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NATIVE DESERT GRASSLAND PLANT SPECIES DECLINES AND ACCELERATED EROSION IN THE PAINT GAP HILLS OF SOUTHWEST TEXAS

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ABSTRACT—Due to the hotter droughts occurring with climate change, grasslands of southwestern deserts and southern plains in the United States are predicted to increasingly lose cover of native plant species, be invaded by nonnative species, and have accelerated soil erosion. We evaluated these predictions for desert grasslands in the Paint Gap Hills of Big Bend National Park, Texas. We used data from 10 monitoring transects established in 1981 and surveyed vegetation composition, canopy cover, and soil surface elevations in 1981, 1983, 1995, and 2014. Four longer and hotter droughts occurred between 1985 and 2014. We found that by 2014 canopy covers of two dominant native warm-season perennial grasses, *Bouteloua curtipendula* and *Bouteloua ramosa*, were reduced to near zero, and the cover of many native shrubs and subshrubs had notably declined. By 2014 two nonnative perennial grasses, *Eragrostis lehmanniana* and *Pennisetum ciliare*, had invaded, and their expansion could have long-term ecological consequences. Soil surfaces changed from accumulating sediments at a rate of +0.7 mm/year for 1983–1995 to eroding at –1.6 mm/year for 1995–2014. These soil and vegetation changes support predictions of major declines in native desert grasslands and emphasize their vulnerability to climate change.

RESUMEN—Debido a las sequías más calientes que ocurren con el cambio climático, se predice que los pastizales desérticos del sudoeste y las llanuras del sur de los EE.UU. perderán especies de plantas nativas, serán cada vez más invadidos por especies no nativas, y tendrán erosión del suelo acelerada. Evaluamos estas predicciones para pastizales desérticos en la región de Paint Gap Hills del Parque Nacional Big Bend en Texas. Utilizamos datos de diez transectos de observación establecidos en 1981 y muestreamos la composición vegetal, cobertura del dosel, y elevaciones de la superficie del suelo en 1981, 1983, 1995 y 2014. Hubo cuatro sequías más duraderas y más calientes entre 1985 y 2014. Encontramos que para el 2014 la cobertura del dosel de dos especies de pastos perennes nativos y dominantes de la estación cálida, *Bouteloua curtipendula* y *Bouteloua ramosa*, se redujo a casi cero, y la cobertura de muchos arbustos y subarbustos nativos había disminuido notablemente. Para el año 2014 dos pastos perennes no nativos, *Eragrostis lehmanniana* y *Pennisetum ciliare*, habían invadido y su expansión podría tener consecuencias ecológicas a largo plazo. Las superficies del suelo cambiaron de acumular sedimentos a una tasa de +0.7 mm/año entre 1983 y 1995 a perderlos por –1.6 mm/año entre 1995 y 2014. Estos cambios de suelo y vegetación respaldan las predicciones de disminuciones importantes en los pastizales desérticos nativos y enfatizan su vulnerabilidad al cambio climático.

Arid and semiarid lands supporting mixed perennial grass-shrub vegetation are referred to globally as desert grasslands (Schmutz et al., 1992). In the southwestern U.S. deserts, these grasslands typically occur around isolated low mountains and hills within basin and range landscapes (McClaran, 1995; Wondzell et al., 1996). In the Chihuahuan Desert, these grass-dominated communities have characteristic shrub and subshrub components, which following the conventions and descriptions

of the U.S. National Vegetation Classification clearly places them in the Chihuahuan Semi-Desert Grassland Macrogroup of the National Vegetation Classification hierarchy (Faber-Langendoen et al., 2017; <http://usnvc.org/>).

Site-based and modeling studies of these semidesert grasslands have reported declines in native perennial grasses and increases in nonnative and opportunistic species following prolonged droughts with below average

precipitation and above average temperatures (Munson et al., 2013; Moran et al., 2014; Gremer et al., 2015). On the Jornada Experimental Range in southern New Mexico, a 2002–2003 drought period with notable below-average precipitation and above-average temperatures greatly reduced native perennial grasses with a subsequent increase in annuals (Peters et al., 2012). After a similar drought in southern Arizona during 2002–2005, changes in desert grasslands on the Walnut Gulch Experimental Watershed included a high mortality of native perennial grasses and an increased dominance by opportunistic forbs and the nonnative grass *Eragrostis lehmanniana* (Moran et al., 2014). Other reported responses to severe droughts were increased native plant mortality and increased soil erosion associated with loss of protective ground cover (Abrahams et al., 1995).

Combining water-balance modeling with vegetation monitoring data from desert sites in the southwestern United States, Gremer et al. (2015) predicted that increasingly extreme drought conditions, similar to those expected with climate change, would negatively impact the grasslands of the Chihuahuan Desert region. Using “climate pivot points” modeling and Chihuahuan Desert site-based monitoring data, Munson (2013) and Munson et al. (2013) predicted that under conditions of low summer precipitation native perennial grasses would markedly decline. Modeling studies of southern Great Plains grasslands sites found that even though these plains grasslands were more resistant to droughts than semidesert grasslands, it was predicted that prolonged droughts would likely cause notable declines in native vegetation (Moran et al., 2014).

The aim of our research was to evaluate whether these predicted and observed responses in desert and plains grasslands would also apply to the semidesert grasslands found in the Paint Gap Hills of Big Bend National Park (Big Bend NP), Brewster County, Texas. The Paint Gap Hills are located in the United States along its border with Mexico, hence their grasslands are at the southern extreme of U.S. Chihuahuan Desert and Great Plains grasslands.

METHODS—Study Area—At the time Big Bend NP was established in 1944, H. M. Ratcliff (1944, in litt.) recorded that vegetation had been overgrazed to a low total ground cover. The National Park Service removed domestic livestock from Big Bend NP after 1944, and vegetation monitoring from 1955–1981 documents that desert grasslands on landforms and soils typical for the Paint Gap Hills had recovered from a total canopy cover of 15% to 47% (Wondzell and Ludwig, 1995).

Our study sites in the Paint Gap Hills are situated about 15 km to the northwest of Panther Junction, Big Bend NP, the closest climate station (U.S. National Climate Data Center, <http://www.ncdc.noaa.gov>). The elevation at the head of our site in the Paint Gap Hills, 1,145 m, is similar to the elevation of 1,110 m at Panther Junction so we have assumed precipitation to be similar in both locations. The area has a semiarid, warm-temperate climate. We estimated annual mean precipitation for

Panther Junction Headquarters to be 331 mm (1947–2015), with summer (May–October) monsoon rains dominating yearly totals (78%). July is the wettest month with a mean of 53.4 mm precipitation. Winters are much drier and the driest month is March with a mean of only 8.7 mm precipitation. Summers are hot (mean July high of 34.3°C) and winters are cool (mean January low of 2.4°C).

Between 1981 and 2014, droughts occurred in 1988–1989, 1994–1995, 1999–2001, and 2009–2012 (Fig. 1). To estimate the severity of these four droughts, we computed average Standardized Precipitation Evapotranspiration Index (SPEI) values for the four drought periods using monthly SPEI data based on Panther Junction climate data available from the Drought Risk Atlas (National Drought Mitigation Center, Lincoln, Nebraska, <http://www.droughtatlas.unl.edu>). Although no single index is ideal for characterizing drought (Knutson and Fuchs, 2016), we chose the SPEI because it is simply based on how precipitation is affected by temperature-driven evaporation demands, and was found to best predict the responses of several ecological, hydrological, and agricultural variables to drought compared to other indices (Vicente-Serrano et al., 2012). The more negative the SPEI the more severe the drought.

The drought of 1988–1989 was characterized by departures of mean annual precipitation from the long-term average of –93 mm in 1988 and –187 mm in 1989, mean annual temperature departures cooler than long-term average, and an SPEI = –0.24 (Fig. 1). This 2-year cool drought ended with wet years in 1990 and 1991. The drought of 1994–1995 had a SPEI = –0.30 because temperature departures were above the long-term average while precipitation departures were below normal (–130 mm in 1994 and –121 mm in 1995). This 1994–1995 drought ended with above-average precipitation in 1996 and 1997. In the 3-year 1999–2001 drought, the SPEI was –0.51 due to precipitation departures being below normal in 1999 (–83 mm) and in 2001 (–137 mm) while temperature departures were well above normal from 1998–2000.

The 4-year 2009–2012 drought was the most extreme in Panther Junction’s climate record with an SPEI = –0.68 (Fig. 1). In 2011 the mean precipitation departure was –201 mm because summer monsoon rains failed and rainfall only totaled 65 mm for the entire year (SPEI = –1.50 in 2011). This severe 2011 drought was of regional extent and 2011 has been recognized as an extreme drought year elsewhere within the Chihuahuan Desert (Peters et al., 2014). At Panther Junction, temperatures in 2011 and 2012 were the hottest on record (Fig. 1). Yet, during the winter of 2011 a hard freeze also occurred. From a nighttime low of –11.7°C on 2 February, the daytime maxima on 3 and 4 February were only –5.6°C and –8.3°C, respectively. Minima on these 2 days, and on 5 February were –13.3°C, –14.4°C, and –11.1°C, respectively. This 3-day freeze event in early February 2011 was extreme. In Panther Junction’s 49-year (1955–2015) climate record, only 6 years had maximum daytime temperatures that remained below freezing for two successive days.

Over the 35-year (1980–2014) climate record for Panther Junction, which covered our study period, we found mean departures for precipitation decreased while temperature increased as indicated by linear regressions (Fig. 1). We also analyzed longer-term regional climate data, which suggested that rather than linear climatic trends occurring in the Big Bend region a shift in climate occurred from wetter-cooler conditions

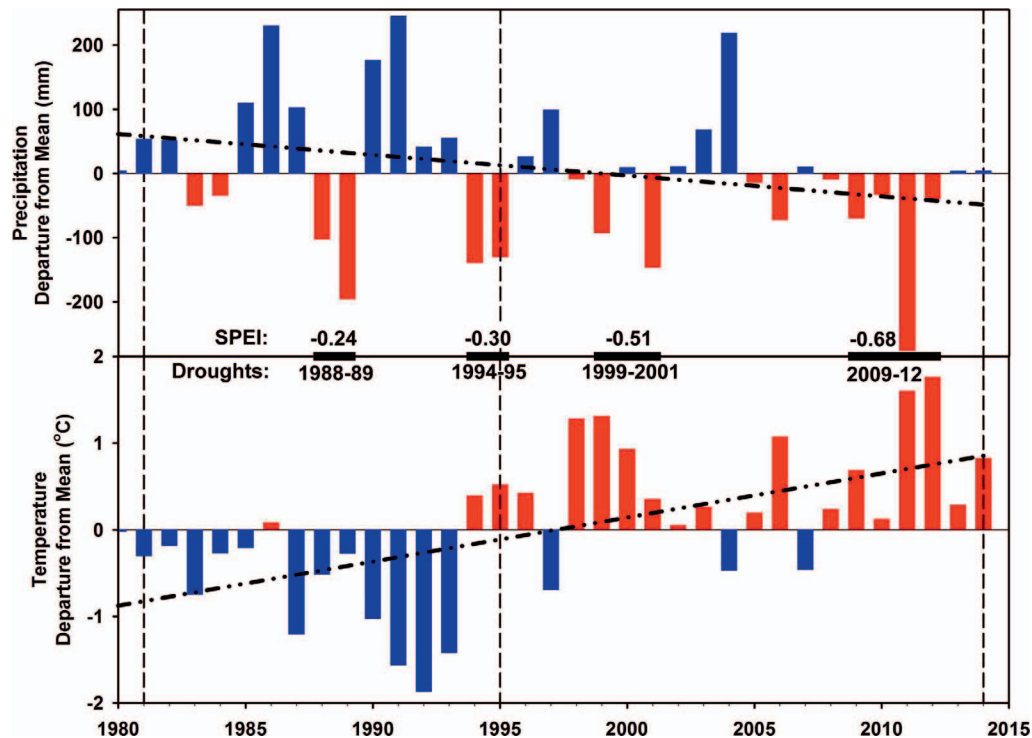


FIG. 1—Annual precipitation and temperature at Panther Junction in Big Bend National Park for 1981–2014 as departures from 60-year (1956–2015) means of 340 mm and 19.1°C, respectively. Standardized Precipitation Evapotranspiration Index (SPEI) values are given for the four drought periods indicated (solid lines), the vertical dashed lines denote that Paint Gap Hills transects were monitored in 1981, 1995, and 2014, and the dash-dot-dot horizontal lines illustrate the linear regression trends in mean precipitation and temperature departures from 1980–2014.

before 1993 to drier-hotter conditions after 1993. Although further climate regime shift analyses are required, this shift in climate after 1993 is evident in the Panther Junction temperature data when departures were above the mean in 18 of the 21 years from 1994–2015 (Fig. 1). These shifts and trends are consistent with expectations of hotter and drier conditions in southwest Texas due to climate change (Breshears et al., 2016).

Data and analyses—In September 1981, in order to sample two landscapes in the Paint Gap Hills characterized by semidesert grasslands (hillslopes and watershed drainages), we established three permanent line transects (T1–T3) down a hillslope below a scarp and seven line transects (T4–T10) along a nearby drainage channel (Fig. 2). The drainage channel extended from the edge of the piedmont slope, into which the drainage channel was incised, up almost to the ridge crest at the head of the watershed drainage. We spaced transects at 45–97-m intervals and oriented transects across the hillslope or drainage.

We permanently located the ends of each transect with steel rods (rebars ~0.5 m long and 12.7 mm in diameter) driven solidly into the soil, or down to bedrock. Transects T1, T2, T3, T5, T9, and T10 were 30 m in length; transects T6, T7, and T8 were reduced to 25 m because they were confined by a narrow section of the drainage; and transect T4 was increased to 45 m so that it extended from an alluvial fan across the wide arroyo onto the opposite alluvial fan.

In October 1981 we drilled, cemented, and sealed permanent benchmarks (galvanized steel bolts) into bedrock. These benchmarks served as fixed elevation reference points for comparing changes in soil surface elevations along our 10

permanent line transects at different survey periods. To maximize surveying precision, we positioned benchmarks in bedrock as close to transect positions as possible and at similar elevations. For transects T5–T10, we were able to position benchmarks in bedrock within 30 m of these six transects. Bedrock at similar elevations to T1, T2, T3, and T4 was farther away, so benchmarks for these transects were positioned at distances of 166, 139, 163, and 143 m, respectively.

The soils on transects T1, T4, and T5 developed on rhyolitic colluvium and alluvium found on the upper piedmont slopes and have been mapped as Chilicotal soils (United States Department of Agriculture–Natural Resources Conservation Service, 2011). The soils that developed in the fractured rhyolitic rocks below the scarp (transects T2 and T3) and along the drainage (transects T6–T9) have been mapped in the Lingua-Rock outcrop complex soil series. The soils on transect T10 developed on deposits of rhyolitic alluvium along the ridge crest and have been mapped as the Leyva-Rock outcrop complex.

We monitored vegetation along each of the 10 transects to identify changes in plant species composition and live-canopy cover over the 33-year period of 1981–2014. We identified plants using Correll and Johnston (1979) and Powell (1988, 1994). We first surveyed vegetation during 24–25 October 1981; resurveys were conducted 19–22 August 1995 and 3–5 October 2014. In 1981, we charted live canopy and basal covers of perennial plants by species in 0.2 × 0.5-m quadrats positioned at 1-m intervals along a measuring tape starting at 0.5 m (for examples of quadrat charting, see Ludwig and Moir, 1987). This detailed

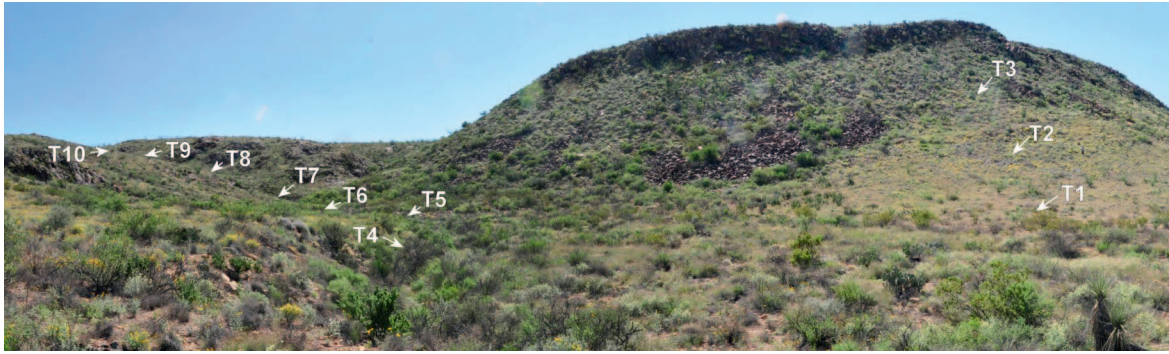


FIG. 2—The Paint Gap Hills desert grassland landscape showing the positions of the 10 permanent transects, T1–T10, within this landscape.

quadrat charting allowed us to estimate species canopy cover in each quadrat to the nearest 1%. During our resurveys, we did not chart quadrats because of time constraints. Instead, we visually estimated species live-canopy covers in quadrats to the nearest 1% if cover was below 10%, to the nearest 5% if cover was from 10% to about 50%, and to the nearest 10% if it was 50–100%. If a plant occurred in a quadrat, but at a very low canopy cover (e.g., a seedling), we assigned it a canopy cover value of 0.1% to denote its presence.

For each transect, we averaged species canopy cover based on the number of quadrats observed. For each year and species, we calculated cover values as means for the 10 transects (three hillslope and seven drainage transects). For each species, we compared differences in mean canopy cover values between the 1981, 1995, and 2014 surveys by simple repeated measures analysis (Quinn and Keough, 2002) using SYSTAT, version 11 (Systat Software Inc., San Jose, California). We evaluated the probability of multiple mean differences using the Huynh-Feldt probability adjustment provided by SYSTAT just in case multivariate assumptions did not hold. We explored for changes in plant community assemblages with nonmetric multidimensional scaling ordinations (McCune and Grace, 2002) using PCORD Version 5 (MJM Software Design, Gleneden Beach, Oregon).

In September 1983 we returned to the Paint Gap Hills after establishing desert grassland monitoring transects on four other Chihuahuan Desert sites (Ludwig and Moir, 1987). During 23–25 September we surveyed soil surface elevations along the 10 Paint Gap Hills transects using a high-precision, auto-leveling transit (Leica Wild NA24) and a stadia rod with millimeter markings. We measured surface elevations at approximately 0.5-m intervals along a fiberglass measuring tape stretched tightly between the two steel rods (rebars) positioned at the ends of transects T1, T2, T3, T9, and T10. To keep the tape close to the soil surface, we positioned two additional rebars within the arroyo on transect T5, and positioned one additional rebar permanently within the drainage channel for V-shaped transects T6, T7, and T8. On transect T4, we positioned three additional rebars within and on the edges of the arroyo. We resurveyed these 10 transects using an auto-level transit during 19–22 August 1995.

During 2–5 October 2014, we surveyed soil surface elevations along the 10 Paint Gap Hills transects using a total survey station (Topcon model GTS 223) and prism-poles. The advantage of surveying with a total survey station in 2014, in addition to its

high-precision optics-prism system, was our ability to measure slope distances so that the relative positions of transects within the watershed could be estimated.

RESULTS—Vegetation Changes—We found substantial vegetation changes from 1981–2014, notably the significant ($P < 0.05$) decline in canopy cover of the two dominant native perennial C_4 grasses, *Bouteloua curtipendula* and *Bouteloua ramosa* (Table 1). From a mean cover of 7.8% in 1981, *B. curtipendula* declined to 1.5% by 1995 and to near zero in 2014, and *B. ramosa* declined from a mean cover of 7.4% in 1981 down to 0.7% in 2014. In contrast, we found that the nonnative perennial bunchgrass *Eragrostis lehmanniana* had a mean canopy cover of 1.9% in 2014, but it was not present on transects in 1981 and 1995. Although it was not found on the three hillslope transects, *E. lehmanniana* was present on all seven drainage transects, especially on upper drainage transect T9 where it had a mean canopy cover of 13.5%. In 2014 we first recorded another nonnative perennial grass, *Pennisetum ciliare*, along drainage transect T7 (canopy cover of 1.6%). The small, short-lived bunchgrass *Tridens muticus* significantly increased from a low mean canopy cover of 0.3% in 1981 to 2.4% in 2014. The bunchgrass *Setaria leucopila* changed in canopy cover from 0.3% in 1981, absent in 1995, to 2.9% in 2014.

Another striking vegetation change was the loss of the succulent *Agave lechuguilla*, which was gone from all 10 transects in 2014, having declined in cover from 3.9% in 1981 to 1.1% in 1995 (Table 1). Of the common native shrubs, the canopy covers of *Florensia cernua*, *Lycium pallidum*, and *Parthenium incanum* significantly declined by 2014. In contrast, cover of *Larrea tridentata* varied below 3.5% over the period of record. *Prosopis glandulosa* also persisted with small cover changes from 1981–2014. *Celtis ehrenbergia* was absent along transects in 2014. Other shrubs and subshrubs, such as *Diospyros texana*, *Jefea brevifolia*, and *Leucophyllum frutescens* appeared to decline in cover by 2014, but these changes were not statistically significant. *Viguiera stenoloba* had a statistically significant low cover in 1995. The cover of the common perennial forb *Bahia absinthifolia* significantly increased from a low

TABLE 1—Mean canopy covers (%) in 1981, 1995, and 2014 for plant species occurring in the Paint Gap Hills, Big Bend National Park, Texas. We have listed species alphabetically within plant lifeforms, with names and codes following the Plants Database (<http://plants.usda.gov>). We have listed only species with a mean canopy cover of >1% in at least 1 year, and we have grouped those with <1% mean canopy cover and summed them under each lifeform as “other.” Statistical significance (P) is indicated as: ns = not significant at $P = 0.05$, $*P < 0.05$, and $**P < 0.01$. When a species was absent on all transects in a year (i.e., zero cover), the statistical analysis was not applicable (na) because of no cover variability. A “—” denotes that we did not apply statistical significance analyses to “other” lifeform categories. We have used the six-letter plant species codes in Fig. 3, which combine the first three letters of the genus name and the specific epithet of species.

Plant species	Annual mean canopy cover (%)			
	1981	1995	2014	P
Grasses				
<i>Aristida purpurea</i> (ARIPUR; purple threeawn)	0.1	<0.1	1.1	ns
<i>Bouteloua curtipendula</i> (BOUCUR; sideoats grama)	7.8	1.5	<0.1	*
<i>Bouteloua ramosa</i> (BOURAM; chino grama)	7.4	2.6	0.7	**
<i>Dasyochloa pulchella</i> (DASPUL; low woollygrass)	1.0	<0.1	0.8	ns
<i>Digitaria californica</i> (DIGCAL; Arizona cottontop)	0.1	0.0	1.2	na
<i>Eragrostis lehmanniana</i> (ERALEH; Lehmann lovegrass)	0.0	0.0	1.9	na
<i>Heteropogon contortus</i> (HETCON; tanglehead)	0.5	0.3	1.1	ns
<i>Setaria leucopila</i> (SETLEU; streambed bristlegrass)	0.3	0.0	2.9	na
<i>Tridens muticus</i> (TRIMUT; slim tridens)	0.3	<0.1	2.4	*
Other grasses	3.3	1.0	1.9	—
Succulents				
<i>Agave lechuguilla</i> (AGALEC; lechuguilla)	3.9	1.1	0.0	na
<i>Dasyllirion leiophyllum</i> (DASLEI; green sotol)	0.0	1.0	0.4	na
Other succulents	0.3	1.7	1.4	—
Shrubs-Subshrubs				
<i>Celtis ehrenbergiana</i> (CELEHR; spiny hackberry)	1.4	1.3	0.0	na
<i>Diospyros texana</i> (DIOTEX; Texas persimmon)	1.7	2.1	0.1	ns
<i>Flourensia cernua</i> (FLOCER; American tarwort)	3.3	2.9	0.3	*
<i>Gymnosperma glutinosum</i> (GYMGLU; gumhead)	2.6	0.1	2.5	ns
<i>Jefea brevifolia</i> (JEFBRE; shortleaf jefea)	2.6	0.7	0.1	ns
<i>Larrea tridentata</i> (LARTRI; creosote bush)	3.4	2.5	3.4	ns
<i>Leucophyllum frutescens</i> (LEUFRU; barometer bush)	2.2	3.3	0.7	ns
<i>Lycium pallidum</i> (LYCPAL; pale desert-thorn)	1.4	1.4	0.4	*
<i>Parthenium incanum</i> (PARINC; mariola)	7.3	4.7	2.7	*
<i>Prosopis glandulosa</i> (PROGLA; honey mesquite)	1.5	2.1	1.4	ns
<i>Viguiera stenoloba</i> (VIGSTE; resinbush)	2.2	0.4	2.6	*
Other shrubs and subshrubs	4.1	2.5	4.9	—
Forbs				
<i>Bahia absinthifolia</i> (BAHABS; hairyseed bahia)	1.3	0.2	3.1	**
<i>Croton pottsii</i> (CROPOT; leatherweed)	0.1	<0.1	1.4	ns
Other forbs	2.4	0.3	4.1	—

of 0.2% in 1995 to 3.1% in 2014. Another common forb, *Croton pottsii*, had low covers in 1981 and 1995, and a cover of 1.4% in 2014, but this increase was not statistically significant.

We found markedly different species assemblages in 2014 compared to 1981 and 1995 (Fig. 3). In 1981 and 1995, the ordination grouped transects T2–T8 together (lower right in the figure) because of an abundance of native perennial grasses (*Bouteloua curtipendula* and *B. ramosa*), a succulent (*Agave lechuguilla*), and shrubs (e.g., *Parthenium incanum* and *Celtis ehrenbergiana*). In 1981, 1995, and 2014, the ordination always grouped transects T1 and T10 together (left center) due to having a

relatively high canopy cover of *Larrea tridentata*, and a low but consistent canopy cover of *Dasyochloa pulchella*, while other species were absent or with sporadic low canopy covers. By 2014, the ordination grouped transects T2–T9 all together (upper right center; Fig. 3) because of their loss of native species and the gain of the invasive, nonnative *Eragrostis lehmanniana* and weedy increasers like *Heteropogon contortus*, *Aristida purpurea*, and *Setaria leucopila* plus the small bunchgrass *Tridens muticus*. Interestingly, transect T9 shifted from the native grass-dominated group in 1981, to the T1 and T10 group in 1995, and then to the nonnative, weedy-dominated group by 2014.

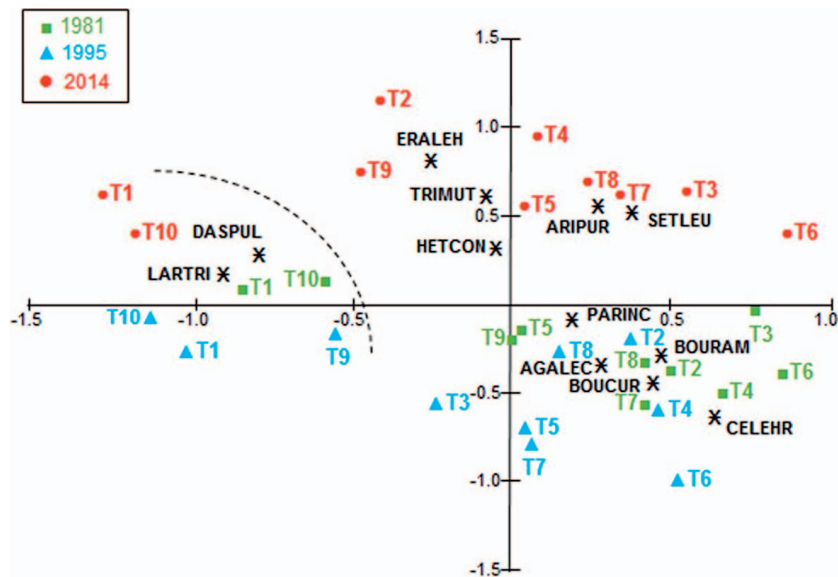


FIG. 3—Ordination of 10 Paint Gap Hills transects (T1–T10) in 1981 (solid squares), 1995 (solid triangles), and 2014 (solid circles) as influenced by the position (X) of dominant desert grassland species (mean canopy cover >1% in 1981, 1995, or 2014). Plant species codes combine the first three letters of the genus name and the specific epithet of species (see Table 1).

Surface Elevation Changes—We found that over the first 12 years of our study (1983–1995), transects T1 and T2 on the grassy hillslope had eroded at rates of -0.4 and -0.6 mm/year, respectively (Table 2). But, transect T3 accumulated sediment at a rate of $+3.0$ mm/year. This resulted in a mean gain of $+0.6$ mm/year on these three transects. Over the next 19 years (1995–2014), transects T1, T2, and T3 eroded at a mean rate of -1.6 mm/year. Although on the same hillslope (Fig. 2), transects T1, T2, and T3 were about 40 m apart and appeared to be eroding independently. For example, we did not observe any evidence that sediment from transect T2 was flowing downslope onto transect T1. Erosion along individual transects was not uniform. For example, on toe-slope

transect T1, surface sediment was mostly lost by the continued erosion of two rills located at about 2 m and 24 m along this 30-m transect.

From 1983–1995, the mean rate of change in surface elevation on the seven drainage transects (T4–T10) was $+0.8$ mm/year (Table 2). Some transects accumulated sediment while others eroded. From 1995–2014, all transects along the drainage eroded, resulting in a mean loss of -1.6 mm/year. Erosion was not uniform between and along transects, with transect T7, located in a lower-drainage position, having the greatest loss rate at -5.0 mm/year. This transect was on a steep slope and had lost a notable amount of sediment from the edges of its channel.

TABLE 2—Mean rate of change (mm/year) in soil surface elevations for the 12 years from 1983–1995 and for the 19 years from 1995–2014 along the 10 transects in two landforms in the Paint Gap Hills, Big Bend National Park, Texas: a hillslope with transects T1–T3, and a drainage channel with transects T4–T10. Based on paired *t*-tests, overall mean differences in surface elevations along the 10 transects between 1983 and 1995, and between 1995 and 2014, were statistically significant (** = $P < 0.01$).

Landform	Transect	Position	1983–1995 (mm/year)	1995–2014 (mm/year)
Hillslope	T1	Toe of slope	-0.4	-0.5
	T2	Midslope	-0.6	-1.7
	T3	Upper slope	$+3.0$	-2.7
		Mean	$+0.6$	-1.6
Channel	T4	Outwash arroyo	-0.01	-0.7
	T5	Head of arroyo	$+1.6$	-1.5
	T6	Base of drainage	$+0.8$	-1.8
	T7	Lower drainage	-0.3	-5.0
	T8	Middrainage	$+0.05$	-1.2
	T9	Upper drainage	$+2.5$	-0.6
	T10	Head of drainage	$+0.7$	-0.6
		Mean	$+0.8$	-1.6
		Overall mean	$+0.7^{**}$	-1.6^{**}

DISCUSSION—Our findings for the Paint Gap Hills in Big Bend NP are in keeping with predicted responses of desert grasslands to the extreme conditions expected with future climate change (Munson et al., 2013; Moran et al., 2014; Gremer et al., 2015). We found that after 33 years (1981–2014) the species composition and dominance by native species on monitored transects was greatly altered. The canopy cover of native perennial grasses *Bouteloua curtipendula* and *B. ramosa* drastically declined while the succulent *Agave lechuguilla* disappeared along all 10 transects. In Big Bend NP, it was observed that many stem-succulent plants, such as *Opuntia phaeacantha*, were killed by the hard freeze in February 2011 (J. Sirotnak, pers. observ.), and that many leaf-succulent plants, such as *Agave lechuguilla* and *Dasyllirion leiophyllum*, may also have died when this freeze was followed by the extremely hot, dry summer of 2011. The shrubs *Parthenium incanum* and *Flourensia cernua* had decreased canopies, although *Larrea tridentata* and *Prosopis glandulosa* cover persisted. Conversely, by 2014, the nonnative perennial grasses *Eragrostis lehmanniana* and *Pennisetum ciliare* were recorded for the first time on transects. The recent proliferation of these exotics in other areas in Big Bend NP is already a serious concern for park managers (J. Sirotnak, pers. comm.). Where these nonnatives dominate desert grasslands in Arizona and New Mexico, they pose major challenges to native perennial grass recovery (Anable et al., 1992; Peters et al., 2012, 2015). We know that recovery of desert grasslands in the southwestern United States after severe droughts is usually slow (Moir, 2011). On the Jornada Experimental Range, for example, recovery of perennial grass biomass after a 2002–2003 drought took 5 years even with above-average precipitation in 2004, 2006, 2007, and 2008 (Peters et al., 2012).

For altered desert grasslands, Moran et al. (2014) stated “there is still no consensus on the underlying mechanisms driving these responses.” For many years the prevailing view was that livestock grazing, in concert with periodic long and severe droughts, drove vegetation changes from desert grassland to shrubland (Buffington and Herbel, 1965; Dick-Peddie, 1993). Recent research using historical photography (McClaran et al., 2010), remote sensing imagery (Browning and Archer, 2011) and broad-scale data syntheses and modeling (Munson, 2013; Moran et al., 2014; Peters et al., 2014; Gremer et al., 2015) provides new evidence. These studies indicate that recent drought periods with below-average precipitation and above-average temperatures are driving major changes in desert grasslands, even when livestock grazing is absent.

Our 1981–2014 findings for the Paint Gap Hills, and our earlier desert grassland monitoring study in Big Bend NP covering the period of 1955–1981 (Wondzell and Ludwig, 1995), support this conclusion. Prior to 1955, vegetation cover in Big Bend NP was low due to a long history of domestic livestock grazing (H. M. Ratcliff, 1944,

in litt.) and the effects of the early 1950s drought. From 1955–1960, a period with below-average precipitation, total canopy cover in desert grassland communities remained at <15%. From 1960–1967 shrub cover increased during a period with wet winters but dry summers. From 1967–1981 summer precipitation was above average and total canopy cover increased to 47%, especially the cover of grasses and forbs. Most shrubs also increased in cover, but *Larrea tridentata* canopy cover declined from about 8% to 4%. Then from 1981–1995 in the Paint Gap Hills, we measured a notable decline in canopy cover of all perennial grass from 20.8% to only 5.5%, which then increased to 14.1% in 2014, but this increase was largely due to the appearance of the nonnative *Eragrostis lehmanniana* and an increase in other invasive grasses such as *Heteropogon contortus*. The total canopy cover of all shrubs and subshrubs declined from 33.6% in 1981 to 18.8% in 2014. Most unexpected was the decline of the succulent *Agave lechuguilla* from 3.9% in 1981 to 0.0% cover on the Paint Gap Hills transects in 2014. These drastic changes in vegetation by 2014 coincide with a shift to progressively longer and hotter-drier drought conditions after 1993 (SPEI drought index increased from −0.24 for 1988–1989 to −0.68 for 2009–2012). Because of the intervals between our vegetation surveys (14 and 19 years), we cannot distinguish whether these observed changes were due to the longer-term effects of climate trends or due to the more immediate impacts of shorter-term drought events.

The processes and drivers of vegetation change in desert grasslands can also influence rates of soil erosion because loss of protective grass cover increases wind and rain-splash erosion and facilitates overland flow of runoff water and sediment (McAuliffe, 1995). Reduced grass cover can also lead to a positive feedback in which surface runoff combines with erosion to clog soil pores thereby reducing infiltration and soil water storage, ultimately reducing grass cover. This positive feedback effect on perennial grasses appears to be critical on sites with shallow soils (due to bedrock or impermeable calcic horizons), such as on the Paint Gap Hills. On shallow soils where water storage is minimal, and if summer monsoon rains fail as they did in Big Bend NP in 2011 when only 58 mm fell at Panther Junction during May–October (22% of the long-term summer average of 258 mm), native warm-season grasses (e.g., *Bouteloua ramosa* and *B. curtipendula*) are negatively impacted (Gremer et al., 2015). These perennial bunch grasses provide a better protective soil cover than nonnative tufted bunchgrasses such as *Eragrostis lehmanniana* and *Pennisetum ciliare*, or the small native *Tridens muticus*.

In keeping with native grass cover declines after the 1994–1995 drought, and continued declines to 2014, we found that surfaces eroded on all 10 transects at a mean rate of −1.6 mm/year from 1995–2014, whereas in the previous 12 years, from 1983–1995, transect surfaces had

accumulated sediment, on average, about +0.7 mm/year. Our findings are consistent with the results from other desert grassland surface erosion monitoring studies in the southwestern United States. A mean soil surface loss rate of −0.4 mm/year was found for six line transects in desert grasslands on Otero Mesa in southern New Mexico (Ludwig et al., 2000). In the Peloncillo Mountains of southeastern New Mexico, two line transects on grassy hillslopes, similar to those we studied in the Paint Gap Hills, had mean soil surface loss rates of −1.4 mm/year and −0.6 mm/year (Moir et al., 2000).

The fact that severe droughts and hard freezes can trigger major vegetation changes in ungrazed native desert grasslands emphasizes their vulnerability to the extreme conditions predicted to occur with climate change in the southwest and southern Great Plains of the United States (Briske et al., 2015). There is a concern that as the frequency and severity of climate extremes intensifies with climate change that species-specific mortality thresholds will be exceeded in grasslands, changing them to alternative states (Breshears et al., 2016). In the Paint Gap Hills desert grasslands we measured a very high mortality of *Agave lechuguilla* and a significant loss of native perennial grasses with an invasion of the nonnative *Eragrostis lehmanniana*, which along with other vegetation changes could be interpreted as an alternative state. Whether the changes we have documented in the Paint Gap Hills will persist or reverse is as yet unknown, and the answer will require further monitoring. If the changes prove to be irreversible or ongoing they will create new and difficult challenges for natural resource managers (Moran et al., 2014; Peters et al., 2015).

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