



Modelling Vegetation Change and Land Degradation in Semiarid and Arid Ecosystems: An Integrated Hierarchical Approach

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ABSTRACT

Despite the dedication of significant human, financial and technological resources, dryland degradation continues unabated in both the developed and developing world. Many of the causes have been described, and the consequences have been extensively documented. In this paper, we argue that the failure of many attempts to stop or reverse dryland degradation can be explained by a failure to (1) recognize when ecosystems have crossed ecological, edaphic or geomorphic thresholds, and (2) identify and address the properties and/or processes at relevant scales that confer resistance and resilience. We illustrate how simulation models can be used to address some of these limitations using examples from one type of model, an individual-based gap dynamics model of grasslands and shrublands (ECOTONE). We used ECOTONE to predict the effects of climatic fluctuations and disturbance frequency on local and regional patterns in species dominance and composition. Our results show that patterns in dominance between two perennial grasses (*Bouteloua gracilis*, *Bouteloua eriopoda*) at semiarid-arid biome transition zone are not predictable based on responses within each biome. An increase in disturbance frequency at the ecotone shifted plant communities to dominance by the short-lived, stoloniferous grass (*B. eriopoda*) from communities codominated by *B. gracilis* or the shrub, *Larrea tridentata*.

We propose a strategy that addresses problems in semiarid and arid ecosystems more effectively than previous approaches based on an integrated, hierarchical modeling approach. This approach employs multiple tools, such as geographic information systems, state and transition models, remote sensing, and expert knowledge, in an iterative approach with simulation models. This strategy is applicable both to research on the processes of dryland degradation, and to management projects to stop or reverse degradation.

KEYWORDS: Chihuahuan Desert, disturbance, ecotone, gap dynamics simulation model, monitoring, Shortgrass Steppe

1.0 INTRODUCTION

Scientists are currently faced with a number of challenges related to dryland assessment, monitoring

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and management. These challenges include, but are not limited to, (1) assessment of ecosystem condition at multiple scales for multiple policy, conservation and management objectives, (2) prioritization of land areas for targeting monitoring and management resources, and (3) prediction of ecosystem responses to future changes in climate and management. None of these issues have been adequately addressed using currently available experimental, analytical and numerical approaches. Powerful tools and approaches are available for prediction (experiments, simulation models), assessment (monitoring, remote sensing, state and transition diagrams, and geographic information systems) and prioritization (expert knowledge, simulation models). However, the complexity of the problems currently facing scientists and managers working in arid and semiarid ecosystems requires a new approach that integrates multiple tools across spatial and temporal scales. Our overall objective was to examine the predictive power of one tool (simulation models) and to develop an approach that integrates these tools in order to make assessments, prioritize resources, and predict ecosystem responses under variable environmental conditions.

Although arid ecosystems are extremely diverse in soils, topography, and plant and animal assemblages, most of these systems share some fundamental characteristics due to the dominant role of moisture as a limiting factor. These characteristics can be used to make generalizations about the response of these systems to both natural and anthropogenic disturbances. A key characteristic of most arid ecosystems is that the relationship between vegetation dynamics and environmental variation in climate, soils or disturbance tends to be extremely non-linear and is defined by thresholds (Westoby *et al.*, 1989). In many arid ecosystems, plant community structure is tightly coupled with the spatial distribution of soil and water resources (Schlesinger *et al.*, 1990; Ludwig and Tongway, 1995). In order to survive in arid environments, most plants harvest water from an area larger than that defined by their canopies; thus their effect on the microenvironment that they occupy is disproportionate to their size (Gile *et al.*, 1997; 1998). Changes in the cover or spatial distribution of one or more species can lead to changes in soil surface hydrology, in particular infiltration and water-holding capacity. In these cases, the re-establishment of plants associated with a previous community is difficult, if not impossible, without addition of external inputs (Tongway and Ludwig, 1996; Davenport *et al.*, 1998). Relatively irreversible transitions are referred to as thresholds (Westoby *et al.*, 1989) that are analogous to chemical transformations in which an energy input is required to return a material to an earlier state.

Another key characteristic of arid and semiarid ecosystems is that they are often strongly affected by both fluctuations and directional changes in climate and disturbance regimes, including grazing, fire and small animal activity (Archer, 1994; Le Houérou, 1996; Weltzin *et al.*, 1997). As a result, arid and semi-arid ecosystems are commonly viewed as highly susceptible to degradation. In some cases this is due to low resistance to change, but it is more frequently due to low resilience or capacity to recover following degradation (*sensu* Pimm, 1984 as modified by Holling & Meffe, 1996). Arid ecosystems tend to recover slowly from degradation due to slow rates of biological production and mineral weathering associated with low moisture availability (Hillel, 1998; Beyer *et al.*, 1999). Although both resistance and resilience to climate and disturbance vary widely across arid and semi-arid ecosystems as a function of interacting soil, geomorphic and vegetation processes (McAuliffe, 1994), previous approaches to understanding and predicting these responses have not often considered spatial and temporal variation among geomorphic surfaces and plant communities.



Simulation modeling, used in conjunction with long-term databases, is a commonly used approach to examining complex ecosystem interactions and to predicting responses to environmental drivers. A variety of modeling approaches are available to predict vegetation response, each with its own strengths and limitations. Biogeographic models are used to predict broad-scale patterns in vegetation for regions, continents, and the globe (e.g., Woodward *et al.*, 1995; Neilson & Drapek, 1998). These models typically operate at the 0.5° latitude by 0.5° longitude grid cell and make a number of simplifying assumptions about controls on vegetation dynamics. In particular, plant growth and tradeoffs between competition for water, nitrogen and light are the key factors controlling plant responses. Soils are assumed to be static with respect to their capacity to support different plant communities. Thus, there are no feedbacks between vegetation, climate and soils, and landscape heterogeneity within grid cells is ignored. Nonetheless, these models are extremely useful for predicting functional group patterns in vegetation at the biome scale.

Species-based successional models that operate on plots scaled to the size of individual plants (< 1 to 100 m^2) represent another type of model used to predict vegetation dynamics (e.g., Shugart, 1984; Coffin & Lauenroth, 1990; Urban & Shugart, 1992). These models simulate the recruitment, growth and mortality of individual plants on grids of plots. Landscape-scale processes, such as seed dispersal and the spread of fire among plots, and feedbacks between vegetation and soil processes are among the complex interactions that can be represented in these models (Coffin & Lauenroth, 1989; Peters & Herrick, 1998; Miller and Urban, 2000). Although these “gap models” are extremely useful in predicting plant- and species-level responses and interactions under a variety of environmental conditions, they are limited computationally in the spatial extent that can be simulated ($< 20 \text{ ha}$) as a result of the small plot size and the detailed processes that they include. Recent attempts to expand the spatial extent of these models include linking gap models with landscape-scale models and deriving statistical meta-models from gap model results that retain fine-scale information, but represent larger areas (He *et al.*, 1999; Urban *et al.*, 1999).

Neither of these types of models is sufficient in scope to address the complex issues associated with land degradation in arid ecosystems. Each model type is restricted to certain spatial and temporal scales that limit the applicability of individual models across the large range of scales needed to address aridland problems. Furthermore, modeling is only one tool of many (i.e., experiments, monitoring, geographic information systems, and remote sensing) that are available and being used, at most in combination with 1-2 other tools. Because each tool has its own strengths and weaknesses, a new approach is needed that effectively integrates simulation modeling with other tools. Our goal was to develop an integrative approach to addressing complex issues in arid ecosystems that provides a general framework for understanding and predicting ecosystem responses to land degradation and other factors. Simulation modeling is a key component of that new approach.

We had two specific objectives: (1) to illustrate the utility of simulation models in addressing key questions in arid and semiarid ecosystems using one type of model. Our approach was to use an individual-based, gap dynamics model (ECOTONE) to predict the effects of climatic fluctuations on regional patterns in vegetation dynamics, and the effects of disturbance on vegetation dynamics at an arid-semiarid ecotone. We focused on two major grassland biomes in North America and their



ecotone for these simulations. (2) to develop a general problem-solving approach to account for the characteristics, heterogeneity, and dynamics of arid ecosystems. Our approach was to link multiple types of models hierarchically and to integrate these simulation models with other types of tools, including geographic information systems, remote sensing, experiments, state and transition models, and expert knowledge in order to make assessments, prioritize research and resources, and make predictions about future ecosystem dynamics. The inclusion of state and transition models helps focus attention on those parts of the landscape which are most sensitive to change. By defining soil-vegetation associations in terms of their resistance and resilience, these models allows us to stratify the landscape based on its dynamics.

2.0 METHODS

2.1 Site descriptions

Our simulation model was parameterized and tested for three sites located along a semiarid to arid gradient in the western U.S. These sites represent one of two grassland biomes and the ecotone between them. The shortgrass steppe, located along the eastern slope of the Rocky Mountains, meets the Chihuahuan desert, located in the central Rio Grande valley and south to Chihuahua, Mexico, at a biome transition zone in central New Mexico (Gosz, 1992; Gosz & Gosz, 1996). The site selected to represent the shortgrass steppe was the Shortgrass Steppe Long Term Ecological Research (SGS-LTER) site located in northcentral Colorado (40.8° N, 104.8° W, 1650 m ASL). This site is located approximately 60 km northeast of Fort Collins, Colorado. Climate of the site is semiarid; long-term (1916-1995) mean annual precipitation was 310 mm/y (SD=86). Mean monthly temperatures over the same time period ranged from -2.8° C in January to 21.7° C in July. The site is characterized by a continental climate where >80% of the annual precipitation occurs during the April through September growing season. The topography is gently rolling with level uplands separated by swales. Surface soil textures range from clay loam to loamy sand. Moderate grazing by cattle occurs throughout the SGS at intensities maintained since 1939 (Klippel & Costello, 1960). Plant communities are dominated by the perennial C₄ grass, *Bouteloua gracilis* (H.B.K.) Lag ex. Griffiths (blue grama) with 60 to 75% of total cover attributed to this species; other grasses, succulents, shrubs, and forbs account for the remainder of plant cover (Lauenroth & Milchunas, 1992). A complete site description is available at <http://sgs.cnr.colostate.edu>.

The Jornada Experimental Range LTER (JRN) in southern New Mexico was selected to represent Chihuahuan desert grasslands and shrublands (Schmutz *et al.*, 1992). This site (32.5° N, 106.8° W, 1350 m ASL) is located approximately 30 km northeast of Las Cruces, NM. Climate is arid to semiarid; long-term (1916-1995) mean annual precipitation was 249 mm/y (SD=87). Mean monthly temperatures ranged from 3.8° C in January to 26.1° C in July. This site is characterized by a monsoonal pattern in precipitation with > 30% of annual rainfall occurring in August and September. Grazing by cattle occurs throughout the region at varying intensities. The JRN is located at the southern end of a hydrologically closed basin and is characterized by a complex system of alluvial fans (bajadas) and ephemeral playa lakes. Much of the basin is dominated by coarse-textured aeolian and fluvial sediments from the Rio Grande. Uplands are dominated by the perennial C₄ grass, *Bouteloua eriopoda* (Torr.) Torr. (black grama). These grasslands occur on sandy loams to loamy



sands with a calcium carbonate layer at depths of 15 to > 50 cm. Bajadas with shallow rocky soils are often dominated by the C_3 shrub, *Larrea tridentata* (DC.) Coville (creosotebush). Other grasses, succulents, shrubs, and forbs account for the remainder of plant cover (Paulsen & Ares, 1962). A complete site description is available at <http://jornada.nmsu.edu>.

The Sevilleta National Wildlife Refuge LTER (SEV; 34.5° N, 106.9° W, 1650 m ASL) located approximately 75 km south of Albuquerque, New Mexico was selected to represent the transition between the shortgrass steppe and the Chihuahuan desert. The climate is semiarid to arid; long-term (1916-1995) mean annual precipitation from a nearby weather station in Socorro, NM (34.1° N, 106.9° W) was 232 mm/y (SD=79). Mean monthly temperatures ranged from 2.6° C in January to 24.6° C in July. Over half of the annual precipitation occurs during July through September. Grazing by cattle has been excluded from the SEV since 1973, although grazing by native herbivores, such as pronghorn and rabbits, occurs at low to moderate intensities. Vegetation of the specific study area, the McKenzie Flats, is typical of the Chihuahuan desert grasslands-shortgrass steppe transition. Patches of vegetation of variable size (<10 m² to >1000 m²) and shape may be dominated or codominated by species from either biome: *B. gracilis*, *B. eriopoda*, and *L. tridentata* (Kröel-Dulay *et al.*, submitted). Other C_3 and C_4 annual and perennial grasses and forbs, subshrubs and succulents occur within patches dominated or codominated by one or more of these three species. The site is located on an alluvial fan deposit with a west-facing aspect and a slope < 2%. The surface soil texture is 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. Complete site description is available at <http://sevilleta.unm.edu>.

Several types of climatic fluctuations occur in the shortgrass steppe-Chihuahuan desert region. The El Niño - southern oscillation phenomenon (ENSO) often strongly influences non-monsoonal precipitation in central and southern New Mexico (Molles & Dahm, 1990; Peters, 2000). In this area, 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 ENSO signal is much weaker in eastern Colorado with less predictability in rainfall amounts between El Niño and La Niña years. Drought also occurs periodically in this region with moderately severe drought occurring on average every 20 years, and more severe drought every 50-60 y (Woodhouse & Overpeck, 1998). Because each of the three sites experiences different climate, the effects of climatic fluctuations (ENSO, drought) on vegetation dynamics are also expected to differ among sites. Furthermore, similarities and differences in species composition along this aridity gradient allow us to test the importance of climate and climatic fluctuations to regional patterns in species dominance and vegetation dynamics.

The disturbance regime throughout the region includes a variety of disturbances operating over a range of spatial and temporal scales. Large disturbances, such as lightning-ignited fire, occur infrequently with low intensity due to the low biomass and fuel load in these arid systems (Bahre, 1995). Soil disturbances created by burrowing animals occur frequently and kill plants in small patches. The most prevalent soil disturbances are mounds created by the burrowing or cutting activities of Western harvester ants, badgers, and several species of kangaroo rats (*Dipodomys*



spectabilis, *D. ordii*). These mounds range in size from 0.5 to 20 m² and at frequencies from < 2 to > 10/ha (Coffin & Lauenroth, 1988; Andersen & Kay, 1999). Although effects of small soil disturbances on short-term vegetation dynamics have been examined in the field at all three sites (Moroka *et al.*, 1982; Coffin & Lauenroth, 1988; Fields *et al.*, 1999), the importance of disturbance frequency has not been well-studied. Because one or more grass species from adjacent biomes can dominate communities at the SEV, we expect that disturbance frequency may be particularly important to shifts in species dominance at this site.

2.2 Simulation model description

Our model, ECOTONE, was developed for arid and semiarid grasslands and shrublands and is described in detail in Peters (submitted). ECOTONE was based on STEPPE, a model used extensively to simulate shortgrass steppe communities of eastern Colorado (Coffin and Lauenroth, 1990; 1994). Similar to gap dynamics models of forests (FORET: Shugart, 1984; JABOWA: Botkin, 1993), ECOTONE simulates recruitment, growth, and mortality of each plant on a small plot at an annual timestep (Fig. 1). Plot size (0.25-1 m²) is determined by the resource space used by a full-size plant of the dominant species. Recruitment and mortality have stochastic elements whereas growth is deterministic and based upon competition for resources. The probability of recruitment for each species is determined by a number of processes, including the production, dispersal, and storage of viable seeds, and the germination and establishment of seedlings. Mortality for each plant depends upon species-specific longevity and slow-growth constraints where insufficient new biomass to support maintenance or growth results in a higher probability of plant mortality (Shugart, 1984). Disturbances are another source of plant mortality that depend upon the type of disturbance agent and its size and frequency of occurrence.

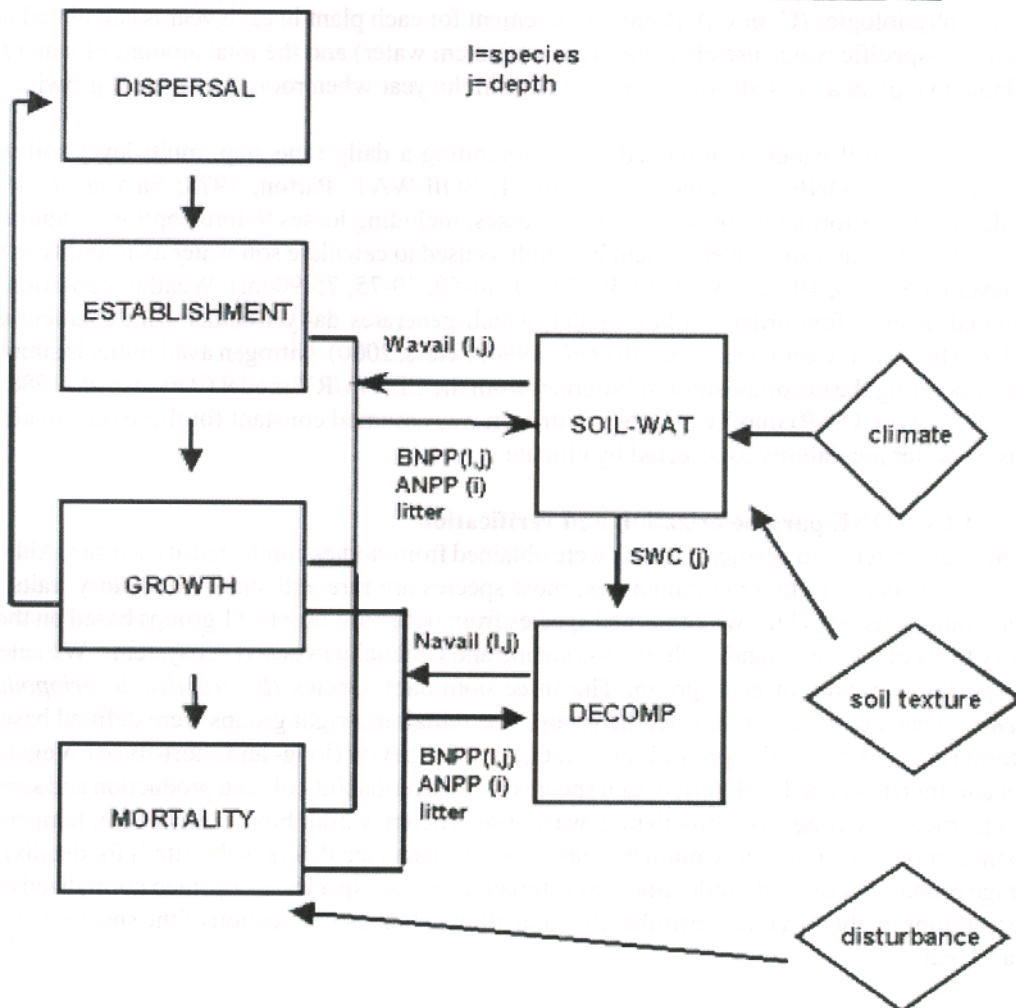


Figure 1. ECOTONE individual plant-based gap dynamics model of arid and semiarid grasslands and shrublands. Major plant processes include seed dispersal, seedling establishment, growth and mortality. Three driving variables (climate, disturbance, soil texture) influence soil and plant processes. Sub-modules of soil water (SOIL-WAT) and decomposition (DECOMP) allow feedbacks between vegetation and soil processes.

Plant growth is deterministic and based on competition for resources. Because light and nitrogen are important less frequently than soil water in arid ecosystems (Noy-Meir, 1973), we simulated only competition for soil water, although the model can also represent competition for these other resources. The amount of water available to each plant at each depth within the soil profile is determined by the proportion of total root biomass at that depth during the time of year when its roots are actively growing. Active root growth is calculated based on temperature response for



different physiologies (C_3 or C_4). Biomass increment for each plant in each year is calculated using the species-specific water-use efficiency (g biomass/cm water) and the total amount of water (cm) available to a plant across all soil layers and days in the year when roots are actively growing.

Plant available soil water is simulated by incorporating a daily time step, multi-layer soil water model into ECOTONE as a sub-module (Fig. 1; SOILWAT: Parton, 1978; Sala *et al.*, 1992). Simulated daily information on soil water processes, including losses to interception, evaporation, and transpiration, and soil water content by depth, is used to calculate soil water availability in each soil layer (0-5, 5-10, 10-15, 15-20, 20-30, 30-40, 40-50, 50-75, 75-90cm). Weather conditions are simulated using a first-order Markov model, which generates daily weather with characteristics similar to historical weather (Lauenroth *et al.*, 1994; Peters, 2000). Nitrogen availability is simulated by incorporating the decomposition subroutines from the CENTURY model (Parton *et al.*, 1988) as a submodule (DECOMP) into ECOTONE. Nitrogen was assumed constant for these runs to allow a focus on water availability as affected by climate.

2.3 ECOTONE parameterization and verification

Species parameters and verification data were obtained from studies conducted at each site. Although >300 species occur in these communities, most species are rare and share life history traits with several other species. Thus, we combined species from both biomes into 11 groups based on the life history traits of species found in shortgrass steppe and Chihuahuan desert ecosystems. We selected one species 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 (long- and short-lived). Vegetation input parameters needed to describe each species include probability of seed production and seedling establishment, seedling size, growth rate, water-use efficiency, root biomass by depth, temperature response, root:shoot ratio, maximum biomass, and life span (see Peters [submitted] for details). The average probability of seed production was estimated for each species group, then normalized to one across groups to obtain a relative probability that allows stochastic selection of the species to recruit in each year.

Driving variables in ECOTONE include climate, soil texture by depth, and disturbance regime. Daily precipitation and temperature were obtained from nearby weather stations. Monthly cloud cover, wind speed, and relative humidity were obtained from long-term estimates based on climate maps (National Oceanic and Atmospheric Administration, 1983). Soil texture (% sand, silt, clay) for each depth needed to simulate soil water dynamics were obtained either from a previous analysis for the climate scenarios across sites (Minnick & Coffin, 1999) or based on county soil maps for the disturbance frequency analysis at the SEV (Soil Survey of Socorro County Area, 1988). Disturbance size and frequency of occurrence were based on the range of values found within communities at the SEV. The model was verified by comparing simulated species composition under climatic conditions of the past 50 y with independent cover data for the same time period (Goslee *et al.*, in review; Peters, submitted). The ability of the model to simulate soil water dynamics through time was also validated (Lauenroth *et al.*, 1994).

2.3.1 Climatic fluctuations in ECOTONE



The model was parameterized for each site using daily climate data from 1942-1995. The same soils parameters were used for all sites to allow us to focus on effects of climate on species dominance (Minnick & Coffin, 1999). Species parameter values for the SGS were based on previous analyses using a similar model (STEPPE; Coffin & Lauenroth, 1990) and more recent analyses using ECOTONE (Goslee *et al.* in review). We used the same species parameters for each group at the SEV and JRN, with the exception of seedling establishment, since these sites contain similar species (Peters, submitted). Seedling establishment has been shown to vary both regionally and within a site for both *B. gracilis* and *B. eriopoda* due to climatic variation (Minnick & Coffin, 1999; Peters, 2000). Thus, the occurrence of a seedling establishment event for each species was determined for each site and climate scenario (see 2.4 Experimental Simulations). We assumed that seeds were available for all species in every year of the simulation; thus germination and establishment were the only constraints on recruitment. Germination and establishment of seedlings depend upon the availability of water near the surface where seeds are located for germination, and in the upper 30 cm where grass root growth is concentrated. Timing of precipitation and temperature and the effects of soil texture on water availability are important controls on the probability of suitable conditions occurring to result in seedling establishment. We used a multi-layer, daily timestep soil water model (SOILWAT; Sala *et al.*, 1992) to determine if seedling establishment occurred in each year for two species where sufficient information was available to conduct this analysis (*B. gracilis*, *B. eriopoda*; following Minnick & Coffin, 1999; Peters, 2000). This analysis was conducted for each site and climate scenario for both species. The probability of establishment for the other species groups were based on data from each site, and were the same for the two climate scenarios.

2.3.2 Disturbance frequency in ECOTONE

The model was parameterized for two soils at the SEV that are representative of grassland and grassland-shrubland soils on the McKenzie Flats. Soils parameters are described in detail in Peters (submitted). Soil texture is incorporated into the model as effects on plant growth and the probability of establishment of seedlings. Plant growth was simulated based on simulated soil water for each texture by depth. The probability of seedling establishment was calculated for the two *Bouteloua* species on each soil type using a 5000 y Monte Carlo simulation analysis based on historical weather from 1942-1995. The SOILWAT model was used to determine the annual probability of seedling establishment for these two species (Minnick & Coffin, 1999; Peters, 2000). This analysis was conducted for each soil type. The establishment probabilities of the other species groups were then renormalized to 1 based on the calculated probability for each *Bouteloua* species. Thus, the establishment probability for each species group differed among sites and climate scenarios. The same 5000 y weather sequence was used for both soils. Disturbance size was assumed to be one plot (0.25 m²). Disturbance frequency was based on the range of frequencies observed at the SEV.

2.4 Experimental Simulations

We conducted two sets of simulations to examine effects of environmental factors on vegetation dynamics. The first set examined effects of climatic fluctuations on regional patterns in species dominance and functional group composition. The second set examined effects of disturbance frequency on site-level patterns in species dominance. Each simulation began by initializing each plot without plants to avoid bias in initial conditions. In each year, we determined the plants to be added to each plot based on the probability of establishment for each species. Growth of each plant



was affected by temperature and competition for soil water where availability by depth was simulated based upon soil texture and precipitation as well as interactions with other plants. Mortality of plants was determined by resource limitation and longevity constraints. Model output included aboveground and belowground biomass for each species group through time.

2.4.1 Simulations of climatic fluctuations

The long-term climate data were grouped in two ways to represent variation in climate at inter-decadal scales. First, two 20 y time periods (1942-61, 1976-95) differing in amounts of precipitation were distinguished (Fig. 2a-c). For all three sites, the first period was drier, on average, than the second period, although a greater difference between periods was observed at the two southern sites (SEV: 6.5 cm/y, JRN: 8.4 cm/y) compared to the northern site (SGS: 3.7 cm/y). Most of the difference between periods occurred during May and the fall growing season (August-October) for the two southern sites whereas precipitation at the northern site was lower throughout most of the year from 1942-61 compared to 1976-1995 (Fig. 3a-c). For the two southern sites, average monthly temperatures were similar for both time periods whereas temperatures were lower at the SGS from 1942-1961 (8.6°C) compared to 1976-1995 (10.3°C). Both time periods contained 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 (Swetnam & Betancourt, 1998).

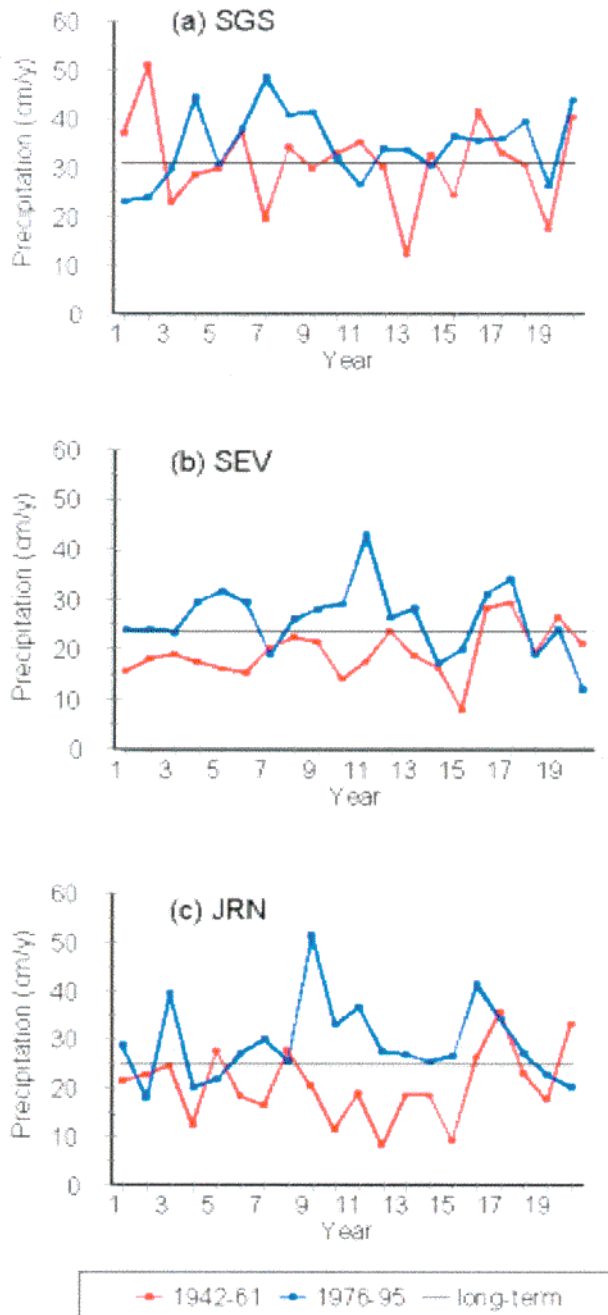


Figure 2. Annual precipitation for two time periods (1942-1961, 1976-1995) and the long-term average (1915-1995) for three sites located along an aridity gradient that represent two major North American biomes and their ecotone: (a) shortgrass steppe [SGS-LTER] (b) Chihuahuan desert ecotone [SEV-LTER] (c) Chihuahuan desert [JRN-LTER].

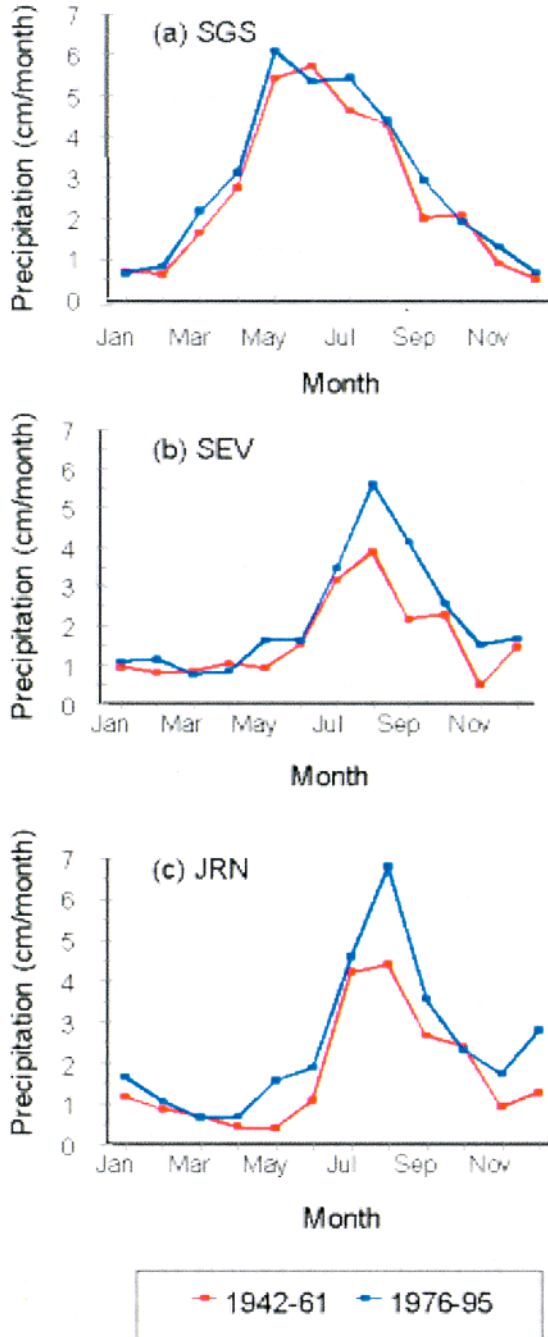


Figure 3. Monthly precipitation for two time periods (1942-1961, 1976-1995) and the long-term



average (1915-1995) for three sites located along an aridity gradient that represent two major North American biomes and their ecotone: (a) shortgrass steppe [SGS-LTER] (b) shortgrass steppe/Chihuahuan desert ecotone [SEV-LTER] (c) Chihuahuan desert [JRN-LTER].

Two simulations were conducted for each site that differed only in the climate parameters and the occurrence of establishment events for each of the two *Bouteloua* species. Each simulation consisted of running ECOTONE for 20 iterations of each sequence of historical weather. Because recruitment and mortality have stochastic elements, each run resulted in different output, except that recruitment of each *Bouteloua* species occurred in the same set of years for all runs within each time period at each site. Model output included aboveground biomass by species group averaged across the 20 iterations. The results presented focus on biomass of the dominant grasses (*B. gracilis*, *B. eriopoda*); remaining species groups were combined into four groups (other perennial grasses, subshrubs, perennial forbs, and annuals) to allow comparisons among sites.

2.4.2 Simulations of disturbance frequency

The model was run for five disturbance frequencies and two soil types (sandy loam, loamy sand) at the SEV to examine the effects of disturbances on species dominance and composition. These frequencies represent the range of natural frequencies observed at this site (0.005, 0.01, 0.05/y) as well as higher rates that may occur in localized areas, such as watering points (0.1, 0.25/y). A 400-y sequence of weather was generated using a first-order Markov weather generator based upon long-term daily precipitation and temperature from the Socorro weather station. Twenty-five replicate plots were simulated for each soil type and disturbance frequency combination with a different weather sequence for each replicate. The results presented focus on aboveground biomass during the last 100y of each simulation, averaged across the 25 replicates for the three dominant species at the SEV (*B. gracilis*, *B. eriopoda* and *Larrea tridentata*). The remaining eight groups of species were combined into one group for ease of presentation.

3.0 RESULTS AND DISCUSSION

3.1 Simulation modeling of vegetation change

3.1.1 Climatic fluctuations

At the shortgrass steppe biome site (SGS), *B. gracilis* dominated biomass throughout the 20 y simulations for 1942-1961, and starting in 1981 for the second time period (Fig. 4). High precipitation in 1942 and 1943 resulted in establishment events of this species in both years that led to rapid dominance that continued for the entire time period (Fig. 4a). This simulated response by *B. gracilis* in the 1940s was observed in eastern Colorado following the severe drought of the 1930s (Albertson & Weaver, 1944). The simulated decrease in *B. gracilis* biomass and increase in other perennial grasses starting in 1953 corresponds with field observations during the drought of the 1950s (Albertson *et al.*, 1957).

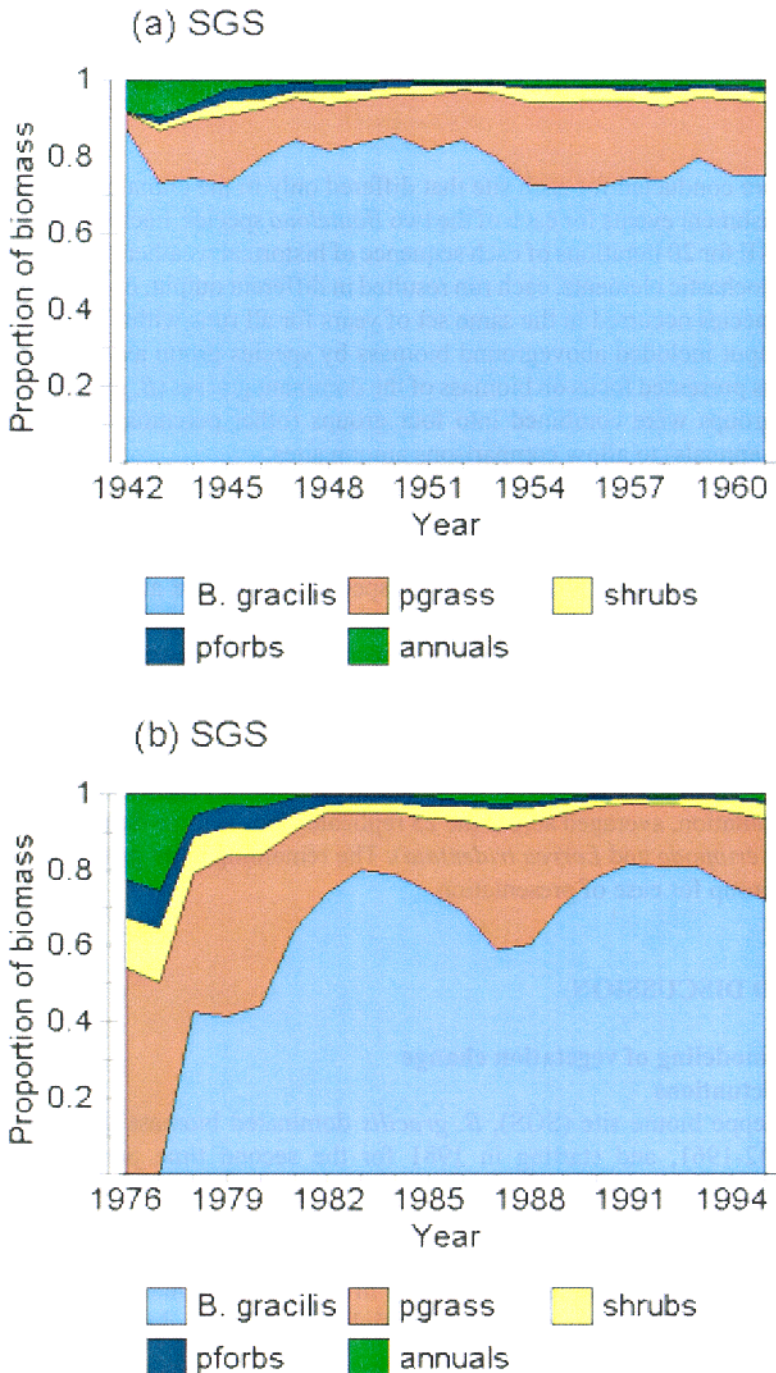


Figure 4. Proportion of total aboveground biomass through time for the dominant species (*Bouteloua gracilis*) and one of four species groups (pgrass: perennial grasses, shrubs, pforbs:



perennial forbs, and annuals) at the SGS-LTER for two time periods: (a) 1942-1961 (b) 1976-1995. Plots initialized without plants in the first year of each simulation.

In the second time period, *B. gracilis* establishment events occurred in 1978 and 1981 that led to dominance by this species on simulated plots within 5 y following disturbance (Fig. 4b). During this initial 5 y, other perennial grasses, in particular short-lived *Aristida* and *Sporobolus* species, dominated biomass on the plots. Following recovery by *B. gracilis*, these other perennial grasses had the highest biomass of the remaining species groups. These results are similar to field observations of disturbed and undisturbed shortgrass steppe communities during this time period (Coffin *et al.*, 1996; 1998). *B. gracilis* is a long-lived bunchgrass (ca. 400 y; Coffin & Lauenroth, 1990) that dominates shortgrass steppe communities for extended periods of time unless plants are killed by disturbance (Coffin & Lauenroth, 1988; Coffin *et al.*, 1996). Because these simulations did not include additional disturbances beyond the initial bare plot, this species was able to dominate simulated biomass within several years following recruitment.

At the Chihuahuan desert biome site (JRN), perennial grasses, perennial forbs and sub-shrubs dominated simulated biomass from 1942 until the establishment of *B. eriopoda* seedlings in 1957 (Fig. 5a). Conditions at this site were too warm and dry during this time period for frequent establishment by *B. eriopoda* (Neilson, 1986); in the model, only three years contained successful establishment by this species. Although model results suggest that recovery by *B. eriopoda* was possible during this time period, this was not observed in southern New Mexico (Gibbens & Beck, 1988). The model assumes a sandy loam soil with relatively high near-surface organic matter and plant available water typically associated with grasslands. Soil texture and soil organic matter content may have changed, however, due to the invasion of shrubs, in particular *L. tridentata* and *P. glandulosa*, in the 1800s and early to mid-1900s, and a large-scale invasion episode following the drought of the 1950s (Buffington & Herbel 1965; Grover & Musick, 1990). Although our model results show that climatic conditions were suitable for the recovery by *B. eriopoda* following this severe drought, altered soil properties and increased soil instability associated with the invasion by shrubs likely precluded this response from occurring in the field (Valentine, 1942; Gibbens *et al.*, 1983). Furthermore, our current model formulation does not include the effects of grazing by cattle. Grazing interacts with drought to promote shrub invasion as well as to inhibit grass recovery by removal of aboveground biomass and seeds (Nelson, 1934; Archer, 1994). Similarly, *B. eriopoda* dominated simulated biomass from 1982-1994 as a result of six years with climatic conditions suitable for successful establishment by this species (Fig. 5b). This response was also not observed in the field due to soil degradation and low availability of *B. eriopoda* seeds following large-scale invasion and dominance by shrubs (Gibbens *et al.*, 1992; 1993).

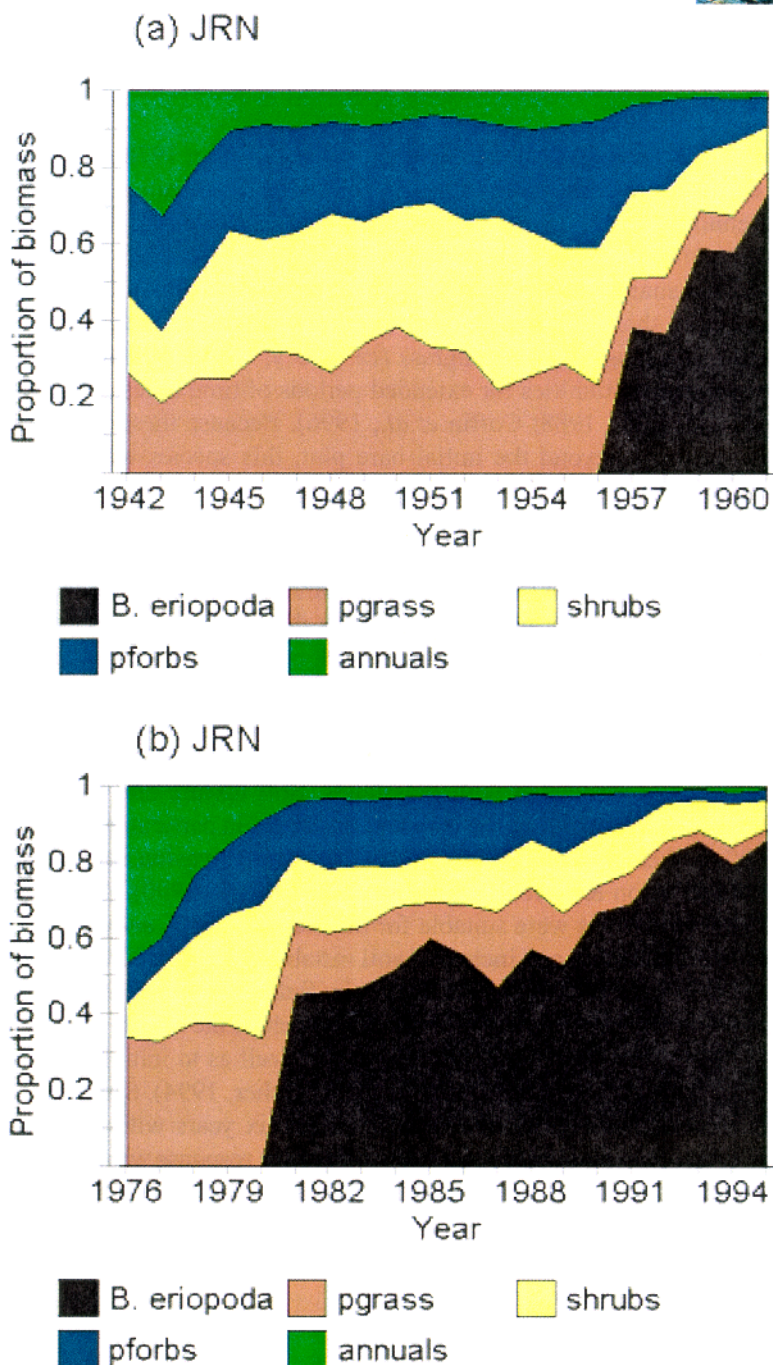


Figure 5. Proportion of total aboveground biomass through time for the dominant species (*Bouteloua eriopoda*) and one of four species groups (pgrass: perennial grasses, shrubs, pforbs:



perennial forbs, and annuals) at the JRN-LTER for two time periods: (a) 1942-1961 (b) 1976-1995. Plots initialized without plants in the first year of each simulation.

Patterns in simulated species dominance at the shortgrass steppe-Chihuahuan desert ecotone (SEV) were not predictable based on simulated responses at the two biome sites. *B. gracilis* had higher simulated biomass at the SEV during the cool, wet period from 1976-1995 (Fig. 6) whereas this species had higher simulated biomass at the SGS during the warmer, drier period from 1942-1961 (Fig. 4). Similarly, *B. eriopoda* had higher simulated biomass at the JRN from 1976-1995 (Fig. 6), but this species had higher simulated biomass at the SEV from 1942-1961 compared to the later time period (Fig. 5). These results are due to complex interactions between climate and two plant processes (seedling establishment and competition for soil water resources). During the dry, warm period from 1942-1961, communities were dominated by *B. eriopoda* since conditions were too harsh for the establishment of *B. gracilis* seedlings (Fig. 6a). The severe drought from 1950-1956 is reflected by the decrease in simulated biomass of *B. eriopoda* and increase in biomass of other perennial grasses.

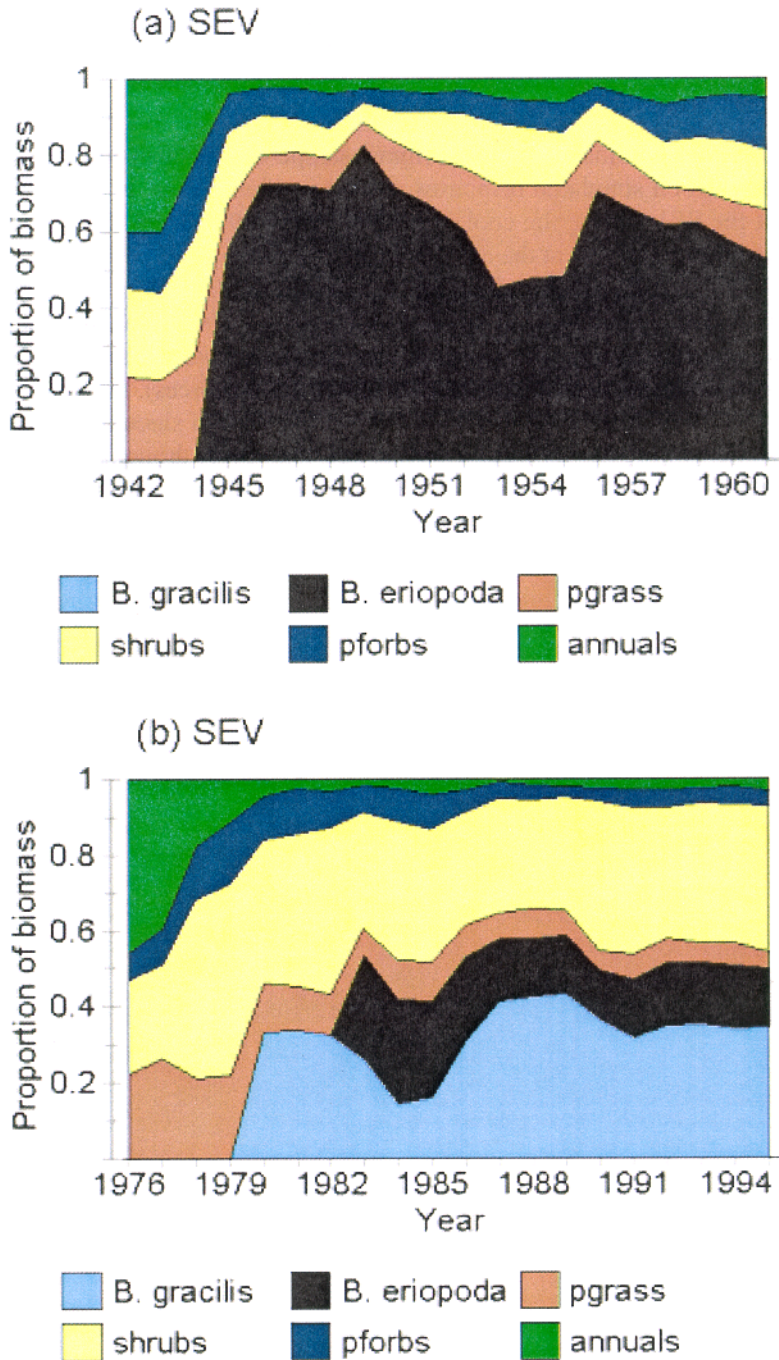


Figure 6. Proportion of total aboveground biomass through time for two dominant species (*Bouteloua gracilis*, *Bouteloua eriopoda*) and one of four species groups (pgrass: perennial



grasses, shrubs, pforbs: perennial forbs, and annuals) at the SEV-LTER for two time periods: (a) 1942-1961 (b) 1976-1995. Plots initialized without plants in the first year of each simulation.

Bouteloua gracilis and the subshrub, *Gutierrezia sarothrae*, codominated biomass on simulated plots at the SEV during the wetter, cooler period from 1976-1995 (Fig. 6b), although *B. eriopoda* was also an important component of these plant communities following its establishment in 1983. The lower simulated biomass of *B. eriopoda* from 1983-1995 compared with 1945-1961 resulted from competitive interactions with other species, in particular with *B. gracilis* that has a similar rooting distribution (Hochstrasser & Coffin, 1997). Coexistence of these two species at ecotones at the SEV may be related to temporal partitioning of water resources that favors *B. gracilis* under cool, wet conditions (Peters, submitted). Long-term data on establishment or dominance patterns of these species do not exist at this site to verify the model results. However, short-term data partly support the results because the cover of *B. gracilis* 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, a greater increase in *B. gracilis* cover was observed both on and off abandoned prairie dog colonies from 1984 to 1996 compared with a small increase in cover of *B. eriopoda* (Gosz *et al.*, 1997).

3.1.2 Disturbance frequency

For both soil types, *B. eriopoda* maintained dominance of simulated biomass at all disturbance frequencies (Fig. 7). Plants of this species can respond vegetatively to soil disturbances that cause mortality by the production of stolons from plants surrounding the disturbed area. Thus, this species can recover following disturbances that occur as frequently as every 4 y. Because seedling establishment events occur infrequently (1/7 y) for this species (Peters, 2000), vegetative spread is the most frequent mode of recovery. By contrast, the bunchgrass *B. gracilis* recovers primarily through seedling establishment since tillering rates are very slow (Samuel, 1985). Because seedling establishment events for this species occur infrequently at the SEV (1/14 y; Peters, 2000), frequent disturbance results in a loss of *B. gracilis* cover and abundance through time.

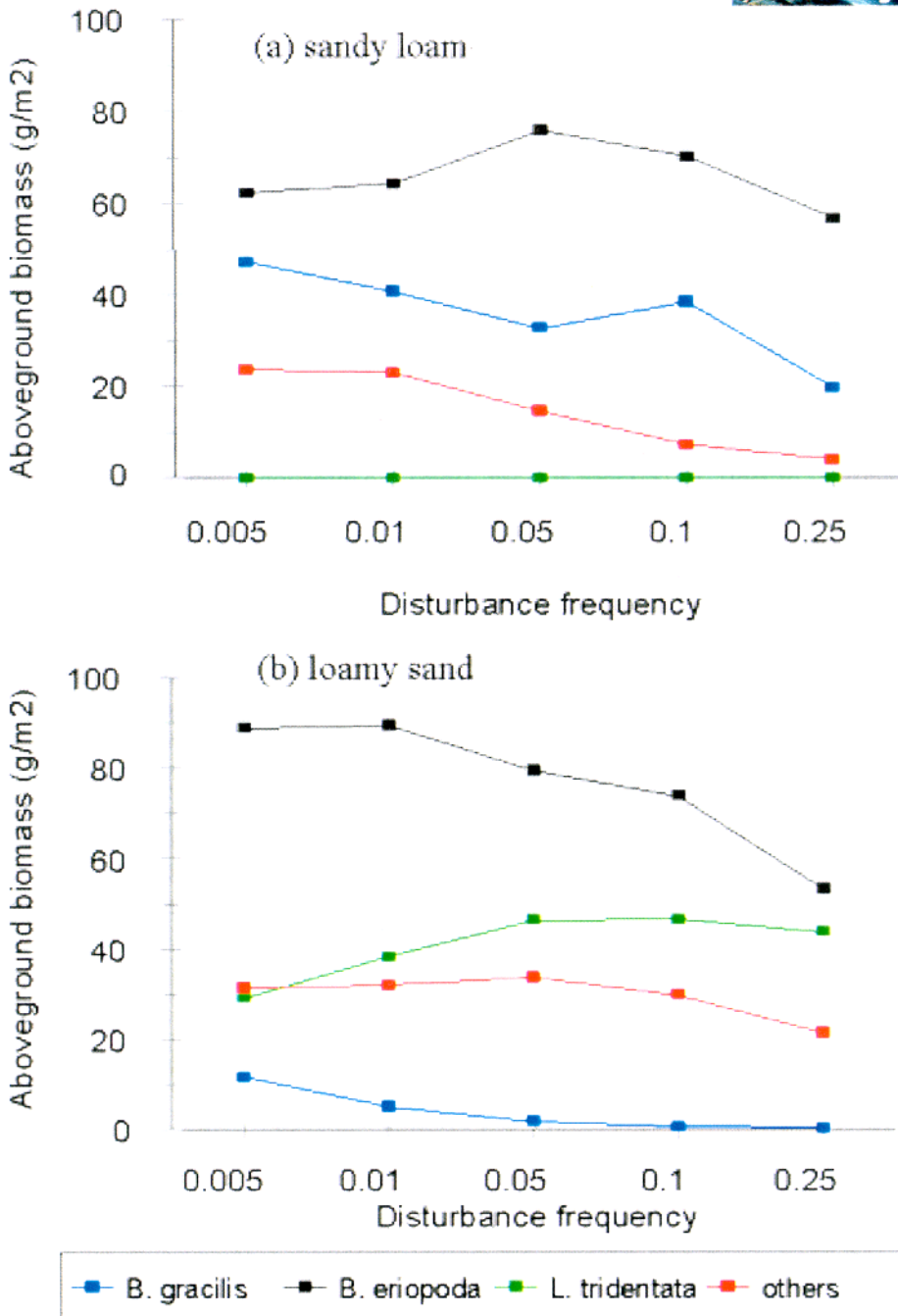


Figure 7. Average biomass of three important species (*B. gracilis*, *B. eriopoda*, *L. tridentata*) and all other species combined for five disturbance frequencies on two soil types: (a) sandy loam (b) loamy sand. Biomass is the average of 25 replicate plots over the last 100 y of each 400 y



simulation. Plots initialized without plants in the first year of each simulation.

On sandy loam soils, disturbance frequencies greater than 0.01 resulted in decreases in simulated biomass of *B. gracilis*, and a shift in dominance to *B. eriopoda* (Fig. 7a). Because seeds of *L. tridentata* are not found in these grassland communities, recruitment by this shrub did not occur on simulated plots; thus this species was unable to respond either positively or negatively in the model to disturbance on this soil type. These model results are supported by a recent field study showing the increased cover of *B. eriopoda* on and around kangaroo rat mounds when compared to the matrix or undisturbed vegetation dominated by *B. gracilis* (Fields *et al.*, 1999). In contrast, *B. gracilis* cover decreased due to the presence of kangaroo rat mounds. These results only apply to soil disturbances created by small animals. Response to grazing by these two species is very different in that *B. gracilis* is more resistant than *B. eriopoda* to heavy grazing by large herbivores (Nelson, 1934; Lauenroth & Milchunas, 1992).

Loamy sand soils were co-dominated by *B. eriopoda* and *L. tridentata* for all disturbance frequencies (Fig. 7b). At low frequencies (0.005), other grasses, forbs and shrubs also had high simulated biomass. Although simulated biomass of *B. eriopoda* decreased as frequency increased, communities experiencing high frequencies of disturbance were co-dominated by this species and *L. tridentata* with 20% of the biomass attributed to other species. Because soil disturbances created by kangaroo rats typically do not kill *L. tridentata* plants and may promote their growth under field conditions (Chew & Whitford, 1992), plants of this species were not killed by disturbance on simulated plots. *B. gracilis* occurred in small amounts under low frequencies, but decreased rapidly as frequency increased due to low rates of seedling establishment on this soil (1/250 y). These results indicate that *B. eriopoda* can persist in the presence of high frequencies of disturbance, although the simulated biomass of *L. tridentata* increases as frequency increases. Although the reduction in perennial grass cover and abundance as a result of grazing by cattle were not included in these simulations, our results suggest that small soil disturbances acting in combination with grazing may further promote the invasion of these communities by *L. tridentata*.

Our model results support previous studies showing that simulation models are extremely useful in predicting responses of different kinds of ecosystems under a variety of environmental conditions (e.g., Shugart, 1998; Mladenoff & Baker, 1999; Tenhunen & Kabat, 1999). However, each type of model is limited in its spatial extent and time frame that restricts its usage to particular situations.

3.2 New approach to understanding and predicting aridland degradation

We propose that a hierarchical linkage among different types of simulation models can be used to improve dryland assessment, prioritization of resource use, and prediction of ecosystem dynamics. By capitalizing on the strengths of each model type, we can simulate ecosystem dynamics over a wide range of spatial and temporal scales needed to address land degradation problems. For example, at the global and continental scales, models such as MAPPS (Neilson & Drapek, 1998) and DOLY (Woodward *et al.*, 1995) can be used to identify regions and biomes which are relatively sensitive to changes in climate or disturbance regime, or which are at or near thresholds. At the sub-regional to landscape scale, meso-scale climate models such as RAMS (Pielke *et al.*, 1991) can be integrated



with landscape-scale vegetation models (He *et al.*, 1999; Urban *et al.*, 1999) to provide information on the sensitivity of specific types of plant communities to change, and on potential vegetation-climate feedbacks. At the patch scale, more traditional gap dynamics models, such as ECOTONE (Peters, submitted), can be used to simulate species composition changes by incorporating fine-scale plant and soil processes. We believe that bottom-up and top-down approaches will need to be applied simultaneously and iteratively in order to generate the types of information required by scientists and managers.

We also propose that multiple tools be integrated to support management and monitoring at multiple spatial scales. We briefly illustrate this approach for landscapes (500 - 500,000 ha; Fig. 8). A similar approach can be applied at regional, national, global and continental scales.

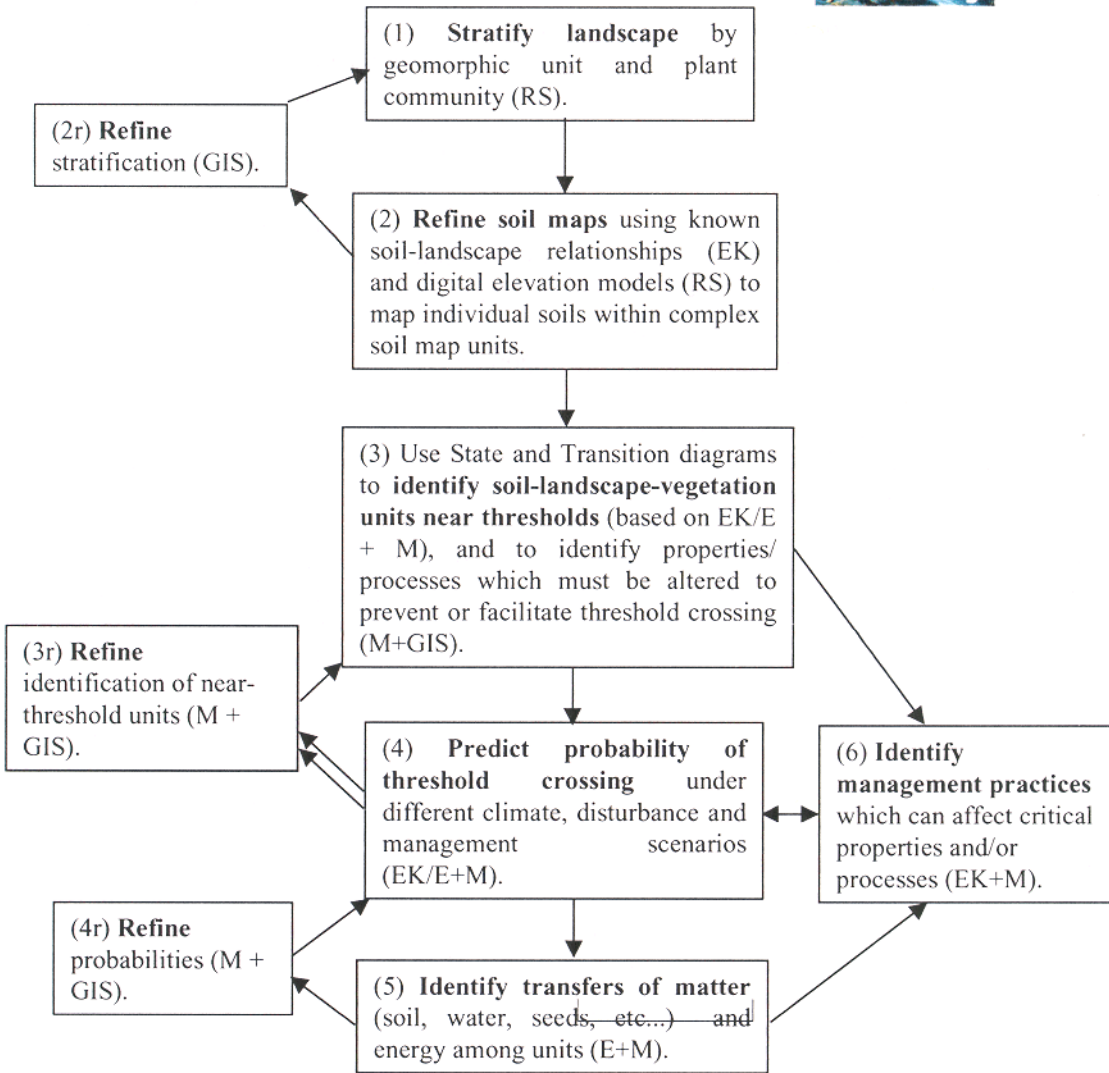


Figure 8. Conceptual figure showing integration of multiple approaches (remote sensing [RS], simulation modelling [M], GIS tools [GIS], experiments [E], and expert knowledge [EK]) to address complex multi-scale problems in arid lands.

Nearly all monitoring and management projects can benefit from stratification of sites among geomorphic, soil, and vegetation units (Fig. 8; Step 1). It is at this stage that remote sensing technologies are most easily and cost-effectively applied. Widely available and easily interpretable imagery, such as aerial photos and LANDSAT, can be used to identify repeating landscape units that can be treated as a group for both monitoring and management. Digital elevation data are now widely available and, when combined with soil maps in a GIS database and interpreted by an expert on local soil-landscape relationships, can be used to refine soils mapped as associations (consisting of 2 or



more soil series) into individual soils (Steps 2 and 2r). This level of stratification facilitates prediction of locations where changes are likely to occur first using State and Transition diagrams or conceptual models (Step 3). These diagrams organize current understanding of the potential transitions, thresholds, and critical processes which control soil-vegetation dynamics (Society for Range Management Task Force on Unity in Concepts and Terminology, 1995).

Identification of the properties and processes which must be altered (Step 3) is one of the most important and difficult tasks in this process. Discussions of this issue frequently focus on the process (such as soil erosion) or property (such as perennial grass species composition) about which the researcher is most knowledgeable rather than on those processes which actually limit change. One way to decide which factors are most likely to be important is to first decide whether the stability of the system depends primarily on its resistance to degradation or on its resilience, or capacity to recover following degradation. This is followed by deciding which part or parts of the system contribute most significantly to resistance or resilience. This process helps focus attention on the most critical properties and processes.

Simulation modeling is essential in both threshold identification (Step 3) and in establishing the probability that a threshold will be crossed (Step 4). For example, Fig. 7b shows a shift from dominance by *B. eriopoda* under low disturbance frequencies (0.005) to co-dominance with *L. tridentata* as disturbance frequency increases. This decrease in grass biomass and increase in shrub biomass with an increase in disturbance frequency is critical information in this region where shrub invasion is a prevalent and pervasive problem. Without models, it is difficult, if not impossible, to address all of the potentially interacting factors for even one climate scenario. Stochastic models, in particular, facilitate the calculation of probabilities and can be easily integrated into risk- and management option cost-benefit analyses because they allow discounting to be explicitly included. Identifying transfers of matter and energy among units (Step 5) represents a further refinement of these predictions which is rarely included in models of vegetation change, but is critically important in arid ecosystems in which resource redistribution plays a significant role. These transfers, and resulting changes in vegetation (Schlesinger *et al.*, 1990), often lead to feedbacks which further alter runoff and erosion (Parsons *et al.*, 1992). Simulation modeling is necessary to both quantify resource redistribution and to account for the different types of feedbacks which are likely to occur (Peters & Herrick, 1998). The diagram shows that identification and prioritization of management options (Step 6) is initially considered at Step 3. This is both because it helps focus modeling efforts on the overall project objectives, and because it encourages the team members who represent these objectives to become involved in the process at a relatively early stage.

4.0 CONCLUSIONS

Our results demonstrate that simulation models can be effectively utilized to predict vegetation transitions associated with land degradation in diverse arid ecosystems. Future advances in our ability to apply model results to land management and monitoring will require extensive integration of different types of bottom-up and top-down models, together with expert knowledge and other types of tools including GIS, remote sensing and field experiments.



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