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Physiological drought tolerance and the structuring of tallgrass prairie assemblages

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Abstract. Drought is a defining characteristic of many grasslands worldwide. Yet we have little understanding of how drought structures grassland communities and the degree to which physiological drought tolerance advantages plants in grasslands. We characterized physiological drought tolerance (Ψ_{crit}) for a large number of species in a mesic grassland community (Konza Prairie, KS, USA). We then examined the relationships between Ψ_{crit} and a number of other key functional traits, and tested whether physiological tolerance of drought underlay success across a number of ecological contrasts—topographic position, burn frequency, and grazing—with 17 years of abundance data. Physiological drought tolerance of Konza species covered almost the full range known to plants globally. Consistently, physiologically drought-tolerant species had thin roots, while associations with other traits were inconsistent across functional groups. In this mesic grassland, physiological drought tolerance appears to increase the abundance of plants in xeric uplands, but does not in the mesic lowlands. Physiological drought tolerance did not alter species responses to changes in burning or grazing. In contrast to Ψ_{crit}, species with high root tissue density were more abundant in uplands and lowlands than species with low root tissue density largely irrespective of grazing or burning regimes. In all, drought appears to have a limited role in structuring the Konza plant community. As such, more severe or frequent droughts in the region would likely restructure the Konza plant community in ways that are currently not observable.

Key words: burning; drought tolerance; ecophysiology; functional traits; grazing; Konza Prairie.

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INTRODUCTION

The episodic nature of precipitation produces moisture stress at multiple scales, from decade-long reductions in precipitation, seasonal dry periods, and daily mid-day inductions of plant water stress (Weaver 1968, Karl and Koscielny 1982, Knapp 1985, Woodhouse and Overpeck 1998). Tropical and Mediterranean grasslands typically have annual dry seasons during which grasses senesce (Gibson 2009). Temperate grasslands are not characterized by a dry dormant season, but periodically experience years with low precipitation as well as soil moisture stress on shorter time scales (Gibson 2009). Across a wide variety of temperate grassland ecosystems, periods of low soil moisture, i.e., drought, reduce productivity (Frank and McNaughton 1992, Briggs and Knapp 1995, Ciais et al. 2005) and alter species abundance (Weaver 1968, Tilman and El Haddi 1992). With projected increases in temperature and reduced water availability during the growing season for temperate grasslands (Christensen et al. 2007), drought is likely to increase in importance as a driver of future grassland community structure.

To predict how grasslands will be structured by drought requires not only forecasts of future climates, but understanding of how drought currently structures communities. One inferential approach is to examine the relationships between species abundance and traits that confer tolerance of drought. Although there are a number of strategies associated with drought (McDowell et al. 2008, Craine 2009), places where soil moisture stress is most frequent and intense tend to be dominated by species that can photosynthesize at low plant water potentials without xylem cavitation (Pockman and Sperry 2000, Bhaskar and Ackerly 2006, Grime et al. 2008, McDowell et al. 2008). This physiological drought tolerance requires sclerification of vascular bundles and small vessel diameter to resist the physical stresses associated with low water potential (Hacke et al. 2001, Sperry et al. 2003). Indirectly, physiological drought tolerance is expected to be linked to other functional traits (Ackerly 2004). For example, stress-tolerant species should have low rates of gas exchange and low maximal growth rates due to inherent tradeoffs in xylem functioning (Grime et al. 1997, Reich et al. 2003*a*). Furthermore, physiologically drought tolerant species should, all other things equal, have higher leaf and root tissue density resulting from the requirement for increased cell wall investment (Cunningham et al. 1999). Thin leaves (Niinemets 2001) and high leaf angle (Ehleringer 1983, Medina et al. 1990, Craine et al. 2002) are also likely associated with drought tolerance.

Despite the potential of drought to structure temperate grassland communities and historic changes in communities, tests of the role of drought-associated traits in determining abundance in grasslands are rare. For example, at Konza Prairie, a North American tallgrass prairie, interannual variation in precipitation drives variation in productivity and flowering (Briggs and Knapp 1995, Nippert et al. 2006, Craine et al. 2010), but seasonal and spatial gradients result in low soil moisture availability even in years with above-average precipitation (Nippert et al. 2011). Topographic position, nutrient availability, fire, and grazing all strongly influence community structure at Konza (Collins et al. 1998, Towne et al. 2005, Spasojevic et al. 2010), but it is unknown whether drought also has a strong influence on community composition at Konza or whether these factors alter the importance of soil moisture stress. At Konza, leaf tissue density from field-collected plants consistently correlated with abundance (Craine and Towne 2010) across a number of ecological contrasts. High leaf tissue density could indicate greater drought tolerance, but also is known to be associated with success in low-nutrient environments (Craine et al. 2001) while providing resistance to herbivory (Wright and Illius 1995, Perez-Harguindeguy et al. 2003). In an irrigation experiment at Konza, dry soils favored species with low N concentrations and high leaf longevity, which is the opposite of geographic patterns where low-precipitation sites tend to be dominated by plants with higher leaf N concentrations and low leaf longevity (Sandel et al. 2010).

To better understand patterns of physiological drought tolerance among grassland species and the role it plays in determining abundance in a mesic grassland, we first measured physiological drought tolerance and a corresponding set of functional traits for a broad suite of grassland species present at a mesic prairie (Konza Prairie) in central North America. We then tested the ability of physiological drought tolerance, other individual traits, and correlated suites of traits to predict the abundance of species across a number of ecological contrasts in a tallgrass prairie. These included xeric uplands and mesic lowlands, frequently and infrequently burned areas, as well as grazed and ungrazed areas.

Regarding the suites of traits that might be associated with physiological drought tolerance, if physiological drought tolerance is dependent on additional allocation to cell walls, then physiologically drought-tolerant species should have high leaf and root tissue density and lower rates of gas exchange. Regarding the role of drought in determining abundance, if periodic or chronically low soil moisture structures the grassland plant communities and plants are reduced in abundance by the physical stresses associated with low soil moisture, then species with greater physiological drought tolerance should be more abundant. As topographic variation can alter plant responses to climate, the importance of drought tolerance is unlikely to be uniform across the landscape (Craine et al. 2010, Debinski et al. 2010). Shallow-soil uplands, burned areas, and ungrazed sites at Konza are the most likely to experience seasonal soil moisture stress (Knapp et al. 1993, Fahnestock and Knapp 1994, Blair 1997, Bremer et al. 2001, Nippert and Knapp 2007*b*) and therefore are the most likely to be dominated by physiologically drought tolerant species. Alternatively, if drought is not an important structuring factor for the grassland communities, or if drought is severe enough to cause mortality for even drought-tolerant species, there might be no relationship or even a negative relationship between physiological drought tolerance and abundance.

METHODS

Site description

Konza Prairie Biological Station is a 3487 ha native tallgrass prairie located in the Flint Hills of northeastern Kansas, USA (39°05′ N, 96°35′ W). The prairie landscape is dominated by a few species of warm-season grasses (*Andropogon gerardii, Sorghastrum nutans, Schizachyrium scoparium,* and *Panicum virgatum*) while cool-season grasses and a diverse suite of forbs comprise a large proportion of the rest of the plant community. Konza receives an average of 835 mm of precipitation annually, most of which (75%) falls during the growing season. Over the last century at Konza, mean annual precipitation regularly deviated from the long term mean by about 25% and reached values as high as 184% of the mean in the wettest year (1533 mm in 1951) and 47% in the driest year (392 mm in 1966). While the mean annual temperature for Konza is 13°C, the mean low for the year is −3°C in January and the mean high of 27°C occurs in July.

Plant cultivation

One hundred and twenty-one herbaceous tallgrass prairie species were chosen for this study. Species chosen for the experiment encompass a broad range of attributes. Phylogeny, life history, and seed availability were all considered during the selection process in order to best represent the floral diversity found on Konza. Seeds were obtained from a variety of sources, including the Kansas Native Plant Society, the National Plant Germplasm System, Chicago Botanic Garden–National Tallgrass Prairie Seed Bank, Taylor Seed Farms (White Cloud, KS), and local collection by the authors at Konza.

Propagules were germinated on damp filter paper in Petri plates at room temperature. Stratified seeds were stored on damp filter paper in a 5°C incubator for at least 30 days while those that required scarification were abraded with sandpaper before being germinated in appropriate conditions. Seedlings were transplanted to 164 mL plastic Cone-tainers (D-40, Stuewe and Sons, Inc. Corvalis, OR) containing standardized, untreated lowland soil from Konza (silty clay loam). Similar to previous experiments (Reich et al. 2003*b*), plants in containers were grown in a Conviron growth chamber (Model PGV 36, Controlled Environments Limited, Winnipeg, Manitoba) with 16-hour days at 25°C and light levels at 1200 μmol m^{-2} s^{-1}. Temperatures at night were held at 20°C. Plants were watered daily and treated with a commercial fertilizer (Miracle Grow 24-8-16 All Purpose Fertilizer) biweekly to eliminate nutrient stress. An average of 8 replicates of each species were maintained, with the level of replication varying from 1 to 24 plants.

Trait measurements

Plants were grown in the growth chamber for 8–12 weeks before data collection. Gas exchange was measured using a Li-6400 infra-red gas analyzer with red/blue LED light source and CO_2 injector (LICOR Biosciences, Lincoln, NE). Light intensity inside the cuvette was 2000 μmol m^{-2} s^{-1}, CO_2 concentration was 400 ppm, and relative humidity was 40%. Measurements were performed on the newest fully-expanded leaves and included maximum photosynthetic rate (A_{max}), stomatal conductance to vapor (g_s), and water use efficiency (WUE; A_{max}/transpiration rate).

Leaf thickness ($Thick_L$) was measured between secondary veins where applicable for 2–3 newly-expanded, mature leaves on each plant using digital calipers (Thermo Fisher Scientific Inc., Waltham, MA). Leaf angle ($Angle_L$) relative to horizontal was measured by averaging 3–5 protractor measurements per plant (Craine et al. 2001).

After 8–12 weeks, plants were divided into sets of 50 and were subjected to a dry-down period with daily monitoring using a steady-state diffusion porometer (Model SC-1, Decagon Devices, Inc., Pullman, WA). Stomatal conductance was recorded daily during dry-down until the conductance rate fell below 5% of the maximum. Following stomatal closure, non-senesced leaf tissue was collected and the hydrostatic pressure potential was measured using a Scholander pressure bomb (PMS Instrument Company, Albany, OR). This leaf pressure potential corresponding to stomatal closure is henceforth referred to as the species' critical water potential (Ψ_{crit}), and is used in the study as an index of physiological drought tolerance. A subset of the leaves was used to measure leaf area (LI-COR Leaf Area Meter, Model LI-3100) and subsequently oven dried and weighed to calculate specific leaf area (SLA).

Leaf tissue density (ρ_L), the ratio of leaf mass to leaf volume was calculated using leaf area and thickness. The remaining biomass was sorted to leaf or stem and dried at 60°C to determine total aboveground biomass (M_L). Roots were sorted into coarse (>2 mm) and fine roots. A representative sample of the fine roots was scanned into a digital root imaging program (Winrhizo; Regent Instruments, Inc., Nepean, Ontario, Canada) which calculated total root length, total root volume, and average root diameter by length. The remainder of the roots was oven dried, weighed, and used to calculate specific root length (SRL), root tissue density (ρ_R), average root diameter ($Diam_R$) and total root biomass (M_R).

Species abundance

As part of the long-term research at Konza, plant composition has been sampled twice annually (late May–June and mid-August–September) since 1983, to capture canopy cover for both early- and late-season species. Twenty watersheds were chosen (Craine and Towne 2010) to represent the six land-management treatments: two topographic positions within grazed and ungrazed watersheds with burn intervals of 1 or 20 years. In each watershed there were eight 50-m permanent transects. Half of the transects were located in shallow, rocky upland soil while the other half were located in deep, fertile lowland soil. Relative cover was sampled in five permanently-marked circular plots (10 m^2) that were evenly spaced along each transect. A modified Daubenmeier cover scale (Bailey and Poulton 1968) was used to visually estimate species cover (Craine and Towne 2010), which is used as the index of abundance here.

Average relative abundance in the watershed for each year was calculated by selecting the larger cover measurement for each species from the two sample periods and using the midpoint of the cover class to average across all upland or lowland plots in the watershed. We averaged across 17 years (1993–2009) to yield a single relative abundance value for each prairie species. Relative abundance for each watershed was combined across similar treatments to gain average values for each treatment. For example, abundance was averaged across all grazed watersheds to gain a single value of relative abundance for the grazing treatment that could be compared to the ungrazed treatment. This was done for grazed, ungrazed, annual burns (burned), 20 year burns (unburned), upland, and lowland treatments. These categories are referred to as contrasts. Finally, we averaged across all treatments to get a single average relative abundance value for each species.

Statistical analysis

Ten functional traits were chosen as the primary functional traits of interest. Encompassing tissue and whole plant morphology and physiology, these traits included root and leaf tissue density, average root diameter, leaf thickness, leaf angle, root mass, shoot mass, Ψ_{crit}, maximum photosynthetic rates and maximum conductance rates. The 10 traits were used in pairwise correlations and in principal component analyses performed on correlations (JMP 8.0.2, SAS Institute, Inc., Cary, NC). Principal component analysis was performed with these 10 traits for the entire species set and then for grasses alone and forbs alone. For the abundance measures, we only examined single-factor contrasts. After determining the average abundance of species for an ecological contrast, e.g., uplands or unburned watersheds, all abundance data were log-transformed to normalize abundance data distributions. We tested whether traits predicted the change in abundance of species across the ecological contrast, which was defined as the difference in log-transformed abundance for a species between the two contrasts. With the abundance data log-transformed, this difference represents the relative change in species abundance independent of its abundance in either contrast. To test which traits best predicted abundance, stepwise multiple linear regressions were performed for each contrast and the most parsimonious model was selected using AIC scores. We tested whether relationships between Ψ_{crit} and abundance in uplands and lowlands differed among years with a repeated measures ANOVA.

RESULTS

Trait relationships

Among species, Ψ_{crit} ranged from −1.1 MPa in *Tradescantia bracteata* to −8.9 MPa in *Bouteloua curtipendula*. Seven species had $\Psi_{crit} \geq -2.0$ MPa while 11 species had $\Psi_{crit} \leq -8.0$ MPa. The grasses that we measured were generally more physiologically tolerant of drought than forbs (−6.8 vs. −4.0 MPa, respectively; $P < 0.001$). Yet, there were several forbs that were as tolerant as the most tolerant grasses, e.g., *Salvia reflexa* ($\Psi_{crit} = -8.6$ MPa), and some grasses such as *Panicum virgatum* and *Eleusine indica* had low physiological drought tolerance (>−3.5 MPa). Annuals were not more drought tolerant than perennials ($P = 0.18$), nor were C_4 species more drought tolerant than C_3 species ($P = 0.32$). Among the other morphological traits, *Xanthium strumarium* had the least dense leaves (0.10 g cm^{-3}) while *Andropogon gerardii* had the most dense (0.86 g cm^{-3}). The thinnest leaves belonged to *Chloris verticillata* (0.08 mm) while *Silphium lacinatum* had the thickest (0.57 mm). Root tissue density (ρ_R) ranged from 0.11 g cm^{-3} in *Euphorbia marginata* to 0.58 g cm^{-3} in *Amorpha cansecens* while average root diameter varied from 0.09 mm (*Lepidium densiflorum*) to 0.45 mm (*Xanthium strumarium*).

Among the 10 main functional traits, 47% of the pairwise correlations were significant (Table 1). The strongest correlation was between the two gas exchange variables as species with high photosynthetic rates had the highest stomatal conductance ($r = 0.70$, $P < 0.001$). Overall, Ψ_{crit} correlated with 4 of the 9 other main functional traits. Species that were more physiologically tolerant of drought (lower Ψ_{crit}) had thin leaves ($r = 0.28$, $P < 0.001$) that were dense ($r = -0.37$, $P < 0.001$) and held at a high angle ($r = -0.39$, $P < 0.001$) as well as thin roots ($r = 0.54$, $P < 0.001$) (Fig. 1). Root tissue density was not directly correlated with Ψ_{crit} ($P = 0.09$), nor were the two gas exchange metrics or biomass amounts.

In the PCA of the 10 main functional traits, the first trait axis separated drought-tolerant species from drought-intolerant species (Table 2). Six traits contributed significantly to the axis, accounting for 28.3% of the total variation in all traits among all species explained by PCA. Species that were physiologically tolerant of drought had thin, dense leaves that were held at a high angle and thin, dense roots. For example, *Hesperostipa spartea* which continued stomatal conductance to −8.0 MPa had leaves that were 0.62 g cm^{-3} and only 0.12 mm thick. In contrast, *Asclepias speciosa* ceased stomatal conductance at −2.0 MPa. Its leaves had a density of only 0.27 g cm^{-3} and were 0.19 mm thick.

On average, grasses had a more drought-tolerant strategy than forbs ($P < 0.001$) and a simple dichotomy of species into grasses and forbs explained 50% of the variation in Axis 1 (Table 3). Neither photosynthetic pathway nor life history was associated with differences in Axis 1 (Table 3). With differences in grasses and forbs explaining a large proportion of the variation in Axis 1, multivariate analyses for the 10 main functional traits were run separately for the two groups. Although Ψ_{crit} was still associated with other functional traits for both grasses and forbs, root diameter and low rates of photosynthesis were the only traits that were consistently associated with Ψ_{crit} (Table 2). For forbs, physiologically drought tolerant species had thin, dense roots and low rates of gas exchange. For grasses, physiologically drought tolerant species had thin dense leaves held at a high angle, thin roots, and a low maximal rate of photosynthesis. Photosynthetic rate was not, however, correlated with physiological drought tolerance ($r = -0.01$, $P = 0.9$) nor was it associated with Ψ_{crit} in the broader principal component analysis.

Axis 2 reflected the correlation among species in gas exchange rates that were largely independent of drought-tolerance (Table 2). As seen in the bivariate relationships, species with high photosynthetic rates also had high rates of stomatal conductance and their leaves were held at a high angle. These species also had a higher fraction of root biomass than those low on the

Table 1. Pair-wise correlations and *P*-values for ten primary traits.

Trait	A_{max}	g_S	Ψ_{crit}	$Thick_L$	$Angle_L$	$Diam_R$	ρ_L	ρ_R	M_S	M_R
A_{max}		**0.001**	0.88	0.10	0.45	0.18	0.30	0.41	0.60	0.82
Gs	**0.70**		0.90	**0.001**	0.43	0.07	**0.02**	**<0.01**	**<0.001**	**0.02**
Ψ_{crit}	−0.01	0.01		**<0.01**	**<0.001**	**<0.001**	**<0.001**	0.09	0.23	0.43
$Thick_L$	0.15	**0.30**	**0.28**		0.72	**<0.001**	**<0.001**	**<0.01**	0.19	0.24
$Angle_L$	0.07	0.08	**−0.39**	−0.04		**<0.01**	0.21	0.74	0.18	0.08
$Diam_R$	0.12	0.17	**0.54**	**0.42**	**−0.26**		**<0.001**	**<0.001**	**<0.01**	0.62
ρ_L	−0.10	**−0.22**	**−0.37**	**−0.53**	0.13	**−0.44**		**0.05**	**<0.001**	0.61
ρ_R	−0.08	**−0.26**	−0.16	**−0.24**	0.03	**−0.30**	**0.18**		0.83	0.11
M_S	−0.05	**−0.33**	−0.12	−0.12	−0.13	**−0.25**	**0.36**	0.02		**<0.001**
M_R	−0.02	**−0.21**	−0.08	0.11	0.17	−0.05	0.05	0.15	**0.45**	

Note: *P*-values in the upper right and correlation coefficients in the lower left are bolded for statistical significance ($\alpha = 0.05$).

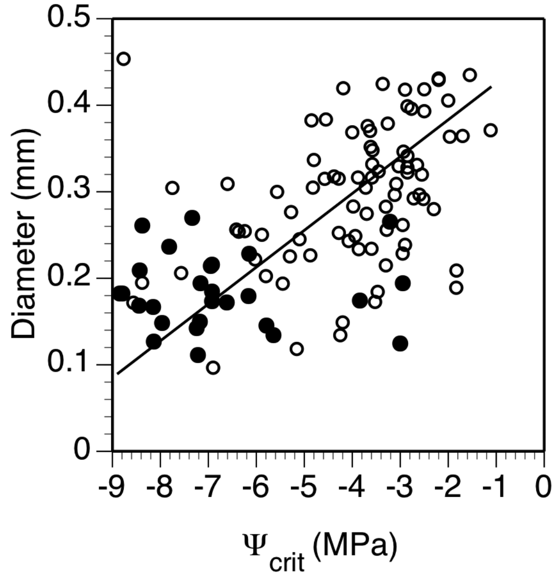

Fig. 1. Bivariate relationships between physiological drought tolerance (Ψ_{crit}) and root diameter ($r = 0.54$, $P < 0.001$). Closed circles are grasses; open circles forbs. Outlier forb is *Verbesina alterniflora*.

axis ($r = 0.32$, $P < 0.001$). On average forbs scored lower than grasses on Axis 2, which reflects their lower rates of gas exchange (Table 3). The third axis primarily separated species based on their size at the end of the experiment and only explained 3.7% more variation than expected by chance (Table 2).

Species abundance

Species that were physiologically tolerant of drought were not more abundant overall at Konza ($P = 0.12$; Fig. 2). Physiologically drought-tolerant species were more abundant in uplands ($y = -2.20 - 0.22 \times \Psi_{crit}$; $r^2 = 0.12$, $P = 0.008$) and infrequently burned areas ($y = -2.55 - 0.19 \times \Psi_{crit}$; $r^2 = 0.09$, $P = 0.01$), while physiologically drought-tolerant species had greater differential abundance in uplands vs. lowlands ($Abund_{Upl} - Abund_{Lowl} = -1.00 - 0.20 \times \Psi_{crit}$; $r^2 = 0.18$, $P = 0.001$). The relationships between Ψ_{crit} and species abundance in the uplands did not vary over time ($P > 0.68$). Physiological drought tolerance did not explain a significant amount of variation in average species abundance for lowlands, frequently burned, grazed, or ungrazed areas, with this lack of relationship consistent across years ($P > 0.5$). Physiological drought tolerance also did not predict the response of species to burning or grazing ($P > 0.9$). There were no relationships between variation in abundance over time for species (here, coefficient of variation for untransformed abundance) and Ψ_{crit} for either uplands ($P > 0.37$) or lowlands ($P > 0.85$).

Of the 9 other metrics measured for each species, root tissue density was consistently the best predictor of abundance (Fig. 3). High root tissue density species were more abundant overall ($r^2 = 0.12$, $P = 0.003$) and were more abundant in each of the six ecological contrasts (Fig. 3). The relative abundance of high root tissue density species did not change any more than low tissue density species when burned or grazed, nor were high root tissue density species relatively more abundant in uplands than lowlands ($P > 0.05$ for all 3 contrasts). Of the remaining 80 combinations of 8 traits and 10 abundance metrics, only 11 were significant. The strongest relationship was between leaf angle and abundance in grazed areas ($r^2 = 0.14$, $P = 0.002$). Axis 1 scores explained just 6.7% of the variation in overall abundance ($P = 0.02$) and it

Table 2. Principal component analysis results for all species, forbs, and grasses.

	Grasses and Forbs			Forbs			Grasses		
Trait	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
Ψ_{crit}	**0.70**	0.30	0.19	**0.47**	−0.24	−0.04	**0.63**	0.11	**−0.44**
$Thick_L$	**0.71**	−0.31	−0.10	0.31	**0.74**	0.28	**0.76**	−0.03	0.05
ρ_L	**−0.71**	−0.13	0.12	−0.32	**−0.62**	0.08	**0.51**	**0.35**	−0.02
$Angle_L$	**−0.40**	**0.47**	0.12	−0.15	**0.76**	−0.15	**0.67**	0.12	−0.18
$Diam_R$	**0.80**	−0.02	−0.10	**0.63**	0.17	0.02	**0.48**	0.25	0.09
ρ_R	**−0.41**	−0.20	0.08	**−0.47**	−0.09	−0.11	−0.30	**0.64**	0.29
A_{max}	0.12	**0.80**	−0.02	**0.80**	0.12	−0.14	**0.37**	0.19	**0.77**
g_s	0.24	**0.82**	−0.29	**0.71**	0.25	**−0.36**	0.00	−0.20	**0.77**
M_S	−0.18	−0.19	**0.76**	−0.06	**−0.39**	**0.80**	0.12	**0.68**	**−0.38**
M_R	0.02	0.05	**0.89**	−0.05	0.24	**0.83**	0.05	**0.82**	−0.08
Eigenvalues	**2.8**	**1.7**	**1.4**	**2.8**	**1.5**	**1.4**	**2.2**	**1.9**	**1.5**

Notes: Axes were rotated to strengthen contrasts among axes. Bold values represent variables that contribute significantly to a given axis (absolute value > 0.33 is equivalent to $P < 0.05$). Eigenvalues represent the ratio of variation explained by a given axis to the amount of variation explained by chance.

Table 3. Multiple regression with categorical variables, general linear model.

	Axis 1			Axis 2			Axis 3		
Variable	P	Partial r^2	LSM	P	Partial r^2	LSM	P	Partial r^2	LSM
Growth Form	<0.001	0.50		<0.001	0.09		0.04	0.03	
Grass			−1.25			0.55			0.39
Forb			−0.00			−0.67			−0.26
Photosynthetic Type	0.24	0.00		0.03	0.04		0.87	0.00	
C_3			−0.48			0.42			0.03
C_4			−0.78			−0.23			0.10
Life History	0.90	0.00		0.77	0.00		0.09	0.02	
Annual			−0.64			0.00			0.22
Perennial			−0.62			0.19			−0.09
GF × PT	0.04	0.02		0.27	0.01		0.05	0.02	
LH × PT	0.13	0.00		0.33	0.01		0.27	0.01	
GF × LH	0.28	0.00		0.99	0.01		0.71	0.00	

Note: For each contrast we report least squares means (LSM) and partial r^2, each contrast's proportion of the total variation explained by the model ($\alpha = 0.05$).

consistently explained less variation than individual traits for the other contrasts (data not shown). Axes 2 and 3 explained no significant variation in abundance overall or for any contrast.

Using backwards-elimination linear regressions to determine the best predictors of abundance, Ψ_{crit} was the best predictor of abundance for uplands and for the difference in abundance between uplands and lowlands (Table 4). In many other cases, root tissue density was the sole predictor of abundance or contributed to the best predictive model (Table 4). For overall abundance, root tissue density and leaf angle jointly described 19% of the variation in abundance. The amount of variation in abundance that was explained by combinations of traits ranged from 8% to 23%. 29% of the difference in abundance between uplands and lowlands was explained by a combination of Ψ_{crit} and leaf tissue density (Table 4).

Discussion

In the xeric uplands at Konza, soil moisture stress appears to be frequent enough and/or sufficiently intense to have favored plant species with greater physiological drought tolerance. Although Ψ_{crit} only explained ~12% of the variation in abundance, the most physiologically drought-tolerant species was predicted to be 50 times more abundant than the least physiologically drought tolerant species. Compared to the over 100,000-fold variation in upland abundance among all species, the amount of variation explained by drought tolerance might appear small, but on an absolute scale it is sizeable nonetheless. Konza upland soils tend to be

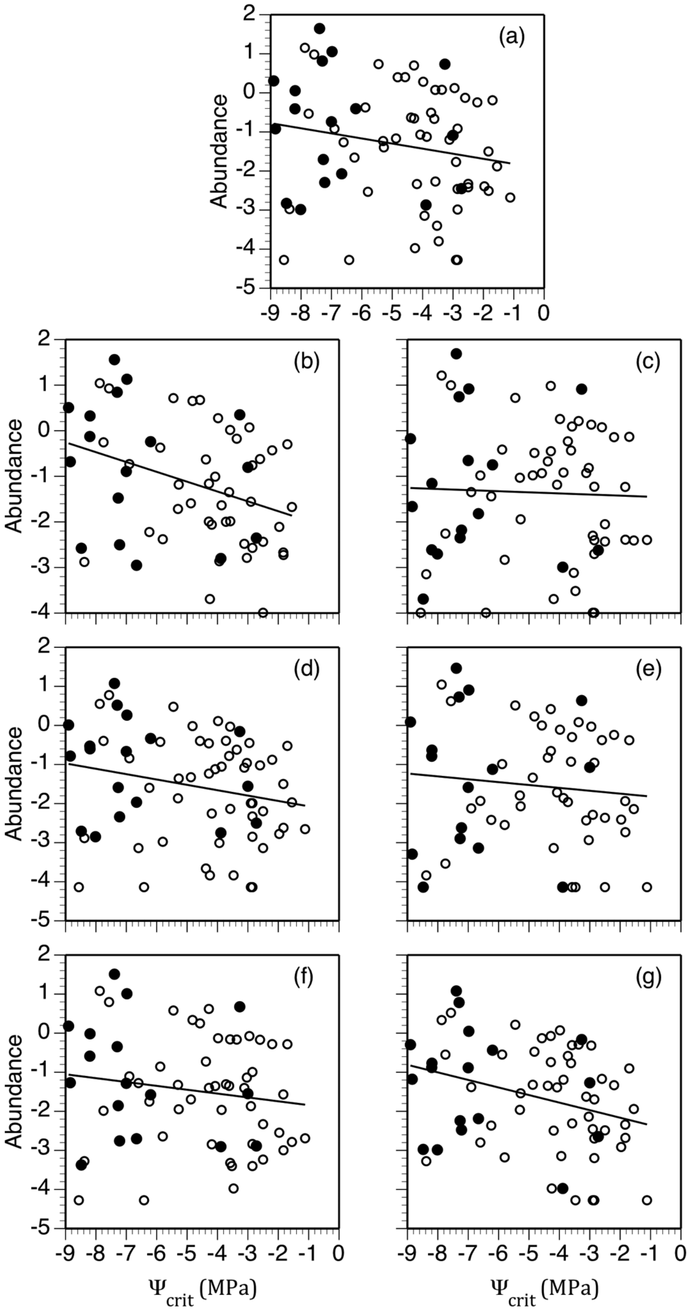

Fig. 2. Relationships between physiological drought tolerance (Ψ_{crit}) and (a) overall abundance at Konza ($P = 0.12$), as well as for (b) uplands ($r^2 = 0.12$, $P = 0.008$) and (c) lowlands ($P = 0.77$); (d) grazed ($P = 0.07$) and (e) ungrazed ($P = 0.43$); and (f) frequently burned ($P = 0.23$)and (g) infrequently burned watersheds ($r^2 = 0.09$, $P = 0.01$). Closed circles are grasses; open circles forbs.

shallow (often <25 cm) (Schimel et al. 1991) and upland species frequently experience low soil moisture (Nippert and Knapp 2007*a*). As such, either the predominance of species with low Ψ_{crit} is a legacy from infrequent, severe droughts or low-intensity soil moisture stress is frequent

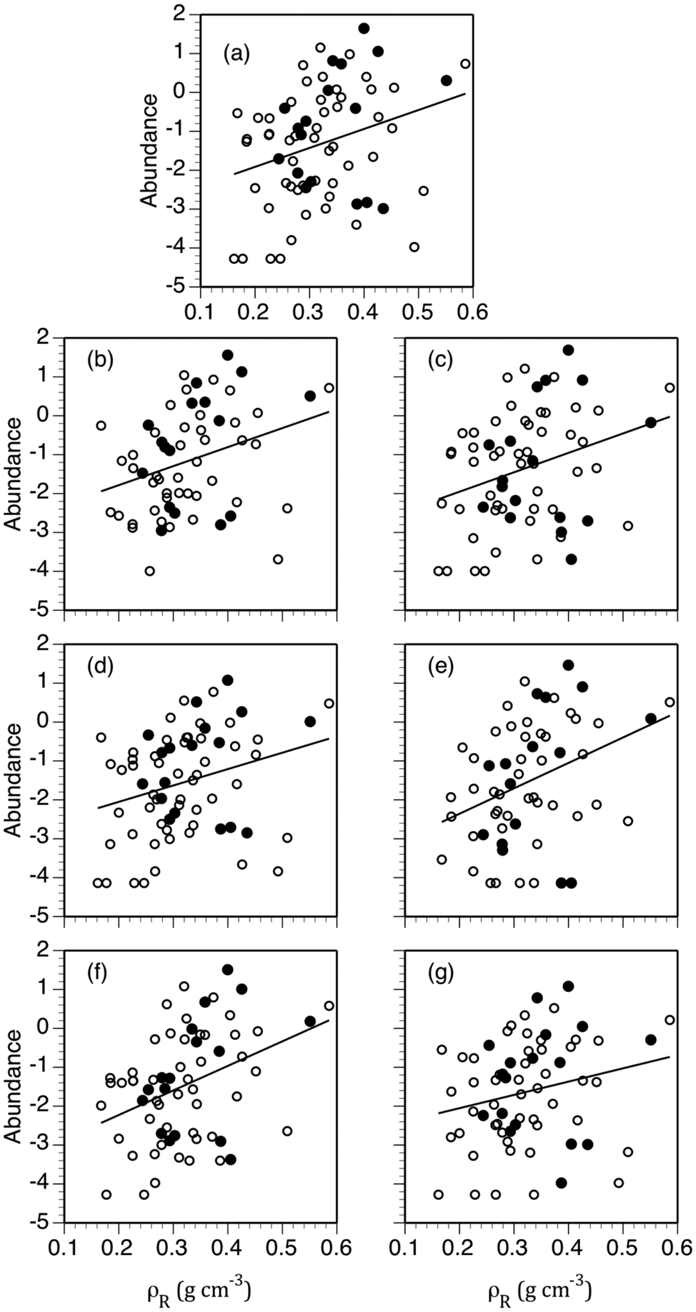

Fig. 3. Relationships between root tissue density (ρ_R) and (a) overall abundance at Konza ($r^2 = 0.12$, $P = 0.003$), as well as for (b) uplands ($r^2 = 0.11$, $P = 0.009$) and (c) lowlands ($r^2 = 0.12$, $P = 0.003$); (d) grazed ($r^2 = 0.09$, $P = 0.009$) and (e) ungrazed ($r^2 = 0.13$, $P = 0.003$); and (f) frequently burned ($r^2 = 0.16$, $P < 0.001$) and (g) infrequently burned watersheds ($r^2 = 0.06$, $P = 0.04$). Closed circles are grasses; open circles forbs.

enough to confer an advantage for physiologically drought-tolerant species.

In contrast, for the more mesic lowlands, physiological drought tolerance did not advantage species on average over the 17 years of the dataset. Drought still might have structured the

Table 4. Stepwise multiple linear regression containing 10 primary traits.

Treatment	r^2	n	Trait	Partial r^2	*P*	Estimate	SS
Abundance	0.19	78	ρ_R	0.10	0.004	5.1	17.4
			Angle_L	0.09	0.01	0.02	15.2
Upland	0.23	65	Ψ_{crit}	0.11	0.003	−0.03	15.3
			ρ_R	0.07	0.01	4.7	10.3
			Diam_R	0.05	0.04	5.1	6.9
Lowland	0.11	73	ρ_R	. . .	0.004	5.3	17.7
Freq.Burn	0.20	72	ρ_R	0.15	0.00	6.251	22.1
			Angle_L	0.05	0.047	0.013	6.9
Infreq.Burn	0.08	72	ρ_L	. . .	0.02	2.7	10.4
Grazed	0.20	75	Angle_L	0.12	0.002	0.02	15.4
			ρ_R	0.08	0.01	4.0	10.0
Ungrazed	0.23	66	Mass_R	0.06	0.03	0.001	10.7
			Thick_L	0.06	0.03	−5.0	10.5
			Mass_S	0.06	0.03	−0.001	10.3
			ρ_R	0.05	0.05	4.2	8.2
ΔUpland	0.29	56	Ψ_{crit}	0.21	<0.001	−0.026	15.4
			ρ_L	0.08	0.008	−2.09	5.7
ΔBurn	n/a						
ΔGraze	0.25	57	Thick_L	0.05	0.01	3.47	5.3
			Angle_L	0.06	0.006	0.015	6.8
			Mass_S	0.07	0.004	0.0088	7.7
			Mass_R	0.06	0.006	−0.0013	6.7

Notes: Abundance data tested also included differences in abundance between uplands and lowlands (ΔUpland), burned and unburned watersheds (ΔBurn), and grazed and ungrazed watersheds (ΔGraze). Partial r^2 is the proportion of model r^2 contributed by each trait. Estimate is the slope of the relationship between the trait and the abundance metric. Sum of Squares represented by SS.

lowland community in the past or in a subset of years. Droughts also might have restricted species presence in the lowlands, filtering sensitive species out of the current community. Only 240 of Konza's ~550 herbaceous species have been observed in the lowland composition plots over the 17 years of monitoring; so historic drought may be responsible for some of the reduction in the observed species set. That said, there was no average difference in Ψ_{crit} between species found in lowland plots and those not found in upland or lowland plots ($P = 0.85$). Alternatively, species with high Ψ_{crit} might possess other adaptations that allow them to recover quickly after drought. If so, drought might structure the community beyond selecting for species with low Ψ_{crit}. At present, there is no evidence that drought has structured the lowland communities in ways that favor physiologically drought-tolerant species as observed for uplands. Plant water potentials are generally higher in the lowlands than uplands at Konza, which supports the conclusion of low importance of drought as a structuring agent in lowland communities. The general pattern of greater drought stress in the uplands than the lowlands is congruent with patterns observed for a grassland in northern England (Buckland et al. 1997). There, shallow soils had much lower soil water potentials during an extreme drought and plants with low physiological drought tolerance showed greater reductions in leaf water than drought-tolerant species.

Regardless of the benefit of drought tolerance in the uplands, for both uplands and lowlands, many physiologically drought-intolerant species were still abundant. Some drought-intolerant species escape drought spatially by occupying microsites where drought is less important (Buckland et al. 1997). Others escape drought phenologically, restricting most of their growth to the wetter, milder spring and fall seasons (Taiz and Zeiger 2002). Annuals can complete their life cycle before severe drought occurs, while some perennial species senesce before drought becomes too severe (Heckathorn and Delucia 1996). Lastly, many of the species with high Ψ_{crit}, such as *Lespedeza capitata*, avoid drought stress by accessing deep soil water (Canadell et al. 1996, Buckland et al. 1997). Soil water is relatively available at depths greater than 1 meter (Briggs and Knapp 1995, Nippert and Knapp 2007*b*) on Konza regardless of antecedent precipitation patterns. Future research that quantifies more specific habitat preferences and/or other related functional traits should shed light into the maintenance of diversity at Konza.

Irrespective of its role in structuring the community, physiological drought tolerance does not appear to be part of an obvious broader plant strategy among Konza species. Outside of thin roots, physiological drought tolerance was not consistently associated with specific functional traits as correlations depended on the groups examined. In addition, the correlated suite of traits that emerged from grasses and forbs predicted less variation in abundance than Ψ_{crit} in the uplands. Still, low Ψ_{crit} and thin roots were consistently associated with one another. The consistent association between low Ψ_{crit} and thin roots was not just a consequence of grasses having thinner roots than forbs for the species studied here as the association held within grasses and within forbs. The low average root diameter of physiologically drought-tolerant species might be a product of thinner xylem elements to prevent cavitation even under very high tension, but could also be associated with a reduced cortex. Distally, the thin roots could represent selection directly related to resistance to low soil water potential, but also could represent selection related to changes in the relative importance of water and nitrogen. A more detailed analysis of the anatomical determinants of interspecific differences in diameter along with models of water and nutrient movement in soils are needed to begin to understand the association between physiological drought tolerance and thin roots.

With our results, one of the key questions to begin to answer is not whether or not drought structures Konza plant communities, but what is the relative role of drought compared to other stresses and disturbances. To this point, root tissue density was consistently associated with abundance in uplands and lowlands, explaining more than twice the variation in abundance than Ψ_{crit} on average. There was no correlation between Ψ_{crit} and root tissue density which implies that high root tissue density is not necessarily a determinant of physiological drought tolerance. High root tissue density has often been linked with low-nutrient environments and tends to be correlated with high leaf tissue density (Wahl and Ryser 2000). Dense roots have low turnover rates (Craine et al. 2002) and are robust due to a high percentage of root stele (Wahl and Ryser 2000). High root tissue density also imparts success when nutrients are limiting. For example, the high root longevity, to which high root tissue density contributes, generates high root length density in soil, which confers the ability to preempt nutrient supplies from competitors (Craine et al. 2005). If high root tissue density is the best trait to indicate importance of low nutrient availability, it is possible that nutrient limitation is more important than drought in structuring the Konza plant community in the lowlands, and of similar importance in uplands. At Konza, both upland and lowland productivity can be limited by N (Seastedt et al. 1991), which would support the importance of nutrients in both landscape positions.

Ultimately, understanding the relative role of drought in structuring the plant communities of grasslands will require monitoring of plant communities during and after severe droughts to determine the immediate stress effects and the community's recovery. At Konza, severe droughts have not occurred since the early 1980s, and for many years the leaf water potential of the dominant grasses has not declined below −3 MPa. As such, although landscape-level variation in soil moisture might structure the grassland community (Silvertown et al. 1999), it is likely that in the more mesic areas at Konza, drought has been less important than other environmental factors such as low nutrient availability, fire, and grazing. If drought becomes more frequent or severe in the future, plant communities might increasingly resemble the uplands and species with low Ψ_{crit} might become more abundant.

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LITERATURE CITED

Ackerly, D. 2004. Functional strategies of chaparral shrubs in relation to seasonal water deficit and disturbance. Ecological Monographs 74:25–44.

Bailey, A. W. and C. E. Poulton. 1968. Plant communities and environmental interrelationships in a portion of Tillamook Burn Northwestern Oregon. Ecology 49:1–13.

Bhaskar, R. and D. D. Ackerly. 2006. Ecological relevance of minimum seasonal water potentials. Physiologia Plantarum 127:353–359.

Blair, J. M. 1997. Fire, N availability, and plant response in grasslands: A test of the transient maxima hypothesis. Ecology 78:2359–2368.

Bremer, D. J., L. M. Auen, J. M. Ham, and C. E. Owensby. 2001. Evapotranspiration in a prairie ecosystem: Effects of grazing by cattle. Agronomy Journal 93:338–348.

Briggs, J. M. and A. K. Knapp. 1995. Interannual variability in primary production in tallgrass prairie: climate, soil moisture, topographic position, and fire as determinants of aboveground biomass. American Journal of Botany 82:1024–1030.

Buckland, S. M., J. P. Grime, J. G. Hodgson, and K. Thompson. 1997. A comparison of plant responses to the extreme drought of 1995 in northern England. Journal of Ecology 85:875–882.

Canadell, J., R. B. Jackson, J. R. Ehleringer, H. A. Mooney, O. E. Sala, and E. D. Schulze. 1996. Maximum rooting depth of vegetation types at the global scale. Oecologia 108:583–594.

Christensen, J. H., B. Hewitson, A. Busuioc, A. Chen, X. Gao, I. Held, R. Jones, R. K. Kolli, W.-T. Kwon, R. Laprise, V. M. Rueda, L. Mearns, C. G. Menéndez, J. Räisänen, A. Rinke, A. Sarr, and P. Whetton. 2007. Regional Climate Projections. *In* S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, and H. L. Miller, editors. Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Ciais, P., M. Reichstein, N. Viovy, A. Granier, J. Ogee, V. Allard, M. Aubinet, N. Buchmann, C. Bernhofer, A. Carrara, F. Chevallier, N. De Noblet, A. D. Friend, P. Friedlingstein, T. Grunwald, B. Heinesch, P. Keronen, A. Knohl, G. Krinner, D. Loustau, G. Manca, G. Matteucci, F. Miglietta, J. M. Ourcival, D. Papale, K. Pilegaard, S. Rambal, G. Seufert, J. F. Soussana, M. J. Sanz, E. D. Schulze, T. Vesala, and R. Valentini. 2005. Europe-wide reduction in primary productivity caused by the heat and drought in 2003. Nature 437:529–533.

Collins, S. L., A. K. Knapp, J. M. Briggs, J. M. Blair, and E. M. Steinauer. 1998. Modulation of diversity by grazing and mowing in native tallgrass prairie. Science 280:745–747.

Craine, J. 2009. Resource Strategies of Wild Plants. Princeton University Press, Princeton, New Jersey, USA.

Craine, J. M., J. Fargione, and S. Sugita. 2005. Supply pre-emption, not concentration reduction, is the mechanism of competition for nutrients. New Phytologist 166:933–940.

Craine, J. M., J. Froehle, D. G. Tilman, D. A. Wedin, and F. S. Chapin III. 2001. The relationships among root and leaf traits of 76 grassland species and relative abundance along fertility and disturbance gradients. Oikos 93:274–285.

Craine, J. M., D. G. Tilman, D. A. Wedin, P. B. Reich, M. J. Tjoelker, and J. M. H. Knops. 2002. Functional traits, productivity and effects on nitrogen cycling of 33 grassland species. Functional Ecology 16:563–574.

Craine, J. M. and E. G. Towne. 2010. High leaf tissue density grassland species consistently more abundant across topographic and disturbance contrasts in a North American tallgrass prairie. Plant and Soil 337:193–203.

Craine, J. M., E. G. Towne, and J. B. Nippert. 2010. Climate controls on grass culm production over a quarter century in a tallgrass prairie. Ecology 91:2132–2140.

Cunningham, S. A., B. Summerhayes, and M. Westoby. 1999. Evolutionary divergences in leaf structure and chemistry, comparing rainfall and soil nutrient gradients. Ecological Monographs 69:569–588.

Debinski, D. M., H. Wickham, K. Kindscher, J. C. Caruthers, and M. Germino. 2010. Montane meadow change during drought varies with background hydrologic regime and plant functional group. Ecology 91:1672–1681.

Ehleringer, J. 1983. Characterization of a glabrate *Encelia farinosa* mutant—morphology, ecophysiology, and field observations. Oecologia 57:303–310.

Fahnestock, J. T. and A. K. Knapp. 1994. Plant responses to selective grazing by bison: Interactions between light, herbivory and water stress. Vegetatio 115:123–131.

Frank, D. A. and S. J. McNaughton. 1992. The ecology of plants, large mammalian herbivores, and drought in Yellowstone National Park. Ecology 73:2043–2058.

Gibson, D. J. 2009. Grasses and Grassland Ecology. Oxford University Press, Oxford, UK.

Grime, J. P., J. D. Fridley, A. P. Askew, K. Thompson, J. G. Hodgson, and C. R. Bennett. 2008. Long-term resistance to simulated climate change in an infertile grassland. Proceedings of the National Academy of Sciences of the United States of America 105:10028–10032.

Grime, J. P., K. Thompson, R. Hunt, J. G. Hodgson, J. H. C. Cornelissen, I. H. Rorison, G. A. F. Hendry, T. W. Ashenden, A. P. Askew, S. R. Band, R. E. Booth, C. C. Bossard, B. D. Campbell, J. E. L. Cooper, A. W. Davison, P. L. Gupta, W. Hall, D. W. Hand, M. A. Hannah, S. H. Hillier, D. J. Hodkinson, A. Jalili, Z. Liu, J. M. L. Mackey, N. Matthews, M. A. Mowforth, A. M. Neal, R. J. Reader, K. Reiling, W. Ross-Fraser, R. E. Spencer, F. Sutton, D. E. Tasker, P. C. Thorpe, and J. Whitehouse. 1997. Integrated screening validates primary axes of specialisation in plants. Oikos 79:259–281.

Hacke, U. G., J. S. Sperry, W. T. Pockman, S. D. Davis, and K. A. McCulloch. 2001. Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. Oecologia 126:457–461.

Heckathorn, S. A. and E. H. Delucia. 1996. Retranslocation of shoot nitrogen to rhizomes and roots in prairie grasses may limit loss of N to grazing and fire during drought. Functional Ecology 10:396–400.

Karl, T. R. and A. J. Koscielny. 1982. Drought in the United States—1895–1981. Journal of Climatology 2:313–329.

Knapp, A. K. 1985. Effect of fire and drought on the ecophysiology of Andropogon gerardii and Panicum virgatum in a tallgrass prairie. Ecology 66:1309–1320.

Knapp, A. K., J. T. Fahnestock, S. P. Hamburg, L. B. Statland, T. R. Seastedt, and D. S. Schimel. 1993. Landscape patterns in soil-plant water relations and primary production in tallgrass prairie. Ecology 74:549–560.

McDowell, N., W. T. Pockman, C. D. Allen, D. D. Breshears, N. Cobb, T. Kolb, J. Plaut, J. Sperry, A. West, D. G. Williams, and E. A. Yepez. 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? New Phytologist 178:719–739.

Medina, E., V. Garcia, and E. Cuevas. 1990. Sclerophylly and oligotrophic environments—relationships between leaf structure, mineral nutrient content, and drought resistance in tropical rain forests of the upper Rio Negro region. Biotropica 22:51–64.

Niinemets, U. 2001. Global-scale climatic controls of leaf dry mass per area, density, and thickness in trees and shrubs. Ecology 82:453–469.

Nippert, J. B. and A. K. Knapp. 2007*a*. Linking water uptake with rooting patterns in grassland species. Oecologia 153:261–272.

Nippert, J. B. and A. K. Knapp. 2007*b*. Soil water partitioning contributes to species coexistence in tallgrass prairie. Oikos 116:1017–1029.

Nippert, J. B., A. K. Knapp, and J. M. Briggs. 2006. Intra-annual rainfall variability and grassland productivity: can the past predict the future? Plant Ecology 184:65–74.

Nippert, J. B., T. W. Ocheltree, A. M. Skibbe, L. C. Kangas, J. M. Ham, K. B. Shonkwiler Arnold, and N. A. Brunsell. 2011. Linking plant growth responses across topographic gradients in tallgrass prairie. Oecologia. [doi: 10.1007/s00442-011-1948-6]

Perez-Harguindeguy, N., S. Diaz, F. Vendramini, J. H. C. Cornelissen, D. E. Gurvich, and M. Cabido. 2003. Leaf traits and herbivore selection in the field and in cafeteria experiments. Austral Ecology 28:642–650.

Pockman, W. T. and J. S. Sperry. 2000. Vulnerability to xylem cavitation and the distribution of Sonoran desert vegetation. American Journal of Botany 87:1287–1299.

Reich, P., I. Wright, J. Cavender-Bares, J. Craine, J. Oleksyn, M. Westoby, and M. Walters. 2003*a*. The evolution of plant functional variation: traits, spectra, and strategies. International Journal of Plant Sciences 164:S143–S164.

Reich, P. B., C. Buschena, M. G. Tjoelker, K. Wrage, J. Knops, D. Tilman, and J. L. Machado. 2003*b*. Variation in growth rate and ecophysiology among 34 grassland and savanna species under contrasting N supply: a test of functional group differences. New Phytologist 157:617–631.

Sandel, B., L. J. Goldstein, N. J. B. Kraft, J. G. Okie, M. I. Shuldman, D. D. Ackerly, E. E. Cleland, and K. N. Suding. 2010. Contrasting trait responses in plant communities to experimental and geographic variation in precipitation. New Phytologist no-no.

Schimel, D. S., T. G. F. Kittel, A. K. Knapp, T. R. Seastedt, W. J. Parton, and V. B. Brown. 1991. Physiological interactions along resource gradients in a tallgrass prairie. Ecology 72:672–684.

Seastedt, T. R., J. M. Briggs, and D. J. Gibson. 1991. Controls of nitrogen limitation in tallgrass prairie. Oecologia 87:72–79.

Silvertown, J., M. E. Dodd, D. J. G. Gowing, and J. O. Mountford. 1999. Hydrologically defined niches reveal a basis for species richness in plant communities. Nature 400:61–63.

Spasojevic, M. J., R. J. Aicher, G. R. Koch, E. S. Marquardt, N. Mirotchnick, T. G. Troxler, and S. L. Collins. 2010. Fire and grazing in a mesic tallgrass prairie: impacts on plant species and functional traits. Ecology 91:1651–1659.

Sperry, J. S., V. Stiller, and U. G. Hacke. 2003. Xylem hydraulics and the soil-plant-atmosphere continuum: Opportunities and unresolved issues. Agronomy Journal 95:1362–1370.

Taiz, L. and E. Zeiger. 2002. Plant Physiology. 3rd edition. Sinauer Associates, Sunderland, Massachusetts, USA.

Tilman, D. and A. El Haddi. 1992. Drought and biodiversity in grasslands. Oecologia 89:257–264.

Towne, E. G., D. C. Hartnett, and R. C. Cochran. 2005. Vegetation trends in tallgrass prairie from bison and cattle grazing. Ecological Applications 15:1550–1559.

Wahl, S. and P. Ryser. 2000. Root tissue structure is linked to ecological strategies of grasses. New Phytologist 148:459–471.

Weaver, J. E. 1968. Prairie Plants and their Environment: a fifty year study in the Midwest. University of Nebraska Press, Lincoln, Nebraska, USA.

Woodhouse, C. A. and J. T. Overpeck. 1998. 2000 years of drought variability in the central United States. Bulletin of the American Meteorological Society 79:2693–2714.

Wright, W. and A. W. Illius. 1995. A comparative study of the fracture properties of 5 grasses. Functional Ecology 9:269–278.

APPENDIX A

Table A1. Data on species information and functional trait data for each species (means ± s.d.). Species information includes functional group (Forb [F] or Grass [G]), life history (Annual [A], Biennial [B], Perennial [P]), and the photosynthetic pathway (C_3 or C_4). Included also are the number of plants grown (N), although not all plants would have generated data for each metric.

Species	Fxnl	LH	Type	N
Achillea millefolium	F	P	C3	8
Ageratina altissima	F	P	C3	5
Amaranthus blitoides	F	A	C4	9
Amaranthus retroflexus	F	A	C4	8
Ambrosia psilostachya	F	P	C3	3
Amorpha canescens	F	P	C3	8
Andropogon gerardii	G	P	C4	13
Antennaria neglecta	F	P	C3	9
Apocynum cannabinum	F	P	C3	6
Aristida oligantha	G	A	C4	7
Aristida purpurea	G	P	C4	5
Artemisia ludoviciana	F	P	C3	6
Asclepias incarnata	F	P	C3	10
Asclepias speciosa	F	P	C3	5
Asclepias sullivantii	F	P	C3	6
Asclepias verticillata	F	P	C3	4
Asclepias viridis	F	P	C3	6
Astragalus canadensis	F	P	C3	5
Baptisia alba	F	P	C3	7
Baptisia australis	F	P	C3	8
Bouteloua curtipendula	G	P	C4	7
Bouteloua gracilis	G	P	C4	5
Bromus inermis	G	P	C3	11
Carex annectens	G	P	C3	12
Chamaecrista fasciculata	F	A	C3	8
Chamaesyce nutans	F	A	C4	13
Chloris verticillata	G	P	C4	7
Cirsium altissimum	F	B	C3	7
Cucurbita foetidissima	F	P	C3	7
Desmanthus illinoensis	F	P	C3	12
Desmodium illinoense	F	P	C3	9
Dichanthelium acuminatum	G	P	C3	4
Echinacea angustifolia	F	P	C3	6
Echinacea atrorubens	F	P	C3	5
Echinacea pallida	F	P	C3	1
Echinodorus berteroi	F	P	C3	3
Eleusine indica	G	A	C4	9
Elymus canadensis	G	P	C3	4
Elymus villosus	G	P	C3	4
Elymus virginicus	G	P	C3	24
Eragrostis pectinacea	G	A	C4	10
Erigeron annuus	F	A	C3	1
Eryngium yuccifolium	F	P	C3	8
Eupatorium altissimum	F	P	C3	8
Eupatorium purpureum	F	P	C3	7
Euphorbia corollata	F	P	C3	1
Euphorbia dentata	F	A	C3	10
Euphorbia marginata	F	A	C3	2
Festuca subverticillata	G	P	C3	5
Helianthus annuus	F	A	C3	8
Helianthus petiolaris	F	A	C3	8
Helianthus salicifolius	F	P	C3	6
Helianthus tuberosus	F	P	C3	8
Heliopsis helianthoides	F	P	C3	8
Hesperostipa spartea	G	P	C3	8
Hordeum jubatum	G	P	C3	12
Hordeum pusillum	G	A	C3	8
Koeleria macrantha	G	P	C3	16
Lactuca canadensis	F	B	C3	4
Lactuca ludoviciana	F	B	C3	2
Lepidium densiflorum	F	A	C3	11
Lepidium virginicum	F	A	C3	8
Lespedeza capitata	F	P	C3	4
Lespedeza violacea	F	P	C3	8
Liatris aspera	F	P	C3	6
Liatris mucronata	F	P	C3	8
Liatris punctata	F	P	C3	4
Liatris pycnostachya	F	P	C3	4
Mirabilis linearis	F	P	C3	5
Monarda fistulosa	F	P	C3	20
Oenothera biennis	F	B	C3	12
Oenothera macrocarpa	F	P	C3	14
Packera plattensis	F	B	C3	4
Panicum capillare	G	A	C4	1
Panicum virgatum	G	P	C4	9
Pascopyrum smithii	G	P	C3	2
Penstemon cobaea	F	P	C3	6
Penstemon digitalis	F	P	C3	11
Penstemon grandiflorus	F	P	C3	4
Penstemon tubiflorus	F	P	C3	9
Physalis pubescens	F	A	C3	4
Plantago rugelii	F	P	C3	8
Poa arida	G	P	C3	8
Poa pratensis	G	P	C3	14
Polygonum virginianum	F	P	C3	12
Prenanthes aspera	F	P	C3	4
Prunella vulgaris	F	P	C3	8
Psoralidium tenuiflorum	F	P	C3	7
Ratibida pinnata	F	P	C3	6
Rudbeckia hirta	F	A	C3	4
Rudbeckia lacinata	F	P	C3	11

Table A1. Continued.

Species	Fxnl	LH	Type	N
Ruellia humilis	F	P	C3	13
Salvia azurea	F	P	C3	19
Salvia reflexa	F	A	C3	9
Schizachyrium scoparium	G	P	C4	14
Senna marilandica	F	P	C3	8
Setaria pumila	G	A	C4	10
Silphium integrifolium	F	P	C3	4
Silphium laciniatum	F	P	C3	14
Solanum carolinense	F	P	C3	6
Solanum rostratum	F	A	C3	12
Solidago canadensis	F	P	C3	1
Solidago missouriensis	F	P	C3	3
Solidago mollis	F	P	C3	3
Solidago nemoralis	F	P	C3	7
Solidago petiolaris	F	P	C3	8
Solidago ulmifolia	F	P	C3	7
Sorghastrum nutans	G	P	C4	18
Sporobolus heterolepis	G	P	C4	1
Stellaria media	F	A	C3	1
Stenosiphon linifolius	F	B	C3	7
Symphyotrichum laeve	F	P	C3	4
Symphyotrichum oblongifolium	F	P	C3	6
Tradescantia bracteata	F	P	C3	8
Tradescantia ohiensis	F	P	C3	5
Tragopogon dubius	F	B	C3	6
Verbesina alternifolia	F	P	C3	5
Vernonia baldwinii	F	P	C3	8
Vulpia octoflora	G	A	C3	6
Xanthium strumarium	F	A	C3	3
Zizia aurea	F	P	C3	1

APPENDIX B

Table B1. Data on physiological drought tolerance (Ψ_{crit}; MPa), average root diameter (Diam_R; mm), root tissue density (ρ_R; g cm^{-3}), shoot mass (M_S; mg), and root mass (M_R; mg).

Species	Ψ_{crit}	Diam_R	ρ_R	M_S	M_R
Achillea millefolium	−5.9 ± 2.1	0.25 ± 0.03	0.35 ± 0.08	881 ± 425	479 ± 224
Ageratina altissima	−2.9 ± 0.7	0.24 ± 0.04	0.16 ± 0.06	309 ± 238	107 ± 125
Amaranthus blitoides	−3 ± 3.1	0.23 ± 0.07	0.53 ± 0.24	411 ± 252	59 ± 19
Amaranthus retroflexus	−4.3 ± 1.6	0.13 ± 0.02	0.49 ± 0.22	904 ± 478	249 ± 97
Ambrosia psilostachya	−7.6 ± 1.8	0.21 ± 0.05	0.37 ± 0.13	2021 ± 432	1076 ± 321
Amorpha canescens	−5.5 ± 2.4	0.19 ± 0.03	0.59 ± 0.2	305 ± 145	159 ± 92
Andropogon gerardii	−7.4 ± 1.9	0.27 ± 0.04	0.4 ± 0.07	1018 ± 749	930 ± 641
Antennaria neglecta	−4.1 ± 1.2	0.24 ± 0.05	0.23 ± 0.06	809 ± 605	222 ± 131
Apocynum cannabinum	−3.7 ± 0.9	0.3 ± 0.05	0.33 ± 0.14	496 ± 267	215 ± 127
Aristida oligantha	−7.2 ± 2.3	0.19 ± 0.04	0.3 ± 0.08	2445 ± 1922	758 ± 548
Aristida purpurea	−8.4 ± 1.5	0.26 ± 0.07	0.33 ± 0.08	397 ± 309	236 ± 189
Artemisia ludoviciana	−4 ± 0.5	0.28 ± 0.07	0.29 ± 0.05	1008 ± 205	333 ± 121
Asclepias incarnata	−2.6 ± 1.4	0.32 ± 0.11	0.33 ± 0.06	755 ± 292	923 ± 431
Asclepias speciosa	−2 ± 1.1	0.41 ± 0.05	0.23 ± 0.02	411 ± 384	340 ± 454
Asclepias sullivantii	−6.6 ± 4.3	0.31 ± 0.05	0.18 ± 0.05	396 ± 160	912 ± 579
Asclepias verticillata	−2.2 ± 1.2	0.43 ± 0.1	0.27 ± 0.07	262 ± 135	380 ± 315
Asclepias viridis	−1.7 ± 1.9	0.36 ± 0.07	0.32 ± 0.12	195 ± 146	268 ± 317
Astragalus canadensis	−2.9 ± 0.5	0.35 ± 0.09	0.31 ± 0.16	719 ± 347	240 ± 139
Baptisia alba	−3.3 ± 1	0.38 ± 0.06	0.22 ± 0.1	696 ± 357	501 ± 287
Baptisia australis	−2.9 ± 0.5	0.34 ± 0.05	0.31 ± 0.07	707 ± 235	314 ± 162
Bouteloua curtipendula	−8.9 ± 1.1	0.18 ± 0.08	0.55 ± 0.11	1099 ± 536	688 ± 326
Bouteloua gracilis	−8.2 ± 3.1	0.17 ± 0.05	0.38 ± 0.11	1072 ± 1264	762 ± 717
Bromus inermis	−6.2 ± 1.6	0.23 ± 0.02	0.25 ± 0.01	838 ± 327	815 ± 330
Carex annectens	−5.8 ± 1.6	0.15 ± 0.02	0.42 ± 0.05	774 ± 369	835 ± 413
Chamaecrista fasciculata	−3.3 ± 0.9	0.26 ± 0.04	0.17 ± 0.05	1344 ± 742	187 ± 87
Chamaesyce nutans	−1.8 ± 0.9	0.19 ± 0.02	0.34 ± 0.07	2048 ± 1299	569 ± 135
Chloris verticillata	−8.5 ± 2.3	0.21 ± 0.03	0.41 ± 0.07	1068 ± 760	533 ± 271
Cirsium altissimum	−4.3 ± 2	0.25 ± 0.07	0.21 ± 0.07	1389 ± 743	1305 ± 699

Table B1. Continued.

Species	Ψ_{crit}	$Diam_R$	ρ_R	M_S	M_R
Cucurbita foetidissima	−2.5 ± 0.8	0.29 ± 0.17	0.4 ± 0.1	1243 ± 490	2297 ± 996
Desmanthus illinoensis	−6.2 ± 3.3	0.25 ± 0.04	0.42 ± 0.08	876 ± 500	394 ± 175
Desmodium illinoense	−5.3 ± 2.4	0.23 ± 0.04	0.26 ± 0.16	756 ± 383	883 ± 285
Dichanthelium acuminatum	−8.5 ± 1.4	0.17 ± 0.02	0.26 ± 0.05	406 ± 577	167 ± 256
Echinacea angustifolia	−5.3 ± 0.7	0.28 ± 0.08	0.34 ± 0.21	378 ± 190	447 ± 373
Echinacea atrorubens	−5.6 ± 0.5	0.3 ± 0.08	0.49 ± 0.14	302 ± 170	476 ± 405
Echinacea pallida	−3.3	0.28	0.33	197	103
Echinodorus berteroi	−2.2	0.43	0.4	221	208
Eleusine indica	−3.1 ± 2.3	0.13 ± 0.02	0.31 ± 0.02	1627 ± 1544	491 ± 313
Elymus canadensis	−7 ± 2.5	0.21 ± 0.02	0.29 ± 0.07	1005 ± 773	493 ± 324
Elymus villosus	−7.2 ± 3.4	0.15 ± 0.02	0.4 ± 0.11	678 ± 197	220 ± 92
Elymus virginicus	−6.7 ± 2.3	0.17 ± 0.02	0.28 ± 0.04	856 ± 548	367 ± 276
Eragrostis pectinacea	−6.2 ± 1.8	0.18 ± 0.04	0.37 ± 0.07	2480 ± 3051	889 ± 370
Erigeron annuus	n/a	0.25	0.33	1449	900
Eryngium yuccifolium	−3.6 ± 1.4	0.37 ± 0.08	0.22 ± 0.07	700 ± 401	506 ± 466
Eupatorium altissimum	−3.6 ± 0.6	0.35 ± 0.07	0.23 ± 0.07	1636 ± 867	867 ± 547
Eupatorium purpureum	−3.9 ± 1.2	0.32 ± 0.03	0.22 ± 0.07	1397 ± 726	757 ± 608
Euphorbia corollata	n/a	0.37	0.35	n/a	283
Euphorbia dentata	−1.8 ± 1.2	0.21 ± 0.03	0.28 ± 0.08	1205 ± 594	233 ± 71
Euphorbia marginata	n/a	0.34 ± 0.02	0.11 ± 0.05	655 ± 339	190 ± 47
Festuca subverticillata	−7 ± 1.9	0.17 ± 0.05	0.27 ± 0.02	1125 ± 964	473 ± 473
Helianthus annuus	−3.1 ± 1.3	0.3 ± 0.09	0.19 ± 0.05	1618 ± 868	403 ± 186
Helianthus petiolaris	−3.6 ± 1.2	0.23 ± 0.07	0.26 ± 0.09	1835 ± 1051	332 ± 165
Helianthus salicifolius	−3.5 ± 1	0.32 ± 0.1	0.27 ± 0.05	633 ± 169	429 ± 235
Helianthus tuberosus	−2.8 ± 0.8	0.4 ± 0.06	0.25 ± 0.05	2005 ± 614	958 ± 542
Heliopsis helianthoides	−4.9 ± 2.5	0.38 ± 0.07	0.17 ± 0.05	550 ± 430	240 ± 235
Hesperostipa spartea	−8 ± 2.8	0.15 ± 0.02	0.44 ± 0.08	624 ± 573	497 ± 412
Hordeum jubatum	−7 ± 2.3	0.19 ± 0.04	0.27 ± 0.03	954 ± 430	379 ± 154
Hordeum pusillum	−8.8 ± 1.2	0.18 ± 0.03	0.28 ± 0.06	1150 ± 665	784 ± 307
Koeleria macrantha	−8.2 ± 2.5	0.13 ± 0.03	0.33 ± 0.08	331 ± 195	302 ± 208
Lactuca canadensis	−2.9 ± 0.8	0.4 ± 0.05	0.23 ± 0.04	839 ± 459	803 ± 957
Lactuca ludoviciana	−2.5	0.42	0.27 ± 0.07	327 ± 172	195 ± 190
Lepidium densiflorum	−6.9 ± 2.8	0.1 ± 0.02	0.45 ± 0.16	744 ± 337	158 ± 59
Lepidium virginicum	−5.2 ± 1.4	0.12 ± 0.03	0.55 ± 0.24	1335 ± 719	387 ± 130
Lespedeza capitata	−2.6 ± 1.7	0.3 ± 0.04	0.36 ± 0.13	524 ± 352	221 ± 84
Lespedeza violacea	−4.3 ± 2.6	0.32 ± 0.05	0.29 ± 0.07	538 ± 341	176 ± 65
Liatris aspera	−6 ± 2.4	0.22 ± 0.03	0.19 ± 0.06	308 ± 147	427 ± 290
Liatris mucronata	−5.1 ± 2.7	0.25 ± 0.05	0.29 ± 0.15	33 ± 23	107 ± 38
Liatris punctata	−7.8 ± 2.5	0.3 ± 0.07	0.17 ± 0.1	49 ± 3	112 ± 93
Liatris pycnostachya	−2.3 ± 0.2	0.28 ± 0.04	0.14 ± 0.02	809 ± 278	358 ± 230
Mirabilis linearis	−5.8 ± 2.5	0.2 ± 0.02	0.51 ± 0.32	534 ± 154	780 ± 580
Monarda fistulosa	−3.9 ± 1.3	0.23 ± 0.03	0.27 ± 0.04	1336 ± 782	741 ± 275
Oenothera biennis	−3.5 ± 2.2	0.18 ± 0.03	0.27 ± 0.12	1561 ± 528	591 ± 33
Oenothera macrocarpa	−3.6 ± 2.1	0.35 ± 0.1	0.31 ± 0.09	1259 ± 624	245 ± 143
Packera plattensis	−2.9 ± 1.3	0.42 ± 0.11	0.27 ± 0.07	137 ± 51	117 ± 3
Panicum capillare	n/a	0.18	0.2	164	n/a
Panicum virgatum	−3.3 ± 0.9	0.27 ± 0.06	0.36 ± 0.07	1103 ± 345	1045 ± 457
Pascopyrum smithii	−3	0.19 ± 0.02	0.28 ± 0.04	947 ± 990	311 ± 131
Penstemon cobaea	−4.2 ± 1	0.42 ± 0.08	0.34 ± 0.1	584 ± 377	410 ± 223
Penstemon digitalis	−3.6 ± 0.7	0.32 ± 0.07	0.31 ± 0.12	1140 ± 558	832 ± 493
Penstemon grandiflorus	−2 ± 1.1	0.36 ± 0.06	0.29 ± 0.02	291 ± 61	133 ± 50
Penstemon tubiflorus	−3.9 ± 1.4	0.25 ± 0.06	0.29 ± 0.06	523 ± 174	572 ± 367
Physalis pubescens	−3.5 ± 1.5	0.17 ± 0.01	0.39 ± 0.09	507 ± 329	805 ± 480
Plantago rugelii	−6.4 ± 1.6	0.25 ± 0.05	0.18 ± 0.02	1651 ± 691	617 ± 141
Poa arida	−5.7 ± 2.2	0.14 ± 0.01	0.3 ± 0.07	1495 ± 667	618 ± 306
Poa pratensis	−7.3 ± 1.5	0.14 ± 0.1	0.34 ± 0.1	1228 ± 419	1542 ± 485
Polygonum virginianum	−4.2 ± 1	0.15 ± 0.03	0.36 ± 0.07	1237 ± 484	295 ± 221
Prenanthes aspera	−3.3 ± 1.7	0.21	0.14	167 ± 240	284
Prunella vulgaris	−6.4 ± 2.6	0.26 ± 0.02	0.18 ± 0.02	1759 ± 860	445 ± 185
Psoralidium tenuiflorum	−4.4 ± 2.9	0.32 ± 0.07	0.43 ± 0.14	111 ± 57	562 ± 214
Ratibida pinnata	−4 ± 0.8	0.37 ± 0.06	0.22 ± 0.07	890 ± 443	474 ± 410
Rudbeckia hirta	−3.7 ± 1	0.27 ± 0.03	0.13 ± 0.03	836 ± 446	386 ± 278
Rudbeckia lacinata	−4.8 ± 2.9	0.34 ± 0.11	0.22 ± 0.04	770 ± 480	748 ± 315
Ruellia humilis	−3.4 ± 1	0.42 ± 0.08	0.41 ± 0.09	908 ± 338	451 ± 188
Salvia azurea	−4.8 ± 2.6	0.3 ± 0.1	0.4 ± 0.15	1026 ± 387	786 ± 336
Salvia reflexa	−8.6 ± 2.3	0.17 ± 0.02	0.25 ± 0.04	n/a	318 ± 74
Schizachyrium scoparium	−7 ± 2.6	0.22 ± 0.06	0.43 ± 0.11	939 ± 578	1144 ± 733
Senna marilandica	−2.9 ± 0.7	0.33 ± 0.03	0.33 ± 0.21	1252 ± 497	481 ± 187

Table B1. Continued.

Species	Ψ_{crit}	Diam$_R$	ρ_R	M_S	M_R
Setaria pumila	−3.9 ± 1.6	0.17 ± 0.02	0.39 ± 0.14	2103 ± 667	1125 ± 646
Silphium integrifolium	−2.5 ± 0.6	0.39 ± 0.04	0.26 ± 0.03	1028 ± 372	1192 ± 557
Silphium laciniatum	−3 ± 1.8	0.33 ± 0.09	0.23 ± 0.11	523 ± 194	1010 ± 361
Solanum carolinense	−4.9 ± 2.4	0.23 ± 0.02	0.31 ± 0.1	606 ± 230	387 ± 201
Solanum rostratum	−8.4 ± 1.5	0.19 ± 0.03	0.23 ± 0.05	900 ± 438	333 ± 167
Solidago canadensis	n/a	n/a	n/a	695	n/a
Solidago missouriensis	−3 ± 0.2	0.26 ± 0.08	0.45 ± 0.3	570 ± 337	637 ± 280
Solidago mollis	−4.6 ± 3.2	0.38 ± 0.05	0.21	174 ± 141	251
Solidago nemoralis	−3.7 ± 1	0.38 ± 0.07	0.2 ± 0.07	591 ± 420	409 ± 351
Solidago petiolaris	−2.7 ± 0.8	0.33 ± 0.04	0.33 ± 0.04	404 ± 277	235 ± 204
Solidago ulmifolia	−3.1 ± 0.4	0.31 ± 0.04	0.32 ± 0.06	1098 ± 525	554 ± 314
Sorghastrum nutans	−7.9 ± 2.2	0.24 ± 0.04	0.32 ± 0.07	702 ± 362	478 ± 258
Sporobolus heterolepis	n/a	n/a	n/a	n/a	n/a
Stellaria media	n/a	n/a	n/a	1170	n/a
Stenosiphon linifolius	−2.7 ± 0.7	0.29 ± 0.11	0.29 ± 0.07	687 ± 224	391 ± 264
Symphyotrichum laeve	−2.9 ± 0.8	0.32 ± 0.12	0.2 ± 0.05	425 ± 427	295 ± 292
Symphyotrichum oblongifolium	−4.6 ± 3.4	0.31 ± 0.05	0.32 ± 0.05	629 ± 249	535 ± 301
Tradescantia bracteata	−1.1 ± 0.7	0.37 ± 0.22	0.34 ± 0.18	456 ± 244	717 ± 357
Tradescantia ohiensis	0 ± 0.3	0.33 ± 0.09	0.24 ± 0.09	267 ± 140	506 ± 388
Tragopogon dubius	−1.6 ± 0.4	0.43 ± 0.11	0.37 ± 0.1	475 ± 120	575 ± 469
Verbesina alternifolia	−8.8 ± 1.8	0.45 ± 0.17	0.31 ± 0.04	1292 ± 1122	942 ± 665
Vernonia baldwinii	−3.6 ± 0.2	0.33 ± 0.08	0.35 ± 0.13	830 ± 526	929 ± 650
Vulpia octoflora	−7.3 ± 2.9	0.11 ± 0.01	0.24 ± 0.03	596 ± 484	293 ± 153
Xanthium strumarium	n/a	0.45 ± 0.13	0.16 ± 0.04	1614 ± 1394	407 ± 65
Zizia aurea	n/a	0.31	0.13	172	60

APPENDIX C

Table C1. Leaf functional trait data for each species (means ± s.d.). Shown are leaf thickness (Thick$_L$; mm), leaf tissue density (ρ_L; g cm^{-3}), leaf angle (A_L; degrees from horizontal), maximum photosynthetic rate (A_{max}; μmol CO_2 m^{-2} s^{-1}), and stomatal conductance (g_s; mol H_2O m^{-2} s^{-1}).

Species	Thick$_L$	ρ_L	A_L	A_{max}	g_s
Achillea millefolium	0.27 ± 0.06	0.28 ± 0.08	49	5.7 ± 5.2	0.08 ± 0.09
Ageratina altissima	0.18 ± 0.13	0.28 ± 0.12	0	8.1 ± 0.5	0.15 ± 0.05
Amaranthus blitoides	0.19 ± 0.05	0.24 ± 0.04	6	7.1 ± 2.5	0.05 ± 0.02
Amaranthus retroflexus	0.19 ± 0.07	0.41 ± 0.23	0	12.6 ± 4.3	0.11 ± 0.04
Ambrosia psilostachya	0.24 ± 0.08	0.45 ± 0.07	40	4.5 ± 0.5	0.06 ± 0.02
Amorpha canescens	0.12 ± 0.01	0.31 ± 0.05	4	2.2 ± 0.8	0.03 ± 0.01
Andropogon gerardii	0.14 ± 0.02	0.86 ± 0.82	69	13.3 ± 5	0.12 ± 0.06
Antennaria neglecta	0.21 ± 0.05	0.32 ± 0.06	52	7.1 ± 2.2	0.22 ± 0.17
Apocynum cannabinum	0.15 ± 0.05	0.55 ± 0.25	0	10.8 ± 3.3	0.11 ± 0.04
Aristida oligantha	0.13 ± 0.03	0.52 ± 0.17	50	16.2 ± 9.1	0.12 ± 0.05
Aristida purpurea	0.12 ± 0.03	0.46 ± 0.2	70	14.5 ± 8	0.1 ± 0.02
Artemisia ludoviciana	0.19 ± 0.05	0.42 ± 0.21	45	8.4 ± 5.6	0.1 ± 0.08
Asclepias incarnata	0.18 ± 0.04	0.34 ± 0.08	11	5.7 ± 3.3	0.09 ± 0.04
Asclepias speciosa	0.19 ± 0.07	0.27 ± 0.07	0	15.2 ± 2.9	0.19 ± 0.06
Asclepias sullivantii	0.31 ± 0.07	0.22 ± 0.04	38	9.9 ± 2.1	0.13 ± 0.04
Asclepias verticillata	0.17 ± 0.04	0.31 ± 0.05	5	13.5 ± 6.2	0.16 ± 0.07
Asclepias viridis	0.2 ± 0.05	0.26 ± 0.11	30	11.7 ± 5.8	0.12 ± 0.07
Astragalus canadensis	0.17 ± 0.04	0.43 ± 0.14	45	13.4 ± 2.5	0.16 ± 0.05
Baptisia alba	0.21 ± 0.05	0.37 ± 0.09	80	6.9 ± 4.4	0.06 ± 0.05
Baptisia australis	0.25 ± 0.06	0.32 ± 0.1	70	6.2 ± 2.8	0.05 ± 0.03
Bouteloua curtipendula	0.12 ± 0.02	0.55 ± 0.13	35	19 ± 6.3	0.17 ± 0.08
Bouteloua gracilis	0.14 ± 0.02	0.47 ± 0.09	72	11 ± 5.7	0.06 ± 0.02
Bromus inermis	0.18 ± 0.03	0.47 ± 0.25	65	9.5 ± 3.8	0.12 ± 0.06
Carex annectens	0.15 ± 0.01	0.48 ± 0.21	78	11.4 ± 2.3	0.24 ± 0.1
Chamaecrista fasciculata	0.11 ± 0.03	0.63 ± 0.11	0	10.8 ± 3.7	0.12 ± 0.06
Chamaesyce nutans	0.1 ± 0.02	0.71 ± 0.11	15	5.8 ± 4	0.04 ± 0.03
Chloris verticillata	0.08 ± 0.03	0.52 ± 0.14	55	17.5 ± 7	0.13 ± 0.05
Cirsium altissimum	0.34 ± 0.1	0.33 ± 0.14	30	11.1 ± 8	0.13 ± 0.1
Cucurbita foetidissima	0.29 ± 0.05	0.3 ± 0.11	20	13.3 ± 5.6	0.15 ± 0.07
Desmanthus illinoensis	0.11 ± 0.07	0 ± 0.87	7	8.7 ± 4.4	0.09 ± 0.05
Desmodium illinoense	0.18 ± 0.02	0.36 ± 0.07	75	5.1 ± 2	0.04 ± 0.02
Dichanthelium acuminatum	0.09 ± 0.03	0.34 ± 0.18	55	6.7 ± 2.2	0.12 ± 0.06

Table C1. Continued.

Species	Thick_L	ρ_L	A_L	A_{max}	g_s
Echinacea angustifolia	0.38 ± 0.1	0.29 ± 0.09	35	16.2 ± 1.7	0.3 ± 0.11
Echinacea atrorubens	0.45 ± 0.07	0.23 ± 0.04	55	11.9 ± 4.4	0.19 ± 0.13
Echinacea pallida	n/a	n/a	0	13.7	0.16
Echinodorus berteroi	0.2	0.26	0	13.7 ± 5.7	0.18 ± 0.08
Eleusine indica	0.08 ± 0.07	0.72 ± 0.32	57	11.3 ± 3.6	0.08 ± 0.03
Elymus canadensis	0.14 ± 0.03	0.47 ± 0.15	35	9.8 ± 1.9	0.13 ± 0.05
Elymus villosus	0.11 ± 0.03	0.41 ± 0.05	70	4.3 ± 3.3	0.08 ± 0.05
Elymus virginicus	0.13 ± 0.03	0.54 ± 0.32	67	12.2 ± 5.3	0.16 ± 0.07
Eragrostis pectinacea	0.16 ± 0.02	n/a	64	10.3 ± 9.1	0.07 ± 0.06
Erigeron annuus	n/a	n/a	0	24.5	0.2
Eryngium yuccifolium	0.43 ± 0.08	0.24 ± 0.07	60	12.5 ± 6.8	0.26 ± 0.29
Eupatorium altissimum	0.24 ± 0.05	0.59 ± 0.39	25	7.7 ± 4.2	0.1 ± 0.1
Eupatorium purpureum	0.16 ± 0.06	0.31 ± 0.16	0	5.1 ± 2	0.05 ± 0.04
Euphorbia corollata	n/a	n/a	0	n/a	n/a
Euphorbia dentata	0.12 ± 0.01	0.54 ± 0.1	10	2.7 ± 2.6	0.03 ± 0.02
Euphorbia marginata	0.25 ± 0.07	0.23 ± 0.08	0	9.8 ± 3	0.14 ± 0.05
Festuca subverticillata	0.09 ± 0.02	0.67 ± 0.15	80	5.4 ± 1.9	0.07 ± 0.01
Helianthus annuus	0.29 ± 0.06	0.41 ± 0.15	15	16.9 ± 6.1	0.2 ± 0.11
Helianthus petiolaris	0.37 ± 0.06	0.35 ± 0.06	0	21 ± 5.3	0.28 ± 0.13
Helianthus salicifolius	0.2 ± 0.07	0.37 ± 0.12	0	6.4 ± 3.1	0.07 ± 0.05
Helianthus tuberosus	0.3 ± 0.02	0.43 ± 0.08	5	7.3 ± 1.4	0.06 ± 0.01
Heliopsis helianthoides	0.21 ± 0.08	0.41 ± 0.16	10	10.7 ± 6.4	0.17 ± 0.13
Hesperostipa spartea	0.12 ± 0.03	0.62 ± 0.22	70	8.2 ± 5.5	0.15 ± 0.1
Hordeum jubatum	0.13 ± 0.04	0.37 ± 0.12	75	12.8 ± 5.3	0.16 ± 0.08
Hordeum pusillum	0.1 ± 0.04	0.56 ± 0.22	70	13.3 ± 3.7	0.22 ± 0.1
Koeleria macrantha	0.14 ± 0.05	0.49 ± 0.21	73	13.2 ± 7.5	0.2 ± 0.15
Lactuca canadensis	0.18 ± 0.03	0.23 ± 0.03	15	14.4 ± 4.7	0.16 ± 0.03
Lactuca ludoviciana	0.23 ± 0.04	0.16 ± 0.02	0	13.1 ± 1.8	0.23 ± 0.1
Lepidium densiflorum	0.13 ± 0.05	0.57 ± 0.35	58	6.8 ± 3.2	0.09 ± 0.05
Lepidium virginicum	0.19 ± 0.06	0.57 ± 0.33	20	6.6 ± 4.7	0.08 ± 0.05
Lespedeza capitata	0.16 ± 0.03	0.41 ± 0.11	0	11.5 ± 4.1	0.23 ± 0.19
Lespedeza violacea	0.1 ± 0.03	0.59 ± 0.23	15	7.3 ± 2.5	0.08 ± 0.03
Liatris aspera	0.35 ± 0.08	0.35 ± 0.11	75	11.4 ± 6.9	0.18 ± 0.11
Liatris mucronata	0.38 ± 0.06	0.4 ± 0.06	90	12.1 ± 3.3	0.23 ± 0.07
Liatris punctata	0.41 ± 0.04	0.39	75	11.9 ± 0.4	0.25 ± 0.05
Liatris pycnostachya	0.28 ± 0.06	0.21 ± 0.02	50	8.2 ± 5.1	0.08 ± 0.06
Mirabilis linearis	0.32 ± 0.14	0.43 ± 0.14	35	13 ± 9.1	0.13 ± 0.11
Monarda fistulosa	0.2 ± 0.06	0.34 ± 0.11	2	5.8 ± 3.8	0.06 ± 0.06
Oenothera biennis	0.26 ± 0.07	0.33 ± 0.1	40	6.6 ± 4.2	0.08 ± 0.06
Oenothera macrocarpa	0.32 ± 0.07	0.32 ± 0.1	8	9.1 ± 6	0.14 ± 0.09
Packera plattensis	0.22 ± 0.04	0.42 ± 0.21	20	11.1 ± 2.4	0.15 ± 0.06
Panicum capillare	0.15	0.21	0	19	0.16
Panicum virgatum	0.15 ± 0.03	0.43 ± 0.11	58	12.2 ± 7	0.08 ± 0.05
Pascopyrum smithii	0.23	0.52	50	20.3 ± 0.2	0.22 ± 0.01
Penstemon cobaea	0.32 ± 0.03	0.41 ± 0.05	10	13 ± 3.5	0.17 ± 0.05
Penstemon digitalis	0.3 ± 0.06	0.34 ± 0.07	42	8.1 ± 2.8	0.13 ± 0.08
Penstemon grandiflorus	0.31 ± 0.06	0.3 ± 0.05	50	11 ± 3.5	0.12 ± 0.06
Penstemon tubiflorus	0.28 ± 0.04	0.34 ± 0.04	49	7.6 ± 4.2	0.1 ± 0.05
Physalis pubescens	0.34 ± 0.04	0.25 ± 0.03	20	2 ± 1.2	0.03 ± 0.01
Plantago rugelii	0.25 ± 0.09	0.37 ± 0.18	0	9.5 ± 3.8	0.16 ± 0.1
Poa arida	0.2 ± 0.05	0.49 ± 0.09	60	10.2 ± 2.7	0.13 ± 0.09
Poa pratensis	0.15 ± 0.01	0.46 ± 0.07	81	11.8 ± 10.9	0.17 ± 0.13
Polygonum virginianum	0.17 ± 0.04	0.4 ± 0.08	23	7.1 ± 2.8	0.08 ± 0.04
Prenanthes aspera	0.21 ± 0.07	0.33 ± 0.21	45	14 ± 8.4	0.3 ± 0.2
Prunella vulgaris	0.21 ± 0.08	0.83 ± 0.73	0	5.6 ± 3.3	0.07 ± 0.06
Psoralidium tenuiflorum	0.29 ± 0.06	0.37 ± 0.1	0	11.6 ± 6.5	0.2 ± 0.13
Ratibida pinnata	0.32 ± 0.12	0.3 ± 0.12	50	11.4 ± 12.3	0.13 ± 0.13
Rudbeckia hirta	0.39 ± 0.1	0.23 ± 0.07	50	11.1 ± 3.6	0.14 ± 0.09
Rudbeckia lacinata	0.23 ± 0.05	0.21 ± 0.09	53	6.8 ± 5.8	0.1 ± 0.09
Ruellia humilis	0.16 ± 0.04	0.36 ± 0.11	15	7.9 ± 3.6	0.13 ± 0.13
Salvia azurea	0.2 ± 0.04	0.44 ± 0.1	27	6.8 ± 4.4	0.09 ± 0.07
Salvia reflexa	0.2 ± 0.02	n/a	1	7 ± 3.3	0.11 ± 0.05
Schizachyrium scoparium	0.1 ± 0.02	0.68 ± 0.23	79	11.9 ± 6.9	0.1 ± 0.04
Senna marilandica	0.14 ± 0.04	0.65 ± 0.23	0	8.6 ± 5.4	0.08 ± 0.06
Setaria pumila	0.11 ± 0.04	0.44 ± 0.23	72	8 ± 2.6	0.05 ± 0.02
Silphium integrifolium	0.34 ± 0.1	0.4 ± 0.1	30	9.4 ± 3.1	0.1 ± 0.04
Silphium laciniatum	0.57 ± 0.05	0.49 ± 0.47	75	8.2 ± 3.4	0.12 ± 0.12
Solanum carolinense	0.16 ± 0.05	0.39 ± 0.18	0	6.5 ± 2.4	0.07 ± 0.02

Table C1. Continued.

Species	$Thick_L$	ρ_L	A_L	A_{max}	g_s
Solanum rostratum	0.16 ± 0.07	0.64 ± 0.25	10	4.9 ± 5.7	0.09 ± 0.1
Solidago canadensis	n/a	n/a	0	n/a	n/a
Solidago missouriensis	0.29	0.26 ± 0.02	40	2.3 ± 1.2	0.03 ± 0.01
Solidago mollis	0.17 ± 0.04	0.39 ± 0.11	40	8 ± 2.5	0.17 ± 0.07
Solidago nemoralis	0.13 ± 0.07	0.45 ± 0.13	0	9.8 ± 4.5	0.15 ± 0.1
Solidago petiolaris	0.16 ± 0.04	0.41 ± 0.09	35	15.8 ± 18.4	0.2 ± 0.2
Solidago ulmifolia	0.12 ± 0.03	0.61 ± 0.14	0	7.2 ± 2.5	0.08 ± 0.04
Sorghastrum nutans	0.14 ± 0.05	0.48 ± 0.2	62	18.4 ± 7.9	0.12 ± 0.06
Sporobolus heterolepis	0.22	n/a	0	5.6	0.06
Stellaria media	n/a	n/a	0	n/a	n/a
Stenosiphon linifolius	0.33 ± 0.04	0.29 ± 0.05	15	12.7 ± 6.7	0.17 ± 0.16
Symphyotrichum laeve	0.26 ± 0.08	0.27 ± 0.12	25	12.2 ± 1.2	0.19 ± 0.1
Symphyotrichum oblongifolium	0.2 ± 0.08	0.46 ± 0.23	25	13.6 ± 5.1	0.18 ± 0.11
Tradescantia bracteata	0.33 ± 0.07	0.18 ± 0.03	65	10.1 ± 6	0.11 ± 0.1
Tradescantia ohiensis	0.27 ± 0.1	0.2 ± 0.06	75	12.7 ± 3.5	0.15 ± 0.06
Tragopogon dubius	0.26 ± 0.08	0.38 ± 0.11	70	13.9 ± 5.3	0.16 ± 0.08
Verbesina alternifolia	0.31 ± 0.02	0.25 ± 0.05	61	4.4 ± 2.7	0.05 ± 0.02
Vernonia baldwinii	0.18 ± 0.02	0.37 ± 0.11	50	6.6 ± 2.9	0.07 ± 0.04
Vulpia octoflora	0.11 ± 0.09	0.73 ± 0.13	70	6.1 ± 3.9	0.11 ± 0.08
Xanthium strumarium	0.55 ± 0.07	0.1	0	21.8 ± 1.6	0.22 ± 0.02
Zizia aurea	0.19	0.36	0	11.7	0.26