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Legacies in Switchgrass Resistance to and Recovery from Drought Suggest That Good Years Can Sustain Plants Through Bad Years

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Abstract The warm-season perennial switchgrass (*Panicum virgatum*) is a candidate bioenergy crop. To be successful, switchgrass production must be maintained on low-quality landscapes with minimal inputs while facing future climates that are expected to be more extreme and more variable. We propose that antecedent rainfall constrains how plants respond to drought, as well as subsequently recover from drought. To test this idea, we examined how six switchgrass genotypes responded to a 1-year severe drought and then recovered under normal rainfall in the following year. These plants had previously grown for 3 years under a range of dry to wet rainfall levels in a shallow-soil common garden with no fertilizer. Plants previously exposed to drought produced less biomass, and basal area after the severe drought was relieved compared to previously well-watered plants. In addition, there were legacy effects caused by plant size: plants that were larger pre-drought were more likely to survive the severe drought, and plants that were larger during the severe drought recovered more biomass, basal area, and tillers post-drought. Although genotypes differed somewhat in their responses, the size constraint was consistent across genotypes. These findings suggest that we can establish more drought-resilient switchgrass stands by, for example, planning for initial irrigation or planting during a wet year to allow plants to grow larger prior to experiencing drought. Additional studies are needed to understand whether these rainfall and size legacies persist or are transient.

Keywords Bioenergy crop · *Panicum virgatum* · Precipitation · Resilience

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Introduction

Perennial bioenergy crops have the potential to substantially contribute to US energy production, but will require low-input systems on degraded or marginal lands to minimize trade-offs with food production and native environments [1–4]. However, a primary challenge for sustainable cellulosic biofuel production in low-input systems is stress such as drought, which reduces yield, decreases yield predictability, and increases costs [5]. Future droughts are predicted to be more extreme with longer duration [6–8] and could further undermine the sustainability of biofuel production. Such extremes are already supported by observed trends [9]. Understanding and maximizing drought resistance and resilience in perennial biofuel crops is therefore a critical aspect of developing economically feasible feedstock systems.

One underexplored aspect of plant drought response and recovery is the potential for legacy effects of previous rainfall. Precipitation legacies occur when the effects of past rainfall carry over into the current year, resulting in plant productivity that is more or less than expected from current conditions [10]. For example, in a desert grassland where precipitation was manipulated, rainfall treatments during the previous 2 years explained 20% of the variation in plant production during year 3 [11]. Legacies in response to short-term antecedent rainfall could occur via physiological, biochemical, or structural mechanisms [12]. The potential for precipitation legacies to affect year-to-year production in bioenergy cropping systems has not been examined. However, in the long term, local adaptation to historical climate conditions can also affect plant responses to rainfall, which has led to efforts to identify locally adapted drought-tolerant genotypes [e.g., 13].

Panicum virgatum L. (switchgrass) is a viable biofuel crop species based on its broad geographic range, diverse ecotypes, perennial life history, high productivity, tissue quality, and conversion characteristics [1, 14–16]. Switchgrass is typically considered drought tolerant; however, establishment and yield depend heavily on water [17–19]. Switchgrass ecotypes also vary in their drought tolerance [13, 20], providing intraspecific diversity that is being targeted to focus on genotypes that are well matched to regional climate conditions. Yet, only a few studies of drought impacts on switchgrass have taken place over more than one growing season [21–23]. Studies have primarily measured recovery after short-term droughts of 2 weeks or less in the greenhouse [19, 24–26], or only tracked responses to natural rainfall variation [27–29].

We addressed three questions in this study. First, how does precipitation applied at differing intensities over 3 years affect subsequent growth (dry weight, number of tiller per plant, and basal area) in year 4 under severe drought with various switchgrass genotypes? Second, following the year 4 drought, do treatment differences in years 1–3 persist to affect recovery under well-watered conditions in year 5? Finally, how do genotypes differ in these responses?

We grew six *P. virgatum* genotypes from 2012 to 2014 (years 1–3) in a rainfall manipulation experiment in central Texas. The plants were grown under four rainfall treatments ranging from 647 to 1322 mm year^{-1}. In 2015 (year 4), all plants were subject to an extreme drought defined as 33% of mean annual precipitation [30]; this treatment mirrored the 2011 extreme drought in the region. In 2016 (year 5), the drought treatment was followed by application of a drought recovery treatment, with rainfall applied at 20% above the historical mean. We hypothesized that plant drought and recovery responses would be affected by the previous year's rainfall, with any effects of prior rainfall treatment (years 1–3) on plant drought responses (year 4) or recovery responses (year 5) indicating rainfall legacies. One possibility is that plants that previously received less water or those in the more variable ambient treatment can better survive and recover from drought based on physiological priming or belowground allocation [12, 17]. Alternatively, previously drought-stressed plants might have reduced carbohydrate reserves and reduced tiller number and thus be more susceptible to future drought [31]. We also expected differences among the genotypes in size and morphology in drought and recovery responses. However, because we focused on southern accessions, we did not anticipate interactions of genotype × previous rainfall [32]. Finally, plant size is known to affect plant physiology and growth [33], and thus, we posited that aboveground biomass 1 or 2 years before measurement might be a more important predictor of plant drought and recovery responses than previous rainfall or genotype per se.

Methods

Experimental site

The study was conducted at the Lady Bird Johnson Wildflower Center in Austin, TX (30° 11′ 0.4″ N, 97° 52′ 35.2″ W). Climate is humid subtropical, with mean annual precipitation of 887 mm and mean annual maximum and minimum temperatures of 26.3 and 13.6 °C. To exclude precipitation, a rainout shelter was constructed (18.3 × 73 m with 1.8-m sidewalls and 7-m central peak height; Windjammer Cold Frame, International Greenhouse Company, Danville, IL, USA). Experimental plots (5 × 5 m) were arranged beneath the shelter in four blocks ($n = 6$ plots per block) spaced 2.76 m apart. Soils at the site are shallow (15–20 cm), limestone-derived rocky clay loam (Speck series; thermic Lithic Argiustolls), with pH 7.9 and low nutrients (NO_3 + NH_4 3.85 ± 0.48 SE μg g^{-1} soil, PO_4 0.41 ± 0.03 SE μg g^{-1} soil). To prevent subsurface water movement and root penetration, plots were surrounded belowground with 1.14-mm-thick synthetic rubber pond liner (PondGard, Firestone Specialty Products, Indianapolis, IN, USA) to a depth of 20 cm; the liner also extends 10 cm aboveground to eliminate overland flow.

Precipitation treatments

The original six precipitation treatments were run from May 2012 to November 2014 (years 1–3) and applied at the plot level, with one treatment per block in a randomized block design. For the current work, we focused on three treatments that were based on the historical range, 1322, 1005, and 657 mm year^{-1}, which were 1.6-, 1.2-, and 0.8-fold of the mean annual precipitation in the region. We also included an ambient treatment that varied annually to mimic actual rainfall (535, 1141, and 729 mm year^{-1} in 2012, 2013, and 2014, respectively). Treatment event sizes and dates were determined using the LARS-WG 5.5 stochastic weather generator [34] that was calibrated using an 87-year precipitation record. All precipitation treatments were delivered via four 90° sprinklers (Hunter HP 2000, Hunter Industries Inc., San Marcos, CA, USA) positioned in the plot corners on 1-m risers and operated with a programmable controller (LEIT XRC, DIG Corporation, Vista, CA, USA).

In 2015 (year 4), we subjected all treatment plots to a severe drought of 284 mm applied between January and June, with no further rainfall applied from July 1, 2015, to January 31, 2016. The drought treatment is one third of historical mean annual precipitation and was applied in a short window to mimic an extreme drought on par with the 2011 drought experienced in the region. In 2016 (year 5), we implemented a drought recovery treatment in all plots. The recovery rainfall amount was 410 mm of rain added from January to July, which was derived from the 1005 mm year^{-1} annual rain treatment. Plants were harvested in July.

Plant genotypes

We included six genotypes of *P. virgatum* that were previously planted in the rainfall experiment for which there were surviving individuals in all four precipitation treatments in year 4. All genotypes were originally clonally propagated from single individuals, collected either from natural populations (ENC, WIL, WWF) or from previously identified populations or cultivars (AP13, KAN, NAS) with minimal domestication [35]. Genotype AP13 is from the "Alamo" cultivar, KAN is from the "Kanlow" cultivar, and NAS is from a population collected from The Nature Conservancy's Clymer Meadow and propagated by Native American Seed Company (Junction, TX). Half of the genotypes (AP13, KAN, WIL) were tetraploid with the "lowland" ecotype morphology of taller, thicker tillers and larger leaves, and half (ENC, NAS, WWF) were octoploid with the "upland" ecotype morphology of short, thinner tillers and smaller leaves [33, 36]. The genotypes originated from Oklahoma and Texas, with climates ranging from 646 to 1110 mm mean annual precipitation and 15.5 to 22.3 °C mean annual temperature (Table 1). Grasses were planted in 2011 with 1-m^2 spacing and allowed to establish under well-watered conditions prior to the initial implementation of rain treatments in 2012 (year 1). For more information on the genotypes and their performance in the rainout shelter prior to this experiment, see Aspinwall et al. [21].

Plant measurements

To assess drought effects in year 4 and post-drought recovery in year 5, aboveground plant parts were measured for height, number of tillers, maximum basal width, and basal width perpendicular to maximum at the end of the growing seasons both years. Basal radii were used to calculate basal area assuming an elliptical shape. In year 5, we also measured survival from the year 4 drought. Aboveground biomass was obtained by harvesting plants in November 2015 (year 4) and again in July 2016 (year 5) and oven drying to constant weight at 60 °C.

Statistics

To examine drivers of plant pre-drought status at the start of the experiment, we analyzed year 3 plant biomass using a linear mixed model (LMM) with restricted maximum likelihood estimation. Genotype, original precipitation treatment, and their interactions were included as fixed factors with type III sums of squares. Block and block interactions were included as random factors with the covariance type set to variance components; a random intercept was included with individual plants as subjects.

To examine how genotype and original precipitation treatment affected plant drought responses (year 4) and recovery responses (year 5), we further analyzed current plant biomass, area, height, and number of tillers using LMMs as above, but with the addition of year as a fixed factor. We also included previous plant biomass 1 and 2 years prior to measurement as covariates. Here, both the original precipitation treatments and the prior size covariates serve as tests of legacy effects on plant drought and recovery responses. Based on previous analysis of year 1 and 2 aboveground biomass [21, 37], we also included the interaction of genotype and prior sizes as covariates; however, this term was never significant and was therefore dropped from the models. All plant measurement data were ln-transformed (dry weights, tillers, height) or square-root-transformed (area) to meet normality and homogeneity criteria; backtransformed means are therefore reported with asymmetric 95% confidence intervals. For significant treatment effects, we used Ryan-Einot-Gabriel-Welsh *F* post hoc tests. When either prior biomass covariate was significant, we used linear regression to examine the relationship with the dependent variable. Plant survival in 2016 was analyzed using the same design as above, but with logistic regression to account for the binary nature of the data. Both logistic regressions used backward elimination procedures with removal

Table 1 Characteristics of the six *Panicum virgatum* genotypes included in this study: ploidy, geographic origin, and climate at geographical origin

Variable[a]	KAN	NAS	WIL	AP13	WWF	ENC
Ploidy	4×	8×	4×	4×	8×	8×
Latitude (°N)	35.1	33.1	29.1	28.3	28.1	26.9
Longitude (°W)	95.4	96.1	98.2	98.1	97.4	98.1
Mean annual precipitation (mm)	1045	1110	701	850	903	646
Mean annual temperature (°C)	15.5	17.2	20.6	21.2	21.2	22.3

[a] Climate data (1971–2000) were obtained from the National Oceanic and Atmospheric Administration weather station closest to the genotype's geographic origin

based on the likelihood ratio statistic. We used a Bonferroni-corrected significance cutoff of α = 0.005 throughout. All statistics were carried out in SPSS v. 24 (IBM Corporation, Armonk, NY).

Results

Pre-drought (year 3)

The pre-drought dry weights (year 3) of switchgrass plants varied across genotypes ($P < 0.001$) and tended to be larger with more rainfall in response to the original precipitation treatments ($P < 0.047$; Table 2, Fig. 1). Biomass varied by 250% between the smallest (NAS) and the largest (ENC/WIL) genotypes, but did not sort by ploidy/ecotype (Fig. 1). Plants increased in dry weight by ~ 60% on average as rainfall was increased from 657 to 1322 mm year^{-1}. The interaction of genotype and rainfall treatment was not significant ($P < 0.167$).

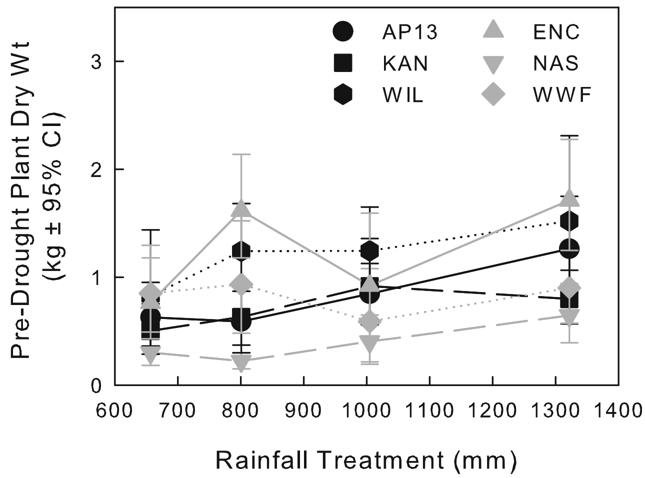

Fig. 1 Switchgrass genotype responses of pre-drought (year 3) dry weight to the rainfall treatments applied in years 1–3. Dry weights are on a per-plant basis. The ambient rain treatment is plotted as its 3-year average (801 mm), but actual applications were 535, 1141, and 729 mm year^{-1} in years 1 to 3, respectively

Drought (year 4) and recovery (year 5)

In the year 4 drought treatment compared to the year 5 recovery period (Table 3), plants on average had 275% more biomass, were 145% taller, and occupied 128% more area (Fig. 2a–d). The magnitude of difference between years typically depended on genotype or rainfall treatment (see below). Mortality was 37% at the end of the year 4 drought.

Genotype effects

Plant genotypes differed significantly in tiller number and basal area (Table 3). The tetraploid lowland ecotypes AP13 and KAN had 37% fewer tillers and occupied 33% of the basal area compared to upland octoploid ecotypes (Fig. 2). In contrast, the lowland tetraploid WIL genotype often grouped with the upland octoploids ENC and WWF.

Some genotype variation in plant responses depended on year or precipitation treatment (Table 3). In the year 4 drought, WIL had the most biomass and NAS had the least; however, there were no significant differences in dry weight during the year 5 recovery treatment (Fig. 2a). Similarly, AP13 and KAN were 40% taller than other genotypes in year 4, but this height difference was only found under the original 1322- and 1005-mm rainfall treatments and disappeared under lower rainfall and altogether in year 5 (Fig. 2d). Genotype variation in basal area across precipitation treatments was driven by NAS, which disproportionately decreased in area as rainfall application declined compared to other genotypes.

Table 2 Results of linear mixed models for pre-drought plant biomass in year 3 as a function of genotype (Gtype), original precipitation treatment (Precip), and their interactions, as well as random effects of block

Source	Num *df*	Biomass	
Fixed effects		*F*	*P*
Gtype	5	*12.288*	*< 0.001*
Precip	3	*6.139*	*0.001*
Gtype × Precip	15	1.405	0.151
Random effects		Wald Z	*P*
Residual		1.458	0.145
Intercept [subject = Plant]		–	–
Block		–	–
Gtype × Block		–	–
Precip × Block		–	–
Gtype × Precip × Block		–	–

Significant factors are in italics (Bonferroni-adjusted $P < 0.005$)

Precipitation legacies

Current plant dry weight and area varied significantly and asymmetrically across the original precipitation treatments, but only in the year 5 recovery period (Table 3, Fig. 3). Plants previously subjected to drought (657 mm year^{-1}) recovered 15% less dry weight in year 5 relative to year 4 compared to plants that previously received more rainfall during years 1–3 (Fig. 3a). Similarly, plants that were previously subjected to drought (657 mm year^{-1}) or to ambient, variable rainfall (535, 1141, 729 mm year^{-1}) occupied 10–35% less basal area in year 5 compared to plants in antecedent treatments receiving more water (Fig. 3b). The precipitation treatments applied from years 1–3 had no significant independent effects on height, tillers, or survival (Tables 3 and 4, Fig. 3c, d).

Table 3 Results of linear mixed models for individual plant measurements as a function of genotype (Gtype), original precipitation treatment (Precip), year, and their interactions, as well as the covariates of previous aboveground dry weight (Biomass) from 2 years or 1 year prior to measurement and the random effect of Block

Source	Num *df*	Dry wt		Area		Tillers		Height	
Fixed effects		*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Gtype	5	1.219	0.307	*22.886*	*< 0.001*	*9.762*	*< 0.001*	1.164	0.339
Precip	3	0.750	0.525	1.179	0.322	0.151	0.926	1.287	0.313
Year	1	0.631	0.429	0.365	0.547	0.67	0.443	2.900	0.133
Gtype × Precip	15	0.754	0.723	*2.887*	*0.001*	2.886	0.010	1.639	0.056
Gtype × Year	5	*4.165*	*0.002*	1.052	0.393	1.316	0.293	3.758	0.006
Precip × Year	3	*6.152*	*0.001*	*5.736*	*0.001*	3.764	0.107	2.573	0.052
Gtype × Precip × Year	15	2.418	0.006	2.335	0.008	2.606	0.011	*3.109*	*< 0.001*
Biomass 2 years prior	1	0.490	0.486	2.096	0.151	2.272	0.137	1.276	0.259
Biomass 1 year prior	1	*88.075*	*< 0.001*	*24.077*	*< 0.001*	*23.553*	*< 0.001*	*7.773*	*0.005*
Random effects		Wald Z	*P*	Wald Z	*P*	Wald Z	*P*	Wald Z	*P*
Residual		*6.595*	*< 0.001*	*6.496*	*< 0.001*	–	–	–	–
Intercept [subject = plant]		–	–	–	–	–	–	–	–
Block		–	–	0.633	0.527	–	–	–	–
Block × Gtype		–	–	–	–	–	–	–	–
Block × Precip		–	–	–	–	1.034	0.301	1.447	0.148
Block × Year		–	–	–	–	1.201	0.230	1.477	0.140
Block × Gtype × Precip		–	–	–	–	0.664	0.507	–	–
Block × Gtype × Year		–	–	–	–	2.369	0.018	*4.714*	*< 0.001*
Block × Precip × Year		–	–	–	–	0.079	0.937	–	–
Block × Gtype × Precip × Year		–	–	–	–	*3.125*	*0.002*	–	–

Significant factors are in italics (Bonferroni-adjusted $P < 0.005$). Dashes indicate redundant parameters

Plant size legacies

Plant biomass in the previous year was a significant covariate for current dry weight, area, tillers, and height (Table 3), explaining 20 to 57% of the variation in these measurements (Fig. 4). Post-drought survival depended on plant size 2 years prior, with surviving plants in year 5 having twice the average dry weight in year 3 as those that died (Table 4, Fig. 5). Because the interaction of genotype and prior size was never a significant covariate, we did not further examine potential differences among genotypes in sensitivity to size legacies.

Discussion

Contrary to our expectations, we did not find legacy effects of previous rainfall on switchgrass drought responses; however, there were legacy effects on plant recovery from drought.

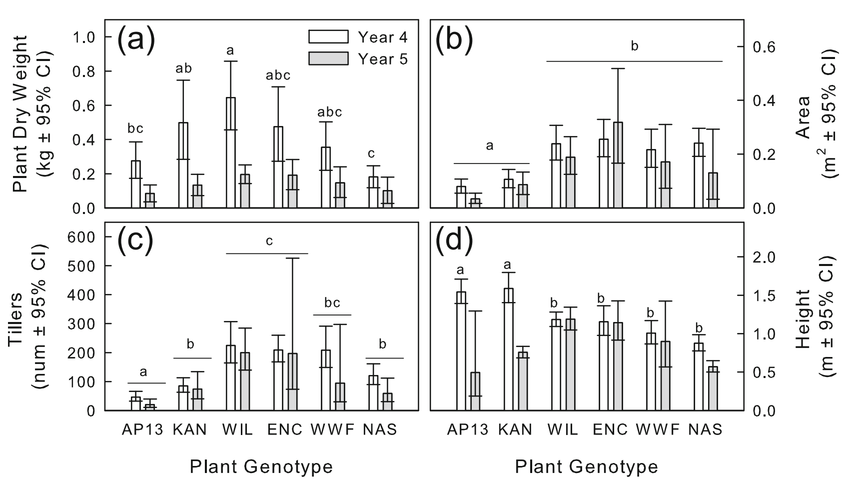

Fig. 2 Plant size by genotypes across years (year 4 = drought, year 5 = recovery). All measurements are reported per plant. Significant differences in post hoc tests are indicated by letters; lines are used to show lack of interaction between genotype and year. Note that the post hoc pattern shown in **d** is for the highest precipitation treatment; this pattern relaxed as original rainfall treatment declined from 1322 to 1005 and disappeared at lower rainfall treatments

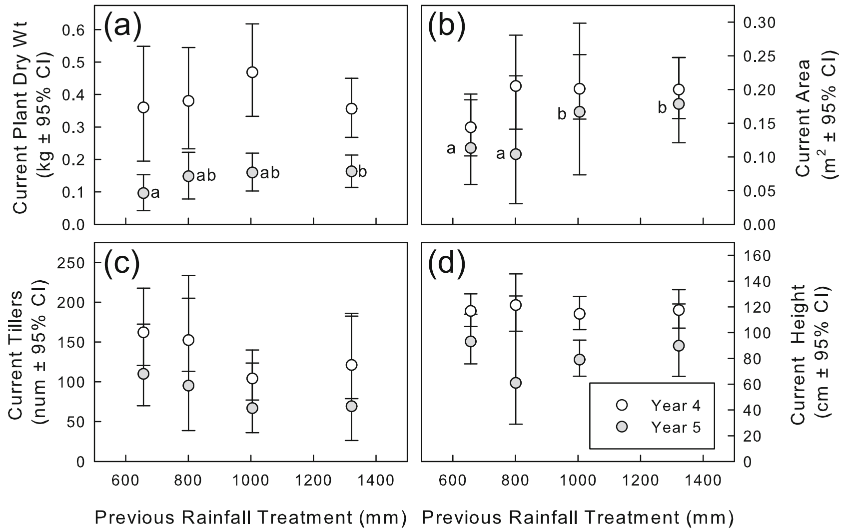

Fig. 3 Effects of previous rainfall on current plant size. Previous rainfall treatment (years 1–3) affected plant dry weight and area in the drought recovery period (year 5), but not during the drought itself (year 4). All measurements are reported on a per plant basis. Letters indicate significant differences among rain treatments in year 5 based on post hoc tests. The ambient rain treatment is plotted as the average annual amount (801 mm) applied, but actual applications were 535, 1141, and 729 mm year^{-1} in years 1 to 3, respectively

Plants that were subjected to stressful drought conditions in years 1 to 3 prior to the severe drought treatment in year 4 were less likely to recover compared to plants that were previously well-watered. Similar asymmetric responses to altered rainfall have been found in other studies [38]; here we demonstrate that such drought effects can persist into future years. In addition, we found that plant biomass 1 year prior to measurement was an important driver of current plant size, with larger plants better able to resist and recover from drought. Moreover, pre-drought plant size in year 3 was an important predictor of post-drought survival in year 5, with only 7% mortality when aboveground dry weight was greater than 1 kg before the drought; in contrast, mortality was 52% for plants less than 1 kg dry weight. In year 1 of the original experiment, plant size increased by 65–245% across genotypes as rainfall increased across treatments [21]. This was also the trend in year 3, when average plant dry weight of the six genotypes increased by 56–382% between the lowest and highest rainfall treatment amounts. Thus, plant size legacies are partly indirect legacies of prior rainfall. In long-lived perennial bioenergy grasses, the effects of prior rainfall on size and the importance of size in drought response suggests an opportunity to enhance stand resilience by providing initial inputs to establish and grow plants prior to drought exposure. Alternatively, initial planting could be planned to take advantage of forecast high rainfall periods, which is a strategy advocated for restoration of degraded arid lands [39].

Increased size, survival, and recovery of plants that received more water or were larger pre-drought were likely due to greater carbon reserves. Switchgrass recovery from drought is partly dependent on remobilization of non-structural carbohydrates typically stored in stem bases and roots [40, 41]. When mild drought follows good rainfall years, reserves can mitigate yield reduction [42]. However, as more extreme or continuing drought reduces carbon reserves [31], post-drought yield drops further. The decline in biomass that we observed between the year 4 drought and year 5 recovery treatments is consistent with reserve depletion proportional to plant size. Drought stress at this site was also exacerbated by the shallow soils, which limit water availability and root depth compared to deeper soils [21, 42]. We harvested earlier in 2016 compared to 2015 to match the size peak during the drought treatment; plants may have grown more if harvested later, but in previous years at the site, maximum size was reached by mid to late July [37]. Alternatively, size dependence could be partly due to the tiller bud bank, the size of which varies with annual rainfall in grasslands [43]. Bud banks can also reflect prior conditions; for example, in the C4 grass *Andropogon gerardii,* 30% of tiller recruitment in a given year arises from buds that are at least 2 years old [44]. We did not measure either carbohydrate or tiller buds in the current study, and additional work is needed to determine the mechanisms underlying size legacies.

As expected, genotype also affected most measurements of plant size. Two of the three lowland tetraploids, AP13 and KAN, were smaller than upland ecotypes; the third lowland genotype, WIL, was larger and more similar to the upland octoploids, particularly ENC and WWF. Aboveground dry

Table 4 Results of logistic regression for plant survival

	Nagelkerke model R^2	Model variables	Wald chi-square	β	SE	Exp(β)	P
Survival	0.255	Biomass per plant 2 years prior	12.196	1.705	0.488	5.503	< 0.001

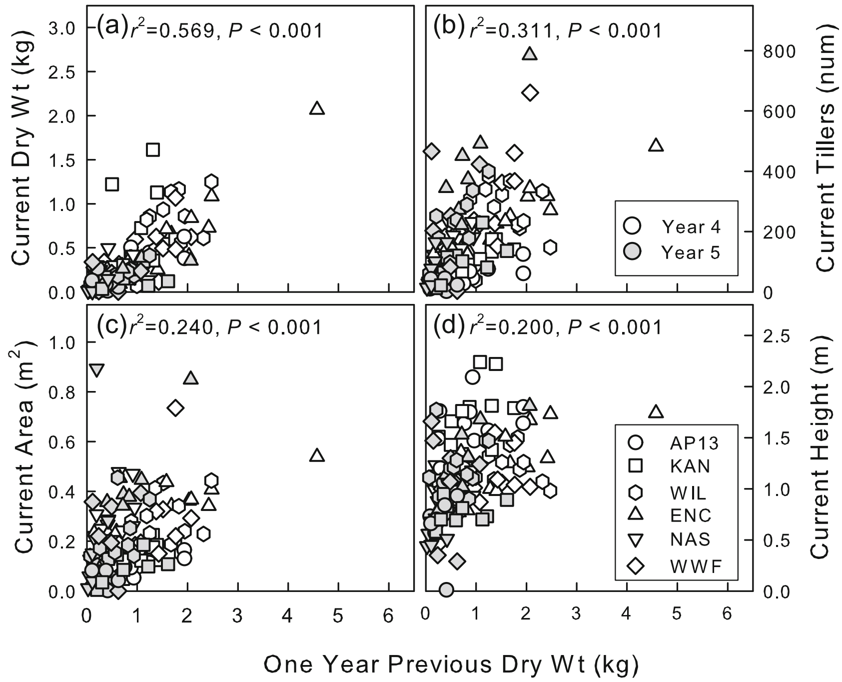

Fig. 4 Relationships between previous plant biomass and current plant **a** biomass, **b** area, and **c** tiller number. All measurements are reported per individual plant. Symbols are coded by genotype and year. Raw data are shown for clarity, but analyses are reported for transformed data

weights reflected different size trait correlations across genotypes; for example, increasing biomass was associated primarily with taller plants for both KAN (r = 0.69) and ENC (r = 0.74), with more area in WIL (r = 0.57), and with more tillers (r = 0.74) and more area (r = 0.76) for AP13. In contrast, biomass increased along with all three size traits, height, tillers, and area, for NAS (r = 0.65, 0.79, 0.61) and WWF (r = 0.60, 0.68, 0.73). Such trait syndromes and the relative performances of the six genotypes are largely consistent with what was observed in previous years, both during establishment [37] and after 1 year of the original precipitation treatments [21]. Although we focused on southern genotypes that were generally considered more drought- and heat-tolerant than ecotypes from northern regions, across-genotype variation in yield, morphology, and physiology remains an important factor [14, 28, 45].

In the current study, the effects of previous plant size were found across all genotypes, suggesting that this could be a

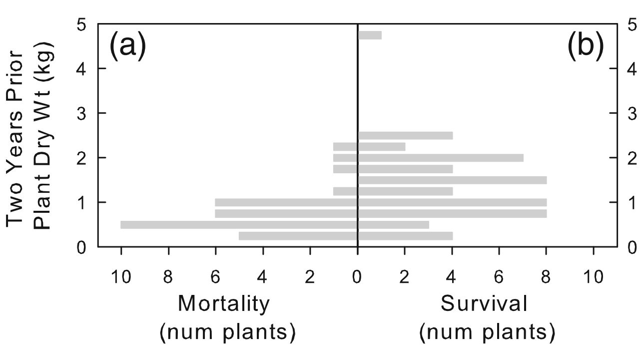

Fig. 5 Numbers of plants that **a** died and **b** survived after drought (year 4) as a function of individual biomass 2 years prior to the recovery year

general phenomenon. However, sample sizes were small due to mortality—particularly in the recovery year—which may constrain our ability to detect such interactions. Based on trends observed here in the degree of relationship between previous and current size, different switchgrass genotypes have the potential to vary in the strength of legacy effects. For example, based on the three-way interaction of genotype, prior rainfall treatment, and year on plant height, the lowland ecotypes AP13 and KAN are more likely to exhibit a legacy component under drought compared to all other genotypes, but only when previously grown under wetter conditions. Additional work is needed to determine whether size legacies generated by drought differentially affect switchgrass genotypes. To our knowledge, neither legacy effects of rainfall nor legacies of previous size (which can be controlled by rainfall) have been incorporated into plant models such as those used to simulate C4 grass production [46–50].

Findings in this study have implications for process-based models used to simulate drought impacts on plant productivity. Severe drought could result in simulated potential leaf area index in the following year below expectations based purely on rainfall, as observed empirically in the drought recovery year in this study. This would decrease the simulated biomass accordingly, and thus potentially carry over into further reductions in potential leaf area index in subsequent years depending on the strength of the legacy. Based on our findings, plant dry weights are constrained by previous rainfall and previous size even with adequate rainfall in the year after drought, suggesting the potential to alter long-term production trajectories. Indeed, precipitation legacies may be one reason previous simulation models have inadequately predicted year-to-year variation in yields of switchgrass and other warm-season grasses [48, 51, 52]. We do not know how the rainfall and size constraints might persist across further years under either additional drought or adequate rainfall. Given the expectation for greater precipitation extremes in the future [6–8], studies that go beyond 5 years will be required to understand the relative importance of both direct and indirect rainfall legacies.

Our findings have limitations. Plant responses to extreme drought and recovery were based on treatments applied between January and June, but the timing of drought can also determine its impact on yield [53, 54]. We also planted switchgrass individuals rather than the dense swards used for large-scale bioenergy crop production, which can overestimate yield. However, a recent analysis based on more than a thousand switchgrass observations from 39 trials found no evidence that plot size affects yield [45], so these patterns may be similar regardless. Finally, we did not directly measure belowground allocation in these plants, which is likely to be an important mechanism for drought recovery [31, 40].

Conclusions

We found that the effect of antecedent rainfall on switchgrass production carries over into subsequent years, both directly and indirectly via plant size. Such legacies have not been previously addressed in switchgrass or other biofuel crops and require multi-year data to identify. Genotypes also varied here, but there were no interactions detected with size, suggesting that size constraints may be universal. However, additional work is needed to confirm that legacies manifest similarly across a broader range of genotypes, ecotypes, and cultivars. These findings will affect how we manage and model switchgrass in a future where climate conditions are expected to be more extreme and more variable.

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