

# Geographic patterns of simulated establishment of two *Bouteloua* species: implications for distributions of dominants and ecotones

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**Abstract.** Our overall objective was to use a soil water model to predict spatial patterns in germination and establishment of two important perennial C<sub>4</sub>-bunchgrasses across the North American shortgrass steppe and desert grassland regions. We also predicted changes in establishment patterns under climate change scenarios. *Bouteloua gracilis* dominates the shortgrass steppe from northeastern Colorado to southeastern New Mexico. *Bouteloua eriopoda* dominates desert grasslands in central and southern New Mexico. Germination and establishment for each species were predicted at 16 sites along the gradient using a daily time step, multi-layer soil water model (SOILWAT) to determine the percentage of years that temperature and soil water criteria for germination and establishment were met. Percentage of years with predicted establishment decreased from north to south for *B. gracilis*, but increased from north to south for *B. eriopoda*, comparable to observed dominance patterns. The 95 % confidence interval around the point at which simulated establishment were equal for the two species was near the location of the shortgrass steppe-desert grassland ecotone where both species are abundant. The intersection in percentage of years with establishment for the two species was predicted to move further north when climate was scaled using three Global Circulation Models (GCMs), indicating a possible northward expansion of *B. eriopoda*. Our results suggest that recruitment by seed may be an important process in determining, at least in part, the geographic distribution of these two species. Changes in climate that affect establishment constraints could result in shifts of species dominance that may or may not be accompanied by changes in species composition.

**Keywords:** *Bouteloua gracilis*; *Bouteloua eriopoda*; Chihuahuan desert grassland; Climate change; Geographic distribution; Shortgrass steppe; Simulation model.

**Nomenclature:** Sutherland (1986).

**Abbreviations:** CPER = Central Plains Experimental Range; GCM = General Circulation Model; GFDL = Goddard Fluid Dynamics Laboratory; NMSU = New Mexico State University; OSU = Oregon State University; UKMO = United Kingdom Meteorological Office.

## Introduction

Environmental factors constrain the geographic ranges of species by affecting the recruitment, growth and mortality of individual plants. Recruitment is an important process in determining the extent of plant species' geographic ranges since recruitment is the dispersal phase of the life cycle (Louda 1982; Neilson & Wullstein 1983; Hengeveld 1990). Seedling survival may reflect identity of adults present in an area, even in the case of long-lived individuals such as the saguaro cactus (*Carnegiea gigantea*) in the U.S. southwest (Turner et al. 1966). In grasslands, dominant perennial grasses can often spread vegetatively on a local scale, although recruitment from seed may be more important in determining broad-scale geographic distributions (Brown & Gersmehl 1985). There may be regional variation in seedling recruitment due to precipitation and temperature gradients, as well as physical barriers such as mountainous regions that may restrict the geographic range (Brown & Gersmehl 1985; Schmutz et al. 1991). There may also be variation in recruitment within a site due to variability in available space, resource patchiness, seed production, and seed bank longevity, as well as annual variation in amount and timing of precipitation and temperature (Rusch & Fernández-Palacios 1995; Wester 1995).

Species at ecotones (relatively sharp transitions, cf. van der Maarel 1990), rather than near the center of their geographic ranges, may be more sensitive to temporal changes in climatic constraints since this is often the geographic and physiological limit of their distributions (Arris & Eagleson 1989). Ecotone location is one indicator of response of plant species to climatic gradients, and changes in ecotone location can be used as an indicator of climate change (Malanson 1997). Ecotones occur at a variety of scales and the most important processes affecting ecotones at these different scales are

hierarchical; biome level ecotones are most often affected by climate and topography, while ecotones at finer scales are more likely constrained by factors such as soil characteristics, inter- and intra-species interactions, microclimate and microtopography (Gosz 1993). We are considering broad-scale ecotones: the transition between vegetation types dominated by one of two species, and thus we are primarily concerned with climatic constraints. Periodic drought as well as directional changes in climate (Weaver & Bruner 1954; Neilson 1993), such as increased temperature predicted with a doubled concentration of atmospheric CO<sub>2</sub>, could shift species distribution through time and space. The detection of change in spatial location of an ecotone with climate change may best be determined over climatic gradients (Delcourt & Delcourt 1992). Because species are already present at all but fine scale and abrupt ecotones, propagule availability may be less important than constraints on germination and establishment in determining species presence at broad-scale ecotones (Gosz 1993; Neilson 1993; Malanson 1997).

Our overall objective was to use a soil water model to predict spatial patterns in germination and establishment of two important perennial C<sub>4</sub>-bunchgrasses across the North American shortgrass steppe and desert grassland regions (Table 1). Shortgrass steppe communities from northern Colorado to central and eastern New Mexico are dominated by *Bouteloua gracilis* (Lauenroth & Milchunas 1991). *Bouteloua eriopoda* dominates Chihuahuan desert grasslands from central New Mexico to Mexico (Schmutz et al. 1991). Because shortgrass steppe and desert grasslands are so overwhelmingly dominated by these two species, the ecotone between the two ecosystems coincides with the transition between dominance by *B. gracilis* to dominance by *B. eriopoda*. The geographic distribution of the two species, as well as the two grassland types, overlap in central New Mexico, resulting in ecotonal transition

zones between the two species (Sims 1988; Gosz 1993). Both species can spread vegetatively by tillers or stolons; recruitment by seedlings occurs infrequently, yet is important for the continued dominance and persistence of species experiencing disturbance or that have short life spans (Wright & Van Dyne 1976; Coffin & Lauenroth 1988; Coffin et al. 1996). Recruitment may explain, at least in part, observed geographic patterns of dominance by these two species since recruitment is related to timing and amount of precipitation and temperature, two factors that vary across the shortgrass steppe-desert grassland region.

We had four specific objectives:

- (1) to simulate germination and establishment of *B. gracilis* and *B. eriopoda* under current climate and to compare these establishment patterns along the gradient to species geographic distribution and dominance patterns;
- (2) to predict ecotone location based on the geographic area where predicted establishment is similar for the two species and to compare this location to a site where the two species codominate;
- (3) to compare effects of climate variables on establishment for the two species; and
- (4) to predict changes in the ecotone location between areas with different dominant species as a result of climate change.

Our approach was to use a daily time-step simulation model of soil water dynamics (SOILWAT; Parton 1978) to predict establishment for each species for sites along a climatic gradient which encompasses the range of dominance for both species. The model uses temporal and spatial dynamics in soil water content and temperatures as an integrative measure of timing and amount of both precipitation and temperature to determine if conditions are sufficient each year for seed germination and seedling establishment. Simulations were conducted under current climate and with climate change scenarios predicted from Global Circulation Models. We assumed seeds were available at all sites and evalu-

**Table 1.** Key characteristics of the two species and, in the case of disturbance, of the shortgrass steppe and desert grassland.

	<i>Bouteloua gracilis</i> / Short-grass steppe	<i>Bouteloua eriopoda</i> / Desert grassland
Distribution	Central grasslands of U.S., Canada and Mexico <sup>1</sup>	U.S. Southwest and Mexico <sup>1</sup>
Dominance	Shortgrass steppe <sup>2</sup>	Desert grassland <sup>3</sup>
Functional Type	C <sub>4</sub> Perennial bunchgrass <sup>1</sup>	C <sub>4</sub> Perennial bunchgrass <sup>1</sup>
Seedling recruitment	Low: 0.0140/yr <sup>4</sup>	Low: 0.295/yr <sup>5</sup>
Vegetative recruitment	Tillers <sup>1</sup>	Tillers and stolons <sup>1</sup>
Vegetative spread	3cm/yr <sup>6</sup>	0.5/yr <sup>5</sup> ; 28%, 7 - 10 cm, 58 % 10 - 20 cm in length <sup>7</sup>
Life-span	Ca. 400 yr <sup>8</sup>	Ca. 28 yr (ramets) <sup>9</sup>
Disturbance	Ant mounds, burrowing animals and cattle fecal pats 0.04 - 0.23% area/yr <sup>8</sup>	Kangaroo rat mounds: 9.4 mounds/ha (2.5 % of area) at Jornada <sup>10</sup> ; 2 - 4 mounds/ha, vegetation influenced for 10 m radius at Sevilleta <sup>11</sup>

<sup>1</sup>Stubbendieck et al. (1992); <sup>2</sup>Lauenroth & Milchunas (1991); <sup>3</sup>Schmutz et al. (1991); <sup>4</sup>Lauenroth et al. (1994); <sup>5</sup>Wright (1972); <sup>6</sup>Samuel & Hart (1995); <sup>7</sup>Nelson (1934); <sup>8</sup>Coffin & Lauenroth (1988); <sup>9</sup>Wright and Van Dyne (1976); <sup>10</sup>Moroka et al. (1982); <sup>11</sup>R. L. Schooley.

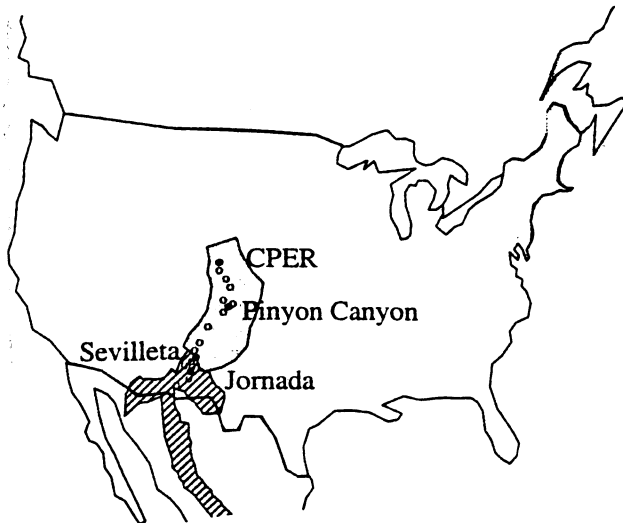


Fig. 1. The geographic extent of shortgrass prairie (shaded) and desert grassland (hatched). The Long-Term Ecological Research Sites and Pinyon Canyon Military Maneuver Site are labeled and appear as closed circles. The other sites in the analysis appear as open circles (redrawn from Sims 1988).

ated if soil water and temperature conditions were sufficient for germination and establishment.

## Methods

### Gradient description

We simulated establishment of *Bouteloua eriopoda* and *B. gracilis* for 16 sites along a climatic gradient from northern Colorado (40° 49' N, 104° 46' W) to southern New Mexico (31° 50' N, 107° 39' W) (Fig. 1). This gradient encompasses three United States National Science Foundation Long-Term Ecological Research Sites (Shortgrass Steppe, Sevilleta, Jornada) as well as the Pinyon Canyon Military Maneuver Site where vegetation has been studied. The gradient includes shortgrass steppe, desert grassland, desert shrubland, and ecotones between these dominant vegetation types. We chose sites at intervals of approximately half degree latitude along the gradient, and limited the analysis to weather stations with few missing data from 1963 to 1992 (Table 2). In general, mean annual temperatures increase while precipitation and mean number of precipitation events per year decrease from north to south (Table 2). Seasonal timing of precipitation also changes along the gradient. At the Colorado sites ( $n = 7$ ) represented by the CPER, precipitation peaks in May, June and July, slightly before the peak in temperature (Fig. 2a). At the New Mexico sites ( $n = 9$ ) represented

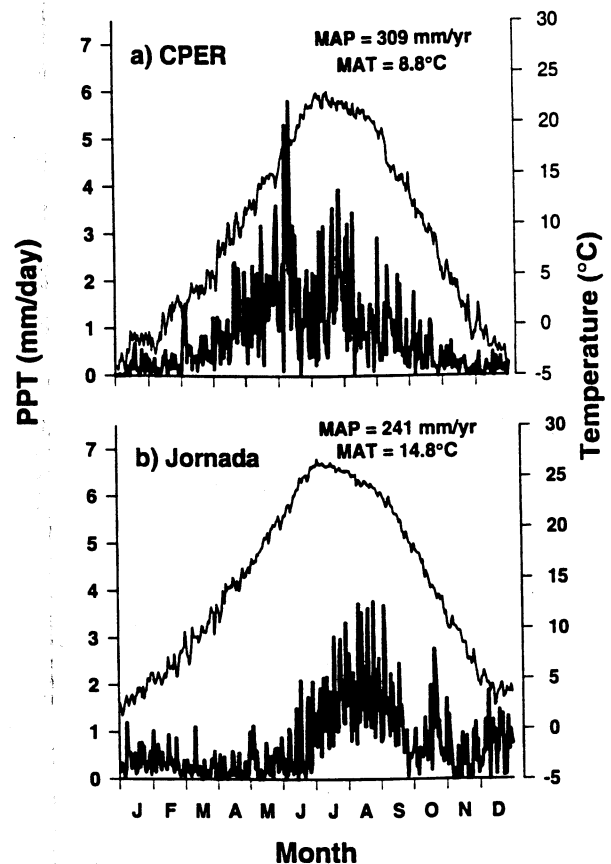


Fig. 2. Daily averages (over 30 yr) of precipitation (heavy line) and average temperature (lighter line) for (a) the Central Plains Experimental Range (CPER) in northern Colorado and (b) the Jornada Experimental Range in southern New Mexico. For the Colorado sites ( $n = 7$ ), precipitation peaks in May, June and July slightly before the peak in temperature, while in New Mexico ( $n = 9$ ) precipitation peaks in July, August and September just after the peak in temperature.

by the Jornada, precipitation is monsoonal and peaks in July, August and September, slightly after the peak in temperature (Fig. 2b). Coarse soil textures predominate along this gradient (Anon. 1991).

### Soil water model

We used the daily time step, multi-layer SOILWAT model (Parton 1978) to predict germination and establishment for each species at each site. SOILWAT has been used to examine long-term soil water dynamics and establishment of *B. gracilis* in the shortgrass steppe, and has also been validated for soil water conditions at the CPER and Socorro, New Mexico (Parton 1978; Sala et al. 1992; Lauenroth et al. 1994; Coffin 1997). Lauenroth et al. (1994) reported a significant linear

**Table 2.** Description of the 16 sites used in the simulation, as well as Pinyon Canyon, CO and Sevilleta, NM, where long-term climate data were not available.

Site	Latitude (N)	Longitude (W)	Altitude (m)	MAP <sup>1</sup> (mm/yr)	PPT events (#/yr)	MAT <sub>MAX</sub> <sup>3</sup> (C)	MAT <sub>AVE</sub> <sup>4</sup> (C)	MAT <sub>MIN</sub> <sup>5</sup> (C)
<b>Colorado</b>								
CPER	40° 49'	104° 46'	1650	314	47.9	17.5	9.4	1.2
Greeley	40° 25'	104° 42'	1440	361	60.8	18.1	9.9	1.7
Byers	39° 45'	104° 08'	1550	401	65.1	18.3	9.4	0.5
Limon	39° 16'	103° 41'	1640	399	71.5	16.6	8.4	0.2
Pueblo	38° 14'	104° 38'	1470	293	58.5	20.4	11.5	2.7
Rocky Ford	38° 02'	103° 42'	1270	281	51.3	21.3	11.8	2.2
Pinyon Canyon	37° 22'	104° 06'	*	*	*	*	*	*
Trinidad	37° 15'	104° 20'	1750	352	69.1	19.4	11.0	2.6
<b>New Mexico</b>								
Alcalde	36° 06'	106° 04'	1730	266	50.5	20.0	10.7	1.4
Albuquerque	35° 03'	106° 37'	1620	238	53.8	21.2	13.5	5.8
Los Lunas	34° 05'	106° 45'	1480	236	46.7	22.3	12.8	3.3
Sevilleta	34° 21'	106° 53'	*	*	*	*	*	*
Socorro	34° 05'	106° 53'	1400	258	44.0	23.0	13.7	4.3
Bosque del Apache	33° 46'	106° 54'	1380	254	39.7	24.6	14.2	3.9
Elephant Butte	33° 09'	107° 11'	1400	257	44.6	23.6	16.0	8.4
Jornada	32° 37'	106° 44'	1300	274	44.6	24.7	14.5	4.3
NMSU	32° 17'	106° 45'	1190	250	44.9	24.9	16.2	7.5
Columbus	31° 50'	107° 39'	1270	263	44.6	25.6	16.8	8.1

<sup>1</sup>Mean annual precipitation; <sup>2</sup>Mean number of precipitation events per yr; <sup>3</sup>Mean annual daily maximum temperature; <sup>4</sup>Mean annual daily average temperature; <sup>5</sup>Mean annual nightly minimum temperature; \*Long-term climate data not available.

relationship between observed and simulated soil water content at the CPER ( $r^2 = 0.66$ ). SOILWAT simulates the interception, infiltration, percolation, evaporation and transpiration of water through the soil profile. Input parameters include daily and monthly climate data, monthly estimates of plant biomass, and soil texture and root distribution by depth.

Daily precipitation and minimum and maximum temperatures were obtained for 30 yr (1963-1992) from a weather station at each site using data from the National Climatic Data Center (Anon. 1993). Monthly values of wind speed, relative humidity and cloud cover, which remained constant from year to year throughout the simulations, were estimated for each site from climate maps (Anon. 1983). Annual above-ground biomass was determined from equations relating above-ground net primary productivity (ANPP;  $g/m^2$ ) and annual precipitation (APPT; mm) developed for a regional analysis across the Central Grasslands as follows (Sala et al. 1988):

$$ANPP = -34 + 0.6 \cdot APPT; r^2 = 0.90 \quad (1)$$

These values were distributed monthly based on a growing season of May to August for the Colorado sites and June to September for the New Mexico sites.

In order to focus on the importance of climatic variation on establishment, soil texture and root distribution by depth parameters were held constant for all sites and

years. We simulated a sandy loam texture (65 % sand, 10 % clay, 25 % silt) which is prevalent throughout the climatic gradient (Anon. 1991). We used 11 soil layers: 0 - 4 cm, 4 - 15 cm, and 9 layers of 15 cm each from 15 - 150 cm. The percentage of the total root biomass found in each layer was the same for both species based on field data for *B. gracilis* dominated shortgrass steppe and for *B. eriopoda* (Bailey 1967; Singh & Coleman 1974).

### Criteria for establishment

#### *Bouteloua gracilis*

Field and laboratory studies and simulation modeling have been used to evaluate conditions required for establishment of *B. gracilis* from seed (Briske & Wilson 1977, 1978; Wilson & Briske 1979; Lauenroth et al. 1994). Because adventitious roots develop near the soil surface where evaporative water losses are high, two periods of moisture near the soil surface are needed for establishment: 2 - 4 days for germination and growth of the seminal root system, and a second 2 - 4 day period of wet soil at 0 - 30 cm depth is needed 2 to 8 weeks later for establishment and growth of the adventitious root system (Wilson & Briske 1979). Air temperatures with the best adventitious root response (e.g., number, total length and weight of adventitious roots), and thus greatest chance for *B. gracilis* establishment,

**Table 3.** Criteria for predicted germination and establishment of *Bouteloua gracilis* and *B. eriopoda*.

	Germ-Day <sup>1</sup>	Swp/Germ/Top (MPa) <sup>2</sup>	Root-Dry <sup>3</sup>	Swp/Germ-Estab/Lower (MPa) <sup>4</sup>	Layers <sup>5</sup>	Min-Init <sup>6</sup>	Max-Init <sup>7</sup>	Estab-Day <sup>8</sup>	Swp/Estab/Top (MPa) <sup>9</sup>	Swp/Estab/Lower (MPa) <sup>10</sup>	Tlow (°C) <sup>11</sup>	Thigh (°C) <sup>12</sup>
<i>B. gracilis</i>	3	-0.5	4	-0.5	3	11	70	3	-0.5	-0.5	15	35
<i>B. eriopoda</i>	5	-1.0	4	-1.0	3	20	50	3	-1.0	-1.0	20	40

<sup>1</sup>Number of wet days needed for germination. <sup>2</sup>Soil water potential necessary in the top soil layer for germination. <sup>3</sup>Maximum number of days between germination and establishment that roots can be dry. <sup>4</sup>Soil water potential necessary in the lower soil layers below which the roots are dry. <sup>5</sup>Number of layers in the lower soil layer. <sup>6</sup>Minimum number of days after germination for initiation of adventitious roots. <sup>7</sup>Maximum number of days after germination for initiation of adventitious roots. <sup>8</sup>Number of wet days needed for establishment. <sup>9</sup>Soil water potential necessary in the top soil layer for establishment. <sup>10</sup>Soil water potential necessary in the lower soil layers for establishment. <sup>11</sup>Lowest temperature at which germination and establishment can occur. <sup>12</sup>Maximum temperature at which germination and establishment can occur.

were 15 - 35 °C (Briske & Wilson 1977).

These experimental findings were used previously to determine establishment criteria for *B. gracilis* to be used in simulation modeling (Table 3; Lauenroth et al. 1994). Seeds were simulated to germinate in the top soil layer since experimental work with *B. gracilis* indicates high germination of seeds in the top soil layer (1 - 2 cm), decreasing with depth (Carren et al. 1987). There are two differences between the germination and establishment criteria for *B. gracilis* used in the current study and the criteria developed previously. First, we added a maximum temperature for establishment (35 °C; Table 3) since the gradient includes areas where bare soil temperatures may exceed 60 °C, and germination of *B. gracilis* has been found to decline at surface temperatures above 35 °C (Knipe 1967). We also used soil temperature in the top soil layer rather than air temperature as the factor affecting establishment since germinating seeds of these species are generally located in the top soil layer. However, air temperatures and not soil temperatures are readily available from weather stations so we then used regression equations (from field data at the CPER - R. D. Alward, unpubl. data) to relate daily maximum and minimum soil temperature at 5 cm depth ( $T_{s-max}$  and  $T_{s-min}$ , respectively) to daily maximum and minimum air temperature at 1.1 m above the soil surface ( $T_{a-max}$  and  $T_{a-min}$ , respectively), as follows:

$$T_{s-max} = 0.87 T_{a-max} + 2.78; r^2 = 0.80 \quad (2)$$

$$T_{s-min} = 0.90 T_{a-min} + 7.35; r^2 = 0.79 \quad (3)$$

Although germination responses to temperature are not square-wave in nature, but vary over the range of suitable temperatures for germination, we used only minimum and maximum temperatures since we are interested in the occurrence of a germination event during a given year, rather than the percentage of seeds available in any given year which germinate. Second, we changed

soil water potentials in all soil layers necessary for establishment from -0.15 MPa to -0.5 MPa. Lauenroth et al. (1994) used the value of -0.15 MPa to be conservative, although Wilson & Briske (1979) suggested that -1.5 MPa was sufficient. In addition, a soil water potential of -1.0 MPa was sufficient for germination under laboratory conditions (Qi & Redmann 1993). Therefore, we selected a value between these that will still result in conservative estimates (-0.5 MPa). Sensitivity analysis has indicated establishment was not sensitive to the soil water potential used for germination, but was sensitive to the soil water potential used for establishment: by changing the soil water potential in the lower soil layers necessary for establishment from -0.1 MPa to -0.7 MPa, establishment probability increased from 0.0140/yr to 0.0754/yr at the CPER in a sandy loam soil (Lauenroth et al. 1994). Thus, our estimates for establishment at the CPER are higher than those of Lauenroth et al. (1994).

#### *Bouteloua eriopoda*

Less information is available on conditions required for establishment of *B. eriopoda* than for *B. gracilis*. Because *B. eriopoda* also develops adventitious roots near the soil surface, we assumed that *B. eriopoda* germination and establishment requirements were similar to those for *B. gracilis* (T.J. Minnick pers. obs.; Table 3). Soil water potential requirements were more negative for *B. eriopoda* than for *B. gracilis* because *B. eriopoda* has high germination under dry conditions: there was 71 % of the germination at -1.1 MPa as compared to -0.03 MPa (Knipe & Herbel 1960). We assumed minimum and maximum temperatures were higher by 5 °C for *B. eriopoda* based on germination trials for both species (Toole 1938). The 20 - 50 days for initiation of adventitious roots by *B. eriopoda* vs. the 11 - 70 days by *B. gracilis*, as well as the 5 days needed for germination by *B. eriopoda* vs. the 3 days necessary for germination by *B. gracilis*, reflects the

slower development following germination of *B. eriopoda* than *B. gracilis* seen under field and greenhouse conditions (T.J. Minnick pers. obs.).

### Experimental simulations

#### Current climate

We used 30 yr of historical weather data from each site to produce 5000 yr of weather data using a first-order Markov weather generator. A long-term weather series was required because establishment are low for both species; thus, 5000 yr resulted in sufficient events for comparison of establishment along the gradient (see Lauenroth et al. 1994 for methods). Each species was simulated at each site separately using the same 5000-yr sequence of weather data to simulate soil water dynamics, and to determine if criteria were met for successful germination and establishment.

We used independent parameter perturbation sensitivity analysis (Rose 1983) to determine if regional patterns of establishment were sensitive to changes in individual model parameters. This sensitivity analysis also indicated if it may be important to consider population-related or distribution-related polymorphism in germination and establishment response to climatic factors. Parameters were varied over a range of values encompassing the original *B. eriopoda* and *B. gracilis* criteria (e.g. soil water potential parameters were varied from  $-0.1$  to  $-1.5$  MPa at  $0.2$  MPa intervals and maximum temperature was varied from  $32$  to  $43$  °C at  $1$  °C intervals). For the sensitivity analysis, we performed 100-yr simulations for each site using the same weather sequence for each species, but varying the establishment criteria one parameter at a time. We used 100-yr simulations in this case because of the large number of different simulations conducted. As an indication of a change in the pattern of germination and establishment across the climatic gradient, separate regressions of latitude versus percentage of years with germination and establishment were performed for each value of each parameter for each species to determine if changes in the sign of the slope of the latitude versus establishment regression line occurred.

To determine the climatic variables explaining the most variation in percentage of years with germination and establishment along the gradient, we performed a multiple regression analysis for the 16 sites. Stepwise selection (Anon. 1997) was used with an  $\alpha = 0.05$  selection level for entry and removal of variables. For each species, we regressed the percentage of years with germination and establishment from each site against 30 year averages from the historical weather

data from each site of five climatic variables. These climatic variables are related to amount and timing of precipitation and temperature: average daily minimum ( $T_{\text{MIN}}$ ), maximum ( $T_{\text{MAX}}$ ), and average ( $T_{\text{AVE}}$ ) temperatures, mean annual precipitation (PPT), and mean number of precipitation events per year (Events).

Although ecotonal boundaries may be difficult to define in the field, the transition zone between dominance by two life-forms likely includes the region where the response variable is similar for both species if the independent variable represents an environmental gradient (Gosz & Sharpe 1989). Therefore, the location of the ecotone between shortgrass steppe and desert grassland was predicted by calculating the intersection of the *B. gracilis* and *B. eriopoda* regression lines of latitude versus percentage of years with predicted establishment. We first determined if regression lines for the two species were different by finding if the slopes of the two lines differed using the general linear model procedure in SAS (Anon. 1997). Next, we calculated the intersection from the equations of the regression lines. Finally, we calculated a 95 % confidence interval for the latitude of the intersection based on methods used in calibration problems (Graybill 1976).

#### Climate change scenarios

We also simulated future establishment under directional changes in climate predicted by general circulation models (GCMs) as a result of doubled atmospheric concentrations of  $\text{CO}_2$ . These simulations were conducted by scaling monthly precipitation, and minimum and maximum temperatures, as well as wind speed, relative humidity, and solar radiation, based upon predictions from three GCMs [Goddard Fluid Dynamics Laboratory (GFDL), Oregon State University (OSU), and United Kingdom Meteorological Office (UKMO)] used in previous model comparison studies (Kittel et al. 1995; Anon. 1995). These GCMs are similar in that they all predict increased temperatures for this region with doubled atmospheric  $\text{CO}_2$ , but they differ in the amount and seasonal timing of changes in temperature and precipitation (Table 4). Because there are many uncertainties in these scenarios, we investigated several of them. We again determined if the slopes of the regression lines of latitude versus percentage of years with predicted establishment of *B. gracilis* and *B. eriopoda* differed. We then calculated the intersection of the regression lines with a confidence interval calculated as outlined above in order to predict shifts in ecotone location with climate change.

**Table 4.** Climate change scenario comparisons for changes in precipitation and temperature by season of year and state; CO = Colorado; NM = New Mexico. Precipitation is shown in percent change, temperature is in °C increase.

	Precipitation (+/- %)			Temperature (+ °C)		
	GFDL	OSU	UKMO	GFDL	OSU	UKMO
Spring <sup>1</sup>						
CO	+18.7	+19.2	+27.4	5.3	2.5	5.8
NM	+15.6	-1.0	+24.1	5.2	2.8	4.9
Summer <sup>2</sup>						
CO	+2.1	+1.3	+7.0	4.5	3.5	5.8
NM	+75.6	-18.9	+29.4	3.3	4.1	5.8
Autumn <sup>3</sup>						
CO	-26.1	-12.4	+11.4	4.3	2.7	6.6
N	-26.0	-11.0	+22.8	3.9	3.0	6.0
Winter <sup>4</sup>						
CO	+30.3	+5.9	+25.5	4.5	2.7	7.0
NM	+7.9	-8.9	+19.9	4.5	2.6	6.3

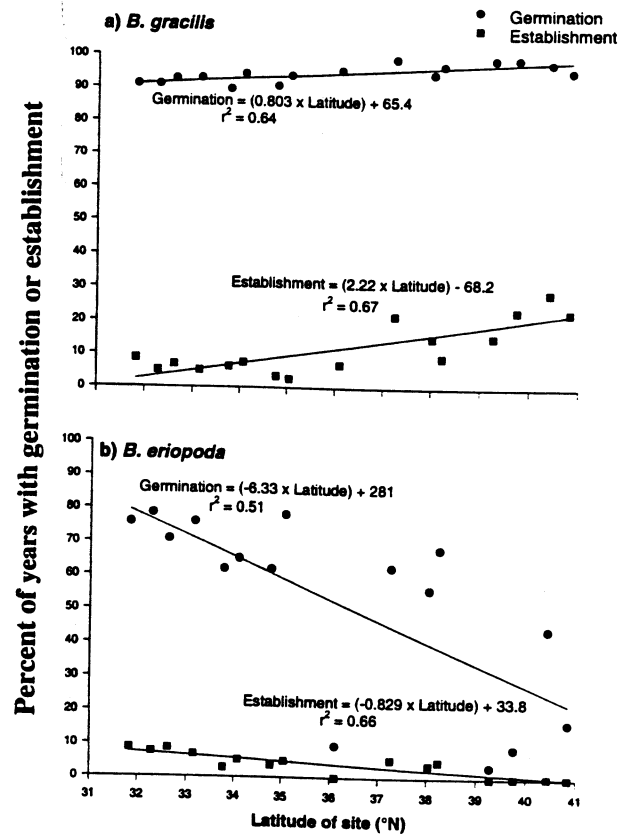
<sup>1</sup>March, April, May; <sup>2</sup>June, July, August; <sup>3</sup>September, October, November; <sup>4</sup>December, January, February.

**Results**

*Current climate*

For *Bouteloua gracilis* percentage of years with predicted germination and establishment decreased from north to south along the climatic gradient (Fig. 3a). Percentage of years with predicted germination ranged from 98.7 % of the 5000 yr at Byers (39° 45' N) and Trinidad, CO (37° 15' N) to 89.5 % at Bosque, NM (33° 46' N). Establishment was predicted to be low throughout the gradient, varying from 28.6 % at Greeley, CO (40° 25' N) to 2.6 % at Albuquerque, NM (35° 03' N). In contrast, percentage of years with predicted germination and establishment of *B. eriopoda* increased from north to south (Fig. 3b). Germination ranged from 3.4 % at Limon, CO (39° 16' N) to 78.5% at NMSU, NM (32° 17' N). Establishment ranged from 0 % at Limon, CO and Alcalde, NM (36° 06' N) to 8.6 % at the Jornada, NM (32° 37' N) and Columbus, NM (31° 50' N).

Temperature variables explained more of the variation in percentage of years with predicted germination and establishment of *B. eriopoda* while precipitation variables explained more of the variation of *B. gracilis* (Table 5). For *B. eriopoda*, T<sub>AVE</sub> explained the most variation in germination while T<sub>AVE</sub> and number of precipitation events per year were both significant in explaining variation in establishment. For *B. gracilis*, both mean number of precipitation events per year and T<sub>MAX</sub> were significant in explaining variation in germination while MAP alone was significant in explaining variation in establishment.



**Fig. 3.** Results from the simulation model showing predicted percent of years with germination or establishment versus the latitude of the site for (a) *Bouteloua gracilis* and (b) *B. eriopoda*. Longitude varies from 103° 41' to 107° 39' W, and altitude from 1190 to 1750 m along the latitudinal gradient.

Slopes of the regression lines of percentage of years with predicted establishment versus latitude were significantly different for *B. gracilis* and *B. eriopoda* ( $F = 47.30; p < 0.0001$ ). Regression lines intersected in central New Mexico at latitude 33.5 °N (95 % CI: 32° 08' N to 34° 28' N) with simulated establishment of 6.0 % (Fig. 4a). In the sensitivity analysis, the sign of the slope of the regression line of *B. eriopoda* changed from negative when minimum temperature was > 18 °C to positive for a minimum temperature of 12 - 18°C. The sign of the slope of the regression line of *B. gracilis* changed from positive when minimum temperature was < 19 °C to negative for a minimum temperature of 19 - 23°C (Table 6). Otherwise, all parameter values were robust in that independently varying them around the original criteria value did not change the sign of the slope of the regression line for either *B. eriopoda* (slope = -) or *B. gracilis* (slope = +) throughout the range of values tested.

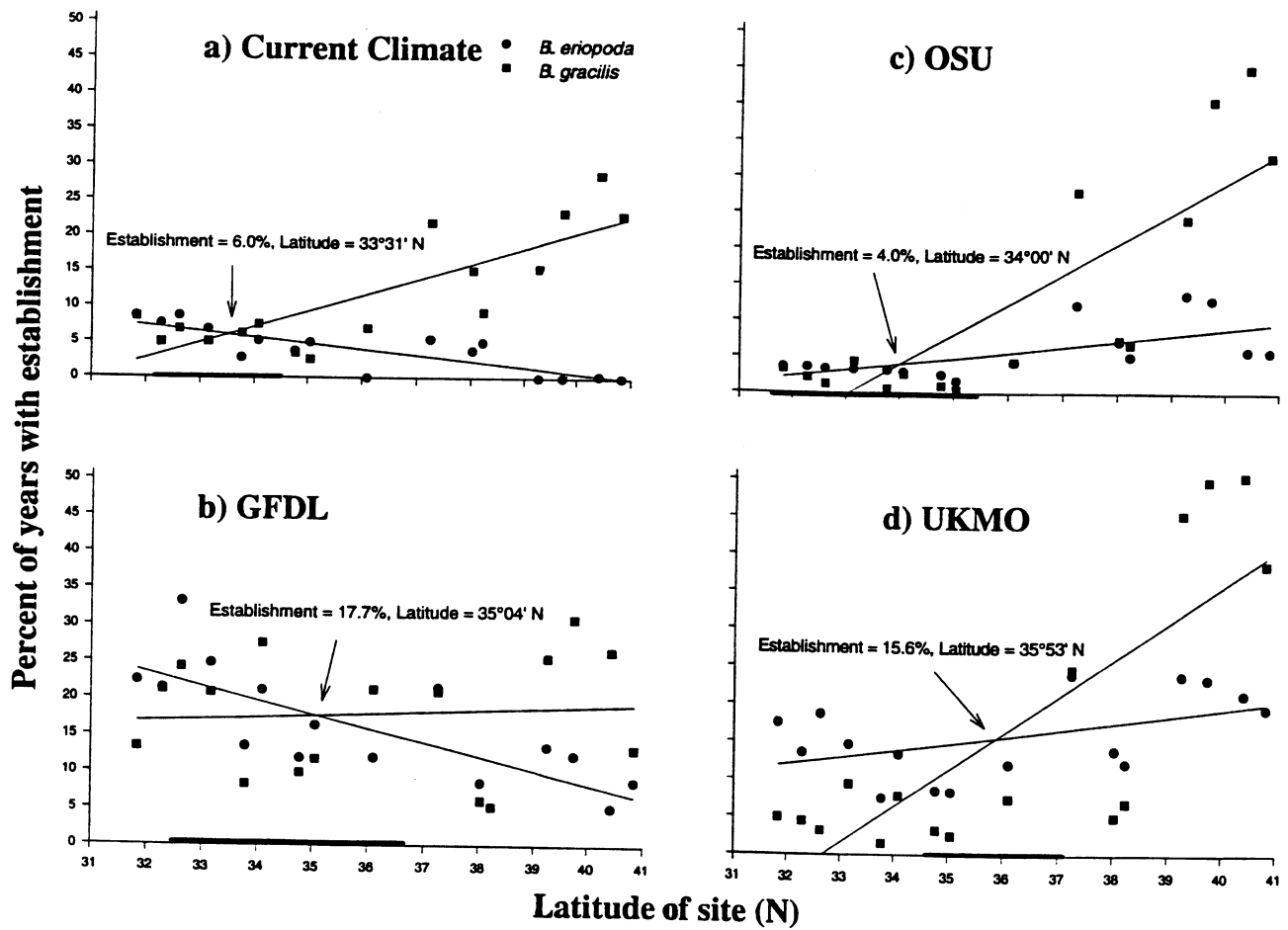


Fig. 4. Simulated establishment for *Bouteloua gracilis* and *B. eriopoda* under (a) current climate, and three climate change scenarios: (b) Goddard Fluid Dynamic Laboratory, (c) Oregon State University, and (d) United Kingdom Meteorological Office. The 95 % confidence interval for the intersection of the two regression lines is shown as a dark bar on the x-axis.

#### Climate change scenarios

Under each of the three climate change scenarios, the slopes of the regression lines of latitude vs. percentage of years with predicted establishment were significantly different for *Bouteloua gracilis* and *B. eriopoda* (GFDL:  $F = 6.58$ ,  $p = 0.016$ ; OSU:  $F = 17.19$ ,  $p = 0.0003$ ; UKMO:  $F = 13.86$ ,  $p = 0.0009$ ). The intersection of the regression lines moved northward to higher latitudes for all three climate change scenarios (Fig. 4 b-d): GFDL (35° 04' N), OSU (34° 00' N), and UKMO (35° 53' N), although the change with the OSU-scenario was slight. In addition, the percentage of years with predicted establishment at the intersection point increased from that predicted under current climate (6.0 %) with both the GFDL- (17.7 %) and UKMO-scenarios (15.6 %), but decreased with the OSU scenario (4.0 %). The 95 % confidence intervals between the current climate (32° 08' N to 34° 28' N) simulations and the UKMO-scenario (34° 36' N to 37° 05' N) did

not overlap, although the intervals overlapped with both the GFDL (32° 33' N to 36° 44' N), and OSU scenarios (31° 35' N to 35° 22' N).

The percentage of years with predicted establishment for both species increased under the climate change scenarios, but there was variation in amount of increase: *B. gracilis* establishment increased by an average of 6.2 % (GFDL), 1.0 % (OSU), and 4.8 % (UKMO), while *B. eriopoda* establishment increased by an average of 11.8 % (GFDL), 1.8 % (OSU), and 11.8 % (UKMO). For *B. gracilis*, both the OSU- and UKMO-scenarios predicted increases in establishment in the northern portion of the gradient, but decreases in the southern, while the GFDL-scenario predicted decreases in the northern and increases in the southern.

For *B. eriopoda*, both the GFDL- and UKMO-scenarios predicted increases throughout the gradient, while the OSU-scenario predicted increases in the northern and decreases in the southern part of the gradient. In addition, signs of slopes of the establishment lines



**Table 5.** Results from the multiple regression analysis showing climate variables best predicting germination and establishment probabilities along the climatic gradient.

Species	Independent Variable	Intercept	Dependent Variable	Coefficient	Partial $R^2$	$P$	Model $R^2$	$P$
<i>Bouteloua gracilis</i>	% germination	93.7	Events <sup>1</sup>	0.184	0.82	< 0.0001	0.88	< 0.0001
			$T_{MAX}$ <sup>2</sup>	-0.417	0.06	0.03		
	% establishment	-25.2	MAP <sup>3</sup>	1.26	0.71	< 0.0001	0.71	< 0.0001
<i>Bouteloua eriopoda</i>	% germination	-54.7	$T_{AVE}$ <sup>4</sup>	8.57	0.69	< 0.0001	0.69	< 0.0001
	% establishment	-20.3	$T_{AVE}$ <sup>4</sup> Events <sup>1</sup>	1.39 0.131	0.75 0.07	< 0.0001 0.03	0.82	< 0.0001

<sup>1</sup>Mean number of precipitation events per y; <sup>2</sup>Mean annual daily maximum temperature, <sup>3</sup>Mean annual precipitation, <sup>4</sup>Mean annual daily average temperature

changed for *B. eriopoda* under the OSU and UKMO climate change scenarios, but remained the same as for current climate for *B. eriopoda* under the GFDL scenario and for *B. gracilis* under all three scenarios.

## Discussion

Recruitment can be important in determining the geographic distributions and abundances of plants (Turner et al. 1966; Louda 1982; Neilson & Wullstein 1983; Hengeveld 1990). Geographic distributions may overlap each other and form an ecotone, the transition between areas of dominance by one species to dominance by another; ecotones exist in hierarchical levels and, when vegetation types are dominated by one or a few species, the ecotone between dominant species may correspond with the ecotone between biomes or vegetation types (Gosz 1993). By integrating amounts and

timing of temperature and precipitation at a daily time scale, we found (1) north-south patterns of simulated establishment along a climatic gradient are similar to the dominance patterns of *B. gracilis* and *B. eriopoda* along the same gradient, (2) predicted ecotone location under current climate between *B. gracilis* and *B. eriopoda* geographic ranges, and hence also between shortgrass steppe and desert grassland, corresponds to a site where the two species codominate, (3) precipitation variables were more important, but not the sole factor, in explaining establishment for *B. gracilis*, while temperature variables were more important for *B. eriopoda*, and (4) the ecotone between *B. gracilis* and *B. eriopoda* is predicted to shift northward under directional changes in climate predicted by several GCMs.

Patterns of establishment simulated in this study broadly correspond to the geographic patterns of dominance by *B. gracilis* and *B. eriopoda*. Plant communities in the northern portion of the gradient in the shortgrass

**Table 6.** Parameter values tested in the sensitivity analysis separately for *Bouteloua gracilis* and *B. eriopoda*. Values encompass and go beyond the differences between the criteria used for the two species. The values tested which changed the slope of the regression line of latitude versus predicted establishment are marked for *B. gracilis* (x) and *B. eriopoda* (y). See Table 2 for explanation of abbreviations.

Parameter	Values tested
GermDay (days)	1, 2, 3, 4, 5, 6
Swp/Germ/Top (-MPa)	0.1, 0.3, 0.5, 0.7, 0.9, 1.1, 1.3, 1.5
RootDry (days)	2, 3, 4, 5, 6, 7, 8, 9, 10
Swp/Germ-Estab/Lower (-MPa)	0.1, 0.3, 0.5, 0.7, 0.9, 1.1, 1.3, 1.5
Layers	2, 3, 4, 5
MinInit (days)	5, 10, 15, 20, 25, 30
MaxInit (days)	30, 40, 50, 60, 70, 80, 90
EstabDay (days)	1, 2, 3, 4, 5, 6
Swp/Estab/Top (-MPa)	0.1, 0.3, 0.5, 0.7, 0.9, 1.1, 1.3, 1.5
Swp/Estab/Lower (-MPa)	0.1, 0.3, 0.5, 0.7, 0.9, 1.1, 1.3, 1.5
Tmin (°C)	12 <sup>y</sup> , 13 <sup>y</sup> , 14 <sup>y</sup> , 15 <sup>y</sup> , 16 <sup>y</sup> , 17 <sup>y</sup> , 18 <sup>y</sup> , 19 <sup>x</sup> , 20 <sup>x</sup> , 21 <sup>x</sup> , 22 <sup>x</sup> , 23 <sup>x</sup>
Tmax (°C)	27, 28, 29, 30, 31, 32, 33, 34, 35, 36, 37, 38

steppe are dominated by *B. gracilis*, and this species decreases in importance in the southern portion of the gradient. In contrast, *Bouteloua eriopoda* is currently not found north of Pueblo, CO (38° 14' N), which corresponds to the part of the gradient where percentage of years with predicted establishment were very low (< 1%). For example, *B. gracilis* dominates the CPER, CO (40° 49' N), the northernmost site of the study gradient, comprising 90% plant basal cover in some areas (Milchunas et al. 1989). Pinyon Canyon Military Maneuver Site in southern Colorado (37° 22' N) also has large areas dominated by *B. gracilis*, with *B. eriopoda* restricted to canyon bottoms and rims (Shaw et al. 1989). The Sevilleta National Wildlife Refuge in central New Mexico (34° 21' N) has areas that are dominated by *B. gracilis*, *B. eriopoda* and a mix of the two species (Gosz 1993). The remnant grassland portion of the Jornada Experimental Range in southern New Mexico (32° 37' N), located near the southern part of the study gradient, is dominated by *B. eriopoda* (Herbel et al. 1972), although *B. gracilis* is found nearby in higher altitude, mountainous regions (T.J. Minnick, pers. obs.). These similarities in patterns suggest that germination and establishment could be responsible, at least in part, for the observed geographic distributions of these species.

Predicted germination results suggest a testable hypothesis with regard to seed bank dynamics in these two species. Predicted germination was nearly 100% of the years for *B. gracilis* throughout the gradient, and 50 - 80% of the years for *B. eriopoda* in the areas in which it is currently found. These results suggest that the seed banks, particularly for *B. gracilis*, may not persist from year to year: once seeds germinate in the spring of the year, current seed production would be necessary to replenish the seed bank. These predictions have some support from temporal seed bank studies at the CPER in which no *B. gracilis* seedlings grew from soil samples collected from July 1984 to July 1985, but were present in September and November 1985, after summer seed production of 1985 (Coffin & Lauenroth 1989). More field studies would need to be done on seed production and seed bank dynamics across the gradient to test this hypothesis. However, many grasslands do not have persistent seed banks, and forbs seem to have longer-lived seeds, in general, than do grasses (see review by Thompson 1992).

These grasses dominate shortgrass steppe and desert grasslands despite observations in the field and simulation analyses that indicate low establishment (Nelson 1934; Hyder et al. 1971; Lauenroth et al. 1994). Life-history characteristics such as lifespan, ability to vegetatively reproduce by tillering or stolons, and low rates of mortality may explain local dominance even with establishment in fewer than 10% of the years

(Table 1). The two *Bouteloua* species have different population dynamics because of their differences in vegetative recruitment: *B. gracilis* populations at the CPER are most likely comprised of mature individuals recruited from seed which then spread by the production of tillers, while *B. eriopoda* populations at the Jornada Experimental Range are comprised of juveniles, primarily recruited from stolons (Lauenroth et al. 1997). However, when life span is taken into account, recruitment from seed may be necessary only periodically in both species (Herbel et al. 1970; Coffin & Lauenroth 1988): *B. gracilis* genets are much longer-lived than are *B. eriopoda* ramets (Table 1). Within the CPER, *B. gracilis* may need only a few establishment events during its long lifespan to replace itself since disturbance rates are low in the shortgrass steppe (Coffin & Lauenroth 1988; Table 1). Similarly, within the Jornada Experimental Range, *B. eriopoda* could spread vegetatively through stolons to maintain its population in the presence of small-scale disturbance and light-to-moderate grazing, with recruitment from seed occurring only periodically (Nelson 1934).

Reproduction from seed, however, is important to consider in broad-scale geographic ranges and dominance patterns because vegetative spread is unlikely to be the sole mechanism determining range expansion (Brown & Gersmehl 1985). For example, in a study of grass demographics and distribution, Laing (1958) found that seedling survival of *Amnophila breviligulata*, a dune grass capable of both vegetative and sexual reproduction, was low in established stands; however, seedling establishment frequently resulted in the establishment of new stands which then increased by vegetative growth. Seedling establishment is also likely important in the recovery of periodic disturbance events, such as extreme drought, which may cause broad-scale mortality: *Bouteloua gracilis* seedlings were critical to the recovery of vegetation in the North American Great Plains after the Great Drought from 1933 to 1940 (Mueller & Weaver 1942; Albertson & Weaver 1944). In northern Colorado, mortality of *B. gracilis* also occurs due to nest sites of ants, burrowing activities of animals and fecal pats from cattle (Coffin & Lauenroth 1988; Table 1). Mortality of *B. eriopoda* likely occurs in the central and southern parts of the study region due to mound-building activities of kangaroo rats (*Dipodomys* spp.) in the Chihuahuan desert (Moroka et al. 1982; Table 1). Recovery of localized dominance patterns from small-scale disturbance of kangaroo rat mound building at the Sevilleta NWR appears to be faster for *B. eriopoda* than for *B. gracilis* (Fields et al. 1999).

Shortgrass steppe and desert grasslands are overwhelmingly dominated by these two species such that

the area of transition in dominance is considered the ecotone between shortgrass steppe and desert grassland vegetation types (Gosz 1993). Gosz (1993) observed ecotones at multiple scales in these two vegetation types, and determined that the key to the transition between types was the presence of both *B. gracilis* and *B. eriopoda*, with each species coexisting within the ecotone rather than the existence of a well-defined transition zone between species and thus between vegetation types. The 95 % confidence interval where the two establishment regression lines cross under current climatic conditions (32° 08' to 34° 28' N) corresponds with an area of transition between shortgrass steppe and desert grassland determined by independent field observations (Gosz & Sharpe 1989). The Sevilleta National Wildlife Refuge in central NM (34° 21' N) is located within this region, and consists of patches of both pure and mixed stands of both species (Gosz 1993).

Simulated recruitment of these species was not due to a single factor, but to the interaction of precipitation and minimum and maximum temperatures. It is likely with increased atmospheric concentrations of CO<sub>2</sub> that temperatures will increase in this region, though the amount of change is uncertain (Kattenberg et al. 1996). The direction and magnitude of change in precipitation is less certain (Kattenberg et al. 1996). Because variation in *B. eriopoda* establishment was explained by temperature variables and variation in *B. gracilis* establishment by precipitation variables, it is likely that the geographic range of *B. eriopoda* would expand to the north based on establishment constraints, while changes in the geographic range of *B. gracilis* is more difficult to predict. Because the current geographic range of *B. gracilis* is large, covering approximately two-thirds of the continental USA. (Stubbendieck et al. 1992), it appears to be adapted to a broad range of climatic conditions; thus it is unlikely that *B. gracilis*' range would contract unless populations are adapted to the local environment.

We assumed no plasticity in germination and establishment criteria within the model. This assumption was based on germination tests under controlled conditions for *B. gracilis* seeds, regardless of origin within the USA. (Anon. 1981). However, plasticity has been found for morphological characteristics and seedling winter survivability for *B. gracilis* (Riegel 1940; Rogler 1943). In particular, results from the sensitivity analysis suggest that minimum temperatures used in these simulations are a key factor in determining the pattern of predicted establishment for both species (Table 6). Thus, refinement of our predictions requires field studies on population- or distribution-related polymorphism in germination and establishment responses to temperature. In addition, other factors such as interspecific competition

and substrate could interact with changing climate in determining dominant species in an area (Graumlich & Davis 1993). Propagule availability and dispersal can also be important in determining ecotone location (Malanson 1997).

Although the three GCMs predicted different climate change scenarios, in particular with regard to precipitation, the intersection between the establishment lines of the two species, and thus the ecotone, shifted northward under all scenarios; however, the 95 % confidence intervals around these points overlapped with the 95% confidence interval from the current climate simulations except in the case of the UKMO-scenario. The shift in dominant species would also shift the location of the shortgrass steppe and desert grassland communities if the two species continued to play such an important role in these vegetation types. However, this shift in ecotone location could lag behind climate change due to the longevity of *B. gracilis*, the species which was predicted to have decreased percentage of years with establishment, in general, using the climate change scenarios. Furthermore, shifts in *B. gracilis* and *B. eriopoda* dominance may not be accompanied by changes in other species. Complex interactions between dominants in a community, other species, and the changing environment may result in new species composition (Davis 1986). Thus, our conclusions about shifts in the ecotone between shortgrass steppe and desert grassland are valid only if these vegetation types continue to be dominated by *B. gracilis* and *B. eriopoda*.

The intersection of the latitude versus establishment regression lines for the two species was predicted under the UKMO- and GFDL-scenarios to have a greater percentage of years with predicted establishment than with current climate; percentage of years with establishment at the intersection was lower with the OSU-scenario than with current climate. This is most likely due to the decreasing precipitation predicted by the OSU scenario, whereas the UKMO- and GFDL-scenarios predicted increasing precipitation throughout the gradient in most seasons. This decreasing precipitation led to decreased establishment predictions at many sites for both *B. gracilis* and *B. eriopoda*, providing further evidence that establishment was a result of the interaction of precipitation and temperature, since in all scenarios temperature was predicted to increase.

### Conclusions

Recruitment may be an important process determining, at least in part, the geographic ranges and dominance patterns of these two important perennial grasses. Although successful recruitment is dependent on a combination of events including seed production and

dispersal, availability of space, and amount and timing of precipitation and temperature, a consideration of only germination and establishment constraints was sufficient to represent dominance patterns similar to those found in the field. Because these species dominate the shortgrass steppe and desert grasslands of North America, changes in the geographic ranges or dominance patterns would be ecologically significant. Alternative climate change scenarios resulted in a similar prediction: a northward shift in the geographic distribution of *B. eriopoda*. Complex interactions between plants of other species with this changing environment may result in different species assemblages than currently found in shortgrass steppe or desert grassland communities. As climate change predictions and our understanding of these interactions improve, our ability to predict consequences of global change will also improve. Consideration of transient change in vegetation type is important in considering the impacts of climate change on terrestrial ecosystems as well as feedbacks to the atmosphere (Steffen et al. 1996; Braswell et al. 1997).

**Acknowledgements.** This material is based upon work supported under a National Science Foundation Graduate Research Fellowship awarded to the first author. Additional support was provided by the Sevilleta LTER (NSF DEB-9411976), the SGS LTER and supplement (NSF BSR-9011659). Thanks to B.T. Milne for comments about ecotones, M. Coleman for assistance with a soil texture map, J. Anderson for access to the Jornada long-term weather data, and P.L. Chapman for assistance with statistical analyses. R.J. Hobbs, M.G. Turner, R. D. Alward, H. Fraleigh, T. Hochstrasser, D.R. Lane, G. Martinez, K. Parker, J.K. Detling, W.K. Lauenroth, T.R. Seastedt, and several anonymous reviewers provided constructive comments on an earlier version of the manuscript. The CPER and Jornada Experimental Range are administered by the USDA Agricultural Research Service. The U.S. Fish and Wildlife Service manages the Sevilleta National Wildlife Refuge. Access to the VEMAP dataset was through the University Corporation for Atmospheric Research's Climate System Modeling Program.

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Received 27 November 1997;

Revision received 12 October 1998;

Accepted 26 October 1998.