Plant species dominance at a grassland–shrubland ecotone: an individual-based gap dynamics model of herbaceous and woody species

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Abstract

Transition zones or ecotones between biomes are predicted to be particularly sensitive areas to directional changes in climate. However, for many ecotones, there is little understanding of the key processes that allow dominant species from adjacent biomes to coexist at transition zones and how differences in these processes affect species responses to changes in environmental conditions. The objective of this study was to examine the relationship between plant life history traits and patterns in dominance and composition at a grassland–shrubland transition zone in order to predict shifts in dominance with directional changes in climate. It was hypothesized that differences in life history traits allow species from adjacent biomes to coexist at this transition zone, and that these dominance patterns are dynamic through time as a result of species-specific responses to changes in climate. A mixed lifeform individual plant-based gap dynamics model (ECOTONE) was developed to examine consequences of differences in recruitment, resource acquisition, and mortality to patterns in species dominance and composition under a variety of soils and climatic conditions. This model is unique because it represents interactions among multiple potential dominant species that include congeneric species of one lifeform as well as herbaceous and woody lifeforms across multiple spatial scales. Similar to other gap models, ECOTONE simulates the recruitment, growth, and mortality of individual plants on a small plot through time at an annual timestep. ECOTONE differs from other gap models in the degree of detail involved in determining successful recruitment by each species and in the simulation of belowground resources. Individual plant root distributions and resource availability by depth are dynamic. Soil water content is simulated on a daily timestep and nitrogen is simulated monthly. Multiple spatial scales can be simulated using a grid of plots connected by seed dispersal. ECOTONE was parameterized for two soil types at the Sevilleta National Wildlife Refuge (SEV), a site located within the transition zone between two major biomes in North America. Shortgrass steppe communities are dominated by the perennial grass *Bouteloua gracilis* (blue grama) and Chihuahuan desert communities are dominated by the perennial grass *Bouteloua eriopoda* (black grama) or the shrub *Larrea tridentata* (creosotebush). Experiments were conducted to provide key parameters related to recruitment and growth that were supplemented with information from the literature for remaining parameters. Model output was verified using field

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estimates of cover and biomass for the three dominant species as well as other groups of species. Simulation analyses were conducted under current climate and for a directional change in climate. Nitrogen was assumed constant for all runs to allow a focus on water availability constraints as affected by climate. Under current climatic conditions, simulated biomass on sandy loam soils was dominated by *B. eriopoda* with smaller biomass of *B. gracilis* and other species groups. By contrast, simulated biomass on a loamy sand soil was codominated by *B. eriopoda* and *L. tridentata* with very small biomass attributed to other species groups. Under a GFDL climate change scenario of increased year-round temperatures and increased summer precipitation, vegetation patterns shifted to a clear dominance of biomass by *B. eriopoda* on both soil types. These results show that temporal partitioning of soil water is important to codominance by the two *Bouteloua* species, and that spatial and temporal partitioning of soil water is important for grass–shrub interactions. The results also suggest that global climate change may provide a mechanism for the recovery of *B. eriopoda* following shrub invasion in the Southwestern U.S. Thus, an individual-based modeling approach is capable of representing complex interactions among herbaceous and woody species as well as between congeneric species with different life history traits at a biome transition zone. This modeling approach is useful in improving our understanding of key processes driving these vegetation dynamics as well in predicting shifts in dominance as environmental conditions change in the future. © 2002 Published by Elsevier Science B.V.

1. Introduction

Biome transition zones, or ecotones between ecosystem types, are areas where dramatic changes in vegetation occur over short distances (Risser, 1995). These vegetation patterns in space are also dynamic through time as the climate fluctuates and plants respond to their changing environment (Neilson, 1991; Noble 1993). Temporal or spatial shifts in ecosystem types at biome transition zones are often characterized by changes in the dominant species or lifeform (Gosz and Sharpe, 1989) that may be accompanied by changes in other ecosystem properties, such as species composition and distribution of soil nutrients (Kröel-Dulay et al., submitted; Kieft et al., 1998). Although vegetation patterns at ecotones have been documented, there is little understanding of the key processes or life history traits involved in driving these dynamics and in allowing coexistence of species from different, yet adjacent biomes. The goal of this study was to examine relationships between plant life history traits and patterns in dominance and composition at a grassland–shrubland transition zone. A mixed lifeform individual plant-based gap dynamics model was developed to predict the consequences of differences in recruitment, competition, and mortality to patterns in species dominance and composition under a variety of soils and climatic conditions.

Ecotones are hierarchical with different environmental constraints operating at different spatial scales (Gosz, 1992, 1993). Large-scale climatic patterns determine geographic distributions of species and ecosystem types (Woodward, 1987; Neilson, 1993). At the landscape scale, the transition zone consists of a mosaic of patches dominated by one or more species (Neilson, 1991; Gosz, 1992, 1993). Patterns in soils and disturbance can have important influences on this mosaic of patches (Neilson, 1991; Brown, 1994; Gosz and Gosz, 1996; Breck and Jenkins, 1997; Fields et al., 1999). Within each patch, species dominance or codominance is determined by interactions between individual plants and the suite of environmental conditions that characterize the patch. These plant-level interactions are influenced by life history traits associated with recruitment, competition, and mortality. Although most studies at ecotones have focused on recruitment and mortality, competition is also expected to be important. In particular, the partitioning of resources, either through time or space, that allows coexistence within biomes (Fitter, 1982, 1986) may provide another mechanism for coexistence of dominant species from different biomes at the transition zone.

In central New Mexico, USA, several biomes meet to form transition zones consisting of dominance by one of two C_4 perennial grass species

(*Bouteloua gracilis* [H.B.K. Lag.] ex Griffiths, *Bouteloua eriopoda* [Torr.] Torr.) and a C_3 shrub (*Larrea tridentata* [DC.] Coville). Shortgrass steppe ecosystems located along the eastern slope of the Rocky Mountains are dominated by the long-lived bunchgrass, *B. gracilis* (blue grama). Chihuahuan desert grasslands located in central and southern New Mexico were historically dominated by the short-lived stoloniferous grass, *B. eriopoda*. A number of shrub species have invaded these grasslands, including the long-lived evergreen, *L. tridentata* (creosotebush), with large-scale shifts in dominance from grasses to shrubs over the past 50–100 years (Buffington and Herbel, 1965). Management of these ecosystems is very different depending on which of these three species dominates. Although, both *Bouteloua* species are important forage for cattle, *B. gracilis* is tolerant of heavy grazing whereas *B. eriopoda* tolerates light to moderate grazing, and suffers high mortality under heavy grazing pressure (Nelson, 1934; Lauenroth and Milchunas, 1992). Shrub-dominated ecosystems provide little forage for cattle, and are typically managed to minimize soil erosion. Thus, understanding factors that shift dominance from one species to another through time is critical to our ability to manage these ecosystems effectively.

Although research has been conducted on each of these dominant species within their respective biomes, little is known about controls on dominance at the shortgrass steppe/Chihuahuan desert transition zone. The landscape at this ecotone consists of patches dominated by combinations of *B. gracilis* and *B. eriopoda* on sandy loam soils and patches containing combinations of *B. eriopoda* and *L. tridentata* on loamy sand soils. Differences between soil types that account for dominance patterns are unknown, although effects of soil water availability on recruitment and growth are expected to be particularly important in these dry ecosystems. Previous studies of recruitment between the two *Bouteloua* species suggest that differences in seedling establishment success due to soil type may be important to dominance (Peters, 2000a); little is known about controls on recruitment by *L. tridentata*. Because all three species are good competitors within their

respective biomes, their coexistence at the transition zone may be facilitated by a partitioning of soil water, either through time or space. Observations suggest temporal partitioning of resources since *B. gracilis* begins growth under cooler temperatures than *B. eriopoda*, although both are C_4 species. Spatial partitioning of soil water based on root distributions has also been documented between grasses and shrubs within biomes of these species (Lee and Lauenroth, 1998; Gibbens and Lenz, 2001). However, these differences in recruitment and acquisition of soil water have not been studied experimentally for co-occurring plants of different species at this semiarid–arid transition zone. Furthermore, the consequences of these differences in life history traits to long-term patterns in species dominance have not been examined.

There were three specific objectives for this study: (1) to develop and parameterize an individual-based model of herbaceous and woody species at biome transition zones; (2) to use the simulation model to examine long-term consequences of differences in life history traits to patterns in dominance and composition under current climatic conditions at a semiarid–arid ecotone; and (3) to predict shifts in dominance under directional changes in climate that modify patterns in soil water availability.

Combining short-term experiments with simulation models provides a powerful approach to examine the long-term consequences of differences in life history traits to species dominance (Coffin et al., 1998). One particular type of model, the individual-based gap dynamics model, explicitly includes recruitment, competition, and mortality processes among individual plants for a range of current and future environmental conditions (Smith and Huston, 1989; Shugart et al., 1992). Thus, gap models are well-suited to addressing vegetation dynamics at ecotones, although they have not been used in this way previously. Most applications have focused on forests (Shugart, 1984, 1998; Urban and Shugart, 1992; Botkin, 1993) with few exceptions, including a grassland model (STEPPE; Coffin and Lauenroth, 1990) and a shrubland model (Higgins et al., 1996; Higgins and Richardson, 1998). The ap-

proach used in this study was to develop an individual-based model of herbaceous and woody species that accounts for differences in life history traits among species. Experiments were conducted to parameterize the model for processes (recruitment, growth) expected to be particularly important to dominance by three species at a biome transition zone. The model was then used to examine long-term species dynamics under variable soil and climatic conditions at a biome transition zone.

2. Site description

The model was parameterized and tested for grasslands and shrublands at the Sevilleta National Wildlife Refuge (SEV; 34.5° N, 106.9° W, 1650 m ASL) located approximately 75 km south of Albuquerque, New Mexico, USA. The SEV 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 supported by the National Science Foundation. Grazing by cattle has been excluded since 1973, although grazing by native herbivores, such as pronghorn antelope and rabbits, occurs at low to moderate intensities. Climate is semiarid to arid with high temporal and spatial variability. Long-term (1916–1995) mean annual precipitation was 23.2 cm per year (SD = 79) and annual temperature averaged 13.6 °C (SD = 0.7 °C). Over half of the annual precipitation typically occurs from July 1 to October 1.

The location selected for study was the McKenzie Flats where vegetation is typical of the Chihuahuan desert/shortgrass steppe transition zone. Patches of variable size (< 10 m^2 to > 1000 m^2) and shape are clearly distinguished based upon their dominance or codominance by *B. gracilis*, *B. eriopoda*, or *L. tridentata* at this location (Gosz, 1995; Gosz and Gosz, 1996; Kröel-Dulay et al. submitted). Other species of C$_3$ and C$_4$ annual and perennial grasses and forbs, cactus, and subshrubs can be found in patches dominated or codominated by one of these three species (Peters, 2000b; Hochstrasser et

al., in press). Complete site description is available at http://www.sevilleta.unm.edu.

3. Simulation model description

An individual-based, gap dynamics simulation model (ECOTONE) was developed to simulate vegetation dynamics at transition zones between communities dominated by herbaceous and woody species. Similar to gap dynamics models of forests and grasslands (JABOWA, Botkin 1993; FORET, Shugart, 1984; STEPPE, Coffin and Lauenroth, 1990, 1994), ECOTONE simulates the recruitment, growth, and mortality of each plant on a small plot at an annual time step (Fig. 1). Recruitment and mortality have stochastic elements whereas growth is deterministic and based upon competition for resources. Recruitment is more complicated than in other gap models since a number of processes are included (seed production, germination and establishment of seedlings) as well as the dispersal of seeds both within- and among-plots. Mortality occurs as a result of limiting resources and longevity constraints as well as disturbances. Individual species are typically simulated that represent the life history characteristics of a similar group of species at a site.

Growth is determined by competition for soil water and nitrogen since these resources most frequently limit plant growth and community structure in arid and semiarid communities (Noy-Meir, 1973; Lauenroth et al., 1978); competition for light is not currently included. ECOTONE is also more complicated than other gap models in the simulation of these belowground resources. ECOTONE contains a daily time step, multi-layer soil water model (SOILWAT; Parton, 1978; Sala et al., 1992) and a monthly time step nutrient cycling model (CENTURY; Parton et al., 1988) as sub-modules. Resources are simulated by layers that represent depths in the soil profile. Thus, seasonal variation in the depth distribution of belowground resources has effects on and is affected by plant growth and root biomass. Climate and soil texture are the driving variables that affect soil water availability.

ECOTONE can either be run as a set of independent plots or as a grid of spatially-interactive plots. Independent plots are simulated using the same weather in each year to represent a landscape, but without connections among plots. A spatially-interactive grid of plots can be used to allow movement of materials among plots, such as the dispersal of seeds.

3.1. Plot size

A key feature of gap dynamics models is plot size, which is based on the resource space associated with a full-size plant of the dominant species (Shugart and West, 1980; Smith and Urban, 1988). Because plant sizes were unknown at this transition zone, an analysis of plant size distributions was conducted for each of the three dominant species at the SEV (*B. gracilis*, *B. eriopoda*, *L. tridentata*) in order to estimate plot size. For the two grass species, basal area (cm^2) was estimated for each plant in five ($n = 829$ plants; *B. gracilis*) or ten ($n = 721$ plants; *B. eriopoda*) 3×4 m^2 plots. Basal area was estimated by measuring the longest diameter and the diameter perpendicular to it, and assuming an ellipsoid shape. For
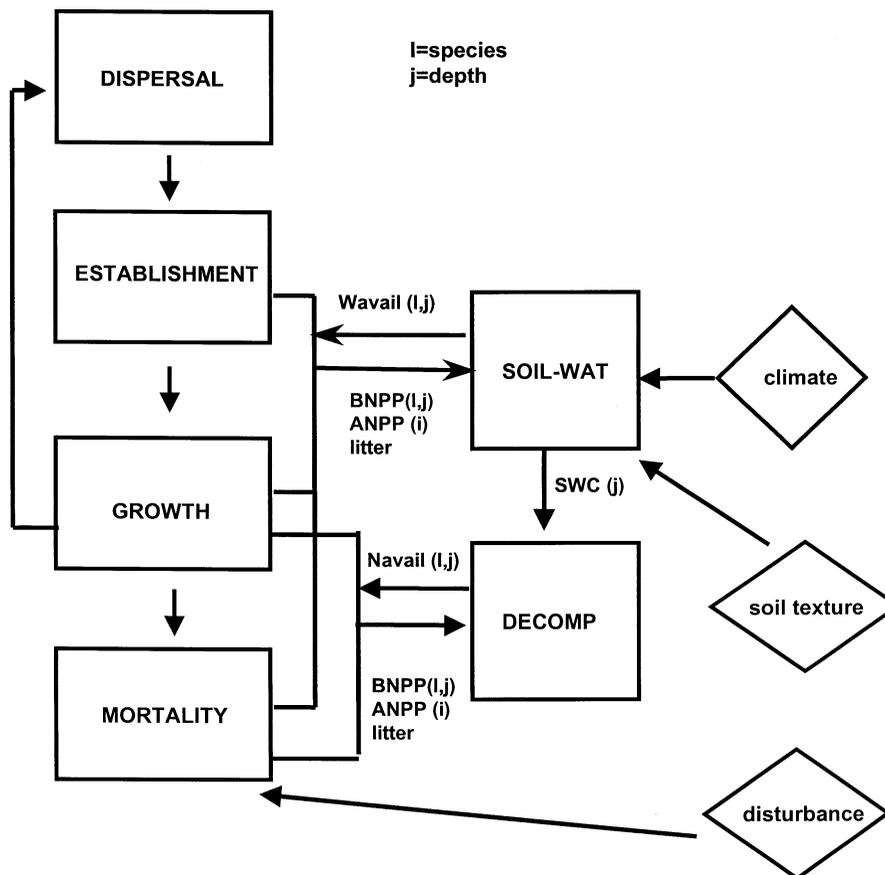

Fig. 1. ECOTONE individual plant-based gap dynamics model of arid and semiarid grasslands and shrublands. Major plant processes include seed dispersal, seedling establishment, growth, and mortality. Three driving variables (climate, soil texture, disturbance) influence soil and plant processes. Two sub-modules of soil water and nitrogen dynamics allow feedbacks between vegetation and soil processes. (Wavail = plant available water by depth; Navail = plant available nitrogen by depth; BNPP = belowground net primary production; ANPP = aboveground net primary production; litter = aboveground dead plant material).
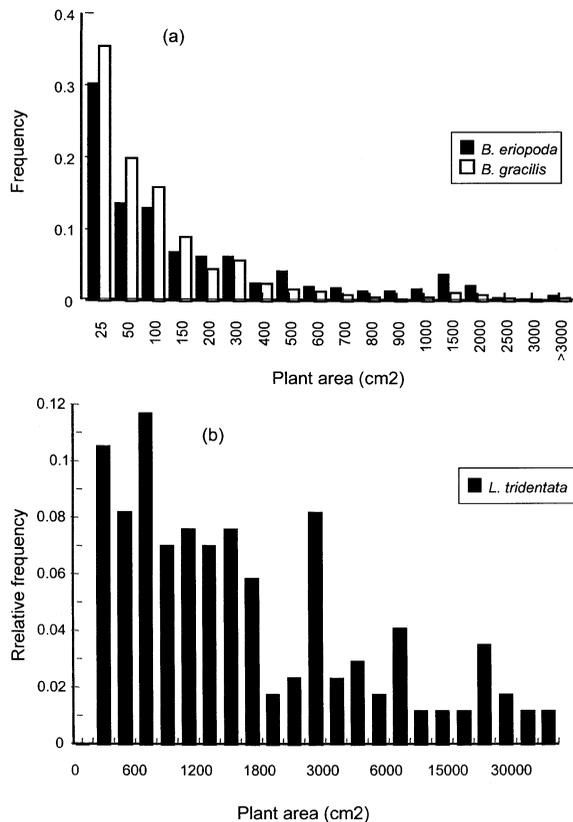
Fig. 2. Plant size distributions from the SEV for: (a) basal area of *B. eriopoda* ($n = 721$) and *B. gracilis* ($n = 829$); and (b) canopy area of *L. tridentata* ($n = 171$).

both species, most plants ($> 70\%$) were small (< 200 cm^2) (Fig. 2a). Average plant size was larger for *B. eriopoda* (244 cm^2) compared to *B. gracilis* (143 cm^2), however, maximum plant sizes were similar in that both species had a few very large plants (> 3000 cm^2). Simulated plot size for grasslands (0.25 m^2) was based upon the total area associated with a large individual of each species where total area was calculated by adding 10 cm to each plant diameter to account for resource space occupied by the root system (Coffin and Lauenroth, 1990). For *L. tridentata*, plant size (cm^2) was estimated by measuring the longest diameter of the canopy and the diameter perpendicular to it, and assuming an ellipsoid shape. Shrub plants were measured in twenty 3×4 m^2 plots ($n = 171$ plants). Average shrub

size (3252 cm^2) was larger than grass plants (Fig. 2b), and the estimated plot size based on the size reached by $> 90\%$ of the measured individuals was 1 m^2. A sensitivity analysis of plot size found no effect on model results over the range of plant sizes estimated from the field (0.25 to 1.0 m^2); thus the same plot size (1 m^2) was used for all simulations. This plot size is sufficiently small that individual grass plants of maximum size (3000 cm^2) can interact with all plants on a plot. The plot size is also sufficiently large for the growth of individual shrub plants. Although shrub roots can extend beyond a 1 m^2 area, these between plot interactions were not included in the model.

3.2. Recruitment

3.2.1. Seedlings

Successful recruitment by seedlings depends on three processes: the production of viable seeds, the dispersal of seeds both within and among plots, and the germination and establishment of seedlings (Fig. 1). Each process is assumed to have a probability of occurrence in each year that is species-specific, and independent from the probabilities associated with other recruitment processes. Each probability can either be constant from year to year, or can vary depending on specified biotic and environmental conditions. Probabilities of seed production are used to determine the relative abundance of seeds of each species on a plot. If seeds are not produced on a plot and an interactive grid of plots is simulated, then probabilities of seed dispersal from neighboring plots are used to determine seed availability to the plot. If seeds are not produced on a plot and an independent grid of plots is used, then no seeds are available and recruitment is not possible for that species. If seeds are available for a species, then microenvironmental constraints are used to determine if seeds can germinate and become established on a plot. After a seedling becomes established and survives until the following year, it is considered an adult plant and constraints on growth and mortality determine its success.

Seed production by a species in the previous year ($k - l$) is assumed to be dependent upon the biomass of plants of that species on a plot and the

amount of precipitation received in that year. In many grassland species, seeds produced in one year are available for germination the following year after overwintering conditions break dormancy. It was assumed that a minimum amount of biomass of species(i) is required on a plot for seeds to be produced. If sufficient biomass is available, then seed production is assumed to increase as the amount of precipitation received in the previous year increases. The form of the curve and the parameters are species-specific:

$$\text{if } \text{ABIO}_{(i,j,k-l)} < \text{MINBIOP}_{(i)}\text{FULBIO}_{(i)}, \quad (1)$$

then $p(\text{SD\_PROD})_{(i,j,k)} = 0$

$$\text{if } \text{ABIO}_{(i,j,k-l)} \geq \text{MINBIOP}_{(i)}\,\text{FULBIO}_{(i)}, \quad (2)$$

then $p(\text{SD\_PROD})_{(i,j,k)} = \text{f}(\text{PPT}_{[k-l]})$

where $\text{ABIO}_{(i,j,k-1)}$ is the biomass of species(i) on plot(j) in year($k-l$), $\text{MINBIOP}_{(i)}$ is the proportion of full-size biomass ($\text{FULBIO}_{[i]}$) required for seed production, $p(\text{SD\_PROD})_{(i,j,k)}$ is the probability of seeds being available in year(k), and $\text{PPT}_{(k-l)}$ is the amount of precipitation received during the previous year. Values of $p(\text{SD\_PROD}_{[i,j,k]})$ range from 0 (no seeds produced) to 1 (maximum number of seeds produced). This function may take a variety of forms (e.g. linear, exponential) that is specific for each species. If insufficient information is known about biotic and abiotic controls on seed production for a species, then a constant is used for every year that represents the average probability of seed production. Probabilities for all species for year(k) are normalized to sum to l to represent relative seed abundance on a plot(j) due to seed production.

Seed dispersal. If seeds are produced on a plot or if an independent set of plots is simulated, then the probability of seed dispersal ($p[\text{SD-DISP}_{(i,j,k)}]$) is 1.0. If seeds are not produced on a plot and an interactive grid is used, then seeds may disperse to the plot from a neighboring plot where seeds were produced the previous year. Dispersal of seeds depends upon the distance between plots, the height of the inflorescence, average wind speed, and aerodynamic properties of seeds (Coffin and Lauenroth 1989, 1994). The probability of at least one seed dispersing to plot(j) decreases exponen-

tially as the distance between plots increases (Werner 1975):

$$p(\text{DISP})_{(i,j,k)} = e^{(-\text{RATE\_D}[i]\,\text{DIST})} \quad (3)$$

where $p(\text{DISP})_{(i,j,k)}$ is the probability of at least one seed of species(i) dispersing to plot(j) in year(k), $\text{RATE\_D}_{(i)}$ is a measure of the dispersability of the seeds, and DIST is the distance (m) between plots. The value of RATE_D is calculated by assuming $p(\text{DISP}) = 0.005$ at the maximum distance ($\text{MAXD}_{[i]}$) that seeds can travel under field conditions. $\text{MAXD}_{(i)}$ is estimated using an equation for wind-dispersed seeds (Greene and Johnson, 1986):

$$\text{MAXD}_{(i)} = \frac{H_{(i)}V_w}{V_{t(i)}} \quad (4)$$

where $H_{(i)}$ is the average release height of the inflorescence for species(i), V_w is the mean horizontal wind speed (cm/s), and $V_{t(i)}$ is the average sinking velocity of the seeds for species(i). $H_{(i)}$ and $V_{(w)}$ are calculated from field data, and $V_{t(i)}$, if unknown, can be estimated using data from wind-dispersed species with similar aerodynamic properties of seeds (Rabinowitz and Rapp, 1981; Fraleigh, 1999). Values of $p(\text{DISP})$ range from 0 (no seeds disperse) to 1 (at least one seed can disperse). The model sequentially checks each neighboring plot within the maximum dispersal distance of each species ($\text{MAXD}_{[i]}$) to determine if seeds were produced on the plot the previous year using Eq. (1) and Eq. (2). Once a plot($j+1$) is found where seed dispersal can occur to a neighboring plot(j), a uniformly distributed random number from 0 to 1 is selected to determine if seed dispersal occurs. If dispersal occurs, then $p(\text{SD\_DISP})_{(i,j,k)} = 1$, and no additional plots are checked. If no seeds disperse from neighboring plots within the maximum dispersal distance of seeds for species(i), then $p(\text{SD\_DISP})_{(i,j,k)} = 0$.

Germination of seeds and establishment of seedlings are based upon the probability that a set of microenvironmental conditions required for these processes will occur each year for species(i) on plot(j) in year (k). This probability [$p(\text{SD\_EST}_{[i,j,k]})$] can be determined in one of three ways depending on the amount of information available. For species where little information is avail-

able, the long-term average probability of establishment is used that is constant from year-to-year and independent of local plot conditions. For species where general responses of seeds and seedlings to microsite conditions are known, the probability of establishment is calculated each year as a function of local conditions on the plot, such as litter amount and plant cover. For species where detailed information on seed and seedling responses to temperature and daily soil water content at multiple depths in the soil profile are known, a multi-layer, daily timestep simulation model of soil water dynamics is used (SOILWAT, Parton, 1978). SOILWAT integrates the effects of precipitation, temperature, litter, plant cover, and soil texture on successful germination and establishment (Lauenroth et al., 1994). (Details on the use of SOILWAT in ECOTONE are described in Section 3.3.1.) If historical weather data are used, then the SOILWAT submodule in ECOTONE is used to dynamically simulate the occurrence of a successful establishment event each year based upon local plot conditions. If stochastically-generated, long-term weather data are used, then the SOILWAT model is run independently to obtain an average long-term probability of establishment based upon plot-level conditions (Minnick and Coffin, 1999; Peters, 2000a). This probability is then used as a constant throughout the ECOTONE runs for that species. After a probability of establishment is determined for each species in each year, the values are normalized to sum to 1 to obtain probabilities relative to the other species.

Selection of species to recruit is determined by calculating a probability of recruitment for each species based on probabilities of seed production, dispersal, and establishment. If seed production occurs on a plot, then the probability of recruitment ($p[\mathrm{RECRUIT}_{(i,j,k)}]$) is calculated by:

$$\text{if } p(\mathrm{SD\_PROD}_{[i,\,j,k]}) > 0,$$
$$\text{then } p(\mathrm{RECRUIT}_{[i,\,j,k]}) = \qquad (5)$$

$$p(\mathrm{SD\_PROD}_{[i,\,j,k]})\, p(\mathrm{SD\_DISP}_{[i,\,j,k]})$$
$$\qquad p(\mathrm{SD\_EST}_{[i,\,j,k]})$$

Alternatively, if seed production does not occur on a plot, but seeds can disperse to the plot from neighbor plots, then the probability of recruitment is calculated by:

$$\text{if } p(\mathrm{SD\_PROD}_{[i,\,j,k]}) = 0 \quad \text{and}$$
$$p(\mathrm{SD\_DISP}_{[i,\,j,k]}) = 1, \quad \text{then} \qquad (6)$$
$$p(\mathrm{RECRUIT}_{[i,\,j,k]})$$
$$= p(\mathrm{SD\_DISP}_{[i,\,j,k]})\, p(\mathrm{SD\_EST}_{[i,\,j,k]})$$

The third possibility is if seeds are not produced on a plot and no seeds are available for dispersal from neighboring plots, then the probability of recruitment is 0:

$$\text{if } p(\mathrm{SD\_PROD}_{[i,\,j,k]}) = 0 \quad \text{and}$$
$$p(\mathrm{SD\_DISP}_{[i,\,j,k]}) = 0, \qquad (7)$$
$$\text{then } p(\mathrm{RECRUIT}_{[i,\,j,k]}) = 0$$

Probabilities for all species are normalized to sum to 1.0 to obtain a relative probability of recruitment for each species on each plot in each year. It is then determined stochastically which species have seedlings recruited to a plot. From 1 to 7 species are randomly selected to have seedlings recruited each year with 0 to 3 seedlings added to the plot for each species. Seedling biomass ($\mathrm{SD\_SZ}_{[i]}$) is based on the estimated size of a one-year-old plant and is a proportion of the aboveground biomass of a fullsize plant ($\mathrm{AFULBIO}_{[i]}$). Variation in seedling biomass is accounted for by randomly selecting a proportional biomass that is $\pm 10\%$ of the seedling biomass. Aboveground biomass of a seedling (g) is calculated by multiplying this proportion by the fullsize biomass of a plant of that species.

Similar to aboveground biomass, belowground biomass of a seedling is determined for each depth in the soil profile as a proportion of the maximum belowground biomass ($\mathrm{BFULBIO}_{[i]}$) for that species. Maximum root biomass values by depth are either entered as parameters, if known, or calculated by the model using general information about the root distribution for each species. Based on analyses of root distributions of a large number of grassland species in the U.S. (Sun et al., 1998), it was assumed that root biomass increases

linearly to a species-specific depth (MID_DEPTH$_{[i]}$), then decreases allometrically to the maximum depth (MAX_DEPTH$_{[i]}$):

$$\text{if } \text{DEPTH}_{(m)} \leq \text{MID\_DEPTH}_{(i)} \tag{8}$$

$$\text{then } \text{PRIO}_{(m,i)} = \text{LIN\_SLOPE}_{(i)}\text{DEPTH}_{(m)} + \text{BIOM\_MIN}_{(i)}$$

$$\text{if } \text{DEPTH}_{(m)} > \text{MID\_DEPTH}_{(i)}, \tag{9}$$

$$\text{then } \text{PBIO}_{(m,i)} = 1 - e^{(\text{RATE\_BIO}[i]\,\text{DEPTH}[m])}$$

where DEPTH$_{(m)}$ is the current depth in cm, PBIO$_{(m,i)}$ is the proportion of peak biomass of species(i) at depth(m), LIN_SLOPE$_{(i)}$ is the slope of the linear part of the function, BIOM_MIN$_{(i)}$ is the proportion of the peak biomass at 0 cm depth, and RATE_BIO$_{(i)}$ is the slope of the allometric part of the function. LIN_SLOPE$_{(i)}$ is calculated using BIOM_MIN$_{(i)}$ at 0 cm and a peak biomass value of 1.0 at MID_DEPTH$_{(i)}$. For each depth, PBIOM$_{(m,i)}$ is multiplied by the total root biomass (g) for a seedling to calculate its biomass (g) in each depth increment. These values are then multiplied by the proportion of the biomass of a fullsize plant that is associated with seedlings to obtain root biomass by depth for each seedling.

3.2.2. Vegetative propagules

Vegetative propagation following plant mortality is possible for clonal grasses that spread through stolons or rhizomes, or for herbaceous and woody plants that regrow or sprout from tap roots. Clonal grasses can also spread vegetatively from adjacent plots containing sufficient biomass if an interactive grid of plots is used. It was assumed that 5% of the aboveground biomass of a fullsize plant of species(i) is required for vegetative spread to occur to an adjacent disturbed plot. The same procedures are used to check plots and add vegetative propagules as for seed dispersal among plots. If vegetative spread is possible, then a random number from 0 to 1 is used and compared with the probability of vegetative spread to determine if spread occurs for species(i). If these conditions are met, then 0–3 plants at the biomass of a seedling are added to the plot. New plants are added to a plot at 10% the total biomass of a full-size plant of that species. The aboveground and belowground biomass are distributed using the same procedure as the addition of seedlings.

3.3. Growth

Increase in biomass of each plant on a plot is a function of temperature, precipitation, and soil texture as well as competition from other plants for soil water and nitrogen. Annual and perennial tissue of above- and belowground organs are simulated separately, and then combined to obtain a growth increment or production for each plant each year. Resources are simulated daily (water) or monthly (nitrogen); plant-level responses are calculated at these time intervals, then aggregated to allow growth to occur annually. It is assumed that plants must maintain and produce perennial tissue first before annual production can occur. Resources that are not used for perennial tissue are available for production of annual biomass.

3.3.1. Soil water

Competition for soil water is determined by the overlap in the distribution of active root biomass by depth for each plant and the depth distribution of water available to a plant. Both root biomass and plant available water are simulated dynamically. Active root biomass by depth for each plant is simulated based on species-specific temperature responses. Parabolic curves are used to calculate the proportion of roots that are active in each 5 day time period using daily temperatures averaged over that period. Five day intervals were used to provide a plant response that integrates extreme temperatures with more typical conditions:

$$\text{TEMP}_{(i,n)} = 1 - (0.00257[\text{AVGTEMP}_{(n)} - \text{OPT\_TMP}_{(i)}]^2) \tag{10}$$

where TEMP$_{(i,n)}$ is the temperature response for species(i) during time period(n), OPT_TMP$_{(i)}$ is the optimum temperature for growth by species(i), and AVGTEMP$_{(n)}$ is average daily tem-

perature (maximum–minimum) averaged over the 5 day period. The constant (0.00257) was selected to allow $TEMP_{(i,n)}$ to range from 0 if temperatures are too cold or hot for growth, to 1 if temperature is optimum for growth.

The temperature effect for each time period is multiplied by the surface area of roots by a plant in each depth to obtain the proportion of roots that are actively growing. Root biomass in each depth is first partitioned into fine and coarse roots; these values are then converted to surface area using species-specific conversion factors. Surface area is used since it is a better representation of uptake than biomass (Nye, 1973; Casper and Jackson, 1997); fine (< 2 mm-diameter) and coarse roots are distinguished since they typically have different potential uptakes of resources (Fogel, 1991; Hendricks et al., 1993). Total root surface area for a plant in each depth is calculated as the sum of the fine and coarse root surface areas. These values are multiplied by the temperature effect for each time period to obtain the surface area of active roots for each plant. The proportion of active roots for each plant in each depth is calculated by dividing the values for each plant by the total surface area of active roots for all plants in each depth and time period.

Soil water availability in each depth at each time period is partitioned among plants based on their proportion of the total surface area of active roots. Soil water availability is simulated by incorporating a daily time step, multi-layer soil water model (SOILWAT; model description can be found in Parton, 1978; Sala et al., 1992) as a sub-module into ECOTONE (Fig. 1). 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 air temperature and precipitation, and monthly wind speed, relative humidity, and cloud cover. Soil temperature is assumed constant for all depths. Monthly aboveground biomass (live and standing dead) and litter obtained from annual amounts are used to simulate interception and evaporation. Annual values are distributed monthly using seasonal distribution of plant growth (Peters, 2000a). Soil texture (% sand, silt, and clay), % rocks by volume, and root biomass by depth are used for simulating evaporation, transpiration, and infiltration. Losses of water to deep drainage are possible, but occur infrequently in upland arid environments.

Total amount of water transpired daily from each depth is used as an estimate of plant available water. These amounts are summed for each 5 day period to represent the time period of plant uptake. Amount of water available to each plant is determined by the proportion of total active surface area attributed to that plant in each depth and 5 day period. These amounts are then summed for the year to obtain a total amount of water available to each plant in each depth based on the time period when the plant is growing. Increment of perennial biomass (g/plant) based on water (WATP_INC) is calculated by multiplying the species-level parameter of water-use efficiency (WUE: g biomass/cm water) by the total amount of water available to the plant across all depths (cm).

3.3.2. Nitrogen

Nitrogen availability is simulated by incorporating the decomposition subroutines from the CENTURY model (Parton et al., 1988) as a submodule (DECOMP) into ECOTONE. CENTURY operates at a monthly time step to simulate nitrogen dynamics in the upper 20 cm of the soil profile (model description can be found in Parton et al., 1988). Input parameters include monthly precipitation and temperature, soil texture and root biomass by depth, and carbon:nitrogen ratios and lignin contents by species. Daily precipitation and temperature used in the SOILWAT submodule are aggregated monthly for use in the DECOMP submodule. Above- and belowground production, and standing dead and litter simulated annually are distributed monthly using seasonal patterns in plant growth, and passed to DECOMP to simulate nitrogen dynamics. Simulated nitrogen availability per month is aggregated to an annual value and summed across depths to obtain a total amount of nitrogen available in each year. Nitrogen availability is partitioned to each plant based on its proportion of total available water for the year. Increment of

perennial biomass increment (g/plant) based on nitrogen (NITP_INC) is calculated by multiplying the species-level parameter of nitrogen-use efficiency (NUE: g biomass/g N) by the total amount of nitrogen available to a plant (g N/plant).

3.3.3. Biomass increment

The actual perennial biomass increment of each plant (PER_INC) is determined according to Liebig's principle as the minimum of the water (WATP_INC) and nitrogen increments (NITP_INC). This biomass increment represents the maintenance of old and production of new perennial tissue. Leftover water or nitrogen is used to support annual production. These resources are distributed to each plant in the same manner as for perennial growth: the total amount of resources are partitioned among plants based on their proportion of the total active roots. Annual production for each plant is calculated for water (WATA_INC$_{[i]}$) and nitrogen (NITA_INC$_{[i]}$) based on the amount of available resource and either WUE or NUE. The minimum of the two annual increments is used for the annual increment (ANN_INC$_{[i]}$). Water or nitrogen that is partitioned to a plant, but not used for annual or perennial production, is made available to other plants on the plot based on their proportion of total biomass. The actual increment of a plant (ACT_INC$_{[i]}$) is the sum of the perennial (PER_INC$_{[i]}$) and annual increments (ANN_INC$_{[i]}$). Final plant biomass is the sum of the initial plant biomass and the actual increment in biomass. Plant biomass is partitioned between above- and belowground based on species-specific root:shoot ratios for production. Belowground biomass is distributed among soil depths using the species-specific root distributions. Total plot biomass is the sum of all individual plant biomass on a plot. Total above- and belowground production on a plot are the sum of these values for all individual plants on a plot.

3.4. Mortality

Three independent sources of mortality are included for each plant in each year of the simulation: longevity, slow growth, and disturbances. Each source of mortality has a probability that is specific to each plant or species. These sources are commonly incorporated into gap models and were based on information in Shugart (1984); modifications for clonal plants were based on Coffin and Lauenroth (1990). In addition, loss of plant tissue due to senescence occurs without plant mortality as a result of the turnover of plant parts (e.g. roots, tillers, leaves).

1. Each species is assumed to have an age-independent likelihood of mortality since a percentage of a cohort growing under optimum conditions will not reach maximum age (MAXAGE). It was assumed that 1% of a cohort reaches maximum age (Shugart, 1984). This results in a constant (4.605) in the equation for calculating the annual probability of mortality for species(*i*):

$$p(\text{MORT\_AGE}_{[i]}) = \frac{4.605}{\text{MAXAGE}_{(i)}}. \tag{11}$$

2. Slow growing plants are assumed to have a greater risk of death due to increased vulnerability to disease, insects, and severe environmental conditions than plants with average growth rates (Shugart, 1984). It was assumed that plants can adjust to short-term stresses due to insufficient resources since soil water is frequently limiting in arid and semiarid ecosystems (Noy-Meir, 1973). Non-clonal plants are assumed to respond differently to slow growth constraints than clonal plants due to differences in their morphology. For non-clonal plants, slow growth constraints do not operate in the model until a plant experiences slow growth for two consecutive years (Coffin and Lauenroth, 1990). Clonal plants must be at least three years of age for slow growth constraints to operate.

   For non-clonal plants, the probability of mortality for a plant (*p*[MORT_SLOWG]) is assumed to increase as the number of consecutive years (NYEARS) that the plant experiences slow growth increases:

$$p(\text{MORT\_SLOWG}) = 0.168 + (\text{NYEARS})0.1,$$
(12)

where slow growth is defined as a biomass increment (ACT_INC]) < 5% of a species maximum growth increment (MAX_INC), which is 90% of its optimum rate of growth (Coffin and Lauenroth, 1990). This equation results in a probability of mortality of 0.57 following four years of slow growth, and a probability of 1.0 after nine years of slow growth. Thus, all plants that experience at least nine years of slow growth are killed. The optimum growth rate of a plant (dR/dt) is calculated based on the intrinsic growth rate ($r_{[i]}$), the maximum biomass of a fullsize plant of that species (FULBIO$_{[i]}$), and the biomass of a plant at time t (ABIO$_{[t]}$):

$$\frac{dR}{dt} = r_{(i)}[\text{FULBIO}_{(i)} - \text{ABIO}_{(t)}].$$
(13)

Intrinsic growth rate for each species (GRO_RATE$_{[i]}$) is estimated from information about the number of years required for an individual to reach its full size while growing under optimum resource conditions. Clonal plants are excluded from this source of mortality since parts of these plants are more likely to die rather than the entire plant (Fair et al., 1999). Because clonal plants can decrease perennial biomass or size if resources are insufficient for growth (Wright, 1972), it was assumed that a proportion of perennial biomass is killed depending on plant growth relative to optimum growth:

$$\text{BIOMRF} = e^{-5.298\,[\text{ACT\_INC/MAX\_INC}]},$$
(14)

where BIOMRF decreases as the actual growth increment of a plant [ACT_INC] approaches its maximum growth increment [MAX_INC]. The value of the slope (-5.298) results in a 77% reduction in biomass if a plant is growing at 5% of its maximum rate, and a 20% reduction if a plant is growing at 30% of its maximum rate.

3. The third source of mortality is due to disturbances that are incorporated into the model based on their size, shape, frequency of occurrence, and the lagtime required before plant recovery can begin. Lagtimes are often due to repeated disturbance, such as mound-building activities of animals, that continue for a period of time following the initiation of the disturbance. Each disturbance also has a species-specific plant biomass below which a plant is killed. In each year, one disturbance event is selected based on the probability associated with its frequency of occurrence. The surface area of a disturbance is selected randomly from its size distribution. The disturbance is randomly located within the grid of plots with the requirement that the entire disturbance must fit within the grid. Continuous plots are aggregated in the shape of the disturbance type until the size is reached. All plants of insufficient biomass are killed on all plots within the disturbed area. Recruitment of plants does not occur on disturbed plots until after the period of time defined by the lagtime for that disturbance type.

4. The final source of tissue loss is associated with parts of plants. For annual plants, all above- and belowground biomass dies each year and is transferred to litter. For perennial plants, species-specific root and leaf (or tiller) turnover rates are used to determine the proportion of these plant parts killed each year. These rates are based on species-specific longevity estimates for each plant part. For herbaceous species, all aboveground biomass except perennial crowns dies each year and is transferred to litter.

4. Model parameterization

Soils, climate and species parameters were obtained from studies conducted at the SEV supplemented with information from other sites in the region. Most supplemental information involved parameters for subordinate species that was obtained from studies conducted either at the Jornada Experimental Range LTER site in southern NM (32.5° N, 106.8° W, 1350 m ASL) where research on Chihuahuan desert communities has been conducted since 1912 or the Shortgrass

Steppe LTER in northern Colorado (40.8° N, 104.8° W, 1650 m ASL) where research has been conducted since 1939. Although, > 300 species occur in these grasslands and shrublands, most species are rare and share life history traits with several other species. Thus, eleven groups were formed by combining species with similar life history traits. One species was selected to represent each group. The three dominant species (*B. gracilis*, *B. eriopoda*, *L. tridentata*) each defined a monospecific group. The remaining eight groups were defined based on lifeform (grass, shrub, forb), physiology (C_3, C_4) and longevity (short- and long-lived).

4.1. Soils and climate

ECOTONE was parameterized for two locations at the SEV with different soil texture. Sand, silt and clay (%) by depth were obtained from county soils maps to represent grasslands (sandy loam) or shrublands (loamy sand) at this site (Soil Survey of Socorro County Area, 1988). The same layer structure (0–5, 5–10, 10–15, 15–20, 20–30, 30–40, 40–50, 50–75 cm depth) was used for both locations. Percentage sand (82 for loamy sand, 58 for sandy loam) and clay (6 for loamy sand, 10 for sandy loam) were assumed to be the same for all layers within each soil type. Evaporation and transpiration from each layer were based on Peters (2000a) and were assumed to be the same for both soil types.

Each location was simulated under current climate and under a climate change scenario predicted from a global climate model (GCM). Historical climate was obtained from a nearby weather station (Socorro, NM; 34.1° N, 106.9° W) with a long-term record (80 years) of daily precipitation and temperature. Monthly cloud cover, wind speed, and relative humidity were obtained from long-term estimates derived from climate maps (National Oceanic and Atmospheric Administration, 1983) and were the same as those used in a previous analysis (Peters, 2000a). The climate change scenario selected for analysis was the Goddard Fluid Dynamics Laboratory (GFDL) since scenarios from this GCM provide conservative estimates for central New Mexico

(Minnick and Coffin, 1999). A GFDL climate change scenario for this region predicts an increase in summer precipitation (June–August) and decrease in fall precipitation (September–October) to result in a total annual increase of 6.6 cm Kittel et al. (1995) (Fig. 3a). Average temperature is predicted to increase 3.1 °C throughout the year (Fig. 3b). Monthly scalars for precipitation and temperature were applied to daily historical weather to obtain a sequence of years with modified climate. Modifications to monthly cloud cover, wind speed, and relative humidity were also based on GFDL predictions for the region.

4.2. Species parameters: recruitment

For these runs, it was assumed that seeds of all species groups were present on each plot and resources were available for establishment every year (Kemp, 1989). The probability that a seedling from a group became established was based upon the occurrence of suitable microenvironmental conditions or the relative abundance of seedlings on a plot; these parameters were assumed to vary by soil texture. Because recruitment was expected to be a key parameter to differentiate the three dominant species, analyses were conducted to obtain estimates of their establishment probability when possible. For the two dominant species where sufficient information is available (*Bouteloua gracilis*, *Bouteloua eriopoda*), their establishment was calculated based on the probability that a set of microenvironmental conditions required for germination and establishment will occur each year (Minnick and Coffin, 1999). A first-order Markov process was used to generate 5000 years of simulated daily precipitation and temperature data with similar characteristics as the long-term historical climate. The same 5000 years weather sequence was used for both soils. The probability of establishment for each *Bouteloua* species was calculated for each soil type using a multi-layer, daily timestep simulation model of soil water dynamics (Peters, 2000a). For both species, the calculated probability of establishment was larger on the sandy loam compared to the loamy sand soil (Table 1). Because little is known about controls on establishment of *L.*

Table 1
Species parameters for the ECOTONE model

Species	G[a]	LS[b]	T[c]	SD_EST[d]	SD_SZ (g)[e]	AFULBIO[f] (g/plant)	BFULBIO[f] (g/plant)	GRO_RATE[g]	OPT_TEMP[h] (°C)	MID-DEPTH[i] (cm)	MAX-DEPTH[i] (cm)	WUE[j]	MAX AGE[k] (y)
Bouteloua gracilis	G	PL	4	0.0444*; 0.004**	3.5	65	108	0.474	15	15	150	15	na
Bouteloua eriopoda	G	PS	4	0.1312*; 0.13**	3.7	75	108	0.6	22	15	75	17.5	35
Aristida purpurea	G	PS	4	0.05	1.6	54	108	0.67	22	20	100	17.5	15
Sporobolus flexuosus	G	PL	4	0.05	1.6	54	108	0.5	22	20	100	17.5	25
Oryzopsis hymenoides	G	PS	3	0.01	1.6	54	108	0.67	10	30	150	12.4	15
Larrea tridentata	S	PL	3	0.0*; 0.01**	1.0	100	100	0.3	10	10	150	12.4	400
Gutierrezia sarothrae	S	PS	3	0.01	1.0	100	100	0.3	10	10	150	12.4	10
Hymenopappus filifolius	F	PS	4	0.15	0.8	25	50	0.67	22	15	100	17.5	15
Sphaeralcea incanum	F	PS	3	0.15	0.8	25	50	0.67	10	15	100	12.4	15
Tidestromia lamuginosa	F	A	4	0.15	0.5	15	30	0.95	22	10	100	17.5	1
Astragalus nuttallianus	F	A	3	0.15	0.5	15	30	0.95	10	10	100	12.4	1

[a] Growth form: G, grass; S, shrub; F, forb;
[b] Lifespan: P, perennial, L, long, S, short; A, annual;
[c] Temperature class: 3 C3, 4 C4;
[d] Seedling establishment probability; *sandy loam soil; **loamy sand soil;
[e] Seedling size (g/plant);
[f] Aboveground and belowground biomass of fullsize plant (g/plant);
[g] Intrinsic growth rate;
[h] Optimum temperature;
[i] MID-DEPTH: depth of maximum root biomass; MAX_DEPTH: maximum depth of roots;
[j] Water use efficiency parameter;
[k] Maximum age (years); na, not applicable.

tridentata seedlings, field observations were used to estimate the probability for each soil type (Table 1).

It was assumed for all other species groups that favorable conditions for establishment occur sometime during each year. The probability of seedling establishment for each species-group was based upon the relative abundance of seedling establishment events by each group using information from the literature and field observations of seed production and seedling success at the SEV (Table 1) (Nava, 1970; Osman, 1982; Coffin and Lauenroth, 1990; Wood et al., 1997; McDaniel et al., 2000). It was assumed that seedling establishment probabilities were the same for both textures for all subordinate species. Probabilities within each texture for all species were normalized to 1, although values for the two *Bouteloua* species remained at their calculated values. An independent set of plots with the same soil texture was simulated for each location to allow a focus on processes that are not spatially interactive among plots. Thus, seed dispersal parameters were not needed.
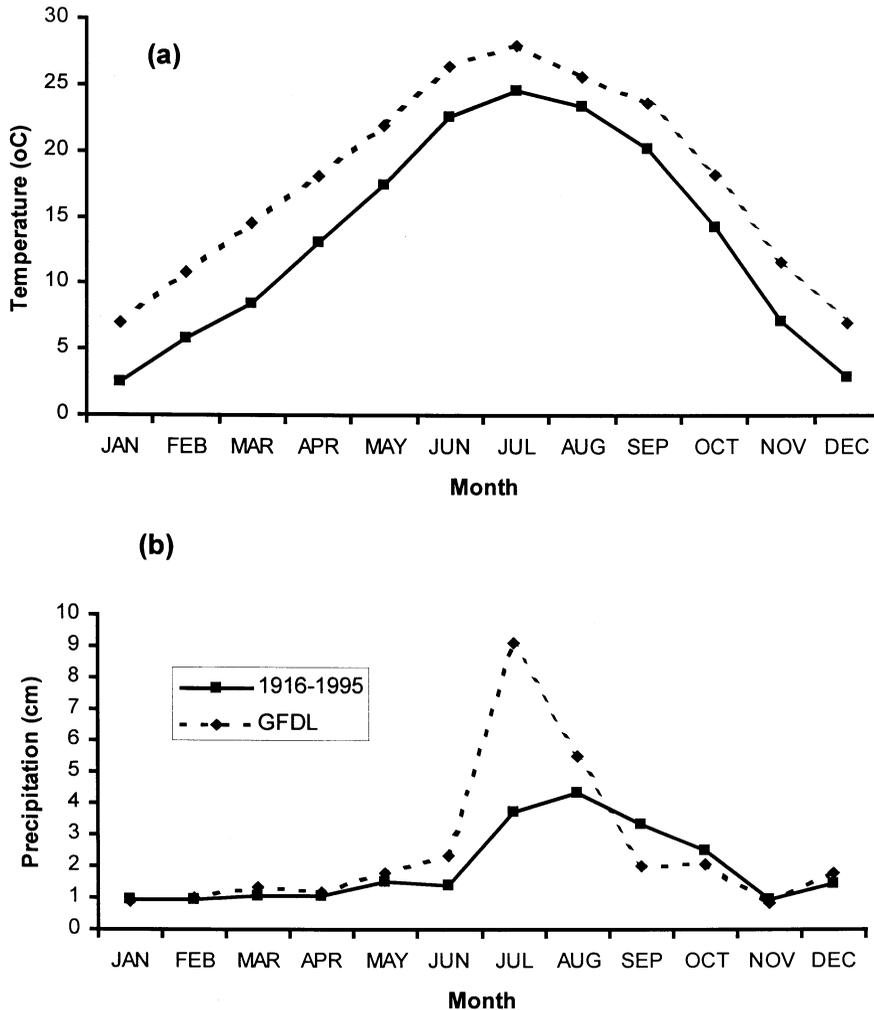
Fig. 3. Long-term historical climate (1916–1995) and directional change in climate based on predictions from the GFDL GCM: (a) average monthly temperature (°C); and (b) average monthly precipitation (cm).

Seedling biomass for each species was assumed to range from 1 to 2% of the above- or below-ground biomass of a full-size plant (Table 1). Maximum above- and belowground biomass values were estimated from the literature (Ludwig et al., 1975, 1989; Coffin and Lauenroth, 1990; Peters, in review). Belowground root biomass was distributed among depths using three parameters: the proportion of peak biomass at 0 cm (BIOM_MIN), the depth of maximum root biomass (MID_DEPTH), and the maximum depth of roots (MAX_DEPTH) for each species (Table 1). BIOM_MIN was assumed to be 0 for all species. The other parameters were based on root distribution data for each species when possible, or for similar species when necessary (Cannon, 1911; Markle, 1917; Bailey, 1967; Gibbens and Lenz, 2001). Vegetative spread was only possible following plant mortality on a plot for *B. eriopoda* through the production of stolons from neighboring plants and for *L. tridentata* as regrowth from tap roots. It was assumed there was a 10% chance of regrowth the following year if a *B. eriopoda* plant was killed and a 75% chance of regrowth if a *L. tridentata* plant was killed.

4.3. Species parameters: growth

Because belowground resource use by the three dominant species was expected to be important to dominance patterns, and little was known about patterns in soil water use through time and space for these species at this transition zone, a watering experiment was conducted in 1996 to provide estimates of growth parameters. For each of the three dominant species (*B. gracilis*, *B. eriopoda*, *L. tridentata*), eight plants were selected within patches dominated by that species. Plants were randomly selected that had similar basal areas (*Bouteloua* spp.) or similar canopy heights and areas (*L. tridentata*). Pairs of stainless steel TDR rods (5 mm-diameter, 2 cm apart) of three lengths (20, 25 and 35 cm) were placed vertically in the soil of each plot with 5 cm of each rod exposed (Nielsen et al., 1995). Two of the depths sampled were selected to correspond to the maximum density (g/cm) of roots (0–15 cm) and ca. 90% of grass root biomass (0–30 cm) (Hochstrasser and

Coffin, 1997). The 0–25 cm rods were used to separate soil water content in the 0–30 cm layer into two sub-layers (0–20 and 20–30 cm). A single pair of wave guides was placed in two microsites of each plot (plant canopy and interspace) to distinguish evaporation and transpiration losses since bare interspaces (50–100 cm-diameter) with low root density are common between plants. Plant canopies were sampled by locating rods within live crowns (grasses) or 10 cm from the woody base of shrubs. Interspace locations were selected within bare areas at the midpoint between the plant of interest and an adjacent conspecific individual.

A 10 mm rainfall event was simulated by adding water two times during the year (mid-April, mid-May). These dates were selected based on observations of the start of photosynthetic activity by C_3 and C_4 species, respectively, at this site. Both average minimum and maximum temperatures were lower during the 3 days of the study in April (3.1, 17.2 °C) compared with the same time interval in May (6.1, 30.5 °C). Water was added to half of the plants within each patch; the other four plants served as controls. Water was added to a 1–1.5 m diameter plot that consisted of an individual plant and its associated interspace. Half of the total amount of water was added to each plot at two times within 30 min to allow infiltration and minimize runoff. Measurements of the propagation velocity along the wave guides were obtained at regular intervals (6, 24, 48 and 72 h) following watering using a Tektronix 1502B cable tester (Beaverton, OR) interfaced to a Campbell Scientific CR10 datalogger equipped with a Multiplexer SDMX50. Measurements were converted to soil water content using standard equations (Topp et al., 1980). Gravimetric soil samples were collected at the same time intervals at two depths (0–5, 5–10 cm) from nearby plant and interspace microsites that were not watered to calculate background soil moisture. Samples were weighed wet, dried at 110 °C for 24 h, and reweighed to calculate gravimetric soil moisture (g water/g soil). The soil was dry at the start of the study since previous measurable precipitation occurred in March (1.8 mm) with only 10.7 mm precipitation occurring throughout the first 3
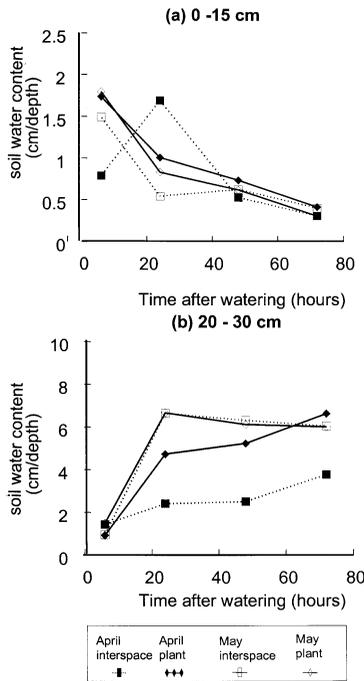
Fig. 4. Soil water content through time following a watering event under *B. gracilis* plants and in bare interspaces for two depths: (a) 0–15 cm; (b) 20–30 cm.

months of 1996. No rainfall occurred during the entire time interval of the study (April–May), thus background soil moisture was minimal.

Changes in soil water content through time at different depths were affected by species, sampling date, and microsite location. Soil water content depends on both plant (transpiration) and soil processes (evaporation, infiltration). Comparing soil water content through time under plants where all three processes operate with bare interspaces where evaporation and infiltration are most important allows the determination of water losses due to actively growing plants. For *B. gracilis* plants, similar rates of decrease in soil water content in the surface soil (0–15 cm) in April and May throughout the sampling period indicate similar transpiration losses due to active root uptake of water (Fig. 4a). Infiltration of water to the deeper depth (20–30 cm) on these dates occurred only within 24 h after watering; soil water content was similar through time in this depth after the 48 h measurement (Fig. 4b). Evap-

oration from the surface layer in April and May was also important for the first 48 h based on water loss in the interspaces (Fig. 4a). However, the continued decrease in water from the surface layer until the end of the sampling period indicates the importance of transpiration in both months (Fig. 4a).

By contrast, infiltration was the predominant process under *B. eriopoda* plants in April based on rapid losses of water from the surface layer (0–15 cm) to the deeper layer (20–30 cm) (Fig. 5a, b). Infiltration to the deeper depth occurred within 6 h after watering with only small changes in water content in either depth after this time. In mid-May, *B. eriopoda* plants were actively growing as evidenced by loss of water under plants from the surface layer (0–15 cm) with minimal infiltration to the 20–30 cm layer after 24 h (Fig. 5a, b). Although loss of water to evaporation in the surface layer of interspaces was also high during this time (Fig. 5a), the lower water content under plants indicates the importance of transpiration to water loss under plants. Evaporative losses from
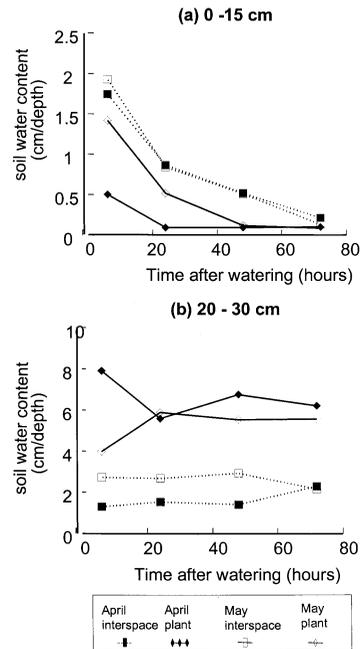

Fig. 5. Soil water content through time following a watering event under *B. eriopoda* plants and in bare interspaces for two depths: (a) 0–15 cm; (b) 20–30 cm.
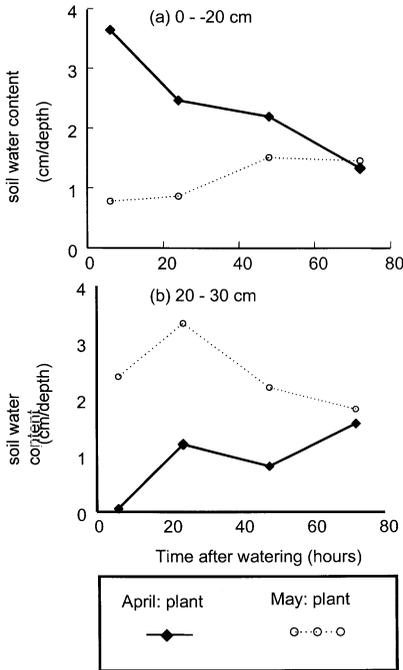
Fig. 6. Soil water content through time following a watering event under *L. tridentata* plants and in bare interspaces for two depths: (a) 0–20 cm; (b) 20–30 cm.

the upper layers were similar for both sample dates based on soil water content in the interspaces where only a small amount of water infiltrated to the deeper depth (Fig. 5b).

For *L. tridentata*, use of soil water by plants occurred during both April and May, however different depths were utilized in each time period. In April, transpiration losses under plants were highest initially from the surface layer whereas losses from the deeper layer were highest after 24 h in May (Fig. 6a, b). In April, the drying of the surface layer under plants continued through time due to transpiration since evaporative losses based on interspace dynamics were low (Fig. 6c), and losses to infiltration were small after 6 h (Fig. 6b). In May, the rapid drying of the surface layer within 6 h was mostly due to infiltration to the deeper depth (Fig. 6b), although evaporative losses within the first 6 h were also possible that were not measured. Decrease in water content in the deeper

layer after 24 h indicates losses to transpiration (Fig. 6b) since the same depth in the interspaces remained wet until 48 h after watering.

These results from the watering experiment were used to estimate plant growth parameters for the three dominant species. Optimum temperatures for plant growth by *L. tridentata* and other C_3 species (10 °C) and by *B. eriopoda* and other C_4 species except *B. gracilis* (22 °C) were based on standard response curves (Table 1) (Williams and Markley, 1973; Salisbury and Ross, 1978; Monson et al., 1983). Optimum temperature for *B. gracilis* was intermediate between C_3 and C_4 species based on results from the watering experiment. These results are supported by field observations of growth of this species at temperatures intermediate to C_3 and C_4 species at the SEV. These results also verify total root distributions of these species used to parameterize seedling biomass by depth where roots of both grasses and shrubs are concentrated in the surface layers (Table 1).

Parameters for partitioning root biomass into coarse and fine components by layer and for converting biomass to surface area were estimated from root studies conducted in the shortgrass steppe and Chihuahuan desert (Gibbens and Lenz, 2001). For all species except *L. tridentata*, it was assumed that 50% of root biomass in each layer are fine roots. For *L. tridentata*, 25% of roots in the upper 10 cm and 50% of roots in the other layers were assumed to be fine roots. For all species, fine root biomass was multiplied by 0.2 cm^2/g to obtain surface area whereas coarse roots had a conversion from biomass to surface area of 0.1 cm^2/g. In these simulations, nitrogen was assumed to be constant for every year in order to focus on competition for soil water; thus parameters were not needed to simulate nitrogen dynamics. Water-use efficiency values (g biomass/cm water) were estimated from the literature using species with similar physiologies (Table 1) (McGinnies and Arnold, 1939; DeGarmo, 1966). Root:shoot production was assumed to be 0.5 for all species (Cunningham et al. 1979; DeGarmo, 1966; Milchunas and Lauenroth, 1992).

4.4. Species parameters: mortality

No disturbances were included in these simulations, thus the only sources of mortality were maximum age and slow growth. Maximum age of each species or species-group was approximated using longevity data for similar species from shortgrass steppe and Chihuahuan desert communities when possible, and for similar species from other semiarid communities when necessary (Table 1; Nelson, 1934; Canfield, 1957; Kerster, 1968; Dittberner, 1971; Wright, 1972). *Bouteloua gracilis* was excluded from this source of mortality because its growth form results in parts of plants dying (tillers) rather than entire plants (Fair et al.,

1999, 2001). Optimum growth rates needed for determination of slow growing plants were estimated based on the number of years required for a plant to reach full size while growing under optimum resource conditions (Dittberner, 1971; Wright, 1972). Root (0.12–0.33) and leaf or tiller turnover rates (0.33) were estimated from Milchunas and Lauenroth (1992) and Reynolds et al. (1999).

5. Experimental simulations

Two sets of simulations were conducted to examine the importance of life history traits to patterns in species dominance. The first set examined effects of soil texture on dominance for current climatic conditions. The second set predicted shifts in dominance under directional changes in climate. Each simulation began by initializing each plot without plants to avoid bias in initial conditions. Twenty-five replicate plots were simulated for each soil texture to obtain a quasi-equilibrium at the landscape scale (Shugart, 1984). The only parameters that changed between soil types were soil texture and the recruitment probability for each species. The same sequence of climate was used for both soil textures. Current climatic conditions were used for the first 300 years of each simulation followed by a 50 years linear ramp in climate until year 350 when the new climatic conditions were used until year 600 (described in Section 4.1). The same species and soils parameters were used as in the current climate runs.

Model output included above- and belowground biomass for each species or group through time. For clarity of presentation, aboveground biomass of plants through time averaged across the 25 plots are shown for the three dominant species separately (*B. gracilis*, *B. eriopoda*, *L. tridentata*) and by combining the remaining species groups into four lifeforms (other perennial grasses, subshrubs, perennial forbs, annuals) (Figs. 7–12). Model results under current climatic conditions were verified using field estimates of cover and biomass from the SEV for each species or group.
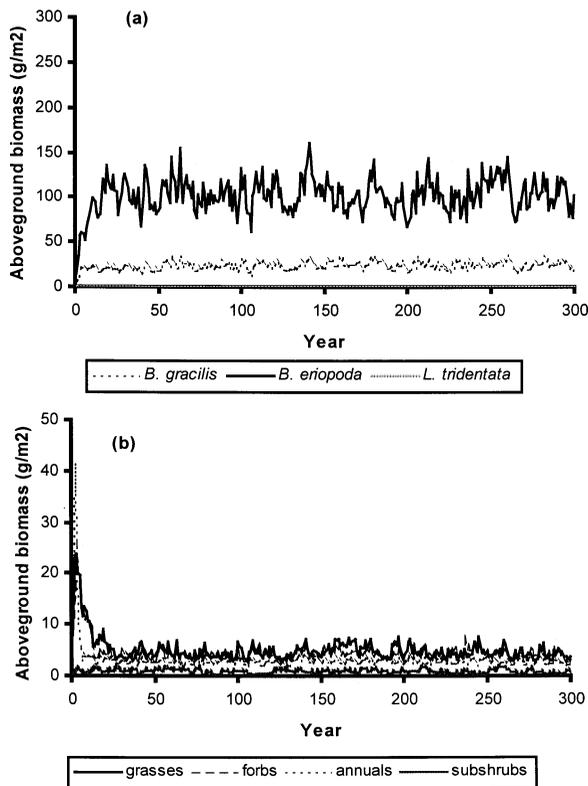

Fig. 7. Average aboveground biomass (g/m²) through time on a sandy loam soil under current climate for: (a) *B. eriopoda*, *B. gracilis* and *L. tridentata;* (b) four species groups (other perennial grasses, perennial forbs, annuals, and subshrubs).
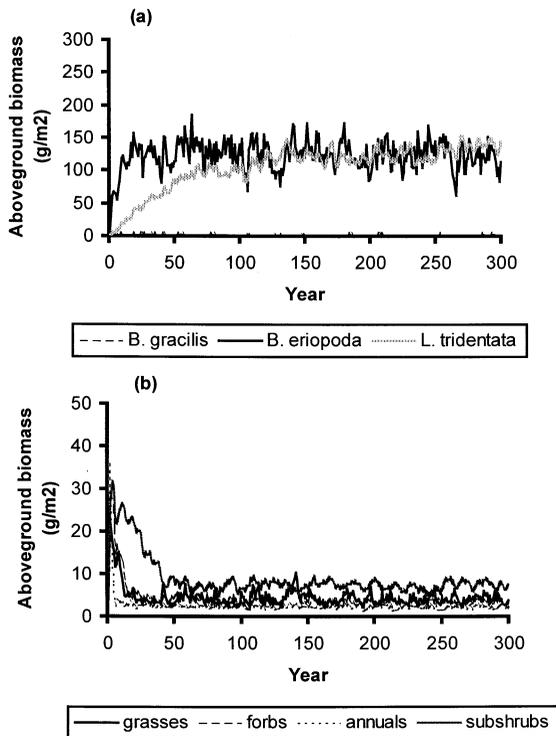
Fig. 8. Average aboveground biomass (g/m²) through time on a loamy sand soil under current climate for: (a) *B. eriopoda*, *B. gracilis* and *L. tridentata;* (b) four species groups (other perennial grasses, perennial forbs, annuals, and subshrubs).

6. Results and discussion

6.1. Consequences of differences in life history traits to dominance under current climate

6.1.1. Sandy loam soil

Under current climatic conditions, *B. eriopoda* dominated simulated biomass on the sandy loam soil with > 70% of total aboveground biomass after the initial 100 years recovery period from a bare plot stage (Fig. 7a). The range in biomass between years 200 and 300 (67–145, average = 104 g/m²) is comparable to field estimates of *B. eriopoda* biomass in mixed grass patches on sandy loam soils at the SEV (85–134 g/m²; Peters, 2000b; in review). High year-to-year variation in *B. eriopoda* biomass resulted from seedling establishment events as well as vegetative growth from stolons. *B. gracilis* had the second highest simu-

lated biomass after year 200 (average = 24 g/m², range = 15–35 g/m²). These values are smaller than field estimates of aboveground biomass for this species (50–119 g/m²; Peters, 2000b; Peters in review). Because *B. gracilis* biomass dynamics are primarily a result of growth and competition for belowground resources rather than establishment and mortality, these underestimates suggest that better information is needed on parameters related to the acquisition of soil water by depth. Although observations suggest that *B. gracilis* is more deeply rooted than *B. eriopoda*, field studies have not been conducted at the SEV to document the depth distribution of active roots, and in particular the maximum rooting depth. The watering experiment conducted as part of this study identified important temporal differences in water uptake between *B. gracilis* and *B. eriopoda* for surface roots (< 30 cm). Model results indicate that similar studies are needed for deeper layers.
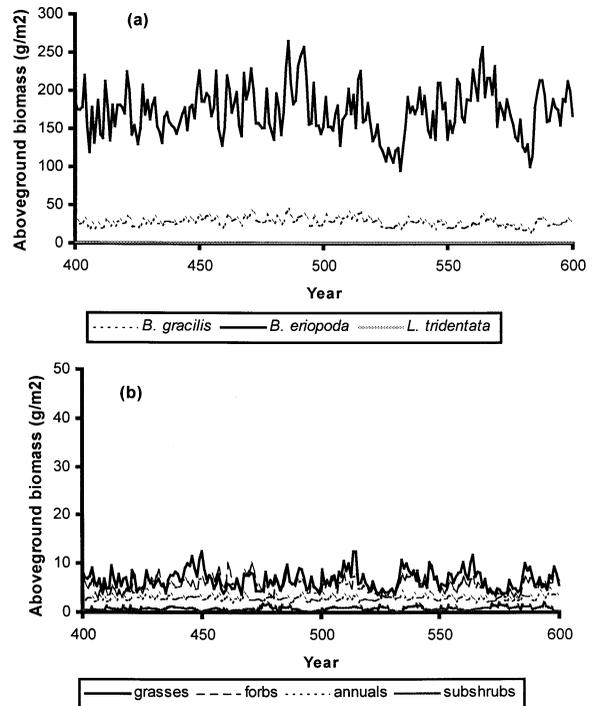

Fig. 9. Average aboveground biomass (g/m²) through time on a sandy loam soil under GFDL climate for: (a) *B. eriopoda*, *B. gracilis* and *L. tridentata;* (b) four species groups (other perennial grasses, perennial forbs, annuals, and subshrubs).
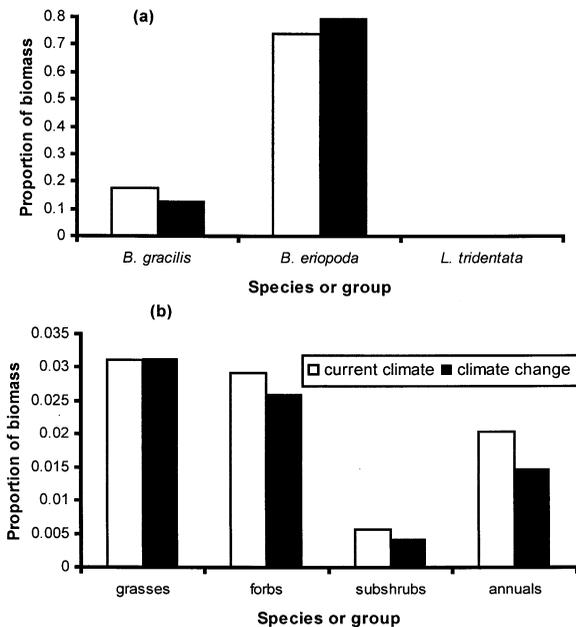
Fig. 10. Proportion of total aboveground biomass through time on a sandy loam soil under current climate and under GFDL climate for: (a) *B. eriopoda*, *B. gracilis* and *L. tridentata;* (b) four species groups (other perennial grasses, perennial forbs, annuals, and subshrubs).

After year 25, other species groups had < 10 g/m² biomass, and in general, subshrubs had the lowest and perennial grasses had the highest biomass of these four groups in any given year (Fig. 7b). The proportion of simulated biomass attributed to each group is similar to field estimated proportions based on cover (0.01–0.09) in patches codominated by *B. gracilis* and *B. eriopoda* on sandy loam soils (Hochstrasser et al., in press). *Larrea tridentata* biomass was 0 throughout the simulation since its probability of seedling establishment was 0 on this soil type.

Dominance by *Bouteloua eriopoda* of plant communities on sandy loam soils is likely related to a combination of life history traits. The ability of this short-lived species (35–40 years; Nelson, 1934) to spread vegetatively through the production of stolons is critical to its dominance through time. A preliminary sensitivity analysis showed that model results are particularly responsive to this parameter. *B. eriopoda* dominance increases

dramatically as the probability of regrowth increases beyond the conservative estimate used in these simulations (0.01). Frequent seedling establishment events (1/7 years) are also important, especially following complete mortality of *B. eriopoda* plants. Because the predicted frequency of establishment for this species at the SEV based on soil water dynamics is higher than observed at a site 200 km to the south with higher annual temperatures (15.1 °C) and similar precipitation (Neilson, 1986), vegetative spread is expected to become increasingly important as temperatures increase and establishment probabilities decrease within the geographic distribution of this species. Most research on *B. eriopoda* has been conducted at this southern site, the Jornada Experimental Range. The extent to which this information can be transferred to other sites is unknown. Because of the importance of establishment and rate of stolon production to dominance by *B. eriopoda*, studies are needed to experimentally examine controls on these processes at this grassland/shrubland transition zone.

For *B. gracilis*, an indeterminate longevity is critical to its dominance and persistence through time. Estimates from the shortgrass steppe (> 400 years; Coffin and Lauenroth, 1990) and mixed-grass prairie (> 100 years; Fair et al. 1999) suggest that *B. gracilis* plants in central New Mexico are very long-lived, although long-term studies are needed to document lifespan at this transition zone. This species grows slowly and is predicted to establish less frequently than *B. eriopoda* at the SEV (1/27 years), but plants are very persistent following establishment. Disturbances are the primary source of mortality and as much as 90% of the tillers can be killed without causing plant mortality (Fair et al., 2001). Similar to *B. eriopoda*, most information about *B. gracilis* is available from a site located within the biome in northern Colorado. Previous work showed geographic variation in *B. gracilis* life history traits using a common garden study (Riegel, 1940), however the ecological significance of this variation to patterns in species dominance at sites located throughout the region has not been examined.

6.1.2. Loamy sand soil

B. eriopoda and *L. tridentata* codominated aboveground biomass on the loamy sand soil after the initial 100 years recovery period (Fig. 8a). Each species had on-average 45–48% of the total aboveground biomass. This codominance based on biomass is supported by field estimates based on cover for loamy sand soils (Peters, 2000b). Simulated biomass from year 200–300 for *B. eriopoda* (average = 122 g/m², range = 61 to 170 g/m²) and for *L. tridentata* (128 g/m²; 107–154 g/m²) were also similar to field measurements on these soils, although average biomass was underestimated by 55–59 g/m² for both species (*B. eriopoda*:178 g/m²; *L. tridentata* 187 g/m²) (Peters, 2000b). Subshrubs, in particular *G. sarothrae*, had the largest biomass of the remaining four groups and contributed 5–10% of the total through time (Fig. 8b). Field measures of cover for these groups showed similar proportions as simulated biomass

(Peters, 2000b). *B. gracilis* was negligible on these soils, both in the model (< 1% of biomass) and in the field (< 5 of cover; Peters, 2000b).

Understanding controls on dominance by *B. eriopoda* and *L. tridentata* is particularly important in central and southern New Mexico since much of this area was grassland prior to the early 1900s (Buffington and Herbel, 1965; Grover and Musick, 1990). Invasion by shrubs, including *L. tridentata* and *Prosopis glandulosa* (honey mesquite), has resulted in changes to soil properties, such as low water-holding capacity, organic matter, and increased potential for erosion, that promote continued shrub dominance through time (Schlesinger et al., 1990). Large-scale changes from grasslands to shrublands have been attributed to a combination of factors, including grazing by cattle, drought, and reduction in fire intensity and frequency (Neilson, 1986; Bahre, 1991; Archer et al., 1995). Although most research
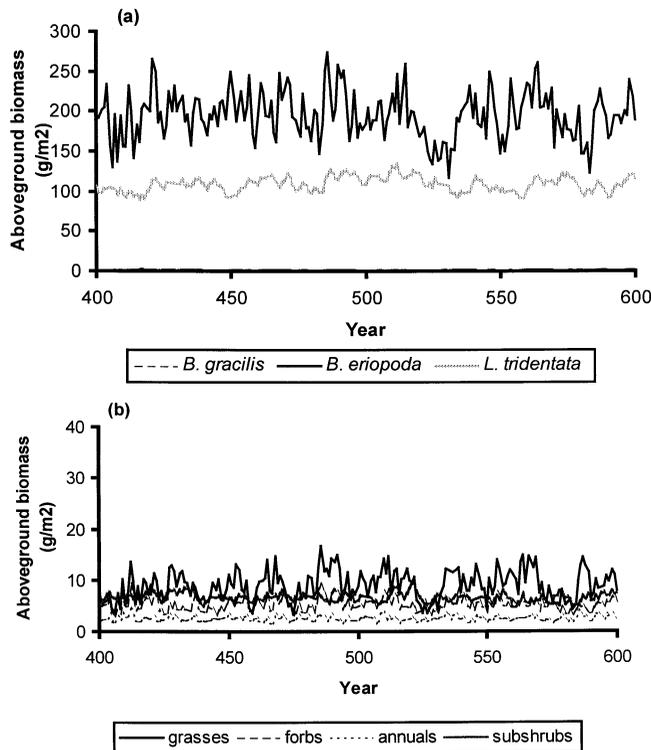

Fig. 11. Average aboveground biomass (g/m²) through time on a loamy sand soil under GFDL climate for: (a) *B. eriopoda*, *B. gracilis* and *L. tridentata;* (b) four species groups (other perennial grasses, perennial forbs, annuals, and subshrubs).
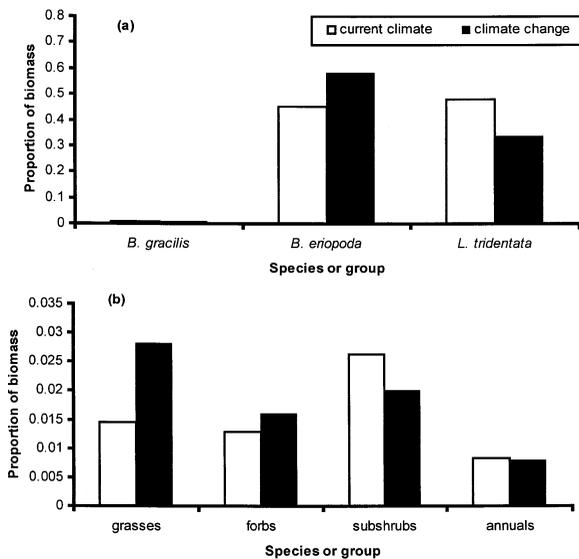
Fig. 12. Proportion of total aboveground biomass through time on a loamy sand soil under current climate and under GFDL climate for: (a) *B. eriopoda*, *B. gracilis* and *L. tridentata;* (b) four species groups (other perennial grasses, perennial forbs, annuals, and subshrubs).

has focused on the factors affecting desertification, recovery of grasslands following shrub invasion is also possible, and has occurred several times over the past 10,000 years (Van Devender and Spaulding, 1979; Monger et al., 1998). Thus, transition zones between dominant grasses (*B. eriopoda)* and shrubs (e.g. *L. tridentata)* are very dynamic. The ability of ECOTONE to represent these grass/shrub transition zones under simple climatic and soils conditions in the current analysis suggests that plant life history traits interacting with the environment play an important role in generating complex vegetation dynamics.

6.2. Predicted patterns in species dominance under GFDL climate

6.2.1. Sandy loam soil

Under a GFDL climate change scenario, plant communities on sandy loam soils were strongly dominated by *B. eriopoda* with small amounts of biomass of *B. gracilis* and other species (Fig. 9). An increase in temperature, particularly during the summer when precipitation also increased,

favored *B. eriopoda* with higher optimum temperatures for growth compared to *B. gracilis*. Average biomass of *B. eriopoda* increased $> 60\%$ to an average of 170 g/m^2 (Fig. 9a). By contrast, *B. gracilis* biomass decreased 12% to an average of 27 g/m^2. Because species and soils parameters remained the same for both sets of climate runs, temporal partitioning of soil water documented from the short-term watering experiment was sufficient to account for the differential response by the two *Bouteloua* species. The proportion of total biomass attributed to *B. eriopoda* also increased whereas the proportion of biomass attributed to all other species groups decreased compared to historical climate runs, except for other perennial grasses (Fig. 10).

6.2.2. Loamy sand soil

A directional change in climate resulted in a shift from codominance by *B. eriopoda* and *L. tridentata* to clear dominance by *B. eriopoda* on the loamy sand soil (Fig. 11a). *B. eriopoda* biomass increased 64% to 190 g/m^2 compared to biomass under current climatic conditions (Fig. 9a). *L. tridentata* biomass decreased on-average 15% to 109 g/m^2. Other species groups had biomass less than 10 g/m^2 with the largest biomass in most years attributed to other perennial grasses and subshrubs (Fig. 11b). The proportion of total biomass attributed to *B. eriopoda* and other perennial grasses and forbs increased whereas the proportion attributed to *L. tridentata* and subshrubs decreased compared to simulated biomass under current climatic conditions (Fig. 12).

These results suggest that directional changes in climate provide one mechanism whereby *B. eriopoda* can dominate a plant community currently codominated by *L. tridentata*. These results are complementary to predictions from a biogeographic modeling analysis of the effects of directional climate change on vegetation dynamics within the continental US (Neilson and Drapek, 1998). This broad-scale analysis predicts an increase in grasslands and decrease in woody vegetation for parts of the Southwestern US. Both the biogeographic analysis and the current gap modeling analysis make a number of simplifying as-

sumptions that may affect the result: seeds are always available, soil properties are appropriate for seed germination and seedling establishment of perennial grasses, and regeneration of grasses is possible immediately after shrub mortality. Recent analyses using a gap dynamics modeling approach suggest the importance of seed availability in changing from grass patches to shrub-dominated areas (Peters and Herrick, 1999a) and of constraints on seedling establishment associated with soil properties on shrub-dominated microsites (Peters and Herrick, 1999b). Both of these processes would reduce the rate of recovery by *B. eriopoda* following shrub invasion, and have not been accounted for in the current model formulation.

7. Summary and conclusions

Interactions among plant life history traits, climate, and soils that generate patterns in species dominance at a biome transition zone are complex. Climate and soil texture interact to affect soil water availability that influences plant establishment, survival and mortality. Individual plants interact through their effects on the availability of soil water by depth in the soil profile. I developed an individual-based simulation model to examine these interactions for multiple lifeforms (herbaceous, woody), soils and climatic conditions. The model successfully simulated species dominance patterns on two soil types under current climatic conditions. Differences among dominant species in establishment and spatial and temporal acquisition of soil water resulted in different combinations of species on different soils. The model also predicted shifts in dominance following directional changes in climate that modifies the availability of soil water. These complex interactions between multiple life history traits and environmental factors would be difficult, if not impossible, to study experimentally. Simulation modeling in combination with key short-term experiments is a powerful tool that can be used to examine the importance of multiple plant and soil

processes as well as environmental factors on dominance patterns at biome transition zones. Because of its generality, the model shows great potential to simulate other ecotones containing mixed species or lifeforms where belowground resources are the primary control on vegetation dynamics. This model was also shown to be useful in simulating dynamics of invasive species in a semiarid grassland (Goslee et al., 2001).

ECOTONE was developed as a synthetic tool to improve our understanding of transitions between Chihuahuan desert and shortgrass steppe biomes in North America. Understanding effects of environmental factors, such as soils and climate, on species dominance is critical to our ability to manage these transitional ecosystems effectively. This information is also useful in predicting shifts in dominance through time as the environment changes. In the model, the Chihuahuan desert grass, *Bouteloua eriopoda*, dominated both soils following a directional change in climate that increased summer precipitation. Alternative climate scenarios have been proposed for central New Mexico including increases in winter precipitation that presumably would favor C_3 shrubs (*L. tridentata*) and grasses that respond to cool temperatures, such as *B. gracilis*. Effects of these alternative climate scenarios on species dominance and composition could also be simulated given that the model successfully represents current conditions. Additional factors not included in the model, including grazing by cattle and soil disturbances, are also expected to affect dominance patterns across the landscape, and can be readily incorporated into future modeling experiments. Integrating these various environmental factors into a model that contains multiple interacting lifeforms results in a powerful tool to both improve our understanding of ecotonal ecosystems and to predict shifts in dominance through time and space.

Most gap dynamics models have been developed for forests (e.g. Bugmann and Solomon, 1995; Starfield, 1996; Liu and Ashton, 1998; Dubé et al., 2001) with few exceptions (Coffin and Lauenroth, 1990; Higgins et al., 1996). One of the

main limitations of gap models is the large number of small plots containing fine-scale demographic data that need to be simulated to represent large landscapes. This limitation is particularly true for herbaceous models where plot or cell size is much smaller than for trees. A number of approaches have been developed recently to overcome these limitations for forested landscapes. Gap models have been used to derive a forest-transition model that is applied to the landscape (Acevedo et al., 1996). Object-oriented programming has also been used to link species floristics of forests with biophysical characteristics of land units (He et al., 1999a,b). More recently, artificial neural networks have been used to link species-specific results of forest gap models to spatially-explicit biophysical conditions (Gullison and Bourque, 2001). These developments are applicable to scaling the ECOTONE model to heterogeneous landscapes and represent a future direction for research.

ECOTONE fits into the dynamic-transient vegetation model class as defined by Bolliger et al. (2000). These dynamic models that account for competition and species-specific life history characteristics are in contrast to static equilibrium models calibrated from large-scale data sets with no detailed physiological mechanisms. Recent analyses comparing the two approaches for ecosystems in Switzerland suggest that similar results can be obtained from both types of models under current climatic conditions (Bolliger et al., 2000). Generally similar results were also obtained using ECOTONE and a static equilibrium model (MAPSS; Neilson and Drapek, 1998) when simulating the response of arid systems to directional changes in climate. Both models show an increase in grasslands in central New Mexico using an equilibrium climate change scenario. A more powerful approach to comparing different kinds of models is to link them hierarchically and take advantage of the strengths of the different kinds of models (Peters and Herrick, 2001). This approach shows great promise in simulating landscape and regional scale dynamics, but has not been rigorously tested or implemented.

Acknowledgements

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