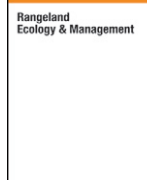




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Original Research

Persistence of a Severe Drought Increases Desertification but not Woody Dieback in Semiarid Savanna<sup>☆</sup>Carissa L. Wonkka<sup>a,\*</sup>, Dirac Twidwell<sup>b</sup>, Trenton E. Franz<sup>c</sup>, Charles A. Taylor Jr.<sup>d</sup>, William E. Rogers<sup>a</sup><sup>a</sup> Department of Ecosystem Science and Management, Texas A&M University, College Station, TX 77843, USA<sup>b</sup> Department of Agronomy & Horticulture, University of Nebraska, Lincoln, NE 68583, USA<sup>c</sup> School of Natural Resources, University of Nebraska, Lincoln, NE 68583, USA<sup>d</sup> Texas A&M Agrilife Research Center, Texas A&M University, Sonora, TX 76950, USA

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## ABSTRACT

Increases in precipitation variability, coupled with higher temperatures, will lead to greater frequencies of severe, prolonged droughts for many regions with the expectation of attendant increases in woody plant die-off events. We took advantage of a 2-yr extension of a severe drought following an initial study of woody plant dieback in a woody-encroached semiarid savanna in west-central Texas, United States. This study tests for the emergence of alternative vegetation trajectories as a result of continued drought persistence: 1) whether additional woody plant dieback occurred following the initial study, leading to a grass-dominated community, or 2) whether desertification became a major feature (defined as a loss of herbaceous cover and increase in bare ground). Neither the emergence of a grass-dominated community nor the prevalence of desertification was observed during the initial study. After 2 additional yr of drought, we found that dieback of woody plants did not increase above previously observed levels, suggesting that the prolongation of drought did not cause the emergence of a grass-dominated community in this heavily encroached rangeland. However, drought severity did lead to increases in desertification, with increases in bare ground owed to declines in grass cover. While previous research at this long-term research site suggests that desertification is transient with grasses rebounding once precipitation returns to predrought levels, rangeland managers should be aware of lags in vegetation response to drought and the increased potential for a shift toward a bare-ground dominated community following extended extreme drought. In this Texas semiarid savanna, major losses in herbaceous cover lagged behind woody plant dieback, so dieback of the woody component might hold promise as an indicator for near-term potential of desertification.

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## Introduction

While there is considerable uncertainty regarding the manner in which climate change will alter future precipitation patterns, there is consensus among models that variability will increase regardless of changes in mean annual rainfall for a particular region (Breshears et al., 2008; Adams et al., 2009). Extreme variability in precipitation patterns increases the likelihood of drought events (Anderegg et al., 2013a). As a result, the frequency, extent (both temporal and spatial),

and severity of drought are likely to increase even in areas with little change in mean annual precipitation (Dai, 2011, 2013). Large-scale forest die-offs could increase in coming decades due to temporal and spatial shifts in soil water availability resulting from increases in precipitation variability and drought events (McDowell et al., 2008). Indeed, there is already evidence of widespread die-off occurring in forested biomes worldwide during the past several decades (Allen et al., 2010; Anderegg et al., 2013b). Drought-induced forest die-offs could have profound disruptive consequences for ecosystem structure and functioning (Allen et al., 2015). While tree dieback occurs periodically in any system, massive die-offs that are species and site specific will potentially have lasting effects on ecosystem heterogeneity (Floyd et al., 2009; Anderegg et al., 2013b), understory composition (Kane et al., 2011; Anderegg et al., 2012), ecohydrological processes (Adams et al., 2012), biogeochemical cycling (Edburg et al., 2012), disturbance dynamics (Bigler et al., 2005), and provision of ecosystem services to human populations (Anderegg et al., 2013b), including carbon sequestration (Allen et al., 2010; Pan et al., 2011).

Drought-induced dieback often manifests abruptly during drought events rather than gradually increasing throughout the duration of a

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prolonged drought (Allen et al., 2010; Carnicer et al., 2011; Anderegg et al., 2013a). This sudden increase in dieback in response to drought events is likely related to physiological tipping-points, or thresholds related to water-stress (Lenton et al., 2008). Plants are adapted to deal with water stress, but prolonged or severe drought stress can lead to xylem cavitation, diminishing water transport to leaves (Pockman and Sperry, 2000; Carnicer et al., 2011). Woody plants experience dieback after crossing a certain species-specific threshold of conductivity loss, resulting in apparently abrupt dieback at some point during the course of an extended drought (Urli et al., 2013). Given that physiological thresholds are species specific, die-off can be sudden and large-scale in forests dominated by a single species. Conversely, die-off in mixed species stands is more likely to occur gradually as species with lower water-stress tolerance succumb to drought-induced hydraulic failure first, followed by those with higher water-stress thresholds as drought intensity or duration increases (Bond and Kavanagh, 1999; Zweifel et al., 2009). Additionally, drought dieback in trees is not necessarily the result of hydraulic failure. Other mechanisms, such as carbon starvation resulting from stomatal closure in response to limited water availability, have been posited to play a role in forest die-offs (McDowell and Sevanto, 2010; Sevanto et al., 2014). Carbon starvation is more likely during prolonged drought events as plants can regulate carbon allocation, but ultimately metabolic needs will exceed input if stomatal closure is long term (McDowell, 2011). This could result in large increases in dieback beyond the initial die-off from hydraulic failure.

An additional concern arising from a potential increase in drought frequency, extent, and severity is the potential for woody plant – encroached semiarid and arid perennial savannas to transition to less productive shrub-dominated deserts with high levels of bare ground and low herbaceous cover (Bestelmeyer et al., 2013; Peters et al., 2013). This widespread conversion, occurring in perennial grasslands in Africa, Australia, and the Americas (D'Odorico et al., 2012; Peters et al., 2013), is thought to result from woody plant – driven redistribution of soil resources that results in so-called “islands of fertility” where high-resource soils occur under patches of shrubs and low-resource soil occurs in bare ground interspaces with limited perennial grass recruitment (Huenneke et al., 2002; Okin et al., 2009; Bestelmeyer et al., 2013). Desertification in these systems is thought to be exacerbated and potentially triggered by severe drought events that further reduce perennial grass cover, strengthening the positive feedback of resource distribution created by encroachment in arid grasslands (Kassas, 1995; Ludwig and Tongway, 1995; Huenneke et al., 2002).

We initially established this study to assess differences in dieback extent and pattern resulting from the droughts of the 1950s and the 2000s after observing a drought-induced die-off of woody plant species in an area where drought dieback had been assessed following a 1950s drought (Merrill and Young, 1959) and land use had remained consistent since that 1959 study. Precipitation in the 2000s was more variable than in the 1950s, but there were three drought episodes associated with woody plant dieback during the periods 1999–2000, 2008–2009, and late 2010 through the time the study was conducted. A comparison of patterns of woody plant dieback during the 1950s and 2000s (through 2011) droughts was detailed in Twidwell et al. (2014). Twidwell et al. (2014) showed that the extended severe drought of the 1950s resulted in greater levels of dieback than that observed in 2011, and that woody plant dieback resulting from periods of drought throughout the 2000s was highly species specific and dependent on topographic characteristics and land management. While high levels of woody plant dieback were observed, the system remained in a grass-tree codominated state in 2011. However, drought conditions persisted through early 2015 (Shaw, 2015). The extended duration of the drought created the potential for altered patterns of woody plant dieback from those observed in 2011 due to continued water stress. Thus, sampling at one point in time could provide a biased view of drought effects given the potential for lags in vegetation response to climatic variability (Goward and Prince, 1995; Bigler et al., 2007; Wu et al., 2015). Additionally, the initial

study did not explore the effect of drought on herbaceous cover or examine the effect of prolonged drought on grass-tree codominance.

Given the additional years of drought that occurred in the region following the initial study and the potential for lagged vegetation responses, this study was established to provide new insights into the role of drought in shaping semiarid Texas savanna. Specifically, our objectives were to test for the emergence of alternative vegetation trajectories with continued drought persistence: 1) whether additional woody plant dieback occurred from 2011 to 2013, leading to a grass-dominated community, or 2) whether desertification became a major feature in 2013 (defined as a loss of herbaceous cover and increase in bare ground), which was not observed while conducting the earlier study by Twidwell et al. (2014). We then discuss the potential to use signals of vegetation response as indicators for climate change adaptation in rangelands on the basis of lags in the response of different vegetation components in savanna to drought.

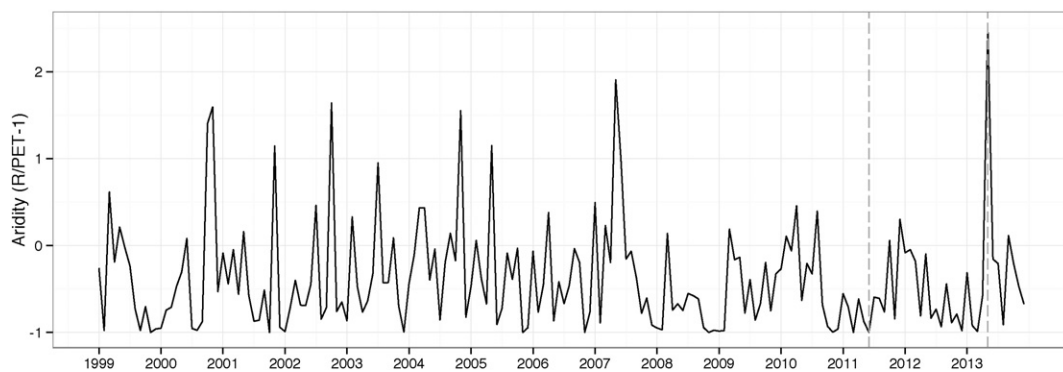
## Methods

### Study Site

This study was conducted at the Sonora, Texas A&M AgriLife Research Station (31°N; 100°W) on the Edwards Plateau of central Texas, United States. Long-term research on rangeland vegetation dynamics has been carried out for more than 90 years at the research station. Additionally, browsing manipulations have been consistently applied in some areas of the station since 1948 (Fuhlendorf and Smeins, 1997; Taylor et al., 2012). Mean annual precipitation is 570 mm (station records, 1919–2013) with high variability within and among years (range = 156–1054 mm). Precipitation is bimodally distributed with peaks occurring in May–June and September–October. However, precipitation is extremely variable and the area experiences frequent prolonged droughts during the summer months. The historically dominant community in the region was live oak savanna, but many areas, including the study location, have transitioned into closed canopy Ashe juniper (*Juniperus ashei* J. Buchholz) forest interspersed among open live oak (*Quercus virginiana* Mill.) savanna. The dominant woody plant species in the study location are live oak (*Quercus virginiana* Mill.), pungent oak (*Quercus pungens* Liebm.), Ashe juniper (*Juniperus ashei* J. Buchholz), Texas persimmon (*Diospyros texana* Scheele), *Celtis* spp., cat-claw (*Acacia greggii* A. Gray), algerita (*Mahonia trifoliolata* [Moric.] Fedde), and downy forestiera (*Forestiera pubescens* Nutt.).

### Experimental Design and Data Collection

In 1949, 10 (30.48 × 0.3048 m) transects were established to estimate the cover of woody plant species in six pastures with different grazing treatments at the Texas A&M AgriLife Research Station (Merrill, 1954). These transects were resampled in 1958 to determine the effect of the drought that occurred in 1951–1957 on woody plant dieback and cover (Merrill and Young, 1959). Three periods of drought throughout the 2000s led to observable large-scale dieback of woody plants in the study region. While precipitation was more variable in the 2000s than in the 1950s, there were several prolonged periods of below-average precipitation in the 2000s including late 1999–2000, 2008–2009, and late 2010–2013 (Fig. 1). Therefore, we decided to resample the pastures included in the Merrill study in June 2011 to compare woody plant dieback caused by the drought of the 1950s with the drought of the 2000s. Ten transects, each 30.48 m long and 0.3048 m wide, were randomly established in each of four pastoral units that have been managed consistently since Merrill and Young (1959) established their study in 1949. We established new transects because transects established in 1949 could not be relocated. Four of these pastoral units were included in the study: a livestock enclosure (accessible to native browsers but not livestock, a deer and livestock enclosure (not accessible to livestock or native browsers), and two pastures annually



**Figure 1.** Aridity index for the Sonora, Texas A&M Agrilife Research Center for 1999–2013. Aridity is defined as  $R/PET-1$ , where a value of 0 indicates rainfall equals potential evapotranspiration, negative values indicate a rainfall deficit, and positive values indicate a sufficient supply of rainfall. Vertical dashed lines indicate sampling periods.

stocked with goats (and accessible to native browsers) and managed under Merrill's four-pasture deferred rotation system since 1949 (Merrill, 1954). In May 2013, we resampled the transects established in June 2011 in order to explore the effects of the continued drought on dieback patterns in vegetation response following the initial 2011 data collection.

Following the sampling protocol of Merrill and Young (1959), woody plants intersecting each transect were classified as: plants alive, plants with main trunks or stems dead but with resprouting stems emerging from the base, and plants dead. Plants were assumed dead if they had no live foliage at the time of the sampling. Canopy cover of each woody species in the understory ( $< 2.1$  m) and overstory ( $> 2.1$  m) and total woody canopy cover were measured along each transect using the line-intercept method (Floyd and Anderson, 1987). Additionally, we measured cover of crown dieback by determining the portion of tree crown intercepting a transect that had no live foliage. A height of 2.1 m was chosen to separate understory and overstory woody plant layers to remain consistent with Merrill and Young (Merrill and Young, 1959). We measured cover of grass and bare ground when either intersected a transect for more than 0.25 m in length. Each transect was characterized as being located on one of three soils: deep Valera soils, which are typically found in the lowland areas; shallow Kavett soils, which are associated with upper divides; and rocky draws, which are large areas of exposed bedrock (sensu Twidwell et al., 2014).

#### Drought Severity

In order to determine the severity of the drought during the course of the study, we developed an aridity index for the Sonora, Texas A&M Agrilife Research Center. Using daily maximum and minimum temperature values from 1919 to 2013, we first computed the monthly potential evapotranspiration rate (PET) using the Hargreaves Equation as described by Maidment (1993). Next we computed cumulative monthly precipitation (R) from the daily values. We define the aridity index (Budyko 1974) as  $R/PET-1$ , where a value of 0 indicates rainfall equal to potential evapotranspiration, negative values indicate a rainfall deficit, and positive values indicate a sufficient supply of rainfall. We also calculated the monthly average divergence from the 30-yr normal monthly mean precipitation for the study region (obtained from the National Oceanic and Atmospheric Administration) for months starting at the beginning of the drought and ending at the time of the 2013 sampling (January 2009–July 2013).

#### Woody Plant Dieback, Woody Plant Cover, and Patch Relationships

First, we assessed differences in total number of woody plants (live, dead, and resprouting); total understory woody plants; and total overstory woody plants between 2011 and 2013. We used a generalized linear mixed-effect model with a poisson distribution to compare total count of woody plants across years as a fixed effect,

with a compound symmetric covariance structure to account for covariation between counts on a given transect in 2011 and 2013. We used a likelihood ratio test comparing the full model with a model reduced by the variable "year" to determine if there were significant decreases in live woody cover and dead woody cover between 2011 and 2013. We used data collected in 2011 and 2013 to assess whether the continued persistence of drought from 2011 to 2013 increased dieback of woody plants and further decreased woody cover. We calculated dieback in 2011 as the number of dead individuals divided by total individuals (live + dead in 2011). We calculated dieback in 2013 as the number of dead individuals in 2013 divided by total number of individuals in 2013 (live + dead in 2013). Dead individuals included only those with no live crown foliage or basal resprouting. This is consistent with calculations of dieback found in other studies of woody plant response to drought (Fensham and Holman, 1999; Allen, 2007; Koepke et al., 2010). We used a general linear mixed-effect model with a compound symmetric covariance structure to account for covariation between 2011 and 2013 data for a given transect to determine if significant increases in dieback had occurred during the 2 yr of drought subsequent to the 2011 sampling period. We looked at differences in total dieback and each dominant species individually. We included pastoral treatment (livestock exclusion, deer and livestock exclusion, and no exclusion); soil category (deep soils, shallow soils, and rock draws); and their interactions with year of sampling to determine if significant increases in dieback in 2013 differed among pastoral treatments or soils. We used a general linear mixed-effect model with a compound symmetric covariance structure to account for covariation between observations on the same transect at different times, together with a likelihood ratio test comparing the full model with a model reduced by the variable "year" to determine if there were significant decreases in live woody cover and dead woody cover between 2011 and 2013. Correlation among dieback of all individuals, understory woody individuals, and overstory woody individuals and the total woody plant cover, total grass cover, and density of patches of cover type along a given transect was determined using Spearman's rank correlation coefficient. We applied the Benjamini-Hochberg procedure for controlling the false discovery rate (rate of type I errors) given the multiple correlations explored. Density of patches of cover type is a measure of the configuration of woody brush and grass along a transect. We counted the number of distinct patches of woody plant cover and grass cover, which intersected the transect for more than 0.25 m, and divided the number by the total cover of woody plants along the transect. We excluded transects that had fewer than five trees to avoid the potential for a high-patch density to be the result of a single or several large trees on the transect. Using this index, we were able to characterize the extent of clustering of woody plants along the transect. Transects with higher patch density

had less clustering of woody plants and instead were composed of more evenly spaced woody plants separated by patches of open grassland.

### Comparing Grass Cover in 2011 and 2013

We used cover data collected during both sampling periods to determine the shift to an alternate state from one with grass-tree codominance to a bare ground – dominated desertified state in this semiarid savanna. We used a general linear mixed-effect model with a compound symmetric covariance structure to account for covariation between observations on the same transect at different times and a likelihood ratio test to determine if significant decreases in grass cover and increases in bare ground had occurred during the 2 yr of drought subsequent to the 2011 sampling period.

## Results

### Drought Severity

Throughout the 2000s, periods of severe droughts leading to woody plant dieback occurred in late 1999 – 2000, late 2007 – 2009, and late 2010 – 2013 (see Fig. 1). While precipitation is highly variable at the site during the 2000s, between late 2007 and 2013, only 9 out of 72 mo had a positive aridity index with the longest negative streak being 13 mo between late 2010 and 2012. Beginning in September 2010, precipitation at the station was below the 1981 – 2010 average for the area every month (Fig. 2). Then, late in 2011 and early in 2012, there were several months with higher than average monthly precipitation, but they were immediately followed by a period of 13 mo, during which precipitation in 11 mo fell below the monthly average and in 2 mo was slightly (< 25 mm) above (see Fig. 2). This 11-month stretch directly preceded the second sampling period in May 2013. Aridity was only slightly positive during 2 mo in the period between sampling dates.

### Woody Plant Dieback, Woody Plant Cover, and Patch Relationships

The continued persistence of drought from 2011 to 2013 did not increase dieback of woody plants or further decrease woody cover. In 2011, the drought of the 2000s had killed 22% of trees (128 of 580 individuals), decreasing woody cover on the transects from  $58\% \pm 4\%$  to  $41\% \pm 4\%$  (Twidwell et al., 2014). Dieback of all woody species present had only increased to 24% (142 out of 583 individuals) by 2013 after 14 additional mo of below-average precipitation in the study area (Table 1). This finding was not the result of new recruits that subsequently died given that total woody plant density along the transects did not differ between 2011 and 2013 (likelihood ratio  $X^2 = 2.12$ ,  $P = 0.15$ ). Similarly, it was not the result of woody plants recruiting into

**Table 1**

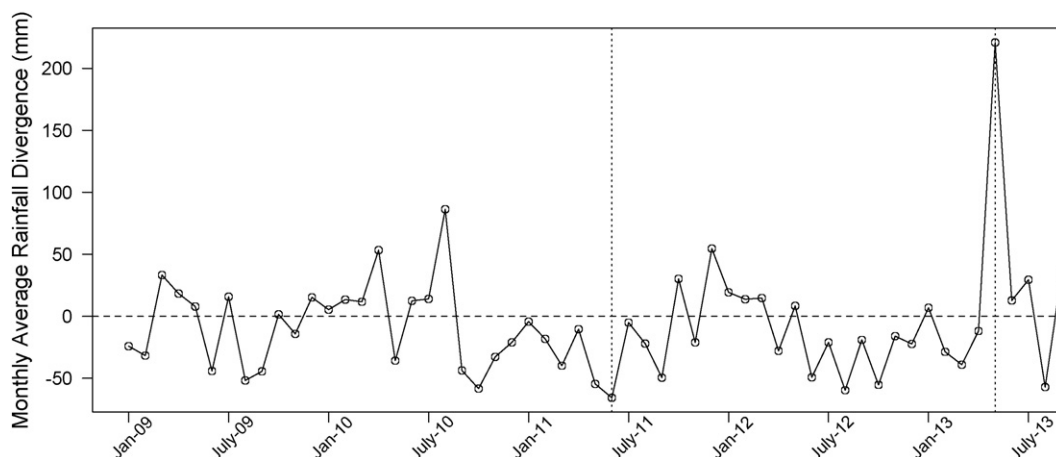
Differences in percent dieback observed in 2011 and 2013 for all species, Ashe Juniper (JUAS), Live Oak (QUVI), and Shin Oak (QUPI). Dieback in 2013 was the number of dead individuals in 2013 divided by total number of individuals in 2013 (live + dead in 2013). Dieback in 2011 was the number of dead individuals in 2011 divided by total number of individuals in 2011 (live + dead in 2011). Differences were estimated using a general linear mixed-effects model with a compound symmetric covariance structure among years, together with a likelihood ratio test comparing the full model with a model reduced by the variable “year” to determine if there were significant decreases in woody dieback between 2011 and 2013

	Estimated difference	Standard error	Likelihood ratio $X^2$	P value
All Species	3.19	9.58	0.70	0.95
JUAS	6.86	11.50	1.10	0.89
QUPI	1.78e-14	0.12	3.48	0.32
QUVI	1.79	13.63	2.86	0.58

the overstory category as total density of understory woody plants did not differ from 2011 in 2013 (likelihood ratio  $X^2 = 0.01$ ,  $P = 0.92$ ) and total density of overstory woody plants did not differ from 2011 in 2013 (likelihood ratio  $X^2 = 0.04$ ,  $P = 0.85$ ). Additionally, dieback of the dominant woody species did not increase significantly following the 2011 sampling period (see Table 1). Ashe juniper dieback increased from 21% to 25%, and Shin Oak dieback increased from 26% to 28%, but these increases were not statistically significant (see Table 1). Live oak dieback did not increase between 2011 and 2013 (see Table 1). Woody plant cover decreased from  $58\% \pm 4\%$  before the drought of the 2000s to  $41\% \pm 4\%$  in 2011 (Twidwell et al., 2014) but did not significantly decrease further between 2011 and 2013, when it fell to  $39\% \pm 4\%$ . Similarly, patterns of dieback did not differ from the patterns in 2011 with higher dieback in deep soils and no significant differences among pastoral treatments or between understory and overstory layers (Twidwell et al., 2014), which was not particularly surprising given that there was not enough additional woody dieback to alter patterns of dieback already established by 2011. Neither total, understory, or overstory woody dieback were correlated with total grass cover or total woody cover (Table 2). However, patch density was correlated positively with overall woody dieback ( $\rho = 0.674$ ,  $P < 0.001$ ), understory woody dieback ( $\rho = 0.432$ ,  $P = 0.028$ ), and overstory ( $\rho = 0.509$ ,  $P = 0.008$ ) woody dieback.

### Comparing Grass Cover in 2011 and 2013

The prolongation of drought conditions caused the system to move toward a community dominated by bare ground in the understory herbaceous layer. Grass cover decreased by  $48.2\% \pm 6.8\%$  between 2011 and 2013 (Table 3). Bare ground increased by  $74.4\% \pm 15.1\%$  between 2011 and 2013 (see Table 3).



**Figure 2.** Precipitation anomaly for the Sonora Agrilife Research Center during January 2009 through September 2013. Points represent monthly divergence from the 30-yr monthly average. Vertical dashed lines indicate sampling periods.

**Table 2**

Differences in grass cover, bare ground, live woody plant cover, and dead woody plant cover along transects between 2011 and 2013. Differences are estimated using a general linear mixed-effects model with a compound symmetric covariance structure among years, together with a likelihood ratio test comparing the full model with a model reduced by the variable “year” to determine if there were significant decreases in cover between 2011 and 2013

	Estimated difference	Standard error	Likelihood ratio $X^2$	P value
Grass	−9.17	2.54	30.56	< 0.001
Bare ground	9.17	2.54	30.56	< 0.001
Live woody	0.91	2.28	0.88	0.93
Dead woody	−0.54	2.84	0.11	1.00

## Discussion

Despite continued prolonged drought for almost 2 yr following the first sampling period in 2011, little additional woody plant dieback occurred between the 2011 sampling period and the 2013 sampling period. This is consistent with other observations of drought-induced dieback where episodic dieback occurred at some point during prolonged drought and little dieback occurred following the initial major dieback event (Suarez et al., 2004; Miriti et al., 2007; Koepke et al., 2010). This type of episodic dieback is consistent with theories of drought-induced hydraulic failure where a threshold of conductivity loss leads to dieback (Urli et al., 2013). While these physiological thresholds vary among species, they are fairly consistent within species because they are driven by the structure of the plant vessels and species-specific responses to reduced water availability (Miriti et al., 2007). On average, loss of 50% of stem conductivity has been found to lead to mortality in conifers while approximately 88% leads to death in many angiosperms (Urli et al., 2013). While physiological thresholds related to conductivity are consistent within species, the stress experienced by a plant during drought is mediated by the interaction of long-term land management practices and the topographic position on the landscape (Twidwell et al., 2014). Therefore, while dieback occurred for all of the dominant species at the site, location on the landscape drove intraspecific patterns of dieback. Regardless of differences in species and topographic position, woody plants that survived the first several months of drought were never pushed over the conductivity loss threshold. This could be the result of greater fluctuation in departure from monthly precipitation normals in the period following the 2011 sampling. Between 2011 and 2013, there was greater variability in precipitation than in the months preceding the 2011 sampling period, which were all far below monthly normals. Another possibility is that

**Table 3**

Spearman's correlation coefficients between percent woody plant dieback on a transect and percent grass cover, percent woody cover, and patch density (a measure of patchiness of woody plant distribution), respectively. P values are corrected using the Benjamini-Hochberg procedure for controlling the false discovery rate

	$\rho$	P
Grass Cover		
All individuals	0.075	0.829
Understory	0.033	0.879
Overstory	−0.122	0.680
Woody Cover		
All individuals	0.025	0.879
Understory	−0.226	0.360
Overstory	0.978	0.398
Patch Density		
All individuals	0.674	< 0.001*
Understory	0.432	0.028*
Overstory	0.509	0.008*

\* Indicates significant correlations.

the high initial dieback resulted in increased water availability for the remaining woody plants despite continued low levels of precipitation. This pattern of dieback with little additional die-off despite continued water stress suggests that carbon starvation was not the dominant mechanism for woody plant dieback observed at the study site. If carbon starvation were responsible for the die-offs observed here, the lengthened drought period would lead to additional dieback as plants exceeded their reserves of carbon and metabolic demands overtook the ability to survive with limited carbon inputs resulting from prolonged stomatal closure (McDowell and Sevanto, 2010; Sevanto et al., 2014). Carbon starvation is less likely in anisohydric species, like our dominant Ashe juniper, which do not regulate leaf water potentials through stomatal closure during periods of limited water availability (McDowell et al., 2008). This increases vulnerability to cavitation but makes carbon starvation less likely as respiration continues throughout the drought (Pockman and Sperry, 2000; McDowell, 2011).

Interestingly, despite a lack of correlation between total woody cover or total grass cover and levels of overstory or understory woody plant mortality, the distribution of woody plants along transects (patch density) did have a significant effect on woody plant dieback. Transects with higher patch density, which are characterized by more even spacing of woody plants, had more dieback than those with a patchy distribution of woody plants (low patch density). Transects with higher patch density, exhibiting lower dieback, have more trees neighboring open grass patches than other trees. Given this, density-dependent effects could be driving the correlation. One hypothesis for explaining inverse density-dependent mortality such as that observed here is that higher woody plant densities facilitate the growth and survival of small trees during drought, when large overstory trees are present. As stress increases, facilitation becomes more important for these individuals (Holzapfel and Mahall, 1999). An alternate hypothesis states that the negative relationship between drought-induced mortality and woody plant density occurs because marginal microsite conditions, which are only able to support low densities of woody plants, experience higher mortality rates than more suitable microsites capable of supporting higher densities (Greenwood and Weisberg, 2008). Correlation between woody plant distribution and dieback is consistent with the finding in Twidwell et al. (2014) that dieback is highly dependent on topographic characteristics of the landscape because woody plant distribution has also been shown to be highly dependent on topographic mediation of resource distribution (Wu and Archer, 2005).

While there was little additional dieback of woody plants during the 2 yr of drought between sampling periods, grass cover declined precipitously. This decline occurred despite a release from competition with trees for light and soil moisture attendant to the 24% decrease in woody plant canopy cover from predrought levels. Given water stress and dieback during the period from 2011 to 2013, grasses were unable to expand into gaps created in loss of Ashe juniper canopy as they did in *Juniperus monosperma* woodland after drought dieback in Arizona (Kane et al., 2011). Grass dieback resulting from prolonged drought is consistent with findings of drought-induced mortality of *Bouteloua gracilis* following severe drought in New Mexico (Allen, 2007) and large-scale mortality of multiple grass species in Arizona throughout a prolonged drought (McAuliffe et al., 2006). However, grasses are highly responsive to fluctuations in precipitation. Dieback observed during drought here is not necessarily indicative of mortality because, even with extensive leaf senescence, grasses can regrow if meristematic tissues remain intact (Volaire et al., 2009). Therefore, grass cover can rebound quickly following an influx of precipitation in the region. In fact, grass production recovered in this system after the longer, more severe drought of the 1950s once precipitation deficits were overcome in the region (Fuhlendorf and Smeins, 1997; Fuhlendorf et al., 2001).

Differences in response to prolonged drought stress between grasses and woody plants highlight the specificity of physiological stress

tolerance. The physiological characteristics of different plant functional types lead them to respond differentially to pulse stressors of varying severity and duration (Schwinning and Sala, 2004). As a result, the interaction between functional groups with unique stress-tolerance thresholds and spatiotemporal partitioning of resource availability drives community dynamics and structure in semiarid and arid systems (Chesson et al., 2004; Schwinning et al., 2004; Knapp et al., 2008). Thus, a dramatic shift in spatiotemporal patterns of precipitation in semiarid regions due to climate change could lead to community composition or even structural shifts depending on mortality and replacement dynamics of the species present at the start of major drought events (Miriti et al., 2007). The balance between grass and woody plants in savanna systems is thought to be greatly influenced by climatic variables (Walker et al., 1981; Walker and Noy-Meir, 1982; Scholes and Archer, 1997; Fensham et al., 2005; Bond, 2008). Arid environments with unpredictable precipitation patterns favor grasses over trees because grasses can take advantage of pulses of precipitation more readily than woody plants (Scholes and Archer, 1997; Chesson et al., 2004). However, as we observed in this study, under severe prolonged drought, grasses experienced high levels of dieback while trees died back in large numbers initially, but little additional dieback occurred with prolonged severe drought. This has potential implications for grass–tree dynamics in savannas in the future with global climate change. While grasses are favored by pulsed rainfall events (Dodd and Lauenroth, 1997; Schwinning and Sala, 2004), trees in semiarid areas might be more adapted to withstand long-term drought conditions (Schwinning et al., 2004; Bréda et al., 2006). Therefore, potential for shifts in dominance to grasses from woody-plant dominated semi-arid savannas under changing climatic conditions will largely depend on patterns of precipitation and drought events. Our study highlights the potential for prolonged drought to reinforce woody dominance in woody plant – encroached grasslands as grasses experience high levels of dieback throughout the drought while trees persist after an initial moderate pulse of dieback.

Prolonged severe drought has the potential to lead to desertification as grass–tree codominated communities (e.g., savannas) transition to less productive ones with low grass cover and high bare ground cover (Okin et al., 2009; Peters et al., 2015). Feedbacks between drought-adapted woody plants and soil resources have been shown to lead to broad-scale shifts from perennial savanna to xerophytic woody plant and bare ground – dominated shrublands (Bestelmeyer et al., 2011, 2013). This type of desertification has been observed in perennial grasslands and savannas globally (Peters et al., 2015). In the southwestern United States, invasion of shrubs into the black grama grasslands of the Jornada Basin occurred abruptly and has proven difficult to reverse (Bestelmeyer et al., 2013). The mechanisms of desertification are currently debated but are largely thought to occur as a result of resource concentration by woody plants (Okin et al., 2001). This creates a feedback that increases growth and recruitment of woody plants and limits perennial grass recruitment (Scheffer and Carpenter, 2003). This process is thought to be exacerbated and potentially triggered by extreme drought events that further reduce perennial grass cover and strengthen the shrub–soil–resource feedback (Peters et al., 2015). In semiarid Texas savanna, data collected following the 1950s drought at our study site suggests that desertification is short-lived and grasses will quickly rebound once the drought subsides (Fuhlendorf and Smeins, 1997; Fuhlendorf et al., 2001). We expect similar vegetation recovery following this present drought. One difference, however, is that woody plant abundance was considerably lower at this site during the 1950s drought (averaging 12% [Smeins and Merrill, 1988]). Woody plant cover is now 41%, and juvenile *Juniperus ashei* trees showed the highest rates of survival among the dominant tree species present at the study site (Twidwell et al., 2014). An outstanding question is therefore whether this drought, combined with high survival and future encroachment of juvenile *J. ashei*, will set the stage for a shift toward a less productive bare ground and woody plant – dominated community.

## Management Implications

Considerable scientific effort has focused on identifying ecological indicators that can be used to guide adaptation measures in the face of future drought and climate change (Bella et al., 1994; Maestre and Escudero, 2009; McKenzie et al., 2012). However, it has been difficult to identify indicators that can serve as signals within a time frame that matches the short-term decision making structure of rangeland managers. In savannas, we propose that woody plant dieback has the potential to be used as an indicator to adjust management for ecosystem services dependent on the herbaceous layer (e.g., livestock production). Dieback in woody cover preceded large losses in herbaceous cover during the prolonged severe drought of this study. This finding is corroborated by a 3-yr lag in grass basal area, which is correlated with cover, that was observed at this study site following droughts in the 1950s and 1980s (Fuhlendorf and Smeins, 1997; Fuhlendorf et al., 2001). The earlier onset of woody plant dieback in this system can be used as an indicator for considering herd size adjustments to accommodate major changes in the forage resource. While managers still have to deal with the decrease in aboveground net primary production that occurs at the onset of the drought, considerable dieback in the woody component signals the potential for future desertification. Increasing interspaces among grasses as a result of desertification can result in negative feedbacks as lower infiltration leads to runoff of water and soil nutrients (Peters and Havstad, 2006). This can lead to lower reestablishment rates of new individuals as resources are not available in grass interspaces for germination even after drought is alleviated (van de Koppel and Rietkerk, 2004). It is under these conditions that livestock operations have faced longer, slower recovery (Castellano and Valone, 2007). Avoiding the tendency to overgraze during severe drought has been shown to lead to faster recovery once the drought is alleviated (Albertson et al., 1957; Fuhlendorf et al., 2001). However, adaptation measures require timely signals to allow managers time to react to changing conditions. Large-scale woody plant dieback might therefore have potential utility as an ecological indicator for timely response to drought, as it provides a signal for managers to initiate earlier adaptation measures.

The long-term research conducted at this study site provides rangeland managers with an expectation of likely trajectories of plant communities to severe prolonged droughts, which are projected to become more frequent in this region as a result of future climate change. Multiple episodic droughts have caused woody plant dieback in the past several decades, but this system has remained woody dominated and has not transitioned to a more grass-dominated community. Instead, continued persistence of the most recent drought resulted in declines in grass cover between 2011 and 2013 and, for now, the emergence of a *Juniperus-Quercus* – mixed-shrub community with high bare ground. Given the high survival of *J. ashei* juveniles during this drought period, rangeland managers should not lose sight of the bigger threat to grassland productivity in this region—woody plant encroachment (Fuhlendorf et al., 2008; Twidwell et al., 2013)—when making near-term adjustments in grazing management in response to drought.

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