mean apparent ages of male and female shrubs in the exclosures were not significantly different from each other, but they were significantly older than shrubs belonging to all four grazed classes (Fig. 1(b)). Winter-grazed females were apparently significantly younger than shrubs in all other classes, except for the winter-grazed males, where differences were not

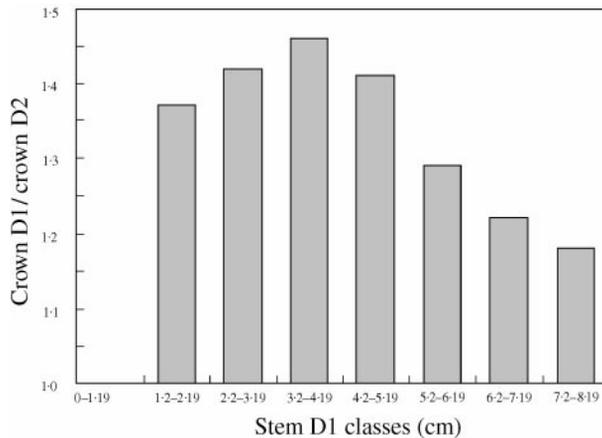


Figure 3. Variation of crown shapes of *Atriplex canescens* shrubs with increasing shrub age.

statistically significant (Fig. 1(b)). Summer-grazed females were significantly younger than summer-grazed males (Fig. 1(b)).

Discussion

In dioecious plants, female and male sexual structures occur on separate individuals. Female reproductive effort is thought to be greater than that of male plants, due to the fact that females must produce both flowers and fruits. This notion is supported by a number of studies showing greater allocation of biomass and nitrogen to reproductive structures of females compared to males (Schlessman, 1988, and references therein; Antos & Allen, 1990).

In a study including *Atriplex confertifolia* (Torr. & Frem.) S. Wats., Freeman & Harper (1980) found that male plants were more abundant inside grazing exclosures than in adjacent grazed pastures. They hypothesized that greater competition for moisture inside the exclosures favoured male shrubs (with less reproductive expenditure) over females. We might have expected to find the pattern described by Freeman & Harper (1980) at this site as well. However, shrub sex ratios within the exclosures (that had double the shrub density of grazed pastures) were significantly more female biased than in adjacent grazed pastures. Variations in the proportion of female shrubs were not related to changes in soil texture. Cattle browsing, apparently overriding the effects of competition between genders and/or small-scale variations in soil moisture availability, may have promoted gender-specific mortality and/or sex shifting toward maleness (McArthur & Freeman, 1982), thus giving rise to the pattern observed here. Intense defoliation can lead to shrub mortality in *A. canescens* (Benjamin *et al.*, 1995). Female shrubs at this research site appear to be subjected to higher levels of herbivory than male shrubs (Cibils, 1999), a phenomenon which has also been shown for *A. vesicaria* (Maywald, 1998). This bias could have promoted greater mortality among female than male shrubs, causing sex ratios of grazed stands to be less female biased than those of the exclosures. The analysis of shrub crown and stem dimensions discussed below appear to substantiate the idea of shrub-gender related mortality.

A number of factors can affect shrub crown dimensions in *Atriplex canescens*. Increases in chromosome numbers are generally associated with a decrease in shrub size (Sanderson *et al.*, 1989). Diploids may grow three to four times taller than tetraploids (Stutz *et al.*, 1975). Furthermore, a relation between soil texture and shrub ploidy level

has also been described in *A. canescens* (Stutz *et al.*, 1975; Dunford, 1984, 1985). Shrubs with lower chromosome numbers (larger crowns) are associated with sandy soils while shrubs with higher chromosome numbers (smaller crowns) are associated with finer-textured soils. Shrub age is another obvious factor affecting shrub size, to the extent that crown sizes have been used as age surrogates in some classifications (Malik *et al.*, 1976). Finally, grazing may also affect shrub dimensions. Both grazing and artificial defoliation experiments in *A. canescens* (Buwai & Trlica, 1977; Trlica *et al.*, 1977; Pieper & Donart, 1978; Price *et al.*, 1989) and in other species of the genus (Eldridge *et al.*, 1990) showed that grazing tends to reduce shrub crown sizes.

Most woody species of the genus *Atriplex* (*A. canescens* included) are fairly short-lived and therefore exhibit moderately high population turnover rates (Crisp, 1978; Eldridge *et al.*, 1990; Chambers & Norton, 1993). At the research site where this study was conducted young shrubs are an important component of the plant community (Cibils *et al.*, 1997). Because population turnover is fairly dynamic and shrub recruitment is frequent, a mosaic of ages (and hence, shrub sizes) can be expected to occur in stands of *A. canescens*. Thus, age-related differences in crown dimensions within local shrub populations are important. At the present research site, no significant association was found between shrub crown size and soil texture, and original chromosome counts of staminate flowers indicated that all sampled individuals were tetraploid. Hence, the observed variation in shrub dimensions could be attributed to age structure. The multivariate analysis of crown and stem dimensions suggested that variations in size and shape of *A. canescens* shrubs at the present study site were basically age related. Winter-grazed shrubs (more heavily utilized) were apparently significantly younger than both summer grazed (less heavily utilized) and protected shrubs. Average apparent age of female shrubs under grazing was in most cases lower than their male counterparts. Such a difference was not evident in the exclosures. Male shrubs of *A. canescens* have been shown to live longer than female shrubs (Freeman *et al.*, 1984), however, at the present site this was apparently the case only with grazed shrubs. Freeman *et al.* (1984) suggested that differences in the longevity of genders in *A. canescens* could be related to differences in fitness of males and females. The data presented here suggest that cattle grazing may enhance gender-specific longevity differences.

The apparently age-related shrub size differences observed here could be magnified by the effects of gender-specific selection pressure imposed by grazing. Since female shrubs appear to be subjected to higher levels of herbivory than males (Cibils, 1999), and because population turnover is fairly dynamic, through time, cattle browsing may have selected for increasingly better defended and, therefore, slower-growing females (Jing & Coley, 1990). Such gender-based differential selection would also tend to exacerbate size differences between sexes. A comparison of levels of chemical defences and/or growth rates of females inside exclosures and in grazed pastures should provide a test for this hypothesis. Under this scenario it would be reasonable to expect slower-growing, better defended female shrubs in grazed pastures than in exclosures. Defence-level differences between protected and browsed males, on the other hand, should be minimal.

Female *Atriplex canescens* shrubs at this site appear to be more negatively affected by cattle grazing than are male shrubs. Higher mortality of females relative to males as a response to sex biased herbivory and/or gender-specific responses to cattle-browsing (females could be more sensitive to defoliation) may be responsible for this process. Sex-shifting could also be partly responsible for the reduction in numbers of females in the grazed pastures at this site. Stresses such as cold winters and heavy seed-sets in previous growing seasons are able to trigger sex phenotype shifting toward maleness in the following flowering season (McArthur, 1977). It would be reasonable to expect that heavy removal of stems and leaves (as might occur in winter-grazed pastures at our site) could jeopardize female reproductive function and promote sex shifts towards maleness. All three mechanisms mentioned above could contribute to the shrub gender-related

pattern of shrub sizes and relative abundance that were observed. Further research is needed to test predictions of hypotheses related to these mechanisms. Such research would certainly make valuable contributions to the understanding of the complexities of animal-plant interactions in dioecious plants, and in *A. canescens* in particular.

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