

Climatic variation and simulated patterns in seedling establishment of two dominant grasses at a semi-arid–arid grassland ecotone

Peters, Debra P.C.

Natural Resource Ecology Laboratory, Department of Rangeland Ecosystem Science, and Graduate Degree Program in Ecology, Colorado State University, Fort Collins, CO 80523, USA; Present address: United States Department of Agriculture-Agricultural Research Service, Jornada Experimental Range, MSC 3JER, NMSU, Las Cruces, NM 88003-0003, USA; Fax +15056465889; E-mail debpeter@nmsu.edu

Abstract. The objective of this study was to predict the effects of climatic variation at multiple temporal frequencies on seedling establishment by two congeneric C_4 perennial grasses (*Bouteloua gracilis* and *B. eriopoda*) at the ecotone between shortgrass steppe grassland and Chihuahuan desert grassland in central New Mexico, USA. The approach was to use a daily time-step simulation model to determine the occurrence of a recruitment event in each year based upon the amount and timing of soil water required for establishment. Historical weather data were used to predict effects of seasonal and interdecadal variation in climate on establishment. A sensitivity analysis was used to predict effects of directional climate change on establishment.

Bouteloua gracilis had a broad pattern of simulated establishment from May through September that included periods with high year-to-year variation in precipitation. *B. eriopoda* establishment events occurred primarily in July when precipitation amounts were most reliable. Climatic conditions from 1949 through 1968 were more favorable for *B. eriopoda* establishment compared to the cooler, wetter conditions from 1969 through 1988 that favored *B. gracilis*. Establishment of *B. eriopoda* was lowest in El Niño years whereas *B. gracilis* establishment was highest in La Niña years. Establishment of *B. gracilis* was most sensitive to temperature when precipitation was higher than current amounts. The greatest response to temperature by *B. eriopoda* for all precipitation amounts occurred at cooler temperatures than found currently.

These results indicate that climatic variation at multiple frequencies has differential effects on seedling establishment for these two perennial grasses, and may account at least in part for patterns in dominance at this biome transition zone.

Keywords: Chihuahuan desert grasslands; Ecotone; ENSO; Global climate change; Recruitment; Shortgrass steppe.

Nomenclature: Stubbendieck et al. (1992).

Abbreviations: ENSO = El Niño Southern Oscillation; SNWR = Sevilleta National Wildlife Refuge.

Introduction

Recruitment processes are important for plant species persistence and dominance, especially in the presence of disturbances (Klinkhamer & de Jong 1988; Clark et al. 1998). Recruitment is particularly important to patterns in species dominance at interfaces between plant community types, such as grassland-forest ecotones, where large-scale mortality events are often balanced through time by small-scale recruitment events (Slatyer & Noble 1992). Although changes in ecotones have been documented, interactions between environmental conditions and recruitment processes underlying the direction and rate of change in species dominance are not well understood.

Ecotones are hierarchical with different environmental constraints operating at different spatial scales (Gosz 1992, 1993). Temporal variation, especially in climate, is also expected to be important to recruitment processes and shifts in species dominance at ecotones; this has not been well tested although inter-annual variation in climate was found to be more important than average climatic conditions to limits in species distributions (Woodward 1997). In this study, it was hypothesized that climatic variation at multiple temporal frequencies has differential effects on recruitment processes of dominant species from adjacent plant communities. Directional changes in climate are expected to affect patterns in recruitment for extended periods of time.

Although there are several processes associated with recruitment, regeneration (i.e. seed germination and seedling establishment) has received less attention compared to seed production, dispersal, and competition for limiting resources (Woodward 1993; Landhauser & Wein 1994). An understanding about the effects of climatic variation on regeneration requires experimental data on physiological responses by seeds and seedlings to micro-environmental conditions; these data exist for very few long-lived, perennial species. One species for which detailed experimental data exist is the C_4 perennial grass *Bouteloua gracilis*, the dominant plant in

shortgrass steppe grasslands of North America (Lauenroth & Milchunas 1991). In this study, regeneration response data for *B. gracilis* and a related species, *Bouteloua eriopoda*, that dominates an adjacent biome (Chihuahuan desert grasslands) were used to predict the effects of temporal variation in climate at multiple frequencies on successful seedling establishment. Because these two species respond differently to drought and heavy grazing, and they overwhelmingly dominate their respective plant communities (Lauenroth & Milchunas 1991; Schmutz et al. 1991), it is important to understand the conditions that favor recruitment by one species over the other.

Thus, there were three objectives for this study: (1) to predict the timing of seed germination and seedling establishment for *B. gracilis* and *B. eriopoda* in response to intra-annual variation in climate; (2) to predict effects of periodic fluctuations in climate at inter-decadal scales (15 to 30 yr) on seedling establishment for each species; and (3) to predict the sensitivity of seedling establishment to long-term directional changes in climate.

Methods

A daily time step simulation model of soil water dynamics was used to integrate long-term daily temperature and precipitation with soil texture data for one site in central New Mexico located near the ecotone between Chihuahuan desert and shortgrass steppe plant communities. The occurrence of a recruitment event in each year was predicted by comparing simulated soil water content through time with amount and timing of soil water required for germination and establishment.

Site description

The model was applied to the Sevilleta National Wildlife Refuge (SNWR; 34.5° N, 106.9° W) located ca. 75 km south of Albuquerque, New Mexico, USA. The SNWR is a 100 000 ha wildlife refuge established in 1973 and managed by the United States Fish and Wildlife Service; the refuge is also a Long Term Ecological Research (LTER) site. Grazing by cattle has been excluded from the SNWR since 1973, although grazing by native herbivores, such as pronghorn antelope and rabbits, occurs at low to moderate intensities. The climate of the SNWR is semi-arid to arid with high temporal and spatial variability (Gosz 1992). The site is characterized by dry, cool winters and springs from January through June. The summer 'monsoon' period from July through September is hot but wet; intense thunderstorms during this time contribute over half of the annual precipitation. Autumn conditions from October to December

are typically cooler and dry. The El Niño southern oscillation phenomenon (ENSO) often strongly influences non-monsoonal precipitation (Molles & Dahm 1990). In central New Mexico, El Niño events are characterized by above-average amounts of precipitation from October through May, and La Niña events are drier than average during the same time period (Molles & Dahm 1990). Growing season precipitation (June through September) is not predictably affected by the ENSO phenomenon.

The study site was the McKenzie Flats (1650 m elevation) where vegetation is typical of the Chihuahuan desert grassland-shortgrass steppe transition zone. Patches of vegetation of variable size (< 10 m² to > 1000 m²) and shape may be dominated or codominated by *B. gracilis* and *B. eriopoda* at this location (Gosz 1995; Kröel-Dulay et al. 1997). The topography is level on a sandy loam soil with > 64% sand to depths of 75–90 cm where a diffuse layer of porous calcium carbonate occurs that affects, but does not restrict, soil water and root penetration to deeper depths.

Climate characteristics

Long-term climate. Mean annual precipitation (234 mm/yr; sd = 704 mm/yr) and average annual temperature (14.1 °C; sd = 0.7 °C) from 1931–1995 were obtained from a nearby weather station (Socorro, NM;

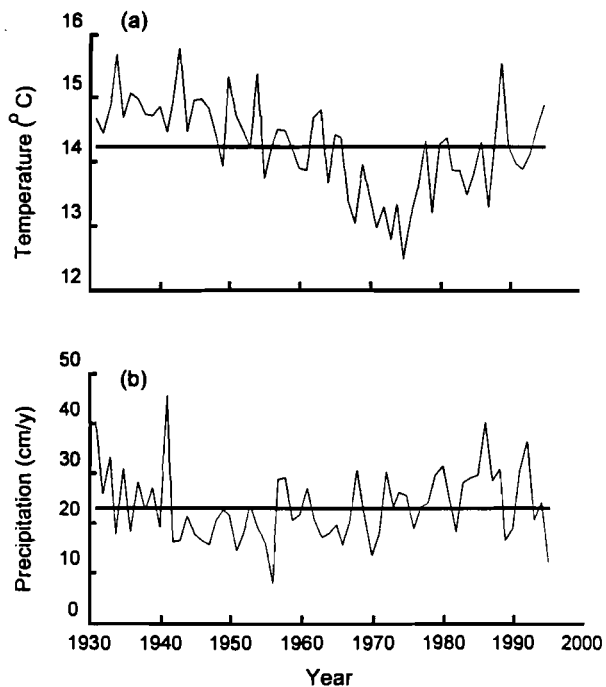


Fig. 1. Long term (1931–1995) climate data from Socorro, NM, USA.: (a) average annual temperature and (b) average annual precipitation.

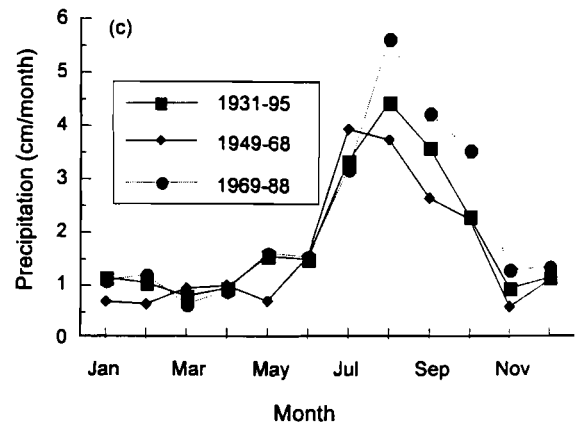
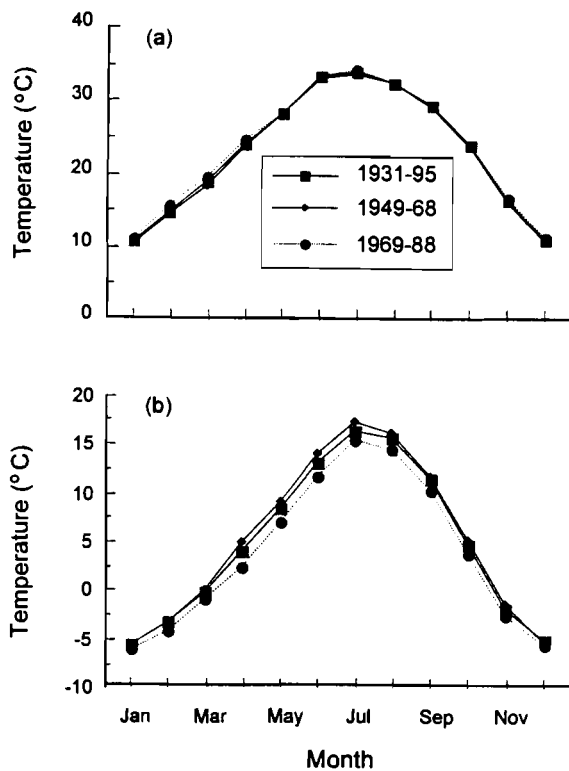


Fig. 2. Average monthly climate data for two time periods (1949-1968, 1969-1988) and the total (1931-1995): (a) maximum temperature; (b) minimum temperature; (c) precipitation.

34.1° N, 106.9° W) (Fig. 1). For the most part, temperatures were above-average until the mid-1960s, and precipitation was above-average until 1941 when a series of drought years extended until 1957 and again from 1961 through 1967. Temperatures have been average or below-average and precipitation has been above-average for most years since 1967.

Inter-decadal climate. The long-term climate data were grouped in two ways to represent variation in climate at inter-decadal scales. First, two 20-yr time periods (1949-1968, 1969-1988) differing in amounts of precipitation and, in particular, temperature were distinguished (Fig. 1). On average, the first period was warm (mean = 14.3 °C) and dry (mean = 203 mm/yr) whereas the second period was cool (mean = 13.6 °C) and wet (mean = 256 mm/yr). Average monthly maximum temperatures were similar for both time periods and for the long-term average (Fig. 2a). By contrast, average monthly minimum temperatures were higher (Fig. 2b), and early (May) and late growing season precipitation amounts (August, September) were lower from 1949–1968 compared to 1969-1988 (Fig. 2c). Both time periods contain El Niño and La Niña events as well as drought, although the two time periods differed in the frequency and intensity of ENSO events that increased starting in 1976 with an anomalous warming of the Pacific Ocean mean)

as El Niño (Molles & Dahm 1990). Years with large positive SOI (≥ 1.0) were defined as La Niña; the remaining years were considered 'other'. El Niño years were characterized by above-average precipitation in the winter and spring whereas La Niña years had below-average precipitation during the same time period (Table 1). Growing season precipitation was unaffected by the ENSO phenomenon, and total annual precipitation was highest in El Niño years.

Intra-annual climate. Highest average monthly temperatures occurred in July (24.7 °C) with lowest mean monthly minimum temperatures in January (2.5 °C). Monthly precipitation is bi-modal with large amounts occurring during the monsoons from July through October, and a small, unreliable peak in April or May. The largest coefficient of variation in average monthly temperature during the growing season occurred in April (Fig. 3). Year-to-year precipitation is least variable from July

Table 1. Average precipitation for three types of years based on ENSO for three time periods from 1932 to 1995¹.

ENSO class	Annual (mm)	Winter-spring (mm) ² (October 1–May 31)	Growing season (mm) (June 1–September 31)
El Niño (n = 13)	296 ^a	155 ^a	141 ^a
La Niña (n = 8)	213 ^b	53 ^c	160 ^a
Other (n = 43)	197 ^b	88 ^b	129 ^a

¹ENSO classes were defined based upon a five-month running mean of the southern oscillation index (SOI) beginning in October 1 of the previous year and continuing until September 31 of the current year.

²Significant differences between classes determined using ANOVA ($P < 0.05$).

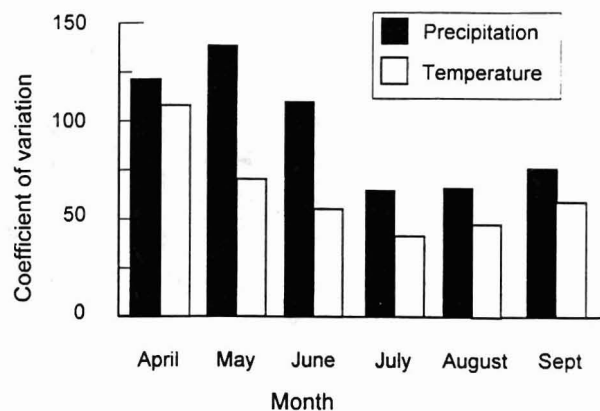


Fig. 3. Coefficient of variation for temperature and precipitation among years (1931-1995) by month for the April through September growing season.

through September with highest variation in April, May, and June (Fig. 3).

Simulation model description

A daily timestep, multi-layer model (SOILWAT) was used to simulate soil water dynamics (Parton 1978; Sala et al. 1992). Processes simulated in SOILWAT include the interception, evaporation, transpiration, and infiltration of water through the plant canopy and soil layers through time. Input parameters include daily temperature and precipitation, and monthly wind speed, relative humidity, and cloud cover. Monthly estimates of above-ground biomass (live and standing dead) and litter are needed to simulate interception and evaporation. Soil texture (% sand, silt, and clay), % rocks by volume, and root distributions by depth are needed for evaporation, transpiration, and infiltration. Losses of water to deep drainage are possible but occur infrequently in upland arid environments.

Model structure, parameterization, and validation have been described in detail for predicting seed germination and seedling establishment events of *B. gracilis* in the northern shortgrass steppe and of both *Bouteloua* species in the shortgrass steppe-Chihuahuan desert region (Lauenroth et al. 1994; Minnick & Coffin 1999). Because the previous use of the model for *B. gracilis* and *B. eriopoda* included a large number of sites along a climatic gradient, a number of generalizations were made in the parameterization that limit its applicability to simulating any one site. Parameters were either held constant among sites (soil texture and root distribution by depth) or were estimated using general equations (above-ground biomass, litter) (Minnick & Coffin 1999). Consistency among sites in climate was obtained using 30 yr of daily weather data. Percentage of

the soil containing rocks also was not included previously, but is important in soil water dynamics of desert grasslands. Thus, in order to predict effects of temporal variation on seedling establishment at the SNWR, it was necessary to collect site-specific data for these parameters. For other parameters, such as those associated with germination and establishment requirements, the same values were used as in the previous study since they were obtained from numerous studies located throughout the gradient. The same monthly weather data were also used as in the previous study since they were obtained from long-term estimates based on climate maps (National Oceanic and Atmospheric Administration 1983).

Site parameters. 65 years of daily historical weather data for air temperature and precipitation were used as input to the model (Fig. 1). Because seeds and seedlings respond to soil temperature, regression equations were used to calculate soil temperature at 5 cm depth from air temperature (Minnick & Coffin 1999). Vegetation and soil parameters were based upon samples collected from mixed stands of *B. gracilis* and *B. eriopoda* at the SNWR. Mixed stands were used to isolate the importance of differences in germination and establishment parameters to species responses rather than differences in stand-specific environmental conditions. In all cases, collection of samples was associated with individual plants of each species, and then averaged to represent a mixed stand.

Maximum above-ground biomass (147.5 g/m²) and litter (80 g/m²) were obtained by clipping 45 plants each of *B. gracilis* and *B. eriopoda* at the SNWR at the time of peak growth in 1996 (D.P.C. Peters submitted). Monthly estimates of these parameters were based upon an extended growing season of March through October with most growth occurring from June through September. For belowground measures, a soil depth structure was selected to correspond to rooting distributions and soil characteristics representative of mixed *B. gracilis*-*B. eriopoda* stands at this site (Table 2). Root biomass by depth was obtained for each species using soil pits (Hochstrasser & Coffin 1997), and then averaged across species for each depth. Soil samples were collected at each depth for texture analyses using the hydrometer method (Day 1965). Soil cores (7.5 cm-diameter) collected at two depths where rocks are most prevalent (0 - 5, 5 - 10 cm) were used to determine the volume of soil where water is potentially unavailable to plants due to the presence of rocks. Volume of rocks was estimated for lower layers based upon extrapolation and field observations. Field capacity (-0.03 MPa) and wilting point (-1.5 MPa) were calculated for each depth using standard regression equations based upon the

Table 2. Soil parameters used in the simulations.

Depth (cm)	Soil texture ¹				Root ³ biomass (%)
	Sand (%)	Silt (%)	Clay (%)	Rocks ² (%)	
0–5	87.6	4.1	8.3	1.45	20
5–15	82.7	6.7	10.6	1.84	56
15–30	70.1	16.8	21.2	1.50	12
30–45	64.8	12.9	22.3	1.50	5
45–60	64.6	10.9	24.5	1.50	4
60–75	65.1	9.2	25.7	1.50	2
75–90	65.1	9.2	25.7	1.50	1

¹Sand, silt, and clay are percentages of total soil particle size;

²Rock volume as percentage of soil volume;

³Hochstrasser & Coffin (1997); biomass is relative to the total across depths.

particle size distribution and adjusted for the percentage of soil volume occupied by rocks (Cosby et al. 1984).

Germination and establishment. Both seed germination and seedling establishment require sufficient amounts of water at appropriate depths in the soil profile and at appropriate times during the year. The most important differences between species are their temperatures and soil water requirements (Lauenroth et al. 1994; Minnick & Coffin 1999). *B. gracilis* has lower daily minimum (15 °C) and maximum (35 °C) temperature constraints compared to *B. eriopoda* (20, 40° C). Minimum soil water potentials sufficient for germination and establishment are lower (more negative) and the number of days of wet soil required before initiation of adventitious roots are greater for *B. eriopoda* (– 1.0, 5) than *B. gracilis* (– 0.5, 3). A smaller range of days between germination and establishment for *B. eriopoda* (30 d) reflects its faster growth and development rates compared to *B. gracilis* (59 days).

Experimental simulations

Three sets of simulations were conducted. Separate simulations were conducted for each species in each year to account for differences in the criteria for germination and establishment. Because the focus of this study was constraints on establishment, seeds were assumed to be available for each species in all years. Only one recruitment event was allowed in each year. The first set of simulations analyzed the effects of intra-annual variation in climate on recruitment in order to determine if there was temporal separation in the timing of establishment events between species. This set involved running the model using historical weather data from 1931 through 1995 to determine the years in which simulated recruitment was successful. In each year, the

soil water content in each depth was simulated through time using the same climate, soils, and vegetation input parameters for each species. Julian day when germination or establishment occurred was compared between species to predict effects of seasonality on recruitment.

The second set of simulations predicted the effects of inter-decadal variation in climate on recruitment. Two scenarios were conducted. First, the model was run using generated weather characteristic of two time intervals (1949–1968, 1969–1988). Because the probability of establishment in any one year is small (< 0.2), few or no establishment events occur when the number of years is small (< 100). Thus, a first-order Markov weather generator was used to produce 5000 years of daily precipitation and temperature data with similar characteristics as the historical weather of each time interval (*sensu* Lauenroth et al. 1994). Five thousand years has been found to be sufficient to estimate and compare probabilities of seedling establishment for these two species under different climatic regimes (Minnick & Coffin 1999). A second scenario was used to determine if establishment by these two species is affected differently by climate in El Niño and La Niña years. The Markov weather generator was used to produce 5000 years of weather for each type of year as well as for the remaining years. For each scenario, the model was run for each species separately using the same sequence of generated weather data for each time interval or type of year. Model output included the number of successful germination and establishment events during each 5000 year run. The probability of successful establishment was calculated by dividing the number of events by 5000. Because the number of years identified as El Niño (13) and La Niña (8) are small relative to the minimum necessary for accurate weather generation using Markov

Table 3. Precipitation and temperature values used in the sensitivity analysis.

Scalar ¹	Average annual temperature (°C)	Annual precipitation (mm/yr)
1.4	na ²	328
1.3	na	304
1.2	na	281
1.1	15.5	258
1.05	14.8	na
1.0 ³	14.1	234
0.95	13.4	na
0.9	12.7	211
0.8	11.3	na
0.7	9.9	na

¹Scalar multiplier on daily precipitation amount. Scalar constant on daily temperature;

²na = not analysed;

³1.0 represents the long-term average.

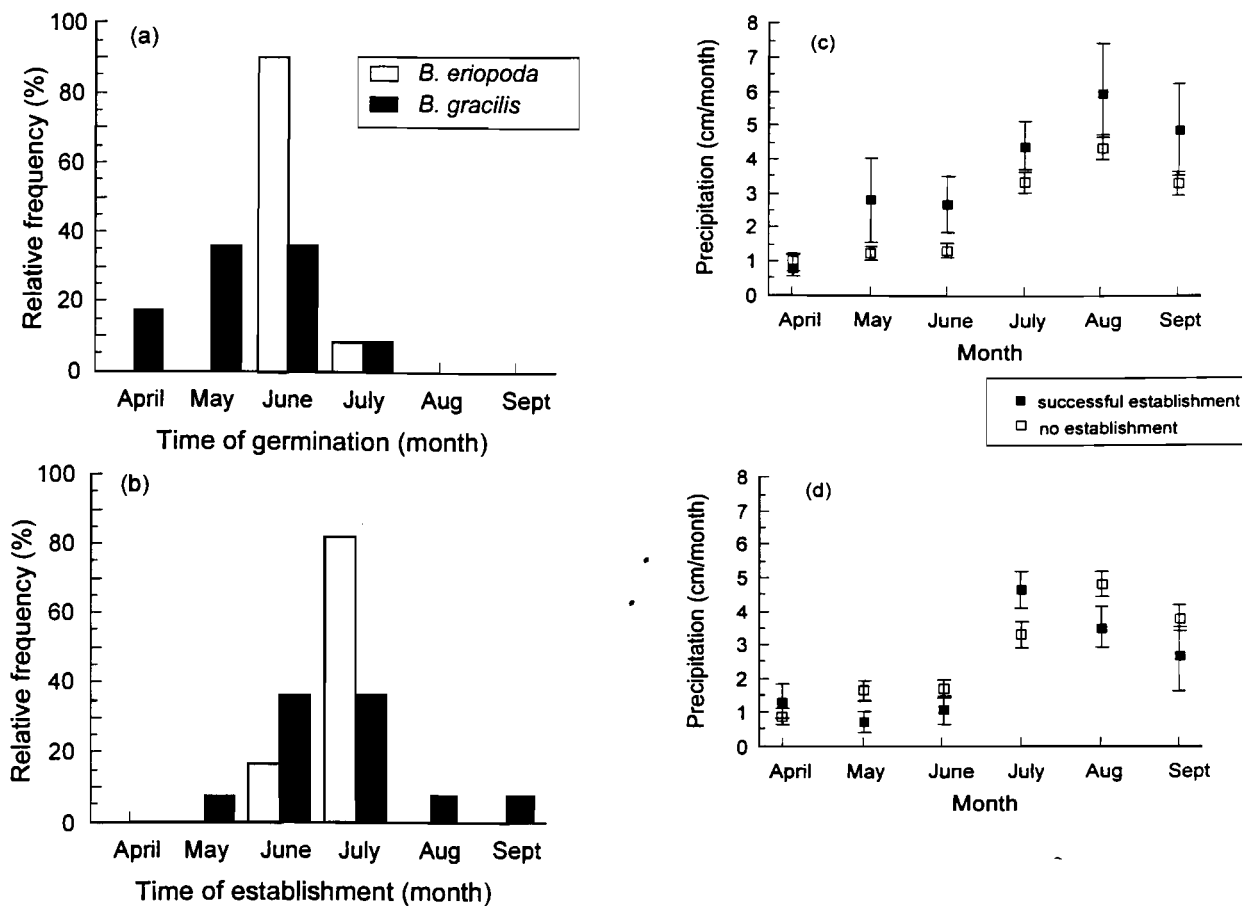


Fig. 4. Frequency of occurrence of events by month for *Bouteloua gracilis* and *B. eriopoda*: (a) germination events for years when establishment was successful and (b) establishment events. Average precipitation amount and standard error in each month for years when establishment was successful or unsuccessful for (c) *B. gracilis* and (d) *B. eriopoda*.

techniques (20; Osborn et al. 1982), the establishment results based upon these small numbers of years are appropriate only for comparison among types of years. The third set of simulations was conducted to determine the sensitivity of establishment to directional changes in climate. Although global circulation models (GCMs) agree in their predictions of altered climate as a result of elevated concentrations of CO_2 , they disagree in the amount and direction of that change (Kittel et al. 1995). Therefore, an alternative approach is to conduct a sensitivity analysis where temperature and/or precipitation are modified sequentially across a range of predicted values to determine the effects on plant processes.

An individual parameter perturbation analysis was used (Rose 1983) where the annual amount of one climatic variable (temperature or precipitation) was modified by a given percentage, and the other climatic variable was maintained at its long-term average. The percentage was applied uniformly to every day of the year, and ranged from -10 to $+40\%$ of the long-

term average for precipitation and from -30 to $+10\%$ for temperature (Table 3). Two additional percentages (-5 , $+5$) were used for temperature based upon the sensitivity of establishment to this factor. These ranges in percentages include those predicted by GCMs for central New Mexico, and represent the range in climate where *B. gracilis* and *B. eriopoda* currently dominate plant communities in the USA. Five thousand years of generated weather were used based upon historical weather, and modified each day by the appropriate percentage. The same weather sequence was used for each species and climatic regime for a total of 48 runs (six temperature values \times four precipitation values \times two species).

Results

Germination occurred later, on average, for *B. eriopoda* (June 14) compared to *B. gracilis* (June 3). The range of days over which germination occurred was broader for *B. gracilis* (April through July) with peaks in May and June (Fig. 4a). For *B. eriopoda*, germination was restricted to June and July with a peak in June. Establishment followed similar patterns as germination with most *B. gracilis* events occurring from May through September; most establishment events for *B. eriopoda* occurred in July (Fig. 4b).

Although these results reflect differences in temperature parameters between the two species, they are not predictable solely from the temperature responses due to interactions with soil properties and timing of precipitation. A comparison of years with successful germination and establishment to years without establishment indicates the importance of sufficient precipitation in May, June, and July for *B. gracilis* (Fig. 4c), and in July for *B. eriopoda* (Fig. 4d). Precipitation amounts in April, August, and September were not important for successful establishment by either species. Furthermore, growing season precipitation (June 1 - September 1) was larger for *B. eriopoda* in years without germination or establishment (136 mm) compared to years with successful establishment (119 mm); the reverse was found for *B. gracilis* where growing season precipitation was higher in successful (180 mm) compared to unsuccessful establishment years (124 mm).

For weather data generated from each of three time periods (1931-1995, 1949-1968, 1969-1988), the simulated probability of establishment was larger for *B. eriopoda* than *B. gracilis* (Fig. 5a). Differences in establishment by the two species were found between the mid- and late-century parts of the record. Establishment probabilities for *B. gracilis* were largest later in the century and establishment probabilities for *B. eriopoda* were larger earlier in the century.

Larger probabilities of establishment were found for *B. gracilis* in El Niño and La Niña years compared to probabilities for *B. eriopoda* (Fig. 5b). The pattern for the remaining years was similar to the long-term average where *B. eriopoda* had larger probabilities. These results for *B. gracilis* in La Niña years likely reflect the large amounts of precipitation in June and July (mean = 67 mm), the months where precipitation was most important to establishment of this species (Fig. 4). Larger probabilities of establishment for *B. gracilis* than *B. eriopoda* in El Niño years (Fig. 5b) likely reflect the cool temperatures (mean = 20.8 °C) and large amounts of precipitation in May and June (34 mm). Low amounts of precipitation in July (mean = 36

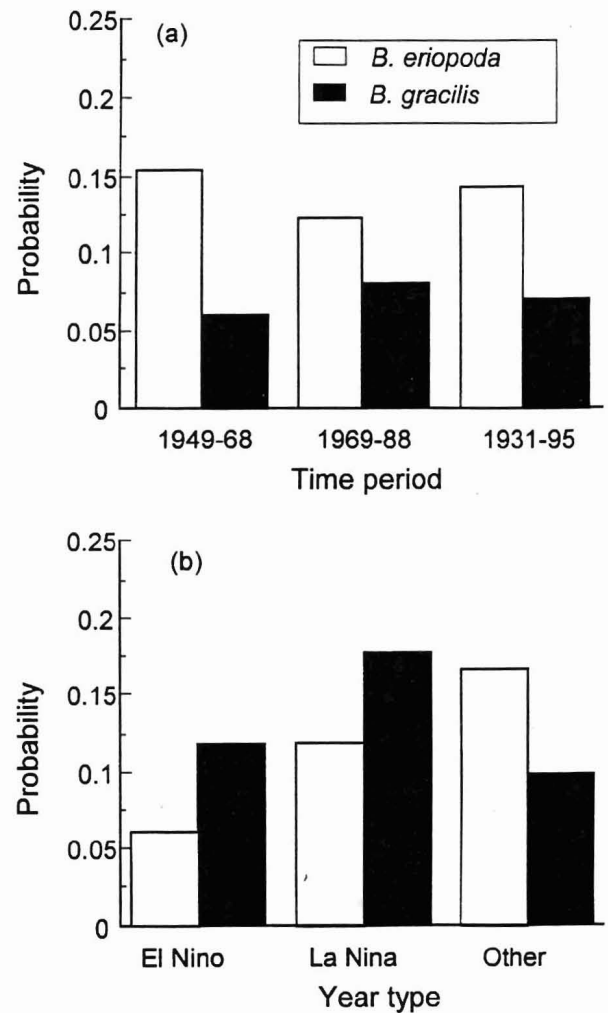


Fig. 5. Simulated probability of establishment for *Bouteloua gracilis* and *B. eriopoda* using weather generated from (a) one of three time periods (1949-1968, 1969-1988, 1931-1995) and from (b) one of three types of years (El Niño, La Niña, Other).

mm/month) in El Niño years would adversely affect both species compared to conditions in La Niña years (50 mm/month) where probabilities were larger.

The probability of establishment of *B. gracilis* was linearly related to annual precipitation in the current year for each value of mean annual temperature (Fig. 6a). However, the rate of change in establishment probability increased as mean annual temperature (MAT) decreased. By contrast, establishment of *B. eriopoda* was not related to precipitation when MAT was low (≤ 12.7 °C) (Fig. 6b). Largest probabilities for *B. gracilis* occurred at coolest temperatures whereas the reverse was found for *B. eriopoda*.

Establishment of *B. gracilis* was most sensitive to temperature when precipitation was high (≥ 281 mm/yr;

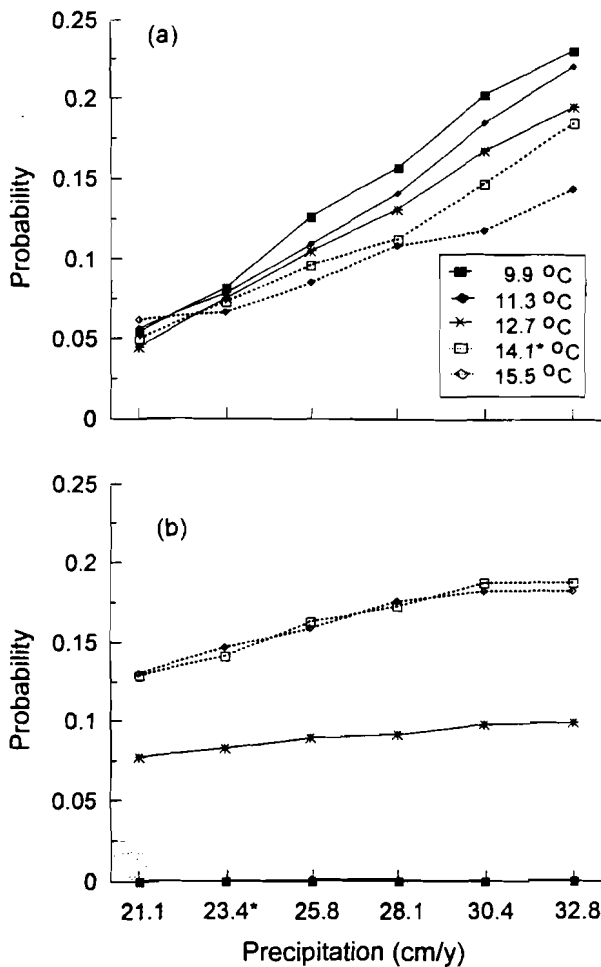


Fig. 6. Simulated probability of establishment using weather generated by adjusting values of precipitation (x-axis) and temperature (shown by different curves) for (a) *Bouteloua gracilis* and (b) *B. eriopoda*. 14.1 °C* and 234 mm/yr* are long-term mean temperature and precipitation, respectively.

Fig. 7a); slopes of the regressions were not significantly different from 0 for lower amounts of precipitation. Probabilities of establishment for this species decreased as temperature increased. By contrast, establishment of *B. eriopoda* was non-linearly related to temperature for all precipitation amounts and approached an asymptote between 13.4 and 14.1 °C (Fig. 7b). The greatest response to temperature occurred between 11.3 and 13.4 °C; these temperatures are commonly found near the northern limit of the geographic distribution of *B. eriopoda* in northern New Mexico and southern Colorado (Stubbenieck et al. 1992).

Response of establishment probabilities by the two species relative to each other to directional changes in temperature and precipitation depended on interactions between these climatic factors. Establishment

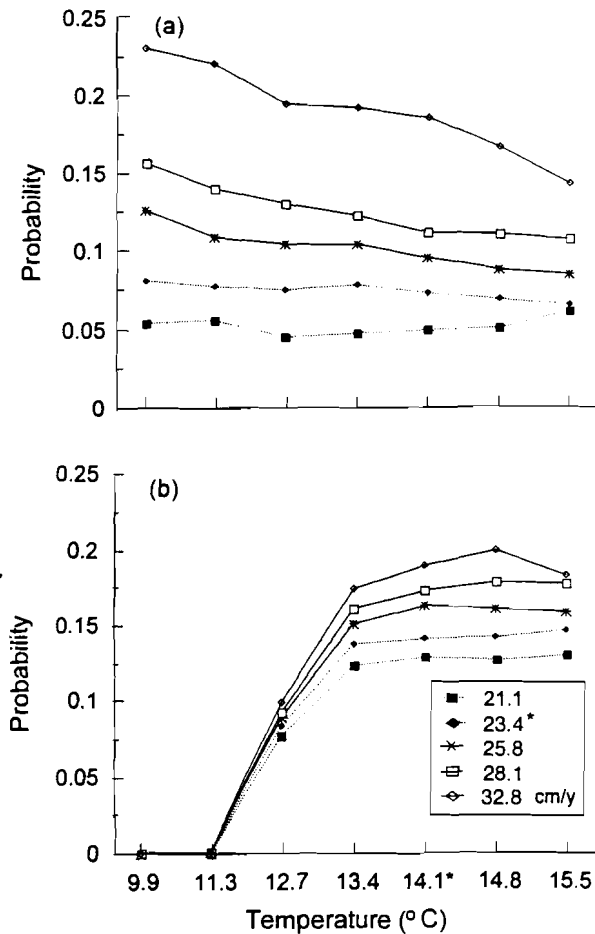


Fig. 7. Simulated probability of establishment using weather generated by adjusting temperature (x-axis) and precipitation (shown by different curves) for (a) *Bouteloua gracilis* and (b) *B. eriopoda*. 14.1 °C* and 234 mm/yr* are long-term mean temperature and precipitation, respectively.

probabilities of *B. gracilis* were higher than *B. eriopoda* for cool temperatures (< 13.4 °C) for all values of precipitation; the reverse was found for warmer temperatures (Fig. 8). For each value of temperature, probabilities increased for both species with increased amounts of precipitation with the exception of *B. eriopoda* below 12.7 °C; no establishment events occurred for this species at low temperatures. The temperature at which the probability of establishment is equal for both species decreased as the precipitation decreased.

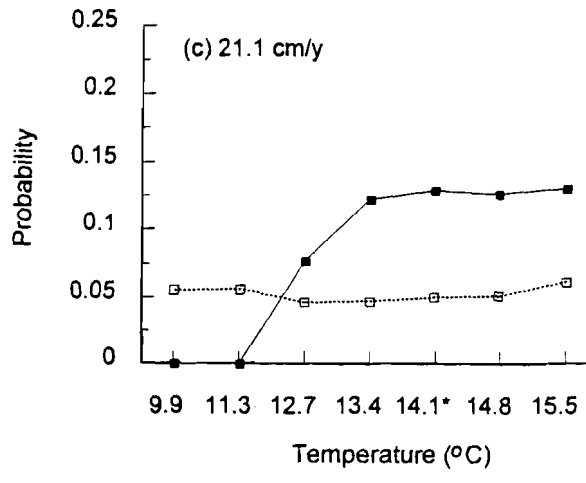
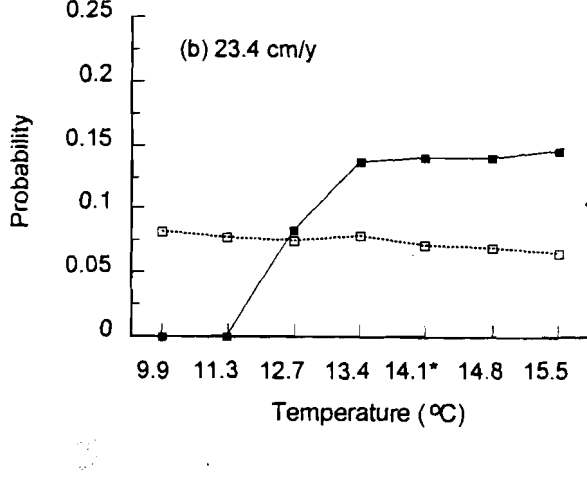
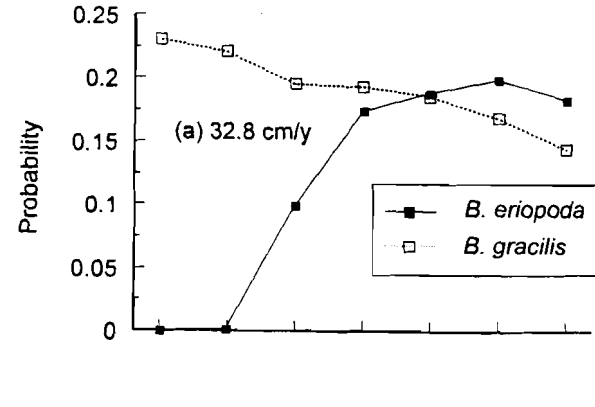


Fig. 8. Simulated probabilities of establishment of *Bouteloua gracilis* and *B. eriopoda* for multiple increments in temperature where 14.1 °C* denotes the long-term average and (a) 10% decrease in precipitation, (b) long-term average precipitation, and (c) 20% decrease in precipitation from the long term mean.

Discussion

Differences in responses by seeds and seedlings of two C_4 perennial grasses to temperature and precipitation resulted in species-specific patterns of simulated recruitment within years, between years, and over sequences of years as climate varied across multiple temporal scales. Recruitment, in particular seedling establishment, has been found to be an important constraint on population and community dynamics for a number of growth forms, including grasses, herbs, and trees (Defossé et al. 1997; Peltier et al. 1997; Tsuyuzaki et al. 1997; Clark et al. 1998). At ecotones, the balance between small-scale recruitment and large-scale mortality events drives much of the variation between different growth forms (Slatyer & Noble 1992; Archer 1994). Results from the current study suggest that differences in recruitment patterns between species of the same growth form may be important to current species distributions and to observed changes in dominance at transition zones between plant communities as climate varies through time. Other factors, including competition for resources, seed production, dispersal, rate of vegetative spread, and differential mortality are also expected to be important to dominance patterns.

Extensive experimentation of both species at the same site is needed to test the regeneration hypothesis relative to the importance of other factors.

Establishment and periodic fluctuations in climate

Overlap in geographic distributions of *B. gracilis* and *B. eriopoda* in central New Mexico results in a mosaic of pure and mixed species patches of variable size and species composition across the landscape (Gosz & Gosz 1996). Processes that determine patch structure based upon dominance by one or both of the *Bouteloua* species are not well-understood, and patterns in dominance are only partially explained by soil properties (J. R. Gosz pers. comm.). Current results suggest that different strategies of recruitment by *B. gracilis* and *B. eriopoda* are one factor that may account for observed patterns in species dominance in response to disturbances (Fields et al. 1999).

Temporal partitioning in soil water resources available to seedlings results from different establishment periods by *B. gracilis* (May through September) compared to *B. eriopoda* (July). The broad temporal distribution for *B. gracilis* is critical to its persistence since precipitation and temperature are most variable

from year-to-year during the months when precipitation is most critical to germination and establishment (May and June). By contrast, establishment by *B. eriopoda* occurs during the most reliable month of precipitation (July). The importance of summer precipitation to *B. eriopoda* establishment was also found using a long-term data set collected from a site in the southern part of the Chihuahuan desert (Neilson 1986). Temporal partitioning in soil water resources needed for plant growth has also been found for these species, and contributes to their ability to coexist at this site (Coffin 1997). Partitioning of resources in time and/or space has been documented in few cases for transition zones between geographic distributions (Neilson & Wullstein 1983).

Results from this study suggest that observed changes in species dominance patterns over multiple years may be explained, at least in part, by regeneration constraints interacting with interdecadal variation in climate. Conditions from 1949 through 1968 are predicted to have been more favorable for *B. eriopoda* establishment compared to cooler, wetter conditions from 1969 through 1988 that favored *B. gracilis*. Long-term data on establishment or dominance patterns for these species do not exist to test this hypothesis generated by the model. However, short-term data support the trend since cover of *B. gracilis* at this site increased from the warm, dry conditions in 1989 to the wet, cool conditions of 1991-1993 (Gosz & Gosz 1996). No directional trends were observed in *B. eriopoda* during this time. Furthermore, these results provide support for the contention that transition zones exist in time as well as space (Neilson 1993), and generate the hypothesis that species-specific responses to periodic fluctuations in climatic extremes can contribute to shifts in dominance patterns through time.

Establishment and directional changes in climate

Based upon results from the sensitivity analysis and species-specific responses of establishment, an increase in average annual temperature as a result of elevated concentrations of atmospheric CO₂ would have little effect on establishment probabilities of the two species relative to each other regardless of the change in precipitation. Increases in precipitation that coincide with increases in temperature would result in proportionally higher probabilities of both species. By contrast, a decrease in annual temperature is expected to result in large changes in seedling establishment. At temperatures < 13 °C, *B. eriopoda* seedlings were unable to establish, yet *B. gracilis* establishment increased as temperature decreased. These results suggest that a decrease in temperature would result in a shift in dominance to *B. gracilis* as the effects of disturbances and plant mortality accumulate

through time and eliminate *B. eriopoda* plants. Although most Global Circulation Models (GCMs) predict an increase in average temperatures globally of 1 - 3 °C (Kittel et al. 1995), not all regions are expected to experience the same magnitude of change, and the slow ramping of temperature may be obscured by natural variation in climate that causes warming and cooling cycles on annual to decadal time scales (Kerr 1998).

Because species are often at their physiological limits in distribution boundary zones, these transition zones have been predicted to be sensitive areas to directional changes in climate and may be used as early indicators of global climate change (Solomon 1986; di Castri et al. 1988). However, recent evidence suggests limits on the conditions under which this sensitivity may occur (Noble 1993). Current analyses indicate that complex interactions among establishment constraints, soil water availability, and temperature may result in changes in patterns of recruitment and species dominance at an ecotone that are not predictable based only on species responses to precipitation and temperature. Simulation modeling provides an opportunity to predict the consequences of these interactions to establishment success.

An aspect of global climate change that was not explicitly considered in this analysis was changes in the frequency, intensity, and duration of interdecadal climatic fluctuations, such as the ENSO phenomenon (Karl 1988). Because the establishment probability of *B. gracilis* was largest in La Niña years, and the probability for *B. eriopoda* was smallest in El Niño years, it is predicted that an increase in the frequency of the cycle of El Niño-La Niña events will favor *B. gracilis* establishment. Other processes, such as seed production and plant growth, may also be affected differently by these types of years.

Patterns in species dominance are affected by a number of processes, including the establishment of seedlings. Current results indicate that temporal partitioning of soil water by seedlings may be important to coexistence of two congeneric *Bouteloua* species. Establishment responses to interdecadal variation in climate may be important to observed changes in cover by these species through time. Long-term directional changes in climate are predicted to alter patterns in establishment only if mean annual temperatures decrease.

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