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Effects of Compounded Precipitation Pattern Intensification and Drought Occur Belowground in a Mesic Grassland

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ABSTRACT

Climate change is altering precipitation regimes globally, with expectations of intensified precipitation patterns (for example, larger but fewer rainfall events) and more frequent and extreme drought. Both aspects of precipitation change can impact ecosystem function individually, but it is more likely that they will occur in combination. In a central US mesic grassland, we imposed an extreme 2-year drought (growing season precipitation reduced by 66%) on plots with a long-term (16-year) history of exposure to either ambient or intensified precipitation patterns (average threefold increase in event size and threefold decrease in event number during the growing season). While this intensified pattern did not alter total precipitation amount, it generally led to ecosystem responses consistent with a drier environment (for example, reduced soil moisture, aboveground net primary production (ANPP), and soil CO_2 flux, but little evidence for altered root biomass). Surprisingly, this history of intensified precipitation patterns did not affect the response of ANPP to the subsequent extreme drought. In contrast, previous exposure to intensified precipitation patterns reduced root production and muted soil CO_2 flux responses to rainfall events during drought. Reduced root production in plots experiencing compounded precipitation extremes was driven not by the dominant C_4 grass species, *Andropogon gerardii*, but collectively by the subdominant species in the plant community. Overall, our results reveal that compound changes in precipitation patterns and amount affected this grassland in ways that were less apparent (that is, belowground) than responses to either change individually and significantly reduced ecosystem carbon uptake.

Key words: belowground net primary production; aboveground net primary production; soil CO_2 flux; carbon cycling; *Andropogon gerardii*; rainfall extremes.

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HIGHLIGHTS

- Rainfall intensity and drought are increasing, with unknown ecological consequences
- Past exposure to intensified rainfall altered the impacts of drought belowground
- Forecasts of drought impacts should include rainfall history and belowground dynamics

INTRODUCTION

Climate change is expected to intensify precipitation regimes by increasing the size of individual rainfall events as well as the number and length of anomalously dry periods (that is, droughts), with evidence for these changes already emerging (Dai 2013; Fischer and Knutti 2016; Huntington 2006; IPCC 2013; USGCRP 2017). For example, much of the world is experiencing larger, more intense precipitation events without corresponding increases in total precipitation amount (Fischer and Knutti 2016; Fowler and others 2021; IPCC 2013). A shift toward fewer but larger precipitation events and longer durations between events can affect myriad ecosystem processes (Fay and others 2008; Knapp and others 2008; Zeppel and others 2014). Concurrently, droughts are becoming more frequent and extreme in many regions. Drought, defined as a period of marked precipitation deficiency relative to the local long-term average, is a well-known climate extreme that has been studied extensively (Dai 2013; Eziz and others 2017; Gao and others 2019; Lei and others 2016; Slette and others 2019; Wu and others 2011). Given that both dimensions of precipitation change are increasing, it is likely that future droughts will occur against a backdrop of intensified precipitation patterns (cf. Harrison and others 2018). However, most research to date has focused on these different aspects of precipitation change individually, and their combined effects are thus unresolved.

Ecosystem responses to combined weather events, or compound events (Seneviratne and others 2012), are likely not predictable from studies that focus on individual events (Dodd and others 2021; Zscheischler and others 2018). Instead, one dimension of change might precondition an ecosystem and alter its response to another (Zscheischler and others 2020). That is, a chronic ''press'' change such as long-term intensification of precipitation patterns might alter the impacts of a ''pulse'' event such as a short-term extreme drought. For example, Hoover and others (2015) found that a short-term extreme ''pulse drought'' had a larger negative impact on plant production and mortality when it occurred against a backdrop of a milder and longer-term ''press drought.'' Other previous studies have also found amplifying impacts of compound climate extremes more generally, though neutral and mitigating effects have also been reported (Anderegg and others 2020; Backhaus and others 2014; Dreesen and others 2014; Hoover and others 2021; Hughes and others 2019). Consensus on the effects of compounded climate changes is therefore lacking. Understanding press–pulse interactions, such as how exposure to intensified precipitation patterns might precondition ecosystem responses to drought, has important implications for improving understanding of carbon cycling in a changing climate.

Grasslands are important ecosystems in which to assess compounded effects of precipitation changes because they are structurally and functionally controlled by water availability (Morgan and others 2008; Mowll and others 2015; Sala and others 1988), they experience high inter- and intra-annual precipitation variability (Knapp and Smith 2001), and they are sensitive to changes in precipitation amount and pattern (Felton and others 2020; Gherardi and Sala 2015; Heisler-White and others 2008, 2009; Hoover and others 2014; Huxman and others 2004a, b, c; Knapp and others 2002, 2008, 2015, 2020; Li and others 2019; Lu and others 2021; Thomey and others 2011). Grass-dominated systems are also globally extensive (Dixon and others 2014; White and others 2000) and play a key role in the global carbon cycle (Pendall and others 2018; Scurlock and Hall 1998). Belowground responses such as belowground net primary production (BNPP) and soil CO_2 flux are of particular interest here because grasslands allocate a substantial portion of total net primary production to roots and store most of their carbon belowground (Hui and Jackson 2006; Risser and others 1981; Silver and others 2010; Smith and others 2008; Soussana and others 2004). Root production and soil CO_2 flux are key factors determining the size of the soil carbon pool, which is at least twice as large as the atmospheric carbon pool and plays an important role in global carbon cycling and climate regulation (Köchy and others 2015; Scharlemann and others 2014). Although root mass production is useful for comparing aboveground versus belowground NPP and their relative contributions to carbon cycling, the capacity of plants to acquire soil resources is likely better reflected by root length than mass because length better reflects the volume of soil that plants can access (Casper and Jackson 1997; Jackson and others 1996; Wilson 2014). We thus assessed both length and mass production of roots.

The objective of this study was to assess the ecosystem impacts of compounded precipitation changes in a mesic grassland. Specifically, we tested how long-term extreme intensification of precipitation patterns might alter ecosystem responses to a subsequent extreme drought, as well as recovery after drought. Our research builds on the Rainfall Manipulations Plots (RaMPs; Fay and others 2000) experiment which altered growing season precipitation patterns, but not amount, for 16 years. The RaMPs experiment intensified precipitation patterns by imposing fewer and larger precipitation events with longer intervening dry periods, compared to ambient patterns. Prior results from the RaMPs study revealed that the intensified precipitation pattern resulted in drier soils, increased plant water stress, reduced aboveground net primary production (ANPP) and soil CO_2 flux, altered soil microbial community composition, and altered genotypic structure of the dominant plant species compared to ambient precipitation patterns (Avolio and Smith 2013; Avolio and others 2013; Evans and Wallenstein 2012; Fay and others 2002, 2003, 2011; Harper and others 2005; Knapp and others 2002; Nippert and others 2009). We predicted that this history of intensified precipitation patterns would exacerbate the impacts of drought, compared to a history of ambient precipitation patterns. To test this prediction, we imposed an extreme 2-year drought (66% reduction in growing season rainfall) in grassland plots with and without previous long-term exposure to an intensified precipitation regime and assessed key carbon cycling processes (for example, ANPP, BNPP and soil CO_2 flux) during and after drought.

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 primarily composed of native C_4 grasses (average 77% of total biomass in the RaMPs experiment over 16 years), dominated by *Andropogon gerardii* and also including *Sorghastrum nutans*, *Sporobolus asper*, and *Panicum virgatum*. The rest of the plant community is composed mostly of an array of C_4 forb species (mainly *Solidago canadensis*, *Aster ericoides*, *S. missouriensis*), with woody species accounting for a very small percent of total biomass and cover in the RaMPs experiment (Fay and others 2000; Knapp and others 1998). The climate is temperate with warm, wet summers and cold, dry winters. The mean annual temperature is 13°C (Knapp and others 1998) and the mean annual precipitation is 851 mm, almost 70% of which occurs during the growing season. Our experiment was located on deep silty clay loam soils in the Tully series (Collins and Calabrese 2012; Ransom and others 1998). Frequent fires are a historical feature of this grassland and are essential for maintaining grass dominance and reducing woody plant encroachment (Briggs and others 2005; Knapp and others 1998), and our experiment was burned annually in mid-March.

The RaMPs Experiment Design and Treatments

The RaMPs experiment included 12 fixed-location shelters (9 × 14 m) arranged in a randomized complete block design (see Fay and others 2000 for details). Each shelter consisted of a clear (UV transparent) polyethylene roof that excluded all precipitation, gutters and storage tanks for rainfall collection, and an overhead irrigation system for rainfall application. Each RaMP was isolated belowground to a depth of 1.2 m via a subsurface barrier. Sampling occurred in a 6 × 6 m area divided into four 2 × 2 m subplots. Each RaMP received either the ambient or intensified precipitation pattern from 1998 to 2013. In RaMPs receiving the ambient precipitation pattern, collected rainfall was applied each time a natural rain event occurred. In RaMPs receiving the intensified precipitation pattern, rainfall timing and event size were altered by delaying rainfall applications. The dry interval between rainfall events was increased by 50% and all ambient rainfall during the lengthened dry interval was collected, stored and applied as a single large event. Thus, the ambient and intense treatments received the same amount of rain, but the intense treatment received fewer and larger rainfall events with longer intervening dry periods. Manipulations occurred only during the growing season (May–September). Rainfall events were defined as daily total > 5 mm, as smaller amounts are almost entirely intercepted by the canopy (Seastedt 1985). The intense treatment imposed a statistically extreme precipitation pattern, compared to long-term ambient rainfall patterns at the KPBS (Nippert and others 2006; Smith 2011).

After 16 years of ambient versus intense precipitation patterns, an extreme drought was imposed on all plots. In 2014 and 2015, total growing season precipitation in all RaMPs was reduced to about 34% of the 1998–2013 experiment average (following Knapp and others 2017). Each rainfall event was reduced in size by 66% and event timing followed the ambient pattern. Similar reductions have imposed statistically extreme droughts at the KPBS in the past (Hoover and others 2014). The size and timing of all rainfall events were the same for all plots, to facilitate direct comparisons of how past exposure to intensified precipitation would impact responses to a common drought treatment. To assess recovery after drought, all ambient precipitation was applied to all RaMPs in 2016 with event size and timing matching the ambient pattern.

Field Measurements

Key ecosystem processes (for example, photosynthesis, ANPP, N mineralization) at the KPBS are strongly linked to soil moisture in the top about 30 cm below the surface (Blair 1997; Briggs and Knapp 1995; Knapp and others 1993; Nippert and Knapp 2007). Thus, soil volumetric water content (VWC) was measured at 15 cm and 30 cm soil depths at 30 min intervals in all RaMPs for the duration of the experiment using Time Domain Reflectometry (TDR) probes (Fay and others 2000).

Annual ANPP was estimated each year (1998–2016) from end-of-growing-season vegetation harvests of 16 total 0.1 m^2 quadrats per RaMP (four per subplot) performed by clipping all vegetation rooted within the quadrat to the soil surface with scissors. Because the site is burned annually and not grazed, the collected biomass represents ANPP. The dominant species, *A. gerardii,* often drives responses in this system (Smith and Knapp 2003), and it was separated from subdominant species. All biomass was dried at 60°C for 48 h and weighed.

The cumulative impact of the ambient versus intense precipitation treatments on total root biomass was estimated by taking four soil cores per RaMP (5 cm diameter, 60 cm deep, one per subplot) at the end of the last growing season before the drought. Each core was divided into 10-cm depth increments. Roots were removed from each increment, washed free of soil, dried at 60°C for 48 h and weighed. Annual BNPP was estimated during the last year of drought (2015) and first year after drought (2016) by using root ingrowth cores to estimate fine root production. At the start of the growing season (late April), three soil cores (5 cm diameter, 30 cm deep) were taken from each plot, plus 10 from unaltered grassland adjacent to the RaMP (for use as controls) and discarded. This depth captures most root production at our study site and other grasslands (Jackson and others 1996; Nippert and others 2012; Schenk and Jackson 2002; Sun and others 1997; Weaver and Darland 1949). A cylindrical mesh basket filled with sieved, root-free soil collected adjacent to the RaMPs and packed to approximate field bulk density was placed into each core hole (5 cm diameter, 30 cm deep, 2 × 2 mm mesh holes). Any space between the ingrowth core and intact soil was filled with sieved, root-free soil. Ingrowth cores were removed at the end of the growing season (late September) and stored at 4°C. Each core was divided into 10-cm depth increments. Soil was washed off roots by wet sieving (0.5 mm sieve) under low water pressure, submerging remaining sample in a shallow bowl of water, picking out roots with forceps, and removing attached soil by hand. *A. gerardii* roots are distinctive (Figure S1), and they were separated from subdominant species' roots. Roots were scanned using an Epson Perfection photo scanner (Epson America Inc., Long Beach, CA, USA) and scans were analyzed for root diameter and length using WinRhizo (Regent Instruments Inc., Québec, Canada). Roots were dried at 60°C for 48 h and weighed. BNPP was calculated as root mass production per m^2 ground area.

Soil CO_2 flux was measured in situ between 10:00 a.m. and 2:00 p.m. local time approximately weekly throughout the 2015 and 2016 growing seasons using a LiCOR 8100 portable gas exchange system (LiCOR Inc., Lincoln, NE, USA). Per RaMP, eight polyvinyl chloride (PVC) collars (two per subplot) were installed (10 cm diameter × 8 cm tall, buried 6 cm into the soil) between plant tillers/stems. Any litter and vegetation within the collar were removed (via clipping with scissors or by hand if loose) so that measurements included only CO_2 flux from the soil. To assess flux responses to rainfall, additional measurements were taken immediately before and approximately 24 h after individual rainfall applications.

Statistical Analyses

We performed all analyses in R (R Core Team 2018), using plot-level and annual-scale data. We used the psych package (Revelle 2020) for summary statistics (Table S1). To determine the impacts of ambient versus intense treatments during 1998–2013 on total, *A. gerardii*, and subdominant species ANPP and on soil moisture at 15 cm and 30 cm, we used linear models (nlme package; Pinheiro and others 2020) and type 3 sum of squares analyses of variance (''ANOVAs''; car package; Fox and Weisberg 2019) to assess the main effects of treatment (nested within block) and year, and the year × treatment interaction. We similarly assessed the main effect of treatment (nested within block) and depth increment, and the treatment × depth increment interaction on root biomass. To determine the impacts of ambient versus intense treatment history during the last year of drought and the first year after drought, we used linear models and type 3 sum of squares ANOVAs to assess the main effects of treatment history (nested within block) and year, and the year × treatment history interaction (Table S2). We analyzed ANPP, BNPP, NPP, and the BNPP:ANPP ratio for all species, *A. gerardii*, and subdominant species in this way, as well as soil moisture at 15 cm and 30 cm and soil CO_2 flux (growing season average, before rainfall events and after rainfall events). In the BNPP model, we also included the main effect of depth increment and the interactions of depth increment with treatment history and with year. For each dependent variable, we used pairwise contrast comparisons (emmeans package; Lenth 2020) to determine in which years there were differences between treatments. We considered p values < 0.05 significant.

RESULTS

Ecosystem Responses to an Intensified Precipitation Pattern

Results from various time periods during the RaMPs experiment have been reported previously (for example, Avolio and others 2013; Fay and others 2000, 2002, 2003, 2011; Harper and others 2005; Knapp and others 2002), but none from its full 16-year duration. We updated a subset of past analyses and here report results from the entire experiment. The intense treatment reduced the number of growing season rainfall events almost threefold (30 ± 2 ambient vs. 12 ± 1 intense) while increasing rainfall event size by a similar proportion (13 ± 1 mm ambient versus 33 ± 2 mm intense; Figure 1), on average. Despite no differences in total rainfall between treatments, the intense pattern led to drier soils at 15 cm during the growing season (22.2 ± 5.9% vwc intense vs. 25.5 ± 4.5% vwc ambient; $F_{1,123} = 49.5$, $p < 0.001$) and a 14% reduction in ANPP (675 ± 17 g m^{-2} intense vs. 737 ± 18 g m^{-2} ambient; $F_{1,7} = 4.93$, $p < 0.001$), averaged over 16 years. *A. gerardii* composed ~ 40% of total ANPP on average during this time (Figure 2). At the end of the experiment, standing crop root biomass did not differ between treatments overall (792 ± 59 g m^{-2} intense vs. 809 ± 61 g m^{-2} ambient; $F_{1,36} = 1.01$, $p = 0.32$) or in any individual depth increment (Figure S2).

How an Intensified Precipitation Pattern Affected Drought Responses

Reducing the size of each ambient precipitation event by 66% resulted in growing season precipitation amounts below the 5th percentile of the RaMPs rainfall record (1998–2013) and the long-term (112-year) KPBS rainfall record (Hoover and others 2014). Thus, based on site-specific historical precipitation amounts, we imposed a statistically extreme drought (Smith 2011).

During the last year of the drought (2015), soil moisture did not differ by treatment history at either 15 cm ($F_{1,17} = 1.13$, $p = 0.30$) or 30 cm ($F_{1,17} = 0.46$, $p = 0.50$) depths, but it was 55% (15 cm) and 40% (30 cm) lower than the pre-drought ambient RaMPs average. Similarly, ANPP during the last year of the drought did not differ by treatment history ($F_{1,8} = 0.086$, $p = 0.78$), but it was 36% lower than the pre-drought ambient RaMPs average. Thus, a history of intensified precipitation did not alter the response of ANPP to drought (Figure 2). In contrast, BNPP during the last year of the drought was lower in historically intense versus ambient plots (Figure 2; $F_{1,8} = 7.14$, $p = 0.028$). BNPP in historically intense plots was 70% of BNPP in historically ambient plots. This was collectively driven by the subdominant species. BNPP of the subdominant species in the historically intense plots was 46% of that in the historically ambient plots ($F_{1,8} = 18.19$, $p = 0.0027$). Surprisingly, BNPP of the dominant species, *A. gerardii*, did not differ by treatment history ($F_{1,8} = 2.43$, $p = 0.16$). Despite differences in BNPP, NPP (ANPP + BNPP; $F_{1,8} = 0.64$, $p = 0.45$) and the overall ratio of BNPP:ANPP did not differ by treatment history ($F_{1,8} = 2.17$, $p = 0.18$). However, the ratio of subdominant species BNPP:ANPP in historically intense plots was just 50% of that in ambient plots ($F_{1,8} = 6.09$, $p = 0.039$). In the last year of the drought, *A. gerardii* was 32 and 59% of total BNPP in historically ambient and intense plots, respectively, and it was 44 and 48% of total ANPP in ambient and intense plots, respectively (Figure 2).

Historical precipitation intensification reduced subdominant species BNPP in each depth increment (Figure 3; 0–10 cm: $p = 0.046$; 10–20 cm:

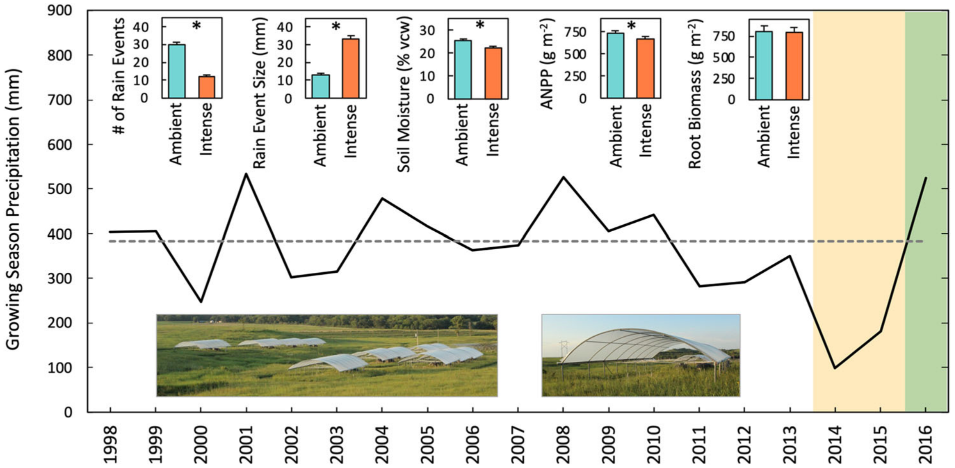

Figure 1. Growing season precipitation in each year of the RaMPs experiment (*solid line*) and 1998–2013 average (*dashed line*). From 1998 to 2013 (*non-shaded area*), the intense treatment received fewer and larger rainfall events. A common drought was imposed on both historical treatments in 2014 and 2015 (*yellow-shaded area*), and all plots received all ambient rainfall in 2016 (*green-shaded area*). Insets: 1998–2013 average (+ 1 standard error) growing season number of rain events, size of rain events, soil moisture at 15 cm, aboveground net primary production (ANPP) and root biomass (2013 only) in ambient and intense precipitation pattern treatments. *Significant difference between ambient versus intense treatments. Photos: the RaMPs experiment (*left*), closer view of a RaMPs experiment shelter (*right*).

$p = 0.0099$; 20–30 cm: $p = 0.021$) in the last year of drought. In addition, there was a significant effect of depth on subdominant species BNPP ($F_{2,28} = 4.37$, $p = 0.022$) but not *A. gerardii* BNPP ($F_{2,28} = 1.80$, $p = 0.18$). That is, *A. gerardii* BNPP was more evenly distributed among depths. In historically intense plots, *A. gerardii* produced more root mass ($p = 0.040$) and a greater proportion of its total root mass ($p = 0.014$) in the deepest increment sampled, compared to subdominant species.

Similar to BNPP, root length production was lower in historically intense versus ambient plots during the last year of drought (Figure 4; $F_{1,7} = 29.6$, $p < 0.001$). This difference was also due to responses of subdominant species ($F_{1,7} = 9.65$, $p = 0.038$), not of *A. gerardii* ($F_{1,7} = 2.65$, $p = 0.65$). *A. gerardii* made up a smaller proportion of total root length versus mass production (20% vs. 30% ambient, 30% vs. 60% intense, respectively), due to its smaller specific root length (SRL; 67.4 ± 7.7 m g^{-1}) compared to subdominant species (160 ± 16 m g^{-1}; $p < 0.001$; Figure S1). There was no difference in root tissue density (RTD) of *A. gerardii* versus subdominant species (Figure S1; $p = 0.25$). There was also no effect of treatment history and no difference between drought versus after-drought years on SRL or RTD of *A. gerardii* or subdominant species ($p > 0.05$).

Growing season average soil CO_2 flux during drought did not differ by treatment history during the last year of drought (Figure 5; $F_{1,8} = 1.34$, $p = 0.28$), but short-term flux increases after rainfall did. Soil CO_2 flux was higher in historically ambient versus intense plots after rainfall ($F_{1,8} = 1.93$, $p = 0.044$). Thus, a history of intensified precipitation dampened the response of soil CO_2 flux to rainfall during drought.

Recovery After Drought

The first year after the drought (2016) was wetter than usual, with ambient precipitation almost 40% higher than the pre-drought RaMPs average (Figure 1). In this year, soil moisture did not differ by treatment history at either 15 cm ($F_{1,7} = 0.013$, $p = 0.91$) or 30 cm ($F_{1,7} = 2.96$, $p = 0.13$) depths. Total ANPP ($F_{1,8} = 0.017$, $p = 0.99$), *A. gerardii* ANPP ($F_{1,8} = 0.162$, $p = 0.70$), and subdominant species ANPP ($F_{1,8} = 0.0041$, $p = 0.95$) also did not differ by treatment history (Figure 2). *A. gerardii* was 50% of total ANPP in both historically ambient and intense plots (Figure 2). As expected, total ANPP was higher after versus during drought, (ambient: $p < 0.001$; intense: $p < 0.001$) as was ANPP of *A. gerardii* and of subdominant species. Compared to the 16-year pre-drought ambient RaMPs average, ANPP during the wet recovery year was slightly (6%) reduced ($F_{1,44} = 2.90$, $p = 0.096$). However, *A. gerardii* ANPP was higher (9.5%) whereas subdominant species ANPP was

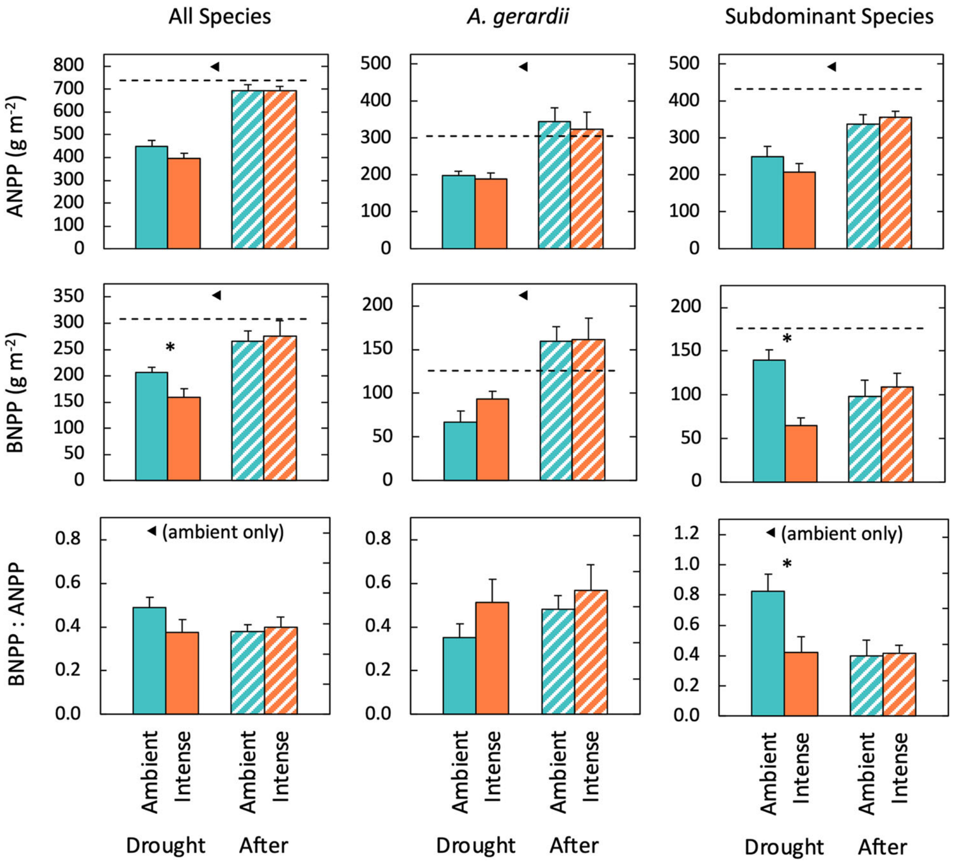

Figure 2. Average (+ one standard error) ANPP, BNPP, and ANPP:BNPP ratio of all species, *A. gerardii*, and subdominant species in historically ambient and intense precipitation treatments in the last year of drought (2015) and the first year after drought (2016). *Horizontal dashed line* = 1998–2013 RaMPs ambient average ANPP or 2015–16 RaMPs-adjacent ambient average BNPP. *Significant difference between historically ambient versus intense precipitation treatments within a year (drought or after-drought). ◀Significant difference between drought versus after-drought years, within historical treatment (ambient or intense).

lower (26%) than the pre-drought ambient average.

After drought, total BNPP ($F_{1,8} = 0.29$, $p = 0.61$), *A. gerardii* BNPP ($F_{1,8} = 0.04$, $p = 0.85$), and subdominant species BNPP ($F_{1,8} = 0.59$, $p = 0.47$) did not differ by treatment history. *A. gerardii* was 60% of total BNPP in both historically ambient and intense plots (Figure 2). Total BNPP (ambient: $p = 0.049$; intense: $p = 0.025$) and *A. gerardii* BNPP (ambient: $p = 0.014$; intense: $p = 0.048$) were higher after versus during drought, but subdominant BNPP did not differ after versus during drought (ambient: $p = 0.14$; intense: $p = 0.10$; Figure 2). The BNPP:ANPP ratio for all species and for subdominants was lower after versus during drought in historically ambient ($p = 0.019$, $p = 0.022$, respectively) but not intense plots ($p = 0.71$, $p = 0.99$, respectively), whereas the BNPP:ANPP ratio for *A. gerardii* did not differ in either historical treatment (ambient: $p = 0.18$; intense: $p = 0.78$).

Consistent with BNPP, root length production did not differ by treatment history in the first year after drought (Figure 4; $F_{1,5} = 0.35$, $p = 0.58$). Total (ambient: $p = 0.049$; intense: $p = 0.019$) and *A. gerardii* (ambient: $p = 0.014$; intense: $p = 0.045$) root length production were higher after versus during drought, but subdominant species root length production was not different after versus during drought (ambient: $p = 0.86$; intense: $p = 0.064$).

Finally, growing season average soil CO_2 flux did not differ by treatment history in the first year after drought (Figure 5; $F_{1,8} = 1.19$, $p = 0.31$) and was higher after versus during drought ($p < 0.001$). The short-term flux increase after rainfall did differ by treatment history. Soil CO_2 flux was higher in historically ambient versus intense precipitation plots after rainfall ($F_{1,92} = 4.49$, $p = 0.037$).

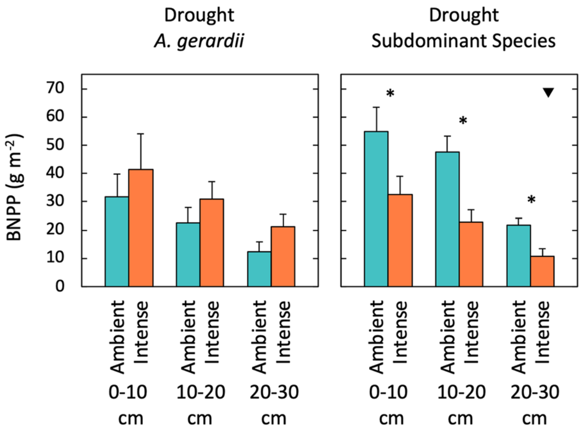

Figure 3. Average (+ one standard error) BNPP of *A. gerardii* and subdominant species by depth in historically ambient and intense precipitation treatments during the last year of drought. *Significant difference between historical treatments in a depth increment. ▼Significant main effect of depth on BNPP. After drought, there were no significant differences between historical treatments in BNPP at any depth, for either *A. gerardii* or subdominant species.

Discussion

Long-term exposure of this mesic grassland to an intensified precipitation pattern reduced soil moisture and ANPP, as reported previously (Fay and others 2002, 2003, 2011; Knapp and others 2002). But when exposure to extreme precipitation patterns was compounded with extreme drought, there were no legacy effects of past precipitation pattern on ANPP. This contrasts sharply with responses belowground, where a history of intensified precipitation patterns amplified reductions in BNPP during drought and reduced the size of the soil CO_2 flux increase following rainfall events both during and after drought. Thus, our findings add to growing evidence that grassland belowground responses to precipitation change should not be inferred from aboveground responses (Byrne and others 2013; Carroll and others 2021; Chou and others 2008; Post and Knapp 2020; Wilcox and others 2015, 2017). The negative effect of past exposure to intensified precipitation belowground has implications for long-term ecosystem carbon cycling and sequestration, given the important role of soils, especially grassland soils, in global carbon storage (Hui and Jackson 2006; Köchy and others 2015; Risser and others 1981; Scharlemann and others 2014; Silver and others 2010; Smith and others 2008; Soussana and others 2004). Our results thus suggest that, as precipitation patterns continue to intensify, the negative impacts of droughts on plant production and ecosystem carbon uptake might be underestimated if belowground dynamics are not fully considered.

Although it is possible that BNPP differed between ambient and intense precipitation plots prior to drought (this was not quantified), root biomass did not differ between treatments in the last year of the experiment (Figures 1, S2), suggesting that any differences in annual root production between treatments were likely small and did not accumulate to affect standing root biomass. However, we found that root production did differ between ambient and intense treatment plots when precipitation intensification was compounded with

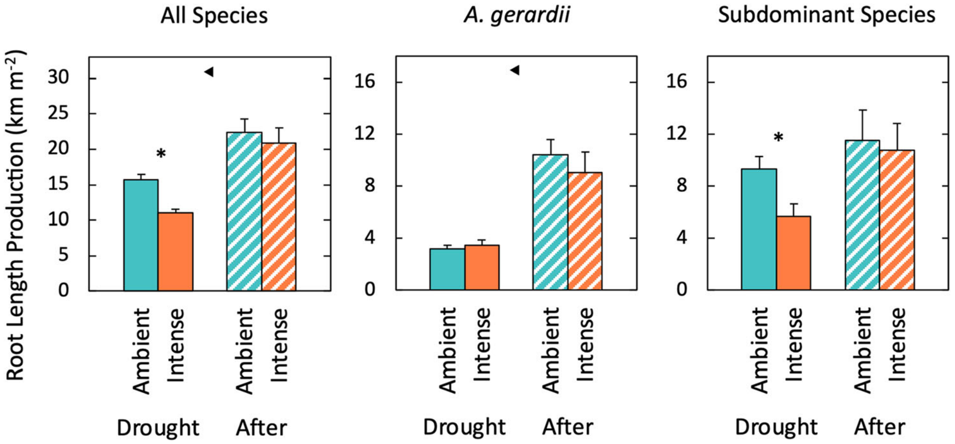

Figure 4. Average (+ one standard error) root length production of all species, *A. gerardii*, and subdominant species from historically ambient and intense treatments in the last year of drought and first year after drought. *Significant difference between historically ambient versus intense precipitation treatments within a year (drought or after-drought). ◀Significant difference between drought versus after-drought years, within historical precipitation treatment (ambient or intense).

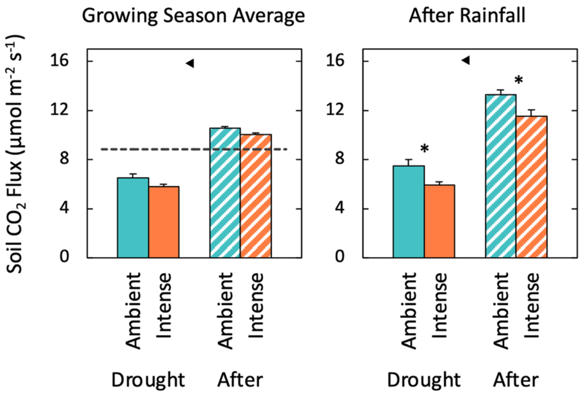

Figure 5. Growing season average (+ one standard error) soil CO_2 flux and average (+ one standard error) soil CO_2 flux approximately 24 h after rainfall in historically ambient and intense treatments in the last year of drought and the first year after drought. *Horizontal dashed line* = pre-drought ambient RaMPs average. *Significant difference between historically ambient versus intense precipitation treatments within a year (drought or after-drought). ◀Significant difference between drought versus after-drought years, within historical precipitation treatment (ambient or intense).

drought. The negative effect of intensified precipitation on BNPP during drought was due to responses of the subdominant species. The BNPP distribution of *A. gerardii* was deeper than that of subdominant species, which likely contributed to the different responses during and after drought. Indeed, previous research has linked changes in root distribution within the top ~ 30 cm to changes in total plant production even when maximum rooting depth is greater than 30 cm (Nippert and Holdo 2015). We also found that *A. gerardii* made up a smaller proportion of total root length production versus root mass production. The lower dominance of *A. gerardii* root length versus mass was driven by its low SRL. A lower SRL likely indicates ''outsourcing'' of resource acquisition to mycorrhizae, versus a ''do-it-yourself'' acquisition strategy of plants with higher SRL (Bergmann and others 2020). We did not assess mycorrhizal abundance, but past research has shown that *A. gerardii* is highly mycorrhizal dependent (Smith and others 1999; Wilson and Hartnett 1997, 1998). It is thus possible that greater mycorrhizal association of *A. gerardii* versus subdominant species also contributed to their different responses during and after drought. BNPP of subdominant species differed between historical ambient versus intense treatments during drought but not after drought, suggesting that the impacts of precipitation pattern intensification are relatively short-lived and reversible. The impact of drought might be longer lasting, as BNPP of subdominant species remained below control plot levels after drought did not increase after drought, even in a wet year.

Previous research and theory have suggested that increased proportional allocation belowground provides an advantage in dry conditions by increasing water uptake (Bloom and others 1985; Chapin and others 1987; Chou and others 2008; Milchunas and Lauenroth 2001; Poorter and others 2012). Based on this, we expected to find higher BNPP:ANPP ratios during versus after drought. However, we only found evidence for this in the former ambient precipitation treatment. This response was driven by an almost twofold higher BNPP:ANPP ratio of the subdominant species during versus after drought. That is, whereas BNPP and ANPP of *A. gerardii* changed by the same relative proportion in both historical treatments, subdominant species shifted to produce proportionally more root mass versus shoot mass during drought, but only in historically ambient precipitation plots. This could indicate greater plasticity of production allocation in response to water availability of subdominant species compared to *A. gerardii*, or that resources other than water (for example, carbon) were also limiting during drought. The mechanism explaining how a history of intensified precipitation altered the responsiveness of BNPP:ANPP allocation patterns to drought remains to be resolved.

Intensified precipitation patterns decreased average soil CO_2 flux (Harper and others 2005), but when intensified precipitation patterns were compounded with drought, there was no effect of past precipitation pattern on growing season average soil CO_2 flux. However, previous exposure to intensified precipitation patterns did decrease the response of soil CO_2 flux to individual precipitation events during and after drought. Our results are consistent with well-documented patterns of soil CO_2 flux correlating with soil moisture, for example, declining during drought and increasing after individual rainfall events, with larger increases after larger rain events and wetter antecedent conditions (for example, after vs. during drought; Birch 1958; Bremer and others 1998; Feldman and others 2021; Fierer and Schimel 2003; Harper and others 2005; Hoover and others 2016; Liu and others 2002; Post and Knapp 2020, 2021). Specifically, the muted response of soil CO_2 flux to precipitation events in historically intense precipitation plots (vs. historically ambient precipitation plots) is consistent with previous research reporting that soils from this treatment were less responsive to moisture pulses pre-drought (Evans and Wallenstein 2012) and had lower microbial respiration following drying and re-wetting (Veach and Zeglin 2020). Thus, this difference in the response of soil CO_2 flux to soil moisture between intense versus ambient treatments appears to be longer lasting than other pre-drought differences (for example, lower ANPP in intense vs. ambient treatments). This has important implications for ecosystem carbon dynamics, given that soil CO_2 flux is a large part of the carbon budget in temperate grasslands and a substantial proportion of soil CO_2 flux occurs after rainfall events (Chen and others 2008, 2009; Gale and others 1990; Ham and others 1995; Huxman and others 2004a, 2004b; Kim and others 1992; Yan and others 2014). Our results indicate that grassland ecosystems might release less total CO_2 from the soil to atmosphere under conditions of increased precipitation pattern intensity and drought.

Drought can have a persistent negative effect on grassland ANPP post-drought, though positive and insignificant impacts of previous droughts have also been reported (Griffin-Nolan and others 2018; Hoover and others 2014; Sala and others 2012). Total ANPP in our study recovered to near the pre-drought average 1 year after drought. This was likely due at least in part to above-average total precipitation in that year. Regardless, our results are consistent with past research identifying the important role of the dominant species in restoring ecosystem function after drought. One year after drought, ANPP of *A. gerardii* was higher than the long-term pre-drought average, while ANPP of the subdominant species remained below average. Previous grassland drought experiments have reported that, aboveground, grasses recover better than forbs (included in ‘‘subdominant species’’) after drought (De Boeck and others 2018; Hoover and others 2014). We expand on this response by showing that BNPP of *A. gerardii* also recovered more than BNPP of subdominant species after drought.

In summary, we found that the compound effects of long-term precipitation pattern intensification and drought were evident primarily belowground in this mesic grassland. We conclude that as precipitation patterns intensify and drought frequency and severity continue to increase globally, predicting and modeling changes in global terrestrial carbon cycling will require greater understanding of how ecosystems respond to multiple compounded precipitation changes, especially belowground.

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