Oecologia (2023) 201:269–278
https://doi.org/10.1007/s00442-022-05281-x

GLOBAL CHANGE ECOLOGY – ORIGINAL RESEARCH

Legacies of precipitation influence primary production in *Panicum virgatum*

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Received: 9 April 2022 / Accepted: 31 October 2022 / Published online: 14 November 2022

Abstract

Precipitation is a key driver of primary production worldwide, but primary production does not always track year-to-year variation in precipitation linearly. Instead, plant responses to changes in precipitation may exhibit time lags, or legacies of past precipitation. Legacies can be driven by multiple mechanisms, including persistent changes in plant physiological and morphological traits and changes to the physical environment, such as plant access to soil water. We used three precipitation manipulation experiments in central Texas, USA to evaluate the magnitude, duration, and potential mechanisms driving precipitation legacies on aboveground primary production of the perennial C_4 grass, *Panicum virgatum*. Specifically, we performed a rainout shelter study, where eight genotypes grew under different precipitation regimes; a transplant study, where plants that had previously grown in a rainout shelter under different precipitation regimes were moved to a common environment; and a mesocosm study, where the effect of swapping precipitation regime was examined with a single genotype. Across these experiments, plants previously grown under wet conditions generally performed better than expected when exposed to drought. *Panicum virgatum* exhibited stronger productivity legacies of past wet years on current-year responses to drought than of past dry years on current-year responses to wet conditions. Additionally, previous year tiller counts, a proxy for meristem availability, were important in determining legacy effects on aboveground production. As climate changes and precipitation extremes—both dry and wet—become more common, these results suggest that populations of *P. virgatum* may become less resilient.

Keywords Bud banks · Precipitation variability · Rainfall manipulation · Switchgrass · Tiller dynamics

Introduction

Worldwide, precipitation is a major determinant of ecosystem function, including primary production (Noy-Meir 1973). Primary production generally increases with precipitation (Huxman et al. 2004; Knapp and Smith 2001). But, plants do not always respond immediately to changes in water availability (Felton et al. 2021b; Sala et al. 2012). In fact, primary production often differs from expectations based solely on the current year's precipitation (Reichmann et al. 2013; Sala et al. 2012). These legacy effects, or time lags in ecosystem responses to changes in annual precipitation, can result from multiple drivers (Sala et al. 2012). These drivers can occur at different levels, from molecular stress responses to meristem dynamics to differences in access to water (e.g., Bruce et al. 2007; Reichmann et al. 2013). As variability in precipitation increases—including longer, more severe droughts and larger, more intense

Communicated by Douglas A Frank .

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rainfall events—the influence of the prior year's precipitation may change as well (Felton et al. 2021b; Gherardi and Sala 2019; Hou et al. 2021). Precipitation legacies also have an applied significance: many ecosystem models assume a linear relationship between precipitation and plant production and do not directly account for legacy effects (Felton et al. 2021a). Furthering our understanding of the drivers of precipitation legacies will improve our ability to predict ecosystem function and carbon (C) sequestration in response to climate change.

Incorporating legacies of previous precipitation regimes can dramatically improve the accuracy of productivity–precipitation relationships within sites (Sala et al. 2012). This may be because a number of mechanisms can alter a system's ability to respond to current-year precipitation. For instance, Reichmann et al. (2013) found that previous-year tiller density accounted for a large portion of precipitation legacy effects on current-year aboveground productivity. In grasses, the presence of meristems (i.e., bud banks) capable of responding to changes in precipitation is critically important (Dalgleish and Hartnett 2006; Ott et al. 2019). Low tiller production in dry years limits the ability of plants to respond to subsequent wet years. Similarly, high tiller production and associated root production resulting from wet years, may buffer larger plants from subsequent drought by enabling greater access to soil water (Sala et al. 2012). Drought may also limit subsequent responses to wet conditions by killing individuals, shifting vegetation structure, or provoking long-term stress responses that limit growth (Bruce et al. 2007; Martin-Benito et al. 2017; Yahdjian and Sala 2006). Previous wet conditions may also buffer against the deleterious effects of drought if soil moisture levels remain high (Cavagnaro 2016; Hoover et al. 2021). Additionally, Hawkes and Kiniry (2018) found that larger plants were better able to survive prolonged drought and recovered more fully when water was made available. Importantly, some mechanisms suggest that legacies of high and low precipitation will be asymmetric (Knapp et al. 2017b; Sala et al. 2012). For instance, the thresholds for plants to deploy new tissue versus abscising old tissue can differ; plants may retain roots grown under high precipitation when conditions become drier, but plants under these same dry conditions would not grow new roots. Thus, plants that had previously experienced wet conditions may produce more biomass than expected under drought, but the reverse may not be true (Sala et al. 2012).

We examined precipitation legacies using a combination of studies with the common C_4 tallgrass species *Panicum virgatum* L. *Panicum virgatum* occurs throughout central North American grasslands, where it has diverged into three ecotypes that occur in different habitats (upland, lowland, and coastal areas) (Casler 2012; Lovell et al. 2021). These ecotypic differences result in varying physiological and whole-plant responses to water availability (Aspinwall et al. 2017; Barney et al. 2009; Heckman et al. 2020), which we leverage to examine the context-dependence of precipitation legacies on aboveground net primary production (ANPP). Specifically, we ask four questions: (1) Does *P. virgatum* exhibit legacy effects of previous precipitation regimes, and are wet and dry legacy effects on ANPP of similar magnitude? (2) Do the effects of antecedent drought or increased precipitation on ANPP persist for multiple years? (3) Are different genotypes of *P. virgatum* more or less resilient to legacy effects of antecedent precipitation? (4) Are precipitation legacy effects on ANPP driven by the availability of plant meristems?

Methods

We examined the impact of precipitation legacies on ANPP in three complementary studies: (1) a rainout shelter study where plants of multiple genotypes were grown under different precipitation treatments at two sites in central Texas; (2) a transplant study where plants that had been growing under a rainout shelter were moved to an unmanipulated common garden; and (3) a mesocosm study, where the impact of switching precipitation regime (wet-to-dry or dry-to-wet) was studied using a single *P. virgatum* genotype. Together, these three studies allow us to assess the generality of precipitation legacies in *P. virgatum* and to assess multiple mechanisms by which legacies can occur.

In combination, these three studies address complementary aspects of the four questions about precipitation legacies on ANPP in *P. virgatum.* Specifically, all three studies can address whether legacy effects of antecedent precipitation regimes occur in *P. virgatum* and whether wet and dry legacy effects on ANPP are of similar magnitude. The transplant and mesocosm studies examine whether the effects of previous precipitation regime on ANPP persist for multiple years. The rainout shelter and transplant studies allow us to test whether there are genotypic differences in the resilience of *P. virgatum* to legacy effects of antecedent precipitation. The rainout shelter and transplant studies allow us to determine whether precipitation legacy effects on ANPP are driven by the availability of plant meristems.

Rainout shelter study

This study was performed at two sites in central Texas, USA that were ~ 110 km apart: the USDA Grassland, Soil and Water Research Lab near Temple, TX, USA and the Lady Bird Johnson Wildflower Center near Austin, TX, USA. Soils at the Temple site were deep (50–100 cm) and fine textured (Austin silty clay, fine silty, carbonatic, Udorthentic Haplustoll), while soils at the Austin site were shallow (35–50 cm) and coarse textured (Speck clay

loam, clayey, thermic Lithic Argiustoll). For Temple, mean annual precipitation is 910 mm, mean maximum air temperature (July–August) is 35.0 °C, and mean minimum air temperature (December) is 3.0 °C. At Austin, mean annual precipitation is 870 mm, mean maximum air temperature (July–August) is 35.0 °C, and mean minimum air temperature (December) is 5.6 °C.

At each site, we planted eight genotypes of *Panicum virgatum* originating between 27° N and 35° N, which spanned the U.S. Central Plains states of Texas and Oklahoma (ESM 1). We clonally propagated individuals of each genotype from a single genet collected at each site. Plants were situated on 1-m centers in duplicate in each plot and constrained so that individuals of the same genotype were never next to one another. During establishment in 2011, plants were well-watered.

At each site, six precipitation treatments were assigned in a randomized complete block design across 24 5 m × 5 m plots arranged in four spatial blocks. Precipitation treatments in the rainout shelter study began in March 2012 and continued throughout 2014 in Austin and 2015 in Temple. Plots at each site were assigned to one of five precipitation treatments representing severe drought to extremely wet conditions. Precipitation treatments were defined from each site's precipitation record (Austin: 1938–2010; Temple: 1900–2002). The low precipitation treatment was the average of the ten driest years and the high precipitation treatment was the average of the 10 wettest years. Precipitation treatments representing the 25th percentile, mean, and 75th percentile of annual precipitation were calculated from the 10 years nearest to these values. These treatments corresponded to annual precipitation amounts of 530–1541 mm at Temple and 349–1330 mm at Austin. The order of rainfall events for each experimental treatment came from a stochastic weather generator, LARS-WG 5.5 (Semenov et al. 1998). These rainfall sequences mimicked the seasonality, size distribution, and spacing of rainfall events in the selected sets of years (Aspinwall et al. 2017).

A sixth, ambient, treatment applied the amount of precipitation received at each site to plots weekly. Unlike the other five treatments, the amount of precipitation that plots received varied among years (Austin: 680, 1141, and 775 mm yr^{-1}, respectively; Temple: 562, 956, 693, and 1187 mm yr^{-1}, respectively; note that the first year's precipitation totals began in March rather than January). This allowed us to estimate legacy effects: each year, we determined the ANPP–precipitation relationship in the five fixed treatments, then used this relationship to predict ANPP in the ambient precipitation plots (based on current year precipitation). The deviation between actual and predicted ANPP as a function of the change in precipitation from $year_{t-1}$ to $year_t$ is an estimate of the legacy of past precipitation (Reichmann et al. 2013). We were able to calculate this legacy effect at each site from the second year of treatments onward (twice in Austin, three times in Temple). For instance, legacies result when plants produce more biomass than expected (positive deviation) when precipitation declines from $year_{t-1}$ to $year_t$ and less biomass than expected (negative deviation) when precipitation increases from $year_{t-1}$ to $year_t$.

Plots within blocks were separated by 0.25 m and blocks were separated by 2.76 m. Pond liner (1.84 mm thick; Firestone Specialty Products, Indianapolis, IN, USA) surrounded each plot. To limit the movement of subsurface water and roots between plots, the pond liner extended to a depth of 120 cm at the Temple site and 20 cm at the Austin site, which reflected differences in soil depth. To limit overland flow of water, the pond liner extended 10 cm above the soil surface. To install the pond liner, we trenched the perimeter of each plot, but otherwise left the soil inside the plots undisturbed. The plots at each site were covered by open-sided 18.3 m × 73.0 m rainout shelters with 2.1-m high walls and 4.2-m high eaves on both ends (Windjammer Cold Frame, International Greenhouse Company, Danville, IL, USA). 150-micron polyethylene greenhouse film excluded natural rainfall all year (Aspinwall et al. 2013). We applied experimental precipitation with programmable 90° sprinklers placed on 1-m risers in all four corners of each plot (LEIT XRC Series Ambient Powered Irrigation Controller, DIG Corporation, Vista, CA, USA; Hunter HP2000, Hunter Industries Inc., San Marcos, CA, USA).

Transplant study

In early 2015, we transplanted a portion of each plant from the Austin rainout shelter to an unmanipulated common garden in Temple. To do this, we excavated a small section of rhizome mass with associated tillers (15–20 tillers per plant) and roots (to a depth of 20 cm) from the crown of each plant. We then planted these individuals into a 25 m × 50 m common garden in a previously fallow field that was tilled to a depth of 15 cm, then tilled again one month later and covered with landscape fabric (Sunbelt 3.2 oz, DeWitt, Sikeston, MO, USA). Plants were randomly assigned to locations in the garden in a honeycomb pattern spaced 1.56 m apart. A round hole 30 cm in diameter was cut in the landscape fabric for each transplant and holes were dug with a shovel. By growing plants of similar starting size in a common environment, we are able to detect legacy effects driven by size-independent mechanisms (e.g., drought stress hormones, physiological or anatomical acclimation to drought).

Mesocosm study

We grew 28 plants of the switchgrass genotype AP13, the reference genotype for lowland *P. virgatum*, in mesocosms under a small rainout shelter at the University of Texas at

Austin's J.J. Pickle Research Campus (Lovell et al. 2016). Plants were grown in cylindrical mesocosms (1.22 m tall × 0.61 m diameter) constructed from gray schedule 40 polyvinyl chloride pipe and exposed to natural lighting, photoperiod, humidity, and temperature changes. Mesocosms were spaced 1.2 m apart and filled with a well-draining soil mixture of rice hulls, compost, sand, and decomposed granite (Ranch Rose Mix, Geo Growers, Austin, TX, USA). This artificial medium had several advantages over the natural clayey soils of central Texas: it is highly uniform and resists compaction, which promotes uniform moisture retention and drainage, and rooting evenly throughout the mesocosms. From 2012 through 2014, half of the plants ($n = 14$) were well-watered (to mesocosm saturation every ten days), while the other half ($n = 14$) received low water—1/3 of the watering frequency in the well-watered treatment (to mesocosm saturation every thirty days). In 2015, after 3 years of treatment, half of the plants in each treatment were switched to the opposite treatment and allowed to grow for 2 more years. The remaining half of the plants in each treatment continued receiving their original watering amounts.

Responses measured

We counted the total number of tillers produced by each plant in the rainout shelter study. In all studies, we measured ANPP as current year aboveground biomass for each plant (kg plant^{-1}). We determined biomass production by clipping at 10 cm above the soil surface in November–December each year, then weighing the biomass after drying at 65 °C for at least 48 h in forage drying ovens.

Data analysis

We quantified legacy effects as the difference between observed plant aboveground biomass and aboveground biomass that would be expected based on the current year's precipitation (Sala et al., 2012). We defined expected biomass in one of three ways based on study design. (1) For the rainout shelter study, we first determined the biomass–precipitation relationship in the five fixed treatments each year using a random regression model that included a random effect of genotype that varied with precipitation treatment (i.e., random slopes and intercepts model) (Arnold et al. 2019); each of the five annual precipitation models explained > 50% of the variation in ANPP ($0.525 <$ conditional $R^2 < 0.626$). We then used this relationship to predict aboveground biomass in the ambient precipitation plots (based on current year precipitation). The deviation between this predicted and observed aboveground biomass is an estimate of legacy of past precipitation. We then compared this deviation in predicted biomass to the change in precipitation from $year_{t-1}$ to $year_t$ at each site from the second year of treatments forward. We also examined whether precipitation legacies on biomass were mediated by meristem availability by including tiller number (a proxy for meristem availability) in $year_{t-1}$ as an additional predictor in the model described above. (2) For the transplant study, we compared plants based solely on their previous precipitation treatment. If plants that had previously been grown under low precipitation (low or 25th treatment) were smaller in a common environment than plants that had previously been grown under high precipitation (high or 75th treatment), this is evidence for a legacy effect. In this study, transplanting similarly sized individuals eliminates the effects of plant size in determining legacy effects. (3) For the mesocosm study, we compared plants that remained under the same precipitation regime (e.g., always high or always low) to plants that switched precipitation regimes (e.g., high, then low; low, then high). If plants with the same current precipitation regime differed in biomass based on their prior precipitation regime, this is evidence for a legacy effect.

For all analyses, we modeled legacies using the nlme package in R version 4.1.0 (Pinheiro et al. 2016; R Core Team 2022). In the rainout shelter study analysis, we examined the interactive effects of genotype identity and change in precipitation between $year_{t-1}$ and $year_t$ on biomass legacy (difference in biomass between observed and expected). Due to the split-plot nature of this experiment (e.g., multiple genotypes within each precipitation whole plot) and the fact that each genotype was replicated twice within each whole plot, this model also included a random effect of individual plant nested within spatial block nested within site. To assess the impact of prior meristem availability on legacies, we ran a second model that included interactions between tiller count in $year_{t-1}$ and the other two predictors, but did not include the three-way interaction. In the transplant study analysis, we examined the interactive effects of prior precipitation treatment and genotype identity on plant biomass, separately each year. These models also included a random effect to account for prior experimental structure (whole plot nested within block). In the mesocosm analysis, we examined the interactive fixed effects of year of observation and precipitation treatment combination (e.g., wet, then dry; dry, then dry; etc.) on plant biomass. For all models, we performed post hoc comparisons using the emmeans package in R (Lenth 2018).

To further evaluate whether precipitation legacies on biomass are mediated by meristem availability, we then performed confirmatory path analysis (Shipley et al. 2006) using the piecewiseSEM package in R (Lefcheck 2016). Using only plants in the ambient precipitation treatment of the rainout shelter study, we examined the impact of precipitation in $year_{t-1}$ on tiller number in $year_{t-1}$ and the impact of tiller number in $year_{t-1}$ on biomass in $year_t$. Each sub-model

included a random effect of plant nested within block nested within site.

Results

Rainout shelter study

Among plants in the ambient precipitation treatment, observed ANPP deviated significantly from ANPP predicted by the five fixed precipitation treatments ($P = 0.005$; ESM 2 Table 2a; Fig. 1), indicating that legacies of previous precipitation are present. Specifically, across all genotypes, plants produced less biomass than expected when the current year was wetter than the preceding year, indicated by a larger negative deviation with larger year-to-year increases in precipitation. Additionally, this effect differed among genotypes ($P < 0.001$; ESM 2 Table 2a; Fig. 1). Three of eight genotypes (ENC, WBC, WIL) exhibited significant legacy effects, while the other five genotypes did not (ESM 2 Table 2b). For every 10 cm increase in $year_t$ precipitation relative to $year_{t-1}$, ANPP declined relative to prediction by 0.10 kg in ENC, by 0.17 kg in WBC, and by 0.08 kg in WIL. Tiller number also had a significant effect on biomass legacies ($P < 0.001$; ESM 2 Table 2c): plants that had more tillers in $year_{t-1}$ had higher current year biomass. However, $year_{t-1}$ tiller count did not interact with the year-to-year change in precipitation to impact biomass production (Tiller count, $year_{t-1} \times$ Change in precipitation, $P = 0.49$; ESM 2 Table 2c). Together, these results suggest that precipitation legacies can be limited by the availability of meristems to promote further growth.

To explore the effect of meristem availability on legacies further, confirmatory path analysis showed that prior year tiller count significantly mediated precipitation legacies. This path model adequately fit the data (Fisher's $C = 5.35$, DF = 2, $P = 0.07$; Fig. 2a). Prior year precipitation positively impacted prior year tiller count ($P < 0.001$; ESM 2 Table 2d; Fig. 2a,b) and prior year tiller count then positively impacted current year biomass ($P = 0.009$; ESM 2 Table2d; Fig. 2a,c). However, both effects were weak (marginal $R^2 = 0.02$ for each).

Transplant study

Among plants that were transplanted from the Austin rainout shelter to an unmanipulated common garden in Temple, we found limited evidence that prior precipitation treatment impacted plant production. There was a significant interaction between genotype and prior precipitation treatment in 2016, but not in 2015 (Genotype × Prior precipitation: 2015, $P = 0.19$; 2016, $P = 0.004$; ESM 2 Table 2e, ESM 2 Table 2f). However, across the two years, only one genotype exhibited significant differences in biomass between the two high precipitation treatments (high, 75th) and the two low precipitation treatments (low, 25th): WIL in 2016 (Post-hoc test: $P = 0.008$; ESM 2 Table 2g, ESM 2 Table 2h; Fig. 3). Because these plants were transplanted at approximately the

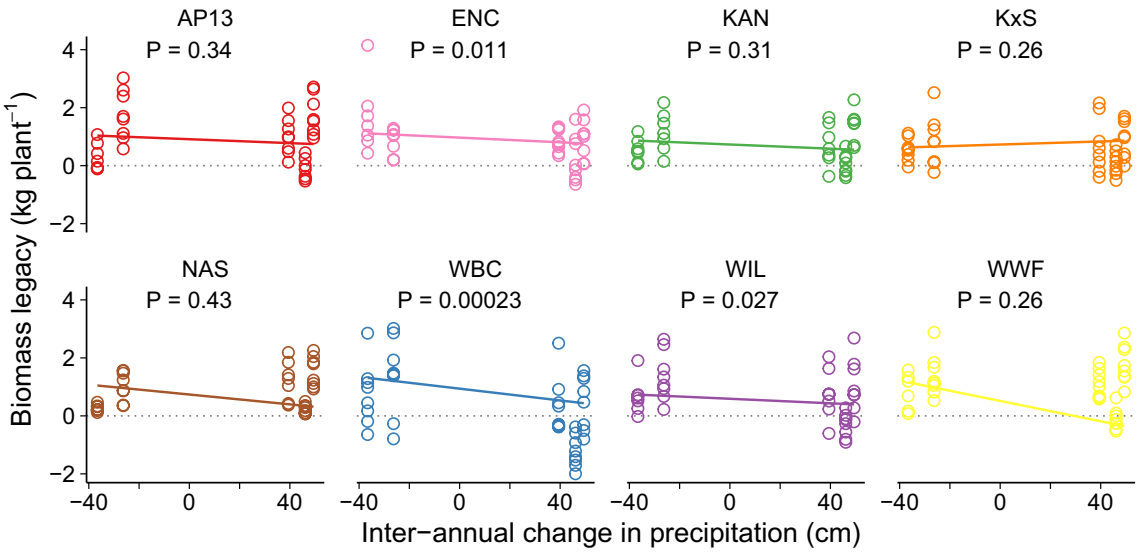

Fig. 1 The effect of inter-annual change in precipitation (cm) on biomass precipitation legacies in a rainout shelter study. Each panel represents a separate *P. virgatum* genotype (see ESM 1 for genotype details). Biomass precipitation legacies were the deviation between expected and observed aboveground biomass responses to precipitation (see Methods for details). Solid lines represent the genotype-level effect of change in precipitation on biomass legacies

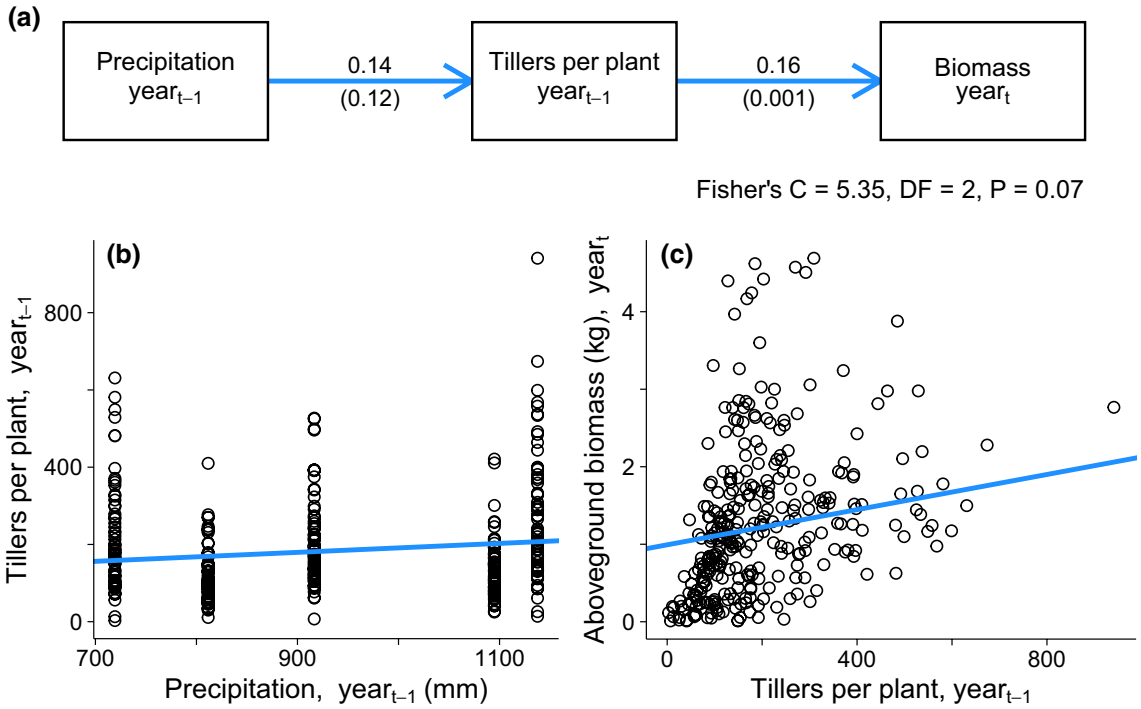

Fig. 2 **a** Confirmatory path analysis relating the legacy effect of precipitation on aboveground biomass as mediated by tiller density in a rainout shelter study. Each path shows standardized coefficients with unstandardized coefficients in parentheses. Panels **b** and **c** show significant bivariate relationships denoted in **a**

same size, this result suggests that plant size-independent mechanisms, like drought stress memory, have little impact on precipitation legacies in this system.

Mesocosm study

In 2013 and 2014, plants in the wet treatment were more than 65% larger than plants in the dry treatment (Post hoc tests: both years, $P < 0.001$; ESM 2 Table 2i, ESM 2 Table 2j), indicating that precipitation substantially impacted biomass production. Although biomass tended to decline over time, indicating that roots may have become increasingly pot-bound in these mesocosms, within-year comparisons provide evidence for a legacy effect of high precipitation on plants subsequently growing under drought. Specifically, plants that had been growing for 3 years under wet conditions, which were then exposed to dry conditions, had 46% higher biomass, on average, than plants that had been growing under continuous dry conditions (Post hoc tests: $P = 0.03$; ESM 2 Table 2j; Fig. 4a). This effect was no longer significant in 2016 (Post hoc tests: $P = 0.95$; ESM 2 Table 2j), indicating that the legacy effect lasted only 1 year. On the other hand, we found no evidence for a legacy effect of drought on plants that subsequently grew under high precipitation (Post-hoc tests: 2015, $P = 0.82$; 2016, $P = 0.32$; ESM 2 Table 2j; Fig. 4b), suggesting that legacy effects on production are asymmetric.

Discussion

Across experiments, we found that *P. virgatum* biomass is constrained by prior precipitation regimes, although the magnitude of this legacy effect was limited and transient. Legacies of past wet years on aboveground biomass under dry conditions tended to be larger than the opposite. Legacies also differed considerably among genotypes. Moreover, in the two studies that examined legacies for multiple years (Mesocosm study, Transplant study), there was no evidence that significant legacies remained after the first year. Additionally, prior tiller count was an important determinant of biomass legacy (Rainout shelter study). Finally, after eliminating differences in plant size (Transplant study), there was little evidence of legacy effects. Together, this suggests that bud banks are important drivers of legacies. These results support the small number of prior studies that examined precipitation legacies in grasses or grassland systems (e.g., Gong et al. 2020; Hawkes and Kiniry 2018; Reichmann et al. 2013).

The results of this study show a number of similarities with other studies that examined legacy effects of

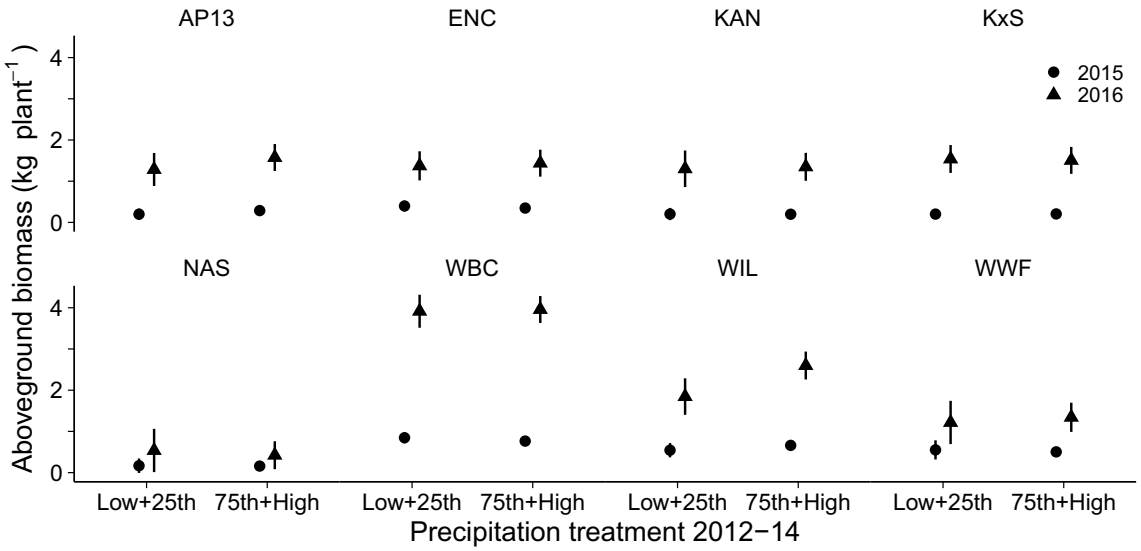

Fig. 3 Effect of prior precipitation treatments on aboveground biomass of plants from a transplant study grown in a common environment in 2015 and 2016. Each panel represents a separate *P. virgatum* genotype (see ESM 1 for genotype details). Means are model-derived and error bars represent 95% confidence intervals

precipitation in herbaceous systems. For instance, Hawkes and Kiniry (2018) found that bigger plants were better able to survive a severe drought and produced more biomass when precipitation occurred again. This was similar to our result in the mesocosm study showing that plants previously growing under wet conditions (i.e., being bigger) performed better in drought than chronically droughted plants. Gong et al. (2020) found a strong linear relationship between current year ANPP and previous year precipitation in a semi-arid grassland system dominated by one grass and one forb. This was similar to our results showing that wetter antecedent conditions increased biomass production, although our results were not as strong.

Our finding that tiller number is an important predictor of precipitation legacies on ANPP is consistent with prior work by Reichmann et al. (2013) and highlights the importance

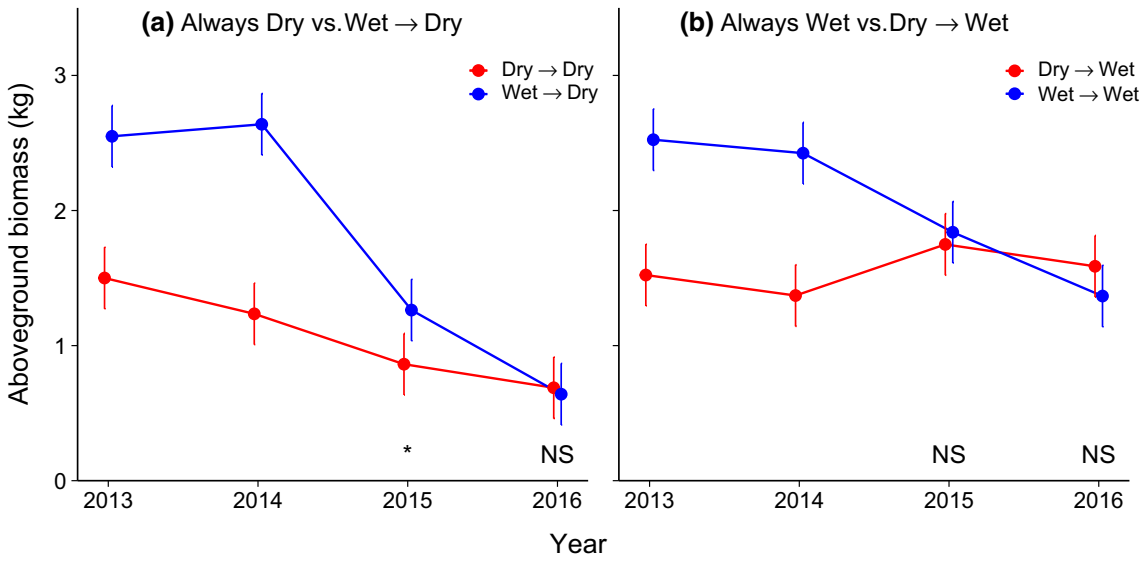

Fig. 4 Effect of swapping precipitation treatments on aboveground biomass in a mesocosm experiment. Plants were grown under either dry or wet conditions from 2012 to 2014. **a** In 2015 and 2016, all plants were grown under dry conditions. **b** In 2015 and 2016, all plants were grown under wet conditions. In 2015 and 2016, asterisk indicates a significant difference in biomass, based on previous treatment differences; NS denotes no statistical significance. Means are model-derived and error bars represent 95% confidence intervals

of meristem availability in understanding how populations and communities will respond to changes in precipitation (Sala et al. 2012). The responses of belowground bud banks to disturbances like drought can vary considerably and have immense impacts on population dynamics (Ott et al. 2019). For instance, bunchgrasses in semi-arid grasslands exhibited greater meristem limitation in response to drought than rhizomatous grasses (Qian et al. 2022), whereas in more mesic grasslands, drought did not alter bud banks (Carter et al. 2012; VanderWeide et al. 2014). Dalgleish and Hartnett (2006) found that bud banks increase with increasing precipitation across North American grasslands. This suggests that legacy effects of precipitation could be larger in drier habitats, especially those prone to high inter-annual variation in precipitation (Qian et al. 2022). Given the broad environmental tolerance that *P. virgatum* exhibits (Casler 2012; Lovell et al. 2021), this species may be less prone to strong legacy effects than other prairie grasses with more stringent environmental requirements.

Here, we examined multiple, complementary studies to assess the role of precipitation legacies in *P. virgatum*. This allowed us to evaluate multiple hypotheses, especially regarding the effect of meristem availability and plant size on legacies (Sala et al. 2012). We also included multiple genotypes with broad geographic origins and extreme precipitation treatments to better examine the range of responses of *P. virgatum* to precipitation (Aspinwall et al. 2017; Heckman et al. 2020). There was some variation among genotypes in legacies. Specifically, three genotypes (ENC, WBC, WIL) exhibited legacies in the rainout shelter study, while five other genotypes did not. These three genotypes were among the southern-most genotypes in the study, suggesting that habitat of origin could impact these responses to precipitation (Aspinwall et al. 2013). Moreover, a separate greenhouse experiment using three of these *P. virgatum* genotypes found that WWF, but not WIL and NAS, exhibited precipitation legacies on biomass production (Crawford and Hawkes 2020). Future work predicting *P. virgatum* responses to variation in precipitation would benefit from considering genotype-specific information.

This study had several limitations. First, our rainout shelter experiment was not long enough to include years of extreme precipitation—ambient treatment applications all fell within 30% of mean annual precipitation. If legacies are driven primarily by drought-induced mortality of ramets or entire plants (Knapp et al. 2017b; Sala et al. 2012), then our study may obscure these effects by focusing on years of less extreme precipitation (Knapp et al. 2017a). There are two alternative approaches that can account for this. Studies can examine legacies over a long enough timescale to include years of extreme precipitation. This may take decades. For instance, the highest and lowest precipitation treatments used in our rainout shelter represent precipitation extremes occurring on average 1–2 times every 20 years (Heckman et al. 2020). Alternatively, as in the mesocosm study, plants can be grown experimentally under precipitation extremes for several years, followed by swapping treatments to examine how plants respond to a wet-to-dry or dry-to-wet shift. This large year-to-year change in precipitation would likely show the strongest evidence of precipitation legacies, albeit in a less realistic context. Second, instead of transplanting plants from a rainout shelter to a common garden, the plants may have responded more strongly to in situ tiller removal. This approach would keep a portion of the plant's crown intact while reducing the number of available meristems, eliminating the confounding effect of transplant stress. Third, impacts of precipitation treatments in the rainout shelters decline over time as *P. virgatum* is able to access deeper soil moisture (Kröel-Dulay et al. 2022). This may flatten the ANPP–PPT relationship in later years in Temple, leading to additional variation in our precipitation legacy calculations. Fourth, biomass of plants in the mesocosm study declined over time, suggesting that plants became root-bound. Given the extensive root systems observed in field-grown *P. virgatum* (Adkins et al. 2016), this is not surprising. Even with this reduced growth capacity, comparing biomass among treatments within years can provide a valid estimate of legacy effects. Fifth, plant-plant competition in the rainout shelters, and to a lesser extent in the transplant study, may have varied among treatments and sites, and increased over time as plants grew. During later years of the rainout shelter study, competition between neighboring plants could have been substantial. In Temple, where plants were generally quite large, higher precipitation plots were often exceptionally dense, far exceeding typical native grassland. Despite these limitations, we still see some compelling evidence for legacy effects.

Precipitation legacies are important determinants of ecosystem functioning that have implications for the resilience of populations and communities to climate change (Sala et al. 2012). Research on precipitation legacies indicates that ecosystem responses to precipitation extremes and more variable climates will be difficult to predict (or these predictions will require more data). Similarly, mechanisms of legacies like meristem banks may make systems more resilient to short-term perturbations (by buffering against the impacts of severe drought for a year or two), but eventually these legacies will give way, leading to collapses in productivity (Reichmann et al. 2013). On the other hand, effects of extended drought, like mortality and large shifts in community structure, may push systems beyond their normal range, making predictions far more difficult (Huxman et al. 2004; Knapp et al. 2017b). These large shifts in community structure may also prevent systems from responding to periods of high precipitation (Knapp et al. 2017b). All these factors make predicting productivity in response

to climate extremes more difficult and show the value of long-term experiments examining different mechanisms of legacy effects.

Conclusions

We demonstrated that precipitation legacies can be important short-term determinants of biomass production in some genotypes of *P. virgatum*. This has implications for our ability to predict responses to future climate change and the resilience of tallgrass ecosystems. Relying on current data may lead to predictions of less severe impacts of drought on biomass production and ecosystem function. However, as precipitation is predicted to become more variable, extended drought may lead to drastic reductions in biomass production (Knapp et al. 2008). Similarly, the ability of plants to respond to large rainfall events may be dampened by long-term drought that reduces meristem banks. This suggests that the resilience of *P. virgatum*-dominated systems may decline with increasing variability of precipitation.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00442-022-05281-x.

Acknowledgements We thank Katherine Banick, Elise Connor, Ken Dodge, Jim Dula, Hannah Giauque, Anne Gibson, Nick Johnson, Martin Lopez, Alicia Naranjo, Lara Reichmann, Haley Smith, Claire Steele, Lauren Taranow, Kyle Tiner, Soren Weber, and Briana Whitaker for their assistance in maintaining these experiments and collecting data. The findings and conclusions of this publication are those of the authors and should not be construed to represent any official USDA or U.S. Government determination or policy.

Author contribution statement RWH and AR analyzed the data; RWH wrote the manuscript with contributions from PAF; CVH, MJA, PAF, and TEJ conceived and implemented the experiments; AK, JEB, and MJA collected data; all authors contributed to revisions of the manuscript.

Funding This research was supported by the Office of Science (BER), U.S. Department of Energy, Grant no. DE-SC0014156, and National Science Foundation Plant Genome Research Program IOS 0922457 and IOS 1444533.

Data and code availability The data and code associated with this study were deposited in figshare under the reference number https://doi.org/10.6084/m9.figshare.19561255.

Declarations

Conflicts of interest The authors declare that they have no conflict of interest.

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