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Drought-induced woody plant mortality in an encroached semi-arid savanna depends on topoedaphic factors and land management

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Nomenclature
Cronquist (1981)

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Abstract

Questions: How do recent patterns of drought-induced woody plant mortality in Texas semi-arid savanna compare to the extended drought of the 1950s? Does the relative composition of the woody plant community shift ubiquitously across the landscape following woody plant mortality and dieback or are shifts dependent on differences among species, soils, land use and plant demography?

Location: Texas Agrilife Research Station, Sonora, Texas, USA (30.1° N 100.3° W).

Methods: Following an exceptional drought from 1951 to 1957, a study was conducted to quantify rates of mortality for various woody plant species. In 2011, we repeated this study within three long-term grazing treatments that were established in 1948. Ten transects were established in each treatment to quantify the frequency and cover of live and dead woody individuals for all woody species. Rates of woody plant dieback were determined for each species and tested for differences among height classes, soil categories, total woody densities and pastoral treatments.

Results: Flash droughts (defined as rapidly intensifying droughts characterized by moisture deficits and high temperatures) from 2000 to 2011 were the second most severe since 1919 (low PDSI = −4) and were only surpassed by the prolonged drought from 1951 to 1957 (low PDSI = −5.17). Drought-induced shifts from one woody plant community to another did not occur uniformly across the landscape. Instead, high mortality rates of mature *Juniperus ashei* trees in deep soils (67.3%, 33 of 49 trees), combined with the recruitment of *Quercus* species where grazing had been excluded for the last 60 yr, were the only patch types to shift from a *Juniperus–Quercus* woodland to an alternate state.

Conclusions: Flash droughts since 2000 resulted in significant mortality and dieback, but dieback in cover was 28% higher following the more severe drought of the 1950s. Legacies from long-term land management practices interacted with localized differences in topoedaphic factors to drive patch-level shifts in woody vegetation following drought.

Introduction

Over the next century, drought events are expected to increase in frequency and duration for many arid and semi-arid regions (IPCC (Intergovernmental Panel on Climate Change) 2007), potentially leading to heightened rates of woody plant mortality and dieback (Allen 2009; Kintisch 2009). Prolonged drought events are expected to increase in the southwestern USA (Gutzler & Robbins 2011), and greater intra-annual variability in precipitation is expected to increase the frequency of extreme climatic episodes in nearby regions (Knapp et al. 2008). With similar climatic extremes anticipated in arid and semi-arid regions of Africa, Asia and Australia (IPCC 2007), there has been increased global recognition of widespread woody plant dieback, or shrub/tree retraction, as a poten-

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tial consequence of future climate change (Fensham et al. 2009). Around the world, drought-induced woody plant dieback has already emerged as an important determinant of rapid plant community shifts in areas with a recent history of woody plant encroachment (Fensham et al. 2009; Bowker et al. 2012). These shifts in vegetation types may swiftly alter the properties and processes within vast semi-arid ecosystems, affecting land–atmosphere feedbacks, carbon and water cycles and disturbance dynamics (Breshears & Allen 2002; Huxman et al. 2005; Allen 2007).

As society becomes confronted with more frequently occurring climatic extremes, it will become increasingly important to understand, predict and plan for major shifts in vegetation (IPCC 2007). Many regional planners rely on predictive climate models, such as species biometric climate models and dynamic global vegetation models (DGVMs), as the basis for understanding climate-induced shifts in vegetation and to develop mitigation efforts (Woodward et al. 1995). However, model projections carry with them a great deal of uncertainty (Allen et al. 2010; McDowell et al. 2011). For example, models of shifts in woody vegetation are dependent on studies that quantify the rates and agents of vegetation change (Fensham et al. 2005), yet experimental data and field observations on woody plant die-off from drought are relatively scarce at both population and ecosystem levels (Allen et al. 2010; McDowell et al. 2011). In addition, such models are typically based on overstorey die-off of woody plants, the most prominent visual feature of the landscape, but it is the loss of juvenile seedlings and saplings that generates the most significant long-term ecological impact by altering demographic, compositional and successional trajectories of the vegetative community (Engelbrecht & Kursar 2003). Current predictions from these models are also at a relatively coarse spatial resolution, which can misrepresent the spatial scale relevant to drought-induced vegetation change in areas where fine-scale variation in topoedaphic factors correspond with variable patterns of tree mortality (Peterman et al. 2013). Addressing these knowledge gaps is therefore critical to refining model predictions of climate-induced vegetation change.

We established this study to assess patterns of woody plant mortality in response to recent flash drought events (defined as rapidly intensifying droughts characterized by moisture deficits and high temperatures; Peters et al. 2002) that have not been observed in Texas for over 50 yr. The last time high rates of woody plant mortality were observed in this region following periods of severe water deficit was after the drought of 1951–1957 (Merrill & Young 1959). A field survey following the 1950s drought showed woody plant cover in *Quercus* savanna decreased 44%, with observed patterns of mortality varying among species and topoedaphic factors (Merrill & Young 1959). Our study is identical to this earlier field survey and is being conducted at the same long-term experiment research site following decades of juniper encroachment. Our study therefore provides a unique opportunity to compare patterns of woody plant die-off before and after juniper encroachment for two of the most exceptional droughts that have occurred over the last 100 yr in the south-central United States. The objectives of this study are to use current and historic field observations from the same research site to address the following questions: (i) how do recent patterns of drought-induced woody plant dieback in Texas semi-arid savanna compare to the exceptional drought of the 1950s; and (ii) does the relative composition of the woody plant community shift ubiquitously across the landscape or are shifts dependent on differences among soils, land use and plant demography? We expand upon our findings and the study of the 1950s (Merrill & Young 1959) to discuss the challenges associated with developing predictions of future vegetation change in this region.

Methods

Study area

We conducted this study at the Sonora, Texas Agrilife Research Station (31° N, 100° W) on the Edwards Plateau, where long-term research on vegetation dynamics has been occurring for over 90 yr and experimental treatments featuring different browsing manipulations have been consistently applied in some pastoral units since 1948 (Fuhlendorf & Smeins 1997; Taylor et al. 2012). The research station (730 m a.s.l., mean frost-free period 240 d) has a mean annual precipitation of 570 mm that is highly variable (range = 156–1054 mm for 1919–2011).

The Edward Plateau ecoregion (i.e. the 'Hill Country') has gently rolling hills with different soil types in close proximity to each other. Shallower Tarrant soils are generally located on hilltops and hillsides and feature a subsoil of porous, fractured limestone. Valera soils occur in the depressions and narrow valleys between hills and sit on petrocalcic horizons 76–91 cm below the soil surface (USDA-NRCS Official Soil Series Descriptions). A petrocalcic horizon is a cemented or hard dolostone layer that can be nearly impenetrable to tree roots (Wilding 1997; Schwinning 2008). Kavett soils (formerly considered a shallow type of Valera soil) also feature a petrocalcic horizon but at a shallower depth of 40–48 cm (USDA-NRCS Official Soil Series Descriptions). Kavett soils are shallow, well-drained soils located on slopes of 0–5%.

Overview of Merrill's 1950s study

In 1949, ten belt transects, 30.48-m long and 0.30-m wide, were established in each of six pastoral units to estimate

the cover of woody plant species at the Texas A&M Agrilife Research Station (Merrill & Young 1959). The dominant woody plant species were *Quercus virginiana* Mill., *Quercus pungens* Liebm., *Diospyros texana* Scheele, *Juniperus ashei* J. Buchholz, *Celtis* spp., *Acacia greggii* A. Gray, *Mahonia trifoliolata* (Moric.) Fedde, *Zanthoxylum fagara* (L.) Sarg., *Forestiera reticulata* Torr. and *F. pubescens* Nutt. Canopy cover of *Juniperus* species was <1% at the time (Merrill & Young 1959). Following the multi-year drought from 1951 to 1957, transects were re-sampled to determine the effect of the drought on woody plant mortality and cover. Woody plants located along each transect were identified to species and classified into three categories: (i) plants alive, (ii) plants with trunks or stems dead but with resprouting stems from the base and (iii) plants dead. Canopy cover was measured for each species in the understorey (<2.1 m) and overstorey ($\geq$2.1 m) layers, and total woody canopy cover was measured along each transect using the line-intercept method.

Data collection

We repeated the design and sampling protocol of Merrill & Young (1959) by establishing 40 belt transects, each 30.48-m long and 0.30-m wide, in four pastoral units that have been managed consistently over the past 60 yr using the treatments the authors established prior to their study in 1949. Ten transects were established in each pastoral unit. We established new transects because the exact locations of the previous transects are no longer known. Transects were randomly established in parallel directions with a minimum of 50 m between transects. Pastoral units were each 40 ha and included a livestock exclosure unit, a high-fenced livestock and deer exclosure unit, and two units that have been annually stocked with livestock under Merrill's four-pasture deferred rotation system (Merrill 1954). Merrill's four-pasture system rotates three herds of livestock among four pastoral units. At any point in time, one pasture is being rested and three pastures are being grazed. In this study, pastoral units are grazed for 12 months and then rested for 4 months. One herd is rotated to a rested pasture every 4 months. Animal units from 1948 to 1982 averaged 32 auy·section^{-1} (640 acres per section). The stocking rate was reduced to 25 auy·section^{-1} during the 1980s, and again in 2000 to 16 auy·section^{-1} due to an increase in *Juniperus* and drought.

In June 2011, following the sampling protocol of Merrill & Young (1959), woody plants intersecting each transect were identified to species and classified into the same health categories as the 1950s analysis: (i) plants alive, (ii) plants with trunks or stems dead but with resprouting stems from the base and (iii) plants dead. Canopy cover of each species in the understorey (<2.1 m) and overstorey ($\geq$2.1 m) layers and total woody canopy cover were measured along each transect using the line-intercept method. Only canopies intersecting at least 0.10 m of the transect were recorded. Measures of cover reached an endpoint when a gap in the canopy of at least 25 cm occurred, meaning that measurements of canopy cover occurred multiple times for individual trees with gaps in the canopy >25 cm. A height of 2.1 m was chosen to separate understorey and overstorey layers to remain consistent with Merrill & Young (1959). Each transect was characterized as being located on one of three soil categories: deep soils, which are typically Kavett and Valera associations found in the lowland areas; shallow soils, which are typically Tarrant soils associated with upper divides; and rock draws, which are large areas, typically >30 m × 10 m, of exposed bedrock and rock outcrops found at any topographic position.

Data analyses

Measurements of canopy cover for each live and dead individual were used to estimate total cover along each transect prior to the drought. Because cover was measured for each individual, the total cover for each transect was calculated as cover of all individuals minus distances where canopies of individual trees overlapped. Percentage reduction in canopy cover was calculated based on comparing our estimate of pre-drought cover with the total cover of live woody plants measured after the drought. Differences between pre-drought and post-drought canopy cover values were analysed using Student's *t*-test at an alpha of 0.05.

Dieback was calculated as the proportion of dead individuals in 2011 relative to the total number of woody plants that occurred prior to the drought (total before drought = alive trees + dead trees in 2011). This definition of dieback is consistent with multiple other studies that have used the term to characterize tree death, stem death or loss of canopy foliage (Rice et al. 2004; Allen 2007; Koepke et al. 2010). Such an approach assumes (i) no recruitment of new individuals after drought-induced mortality of woody plants was first observed (in the year 2000 at this site), and (ii) all mortality was a function of the drought. These assumptions are reasonable in the present study because (i) recruitment of new woody plants is severely limited in the pastoral units sampled because the communities had already reached a highly encroached steady state of *Juniperus–Quercus* woodland prior to the drought; (ii) few juvenile trees were recorded during our sampling efforts; and (iii) tree mortality is rarely observed at this site in years without drought.

Differences in dieback among species, height classes, soil categories and pastoral treatments were analysed using

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Pearson's chi-squared test with an alpha level of 0.05, using the R statistical computing package (R Foundation for Statistical Computing, Vienna, AT). For each comparison, dieback data were pooled for all transects within a given category. Categories were omitted from analyses when their total sample sizes were ≤ 5. Identical results were obtained when statistical output for chi-square tests were compared to results obtained for Fisher's exact test (data not shown), which is often preferred over chi-square tests when sample sizes are low (Fisher et al. 1990). We used chi-square over traditional one-way ANOVA because using ANOVA would require pseudo-replication of this 1940s experimental design (treatments are at pastoral level, $n = 1$). Moreover, dieback was calculated in this study as proportions and chi-square is typically preferred over ANOVA for proportion data (Fienberg 1979; Zar 1984).

Density-dependent mortality resulting from the drought was tested for each species. The proportion of variation (R^2) in mortality of (i) all individuals, (ii) understorey individuals and (iii) overstorey individuals explained by the total number of woody plants along a given transect was determined for each species. For illustration purposes, only significant relationships ($P < 0.05$) are shown and discussed.

Palmer drought severity index (PDSI) values were computed for the history of the Sonora, Texas Agrilife Research Station using the self-calibrating Palmer drought severity index (SC-PDSI; available at http://greenleaf.unl.edu/). On-site weather records dating back to 1919 were used to calculate weekly PDSI values. This PDSI method can overestimate changes in drought occurring over time because it uses a simplified model of evapotranspiration (Sheffield et al. 2012). However, historical on-site weather records were not available to use more physically complex PDSI methods (e.g. Penman–Monteith equation; Shuttleworth 1993). The SC-PDSI requires the user to input a single value corresponding to the available water capacity of the site. We used the available water capacity of Tarrant soils (8 mm·cm^{-1}; USDA-NRCS Official Soil Series Descriptions), the dominant soil type in this region (USDA-NRCS Official Soil Series Descriptions).

Results

The PDSI from on-site records since 1919

The drought of the 1950s was more prolonged and severe than any period since the station was established in 1919 (Fig. 1). For 132 consecutive weeks (1951–1954), PDSI values were less than or equal to −3 (the PDSI value associated with 'severe drought'; Heim 2002). In fact, 99 of the top 100 drought weeks, according to PDSI calculations from 1919 to 2011, occurred between 1951 and 1956.

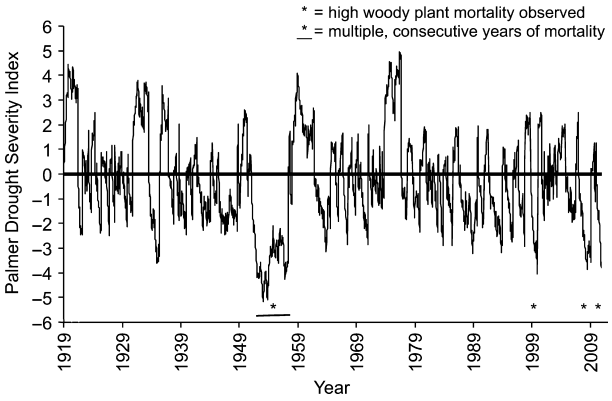

Fig. 1. Weekly Palmer drought severity index (PDSI) values from 1919 to 2011 at the Sonora, Texas Agrilife Research Station, and years when drought was known to cause high levels of woody plant mortality.

Ninety-seven of those weeks had PDSI values less than or equal to −4. This extended drought period was followed by a second severe drought (PDSI ≤ -3) that occurred for 32 consecutive weeks from 1957 to 1958. In more recent years, PDSI values have exhibited high intra-annual variability, with severe but short flash droughts occurring in 2000, 2008, 2009 and 2011 (Fig. 1).

Patterns of vegetation change

Drought events since 2000 killed 22% of woody plants (128 of 580 individuals died), which significantly decreased woody plant cover from 58 ± 4% to 41 ± 4% ($t = 2.78$, df = 78, $P = 0.007$) in this *Juniperus–Quercus* woodland. Woody plant mortality occurred throughout the landscape (33 of 40 transects). Woody plant mortality was significantly higher in deep soils than in the other two soil types (Fig. 2). Dieback did not differ among pastoral treatments or between understorey and overstorey layers (Fig. 2).

Even with high woody mortality, vegetation shifts where the density of a subdominant species displaced *Juniperus* as the dominant species were uncommon. Vegetation shifted in deep soils within the livestock–deer exclosure treatment from a *Juniperus*-dominated overstorey to a *Q. virginiana*-dominated overstorey with a diverse mixture of small shrubs dominating the understorey (Fig. 3). In contrast, patches of vegetation in deep soils with both deer and goats continued to be dominated by *Juniperus* (Fig. 3), albeit at lower densities, because long-term exposures to high densities of browsers reduced the abundance of the subdominant short-growing woody species. Vegetation shifts were not observed in other patch types (Fig. 3). In the forthcoming section, we evaluate species-level responses to the drought to explain the differential patterns of dieback observed across the study area.

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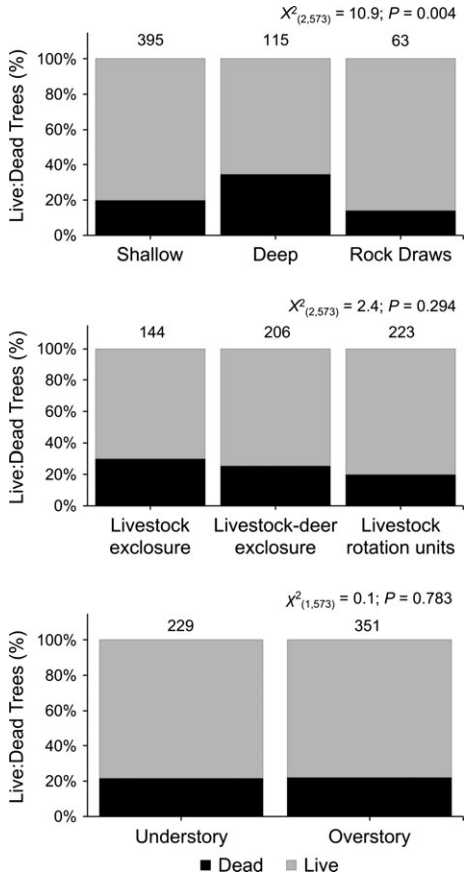

Fig. 2. Differences in the proportion of live and dead trees among soil types, livestock management histories, and tree height classes (total sample size shown above columns).

Species-specific patterns of dieback and interactions with edaphic factors

Three of the four dominant species in this study area exhibited context-specific patterns of dieback across soils, pastoral treatments and woody plant densities. *Juniperus* dieback differed among soil types (Fig. 4) but not pastoral treatments (Fig. 5). *J. ashei* was the only species that tended to have higher mortality for trees in the overstorey than in the understorey (Fig. 4). This relationship was magnified in deep soils (Fig. 4), leading to dissimilar levels of overstorey mortality across soil types (χ^2 = 51.1, df = 2, $P < 0.001$). In comparison, understorey mortality of *Juniperus* was not significantly different among soil types (χ^2 = 4.1, df = 2, P = 0.13). *Q. pungens* and *Diospyros* dieback differed among pastoral treatments, but exhibited contrasting patterns. *Q. pungens* mortality was highest within the livestock exclosure (Fig. 5) when transects were located in shallow soils where woody plant density was low relative to other areas [nearly all *Q. pungens* trees were located on shallow soils (116 of 123; Fig. 4) and mortality of understorey *Q. pungens* trees on shallow soils was negatively related to total woody plant density; R^2 = 0.55; $P < 0.05$]. The same outcome would be expected in similar areas in other treatment units (e.g. livestock rotation treatment), but long-term browsing masked this effect by greatly lowering the abundance of understorey *Q. pungens* plants within the livestock rotation units compared to other pastoral units (Fig. 4). Opposite mortality patterns were observed for *Diospyros*, which was the least abundant species of those that were killed by the drought and was predominantly found on both shallow and deep soils (Fig. 4). *Diospyros* dieback was highest in the livestock rotation treatment, whereas low rates of mortality were observed in the livestock exclosure (Fig. 5). *Q. virginiana* dieback did not differ among soil types, height classes or pastoral treatments (Figs 4,5). Other species were in low abundance ($n < 13$) and were not killed by the drought.

Discussion

Over the last 60 yr, only the severe drought of the 1950s and the flash droughts from 2000 to 2011 were known to cause significant levels of woody plant mortality in this ecosystem (Fig. 1; observations from C.A. Taylor Jr, site superintendent, and his conversations with L. Merrill, previous site superintendent). The extended drought of the 1950s was more severe than any period before (dating back to 1919) or after (to 2011; Fig. 1). Measurements taken after the 1950s drought ended showed woody plant cover had decreased 44% compared to pre-drought estimates taken in 1949 (Merrill & Young 1959). In comparison, we estimate droughts since 2000 have reduced woody plant cover by 16%, about one-third of the reduction observed following the 1950s drought. However, the current drought continued many months beyond our June 2011 sampling date, which may have resulted in additional mortality.

A common finding between this study and Merrill & Young's (1959) was that patterns of dieback for individual species were contingent on interrelationships among topo-edaphic factors. However, differential mortality among livestock treatments was not observed for any species following the 1950s drought (Merrill & Young 1959), likely because livestock treatments were established in 1949 and effects of browsers on woody plant recruitment had yet to cause changes to the composition of the woody plant community. Considering that dieback differed among livestock treatments in 2011 for *Q. pungens* and *Diospyros*, long-term livestock management practices can alter the trajectory of drought-induced change for some species.

Taller, overstorey trees were more vulnerable to drought than understorey shrub species. A total of 54% of

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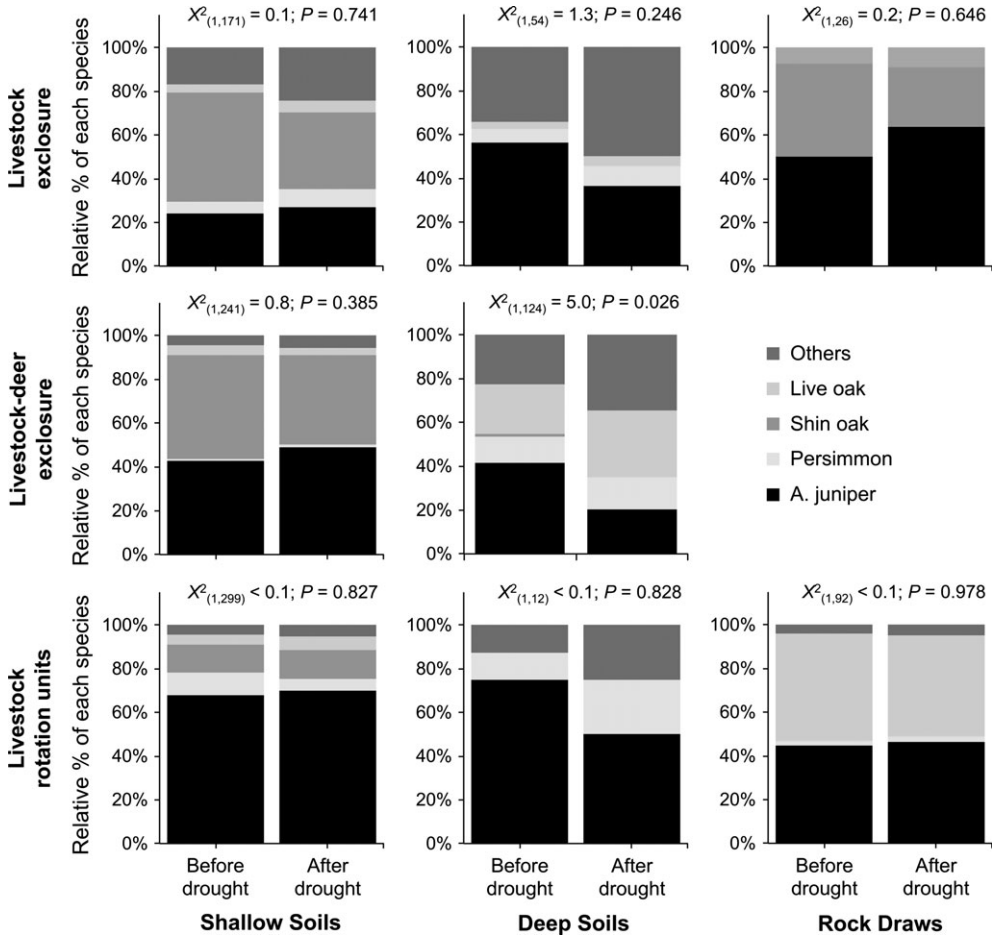

Fig. 3. Drought-induced vegetation shifts of the relative density of woody species before and after the drought for patches in different soil types and livestock management treatments. No transects occurred on rock draws in the livestock-deer exclosure.

Q. virginiana trees had died by 1958 vs 14% by 2011, while *Q. pungens* mortality was similar after both droughts (30% in 1958, 32% in 2011). *Juniperus* was the only woody plant to have higher mortality in the overstorey than in the understorey, a trend observed following both droughts. The most striking difference between the droughts of the 1950s and 2000s was that *Diospyros*, which was not killed in the drought of the 1950s and subsequently doubled in relative abundance from 1949 to 1958, was the least drought resistant species in 2011. No individuals of other shrub species were killed in either drought period.

The relative abundance of woody plants in our recent survey changed considerably from Merrill and Young's initial study on the effects of the 1950s drought on woody plant mortality (Merrill & Young 1959). Prior to the drought, total woody cover was estimated to be 12% (Smeins & Merrill 1988). *Q. virginiana* and *Q. pungens* dominated the woody plant community, collectively accounting for 90% of the relative cover of all woody plants, and *Juniperus* was rare (2% relative cover in 1949 and 1958; Merrill & Young 1959). By 2011, the plant community had transitioned from a *Quercus* savanna to a *Juniperus* woodland interspersed with clusters of *Quercus* trees in the overstorey and various understorey shrubs. Total woody cover was 58 ± 4% before the flash droughts and only dropped to 41 ± 4% after them in 2011. *Q. virginiana* and *Q. pungens* accounted for only 18% of the relative cover, whereas *Juniperus* had increased to 68% of the relative cover of all woody plants. *Diospyros*, the most frequently occurring shrub in 1949 and 2011, had the same relative cover in 1949 and 2011 (4%).

Pattern and scale of state change

The findings of this study and that of Merrill & Young (1959) indicate that the exceptional drought events in the 1950s and 2000s caused major vegetation shifts in patches within the western Edwards Plateau landscape, but not at the community level. Shifts in community types occur when a dominant species becomes a subdominant species

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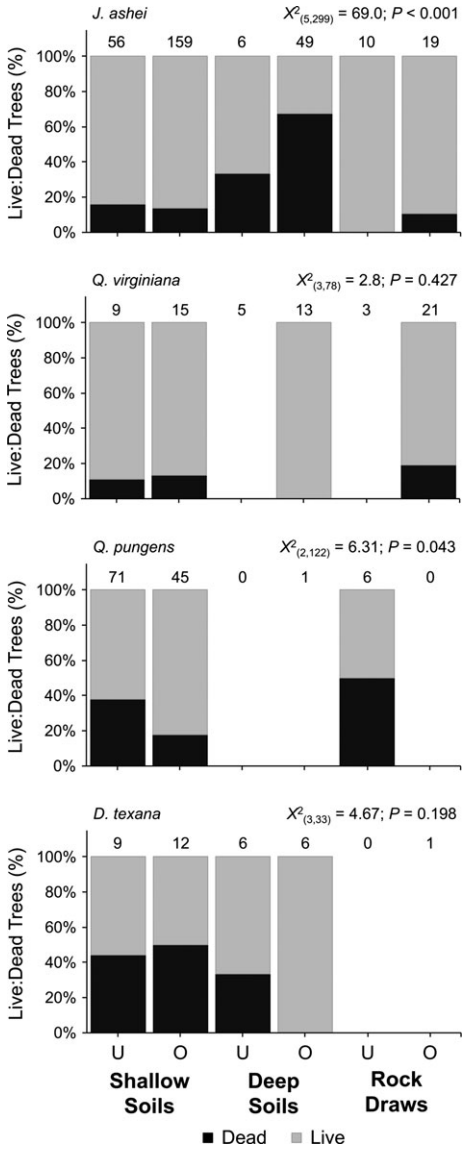

Fig. 4. Differences in the proportion of live and dead trees for understory (U) and overstory (O) individuals of each species across soil categories (total sample size shown above columns). Data were excluded for cases where the expected values were too low to include in chi-square tests.

(Allen & Breshears 1998). This type of vegetation shift was not observed following droughts in the 1950s or 2000s. In both cases, there was no change in the dominant woody species. Even with reductions in cover of 44% and 18% following the droughts of the 1950s and 2000s, respectively, the community did not transition to a grassland or savanna state or an alternate woody-dominated plant community. Rather, the system remained as a *Quercus* savanna in 1958 (Merrill & Young 1959) and a *Quercus–Juniperus* woodland in 2011. Studies at this site instead suggest that drought-induced shifts in woody vegetation are primarily driven by major differences in ecohydrology among the highly heterogeneous soil types of the Edwards Plateau and the water use strategy of the dominant woody species.

The patterns of woody plant die-off observed here may reflect feedbacks between topoedaphic factors and species-specific water regulatory pathways. Drought-induced tree mortality is directly affected by rooting zone available water and the efficiency with which plants utilize this water during drought. Collectively, topoedaphic factors (soil depth, soil texture and its topographic location) and plant specific traits will affect patterns and rates of mortality within a site under the same drought event (Peterman et al. 2013). For the two main soil types in this site, water flows more readily through coarse-textured Tarrant soils as it escapes through cracks in the limestone fragments, while water remains trapped by the petrocalcic horizon in the finer-textured Valera and Kavett soils. This contributes to decreased available water capacity of Tarrant soils relative to Kavett–Valera soils for the same soil volume (0.08 $m^3 \cdot m^{-3}$ vs 0.18 $m^3 \cdot m^{-3}$ of available water capacity, respectively; USDA-NRCS Official Soil Series Descriptions) in the mineral soil matrix. However, the Tarrant soil allows a deeper rooting system to develop through the fractured bedrock underlying the Tarrant soils. In contrast, the petrocalcic horizon under the Valera and Kavett soil types can restrict the development of deeper rooting systems (Schwinning 2008). This edaphic difference and corresponding ecohydrology is fundamental in understanding how flash drought events influence plant community dynamics in areas that have recently experienced woody plant encroachment.

Differences in water flow between soil types can lead to large disparities in the root:shoot ratios and water use of *Juniperus* trees. Rooting depths can be considerably deeper in the shallower Edwards limestone soils, as *Juniperus* roots penetrate cracks in the fractured bedrock beneath the thin limestone layer (Schwinning 2008). This results in shrub-like *Juniperus* trees that rely on extensive root systems to take up available water from both soil and bedrock, and are more tolerant to high variation in root zone water potential (Schwinning 2008). In contrast, *Juniperus* trees are considerably taller on the Edwards Plateau in deeper soils, do not have substantial roots other than those above the petrocalcic horizon, and are likely to be more reliant on the availability of soil water in the soil matrix above the petrocalcic layer (Heilman et al. 2009; Schwinning 2010). Under normal rainfall and climatic condition, these trees have access to a relatively larger and more stable available soil water capacity and are able to grow taller than trees in shallower soils, which is typical of trees in other deep soil environments (Fravolini et al. 2005). A protracted drought episode alters this ecohydrological interaction and likely led to the higher rates of mortality in the deeper soils in

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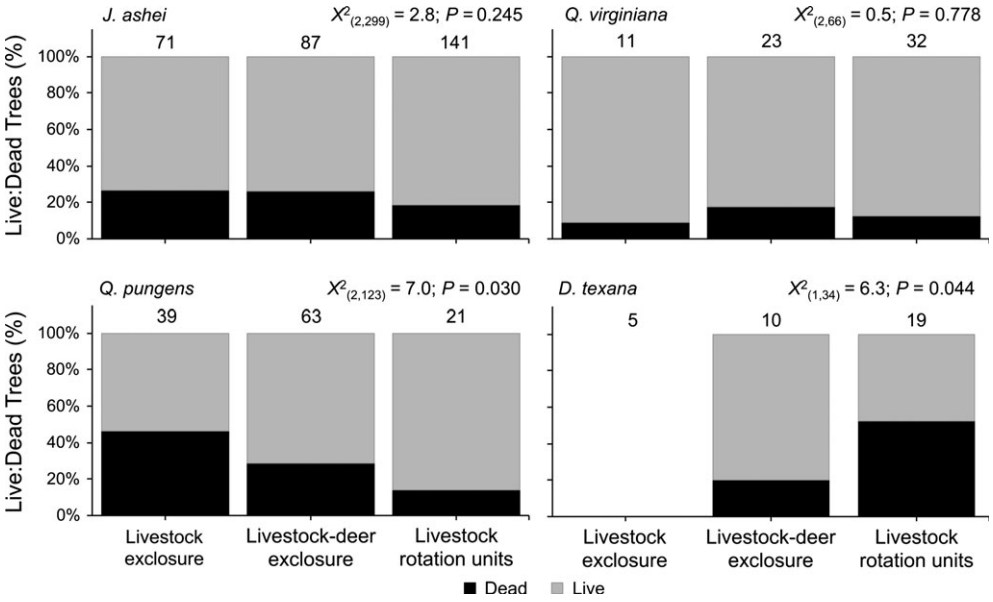

Fig. 5. Differences in the proportion of live and dead trees for each species across pastoral units (total sample size shown above columns). Data were excluded for cases where the expected values were too low to include in chi-square tests.

this study. Higher transpiration demands from taller trees and a confined soil buffer that restricts available water at greater rooting depths combine to induce more severe water stress than occurs in shrub-like trees with preferential flow from deeper roots in fractured bedrock (Taucer et al. 2008).

Large *Juniperus* trees tend to be more susceptible to mortality from drought than juveniles, which is not typical of most other woody species (Pook & Forrester 1984). Drought-induced mortality generally decreases as trees increase in size, because larger trees are better competitors for water and nutrients (Moore et al. 2004). One explanation for the higher mortality rates of large *Juniperus* trees is that clusters of *Q. virginiana* and *Q. pungens* trees may provide a nurse plant environment that facilitates the survival of small *Juniperus* trees during drought. Such clusters are typically the first areas to be colonized by encroaching *Juniperus* trees (Van Auken et al. 2005), and provide microsites with increased nutrients and moisture in soils, reduced evapotranspiration because of shade and reduced tissue water loss by protecting individuals from wind (Zou et al. 2005; Raventos et al. 2010). A second possible explanation for increased mortality in larger *Juniperus* is that taller trees may suffer larger water restrictions due to longer hydraulic pathways, although this explanation has typically been applied to trees considerably taller than *J. ashei* (McDowell et al. 2008).

This study demonstrates that high levels of *Juniperus* mortality following drought can lead to shifts in vegetation on the deeper Kavett and Valera soils, but patterns of dieback are contingent on long-term livestock management practices in these patches. Goats and deer are major livestock and wildlife species on the Edwards Plateau that selectively browse on low-growing woody vegetation. On the Edwards Plateau, ca. 50% of the diet of goats and up to 92% of the diet of whitetail deer consists of woody browse (Bryant et al. 1979, 1981; Taylor & Fuhlendorf 2003). This preference for woody vegetation has limited or eliminated the recruitment of small shrubs on the Edwards Plateau when goats are stocked at high densities (Taylor & Fuhlendorf 2003; Allred et al. 2012). As many areas on the Edwards Plateau have been heavily browsed by goats and deer, our findings suggest that the potential drought-induced shifts on Kavett and Valera soils from *Juniperus*-dominated patches to mixed brush patches will not occur over much of the region. *Juniperus* will likely continue to dominate patches of woody vegetation on both shallow and deep soil areas on much of the Edwards Plateau following the most recent drought, albeit at lower densities, as a result of long-term livestock management. However, recent widespread changes in land management on the Edwards Plateau from mostly livestock production to wildlife and hunting enterprises (Wilkins et al. 2009) may sufficiently decrease browsing pressure to allow a shift from *Juniperus* to mixed-brush patches in some areas.

Patterns of dieback among subdominant species

It is difficult to develop causal explanations for many of the specialized patterns of dieback that were observed among

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many of the subdominant woody plant species. It is not clear why *Q. virginiana* was the only large tree to exhibit consistent patterns of dieback across all potential interactions among soil types, pastoral treatments and woody plant densities. Even more perplexing is why *Q. pungens* and *Diospyros* showed contrasting patterns of dieback in the long-term livestock pastoral treatments. To better understand these patterns, more detailed, manipulative studies (*sensu* Volder et al. 2010) are needed to isolate factors associated with the interactions among legacy effects related to long-term land management, woody plant densities, plant demography, differences in ecohydrology among soil types, and numerous other factors that were not measured in this study but potentially contribute to woody dieback.

Conclusions

Pulse drought events from 2000 to 2011 were the second most severe since 1919 and were only surpassed by the prolonged drought from 1951 to 1957. While dieback in woody cover was nearly three times as high in the more severe drought of the 1950s, patterns of woody mortality were relatively similar following both drought periods. Neither resulted in widespread shifts in woody vegetation, and species-specific patterns of dieback were contingent on localized interactions between topoedaphic factors and long-term land use.

Findings from this study suggest multi-scale assessments are needed to understand and predict vegetation shifts as a result of climate change. In this *Juniperus*-dominated woodland, broad patterns of vegetation change from intense drought hinged upon the response of the dominant woody species, *J. ashei*. These types of general patterns can be reasonably predicted with current modelling approaches that use a single integrated metric, such as a change in woody canopy cover. Yet, the broader resolution of current climate–vegetation models is unlikely to consistently capture the spatially variable responses observed in this study. Improving predictions of climate–vegetation models at finer scales will be a challenge. Researchers are tasked with identifying unique species responses (Volder et al. 2010) but are confronted with the challenge of disentangling the effects of multiple ecological processes operating across a variety of spatial and temporal scales. In this study alone, specialized species-specific responses to drought occurred as a result of differences in ecohydrology among soil types, species-specific water use strategies, density-dependent mortality relationships and legacy effects resulting from long-term livestock management practices. Interactions among these drivers resulted in a shift from a *Juniperus*-dominated woody state to a *Quercus*-dominated state at a patch size that is relevant to land managers, but this shift would have gone undetected with a landscape-only perspective. To improve our understanding of climate-induced vegetation change at multiple scales, projections need to be down-scaled to a finer spatial resolution than is currently featured in most climate change models (Gutzler & Robbins 2011).

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References

Allen, C.D. 2007. Interactions across spatial scales among forest dieback, fire, and erosion in northern New Mexico landscapes. *Ecosystems* 10: 797–808.

Allen, C.D. 2009. Climate-induced forest dieback: an escalating global phenomenon. *Unasylva* 60: 43–49.

Allen, C.D. & Breshears, D.D. 1998. Drought-induced shift of a forest–woodland ecotone: rapid landscape response to climate variation. *Proceedings of the National Academy of Sciences of the United States of America* 95: 14839–14842.

Allen, C.D., Macalady, A.I., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.H., Allard, G., Running, S.W., Semerci, A. & Cobb, N. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management* 259: 660–684.

Allred, B.W., Fuhlendorf, S.D., Smeins, F.E. & Taylor, C.A. 2012. Herbivore species and grazing intensity regulate community composition and an encroaching woody plant in semi-arid rangeland. *Basic and Applied Ecology* 13: 149–158.

Bowker, M., Muñoz, A., Martinez, T. & Lau, M. 2012. Rare drought-induced mortality of juniper is enhanced by edaphic stressors and influenced by stand density. *Journal of Arid Environments* 76: 9–16.

Breshears, D.D. & Allen, C.D. 2002. The importance of rapid, disturbance-induced losses in carbon management and sequestration. *Global Ecology and Biogeography* 11: 1–5.

Bryant, F.C., Kothmann, M.M. & Merrill, L.B. 1979. Diets of sheep, Angora goats, Spanish goats, and white-tailed deer under excellent range conditions. *Journal of Range Management* 32: 412–417.

Doi: 10.1111/avsc.12044 © 2013 International Association for Vegetation Science

Bryant, F.C., Taylor, C.A. & Merrill, L.B. 1981. White-tailed deer diets from pastures in excellent and poor range condition. *Journal of Range Management* 34: 193–200.

Cronquist, A. 1981. *An integrated system of classification of flowering plants*. The New York Botanical Garden, Columbia University Press, New York.

Engelbrecht, B.M.J. & Kursar, T.A. 2003. Comparative drought-resistance of seedlings of 28 species of co-occurring tropical woody plants. *Oecologia* 136: 383–393.

Fensham, R., Fairfax, R. & Archer, S. 2005. Rainfall, land use and woody vegetation cover change in semi-arid Australian savanna. *Journal of Ecology* 93: 596–606.

Fensham, R., Fairfax, R. & Ward, D. 2009. Drought-induced tree death in savanna. *Global Change Biology* 15: 380–387.

Fienberg, S.E. 1979. The use of chi-squared statistics for categorical data problems. *Journal of the Royal Statistical Society, Series B* 41: 54–64.

Fisher, R.A., Bennett, J.H. & Yates, F. 1990. *Statistical methods, experimental design, and scientific inference: a re-issue of statistical methods for research workers – the design of experiments, and statistical methods and scientific inference*. Oxford University Press, Oxford, UK.

Fravolini, A., Hultine, K.R., Brugnoli, E., Gazal, R., English, N.B. & Williams, D.G. 2005. Precipitation pulse use by an invasive woody legume: the role of soil texture and pulse size. *Oecologia* 144: 618–627.

Fuhlendorf, S.D. & Smeins, F.E. 1997. Long-term vegetation dynamics mediated by herbivores, weather and fire in a *Juniperus–Quercus* savanna. *Journal of Vegetation Science* 8: 819–828.

Gutzler, D.S. & Robbins, T.O. 2011. Climate variability and projected change in the western United States: regional downscaling and drought statistics. *Climate Dynamics* 37: 835–849.

Heilman, J.L., McInnes, K.J., Kjelgaard, J.F., Owens, M.K. & Schwinning, S. 2009. Energy balance and water use in a subtropical karst woodland on the Edwards Plateau, Texas. *Journal of Hydrology* 373: 426–435.

Heim, R.R. Jr 2002. A review of twentieth-century drought indices used in the United States. *Bulletin of the American Meteorological Society* 83: 1149–1165.

Huxman, T.E., Wilcox, B.P., Breshears, D.D., Scott, R.L., Snyder, K.A., Small, E.E., Hultine, K., Pockman, W.T. & Jackson, R.B. 2005. Ecohydrological implications of woody plant encroachment. *Ecology* 86: 308–319.

IPCC (Intergovernmental Panel on Climate Change). 2007. Contribution of Working Group I to the fourth assessment report of the Intergovernmental Panel on Climate Change. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M.C., Averyt, K.B., Tignor, M. & Miller, H.L. (eds.) *Climate change 2007: the physical science basis*. Cambridge University Press, Cambridge, UK.

Kintisch, E. 2009. Global warming: Projections of climate change go from bad to worse, scientists report. *Science* 323: 1546–1547.

Knapp, A.K., Beier, C., Briske, D.D., Classen, A.T., Luo, Y., Reichstein, M., Smith, M.D., Bell, J.E., Fay, P.A., Heisler, J.L., Leavitt, S.W., Sherry, R., Smith, B. & Weng, E. 2008. Consequences of more extreme precipitation regimes for terrestrial ecosystems. *BioScience* 58: 811–821.

Koepke, D.F., Kolb, T.E. & Adams, H.D. 2010. Variation in woody plant mortality and dieback from severe drought among soils, plant groups, and species within a northern Arizona ecotone. *Oecologia* 163: 1079–1090.

McDowell, N.G., Pockman, W., Allen, C., Breshears, D., Cobb, N.S., Kolb, T.E., Plaut, J., Sperry, J., West, A., Williams, D.G. & Yepez, E.A. 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytologist* 178: 719–739.

McDowell, N.G., Beerling, D.J., Breshears, D.D., Fisher, R.A., Raffa, K.F. & Stitt, M. 2011. The interdependence of mechanisms underlying climate-driven vegetation mortality. *Trends in Ecology & Evolution* 23: 523–532.

Merrill, L. 1954. A variation of deferred rotation grazing for use under southwest range conditions. *Journal of Range Management* 7: 152–154.

Merrill, L. & Young, V. 1959. Effect of drought on woody plants. *Texas Agricultural Progress* 3: 9–10.

Moore, J.A., Hamilton, D.A. Jr, Xiao, Y. & Byrne, J. 2004. Bedrock type significantly affects individual tree mortality for various conifers in the inland Northwest, USA. *Canadian Journal of Forest Research* 34: 31–42.

Peterman, W., Waring, R.H., Seager, T. & Pollock, W.L. 2013. Soil properties affect pinyon pine–juniper response to drought. *Ecohydrology* 6: 455–463.

Peters, A.J., Walter-Shea, E.A., Lei, J., Vina, A., Hayes, M. & Svoboda, M.R. 2002. Drought monitoring with NDVI-based standardized vegetation index. *Photogrammetric Engineering and Remote Sensing* 68: 71–75.

Pook, E. & Forrester, R. 1984. Factors influencing dieback of drought-affected dry sclerophyll forest tree species. *Australian Forest Research* 14: 201–217.

Raventos, J., Wiegand, T. & De Luis, M. 2010. Evidence for the spatial segregation hypothesis: a test with nine-year survivorship data in a Mediterranean shrubland. *Ecology* 91: 2110–2120.

Rice, K.J., Matzner, S.L., Byer, W. & Brown, J.R. 2004. Patterns of tree dieback in Queensland, Australia: the importance of drought stress and the role of resistance to cavitation. *Oecologia* 139: 190–198.

Schwinning, S. 2008. The water relations of two evergreen tree species in a karst savanna. *Oecologia* 158: 373–383.

Schwinning, S. 2010. The ecohydrology of roots in rocks. *Ecohydrology* 3: 238–245.

Sheffield, J., Wood, E.F. & Roderick, M.L. 2012. Little change in global drought over the past 60 years. *Nature* 491: 435–438.

Shuttleworth, W.J. 1993. Evaporation. In: Maidment, D.R. (ed.) *Handbook of hydrology*, pp. 4.1–4.53. McGraw-Hill, New York, NY, US.

Smeins, F.E. & Merrill, L. 1988. *Long-term change in a semi-arid grassland – Edwards Plateau vegetation*. Baylor University Press, Waco, TX, US.

Taucer, P., Munster, C. & Wilcox, B. 2008. Large-scale rainfall simulation experiments on juniper rangelands. *Transactions of the American Society of Agricultural and Biological Engineers* 51: 1951–1961.

Taylor, C.A. Jr & Fuhlendorf, S.D. 2003. *Contribution of goats to the sustainability of Edwards Plateau Rangeland* [Texas Agricultural Experiment Station Technical Report 03–1]. Sonora, TX, US.

Taylor, C.A. Jr, Twidwell, D., Garza, N.E., Rosser, C., Hoffman, J.K. & Brooks, T.D. 2012. Long-term effects of fire, livestock herbivory removal, and weather variability in Texas semiarid savanna. *Rangeland Ecology and Management* 65: 21–30.

Van Auken, O.W., Jackson, J.T. & Jurena, P.N. 2005. Survival and growth of *Juniperus* seedlings in *Juniperus* woodlands. *Plant Ecology* 175: 245–257.

Volder, A., Tjoelker, M.G. & Briske, D.D. 2010. Contrasting physiological responsiveness of establishing trees and a C_4 grass to rainfall events, intensified summer drought, and warming in oak savanna. *Global Change Biology* 16: 3349–3362.

Wilding, L.P. 1997. A reappraisal of the Bracket Soil Series. In: Woodruff, C.M.J. (ed.) *Environment and Land Restoration in the Central Texas Hill Country, a Geologic Excursion to Selah, Bamberger Ranch, Blanco County, Texas*. Austin Society Geological Guidebook 19: 59–68.

Wilkins, R.N., Snelgrove, A.G., Fitzsimons, B.C., Stevener, B.M., Skow, K.L., Anderson, R.E. & Dube, A.M. 2009. *Texas land trends*. Texas A&M Institute of Renewable Natural Resources, Texas A&M University. URL: http://texaslandtrends.org/ (accessed 6 September 2012).

Woodward, F.I., Smith, T.M. & Emanuel, W. 1995. A global land primary productivity and phytogeography model. *Global Biogeochemical Cycles* 9: 471–490.

Zar, J.H. 1984. *Biostatistical analysis*, 2nd ed. Prentice Hall, Englewood Cliffs, NJ, US.

Zou, C., Barnes, P., Archer, S. & McMurtry, C. 2005. Soil moisture redistribution as a mechanism of facilitation in savanna tree–shrub clusters. *Oecologia* 145: 32–40.

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