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Different clades and traits yield similar grassland functional responses

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Plant functional traits are viewed as key to predicting important ecosystem and community properties across resource gradients within and among biogeographic regions. Vegetation dynamics and ecosystem processes, such as aboveground net primary productivity (ANPP), are increasingly being modeled as a function of the quantitative traits of species, which are used as proxies for photosynthetic rates and nutrient and water-use efficiency. These approaches rely on an assumption that a certain trait value consistently confers a specific function or response under given environmental conditions. Here, we provide a critical test of this idea and evaluate whether the functional traits that drive the well-known relationship between precipitation and ANPP differ between systems with distinct biogeographic histories and species assemblages. Specifically, we compared grasslands spanning a broad precipitation gradient (~200–1,000 mm/y) in North America and South Africa that differ in the relative representation and abundance of grass phylogenetic lineages. We found no significant difference between the regions in the positive relationship between annual precipitation and ANPP, yet the trait values underlying this relationship differed dramatically. Our results challenge the trait-based approach to predicting ecosystem function by demonstrating that different combinations of functional traits can act to maximize ANPP in a given environmental setting. Further, we show the importance of incorporating biogeographic and phylogenetic history in predicting community and ecosystem properties using traits.

functional traits | grasslands | phylogenetics | ecosystem function | biogeography

Net primary productivity (NPP), or the biomass produced by the conversion of CO_2 via photosynthesis minus that lost to respiration, is a fundamental link between the atmosphere and the biosphere. Understanding and predicting the drivers of terrestrial NPP is of the utmost importance, especially for grasslands, which cover more than 40% of terrestrial land surface, constitute upwards of 30% of terrestrial gross primary productivity (1, 2), and are responsible for important ecosystem services such as carbon sequestration and forage production. Precipitation is the primary driver of variation in aboveground NPP (ANPP) in grasslands across broad spatial scales (3–6), and a consistent relationship has been observed between ANPP and precipitation across biogeographic regions (7). However, our understanding of the factors that underlie this emergent pattern remain limited.

Recently, ecosystem processes, including ANPP, have been modeled as a function of the quantitative traits of organisms that reflect adaptations to environmental variation, and are often proxies for photosynthetic rates, and nutrient and water-use efficiency (8–11). Although these approaches are promising, they rely on the assumption that a certain trait value confers a specific function or response in a given environment, regardless of differences among species in other traits or interactions among traits. Furthermore, these "trait-based" approaches assume robust trait–environment and trait–ecosystem function associations across broad spatial scales and/or biogeographic regions (12, 13). Here, we test these

assumptions by measuring stand-level ANPP and functional and phylogenetic turnover of the grass community across broad precipitation gradients in grassland ecosystems of South Africa (SA) and North America (NA). These two regions differ dramatically in their geological, evolutionary, and biogeographic histories (14, 15), which has resulted in significant differences in the representation of different grass species and major lineages (Fig. 1 and Fig. S1). Despite these differences, these regions harbor grasslands that span a similar rainfall gradient and are dominated by grasses that use the C_4 photosynthetic pathway, making them ideal for determining whether functional traits map similarly to environmental conditions and ecosystem function in disparate regions (Table S1 and Fig. S2).

Ten grassland sites were selected on each continent, spanning a mean annual precipitation gradient of ~200–1,000 mm (Fig. 1). All sites were ungrazed at the time of sampling and had no history of overgrazing. Twenty plots at each site were sampled for grass community composition and ANPP, and functional traits associated with relative growth rate and nutrient and water use strategies were quantified for the common grass species at each site. Whole community ANPP was collected at 17 of the 20 sites, because sampling was limited at three sites due to environmental constraints during collection years. Voucher specimens of each species were collected for DNA sequencing and phylogenetic

Significance

Plant functional traits—characteristics that influence performance or fitness—are increasingly being used to model important ecosystem properties such as primary production. These approaches assume that traits confer specific functions or responses under given environmental conditions, and that these trait–environment and trait–function relationships can be generalized globally irrespective of a region's history or differences in species assemblages. Here, we test this assumption in grasslands with distinct histories and find that different combinations of trait values can yield similar productivity–precipitation relationships. Our study highlights a missing link in the development of trait-based approaches to modeling ecosystem function, namely that there is not necessarily a single solution or set of traits that yields higher function in a given environment.
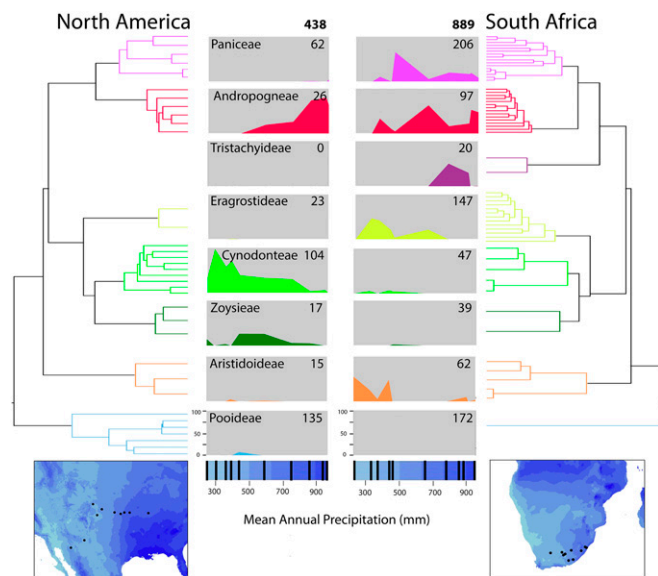
Fig. 1. Regional Bayesian maximum clade credibility phylogenies of grass species present within plots across all sites in NA and SA. The subimages represent the percent of total relative abundance represented by each major grass clade across the sampled precipitation gradient. Numbers within the subimages represent the number of species within each clade present in each region based on surveys of floras of the Great Plains of NA (including New Mexico and Arizona) and SA. Maps of each region show mean annual precipitation and sampled sites.

inference (*Methods*). We used this dataset to test whether the relationship between traits and environment (precipitation) is consistent across the two regions, to determine which traits best predict ANPP, and to assess whether these trait–environment and trait–function relationships can be explained by the representation, diversity, and/or ecological dominance of grass lineages within each region.

Because we focused on the grass component of the plant community, we first tested whether grass production largely accounted for ANPP in our communities and was a strong predictor of total ANPP. In NA and SA, we found that grasses constitute an average of 74% (SD = 22) and 85% (SD = 13) of total ANPP, respectively. Furthermore, grass ANPP predicted 91% of the plot-level variation in total ANPP in NA, and 97% in SA (Fig. S3).

Whereas multiple environmental variables were measured (Table S1 and Fig. S2), annual precipitation in the current year was the main variable used as a predictor of variation in ANPP across sites, because it is widely recognized to be an important driver of variation in productivity in grassland ecosystems (4–7). The current year's annual precipitation explained most of the variation in ANPP at both sites (98% and 83% in NA and SA, respectively; Fig. 2A), and we found no significant difference in the slope ($t_{13} = -0.672$, $P = 0.514$) or intercept ($t_{13} = -0.500$, $P = 0.625$) of the relationship in NA versus SA grasslands. When a single model was fit to the combined data from both NA and SA, the slope of the overall relationship between the current year's precipitation and ANPP was estimated to be 0.69 [95% CI (0.599, 0.786); Fig. 2B], which is similar to estimates from previous studies (4–7).

Despite a highly similar relationship between annual precipitation and ANPP, the regions differed in their phylogenetic and functional representation across the precipitation gradients. SA grasslands were more diverse with a total of 62 grass species identified across all sites, whereas only 35 were found in NA sites (Fig. 1), perhaps largely reflecting differences in biogeographic history, the evolutionary history of large herbivores, and recent glaciation in NA (14, 15). Although there was overlap in the representation of major

grass clades across the regions, they differed significantly in their relative abundance across the precipitation gradients (Fig. 1). Andropogoneae and Cynodonteae were responsible for the bulk of the grass abundance (and thus productivity) in the mesic and xeric sites of NA, respectively. In contrast, SA grassland sites exhibited higher phylogenetic diversity with multiple clades present in high abundance across the precipitation gradient. Aristidoideae and Eragrostideae were most abundant in the more xeric sites in SA, whereas Paniceae, Andropogoneae, and Tristachyideae were abundant in more mesic sites (Fig. 1). We also found significant phylogenetic lineage turnover along the precipitation gradients (Table S2; NA: $r = 0.539$, $P = 0.001$; SA: $r = 0.398$, $P = 0.001$). Although this general pattern of phylogenetic turnover across climatic gradients among major C4 lineages has been observed in other regions as well (16–18), our study shows how phylogenetic turnover differs between grasslands with broadly divergent evolutionary and biogeographic histories. These results underscore the diversity of climatic tolerances that are found within a single photosynthetic type (i.e., C4 grasses), and the promise of integrating a phylogenetic perspective in the classification of grasses into functional groups for climate and vegetation modeling (19, 20).

In step with phylogenetic diversity, we found that the representation of functional traits across the precipitation gradients varied significantly for NA and SA grasses. We used community weighted trait means (CWM) of the grasses to model the response of community function to precipitation. The CWM of a trait value is the mean trait value of each species present in the community weighted by its relative abundance. The use of CWMs aligns with the mass ratio hypothesis wherein the dominant species in the community and their traits are sufficient to describe how a community will respond to environmental conditions (21). Mean annual precipitation (MAP) was used for the analysis of trait–environment relationships, because these grasses are largely perennial long-lived species that are not establishing over a single season and, thus, their presence is influenced by longer-term climate conditions. Trait–MAP relationships were inconsistent in NA versus SA (Fig. 3 and Table S3), and for 6 of the 11 traits measured, region was a significant covariate. In SA, MAP was a significant predictor of leaf area (LA), leaf % carbon (leaf C), and stomatal pore index (SPI), whereas MAP was a significant predictor of height, LA, $\delta^{13}C$, leaf C, leaf % nitrogen (leaf N), leaf carbon to nitrogen (C:N), stomatal size, and SPI in NA (Fig. 3). SLA, a widely measured and commonly accepted key plant trait related to resource availability (10), exhibited no significant association with MAP in either NA or SA (Fig. 3C and Table S3). Also height, which has been found to exhibit a positive association with water availability (22), was significantly
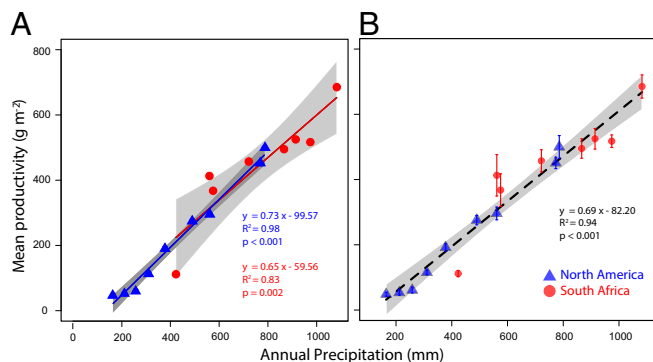

Fig. 2. Relationships between current year's annual precipitation and ANPP for grasslands in central NA and SA. Gray area shows the 95% confidence intervals for the fitted relationship. *A* shows models fitted separately for NA and SA, and *B* shows a single model fit with data from both regions. Error bars in *B* represent the SEM ANPP across all plots at each site.
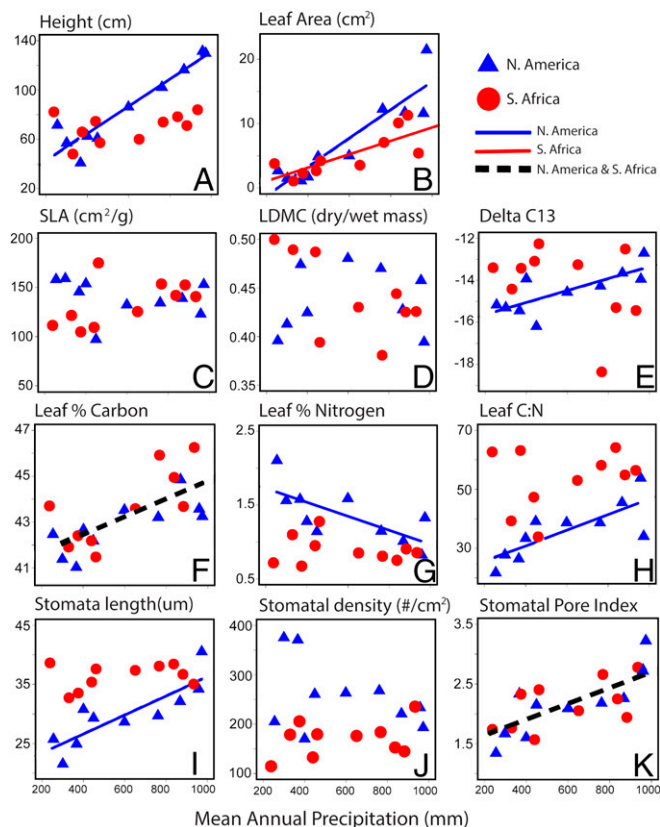
Fig. 3. Community weighted means (CWMs) of the grasses across the broad precipitation gradients in NA and SA. CWMs were calculated by averaging the trait value of all species within a plot weighted by their abundance, with all plots averaged to generate a site-level trait mean. ANCOVA model results are shown for each trait (A–K). Fitted lines represent the model fits for NA, SA, and both (for instances when there was no significant difference in slopes or intercepts for NA and SA). Those graphs without a given line represent instances where there was no significant relationship. Complete statistical results for the ANCOVAs are reported in Table S3.

current extent and species composition of NA grasslands was achieved primarily in the postglacial period when there was a lower diversity of grazers (15). In mesic grasslands of NA, the lower grazing pressure combined with high fire frequency likely resulted in the filtering and selection of species with traits associated with reduced grazing tolerance and higher potential growth rates (i.e., taller plants; greater leaf area; ref. 26).

As was the case for trait–environment associations between the two regions, we found that different sets of traits were the best predictors of ANPP in NA versus SA. In NA, a model that included only height and LA was the best fit by using Bayesian Information Criterion (BIC) (marginal $R^2 = 0.56$, conditional $R^2 = 0.80$), and leaf C was also included in the best fit model by using the Akaike Information Criterion corrected for small sample sizes (AICc; Table S5). In combination, these traits accounted for 60% of the variation in total ANPP across plots and sites (i.e., marginal R^2). In SA, a model that included SLA and SPI was the best fit by using BIC (marginal $R^2 = 0.29$, conditional $R^2 = 0.59$), and height, LA, LDMC, and leaf C were also included in the best fit model by using AICc (Table S5). These traits accounted for 48% of the variation in ANPP. In NA, taller grasses resulted in greater ANPP, whereas greater LA yielded increased ANPP in both NA and SA. In SA, leaf C, SLA, LDMC, and SPI were positively associated with greater ANPP (Table S5). Interestingly, when including variation across plots, height had a slightly negative relationship with ANPP in SA in the AICc best fit model. The significant amount of variation in ANPP that could be predicted by functional traits of the grasses supports the utility of a functional trait approach to vegetation and ecosystem modeling. However, the fact that different sets of traits drive these patterns in regions with different histories and phylogenetic compositions highlights the potential difficulties in using the same traits to predict ecosystem function across biomes globally, and it emphasizes the importance of fitting models on a regional basis or reconsidering the use of trait-based approaches to modeling ecosystem function (27).

Although there was a significant correlation between phylogenetic and functional trait turnover in NA ($r = 0.790$, $P = 0.001$) and SA ($r = 0.348$, $P = 0.006$), these correlations were driven by
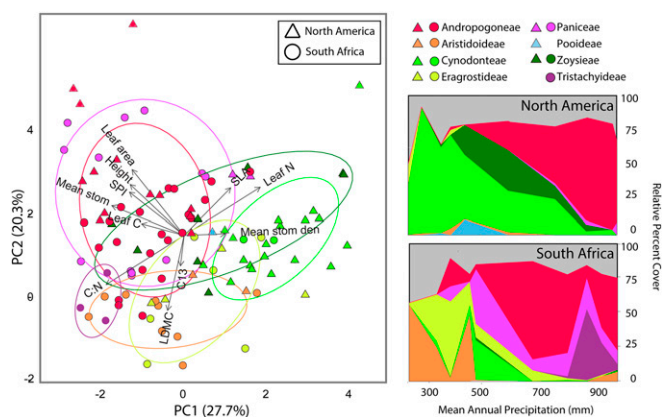
related to MAP only in NA (Fig. 3A). In more mesic grasslands (MAP > 500 mm), grasses were shorter in SA than in NA, but were able to attain similar levels of production as the taller grasses of NA (i.e., vegetation was generally denser in SA). This difference in height response was primarily driven by the mesic-adapted Andropogoneae, which were on average shorter in SA than in NA, and the shorter Tristachydeae species, which were only present in SA. Additionally, at the xeric end of the gradient, the Aristidoideae of SA were on average taller than the Cynodonteae species of NA (Fig. 4 and Fig. S4). The only traits that had similar relationships with MAP in NA and SA were leaf C and SPI. The latter is a dimensionless index of stomatal pore area per lamina area and has been found to be related to drought tolerance and water-use efficiency (23). In this case, SPI was negatively related to MAP.

The interaction of grazing history, fire, and water availability likely played a role in the evolution of these functional trait strategies along gradients of precipitation (24), because grasses in both NA and SA have coevolved with large grazing herbivores and fire. Consequently, the origin of traits associated with drought tolerance and grazing responses cannot necessarily be disentangled (25, 26). Specifically, short plants with small and/or tough leaves can be associated with adaptation to both drought and grazing (25, 26). Further, the differences in height between NA and SA grasses at the mesic end of the gradient could in part be the result of differences in climatic, fire, and grazing histories. Whereas both NA and SA have historically harbored a comparable diversity of large herbivores, the

Fig. 4. A principal components analysis of functional trait values for each common grass species from the NA and SA sites, with stacked relative abundance plots of all grasses subdivided by major clades. The gray portion of the graph represents the relative abundance represented by the remainder of the community. Ellipses represent 68% confidence intervals for the data from each clade. See Fig. S4 for species complete names and Table S4 for clade-level comparisons of trait values. Trait abbreviations: C13, stable carbon isotope ratio; Height, maximum culm height; LDMC, leaf dry matter content; Leaf C, percent leaf carbon by mass; Leaf C:N, percent leaf percent carbon to nitrogen ratio; Leaf n, percent leaf nitrogen by mass; SLA, specific leaf area; SPI, stomatal pore index; Stom. density, stomatal density; Stom. length, stomatal length.

different sets of traits in each region (Table S2). Further, differences in the trait–environment and trait–ANPP associations were driven by different factors at the mesic and xeric ends of the precipitation gradient. At the mesic end, there was overlap in the representation of phylogenetic lineages (i.e., Andropogoneae), and it was the greater variation in trait values and functional diversity within the dominant lineages that drove differences in trait responses, specifically in LA and height (Figs. 3 and 4). At the xeric end of the gradient, it was the more conserved functional strategies of different clades in NA and SA that drove differences in the trait–environment and trait–ANPP relationships (Fig. 4 and Fig. S4). For the xeric-adapted clades, Aristidoideae dominate in SA, whereas Cynodonteae, a major subclade of the dry-adapted Chloridoideae, dominate in NA. Despite occupying a similar precipitation niche, these clades differ significantly in key functional traits such as height, SLA, stomatal density, LDMC, and leaf %N (Fig. 4 and Table S4). Cynodonteae exhibit some trait values commonly associated with grazing and/or drought tolerance such as small stature, lower LDMC, higher SLA, and higher leaf %N, whereas Aristidoideae exhibit trait values such as higher LDMC and lower N that are more commonly associated with grazing resistance. There is also evidence that different dry-adapted C_4 lineages have evolved different physiological and functional strategies to cope with low water availability (28), and these trait differences could have arisen as divergent strategies to cope with both drought and grazing pressure (25, 26). Regardless of the specific strategies used, these two lineages occupy distinct functional trait space despite occupying a similar precipitation niche (Fig. 4).

Importantly, the traits that differ between these two clades (Aristidoideae and Cynodonteae), such as SLA, LDMC, and leaf N, are increasingly being used in global climate and vegetation models (29, 30). Without considering such regional differences in clade and species representation, trait-based models could yield poor global estimates of important ecosystem properties. For example, if one were to produce a model of global production potential based on the SLA–environment relationship, assuming that there is a universal relationship (i.e., species with higher SLA have greater maximum photosynthetic capacity and, therefore, greater production potential), one would greatly underestimate the variation. Our results show that SLA, among other traits, does not vary consistently across the precipitation gradient in different biogeographic regions (Fig. 3), and highlights a missing link in the development of trait-based approaches to modeling ecosystem function, namely that there is not necessarily a single solution or set of traits (i.e., "adaptive optima") that yields higher fitness or function in a given environment (31). Instead, even within a single grass clade, there are multiple evolutionary trajectories that can lead to alternative functional syndromes under a given precipitation regime.

Our results document a consistent relationship between precipitation and productivity in NA and SA, and show that annual precipitation alone adequately predicts grassland ANPP, despite underlying differences in clade representation and functional trait values between the two regions. Further, our results highlight the complexity of relationships among environmental tolerances, productivity, and organismal attributes. There is a growing consensus that a small set of plant characteristics can explain the major axes of ecosystem function, yet these characters failed to consistently predict even the simplest of ecosystem productivity gradients in systems dominated by a single, relatively specialized lineage, the grasses. Whereas plant functional attributes must be central in establishing the dramatic clade turnover observed along precipitation gradients, the set of commonly measured "plant functional traits" are not adequate to explain general rules dictating ecosystem function. Moreover, we must integrate knowledge of differences in phylogenetic diversity between regions, which ultimately trace to differences in the historical assembly of

biotas, to make accurate predictions of overall ecosystem function from functional traits.

Methods

Study Systems. The grasslands of NA and SA both span a broad precipitation gradient (∼200–1,000 mm/y), exhibit a strong productivity gradient that reflect east-west increases in precipitation, and overlap considerably in the climatic space occupied (4, 32; Fig. S1). The primary growing season in NA grasslands is from May through mid-September (33), and in SA is from mid-November through March (34). Mean annual temperature was slightly higher at sites in SA, because of the presence of milder winters, but mean growing season temperatures were similar. These environmental similarities, in conjunction with their disparate geological and biogeographic histories, render them ideal systems to test for the role that historical contingencies play in driving the turnover in the functional and phylogenetic composition of communities and their effect on a key ecosystem function, ANPP. Ten natural grassland sites were selected per region (NA, SA) that spanned a mean annual precipitation gradient from 255 to 973 and 238 to 934 mm/y for NA and SA, respectively. Sites were selected based on the maintenance of the historical fire regime (1- to 3-y fire return intervals at mesic sites, and >15-y fire return interval at xeric sites) and grazing history. All sites were ungrazed at the time of sampling, but had a history of grazing in the past (yet no history of plowing or overgrazing). We chose to focus on ungrazed sites to avoid confounding effects of differences in herbivore assemblages, densities, and grazing pressure that could affect grass community composition and estimates of ANPP. NA sites spanned the Central Great Plains and the desert grasslands of the Southwestern United States. SA sites spanned the grasslands of Kwazulu-Natal, the Free State, the Eastern Cape, and the desert grasslands of the Little Karoo in the Northern Cape (Table S1 and Fig. S2). Within each native grassland site, four 10-m transects of five plots that were each 1 m² (5 plots and 4 transects per site for each region; $n = 20$ plots per site, 200 plots per region) were established in an average area of 30 × 12 m. At each site, a relatively homogeneous upland area dominated primarily by grasses, which was representative of the broader community, was chosen to control for heterogeneity in topography and soil moisture. All sites in both SA and NA are dominated by C4 grasses (accounting for the bulk of the relative cover and production). No single species occurred in both NA and SA, with the exception of *Eragrostis lehmannia*, a native SA species that was introduced and has become invasive in the Southwestern United States. There were 62 grass species identified in our plots in SA and 35 in NA. GPS coordinates, climate, and specific site details are included in Table S1.

Data Collection.

Community composition and productivity. In NA, all community data were collected in the 2011 field season between May and September. In SA, data were collected in the 2011–2012 field season between December and March. Plant species composition was measured for all 1 × 1 m plots twice per growing season in NA and SA, once at the beginning of the season (late May and early January, respectively) to capture early season species and once at the end to capture late season species (August and March, respectively). Percent aerial cover was estimated for each plot to the nearest 1% (for cover less than 50%) and 5% (for cover more than 50%) for each species rooted therein (35). Maximum cover values for each species across the season were used to calculate relative cover for each species (relative cover equals the cover of a species divided by the total cover in a plot).

ANPP was estimated by collecting all aboveground biomass at the end of the growing season. ANPP was collected at 8 of the 10 sites in SA and 9 of the 10 sites in NA, because sampling was limited at three sites due to environmental constraints during collection years. Specifically, two 0.1 m² quadrats were clipped at ground level within each plot at the time of peak biomass accumulation (August–September for NA; March for SA). Biomass was separated into current and previous year's biomass. Current year's biomass was separated into functional groups (woody, forb, and graminoid), with common grasses sorted to species, and subsequently dried and weighed. Common grass species are defined as consisting of >2% mean relative cover at site level, or >10% relative cover in any individual plot. ANPP was estimated as the sum of all current year's biomass and was averaged across two quadrats within each plot. Site level estimates of ANPP were calculated as the mean across all plots. Thirty-one and 22 species were considered common and sampled for productivity and traits in SA and NA, respectively. These species were collectively sampled a total of 59 times in SA and 43 times in NA across all sites.

Environmental data. Total soil nitrogen and organic carbon were determined from soil cores collected from each plot in June 2011 in NA and January 2012 in SA. Four cores at 15 cm depth were collected from the four corners

of a 1×1 m plot adjacent to the sampled plot. Soil cores were aggregated by plot and sieved with a 2-mm sieve. Samples were dried, weighed, and shipped to Kansas State University Soil Testing Laboratories to be analyzed for soil nitrogen and organic carbon content via dry combustion (www.agronomy.k-state.edu/services/soiltesting/).

Long-term averages for annual precipitation and temperature for all sites in NA and SA were obtained from WorldClim at 30° arc resolution (www.worldclim.org). Monthly annual precipitation data in SA were obtained from a combination of landowners (i.e., academic institutions, farmers, government) and the SA weather service (www.weathersa.co.za). Annual precipitation data in NA were obtained from landowners and the US Climatic Reference Network (USCRN) online database (https://www.ncdc.noaa.gov/crn/). Monthly annual temperature was obtained from the Climatic Research Unit CRU v 3.21 (www.cru.uea.ac.uk; ref. 36). Only monthly estimates of precipitation were available for most sites in SA, so monthly estimates were used in our analyses for all sites. Total annual precipitation from each site was calculated as the sum of monthly precipitation totals from the end of one growing season to the end of the following growing season to more accurately represent the precipitation that could affect ANPP. Growing season temperature and precipitation were calculated for both regions as the mean values of months in the growing season (May through September for NA, November through March for SA).

Trait data collection. At both sites, data on maximum height, growth habit, photosynthetic pathway, specific leaf area, leaf dry matter content, stomatal pore length, stomatal density, stomatal pore index, foliar %N, %C, C:N, and δC_{13} were collected during the 2010–2012 field seasons as close to peak flowering as possible for all common grass species (see above) at each site (peak flowering ranged from June to September for NA and from December to March for SA). A minimum of 10 individuals per common grass species was measured at each site. Specimens were collected for functional trait analysis adjacent to survey plots. Many species were common at several sites. Thus, those species that were abundant across a broad climatic range were collected at several sites to incorporate intraspecific trait differences because of environmental differences. Flowering stage, height, and collection location were also recorded for each species.

Standard methods were used for the collection and processing of all leaf traits (37, 38). Four fully expanded green leaves in full sun were collected per individual plant and immediately placed in plastic bags with a wet paper towel in a cooler. Two leaves were rehydrated for 24–48 h following collection. Subsequently, leaf area and weight were recorded, and the leaves were dried at 60 °C for at least 48 h. Specific leaf area (leaf area divided by dry mass) and leaf dry matter content (dry mass divided by wet mass) were calculated for each leaf. The dried leaves were also ground for foliar C, N, C:N, and C-13 isotope analysis. Organic carbon and nitrogen isotope samples were analyzed by using a Costech ESC 4010 Elemental Combustion System (Costech Anlaytcial Technologies) interfaced with a Thermo Finnigan Delta Plus Advantage isotope mass spectrometer (Thermo Finnigan-MAT) at Yale University's Earth System Center for Stable Isotopic Studies (earth.yale.edu/yasic-yale-analytical-and-stable-isotope-center). Ultimately, 5 of the 10 leaves per species and treatment were subjected to leaf tissue analysis.

The other two leaves were preserved in 70% (70 mL 200 proof ethanol/30 mL distilled water) ethanol solution for analysis of stomatal size, density, and pore index. Dental putty (President Plus-light body; Coltene/Whaledent Ltd., Burgess Hill) impressions were taken from the abaxial surface of the midsection of five individuals and two preserved leaves per individual ($n = 10$) from each species and treatment. Nail polish peels produced from the impressions were transferred onto microscope slides and imaged by using a Zeiss SteREO Discovery.V12 Stereoscope and AxioCam HRc at 200× magnification. Along each peel, six stomata were measured for length and stomata were counted in two fields of view located on either side of the midrib to calculate stomatal density. Stomatal pore index, an index of total stomatal pore area per leaf area, was quantified as stomatal density × the square of the mean guard cell length (23).

Phylogenetic inference. We estimated phylogenetic relationships for species at the NA and SA sites together by using the nuclear ribosomal internal transcribed spacer (ITS) region and *mat*K, *ndh*F, and *rbc*L chloroplast markers. These four markers were retrieved from GenBank and supplemented by sequences obtained from specimens collected at each site. We sequenced only the three chloroplast markers for our specimens, which matched the gene regions used by the Grass Phylogeny Working Group (GPWG) II (39). Total genomic DNA was isolated from dried plant tissue and amplified following the protocol and using the primers specified in GPWG 2011. PCR products were sequenced by using Applied Biosystems Big Dye Chemistry and 3730 xL DNA analyzers (Applied Biosystems) at the Keck Biotechnology Resource Laboratory (Yale University). All new sequences are deposited in GenBank; voucher specimen information and GenBank accession numbers are deposited in Dryad (http://dx.doi.org/10.5061/dryad.q1b6v). The four markers were aligned by using MUSCLE v 3.7 (40) and manually edited. Individual alignment files were concatenated using Phyutility (41). Our aligned sequence matrix consisted of 8,606 base pairs. Models of nucleotide substitution and optimal partitioning strategies were chosen simultaneously under the BIC using heuristic search algorithms in PartitionFinder (42). The noncoding nuclear gene region ITS was treated as its own partition. For the coding genes *rbc*L, *mat*K, and *ndh*F, all five combinations of codon partitions were considered as candidate partitions. Alternative nucleotide substitution models considered were those available in BEAST v.1.6.2 (43). The best-fit partition strategy according to BIC was a SYM + I for ITS and a GTR+I+G model for all other partitions. Phylogenetic relationships were reconstructed by using Bayesian methods in BEAST v.1.6.2 (43). Mixed partition analyses were performed for each of the sampled genes and on the concatenated matrices using the optimal partition strategies identified by PartitionFinder (42). Trees were unlinked by gene region and analyses were conducted under a model of uncorrelated rates and a log-normal distribution. Following the BEAST dating analysis of Christin et al. (44), our tree was time-calibrated by using normally distributed calibrations for the following four clades: (*i*) Bambusoideae/Ehrhartoideae, Pooideae-Panicoideae/Aristidoideae/Chloridoideae/Micrairoideae/Arundinoideae/Danthonioideae (BEP-PACMAD) split (mean = 49.8, SD = 3.0), (*ii*) Andropogoneae (mean = 18.0, SD = 3.7), (*iii*) Chloridoideae (mean = 34.7, SD = 3.75), and (*iv*) Aristideae (mean = 8.6, SD = 10.5). The MCMC chain was run for 20 million generations and sampled every 10,000 generations. Convergence of the chain was assessed by visualizations of the state likelihoods using Tracer v1.5 (43). Effective sample sizes (ESS) for all model parameter estimates were examined to ensure adequate mixing of the chain, with ESS values more than 200 indicating appropriate sampling. One million generations were discarded as burn-in, and the remaining trees were combined to generate a maximum clade credibility tree that was used for all analyses.

Statistical Analyses.

Relating grass productivity to total ANPP. Using linear mixed models, we first estimated how well grass ANPP predicted variation in total ANPP where plot-level production of the grass community was treated as the predictor, and plot was nested within site, which was treated as a random variable. Percent of total ANPP attributable to grasses was also calculated for all plots.

Annual precipitation as a predictor of ANPP. Using linear regression models, we explored across-site variation in total ANPP in different regions (NA versus SA) in response to annual precipitation. Mean site-level ANPP (averaged across all plots at each site) was treated as the response variable in all models. In the first set of models, separate models were run for NA and SA, and slopes and intercepts were compared by using Welch's t test statistic. After finding that there were no statistically significant differences between NA and SA slopes and intercepts in the first set of models, a model was fit that combined data from both regions.

Modeling functional turnover along the precipitation gradient. We explored how variation in precipitation drives community functional turnover on each continent by fitting ANCOVA's where the predictor variable was mean annual precipitation, and the response variable was the community weighted mean of a given functional trait, with continent treated as a covariate. Separate models were fit for each individual trait. First, we calculated site-level CWMs of the grass community for all 11 traits (height, leaf area, specific leaf area, leaf dry matter content, leaf N, leaf C, leaf C:N, stomatal length, stomatal density, stomatal pore index, and ^{13}C). We used CWM of the grasses to model the response of community function to precipitation. MAP was used for the analysis of trait–environment relationships, because these grasses are largely long-lived perennial plants that are not establishing over a single season. The CWM of a trait value is the mean trait value of each species present in the community weighted by its relative abundance. To incorporate intraspecific trait variation, trait means for each site or precipitation level were calculated from the dominant grass species collected at that site.

Modeling community function and plot-level production. We explored whether within- and across-site variation in ANPP was driven by the functional traits of each plot and by the constituent species of sites within each region. First, we calculated plot-level CWMs of the grass community for all 11 traits by using mean trait values of dominant species from each site. Multiple mixed-effects model regressions were performed with ANPP as the response variable, CWMs for each trait as the predictor variables, and site as a random variable. Leaf C:N was removed from the analysis because it was highly correlated with leaf C ($r = 0.95$). All other correlation coefficients between trait variables were <0.7. Separate models were fit for NA and SA, and all possible models were compared by using BIC and AICc. All models were fit with the lmer library (45) and the basic statistical package of R v. 3.0.3. (https://cran.r-project.org). Model comparisons were carried out by using the dredge

function in the MuMIn package of R (46). For all linear mixed models, the marginal and conditional coefficients of determination, which correspond to the variation explained by the fixed factors alone and the fixed and random factors together, respectively, were calculated by using the r.squaredGLMM function in MuMIn.

Multivariate trait space of clades/species. To compare the functional space occupied by the common grass species/clades represented at each site, a principal component analysis was carried out by using the prin.comp function in the base package of R with species trait values of common grass species at each site from both NA and SA.

Correlations among phylogeny, functional traits, and MAP. To test for correlations between phylogenetic and functional turnover along the precipitation gradient on each continent, matrix correlations among a phylogenetic dissimilarity matrix, a trait dissimilarity matrix, a species-level abundance community matrix that included all plots, and the mean annual precipitation values of each plot were calculated for NA and SA separately (47, 48). Specifically, we tested for: (*i*) convergence in trait values in response to similar levels of mean annual precipitation, (*ii*) phylogenetic signal in trait values at the species level, (*iii*) correlations between phylogenetic turnover and MAP (i.e., environmental filtering of clades), and (*iv*) correlations between phylogenetic turnover and trait convergence patterns (i.e., correlation of clade and trait turnover). Analyses were carried out in the SYNCSA v 1.3.2 package in R (49).

Clade-level functional trait comparison. To test for differences between clades in the functional trait space they occupy, we conducted ANOVAs on principal components 1–4 from the principal component analysis of 11 functional traits on the dominant grasses at each site in NA and SA (Fig. 4). A separate model was run for each principal component, and clade was treated as a fixed effect in each model. All analyses were conducted by using the basic statistical package of R v. 3.0.3. (https://cran.r-project.org). For those principal components where clade was a significant effect, we conducted Tukey's post hoc test to control for multiple comparisons and test all pairwise differences between clades.

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