



Response of semi-desert grasslands invaded by non-native grasses to altered disturbance regimes

Erika L. Geiger* and Guy R. McPherson

School of Natural Resources, University of Arizona, Tucson, AZ, USA

ABSTRACT

Aim Using a long-term data set we investigated the response of semi-desert grasslands to altered disturbance regimes in conjunction with climate patterns. Specifically, we were interested in the response of a non-native grass (*Eragrostis lehmanniana*), mesquite (*Prosopis velutina*), and native species to the reintroduction of fire and removal of livestock.

Location The study site is located on the 45,360-ha Buenos Aires National Wildlife Refuge (31°32' N, 110°30' W) in southern Arizona, USA. In 1985, livestock were removed and prescribed fires were reintroduced to this semi-desert grassland dominated by non-native grasses and encroaching mesquite trees.

Methods Plant species cover was monitored along 38, 30-m transects five times over a period of 15 years. Data were analysed using principal components analysis on the variance–covariance and correlation matrix, multivariate analysis of variance for changes over time in relation to environmental data, and analysis of variance for altered disturbance regimes.

Results Reintroduction of fire and removal of livestock have not led to an increase in native species diversity or a decrease in non-native grasses or mesquite. The cover of non-native grass was influenced by soil type in 1993.

Main conclusions Variability of plant community richness, diversity, and cover over time appear to be most closely linked to fluctuations in precipitation rather than human-altered disturbance regimes. The effects of altered grazing and fire regimes are likely confounded by complex interactions with climatic factors in systems significantly altered from their original physiognomy.

Keywords

Arizona, climate, disturbance, *Eragrostis lehmanniana*, fire, grazing, long-term monitoring, non-native, semi-desert grassland.

*Correspondence: Erika L. Geiger, School of Natural Resources, University of Arizona, 325 Biological Sciences East, Tucson, AZ 85721, USA.
E-mail: elg@ag.arizona.edu

INTRODUCTION

Similar to other biomes across the globe, grasslands in the American Southwest have experienced significant changes to their historic composition and processes (Bahre, 1991; McPherson & Weltzin, 2000). Plant communities have been shaped by disturbances such as fire, grazing, and their interactions with climate. 'Disturbance is a change in physical or biological factors that ultimately affects the structure and function of plant communities' (McPherson & Weltzin, 2000). Different processes come into play over long time-scales,

therefore altered disturbance regimes, compared with individual disturbance events, may have novel influences on vegetation (Clark, 1996).

During the last several hundred years, most grasslands of the American Southwest experienced a novel disturbance type when cattle, coincident with the extirpation of prairie dogs, became a significant influence. Ecologists have argued about the detrimental effects of livestock grazing on plants (Belsky, 1986) vs. potential benefits to plant fitness (McNaughton, 1979) with evidence from systems that evolved with grazing by large herbivores. Grazing affects grasslands directly through the

removal of biomass, stressing of plants and altering of soil properties. In addition, plant community composition can be strongly influenced by intensity, duration and frequency of livestock grazing (Heitschmidt & Stuth, 1991), and the climatic conditions under which the grazing occurs. Herbivory in mesic systems typically results in short-term decreases in plant cover and increases in community richness and diversity (Huston, 1994). In arid systems and under drought conditions, the effects of grazing are intensified because of the additional stress caused by lack of moisture. After defoliation, relatively less carbon is translocated to the root system, and during drought periods the root extension rate may not be sufficient to maintain access to soil moisture (Sosebee & Wan, 1988). This stress on the plants may lead to a decline or death of perennial grasses. Damage to grasslands by livestock in the late 1800s, followed by severe drought in the early 1900s, may have caused so much damage to soils and vegetation that when livestock were removed vegetation response was 'not continuous, not reversible, or not consistent' and had entered a new 'state' (Westoby *et al.*, 1989).

Livestock also contributed to altered fire regimes by reducing fine fuels which, along with heat and oxygen, are required for fire. Livestock-induced declines in plant abundance limit fire occurrence and intensity relative to conditions that preceded Anglo settlement (McPherson & Weltzin, 2000). Roads, houses and other elements of the Anglo conquest of the region further limited fire spread. Therefore, fire, a common disturbance in grassland and savanna systems, no longer occurs at historic frequency, intensity or extent (McPherson, 1995). Woody species increased following changes in fire regimes and grazing under the influence of climate (Archer, 1994). Although managers are attempting to incorporate fire into their management plans as a way to restore areas now dominated by woody species, new fire regimes do not match historic regimes. Prescribed fires are often set in spring, autumn or winter, when cool and moist conditions are particularly conducive to controlling fire behaviour. Wildfire in southern Arizona occurs primarily between May and July during the hottest and driest period of the annual cycle prior to the onset of the summer 'monsoonal' rains (Swetnam & Betancourt, 1990; Westerling *et al.*, 2003). Additionally, the extent, location and frequency of fires are selected by managers rather than being subject to characteristics of the vegetation and landscape. Finally, landscapes are continually affected by humans and these effects may alter the influence of fire.

Climate also acts as a disturbance alone (e.g. extreme events) or in concert with the disturbances discussed above. Climate is the primary driver behind wildfire in the western United States (Westerling *et al.*, 2003). Years that are drier than normal create conditions conducive to wildfires, with fine fuels of extremely low moisture, and if preceded by a year of abundant rainfall that creates high fuel loads, the fire may be intense and widespread. Because of its effect on vegetation, climate can influence the impact of livestock on semi-arid grasslands in conjunction with management, such as stocking

rates. The interaction of climate and grazing in the Southwest during the drought at the turn of the twentieth century resulted in sharp declines of plant biomass and subsequent soil loss. Ecosystem processes are highly influenced by precipitation events (Noy-Meir, 1973; Crawford & Gosz, 1982) because of the variability and scarcity of rainfall (Weins, 1977) in arid systems. Shifts in climate averages or extremes can lead to the expansion of ranges or extirpation of species. For example, an increase in winter precipitation and rising carbon dioxide levels reportedly influenced historic encroachment by mesquite in addition to fire suppression and livestock (Archer, 1994).

In addition to woody species encroachment altering grassland physiognomy in the American Southwest (Hastings & Turner, 1965; Archer, 1989; McPherson & Weltzin, 2000), non-native species dominate many of these grasslands. These changes to plant community structure have been mediated by soil characteristics (McAuliffe, 1995), grazing, fire suppression and climate. Non-native grasses were introduced to rehabilitate the degraded grasslands and the most successful species appear to be those that tolerate drought, grazing and fire. In southern Arizona, Lehmann Covegrass, *Eragrostis lehmanniana* Nees, a perennial grass from South Africa, was introduced to provide erosion control and forage for cattle (Crider, 1945). In contrast to native grasses, *E. lehmanniana* exhibited no reduction in biomass production during an experimental drought (Fernandez & Reynolds, 2000). Additionally, this introduced grass evolved with and is very tolerant of grazing pressure (Cox *et al.*, 1992). Livestock in southern Arizona are known to selectively graze native species in preference to *E. lehmanniana* because of their high nutrition and moisture content (Cable & Bohning, 1959; Cable & Schumway, 1966; Cox, 1992). *Eragrostis lehmanniana* appears to dominate many semi-arid grasslands in southern Arizona and apparently has reduced or eliminated indigenous plants and animals, thereby contributing to permanent changes in diversity and species composition (e.g. Bock *et al.*, 1986).

Researchers estimate the species spread from 69,000 ha sown to an additional 76,000 ha in 50 years (Cox & Ruyle, 1986), and fires enhance its establishment (e.g. Cable, 1965, 1971; Ruyle *et al.*, 1988; Sumrall *et al.*, 1991; Robinett, 1992). *Eragrostis lehmanniana* may influence fire regimes by producing more biomass than native grasses (Cable, 1971; Cox *et al.*, 1984; Fernandez & Reynolds, 2000) and therefore enhance fire continuity and spread, intensity and frequency. Its spread is expected to continue under current climate conditions and land-management practices (Anable *et al.*, 1992): the species does not require disturbance to invade new areas (McClaran & Anable, 1992). However, the degree to which *E. lehmanniana* dominates plant communities has been linked to soil characteristics: *E. lehmanniana* is restricted to specific soil types in the south-western US and northern Mexico (Cox *et al.*, 1989) and in south-eastern Arizona soil permeability and water-holding capacity influence its abundance and rate of increase (Anable, 1990). Conservation of native grasslands will require considerable

knowledge of the response of *E. lehmanniana* to disturbance. The short- and long-term effects of non-native species and their response to management techniques remain a mystery in many systems.

In an effort to restore native semi-desert grasslands in Arizona, land managers have reintroduced fire with the goal of reducing abundance of these undesirable plants. However, if managers implement fires in these vastly altered systems (e.g. overgrazed, dominated by mesquite and Lehmann lovegrass) at seasons, frequencies and extents contrary to historic fire regimes they may have unknown consequences. Some systems may have passed thresholds whereby simply reintroducing the process that maintained the system no longer creates the expected effect (Archer, 1989; Westoby *et al.*, 1989). For example, woody plants such as *Prosopis velutina* Wooten (velvet mesquite) may have surpassed a size by which they can be killed by fire. Another difficulty in reintroducing disturbances is that they can facilitate invasion by non-native species; several studies have shown an increase in abundance of non-native grasses following fire (reviewed by D'Antonio & Vitousek, 1992).

The ability of scientists and managers to understand the role of disturbances in altered semi-desert grasslands has been hindered by lack of knowledge of the climate as a disturbance in conjunction with other disturbances. Additionally, we lack sufficient data that reveal time lags in the response of vegetation to disturbances. We examined the response of semi-desert grasslands in southern Arizona to altered fire and grazing regimes using a long-term data set that encompassed 15 years of climatic trends. Specifically, we investigated the following questions: How have plant communities changed over time since the removal of livestock and reintroduction of fire? Has the cover of *P. velutina* changed over time? How has cover of *E. lehmanniana* changed in response to the removal of livestock and reintroduction of fire? How do environmental variables such as slope, aspect, or soil texture influence the response of *E. lehmanniana* to altered disturbance regimes?

METHODS

Study area

The study site is located on the 45,360-ha Buenos Aires National Wildlife Refuge (BANWR) (31°32' N, 110°30' W) in southern Arizona, USA. In 1985, the US Fish and Wildlife Service established BANWR to preserve native vegetation and open space to support populations of the federally endangered masked bobwhite quail (*Colinus virginianus ridgwayi*) (United States Fish and Wildlife Service, 1995). Most of BANWR lies between 950 and 1150 m elevation, but some areas reach 1400 m. The most common soil orders are Aridisols and Mollisols and dominant subgroups are Ustollic Haplargids, Ustollic Camborthids, Aridic Calcistolls, Lithic Haplustolls. The majority of the grassland at BANWR has been modified by the invasion of mesquite (*P. velutina*) and non-native grasses

including *E. lehmanniana*, *E. chloromelas*, and *Sorghum halepense* (McLaughlin, 1992).

According to a detailed history of BANWR and the Altar Valley by Sayre (2002), the area supported livestock grazing since the late 1800s, with stocking rates varying by year and owner. The area was severely overgrazed during the drought years of 1898–1904. During the 1970s, ranch managers attempted to reduce mesquite and encourage grass production through chaining and grubbing of mesquite, applying herbicides, and prescribed fire followed by seeding of native and non-native grasses, although the estimates of these treatments and precise locations are impossible to determine. Presumably, grazing was very intense in the two years prior to refuge establishment based on statements made by the ultimate owner and by Refuge staff in internal memos. Following Refuge establishment, Refuge staff altered disturbance regimes by removing livestock and initiating an ambitious prescribed-fire programme. Since 1986, 300–3900 ha have been burned annually.

Since BANWR's establishment, biologists have collected data on species composition along permanent transects. Transect locations were selected either to provide broad representation of the area or because they captured the interest of early biologists. Basal and foliar cover of each species were measured along each of 38, 30-m transects according to methods described by Canfield (1941) at the end of the growing season (August–November) in 1987, 1989, 1993, 1997 and 2002.

Weather data were collected from the Western Regional Climate Center (<http://www.wrcc.dri.edu/summary/climsmaz.html>) and are 50-year averages from Anvil Ranch and Sasabe stations. Mean monthly temperature ranges from 9 °C (0 °C average minimum) in December and January to 29 °C (38 °C average maximum) in June and July. Just over half of the annual 360 mm of precipitation falls between July and September, and a quarter falls between December and February.

Environmental data collected at the time of transect establishment include range site, soil texture, slope and aspect. A range site is a description of land based on soil characteristics, site characteristics, climate and site potential (United States Soil Conservation Service, 1976). Because of the limited sample size (i.e. few transects on each soil texture) we classified soil textures into two groups based on clay content and another two groups based on sand content based on divisions for soil textures. The divisions are: soils containing > 28% clay are high clay content; soils with < 27% are low clay content; soils containing > 45% sand are high sand content; and soils containing < 44% sand are low sand content. Low clay content did not translate to high sand content and vice versa because of the silt component of most soil textures. We determined available water holding capacity (AWHC) based on soil textures and again grouped the transects because of low sample size. Dates and spatial extents of prescribed fires and wildfires were also recorded and were used to determine the fire history of each transect. Fire

frequency refers to the number of times a transect burned since Refuge establishment in 1985. Time-since-fire refers to the number of years between the date of the most recent fire and the year 2002.

Analysis

We used principal components analysis (PCA), both on the variance–covariance matrix and correlation matrix, as an exploratory tool to search for patterns in species cover over time. PCA on the variance–covariance matrix assigns a weight to species on the basis of abundance and therefore is highly influenced by dominant species. PCA on the correlation matrix standardizes data and therefore increases the influence that uncommon species have on resulting scores (McPherson & DeStefano, 2003). We determined correlations between components, species scores and environmental variables. We calculated species richness (s) and estimated diversity with Simpson's (c) and Shannon's (H) indices (Greig-Smith, 1983) using basal cover data for each transect on each sampling period; c and H were highly correlated ($r^2 = 0.86$), therefore only H is reported.

We analysed basal-cover data collected on the same transects over the five sampling periods with repeated-measures analysis of variance (ANOVA). Failure to relocate some transects each year restricted analysis to 21 transects. Basal cover is more representative of actual changes to herbaceous plant communities over time than aerial cover, which is highly variable. Because the data did not meet the assumptions of ANOVA, we transformed the data with the equation: $1/(\text{basal cover} + 1)^2$. Transformed data were distributed normally and had homogeneous variances. We examined the relationship between basal cover of *E. lehmanniana* in 1987, 1989, 1993, 1997, 2002 and slope, AWHC, sand content and clay content.

Additionally, we determined fire frequency and time-since-fire for each transect for each year. Transects that had not burned since Refuge establishment were assigned a value of 17 (years) and all time-since-fire values were treated as ordinal. We used ANOVA to test for the effects of fire frequency and time-since-fire on basal cover of *E. lehmanniana*, basal richness and diversity, and aerial cover of *P. velutina* ($n = 36$ for fire frequency and $n = 35$ for time-since-fire) in 2002.

RESULTS

Species abundance and distribution

PCA on the correlation and variance–covariance matrix revealed that most transects and species clustered around the origin of the ordination axes. Many transects in 1993 were dissimilar from transects associated with other sampling years. PCA on the correlation matrix revealed two distinct plant assemblages based on depth of soil (Fig. 1). PCA on the correlation matrix revealed transects separated by range site (United States Soil Conservation Service, 1976). Axis 1 reflected transects typically found on Shallow Uplands (areas

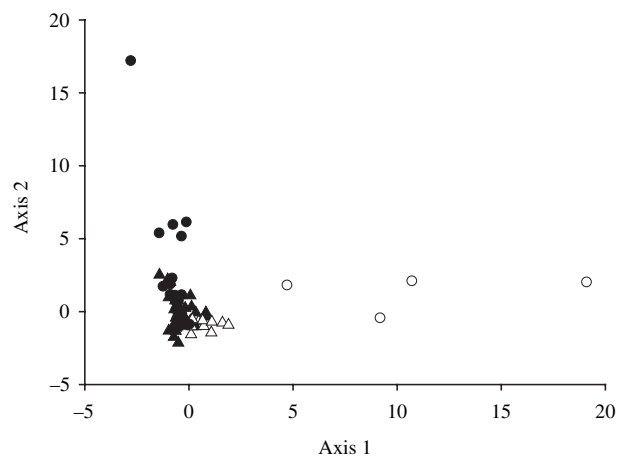


Figure 1 Principal components analysis on the correlation matrix. Circles represent transect data collected in 1993 and triangles represent 1987, 1989, 1997, 2002 data on plant communities. Filled symbols represent transects on deep soils, empty symbols represent transects on shallow soils at the Buenos Aires National Wildlife Refuge, Arizona.

with shallow soils and slopes of 1–15%) that permit the growth of relatively small bunchgrasses such as *Hilaria belangeri* and several *Bouteloua* species. Axis 2 reflected transects found on deep-soiled uplands (Loamy Uplands and Sandy Loam Uplands), on which good plant–soil moisture relationships allow for the growth of tall, robust perennial grasses such as *Digitaria californica* and *Bothriochloa barbinodis*. The latter transects also have a great number of herbaceous dicots and shrubs, whereas transects represented along Axis 1 are dominated almost exclusively by perennial short-grasses.

PCA on the variance–covariance matrix (not shown), which weights species by abundance and therefore is sensitive to dominant species, reflected cover of two of the most abundant species at BANWR. In the latter analysis, Axis 1 represented the cover of *E. lehmanniana* and Axis 2 represented the cover of the native congener, *E. intermedia*. A correlation between *E. lehmanniana* and the coefficients for principal component 1 ($r^2 = 0.9987$) and a correlation between *E. intermedia* and the coefficients for principal component 2 ($r^2 = 0.9491$) further confirmed this relationship. Principal component 3 weakly reflected transects monitored in 1993 in which an association of small-statured perennial grasses peaked in cover ($0.6741 > r^2 > 0.1436$).

No trends were evident on either PCA for cover, richness or diversity in relation to time since Refuge establishment. Between 1985 and 2002, basal-cover richness ranged from 0 to 13 species along individual transects. Mean richness was $2.9 < s < 5.3$ for all sampled years. Cover and richness were highest in 1993. Year-to-year diversity (Shannon's index) appeared to decline until 2002 ($H' = 1.04, 0.95, 0.8, 0.7, 1.1$).

No interpretable relationship between transects and fire frequency or time-since-fire was evident on either PCA. Likewise, no trend reflected a cumulative change following removal of livestock.

Abiotic factors and *Eragrostis lehmanniana*

An interaction between soil clay content and year was associated with differences in cover of *E. lehmanniana* in 1993 (Fig. 2, $P = 0.02$, $F_{4,14} = 4.20$) as compared with the other sampling years. Cover was seven times higher on soils with low clay content than on soils with high clay content (mean = 8.13, SE = 2.7; mean = 1.16, SE = 1.1). In contrast, across the five sampling dates, basal cover of *E. lehmanniana* was not related to soil sand content ($P = 0.26$, $F_{4,14} = 1.50$), AWHC of the soil ($P = 0.51$, $F_{4,14} = 0.73$), or slope ($P = 0.43$, $F_{4,14} = 1.02$). Total percentage cover of *E. lehmanniana* across all plots did not change substantially from year to year (repeated measures ANOVA, $P = 0.99$, $F_{4,14} = 0.29$).

Fire regime

In 2002, fire frequencies since 1985 included 0 ($n = 10$), 1 ($n = 4$), 2 ($n = 8$), 3 ($n = 12$), and 4 ($n = 2$). Time-since-fire ranged from 0 to > 17 years (i.e. unburned since Refuge establishment). Since Refuge establishment, almost half of the transects had burned < 4 years ago, 1/4 had burned between 5 and 14 years ago and 1/4 had not burned. There was no relationship between basal-cover richness in 2002 and fire frequency ($P = 0.2259$, $F_{4,31} = 1.5016$, ANOVA) or time-since-fire ($P = 0.3391$, $F_{10,25} = 1.1969$, ANOVA). ANOVA revealed no effects of fire frequency ($P = 0.4482$, $F_{4,31} = 0.9506$) or time-since-fire ($P = 0.5503$, $F_{10,25} = 0.8960$) on percentage cover of *E. lehmanniana*. Cover of *P. velutina* was also unrelated to fire frequency ($P = 0.3764$, $F_{4,31} = 1.0949$, ANOVA) and time-since-fire ($P = 0.4867$, $F_{9,25} = 0.9703$, ANOVA).

Climate

The two years prior to Refuge establishment, 1983–84, were among the wettest on record; between 600 and 850 mm of rainfall, double the annual average of 360 mm. In 1993,

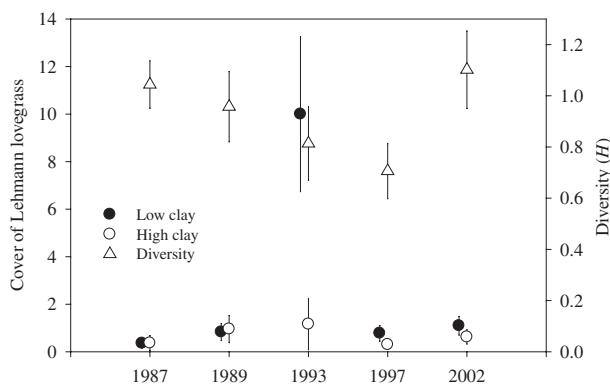


Figure 2 Percentage basal cover of *Eragrostis lehmanniana* (mean ± SE) on soils of low (< 27%) clay content (filled circles) and high (> 28%) clay content (open circles) and plant community diversity (open triangles, mean ± SE) at the Buenos Aires National Wildlife Refuge, Arizona.

precipitation was above the annual average by 180 mm (543 mm), while 1987 (348 mm), 1989 (302 mm), and 1997 (289 mm) experienced below average precipitation. The lowest annual precipitation for the 15-year data set was 181 mm in 2002. A precipitation gradient is also evident in some years, with southern portions of the Refuge receiving up to 1.6 times the amount of rainfall received by northern portions (data not shown).

DISCUSSION

Climate variability strongly influences the structure and function of arid systems (McPherson & Weltzin, 2000). Long-term monitoring in the American Southwest is essential to understanding the interaction between climate and other disturbances. Climatic conditions preceding, following, or interacting with a disturbance event may enhance or lessen the effects of disturbance. An indication of the importance of climate as a disturbance over altered land management is revealed by the separation of transect scores from the year 1993 in the PCA using both the correlation and variance–covariance matrices. These transects had no consistent relationship to fire or cessation of grazing. Using the variance–covariance matrix (not shown), the first two axes express dominance by the non-native (axis 1) and native (axis 2) lovegrass. Using the correlation matrix (Fig. 1), the axes represent specific range sites, but this pattern is evident only in 1993. The separation of range sites between axis 1 and axis 2 likely reveals an interaction between climate and range site, with the particularly wet year clearly differentiated. Range site represents a suite of environmental characteristics, including soil texture and landscape position, which would interact with precipitation to influence available soil moisture and therefore underlie expression of plant associations.

We expected plant communities to express changes in species composition or cover over time, particularly on transects that had not burned since refuge establishment (i.e. where fire was not a confounding factor). Livestock influence the cover and density of woody and herbaceous species in the American Southwest (McPherson & Weltzin, 2000). Anecdotal accounts of the Buenos Aires Natural Wildlife Refuge indicate that cattle have had greater impact during drought than under average conditions (Sayre, 2002). Two years prior to Refuge establishment the area experienced rainfall double the average, which probably encouraged regrowth. Had the years immediately prior to the purchase of BANWR been drought years the impact of the intense grazing that occurred in 1983–1984 likely would have impacted the land substantially. Alternatively, perhaps these areas have passed a threshold (Archer, 1989; Westoby *et al.*, 1989) and even removing or introducing disturbances no longer has an effect on species composition (McPherson & Weltzin, 2000).

Fires were reintroduced into some grasslands, including those at BANWR, as a restoration tool after managers had noticed changes in community structure that likely resulted from fire suppression. Land managers at BANWR predicted

that prescribed fires would alter plant community composition by favouring native grasses and reducing non-native grasses and woody species. Fire may meet other management goals, including reduction of fuel loads, stimulation of new growth, maintenance of species that may not have been monitored and reduced cover of woody species (McPherson, 1995). Although prescribed fire has been proposed as a restoration tool in these semi-arid systems, it may not produce the same results as historic wildfires because of significant changes in soils and plant community composition and differences between seasonal timing and behaviour of prescribed vs. pre-settlement fires. We found no effect of fire regime on plant communities or cover of *P. velutina* or *E. lehmanniana*. We might not expect that *P. velutina* would respond to introduced fires because this tree is capable of resprouting at 1 cm in diameter (Glendening & Paulsen, 1955) or over 3 years old (Wright *et al.*, 1976). Additionally, if the land had already passed a threshold from grassland to scrubland, fire alone cannot eliminate *P. velutina* (Archer, 1989; Westoby *et al.*, 1989). Although researchers have suggested that germination and establishment of *E. lehmanniana* is enhanced by fire (Cable, 1965, 1971; Ruyle *et al.*, 1988; Sumrall *et al.*, 1991; Robinett, 1992), we found no positive or negative influence of fire. Currently, there is little experimental evidence of the response of *E. lehmanniana* to fire; further research about the effects of prescribed fire on native and non-native plant communities is necessary as they are reintroduced to semi-desert grasslands.

Non-native species also have substantial impacts on ecosystem dynamics, and they often result in decreased cover, richness and diversity of native species (Office of Technology Assessment, 1993). Livestock were removed and fire reintroduced to BANWR in an attempt to restore high herbaceous cover and diversity and low cover of woody species, and to reduce non-native species. However, this research suggests that plant community structure in semi-desert grasslands at BANWR has not markedly changed following the introduction of prescribed fires and removal of livestock. Rather, changes in cover and diversity were associated with variability in precipitation (Fig. 2) and range site (Fig. 1). Little is known about the interactive effects of disturbance and *E. lehmanniana* on native plant communities, although it is known that disturbance is not required for spread (McClaran & Anable, 1992).

Researchers suggest that the persistence of *E. lehmanniana* may be limited to loamy sand, sandy loam or sandy soils (Cox *et al.*, 1984; Cox & Ruyle, 1986). On transects at BANWR, we found cover of *E. lehmanniana* to be higher on soils of low clay content than on soils of high clay content in 1993, a year of abundant summer precipitation (Fig. 2). Other research shows that plant height and biomass of *E. lehmanniana* increased at least threefold when grown on sand vs. silty clay (Flores-Ortiz, 1997). Soils with large particles and therefore large pore spaces have greater water-holding capacities and different nutrient availability than soils with small particles. Soil depth and topography also influence these characteristics; at BANWR, *E. lehmanniana* was rarely present on shallow uplands with sandy loam soils but was common on uplands with deep sandy

loam soils. *Eragrostis lehmanniana* was less common on clay loam soils and did not increase in cover in 1993 on these soils (Fig. 2). Rogstad (1998) found that *E. lehmanniana* was able to germinate on two different soil textures (one with a 26% clay fraction) given sufficient moisture during the summer, while Cox & Martin (1984) found that germination was limited depending on the type of clay present. Various studies have noted the ability of *E. lehmanniana* to be active earlier and later than native grasses during the year (Cable & Bohning, 1959; Cable, 1971; Anable, 1990; Rogstad, 1998). Potential access and use of resources by *E. lehmanniana* over a longer growing season than most native grasses may allow this non-native grass to dominate certain habitats. Moreover, predicted alterations to seasonality of rainfall, and increases in the intensity of precipitation events and of the frequency of extreme events across the globe (Easterling *et al.*, 2000) will further alter the ability of species to access resources. Studies on the effects of altered precipitation regimes on interactions among species are critical to the future management of these systems.

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BIOSKETCHES

Erika Geiger is a doctoral candidate at the University of Arizona's School of Natural Resources. She is interested in conservation biology, biogeography and the response of ecosystems to disturbance. Her research focuses on the effects of fire regime and a non-native grass on native plants in semi-desert grasslands.

Guy McPherson is a professor at the University of Arizona's School of Natural Resources and Department of Ecology and Evolutionary Biology. He teaches courses and conducts research in ecology. Specifically, he focuses on the creative application of ecological principles to the management of natural resources, including the conservation of biological diversity.

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