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Original Research

Persistence of a Severe Drought Increases Desertification but not Woody Dieback in Semiarid Savanna☆

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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.

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 topoedaphic 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., catclaw (*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 exclosure (accessible to native browsers but not livestock, a deer and livestock exclosure (not accessible to livestock or native browsers), and two pastures annually

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