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Research article

Repeated extreme droughts decrease root production, but not the potential for post-drought recovery of root production, in a mesic grassland

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Global climate change is expected to cause more frequent extreme droughts in many parts of the world. Despite the crucial role of roots in water acquisition and plant survival, our understanding of ecosystem vulnerability to drought is primarily based on aboveground impacts. As return intervals between droughts decrease, root responses to one drought might alter responses to subsequent droughts, but this remains unresolved. We conducted a seven-year experiment that imposed extreme drought (growing season precipitation reduced 66%) in a mesic grassland. Plots were droughted during years 1–2 ('Drought 1'), or years 5–6 ('Drought 2') or both. We quantified root production during year 6 (final year of Drought 2) and year 7 (first year after Drought 2), when all plots received ambient precipitation. We found that repeated drought decreased root mass production more than twice as much as a single drought (−63% versus −27%, respectively, relative to ambient precipitation). Root mass production of the dominant C_4 grass *Andropogon gerardii* did not decrease significantly with either one or two droughts. *A. gerardii* root traits differed from subdominant species on average across all treatments, but drought did not alter root traits of either *A. gerardii* or the subdominant species (collectively). In year 6, root production in plots droughted 4 years ago had not recovered (−21% versus control), but root production recovered in all formerly droughted plots in year 7, when precipitation was above average. Our results highlight the complexity of root responses to drought. Drought-induced reductions in root production can persist for years after drought and repeated drought can reduce production even further, but this does not preclude rapid recovery of root production in a wet year.

Keywords: *Andropogon gerardii*, belowground net primary production, climate extremes, precipitation, traits

Introduction

Globally, more frequent and extreme droughts are expected as climate change alters precipitation and evapotranspiration patterns, with evidence for this already emerging

(Dai 2013, IPCC 2013, USGCRP 2017). Drought, defined as a period of marked precipitation deficiency relative to the local long-term average, has been studied extensively and shown to impact myriad ecosystem functions (Wu et al. 2011, Dai 2013, Lei et al. 2016, Eziz et al. 2017, Gao et al. 2019, Slette et al. 2019). But much of what we know is based on aboveground-focused studies of single droughts. As the time between droughts decreases, it will be important to understand how ecosystems respond to not only single, but also recurrent drought. Legacies from past climate anomalies can precondition ecosystems and alter responses to subsequent events, so it is likely that responses to recurrent drought, or compound events more generally, are not predictable from studies of individual events (de Vries et al. 2012, Sala et al. 2012, Seneviratne et al. 2012, Zscheischler et al. 2018, 2020, Hughes et al. 2019, AghaKouchak et al. 2020).

Previous studies of recurrent drought are relatively few and their results vary, depending on the ecosystem and species (Backhaus et al. 2014, Dreesen et al. 2014, Anderegg et al. 2020, Hoover et al. 2021, Sánchez-Pinillos et al. 2021). Thus, the potential consequences of repeated drought, ranging from increased acclimation to increased sensitivity, remain unresolved. For example, some studies have found increased plant drought tolerance following adaptation of soil microbial communities to previous drought (Marulanda et al. 2009, Lau and Lennon 2012, Meisner et al. 2013), but this is not always the case (Kaisermann et al. 2017).

Community responses might impact the effects of repeated drought. For example, because dominant species make up the largest proportion of biomass, overall drought sensitivity might be lower if the dominant species is relatively resistant to drought (i.e. mass-ratio hypothesis; Grime 1998, Hillebrand et al. 2008). Variation in responses to repeated drought among different sites and studies might thus be partially attributable to differences in dominant species responses. However, the effects of plant community composition on ecosystem functioning during and after drought have mostly been studied aboveground (Hoover et al. 2014a, b) and understanding of belowground community dynamics during drought remains limited.

A primary function of roots is to acquire water and nutrients. Differences in root characteristics such as rooting depth, root length density and specific root length can affect how plants acquire soil resources and drive differences in ecosystem processes including carbon and nutrient cycling (Bardgett et al. 2014, Bristiel et al. 2019, Lynch et al. 2021). For example, root depth can determine whether plants acquire water from shallow or deep soil depths and differences in root length production can indicate differences in the volume of soil that plants can access, with consequences for their ability to acquire water and nutrients (Jackson et al. 1996, Casper and Jackson 1997, Wilson 2014, Zwicke et al. 2015, Fort et al. 2017, Freschet et al. 2021). Roots also sense and signal water deficits (Davies and Zhang 1991, Tardieu and Simonneau 1998) and play key roles in carbon and nutrient cycling and soil formation (Russell et al. 2004, Clemmensen et al. 2013, Freschet et al. 2013, Bardgett et al. 2014). Root dynamics are thus key determinants of the size of the soil carbon reservoir, which is at least twice the size of the atmospheric carbon reservoir and important for global carbon sequestration and climate regulation (Scharlemann et al. 2014, Köchy et al. 2015). Despite growing recognition of the importance of root dynamics to ecosystem functioning, root responses remain less well-studied than aboveground responses. Several previous studies have found negative impacts of drought on root production and biomass, but other have found no effect of drought or even positive responses (Pilon et al. 2013, Xu et al. 2013, Wilcox et al. 2015, 2017, Balachowski et al. 2016, de Vries et al. 2016, Balachowski and Volaire 2018, Garbowski et al. 2020). More research is thus needed to develop a broad understanding of root dynamics in a changing climate. An improved understanding of root traits (e.g. specific root length, rooting depth, etc.) could help produce a framework for predicting root responses to change and linking those responses to broader ecosystem processes such as NPP and carbon cycling. Studies of root traits will therefore be particularly useful in advancing root ecology (Bardgett et al. 2014, Iversen et al. 2017, Freschet et al. 2021).

Grass-dominated ecosystems allocate a substantial portion of total primary production to roots, store most of their carbon belowground (Risser et al. 1981, Jones and Donnelly 2004, Soussana et al. 2004, Hui and Jackson 2006, Smith et al. 2008, Silver et al. 2010), and are globally extensive (White et al. 2000, Dixon et al. 2014). They thus play a key role in the global carbon cycle (Scurlock and Hall 1998, Pendall et al. 2018). Most grassland are water-limited, climatically variable and sensitive to precipitation, particularly drought (Sala et al. 1988, Knapp and Smith 2001, Morgan et al. 2008, Knapp et al. 2015, 2020, Mowll et al. 2015, Li et al. 2019, Felton et al. 2020). Understanding grassland root responses to drought, especially extreme drought, thus has important implications for predicting both ecosystem- and global-scale changes to carbon dynamics under an increasingly variable climate.

Here we report the results of a study focused on assessing fine root responses to single versus recurrent extreme droughts, and recovery after drought, in a mesic grassland. Our research builds on the climate extremes experiment (CEE; Hoover et al. 2014a) which imposed an extreme two-year drought ('Drought 1') and focused on quantifying primarily aboveground responses during and after drought. Taking advantage of the CEE platform, we imposed another extreme drought ('Drought 2') in plots both with and without previous drought exposure and assessed root production and traits during and after drought. Drought 1 altered plant community composition and increased the relative abundance of dominant C_4 grass species with high water-use-efficiency (Hoover et al. 2014a, Turner and Knapp 1996). We predicted that this shift to a more drought-resistant plant community would cause plots that were droughted during Drought 1 to be generally more resistant to Drought 2 than plots that were not droughted during Drought 1.

Methods

Study site

The Konza Prairie Biological Station (KPBS) is a 3487-ha unplowed tallgrass prairie in northeast Kansas, USA (39°05′N, 96°35′W) and is a USA Long-Term Ecological Research (LTER) site. The plant community is composed primarily of native C_4 grasses, dominated by *Andropogon gerardii*, which drives many community and ecosystem dynamics aboveground (Knapp et al. 1998, Smith and Knapp 2003, Silletti et al. 2004). The climate is temperate mid-continental with warm, wet summers and cold, dry winters. The mean annual temperature is 13°C (Knapp et al. 1998) and the mean annual precipitation is 851 mm, almost 70% of which (559 mm) falls during the growing season (April–August). Frequent fires are a historical feature of this grassland and are key for maintaining grass dominance and reducing woody plant encroachment (Knapp et al. 1998, Briggs et al. 2005).

The CEE design and treatments

The CEE was located in a lowland area with deep, silty clay loam soils in the Tully series (Ransom et al. 1998, Collins and Calabrese 2012) and was burned annually in mid-March. *Andropogon gerardii* made up about 40% of total ANPP in the CEE. The CEE consisted of four shelters (6 × 24 m) constructed from greenhouse frames with 10 plots (2 × 2 m) in each shelter (see Hoover et al. 2014a for details). Each shelter was hydrologically isolated to a depth of 1 m below the soil surface via a plastic barrier, and via metal flashing installed aboveground. During Drought 1, each rainfall event during the growing seasons (April–August 2010 and 2011) was reduced in size by ~66% in two shelters by covering the frame with evenly spaced strips of clear polycarbonate plastic, based on Yahdjian and Sala (2002). The other two shelters received ambient precipitation and were covered with deer netting that reduced photosynthetically active radiation by ~10% (equivalent to the reduction in the drought shelters) while allowing all rain to pass through. All plots received ambient precipitation in the next two years (2012 and 2013; plastic strips were not installed over the plots to reduce rainfall in these years). Ambient precipitation plots were watered weekly by hand if total rainfall during that week was less than the long-term average (in which case the deficit was added). During Drought 2 (2014 and 2015), each rainfall event during the growing seasons was reduced in size by ~66% in half of each shelter by covering half of the frame with evenly spaced strips of clear polycarbonate plastic (covering 5 of 10 contiguous plots), and the other half was covered with deer netting (Fig. 1). As such, half of the plots that had been droughted and half of the plots that hadn't been droughted during Drought 1 were droughted during Drought 2. This resulted in four treatments: never droughted (Ambient→Ambient), droughted only during Drought 1 (Drought→Ambient), droughted only during Drought 2 (Ambient→Drought) and droughted during both Drought 1 and Drought 2 (Drought→Drought). All plots received ambient precipitation in the year after Drought 2 (2016; Fig. 1).

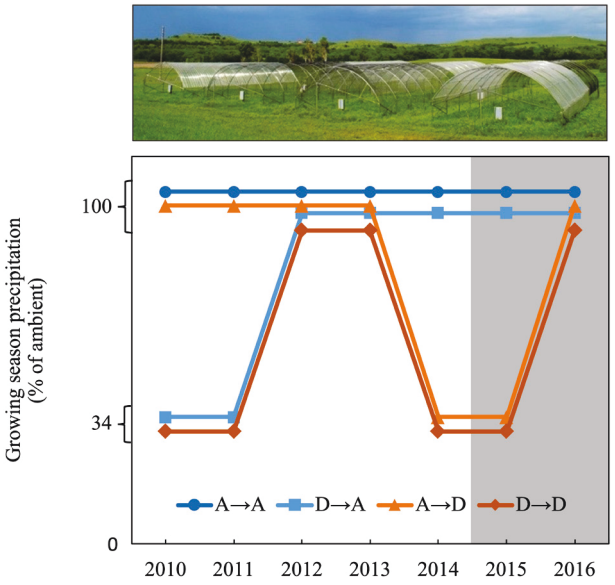

Figure 1. Photo and treatment schematic of the climate extremes experiment. Two 2-year droughts were imposed in half of all plots in 2010–2011 ('Drought 1') and 2014–2015 ('Drought 2'), separated by 2 years of ambient precipitation. A = Ambient, D = Drought (during Drought 1 and Drought 2). The shaded area indicates the time period when root responses were measured.

Root measurements

We estimated BNPP in 2015 (the final year of Drought 2) and in 2016 (the first year after Drought 2) by using root ingrowth cores to estimate fine root production. At the start of each growing season (early April), we took a soil core (5 cm diameter, 30 cm deep) from every plot. This depth captures most root production at our site and in other grasslands (Weaver and Darland 1949, Jackson et al. 1996, Sun et al. 1997, Schenk and Jackson 2002, Nippert et al. 2012), and research has linked differences in root distribution within this depth to differences in production even when maximum rooting depth is deeper (Nippert and Holdo 2015). We placed a cylindrical mesh basket filled with sieved, root-free soil (collected adjacent to the CEE) packed to approximate field density into each core hole and filled the space between the ingrowth core and intact soil with sieved, root-free soil. We removed the ingrowth cores at the end of the growing season (early September) and stored them at 4°C. We cut each core into 10-cm depth increments that we processed separately. We washed all roots free of soil by wet sieving (0.5 mm sieve) under low water pressure, then submerging remaining sample in a shallow bowl of water, picking out roots with forceps and removing attached soil by hand. Roots of the dominant plant species, *A. gerardii*, are visibly distinguishable from roots of other species in this plant community (Supporting information), and we separated these from the roots of all other species. We scanned all roots using a photo scanner and analyzed

scans for root diameter and length using WinRhizo (Regent Instruments Inc., Québec, Canada). We dried roots at 60°C for 48 h and weighed them. We calculated BNPP as root mass production per m^2 ground area.

Statistical analyses

We used annual plot-level data for all analyses, which we performed in R (www.r-project.org). We used the psych package (Revelle 2020) for summary statistics (Supporting information). We used linear mixed effects models with plot (nested within shelter) as a random variable (lme4 package, Bates et al. 2015) and type 3 sum of squares analyses of variance ('ANOVAs') to assess the main effects of treatment (Ambient→Ambient, Drought→Ambient, Ambient→Drought, Drought→Drought) and year (2015, 2016), as well as the year × treatment interaction. We analyzed total, *A. gerardii*, and subdominant species BNPP and root length production in this way (Supporting information). We used additional models which included the main effect of depth increment and the interactions of depth increment with treatment and with year to assess differences in BNPP depth distribution. We used pairwise contrast comparisons with Holm adjustment to determine in which years there were differences among treatments and in which treatments there were differences between years (emmeans package, Lenth 2021). We considered p-values < 0.05 indicative of significant effects.

Results

Growing season precipitation during the experiment

The Drought 2 treatment (66% reduction in the size of each precipitation event during the 2014 and 2015 growing seasons), resulted in growing season total precipitation amounts below the 5th percentile of the long-term (112-yr) KPBS rainfall record (Hoover et al. 2014a) in each year. Thus, based on site-specific historical precipitation amounts, Drought 2 was statistically extreme (Smith 2011, Slette et al. 2019), similar to Drought 1 (Hoover et al. 2014a). The first year after Drought 2 (2016) was unusually wet, with ambient growing season precipitation almost 30% above the long-term average (710 mm versus 559 mm, respectively; Fig. 2).

Root production and traits at the end of Drought 2

BNPP followed the pattern Ambient→Ambient > Ambient→Drought = Drought→Ambient > Drought→Drought (Fig. 3). There was a significant effect of treatment on BNPP ($F_{3,49} = 19.3$, $p < 0.001$). Relative to ambient precipitation, a single drought reduced BNPP by 27% ($p = 0.021$), and a second drought reduced BNPP by 63% ($p < 0.001$). BNPP in plots droughted four years earlier (Drought→Ambient) was 21% lower than in Ambient→Ambient plots ($p = 0.044$). The impacts of repeated droughts were additive ($p > 0.05$ for interaction term of two-way ANOVA of Drought 1 treatment and Drought 2 treatment). Reductions in BNPP were largest in shallow soil increments (Fig. 3, Supporting information). There was an effect of treatment at 0–10 cm ($p = 0.002$), but not at 10–20 cm ($p = 0.11$) or 20–30 cm ($p = 0.28$) below the surface. BNPP in Drought→Drought plots was reduced by approximately 70, 60 and 50% in the 0–10, 10–20 and 20–30 cm depth increments, respectively, compared to Ambient→Ambient plots. *Andropogon gerardii* BNPP followed the same pattern as total BNPP, but there was not a significant effect of treatment on *A. gerardii* BNPP ($F_{3,47} = 0.943$, $p = 0.82$). Compared to Ambient→Ambient plots, *A. gerardii* BNPP in Drought→Drought plots was reduced by approximately 50% while subdominant species BNPP was reduced by approximately 70%.

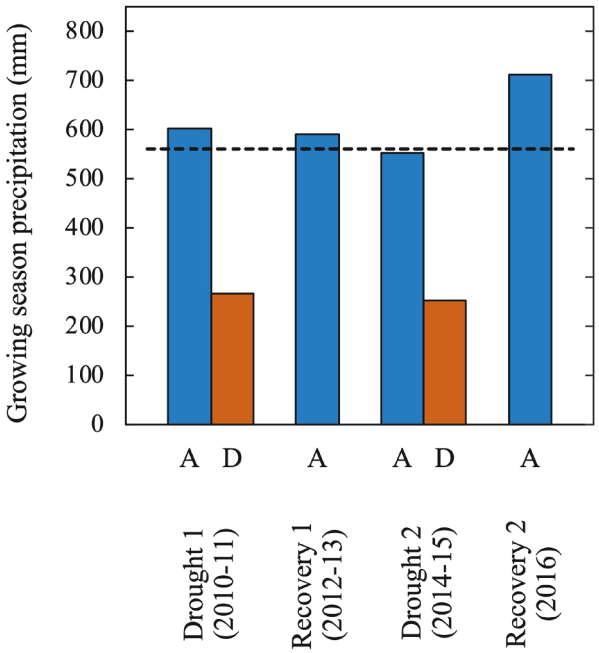

Figure 2. Growing season precipitation in Ambient (A) and Drought (D) treatments throughout the climate extremes experiment, and the long-term site average (horizontal dashed line).

There was a significant effect of treatment on root length production ($F_{3,39} = 20.8$, $p < 0.001$). A single drought reduced root length production by 52% ($p = 0.0011$) and a second drought reduced root length production by 63% ($p = 0.0002$), relative to ambient precipitation (Fig. 3). In contrast to BNPP, root length production did not differ between Ambient→Drought and Drought→Drought plots ($p = 0.33$; Fig. 3). Root length production in plots droughted only during Drought 1 was 30% lower than in Ambient→Ambient plots, but this difference was only marginally significant ($p = 0.056$). The magnitude of reduction was thus the same for root mass and length production in Drought→Drought plots (63%), but root length production was reduced more than root mass production in Ambient→Drought plots (52% versus 27%, respectively).

Root diameter, root tissue density (RTD) and specific root length (SRL) all differed between *A. gerardii* versus subdominant species, averaged across all treatments ($p < 0.001$

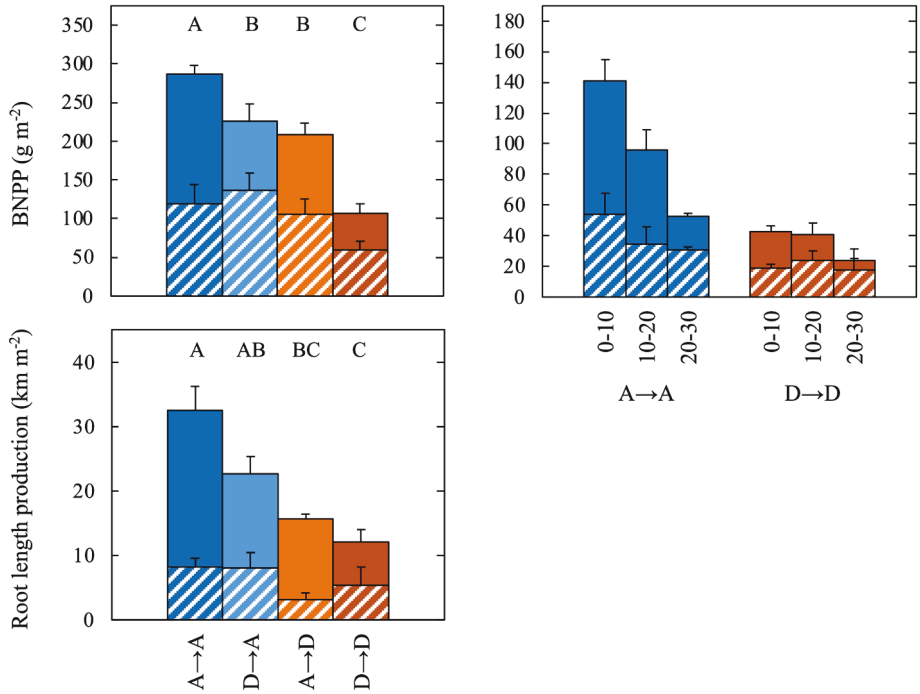

Figure 3. Average BNPP (+ one standard error) in the top 30 cm of the soil in the final year of Drought 2 for all treatments (top left). Average BNPP (+ one standard error) by depth in 10-cm increments for Ambient→Ambient and Drought→Drought treatments (top right). And average root length production (+ one standard error) by treatment in the final year of Drought 2 (bottom left). The dashed portion of each bar indicates *A. gerardii* BNPP or root length production. Different letters indicate significant differences in total BNPP or root length production among treatments. There was no effect of treatment on *A. gerardii* BNPP or root length production.

for each trait, Fig. 5). *Andropogon gerardii* roots had larger diameter, higher RTD and lower SRL than the collective subdominant species. There was no effect of treatment on root diameter, RTD or SRL of *A. gerardii* or of subdominant species ($p > 0.05$ for each trait).

Root production and traits after Drought 2

There was a significant main effect of year on BNPP ($F_{1,49} = 4.00$, $p = 0.045$). BNPP in the year after Drought 2 was higher in all formerly droughted plots compared to the previous year, regardless of drought history ($p = 0.0057$ A→D, $p < 0.001$ D→D, $p = 0.020$ D→A; Fig. 3 versus Fig. 4). BNPP was also higher in Ambient→Ambient plots during this year compared to the previous year, but statistical significance was marginal ($p = 0.059$). There were no differences among the four treatments in total BNPP ($p > 0.05$) or in *A. gerardii* BNPP ($p > 0.05$; Fig. 4) in this year. There were also no differences among the four treatments in total root length production ($p > 0.05$) or in *A. gerardii* root length production ($p > 0.05$; Fig. 4).

As during the previous year, root diameter, RTD and SRL all differed between *A. gerardii* versus subdominant species in this year, averaged across all treatments ($p < 0.001$ for each trait, Fig. 5). *Andropogon gerardii* roots again had larger diameter, higher RTD and lower SRL than the collective subdominant species. There was no effect of treatment on diameter, RTD or SRL of *A. gerardii* or of other species in this year ($p > 0.001$ for each trait).

Discussion

Our study revealed that previous drought exposure decreased resistance of root production to a subsequent drought. Two 2-year extreme droughts, separated by two years with average precipitation, decreased total BNPP by more than twice as much as a single 2-year extreme drought. This is contrary to our hypothesis that plots droughted previously would be more resistant to a second drought and suggests that less adaptation to low-water conditions occurred during Drought 1 than we expected. Drought impacts in this ecosystem may thus be underestimated if climatic history is not considered. Our results expand upon studies showing that drought can decrease root production and show that two droughts can decrease root production even more. Increasingly larger declines in BNPP with repeated droughts could decrease ecosystem carbon cycling and storage. This could have substantial global implications, given the importance of root dynamics to soil organic matter formation and the key role of grassland soils in global carbon sequestration (Risser et al. 1981, Soussana et al. 2004, Hui and Jackson 2006, Smith et al. 2008, Silver et al. 2010, Scharlemann et al. 2014, Köchy et al. 2015).

Root length production and root mass production responded to drought in slightly different ways. Compared to ambient precipitation plots, root length production declined more than root mass production in plots only droughted during Drought 2 (52% versus 27%, respectively), while root

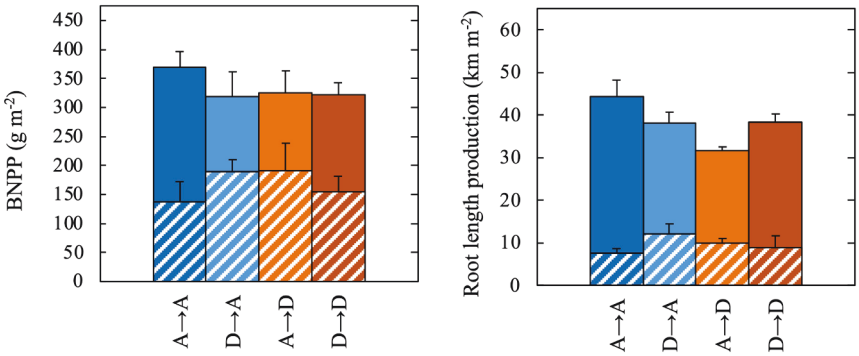

Figure 4. Average BNPP (+ one standard error) in the year after Drought 2 (left). Average root length production (+ one standard error) in the year after Drought 2 (right). There were no differences among treatments in total or *A. gerardii* (dashed portion of bars) BNPP or root length production.

length and mass production declined equally in plots droughted during both Drought 1 and Drought 2 (63%). Though less commonly quantified than mass production, root length production is likely a better indicator of the capacity of plants to acquire soil resources, as length reflects the volume of soil that plants can access (Jackson et al. 1996, Casper and Jackson 1997, Wilson 2014, Freschet et al. 2021). A single drought might thus have a larger negative impact on plant water and nutrient acquisition than on ecosystem carbon cycling, while a second drought substantially impacts both.

Though total root production declined with drought, root production of the dominant species, *A. gerardii*, did not (Fig. 3). *Andropogon gerardii* has relatively high water use efficiency (Turner and Knapp 1996), and photosynthesis and ANPP of *A. gerardii* declined less than that of other species in the CEE during Drought 1 (Hoover et al. 2014b). We build upon that finding and show that root production of *A. gerardii* also declined less than that of the other species in the community (collectively) during Drought 2. This suggests that *A. gerardii* could play an important role in maintaining ecosystem functioning in a changing climate.

A major goal of trait-based ecology has been to link plant traits with key ecosystem functions but establishing such links has been challenging, particularly for root traits (Freschet et al. 2021). *Andropogon gerardii* roots in our study were thicker and denser and more deeply distributed than those of the collective subdominant community (Fig. 3 and 5). This trait combination might be advantageous during drought. Given that shallow BNPP was most negatively affected by drought (Fig. 3, Supporting information), a deeper BNPP distribution likely increases water uptake and drought resistance in this grassland. This is consistent with previous research linking differences in root depth distribution with differences in plant production (Nippert and Holdo 2015) and with research demonstrating that deeper roots increase plant water uptake during dry periods (Fort et al. 2017). Thicker, low-SRL roots generally indicate more 'outsourcing' of resource acquisition to mycorrhizae (Bergmann et al. 2020). Previous research has shown that *A. gerardii* is indeed strongly mycorrhizal dependent (Wilson and Hartnett 1997, 1998, Smith et al. 1999), so greater mycorrhizal association of *A. gerardii* versus other species might have also contributed to its greater drought resistance (Begum et al. 2019). We did not find any evidence of either *A. gerardii* or the collective subdominant community altering root traits to adapt to drought (Supporting information). Thus, though certain traits appear to be beneficial in maintaining root production during drought, the species in this community might have

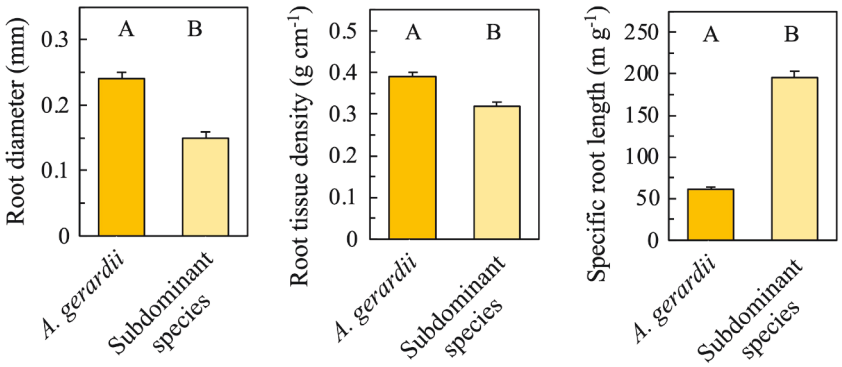

Figure 5. Average (+ one standard error) root diameter, specific root length and root tissue density of *A. gerardii* and of subdominant species (collectively). Trait values are averaged across treatments and years because there was no significant effect of treatments or of year or any trait. Different letters indicate significant differences between *A. gerardii* versus the rest of the species in the community.

little capacity to adjust the root traits assessed in this study in response to drought. Previous studies have found a variety of root trait responses to drought and more research is needed to fully understand the role of species identity and environmental context in modifying root trait responses to drought and the consequences for important plant and ecosystem functions (de Vries et al. 2016, Garbowski et al. 2020, Freschet et al. 2021, Funk et al. 2021).

After Drought 1 (2010–2011), ANPP in the CEE recovered in just one year (2012; Hoover et al. 2014a) and remained recovered in every following year (i.e. ANPP in formerly droughted plots was not different from ANPP in ambient precipitation plots in every year from 2012 to 2016; Smith et al. unpubl.). In contrast, our results show that BNPP was lower in Drought→Ambient plots than in Ambient→Ambient plots four years after Drought 1 (2015; Fig. 3). This slow recovery of BNPP was a less apparent (i.e. belowground) but much more persistent effect of Drought 1. Therefore, drought-driven decreases in production might be underestimated if forecasts consider only aboveground effects and not the large and persistent impact of drought belowground. However, BNPP did recover in the year after Drought 2 (Fig. 4), likely due to above-average precipitation in this year, compared to near-average precipitation in the previous four years (Fig. 2). Thus, reductions in BNPP following two sequential droughts did not preclude rapid post-drought recovery when resource availability was high. Along with BNPP, ANPP also decreased in Ambient→Drought and Drought→Drought plots during Drought 2 but recovered in just one year (2016; Smith et al. unpubl.). The different recovery patterns of ANPP versus BNPP over time suggest that while average precipitation amounts appear to be sufficient for ANPP recovery after extreme drought, BNPP recovery might be more resource demanding. This adds to the growing evidence that precipitation change has different impacts on grassland primary production aboveground versus belowground (Chou et al. 2008, Byrne et al. 2013, Wilcox et al. 2015, 2017, Post and Knapp 2020, Carroll et al. 2021, Slette et al. 2022a). It will be important to consider dissimilarity of aboveground versus belowground production responses when forecasting impacts of increasing climatic variability.

Our results suggest several topics for future studies of root responses to repeated drought. For example, we found no change in several root morphological traits in response to drought, but this does not preclude change in other traits or in root physiology or mycorrhizal association (Feng et al. 2022). Future studies could investigate changes in a variety of additional root traits in response to drought and how these relate to plant and ecosystem processes. Also, our results indicate that recovery of root production after drought depends on precipitation amount after drought, and this could be quantified more rigorously in future research. Studies that track recovery of root production for multiple years after drought will be particularly useful, as our results indicate that recovery can sometimes take years. We only measured root production for one year after Drought 2 and, though we found complete recovery in that year, this might not have been the case if precipitation had been closer to average in this year, and root production might differ among former treatment in later years (another legacy effect of drought). Finally, we speculate that grasslands with different climates (e.g. mean annual precipitation) would respond differently to repeated experimental droughts, because grasslands with different climates respond differently to drought aboveground (Knapp et al. 2015, 2020, Wilcox et al. 2015, Carroll et al. 2021).

In summary, we found that previous exposure to an extreme drought decreased drought resistance of mesic grassland root production. After drought, root production recovered to ambient levels only when precipitation was above average. As climatic variability increases, causing greater drought frequency and severity as well as more extreme wet years, predicting and modeling changes in key aspects of global terrestrial carbon and water cycling will require understanding the unique dynamics of roots (in addition to more commonly measured aboveground dynamics) and responses during and after not only single but also multiple climate extremes.

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Author contributions

Ingrid J. Slette: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Writing – original draft (lead); Writing – review and editing (lead). **David L. Hoover**: Conceptualization (equal); Writing – review and editing (equal). **Melinda D. Smith**: Conceptualization; Writing – review and editing. **Alan K. Knapp**: Conceptualization; Writing – review and editing.

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.25349/D99C85 (Slette et al. 2022b).

Supporting information

The Supporting information associated with this article is available with the online version.

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