Recruitment potential of two perennial grasses with different growth forms at a semiarid-arid transition zone[1]

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The objective of this study was to quantify differences in recruitment potential (seed production, seed presence in the soil) for two congeneric perennial grasses (*Bouteloua gracilis*, *Bouteloua eriopoda* [Poaceae]) that dominate adjacent arid and semiarid grassland biomes. It was hypothesized that these species have different recruitment strategies at the biome transition zone that are related to differences in their growth form and longevity. Recruitment potential for each *Bouteloua* species was compared in patches dominated by one or both species or codominated by the invasive shrub, *Larrea tridentata* (Zygophyllaceae). Regional variation in recruitment was examined for *B. gracilis* for cases in which comparable data were available in the literature for a site located within the semiarid grassland biome. The short-lived stoloniferous species *B. eriopoda* produced more seeds per plant than the long-lived bunchgrass *B. gracilis*, yet seed viability (<60%) and presence in the soil were lower. Mean viability of *B. gracilis* was higher (>90%) than that of *B. eriopoda*, and a greater percentage of seeds produced on a square meter basis was found in the soil (10–25%). Similar patterns were found for both species in all grass-dominated patches. *Bouteloua eriopoda* plants growing in patches codominated by *L. tridentata* produced fewer seeds per plant with lower viability, and fewer seeds were found in the soil compared to grass-dominated patches. Regional comparisons found greater seed production per square meter and more seeds in the soil for *B. gracilis* at the transitional site compared with a cooler, wetter site located within the semiarid grassland biome. These differences in recruitment potential along with published differences in rates of seedling establishment and vegetative spread may explain, at least in part, localized patterns in species dominance.

Key words: *Bouteloua eriopoda*; *Bouteloua gracilis*; Chihuahuan Desert grasslands; grass–shrub interactions; intra- and interspecific interactions; Poaceae; seed production; shortgrass steppe.

In North America, two major grassland biomes are dominated by one of two perennial C_4 grasses with different growth forms and longevities. Chihuahuan Desert grasslands of southern New Mexico and northern Mexico are dominated by *Bouteloua eriopoda* (Torr.) Torr. (Poaceae), a short-lived (35–40 yr; Wright and Van Dyne, 1976) stoloniferous grass. Shortgrass steppe grasslands located along the Front Range of the Rocky Mountains are dominated by the long-lived (400 yr; Coffin and Lauenroth, 1990) bunchgrass *Bouteloua gracilis* (H.B.K.) Lag. ex Griffiths. A transition zone between biomes dominated by these species occurs in central New Mexico. Controls on patterns in species dominance at this transition zone are unknown, although soil disturbances caused by ban-nertail kangaroo rats (*Dipodomys spectabilis*) result in an increase in localized dominance by *B. eriopoda* and a decrease in *B. gracilis* that cannot be explained by differences in vegetative spread alone (Fields, Coffin, and Gosz, 1999). Thus, it was hypothesized that these small-scale dominance patterns are due to species-specific differences in recruitment. Specifically, seed production per plant was expected to be larger for the bunchgrass *B. gracilis* than for the stoloniferous *B. eriopoda* as a result of differences in energetic demands for vegetative propagules (Schmid et al., 1988). By contrast, seed availability in the soil on a square meter basis, one measure of recruitment success, was expected to be greater for the short-lived *B. eriopoda* compared to the long-lived *B. gracilis* since populations consisting of short-lived genets must replace plants more frequently than populations where genets live indefinitely.

At the shortgrass steppe/Chihuahuan Desert transition, the landscape consists of a mosaic of grass patches that may be dominated by one or both *Bouteloua* species. Another patch type of particular importance is codominance of *B. eriopoda* with *Larrea tridentata* (DC.) Coville (Zygophyllaceae), a common invasive shrub in the Chihuahuan Desert (Buffington and Herbel, 1965). Because patch types differ in microenvironmental conditions (Kröel-Dulay, Hochstrasser, and Coffin, 1997; Kieft et al., 1998), recruitment processes may also differ by patch type. Alternatively, one or more processes may be primarily constrained genetically, in which case plants growing in different patch types may exhibit similar responses. Effects of grasses on shrub seedling establishment have been studied (Brown, Scanlon, and McIvor, 1998); however, little is known about the effects of shrubs such as *L. tridentata* on

B. eriopoda recruitment and how these grass–shrub interactions may differ from intra- and interspecific interactions among grasses.

Both *Bouteloua* species have been well studied within the biome where each dominates (Gadzia, 1979; Coffin and Lauenroth, 1989, 1992; Lauenroth et al., 1994). However, it is not known whether studies conducted in different parts of the geographic distributions of these species are applicable at the biome transition zone (Minnick and Coffin, 1999). Plants growing near the edge of their species range may be near the limits of their physiological tolerance (Arris and Eagleson, 1989). Thus, recruitment potential may be lower at a biome transition zone compared with the core of a biome.

The three specific objectives for this study were: (1) to compare seed production and presence in the soil of *B. gracilis* and *B. eriopoda* at a biome transition zone; (2) to evaluate recruitment potential in different patch types for each *Bouteloua* species, either with or without the other *Bouteloua* species or *L. tridentata*; (3) to evaluate regional variation in recruitment potential for one species, *B. gracilis*, in cases for which similar data are available from a site located within the shortgrass steppe biome.

MATERIALS AND METHODS

Biome transition zone: species and patch type comparisons—*Study site*—Studies to represent the shortgrass steppe/Chihuahuan Desert transition zone (SGS/CD) were conducted at the Sevilleta National Wildlife Refuge (34.5° N, 106.9° W) located approximately 75 km south of Albuquerque, New Mexico, USA. Grazing by cattle has been excluded from this site since 1973, although grazing by native herbivores occurs at low to moderate intensities. Long-term (65 yr) mean annual precipitation was 234 mm (SD = 70 mm) with >60% occurring from July through October (Peters, 2000a). Annual temperatures averaged 14.1°C (SD = 0.7°) over the same time period. During the time of this study (November 1995–April 1997), temperatures were above average and summer precipitation was below average in 1995. Summer precipitation was above average in 1996 and 1997. Mean daily temperatures were above average in the summer of 1996 and fall of 1997 and below average in the winter of 1996–1997.

A 2.5-km² area on the McKenzie Flats (1650 m above sea level) was randomly selected containing patches that were either: (1) dominated by *B. gracilis* (blue grama); (2) codominated by *B. gracilis* and *B. eriopoda*; (3) dominated by *B. eriopoda* (black grama); or (4) codominated by *B. eriopoda* and *Larrea tridentata* (creosotebush). Patches codominated by *B. gracilis* and *L. tridentata* rarely occur. One patch of each type was randomly selected for sampling. Species composition and cover within each patch, measured annually since 1995, were compared with a large number of patches (60) to confirm the representativeness of each sampled patch to its type (Kröel-Dulay, Hochstrasser, and Coffin, 1997; Peters, 2000b). Soil sampling showed that sand contents in the upper 10 cm (83–86%) and 30 cm depths (73–75%) were similar for the three grass patches and higher than the *B. eriopoda–L. tridentata* patch (73% and 61%, respectively). Percentage clay content ranged from 5 to 9% (0–10 cm) and from 12 to 18% (0–30 cm) for grass-dominated patches, and from 11 to 12% for both depths in the grass–shrub patch.

Plant-level sampling of seed production and reproductive effort—Sampling was conducted in 1996 on 20 September (*B. eriopoda*) and 18 October (*B. gracilis*) to correspond to the peak of seed maturation, yet prior to dispersal. Sampling and experimental design were based upon a previous study of *B. gracilis* (Coffin and Lauenroth, 1992) to allow comparisons between data sets. Three plants of each dominant species were randomly selected within each of five 10-m transects in each of three blocks for each patch; thus, a total of 45 plants was sampled for each species from each patch where it dominates or codominates. Individual plants of *B. gracilis* were defined as all tillers currently connected by a crown (Coffin and Lauenroth, 1988). Because *B.*

eriopoda is stoloniferous, individual clumps can be quite large (100 cm diameter) and diffuse with many loosely connected ramets (Peters, 2002). Only small, well-defined clumps from each genet that were similar in size to *B. gracilis* plants (mean = 12.8 cm diameter) were selected.

Numbers of seeds and inflorescences and biomass (measured as grams of dry mass) of aboveground reproductive (inflorescences including seeds) and vegetative structures (nonreproductive tillers and crowns) were assessed for each plant by clipping material at the soil surface, separating it, then either counting or weighing it. Distribution of biomass to reproduction was calculated in two ways. First, reproductive biomass was divided by total biomass (reproductive + vegetative) as a measure of energy invested in reproductive structures. Second, the number of seeds produced was divided by total aboveground biomass as a measure of energy invested in seed availability for recruitment. Seed viability (as a percentage) for each species–patch type combination was determined using species-specific standardized procedures to break dormancy followed by a 28-d germination test and a tetrazolium test for viability. Fifty seeds were randomly selected for testing from a combined sample of all seeds collected by each species in each patch type. Mean seed mass (in milligrams) was calculated from the seeds tested for viability.

Analysis of variance (ANOVA) was used to evaluate differences between species and patch type with respect to indicators of reproductive effort. Plants were averaged within transects and the means were analyzed in a two-fold design with patch type, block within patch type, and transect within block as factors. The residuals were normally distributed for most variables. Response variables where residuals were not normally distributed were log-transformed prior to the analysis.

A priori contrasts were used to test for effects of species or patch type on the response variables (Sokal and Rohlf, 1998). Five separate contrasts were conducted for each ANOVA if the overall *F* test for patch type was significant. The first contrast tested the significance of species for all patch types. The second contrast tested for the significance of the two patch types containing *B. gracilis* on responses of this species. The third contrast tested for the significance of the three patch types containing *B. eriopoda* on responses of this species; if this test was significant, then two additional contrasts were conducted to determine if responses for each pair of patches were different. A significance level of $\alpha = 0.05$ was used for all analyses.

Because sampling for seed production per plant is very time consuming, patch types were also compared using regression to analyze the relationship between seed production and one of several easily obtained measures per plant. Inflorescence density, basal area, and total aboveground biomass (reproductive and vegetative) were selected as the predictor variables. Separate regressions were first conducted for each species in each patch type. The influence of patch type on the slope and intercept of each relationship was then tested (Sugiyama and Bazzaz, 1998). Slopes were compared pairwise using a Tukey-Kramer minimum significant difference procedure (Sokal and Rohlf, 1998). ANOVA was used to test for differences in intercepts for those patch types where the slopes were not significantly different. Regressions for which the slope and intercept were not significantly different between patch types and within species resulted in a pooling of patch types.

Community-level sampling of seed production—Density of seeds produced on a square metre basis was calculated for each species and patch type to allow comparisons with the density of seeds found in the soil per square metre (see below). Density of seeds per unit of *B. gracilis* or *B. eriopoda* basal area was obtained using the basal area of each plant measured prior to clipping. Seed density per square meter was calculated using the average basal area of all plants (in square centimeters per square meter; *N* = 1500) within five 3 × 4 m quadrats in each patch type in September 1996 (Peters, 2002). Because measures of reproductive effort obtained at the community level were estimated using one value of basal area for each patch type–species combination, statistical analyses were not possible and only general comparisons can be made when comparing seed production and seed presence in the soil.

Seed presence in the soil—Soil samples were collected three times over 18 mo to assess temporal variation in seed presence. Fifteen randomly located samples were collected from each patch type in November 1995 and 1996
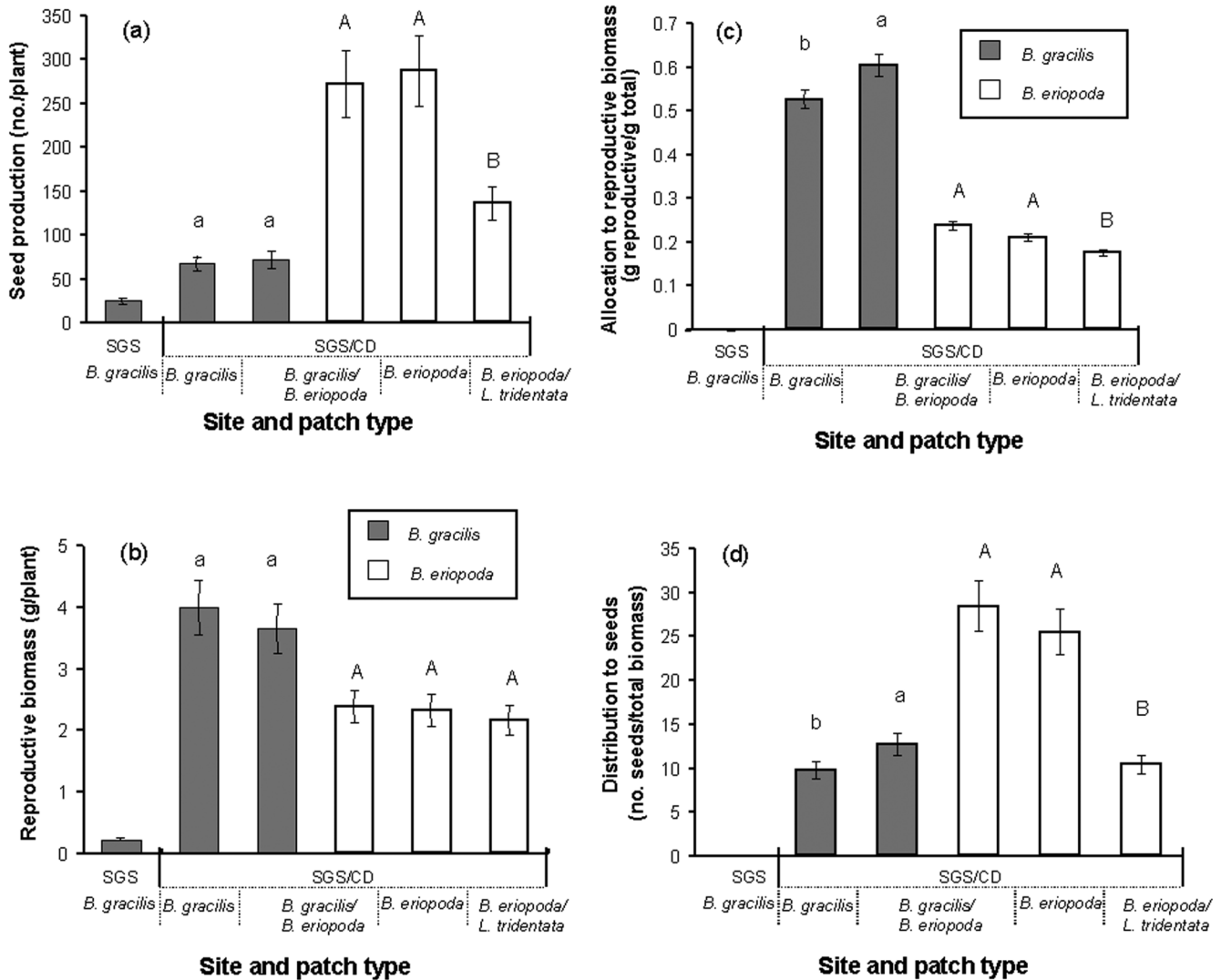
Fig. 1. Measures of reproductive potential at the plant level: (a) seed production, (b) reproductive biomass, (c) allocation to reproductive biomass, and (d) distribution of biomass to number of seeds for *Bouteloua gracilis* as an average of five plant communities at a shortgrass steppe site in northern Colorado (SGS) and for *B. eriopoda* in four patch types at a shortgrass steppe/Chihuahuan Desert transition in central New Mexico (SGS/CD). Means and standard errors are shown. Species are significantly different for all measures at the SGS/CD site. Different small letters indicate significant differences between patch types for *B. gracilis* at the SGS/CD. Different capital letters indicate significant differences among patch types for *B. eriopoda* at the SGS/CD.

and April 1997. The first date represents seed presence in the soil following a drought year when very few seeds were produced. The second date represents seed presence during a year with average precipitation, and the final sampling represents seeds available for establishment after overwintering. Each sample consisted of two 7.5 cm diameter soil cores taken to a depth of 5 cm (methods follow Coffin and Lauenroth, 1989). Microsite effects on seed presence in the soil were accounted for in two ways. One core of each sample was obtained within a plant of *B. gracilis* or *B. eriopoda*, and one was taken in an adjacent bare area to account for differences due to plant presence (Coffin and Lauenroth, 1989); cores were combined for the analysis. The importance of species identity was accounted for by collecting samples either under *B. gracilis* or under *B. eriopoda* for the patch type codominated by these species and either under *B. eriopoda* and *L. tridentata* for the patch type codominated by these species.

Samples were sieved using a 1-cm mesh screen to remove plant material, allowed to air dry, and stored for 7 d at 0°C to break dormancy (Coffin and Lauenroth, 1989). Each sample was then spread in a 1-cm deep layer over a potting soil–sand mixture in plastic trays in a greenhouse maintained at suit-

able conditions for germination of both species. Samples were watered daily and one-third strength Hoagland's solution was applied once per week. Seedlings were counted at weekly intervals for 12 wk. Identified seedlings were removed from a tray. Sieving of soil after completion of the experiment resulted in no additional seeds of these species, thus all seeds in the samples were germinable.

The total number of seedlings per square meter found in the soil was calculated for each *Bouteloua* species on each date and averaged across microsite (plants of *B. gracilis* or *B. eriopoda*, bare interspaces) within each patch type. This pooling was necessary because of high inter-sample variation that precluded statistical comparison of patch types (Coffin and Lauenroth, 1989). Regression analyses were not possible to predict seed presence in the soil since samples were not collected from the same plants where the predictor variables were obtained.

Regional variation in recruitment—Published data on *B. gracilis* collected from the Central Plains Experimental Range (40.8° N, 107.8° W) in north-central Colorado were used to represent the shortgrass steppe biome (SGS)

TABLE 1. Characteristics of *Bouteloua gracilis* at a shortgrass steppe site (SGS)[a] and of *B. gracilis* and *B. eriopoda* for four patch types at a shortgrass steppe/Chihuahuan Desert transition (SGS/CD). NA: not available. An asterisk indicates significant difference between *B. gracilis* and *B. eriopoda* at the SGS/CD site. Different superscripts indicate significant differences between patch types at the SGS/CD site for *B. gracilis*. Different subscripts indicate significant differences between patch types at the SGS/CD site for *B. eriopoda*.

	SGS	SGS/CD			
Characteristic	*B. gracilis*	*B. gracilis*	*B. gracilis/ B. eriopoda*	*B. eriopoda*	*B. eriopoda/ L. tridentata*
Seed mass (mg)					
B. gracilis	0.28	0.41	0.40		
B. eriopoda			0.23	0.40	0.17
Seed viability (%)					
B. gracilis	80	86	90		
B. eriopoda			66	58	38
Inflorescence biomass (g/stem)					
B. gracilis*	0.05	0.15[A]	0.14[A]		
B. eriopoda			0.04[A]	0.04[A]	0.04[A]
Cover (%)					
B. gracilis	NA	36[A]	28[B]	0	0
B. eriopoda	0	0	12[B]	45[A]	14[B]

[a] Mean of five ungrazed locations in Coffin and Lauenroth (1992).

and to allow comparisons with data collected at the SGS/CD site. Long-term (57 yr) mean annual precipitation was 326 mm (SD = 86 mm) with >75% occurring during the April through September growing season. Annual temperatures averaged 9.0°C (SD = 1.2°C) over the same time period. Plant and soil sampling are described in detail in Coffin and Lauenroth (1989, 1992). Because the SGS/CD site has not been grazed by cattle since 1973, data on *B. gracilis* reproductive effort at the SGS were collected from five cattle exclosures that had not been grazed for at least 5 yr (Coffin and Lauenroth, 1992); these data were averaged for the regional comparison. Soil samples were obtained from two moderately grazed pastures on different soils (sandy loam, sandy clay loam); the numbers of seeds in the soil were averaged for the regional analysis (Coffin and Lauenroth, 1989). Sand (74%) and clay contents (15%) were similar to grass-dominated patches at the SGS/CD site for the 0–30 cm depth where data were available.

Because seed presence in the soil (1985) and seed production data (1989) were collected in different years at the SGS, it was not possible to compare inputs and losses of seeds from the soil. Because the data were collected in different years at the SGS and SGS/CD, between-site comparisons should be treated with caution, although the sites do not necessarily experience similar weather patterns even in the same year.

RESULTS

Seed production and reproductive effort—At the SGS/CD site, total seed production was significantly greater for *B. eriopoda* (Fig. 1a) whereas seed viability and mass, and measures of reproductive biomass (inflorescence and total) were greater for *B. gracilis* (Fig. 1b, Table 1). Because the mean biomass of an inflorescence (Table 1) and the mean reproductive biomass per plant (Fig. 1b) were larger for *B. gracilis*, greater allocation of biomass to reproductive structures was found compared with *B. eriopoda* (Fig. 1c). The larger number of seeds produced per plant and lower reproductive biomass by *B. eriopoda* resulted in a greater distribution of biomass to seeds compared with *B. gracilis* (Fig. 1d).

All measures of reproductive effort for *B. gracilis* were greater at the SGS/CD compared with the SGS site (Table 1,

Fig. 1). Although average viability of *B. gracilis* was lower at the SGS, maximum viability was similar between sites (SGS: 54–90%; Coffin and Lauenroth, 1992; SGS/CD: 86–90%).

Most measures of reproductive potential were similar among grass-dominated patches for both species. The exceptions for *B. gracilis* were the larger allocation to reproductive biomass and distribution of biomass to seeds in the patch codominated by *B. eriopoda* (Fig. 1c and d). The exception for *B. eriopoda* was the heavier seeds found in the patch dominated by this species compared with the patch codominated by *B. gracilis* (Table 1). By contrast, most measures for *B. eriopoda* were significantly less in patches codominated by *L. tridentata* compared with grass-dominated patches. The exceptions were the biomass of inflorescences and all reproductive structures that were similar for all patches. Smallest allocation of *B. eriopoda* biomass to reproductive biomass in the patch codominated by *L. tridentata* was due to greater vegetative biomass of these plants compared to those in grass-dominated patches.

Patch type based on presence or absence of shrubs was also important to the relationships between seed production per plant and inflorescence density, aboveground biomass, or basal area for *B. eriopoda* (Fig. 2). All grass patches had similar regression coefficients; however, these coefficients were significantly different than coefficients for patches codominated by *L. tridentata*. Thus, two groups were formed for the final analysis for *B. eriopoda*: one group consisted of the two grass-dominated patches pooled, and the second group consisted of the *B. eriopoda–L. tridentata* patch only. For *B. gracilis*, patch type was not important to the slopes and intercepts for relationships between seed production and biomass or culm density; thus data were pooled across patch type for the final analysis.

For both species and all patch types, inflorescence density was the best predictor of seed production, although significant regressions were also found for total aboveground biomass (Fig. 2). In grass-dominated patches, higher r^2 values were found for *B. eriopoda* ($r^2 > 0.57$) than for *B. gracilis* ($r^2 < 0.27$). Similar r^2 values were found regardless of patch type for *B. eriopoda*. Significant regressions were not found for either species between the number of seeds produced and basal area.

Seed presence in soil—Both *Bouteloua* species had variable numbers of germinable seeds in the soil through time that were not predictably related to the timing of seed production and dispersal in September and October (Table 2). Because sampling was not conducted in spring 1996 at the SGS/CD site, it is not possible to distinguish the persistent component of the seed bank (Thompson and Grime, 1979). However, the lack of *B. eriopoda* seeds and low numbers of *B. gracilis* seeds in three of four patch types (≤ 53 seeds/m^2) in November 1995 following a year-long drought suggests that both species have transient seed banks.

In November 1996 and April 1997, *B. gracilis* had more seeds in the soil than *B. eriopoda* for all patch types, except the patch dominated by *B. eriopoda*. Furthermore, the number of germinable *B. eriopoda* seeds increased for all patch types over winter whereas the number of *B. gracilis* seeds decreased in most patch types. Because samples were exposed to a cold treatment prior to germination, increases in the number of seeds over winter likely represent a lag in the time between seed maturation, dispersal, and redistribution from the litter to
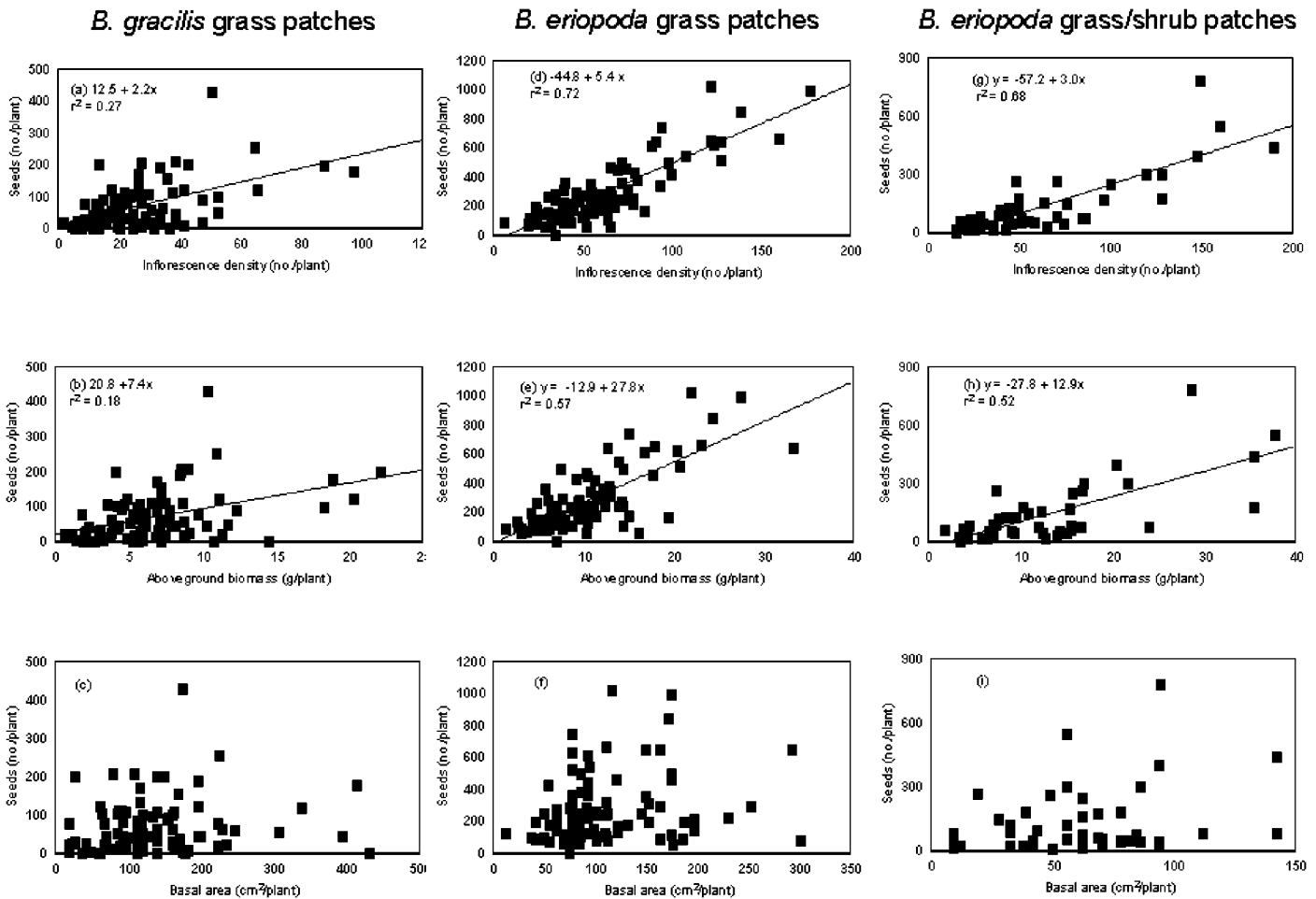
Fig. 2. Relationship between seed production and inflorescence density, aboveground biomass, or basal area for *Bouteloua gracilis* in patches dominated by *B. gracilis* or *B. eriopoda* (a–c) ($N = 90$), for *B. eriopoda* in patches dominated by *B. gracilis* or *B. eriopoda* (d–f) ($N = 90$), and for *B. eriopoda* in patches dominated by *B. eriopoda* and *L. tridentata* at a SGS/CD transition (g–i) ($N = 45$). Significant regressions ($P \leq 0.05$) are shown.

the soil that was more pronounced for *B. eriopoda* than for *B. gracilis*.

Dispersal of seeds among patch types is indicated for both species. No *B. gracilis* plants were found in the patch codominated by *B. eriopoda* and *L. tridentata* (Table 1), although more germinable seeds of this species than of *B. eriopoda* were found in the soil (Table 2). Small numbers of germinable *B. eriopoda* seeds were found in the *B. gracilis*-dominated patch type where *B. eriopoda* plants did not occur (Table 1). Similar numbers of germinable *B. gracilis* seeds were found at the SGS (0–174) and SGS/CD sites (0–548), except for the large number of seeds from November 1996 in the patch dominated by this species (1065).

Comparison of seed production and seed presence in the soil—For most patch types at the SGS/CD, higher viability by *B. gracilis* (Table 1) offset the lower number of seeds produced to result in a similar production of viable seeds as *B. eriopoda* on a square meter basis (Fig. 3a). The exception is the large number of viable seeds produced by *B. eriopoda* in the patch type dominated by this species that was primarily due to its high cover (Table 1). Seed production by *B. gracilis*

was similar between patch types at the SGS/CD and higher than at the SGS.

Although the patch dominated by *B. eriopoda* had the largest number of seeds produced of all patches (Fig. 3a), this patch had the smallest percentage of seeds in the soil (Fig. 3b). For all patch types, <15% of the *B. eriopoda* seeds produced in the fall were found in the soil the following spring. By contrast, *B. gracilis* produced fewer seeds with higher viability than *B. eriopoda*, and 10–25% of the number of seeds produced in the fall were found in the soil the following spring. These comparisons assume that the number of seeds dispersed into and out of a patch are similar and that all seeds in the soil were produced the previous year. Because viability was not determined on a per-plant basis, statistical analyses were not possible on these data.

DISCUSSION

Recruitment processes have not been well studied for species with different growth forms, and the examination of multiple populations or species at biome transition zones or localized ecotones is even more rare (Neilson and Wullstein, 1983; Goldberg, 1985; Breck and Jenkins, 1997). In this study,

TABLE 2.   Seed presence in the soil (measured as number of seeds per square meter) by sampling date for *Bouteloua gracilis* as the mean of two plant communities at a shortgrass steppe site (SGS)[a] and for *B. gracilis* or *B. eriopoda* in four patch types dominated or codominated by these species at a shortgrass steppe/Chihuahuan Desert transition (SGS/CD). NA: not available.

Date and species	SGS *B. gracilis*	SGS/CD *B. gracilis*	SGS/CD *B. gracilis/ B. eriopoda*	SGS/CD *B. eriopoda*	SGS/CD *B. eriopoda/ L. tridentata*
May 1985					
B. gracilis	0	NA	NA	NA	NA
November 1985					
B. gracilis	174	NA	NA	NA	NA
November 1995					
B. gracilis	NA	0	8	45	53
B. eriopoda	NA	0	0	0	0
November 1996					
B. gracilis	NA	1065	548	101	65
B. eriopoda	NA	0	106	181	5
April 1997					
B. gracilis	NA	261	382	231	211
B. eriopoda	NA	60	201	392	121

[a] Colorado data from Coffin and Lauenroth (1989); mean of two locations with different soil textures.

recruitment potential differed between two perennial grass species with different growth forms, with important implications for patterns in species dominance and recovery after disturbance. In contrast to expectations, seed production per plant was greater and seed presence in the soil was less for the short-lived, stoloniferous species *B. eriopoda* compared with the long-lived bunchgrass *B. gracilis*. High seed production per plant, yet low seed viability by *B. eriopoda* was accompanied by few germinable seeds in the soil, whereas *B. gracilis* produced fewer seeds per plant with higher viability, and a greater percentage of seeds produced in the fall were found in the soil the following spring. These results suggest that recruitment processes are complex and not easily explained by energetic models or life history traits. Recent simulation model analyses of grass-dominated patches at the SGS/CD that assumed seeds were available found higher mean probabilities of *B. eriopoda* seedling establishment (0.14 seedlings/yr) than for *B. gracilis* (0.07 seedlings/yr) over the past 65 yr (Peters, 2000a). A consideration of all three processes (seed production, presence in the soil, and establishment) suggests that recruitment by *B. eriopoda* may be more limited by the availability of germinable seeds in the soil, and *B. gracilis* may be constrained more by seedling establishment. Long-term studies that examine multiple processes are needed under a variety of climatic and soil conditions to support this hypothesis. Furthermore, the key process in any given year will likely depend upon the specific conditions of that year (Fair, Lauenroth, and Coffin, 1999).

The importance of vegetative spread relative to recruitment may also differ between the two species. Heavier seeds, larger reproductive biomass allocation per plant, and higher seed viability by *B. gracilis* compared with *B. eriopoda* suggests that more energy is allocated to seedling recruitment than vegetative spread. Although tillering rates have not been measured at the SGS/CD site, *B. gracilis* spreads very slowly through the production of tillers in the northern mixed-grass

prairie (<2 cm/yr; Samuel, 1985), and most recovery following disturbance in the shortgrass steppe is through seedling establishment (Coffin and Lauenroth, 1990). By contrast, a greater energetic commitment to vegetative compared with reproductive biomass was found for *B. eriopoda* compared with *B. gracilis*. Large numbers of inflorescences (not shown) and high vegetative biomass per plant would result in high rates of tiller and stolon production since inflorescences in *B. eriopoda* often become rooted and function as stolons (Gadzia, 1979). These results are supported by previous studies in the Chihuahuan Desert where *B. eriopoda* can spread rapidly through the production of stolons (Nelson, 1934). Because *B. eriopoda* is short-lived, replacement after plant mortality through seedling establishment must also occur, even if only at low frequencies. Thus, response to disturbance by *B. eriopoda* at the shortgrass steppe/Chihuahuan Desert transition zone likely includes both reproductive and vegetative modes of reproduction, whereas *B. gracilis* most likely responds through seedling establishment.

Significant regressions between seed production and inflorescence density or aboveground biomass per plant provide easily obtained metrics to estimate total seed production for *B. gracilis* or *B. eriopoda* plants in patches dominated by these species. Between-plant variation in viability needs to be determined before regressions with viable seed production can be evaluated. Positive relationships between aboveground biomass and production of seeds have been found for other annual and perennial grasses and forbs (Mack and Harper, 1977; Escarré and Thompson, 1991). The lack of relationship between plant basal area and seed production is not surprising because basal area consists primarily of perennial organs (tillers) that reflect environmental conditions over a number of growing seasons (Hyder et al., 1975).

Patch type comparisons—Most measures of reproductive potential were not affected by different types of grass patches for either species. The exception for *B. gracilis* was its larger allocation of biomass to reproductive structures and greater distribution of biomass to seeds in patches codominated by *B. eriopoda* that suggests a shift towards a more reproductive strategy compared to plants located in *B. gracilis* patches. For *B. eriopoda*, patch type was most important when comparing grass- and shrub-dominated patches. *Bouteloua eriopoda* plants growing in patches codominated by *L. tridentata* produced fewer seeds per plant with lower viability, and fewer seeds were found in the soil compared to grass-dominated patches. This shift in carbon allocation from sexual to vegetative biomass as a result of the presence of shrubs has not been observed previously for *B. eriopoda*, but may be an important factor contributing to its continued decline as shrubs invade (Buffington and Herbel, 1965). A number of factors are important to shrub invasion, including drought, grazing by cattle, and lack of fire (Humphrey, 1958; Archer, Schimel, and Holland, 1995). Current results suggest that a negative feedback exists between the presence of shrubs and recruitment by *B. eriopoda* that would further reduce the ability of this grass species to persist through time. These negative effects are likely due to biotic interactions between *L. tridentata* and *B. eriopoda* (Knipe and Herbel, 1966) because soil texture differences were small between patch types.

Because both *Bouteloua* species had seeds in the soil of patches where they had very little aboveground cover, seed dispersal was prevalent throughout the study area. Large num-
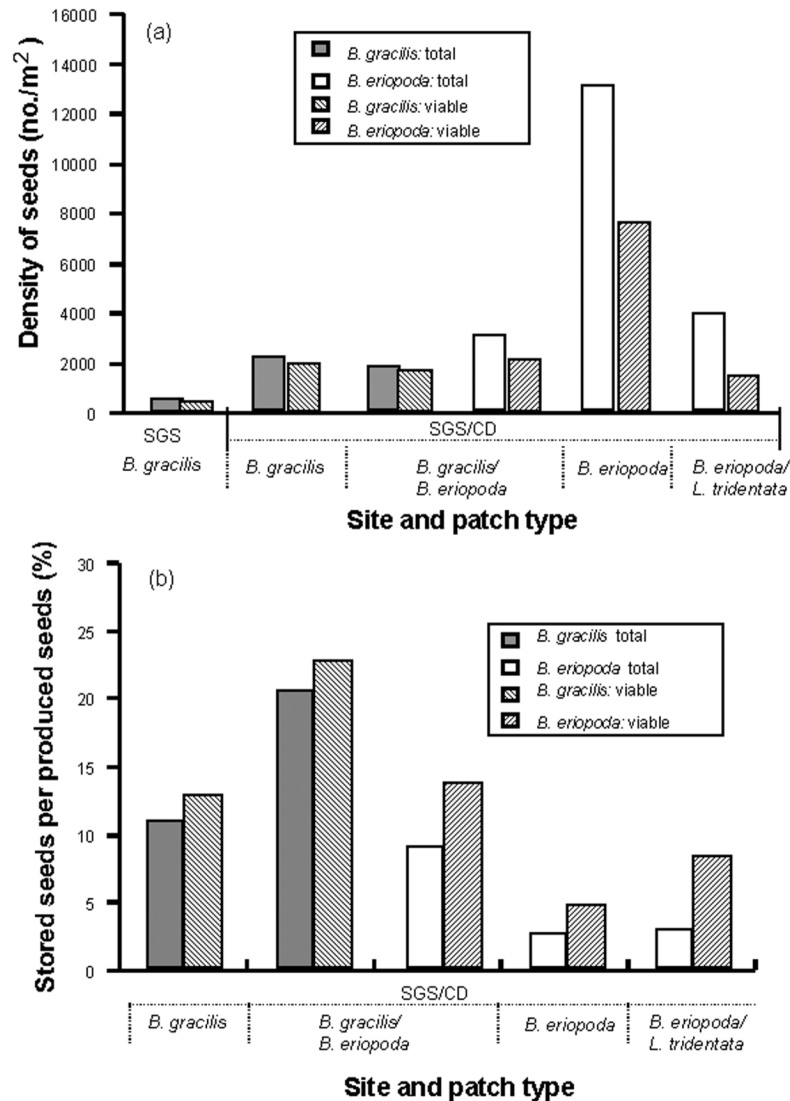
Fig. 3.   (a) Seed production (total and viable) for *Bouteloua gracilis* as an average of five plant communities at a shortgrass steppe site (SGS) and for *B. gracilis* and *B. eriopoda* in four patch types at a shortgrass steppe/Chihuahuan Desert transition (SGS/CD) and (b) presence of germinable seeds in the soil in April 1997 as a percentage of seeds produced in a patch (total and viable) in fall 1996 for *B. gracilis* and *B. eriopoda* in four patch types at a shortgrass steppe/ Chihuahuan Desert transition in central New Mexico.

bers of *B. gracilis* seeds found in the soil of patches dominated by *B. eriopoda* and *L. tridentata* were surprising and supports the contention that *B. gracilis* is primarily constrained by seedling establishment rather than by seed availability.

Regional comparisons—The greater magnitude of response by *B. gracilis* for most variables at the transitional site in New Mexico compared to a site within the shortgrass steppe is in contrast to predicted responses based upon physiological constraints (Arris and Eagleson, 1989). One explanation for these results is the single year of sampling; high interannual variation in seed production has been observed for *B. gracilis* at both sites. However, annual censuses of this species at the SGS (1989–1997) indicate that seed production in 1989 was above average (D. P. C. Peters and W. K. Lauenroth, unpublished data); seed production at the SGS/CD in 1996 was also above average (D. P. C. Peters, unpublished data). Another possibility

is that the production and storage of *B. gracilis* seeds are favored by warmer temperatures found in central New Mexico compared with northern Colorado.

Summary of conclusions—In contrast to expectations, seed production per plant was greater and seed presence was lower in the short-lived stoloniferous species (*B. eriopoda*) compared with the long-lived bunch grass (*B. gracilis*) at a shortgrass steppe/Chihuahuan Desert transition zone. However, most measures of reproductive potential were larger for *B. gracilis* than *B. eriopoda* plants. These results, combined with published rates of seedling establishment, suggest that the key process limiting recruitment differs for these species. Seedling establishment is expected to constrain successful establishment by *B. gracilis* whereas the availability of germinable seeds in the soil may be more important for *B. eriopoda*. Successful recruitment is affected by a suite of biotic processes interacting

with the environment of a plant. A subset of these processes was examined here. A long-term study conducted under variable environmental conditions that includes the complex of processes is needed to fully elucidate the key process or processes limiting recruitment for these species.

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