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Title: 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 southwestern USA have shifted to sparse shrublands dominated by drought-tolerant woody species over the last 150 years, accompanied by accelerated soil erosion. An important step towards 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 m⁻²), although is largely concentrated in densely vegetated areas (with peaks up to 800-1200 seeds m⁻² 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 years 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 5-6 consecutive weeks) constrain shrub-recruitment pulses to localized and episodic decadal events (9-25 years 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 semi-arid grasslands throughout central Australia, southern Africa, southwestern United States of America, 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 USA, where drought-tolerant C_3 shrub species (mainly honey mesquite, *Prosopis glandulosa*, and creosotebush, *Larrea tridentata*) have colonized large areas of C_4 semi-arid 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 CO_2 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 2015); e.g., the severe multiyear drought between 1950 and 1960 caused rapid regional changes in Chihuahuan landscapes across southwestern USA (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 *B. 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 1960-70, 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 towards 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 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 (approx. 400 years life-span) shrub appears to depend exclusively on seed reproduction (Miller and Huenneke 2000, Pendleton et al. 2008, Peters and Yao 2012). Seedling recruitment has been shown to occur infrequently for *B. eriopoda*, a perennial and relatively short-lived (20-40 years life-span) C₄ 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 the 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 approx. 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 for analysis four study sites 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 years, 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 years of rangeland use.

The study sites (each 30×10 m, Fig. 1c) represent a *L. tridentata*-encroachment gradient (Turnbull et al. 2008, 2010a, 2010b), 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 (supplement Table ST1 for soil characteristics in the online appendix). Surface stoniness and soil organic carbon contents in shrub, grass and bare soil interpatches reflect the typical spatial patterns of erosion/sedimentation and resource-island development in shrub-encroached dry grasslands (Schlesinger et al. 1990, Reynolds et al. 1999, Turnbull et al. 2010a, 2010b).

Characterization of vegetation cover and soils

We used the point-intercept method to estimate the distribution of surface types (% 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 ($\Psi = -0.0002, -0.01, -0.03, -0.05, -0.08, -0.4, -0.8$ and -1.45 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 the supplement Fig. SF1 and Table ST2 (online appendix).

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 cm^2 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° 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, $20\text{-}25^\circ\text{C}$). The samples were watered to field capacity at the start of the experiment, in January 2014. Then, bottom-up watering was provided as required to keep soil moisture near field capacity. After

the first six weeks, we added 40 ppm of fertilizer (5 ml /10 l; NPK 3.5:3.5:3.5) mixed with water every month. We counted emerged seedlings at weekly intervals until August 2014.

Non-metric 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). *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 (approx. 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°, 20°, 25° and 30°C) and eight water potentials representing soil-moisture values between saturation and the wilting point (Ψ = 0, -0.2, -0.4, -0.6, -0.85, -1.1, -1.3 and -1.5 MPa). Water-potentials were simulated using polyethylene glycol (PEG) concentrations following the standard equations of

Michel et al. (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, $150 \mu\text{mol m}^{-2} \text{s}^{-1}$ lighting intensity, 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, days) 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°, 20°, 25° and 30°C) as factors, water potential (Ψ) as a co-variable, and their interactions to test for their effects on germination rate (Gr). The Sp: Ψ interaction indicates whether Ψ_g differs for *B. eripoda* 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. eripoda* 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. eripoda* 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).

(i) 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, <http://www.nrel.colostate.edu/projects/daycent-home.html>) 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 (supplement Table ST3 in the online appendix). Root distribution by depth was parametrized using typical root-density values of Chihuahuan *B. eriopoda* grasslands and *L. tridentata* shrublands (supplement Table ST4 in the online appendix). Application of the parameterized model using 2005-06 onsite daily records of precipitation and air temperature (SNWR Five Points station, Fig. 1b, <http://sev.lternet.edu/data/sev-1>) yields a low root-mean-square error (0.02 vol/vol, 9% NRMSE) for soil moisture prediction (supplement Fig. SF2a in the online appendix).

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 supplement Fig. SF2b and c of the online appendix). 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% NMRSE) 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, US Western Regional Climate Center station code 298387, 237 mm mean annual precipitation, <http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?nm8387>).

(ii) 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 2011). Thus, seedling emergence conditions were derived from our seed-germination experiments. A wet period with water potential $\geq \Psi_g$ MPa and length G_t (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) G_r and G_t 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* 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.

(iii) Data analysis of simulated seedling emergence and early establishment:

We calculated the seedling emergence/establishment frequency (years⁻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 to 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 1948-59, which includes the 1950s dry period plus three years immediately before/after that period.

RESULTS

Soil seed-bank

We identified a total of 21 different plant species in the soil seed-bank, comprising twelve forbs, five grasses and four subshrub/shrub species (supplement Table ST5 in the online appendix). 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 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). Overall, 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 x 5 m) seed-bank plots (Fig. 2a).

Average density of viable seeds in the soil ranges 200-400 seeds m⁻² (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 m⁻², Fig. 3a). *B. eriopoda* seed density varies significantly between sites ($H=9.7$, 3 d.f., $P=0.02$), decreasing from sites 1 and 2 to sites 3 and 4 (from 50-40 to 7-0 seeds m⁻², Fig. 3b). *L. tridentata* soil seed abundance differs marginally between sites ($H=6.3$, 3 d.f., $P=0.08$), with 20 seeds m⁻² in the shrubland, 6-2 seeds m⁻² 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 d.f., $P<0.01$). Bare soil interpatches show very low densities (typically <150 seeds m⁻²), while vegetated clumps concentrate most viable seeds, peaking up to maxima of 800 and 1200 seeds m⁻² for grass and shrub patches, respectively (Fig. 3d). *B. eriopoda* seeds are preferentially distributed in the grass patches ($H=13.9$, 2 d.f., $P<0.01$, 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 $P<0.05$ (supplement Table ST6 in the online appendix).

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 and 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 and b, and supplement Table ST7 in the online appendix). The interaction between species and water

potential (Ψ_g , $F_{1, 432}=10.8$, $P<0.01$) 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, supplement Table ST3 in the online appendix).

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 ten 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 years⁻¹ (recurrence time 2-3 years) for *B. eriopoda* and 0.08-0.15 years⁻¹ (recurrence time 6-12 years) for *L. tridentata* (Fig. 5a, supplement Tables ST8 and ST9 in the online appendix). Modelled early seedling-recruitment events show a frequency of 0.13-0.22 years⁻¹ (recurrence time 5-8 years) for *B. eriopoda*, and 0.04-0.12 years⁻¹ (recurrence time 9-25 years) for *L. tridentata* (Fig. 5b, supplement Tables ST8 and ST9 in the online appendix). 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 approx. 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 1948-59 indicates that the soil-surface temperature and soil-moisture dynamics in (the grass-transition) Site 2 meet episodically the creososebush 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 (1951-56 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 1948-59 (years 1949, 1950, 1954 and 1957). Recruitment simulations in sites 1, 3 and 4 show similar patterns (supplement Fig. SF3 in the online appendix).

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 semi-arid environments, for example the Shortgrass Steppe and Mediterranean grasslands, which have average densities generally above 1000 seeds m⁻² (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 semi-arid 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, 2010b). 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 (Table 1).

Our observations of low viable seed availability for *B. eriopoda* and *L. tridentata* (<100 seeds m⁻²; Fig. 3b and 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 m⁻² for dry years to 200-400 seeds m⁻² for very wet years (Peters 2002a). Our soil seed-bank analysis reflects limited amounts of viable *B. eriopoda* seeds for 2013 (average 50 seeds m⁻² 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 -that is not available to grass species- for plant production, limiting the inter-annual 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. 2). 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 semi-arid 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 years (Fig. 5b). This result is comparable to that of Neilson (1986), who in a 55-year field study in a northern Chihuahuan site obtained a *B. eriopoda* seedling recruitment recurrence time of 8 years. Similarly, Peters (2000) in a simulation study reported *B. eriopoda* recurrence times ranging from 4 to 10 years 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 (supplement Table ST8 in the online appendix).

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 years, Fig. 5b), which could be expected considering the extremely high life-span (about 400 years) 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 years in the Jornada Experimental Range (southern New Mexico), which is in line with our modeled *L. tridentata*-seedling emergence frequency of 6-12 years (Fig. 5a). Analysis of *L. tridentata* age and size frequency in a variety of sites across southwestern USA 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; Scott 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 (supplement Table ST8 in the online appendix).

Field observations of *L. tridentata* seedlings in southwestern USA 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 and 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 USA from late-August until October (Ritchie et al. 2011).

Whilst 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 5-6 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, Collins and Xia 2015, Bochet 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 been 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 southwestern USA 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 impedes 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 years⁻¹ in the grassland sites down to 0.13 years⁻¹ in the shrub-transition and shrubland landscapes (Fig. 5a). 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 1990, Reynolds 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, 2010b). Furthermore, the lack of viable *B. eriopoda* seeds in those landscapes (Fig. 2b) 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 years 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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LITERATURE CITED

Allen, A. P., W. T. Pockman, C. Restrepo, and B. T. Milne. 2008. Allometry, growth and population regulation of the desert shrub *Larrea tridentata*. *Functional Ecology*, 22:197-204.

700 Baez, S., and S. L. Collins. 2008. Shrub invasion decreases diversity and alters community
701 stability in northern Chihuahuan Desert plant communities. PLoS ONE, 3(6):e2332,
702 doi:10.1371/journal.pone.0002332

703 Barbour, M. G. 1968. Germination requirements of the desert shrub *Larrea divaricata*. Ecology,
704 49:915-923.

705 Barbour, M. G. 1969. Age and space distribution of the desert shrub *Larrea divaricata*. Ecology,
706 50: 679-685.

707 Brooks, R. H., and A. T. Corey. 1964. Hydraulic properties of porous media. Hydrology Papers,
708 3. Colorado State University, Fort Collins.

709 Bochet, E. 2015. The fate of seeds in the soil: a review of the influence of overland flow on seed
710 removal and its consequences for the vegetation of arid and semiarid patchy ecosystems.
711 Soil, 1:131-146.

712 Boyd, R. S., and G. D. Brum. 1983. Postdispersal reproductive biology of a Mojave Desert
713 population of *Larrea tridentata* (Zygophyllaceae). American Midland Naturalist, 110:25-36.

714 Bowers, J. E., R. M. Turner, and T. L. Burgess. 2004. Temporal and spatial pattern in emergence
715 and early survival of perennial plants in the Sonoran Desert. Plant Ecology, 172:107-119.

716 Carter, M. R., and E. G. Gregorich. 2008. Soil Sampling and Methods of Analysis, 2nd Ed.,
717 Canadian Society of Soil Science, CRC Press, Boca Raton.

718 Chew, R. M. and A. E. Chew. 1965. The primary productivity of a desert-shrub (*Larrea*
719 *tridentata*) community. Ecological Monographs, 35:355-375.

720 Coffin, D. P., and W. K. Lauenroth. 1989. Spatial and temporal variation in the seed bank of a
721 semiarid grassland. American Journal of Botany, 76:53-58.

722 Collins, S. L., and Y. Xia. 2015. Long-term dynamics and hotspots of change in a desert
723 grassland plant community. The American Naturalist, 185:E30-E43.

724 D'Odorico, P., G. S. Okin, and B. T. Bestelmeyer. 2012. A synthetic review of feedbacks and
725 drivers of shrub encroachment in arid grasslands. Ecohydrology, 5:520-530.

726 Dwyer, D. D. and E. Aguirre. 1978. Plants emerging from soils under three range condition
 727 classes of desert grasslands. *Journal of Range Management*, 31: 209-212.

728 Espigares, T., and B. Peco. 1993. Mediterranean pasture dynamics: the role of germination.
 729 *Journal of Vegetation Science*, 4:189-194.

730 Garfin, G. A., A. Jardine, R. Merideth, M. Black, and S. LeRoy. 2013. Assessment of Climate
 731 Change in the Southwest United States: A Report Prepared for the National Climate
 732 Assessment. Southwest Climate Alliance. Island Press, Washington.

733 Gibbens, R. P., and R. F. Beck. 1988. Changes in grass basal area and forb densities over a 64-
 734 year period on grassland types of the Jornada Experimental Range. *Journal of Range*
 735 *Management*, 41: 186-192.

736 Gosz, J. R. 1992. Ecological functions in a biome transition zone: translating local responses to
 737 broad-scale dynamics. Pages 56-75 in A. J. Hansen, and A. J. di Castri, editors. *Landscape*
 738 *Boundaries: Consequences for Biotic Diversity and Ecological Flows*. Springer, New York.

739 Guo, Q., P. W. Rundel, and D. W. Goodall. 1998. Horizontal and vertical distribution of desert
 740 seed banks: patterns, causes, and implications. *Journal of Arid Environments*, 38:465-478.

741 Herbel C. H. and R. E. Sosebee. 1969. Moisture and temperature effects on emergence and
 742 initial growth of two range grasses. *Agronomy Journal*, 61:628-631.

743 Herrick, J. E., K. M. Havstad, and D. P. Coffin. 1997. Rethinking remediation technologies for
 744 desertified landscape. *Journal of Soil and Water Conservation*, 52:220-225.

745 Kigel, J. 1995. Seed germination in arid and semiarid regions. Pages 645-699 in J. Kigel, and G.
 746 Galili, editors. *Seed Development and Germination*. Marcel Dekker, New York.

747 Klute, A. 1986. Water retention: laboratory methods. Pages 635-662 in A. Klute, editor.
 748 *Methods of Soil Analysis: Part 1, Physical and Mineralogical Methods*. Soil Science Society
 749 of America, Madison.

750 Knipe, D. and C. H. Herbel. 1960. The effects of limited moisture on germination and initial
 751 growth of six grass species. *Journal of Range Management*, 13:297-302.

752 Koontz, T. L., and H. L. Simpson. 2010. The composition of seed banks on kangaroo rat
 753 (*Dipodomys spectabilis*) mounds in a Chihuahuan Desert grassland. *Journal of Arid*
 754 *Environments*, 74:1156-1161.

755 Lauenroth, W. K., O. E. Sala, D.P. Coffin, and T. B. Kirchner. 1994. The importance of soil
 756 water in the recruitment of *Bouteloua gracilis* in the shortgrass steppe. *Ecological*
 757 *Applications*, 4:741-749.

758 Leyendecker, P. J. 1975. Nogal Blackgrama. NMSU Cooperative Extension Service Circular
 759 460. New Mexico State University, Las Cruces.

760 Martinez-Vilalta J., and W. T. Pockman. 2002. The vulnerability to freezing-induced xylem
 761 cavitation of *Larrea tridentata* (*Zygophyllaceae*) in the Chihuahuan Desert. *American*
 762 *Journal of Botany*, 89:1916-1924.

763 Michel, B. E. 1983. Evaluation of the water potentials of solutions of Polyethylene Glycol 8000
 764 both in the absence and presence of other solutes. *Plant Physiology*, 72:66-70.

765 Miller, R. E., and L. F. Huenneke. 2000. Demographic variation in a desert shrub, *Larrea*
 766 *tridentata*, in response to a thinning treatment. *Journal of Arid Environments*, 45:315-323.

767 Minnick, T. J., and D. P. Coffin. 1999. Geographic patterns of simulated establishment of two
 768 *Bouteloua* species: implications for distributions of dominants and ecotones. *Journal of*
 769 *Vegetation Science*, 10:343-356.

770 Moore, D. 2011. *Larrea* Seedling Monitoring Study at the Sevilleta National Wildlife Refuge,
 771 New Mexico (1999-). Long Term Ecological Research
 772 Network. <http://dx.doi.org/10.6073/pasta/751d60c674f8750c1d3dfaca1e78839e>

773 Moreno-de las Heras, M., T. Espigares, L. Merino-Martin, and J. M. Nicolau. 2011. Water-
 774 related ecological impacts of rill erosion processes in Mediterranean-dry reclaimed slopes.
 775 *Catena*, 84:114-124.

776 Moreno-de las Heras, M., R. Díaz-Sierra, L. Turnbull, and J. Wainwright. 2015. Assessing
 777 vegetation structure and ANPP dynamics in a grassland-shrubland Chihuahuan ecotone
 778 using NDVI-rainfall relationships. *Biogeosciences*, 12:1-19.

779 Neilson, R. P. 1986. High-resolution climatic analysis and southwest biogeography. *Science*,
 780 232:27-34.

781 Nelson, E. W. 1934. The influence of precipitation and grazing upon black grama grass range.
 782 US Department of Agriculture Technical Bulletin, 409. Washington, D. C.

783 Ogle, K. and J. F. Reynolds. 2004. Plant responses to precipitation in desert ecosystems:
 784 integrating functional types, pulses, thresholds and delays. *Oecologia*, 141:282-294.

785 Parton, W. J., M. Hartman, D. S. Ojima, and D. S. Schimel. 1998. DAYCENT: Its land surface
 786 submodel: description and testing. *Global Planetary Change*, 19:35-48.

787 Pendleton, R. L., B. K. Pendleton, K. R. Wetherill, and T. Griswold. 2008. Reproductive biology
 788 of *Larrea tridentata*: a preliminary comparison between core shrubland and isolated
 789 grassland plants at the Sevilleta National Wildlife Refuge, New Mexico. Pages 131-135 in
 790 S. G. Kitchen, R. L. Pendleton, T. A. Monaco, and J. Vernon, editors. *Shrublands under*
 791 *Fire: Disturbance and Recovery in a Changing World*. US Department of Agriculture, Fort
 792 Collins.

793 Peters, D. P. C. 2000. Climatic variation and simulated patterns in seedling establishment of two
 794 dominant grasses at a semi-arid-arid grassland ecotone. *Journal of Vegetation Science*,
 795 11:493-504.

796 Peters, D. P. C. 2002a. Recruitment potential of two perennial grasses with different growth
 797 forms at a semi-arid transition zone. *American Journal of Botany*, 89:1616-1623.

798 Peters, D. P. C. 2002b. Plant species dominance at a grassland-shrubland ecotone: an individual-
 799 based gap dynamics model of herbaceous and woody species. *Ecological Modelling*, 152:5-
 800 32.

801 Peters, D. P. C., and J. Yao. 2012. Long-term experimental loss of foundation species:
 802 consequences for dynamics at ecotones across heterogeneous landscapes. *Ecosphere*, 3:27,
 803 <http://dx.doi.org/10.1890/ES11-00273.1>

804 Peters, D. P. C., K. M. Havstad, S. R. Archer, and O. E. Sala. 2015. Beyond desertification: new
 805 paradigms for dryland landscapes. *Frontiers in Ecology and the Environment*, 13:4-12.

806 Rango, A., L. Huenneke, M. Buonopane, J. E. Herrick, and K. M. Havstad. 2005. Using historic
 807 data to assess effectiveness of shrub removal in southern New Mexico. *Journal of Arid*
 808 *Environments*, 62:75-91.

809 Reynolds, J. F., R. A. Virginia, P. R. Kemp, A. G. de Soyza, and D. C. Tremmel. 1999. Impact
 810 of drought on desert shrubs: effects of seasonality and degree of resource island
 811 development. *Ecological Monographs*, 69:69-106.

812 Ritchie, E. A., K. M. Wood, D. S. Gutzler, and S. R. White. 2011. The influence of Eastern
 813 Pacific tropical cyclone remnants on the southwestern United States. *Monthly Weather*
 814 *Review*, 139:192-210.

815 Rivera, R.L., and C. E. Freeman. 1979. The effects of some alternating temperatures on
 816 germination of creosotebush (*Larrea tridentata* [D.C.] Con.: *Zygophyllaceae*). *The*
 817 *Southwestern Naturalist*, 24:711-714.

818 Schlesinger, W. H., J. F. Reynolds, G. L. Cunningham, L. F. Huenneke, W. M. Jarrell, R. A.
 819 Virginia, and W. G. Whitford. 1990. Biological feedbacks in global desertification. *Science*
 820 247:1043-1048.

821 Stewart, J., A. J. Parsons, J. Wainwright, G. S. Okin, B. T. Bestelmeyer, E. L. Fredrickson, and
 822 W. H. Schlesinger. 2014. Modeling emergent patterns of dynamic desert ecosystems.
 823 *Ecological Monographs*, 84:373-410.

824 Thompson, S. E., S. Assouline, L. Chen, A. Trahtenbrot, T. Svoray, and G. Katul. 2014.
 825 Secondary dispersal driven by overland flow in drylands: Review and mechanistic model
 826 development. *Movement Ecology*, 2:1-13.

827 Tipton, J. L. 1985. Light, osmotic stress, and fungicides affect hulled creosotebush mericarp
828 germination. *Journal of the American Society of Horticultural Science*, 110:615-618.

829 Turnbull, L., Brazier, R. E., J. Wainwright, L. Dixon, and R. Bol. 2008. Use of carbon isotope
830 analysis to understand semi-arid erosion dynamics and long-term semi-arid degradation.
831 *Rapid Communications in Mass Spectrometry*, 22:1697-1702.

832 Turnbull, L., J. Wainwright, and R. E. Brazier. 2010a. Changes in hydrology and erosion over a
833 transition from grassland to shrubland. *Hydrological Processes*, 24:393-414.

834 Turnbull, L., J. Wainwright, R. E. Brazier, and R. Bol. 2010b. Biotic and abiotic changes in
835 ecosystem structure over a shrub-encroachment gradient in the southwestern USA.
836 *Ecosystems*, 13:1239-1255.

837 Turnbull, L., J. Wainwright, and S. Ravi. 2014. Vegetation change in the southwestern USA:
838 patterns and processes. Pages 289-313 in E. N. Mueller, J. Wainwright, A. J. Parsons and L.
839 Turnbull, editors. *Patterns of Land Degradation in Drylands, Understanding Self-Organised
840 Ecogeomorphic Systems*. Springer, New York.

841 Valentine, K. A., and J. B. Gerard. 1968. Life-history Characteristics of the Creosotebush,
842 *Larrea tridentata*. New Mexico State University Agricultural Experiment Station Bulletin,
843 526. Las Cruces.

844 Van Auken, O. W. 2000. Shrub invasions of North American semiarid grasslands. *Annual
845 Review of Ecology and Systematics*, 12:352-356.

846 Vasek, F. C. 1980. Creosote bush: long-lived clones in the Mojave Desert. *American Journal of
847 Botany*, 67:246-255.

848 Woods, S. R., S. R. Archer, and S. Schwinning. 2011. Early taproot development of a xeric
849 shrub (*Larrea tridentata*) is optimized within a narrow range of soil moisture. *Plant
850 Ecology*, 212:507-517.

FIG. 1. Study area: (a) location of the Sevilleta National Wildlife Refuge (SNWR) and distribution of New Mexico biomes, (b) location of the study sites (Five Points area, McKenzie Flats), and (c) study sites (10 x 30 m each). Biome distribution in panel (a) follows the Sevilleta LTER classification (<http://sev.lternet.edu/content/new-mexico-biomes-created-sevlter>). Spatial distribution of surface types (%) was determined in the field by applying the point intercept method (details in methods). Graphical representation of surface types 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⁻¹) aerial image that is freely available through GoogleEarth™ (<http://www.google.com/earth/>). Source for background image in panels (a) and (b): 2014 National Aerial Imagery Program (USDA Farm Service Agency).

FIG. 2. NMS (non-metric multidimensional scaling) ordination of the soil seed-bank data: (a) projection of cases (5 x 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 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*. Sig. codes: **, $P < 0.01$.

FIG. 3. Differences in soil seed density (viable seeds m⁻²) 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 colors in

panels (a) and (b). Different letters indicate differences at $P < 0.05$. Tested using Kruskal-Wallis ANOVA and post-hoc Mann-Whitney tests.

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 the supplement Table ST7 in the online appendix), (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 in different colors 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. Sig. Codes for panels (a) and (b): ‘***’, $P < 0.01$.

FIG. 5. Simulated seedling emergence and early establishment for *B. eriopoda* and *L. tridentata*: frequency (year^{-1}) and relative frequency by month (%) of seedling emergence (a) and establishment (b) for the studied sites, (c) differences in event (seedling emergence/establishment) triggering rainfall between species, (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, daily rainfall, and simulated seedling establishment events). Seedling recruitment simulation results for Site 1, 3 and 4 can be found in the supplement Figure SF3 in the online appendix. 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.

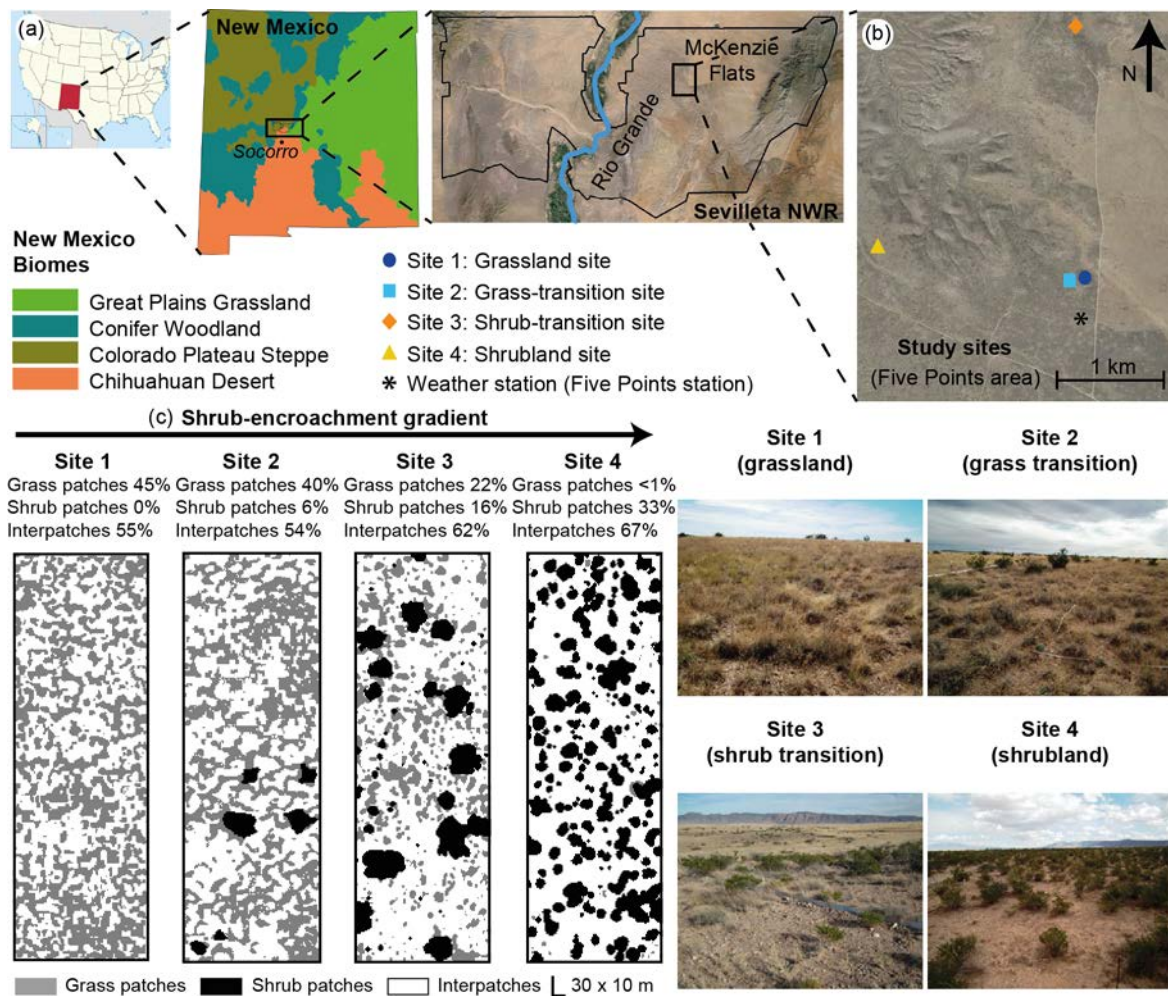


Figure 1.

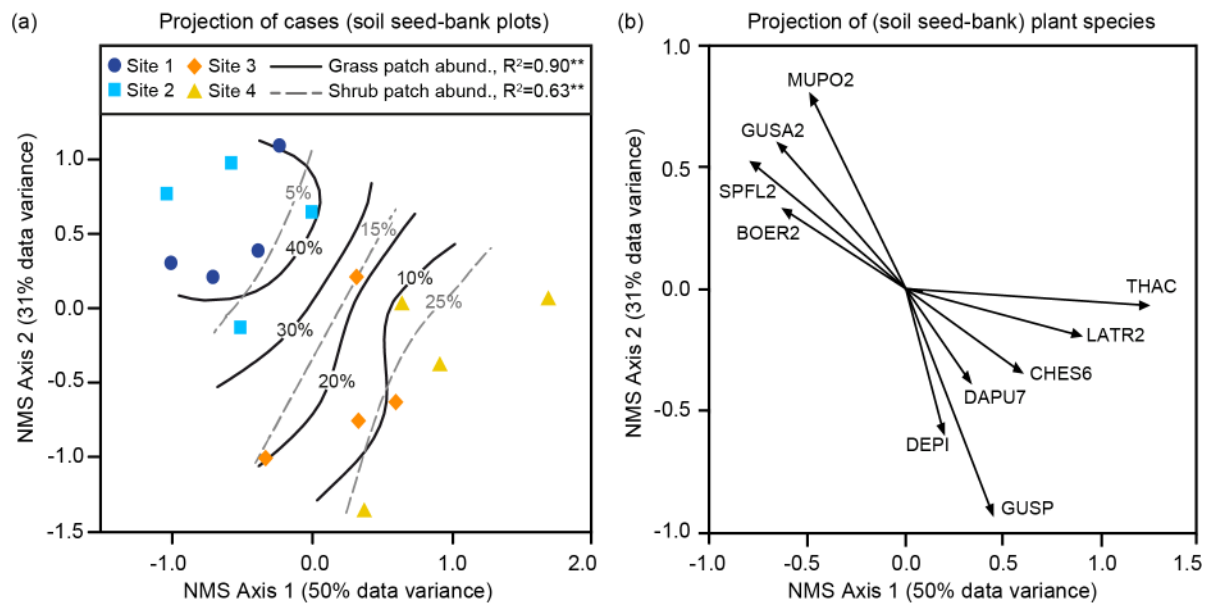


Figure 2.

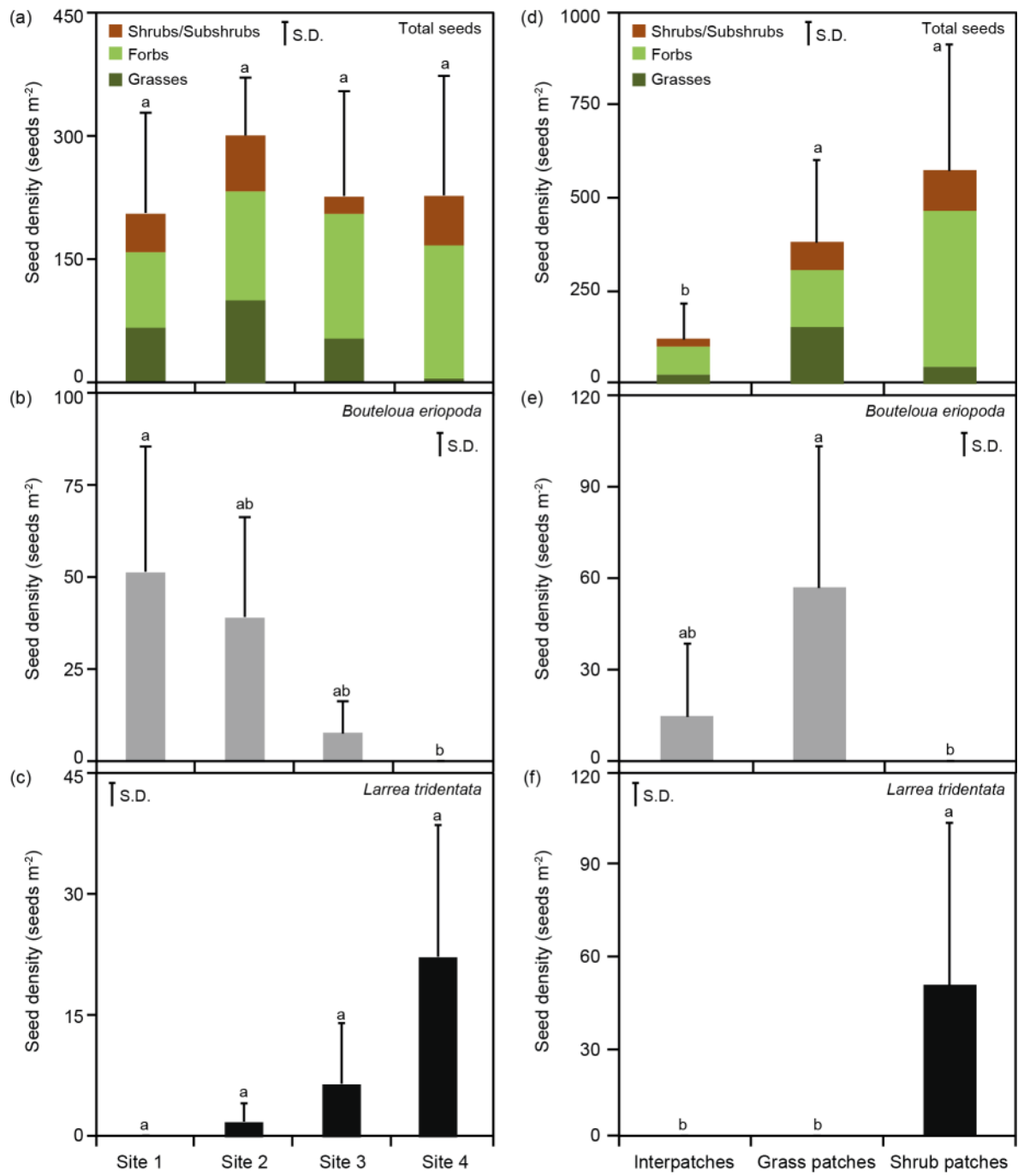


Figure 3.

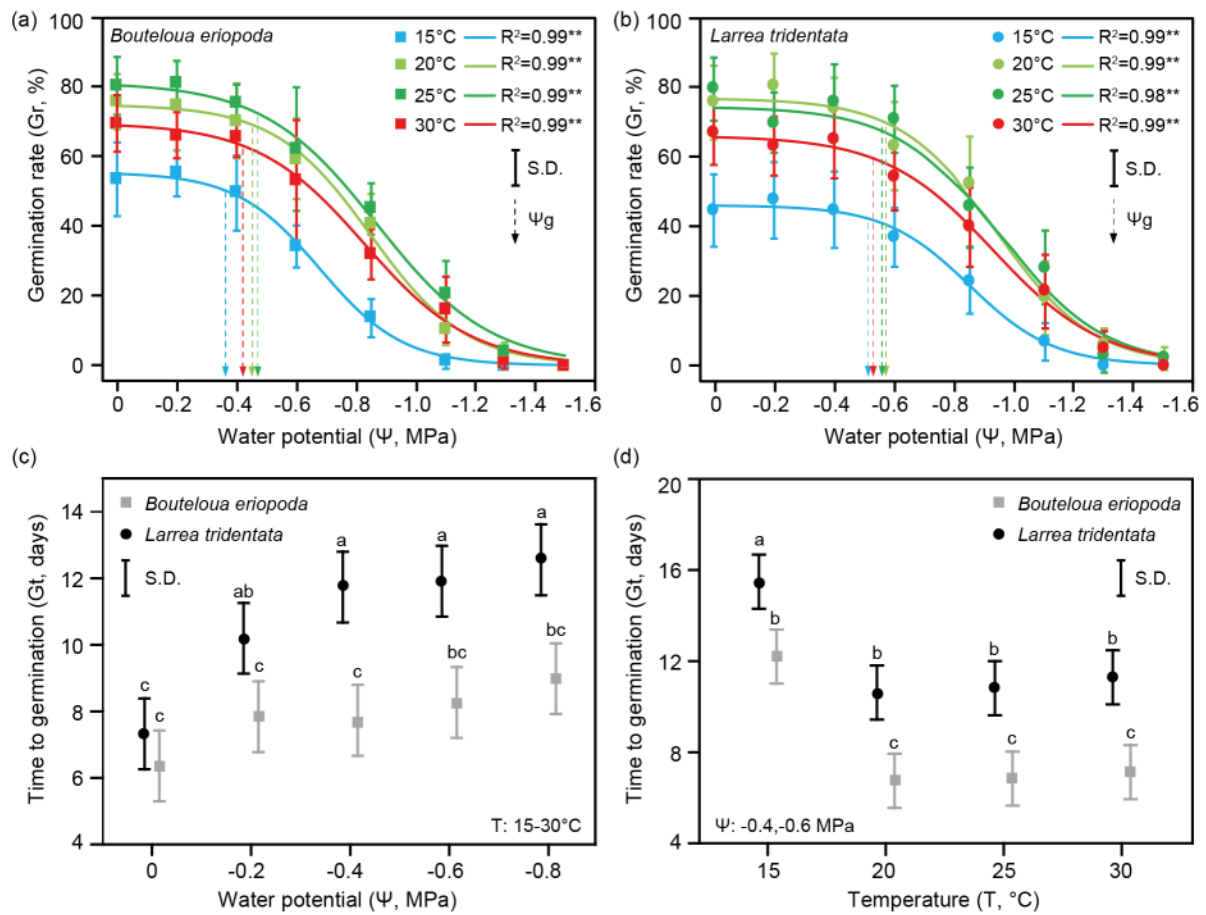


Figure 4.

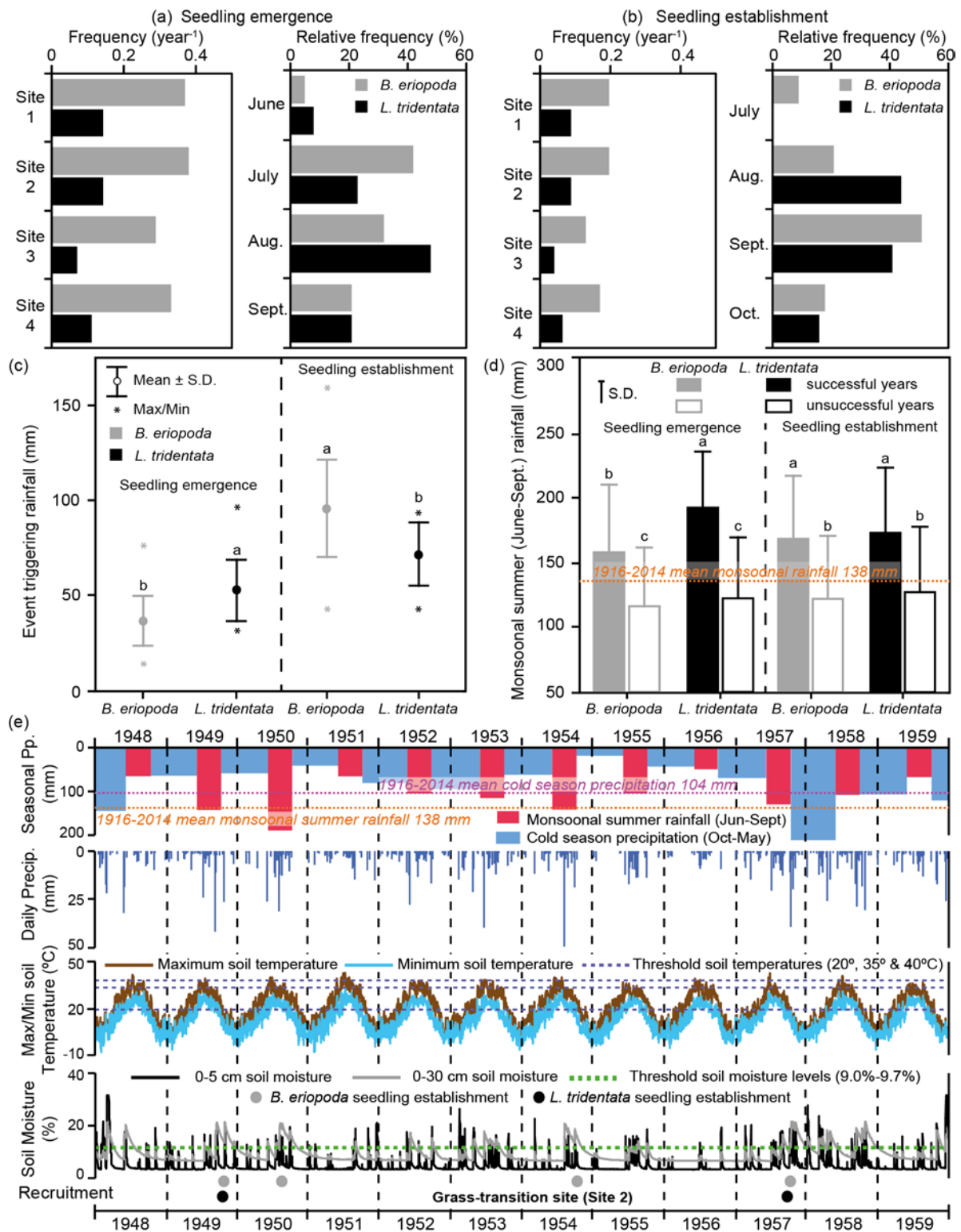


Figure 5.

This appendix contains supporting and supplementary information for our study, including: a detailed characterization of soils (Table ST1) and soil-water retention curves for our study sites (Table ST2 and Fig. SF1), parameterization (Tables ST3 and ST4) and error-assessment details (Fig. SF2) for the soil-moisture and soil-surface-temperature simulations that were applied in our study, supplementary information on soil seed-bank data (Tables ST5 and ST6) and seed germination tests (Table ST7), and detailed records of our black grama and creosotebush seedling emergence and early establishment simulations in the study sites along 1948-1959 (Fig. SF3) and 1914-2014 (Tables ST8 and ST9).

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TABLE ST1. Soil characteristics (mean values and S.D.) for the surface types (interpatches, grass and shrub patches) in the studied sites.

		Site 1		Site 2			Site 3			Site 4	
		Ip	Gp	Ip	Gp	Sp	Ip	Gp	Sp	Ip	Sp
Stoniness (>2 mm particles, %)	Mean	35.2	9.6	32.8	9.7	25.1	40.0	16.5	21.1	37.7	14.0
	S.D.	4.7	3.5	3.4	5.2	6.6	3.2	5.3	9.8	3.7	4.8
	Sig. dif.	a	b	a	b	a	a	b	b	a	b
Sand (2 mm-50 μ m, %)	Mean	40.5	65.9	42.2	62.4	58.1	38.6	60.1	51.6	38.7	62.1
	S.D.	5.3	2.6	4.6	4.7	4.8	5.3	9.0	3.2	3.2	2.3
	Sig. dif.	a	b	b	a	ab	b	a	ab	b	a
Silt (50-2 μ m, %)	Mean	18.3	19.9	20.4	23.6	12.9	17.7	20.0	20.8	17.8	18.5
	S.D.	1.2	0.8	3.6	1.9	3.2	2.3	5.0	5.8	2.4	5.9
	Sig. dif.	a	a	a	a	b	a	a	a	a	a
Clay (<2 μ m, %)	Mean	6.0	4.5	4.6	4.3	3.9	3.7	3.3	6.5	5.8	5.5
	S.D.	1.6	0.2	0.3	0.3	0.5	0.5	0.5	1.7	1.6	1.5
	Sig. dif.	a	a	a	a	a	a	a	a	a	a
Soil Texture		SL	SL	SL	SL	LS	SL	SL	SL	SL	SL
pH (w/v:1/2)	Mean	8.7	8.4	8.6	8.2	8.4	8.8	8.6	8.5	8.8	8.6
	S.D.	0.1	0.1	0.1	0.1	0.1	0.1	0.2	0.1	0.1	0.1
	Sig. dif.	a	b	a	b	ab	a	a	a	a	a
Electrical Conductivity (w/v:1/2; dS m ⁻¹)	Mean	0.33	0.32	0.35	0.32	0.47	0.32	0.36	0.58	0.30	0.41
	S.D.	0.04	0.02	0.06	0.01	0.06	0.01	0.04	0.12	0.01	0.02
	Sig. dif.	a	a	ab	b	a	b	ab	a	a	b
Inorganic C (%)	Mean	0.84	0.47	0.89	0.35	0.59	1.16	0.96	1.17	1.11	0.91
	S.D.	0.25	0.01	0.16	0.03	0.04	0.12	0.03	0.04	0.11	0.10
	Sig. dif.	a	b	a	b	ab	a	b	a	a	b
Organic C (%)	Mean	0.49	0.52	0.52	0.57	0.73	0.46	0.58	1.01	0.42	0.62
	S.D.	0.11	0.07	0.06	0.08	0.07	0.03	0.09	0.17	0.05	0.03
	Sig. dif.	a	a	b	b	a	b	b	a	b	a
Total N (%)	Mean	0.04	0.04	0.05	0.05	0.07	0.04	0.05	0.10	0.03	0.05
	S.D.	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
	Sig. dif.	a	a	b	ab	a	b	ab	a	a	b
Plant available P (mg Kg ⁻¹)	Mean	8.1	5.8	10.0	5.7	10.1	8.6	5.7	10.1	9.4	10.2
	S.D.	0.7	1.0	0.5	0.6	3.0	1.7	0.5	3.0	2.1	2.5
	Sig. dif.	a	a	a	a	a	a	a	a	a	a

Abbreviations: Ip, interpatches; Gp, grass patches; Sp, shrub patches; w/v, soil (weigh) to water (volume) ratio; SL, sandy loam; LS, loamy sand. *Notes:* Different letters indicate surface type differences within each site at $P < 0.05$. Tested using Kruskal-Wallis ANOVA and post-hoc Mann-Whitney tests.

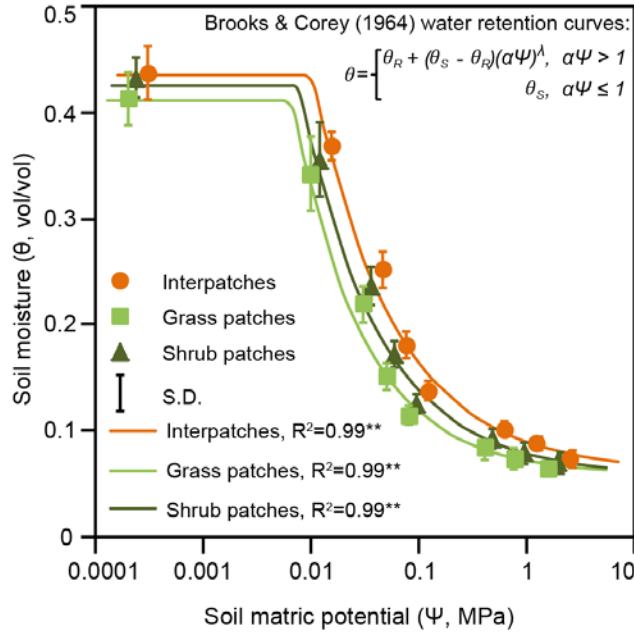


FIG. SF1. Parameterized Brooks and Corey (1964) soil-water-retention curves for the different surface types (interpatches, grass and shrub patches) in the studied sites. Curve parameters: θ_R and θ_S are the residual and saturated soil-water contents (vol/vol), respectively; α is an empirical parameter (MPa^{-1}), and λ is a pore-size distribution coefficient (dimensionless) affecting the shape of the curve. For simplification, soil matric potential (suction, Ψ , MPa) takes positive values in the represented Brooks and Corey curves. Sig. codes: '**', $P < 0.01$.

TABLE ST2. Parameter estimates (S.E. in parentheses) and R^2 for the fitted Brooks and Corey soil-water-retention curves.

	θ_R (vol/vol)	θ_S (vol/vol)	α (MPa^{-1})	λ	R^2
Interpatches	0.064 (0.005)	0.438 (0.004)	139 (5)	0.57 (0.03)	0.99**
Grass patches	0.061 (0.004)	0.414 (0.005)	138 (5)	0.66 (0.03)	0.99**
Shrub patches	0.059 (0.005)	0.433 (0.005)	144 (7)	0.60 (0.03)	0.99**

Abbreviations: θ_R and θ_S are the residual and saturated soil-water contents (vol/vol), respectively; α is an empirical parameter (MPa^{-1}), and λ is a pore-size distribution coefficient (dimensionless) affecting the shape of the curve. Sig. codes: '**', $P < 0.01$.

TABLE ST3. Soil-moisture estimates (% vol/vol) and S.E. of estimates (in parentheses) at field capacity (-0.03MPa), wilting point (-1.5 MPa), and experimental water potential threshold levels for seed germination of black grama (*B. eriopoda* Ψ_g , -0.45 MPa) and creosotebush (*L. tridentata* Ψ_g , -0.55 MPa) in the studied sites.

	-0.03 MPa	-1.5 MPa	-0.45 MPa	-0.55 MPa
Site 1	22.0 (0.9)	7.7 (0.9)	9.3 (0.9)	9.0 (0.9)
Site 2	22.0 (0.9)	7.8 (0.9)	9.3 (0.9)	9.0 (0.9)
Site 3	22.4 (0.9)	7.9 (0.9)	9.5 (0.9)	9.2 (0.9)
Site 4	22.8 (0.9)	8.0 (0.9)	9.7 (0.9)	9.3 (0.9)

Notes: data derived from the soil water retention curves parameterized at the surface-type scale (i.e., interpatches, grass and shrub patches, Fig. SF1) and the distribution of surface types (% cover, Fig. 1) in the study sites.

TABLE ST4. Depth distribution of root biomass (%) across the soil profile that was represented for the studied sites in the DayCent soil-moisture simulations.

Soil depth (cm)	Site 1	Site 2	Site 3	Site 4
0-2	5	5	4	2
2-5	15	14	10	3
5-10	36	34	22	5
10-20	23	22	18.5	14.5
20-30	8	9	13	19.5
30-45	5	8	17.5	33
45-60	5	5	9	14
60-75	2	2	4	6
>75	1	1	2	3

Notes: Root distribution in Site 1 (grass-dominated site) represents typical values of Chihuahuan black grama grasslands (Peters 2002a). Root distribution in Site 4 (shrub-dominated site) represents typical values for Chihuahuan creosotebush shrublands (Ogle and Reynolds 2004, and references therein). Root distribution in sites 2 and 3 (i.e., the grass- and shrub-transition sites, respectively) were obtained weighing the root distribution of the end-member sites 1 and 4 by the grass and shrub abundances in the transition sites 2 and 3 (% cover, Fig. 1).

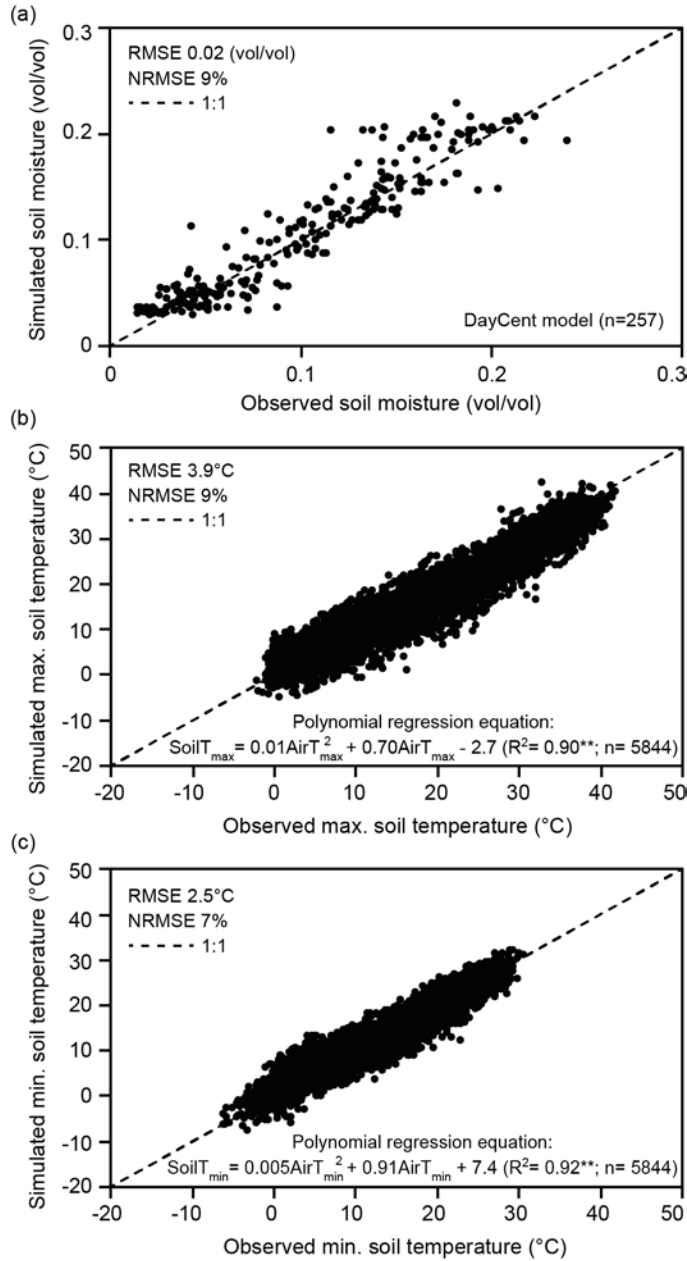


FIG. SF2. Error assessment of modeled soil moisture and surface temperatures: simulated against observed (a) soil moisture, and (b) maximum and (c) minimum soil surface temperature (1:1 relationship, root-mean square error, RMSE, and normalized error, NRMSE, of the estimates are shown within the scatter plots). Soil-moisture dynamics (a) were simulated by applying the parameterized DayCent model. Surface soil temperature dynamics (b and c) were simulated by using field-based air-soil surface polynomial regression equations (equation details are provided within the scatter plots). Observed soil-moisture and soil-surface-temperature data for the sites was taken from Turnbull et al. (2010a) and a local weather station (SNWR Five Points station, <http://sev.lternet.edu/data/sev-1>), respectively. Sig. codes: ‘**’, $P < 0.01$.

TABLE ST5. Plant species identified in the soil seed-bank samples for the studied sites. Species symbols, common names, life-forms and life-patterns follow the plant descriptions of the USDA Plant Database (<http://plants.usda.gov/java/>).

N	Scientific name	Family	USDA symbol	Common name	Life-form	Life-pattern	Sites
		Asteraceae					
1	<i>Laennecia coulteri</i>		LACO13	Coulter's horseweed	Forb	Annual	1, 2
2	<i>Macharanthera tatanacetifolia</i>		MATA2	Tanseyleaf tansyaster	Forb	Annual	4
3	<i>Gutierrezia sarothrae</i>		GUSA2	Broom snakeweed	Subshrub	Perennial	1, 2
4	<i>Gutierrezia sphaerocephala</i>		GUSP	Roundleaf snakeweed	Subshrub	Perennial	3, 4
5	<i>Thymophylla acerosa</i>		THAC	Pricklyleaf dogweed	Subshrub	Perennial	4
		Brassicaceae					
6	<i>Descurainia pinnata</i>		DEPI	Western tansymustard	Forb	Annual	2, 3, 4
		Boraginaceae					
7	<i>Cryptantha crassisejala</i>		CRCR3	Thicksepal cryptantha	Forb	Annual	1, 2
		Euphorbiaceae					
8	<i>Chamaesyce serpyllifolia</i>		CHSE6	Thymeleaf sandmat	Forb	Annual	2, 3, 4
		Hydrophyllaceae					
9	<i>Nama hispidum</i>		NAHI	Bristly nama	Forb	Annual	2
10	<i>Phacelia integrifolia</i>		PHIN	Gypsum phacelia	Forb	Annual	1, 2, 3, 4
		Onagraceae					
11	<i>Oenothera caespitosa</i>		OECA10	Tufted evening primrose	Forb	Perennial	3
		Plantaginaceae					
12	<i>Plantago patagonica</i>		PLPA2	Woolly plantain	Forb	Annual	1, 2, 3, 4
		Poaceae					
13	<i>Bouteloua eriopoda</i>		BOER2	Black gramma	Grass	Perennial	1, 2, 3
14	<i>Dasyochloa pulchella</i>		DAPU7	Low woollygrass	Grass	Perennial	2, 3
15	<i>Sporobolus flexuosus</i>		SPFL2	Mesa dropseed	Grass	Perennial	1, 2
16	<i>Sporobolus contractus</i>		SPCO4	Spike dropseed	Grass	Perennial	3, 4
17	<i>Muhlenbergia torreyi</i>		MUPO2	Ring muhly	Grass	Perennial	2
		Polemoniaceae					
18	<i>Ipomopsis pumila</i>		IPPU4	Dwarf ipomopsis	Forb	Annual	1
		Portulacaceae					
19	<i>Portulaca halimoides</i>		POHA5	Silkcotton purslane	Forb	Annual	4
		Typhaceae					
20	<i>Typha domingensis</i>		TYDO	Southern cattail	Forb	Perennial	1, 2, 3, 4
		Zygophyllaceae					
21	<i>Larrea tridentata</i>		LATR2	Creosotebush	Shrub	Perennial	2, 3, 4

TABLE ST6. Mean soil seed density (viable seeds m⁻²) and S.D. for the surface types (interpatches, grass and shrub patches) in the studied sites.

		Site 1		Site 2			Site 3			Site 4	
		Ip	Gp	Ip	Gp	Sp	Ip	Gp	Sp	Ip	Sp
Grasses (seeds m ⁻²)	Mean	52	87	17	208	93	17	173	35	0	17
	S.D.	34	87	35	126	40	35	165	40	0	35
	Sig. dif.	a	a	b	a	ab	b	a	ab	a	a
Forbs (seeds m ⁻²)	Mean	87	104	87	156	208	35	173	694	104	295
	S.D.	35	89	35	173	208	40	132	380	165	87
	Sig. dif.	a	a	a	a	a	b	ab	a	a	a
Shrubs/Subshrubs (seeds m ⁻²)	Mean	17	87	52	104	46	0	35	87	0	174
	S.D.	35	35	66	40	40	0	69	104	0	120
	Sig. dif.	b	a	a	a	a	a	a	a	b	a
Total (seeds m ⁻²)	Mean	156	278	159	469	347	52	382	816	104	486
	S.D.	35	196	66	199	250	35	269	433	165	98
	Sig. dif.	a	a	b	a	ab	b	ab	a	b	a
<i>B. eriopoda</i> (seeds m ⁻²)	Mean	35	69	17	69	0	0	34	0	0	0
	S.D.	40	57	35	57	0	0	40	0	0	0
	Sig. dif.	a	a	ab	a	b	a	a	a	a	a
<i>L. tridentata</i> (seeds m ⁻²)	Mean	0	0	0	0	46	0	0	52	0	69
	S.D.	0	0	0	0	40	0	0	66	0	57
	Sig. dif.	a	a	a	a	b	a	a	a	b	a

Abbreviations: Ip, interpatches; Gp, grass patches; Sp, shrub patches. *Notes:* For each experimental site, different letters indicate differences between surface types at $P<0.05$. Tested using Kruskal-Wallis ANOVA and post-hoc Mann-Whitney tests.

TABLE ST7. Experimental water potential-seed germination curves for *B. eriopoda* and *L. tridentata* at 15°, 20°, 25° and 30°C: parameter estimates and S.E. (between brackets).

	G _m (%)	a (MPa)	b	Ψ _g (MPa)	R ²
<i>Larrea tridentata</i>					
15°C	45.2 (1.2)	-0.85 (0.02)	0.14 (0.02)	-0.51 (0.06)	0.99**
20°C	75.4 (2.4)	-0.94 (0.03)	0.16 (0.02)	-0.57 (0.07)	0.99**
25°C	75.1 (3.4)	-0.95 (0.03)	0.17 (0.03)	-0.56 (0.09)	0.98**
30°C	64.8 (2.0)	-0.93 (0.03)	0.18 (0.03)	-0.53 (0.09)	0.99**
<i>Bouteloua eriopoda</i>					
15°C	55.6 (1.2)	-0.68 (0.01)	0.14 (0.01)	-0.36 (0.03)	0.99**
20°C	75.1 (1.8)	-0.85 (0.01)	0.16 (0.02)	-0.47 (0.06)	0.99**
25°C	81.5 (2.4)	-0.87 (0.02)	0.19 (0.02)	-0.43 (0.09)	0.99**
30°C	69.8 (2.3)	-0.83 (0.03)	0.18 (0.02)	-0.42 (0.07)	0.99**

Abbreviations: G_m, maximum germination rate; a, inflection point; b, shape coefficient; Ψ_g, water-potential threshold for seed germination. Sig. Codes: ‘**’, *P*<0.01.

TABLE ST8. Simulated *B. eriopoda* (black grama) seedling emergence and early establishment pulses by month along 1916-2014 in the studied sites.

	Site 1		Site 2		Site 3		Site 4	
	Emerg.	Estab.	Emerg.	Estab.	Emerg.	Estab.	Emerg.	Estab.
1916	---	---	---	---	---	---	---	---
1917	---	---	---	---	---	---	---	---
1918	---	---	---	---	---	---	---	---
1919	---	---	---	---	---	---	---	---
1920	---	---	---	---	---	---	---	---
1921	July	August	August	August	August	---	July	---
1922	---	---	---	---	---	---	---	---
1923	---	---	---	---	---	---	---	---
1924	---	---	---	---	---	---	---	---
1925	---	---	---	---	---	---	---	---
1926	---	---	---	---	---	---	---	---
1927	Sept.	---	Sept.	---	Sept.	---	Sept.	---
1928	Sept.	---	Sept.	---	---	---	Sept.	---
1929	July	Sept.	July	Sept.	July	Sept.	July	Sept.
1930	August	---	August	---	---	---	---	---
1931	July	August	July	Sept.	July	---	July	Sept.
1932								
1933	June	July	June	July	June	July	June	July
1934	August	Sept.	August	Sept.	August	Sept.	August	Sept.
1935	Sept.	Sept.	Sept.	Sept.	Sept.	Sept.	Sept.	Sept.
1936	July	---	July	---	July	---	July	---
1937	---	---	---	---	---	---	---	---
1938	July	Sept.	July	Sept.	Sept.	October	July	Sept.
1939	---	---	---	---	---	---	---	---

TABLE ST8 continuation (1).

	Site 1		Site 2		Site 3		Site 4	
	Emerg.	Estab.	Emerg.	Estab.	Emerg.	Estab.	Emerg.	Estab.
1940	---	---	---	---	---	---	---	---
1941	---	---	---	---	---	---	---	---
1942	---	---	---	---	---	---	---	---
1943	July	---	July	---	---	---	July	---
1944	---	---	---	---	---	---	---	---
1945	---	---	---	---	---	---	---	---
1946	---	---	---	---	---	---	---	---
1947	---	---	---	---	---	---	---	---
1948	August	---	August	---	August	---	August	---
1949	Sep.	October	Sep.	October	Sep.	October	Sep.	October
1950	July	August	July	August	July	August	July	August
1951	August	---	August	---	August	---	August	---
1952	---	---	---	---	---	---	---	---
1953	---	---	---	---	---	---	---	---
1954	August	October	August	October	August	October	August	October
1955	July	---	July	---	July	---	July	---
1956	---	---	---	---	---	---	---	---
1957	Sept.	October	August	October	N.A	---	Sep.	---
1958	---	---	---	---	---	---	---	---
1959	---	---	---	---	---	---	---	---
1960	---	---	---	---	---	---	---	---
1961	August	Sep.	August	Sep.	August	---	August	Sep.
1962	---	---	---	---	---	---	---	---
1963	---	---	---	---	---	---	---	---
1964	---	---	---	---	---	---	---	---
1965	Sep.	---	Sep.	---	Sep.	---	Sep.	---
1966	---	---	---	---	---	---	---	---
1967	---	---	---	---	---	---	---	---
1968	July	August	July	August	July	---	July	August
1969	July	August	July	August	July	---	July	---
1970	---	---	---	---	---	---	---	---
1971	---	---	---	---	---	---	---	---
1972	Sep.	October	Sep.	October	---	---	Sep.	October
1973	---	---	---	---	---	---	---	---
1974	---	---	---	---	---	---	---	---
1975	Sept.	---	Sept.	---	Sept.	---	Sept.	---
1976	July	---	July	---	July	---	July	---
1977	---	---	---	---	---	---	---	---
1978	---	---	---	---	---	---	---	---
1979	---	---	---	---	---	---	---	---
1980	---	---	---	---	---	---	---	---
1981	---	---	---	---	---	---	---	---
1982	---	---	---	---	---	---	---	---
1983	---	---	---	---	---	---	---	---
1984	---	---	---	---	---	---	---	---

TABLE ST8 continuation (2).

	Site 1		Site 2		Site 3		Site 4	
	Emerg.	Estab.	Emerg.	Estab.	Emerg.	Estab.	Emerg.	Estab.
1985	---	---	---	---	---	---	---	---
1986	June	July	June	July	---	---	June	July
1987	---	---	---	---	---	---	---	---
1988	August	Sep.	August	Sep.	August	Sep.	August	Sep.
1989	July	Sep.	July	Sep.	---	---	---	---
1990	---	---	---	---	---	---	---	---
1991	August	Sep.	August	Sep.	August	Sep.	August	Sep.
1992	---	---	---	---	---	---	---	---
1993	August	---	August	---	---	---	---	---
1994	---	---	---	---	---	---	---	---
1995	---	---	---	---	---	---	---	---
1996	July	---	July	---	July	---	July	---
1997	---	---	August	---	---	---	August	Sep.
1998	July	August	July	August	July	August	July	August
1999	August	Sep.	August	Sep.	August	Sep.	August	Sep.
2000	---	---	---	---	---	---	---	---
2001	---	---	---	---	---	---	---	---
2002	---	---	---	---	---	---	---	---
2003	---	---	---	---	---	---	---	---
2004	---	---	---	---	---	---	---	---
2005	---	---	---	---	---	---	---	---
2006	July	---	July	---	July	---	July	---
2007	---	---	---	---	---	---	---	---
2008	August	Sep.	August	Sep.	August	Sep.	August	Sep.
2009	---	---	---	---	---	---	---	---
2010	---	---	---	---	---	---	---	---
2011	---	---	---	---	---	---	---	---
2012	---	---	---	---	---	---	---	---
2013	July	---	July	---	July	---	July	---
2014	---	---	---	---	---	---	---	---

TABLE ST9. Simulated *L. tridentata* (creosotebush) seedling emergence and early establishment pulses by month along 1916-2014 in the studied sites.

	Site 1		Site 2		Site 3		Site 4	
	Emerg.	Estab.	Emerg.	Estab.	Emerg.	Estab.	Emerg.	Estab.
1916	---	---	---	---	---	---	---	---
1917	---	---	---	---	---	---	---	---
1918	---	---	---	---	---	---	---	---
1919	---	---	---	---	---	---	---	---
1920	---	---	---	---	---	---	---	---
1921	---	---	---	---	---	---	---	---
1922	---	---	---	---	---	---	---	---
1923	---	---	---	---	---	---	---	---

TABLE ST9 continuation (1).

	Site 1		Site 2		Site 3		Site 4	
	Emerg.	Estab.	Emerg.	Estab.	Emerg.	Estab.	Emerg.	Estab.
1924	---	---	---	---	---	---	---	---
1925	---	---	---	---	---	---	---	---
1926	---	---	---	---	---	---	---	---
1927	---	---	---	---	---	---	---	---
1928	---	---	---	---	---	---	---	---
1929	August	August	August	August	---	---	August	August
1930	---	---	---	---	---	---	---	---
1931	---	---	---	---	---	---	---	---
1932	---	---	---	---	---	---	---	---
1933	June	---	June	---	June	---	June	---
1934	---	---	---	---	---	---	---	---
1935	---	---	---	---	---	---	---	---
1936	---	---	---	---	---	---	---	---
1937	---	---	---	---	---	---	---	---
1938	July	August	July	August	July	August	July	August
1939	---	---	---	---	---	---	---	---
1940	---	---	---	---	---	---	---	---
1941	---	---	---	---	---	---	---	---
1942	---	---	---	---	---	---	---	---
1943	---	---	---	---	---	---	---	---
1944	---	---	---	---	---	---	---	---
1945	---	---	---	---	---	---	---	---
1946	---	---	---	---	---	---	---	---
1947	---	---	---	---	---	---	---	---
1948	---	---	---	---	---	---	---	---
1949	Sep.	October	July	August	---	---	July	August
1950	---	---	---	---	---	---	---	---
1951	---	---	---	---	---	---	---	---
1952	---	---	---	---	---	---	---	---
1953	---	---	---	---	---	---	---	---
1954	---	---	---	---	---	---	---	---
1955	---	---	---	---	---	---	---	---
1956	---	---	---	---	---	---	---	---
1957	Sep.	Sep.	Sep.	Sep.	---	---	Sep.	Sep.
1958	---	---	---	---	---	---	---	---
1959	---	---	---	---	---	---	---	---
1960	---	---	---	---	---	---	---	---
1961	August	Sep.	August	Sep.	---	---	August	Sep.
1962	---	---	---	---	---	---	---	---
1963	---	---	---	---	---	---	---	---
1964	---	---	---	---	---	---	---	---
1965	---	---	---	---	---	---	---	---
1966	---	---	---	---	---	---	---	---
1967	---	---	---	---	---	---	---	---
1968	July	August	July	August	---	---	July	August
1969	---	---	---	---	---	---	---	---

TABLE ST9 continuation (2).

	Site 1		Site 2		Site 3		Site 4	
	Emerg.	Estab.	Emerg.	Estab.	Emerg.	Estab.	Emerg.	Estab.
1970	---	---	---	---	---	---	---	---
1971	---	---	---	---	---	---	---	---
1972	Sep.	October	Sep.	October	---	---	Sept.	---
1973	---	---	---	---	---	---	---	---
1974	---	---	---	---	---	---	---	---
1975	---	---	---	---	---	---	---	---
1976	---	---	---	---	---	---	---	---
1977	---	---	---	---	---	---	---	---
1978	---	---	---	---	---	---	---	---
1979	---	---	---	---	---	---	---	---
1980	---	---	---	---	---	---	---	---
1981	---	---	---	---	---	---	---	---
1982	---	---	---	---	---	---	---	---
1983	---	---	---	---	---	---	---	---
1984	---	---	---	---	---	---	---	---
1985	---	---	---	---	---	---	---	---
1986	July	August	July	August	July	August	July	August
1987	---	---	---	---	---	---	---	---
1988	August	---	August	---	July	---	August	---
1989	---	---	---	---	---	---	---	---
1990	---	---	---	---	---	---	---	---
1991	August	---	August	---	August	---	August	---
1992	---	---	---	---	---	---	---	---
1993	---	---	---	---	---	---	---	---
1994	---	---	---	---	---	---	---	---
1995	---	---	---	---	---	---	---	---
1996	---	---	---	---	---	---	---	---
1997	August	Sep.	August	Sep.	August	Sep.	August	Sep.
1998	---	---	---	---	---	---	---	---
1999	August	Sep.	August	Sep.	August	Sep.	August	Sep.
2000	---	---	---	---	---	---	---	---
2001	---	---	---	---	---	---	---	---
2002	---	---	---	---	---	---	---	---
2003	---	---	---	---	---	---	---	---
2004	---	---	---	---	---	---	---	---
2005	---	---	---	---	---	---	---	---
2006	August	---	August	---	August	---	August	---
2007	---	---	---	---	---	---	---	---
2008	---	---	---	---	---	---	---	---
2009	---	---	---	---	---	---	---	---
2010	---	---	---	---	---	---	---	---
2011	---	---	---	---	---	---	---	---
2012	---	---	---	---	---	---	---	---
2013	Sept.	October	Sept.	October	---	---	Sept.	October
2014	---	---	---	---	---	---	---	---

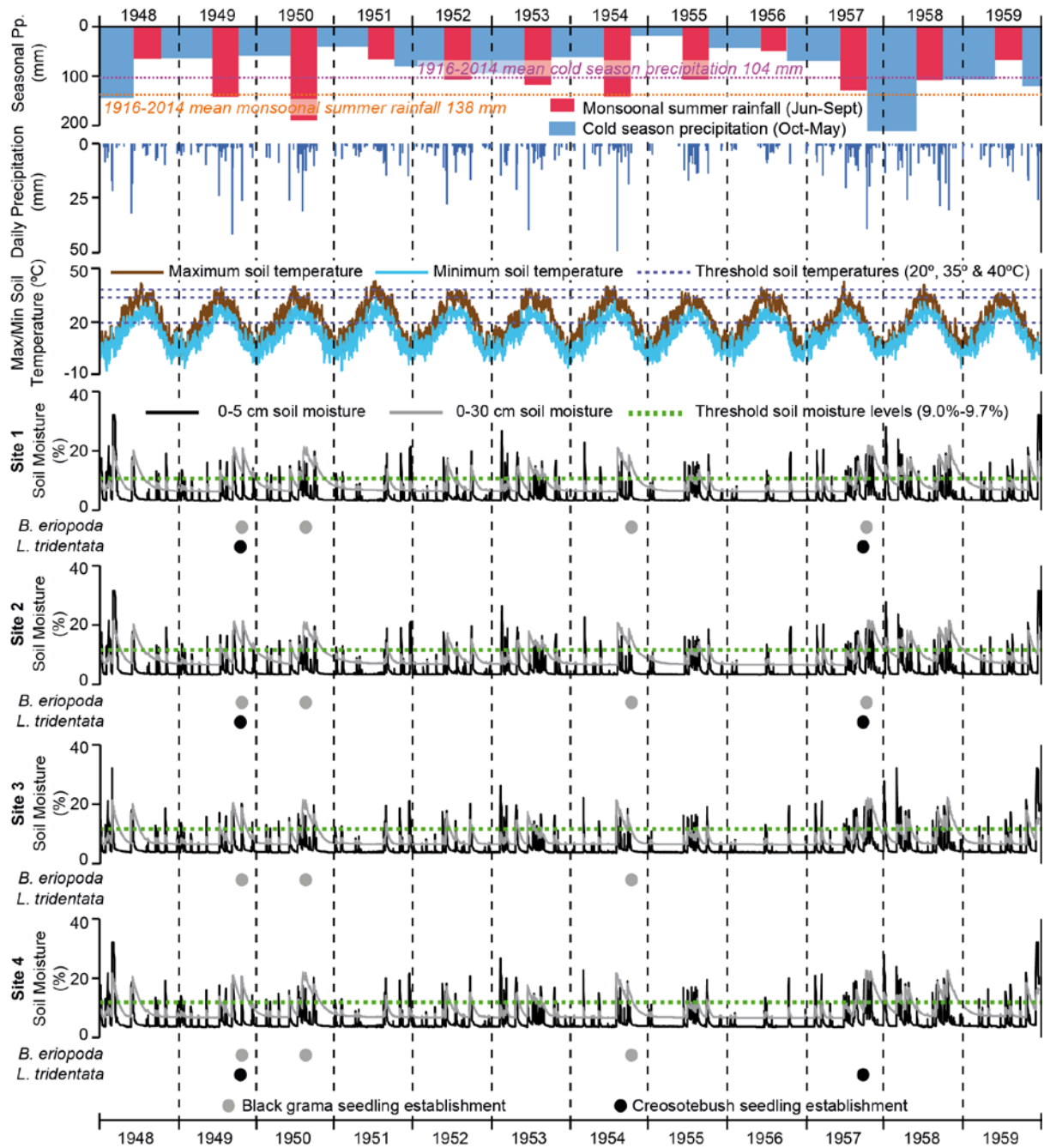


FIG. SF3. Simulated 1948-1959 seedling recruitment dynamics for *B. eriopoda* (black grama) and *L. tridentata* (creosotebush) in the studied sites. Modeled soil surface temperature and soil moisture at 0-5 cm and 0-30 cm are shown along with seasonal precipitation (winter and summer monsoonal precipitation), daily rainfall, and simulated seedling emergence and establishment events.