

Soil-vegetation-climate interactions in arid landscapes: Effects of the North American monsoon on grass recruitment

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ABSTRACT

We used a daily time step, multi-layer simulation model of soil water dynamics to integrate effects of soils, vegetation, and climate on the recruitment of *Bouteloua eriopoda* (black grama), the historically dominant grass in the Chihuahuan Desert. We simulated landscapes at the Jornada ARS-LTER site with heterogeneous soil properties to compare: (1) a grass-dominated landscape in 1858 with the current shrub-dominated landscape (i.e., a change in vegetation structure), and (2) the current shrub-dominated landscape with future landscapes over a range of climate scenarios associated with the North American monsoon (i.e., a change in climate). A historic shift from high productivity grasslands to low productivity shrublands decreased simulated recruitment for most of the site; the amount of reduction depended on location-specific soil properties and changes in production. In some cases, soil properties interacted with vegetation structure: soils high in clay content maintained high recruitment even with a decrease in production. Wetter summers would increase recruitment in all vegetation types. Drier summers below 25% of current rainfall would decrease recruitment to negligible values (<0.03) throughout the landscape. We used our results to identify the conditions where recruitment of *B. eriopoda* is possible with and without significant modifications to soil and vegetation.

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1. Introduction

Woody plant encroachment into perennial grasslands has occurred globally throughout arid and semiarid regions over the past several centuries (Reynolds and Stafford Smith, 2002). Although the causes of this state change resulting in desertification are often site specific, the consequences are clear and consistent: conversion from grasslands to woody plant dominance results in increased wind and water erosion of soil and nutrients (Bird et al., 2007; Okin and Gillette, 2001; Wainwright et al., 2002), spread of invasive species (Masters and Sheley, 2001), changes in carbon dynamics (Jackson et al., 2002; Knapp et al., 2008) and loss of biodiversity and forage production (Ricketts et al., 1999). Reversal from woody plant-dominated systems back to perennial grasslands is difficult, and remediation efforts are often unsuccessful (Herrick et al., 2006).

Woody plant persistence following invasion is typically attributed to feedbacks between plants and soils that positively affect shrub growth and persistence (Schlesinger et al., 1990).

Redistribution of soil, water, and nutrients from bare interspaces to beneath woody plant canopies results in “islands of fertility” that favor woody plants (Bhark and Small, 2003; Huxman et al., 2005; Kieft et al., 1998). However, shifts to woody plant dominance may also influence plant processes that limit grass recovery. Microenvironmental conditions associated with shrub invasion have been found to reduce grass viability, production, and storage of seeds in the soil compared with neighboring grasslands (Peters, 2002). Effects of shrublands on two key aspects of grass recruitment, seed germination and seedling establishment, may provide additional constraints on the ability of grasses to recover following shrub invasion, in particular for perennial grasses with low rates of seedling recruitment (Minnick and Coffin, 1999; Peters, 2000).

Recruitment of grass seedlings is expected to be affected by changes in vegetation structure and soil properties that influence soil water availability following grassland to shrubland conversion. Shrublands on the same soil type as arid grasslands likely have lower interception and transpiration losses due to lower leaf area, yet higher rates of evaporation as a result of lower production (Knapp et al., 2008). Because evaporation is often the primary control on water availability in arid regions (Loik et al., 2004), a shift to shrublands is expected to decrease water available to seedlings and reduce rates of establishment. However, if water available for

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transpiration exceeds losses to evaporation, then shrub encroachment could increase rates of grass establishment if more water is available to seedlings.

Effects of shrubs on water availability and grass recruitment may be either offset or amplified by future changes in climate. Although temperatures are increasing globally as a result of elevated concentrations of atmospheric carbon dioxide and other greenhouse gases, changes in precipitation are more uncertain (IPCC, 2007). For example, in the southwestern US and northwestern Mexico, there is no consistent pattern in global climate model scenario results for precipitation, and even the latest generation of models contained in the IPCC AR4 suite (IPCC, 2007) do not show significant model agreement for summer precipitation in the future. Directional changes in precipitation, particularly during the North American monsoon, are expected to affect rates of recruitment of perennial grasses based on previous studies of the timing of grass germination and establishment during the rainy monsoon season (Peters, 2000).

Simulation modeling provides one approach to integrating multiple drivers (climate, soils) and processes (evaporation, transpiration, infiltration) to investigate the effects of shrub encroachment on grass recruitment. A landscape approach is necessary to capture both spatial and temporal heterogeneity in arid systems (Peters et al., 2006a). We had two objectives for this study. *First*, we evaluated effects of historic changes in vegetation structure on the simulated probability of establishment of the perennial grass, *B. eriopoda* (black grama), a historic dominant in the Chihuahuan Desert. We simulated a landscape with heterogeneous soils that was predominantly grasslands in 1858, and compared these results with the same area that is currently shrub dominated. We expected that the probability of establishment would decrease, in general, following broad-scale shrub invasion, but that certain soil-vegetation combinations would be more sensitive to vegetation change than other locations because of differences in plant production and soil properties. *Second*, we evaluated effects of changes in climate on simulated probabilities of establishment of *B. eriopoda*. We compared spatial variation in recruitment under current climate with future predicted probabilities under an increase in temperature and either a directional increase or decrease in precipitation during the monsoon period (July 1–October 1). We expected that the probability of recruitment would have a positive relationship with precipitation, but that climatic effects would interact with vegetation and soils to create spatial variability in recruitment.

2. Data and methods

2.1. Study site

We evaluated the change in probability of recruitment of *B. eriopoda* through time for a site located in the northern Chihuahuan Desert, the Jornada ARS-LTER site (32.5 N, 106.8 W, 1188 m a.s.l.) in southern New Mexico, USA. Three shrubland types have replaced two grassland types throughout much of the Chihuahuan Desert, including the Jornada site. Shrub invasion of both grassland types is associated with significant soil loss and degradation. *Bouteloua eriopoda* grasslands have been replaced by *Prosopis glandulosa* (honey mesquite) on sandy basin soils, while *Pleurophis mutica* (tobosa) grasslands have been replaced by *Flourensia cernua* (tarbush) on clay loam soils in lower landscape positions. *Larrea tridentata* (creosotebush) now dominates gravelly and loamy soils formerly dominated by *P. mutica* and/or *B. eriopoda*.

The Jornada is typical of much of the American Southwest in that it was dominated by grasslands in 1858 (81% of the 100,000 ha area) and is currently dominated by shrublands (92% of the area) (Gibbens et al., 2005). Reasons for this shift in lifeform include

overgrazing by livestock in the late 1800s to early 1900s combined with periodic drought, and reduction in fire frequency and increase in small animal population densities (Van Auken, 2000). Current livestock grazing intensities are much lower than historically (Fredrickson et al., 1998). In our analysis, seedling herbivory by animals was assumed to be negligible and seeds were assumed to always be available in order to focus on germination and establishment processes.

Climate at the Jornada is arid to semiarid with low annual precipitation (80 y avg = 23 cm/y) and high summer temperatures (80 y avg = 36 °C avg maximum in June). Most precipitation (60–80%) occurs during the North American monsoon that typically occurs from July 1 to October 31 (Wainwright, 2006). Global circulation models predict an increase of 3 °C in temperature for this region (IPCC, 2007), and either a decrease or an increase in precipitation as a result of elevated concentrations of atmospheric gases associated with global climate change (Kunkel et al., 1999; Seager et al., 2007).

2.2. Soil water simulation model

We used a multi-layer, daily time step simulation model (SOILWAT; Parton, 1978) to determine the probability of recruitment of *B. eriopoda* for spatially variable soils and vegetation in different time periods. Climate and soil texture are drivers, and vegetation structure is an input parameter. Processes simulated in

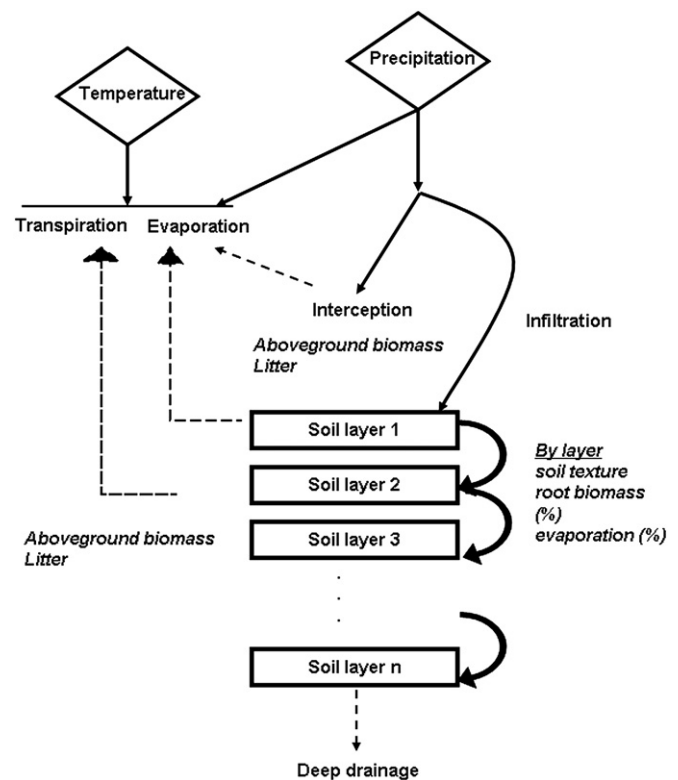


Fig. 1. The SOILWAT model simulates precipitation inputs, losses (dashed arrows) by interception from the plant canopy, bare soil evaporation, plant transpiration, and loss of water to deep drainage, and vertical redistribution of water between multiple layers of variable depth (modified from Parton, 1978). Infiltration is simulated using a tipping bucket approach where water moves vertically into the next layer after an upper layer becomes saturated. Climatic drivers are daily precipitation and air temperature. Input parameters include soil texture (% sand, silt, clay), percentage evaporation and percentage transpiration (i.e., root biomass) by depth in the soil profile, and monthly aboveground biomass and litter. Aboveground biomass and litter change with grass to shrub conversion from 1858 to present. Temperature and precipitation change with climate change scenarios between present and 2150.

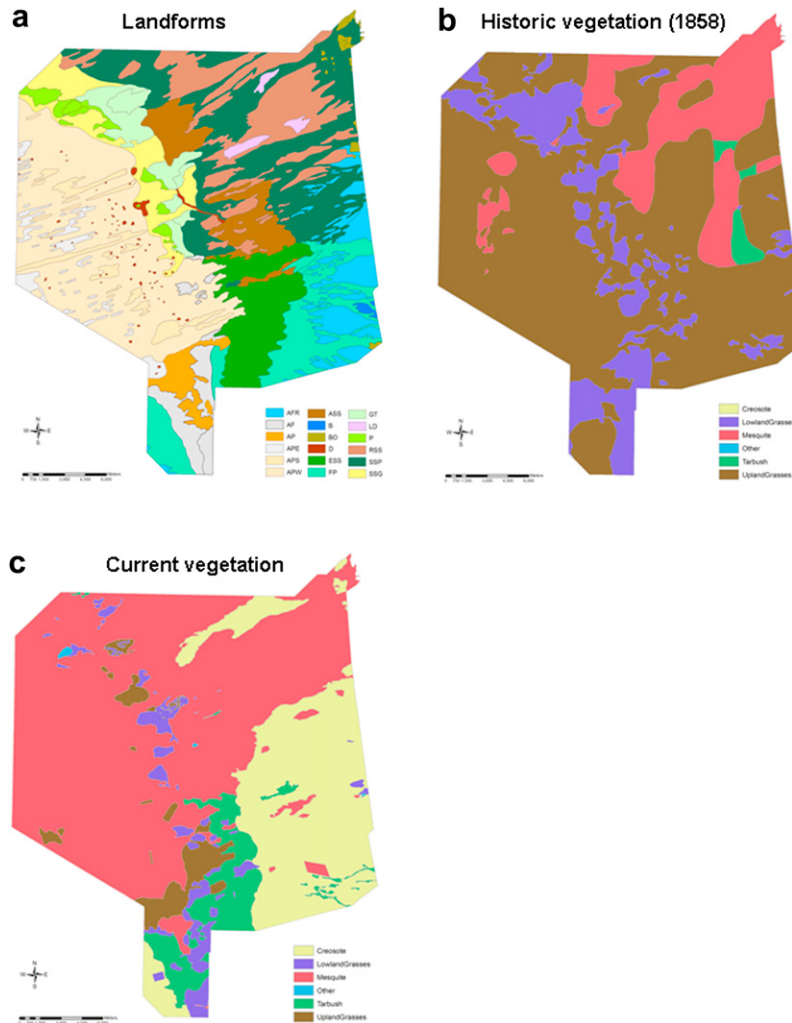


Fig. 2. Input maps from the Jornada ARS-LTER site: (a) landform map from Monger et al. (2006), (b) vegetation map in 1858, and (c) vegetation map at present from Gibbens et al. (2005).

SOILWAT include evaporation, transpiration, interception, and infiltration of water through the plant canopy and soil layers through time (Fig. 1). Input parameters include daily temperature and precipitation, and monthly wind speed, relative humidity, cloud cover, aboveground biomass, and litter. Soil texture (% sand, silt, clay), % rocks by volume, and root distribution by depth are additional input parameters. Loss of water to deep drainage occurs infrequently in arid systems, and is not simulated. The occurrence of a recruitment event in each year is predicted by comparing simulated soil water content through time with amount and timing of soil water required for germination (0–5 cm depth) and establishment (0–30 cm depth) by *B. eriopoda* (*sensu* Peters, 2000). The model has been tested for dry grasslands in the US, both for soil water dynamics (Lauenroth et al., 1994) and for recruitment of *B. eriopoda* (Minnick and Coffin, 1999).

2.3. Model parameterization

The model was parameterized using spatial data layers in a geographic information system combined with data collected primarily from the Jornada. A landform map (Fig. 2a; Monger et al., 2006) and soil texture data from the Jornada (Monger, 2006; SCS, 1963; <http://ssldata.nrcs.usda.gov>) were used to create soil texture input variables by depth for each landform (Table 1). We created the

same depth structure for each soil type (0–5, 5–10, 10–15, 15–20, 20–30, 30–50, 50–75, 75–100 cm) by either combining or linearly extrapolating texture values across soil depths in the database.

Table 1

Soil texture input parameters to SOILWAT (Monger, 2006; Monger et al., 2006; SCS, 1963). Average percentage sand, clay, and rocks are shown across depths; actual values used in the simulations varied by depth. Map code refers to legend in Fig. 2.

Landform	Sand (%)	Clay (%)	Rocks (%)	Map Code
Alluvial fan remnant	0.72	0.13	0.48	AFR
Alluvial flat	0.43	0.31	0.00	AF
Alluvial plain	0.59	0.22	0.00	AP
Alluvial plain eroded	0.71	0.14	0.00	APE
Alluvial plain sand sheet	0.76	0.17	0.00	APS
Alluvial plain wind reworked	0.83	0.10	0.00	APW
Arcuate sand ridges and sand sheets	0.84	0.10	0.00	ASS
Ballena	0.72	0.13	0.48	B
Bedrock outcrop	0.63	0.23	0.48	BO
Depression	0.48	0.32	0.00	D
Fan piedmont	0.46	0.29	0.00	FP
Longitudinal dunes	0.84	0.10	0.00	LD
Reddish brown sand sheets and dunes	0.84	0.10	0.00	RSS
Sand sheet and dunes on fan piedmont	0.73	0.11	0.00	SSP
Gypsiferous terrace	0.52	0.21	0.00	GT
Playa	0.11	0.63	0.00	P
Erosional scarplets and sand ridges	0.42	0.34	0.00	ESS
Sand sheet over gypsum	0.83	0.09	0.00	SSG

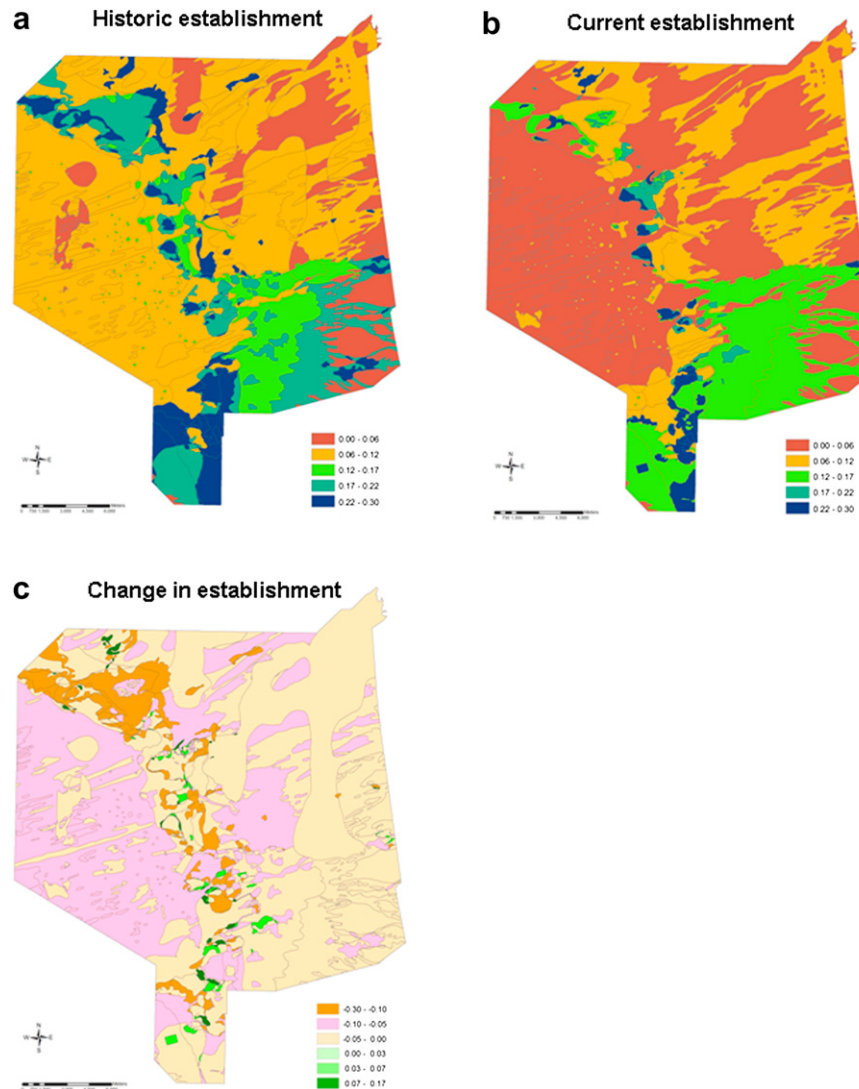


Fig. 3. Simulated probabilities of recruitment of *B. eriopoda* at the Jornada ARS-LTER site in: (a) 1858 grassland-dominated landscape, (b) current shrubland-dominated landscape, and (c) the difference in probability between present day and 1858.

Vegetation maps from 1858–1998 (Fig. 2b, c) were combined with average annual aboveground production data from 1989 to 2005 for each of the five vegetation types (upland grasslands = 100 g/m²/y; lowland grasslands = 175 g/m²/y; three shrubland types = 80 g/m²/y; <http://jornada-www.nmsu.edu/>) to determine annual aboveground biomass values for each landform-vegetation type combination. We assumed biomass corresponds with production, and that the same amount of biomass occurs in each month. Percentage live biomass by month was based on phenological patterns of the vegetation. Monthly litter values were assumed to be the same as monthly biomass. Monthly wind speed, cloud cover, and relative humidity, and average annual evaporation and transpiration rates by depth were obtained from runs conducted for a site with similar climate and vegetation (Sevilleta National Wildlife Refuge; 34° 21'; 106° 53') (Peters, 2000); these parameters remained the same for all runs.

To address our first objective, we used daily temperature and precipitation data from 1915 to 2006 in a first-order Markov analysis to create 2000 years of weather that was the same for historic (1858) and present runs. The only difference between runs was the change in production associated with a change in vegetation type through time. To address our second objective, climate

change was invoked by adding 3 °C to the maximum and minimum temperature value for each day. Precipitation was modified by either increasing or decreasing the daily monsoonal amount of rainfall (July 1 through Oct 31) by 5, 10, 25, and 50%. These values represent the natural variation in rainfall at the Jornada where 10% of the years since 1915 have exceeded 50% of the long-term mean, and 5% of the years have been less than 50% of the long-term mean. These values were selected to allow us to evaluate either increases or decreases in rainfall amount rather than to represent any particular output from a global climate model. Because we used the Markov analysis based on historical climate, our climate change scenarios only include changes in amount of rainfall and not changes in intensity (smaller or larger rain events) or frequency (fewer or more frequent rain events) that are predicted in some climate models (IPCC, 2007). More intense rain events within a day (mm/hour) or an increase in frequency of large events (>25 mm) may result in runoff and runoff of water in some landscape locations, but these horizontal water redistribution processes were not simulated here. The probabilities of germination and establishment were calculated as the total number of successful events in each 2000 year run (*sensu* Minnick and Coffin, 1999; Peters, 2000).

2.4. Experimental simulations

2.4.1. Obj. 1 Effects of vegetation structure and soil properties on recruitment

We compared simulated probabilities of recruitment of *B. eriopoda* in 1858 with those under present conditions (based on the 1998 vegetation map) for all 75 combinations of soil types ($n = 15$) and vegetation types ($n = 5$). We assumed that soils associated with each vegetation type did not change over time; thus the only change between years was the spatial distribution and areal extent of the different vegetation types.

2.4.2. Obj. 2. Effects of climate change on recruitment

We compared simulated probabilities of recruitment for current landscapes with an increase in temperature for a range of precipitation scenarios for all soil type-vegetation type combinations. We assumed that soils and vegetation type did not change over time; thus the only change between runs was daily precipitation amount and a 3° increase in average daily temperature.

3. Results and discussion

3.1. Effects of changes in vegetation structure and soil properties on recruitment

In general, probabilities of germination (not shown) and establishment were greater in 1858 than at present as a result of changes in plant production and interactions with soil properties that influence water availability to seedlings (Fig. 3). In 1858, most of the Jornada was dominated by grasslands (Fig. 2b) with simulated establishment probabilities greater than 0.06 (Fig. 3a). In general, largest probabilities were found on high productivity lowland grasslands and upland grasslands on soils high in clay content. Smallest probabilities were found on grasslands located on alluvial fan remnants with gravelly soils and high percentage of rocks (Fig. 2a), and on low productivity mesquite-dominated areas regardless of soil type (Fig. 2b). These soils have the lowest near-surface water holding capacities and highest evaporative losses. Current landscapes dominated by shrublands have lower probabilities of establishment compared to the historic landscape; most of the site had values less than 0.06 (Fig. 3c). Smallest probabilities were again found on gravelly soils where a shift in vegetation to shrublands had little effect on recruitment.

In general, most of the site experienced small decreases in recruitment as a result of a shift from grasslands to shrublands (Fig. 3c), although even small changes in small establishment probabilities (<0.19) can have significant effects on system dynamics (Coffin and Lauenroth, 1990). These results suggest that an increase in evaporative losses has a greater negative effect on soil water availability and recruitment compared to transpiration and interception. Simulated evaporative losses increase, with resulting decreases in recruitment, with a decrease in plant production following a shift from grasses to shrubs. Increased evaporation, and an increase in the evaporation/transpiration ratio, can have dramatic effects on grass establishment because evaporative losses are concentrated in the soil surface layers to which grass seedling roots are confined during the early phases of establishment (Briske and Wilson, 1978).

In some cases, soil properties interacted with vegetation structure to drive dynamics: playa soils with high clay content (63%) and high production in 1858 (Fig. 2a, b) had the largest decrease in recruitment following conversion to shrublands (Fig. 3c). By contrast, soils with moderate amounts of clay (29–34%; erosional scarplets and sand ridges, fan piedmont) maintained relatively high recruitment even as production decreased with a loss of grasslands

and increase in shrubs. Locations where establishment increased (green colors) should be targeted for restoration efforts since they have the greatest potential for establishment by *B. eriopoda*. Additional constraints, such as seed availability, will need to be considered, although remnant *B. eriopoda* plants exist even in shrublands that can provide seeds for recovery (Peters et al., 2006b).

Because root distributions were assumed to be similar for grasses and shrubs, and all precipitation was assumed to enter the soil with no run-on or runoff of water, effects of a shift from grasslands to shrublands on infiltration could not be examined in this study. Including increased infiltration losses from shrub-dominated communities (Wainwright et al., 2002) would tend to strengthen the general pattern of reduced grass establishment with shrub invasion.

3.2. Effects of climate change on recruitment

In general, probabilities of germination (not shown) and establishment decreased with a decrease in monsoonal precipitation and increased with an increase in precipitation after averaging across all soil types for each vegetation type (Fig. 4). The largest increases in recruitment were found for the most productive vegetation type (lowland grasslands) where a 50% increase in rainfall resulted in a 52% increase in recruitment compared with 24–27% increase in recruitment for the other vegetation types. Because these grasslands can receive runoff of water from upslope locations (Peters et al., 2006a), simulated probabilities without runoff are conservative estimates. Restoration efforts focused on lowland grasslands following runoff events are expected to have the greatest likelihood of success of all landscape locations. Proportionally similar reductions in recruitment (73–80%) were found for all vegetation types with 50% less rainfall. Drier summers below 25% of current rainfall amounts would decrease recruitment to near negligible values (<0.03) throughout the landscape. These values are smaller than the simulated probabilities for the current geographic distribution of *B. eriopoda* (Minnick and Coffin, 1999). This species of grass has been suggested to have established under cooler climates of the “little Ice Age”, and is only marginally supported under present climatic conditions (Neilson, 1986). Thus,

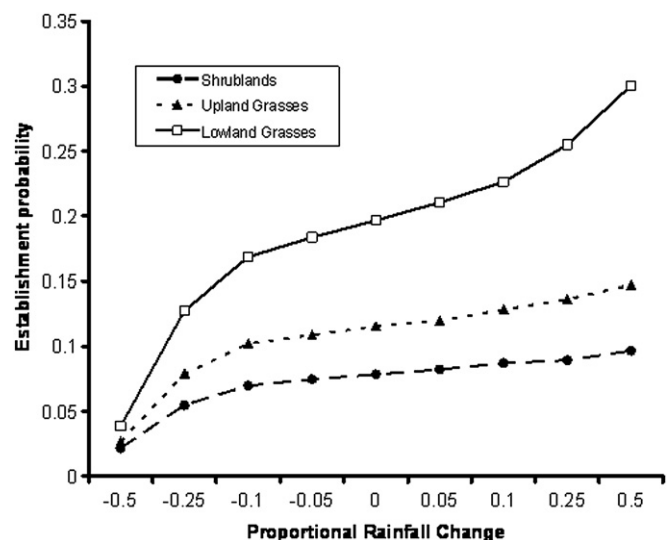


Fig. 4. Simulated establishment for a 3°C increase in temperature and a range of either a decrease or increase in precipitation for five vegetation types averaged across soil types; same values obtained for all three shrubland types with the same production values.

shifts to warmer and drier conditions that reduce recruitment even further may push these grasslands past a threshold where *B. eriopoda* can not persist. However, a small decrease in rainfall coupled with fewer but more intense storms may result in an increase in establishment. These changes in distribution of event sizes and intensity need to be examined in future studies.

4. Conclusions

Although most studies of state changes in arid and semiarid systems have focused on plant-soil feedbacks that favor shrub growth, our results show that soil water availability effects on the germination and establishment of grass seedlings is another important constraint. Reduced probabilities of establishment for *B. eriopoda* between 1858 and present day in the presence of broad-scale shrub invasion may help explain the challenges associated with restoration of this grass species. However, this pattern was not true for all locations; some locations had no change or an increase in the probability of establishment as a result of interactions between vegetation and soil properties. In particular, locations with intermediate clay content should be targeted for restoration efforts after taking into consideration other factors, such as grass seed availability, herbivory pressure, and water losses associated with increased runoff in some shrub communities.

According to the simulation model used here, directional changes in climate that increase rainfall during the North American monsoon, but with no change in frequency of intensity of rain events, will have the greatest effect on increased recruitment of *B. eriopoda* in lowland grasslands that comprise only a small part of the overall landscape. The increase in temperature under all simulated climate scenarios resulted in drier soils, in general, for all locations. However, vegetation-soil interactions in lowland grasslands allowed an increase in precipitation to overwhelm the increase in temperature for these grasslands. Reductions in monsoonal rainfall below 25% of current amounts would reduce recruitment to low levels (<0.03) across all vegetation types with significant impacts on the ability of *B. eriopoda* to persist in Chihuahuan Desert ecosystems. Additional factors that influence grass-shrub interactions, such as livestock grazing and increases in atmospheric carbon dioxide, need to be considered in future studies.

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