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Global diversity of drought tolerance and grassland climate-change resilience

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Drought reduces plant productivity, induces widespread plant mortality and limits the geographic distribution of plant species[1-7]. As climates warm and precipitation patterns shift in the future[8,9], understanding the distribution of the diversity of plant drought tolerance is central to predicting future ecosystem function and resilience to climate change[10-12]. These questions are especially pressing for the world's 11,000 grass species[13], which dominate a large fraction of the terrestrial biosphere[14], yet are poorly characterized with respect to responses to drought. Here, we show that physiological drought tolerance, which varied tenfold among 426 grass species, is well distributed both climatically and phylogenetically, suggesting most native grasslands are likely to contain a high diversity of drought tolerance. Consequently, local species may help maintain ecosystem functioning in response to changing drought regimes without requiring long-distance migrations of grass species. Furthermore, physiologically drought-tolerant species had higher rates of water and carbon dioxide exchange than intolerant species, indicating that severe droughts may generate legacies for ecosystem functioning. In all, our findings suggest that diverse grasslands throughout the globe have the potential to be resilient to drought in the face of climate change through the local expansion of drought-tolerant species.

Despite widespread agreement on the importance of drought in grasslands, predictions of grassland functioning under future climates is limited by our understanding of how grasses respond to drought and the geographic distribution of grasses with different functional traits. For example, plant productivity in Kansas and Nebraska grasslands was maintained during drought in the 1930s not by the immigration of drought-tolerant species, but by local expansion of these species after less-tolerant species perished[15,16]. Yet, it is unknown how diversity of drought tolerance among grassland species varies along climate gradients globally. Further research on the effects of functional diversity on resilience is still necessary, but grasslands containing a large range of drought tolerance among species should have greater resilience to drought compared with grasslands with less functional diversity. Grasslands without drought-tolerant species present are more likely to experience major declines with drought in grassland ecosystem function such as carbon uptake, productivity, soil retention and provision of forage to grazers following drought. Droughted grasslands may require long-distance migrations to restore such functions[17,18], which may not be able to keep pace with the velocity of climate change[19]. Additionally, if drought-tolerant species have unique sets of functional traits beyond drought tolerance[20-22], droughts might alter both the functional composition of grasslands and important grassland processes after cessation of drought. However, present functional trait data are insufficient to predict how drought may alter the functional composition of grasslands.

To better understand drought tolerance in grasslands, we assessed physiological drought tolerance and a number of other leaf functional traits for 426 grass species. Plants can tolerate environmental drought by accessing stable or stored water sources or even speeding reproduction to precede drought-induced mortality. Because grasses store too little water or carbon to maintain shoots during extended droughts, long-term resistance for grasses to low water potentials is probably first approximated by their physiological tolerance of drought. Here, physiological drought tolerance was assessed as the critical leaf water potential (Ψ_{crit}) at which stomatal conductance fell below an ecological threshold for functioning[23,24]. As leaf water potential (Ψ) is expressed as a negative number representing the tension on the water column in a plant, lower values of Ψ_{crit} indicate greater physiological tolerance of plants to dry soils. To understand the distribution of functional diversity for drought tolerance within grasslands, we examined the global bioclimatic patterns of grass physiological drought tolerance and its phylogenetic distribution. We then examined the relationships between Ψ_{crit} and other leaf functional traits to test whether changes in the prevalence of drought-tolerant species would change the functional composition of grasslands beyond drought tolerance.

The diversity of physiological drought tolerance was high throughout the bioclimatic range that grasslands occupy such that changes in the prevalence of drought could be accompanied by changes in local abundance that may help preserve ecosystem function. Across 426 grass species, the median Ψ_{crit} was -4.1 MPa and ranged from -1.4 MPa to -14 MPa—our minimum detection limit that was met by 26 species (Fig. 1a). Available species-distribution data allowed climate envelopes to be generated for 52% of these species. For this subset of species, we examined how the diversity of grass physiological drought tolerance varied across the range of mean annual precipitation (MAP) associated with grasslands (250–1,500 mm). Both the upper and lower bound of Ψ_{crit} for species present within a 50-mm interval of MAP increased with increasing MAP ($P < 0.001$; Fig. 2). Although wetter regions within the grassland precipitation range had fewer physiologically drought tolerant and more intolerant species, the shift in maximum and minimum Ψ_{crit} was only 1.0 MPa, which was just 8% of the 12.4 MPa mean range (central 95%) of drought tolerance. There were no shifts, for example, in minimum or maximum Ψ_{crit} when using the 10th and 90th percentile as the bounds (means $= -2.3$ and -10.8 MPa, respectively; $P > 0.3$ for both), whereas shifts in the inner quartile ranges (25–75%) were less than 0.5 MPa from 250 to 1,500 mm (Fig. 2).

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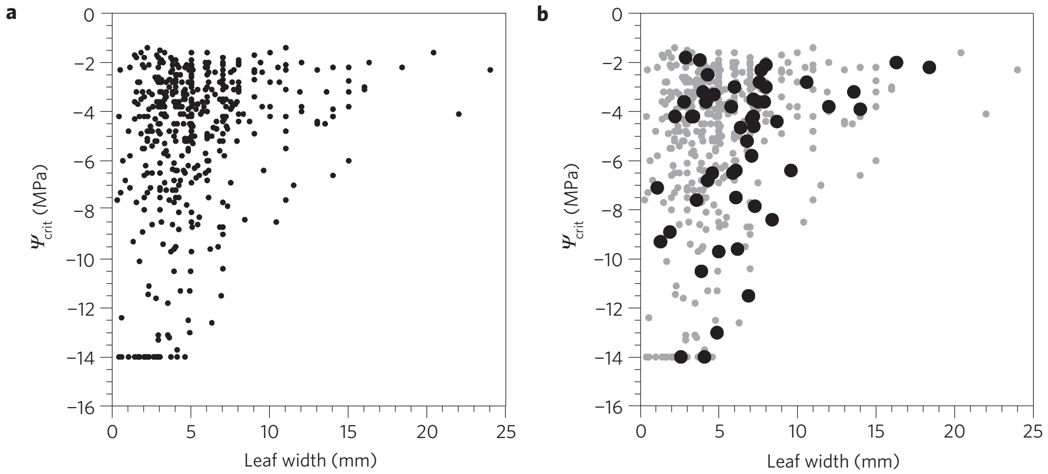

Figure 1 | Relationship between maximum leaf width and $\Psi_{\rm crit}$. a, $\Psi_{\rm crit}$ for 426 species and **b**, same species set with species present at Konza Prairie ($n = 52$) highlighted in black. Minimum Ψ that could be measured was −14 MPa.

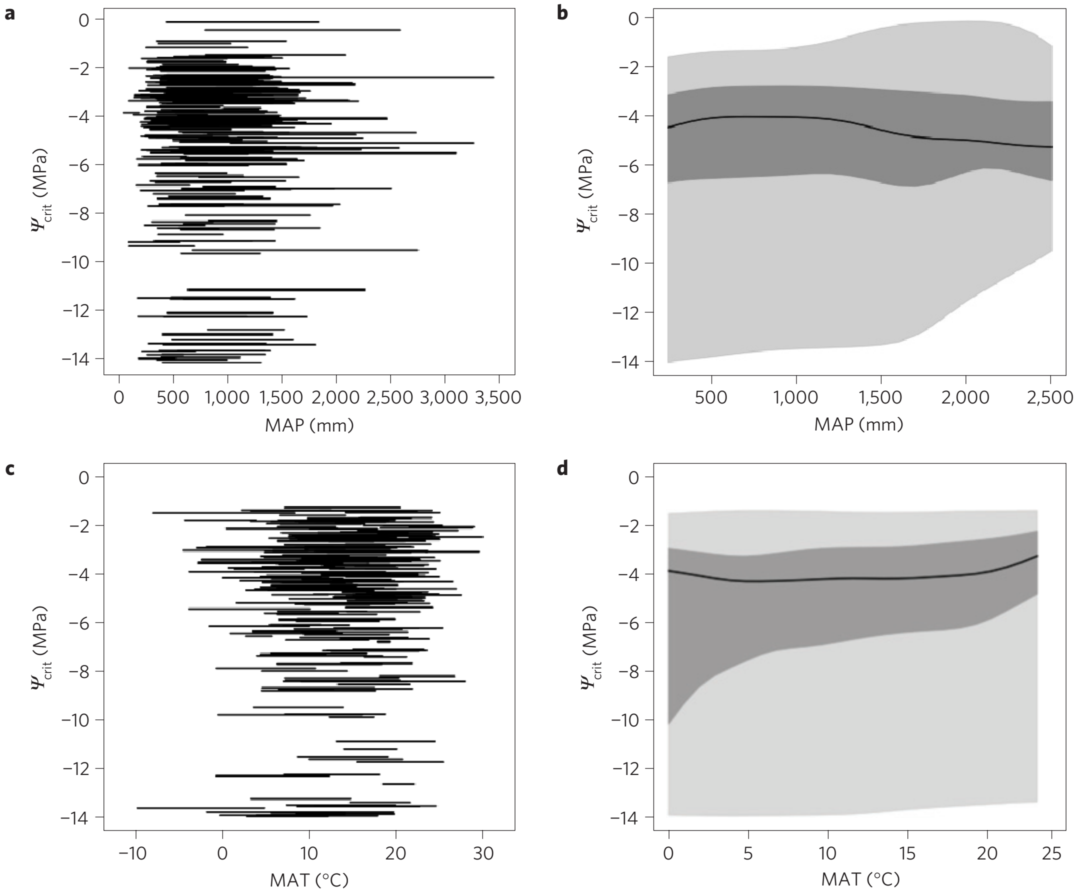

Figure 2 | Bioclimatic ranges of $\Psi_{\rm crit}$. a–d, Ranges of $\Psi_{\rm crit}$ for individual grasses shown versus MAP (**a**) and MAT (**c**). Also shown are median $\Psi_{\rm crit}$ as well as inner quartile range (dark grey) and 95% of the range (light grey) in $\Psi_{\rm crit}$ calculated every 50 mm for MAP (**b**) or 1 °C for MAT (**d**). The centre line is the median $\Psi_{\rm crit}$. Approximate precipitation ranges for different ecosystems: grasslands (250–1,500 mm), savannas (750–2,500 mm) and forests (>1,000 mm; ref. 25). Data compiled from 223 species.

In only the ecosystems with the highest precipitation (MAP > 1,500 mm), representing primarily more humid savannas and forests, but also some high-precipitation grasslands[25,26], would functional responses to severe drought be potentially constrained by the drought tolerance of grass communities. As revealed by piecewise linear regression, maximum drought tolerance declined with increasing MAP for ecosystems with MAP > 1,913 ± 44 mm (Supplementary Table S1) at a rate that was nearly an order of magnitude higher than lower-precipitation ecosystems (0.0065 versus 0.0008 MPa mm^{-1} MAP; Fig. 2, $P < 0.001$). Although caution should be applied to these results owing to the relatively few species that extend into these regions (∼10% of the species sampled for which climate envelopes could be generated), reductions in precipitation might require an immigration of grass species into

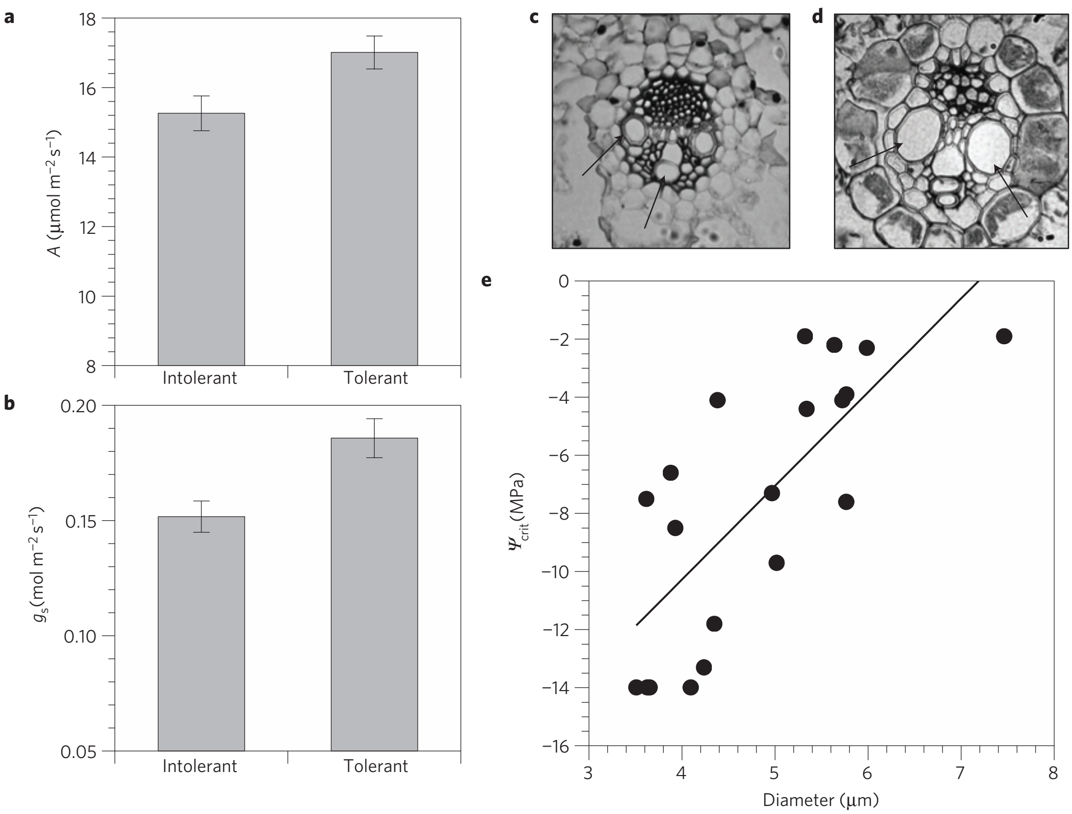

Figure 3 | Ψ_{crit} and functional traits. a,**b**, Differences (± standard error) between physiologically drought-intolerant ($\Psi_{\mathrm{crit}} > -4.1$ MPa) and -tolerant grasses ($\Psi_{\mathrm{crit}} < 4.1$ MPa) in **a**, rates of photosynthesis (A) and **b**, stomatal conductance (g_s). **c**–**e**, Relationship between typical diameter of xylem vessel elements and Ψ_{crit} (**e**) with examples of species that have (**c**) narrow vessel elements (*Koeleria glauca*; 3.5 μm) and (**d**) wide vessel elements (*Panicum queenslandicum*; 7.5 μm). Arrows show largest xylem vessel elements.

high-precipitation ecosystems to maintain ecosystem function. There were no ecologically significant changes in the range of drought tolerance present in grasslands along temperature gradients (<2% of range of Ψ_{crit}; Fig. 2).

Examining the variation in physiological drought tolerance for species collected from a single grassland supports our global evidence that local variation in physiological drought tolerance in grasslands should be high[23,24]. Of the 426 species grown for this experiment, 52 were collected from a single grassland, Konza Prairie, a humid grassland in central North America, representing 60% of Konza's Poaceae species. Comparing the distribution of Ψ_{crit} from the Konza flora with the global distribution reveals that almost the entire global range of physiological drought tolerance is present at just a single grassland site (Fig. 1b).

Physiological drought tolerance was not only widespread geographically, but also phylogenetically (Supplementary Fig. S1). Thus, if specific clades were to become less abundant, the functional diversity of physiological drought tolerance should still be preserved. For 165 species that could reliably be placed in a phylogeny, physiological drought tolerance had evolved numerous times and was widespread throughout the grass phylogeny. There was no more phylogenetic signal in Ψ_{crit} than expected by chance ($K = 0.002$, $P > 0.2$). Similarly, there was no difference in Ψ_{crit} between major clades (BEP versus PACMAD; $P = 0.16$), nor among the four subfamilies for which we had sampled extensively ($P > 0.05$). C_4 species were not on average more or less physiologically drought tolerant that C_3 species (-4.9 ± 0.2 versus -5.2 ± 0.2 MPa, $P = 0.27$; Supplementary Table S2).

Examination of functional traits associated with physiological drought tolerance reveals a unique combination of traits in physiologically drought-tolerant species. Physiologically drought-tolerant grasses ($\Psi_{\mathrm{crit}} < -4.1$ MPa) had higher photosynthetic rates (17.0 ± 0.5 versus 15.3 ± 0.5 μmol m^{-2} s^{-1}, $P = 0.01$; Fig. 3) and higher stomatal conductance (0.185 ± 0.008 versus 0.152 ± 0.008 mol m^{-2} s^{-1}, $P = 0.002$; Fig. 3) compared with physiologically drought-intolerant species ($\Psi_{\mathrm{crit}} > -4.1$ MPa). This suggests that droughts may select for species that, under non-drought conditions, will have higher gas-exchange rates per unit leaf area, perhaps aiding in the recovery of primary productivity following drought.

Considering the relationships among functional traits associated with physiological drought tolerance, among 426 grass species, a trade-off boundary was apparent between physiological drought tolerance and leaf width (Fig. 1). The corners of the relationships describe endpoints of selection: wide-leaved species that were drought intolerant, narrow-leaved physiologically drought-intolerant species and narrow-leaved physiologically drought-tolerant species. There were no examples of physiologically drought-tolerant species with wide leaves. Although wide-leaved species were not physiologically drought tolerant, the main physical adaptations to drought seem to be structural rather than morphological (Supplementary Text). Across 20 measured species, physiologically drought-tolerant grass species had narrow xylem elements (Fig. 3), consistent with mechanisms of cavitation resistance in other taxonomic groups[27].

In all, our results reveal the basic patterns of physiological drought tolerance in grasses and grasslands. Grass physiological drought tolerance has probably evolved numerous times and is widely distributed phylogenetically and geographically. Consequently, throughout a broad bioclimatic range of grasslands, local species may help maintain ecosystem functioning in the face of drought, even without large migrations of grass species.

This suggests that the observed widespread functional diversity of drought tolerance in native grasslands should help provide resilience to drought, rather than requiring immigration of physiologically drought-tolerant species to help maintain ecosystem function. The observed higher photosynthetic and stomatal conductance rates of drought-tolerant species would require parameterizing models of carbon and water dynamics and surface energy balance differently when assessing the responses of grasslands to drought.

Additional research on both drought tolerance and intolerance will be needed to predict how grassland communities will respond to climate change. The triangular relationship between physiological drought tolerance and leaf width raises questions about the ecological strategies associated with physiologically drought-intolerant species. For example, species with wide leaves had long, thick, low-tissue-density leaves with higher photosynthetic rates and water-use efficiency (Supplementary Table S3). This might indicate tolerance of shade or advantages under high nutrient availability[28], but the associations of both ends of the drought-intolerant, leaf-width axis with other important ecological factors remains to be determined. Grass species that extended into (or were confined to) drier regions were not more physiologically drought tolerant but did have longer, narrower leaves ($P < 0.01$ for all comparisons, Supplementary Fig. S2), which suggests that reductions in precipitation might promote species associated with these traits[29]. Yet, additional research is required to understand the functional significance of these trait patterns in grassland communities.

Although drought would shift the functional composition of grassland communities in ways that we do not yet understand, bioclimatic patterns suggest that species-rich grasslands should have sufficient functional diversity with respect to drought to help maintain ecosystem function with changes in climate. Although more research is necessary to better understand how plant communities of different functional composition and diversity respond to drought, the ability of grasslands to respond to severe droughts is likely to depend on grasslands maintaining their plant diversity in light of other global change factors. Understanding the role of drought in patterns of plant diversity, community structure and ecosystem function will require better understanding of the spatiotemporal responses of plant communities to drought[30] and the mechanisms that maintain functional diversity in grasslands. This knowledge could be used to help promote resilient ecosystems and better model the consequences of future drought to grassland ecosystems.

Methods

Plants were grown from seeds acquired from the United States Department of Agriculture (392 species) and hand-collected in New Zealand (three species). Seeds originated from all six continents ranging from 8% from Australia to 33% from Asia. Seeds were germinated in 164 ml plastic pots (D-40 Cone-tainers, Stuewe and Sons) containing commercial potting mix (Scotts). Two replicates were grown for each species with only two seedlings per pot. Plants were grown in a Conviron growth chamber (model PGV 36, Controlled Environments) with 16-hour days at 25 °C and light levels at 1,200 μmol m^{-2} s^{-1}. Temperatures at night were held at 20 °C. Plants were watered daily and treated with a commercial fertilizer (Miracle Gro 24-8-16 All Purpose Fertilizer, Scotts) biweekly to eliminate nutrient stress. During the 2011 growing season, for 52 grass species, perennating organs were collected from Konza Prairie, a 3487-ha native tallgrass prairie located in northeastern Kansas, USA (39.08° N, 96.56° W). Mean annual temperature (MAT) is 13 °C, with average monthly temperatures ranging from −3 °C in January to 27 °C in July. Annual precipitation for Konza Prairie averaged 844 mm from 1983 to 2009, with approximately 75% falling in the April to September growing season and peak precipitation occurring in June. Konza grasses were planted directly in the same medium and grown under the same conditions as plants started from seeds. 21 species were grown from both seeds and vegetative parts and their values averaged.

After an average of five weeks post-germination or planting, maximum rates of photosynthesis (A_{a}) and stomatal conductance (g_{s}) were measured on a recently expanded leaf for each species using a Li-6400 infrared gas analyser with red/blue-light-emitting diode light source and CO$_2$ injector (LICOR Biosciences). Light intensity inside the cuvette was 2,000 μmol m^{-2} s^{-1}, CO$_2$ concentration was 400 ppm and relative humidity was 45%. Leaf thickness ($\mathrm{Thick}_{\mathrm{L}}$) was measured for two to three newly expanded, mature leaves on each plant using digital calipers (Thermo Fisher Scientific) along with length ($\mathrm{Length}_{\mathrm{L}}$) and maximum width ($\mathrm{Width}_{\mathrm{L}}$). Leaves were scanned for area (LI-COR leaf area meter, Model LI-3100), dried and then weighed to determine leaf-tissue density.

After this time, watering was ceased for one pot of each species. Leaf conductance was measured daily with a steady-state diffusion porometer (model SC-1, Decagon Devices). Leaf conductance was measured daily for each plant until $g_{\mathrm{s}} < 5$ mmol m^{-2} s^{-1}, which represented stomatal closure. Following stomatal closure, one to three leaves were collected and the hydrostatic pressure potential was measured using a Scholander pressure bomb (PMS Instrument). The leaf water potential corresponding to stomatal closure is considered the Ψ_{crit} of the species, representing an index of physiological drought tolerance. The average time to Ψ_{crit} after cessation of watering was 5.7 days. Although we focused on minimum water potentials, the lowest Ψ_{crit} values are associated with reasonable exponential declines in conductance across a wide range of plant water potentials. (Supplementary Fig. S2).

At the end of the growth period one leaf per species was harvested and placed in a fixative (formalin: ethanol: glacial acetic acid) until the tissue could be further processed for anatomical analyses. A ∼5-mm-thick section was taken from the centre of each leaf, embedded with paraffin, mounted on slides and stained with toluidine blue. Anatomical images were taken using a digital camera (Leica DFC 290, Leica Microsystems GmbH) coupled to a light microscope (Leica DM1000, Leica Microsystems GmbH) and analysed with ImageJ (http://rsbweb.nih.gov/ij/). The diameter of each vessel was calculated as an ellipse from measurements of the long and short axis of every vessel in the leaf. A Weibull distribution was fit to the vessel diameter data and the diameter where the distribution peaked was identified and used in our analysis. Vascular-bundle diameters were bimodally distributed in each species allowing division of vascular bundles into just two size classes: major and minor.

Two separate sets of principal component analyses were run on the correlations of the seven functional traits (Ψ_{crit}, $\mathrm{Width}_{\mathrm{L}}$, $\mathrm{Thick}_{\mathrm{L}}$, $\mathrm{Length}_{\mathrm{L}}$, leaf tissue density, photosynthetic rate (A) and g_{s}). One principal component analysis was run for narrow-leaved species (<4.6 mm) that varied primarily in drought tolerance and another for drought-intolerant species ($\Psi_{\mathrm{crit}} > 4.1$ MPa) that varied primarily in their leaf width. Transverse sections of leaves were used to determine the most common diameter of xylem elements. For each species, climate envelopes were generated from global occurrence data. For each species occurrence, we extracted 50-year MAT and MAP and then determined upper and lower bounds of each to describe the climate envelope of the species. Taxonomic information for each species was acquired from the uniprot database (www.uniprot.org). Phylogenetic signal in Ψ_{crit} was quantified by calculating the K statistic for species with measured Ψ_{crit} values.

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Author contributions

J.M.C., T.W.O. and J.B.N. conceived the research and carried out the measurements of grasses. E.G.T. and J.M.C. collected plants from Konza. A.M.S. and J.M.C. generated climate envelopes for each species. S.W.K. carried out the phylogenetic analyses. J.M.C. and T.W.O. analysed the data and generated the figures. All authors contributed to the preparation of the manuscript.

Additional information

Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to J.M.C.

Competing financial interests

The authors declare no competing financial interests.