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ARTICLE

Special Feature: Dynamic Deserts

Simulated distribution of *Eragrostis lehmanniana* (Lehmann lovegrass): Soil–climate interactions complicate predictions

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Abstract

The invasive perennial grass *Eragrostis lehmanniana* has expanded rapidly throughout the Sonoran Desert (SD) while remaining sparse and patchily distributed in the neighboring Chihuahuan Desert (CD). As temperatures and patterns in precipitation change, identifying the drivers limiting spread in the CD is needed. Our objectives were (1) to identify the climatic and edaphic factors limiting recruitment of *E. lehmanniana* throughout the CD and (2) to predict the edaphic and climatic locations in the CD where this species is expected to have higher probabilities of recruitment under future climatic conditions. Recruitment was simulated at 57 locations throughout the CD with a daily, multilayer soil water model (SOILWAT) that was parameterized and tested to develop recruitment parameters for *E. lehmanniana* using long-term data from research stations in the SD and CD. Logistic regression was used to predict recruitment across the CD using climate and soil factors to create a map of simulated recruitment under current and alternative climate scenarios. Simulated recruitment under current climate was low for most of the CD. However, localized areas with high probabilities (>0.8) occurred along the western transition between the CD and the SD, and in the southern extent of the CD. In general, the CD climate is too cool and dry for rapid and widespread invasion. However, increases to temperature and precipitation are likely to increase recruitment success. Interactions among soil, temperature, and precipitation were important to increases in recruitment of *E. lehmanniana* and are expected to lead to heterogeneous increases in abundance as climate continues to change. This patchy increase in abundance will result in changes in its geographic distribution that will make predictions in the future challenging.

KEYWORDS

Chihuahuan Desert, climate change, geographic distribution, numerical model, recruitment, seedling establishment, Special Feature: Dynamic Deserts

INTRODUCTION

Invasion by non-native species and changes in climate regimes are important global change drivers in terrestrial ecosystems (Hobbs et al., 2009). These drivers often interact to result in increases in both the local abundance and the geographic distribution of invasive species (Kriticos et al., 2003; Mack et al., 2000). Most studies of non-native species are conducted at local scales where their ecological consequences have been well-documented (Hobbs et al., 2006; Seastedt et al., 2008). Changes in the geographic distribution of invasive species are challenging to predict and require information throughout their spatial extent about the environmental drivers (climate, soils, and disturbance) and species-level processes limiting or promoting their range expansion (Gallien et al., 2010). Invasion dynamics can be complex and surprising when invasive species recruit unexpectedly in some locations and do not occur when expected in other locations. Our goal was to improve predictions of invasive species dynamics using a macro-ecology perspective that combines broad-scale patterns across the geographic distribution of a species with an underlying process-based understanding derived from individual locations (Heffernan et al., 2014; Peters et al., 2008).

In the deserts of North America, invasive species from South Africa, southern Europe, and South Asia have had variable invasion success across the broad environmental conditions characteristic of these deserts. Low elevation locations (<1500 m above sea level [asl]) of the Sonoran Desert (SD) have been susceptible to invasion by annual and perennial grasses leading to losses in biodiversity and increases in frequency and severity of wildfire (Anable et al., 1992; D'Antonio & Vitousek, 1992). *Eragrostis lehmanniana* (Lehmann lovegrass), *Cenchrus ciliaris* (buffel grass), *Bromus madritensis rubens* (red brome), and *Bromus tectorum* (cheatgrass) have invaded hundreds of thousands of hectares of native Sonoran ecosystems since the 1800s with subsequent losses in plant and animal biodiversity (Billings, 1990; Bock et al., 1986; Marshall et al., 2012; Simonin, 2001). Interestingly, the Chihuahuan Desert (CD) located on the eastern border of the SD (Figure 1) is a high elevation desert (>1500 m) with fall monsoonal rainfall and a low susceptibility to invasion by these same species. Because the SD has a bimodal pattern in precipitation and is generally 2–3°C warmer than the CD, it is generally believed that climatic differences are primarily responsible for differences in invasion success of these grasses between deserts. Continued changes in climate could lead to an increase in invasion by these species in the CD in future, in particular as temperatures in this desert become more similar to the warmer SD. We sought to identify factors limiting

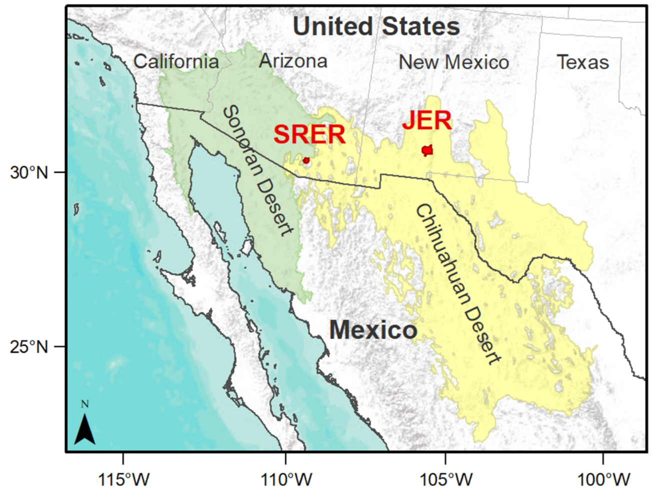


FIGURE 1 Map of the Chihuahuan Desert in the United States and Mexico, and the Jornada USDA-LTER research site (JER), and the Santa Rita research site (SRER) along the western ecotone between the Sonoran and Chihuahuan Deserts

invasion by one particularly invasive non-native perennial grass (*E. lehmanniana*) in the CD in order to predict changes in its local invasion success and geographic distribution with changes in climate.

Both deserts have undergone major shifts in vegetation from dominance by perennial grasses in the 1800s prior to European settlement to dominance by xerophytic, drought-tolerant woody plants following livestock overgrazing and periodic drought (Gibbens et al., 2005; McClaran et al., 1997; Van Auken, 2000, Van Devender & McClaran, 1995; Wooton, 1908). In the SD over the past several decades, *E. lehmanniana* and other non-native grasses have invaded shrublands dominated by several species of mesquite (e.g., *Prosopis velutina*), and grasslands dominated by mainly caespitose grasses (*Boutella* spp. and *Aristida* spp.) (Anable et al., 1992; Humphrey, 1958; Van Devender & McClaran, 1995). Invasion by *E. lehmanniana* often leads to monospecific stands dominated by this species with low biodiversity of native species (Steidl et al., 2013). These monospecific stands of *E. lehmanniana* led to increases in the number and spatial extent of wildfires with feedback to increases in cover and abundance of non-native grasses that maintain and increase their dominance through time (Anable et al., 1992; Kupfer & Miller, 2005; Mack & D'Antonio, 1998).

Similar vegetation changes have occurred throughout the CD where large expanses of perennial grasslands in the mid-1800s converted to woody plant dominance by the early 1900s as livestock overgrazing occurred during periods of severe drought (Buffington & Herbel, 1965; Dick-Peddie, 1993). Thresholds in grass cover and soil properties were crossed such that shrub cover continued to increase throughout the 20th century even after grazing intensity decreased throughout the region (Fredrickson et al., 1998). Currently, much of the CD is dominated by one of three shrub species, each of which is generally associated with a different soil type and topographic position: honey mesquite (*Prosopis glandulosa*) on the basin floor sand sheet; tarbush (*Flourensia cernua*) on sandy loams of the lower bajada; and creosote bush (*Larrea tridentata*) on the loamy soils of the upper bajada (Wondzell et al., 1987). Remnant grasslands are primarily located on the sandy uplands of the basin floor and in playas (Gibbens et al., 2005). Vegetation dynamics in the CD are often related to soil properties and topography interacting with climate (Miao et al., 2009; Monger & Bestelmeyer, 2006; Peters et al., 2009). For native perennial grasses, soil textural properties are major determinants of the ability of perennial grasses to respond to multi-year precipitation events in grasslands and shrublands (Peters et al., 2012, 2014) and presumably are important to the ability of these grasses to resist invasion by non-native grasses, although this has not been tested.

Non-native grasses have primarily expanded into grasslands and shrublands in the southern parts of the CD within the United States near Big Bend National Park with small, isolated patches occurring throughout the rest of the biome (Barkworth et al., 2003; Correll & Johnston, 1970; Peterson, 2003). The depth to an impenetrable clay layer can influence seedling establishment of *E. lehmanniana* (Cox & Ruyle, 1986). Recent studies have shown that adult plants of *E. lehmanniana* can outcompete established plants of native grasses, although native perennial grasses are better competitors with *E. lehmanniana* seedlings compared with shrubs (Anable et al., 1992; Biedenbender et al., 2003). Thus, the rate and pattern of spread of *E. lehmanniana* is expected to vary across the CD and to depend on interactions among climate, soil properties, and ecosystem type.

Global circulation models predict an average temperature increase of 3°C for the American Southwest (IPCC, 2014). However, there is not a consensus on whether global warming will result in increased or decreased precipitation in this region (Donat et al., 2016; Konapala et al., 2020; Kunkel et al., 1999; Seager et al., 2007). Analyses of observed patterns in rainfall show that precipitation has generally increased over large parts of the CD in recent decades compared with earlier in the 1900s, whereas precipitation has decreased for most of the SD over the same time period (Karl & Knight, 1998). This spatial variability in observed and predicted patterns in precipitation makes predictions of future changes in distributions of non-native species challenging. Studies of future distributions need to account for both increases and decreases in precipitation along with increases in temperature.

Simulation modeling combined with long-term data and geospatial data enables exploration of relationships among a broad range of environmental drivers and invasive species success across a much larger spatial extent than is feasible experimentally (Egli et al., 2019; Grant et al., 1997). This approach is particularly effective when examining constraints on the geographic distribution of an invasive species and predicting changes in its spatial distribution as climate continues to change (Morin & Lechowicz, 2008). Long-term research sites also provide detailed site-based understanding of local ecological processes developed through multi-disciplinary research that can guide broader investigations (D'Antonio & Flory, 2017; Peters et al., 2018). Sites also have an abundance of long-term data that are available for model development and testing of complex processes and principles (Franklin, 1989; Moran et al., 2008). Focusing on a landscape scale enables the identification and comparison of the broader regional relationships constraining invasion.

Our overall objective was to identify the climatic, edaphic, and biotic factors important to recruitment of *E. lehmanniana* in the CD and to apply this information to predict its potential geographic distribution under current and alternative climate scenarios. We focused on recruitment as the process required for *E. lehmanniana* establishment because it involves the developmental processes necessary for successful reproduction. We assumed after plants became established, they can outcompete native plants based on studies in the SD and observations from the CD (Anable et al., 1992). We also assumed that viable seeds of *E. lehmanniana* are produced each year to allow us to focus on seed germination and seedling establishment as the recruitment processes of interest (Cable, 1971). We had three specific objectives: (1) to identify site-scale processes limiting *E. lehmanniana* recruitment in the CD under current climate, (2) to determine factors related to broad-scale patterns of *E. lehmanniana* across the CD under current climate, and (3) to predict future patterns in *E. lehmanniana* recruitment under alternative climate scenarios.

METHODS

General approach

Our approach was to use a well-established simulation model of soil water dynamics (SOILWAT) that generates probabilities of germination and establishment of perennial grasses in drylands (Lauenroth et al., 1994; Minnick & Coffin, 1999; Peters et al., 2010). We developed model parameters for germination and establishment of *E. lehmanniana* based on field and laboratory data from the Santa Rita Experimental Range (SRER) site that was initially invaded by *E. lehmanniana* in 1937

(Cable, 1971). We then tested the model at the Jornada site in the CD by simulating recruitment under current climate for three long-term primary production locations. The spatial distribution of *E. lehmanniana* was estimated by developing regression equations for the simulated probability of establishment using site-based climate and soil data under current climate and alternative climate scenarios. We then mapped the probability of simulated establishment across the Jornada and CD for current and alternative climate scenarios by applying equations to geospatial climate (PRISM) and soil (SSURGO) data.

Study sites

Santa Rita, AZ, USA

The SRER located in southern Arizona, USA (31.8°N, 106.5°W, 884 m asl) experienced a rapid expansion by *E. lehmanniana* during the late 1980s (Anable et al., 1992). The 21,000 ha research site has a mean annual precipitation of 28 cm with two modes (winter and summer) typical of the SD. Average monthly temperatures range from 3°C in January to 34°C in June. Livestock grazing occurs on 90% of the experimental range, and livestock numbers have been intensively managed since 1915 (McClaran, 2002). The current vegetation at SRER is a mix of short trees, shrubs, cacti and other succulents, perennial grasses, and other herbaceous species. Over the last 100 years, mesquite tree abundance has steadily increased across the SRER (McClaran, 2003). Dominant species are *L. tridentata*, *P. velutina*, *and Zinnia acerosa* (McClaran, 2003).

Jornada, NM, USA

The Jornada USDA-LTER site (JRN) located 397 km to the east of the SRER in southern New Mexico, USA, occurs in the northern CD (32.5°N, 106.45°W, 1219 m asl) (Figure 1). The Jornada is a high elevation desert that receives >60% of its average precipitation (24 cm/year) from July to October (Wainwright, 2006). Average monthly temperatures range from means of 6°C in January to 26°C in June. The site is principally dominated by one of three shrubs on different soil-geomorphic locations: *P. glandulosa* (honey mesquite) on sandy uplands, *F. cernua* (tarbush) on lower bajadas, and *L. tridentata* (creosote bush) on upper bajadas. Perennial grasses that historically dominated this landscape are now restricted either to sandy uplands (*Bouteloua eriopoda* [black grama] and *Sporobolus flexuosa* mesa dropseed]) or playas (*Pleuraphis mutica* [tobosa grass]) (Gibbens et al., 2005). Livestock are managed to maintain low-intensity grazing relative to historic practices (Fredrickson et al., 1998). Historically, *E. lehmanniana* has been used as a revegetation species throughout the CD, although with variable success. Revegetation efforts from the 1930s resulted in small patches of this species at the Jornada primarily on sandy uplands dominated by honey mesquite and black grama or on upper bajada locations dominated by creosote bush.

Chihuahuan Desert ecoregion

The CD ecoregion within the United States includes southern New Mexico, western Texas, and parts of southeastern Arizona (Figure 1). Like the Jornada, this region has a mean annual temperature of −2 to 12.1°C and receives 19–69 cm of average annual rainfall primarily occurring during the summer to fall monsoon. Vegetation patterns are comparable to those found on the Jornada where shrublands are typically separated by soil-geomorphic unit (creosote bush, tarbush, and mesquite), and perennial grasslands are found on sandy uplands or playas. Studies of invasive grasses have been primarily conducted in the southern parts of the CD in and near Big Bend National Park where temperatures are the warmest of the region (Young et al., 2013).

Soil water simulation model description

Soil moisture processes and recruitment of *E. lehmanniana* were simulated using a daily time step model parameterized with climate, soil properties, and vegetation structure as input (SOILWAT; Parton, 1978 as modified by Peters et al., 2010). Soil moisture processes (canopy interception, bare soil evaporation, transpiration, and infiltration) are simulated across multiple soil layers using daily (temperature and precipitation) and monthly parameters (wind speed, relative humidity, cloud cover, aboveground biomass, and litter). Static parameters in the model are soil texture (%sand, %silt, and %clay), %rocks by volume, evaporation potential, and root distribution by depth. Deep drainage is not common in these arid systems and was not simulated. Model outputs include estimates of water content by depth and probability of *E. lehmanniana* seed germination and seedling establishment through time. Recruitment success of *E. lehmanniana* for each year is determined by comparing daily soil water content by depth with germination (0–5 cm depth) and establishment criteria (0–30 cm). This approach has performed well in accurately simulating soil water content (Lauenroth et al., 1994) and recruitment of native perennial grasses, *B. eriopoda* (black grama) and *B. gracilis* (blue grama), in arid grasslands in the United States (Minnick & Coffin, 1999; Peters et al., 2010).

Model parameterization

The SOILWAT parameterization to simulate soil water processes has been described previously for the Jornada (Peters et al., 2010). Here, we focus on the details of the parameters needed to simulate germination and establishment of *E. lehmanniana*. Soil and climate criteria for *E. lehmanniana* were estimated using field and laboratory data from the SRER. We used a two-step process to parameterize SOILWAT that integrated published data to establish a range of values that were then analyzed using a probabilistic approach to optimize the input value.

First, data from laboratory and field experiments were used to define germination and establishment criteria for *E. lehmanniana* in the model (Table 1). Laboratory experimentation suggests that germination of *E. lehmanniana* in the surface soil begins at −1.0 MPa (Adams, 1997). In the absence of published data, germination moisture requirements of lower layers and establishment requirements of top and lower layers were assumed to be the same as Minnick and Coffin (1999) for *B. eriopoda* in the top and lower soil layers ($n = 10$). We assumed five consecutive wet days were needed for germination based on data from Adams (1997). We assumed the minimum temperature (20°C) and maximum temperature (40°C) for germination and establishment were based on studies by Cox (1984) and Roundy et al. (1992).

Greenhouse experiments of *E. lehmanniana* were used to determine the maximum number of days that the seminal root can survive following germination before another rain event (Cox, 1984; Frasier et al., 1985). Laboratory experiments showed that seminal roots exhibit 100% mortality after 7 days without rainfall, and survival is decreased to less than 1% after 0.5–3 days of dehydration (Adams, 1997; Frasier et al., 1987). For this analysis, we assumed the maximum number of days between germination and establishment that seminal roots can be dry was 4 days.

Similar to previous studies of perennial grasses, we assumed successful establishment of *E. lehmanniana* seedlings when adventitious roots develop. However, we are not aware of research on the development of adventitious roots of *E. lehmanniana* leading to seedling establishment. Thus, we assumed the same minimum (20) and maximum (50) number of days after germination for a second precipitation event to initiate adventitious roots based on values for *B. eriopoda* (Minnick & Coffin, 1999).

Second, germination and establishment parameters values were optimized for the CD using a simulated annealing algorithm (Table 1). We used >80,000 runs of SOILWAT spanning a large search of parameter space to identify the germination and establishment parameters that corresponded with field data (Peters & Huenneke, 2019). We also included a parameter for soils with high clay content that can impede vertical root growth of *E. lehmanniana* based on field observations (Cox et al., 1983, 1988; Cox & Ruyle, 1986). To integrate this soil property into SOILWAT, we assumed for any event where the criteria for establishment were met based on soil water conditions, the probability of seedling emergence is a function of clay content:

$$\text{Probability of emergence} = \frac{0.024+1}{1+0.025^{X/6.5}}$$

where X equals clay content.

TABLE 1 Parameters used to run soil water model (SOILWAT) and estimate germination and establishment of *Eragrostis lehmanniana*

Parameter	Explanation	Value
bar1	Top layer requirement for germination (bar)	10
bar2	Lower layer requirement for germination (bar)	10
bar3	Top layer requirement for establishment (bar)	10
bar4	Lower layer requirement for establishment (bar)	10
lyrestab	Number of layers in the lower soil layer (*N*)	3
maxint	Maximum number of days after germination for initiation of adventitious roots (No. days)	50
minint	Minimum number of days after germination for initiation of adventitious roots (No. days)	20
nestabdy	Number of wet days needed for establishment (No. days)	3
ngermdy	Number of wet days needed for germination (No. days)	5
numwait	Maximum number of days between germination and establishment that roots can be dry (No. days)	4
tmpmax	Maximum temperature at which germination and establishment can occur (in degree Celsius)	40
tmpmin	Lowest temperature at which germination and establishment can occur (in degree Celsius)	20

Eragrostis lehmanniana recruitment verification

The model was tested at two sites: the SRER in the CD where *E. lehmanniana* has occurred at high cover in some locations since the 1950s (Cable, 1971), and at the Jornada in the CD where cover of this species is typically low, and highly variable in time and space. We first tested the model at the SRER where simulations were conducted to estimate *E. lehmanniana* establishment probabilities for the years 1976 to 2009 by parameterizing SOILWAT using daily precipitation and temperature, and monthly climate variables using data from National Oceanic and Atmospheric Administration (NOAA), National Centers for Environmental Information, and the Global Historical Climatology Network Daily Database (Climate Data Online: https://www.ncei.noaa.gov/products/land-based-station/global-historical-climatology-network-daily). Soil properties for the site were obtained from Breckenfeld and Robinett (1998). Field estimates of cover and frequency of *E. lehmanniana* from 1990 to 2012 (Biedenbender et al., 2003; McClaran, 2002) showed a good correspondence with simulated establishment events. We then used the annealing algorithm to modify the recruitment parameters for the CD and used the climate and soil input parameters from Peters et al. (2010) to simulate *E. lehmanniana* germination and establishment through time at two long-term research sites at the Jornada (G-IBPE and G-SUMM) from 1990 to 2012 (e.g., Peters et al., 2014) to verify model results.

Experimental simulations

Objective 1: To identify site-scale processes influencing *E. lehmanniana* recruitment under current climate

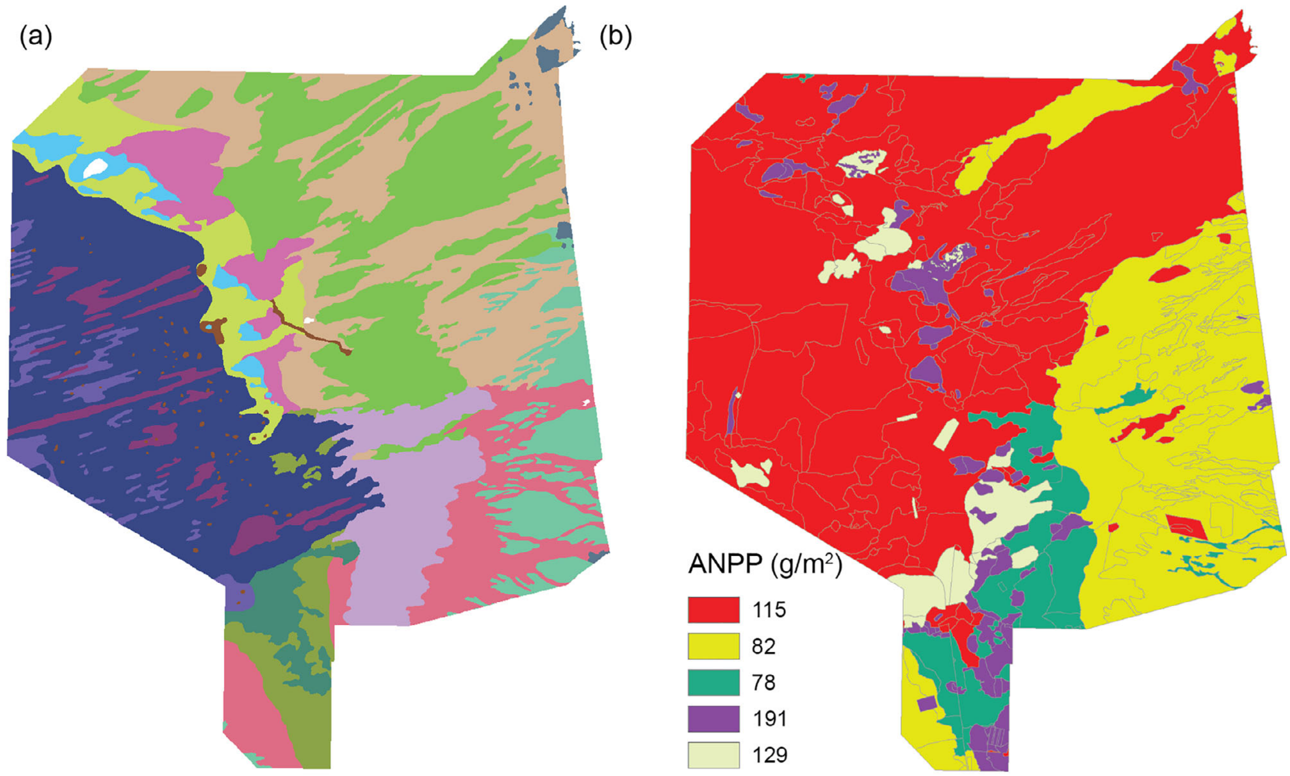
The simulated probabilities of *E. lehmanniana* recruitment for the current climate regime were conducted for 75 unique combinations of soil based on landform ($n = 15$) and vegetation types with different mean annual net primary production ($n = 5$) at the Jornada research site (Figure 2). Current patches of *E. lehmanniana* were georeferenced to determine how well patterns in establishment represent long-term patch dynamics of this species.

Objective 2: To determine factors related to patterns of *E. lehmanniana* across the CD under current climate

To construct a continuous surface of spatially explicit estimates of simulated probabilities of *E. lehmanniana* recruitment, we used a three-step process. First, we used SOILWAT to estimate the probabilities of establishment for 12 standard soil types (silt, silty loam, sandy loam, loam, loamy sand, sand, sand clay loam, silty clay loam, clay loam, sandy clay, silty clay, and clay) at 57 meteorological stations located across the CD. Soil class was based on texture (%sand, %silt, and %clay) by either combining or linearly extrapolating SSURGO values across horizons (USDA NRCS; https://gdg.sc.egov.usda.gov/). Climate was represented by 30 years (1981–2010) of NOAA daily precipitation, and minimum and maximum temperature from each station (Appendix S1: Table S1, Figure 3). Missing climate data were estimated using a multivariable Markov weather model and a gap-filling procedure based on the daily Markov chain for precipitation and bivariate normal random variable processing from weekly bi-covariance matrix of daily min and max temperature.

Second, we developed logistic regression models to estimate the simulated probability of *E. lehmanniana* seedling establishment for each of the 12 soil and 52 climate variables. A total of 13 variables per category (12 monthly means plus one annual mean) × four categories of variables (precipitation; maximum, mean, and minimum temperature) were considered for each model. Interannual variability was minimized by calculating monthly and annual 30-year mean precipitation and minimum and maximum temperature from daily data. To identify collinearity among explanatory variables and to reduce the number of explanatory variables, we used Pearson's correlation analysis and a principal component analysis with 36 climate variables as input (12 monthly mean precipitation, 12 monthly maximum temperature, and 12 monthly minimum temperature). This analysis resulted in the selection of five uncorrelated variables ($|R| < 0.7$) in the following logistic regression analysis: (1) minimum temperature in nonsummer (January–June, September–December), (2) maximum temperature of nonsummer (January–May, September–November), (3) precipitation during spring and fall (April–June, September–October), (4) precipitation during winter (January–March, November–December), and (5) precipitation during summer (July–August).

Third, we used the logistic regression models to create a continuous surface of spatial estimates of the probability of seedling establishment across the CD using PRISM interpolated climate surfaces (PRISM Climate Group, 2004) (800-m^2 30-year current data from 1981 to 2010) and gridded SSURGO soil data in the logistic models. The degree of similarity between daily meteorological station data and PRISM data was assessed using Pearson's correlation analysis. Pearson's correlation of mean annual climate (aggregated from daily data) and PRISM data were very high: 0.99 for precipitation, 0.97 for maximum temperature, 0.94 for mean temperature, and 0.95 for minimum temperature.



Pedon	Geomorphic unit	Soil texture
01N0519	Basin Floor Sand Sheet	Loamy Sand
01N0542	Basin Floor Sand Sheet	Loam
04N0946	Piedmont Slope (Bajada)	Sandy Clay Loam
04N0947	Basin Floor Sand Sheet	Clay Loam
04N0950	Basin Floor Sand Sheet	Loamy Sand
04N0953	Piedmont Slope (Bajada)	Loamy Sand
63LF001	Basin Floor Sand Sheet	Loamy Sand
63LF002	Piedmont Slope Sand Sheet	Loamy Sand
63LF003	Transition Zone	Clay Loam
63LF004	Piedmont Slope Sand Sheet	Loamy Sand
90P0496	Basin Floor Sand Sheet	Loamy Sand
90P0498	Basin Floor Sand Sheet	Loamy Sand
97P0155	Basin Floor Sand Sheet	Sandy Loam
97P0162	Basin Floor Sand Sheet	Sand
S70NMex-7-1	Mountain & Hills	Sandy Loam

FIGURE 2 Distribution of the Jornada's (a) 1963 pedons, the corresponding geomorphic unit, and dominant soil texture class (Monger et al., 2006); and (b) mean annual production from 1989 to 2010 by ecosystem type (Peters et al., 2010; Peters & Huenneke, 2019): mesquite (red), creosote bush (yellow), tarbush (turquoise), lowland grasses (violet), and upland grasses (beige)

Objective 3: To predict future patterns in *E. lehmanniana* recruitment under alternative climate scenarios

Jornada USDA-LTER site

We simulated effects of climate change by increasing temperature by 2.4°C above present-day maximum and minimum temperature values. Precipitation was modified by either increasing or decreasing daily total rainfall by 25%. These values were selected to represent natural variation in rainfall at the Jornada where 24.2% of the years since 1915 have exceeded 25% of the long-term mean, and 26.3% of the years have been less than 25% of the long-term mean. This approach enabled evaluation of

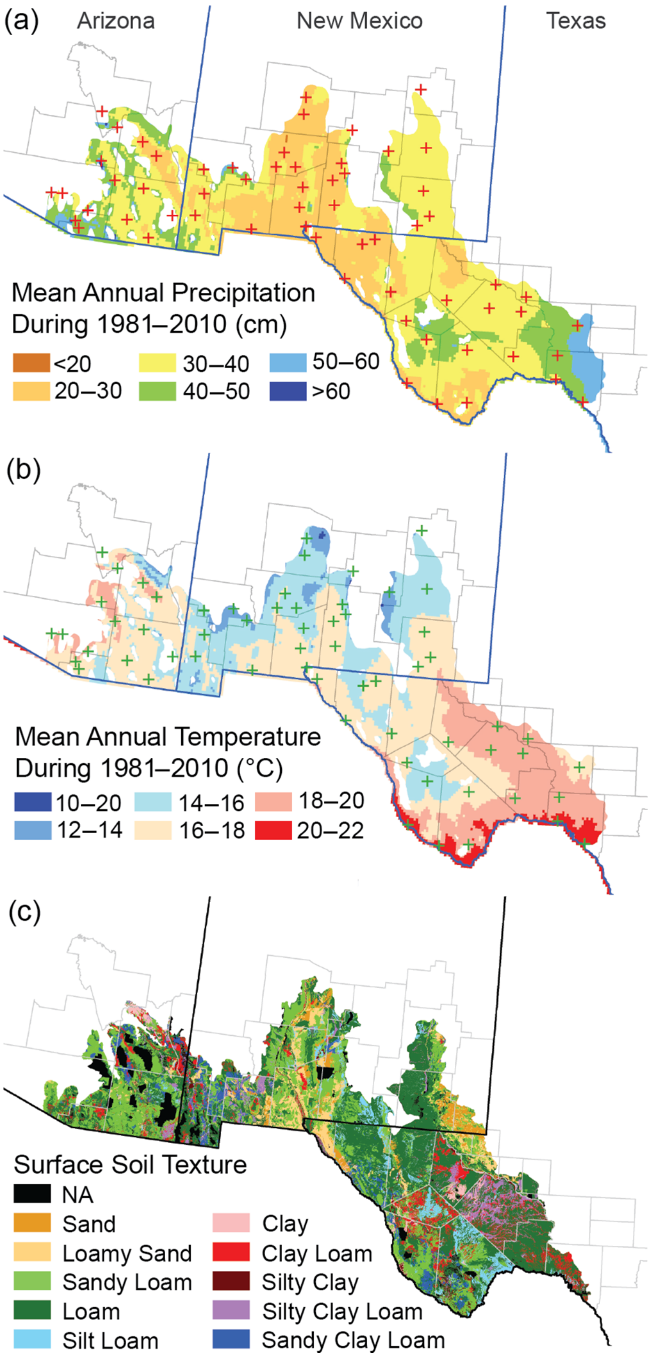


FIGURE 3 Soil water model (SOILWAT) input parameters for the northern Chihuahuan Desert in the United States at each of the 57 meteorological stations (+) (a) mean annual precipitation, (b) mean annual temperature, and (c) 11 standard soil texture classes

directional changes in rainfall totals instead of changes in intensity and frequency. For further explanation, see Peters et al. (2010).

Chihuahuan Desert

We simulated how changes in climate may impact *E. lehmanniana* recruitment across the CD by uniformly varying the climate parameters in the logistic regression model. Temperature was increased by 2.5°C, and precipitation was varied by 90%, 95%, 105%, and 110% of current observed totals. These modifications represent modest temperature and precipitation change projections for the reference period (2077–2099) for the southwest region under the low-emission scenarios (Cayan et al., 2013). We then reestimated establishment under novel climates following the same approach used to simulate establishment under current climate. Differences in simulated probability of establishment were then compared to evaluate changes resulting from alternative climate scenarios. Comparisons of germination and establishment estimates were conducted using estimated plant available water from the SPAW model (Saxton et al., 2006) for both current and alternative climate scenarios.

RESULTS

Objective 1: To identify site-scale factors related to *E. lehmanniana* recruitment under current climate

Simulated *E. lehmanniana* probabilities of establishment were not uniform across the Jornada landscape under current climatic conditions (Figure 4). These patterns in establishment were not simply related to ecosystem or soil type (Figure 2). Vegetation production and soil texture interacted to affect water availability to seedlings that led to complex patterns in simulated establishment across the landscape. Fine-textured soils, such as erosional scarplets, arcuate sand ridges, alluvial plains, fan piedmonts, and playas with lower sand and higher silt content, had higher probabilities of establishment compared with sandy soils with lower plant available water and high losses of water to evaporation (Snyder et al., 2006). Higher establishment probabilities also occurred on high productivity areas dominated by upland grasslands or in playas with lowland grasses. The lowest probabilities (<0.06) were found on alluvial fan remnants on gravelly upper bajadas dominated by low productivity creosote bush or wind-scoured eolian sand sheets on the sandy basin floor dominated by mesquite shrublands (0.07–0.12).

Higher simulated probabilities of establishment were found where current patches of *E. lehmanniana* occur compared to areas without this species (Figure 4). These patches represent known suitable habitats for recruitment and growth and are not all possible locations where *E. lehmanniana* can occur. This species was seeded unevenly across the Jornada landscape beginning in the late 1930s for grass revegetation efforts (Humphrey, 1994). The locations may have undergone patch dynamics (expansion and losses of plants) through time that are not captured by this map.

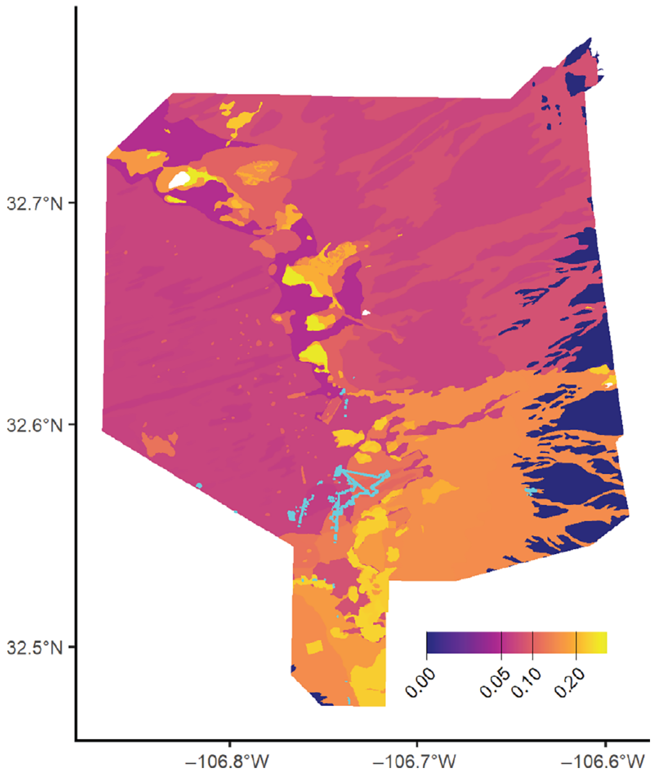


FIGURE 4 Simulated probability of establishment and the perimeter of current patches of *Eragrostis lehmanniana* (light blue) on the Jornada research site. Linear features in current *E. lehmanniana* patches correspond to roads

Objective 2: To determine factors related to patterns of *E. lehmanniana* across the CD under current climate

Across the CD, simulated probabilities of establishment increased with silt and sand content, monthly minimum temperature, precipitation of winter, spring, and fall, but decreased with monthly maximum temperature and summer drought (Table 2). These relationships led to nonuniform patterns in germination and establishment across the CD. These simulated patterns in recruitment are consistent with observed patterns in this species where low probabilities were found for most of southern New Mexico and western Texas in locations where this species rarely occurs, but there were localized areas with high probabilities (>0.8) (e.g., north of Big Bend, Texas) where cover of *E. lehmanniana* can be high (Figure 5).

Objective 3: To predict future patterns in *E. lehmanniana* recruitment under alternative climate scenarios

Jornada USDA-LTER site

Changes in establishment at the Jornada site resulting from modifications to precipitation and temperature were not uniform on all landforms (Figure 6). In general, changes in temperature that accompanied changes in precipitation (e.g., Figure 6c,d) had larger effects on

TABLE 2 Statistics of logistic regression Logit (simulated probability of *Eragrostis lehmanniana* seedling establishment) = *f*(soil texture, climate) for current climate and alternative climate scenarios

	Climate scenario[a]					
Regression statistic	**TcurP100**	**TcurP090**	**TcurP110**	**TincP100**	**TincP090**	**TincP110**
Y-intercept	−10.15	−10.12	−10.24	−10.49	−10.41	−10.59
Slope_%silt	0.11	0.10	0.11	0.12	0.11	0.12
Slope_%sand	0.15	0.14	0.15	0.15	0.15	0.16
Slope_%sand × %sand	−0.0007	−0.0006	−0.0007	−0.0007	−0.0007	−0.0007
Slope_climate PC1[b]	−0.18	−0.16	−0.18	−0.30	−0.29	−0.31
Slope_climate PC2	0.34	0.35	0.33	0.18	0.19	0.16
Slope_climate PC3	0.44	0.47	0.42	0.53	0.56	0.50
Slope_climate PC4	0.25	0.25	0.26	0.33	0.33	0.33
Slope_climate PC5	0.28	0.28	0.28	0.35	0.36	0.34
Generalized R^2	0.91	0.91	0.91	0.93	0.93	0.93

Note: Simulated probability of seedling establishment results from soil water model (SOILWAT) simulation with input of climate data at 43 meteorological stations in the Chihuahuan Desert and 12 standard soil texture types ($N = 43 \times 12 = 516$ for each climate scenario).

[a]Tcur: current temperature (1981–2010); Tinc: daily temperature increased by 2.5°C; P100: 100% of current daily precipitation (1981–2010); P090: 90% of current daily precipitation; P110: 110% of current daily precipitation.

[b]Climate PC1: First principal component of climate variables, interpretation: maximum temperature and dry August; climate PC2: minimum temperature; climate PC3: spring and fall precipitation; climate PC4: winter precipitation; climate PC5: wet July and cool July–August.

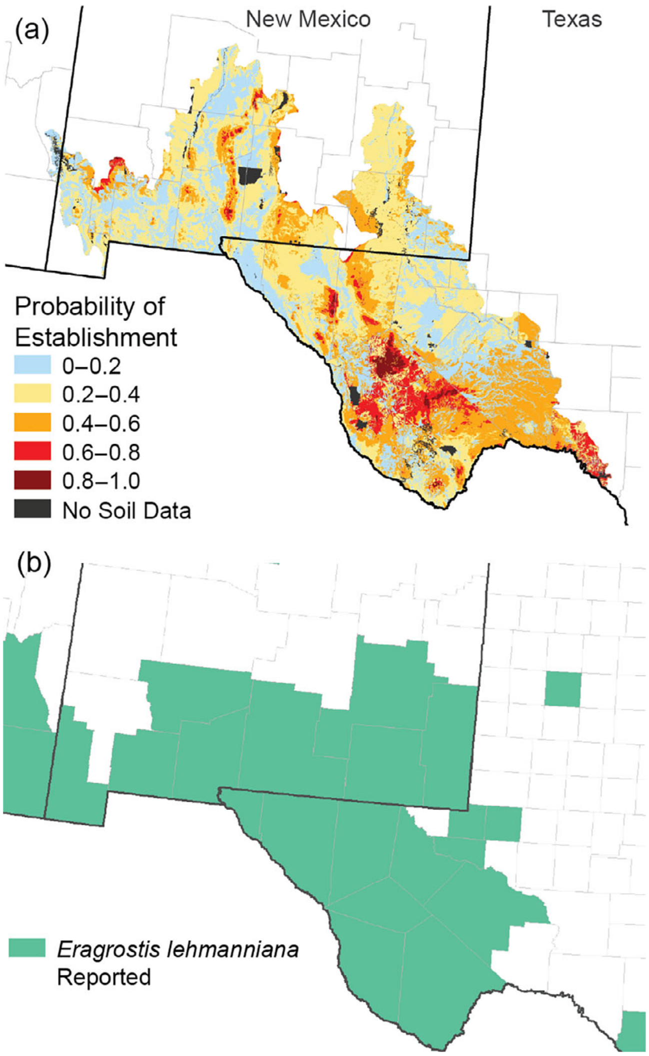


FIGURE 5 Map of (a) the probability of *Eragrostis lehmanniana* seedling establishment for the northern Chihuahuan Desert in the United States under current climate and (b) counties which have reported at least one occurrence of *E. lehmanniana* shown in green (USDA NRCS, 2021), which is the most detailed distribution map available during the time of this analysis

establishment compared with increases in precipitation alone (e.g., Figure 6a,b). Patterns in establishment were complex when both changes in climate and soil properties were considered. The largest percentage increases (and decreases) in establishment (nearly 50%) occurred following increases (or decreases) in precipitation and increases in temperature on the silty loam soils of the lower bajada and on playas (Figure 6c,d). Establishment on these geomorphic units also responded to increases or decreases in precipitation alone (Figure 6a,b). Sandy soils were least affected by changes in precipitation, either with or without changes in temperature.

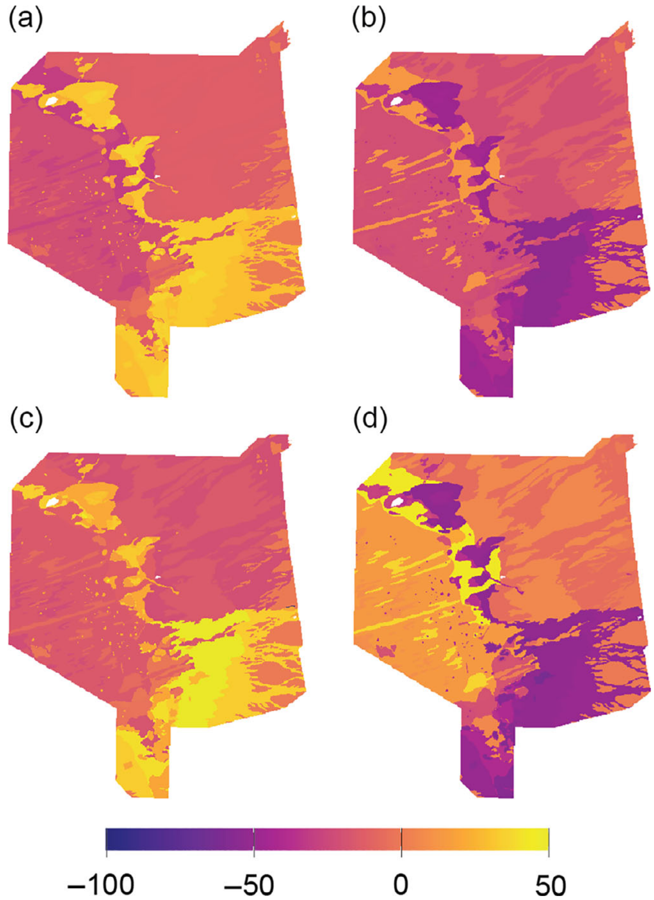


FIGURE 6 Changes in simulated probability of establishment for *Eragrostis lehmanniana* on Jornada research site ([(modified climate – current climate)/current climate] × 100): (a) 25% increase in precipitation and (b) 25% decrease in precipitation with no change in temperature; (c) 25% increase in precipitation and (d) 25% decrease in precipitation with 2.5°C increase in temperature

Chihuahuan Desert

In general, changes in simulated probability of seedling establishment with changes in climate were heterogeneous across the CD (Figure 7). Areas with relatively higher probabilities of establishment under current climate (e.g., the southern and northern borders of the CD; Figure 5) experienced the greatest increases when the climate changed, in particular when both precipitation and temperature increased (Figure 7e). An increase in temperature of 2.5°C without changes in precipitation resulted in increases in establishment for large parts of the CD (Figure 7c); adding a decrease in precipitation to an increase in temperature resulted in smaller increases or decreases for most of the area (Figure 7d). Changes in precipitation without changes in temperature had small effects on establishment throughout the CD (Figure 7a,b).

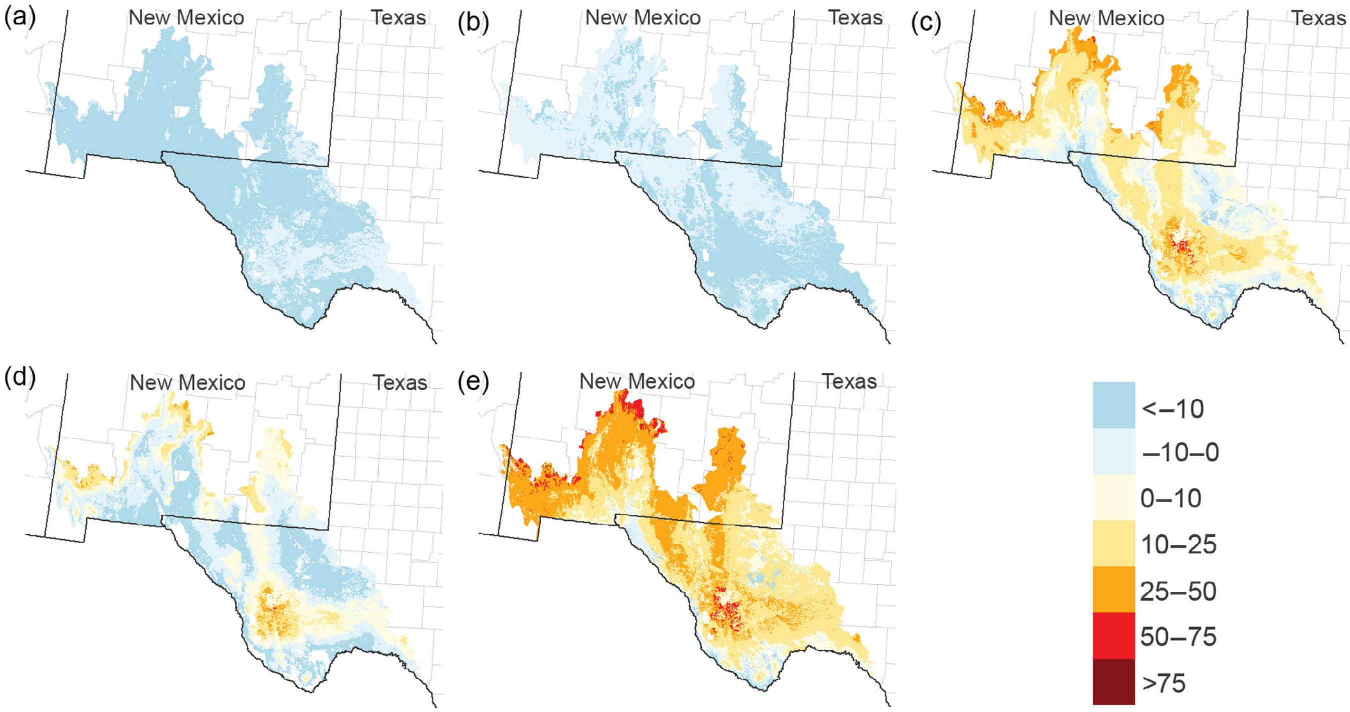


FIGURE 7 Maps of percentage change simulated probability of *Eragrostis lehmanniana* seedling establishment in the northern Chihuahuan Desert in the United States calculated as ([modified climate estimate − current climate estimates]/current climate estimates) × 100 for: (a) current temperature and a 10% decrease in precipitation, (b) current temperature and a 10% increase in precipitation, (c) 2.5°C increase in temperature and current precipitation levels, (d) 2.5°C increase in temperature and a 10% decrease in precipitation, and (e) 2.5°C increase in temperature and a 10% increase in precipitation

Complex relationships were found between changes in climate when considering the 11 soil texture classes (Figure 8). For silt, loam, and sandy soils, simulated probability of establishment increased (decreased) as precipitation increased (decreased), reflected by the positive slopes of the lines; soils high in clay content had little change in establishment as climate changed (Figure 8). Additionally, simulated probabilities were higher when an increase in daily temperature by 2.5°C was combined with a change in precipitation as reflected by the higher *Y*-intercepts (Figure 8).

For sandy and silty soils, simulated probabilities were higher under increased temperature than under current temperature for the same precipitation amount, and the effects of 2.5°C increased temperature resulted in greater establishment than the effects of 10% increased precipitation (Figure 9a). Simulated probabilities for sandy and silty soils under increased precipitation were positively associated with simulated plant available water from the SOILWAT model for all precipitation scenarios ($R^2 = 0.8706$, $R^2 = 0.8905$, $R^2 = 0.859$, for 90%, current, and 110% current precipitation, respectively), and there was no interaction between temperature and precipitation (Figure 9b).

DISCUSSION

Eragrostis lehmanniana (Lehman lovegrass) represents a class of grasses endemic to South Africa that were originally introduced to the western United States in the early to mid-1900s for livestock forage and erosion control (USDA Forest Service, 2017). Many of these species, including buffel grass (*C. ciliaris* and *Pennisetum ciliare*), kleingrass (*Panicum coloratum*), and two species of lovegrass (*E. lehmanniana* [Lehman lovegrass] and *E. curvula* [weeping lovegrass]) are invasive throughout the southwestern United States. Most of these invasive grasses are listed as noxious weeds in parts of the Sonoran and Chihuahuan Deserts because of their impacts on the local biodiversity, wildfire regime, and biogeochemical cycling (USDA, 2018; USDA Forest Service, 2017). Changes in climate are expected to influence the distribution of these introduced species beyond their current range (Hellmann et al., 2008). For *E. lehmanniana*, we found that its current regional distribution in the Chihuahuan Desert and local distribution at the Jornada USDA-LTER site correspond with simulated probability of establishment based on processes governed by precipitation, temperature, and soil texture.

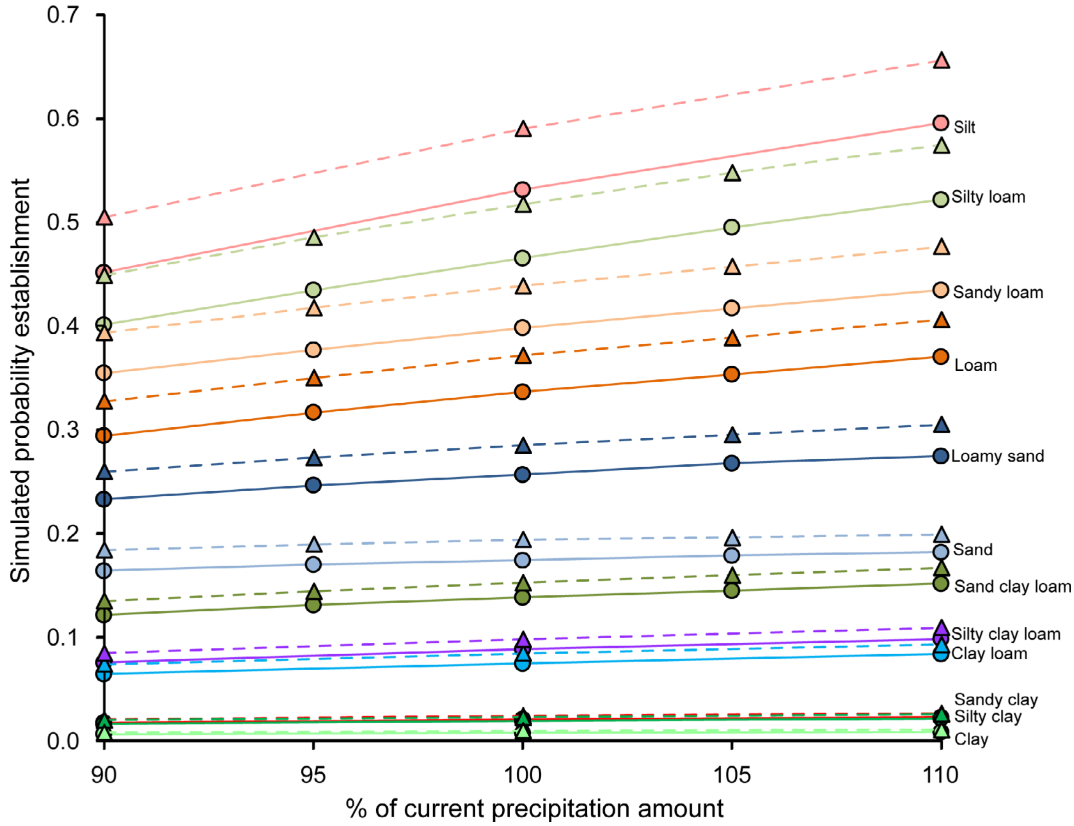


FIGURE 8 Soil water model (SOILWAT) simulated probability of *Eragrostis lehmanniana* seedling establishment (mean, $N = 43$) by soil texture type and climate scenario (current temperature represented with solid lines and circles and 2.5°C temperature increase represented with dashed lines and deltas), with the subroutine of soil barrier for seedling establishment. Current daily climate data during 1981–2010 at 43 meteorological stations in the northern Chihuahuan Desert in the United States and 12 standard soil texture types were the main input to the SOILWAT

At the landscape scale, *E. lehmanniana* establishment is driven by soil physical properties affecting plant available water that can be overwhelmed by climate. Complex relationships between production, soil, and climate interact to affect plant available water (Peters et al., 2010) and result in relatively low establishment estimates across the JRN under current environmental conditions. Soils with higher silt content and increased production had higher probabilities of *E. lehmanniana* recruitment that threaten the few remaining areas still dominated by upland grasses. Across the CD, simulated *E. lehmanniana* success was highest in the warmest parts of the CD with moderate amounts of rainfall. While current temperature and precipitation levels are not conducive to rapid invasion for the JRN or CD region, increases in precipitation and temperature are likely to result in increased establishment probabilities, especially on the lower bajada landscape location of the JRN and southwestern Texas, and would be expected to allow the expansion of this invasive species.

Land management, such as seeding and other range improvement treatments, may also impact the distribution of this species; establishment probabilities were largest on lower bajada locations on fine loamy soils where this species does not occur. Ubiquitous seed dispersal is assumed by our model; however, the uneven human dispersal of *E. lehmanniana* may have led to established plants outside of the optimal climatic range (Bradley et al., 2015) and resulted in linear patch features (e.g., when seeded along roads). This mechanism can explain the relatively slow invasion of *E. lehmanniana* across the JRN when compared to the SRER. The importance of incorporating site-based knowledge is underscored in our approach where broad-scale analyses that omit site-level information may be confounded by the broad environmental distributions of non-native invasives that are not solely due to their niche traits. This approach also illustrates the risk posed by long-term changes to the climate regime that can release processes limiting invasion.

Our study shows that the future distribution of *E. lehmanniana* in the Chihuahuan Desert will depend on the amount and direction of changes in annual precipitation and temperature. Increases in temperature and precipitation are likely to result in increased invasible area

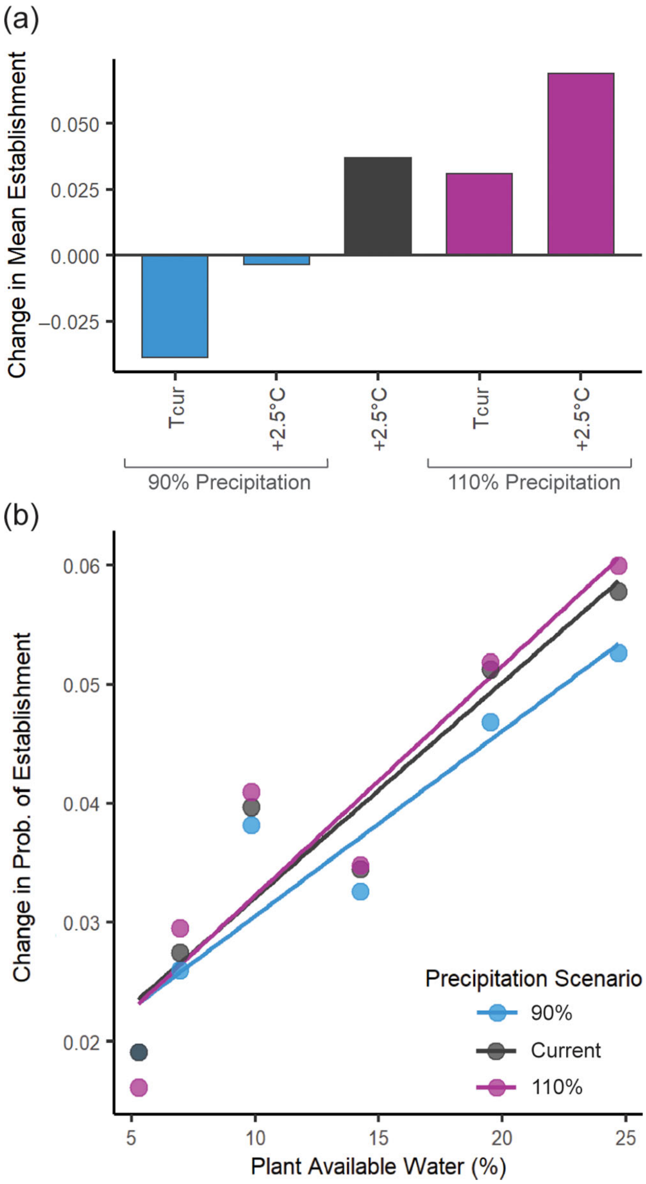


FIGURE 9 (a) The change in the northern Chihuahuan Desert mean simulated probability of *Eragrostis lehmanniana* seedling establishment from current climate estimates for each precipitation scenario (90%, current, and 110%) under the current temperature (Tcur) and increased temperature (+2.5°C) scenarios. (b) The linear relationship between the change in the simulated probability of *Eragrostis lehmanniana* seedling establishment due to +2.5°C increase in temperature and plant available water (%) of each northern Chihuahuan Desert soil class (fine-textured soils that deterred radicle development excluded). The linear relationship for the 90% precipitation scenario is $y = 0.0015531 \times$ plant available water (PAW) $+ 0.0150288$, $R^2 = 0.8706$, and p value $= 0.006571$; for current precipitation is $y = 0.0018063 \times \text{PAW} + 0.0140333$, $R^2 = 0.8905$, and p value $= 0.00467$; and for 110% of current precipitation is $y = 0.0019261 \times \text{PAW} + 0.0130222$, $R^2 = 0.859$, and p value $= 0.007831$

and establishment of *E. lehmanniana* across the Chihuahuan Desert. Silty and loamy soils will be especially vulnerable. Fine-textured soils will be least responsive to *E. lehmanniana* invasion with climate change. This uncertainty in the projected distribution adds one more challenge to land management of this invasive grass under climate change. Our study shows that the distribution of *E. lehmanniana* in the Chihuahuan Desert will depend on the amount and direction of changes in future temperature and precipitation. This uncertainty in the projected distribution adds one more challenge to land management of this invasive grass under climate change.

CONCLUSIONS

Our approach integrates site-specific understanding of process-based relationships with a spatially explicit simulation model to identify landscape-scale relationships and generate regional prediction of the potential distribution of a non-native invasive species. Our results show that multiple scales of drivers can influence non-native invasion. For example, fine-scale soil moisture processes facilitating germination and establishment can be overwhelmed by climate. This approach enables assessment of the relative importance of drivers and can be used to identify broad environmental relationships, inform land managers, and evaluate effectiveness of board-scale biological control strategies.

The integration of detailed long-term data offers site-based detail on ecosystem processes driving the current distribution of Lehmann's lovegrass from the SRER and JER. This lends itself to robust assessments and increased confidence in the accuracy and reproducibility of our findings (Franklin, 1989). The fine level of understanding developed through long-term, and often multidisciplinary, research provides a strong foundation for extrapolating to the regional extent and illustrating how novel environmental conditions influence invasion success for *E. lehmanniana*.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Burruss, 2021) are available from Zenodo: https://doi.org/10.5281/zenodo.5750300.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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