



# Traits that distinguish dominant species across aridity gradients differ from those that respond to soil moisture

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## Abstract

Many plant traits respond to changes in water availability and might be useful for understanding ecosystem properties such as net primary production (NPP). This is especially evident in grasslands where NPP is water-limited and primarily determined by the traits of dominant species. We measured root and shoot morphology, leaf hydraulic traits, and NPP of four dominant North American prairie grasses in response to four levels of soil moisture in a greenhouse experiment. We expected that traits of species from drier regions would be more responsive to reduced water availability and that this would make these species more resistant to low soil moisture than species from wetter regions. All four species grew taller, produced more biomass, and increased total root length in wetter treatments. Each species reduced its leaf turgor loss point (TLP) in drier conditions, but only two species (one xeric, one mesic) maintained leaf water potential above TLP. We identified a suite of traits that clearly distinguished species from one another, but, surprisingly, these traits were relatively unresponsive to reduced soil moisture. Specifically, more xeric species produced thinner roots with higher specific root length and had a lower root mass fraction. This suggests that root traits are critical for distinguishing species from one another but might not respond strongly to changing water availability, though this warrants further investigation in the field. Overall, we found that NPP of these dominant grass species responded similarly to varying levels of soil moisture despite differences in species morphology, physiology, and habitat of origin.

**Keywords** Drought · Grass · Leaf hydraulics · Root traits · Primary production

## Introduction

Plants depend on water for gas exchange, cellular integrity, solute transport, and temperature regulation. This physiological dependence underlies the predominant role of precipitation in controlling rates of net primary production (NPP) globally (Sala et al. 2012; Anderegg et al. 2015; Knapp et al. 2017). Species vary in their responses to altered water availability which in turn influences their potential distributions and their impacts on ecosystem properties (Lavorel and Garnier 2002). For example, grasslands vary in their sensitivity of NPP to drought (Knapp et al. 2015; Maurer et al. 2020), with up to 70% of this variation in sensitivity at regional scales explained by the traits and relative abundances of resident plant species (Griffin-Nolan et al. 2019a).

Dominant plant species have the greatest impact on NPP and ecosystem responses to environmental change (“mass-ratio hypothesis”, Grime 1998), particularly in plant communities with low species evenness (Avolio et al. 2019; Smith et al. 2020). In a tallgrass prairie, for example,

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experimentally removing half of the stems of the dominant C<sub>4</sub> grass led to a > 50% loss of aboveground NPP (i.e., subordinate species did not compensate for loss of NPP), while removal of less common species had little-to-no effect on production (Smith and Knapp 2003). Furthermore, aboveground NPP was unable to fully compensate for the loss of this dominant species even after alleviating resource limitation via irrigation and nutrient fertilization (Chaves and Smith 2021). Thus, understanding how the traits of dominant grass species from different grassland types respond to changes in water availability will be important for forecasting ecosystem responses to expected climate changes (Smith et al. 2009, 2020; Hoover et al. 2014a).

Grasses are a highly diverse family of plants (~ 11,500 species of Poaceae worldwide; Soreng et al. 2017) and contribute disproportionately to the terrestrial carbon sink (Fisher et al. 1994; Still et al. 2003; Wigley et al. 2020). While grasses are present across all biomes, they are particularly successful in water-limited ecosystems (Bond et al. 2005), making them an ideal group for exploring plant adaptations to water stress. Species that are chronically exposed to water limitation are expected to be tolerant of changes in water availability (Grime 2000, Tielborger et al. 2014). For example, grass species that inhabit drier regions are more resistant to leaf turgor loss (i.e., wilting) than grasses from wetter regions (Griffin-Nolan et al. 2019b). However, global analyses suggest that physiological drought tolerance is widespread, meaning that drought tolerant species are not constrained to xeric ecosystems (Craine et al. 2013). Indeed, both observational and experimental evidence suggests that NPP of xeric grasslands is more sensitive to changes in water availability than mesic ecosystems (Huxman and Smith, 2004; Knapp et al. 2015; Griffin-Nolan et al. 2019a; Maurer et al. 2020), suggesting that dominant grass species in xeric ecosystems may be less drought tolerant, although this is understudied. Measuring traits and NPP of both xeric- and mesic-adapted grass species along a controlled gradient of soil moisture may help explain this pattern of differential sensitivity.

Given the large number of potential traits to measure for a single species/individual (Perez-Harguindeguy et al. 2016), trait selection should be based on the environmental context of the hypothesis being tested (Rosado et al. 2013; Griffin-Nolan et al. 2018). For example, some traits explain a species' response to environmental change, while others are related to a species' influence on certain ecosystem functions (Suding et al. 2008). Additionally, certain traits may be 'static', in that they uniquely identify a species or groups of species but do not change in response to the environment (e.g., photosynthetic pathway or lifespan). In the context of water availability, both hydraulic and root traits have proven critical for predicting species responses to water stress (Reich 2014; Griffin-Nolan et al. 2018; Garbowski et al.

2020). However, few studies have measured both hydraulic and root traits of dominant grass species along a gradient of water availability (Jardine et al. 2021). Additionally, many studies have collected trait and production data on adult grasses, despite recognition that seedlings are a critical yet understudied stage of development (Harrison and LaForgia 2019; Larson et al. 2020). Indeed, grass ontogeny and life stage can influence a species response to drought as much as drought severity and/or duration (Lemoine et al. 2018).

In this study, we aimed to understand how water availability influences hydraulic and root traits of dominant grass seedlings from both xeric and mesic biomes. We measured biomass production, root and shoot morphology, and leaf hydraulics of seedlings of four dominant North American prairie grasses (*Bouteloua eriopoda*, *Bouteloua gracilis*, *Pascopyrum smithii*, and *Andropogon gerardii*) in response to four different levels of soil moisture. We selected these species, because they are all widespread throughout the U.S. central Plains, but each one is dominant in a different one of the four distinct grassland ecosystems in the region: desert grassland, shortgrass prairie, mixed grass prairie, and tallgrass prairie (Table 1). Studying these four species thus provides important insight into how common species dominating different habitats respond to changing water availability. We explored the coordination of production and morphological traits above- and belowground with the goal of identifying traits that respond to soil moisture, as well as static traits that differentiate species from one another. For all species, we expected biomass production would be reduced and biomass allocation belowground increased in drier treatments. We tested the hypotheses that grasses from drier regions (*Bouteloua* spp.) would be more resistant to drier conditions than those from wetter regions (*A. gerardii* and *P. smithii*) (Grime 2000). We expected each species would adjust osmotically in drier conditions leading to lower (more negative) leaf turgor loss point (TLP) (Knapp 1984) and tested the hypothesis that grasses from drier sites would have lower TLP (Lenz et al. 2006; Griffin-Nolan et al. 2019b). Additionally, we expected species from drier regions to maintain midday leaf water potential ( $\psi_{leaf}$ ) above TLP.

**Table 1** Mean annual temperature and mean annual precipitation of the ecosystems which the species in this study dominate (from Griffin-Nolan et al. (2019a))

Ecosystem	Representative species	MAP (mm)	MAT (°C)
Desert grassland	<i>Bouteloua eriopoda</i>	244	13.4
Shortgrass prairie	<i>Bouteloua gracilis</i>	366	9.5
Mixed grass prairie	<i>Pascopyrum smithii</i>	415	7.9
Tallgrass prairie	<i>Andropogon gerardii</i>	864	13

MAP mean annual precipitation, MAT mean annual temperature

## Materials and methods

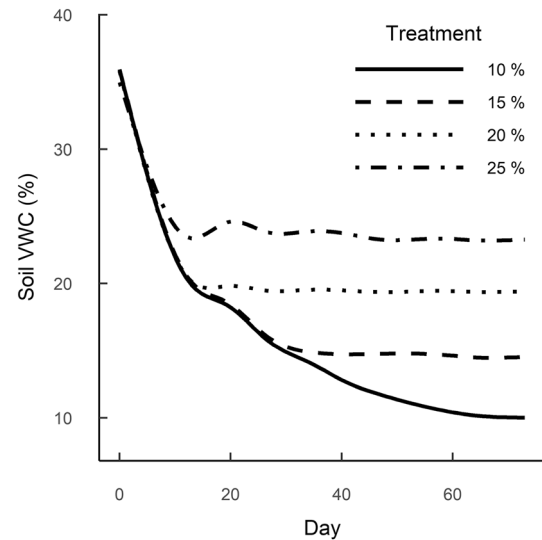
### Study species

We selected species that are representative of the four major grassland types that occur in the US central Plains (Knapp et al. 2015): *Bouteloua eriopoda* (desert grasslands), *Bouteloua gracilis* (shortgrass prairie), *Pascopyrum smithii* (mixed grass prairie), and *Andropogon gerardii* (tallgrass prairie). These species are widespread throughout the Great Plains and are each dominant in a different ecosystem, where they are the most important contributor to ecosystem functions including primary production and C cycling. We obtained seeds from a common garden environment to minimize environmental influences on seedling variability (Prairie Moon Nursery; Winona, MN).

### Treatments

We germinated seeds ( $n=20/\text{species}$ ) in SC7 cone-tainers (Greenhouse Megastore, Danville, IL) filled with Pro-Mix<sup>®</sup> potting soil and placed under a germination mister until each individual had at least 3 fully emerged leaves ( $\sim 3$  weeks). We then transplanted individuals to 34.5 cm deep pots containing  $\sim 1600$  g of greens-grade natural porous ceramic soil (bulk density  $0.576 \text{ g/cm}^3$ , Profile, Buffalo Grove, IL) and 16 g of slow-release Osmocote NPK fertilizer (Scotts Miracle-Gro, Marysville, Ohio), and relocated them to a greenhouse with fixed environmental conditions (16H/8H-day/night light cycle,  $25^\circ\text{C}$ , and 40% relative humidity). This pot depth captures the majority of grassland root production in the field (Weaver and Darland 1949; Jackson et al. 1996; Sun et al. 1997; Schenk and Jackson 2002; Nippert et al. 2012). We allowed seedlings to acclimate for 2 weeks, during which we watered pots to holding capacity [ $\sim 36\%$  volumetric water content (VWC)] every day.

Following acclimation, we imposed soil moisture treatments by withholding water until soil moisture declined to four different levels: 25, 20, 15, and 10% VWC. We weighed each pot daily and calculated VWC as:  $(\text{soil wet weight} - \text{soil dry weight}) / \text{soil dry weight} \times \text{soil bulk density} \times 100$ . Once a pot reached its assigned treatment level, we maintained soil moisture at that level by weighing pots daily and adding water to account for loss via evapotranspiration. All treatments were maintained at their target soil moisture content until the driest treatment (the last to reach its target level) had been at its target level for 2 weeks (Fig. 1). As a result of our study design, each treatment spent a different amount of time at its target soil moisture level.



**Fig. 1** Soil volumetric water content (VWC) in the four treatments over the course of the study. Treatments are expressed as % VWC

### Production and morphological traits

At the end of our treatments, we quantified maximum stretched plant height (i.e., distance from the soil to the tip of the most recently emerged leaf extended vertically), number of tillers, number of flowers, and proportion of total leaves that were green on ten individuals per species. We also estimated above- and belowground biomass production of these individuals. We harvested all aboveground plant material by clipping at the soil surface and drying all collected material at  $60^\circ\text{C}$  for 48 h prior to weighing. We carefully washed all soil off of all roots by submerging the root system of each individual plant in a shallow bowl of water, and removing attached soil by hand. We scanned roots with an Epson Perfection V600 scanner (Epson America Inc., Long Beach, CA, USA) and analyzed scans to determine average root diameter and total root length production per plant using WinRhizo (Regent Instruments Inc., Quebec, Canada). We then dried at  $60^\circ\text{C}$  for 48 h and weighed them. We also estimated specific root length (SRL; root length/root dry mass) and root tissue density (RTD; root dry mass/root wet volume) per individual plant. To estimate specific leaf area (SLA; leaf area/leaf dry mass), we sampled two additional leaves from five individuals per species and treatment and scanned them for leaf area (Epson V600 scanner), which was determined using ImageJ software. We oven-dried the same leaves at  $60^\circ\text{C}$  for 48 h prior to weighing.

## Leaf hydraulics

We measured physiological responses to the treatments using the remaining ten individuals per species. To determine water stress, we estimated midday leaf  $\psi_{leaf}$  ( $\psi$ ) using a Scholander-style pressure chamber (PMS Instruments, Albany, OR, USA) after pots had reached their target soil moisture content. Briefly, we clipped two recently emerged and fully expanded leaves from 5 pots per species and treatment, and sealed the leaves in a plastic bag with a moist paper towel to avoid desiccation. Within 20 min of clipping, we inserted the leaf into the pressure chamber with the cut end facing out and increased the pressure inside until xylem water was exuded out of the cut end.

Once pots were at treatment level for at least 2 weeks, we estimated the leaf osmotic potential at full turgor ( $\pi_o$ ) using a vapor pressure osmometer following Bartlett et al. (2012). We watered 5 pots per species and treatment (i.e., those not used for water potential measurements) to holding capacity and covered them in plastic bags for ~12 h to allow leaves to fully rehydrate. Following rehydration, we sampled a leaf disk from one fully emerged leaf per pot using a biopsy punch. To rupture cell walls, we wrapped the disk in tin foil and held it under liquid nitrogen for 1 min. Immediately following treatment with liquid nitrogen, we placed the leaf disk into the osmometer chamber (VAPRO 5520, Wescor). We left samples in the closed chamber for ~10 min to allow equilibration and then recorded osmolarity every 2 min until equilibrium was reached (<5 mmol/kg change in osmolarity between measurements). We converted osmolarity to leaf osmotic potential at full turgor ( $\pi_o$ ) ( $\pi_o$  = osmolarity  $\times$  -2.3958/1000) and further converted to leaf turgor loss point (TLP, the leaf water potential at which cells lose turgor and wilting occurs) using a linear model developed specifically for grasses (Griffin-Nolan et al. 2019b):  $TLP = 0.944\pi_o - 0.611$  ( $r^2 = 0.96$ ).

## Statistical analysis

To test for differences in production and traits among species and treatments, we fit linear models including treatment, species, and their interaction and performed pairwise comparisons among species within treatments and among treatments within species using Tukey-adjusted p values to account for multiple comparisons. We log-transformed data when necessary. Proportion data, such as % green leaves, required an arc-sin transformation to meet assumptions of normality of residuals. We ran a principal component analysis (PCA) including production and morphological traits (excluding SLA which was measured on separate individuals) using the *prcomp* function. Transformed and scaled data were used for the PCA. To assess species and treatment differences in multivariate space, we extracted the scores of

each individual along the first and second principal components and ran non-parametric Kruskal–Wallis tests and made pairwise comparisons using Bonferroni-adjusted p values. Finally, we assessed potential tradeoffs between traits using Pearson's r correlation. All analyses were run in R Statistical Programming language version 4.0.3 (R Core Team 2020).

## Results

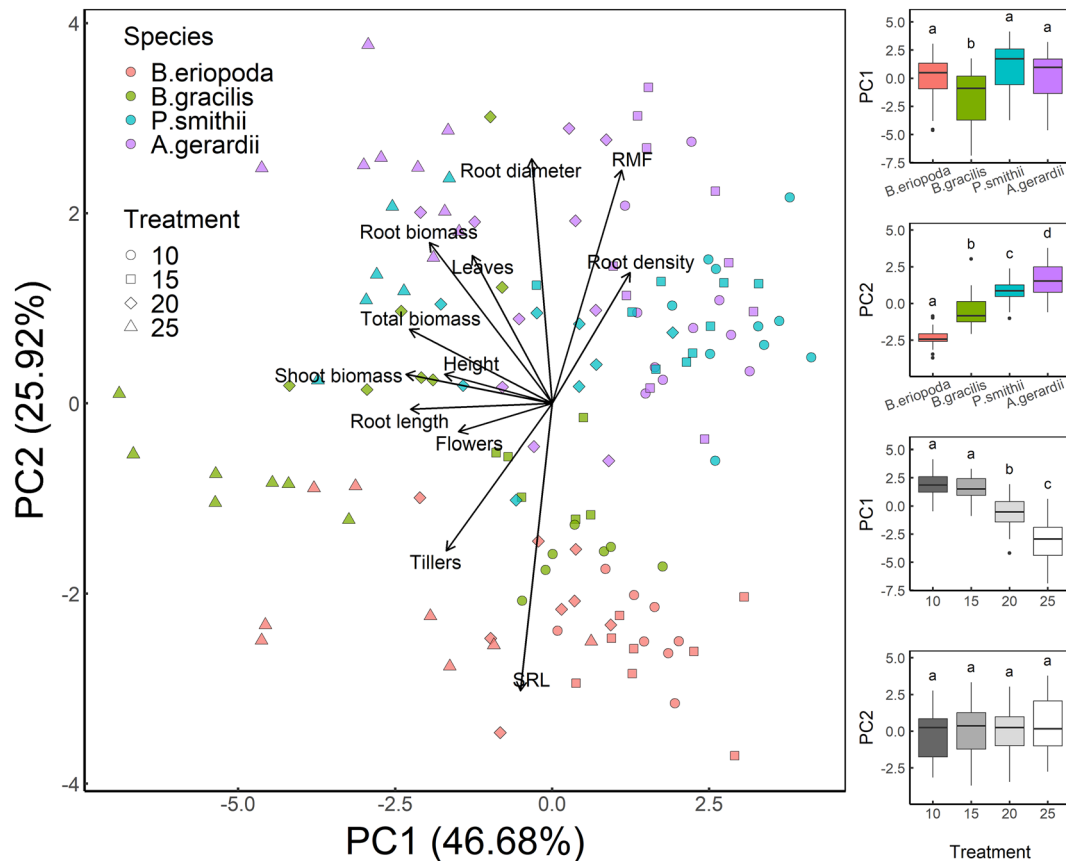
We found a significant main effect of the soil moisture treatments on plant biomass and all traits measured, except SRL, and a significant effect of species on biomass and all traits measured (Table 2). The effect of soil moisture on shoot mass production, height, number of flowers, root length production, root diameter, root tissue density, and TLP did not vary by species (i.e., no significant treatment  $\times$  species interaction), meaning that all species responded to treatments similarly for those traits (Table 2). However, the effect of treatment on root mass production, total mass production, RMF, number of tillers, % green leaves, SRL, SLA, and midday leaf water potential did vary by species (i.e., significant treatment  $\times$  species interaction) (Table 2). The PCA assessing associations among morphological traits and production in multivariate space indicated strong separation among

**Table 2** Results from Analysis of Variance (ANOVA). For models with significant interactions, we ran a type-III ANOVA; otherwise, type-II ANOVA results are shown

Traits	Treatment	Species	Treatment*Species
Shoot biomass (g)	156.03***	11.17***	1.7438
Root biomass (g)	30.47***	4.71**	2.15*
Total biomass (g)	37.99***	4.35**	1.56*
RMF	5.81***	24.60***	2.72**
Height (cm)	43.44***	24.89***	1.30
# of Tillers	5.09**	35.06***	4.43***
# of Flowers	288.11***	450.60***	7.34
% Green leaves	100.15***	39.54***	8.47***
Root length (m)	92.69***	14.34***	0.88
Root diameter (mm)	3.76*	28.74***	0.75
SRL (cm mg <sup>-1</sup> )	2.21	25.96***	4.39***
Root tissue density (g cm <sup>-3</sup> )	6.11***	7.60***	2.24
SLA (m <sup>2</sup> kg <sup>-1</sup> )	12.15***	54.01***	11.83***
TLP (MPa)	51.30***	12.09***	1.79
Midday $\psi$ (MPa)	55.16***	31.96***	14.06***

RMF root mass fraction, SRL specific root length, SLA specific leaf area, TLP turgor loss point,  $\psi$  leaf water potential

Values are F-statistics and asterisks denote statistical significance (\*\*\* $p$  < 0.001; \*\* $p$  < 0.01; \* $p$  < 0.05). For the # of Flowers, values represent Chi square test statistics from a Poisson regression (glm function)



**Fig. 2** Biplot of the principal component analysis explaining a total of 73% of variation in morphological traits and biomass across all pots (each point represents a pot). Different colors and shapes represent different species and treatments, respectively. The 1<sup>st</sup> principal component is primarily negatively associated with biomass production (above and belowground), root length production, height, and number of tillers. The 2<sup>nd</sup> principal component is primarily associated with specific root length (SRL), root diameter, root mass fraction (RMF), and belowground production. The box plots to the right show species and treatment separation on PC1 and PC2 with letters denoting

statistically significant differences following Kruskal–Wallis tests (Bonferroni-adjusted  $p$  values at  $\alpha=0.05$ ). Separation among treatments was observed along PC1, but not PC2, suggesting drier treatments resulted in less productive, shorter plants, with fewer tillers and less total root length. Differences among species were observed along both axes of variation, but mostly along PC2. Species separation along PC2 suggests xeric-distributed species (e.g., *B. eriopoda* and *B. gracilis*) had higher SRL and lower root diameter and RMF than mesic-distributed species

treatments based on mass production (shoot, root, and total), root length production, height, and number of tillers, and strong separation among species based on SRL, root diameter, RMF, and root mass production (Fig. 2).

### Production and morphological traits

The first two components of the PCA explained ~73% of total variation across individuals (Fig. 2). The first principal component (PC1), which explained 46.68% of variation, was primarily negatively associated with biomass production, root length production, height, and tiller density (Figure S1; Table S1). We observed clear treatment separation along this axis (Fig. 2; Kruskal–Wallis;  $p < 0.001$ ), with the only exception being that the two driest treatments were statistically similar to one another. Species differences along this

axis were less apparent, with only *B. gracilis* having statistically lower PC1 scores (i.e., being larger) than other species on average (Fig. 2; Kruskal–Wallis;  $p < 0.001$ ). The second principal component (PC2) explained 25.92% of variation and was primarily associated with SRL, root diameter, and RMF (Fig. 2). We observed no differences in PC2 scores based on treatment ( $p = 0.52$ ); however, we did observe clear species separation along this axis (Kruskal–Wallis;  $p < 0.001$ ). Notably, the more mesic-distributed species (*P. smithii* and *A. gerardii*) were clustered with high RMF and root diameter, and low SRL, and were not significantly different from each other. Individuals of *B. gracilis* and *B. eriopoda* were clustered with lower RMF and root diameter, yet high SRL.

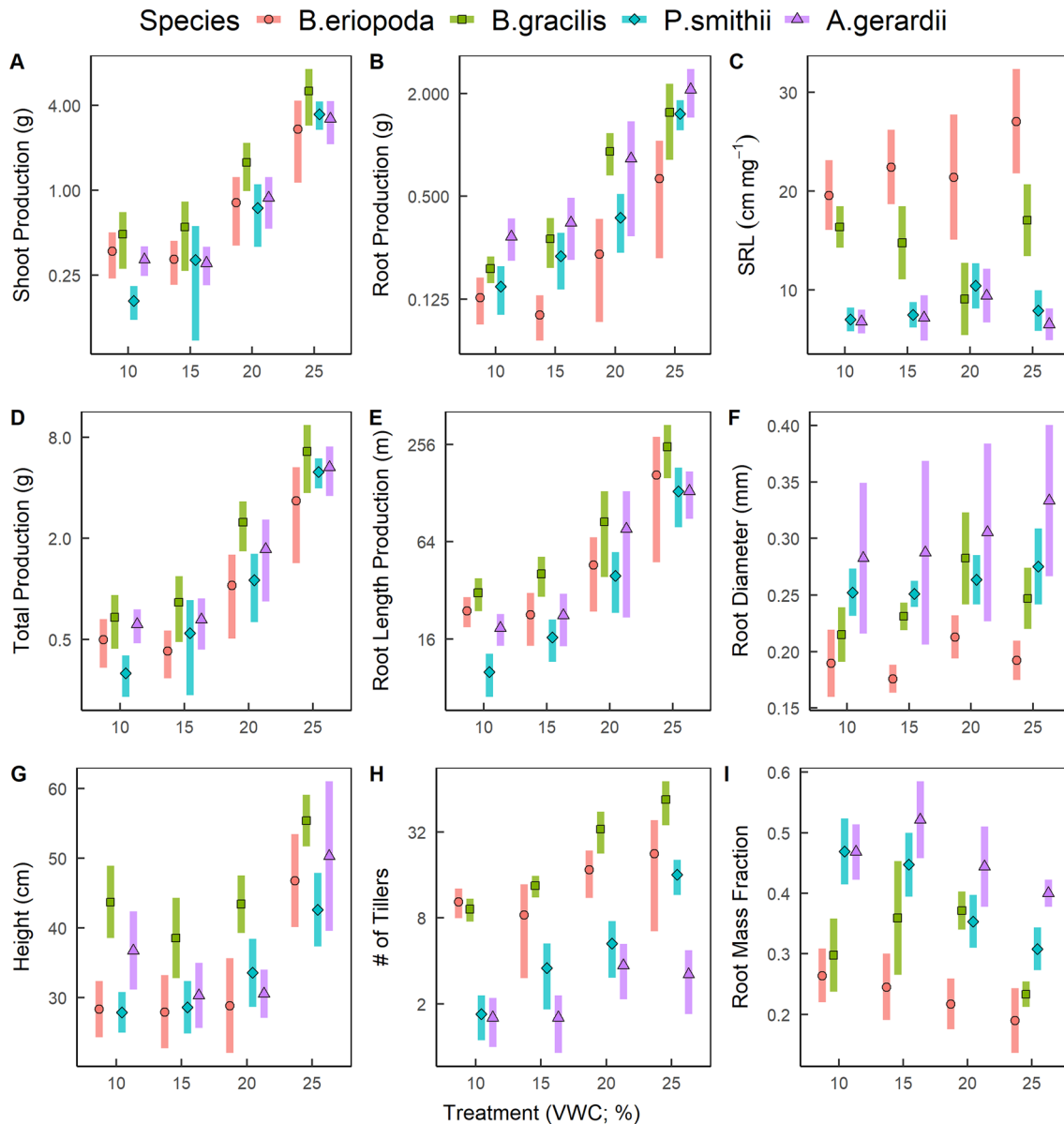
While our soil moisture dry-down treatments decreased aboveground, belowground, and total biomass production



of all study species (Fig. 3), there were no production differences between the two driest treatments for any species (Table S2), and there was no difference in root biomass of *B. gracilis* between the two wettest treatments (Table S2). Treatment effects on biomass allocation were species-specific. For example, there was no effect of treatment on root mass fraction (RMF) of *B. eriopoda*, while RMF of *P. smithii* increased in drier vs. wetter treatments (Fig. 3; Table S2). There was no consistent pattern of RMF among treatments for *A. gerardii* or *B. gracilis*. Within treatments,

we observed clear differences among species (Table S2). Importantly, root growth was not visibly pot-limited in any pot at the time of harvesting.

Treatments had a significant effect on plant height (Table 2) whereby all species grew taller in the wettest treatment (Fig. 3) vs. the other treatments (Table S3). In both wet and dry treatments, *B. gracilis* was tallest and *P. smithii* was shortest (Table S3). In general, higher soil moisture also led to greater production of tillers across all species (Fig. 3; Table S3). Flower production was also higher with



**Fig. 3** The response of biomass production and morphological traits to each treatment for each species. Shown are the variables that contributed most to PC1 (A, B, D, E, G, and H) and PC2 (B, C, F, and I) (see Fig. 2 and Figure S1). Error bars represent 95% confidence intervals around the mean. Significant differences among species for

each treatment, and among treatments for each species can be found in the supplementary materials. Variables include: shoot mass production, root mass production, total mass production, root mass fraction, root length production, root diameter, specific root length (SRL), height, and the number of tillers

higher soil moisture, but this effect was species-specific. For example, *B. gracilis* produced more flowers than any other species and produced more flowers with each increase in soil moisture, *A. gerardii* only produced flowers in the wettest treatment, and *P. smithii* did not produce flowers in any treatment (Table S3).

We observed clear treatment effects on leaf production (Table 2), with all species having a higher proportion of green leaves at higher soil moisture levels (Table S3). In wet and dry conditions, *B. eriopoda* produced fewer green leaves than any other species (Table S3). We observed lower SLA at lower soil moisture levels only for *B. gracilis* and *A. gerardii* (Table S3). In the wettest treatment, *A. gerardii* had higher SLA than all other species, while *B. gracilis* had the lowest SLA in the driest treatment (Table S3).

Root length production was higher with higher soil moisture for all species (Fig. 3; Table S4). Root length production did not differ by species under wetter conditions, but *P. smithii* had significantly lower root length production in the driest treatment (Table S4). In contrast, root diameter and SRL were not responsive to soil moisture (Table S4). We observed clear species differences in root diameter, with both *A. gerardii* and *P. smithii* producing thicker roots than *B. eriopoda* in both the driest and wettest treatments (Table S4). Additionally, SRL was highest for *B. eriopoda* and *B. gracilis* and lowest for *A. gerardii* and *P. smithii* (Table S4). Finally, root tissue density was generally higher for *A. gerardii* and *P. smithii* compared to the two *Bouteloua* species (Table S4).

### Leaf hydraulics

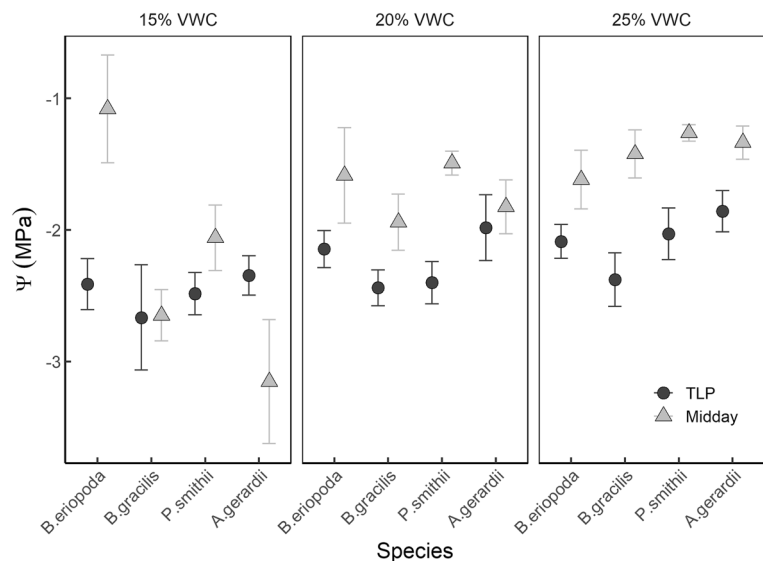
All four species exhibited osmotic adjustment and corresponding declines in leaf turgor loss point as well as lower

midday  $\psi_{leaf}$  in drier conditions (Fig. 4; Table S5). Notably,  $\psi_{leaf}$  remained higher than TLP (often a proxy for stomatal closure) for *B. eriopoda* and *P. smithii* in all treatments, yet dropped to within or below the 95% confidence interval of TLP for *A. gerardii* and *B. gracilis* in the drier treatments (Fig. 4; Table S5). Due to leaf senescence, we were unable to assess  $\psi_{leaf}$  in the driest treatment. In well-watered conditions, *B. gracilis* had the lowest TLP, although species converged to a similar TLP under drier conditions (Table S5).

### Discussion

We explored the morphological and physiological responses of four dominant grass species to a gradient of soil moisture. Our study suggests that the plant traits which distinguish dominant species from each other (i.e., static traits) differ from those that are sensitive to variability in soil moisture. Overall, aboveground NPP of these species responded similarly to four different levels of soil moisture despite differences in species morphology, physiology, and habitat of origin. We identified a suite of morphological traits that distinguished the four species from one another, namely SRL, root diameter, and root mass fraction. Further, we found that these same traits were relatively unresponsive to soil moisture dry-down. Variables related to plant size (e.g., biomass, height, root length production, tiller density, and flower production) were strongly correlated with each other (Figure S2) and all declined in drier conditions, while biomass allocation belowground generally increased, albeit not consistently. Each species had lower TLP in drier treatments, as expected, although *B. eriopoda* was the only species that maintained high  $\psi_{leaf}$  in all soil moisture conditions. Taken together, these

**Fig. 4** The response of midday leaf water potential and leaf turgor loss point (TLP) to each treatment for each species. Error bars represent 95% confidence intervals around the mean. Too few leaves were produced in the driest treatment (10% VWC) for measurements of midday leaf water potential for *B. gracilis* and *P. smithii* (see Table S5). Significant differences among species at each treatment, and among treatments for each species can be found in the supplementary materials



results suggest root traits are key for distinguishing grass species from one another but may not respond strongly to soil moisture change, and that different suites of traits can lead to similar NPP responses to soil moisture dry-down (Forrestel et al. 2017).

Our data support previous studies which have demonstrated that grass biomass production is sensitive to water availability (Sala et al. 1988; Fay and Schultz 2009; Hoover et al. 2014b; Knapp et al. 2015; 2020; Carroll et al. 2021), and that aboveground and belowground biomass production can respond differently to altered water availability (Chou et al. 2008; Byrne et al. 2013; Wilcox et al. 2015, 2017; Post and Knapp 2020; Carroll et al. 2021, Slette et al. 2022b). However, we expected that *B. eriopoda* and *B. gracilis* would be less sensitive to altered water availability given their long-term exposure to water limitation (Grime 2000), but this was not the case. This was particularly surprising given that each species in our study was characterized by different traits and thus might be expected to respond to their environment differently (Suding et al. 2008). For example, the two species from more xeric habitats, *B. eriopoda* and *B. gracilis*, both invested heavily in tiller production and invested proportionally less biomass belowground (low RMF) compared to the species from more mesic habitats. However, *B. eriopoda* senesced a majority of its leaves in drier treatments and maintained high relative water status of its remaining leaves (Fig. 4), a strategy characteristic of drought avoidance (Kooyers 2015), while *B. gracilis* maintained leaf production and reduced its SLA, likely to avoid additional water loss, at least in moderately dry conditions (Fig. 4). The C<sub>3</sub> grass, *P. smithii*, also maintained high leaf production in drier treatments but had a different rooting strategy (low SRL and high root diameter) and invested in highly drought tolerant leaves that did not lose turgor in drier conditions (Fig. 4). Finally, *A. gerardii* produced relatively drought intolerant leaves yet had the greatest relative biomass investment in roots as well as the lowest SRL and highest root diameter (Fig. 3), traits that have been associated with high water uptake rates in other grasses (Bristiel et al. 2019). These differences demonstrate that different suites of plant traits can result in similar NPP responses to soil moisture, at least aboveground.

Notably, a suite of root traits (PC2) clearly differentiated species from one another, but these same traits did not respond strongly to soil moisture in our study and were not strongly associated with total or aboveground biomass production in our PCA. In other words, traits which distinguished species occupying drier vs. wetter habitat types did not distinguish individuals within a species growing in drier vs. wetter conditions in our study. Thus, our results suggest that these traits might be more useful in explaining long-term species distributions than short-term responses

to altered water availability (Sandel et al. 2010). It is possible that root traits might respond more strongly to altered water availability in the field, where there might be greater spatial heterogeneity in soil moisture and less restriction on root growth. However, our finding that the root traits we measured (e.g., root diameter and SRL) were relatively unresponsive to soil moisture dry-down is generally consistent with recent research demonstrating little impact of experimental drought on root traits under field conditions, including for *A. gerardii* (Slette et al. 2022a, b). This suggests that these might be “static” traits that distinguish among species but do not respond strongly to environmental changes (Suding et al. 2008). More research is needed to fully understand the roles of species and environmental context in determining root responses to climatic changes and their effect on key plant and ecosystem processes, especially in the field, where such measurements are difficult to make and are thus relatively rare (de Vries et al. 2016; Iversen et al. 2017; Garbowski et al. 2020; Freschet et al. 2021; Funk et al. 2021).

Contrary to our hypothesis that RMF would increase in dry conditions, only *P. smithii* consistently allocated more biomass belowground in drier conditions (Fig. 3). Theory suggests that higher proportional allocation belowground increases water uptake and is advantageous in dry conditions (Bloom et al. 1985; Chapin et al. 1987; Chou et al. 2008; Milchunas and Lauenroth 2001; Poorter et al. 2012); however, previous studies have demonstrated that RMF actually responds to changing water availability in a variety of ways (Garbowski et al. 2020), which is consistent with our finding of different species responding differently. This could be due to greater plasticity of RMF of some species than others, or to factors other than water limiting growth of different species to different extents.

The biomass response of *P. smithii* to reduced soil moisture was similar to the three C<sub>4</sub> grass species, which was unexpected. The northern mixed grass prairie that *P. smithii* dominates is resistant to extreme drought (Carroll et al. 2021), as are many C<sub>3</sub>-dominated grasslands (Frank 2007). However, our results suggest that this resistance is likely not due to differences between this species and grasses that dominate more drought-sensitive regions (i.e., desert grasslands). Rather, the high resistance of northern mixed grass prairie likely reflects the tendency of drought to occur during summer months when the lifecycle of C<sub>3</sub> grasses is nearly complete (Knapp et al. 2020). Based on our measurements, a drought that reduced early spring soil moisture would lead to reduced NPP of *P. smithii* and likely total ecosystem NPP.

Notably, only *B. gracilis* differed from the other species along the axis associated with size, being relatively larger than the other three species. This was an unexpected result given that *B. gracilis* is the dominant species of the short-grass prairie and is much less productive than tallgrass



prairie species, such as *A. gerardii*, in the field. This may reflect different growth potentials of seedlings vs. tillers emerging from buds. Previous studies have observed limited seedling germination for *A. gerardii* in greenhouse conditions (Ocheltree et al. 2016), and *A. gerardii* biomass production in our study may be normal for individuals grown from seeds, though it is relatively less than the amount observed in the field, where most tillers arise from buds on overwintering rhizomes (Benson 2004). Finally, the comparatively strong growth response of *B. gracilis* to higher moisture availability is not surprising given this species' high sensitivity to moisture at any time of the season (Post and Knapp 2019), particularly as it was grown in the absence of grazing pressure and high vapor pressure deficits that occur in the shortgrass prairie.

The effect of treatment on SLA was species-specific, but largely met our expectations. We observed lower SLA with increasing water stress for only *B. gracilis* and *A. gerardii* (Table S3). Decreasing SLA in response to water stress is a common strategy for reducing evaporative leaf surface area (Dwyer et al. 2014; Wellstein et al. 2017). Some species may not reduce SLA as soil moisture declines, but rather senesce leaves entirely to avoid water loss (Volaire and Norton 2006)—a response we observed across all four species, but particularly the  $C_4$  grasses (Table S3). Shifts in SLA of herbaceous plants can also be driven by dry weight adjustments, through altered structural components (Meziane and Shipley 1999) and/or non-structural investments in solutes, which accumulate in cells during drought to avoid turgor loss (Bartlett et al. 2012).

Osmotic adjustment is common across many grasses as a mechanism for tolerating dehydration (Knapp 1984; da Silva and Arrabaca 2004; Májeková et al. 2019). We found that each species reduced their osmotic potential and TLP in drier conditions (Fig. 4). Interestingly, however, not all species experienced reduced  $\psi_{leaf}$  in drier conditions. Specifically, *B. eriopoda* maintained constant  $\psi_{leaf}$  (or even increased  $\psi_{leaf}$ ) as soil moisture declined (Fig. 4). Species that maintain high  $\psi_{leaf}$  in dry conditions tend to have tight stomatal regulation of leaf hydration status (Martínez-Vilalta and Garcia-Forner, 2017). We did not measure stomatal conductance or diurnal variation in  $\psi_{leaf}$  which would have allowed us to make this conclusion regarding the stomatal strategy of *B. eriopoda*. However, in the warm desert grasslands that *B. eriopoda* dominates, grass NPP is largely determined by pulses in soil moisture from monsoon rains following long dry spells (Muldavin et al. 2008). A drought avoidant stomatal strategy, coupled with drought avoidant root traits that *B. eriopoda* exhibits (Fig. 3), would likely be adaptive for long periods without rainfall. Similarly, *P. smithii* maintained turgor in drier conditions (i.e.,  $\psi_{leaf}$  above the 95% CI of TLP), which corresponded with a large proportion of its leaves staying

green (Table S3). Whether or not these divergent strategies impact plant fitness depends on plant survival following drought (Norton et al. 2016), which was not assessed in this study and warrants further investigation.

## Conclusions

Dominant species responses to soil moisture change will have important consequences for grassland ecosystem responses to climate change across the U.S. Great Plains (Smith et al. 2020). This region is expected to experience more extreme droughts and larger storms due to climate change (IPCC 2021), with evidence that this is already occurring (Williams et al. 2022). We found that four prairie grass species (each one dominant in a different ecosystem type) possess unique trait syndromes related to root morphology and leaf hydraulics. Because root traits were critical for distinguishing dominant species from one another in our study, and because species-specific root trait measurements are relatively rare (Griffin-Nolan et al. 2018; Garbowski et al. 2020), measuring these should be a priority for future studies, especially field studies. Despite their trait differences, aboveground NPP of all four species responded similarly to a common gradient of soil moisture. Thus, our results suggest that different sets of plant traits do not necessarily translate into different production responses to soil moisture change.

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**Data availability** Data and relevant R code can be found in the supplementary information.

## Declarations

**Conflict of interest** The authors declare that they have no conflict of interest.

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