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Comparing water-related plant functional traits among dominant grasses of the Colorado Plateau: Implications for drought resistance

David L. Hoover · Kelly Koriakin · Johanne Albrigtsen · Troy Ocheltree

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Abstract
Background and aims Water is the primary limiting factor for plants in drylands, which are projected to become even drier with climate change. Plant functional traits related to water influences individual performance, community composition, and can provide insight into which species will be most vulnerable to drought.
Methods Here, we used a trait-based approach to examine key water-related traits of five perennial grasses of the Colorado Plateau, with the goals of identifying functional trait syndromes, and assessing vulnerability to drought. We examined 14 traits including hydraulic, above- and belowground biomass, and morphology, then assessed how these traits varied by species, and photosynthetic pathway.
Results Individual water-related traits varied widely, but did not consistently vary by photosynthetic pathway. We identified three unique functional trait syndromes that could be classified as either conservative or non-conservative with regard to water use.
Conclusions Variation in water-related traits may be key to the coexistence of species in drylands, but there is uncertainty as which traits or functional trait syndromes will be most vulnerable to changes in climate. Based on the traits examined here, and forecast changes in climate for the region, we predict that the cool-season, C_3 grasses will be most vulnerable in this drying, more drought-prone region.

Keywords Drylands · Hydraulic · Morphology · Roots · Aboveground · Belowground

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D. L. Hoover (✉)
Rangeland Resources & Systems Research Unit, U.S. Department of Agriculture, Agricultural Research Service, Fort Collins, CO, USA
e-mail: David.Hoover@usda.gov

K. Koriakin
Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, FL, USA

J. Albrigtsen
Department of Ecology & Evolutionary Biology, University of Colorado, Boulder, CO, USA

T. Ocheltree
Department of Forest & Rangeland Stewardship, Colorado State University, Fort Collins, CO, USA

Introduction

Water availability is the one of the primary limiting factors to growth and survival of terrestrial plants, and in no environment is water more limiting than in drylands (Safriel and Adeel 2005; Aschehoug et al. 2016). Global climate models predict an increase in temperature, aridity, and the frequency and magnitude of droughts, all of which will exacerbate water limitations (IPCC 2013). Such changes in water availability in drylands will likely alter plant community composition and the critical ecosystem functions they provide (Maestre et al. 2016). Thus, understanding which species are most vulnerable to drought (e.g. low drought resistance), is key to predicting ecological impacts of climate change in drylands.

Functional traits related to water in plants reflect evolutionary history, and influence individual performance, community composition, ecosystem function, and provide insight into which plants will most likely be affected by changes in water availability (Reich 2014). In many dryland regions, stable coexistence of species within a plant community is due to variation in the functional traits, which can lead to spatial and temporal niche partitioning (Schwinning and Ehleringer 2001; Silvertown et al. 2015; Butterfield et al. 2017). Variation in water-related functional traits may include: 1) occupying unique soil moisture regimes, 2) varied recruitment patterns, and 3) different acquisition strategies (e.g. rooting depth, phenology; Silvertown et al. 2015). Therefore, assessing variation in such traits may provide key insights into evolutionary strategies and help identify which species are most vulnerable to drought.

Plant species occupying a given hydrological niche are predicted to coordinate physiological, hydraulic, and morphological traits (Reich 2014; Silvertown et al. 2015). However, tradeoffs exist, leading to functional trait syndromes, such as fast growing species with resource-acquisitive traits, or slow growing species with resource-conservative traits (Fort et al. 2013; Reich 2014). The "safety vs efficiency" tradeoff suggests that plants can either have high rates of hydraulic conductance, which supports high growth rates but are prone to hydraulic failure (cavitation), or low rates of hydraulic conductance, with low growth rates but high resistance to cavitation (Manzoni et al. 2013). Thus species with resource-acquisitive trait syndromes may be more vulnerable to water stress and mortality when conditions are dry than those with resource-conservative trait syndromes. It is hypothesized that these syndromes arise from selection along trait tradeoffs, resulting in coordination among above- and belowground traits (Reich 2014).

Plant functional types (PFTs) aggregate plant species into different classes based on particular traits that differentiate in terms of functional responses to the environment (Verheijen et al. 2016). PFTs are defined using many classes and combinations of classes including: photosynthetic pathway (C_3 vs C_4), growth form (grass, shrub, tree), and life history (annual, perennial). For example, differences in photosynthetic pathways suggest that C_4 plants should have higher drought tolerance than C_3 plants, due to higher water use efficiencies and differences in growth and allocation patterns (Pearcy and Ehleringer 1984; Sage 2004; Atkinson et al. 2012). Much like traits or functional trait syndromes, classifying species into PFTs makes predicting responses to environmental change simpler. However, PFTs are often broad classifications, and include multiple functional trait syndromes (or plant strategies), which may be insufficient to capture functional differences (Verheijen et al. 2016). Therefore it is important to use a trait-based approach to identify potential vulnerabilities of plant species to drought in drylands.

The Colorado Plateau of the southwestern US, is predicted to become hotter and drier with climate change (Seager et al. 2007; USGCRP 2017). The unique ecohydrology of this semi-arid dryland allows for mixed communities of shrubs, forbs, and perennial grasses, which may be differentially impacted by increased water limitations (Munson et al. 2011; Gremer et al. 2015; Hoover et al. 2015, 2017; Witwicki et al. 2016; Thoma et al. 2018). Perennial grasses with C_3 and C_4 photosynthesis co-occur in this region and even overlap phenologically for much of the year. Although cool, wet springs are ideal growing times for C_3 grasses, C_4 grasses often initiate growth and can complete all phenological stages during that period (Comstock and Ehleringer 1992). Conversely, if monsoons deliver sufficient moisture during the hot summer, both grass types can be active, despite hotter conditions often favoring C_4 grasses (Comstock and Ehleringer 1992; Schwinning et al. 2008). Climate projects for this region suggest that water availability will decrease due to increases in temperature and changes in precipitation (Seager et al. 2007; IPCC 2013; USGCRP 2017). Increased droughts due to hotter summers and reduced cool-season precipitation may have large impacts on grasses in this region. Indeed, recent observations and experiments suggest that both C_3 and C_4 grasses may decline with continued warming and more frequent drought (Munson et al. 2011; Hoover et al. 2015; Witwicki et al. 2016). However, uncertainty remains if such classifications based on photosynthetic pathway alone is sufficient to predict responses to drought.

Here, using a trait-based approach, we examined key hydraulic, biomass, and morphological traits of five dominant perennial grass species of the Colorado

Plateau to identify water-related functional trait syndromes and identify species vulnerable to drought. This research addressed three questions: 1) How do the water-related traits vary by species and photosynthetic pathway? 2) Is there evidence for unique trait syndromes? and 3) What are the implications for drought vulnerability? To accomplish this, we focused on two general types of traits. First, we examined hydraulic traits, because they are mechanistically linked to water transport and provide insights into plant responses to changes in water availability (Griffin-Nolan et al. 2018). Second, we examined above- and belowground biomass and morphological traits to identify allocation patterns.

Methods

Site description

The study was conducted on the Colorado Plateau in southeastern Utah, near Canyonlands National Park. The climate is continental with warm, dry summers, cool winters, low precipitation falling evenly throughout the year (221 mm $yr.^{-1}$; Gremer et al. 2015), and highly variable summer monsoons (Comstock and Ehleringer 1992). The study site (~3.2 ha) was located on deep (>1.5 m) loamy fine sand soils with little spatial variability in soil texture. The area had a history of light winter cattle grazing prior to 2015 when a fence was added. The plant community consisted of shrubs, forbs, and five perennial grass species; two with C_3 (cool-season) and three with C_4 (warm-season) photosynthetic pathways (Table 1). All samples were collected from seven 5 × 10 m blocks, with individuals of each species paired within a block to be morphologically similar. Sample collection occurred in May and June of 2016, which was preceded by a period of near-average cool-season precipitation (December – May 2016 = 86.6 mm; long-term mean = 102.0 mm; Hoover et al. 2015). During sampling, average soil moisture from 5 to 30 cm was 13.0% volumetric water content, slightly below field capacity (15.3% volumetric water content; Saxton et al. 1986).

Hydraulic trait measurements

Pressure volume curves were conducted on 7 individuals per species collected from each block. Whole tillers of individuals were dug up and immediately placed in 50 ml tubes of deionized (DI) water and kept cool in the shade until they were transported back to the lab. In the lab, stems were cut under DI water and placed in vials overnight in the dark to fully rehydrate. The next day, each sample was freshly cut under water, the leaf surface was then dried, the sample was weighed immediately, and water potential was measured with a Scholander-type pressure chamber (PMS Instruments, Albany, OR, USA). The leaf surface was then placed on lab bench to dry in order to generate a range of leaf water potential values. Measurements of leaf water potential and leaf weight were repeated and continued at ~0.3 MPa increments to −3.25 to −3.75 MPa. Following this, the leaf was rehydrated, scanned on a flatbed scanner and analyzed for leaf area (Image J software; National Institutes of Health, Bethesda, MD, USA). The leaf was then dried for 24 h at 60 °C and reweighed. Leaf dry matter content (LDMC) was calculated as the oven-dried mass of the leaf, divided by its saturated fresh mass. Pressure volume curves (relative water content vs. leaf water potential), were generated and any points that were indicative of a plateau effect removed and then used to calculate the turgor loss point (Π_{TLP}), osmotic potential at full turgor (Π_o), apoplastic water fraction, and leaf capacitance at full turgor (C_{FT}; normalized by leaf area; Bartlett et al. 2012a). Because we utilized rehydrated tissue for our pressure volume curves, it is likely that our values are slightly less negative than if we used partially dehydrated tissues (Kubiske and Abrams 1991; Bartlett et al. 2012b). Despite this offset, the ranking of species should not change and can be used for categorizing species by drought tolerance traits.

Hydraulic conductivity (K_{leaf}) values were calculated using the rehydration by relaxation technique (Ocheltree et al. 2016). Within each of the 7 blocks, 6–9 tillers were collected for each species, placed in 50 ml tube of DI water, and kept cool and in the shade. Back in the lab, tillers were recut under degassed DI water and placed in the dark overnight for rehydration. The next day, tillers were placed on the lab bench and allowed to dry for varying durations. Prior to measurement, each tiller was placed in a sealed bag in the dark for 15 min to allow water potentials to equilibrate. For each tiller, leaf water potentials were measured on adjacent leaves, which were assumed to be hydraulically equivalent (Ocheltree et al. 2016). The first leaf was cut and measured for pre-rehydration leaf water potential. The second leaf was cut under degassed DI water and allowed to rehydrate 30–120 s, depending on hydration status,

Table 1 Grasses used in this study

Species	*Achnatherum hymenoides*	*Hesperostipa comata*	*Sporobolus spp.*	*Aristida purpurea*	*Pleuraphis jamesii*
					
Common name	Indian Ricegrass	Needle and Thread		Purple Three-Awn	James' Galleta grass
Photosynthetic pathway	C_3	C_3	C_4	C_4	C_4
Season	Cool-season	Cool-season	Warm-season	Warm-season	Warm-season
Growth form	Bunchgrass	Bunchgrass	Bunchgrass	Bunchgrass	Rhizomatous

cut again, and placed in a bag with a moist towel to equilibrate for 15 min. Following this, post-rehydration leaf water potential was measured. K_{leaf} was calculated using the following equation:

$$K_{leaf} = \frac{C_{FT}\ln\left[\frac{\Psi_0}{\Psi_f}\right]}{t} \qquad (1)$$

Where C_{FT} is the leaf capacitance at full turgor (calculated from pressure volume curves), Ψ_0 is the pre-rehydration, Ψ_f is the post-rehydration leaf water potentials, and t is the rehydration time. Saturated hydraulic conductivity (K_{sat}) was calculated by taking the mean of the five highest K_{leaf} that occurred above the turgor loss point.

Biomass and morphological traits measurements

As with the hydraulic traits, one individual of each species were sampled from 7 blocks for the biomass and morphological traits. Basal circumference, height, length and width were measured on each individual and used to estimate the plant volume (calculated using the volume of a conical frustum). Aboveground biomass was clipped at the surface, and all previously dead litter was removed. Belowground biomass was collected by carefully extracting each root throughout the soil profile. The deep sandy soils and low belowground biomass made whole root system excavation possible. If a root was broken during excavation, we continued to excavate it until its terminus. For each individual, we measured the maximum rooting depth and one-way lateral spread of the deepest and longest roots, respectively. Following excavation, belowground biomass was washed in a 1 mm sieve, roots were separated from the crown or rhizome (depending on species), dead roots were removed (based on color and structure) and live roots were preserved in a 50:50 mixture of ethanol and DI water. Roots were imaged within several days on a Cannon CanoScan 9000F MarkII photo scanner and analyzed using WinRHIZO Regular software (Regent Instruments, Quebec, ON, Canada). After processing, all plant materials were dried in at 60 °C for 48 h and weighed.

Statistical analyses

Hydraulic, biomass, and morphological traits were first checked for normality, and those not fitting a normal distribution (aboveground volume, root:shoot), were log-transformed prior to analysis. Each of the 14 traits were analyzed using a one-way ANOVA with species as a main effect (function 'aov', R version 3.3.2, R Foundation for Statistical Computing, Vienna, Austria). Tukey-adjusted pairwise comparisons were made for traits with significant main effects ($P < 0.05$) to test for differences among the grass species (package 'lsmeans', R version 3.3.2, R Foundation for Statistical Computing, Vienna, Austria). We performed a canonical discriminant analysis (CDA) using the package 'candisc' (R version 3.3.2, R Foundation for Statistical Computing, Vienna, Austria) to assess the relationships among 10 biomass and morphological traits for the five species, and determine the species functional trait syndromes. We did not include the hydraulic traits in the CDA analysis because they were collected on different individuals than the biomass/morphological traits and our analysis.

Results

Hydraulic traits

We observed significant differences among the five grass species for the hydraulic traits LDMC ($P < 0.001$), Π_{TLP} ($P = 0.034$), and K_{sat} ($P < 0.001$), while Π_o was only marginally significant ($P = 0.068$; Fig.1; Table S1). These differences did not appear related to photosynthetic pathway. For example, the lowest (*A. purpurea*) and highest (*P. jamesii*) Π_{TLP} were both C_4 grasses, while the C_3 grasses were intermediate (Fig. 1). Although we did not use apoplastic water fraction to compare our species, values were within the range of expected values for grasses and forbs (Table S2). Likewise, K_{sat} for the C_3 grass, *A. hymenoides*, was nearly three-fold greater than the other C_3 grass, *H. comata*, while the C_4 grasses were intermediate. We examined the relationship among hydraulic traits and only found Π_{TLP} and Π_o were significantly correlated ($r = 0.93$; $P < 0.001$), which is not surprising given they are predicted from the same linear relationship.

Biomass and morphology traits

There were significant differences among the species for total biomass ($P < 0.001$), aboveground biomass ($P < 0.001$), and crown/rhizome biomass ($P = 0.005$), while root biomass was not significantly different ($P = 0.134$; Fig. 2; Table S3). Across the species, biomass varied widely: total biomass ranged from 6.3 g individual^{-1} (*P. jamesii*) to 32.9 g individual^{-1} (*A. hymenoides*), aboveground biomass ranged from 1.0 g individual^{-1} (*P. jamesii*) to 14.5 g individual^{-1} (*H. comata*), and crown/rhizome biomass ranged from 4.3 g individual^{-1} (*P. jamesii*) to 23.4 g individual^{-1} (*A. hymenoides*). The C_3 grasses tended to have higher non-root biomass than the C_4 grasses, particularly *P. jamesii*, which consistently had the lowest biomass values (Fig. 2). In terms of allocation, the C_4 grasses, especially *P. jamesii*, tended to have relatively more biomass belowground, as the root:shoot ratio was highest for the C_4 grasses and lowest for the C_3 grasses. To focus more on traits related to water acquisition, it should be noted that root:shoot values are only root biomass and did not include crown/rhizome biomass (Fig. 2).

Across the morphological traits we examined, there was substantial variability in the patterns of difference among the species. Much like the aboveground biomass traits, there were significant differences among the species in height ($P < 0.001$) and aboveground volume ($P < 0.001$), with the C_3 grasses being taller and tending to have higher volume than the C_4 grasses (Fig. 3; Table S4). Total root length significantly differed between the species ($P = 0.007$), while differences in specific root length were only marginally significant ($P = 0.079$; Fig. 3; Table S4). The pattern of both total and specific root length among the species differed from the aboveground morphological traits with the C_3 grass, *A. hymenoides* and C_4 grass, *P. jamesii* both the lowest values, while the others were higher (Fig. 3). While the species were not significantly different with regard to lateral root spread ($P = 0.127$), there were differences in rooting depth ($P = 0.006$). Unlike the trends in other morphological traits, the C_4 grass, *P. jamesii* had the deepest rooting depth (42 cm), while the C_3 grass, *A. hymenoidies* and C_4 grass, *Sporobolus spp.* had the shallowest rooting depth (21 and 26 cm, respectively; Fig. 3).

Canonical analysis

Using 10 biomass and morphological traits for the CDA analysis, we found the first two axes explained 94% of the variation among the species (Fig. 4). The C_3 grasses were distinct from the C_4 grasses and closely grouped together with traits such aboveground biomass and

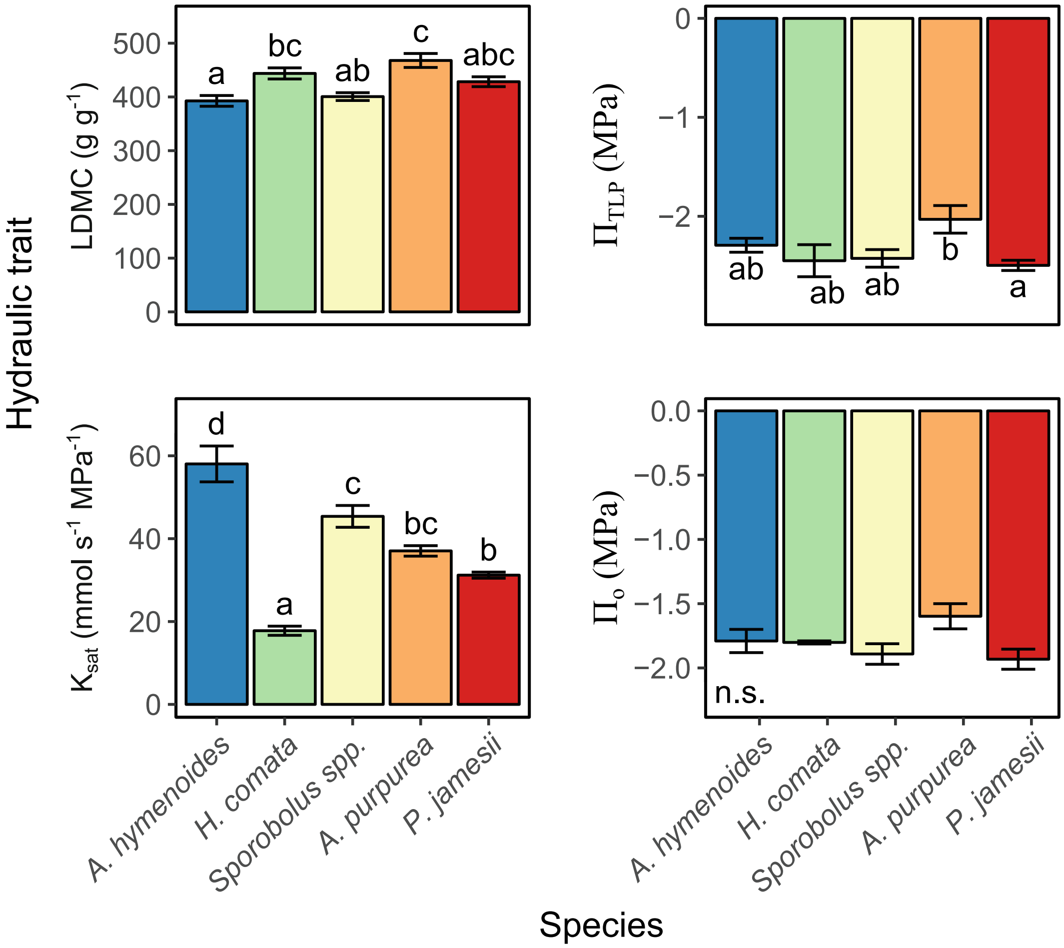

Fig. 1 Hydraulic traits of the five grasses including leaf dry matter content (LDMC), turgor loss point (Π_{TLP}), saturated hydraulic conductivity (K_{sat}) and osmotic potential at full turgor (Π_o). Bars represent means (± 1 SE), and letters denote significant differences among the species

volume, height and crown/rhizome biomass. There were two distinct groupings among the C_4 grasses. The two bunchgrasses, *Sporobolus spp.* and *A. purpurea* clustered together and were associated with root traits such as root biomass, specific root length and total root length (Fig. 4). The rhizomatous species, *P. jamesii* was distinct from the other grass species and was associated with high lateral root spread, deep roots and high root:shoot ratio (Fig. 4).

Discussion

Here, we used a trait-based approach to identify the unique water-related trait syndromes and assess drought vulnerability of five dominant perennial grass species of the Colorado Plateau. There were two main results. First, individual water-related traits varied among the grasses, but did not consistently vary by photosynthetic pathway. Second, when the traits were grouped together, we found evidence for three unique functional trait syndromes. These results suggest that while individual water-related traits can be decoupled from photosynthetic pathway, variation in the functional traits that lead to unique morphological trait syndromes may allow spatial and/or temporal niche partitioning and the coexistence of these five grasses.

Trait variation across species and photosynthetic pathway

Across the 14 water-related traits examined here, while there were many differences among the grasses species, only a few were distinctly separated by photosynthetic

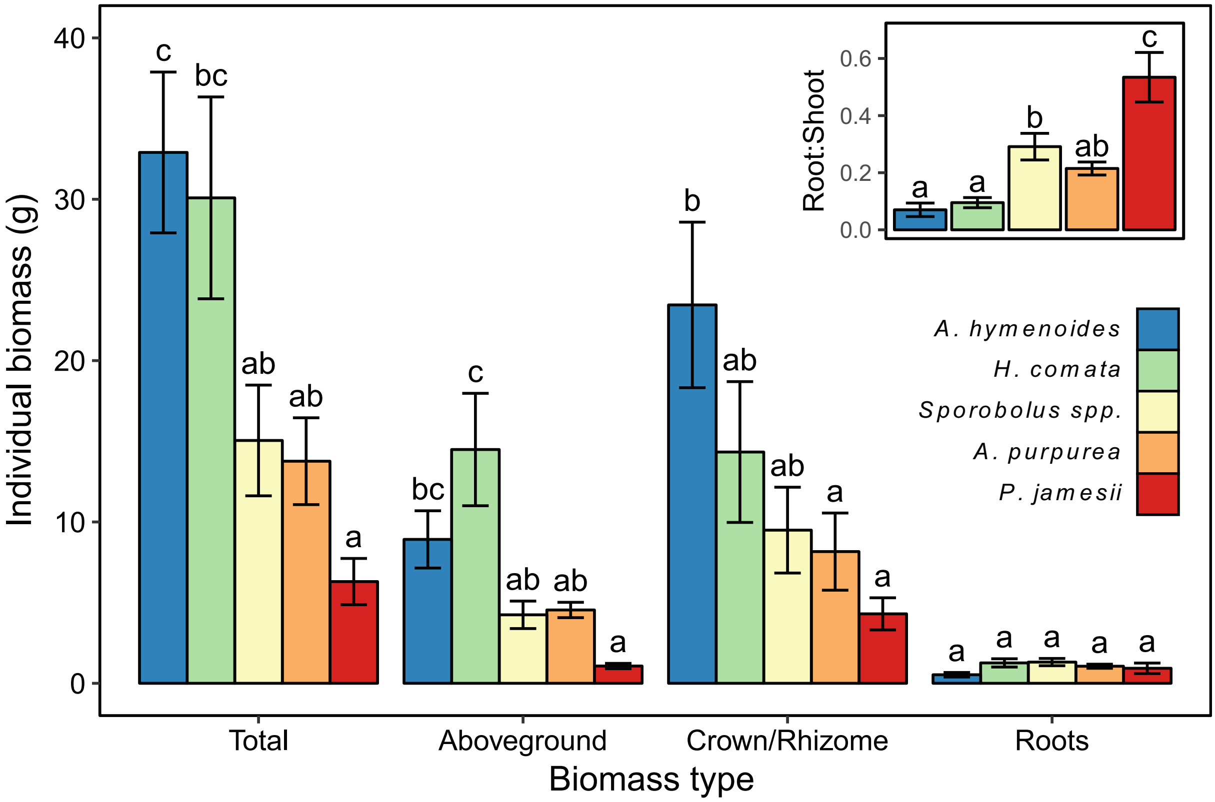

Fig. 2 Individual biomass for each grass species. Total biomass represents the sum of aboveground, crown/rhizome and roots. Root:shoot is the ratio of roots to aboveground biomass. Bars represent means (± 1 SE), and letters denote significant differences among the species

pathway. There was no clear divergence between the C_3 and C_4 grasses for either hydraulic traits (Fig. 1; Table S1), root biomass (Fig. 2; Table S3), or root morphology (Fig. 3; Table S4). The only traits differed by photosynthetic pathway were mostly related to allocation strategies: relative to the C_4 grasses, the C_3 grasses tended to allocate more biomass to non-root structures (e.g. aboveground biomass, crown/rhizome biomass, height; Figs. 2 and 3; Tables S3 & S4). In a recent review, Verheijen et al. (2016) found that trait-based misclassification of plant functional types were most common among closely related growth forms such as within graminoids and forbs, and suggest that such ambiguity could arise due to the functional significance of the traits chosen. Therefore, the lack of divergence in traits by photosynthetic pathway in the study may reflect the traits selected rather than convergence in function of C_3 and C_4 grasses.

K_{sat} of leaves has been correlated with photosynthetic rates across a range of species (Brodribb et al. 2007), but often this relationship does not appear among closely-related species (Gleason et al. 2016; Ocheltree et al. 2016). Hydraulic efficiency can minimize the decrease in water potential from the soil to sites of evaporation within leaves, and so may allow plants to maintain higher rates of stomatal conductance despite high aridity in some systems. Our limited set of species prevents us from determining physiological correlates with K_{sat}, but the large range of variability suggests it may be important to understanding different drought resistance strategies in this system.

Functional trait syndromes and regional ecohydrology

Overall, the water-related traits varied widely, both in terms of difference by species or photosynthetic pathway, and the absolute range in values. Such variation in functional traits may help drive niche partitioning and coexistence in water-limited ecosystems like the Colorado Plateau (Schwinning and Ehleringer 2001; Silvertown et al. 2015; Brum et al. 2017; Butterfield et al. 2017). Despite the large variation in the water-related traits we examined, three functional trait syndromes emerged including: (Syndrome 1) high

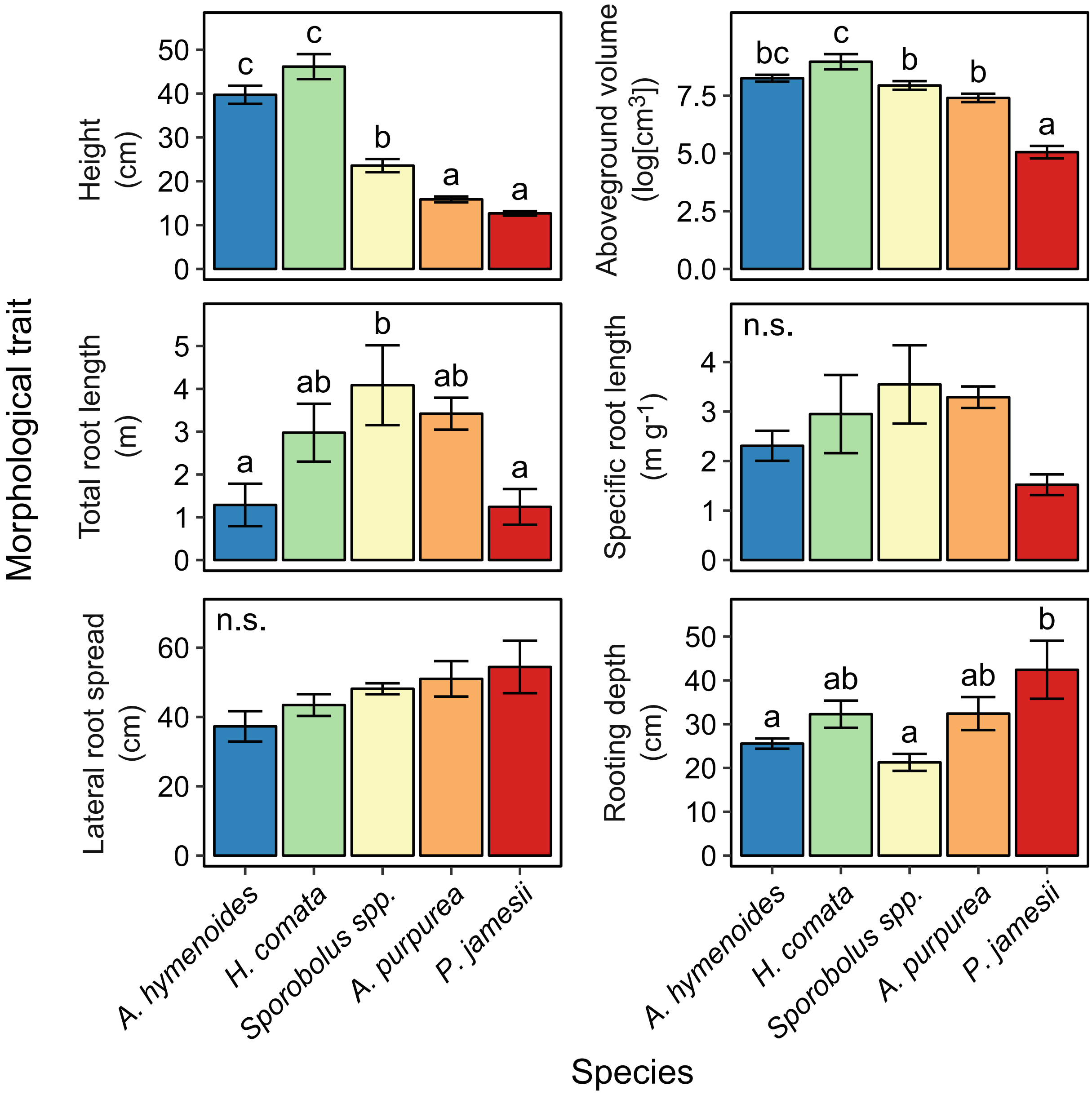

Fig. 3 Morphological traits for each of grass species. Bars represent means (± 1 SE), and letters denote significant differences among the species

aboveground biomass allocation and crown/rhizome biomass (*A. hymenoides*, *H. comata*), (Syndrome 2) dense roots (*Sporobolus spp.*, *A. purpurea*), and (Syndrome 3) high root:shoot ratio and root spread/depth (*H. jamesii*; Fig. 4). Here a pattern emerged that diverged along photosynthetic pathway; the C_3 grasses had high above ground biomass allocation (Syndrome 1) while the C_4 grasses devoted more resources belowground (Syndrome 2 & 3). One interpretation for this dichotomy is a trade-off between rapid growth and water stress tolerance, where the less conservative strategy of cool-season C_3 grasses is optimized for fast growth rates while the more conservative strategy of warm-season C_4 grasses is optimized for drought tolerance. Coordination among plant traits is predicted to occur if it results in a selective advantage at the whole-plant scale (Reich 2014). For example, Fort et al. (2013) observed evidence for coordination of above- and belowground traits with regard to drought

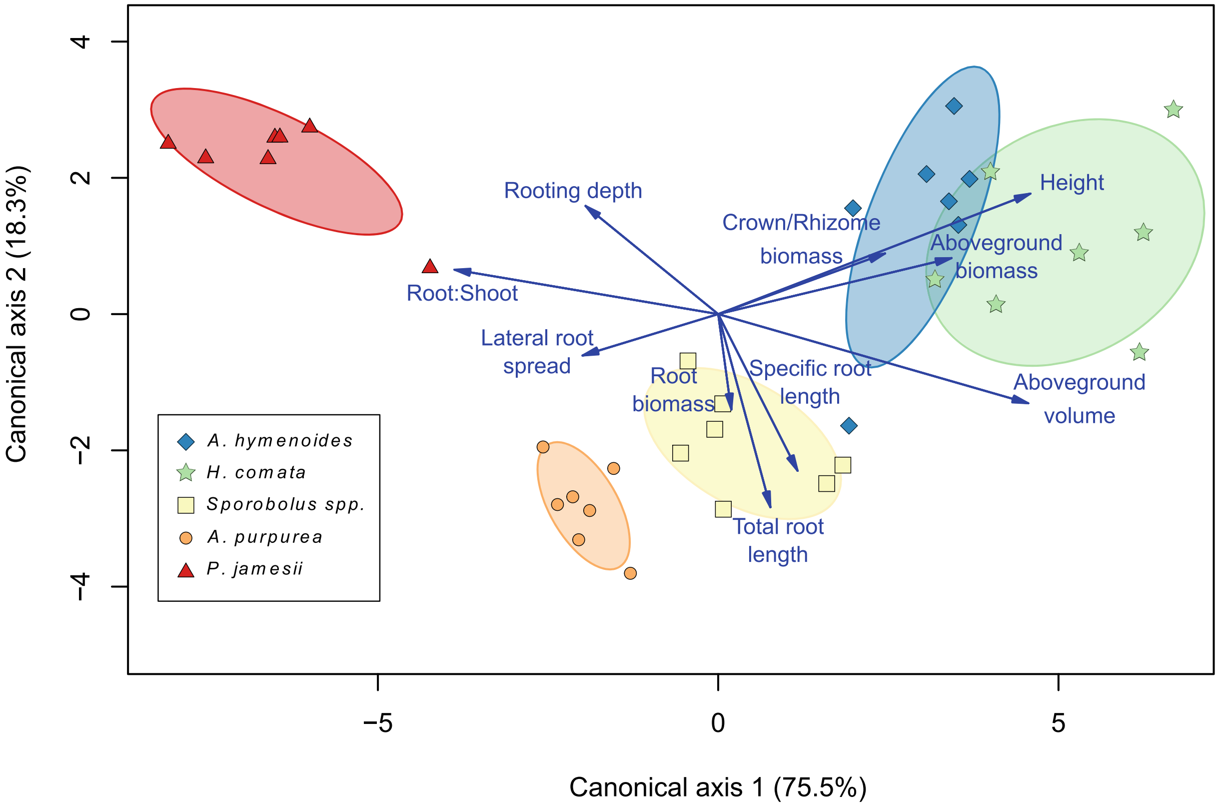

Fig. 4 Canonical discriminant analysis (CDA) for 10 biomass and morphological traits for the five grasses. Each point represents and individual (7 replicates per species). The first and second axes explained 94% of the variation among the grasses. Colors and symbols indicate species and ovals highlight the 95% confidence interval around the means for each species

tolerance in eleven grass species from a wide range of habitats and drought tolerance.

The patterns of above- and belowground trait coordination observed in this study may best be explained when placed in the context of the ecohydrology of the Colorado Plateau. During the winter, while cold temperatures limit plant activities, low rates of potential evapotranspiration permit spring recharge of soil moisture. Most plants, including both C_3 and C_4 grasses initiate growth in March when water is available and day time temperatures are above freezing (5–15 °C). Distinct dry periods and senescence are common early summer (June/July), followed by a second green-up in late summer (August/September) with monsoon rain (Comstock and Ehleringer 1992). The cool, wet springs are ideal growing conditions for C_3 grasses, but because the monsoons are highly variable, C_4 grasses are able to complete all phenological stages during that period, even though they delay growth initiation relative to the C_3 grasses (Comstock and Ehleringer 1992). Therefore, the quick growth, low root biomass syndrome of the C_3 grasses can take advantage of the transient, reliable water availability in the spring time. On the other hand the C_4 grasses have traits that allow for drought tolerance during the hot and dry period of the monsoon such as deep roots, high root density and low root:shoot ratios.

Implications for drought resistance

In the southwestern US, mean annual temperature has risen 0.9 °C over the past thirty years while mean annual precipitation has decreased by 0 to 15% (USGCRP 2017). Over the next century, water availability is projected decrease as the balance between precipitation and evaporation shifts the region to a more arid climate (Seager et al. 2007). While changes in mean annual precipitation remain uncertain, precipitation in the southwestern US is projected to decrease in the winter and spring (USGCRP 2017). In addition to changes in climate means, extreme events such as heat waves and droughts are also predicted to increase (IPCC 2013; USGCRP 2017), with the potential for unprecedented droughts, even exceeding the driest periods of the Medieval Climate Anomaly (1100–1300 CE; Cook et al. 2015).

While the variation in water-related traits in the Colorado Plateau grasses examined here may have permitted their current stable coexistence, such predicted changes in climate and water availability could result in species with traits poorly suited to the altered environmental conditions. Forecasts suggest the region will become hotter and drier with precipitation deficits in the winter and spring (Seager et al. 2007; USGCRP 2017). These changes may have the greatest impact on the C_3 grasses with traits that favor high growth rates during the cool, moist conditions of the spring. Indeed, experiments and observations suggest that cool-season C_3 grasses may have greater sensitivity to increases in temperature and decreases in precipitation (Munson et al. 2011; Hoover et al. 2015). Furthermore, the hydraulic traits examined here suggest that these conditions may be favorable to warm-season C_4 grasses, leading to shifts in grass community composition.

Changes in the abundance of grasses on the Colorado Plateau with increased water limitations may have significant ecological and economic impacts. For example, the balance of cool- and warm-season grasses is important to livestock production as ranchers rotate cattle to utilize the highly nutritious cool-season C_3 grasses in the spring (Witwicki et al. 2016). Therefore loss of a key cool-season species, such as *A. hymenoides*, with drier conditions may have large impacts on livestock production in the region. Loss in grass cover has also been linked to higher rates of wind erosion and dust transport (Munson et al. 2011). Increased dust production can have a wide range of effects including accelerated soil erosion in agriculture, increased snow albedo and runoff rates, higher non-accident mortality rates, and increased automobile accidents during dust storms (Painter et al. 2010; Crooks et al. 2016; Middleton 2017). Thus loss of these key grass species can have large impacts from local to the regional scales.

While this study focuses on resistance to drought, the future of the community will also be shaped by drought resilience mechanisms. Recent observations suggests that grasslands may have low resistance yet high resilience to drought; a characteristic that may provide long-term stability in the face of a variable and changing climate (Van Ruijven and Berendse 2010; Hoover et al. 2014; Yang et al. 2016; Stampfli et al. 2018; Stuart-Haëntjens et al. 2018). Reduced density or mortality of individuals due to drought may be compensated post-drought by recovery of extant individuals (via vegetative regrowth) or through seed recruitment (Gonzalez and Loreau 2009; Lloret et al. 2012; Silvertown et al. 2015). Thus while the cool-season C_3 grasses in this study may have low resistance to drought, they may possess traits related to drought resilience (e.g. high crown biomass or prolific seedbank), which provide long-term stability of this key functional group.

Summary

In this study, we observed wide variation in water-related traits of the dominant perennial grasses, which did not consistently differ by photosynthetic pathway. Such differences may be key to the coexistence of the species. Using these traits we identified three functional trait syndromes and assessed the vulnerability of these grasses to future climate. The cool-season C_3 grasses have traits with the least conservative water strategy and their growing season during the winter and spring is predicted to have the greatest decrease in water availability relative to the summer and fall. This portends changes in both community composition with the potential for large and long lasting ecological and economic impacts for the Colorado Plateau.

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