

Seed-bank structure and plant-recruitment conditions regulate the dynamics of a grassland-shrubland Chihuahuan ecotone

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Abstract. Large areas of desert grasslands in the southwestern United States have shifted to sparse shrublands dominated by drought-tolerant woody species over the last 150 yr, accompanied by accelerated soil erosion. An important step toward the understanding of patterns in species dominance and vegetation change at desert grassland–shrubland transitions is the study of environmental limitations imposed by the shrub-encroachment phenomenon on plant establishment. Here, we analyze the structure of soil seed banks, environmental limitations for seed germination (i.e., soil-water availability and temperature), and simulated seedling emergence and early establishment of dominant species (black grama, *Bouteloua eriopoda*, and creosotebush, *Larrea tridentata*) across a Chihuahuan grassland–shrubland ecotone (Sevilleta National Wildlife Refuge, New Mexico, USA). Average viable seed density in soils across the ecotone is generally low (200–400 seeds/m²), although is largely concentrated in densely vegetated areas (with peaks up to 800–1,200 seeds/m² in vegetated patches). Species composition in the seed bank is strongly affected by shrub encroachment, with seed densities of grass species sharply decreasing in shrub-dominated sites. Environmental conditions for seed germination and seedling emergence are synchronized with the summer monsoon. Soil-moisture conditions for seedling establishment of *B. eriopoda* take place with a recurrence interval ranging between 5 and 8 yr for grassland and shrubland sites, respectively, and are favored by strong monsoonal precipitation. Limited *L. tridentata* seed dispersal and a narrow range of rainfall conditions for early seedling establishment (50–100 mm for five to six consecutive weeks) constrain shrub-recruitment pulses to localized and episodic decadal events (9–25 yr recurrence intervals) generally associated with late-summer rainfall. Re-establishment of *B. eriopoda* in areas now dominated by *L. tridentata* is strongly limited by the lack of seeds and decreased plant-available soil moisture for seedling establishment.

Key words: black grama; Chihuahuan Desert; creosotebush; seedling recruitment; Sevilleta LTER; shrub encroachment; soil seed bank.

INTRODUCTION

The encroachment of native woody species has affected several hundred million hectares of arid and semiarid grasslands throughout central Australia, southern Africa, southwestern United States, South America, and the Mediterranean Basin over the last 150 years (Van Auken 2000, D'Odorico et al. 2012, Turnbull et al. 2014). This process is well documented in the Chihuahuan Desert, southwestern United States, where drought-tolerant C₃ shrub species (mainly honey mesquite, *Prosopis glandulosa*, and creosotebush, *Larrea tridentata*) have colonized large areas of C₄ semiarid grasslands since 1850 (Schlesinger et al. 1990, Van Auken 2000, D'Odorico et al. 2012, Turnbull et al. 2014). Shrub encroachment in this

region has caused largely irreversible changes in ecosystem function (e.g., alterations in landscape net primary production patterns and reductions in biodiversity) accompanied by accelerated wind and water erosion, which is perceived to be symptomatic of land degradation and desertification (Baez and Collins 2008, Turnbull et al. 2010a, Moreno-de las Heras et al. 2015, Peters et al. 2015).

A range of mechanisms has been suggested to explain the encroachment of desert shrubs in north Chihuahuan grasslands, including overgrazing, drought, changes in the frequency of rainfall, climate variability, fire suppression, and increased atmospheric CO₂ concentrations (Van Auken 2000, D'Odorico et al. 2012, Turnbull et al. 2014, Peters et al. 2015). Directional changes in these environmental conditions can cause either gradual or sudden alterations in ecosystem structure, promoting the shrub-encroachment phenomenon (D'Odorico et al. 2012, Collins and Xia

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2015); e.g., the severe multiyear drought between 1950 and 1960 caused rapid regional changes in Chihuahuan landscapes across the southwestern United States (Peters et al. 2015). In the Sevilleta National Wildlife Refuge (SNWR, central New Mexico), the 1950s drought led to the conversion of large areas of grasslands dominated by *Bouteloua eriopoda* into sparse desert shrublands dominated by *L. tridentata* (Gosz 1992). Remote sensing explorations of vegetation and field study of both shrub architecture and vegetation dynamics indicates that the SNWR grassland–shrubland ecotone (i.e., the transition between the *B. eriopoda*- and *L. tridentata*-dominated communities) has remained stable for long periods after 1960–1970, showing little changes in either shrub progression or grass recovery (Allen et al. 2008, Peters and Yao 2012, Moreno-de las Heras et al. 2015).

An important step toward understanding patterns in plant-species dominance and vegetation change at desert grassland–shrubland ecotones is determining plant-recruitment limitations imposed by the shrub-encroachment process. Seed availability and the dynamics of seed germination and early seedling establishment are critical plant recruitment processes that can condition species dominance, plant-regeneration patterns, and the rates of vegetation change in drylands (Coffin and Lauenroth 1989, Espigares and Peco 1993, Kigel 1995, Bowers et al. 2004, Koontz and Simpson 2010, Peters et al. 2014, Bochet 2015). Previous studies of *L. tridentata* plant-age structure in a variety of North American desert sites suggests that recruitment of seedlings occurs primarily as rare episodic events that may influence shrub-expansion rates and the frequency of active encroachment pulses for the region (Chew and Chew 1965, Barbour 1969, Allen et al. 2008). Polyploid *L. tridentata* shows vegetative shrub reproduction by clonal growth in the Mojave Desert (Vasek 1980). However, there is no evidence that Chihuahuan (diploid) *L. tridentata* spreads clonally, and consequently, colonization in the Chihuahuan Desert of this long-lived (approximately 400-yr life span) shrub appears to depend exclusively on seed reproduction (Miller and Huenneke 2000, Pendleton et al. 2008, Peters et al. 2012). Seedling recruitment has been shown to occur infrequently for *B. eriopoda*, a perennial and relatively short-lived (20–40 yr life span) C_4 grass species that mostly regenerates through stoloniferous expansion (Nelson 1934, Neilson 1986, Collins and Xia 2015). However, analysis at large-scale biome transitions indicates that recruitment of *B. eriopoda* from seed accounts for localized patterns in the dominance of grass species across Chihuahuan landscapes and shortgrass steppe, and may also impact plant-colonization patterns in areas where *B. eriopoda* patches are locally extinct, which prevents vegetative grass recovery (Minnick and Coffin 1999, Peters 2000, 2002a). Shrub encroachment promotes alterations in soil properties, soil-moisture patterns, and the availability of plant propagules, which may constrain the re-establishment of *B. eriopoda* in areas now dominated

by desert shrubs (Schlesinger et al. 1990, Turnbull et al. 2010b, Peters and Yao 2012).

The aim of this study is to analyze how seedling recruitment for *B. eriopoda* and *L. tridentata* can impact shrub encroachment in a Chihuahuan grassland–shrubland ecotone (SNWR, New Mexico). To achieve this aim, we study the soil seed-bank structure and environmental limitations for seed germination, and simulate plant emergence and early establishment of *B. eriopoda* and *L. tridentata* over the ecotone.

MATERIALS AND METHODS

Site description

This study was carried out in the SNWR, central New Mexico (Socorro County), USA, the location of a National Science Foundation Long Term Ecological Research (LTER) site (Fig. 1a). The SNWR is a biome transition zone between the Chihuahuan Desert, the Great Plains grasslands, the Colorado Plateau steppe, and the Mogollon coniferous woodland. Annual precipitation is 230 mm, with approximately 60% falling in the form of high-intensity convective storms in the summer monsoon (from late-June to September). Average annual air temperature is 14°C (2°C in January and 26°C in July). Peak vegetation growth in the area is concentrated in July–September, coinciding with the summer monsoon (Moreno-de las Heras et al. 2015).

We selected four study sites for analysis within a 5-km² grassland–shrubland ecotone (*B. eriopoda*-dominated grassland and *L. tridentata*-dominated shrubland) in the SNWR McKenzie Flats (Five Points experimental area), a zone of gently sloping (<5°) terrain (Fig. 1b). Analysis of soil carbon isotopes, shrub architecture, and photographic evidence indicates that *L. tridentata* expanded over the Five Points area in the past 80 yr, particularly in a major shrub-encroachment pulse that took place along a deep and prolonged drought from 1951 to 1956 (Gosz 1992, Allen et al. 2008, Turnbull et al. 2008). Livestock grazing was excluded from the area in 1973, following 37 yr of rangeland use.

The study sites (each 30 × 10 m; Fig. 1c) represent a *L. tridentata*-encroachment gradient (Turnbull et al. 2008, 2010a, b), and encompass a grassland end-member (Site 1, 45% and 0% grass and shrub cover, respectively), two transition landscapes (Sites 2 and 3, 40–22% grass and 6–16% shrub cover), and a shrubland end-member (Site 4, <1% and 33% grass and shrub cover, respectively). Vegetation cover is organized in a mosaic of grass and shrub patches (typically <1 m² and 0.5–5 m² for grass and shrub) interspaced by bare soil interpatches (with average diameter ranging from 0.2 m in Sites 1 and 2 to >1 m in Sites 3 and 4). Soils are alkaline, sandy loams with <10% clay content (Appendix S1: Table S1 for soil characteristics). Surface stoniness and soil organic carbon contents in shrub, grass, and bare soil interpatches reflect the typical spatial patterns of erosion/sedimentation and

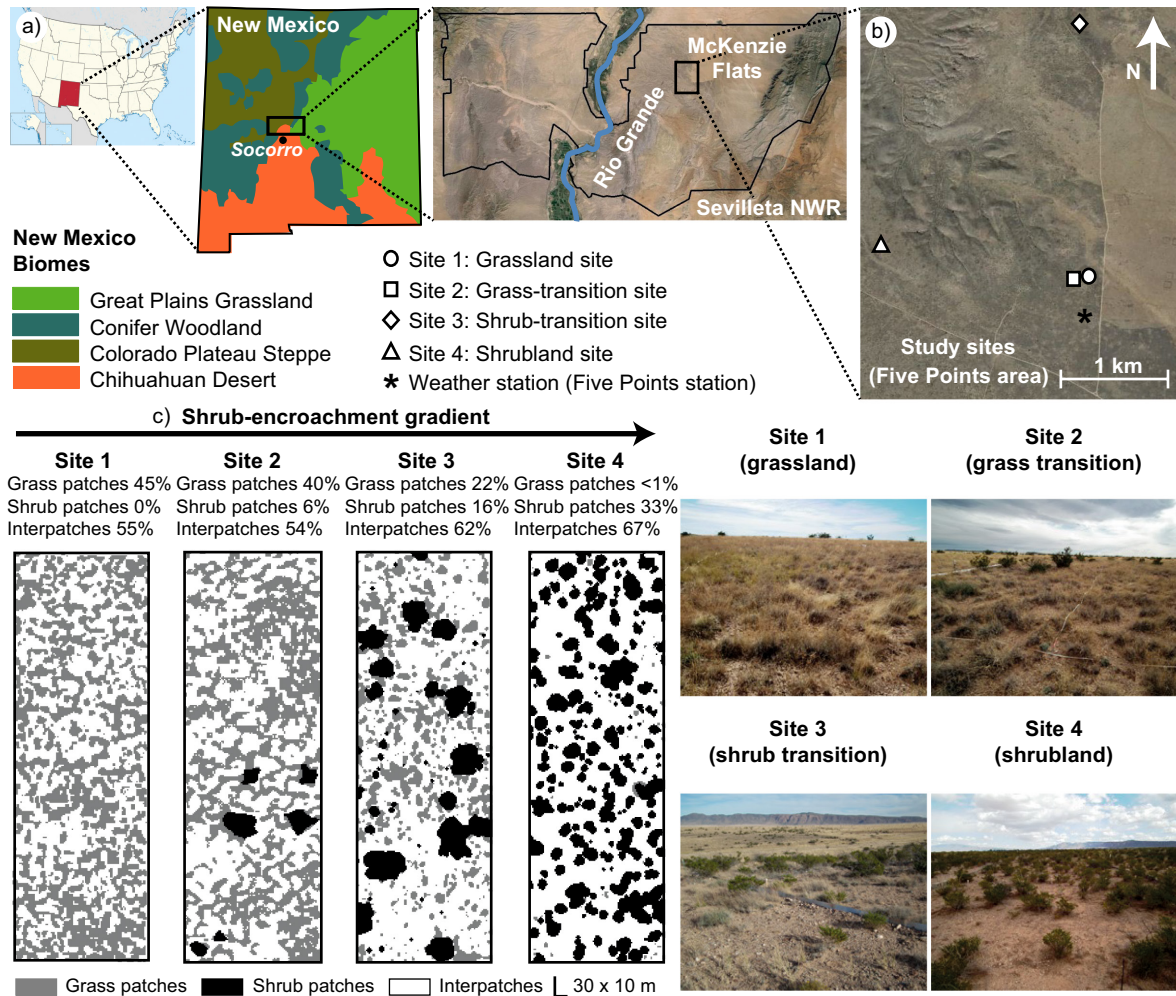


FIG. 1. Study area. (a) Location of the Sevilleta National Wildlife Refuge (SNWR) and distribution of New Mexico, USA, biomes. (b) Location of the study sites (Five Points area, McKenzie Flats), and (c) maps and photos of study sites (10 × 30 m each). Biome distribution in panel (a) follows the Sevilleta LTER classification (<http://sev.lternet.edu/about>). Spatial distribution of surface types (percentage of surface) was determined in the field by applying the point intercept method (details in *Methods*). Graphical representation of surface types (panel c) for Sites 1, 3, and 4 was taken from Turnbull et al. (2010a). For Site 2, surface types were digitalized from a recent (2014) high-resolution (20 cm/pixel) aerial image available through GoogleEarth. Source for the background image in panels (a) and (b): 2014 National Aerial Imagery Program (USDA Farm Service Agency).

resource-island development in shrub-encroached dry grasslands (Schlesinger et al. 1990, Reynolds et al. 1999, Turnbull et al. 2010a, b).

Characterization of vegetation cover and soils

We used the point-intercept method to estimate the distribution of surface types (percent cover, relative abundance) in our four sites. Presence of grass patches (Gp), shrub patches (Sp), and bare soil interpatches (Ip) was recorded every 50 cm using a metal rod pointer (2 cm diameter) along five parallel, 30 m long, linear transects regularly distributed at each site.

We collected three composite soil samples per surface type and site (each sample formed by six

homogeneously mixed subsamples) from the top 10 cm to characterize soil traits (i.e., soil granulometry and texture, pH, electrical conductivity, inorganic and organic C, total N, and plant available P) using standardized methods of soil analysis (Carter and Gregorich 2008). Soil water retention at a range of matric potentials ranging from saturation to the permanent wilting point ($\Psi = -0.0002, -0.01, -0.03, -0.05, -0.08, -0.4, -0.8, \text{ and } -1.45 \text{ MPa}$) was determined using the pressure chamber method (Klute 1986). Parametrization of the soil-water-retention characteristic curves was made according to Brooks and Corey (1964). Details of the parameterized Brooks and Corey curves can be found in Appendix S1: Fig. S1 and Table S2.

Soil seed-bank sampling and analysis

In each site, we established four 5×5 m plots that were randomly distributed (without overlapping) to measure the soil seed bank. Gp, Sp, and Ip surface cover (%) were visually estimated in nine (0.5×0.5 m) quadrats distributed at random within each plot.

In November 2013, following seed production and dispersal at the SNWR (Pendleton et al. 2008, Koontz and Simpson 2010) and after the course of an exceptionally wet growing season (June–September rainfall was 243 mm, 75% above the 1988–2015 average), we collected soil samples (36 cm² surface area and 3 cm depth) to analyze the composition of the soil seed bank. In each plot, we collected four soil samples per surface type, totaling 156 samples. Soil samples were air dried, carefully disaggregated and sieved (to 4 mm) to remove big pebbles and coarse plant fragments. Excluded material was examined manually for seeds and fruits. Some Chihuahuan species need exposure to low temperature to break seed dormancy (Peters 2002a) and therefore the soil samples were stored for four weeks at low temperature (ranging from 0°C to 4°C) to break seed dormancy (Coffin and Lauenroth 1989). The samples were then spread out over a 5-cm vermiculite layer in plastic pots. Availability of viable seeds and floristic composition of the soil seed bank was determined after germination in a greenhouse with controlled day length and temperature (12 h day length, 20–25°C). The samples were watered to field capacity at the start of the experiment in January 2014. Bottom-up watering was then provided as required to keep soil moisture near field capacity. After the first six weeks, we added 40 ppm of fertilizer (5 mL fertilizer/10 L water; NPK 3.5:3.5:3.5) mixed with water every month. We counted emerged seedlings at weekly intervals until August 2014.

Nonmetric multidimensional scaling (NMS) ordination was used to explore differences in floristic composition of the soil seed bank for the studied sites. The relation between the floristic composition of the soil seed bank to the distribution of cover types on the plot surface (i.e., Gp, Sp, and Ip abundance) was analyzed by fitting thin plate splines to the NMS ordination using general additive models. Differences in soil seed densities of viable grass, forb, shrub/subshrub, *B. eriopoda*, *L. tridentata*, and total seeds between sites and surface types were tested using Kruskal-Wallis ANOVA and post-hoc Mann-Whitney tests.

Seed-germination tests and analysis for *B. eriopoda* and *L. tridentata*

Native *B. eriopoda* seeds (unimproved Chihuahuan ecotype “Nogal”; Leyendecker 1975) for the germination tests were obtained from a local seed supplier (USDA Los Lunas Plant Materials Center, Los Lunas, New Mexico, USA). *L. tridentata* seeds for this study were collected in the field. Chihuahuan *L. tridentata* fruits are

generally shed when ripe throughout summer and fall, although *L. tridentata* shrubs can keep small seed crops un-shed for after-ripening periods beyond fall (Barbour 1968, Pendleton et al. 2008). At the time of soil seed-bank sampling for this study (November 2013), we observed significant amounts of ripe, un-shed fruits in SNWR *L. tridentata* shrubs. We therefore collected freshly ripe *L. tridentata* fruits in the Five Points shrublands for our seed-germination tests (approximately 30 fruits per shrub from 50 adult shrubs). Each *L. tridentata* fruit is split into five mericarps, containing one seed per mericarp. The seeds’ husks were removed by rubbing the mericarps with sandpaper.

Seedling germination was studied under four temperature levels (15°C, 20°C, 25°C, and 30°C) and eight water potentials representing soil-moisture values between saturation and the wilting point ($\Psi = 0, -0.2, -0.4, -0.6, -0.85, -1.1, -1.3, \text{ and } -1.5$ MPa). Water potentials were simulated using polyethylene glycol (PEG) concentrations following the standard equations of Michel (1983). Seven replicates for each water potential and temperature level were prepared. Each replicate consisted of 25 (15) *B. eriopoda* (*L. tridentata*) seeds placed in a 9 cm diameter Petri dish, on a bed composed of a layer of hydrophilic cotton and filter paper. Replicates were moistened with 30 mL of PEG solutions. The experiment took place inside a phytotron under controlled conditions (temperature level $\pm 1^\circ\text{C}$, 12-h day length, 150 $\mu\text{mol}/\text{m}^2/\text{s}$ lighting intensity (i.e., photon flux density), 75% relative air humidity for four weeks). Germination was monitored every three days, with germination considered successful when a minimum of 4 mm of embryonic root had emerged (at the time of germination, the seedling green cotyledons were, at least, partially visible). Germination rate (Gr, %) was calculated as the total percentage of germinated seeds during the (four-week) germination tests. Time to germination (Gt, d) was determined as the time to reach 90% of total seed germination for each test, which provides a conservative approach to approximate time to seedling emergence in the field using laboratory tests (Moreno-de las Heras et al. 2011).

To study the influence of water potential (Ψ , MPa) on seed-germination rate (Gr, %), a sigmoid-shape response function (Moreno-de las Heras et al. 2011) was fitted to the germination results obtained for each species and temperature level

$$G_r = \frac{G_m}{1 + e^{\frac{\Psi - a}{b}}} \quad (1)$$

where G_m (%) is the maximum germination rate that is reached at $\Psi = 0$ MPa, a is the inflection point (MPa), and b is a shape coefficient.

Germination rate in Eq. 1 rapidly decreases below a particular level of water potential (hereafter defined as the water-potential threshold for seed germination, Ψ_g , MPa), which can be mathematically determined by

equating the fourth derivate of the response function to zero

$$\psi_g = -\ln(5 - 2\sqrt{6})b + a. \quad (2)$$

We applied a generalized linear model (quasi-binomial distribution and logit-link function) with species (Sp, two levels: *B. eriopoda* and *L. tridentata*) and temperature (*T*, four levels: 15°C, 20°C, 25°C, and 30°C) as factors, water potential (Ψ) as a covariable, and their interactions to test for their effects on germination rate (Gr). The Sp $\times$ Ψ interaction indicates whether Ψ_g differs for *B. eriopoda* and *L. tridentata*. We also applied factorial ANOVA to test for the effects of Sp, *T*, and Ψ and their interactions on germination time (Gt).

Seedling emergence and early establishment simulations and analysis

Early plant dynamics for *B. eriopoda* and *L. tridentata* are largely controlled by soil moisture dynamics in the top 5 cm of the soil profile for seed germination and field emergence, and in the top 30 cm for early root growth and seedling establishment (Minnick and Coffin 1999, Peters 2000, Woods et al. 2011). Seed germination in arid environments is also influenced by the temporal dynamics of maximum and minimum soil-surface temperature, which constrain the opportunity time for field seedling emergence and further plant establishment (Kigel 1995). We model long-term (centennial) soil-moisture contents and soil surface temperature to simulate seedling emergence and early establishment of *B. eriopoda* and *L. tridentata*. We use results of these simulations to analyze the influence of shrub-encroachment stage, and growing season rainfall on the early dynamics of both species, with particular detail for the 1950s severe drought, which is recognized as the period with the most important *L. tridentata*-encroachment pulse for the Five Points experimental area (Gosz 1992, Allen et al. 2008).

Soil moisture and soil surface temperature simulations.— We applied an ecohydrological model, DayCent (Parton et al. 1998), parameterized for our field sites, to simulate soil-moisture dynamics at a daily time step (at 0–5 cm and 0–30 cm) using daily precipitation records. The model (DayCent version 4.5) was set up to represent soil-moisture records obtained in 2005–06 for our sites (Turnbull et al. 2010a). Soil parameters (i.e., soil particle-size distribution and bulk density) were obtained from intensive soil surveys carried out by Turnbull et al. (2010b). Soil-water content at field capacity and the wilting point were obtained from the Brooks and Corey soil-water retention curves determined in this study (Appendix S1: Table S3). Root distribution by depth was parametrized using typical root-density values of Chihuahuan *B. eriopoda* grasslands and *L. tridentata* shrublands (Appendix S1: Table S4). Application of the parameterized model using 2005–2006 onsite daily records of precipitation and

air temperature (SNWR Five Points station; Fig. 1b) yields a low root-mean-square error (0.02 vol/vol, 9% normalized root-mean-square error, NRMSE) for soil-moisture prediction (Appendix S1: Fig. S2a).

Maximum and minimum soil temperatures were estimated using field-based air–soil temperature relations. Our empirical air–soil equations were derived from the application of polynomial regression of the historic 1997–2014 air and soil surface records of the SNWR Five Points station (equations and error details in Appendix S1: Fig. S2b and c). Analysis of the field-parameterized air–soil temperature equations yield low levels of root-mean-squared error for the estimation of maximum (3.9°C, 9% NRMSE) and minimum (2.5°C, 7% NRMSE) soil-surface temperature.

We simulated soil moisture and soil surface temperature dynamics in our four experimental sites by applying a centennial (1916–2014) series of daily (maximum and minimum) air temperature and precipitation of a nearby (30 km from the study area) reference weather station (Socorro, U.S. Western Regional Climate Center station code 298387, 237 mm mean annual precipitation).

Modeled seedling emergence and early establishment requirements.— Occurrence of emergence and early establishment of *B. eriopoda* and *L. tridentata* seedlings was simulated by comparing modelled soil-surface temperature and soil-moisture contents through time with the plant recruitment conditions of the species. The application of conservative criteria derived from seed-germination laboratory tests provides a practical way to simulate seedling emergence in the field (Lauenroth et al. 1994, Kigel 1995, Moreno-de las Heras et al. 2011). Thus, seedling emergence conditions were derived from our seed-germination experiments. A wet period with water potential $\geq \Psi_g$ MPa and length Gt (days) at 0–5 cm of the soil profile is required for seedling emergence. Threshold water-potential values for our sites, Ψ_g , were transformed into soil-moisture content (% vol/vol) for analysis, by applying the parameterized water-retention curves. We constrained the timing of seedling emergence by imposing a tolerance range of soil-surface temperatures. Species-specific minimum soil-surface temperature ($T_{\min}$) was obtained in our seed germination experiments as the lowest temperature level that showed optimal (i.e., not statistically different from peak) Gr and Gt responses. Maximum soil-surface temperature ($T_{\max}$) for our simulations was established at 35°C for *L. tridentata* and 40°C for *B. eriopoda*, which constitute the upper tolerance limit for the species (Rivera and Freeman 1979, Minnick and Coffin 1999).

Early seedling establishment for both *B. eriopoda* and *L. tridentata* largely depends on root development, which has been shown to occur at minimum soil-moisture levels similar to those required for seedling emergence (Herbel and Sosebee 1969, Woods et al. 2011). We therefore applied the experimental Ψ_g water-potential threshold as minimum soil-moisture level to simulate early seedling establishment. *B. eriopoda*

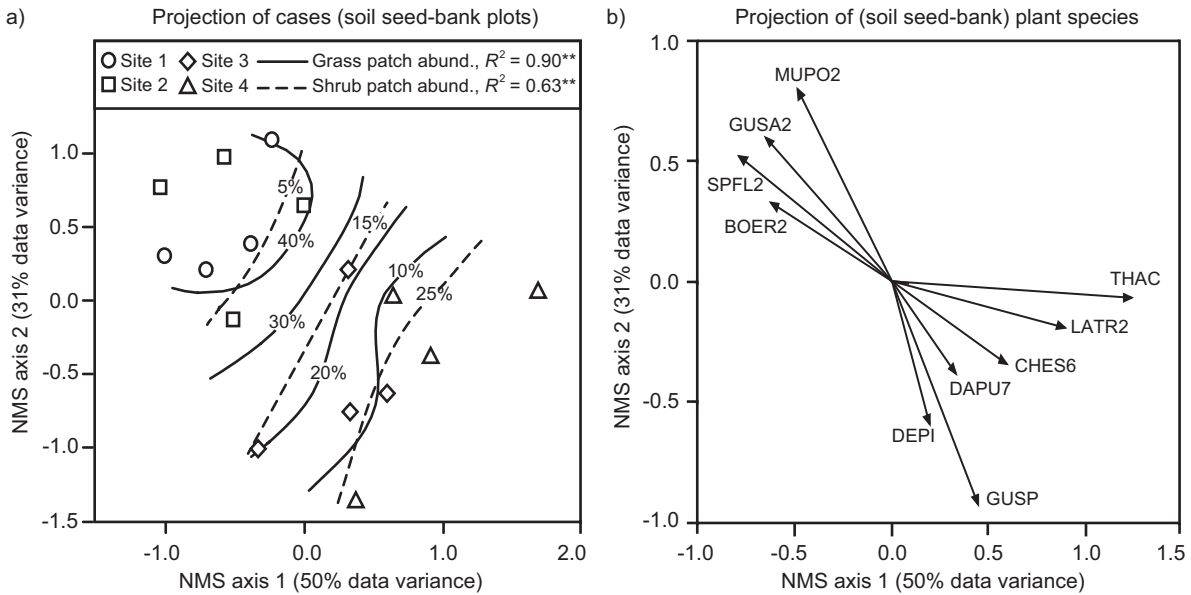


FIG. 2. Nonmetric multidimensional scaling (NMS) ordination of the soil seed-bank data: (a) projection of cases (5 × 5 m soil seed-bank plots) and (b) projection of plant species (for simplification, only plant species that significantly correlate with the ordination axes at $P < 0.05$ are shown; tested using Spearman's R). Grass and shrub patch abundances are represented (as cover percentages) in panel (a) by the fitted thin plate spline surfaces (R^2 and significance of the fitted surfaces is shown). Species symbols in panel (b) follow the USDA Plant Database codes (<http://plants.usda.gov/java/>): MUPO2, *Muhlenbergia torreyi*, GUSA2, *Gutierrezia sarothrae*, SPFL2, *Sporobolus flexuosus*, BOER2, *Bouteloua eriopoda*, DEPI, *Descurainia pinnata*, GUSP, *G. sphaerocephala*, DAPU7, *Dasyochloa pulchella*, CHES6, *Chamaesyce serpyllifolia*, LATR2, *Larrea tridentata*, THAC, *Thymophylla acerosa*. ** $P < 0.01$.

seedling establishment depends on the occurrence of suitable soil-moisture conditions for promoting the development of both the seminal and adventitious root systems in the soil (Minnick and Coffin 1999, Peters 2000). Early growth of the seminal roots requires wet conditions (i.e., water potential $\geq \Psi_g$ MPa) at 0–30 cm during four consecutive days after seedling emergence (Minnick and Coffin 1999, Peters 2000). Growth of the adventitious roots typically is initiated from the near surface 20 to 50 days after field emergence, and requires three consecutive days with water potential at or above Ψ_g at 0–5 cm and a subsequent four-day period with suitable soil moisture at 0–30 cm (Peters 2000). The seminal root system has little capacity to support vegetation growth under dry conditions. Hence, seedlings were simulated to die if soil moisture at 0–30 cm drops below Ψ_g for more than four days between the dates of seedling emergence and adventitious root growth (Minnick and Coffin 1999).

Early seedling establishment of *L. tridentata* is also strongly dependent on the occurrence of suitable soil-moisture conditions for the development of the root system in the 0–30 cm soil profile. Creosotebush requires four weeks of wet conditions for taproot development in the top 30 cm of the soil (Woods et al. 2011). Death of modeled seedlings was simulated if soil moisture at 0–30 cm drops below Ψ_g for more than four days within four weeks after the seedling-emergence date, applying a conservative seedling

root-desiccation criterion analogous to those described by Minnick and Coffin (1999). *L. tridentata*-root growth requires unusually high oxygen and may also be affected by fungal intrusion due to excessive soil moisture (Valentine and Gerard 1968, Woods et al. 2011). Seedlings were therefore simulated to die if soil moisture at 0–30 cm remains at or above field capacity (-0.03 MPa) for more than four days in the (four-week) taproot-development period.

Data analysis of simulated seedling emergence and early establishment.— We calculated the seedling emergence/establishment frequency (yr^{-1}) and relative frequency by month (%) for the modelled plant-recruitment dynamics in our sites between 1916 and 2014. Event-triggering rainfall for modelled seedling emergence (establishment) was determined as the cumulative rainfall amount between the start date of seed germination and seedling emergence (establishment) date. We analyzed the effects of species (two levels: *B. eriopoda* and *L. tridentata*) and site (four levels: Sites 1–4) on event-triggering rainfall by applying factorial ANOVA. Factorial ANOVA was also applied to test for site effects and differences in monsoonal summer rainfall (i.e., June–September precipitation) between successful and unsuccessful years (i.e., years with and without seedling emergence/establishment, respectively). Finally, we explored in detail the modeled *B. eriopoda* and *L. tridentata* seedling-recruitment dynamics for the series 1948–1959, which includes the 1950s dry period plus three years immediately before/after that period.

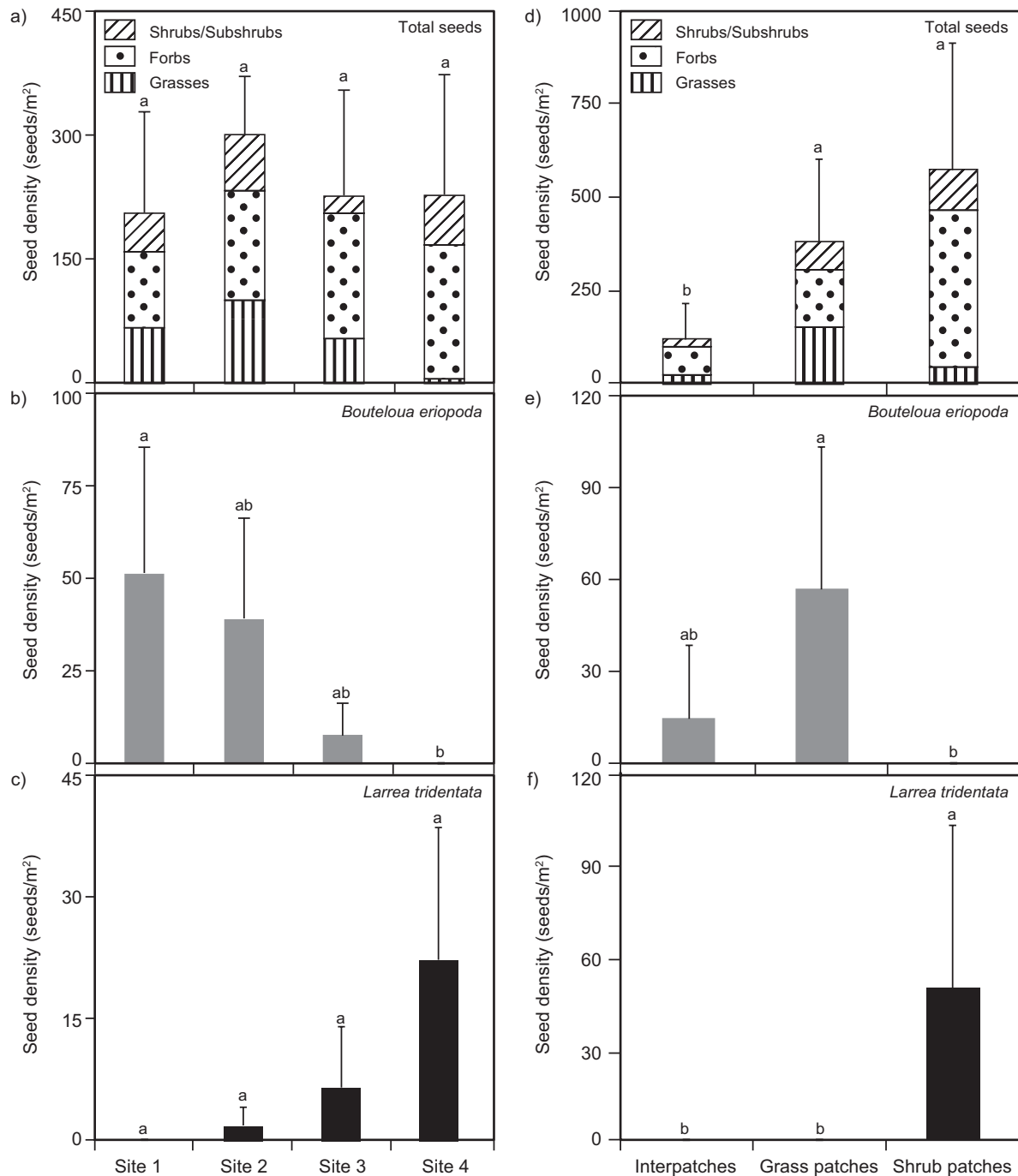


FIG. 3. Differences in soil seed density (viable seeds/m²) for (a–c) sites (area-weighted values) and (d–f) surface types. Total seeds (a and d), *B. eriopoda* seeds (b and e), and *L. tridentata* seeds (c and f). Shrub/subshrub, forb, and grass seed densities are detailed in different patterns in panels (a) and (b). Different letters indicate significant differences at $P < 0.05$. Tested using Kruskal-Wallis ANOVA and post-hoc Mann-Whitney U tests. Error bars show SD.

RESULTS

Soil seed bank

We identified a total of 21 different plant species in the soil seed bank, comprising 12 forbs, five grasses, and

four subshrub/shrub species (Appendix S1: Table S5). The soil seed bank at all sites is dominated by seeds of annual forbs (particularly *Plantago patagonica*). Although species richness is similar in all sites (about 9–14 species), the floristic composition and heterogeneity of the soil seed bank are significantly affected by

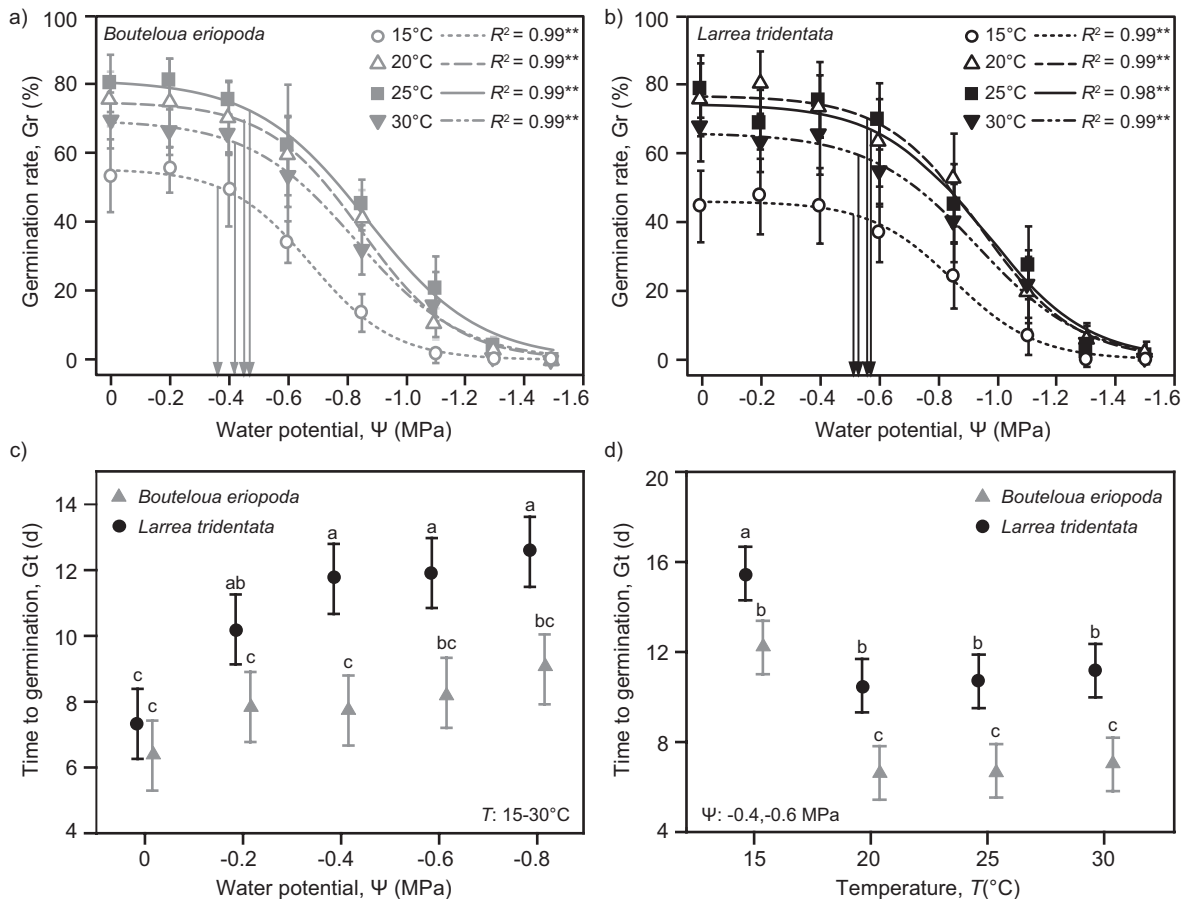


FIG. 4. Seed germination environmental conditions: germination vs. water potential curves for (a) *B. eriopoda* and (b) *L. tridentata* (parameter estimates of the fitted curves are detailed in Appendix S1: Table S7), (c) impact of water potential level on seed germination time (pooled data for the studied range of temperatures), and (d) impact of temperature on seed germination time (pooled data for water potential at -0.4 and -0.6 MPa). Different temperatures are indicated by different markers and line patterns in panels (a) and (b). Water potential threshold for seed germination (Ψ_g) is indicated in each curve by the vertical arrows (panels a and b). Different letters indicate differences at $P < 0.05$ (plots c and d), tested using factorial ANOVA and post-hoc Tukey HSD tests. Error bars show SD. $^{**} P < 0.01$.

shrub encroachment (Fig. 2). NMS ordination of the soil seed-bank data (81% of total data variance) shows important differences in the floristic composition of the sites. Three grass species (*Sporobolus flexuosus*, *Bouteloua eriopoda*, and *Muhlenbergia torreyi*) and a subshrub (*Gutierrezia sarothrae*) are indicative of the seed-bank floristic composition in the grass-dominated and transition sites (Site 1 and 2, respectively; Fig. 2b). The soil seed-bank structure in the shrub-transition and dominated sites (Site 3 and 4, respectively) is characterized by the presence of two annual forb species (*Descurainia pinnata* and *Chamaesyce serpyllifolia*), a perennial grass (*Dasyochloa pulchella*), two subshrubs (*Thymophylla acerosa* and *Gutierrezia sphaerocephala*), and a shrub species (*Larrea tridentata*; Fig. 2b). Heterogeneity of the soil seed-bank floristic composition (assessed on the basis of mean Euclidean distances for each site in the NMS ordination) increases from the grassland to the shrubland site (0.7, 0.9, 0.9, and 1.2 NMS distance units for Site 1, 2, 3, and 4,

respectively). The NMS representation of the soil seed-bank floristic structure can be explained to a large extent by the abundance of grass and shrub patches in the (5×5 m) seed-bank plots (Fig. 2a).

Average density of viable seeds in the soil ranges 200–400 seeds/m² (no differences were found between sites at $P < 0.05$) and is mainly dominated by annual forbs (Fig. 3a), particularly *Plantago patagonica* and *Phacelia integrifolia* (largely distributed in all sites) and *Descurainia pinnata* and *Chamaesyce serpyllifolia* (broadly distributed in Sites 3 and 4). Grass seed abundance in the shrub-dominated Site 4 is negligible (5 seeds/m², Fig. 3a). *B. eriopoda* seed density varies significantly between sites (Kruskal-Wallis $H = 9.7$, 3 df, $P = 0.02$), decreasing from Sites 1 and 2 to Sites 3 and 4 (from 50–40 to 7–0 seeds/m², Fig. 3b). *L. tridentata* soil seed abundance differs marginally between sites ($H = 6.3$, 3 df, $P = 0.08$), with 20 seeds/m² in the shrubland, 6–2 seeds/m² in the transition sites, and no *L. tridentata* seeds in the grassland (Fig. 3c).

Availability of viable seeds differs between surface types ($H = 19.8$, 2 df, $P < 0.01$). Bare soil interpatches show very low densities (typically <150 seeds/m²), while vegetated clumps concentrate most viable seeds, peaking up to maxima of 800 and 1,200 seeds/m² for grass and shrub patches, respectively (Fig. 3d). *B. eriopoda* seeds are preferentially distributed in the grass patches ($H = 13.9$, 2 df, $P < 0.01$, Fig. 3e). We did not find any *L. tridentata* seeds outside the shrub patches (Fig. 3f). Seed availability in all sites follows the same surface-type trends, although for Site 1 we did not find in general significant differences between interpatches and vegetated (grass) patches at $P < 0.05$ (Appendix S1: Table S6).

Seed-germination conditions for *B. eriopoda* and *L. tridentata*

Maximum germination rate for both *B. eriopoda* and *L. tridentata* ranges from 75% to 80% and is reached at 20–25°C (Fig. 4a, b). We did not find significant differences in seed germination between species at $P < 0.05$. Seed germination is affected by temperature ($F_{3, 432} = 52.0$, $P < 0.01$), and decreases abruptly below 20°C. Seed germination is also affected by water potential ($F_{1, 432} = 2042.2$, $P < 0.01$), and decreases rapidly below threshold Ψ_g levels of about -0.45 and -0.55 MPa for *B. eriopoda* and *L. tridentata*, respectively (Fig. 4a, b; Appendix S1: Table S7). The interaction between species and water potential ($\text{Sp} \times \Psi$, $F_{1, 432} = 10.8$, $P < 0.01$) indicates that threshold Ψ_g is significantly higher for *B. eriopoda*. Soil moisture at Ψ_g for our sites ranges from 9.0% (for -0.55 MPa in Site 1) to 9.7% (for -0.45 MPa in Site 4; Appendix S1: Table S3).

Time to germination is affected by species ($F_{1, 240} = 72.4$, $P < 0.01$) and water potential ($F_{4, 240} = 14.3$, $P < 0.01$). *L. tridentata* shows generally longer seed-germination times than *B. eriopoda* (Fig. 4c). Time to germination increases for both species significantly by reducing water potential (Fig. 4c). Seed germination time is also affected by temperature ($F_{3, 240} = 51.2$, $P < 0.01$), and is significantly longer at 15°C (Fig. 4d). The lowest temperature level that shows a quick and strong seed germination response ($T_{\min}$) is 20°C for both species. Time to germination (Gt) at 20–30°C and threshold Ψ_g water potential (*B. eriopoda*: -0.45 MPa, 9.3–9.7% soil moisture for the study sites; *L. tridentata*: -0.55 MPa, 9.0–9.3% soil moisture) is about six and 10 days for *B. eriopoda* and *L. tridentata*, respectively (Fig. 4d).

Simulated seedling emergence and establishment for *B. eriopoda* and *L. tridentata*

Simulated conditions for seedling emergence in the study sites take place at a frequency of 0.29–0.37 yr⁻¹ (recurrence time 2–3 yr) for *B. eriopoda* and 0.08–0.15 yr⁻¹ (recurrence time 6–12 yr) for *L. tridentata*

(Fig. 5a; Appendix S1: Tables S8 and S9). Modelled early seedling-recruitment events show a frequency of 0.13–0.22 yr⁻¹ (recurrence time 5–8 yr) for *B. eriopoda*, and 0.04–0.12 yr⁻¹ (recurrence time 9–25 yr) for *L. tridentata* (Fig. 5b; Appendix S1: Tables S8 and S9). Sites 3 and 4 show in general longer recurrence times for seedling emergence and establishment than Sites 1 and 2. Simulated seedling emergence takes place primarily in July and August for both species (Fig. 5a), while early seedling establishment occurs mainly in September for *B. eriopoda* and throughout August and September for *L. tridentata* (Fig. 5b).

Triggering rainfall for seedling emergence differs for *L. tridentata* and *B. eriopoda* ($F_{1, 182} = 37.9$, $P < 0.01$). *B. eriopoda* seedling emergence requires less rainfall than *L. tridentata* (a minimum of 15 mm and 35 mm average rainfall for *B. eriopoda*, compared with 30 mm minimum and 50 mm average for *L. tridentata*; Fig. 5c). Triggering rainfall for seedling establishment is also affected by species ($F_{1, 103} = 17.3$, $P < 0.01$). *B. eriopoda* early seedling establishment takes place in a wide rainfall range (from approximately 50 to 160 mm), while *L. tridentata* seedling establishment occurs within a narrower window of rainfall amount (from about 50 to 100 mm; Fig. 5c). We did not find any differences between sites at $P < 0.05$ on triggering rainfall requirements for both seedling emergence and early establishment.

Monsoonal summer rainfall differs for successful and unsuccessful years at both the seedling emergence ($F_{1, 776} = 162.4$, $P < 0.01$) and early establishment ($F_{1, 776} = 72.8$, $P < 0.01$) stages. In general, successful seedling emergence and establishment for both *B. eriopoda* and *L. tridentata* takes place in years with above-average summer rainfall, while unsuccessful years commonly have lower monsoonal rainfall (Fig. 5d). *L. tridentata* emergence occurs in years with higher monsoonal rainfall than *B. eriopoda* seedling emergence ($F_{1, 776} = 21.3$, $P < 0.01$), however we did not find differences between species in summer precipitation for seedling establishment (Fig. 5d). Site does not affect monsoonal requirements for successful seedling emergence/establishment of the species at $P < 0.05$.

Detailed exploration of seedling emergence and early establishment simulations for 1948–1959 indicates that the soil-surface temperature and soil-moisture dynamics in (the grass-transition) Site 2 meet episodically the creosotebush recruitment conditions during that period (Fig. 5e). Particularly, modelled dynamics show successful recruitment of *L. tridentata* for 1949 and 1957, immediately before and after the 1951–56 drought (1951–1956 average yearly precipitation is 160 mm, 35% less than the 1916–2014 annual mean). Surface temperature and soil-moisture conditions for *B. eriopoda* seedling recruitment are also episodically met in Site 2 within 1948–1959 (years 1949, 1950, 1954, and 1957). Recruitment simulations in Sites 1, 3, and 4 show similar patterns (Appendix S1: Fig. S3).

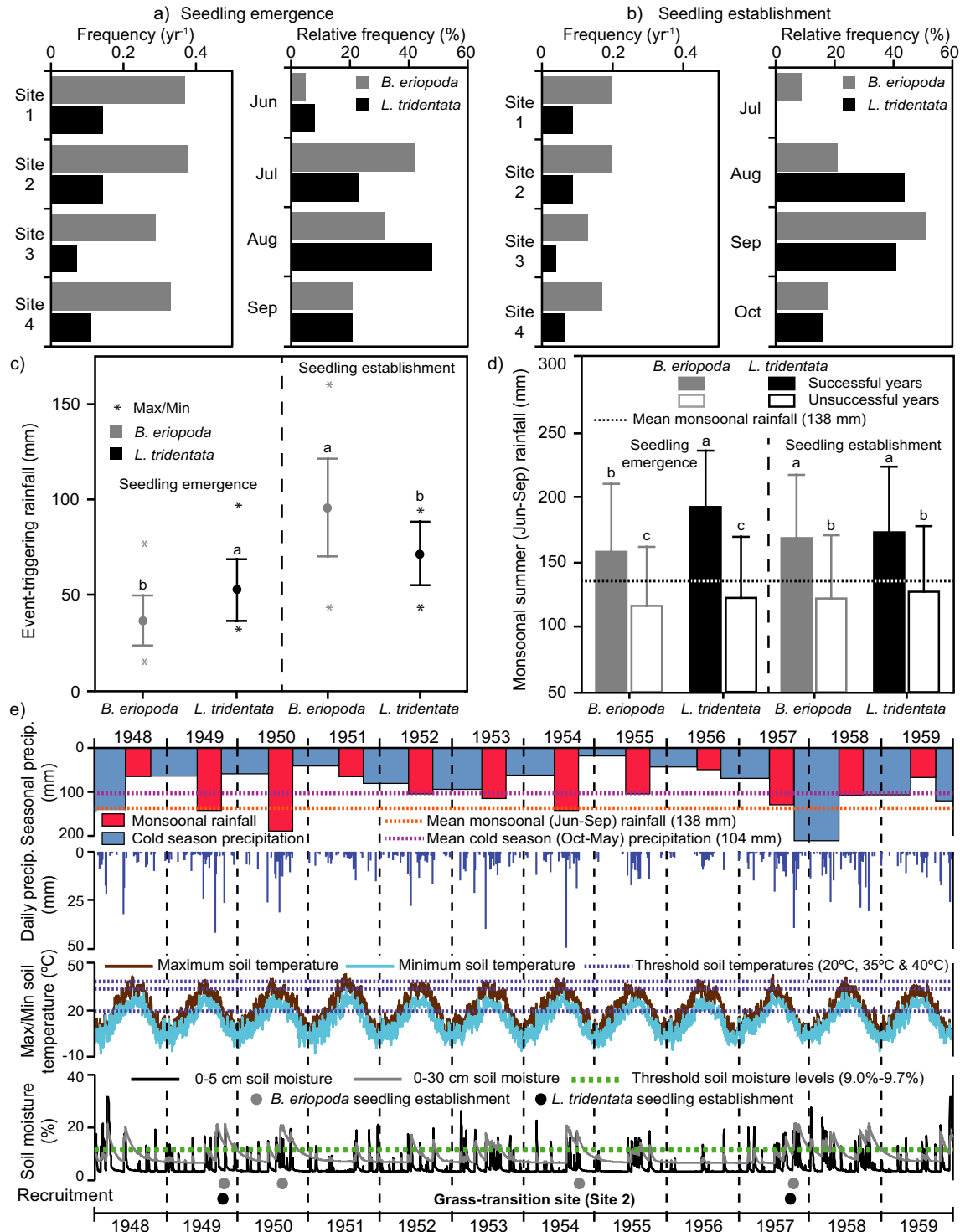


FIG. 5. Simulated seedling emergence and early establishment for *B. eriopoda* and *L. tridentata*: frequency (yr^{-1}) and relative frequency by month (%) of (a) seedling emergence and (b) establishment for the studied sites, (c) differences in event-triggering rainfall between species (where events are seedling emergence/establishment), (d) differences in monsoonal summer rainfall (from June to September) between years that showed successful seedling emergence/establishment (successful years) and years without occurrence of seedling emergence/establishment (unsuccessful years), (e) simulated 1948–1959 seedling recruitment dynamics for Site 2 (modeled soil surface temperature and soil moisture at 0–5 cm and 0–30 cm are shown along with seasonal precipitation (precip.), daily rainfall, and simulated seedling establishment events). Seedling recruitment simulation results for Site 1, 3, and 4 can be found in the supplement Appendix S1: Fig. S3. Different letters in panels (c) and (d) indicate differences within event type (seedling emergence or establishment) at $P < 0.05$, tested using factorial ANOVA and post-hoc Tukey HSD tests. Error bars are SD.

DISCUSSION

Structure of the soil seed bank and availability of B. eriopoda and L. tridentata seeds

Shrub encroachment in Chihuahuan landscapes promotes large changes in the structure and spatial pattern of plant communities (Schlesinger et al. 1990, Reynolds et al. 1999, Baez and Collins 2008, Peters et al. 2015). Overall, the observed variations in floristic composition of the soil seed bank over the study grassland–shrubland ecotone (Fig. 2) are consistent with aboveground variations in species composition and also reflect the higher spatiotemporal heterogeneity of subdominant plant communities in areas invaded by *L. tridentata* (Baez and Collins 2008).

Soil seed-density records in our Chihuahuan study are considerably smaller than typical viable seed amounts in other semiarid environments, for example the shortgrass steppe and mediterranean grasslands, which have average densities generally above 1,000 seeds/m² (Coffin and Lauenroth 1989, Espigares and Peco 1993), although they are within the range of viable soil seed densities reported to occur in desert sites (Dwyer and Aguirre 1978, Koontz and Simpson 2010). Concentration of the soil seed bank in densely vegetated microsites is characteristic of many arid and semiarid landscapes, where vegetation patches generally act as a sink for water, nutrients, and sediments, leading to improved soil properties (Bochet 2015). Spatial heterogeneity of soil seed density in these systems is usually explained by the patchy distribution of parental plants (i.e., seed pools generally decrease rapidly away from the parental plants for most gravity dispersed seeds) and patch-to-patch transmission of seeds by wind and/or runoff (Guo et al. 1998, Koontz and Simpson 2010, Thompson et al. 2014). Spatial heterogeneity of soil properties (i.e., abundance of fine soil particles, organic matter and nutrients) in Chihuahuan landscapes generally increases with the progression of shrub encroachment, as does the size of bare soil interpatches and intensity of water and wind erosion (Schlesinger et al. 1990, Reynolds et al. 1999, Turnbull et al. 2010a, b). These observations are in agreement with our results, which show that the differences in seed density between vegetated and bare soil patches are more pronounced in the shrub-transition and shrubland sites where bare soil interpatches are in general longer than 1 m (Appendix S1: Table S6).

Our observations of low viable seed availability for *B. eriopoda* and *L. tridentata* (<100 seeds/m²; Fig. 3b, c) are in agreement with other studies carried out in Chihuahuan landscapes (Dwyer and Aguirre 1978, Guo et al. 1998, Koontz and Simpson 2010). Previous analysis of *B. eriopoda* seed production and soil seed-bank dynamics in the SNWR indicates that *B. eriopoda* has (short-lived) transient seed banks, and that viable seed availability in the soil is strongly dependent on the amount of growing season (June–September) precipitation, ranging from 0

seeds/m² for dry years to 200–400 seeds/m² for very wet years (Peters 2002a). Our soil seed-bank analysis reflects limited amounts of viable *B. eriopoda* seeds for 2013 (average 50 seeds/m² in the grassland and grass-transition sites) despite high growing season precipitation (243 mm, 75% above the historical average), and suggests legacy effects of preceding dry years 2011 and 2012 (80–90 mm summer rainfall, 35% below the historical mean). *B. eriopoda* growth and seed production frequently shows legacy effects on previous year's rainfall conditions (Nelson 1934). *L. tridentata* seeds are also relatively short-lived and, although this shrub species does not show in general persistent soil seed banks, *L. tridentata* growth and seed production are quite stable in time, producing year-round small crops of viable seeds except for growing seasons preceded by extremely low winter temperatures (Valentine and Gerard 1968, Boyd and Brum 1983). *L. tridentata* has a bimodal rooting system (encompassing near-surface and >70 cm depth active roots) that facilitates the use of both (ephemeral) shallow soil water-resources derived from summer rainfall and (more stable) winter-derived deep soil moisture (which is not available to grass species) for plant production, limiting the interannual variation in shrub seed production (Reynolds et al. 1999, Ogle and Reynolds 2004, Moreno-de las Heras et al. 2015).

The availability of *B. eriopoda* and *L. tridentata* seeds varies at both the plant-patch scale and broader landscape scale over the shrub-encroachment gradient (Fig. 3). This variation may be explained by primary and secondary seed dispersal mechanisms. Primary seed dispersal of *L. tridentata* is typically limited to a few centimeters from the shrubs, thus yielding patch-scale variations in seed abundance, whereas secondary dispersal by runoff during early summer storms may facilitate patch-to-patch transport of significant amounts of *L. tridentata* seeds over longer distances (Chew and Chew 1965, Valentine and Gerard 1968, Boyd and Brum 1983, Thompson et al. 2014). *B. eriopoda* seeds are dispersed more widely by wind (Peters and Yao 2012). However, low flowering and seed-production capacity of *B. eriopoda* plants growing in areas co-dominated by *L. tridentata* may strongly limit the availability of viable *B. eriopoda* seeds in transition and shrubland landscapes (Nelson 1934, Peters 2002a).

Seed-germination conditions for B. eriopoda and L. tridentata

Soil-water potential and temperature broadly limit seed germination in arid and semiarid landscapes (Kigel 1995) and control the time and rates of seed germination for *B. eriopoda* and *L. tridentata* (Fig. 4). Threshold soil moisture for seed germination obtained in our study for *B. eriopoda* (Ψ_g : -0.45 MPa) is higher than that applied by Minnick and Coffin (1999) and Peters (2000) to simulate the seedling-emergence dynamics of *B. eriopoda* across the shortgrass steppe and Chihuahuan landscapes. They used a threshold water-potential level of -1.0 MPa based on

laboratory tests on seeds by Knipe and Herbel (1960), which reported a strong *B. eriopoda* germination response at -1.1 MPa applying a non-conservative criterion (a seed was considered germinated when the radicle had perforated the pericarp, irrespective of radicle elongation). Our seed-germination criterion is more conservative, and requires the elongation of at least 4 mm of radicle. Knipe and Herbel (1960) found very little radicle extension (≤ 2 mm) at water-potential levels below -0.7 MPa, which can hardly support seedling emergence in the field. Laboratory observations of *B. eriopoda* seedling emergence and early growth under controlled conditions indicate that emergence does not occur if daily average soil water potential drops below -0.5 MPa (Herbel and Sosebee 1969), which is in agreement with our estimate of Ψ_g for *B. eriopoda*. Our experimental *L. tridentata* Ψ_g threshold level for seed germination (-0.55 MPa) is also within the range of critical osmotic potential (from -0.4 to -0.6 MPa) reported by other studies (Tipton 1985). Similarly, experimental *B. eriopoda* and *L. tridentata* seed-germination time in our study (6 and 10 days, respectively; Fig. 4d) is consistent with field and laboratory observations of seed germination and seedling emergence of these species (Barbour 1968, Rivera and Freeman 1979, Minnick and Coffin 1999).

Recruitment recurrence times and environmental conditions for field emergence and early establishment dynamics of B. eriopoda and L. tridentata

Our results show that environmental conditions for *B. eriopoda* seedling recruitment have recurrence times ranging from 5 to 8 yr (Fig. 5b). This result is comparable to that of Neilson (1986), who, in a 55-yr field study in a northern Chihuahuan site, obtained a *B. eriopoda* seedling recruitment recurrence time of 8 yr. Similarly, Peters (2000) in a simulation study reported *B. eriopoda* recurrence times ranging from 4 to 10 yr for Chihuahuan grasslands with 210–330 mm annual precipitation. Our results are also consistent with field observation of bi-decadal (1989–2010) *B. eriopoda* dynamics in grass-dominated landscapes within the SNWR experimental Five Points area, where *B. eriopoda* has increased in cover via both stoloniferous expansion and occasional seed reproduction (Peters and Yao 2012, Collins and Xia 2015). The two most important pulses of *B. eriopoda* cover expansion over the Five Points grasslands took place in 1991 and 1999 (Collins and Xia 2015), which coincide with two major pulses of simulated *B. eriopoda* recruitment for our experimental sites, also located within the Five Points area (Appendix S1: Table S8).

Our simulations suggest that *B. eriopoda* seedling emergence occurs primarily in July and August (Fig. 5a). Peters (2000) simulated *B. eriopoda* seedling emergence centered in June, by applying less conservative water potential requirements (-1.0 MPa Ψ_g); however, June is in general a dry month compared to July and August (1919–2014 average precipitation in the area for June is 15 mm and 40–50 mm for July and August). Field observations in

north Chihuahuan grasslands and experimental *B. eriopoda* plantings indicate that seedling emergence and plant growth for *B. eriopoda* usually does not start until July (Nelson 1934, Leyendecker 1975, Dwyer and Aguirre 1978). Our simulations indicate that *B. eriopoda* seedling establishment primarily takes place in September (Fig. 5b), which also matches *B. eriopoda* early establishment observations in Chihuahuan landscapes during late-summer and early-fall rains (Neilson 1986).

Our results suggest that *L. tridentata* recruitment events across the grassland–shrubland ecotone appear to be sporadic, although with considerably longer recurrence times than for *B. eriopoda* (9–25 yr; Fig. 5b), which could be expected considering the extremely high life span (about 400 yr) of adult Chihuahuan *L. tridentata* shrubs (Miller and Huenneke 2000). There is little field information on the recurrence times of seedling emergence and establishment for *L. tridentata*. Valentine and Gerard (1968) estimated effective *L. tridentata* seedling emergence pulses to occur with a time-span of 7 yr in the Jornada Experimental Range (southern New Mexico), which is in line with our modeled *L. tridentata*-seedling emergence frequency of 6–12 yr (Fig. 5a). Analysis of *L. tridentata* age and size frequency in a variety of sites across the southwestern United States suggests that *L. tridentata* seedling recruitment occurs primarily during rare and episodic events, which supports our low-frequency early seedling establishment simulations (Chew and Chew 1965, Barbour 1969, Allen et al. 2008). LTER vegetation surveys between 1990–2012 within the SNWR Five Points area indicate that seedling emergence and establishment of *L. tridentata* appears to be low, sporadic and very localized, accounting for a small recruitment pulse that took place at the end of the 1990s (Moore 2011, Peters and Yao 2012). Recent vegetation surveys in the area indicate that other sizeable *L. tridentata* emergence events also took place in 2013 and 2014, although showing variable recruitment success (for the 2014 event all seedlings died within 4–6 months of field emergence; S. L. Collins, *personal communication*). Our *L. tridentata* modelling results suggest that the most recent effective recruitment events for the area took place in years 1997, 1999, and 2013 (Appendix S1: Table S9).

Field observations of *L. tridentata* seedlings in southwestern U.S. landscapes indicate that emergence and early plant establishment can take place broadly between early July and the beginning of October, with timing frequently synchronized with the occurrence of late-summer heavy rainfall (Rivera and Freeman 1979, Boyd and Brum 1983, Bowers et al. 2004). Our simulations reproduce field-observed temporal patterns, with *L. tridentata* seedling emergence and early establishment concentrated principally in late summer (August and September; Fig. 5a, b). *L. tridentata* seedling establishment may be facilitated by the activity of Eastern Pacific tropical cyclone remnants, which provide supplemental soil moisture in the arid southwest United States from late August until October (Ritchie et al. 2011).

While our modelling results suggest that seedling recruitment of both *B. eriopoda* and *L. tridentata* is generally associated with the occurrence of strong monsoons (Fig. 5d), triggering rainfall for field emergence and early plant establishment are different for the two species (Fig. 5c). *B. eriopoda* requires moderate amounts of rainfall for seedling emergence (minimum 15 mm, and 35 mm average rainfall), and early plant establishment occurs within a broad range of precipitation during the seedling development period (from 50 to 160 mm). These requirements match the rainfall conditions empirically determined by Herbel and Sosebee (1969) for *B. eriopoda* seedling emergence (20–30 mm within six days) and early survival (70–150 mm within a month of seed planting) under typical summer temperatures for northern Chihuahuan landscapes (20–50°C). Conversely, *L. tridentata* seedling emergence requires a minimum of 30 mm and average 50 mm rainfall, which also agrees with field observations and controlled laboratory analysis of *L. tridentata* early plant development (Rivera and Freeman 1979, Boyd and Brum 1983, Bowers et al. 2004, Woods et al. 2011). The smaller range of rainfall conditions for *L. tridentata* early establishment (from 50 to 100 mm for five to six consecutive weeks) reflects its low seedling tolerance to high soil moisture. Laboratory rhizotron and field experiments indicate that *L. tridentata* has unusually high oxygen requirements for root development, which, together with fungal intrusion under high soil moisture regimes, can produce high seedling mortality and/or weaken early-established shrubs for longer-term survival (Valentine and Gerard 1968, Woods et al. 2011). Extreme winter temperatures (i.e., cold spells with minimum air temperature below -14°C) may cause further seedling mortality due to freezing-induced xylem cavitation in the SNWR, where *L. tridentata* is close to its northern Chihuahuan distribution limit (Martinez-Vilalta and Pockman 2002).

Implications for vegetation dynamics at Chihuahuan grassland-shrubland boundaries

Early seedling dynamics can have a great influence on the spatial pattern and rates of vegetation change in drylands (Espigares and Peco 1993, Kigel 1995, Peters 2002b, Bowers et al. 2004, Bochet 2015, Collins and Xia 2015). Our *L. tridentata* seedling simulations along 1948–1959 suggest that the 1950s dry period provided an ideal window for the expansion of *L. tridentata* over the SNWR Five Points area (Fig. 5e), with shrub recruitment taking place immediately before and after the 1951–1956 dry period. Soil moisture and surface-soil-temperature dynamics also episodically meet the conditions for *B. eriopoda* recruitment along the 1950s dry decade. However, it is unlikely that grass recruitment pulses would have taken place, as a result of a lack of persistent *B. eriopoda* soil seed banks and deficiency of viable seed production in dry years with below-average summer monsoonal precipitation (Nelson 1934, Peters 2002a). In fact, field analysis of *B. eriopoda* basal cover in north Chihuahuan grasslands indicates that, although

relatively high summer rainfall in 1949 and 1950 resulted in a small increase in *B. eriopoda* cover, the abundance of perennial grass (also affected by cattle grazing in the SNWR at that time) was reduced to very low levels along the 1951–1956 dry period (Gibbens and Beck 1988). High drought tolerance of *L. tridentata* plants and synchronization of active shrub recruitment at the temporal boundaries of the dry period may have been contributing factors in facilitating widespread expansion of *L. tridentata* over damaged *B. eriopoda* grasslands in the SNWR Five Points area during and shortly after the 1950s severe multiyear drought. Accordingly, analysis of shrub architecture and age-structure indicates that local *L. tridentata* populations are dominated by shrubs that were recruited primarily within or soon after the 1950s (Allen et al. 2008).

Observed spatial structure of the *L. tridentata* seed bank and simulated temporal patterns of shrub recruitment for the study sites suggest that shrub colonization is an episodic and localized phenomenon associated with the occurrence of late-summer strong precipitation. Viable soil seed concentration near adult shrubs due to limited *L. tridentata* large-range seed dispersal (Fig. 3f) can constrain the spatial extension of active shrub recruitment events. Similarly, the narrow range of rainfall conditions for early seedling establishment (Fig. 5c) strongly limit effective *L. tridentata* recruitment pulses to episodic decadal events, especially in Chihuahuan landscapes where local (diploid) *L. tridentata* populations appear to establish and regenerate exclusively by seed reproduction (Miller and Huenneke 2000, Pendleton et al. 2008, Peters and Yao 2012). In support of this result, field observations at the SNWR area indicate that *L. tridentata* infill across the Five Points area happens slowly, and is characterized by the occurrence of rare and sporadic events that are localized in space (Allen et al. 2008, Moore 2011, Peters and Yao 2012). Erratic spacing of summer storms may also be partially responsible of the localized nature for the observed recruitment events (Valentine and Gerard 1968). Overall, the grassland-shrubland boundary at the Five Points area appears to be stable at present (Moreno-de las Heras et al. 2015). In the absence of cattle overgrazing, no significant shrub encroachment is expected for the area unless extensive grass suppression by an extreme event similar to the severe and prolonged 1950s drought occurs (Peters 2002b). However, an increment of the activity of tropical cyclones that provide supplemental late-summer and fall precipitation for the area may facilitate *L. tridentata* infill and long-term destabilization of *B. eriopoda*–*L. tridentata* transition landscapes in the region, particularly under the future context of increased aridity in the southwestern United States due to higher summer temperatures and increased drought frequency (Garfin et al. 2013).

Environmental conditions for seedling recruitment and soil seed-bank structure also have a critical role for the re-establishment of *B. eriopoda* in landscapes now dominated by *L. tridentata*, and particularly for those areas lacking *B. eriopoda* remnants that impede vegetative plant recovery via stolons. Our simulations indicate that shrub encroachment has a net impact on *B. eriopoda* seedling

dynamics, reducing the frequency of soil-moisture conditions for early establishment from 0.22 yr^{-1} in the grassland sites down to 0.13 yr^{-1} in the shrub-transition and shrubland landscapes (Fig. 5b). The longer seedling recurrence times in areas where shrubs are dominant can be explained by site variations in soil properties and soil-surface hydrology that are induced by the shrub-encroachment process (Schlesinger et al. 1990, Reynolds et al. 1999, Peters 2002b, Stewart et al. 2014). Previous analysis of soil-surface hydrology of our study sites indicates that increased (bare soil) interpatch size and surface stoniness for the shrub-transition and dominated Sites 3 and 4 intensify runoff production and soil erosion, which feedbacks into plant dynamics by reducing plant-available soil moisture (Turnbull et al. 2010a, b). Furthermore, the lack of viable *B. eriopoda* seeds in those landscapes (Fig. 3b) makes *B. eriopoda* seedling recruitment highly unfeasible in areas now dominated by the shrubs. In fact, recent bi-decadal field observations of *B. eriopoda* dynamics across the Five Points area indicate that although *B. eriopoda* cover has broadly increased since 1989 in grassland sites via both stoloniferous expansion and episodic seed reproduction, no *B. eriopoda* recovery has been detected in shrubland and shrub-transition sites, even 16 yr after the application of experimental shrub removal (Peters and Yao 2012, Collins and Xia 2015). Similarly, long-term (1930-present) experiments of (spatially extensive) *L. tridentata* removal in other Chihuahuan shrublands have shown little impact on grass recovery (Rango et al. 2005). Peters (2002b), using a dynamic vegetation model, proposed that increases in summer precipitation could facilitate the re-establishment of *B. eriopoda* in areas now dominated by *L. tridentata*. However, lack of viable *B. eriopoda* seeds and tighter environmental conditions for grass establishment in shrubland sites may greatly limit the rates of *B. eriopoda* recovery even under favorable climate conditions, which thus has significant implications for the restoration of native grasslands. Re-seeding in targeted areas (e.g., shallow gullies, gently sloping arroyos, and small artificial dikes) strategically applied with punctual supplemental irrigation may help re-establish *B. eriopoda* patches in areas invaded by *L. tridentata* (Herrick et al. 1997). Our study provides biophysical criteria to regulate supplemental irrigation efforts for satisfying soil-moisture conditions along the *B. eriopoda* emergence and early seedling establishment stages.

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