Species composition but not diversity explains recovery from the 2011 drought in Texas grasslands

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Abstract
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Keywords
aboveground biomass, C3 forbs, drought, drought legacy, native and exotic grasslands, plant composition, recovery, short grasses, the transient maxima hypothesis

Disciplines
Atmospheric Sciences | Climate | Ecology and Evolutionary Biology | Plant Biology | Terrestrial and Aquatic Ecology

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Species composition but not diversity explains recovery from the 2011 drought in Texas grasslands

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Abstract. Extreme droughts can have profound direct consequences for grassland ecosystems, but it is poorly known how ecosystems recover from drought and what ecological factors are associated with recovery. Recovery occurs when ecosystem functioning returns to values observed prior to a perturbation. Here, we tested for ecosystem recovery after an extreme drought in 2011 in previously established native and exotic experimental communities in Central Texas. Planted mixtures of all native and all exotic species were crossed with a summer irrigation treatment, with eight community compositions (random draws) per treatment. Prior to the drought, native plots had higher diversity than exotic plots, which sets up the prediction that the high-diversity native plots will recover more quickly than exotics. The extreme drought decreased rain-use efficiency ([RUE], annual biomass production per unit of rainfall) by 82%. Rain-use efficiency remained well below pre-drought levels during the growing season after the drought. However, on average, RUE recovered to pre-drought levels by the second growing season following drought. Exotic communities showed higher RUE than native communities, and irrigation significantly reduced RUE in both exotic and native communities across years. Interestingly, not all of the mixtures recovered from the drought, and recovery was associated with species composition, but not diversity. Rain-use efficiency recovery from drought was greatest in native communities in which the proportion of C3 forb biomass increased during and following drought and in exotic communities with a low proportion of short grass biomass. Extreme droughts can exert differential impacts on plant functional groups, leading to a drought legacy effect that reduces recovery with possible long-term repercussions.

Key words: aboveground biomass; C3 forbs; drought; drought legacy; native and exotic grasslands; plant composition; recovery; short grasses; the transient maxima hypothesis.

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INTRODUCTION

Droughts can have profound direct impacts as well as indirect effects on ecological systems (Seastedt and Knapp 1993, Blair 1997, Breshears et al. 2005, Hanson et al. 2006, Phillips et al. 2009, Smith 2011, Sala et al. 2012a, Schwalm et al. 2012, Frank et al. 2015). Indeed, impacts of extreme droughts such as the droughts in the western North America from 2000 to 2004 (Breshears et al. 2005, Schwalm et al. 2012), in Europe in 2003 (Ciais et al. 2005), in the Amazon Basin in 2005 (Phillips et al. 2009) and 2010 (Lewis et al. 2011), in Greece in 2007 (Founda and Giannakopoulos 2009), and in the Central United States in 2012 (Knapp et al. 2015) have been well documented. Moreover, extreme droughts are consistently predicted to increase in frequency and intensity by global climate models (IPCC 2013, Fischer and Knutti 2014). Understanding the likely mechanisms and processes associated with drought impacts on ecosystems is therefore

The indirect impacts of extreme droughts on ecosystems can be due to drought-associated changes in plant community composition. These shifts in community composition can in turn indirectly affect ecosystem process rates if the shifts are toward species with trait values that differ significantly from those of remaining species (Polley et al. 2014). These “legacy effects,” which result in reductions in process rates below expected values (Sala et al. 2012b), are much less studied in comparison with direct impacts of drought. Legacy effects can operate over multiple time frames, from days to centuries, but typically manifest themselves as reduced production of aboveground biomass (AGB) relative to the levels expected for a given amount of precipitation in the years following a drought. These reductions can be due to the community and species–trait shifts that occur during and after a drought. Alternatively, some theoretical work (transient maxima hypothesis) predicts that AGB will be higher in the growing seasons after the drought due to nutrient buildup during the drought (Seastedt and Knapp 1993, Blair 1997). This increase in AGB could lead to higher production for some time after the drought has concluded. Whether they are positive or negative, the underlying mechanisms behind legacy effects are poorly understood (Smith 2011, Anderegg et al. 2015).

The impacts of droughts on ecosystem processes also may differ between exotic and native plant communities and could shift if climate change alters precipitation regimes. The invasion of habitats by exotic species is among the most serious global change issues, potentially leading to exotic dominance and the degradation of native communities (Xu et al. 2015), but few studies have compared the responses of exotic and native plant communities to extreme drought. Exotic grasslands in the tallgrass region have lower diversity and forb abundance than native grasslands (Wilsey et al. 2011, Martin et al. 2014), and this reduced diversity may leave them more vulnerable to drought (Tilman and Downing 1994, Isbell et al. 2015). Climate change is projected to shift the seasonality of precipitation in the southern Plains of the United States, resulting in wetter summers (Karl and Knight 1998, Allan and Soden 2008, Seager and Vecchi 2010). Whether such a shift in precipitation will differentially impact exotic and native plants and the responses of exotic and native communities to episodic drought is unknown.

A severe drought occurred in 2011 during a long-term grassland experiment in Central Texas (National Oceanic and Atmospheric Administration 2011, Wilsey et al. 2011, 2014, Xu et al. 2015; Appendix S1: Fig. S1). Tree-ring records show that the 2011 drought was matched in extremity only by drought in the year 1789 (records dating from 1550; National Oceanic and Atmospheric Administration 2011). Our ongoing experiment comparing pure native or exotic species mixtures with replicated species compositions provided us with a unique opportunity to study direct drought impacts as well as potential drought legacies. Specifically, we hypothesized that (1) drought would reduce biomass production and rain-use efficiency ([RUE], annual AGB production per unit of rainfall) more in species-poor than in species-diverse communities and (2) drought-caused shifts in community composition and diversity would contribute to a legacy effect that slowed the recovery of RUE from drought. We expected drought effects on plant community composition to differ between native and exotic communities.

**Materials and Methods**

**Maintenance of exotic vs. native diversity experiment**

We conducted the experiment at the USDA-ARS Grassland, Soil, and Water Research Laboratory in Central Texas. For a full description of the experimental design, see Wilsey et al. (2011), Xu et al. (2015). Briefly, we established the experiment in two blocks planted in October 2007 and March 2008 using 36 widely distributed native
and exotic grassland species (Appendix S1: Table S1, Fig. S2). A two-way factorial treatment (origin × irrigation) was applied to plots (1 × 1 m) with a randomized block design, using random draws to vary species composition. There were eight random draws for each of the four treatments. Draws were created by randomly selecting species from each of four functional groups (C3 forbs, C3 grasses, C3 legumes, and C4 grasses) to populate nine-species communities of perennial plants. Native and exotic species were selected using a paired species approach that controlled for phylogeny and growth form between pairs of native and exotic species. We used a large pool of native and exotic species; all exotic species used were already present in the Texas flora (Diggs et al. 1999). The species composition of our plots (mixtures) was very similar to species composition of fields in the area, and our study used all of the non-native species in the area (Wilsey et al. 2011) that could be paired with native species. Biomass did not differ significantly among species at planting (72 seedlings/m²). Survival rate was high during the initial growing period (Wilsey et al. 2011). We thus compared native and exotic communities while controlling for soil type, disturbance rate, and phylogeny (i.e., without confounding factors present). Mixtures were replicated at both the species draw (composition) and true replicate levels for a total of 64 mixtures (2 origins × 2 irrigation levels × 2 blocks × 4 replicate draws (block) × 2 true replicates). Annual precipitation is 878 mm with a bimodal pattern with a large peak in the spring and a smaller peak in the autumn. Soils are Vertisol ustepts.

Half of the mixtures received water additions during each summer of the experiment to match predictions from global change models of increased rainfall in summer months (Allan and Soden 2008). Irrigated plots were hand-watered from mid-July to mid-August each year beginning in 2008 at a rate of 128 mm per month in eight applications of 16 mm. Preliminary testing of our technique showed no lateral water flow across the flat field. Soil cores (5 cm in depth) taken the day following irrigation from irrigated plots had consistently higher soil moisture than those from control plots (Wilsey et al. 2011). All plots were burned during winter on a five-year cycle (first time in February 2013). In order to maintain the native and exotic status of the plots, weeds were removed by hand while small. Thus, our study focused on recovery from drought by the planted species and did not include the effects of plant invaders.

Data collection

Aboveground biomass and species composition were determined twice per year (late June and October) in each plot using point intercept techniques from June 2008 to June 2015 (Wilsey et al. 2011). Briefly, point intercept was done by dropping pins vertically 25 times in a systematic fashion in the inner 90 × 90 cm (1 × 1 m) portion of each plot and noting all plant hits. Pin drops were spaced 20 cm apart and dropped in a 5 × 5 grid. All species were counted in each plot to determine species richness. Species that were present but not hit were given a value of 0.5 hits (Bowman et al. 2006, Yurkonis et al. 2010). Point intercept hits were converted to biomass with regression equations based on concurrent point intercept sampling and biomass harvesting in October 2008 (Appendix S1: Table S2). Relationships between number of hits and biomass were linear and strong across species (mean $r^2$ across 35 species was 0.89 ranging from 0.69 to 0.99, not including Trifolium repens, which became locally extant during the first summer; Appendix S1: Table S2). Climate variables (1914–2013), including daily precipitation, maximum and minimum temperatures, were downloaded from the weather station at the Grassland, Soil, and Water Research Laboratory (http://www.ars.usda.gov). The year prior to sampling was defined from June 16th to next June 15th for the June sampling and from October 16th to next October 15th for the October sampling. We used RUE, rather than AGB, an index of ecosystem functioning because inter-annual variability in precipitation is large at our site. Rain-use efficiency is defined as AGB divided by annual precipitation in un-irrigated plots or annual precipitation plus irrigation in irrigated plots. This value gives the amount of biomass produced per unit of yearly precipitation, and thus could be used to compare plots across years that varied in precipitation. Our results were qualitatively similar whether we used RUE or AGB.
Statistical analysis

Experimental response variables were analyzed using a mixed-model ANOVA with PROC MIXED in SAS 9.2 (SAS Institute, Cary, North Carolina, USA) with grassland origin (native vs. exotic), irrigation, and block as fixed factors, and species composition (draw [block]) and its interactions as random factors (Wilsey et al. 2011), using the Kenwood-Roger correction method. We used repeated-measures ANOVA with a first-order autoregressive (1) covariance structure to analyze responses of RUE, species richness, Simpson’s diversity, biomass of different functional groups—C3 grasses, C3 forbs, C3 legumes, C4 grasses, and short (<45 cm) grasses (overlapped with the C3 and C4 grasses)—to drought (Diggs et al. 1999). Plant functional groups were used in analyses rather than individual species because all of the species were not included in all mixtures. Recovery was tested by contrasting RUE in 2010 with RUE in subsequent growing seasons (2012, 2013, etc.). The year 2010, the growing season immediately prior to the drought, was considered as the pre-drought period in comparisons. Relationships between changes in RUE (ΔRUE) and functional group composition were analyzed with PROC REG in SAS 9.2 followed by confirmatory analyses using structural equation modeling (SEM) as described below.

Structural equation modeling was applied to quantify indirect effects of drought on RUE. We created a conceptual model based on a priori and theoretical knowledge. Four major pathways were constructed to explore the effect of pre- vs. post-drought changes in native and exotic communities on ΔRUE. Among them were differences in species richness, Simpson’s diversity, proportion of C3 forb biomass, and proportion of short grass biomass. These pathways tested whether high species diversity or functional group composition (Polley et al. 2014) was correlated with recovery. The proportion of short grasses was used as a predictor because monoculture biomass was lower for these species than for tall grasses, implying that a shift to short grasses could reduce post-drought productivity and RUE (Polley et al. 2014). We did not include proportion biomass of C3 grasses and C3 legumes in the SEM, because these groups contributed little to AGB. Proportion biomass of C4 and tall grasses were also excluded from the SEM because they were the inverse of the variables that we did use. Data were fitted to the model using the maximum-likelihood estimation method. Adequate model fit was indicated by a non-significant chi-square test (P > 0.05). Structural equation modeling analysis was performed using AMOS 21.0 software (IBM, SPSS, Armonk, New York, USA).

RESULTS

Climatic variables

The year 2011 was an extreme drought year, with a <2% statistical probability of occurrence (Fig. 1a). Our site only received 405 mm of precipitation, which was approximately 46% of the long-term mean (878 mm). Neither the amount of precipitation nor temperatures differed between pre- and post-drought periods (P > 0.05; Fig. 1a). Mean maximum and minimum daily temperatures in 2011 were higher than those in the pre-drought period (Fig. 1b, c).

The drought impacts in 2011

The drought in 2011 reduced RUE by 84% and 80% in native and exotic communities, respectively (all P < 0.001; Fig. 2). Aboveground biomass was reduced by 93% in native communities and 92% in exotic ones (all P < 0.001; Appendix S1: Fig. S3). Rain-use efficiency and AGB were also significantly reduced in the first growing season (2012) after the drought (contrast P < 0.001; Table 1). On average, RUE of native and exotic communities recovered by the second growing season (contrast P > 0.05; Table 1), although species richness and diversity remained below pre-drought levels (Figs. 2 and 3). Exotic communities showed significantly higher RUE than native communities across years (Table 2, Fig. 2). The main effects of origin and irrigation on RUE were consistent across years. Irrigation significantly decreased RUE (P < 0.05; Table 2, Fig. 4), more so in exotic than in native communities.

Underlying mechanisms

Interestingly, not all mixtures recovered from the drought. Differences in recovery were associated with differing shifts in species composition in both native and exotic communities. However, the species involved differed by grassland origin
Drought initiated a shift toward greater forb and short grass abundance that continued following drought relief in native and exotic communities, respectively. Forbs such as *Vernonia baldwinii* contributed as much as 40% of community ABG following drought in native communities (Appendix S1: Fig. S4a, b). Exotic short grasses, such as *Cynodon dactylon*, continued to increase following drought relief to the near exclusion of other species in some exotic plots (Appendix S1: Fig. S4a, c). Rain-use efficiency recovered the most in native communities that had the largest increases in C₃ forb fraction ($P < 0.01$; Fig. 5). Rain-use efficiency recovered the most in exotic communities that had no increase in short grass fraction following drought ($P < 0.001$; Fig. 6).

**DISCUSSION**

We found significant direct and indirect (i.e., legacy) effects of the 2011 drought on grassland functioning. The drought decreased RUE by 82% in 2011. Rain-use efficiency remained lower than pre-drought levels through the 2012 growing season. The drought legacy in our sub-humid...
Table 1. Contrast results (F tests, a priori) on rain-use efficiency (RUE, g·m⁻²·mm⁻¹) of pre-drought period (2010) with the post-drought years 2012 and 2013 across treatments (whole), and for native and exotic communities separately.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>df</th>
<th>Pre vs. 12 F, P</th>
<th>Pre vs. 13 F, P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Whole</td>
<td>1, 370</td>
<td>35.98*** 0.07</td>
<td></td>
</tr>
<tr>
<td>Natives</td>
<td>1, 370</td>
<td>12.64*** 1.27</td>
<td></td>
</tr>
<tr>
<td>Exotics</td>
<td>1, 370</td>
<td>24.28*** 0.55</td>
<td></td>
</tr>
</tbody>
</table>

*** P < 0.001.

The grassland system was negative, as predicted by Sala et al. (2012b). The continued reduction in biomass throughout 2012 did not support the predictions of the transient maxima hypothesis (Seastedt and Knapp 1993), perhaps because the drought was so extreme. On average, RUE in both exotic and native communities recovered to pre-drought levels, but species richness and functional composition did not. The key mechanism explaining mixture differences in recovery was species reorganization within plant communities, although the functional groups that were important to recovery differed between native and exotic communities.

Table 2. Results of mixed-model ANOVA (F tests) that compared rain-use efficiency (RUE, g·m⁻²·mm⁻¹) between native and exotic plots (Origin) that received summer irrigation or not (Irig) yearly for the entire time (Time) period (2008–2015).

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>F, P</th>
</tr>
</thead>
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<tr>
<td>Block</td>
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<tr>
<td>Origin</td>
<td>1, 12.7</td>
<td>0.69</td>
</tr>
<tr>
<td>Irrig</td>
<td>1, 7.4</td>
<td>15.03**</td>
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<td>O × I</td>
<td>1, 371</td>
<td>6.76*</td>
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<tr>
<td>Time</td>
<td>13, 371</td>
<td>81.79***</td>
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<tr>
<td>Time × O</td>
<td>13, 371</td>
<td>2.39*</td>
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<tr>
<td>Time × I</td>
<td>13, 371</td>
<td>1.26</td>
</tr>
<tr>
<td>Time × O × I</td>
<td>13, 371</td>
<td>0.63</td>
</tr>
</tbody>
</table>

* P < 0.05, ** P < 0.01, and *** P < 0.001.

Fig. 3. Species richness (a) and Simpson’s diversity (b) in June (J) and October (O) of each year in native and exotic communities.

Fig. 4. Effects of irrigation on rain-use efficiency (RUE) during pre- and post-drought years. Summer irrigation consistently decreased RUE. * P < 0.05, ** P < 0.01.
Fig. 5. Path analysis of relationships among post- to pre-drought differences in species richness (\(\Delta S\)), Simpson’s diversity (\(\Delta D\)), proportion biomass of C3 forbs (\(\Delta \% C_3\) forbs), short grass (\(\Delta \%\) short grasses), and rain-use efficiency (\(\Delta\)RUE, mostly negative) across plots in native communities (a, \(\chi^2 = 4.78, P = 0.44\)). Panel b shows relationships of post- to pre-drought differences in RUE (\(\Delta\)RUE) and \(\% C_3\) forbs (\(\Delta \% C_3\) forbs) and the 95% confidence lines (dashed) in native communities. Solid and dashed arrows in panel a represent significant (\(P < 0.05\)) and non-significant (\(P > 0.05\)) paths in a fitted structural equation model depicting impact of variables on RUE. The post- to pre-drought differences (\(\Delta\)) in the variables in this figure were calculated as the differences between post- and pre-drought years (post – pre).

Fig. 6. Path analysis of relationships among the post- to pre-drought differences in species richness (\(\Delta S\)), Simpson’s diversity (\(\Delta D\)), proportion biomass of C3 forbs (\(\Delta \% C_3\) forbs), short grass (\(\Delta \%\) short grasses), and rain-use efficiency (\(\Delta\)RUE, mostly negative) across plots in exotic communities (a, \(\chi^2 = 2.67, P = 0.45\)). Panel b shows relationships of the post- to pre-drought differences between RUE (\(\Delta\)RUE) and \% short grasses (\(\Delta \%\) short grasses) and the 95% confidence lines (dashed) in exotic communities. Solid and dashed arrows in panel a represent significant (\(P < 0.05\)) and non-significant (\(P > 0.05\)) paths in a fitted structural equation model depicting impact of variables on RUE. The post- to pre-drought differences (\(\Delta\)) in the variables in this figure were calculated as the differences between post- and pre-drought years (post – pre).
Extreme droughts can reduce biomass production and alter plant community composition (Weaver 1954, Hoover et al. 2014). The 2011 drought reduced AGB by >92%, and triggered shifts in plant species composition. C₃ forbs were resilient to drought in native communities and often increased in relative abundance, especially in diverse mixtures (Wilsey et al. 2011, 2014). C₃ forbs typically concentrate roots deeper than C₄ grasses (Nippert and Knapp 2007, Xu et al. 2014), which may have enabled C₃ forbs to suffer less during the drought. In contrast, exotic communities were highly dominated by C₄ grasses and had low forb abundance (Wilsey et al. 2014). Short grasses increased during and after the drought in a subset of exotic communities. Composition of some of these exotic mixtures approached that of Cynodon dactylon (short grass) monocultures (Appendix S1: Fig. S4c). This shift to short-statured species with lower-than-average RUE strongly limited drought recovery. Feedbacks from functional group change (Polley et al. 2014) can have important legacy effects on drought recovery.

Drought may lead to community-level responses, including compositional changes, that affect subsequent community function (Smith et al. 2009, Smith 2011). Survivorship among different species could vary due to their differential tolerance to droughts, leading to persistent changes in species composition (Niu et al. 2014). A representative example is the gradual replacement of tallgrass prairie in central Kansas, eastern Nebraska, and eastern South Dakota, United States, by mixed prairie with its dominant mid-grasses and sub-dominant short grasses following the driest consecutive 2-year period (1933–1934) during 1930s drought (Weaver 1954, 1968). In an experimentally imposed extreme drought, a perennial forb (Solidago canadensis) and the dominant grass (Andropogon gerardii) reordered and the reordering persisted post-drought (Hoover et al. 2014). In the Swiss Alps, extremely dry years led to long-term reductions in grass percent cover (and increases in forbs). This reduction persisted for decades after the drought occurred (Stampfl and Zeiter 2004). Drought increased abundance of C₃ forb in native communities and short grasses in some exotic communities, but on average, RUE of plant communities recovered to pre-drought levels within 2 yr. Drought also changed community composition of tallgrass prairie, but aboveground productivity recovered rather quickly to pre-drought levels (Hoover et al. 2014).

Species diversity was much higher in native than in exotic communities in our study (Appendix S1: Table S3; Wilsey et al. 2014), but RUE recovery from drought was no quicker in native than in exotic mixtures. Isbell et al. (2015) found that resistance and stability to extreme precipitation years were higher in plots with high species richness, but that resilience to drought was unaffected by species richness. Our finding that resilience (recovery) was no greater in diverse than in depauperate communities implies that either resilience to drought is relatively insensitive to species richness or is not affected by richness declines among invasive exotic species. Exotic communities persisted through a major drought that might have been expected to “reset” the system. Interestingly, RUE in some of the exotic and native communities did not recover to the pre-drought level. The amount of precipitation received did not differ between pre- and post-drought periods and was within the normal range, implying that the pre- to post-drought reduction in RUE was linked to community change. Such changes are predicted to have the largest impact on ecosystem functions post-drought (Smith 2011, Anderegg et al. 2015). Differences in plant community structure can drive substantial differences in sensitivity of AGB to precipitation (Veron et al. 2002). For example, the mean proportion of C₃ forb and short grass biomass across plots was significantly higher post-drought in native and exotic communities, respectively (Appendix S1: Fig. S5). Although the physiological mechanisms that explain why drought favored C₃ forbs in native and short grasses in exotic communities are yet to be revealed, our results indicate that changes in plant community composition in response to drought can alter ecosystem function for years thereafter (Kreyling et al. 2008, van der Molen et al. 2011).

The observed differences in plant community composition between pre- and post-drought periods strongly defined the drought legacies of the system. Unfortunately, our native–exotic design precluded the opportunity for invasion of
non-planted species. Invaders can have strong influences on species compositions during and after droughts, and further work should be done with plots that can be invaded. Invaders could enhance this legacy effect or could cause a community shift back toward the original composition. Nevertheless, changes in community composition and associated legacy effects following extreme droughts conflict with the implicit assumption in coupled climate-C cycle models that vegetation recovery from extreme droughts is immediate and complete (Anderegg et al. 2015).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1704/full