

Positive feedback between microclimate and shrub encroachment in the northern Chihuahuan desert

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Abstract. Woody plant encroachment is affecting vegetation composition in arid grasslands worldwide and has been associated with a number of environmental drivers and feedbacks. It has been argued that the relatively abrupt character (both in space and in time) of grassland-to-shrubland transitions observed in many drylands around the world might result from positive feedbacks in the underlying ecosystem dynamics. In the case of the Chihuahuan Desert, we show that one such feedback could emerge from interactions between vegetation and microclimate conditions. Shrub establishment modifies surface energy fluxes, causing an increase in nighttime air temperature, particularly during wintertime. The resulting change in winter air temperature regime is important because the northern limit of the dominant shrub in the northern Chihuahuan Desert, *Larrea tridentata*, presently occurs where minimum temperatures are sufficiently low to be a potential source of mortality. Using freezing responses from published studies in combination with observed temperature records, we predict that a small warming can yield meaningful changes in plant function and survival. Moreover, we also suggest that the effect of the change in air temperature on vegetation depends on whether plants experience drought during winter. Thus, in the Chihuahuan region a positive feedback exists between shrub encroachment and changes in microclimate conditions, with implications for the response of this ecosystem to regional changes in temperature and precipitation.

Key words: Chihuahuan Desert; feedbacks; microclimate; shrub encroachment; state shift; warming.

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INTRODUCTION

Shrub encroachment is contributing to major changes in vegetation cover in many arid and semiarid grasslands around the world, including Africa, North and South America, and Australia (van Auken 2000, Knapp et al. 2008). In the southwestern USA, for example, the (native) creosote bush (*Larrea tridentata*) has been replac-

ing the native C₄ grasses of the Chihuahuan Desert (e.g., Buffington and Herbel 1965). These changes in land cover have “undesirable” effects, including increased erosion, decreased rangeland productivity, and loss of other ecosystem services. Major changes in land cover are also known for their ability to modify the regional climate, as reported in the case of tropical deforestation, ecosystem succession, and desertification (e.g.,

Bonan 2002). The climatic implications of woody plant encroachment in arid grasslands, however, remains poorly investigated (Beltran-Przekurat et al. 2008) and it has seldom been recognized as one of the drivers of the shift from grass to shrub dominance (He et al. 2010). Mechanisms commonly invoked to explain these regional shifts in plant community composition include overgrazing, fire suppression, atmospheric carbon dioxide enrichment, nitrogen deposition, and regional climate change (e.g., van Auken 2000). Due to its relatively abrupt character, the ensuing land cover change has often been associated with a state shift in an ecosystem known to exhibit alternative stable states (Westoby et al. 1989). Thus, grass and shrub dominance would both be stable configurations of the landscape. Changes in environmental conditions or disturbance regime would cause an abrupt and highly irreversible shift to the shrubland state (Walker and Noy-Meir 1982, Westoby et al. 1989, Anderies et al. 2002, van Langevelde et al. 2003, Okin et al. 2009).

Bistable dynamics often emerge as an effect of positive feedbacks between ecosystems and their external drivers, including disturbance and climate forcing (e.g., Wilson and Agnew 1992). Feedbacks between fires and vegetation dynamics (Anderies et al. 2002, D'Odorico et al. 2006) or between soil erosion and vegetation cover (Schlesinger et al. 1990, Okin et al. 2009) are often invoked to explain the state shift from grassland to shrubland. Both of these feedbacks are plausibly involved in the transition from grass to shrub cover and, to date, it has not been possible to conclusively identify the dominant mechanism responsible for favoring and sustaining shrub encroachment in North American deserts.

Here, we propose that this dynamic change in plant community composition modifies the microclimate with the net result of increasing minimum nighttime air temperature, thereby favoring the survival and growth of shrubs at the expense of grasses. In fact, as a consequence of the shift in plant dominance, structural land surface changes occur that have the potential to influence microclimatic conditions whose effects further drive and sustain the change in vegetation cover. Vegetation shifts affect surface albedo and emissivity, leaf area, surface aerodynamic

characteristics, root depth, and soil water balance (Asner and Heidebrecht 2005, Beltran-Przekurat et al. 2008). These changes can also alter surface heat fluxes (Dugas et al. 1995) and longwave radiation, with possible feedbacks to the change in vegetation cover (e.g., Bonan 2002).

We propose that shrub encroachment in Chihuahuan Desert grasslands modifies microclimatic conditions, initiating a positive feedback loop that reinforces the survival of shrubs (Fig. 1) by increasing bare soil area (Grover and Musick 1990, Huenneke et al. 2002). The mechanism behind the change in microclimate is revealed by differences in vegetative cover with 50–60% cover in grass-dominated vegetation, roughly 25% cover in shrub-dominated areas, and large patches of bare soil around shrubs in the ecotone between grassland and shrubland (Bhark and Small 2003, Pockman and Small 2010). During the day, the large areas of bare soil in shrubland absorb greater amounts of solar radiation, which is transformed into thermal energy and stored in the soil. Therefore, at night shrublands experience greater transfer of thermal energy and irradiance from the soil to the overlying atmosphere than the adjacent grasslands resulting in higher nighttime, near-surface air temperature over the shrubland (He et al. 2010). Because the establishment and survival of *Larrea tridentata* (creosote bush), a dominant native shrub species in the southwestern U.S.A., is strongly influenced by cold wintertime conditions (Pockman and Sperry 1997; Medeiros and Pockman, *in press*), the nocturnal warming associated with the shift to shrub dominance has a positive feedback on shrub encroachment. In this paper we test the hypothesis that shrub establishment creates conditions that facilitate continuing survival of *Larrea tridentata* by modifying the local microclimate and effectively reducing exposure to potentially lethal minimum air temperatures that occur in nearby grass-dominated sites. To this end, we analyzed measurements of near surface air temperatures taken in shrub and grass dominated areas in the Northern Chihuahuan Desert. To assess the scale at which vegetative cover is able to induce a detectable change in wintertime temperatures in this region, we considered temperature data collected at patch, landscape and sub-regional scales.

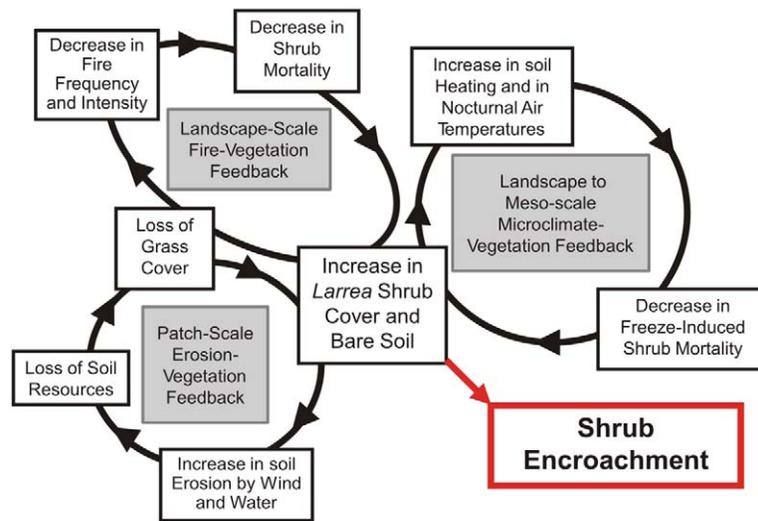


Fig. 1. Positive feedbacks contributing to shrub encroachment at different scales. This study provides evidence for the feedback loop between shrub encroachment and microclimate in the northern Chihuahuan Desert.

METHODS

Field measurements were conducted at the Sevilleta National Wildlife Refuge (SNWR) in the northern Chihuahuan Desert, New Mexico (34°22' N, 106°4' W, elevation of 1610 m above sea level). Average annual precipitation is 250 mm, about 60% of which occurs during the monsoon season from July through September (Gosz et al. 1995, Pennington and Collins 2007). Average annual temperature is 13.2°C (average daily temperature is 1.6°C in January and 25.1°C in July). Mean daily maximum/minimum temperatures from 1999 to 2007 varied from 34/14°C in summer to 10/−7°C in winter. Located in the Rio Grande Valley approximately 80 km south of Albuquerque (NM), the SNWR exhibits an abrupt change in land cover along a dynamic transition zone between grass and shrub dominance (Fig. 2) with an encroachment front of *Larrea tridentata* into desert grassland. Thus, this field site is an ideal location to investigate differences in microclimate associated with the two different land cover states.

Historical temperature records in this region were available at the Los Lunas and Socorro stations located in central New Mexico at a similar elevation, about 30 km north and south of the current location of the grassland-shrubland boundary. Los Lunas (34.7675° N, 106.7611° W,

1475 m MSL) is surrounded by grassland, whereas Socorro (34.0828° N, 106.8831° W, 1397 m MSL) is in an area completely surrounded by *Larrea tridentata*. Although data do not exist from this time, we assume that creosote bush has occurred in the Socorro area at least since the beginning of the 19th century. Indeed, creosote-bush has expanded at the Sevilleta between 1920s and 1970s suggesting that it was previously more abundant to the south. Temperature records were obtained from the U.S. Historical Climatology Network version 2 serial monthly dataset (Menne et al. 2009). Data quality evaluation included the adjustment of bias in the time of observation, estimation of missing data (Menne et al. 2009), and application of a homogenization algorithm to effectively minimize urbanization impact on the temperature record (Menne and Williams 2009, Menne et al. 2010).

Data from the long-term record for the Five Points (ecotone, 1610 msl) and Deep Well (grassland, 1596 msl) micrometeorological stations operated by the Sevilleta LTER were used to investigate differences in winter temperature regime between grassland and shrubland within the SNWR. These stations are separated by 4.4 km from ecotone to grassland and are at about the same elevation. Moreover, to assess whether possible temperature differences between these two stations are a result or a cause of the different



Fig. 2. A view of a grassland-shrubland transition zone (ecotone) in the northern Chihuahuan Desert (Sevilleta Wildlife Refuge, NM).

vegetation at the two sites, we established a network of near-ground temperature measurement in the proximity of the encroachment front. To this end, three additional field sites were established within the SNWR: in the grassland, in the creosote bush (*Larrea tridentata*) shrubland, and at the encroachment front (ecotone site). The sites were less than 1 km apart on flat terrain and several kilometers away from any major topographic features or slopes. Black grama (*Bouteloua eriopoda*) dominated the grassland site and covered approximately 60% of the ground surface, with bare soil in the remaining 40%. Other plant species (e.g., *Gutierrezia sarothrae*) were intermingled with the grasses. Overall, the grassland site exhibited a relatively uniform grass cover with a typical grass canopy height of 0.1 m. Less vegetation cover occurred at the creosote site—around 30%, with 70% bare soil

(Bhark and Small 2003)—and cover was more discontinuous, with a mosaic of shrub-dominated patches interspersed in a matrix of bare soil. The average shrub canopy height was about 1.0 m. The ecotone site was a mixture of *B. eriopoda* and *L. tridentata* cover with about 50% bare soil. At each site six temperature sensors (model H08-031-08, HOBO®Temp sensors, Contoocook, NH) were mounted on a pole at a height of 80 cm above the ground: three sensors were placed in the middle of bare soil patches (diameter > 1.5m) and the other three sensors were in the middle of vegetated patches (i.e., in grass patches at the grassland site and in shrub-dominated patches at the ecotone and shrubland sites). Sensors were previously tested in the laboratory using a water bath: all sensors measured the same temperature, with errors within the accuracy range indicated by the manufacturer ($\pm 0.2^{\circ}\text{C}$). Data were logged

at 5-minute intervals. The records used in this study refer to the season between December 15, 2008 and February 28, 2009 (i.e., 75 days). In particular, we focused on nighttime measurements (18:00–06:00 Local Standard Time (LST), 12 hours per day), as the sensitivity of *Larrea tridentata* to surface temperature has been reported to be due to freezing-induced xylem cavitation associated with minimum winter temperatures (Pockman and Sperry 1997).

RESULTS

Long-term minimum temperature data (Fig. 3) show significantly higher ($t = 8.066$, $p < 0.0001$) annual low temperatures in the shrub-dominated region (Socorro, open circles) compared to the grass-dominated area (Los Lunas, filled circles). The minimum temperatures measured in Los Lunas and Socorro in the 1896–2009 period of record (nighttime and wintertime only) were -15.2°C and -12.00°C , while the means of the minimum annual values (nighttime and wintertime only) were -10.0°C and -7.9°C in Los Lunas and Socorro, respectively. Although these long-term data must be interpreted with caution because of the idiosyncrasies of site selection

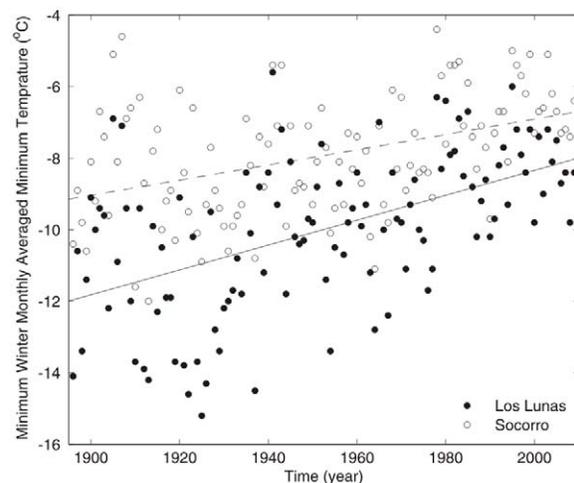


Fig. 3. Historic minimum winter temperature at Los Lunas (filled circles) and Socorro (open circles), New Mexico, USA. The minimum temperatures are calculated as the minimum values of the monthly average minimum temperatures of winter months reported in the U.S. Historical Climatology Network.

within villages and changes in measurement technology over the period of record, they are consistent with the hypothesis that minimum temperature is higher in shrub dominated sites compared to grass dominated sites.

Additional support for the hypothesized temperature differences between shrub- and grass-dominated vegetation comes from measured minimum air temperature at the ecotone and grassland sites (4.4 km apart) at the SNWR (Fig. 4). Monthly means of daily differences in minimum temperature between the locations of Five Points (ecotone) and Deep Well (grassland) show a seasonal pattern with the largest differences ($\approx 2^{\circ}\text{C}$) occurring during the period between November and April. During the summer, the mean difference between the two met stations was roughly 0.5°C .

Data from HOBO sensors deployed at the grassland, shrubland and ecotone sites within the same landscape (a total span of roughly 5 km) showed no significant difference in mean temperature between the vegetated or bare soil microsites within each site (shrubland: $p = 0.41$; ecotone: $p = 0.65$, grassland; $p = 0.25$). The mean temperatures, however, were significantly different across sites, indicating that vegetation cover affects microclimate conditions at the landscape scale, but not at the patch scale. Between mid-December and the end of February, mean nocturnal temperature (1.1°C) at the shrubland site remained significantly higher than the mean nocturnal temperature at the ecotone site (0.8°C ; $p = 0.0004$) and at the grassland site (-0.7°C ; $p < 0.0001$). Moreover, the mean temperature at the ecotone site was significantly higher than that at the grassland site ($p < 0.0001$). Within each site temperature differences between microsites (measured at 80 cm from the ground) were not significant and were much smaller than the significant differences in average temperatures among sites (Fig. 5).

Temperature differences between sites were larger (on average by about 0.4°C) in the first half of the night (18:00–24:00 LST) than in the second half (0:00–6:00 LST). Moreover, temperature differences were larger (on average by about 1.3°C) between grassland and ecotone, than between ecotone and shrubland (Fig. 5). Similarly, the minimum temperatures of every half hour measured between December 15, 2008 and

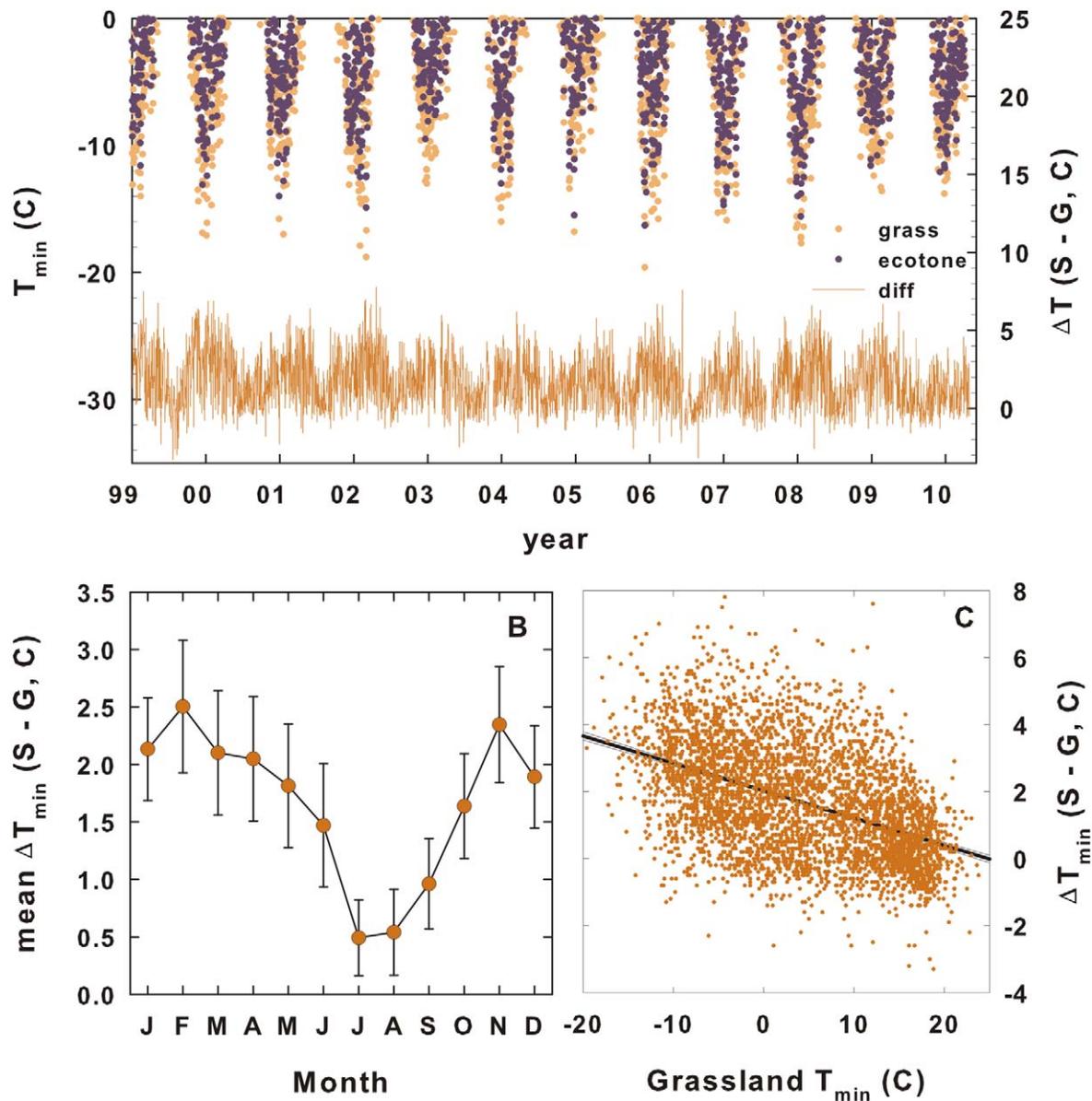


Fig. 4. (A) Sub-zero temperatures in grassland (G) and shrubland (S) sites, 1999 to winter 2010. (B) Monthly mean of the daily difference between ecotone and grassland minimum temperature (T_{\min}), where positive values reflect higher minimum temperature in the shrubland. Data were from the Five Points (shrubland, 1610 m) and Deep Well (grassland, 1596 m) micrometeorological stations operated by the Sevilleta LTER. (C) Correlation between the difference in minimum temperature between grassland and shrubland and minimum temperature at the grassland site, showing that the greatest differences in temperature tend to occur on the coldest nights.

February 28, 2009 showed consistently lower values (about 1–2°C) at the grassland sites than at the shrubland site and intermediate values at the ecotone site. However, no significant differences between the bare and the vegetated soil patches

were detected at any site. Moreover, Kolmogorov-Smirnov tests indicated that there were no significant differences in the probability distributions of daily minimum temperatures for different micro-sites within one land cover. Similarly,

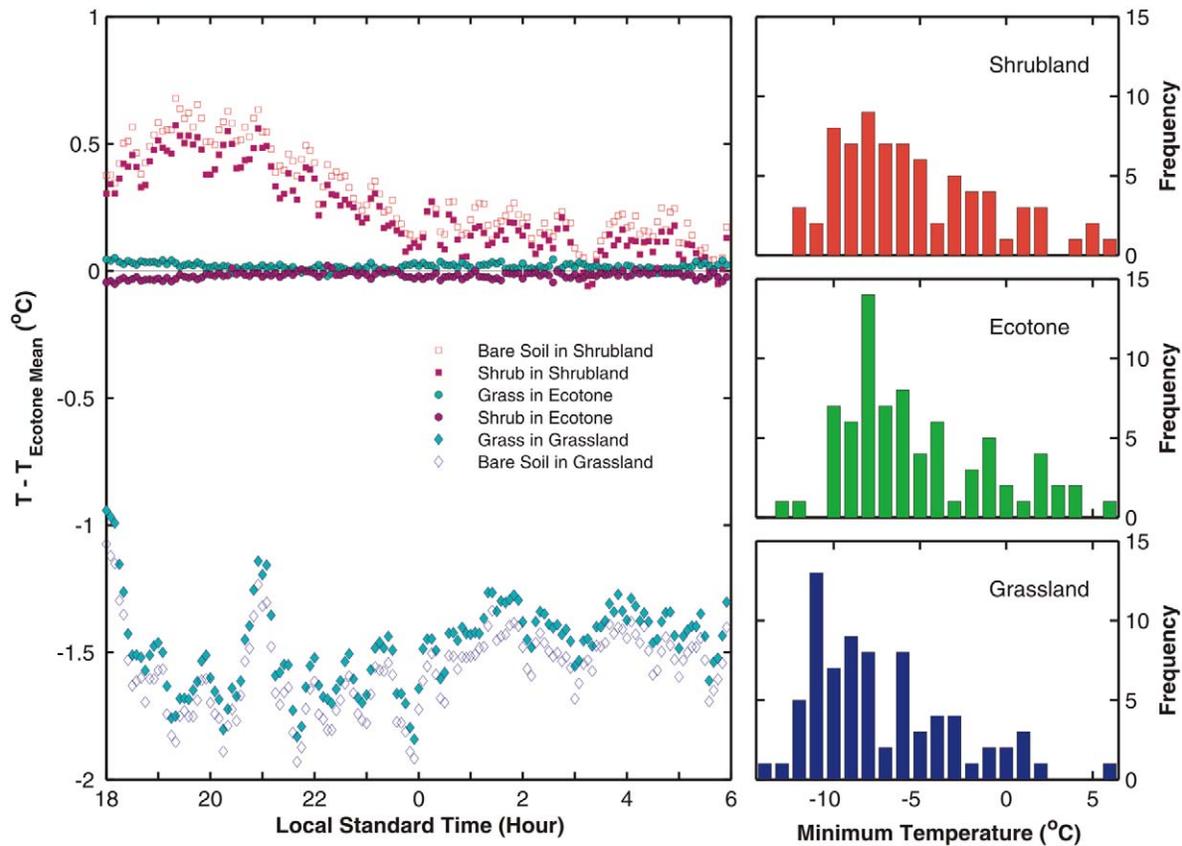


Fig. 5. Left panel: difference between mean temperatures measured at different times of the night at the shrub-dominated (squares), ecotone (circles), and grass-dominated (diamonds) sites, and the average nighttime temperature measured at the ecotone site (December 15, 2008 to February 28, 2009). Right panels: distribution of daily minimum temperature of shrub-dominated (top), ecotone (middle), and grass-dominated (bottom) sites.

the distribution of minimum temperatures measured at the shrubland and ecotone sites were not significantly different, while in the same time period, the grassland had a significantly different distribution of minimum temperature than either the shrubland or ecotone. The minimum temperatures in the shrubland and ecotone dropped below -10°C on 10% and 5% of the nights, respectively, while in the grassland the temperature dropped below -10°C on about one third of the winter nights.

DISCUSSION

Our analysis of long term data from stations representing grassland and shrubland sites, intermediate term air temperature data from these vegetation types at SNWR and short term

measurements of cover types within grassland and shrubland shows a significant difference in nocturnal winter temperatures between the grass and shrub dominated sites. Mean and mean minimum temperatures in the shrubland were roughly 2°C higher than in the grassland (Fig. 3), with daily differences between sites reaching more than 8°C and the largest differences occurring, on average, on the coldest nights (Fig. 3). These differences existed at the field-to-landscape scale (i.e., 100–1000 m) but were not evident at the patch scale (Fig. 4, i.e., 1–5 m). The differences in minimum temperature from the long-term climatological measurements at the SNWR are not the result of elevation differences, which were less than 15 m across 5 km separation. Even smaller elevation differences existed among the locations where the HOBO

sensors were deployed. Similarly, landscape-scale warming at the shrubland site cannot be explained by its lower latitude with respect to the grassland, as the two sites are only a few kilometers apart. Rather, the difference in nighttime temperatures between grass- and shrub-dominated sites is the result of a higher fraction of bare soil in the shrubland (He et al. 2010). Bare soil exhibits larger ground heat fluxes and soil heating during the day. This energy is then released at night in the form of longwave radiation, maintaining higher nighttime near-surface temperatures at the shrub site. While this process is operating in bare soil patches in both the grassland and shrubland sites, the increased areal coverage of bare soil in the shrubland is likely responsible for the observed nighttime temperature differences. Based on surface energy flux measurements, this interpretation (He et al. 2010) is only apparently in contrast with the lack of nocturnal temperature differences between vegetated and bare soil microsites reported in this paper. In fact, these results indicate that, although He et al. (2010) reported differences in soil heat fluxes between vegetated and bare soil microsites, their impact on near-surface air temperatures is not detectable at the height of 80 cm.

The increase in minimum temperature observed with increasing shrub dominance (Figs. 3–5) suggests that changes in community structure and cover create a positive feedback with surface energy balance and microclimate that favors continuing shrub growth and survival. The shrubland and ecotone sites occur near the northern limit of *Larrea tridentata*. Juvenile and mature individuals exhibit increasing damage to leaves and xylem as minimum temperature decreases (Pockman and Sperry 1997, Martinez-Vilalta and Pockman 2002; Medeiros and Pockman, *in press*), with the critical temperatures for this response falling in the range of temperatures that occurred at our study sites. These measured physiological limits have previously been suggested as one of the mechanisms defining the northern limit of *Larrea tridentata* (Pockman and Sperry 1997, Martinez-Vilalta and Pockman 2002). The difference in minimum temperature observed between the grassland and ecotone/shrubland sites (2–8°C) is large enough to affect the level of damage experienced by juvenile

Larrea tridentata on the coldest nights of the year. Thus, by increasing the minimum temperatures that occur in the shrubland and ecotone, the microclimate changes associated with shrub establishment may reduce juvenile mortality and favor continuing shrub growth and survival.

As a preliminary assessment of this mechanism, we combined the 11 year (1999–2010) instrumental record of minimum temperature from meteorological stations in grassland and the ecotone (see Fig. 4) with recent data describing juvenile mortality as a function of minimum temperature under well-watered and drought conditions (Medeiros and Pockman, *in press*). Using simple linear interpolation between observed mortality as a function of minimum treatment temperatures (Fig. 6C inset), we estimated cumulative juvenile mortality using the long term T_{\min} data from the field site (Fig. 6B). In both well-watered (Fig. 6A) and drought conditions (Fig. 6C), this approach predicted greater juvenile mortality in the grassland than in the shrubland/ecotone. Because drought effectively increases freezing tolerance, our simple model predicted greater mortality at both sites when freezing occurred and plant water potential was high (approx –2 MPa, see Medeiros and Pockman, *in press*). During drought years, little mortality was predicted in the shrubland/ecotone while substantial mortality was predicted to occur at grassland temperatures (Fig. 6). Thus, *Larrea tridentata* shrubs benefit from the changes they induce in the physical environment. In fact, the nighttime warming induced by shrub establishment favors the success of juvenile *Larrea tridentata* (Fig. 1), and decreases potential for mortality due to freezing.

CONCLUSIONS

We conclude that at the high latitude limits of *Larrea tridentata*, the modification of microclimatic conditions that accompany shrub establishment favors continuing growth and survival of juveniles. The existence of the feedback described in this paper could explain the relatively sharp shift between the two land covers, consistent with similar sharp changes reported for other systems affected by similar feedbacks (Wilson and Agnew 1992).

Ecosystem engineering (Jones et al. 1994), the

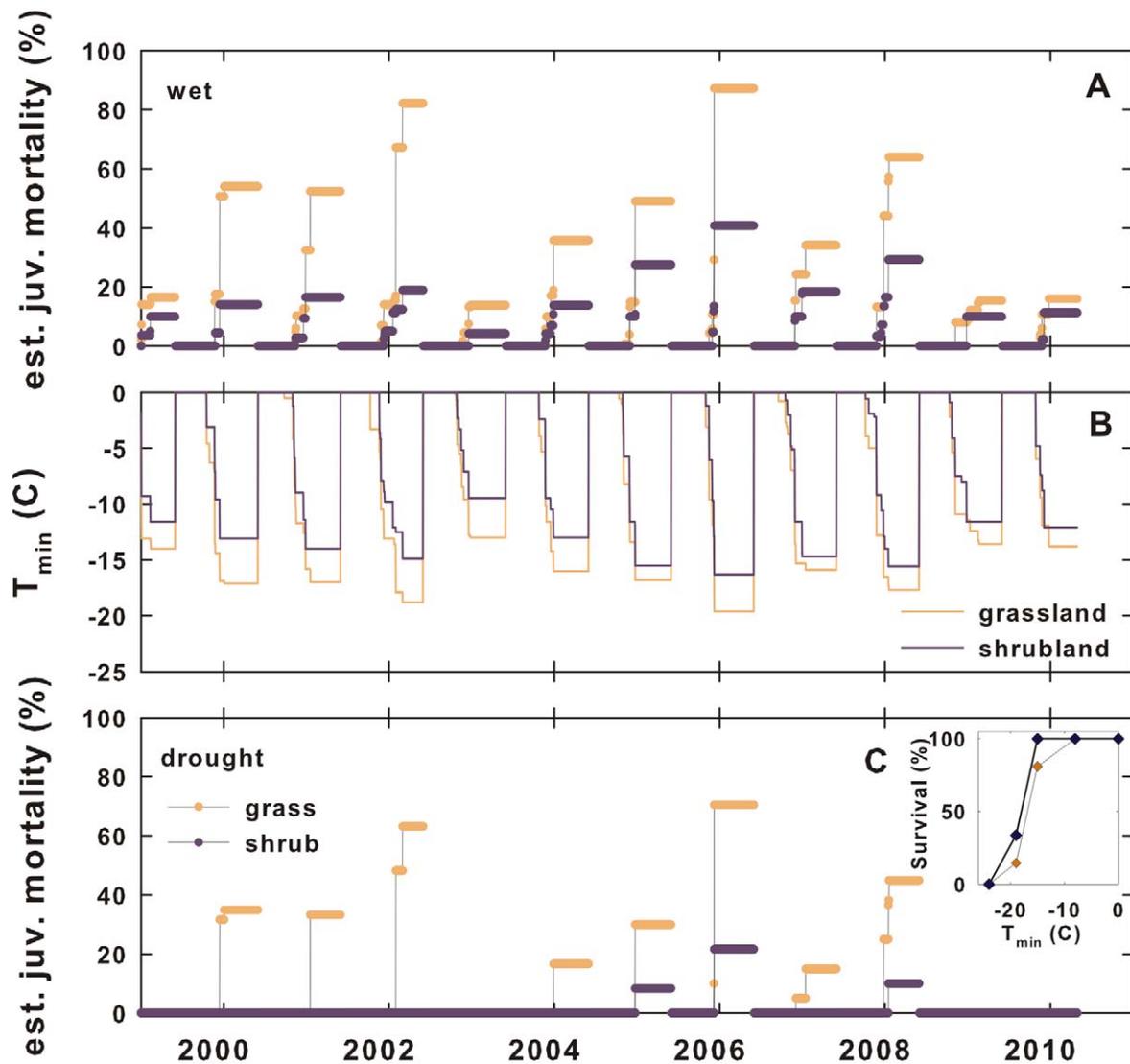


Fig. 6. Juvenile mortality from 1999–2010, estimated by combining response functions of survival of juvenile *Larrea tridentata* as a function of minimum temperature (Medeiros and Pockman, *in press*) with long-term minimum temperature data at Five Points (ecotone) and Deep Well (grassland) meteorological stations at the Sevilleta LTER. Plants used for survival measurements were 1 year-old juveniles grown from seed collected at Five Points. A. Estimated mortality under well watered conditions, B. Lowest daily temperature measured at Deep Well and Five Points since the previous spring season (i.e., minimum temperature to date during each year, and reset to zero each spring), and C. Estimated mortality under drought conditions, which actually favor survival. Under well watered conditions, this approach predicts significant mortality in both locations while under drought conditions significant mortality is still predicted for the grassland site while only low levels of mortality are predicted in the ecotone and then only in some years.

ability of organisms to modify their habitat to their own advantage as well as that of other species can induce bistability in ecosystem dynamics (Wilson and Agnew 1992). In the

northern Chihuahuan Desert, bistability would result in shrub-dominated areas with relatively warm conditions during the winter, grass-dominated areas with colder microclimates, and

ecotones where shrubs are encroaching into grassland (e.g., Peters et al. 2006). Thus, shrub encroachment could occur as a state shift from stable grassland to stable shrubland conditions, consistent with a number of models of rangeland dynamics (e.g., Westoby et al. 1989, Anderies et al. 2002, van Langevelde et al. 2003, Okin et al. 2009), which explain the relatively abrupt character of this transition. As noted, these models invoke two feedback mechanisms as the possible cause of bistability, namely the feedback between vegetation and fire dynamics (Anderies 2002, D'Odorico et al. 2006, Ravi et al. 2009), or the feedback between vegetation cover and the erosion-induced loss of soil resources (Schlesinger et al. 1990). Here we showed that this ecosystem exhibits another important feedback mechanism, which involves the interaction between plant community composition and microclimate conditions. Changes in climate can interact with this feedback, with regional warming further reinforcing these effects of microclimate on the distributional limits of *Larrea tridentata* while changes in precipitation may favor juvenile survival following freezing if drought prevails during cold wintertime conditions or increase mortality if water availability is high during the winter.

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