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Soil precipitation legacies influence intraspecific plant–soil feedback

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Abstract. Feedbacks between plants and soil microbial communities can play an important role in structuring plant communities. However, little is known about how soil legacies caused by environmental disturbances such as drought and extreme precipitation events may affect plant–soil feedback or whether plant–soil feedback operates within species as it does between species. If soil legacies alter plant–soil feedback among genotypes within a plant species, then soil legacies may alter the diversity within plant populations. We conducted a fully factorial pairwise plant–soil feedback experiment to test how precipitation legacies influenced intraspecific plant–soil feedbacks among three genotypes of a dominant grass species, *Panicum virgatum*. *Panicum virgatum* experienced negative intraspecific plant–soil feedback, i.e., genotypes generally performed worse on soil from the same genotype than different genotypes. Soil precipitation legacies reversed the rank order of the strength of negative feedback among the genotypes. Feedback is often positively correlated with plant relative abundance. Therefore, our results suggest that soil precipitation legacies may alter the genotypic composition of *P. virgatum* populations, favoring genotypes that develop less negative feedback. Changes in intraspecific diversity will likely further affect community structure and ecosystem functioning, and may constrain the ability of populations to respond to future changes in climate.

Key words: climate change; genetic diversity; grasslands; Panicum virgatum*; pathogens; plant–soil feedback; soil microbial communities.*

Introduction

Plant–soil feedback plays an important role in structuring plant communities (Reynolds et al. 2003, Bever et al. 2010). Species-specific soil communities assemble on and around plant roots (Bever et al. 2012) and can differentially influence plant performance (Bever et al. 1997). Negative plant–soil feedback (i.e., changes in soil communities that favor heterospecifics over conspecifics) can promote coexistence among species (Bever et al. 1997, Petermann et al. 2008), and variation in the strength of plant–soil feedback among species can predict species abundance distributions: rarer species generally have more negative plant–soil feedback (Klironomos 2002, Mangan et al., 2010, Bennett et al. 2017, Teste et al. 2017, but see Reinhart 2012). Despite its importance, we know little about how plant–soil feedback will be altered by expected climate changes, such as shifts in precipitation (Smith-Ramesh and Reynolds 2017, Crawford et al. 2019). Changes in precipitation, either persistent or in the form of extreme events, can have long lasting effects on both plants and soil microbes, which likely influence plant–soil feedback.

Precipitation is a key driver of microbial community structure and function. Experimental manipulations have revealed large changes in microbial community composition and function with changing precipitation (Fierer et al. 2003, Kardol et al. 2010, Barnard et al. 2013), and surveys along climate gradients have shown that the environment plays a strong role in influencing microbial community structure and function (Bradford et al. 2008, de Vries et al. 2012, Averill et al. 2016), which can be independent from changes in the plant community (Hawkes et al. 2017). Changes in microbial communities created by shifts in rainfall may have consequences for plant–soil feedbacks, especially if groups of microbes that differ in their influence on plant–soil feedbacks respond differently to changes in precipitation (Revillini et al. 2016, van der Putten et al. 2016). Importantly, changes in microbial community structure and function can be long lasting, producing microbial legacies in the soil (Martiny et al. 2017, Wubs et al. 2019). Soil microbial communities that are created or altered by precipitation can generate legacy effects. Legacy effects are the effects of prior conditions or disturbances on current ecological responses. Precipitation legacy effects can have a lingering influence on plant community composition (Meisner et al. 2013), may constrain future plant–soil feedbacks (Kaisermann et al. 2017, De Long et al.

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2019*a*), and may make changes in plant–soil feedback more difficult to predict across a landscape.

In addition to creating soil legacies that influence the outcome of plant–soil feedback, precipitation can also cause legacies in perennial plants (Sala et al. 2012). Grassland productivity can be more strongly correlated to past precipitation than current precipitation (Sala et al. 2012, Reichmann et al. 2013). This is at least partly explained by how precipitation affects resource storage in grasses, so they have a greater capacity to reproduce vegetatively after wetter years than drier years (Reichmann et al. 2013, Reichmann and Sala 2014, Hawkes and Kiniry 2018). Recent work has shown that biotic interactions can modify the effects of plant legacies on productivity (Grinath et al. 2018). However, it is largely unknown whether legacies in soil microbial communities can interact with plant legacies to influence plant performance (but see De Long et al. 2019*b*). A legacy of drought may hinder the ability of plants to combat pathogens (Jactel et al. 2012) or provide resources to mutualists (Sendek et al. 2019).

Plant–soil feedback is generally applied to heterospecific comparisons, but in perennial ecosystems intraspecific variation may dominate climate change responses. Variation within species is increasingly recognized as ecologically important (Hughes et al. 2008, Bolnick et al. 2011), but few experiments have tested whether genotypes within a species can generate plant–soil feedback (Crawford et al. 2019). Within a species, plants can culture genotype-specific soil communities (Schweitzer et al. 2008). Plant genotypes can also differ in their susceptibility to pathogens (Busby et al. 2013, Slinn et al. 2017) or ability to form associations with mutualists (Ronsheim 2016). Therefore, it seems likely that intraspecific plant–soil feedbacks may influence the coexistence and relative abundance of genotypes within a population, much as plant–soil feedback can influence the coexistence and relative abundance of species within communities. If precipitation legacies differentially alter plant–soil feedbacks for different plant genotypes, they could alter the diversity or composition of plant populations. In addition to having important evolutionary consequences, changes in the genotypic composition of plant populations can have cascading consequences for communities and ecosystem functioning (Hughes et al. 2008). For example, plant–soil feedback may shift plant composition to favor more or less productive genotypes, which may either dampen or exacerbate the consequences of climate disturbances on primary production.

Here, we tested how precipitation legacies influenced plant–soil feedback among genotypes of *Panicum virgatum* (switchgrass). *Panicum virgatum* is a native perennial bunchgrass that is common throughout grasslands in North America. The three genotypes in our study differed in ploidy level and ecotype, and previous work has shown that they also differed considerably in phenotypic traits (Aspinwall et al. 2013) and responses to precipitation (Aspinwall et al. 2017). Furthermore, prior precipitation generates a legacy effect on the ability of *P. virgatum* to recover from drought (Hawkes and Kiniry 2018). In order to address the role of intraspecific variation and precipitation legacies on plant–soil feedback, we conducted a two-phase fully factorial plant–soil feedback experiment in the greenhouse using soils and plants collected from a field experiment that manipulated precipitation applied to multiple switchgrass genotypes. We tested the following specific questions: (1) Do genotypes of *P. virgatum* generate intraspecific plant–soil feedbacks? (2) Do plant precipitation legacies and/or microbially mediated soil precipitation legacies influence intraspecific plant–soil feedbacks? (3) Do plant and soil precipitation legacies interact to influence plant–soil feedback?

METHODS

Plant and soil collection

In mid-May 2015, we collected soil and tillers from three genotypes of *Panicum virgatum*: WIL, WWF, and NAS (for details on the genotypes, see Aspinwall et al. 2013). These plants were part of a 3-yr experiment that tested how *P. virgatum* genotypes responded to a range of precipitation regimes. The grass genotypes originated from natural populations throughout Texas. While these genotypes are unlikely to locally co-occur, results from our experiments serve as a proof of concept for how climate legacies may influence intraspecific feedback. The *P. virgatum* populations were planted in four blocks of 5 × 5 m plots under a rainout shelter at Lady Bird Johnson Wildflower Center (Austin, Texas) where soils are shallow rocky clays (Speck series). Two clones of each genotype were planted in every plot, and plants were separated by 1 m. Soil microbial community composition was not measured in the blocks prior to establishing the experiment, but precipitation treatments were replicated across blocks. Plots within a block were randomly assigned to one of six precipitation treatments; here we sampled plants and soils from two treatments: 1,322 mm/yr (“high”) and 657 mm/yr (“low”). The high precipitation treatment was based on average precipitation during the 10 wettest years in the 100-yr local rainfall record, and the low precipitation treatment was based on average precipitation during 10 yr most closely matching the 25th percentile of years in the 100-yr local rainfall record. For comparison, the average annual rainfall in Austin, Texas is 864 mm and the amount of rainfall during a major drought in 2011 was 500 mm. For more details of the experimental design, please see Aspinwall et al. (2017). After 3 yr of exposure to the precipitation treatments, we collected tillers and soil from one clone per genotype per precipitation treatment per block. Plants and soils were stored on ice and shipped to the University of Houston. At the University of Houston, we immediately split the clones and planted individual tillers in 260-mL conical pots (5 cm diameter × 18 cm deep; Stuewe and Sons, Tangent, Oregon, USA) filled with autoclaved Metro-Mix 360 (Sun Gro Horticulture, Agawam, Massachusetts, USA), which contains a mix of *Sphagnum* peat moss, bark, and vermiculite. We grew the plants for six weeks prior to initiation of the experiment to acclimate them to greenhouse conditions. During this time, we stored soil from the plants in a refrigerated room (4°C) to slow microbial processes and minimize changes in soil community composition. According to the International Culture Collection of (Vesicular) Arbuscular Mycorrhizal (AM) Fungi (INVAM), AM fungi can remain viable for up to 1 yr when refrigerated (data *available online*),[5] and soil bacterial communities remain distinct from one another under a variety of storage temperatures and times (Rubin et al. 2013). At the onset of the experiment, plants varied in size (3.5–285 cm), but initial plant height was not significantly different across genotypes ($F_{2,\ 338} = 0.47$, $P = 0.63$) or precipitation treatments ($F_{1,\ 338} = 0.46$, $P = 0.50$).

Feedback experiment

To test how putative precipitation-induced plant and microbial legacies generated in the field experiment influenced intraspecific plant–soil feedback, we established a factorial experiment where plants of each genotype in each precipitation treatment were grown in soil collected from under each genotype in each precipitation treatment. Thus, we had 36 total treatment combinations comprised of six plant treatments (three plant genotypes originating from the two field precipitation treatments) fully crossed with six soil treatments (conditioned by the three plant genotypes grown in the two field precipitation treatments). Each treatment combination was replicated between 7 and 10 times, depending on the availability of plant material. The collected soils likely differed in both biotic and abiotic properties. To isolate microbially mediated plant–soil feedback effects from plant–soil feedback caused by differences in soil nutrients or soil structure, we added a small amount (5% by volume) of the treatment soil to a common, sterilized, background soil. This standardized nutrients and soil structure across treatments while allowing biotic communities to vary based on plant genotype and the soil precipitation legacies. The background soil was collected from the University of Houston Coastal Center (La Marque, Texas, USA), where soils are deep clays (Ijam series). Background soil was autoclaved twice with a 24-h resting period between autoclave cycles. Plants were grown in 260-mL conical pots (5 cm diameter × 18 cm deep; Stuewe and Sons). Live treatment soil was added directly to the rooting zone of the plants to ensure rapid colonization by soil microbes. The conical pots were suspended in racks (Stuewe and Sons), and every other position in the rack was left empty to prevent cross-contamination from splash-over during watering. To prevent water limitation, plants were watered to saturation once a day. After 12 weeks, we harvested aboveground plant biomass.

Statistical analyses

The plant–soil feedback metric, I_s, (the relative response of *P. virgatum* genotypes when associated with soils from their “own” genotypes vs. soils from “other” genotypes, relative to how the “other” genotypes responded across the same soils) was calculated using a priori contrasts following significant interactions in a general linear model for aboveground biomass (Bever et al. 1997). We chose this plant–soil feedback metric because it is directly linked to coexistence criteria: negative feedback stabilizes diversity while positive feedback erodes diversity. The general linear model included the fixed effects of plant response genotype (*P. virgatum* genotype that was tested in the current experiment), soil conditioning genotype (*P. virgatum* genotype that conditioned the soil in the field experiment), plant precipitation legacies (whether the *P. virgatum* was from a high or low precipitation treatment), soil precipitation legacies (whether the soil inoculum was from a high or low precipitation treatment) and all possible interactions (Proc GLM, SAS 9.4; SAS Institute, Cary, North Carolina, USA). The initial summed tiller heights for each plant were included as a covariate to control for differences in plant size at the start of the experiment. Significant plant–soil feedback is indicated by a significant plant response genotype × soil conditioning genotype interaction, i.e., the performance of different *P. virgatum* genotypes depended on the genotype of *P. virgatum* that conditioned the soil. A significant interaction between plant response genotype × soil conditioning genotype and plant or soil precipitation legacies indicates that those factors affected the strength or direction of plant–soil feedback. To quantify plant–soil feedback and test whether feedback for each genotype was significantly different from zero, we used a priori contrasts within the significant plant response genotype × soil conditioning genotype × soil precipitation legacy interaction that isolated the strength and direction of the interaction between plant response genotype and soil conditioning genotype for each possible pair of genotypes (i.e., pairwise plant–soil feedbacks among genotypes) within both soil precipitation legacy treatments (Mangan et al. 2010, Smith and Reynolds 2015, Crawford and Knight 2017). Results from statistical models containing block (in the field experiment) were not qualitatively different (Appendix S1: Table S1), so models excluding block are presented for clarity. Data from the experiment can be found in the supplementary materials (Data S1, Metadata S1).

RESULTS

Results from the general linear model of aboveground biomass showed that plant–soil feedback among

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[5] https://invam.wvu.edu

genotypes of *P. virgatum* was significantly influenced by soil precipitation legacies (significant interaction of plant response genotype × soil conditioning genotype × soil precipitation legacy; Table 1). Averaged across all genotypes, plant–soil feedback was negative in both soil precipitation legacies (low precipitation −1.05 ± 0.44 [mean ± SE]; high precipitation −0.90 ± 0.45). However, soil precipitation legacies reversed the rank of the strength of plant–soil feedback responses for each genotype (Fig. 1). In soils with a legacy of low precipitation, genotypes WIL and WWF had significantly negative feedback whereas feedback for NAS was negative but not significantly different from zero. In soils with a legacy of high precipitation, feedbacks for WIL and WWF were negative but not significantly different from zero while feedback for NAS was strongly negative.

TABLE 1. Results from general linear models testing how plant response genotype (P), soil conditioning genotype (S), soil precipitation legacy (SL), and plant precipitation legacy (PL) influenced aboveground plant biomass.

Factor	df	*F*	*P*
P	2	4.72	**0.01**
S	2	1.85	0.16
SL	1	0.42	0.52
PL	1	11.82	**0.0007**
P × S	4	2.72	**0.03**
P × SL	2	0.79	0.46
P × PL	2	7.61	**0.0006**
S × SL	2	0.66	0.52
S × PL	2	0.58	0.56
SL × PL	1	0.69	0.41
P × S × SL	4	2.98	**0.02**
P × S × PL	4	1.83	0.12
P × SL × PL	2	1.12	0.33
S × SL × PL	2	0.09	0.92
P × S × SL × PL	4	0.80	0.52
Initial height	1	573.85	**<0.0001**
Error	305		

Note: Boldface type highlights significant *P* values ($P < 0.05$).

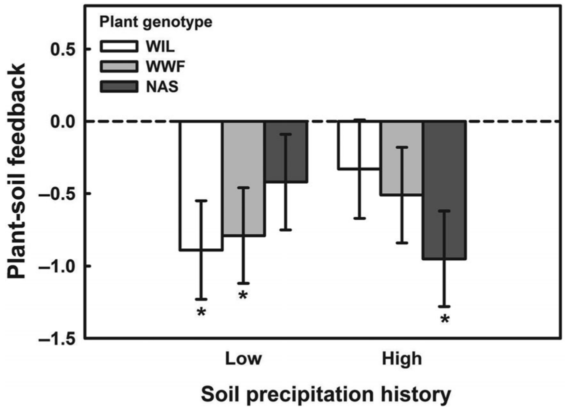

FIG. 1. Variation in plant–soil feedback among *Panicum virgatum* genotypes in soils with histories of low and high precipitation. Bars indicate mean plant–soil feedback ± SE. Asterisks indicate plant–soil feedback that was significantly different from zero at $P < 0.05$.

Examining how the aboveground biomass of the *P. virgatum* genotypes changed depending on soil conditioning genotype and soil precipitation legacies helps uncover what responses drove the differences in plant–soil feedback (Fig. 2). In soils with a legacy of low precipitation, WIL and WWF performed the worst on conspecific soils, contributing to negative plant–soil feedback, while there was little variation in response of NAS, contributing to neutral plant–soil feedback. In soils with a legacy of high precipitation, NAS performed the worst on conspecific soil, contributing to negative plant–soil feedback, while there was little variation in response of WIL, contributing to neutral plant–soil feedback. In high precipitation soil legacies, there was a tendency for WWF to perform better on the soil of a heterospecific, NAS, contributing to negative, but not significantly negative, plant–soil feedback.

Plant precipitation legacies also influenced the aboveground biomass of the *P. virgatum* genotypes (Table 1, Fig. 3). WWF clones produced 22% less biomass when they had a legacy of high precipitation relative to a legacy of low precipitation (Tukey's hsd < 0.0001). The other two genotypes did not respond to plant precipitation legacies. Plant precipitation legacies did not influence plant–soil feedback.

DISCUSSION

We found that *P. virgatum* experienced intraspecific plant–soil feedback and that the strength of feedback for individual genotypes depended on soil precipitation legacies. Average plant–soil feedback across genotypes was negative, suggesting that soil microbes may promote coexistence among these genotypes. However, microbially mediated soil precipitation legacies reversed the rank order of intraspecific plant–soil feedback for the three *P. virgatum* genotypes. If the strength of intraspecific plant–soil feedback is correlated with relative abundance, as it often is for interspecific plant–soil feedback (Klironomos 2002, Mangan et al. 2010, Bennett et al. 2017, Teste et al. 2017), then soil legacies may cause changes in the genetic composition (i.e., evolution) of *P. virgatum* populations. Unlike soil precipitation legacies, plant precipitation legacies were only apparent for one genotype (WWF), which produced less biomass with a history of high precipitation, and did not influence plant–soil feedback.

While we did not attempt to identify the soil microbes underlying the feedback responses, negative plant–soil feedback can be driven by specialized pathogens (Petermann et al. 2008, Bever et al. 2015, Crawford et al. 2019). Pathogens tend to proliferate in wetter environments (Augspurger 1984, Tedersoo et al. 2014), so it

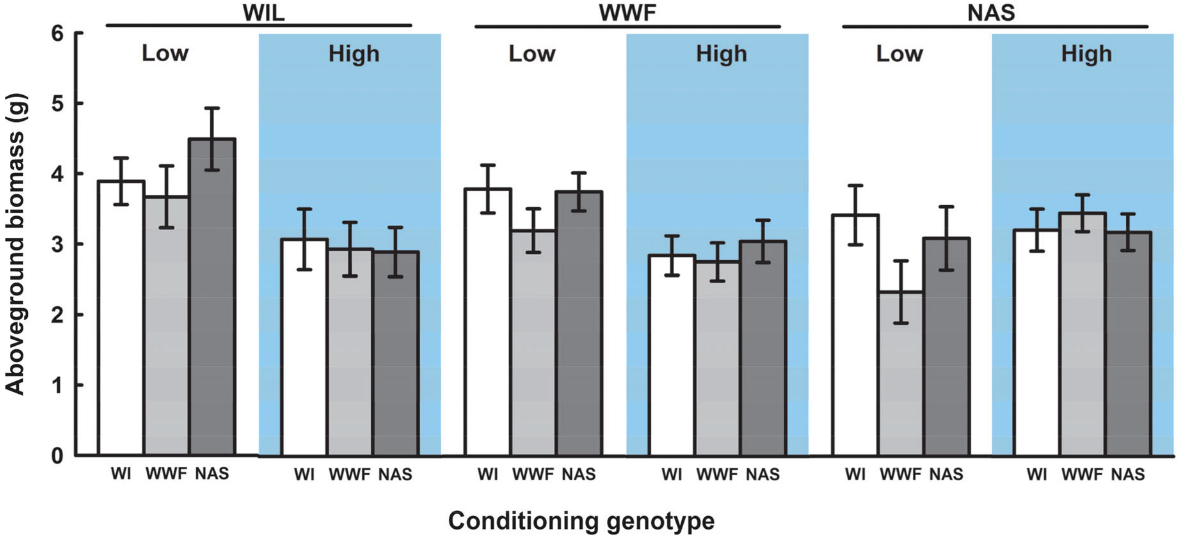

FIG. 2. Effect of soil conditioning genotype and soil precipitation legacies on aboveground biomass of each *Panicum virgatum* genotype. Response genotypes are labeled at the top of the graph, as are soil precipitation legacies (low, white background; high, blue background). Bars indicate lsmeans for aboveground biomass ± SE.

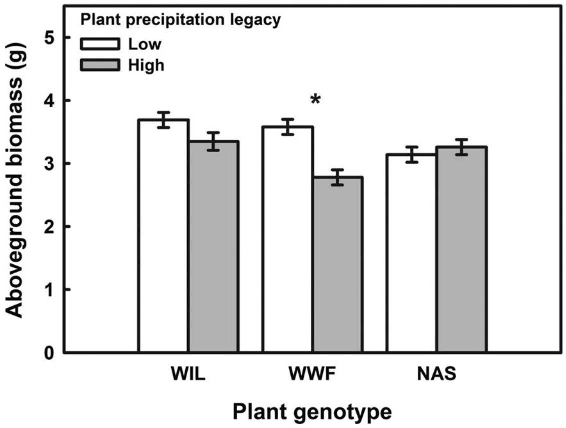

FIG. 3. Effect of plant precipitation legacy on the aboveground biomass of the *Panicum virgatum* genotypes. Bars indicate lsmeans for aboveground biomass ± SE. Asterisks indicate significant differences ($P < 0.05$) in biomass within a genotype.

follows that plant–soil feedback may become more negative with increased water availability. However, negative feedback was generally stronger in soils with a legacy of low precipitation. Many plant pathogens, such as oomycetes, form long-lasting spores. Dormant spores may have accumulated in the low precipitation treatment and became active during the favorable conditions in the greenhouse, magnifying negative plant–soil feedbacks. Alternatively, mutualists could be driving negative plant–soil feedback. For example, AM fungi that benefit competing plant species more than their hosts can generate negative feedback (Bever 1999, Umbanhowar and McCann 2005). Genotypes of *P. virgatum* can have sevenfold differences in their amount of colonization by AM fungi (C. V. Hawkes, *unpublished data*) and differ in the identity of associated microbial mutualists, including AM fungi (Revillini et al. 2019). If the costs and benefits of mutualism change with precipitation (Hoeksema et al. 2010), e.g., AM fungi can benefit plants more during drier conditions (Auge 2001), then changes in precipitation may alter mutualist-driven feedbacks. Future work that characterizes microbial community responses to plant identity and changes in precipitation may help uncover the mechanisms driving plant–soil feedback (van der Putten et al. 2016).

To our knowledge, no study has tested how precipitation influences intraspecific feedbacks, and the few studies that have tested how precipitation influences interspecific feedbacks have produced mixed results. Experiments that tested for contemporary precipitation effects (rather than precipitation legacies) found that drought neutralized negative pairwise plant–soil feedback (Snyder and Harmon-Threatt 2019) and neutralized negative and positive conspecific plant–soil feedback (Fry et al. 2018). However, a test of precipitation legacies found that drought switched conspecific plant–soil feedbacks from positive to negative (Kaisermann et al. 2017). One possible explanation for the difference in results is that the rewetting of drought-stressed soils changes the microbial community in a way that contemporary droughts do not (Evans and Wallenstein 2012), e.g., by causing increases in previously dormant plant pathogens. An interesting avenue for future research is testing whether historical and contemporary precipitation interact to influence plant–soil feedback responses. Adaptation of soil microbial communities to environmental conditions can influence plant responses to changes in precipitation (Lau and Lennon 2012, Tomiolo et al. 2015). For example, during droughts, soil microbial communities that have previously experienced dry conditions can buffer plant fitness (Lau and Lennon 2012). We did not manipulate contemporary precipitation in our experiment, but if we had we suspect that "mismatches" between soil legacies and contemporary precipitation may decrease plant growth. If decreased plant performance caused by soil legacy mismatches are unequal across genotypes, it could generate stronger negative plant–soil feedback. It is also likely that the type of precipitation disturbance (e.g., press vs. pulse, change in mean vs. change in variance) influences soil legacies and plant–soil feedbacks. While potentially complex, plant–soil feedback experiments that manipulate disturbance types could help provide insights into how soil communities and plant communities will respond to changing climates.

The genotype-specific differences in plant–soil feedback we observed may be driven by a combination of plant traits and maternal environment. The three *P. virgatum* genotypes in our study differed in ploidy level and ecotype (Aspinwall et al. 2013, 2017). "Upland" ecotypes are usually octoploid and have short, thin tillers and small leaves; "lowland" ecotypes are usually tetraploid and have tall, thick tillers and large leaves (Porter 1966, Brunken and Estes 1975). NAS is octoploid with an upland ecotype, WIL is tetraploid with a lowland ecotype, and WWF is octoploid but intermediate in plant traits (Aspinwall et al. 2017). Interestingly, WWF also responded intermediately to plant–soil feedback and was the only genotype that had a significant plant precipitation legacy. Linking plant traits to feedback responses has the potential to improve our ability to predict how plant–soil feedback structures communities (Ke et al. 2015, Cortois et al. 2016, Teste et al. 2017). The wide trait variation characterized in *P. virgatum* may make it an ideal species for testing how plant traits influence plant–soil feedback. The three genotypes were also from maternal environments that differed in their average water availabilities (Aspinwall et al. 2013). Genotypes tended to have the more negative feedback in soils with precipitation legacies that more closely matched their natural maternal environment, suggesting that there may be adaptation in plant–microbe interactions to local conditions (terHorst et al. 2014, terHorst and Zee 2016).

There is mounting evidence that plant–soil feedback plays an important role in structuring plant communities. Our work shows that soil precipitation legacies alter intraspecific plant–soil feedback within a dominant grass species, *P. virgatum*, which may change the relative abundance of genotypes within *P. virgatum* populations. If strength of feedback is positively correlated with relative abundance (Mangan et al. 2010), then WWF and WIL may become rarer with decreased precipitation. These two genotypes tend to be more productive than NAS (Aspinwall et al. 2013). Therefore, plant–soil feedback driven changes in population structure may magnify the negative effect of drought on *P. virgatum* productivity. While previous work has found that drought may cause rapid evolutionary change in a foundational grass (Whitney et al. 2019), the genotype-dependent soil legacies we found suggest that precipitation and soil microbes jointly drive evolution in *P. virgatum* populations. Subsequent changes in the microbial community caused by microbially driven changes in *P. virgatum* populations sets up the potential for strong eco-evolutionary dynamics in this system. With the anticipated global changes in climate, it is important that we better understand how abiotic factors, such as precipitation, modify plant–soil feedbacks so that we can make better predictions for how climate change will restructure ecological communities.

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