Abstract: Plant traits are useful for predicting how species may respond to environmental change and/or influence ecosystem properties. Understanding the extent to which traits vary within species and across climatic gradients is particularly important for understanding how species may respond to climate change. We explored whether climate drives spatial patterns of intraspecific trait variation for three traits (specific leaf area (SLA), plant height, and leaf nitrogen content (Nmass)) across 122 grass species (family: Poaceae) with a combined distribution across six continents. We tested the hypothesis that the sensitivity (i.e., slope) of intraspecific trait responses to climate across space would be related to the species' typical form and function (e.g., leaf economics, stature, and lifespan). We observed both positive and negative intraspecific trait responses to climate with the distribution of slope coefficients across species straddling zero for precipitation, temperature, and climate seasonality. As hypothesized, variation in slope coefficients across species was partially explained by leaf economics and lifespan. For example, acquisitive species with nitrogen-rich leaves grew taller and produced leaves with higher SLA in warmer regions compared to species with low Nmass. Compared to perennials, annual grasses invested in leaves with higher SLA yet decreased height and Nmass in regions with high precipitation seasonality. Thus, while the influence of climate on trait expression may at first appear idiosyncratic, variation in trait-climate slope coefficients is at least partially explained by the species' typical form and function. Overall, our results suggest that a species' mean location along one axis of trait variation (e.g., leaf economics) could influence how traits along a separate axis of variation (e.g., plant size) respond to spatial variation in climate.

Key words: functional traits, grass, intraspecific trait variation, Poaceae, climate, specific leaf area, leaf nitrogen, plant height

Introduction

Characteristics of individual plants (i.e., traits) can influence both their response to environmental change and their effect on climate and ecosystem processes (Suding et al. 2008). Globally, plant traits are coordinated such that three quarters of trait variation between species can be explained by a two-dimensional spectrum of plant form and function describing a species relative size and its leaf economic strategy (Diaz et al. 2016). Size-related traits, such as plant height, can reflect competitive ability, particularly with regards to light acquisition (Westoby 1998). Traits of the leaf economic spectrum separate species along a continuum of conservative to acquisitive resource-use strategies, where acquisitive species are generally short-lived and have higher specific leaf area (SLA; leaf area per gram of dry leaf mass), mass-based leaf nitrogen content (Nmass), and rates of photosynthesis (Wright et al. 2004; Shipley 2006). Such traits can be predictive of where species grow and how they respond to climate. For example, low SLA species tend to be more abundant in arid environments and reduce their SLA further during drought (Reich 2014; Dwyer et al. 2014). Importantly, these traits can also vary considerably within species (up to 40% of total variation for some traits), reflecting genetic diversity and phenotypic plasticity (Kattge et al. 2011; Siefert et al. 2015). Characterizing how plant traits vary intraspecifically with climate is not only important for understanding physiological adaptations to climate change (Dong et al. 2020), but can also inform predictions of plant trait values in regions where measurements are still lacking (Sandel et al. 2021).

Here, we examine the global patterns of intraspecific trait variation and its association with climate for grasses (family: Poaceae), a species-rich and globally distributed plant family with massive ecological and economic importance (Clayton and Renvoize 1986). Grasses are a highly successful group of plants from an evolutionary perspective with ~11,500 species worldwide (Soreng et al. 2017). They are the dominant growth form of grasslands, which cover 52 million km², or roughly 40% of Earth's terrestrial land surface (Gibson 2009), and make a significant contribution to the terrestrial carbon sink (Fisher et al. 1994; Still et al. 2003; Wigley et al. 2020). Humans are heavily dependent on grasses for food (e.g., corn, rice, and wheat), building materials (e.g., bamboo), and forage for livestock (Hodkinson et al. 2018). Despite their ecological, economic, and cultural importance (Nowak-Olejnik et al. 2020), grasses have received relatively little attention in the plant traits literature, with most analyses focusing on interspecific comparisons (Sandel et al. 2016, Jardine et al. 2020). Therefore, many of our expectations about how climate influences intraspecific variation in grass traits are informed by interspecific comparisons.

Our understanding of trait responses to climate stems from analyses of spatial patterns in species mean traits along broad environmental gradients (Reich and Oleksyn 2004). For example, grass species with high Nmass often inhabit arid climates with high temperature and low precipitation (Jardine et al. 2020). This is likely because a large portion of leaf N is allocated to Rubisco (Evans 1989; Hikosaka 2004; Funk et al. 2013), and higher Rubisco content improves water-use efficiency by allowing plants to achieve higher carbon assimilation at lower rates of stomatal conductance (Wright et al. 2001). Similar spatial analyses suggest that variation in SLA is not (or only weakly) correlated with climate (Wright et al. 2004; Jardine 2020), although positive relationships between SLA and both precipitation and temperature were observed *within* grass species in California (Sandel et al. 2021). Taller grass species often inhabit wetter and warmer regions (Sandel et al. 2016; Jardine et al. 2020). Within species, however, grass individuals are generally taller in warmer regions, but not necessarily wetter regions (Sandel et al. 2021). A lack of a general pattern between height and precipitation within species may be due to individuals of some grass species growing taller in dry areas where they’re supported by deeper rooting systems (Hoffman et al. 2020).

While we’d expect intraspecific trait-climate relationships to generally match those observed between species, the sensitivity of traits to climate is likely highly variable among species. This could be due to genetic constraints on trait variability, interactions with neighboring biota, or differences in microclimate that mask broad environmental gradients (Westerband et al. 2021). We aimed to better understand variation in trait-climate relationships and potential modifying effects. First, we test a novel hypothesis that the strength (slope) and direction (sign) of intraspecific trait-climate relationships for a species depend on its relative location along the two major axes of the global spectrum of plant form and function (leaf economics and stature; Fig. 1). For example, if we consider two species of similar stature but on opposite ends of the leaf economic spectrum, individuals of the acquisitive species should theoretically be able to capitalize on greater resource availability in wetter areas and grow taller compared to a more conservative species. In this scenario, we would expect to observe a higher slope for the intraspecific relationship between height and precipitation for species with high SLA and leaf Nmass (Fig. 1). Second, we explored differences in trait-environment relations based on a species’ lifespan (annual vs. perennial) and photosynthetic pathway (C_4 vs. C_3) given the known linkages between these categorical traits and leaf economics (Still et al. 2003; Frenette-Dussault et al. 2012; Kooyers 2015). A species’ lifespan is an important determinant of resource use strategies; annuals must complete their reproductive lifecycle within a limited period of time compared to perennials, which may influence their trait expression along climate gradients. Similarly, we’d expect photosynthetic pathway to modify trait responses to climate given C_4 grasses are generally more tolerant of high temperatures and drought (Still et al. 2003).

We tested these hypotheses by analyzing intraspecific relationships between commonly measured traits (SLA, Nmass, and height) and temperature, precipitation, and climate seasonality using a global trait dataset for 122 grass species. We expected individuals of a species to grow taller and have higher SLA in wetter and warmer climates (i.e., positive intraspecific trait-climate relationships for SLA and Height) (Moles et al. 2014; Jardine et al. 2020; Sandel et al. 2021). Additionally, we expected individuals in warmer and drier regions to produce leaves with high Nmass to increase water-use efficiency (i.e., negative intraspecific trait-climate relationships for Nmass) (Wright et al. 2001). Finally, we hypothesized that variation among species in the strength and direction of these intraspecific trait-climate relationships would be related to their typical form and function (Fig. 1).

Methods

Trait and climate data

We measured traits of grasses across the Bay Area of California and obtained additional records from published papers (Appendix 1) and trait databases, including TRY (Kattge et al. 2011), TTT (Bjorkman et al. 2018), BIEN (Maitner et al. 2018), BROT2 (Tavşanoğlu and Pausas 2018), and AusTraits (Falster et al. 2021). For this analysis, we focus on three traits of interest: specific leaf area (SLA), plant height, and mass-based leaf nitrogen content (Nmass). All trait measurements were georeferenced with latitude and longitude coordinates. For each trait measurement, we extracted and paired the following high resolution (30 arc sec, ~1km) climate statistics from CHELSA V2.1 (Karger et al. 2017; https://chelsa-climate.org/): mean annual precipitation (MAP), mean annual temperature (MAT), precipitation seasonality (PS; the standard deviation of the monthly precipitation estimates expressed as a percentage of the mean of those estimates (i.e. the annual mean)), temperature seasonality (TS; standard deviation of the monthly mean temperatures), mean monthly precipitation of the warmest and coldest quarter of the year (P_{warm} and P_{cold}, respectively), and mean monthly temperature of the warmest and coldest quarter of the year (T_{warm} and T_{cold}, respectively).

To avoid over-weighting regions that were heavily sampled (i.e., parts of Europe and North America, see Fig. 2), we aggregated our trait-climate dataset by rounding latitude-longitude coordinates to the nearest first decimal point and averaging climate and trait values for a species within that binned coordinate. We then subset this binned dataset to include only species for which we had at least 10 records spanning a MAP gradient of 100 mm, a MAT gradient of 2°C, and a correlation between MAP and MAT of no more than 0.8. This was done to prevent fitting models when MAP and MAT were highly collinear or when all measurements were made over a narrow range of climate values which might result in extreme slope coefficients (Sandel et al. 2021). Based on these criteria, our final global grass trait-climate dataset spanned six continents, covered all of Earth's major terrestrial biomes, and included 2,648 measurements of SLA (n= 109 species), 1,359 measurements of Nmass (n = 61 species), and 1,439 measurements of plant height (n = 66 species) (Fig. 2).

Analysis

Trait data were log-transformed prior to analyses to meet assumptions of normality. For each species and trait, we ran two separate simultaneous autoregressive (SAR) models predicting trait values from climate variables using the errorsarlm() function in the *spdep* package (Bivand et al. 2015), with the neighborhood of a point being defined as the three nearest points. The first model included mean climate characteristics (MAP, MAT, PS, TS) while the second included mean monthly climate of the warmest and coldest quarters of the year (P_{warm}, P_{cold}, T_{warm}, and T_{cold}). The use of SAR models accounts for spatial autocorrelation in our data, a common phenomenon in ecology where nearby observations are more similar than would be expected by chance (Legendre 1993). These models each produced 12 trait-climate slope coefficients (3 traits, 4 climate variables). Using Student t-tests, we assessed whether the mean of each SAR slope coefficients across species was significantly different from zero (Bonferroni-adjusted p-values for 12 independent tests; $\alpha = 0.004$).

To test whether variation in intraspecific sensitivity of traits to climate could be explained by mean species traits, we ran phylogenetic generalized least squares (PGLS) regression models with the intraspecific trait-climate slope coefficients (e.g., MAP vs. SLA slope) as the dependent variable and the following mean species traits as independent variables: SLA, Nmass, height, lifespan (i.e., perennial or annual), and photosynthetic pathway (i.e., C_4 or C_3 photosynthesis). We used PGLS models to account for the possibility that more closely related species have more similar responses to climate than would be expected by chance (see Fig. S1 for complete phylogenetic tree). In our models, we log transformed continuous mean traits (SLA, Nmass, and Height). To simplify these global models and determine which mean traits were most important for understanding variability in the trait-climate slope coefficients, we performed an automated model selection using the dredge() function in the *MuMln* package (Barton and Barton 2015). We then performed model averaging on those models with a delta AICc of <2, and produced partial residual plots to visualize the effects of individual significant predictor variables on variation in the slope coefficients while also considering other components of the final model.

Finally, we explored the correlation between mean continuous traits for all species used in this study (n=122) using standard major axis (SMA) regression (sma function in the *smatr* package; Warton et al. 2018) and tested for trait differences based on photosynthetic pathway and lifespan using two-sample t-tests. This was done to confirm that the mean traits for our species were similarly coordinated according to global spectrum of plant form and function (Diaz et al. 2016). All statistical analyses and data visualization were performed in R (version 4.2.2).

Results

Across the 122 grass species included in this study, mean leaf trait associations broadly met the assumptions of the global spectrum of plant form and function (Reich 2014; Diaz et al. 2016). As expected, we observed a positive relationship between SLA and Nmass ($R^2 = 0.181$), suggesting acquisitive grass species with high SLA also have high leaf Nmass (Fig. 3a). Leaf Nmass of annuals was higher than that of perennials ($p < 0.01$; Fig. 3b) and C_3 grasses had higher Nmass than C_4 grasses ($p < 0.01$; Fig. 3c) reflecting the higher nitrogen-use efficiency of C_4 photosynthesis. We observed no significant relationship between SLA and plant height (Fig. 3d). Annuals had higher SLA than perennials ($p < 0.01$; Fig. 3e) while SLA did not differ based on photosynthetic pathway (Fig. 3f). We observed a weak negative relationship between leaf Nmass and height ($R^2 = 0.036$, $p = 0.04$, Fig. 3g). This negative relationship is perhaps due to the taller stature of C_4 species (Fig. 3i) which also had lower leaf Nmass than C_3 species (Fig. 3 c).

Across species, the trait-climate SAR slope coefficients straddled zero and were, on average, not significantly different from zero (Fig. 4, Fig. S2). However, this was driven by similar numbers of positive and negative relationships, many of which were individually statistically significant (Table 1). Variation across species in their trait responses to mean annual climate was partially explained by a species' typical form and function (Table S1). For example, individuals of species with high Nmass grew taller in warmer areas (Fig. 5a). Annual grasses, short species, and those with low SLA grew shorter in regions with high precipitation seasonality (Fig. 5 b, c, and d), and perennials grew taller in regions with high temperature seasonality (Fig. 5e). Species with low Nmass grew shorter in regions with high T_{warm} (Fig. S3). Compared to perennials, annuals grew taller in regions with high T_{cold} and P_{warm} but low P_{cold} (Fig. S3).

We observed similarly species-specific slope coefficients for intraspecific Nmass-climate relationships (Fig. 4, Table 1), with mean traits explaining some of the variability across species (Table S2). For example, annual grasses and tall species decreased leaf Nmass in regions with greater precipitation seasonality (Fig. 5 f and g). Species with high SLA increased Nmass in regions with high T_{warm} but decreased Nmass in regions with high T_{cold} (Fig. S3). The opposite response was observed for species with high Nmass (Fig. S3), which was surprising given the correlation between Nmass and SLA (Fig. 3). Annuals increased Nmass in regions with high P_{warm}, more so than perennials (Fig. S3).

Finally, both positive and negative relationships between SLA and mean climate were observed (Fig. 4, Table 1), with lifespan and leaf Nmass explaining some of this variation (Fig. 5; Table S3). Species with high leaf Nmass increased SLA in warmer regions (Fig. 5h) as well as regions with low precipitation seasonality (Fig. 5j). Annuals increased SLA in areas with high precipitation seasonality and low MAT, while SLA of perennials was less responsive (Fig. 5 i and k). Compared to perennials, annuals decreased SLA more in regions with high T_{warm} (Fig. S3). Finally, species with high Nmass and/or low SLA increased SLA in regions with high P_{warm} (Fig. S3)

Discussion

Using a trait dataset for 122 globally distributed grass species, we investigated how the typical form and function of a species modifies its intraspecific trait responses to climate. On average, traits did not respond consistently to climate as both positive and negative responses were observed across species; however, some of this variation was explained by a species' mean traits. For example, acquisitive species with high leaf Nmass grew taller and produced leaves with higher SLA in warmer regions compared to species with less nitrogen-rich leaves. Compared to perennials, annual grasses invested in leaves with higher SLA yet decreased height and Nmass in regions with high precipitation seasonality. These findings suggest that intraspecific trait responses to climate are variable (both positive and negative responses observed) but both the direction and magnitude of responses can depend on a species' lifespan as well as its mean traits.

While we expected certain grass traits would respond consistently to climate, this was not the case (Fig. 4). The lack of a consistent relationship between height and climate across grasses could be due to the variable growth strategies grasses exhibit (e.g., caespitose, rhizomatous, or stoloniferous). For example, grasses can increase aboveground biomass without growing taller if lateral spread is more advantageous (Navas et al. 2005). We also did not find support for our hypothesis that species would produce N-rich leaves in warm dry regions (Jardine et al. 2020; Sandel et al. 2021). Nitrogen in plant leaves can be allocated to a variety of processes including photosynthesis, defense against herbivory (e.g., secondary metabolites), and leaf structure (e.g., investment in cell wall proteins) (Funk et al. 2013). Thus, intraspecific variation in allocation to these processes may have masked some relationships between climate and water-use efficiency as it relates to total Nmass. Alternatively, temperature may not reflect water stress as well as other climate variables such as vapor pressure deficit. Indeed, recent work suggests Nmass is negatively related to temperature, but positively related to vapor pressure deficit (Dong et al. 2020). Our results generally corroborate previous findings that SLA is not strongly correlated with precipitation (Wright et al. 2004; Sandel et al. 2021). Interspecific variation in SLA is often better explained by temperature (Wright et al. 2004; Moles et al. 2014), such that warmer regions support grasses with higher SLA (Sandel et al. 2021). However, our analysis did not reveal consistently positive intraspecific responses of SLA to temperature either (Fig. 4).

There are many reasons why mean climate statistics may not explain variation in plant traits. For instance, two sites with the same mean climate can have drastically different soil water holding capacity depending on soil texture (Noy-Meir 1973; English et al. 2005) which may lead to different trait expressions. Additionally, differences in topographical slope or aspect can alter the local temperature and soil moisture of microclimates within a landscape (Stark and Fridley 2022), which may not be accounted for in the coarse climate data from CHELSA (~1 km grid). Plants may also be more responsive to antecedent precipitation and temperature than the mean climate at the time of measurement (Walter et al. 2013). And finally, canopy cover and the presence or absence of vegetation and associated competitive vs. facilitative interactions with neighboring plants can influence resource availability and an individual’s realized functional niche (Sthultz et al. 2007). These biotic and abiotic factors can alter local resource availability and plant trait expression leading to unexpected global patterns. Additionally, species vary in their potential for plastic adjustment, a major driver of intraspecific trait variability (Hoffman et al. 2020).

Despite these potential caveats and the lack of consistency in trait-climate relationships across species, we did observe many significant individual positive and negative relationships

(Table 1). As we hypothesized, variation across species in the direction and strength of these slope coefficients was partially explained by a species' typical form and function. We predicted that species with more acquisitive leaf economics traits (e.g., high Nmass and SLA) would grow taller in warmer and wetter regions (Wright et al. 2004; Shipley 2006). We found some support for this as MAT-height coefficients (and T_{warm}-height coefficients; Fig. S3) across species was positively correlated with a species' mean leaf Nmass (Fig. 5a). Given that species with high Nmass are generally more water-use efficient (Wright et al. 2001), this result could indicate water-use efficient grasses have greater growth potential in areas with higher evaporative demand. Furthermore, species with high SLA grew taller in regions with higher precipitation seasonality, suggesting the height of acquisitive species is maximized in warmer regions with variable climates. Regions with high precipitation seasonality are often characterized by either winter growing seasons (e.g., Mediterranean climate) or monsoon rains (e.g., desert ecosystems) where pulse dynamics drive ecosystem properties and plant resource use strategies (Noy-Meir 1973). To be successful in such an environment, many plant species adopt a drought escape strategy characterized by acquisitive traits (e.g., high SLA and Nmass) which allow them to grow quickly and take advantage of temporally scarce soil moisture resources (Kooyers, 2015). The height of such species may be maximized in highly seasonal regions where this strategy is most advantageous. Taken together, this pattern suggests a grass species' mean location along one axis of the global spectrum of plant form and function (e.g., leaf economic traits such as Nmass and SLA) could influence how its traits along a separate axis of variation (e.g., plant size traits such as height) respond to spatial variation in climate. While the data presented in the original global spectrum of plant form and function incorporated many more species with a range of heights (including woody species) (Diaz et al. 2016), our global grass dataset covers a large portion of the herbaceous plant functional space, at least for these three traits (Fig. 1).

Interestingly, intraspecific responses of SLA and Nmass to climate also depended on a species' relative location along the leaf economic spectrum. For example, species with high leaf Nmass increased SLA in warmer regions (Fig. 5 h). Higher temperatures impose greater evaporative water stress (De Boeck et al. 2011), so increasing SLA may seem maladaptive. However, species with high Nmass are generally more water-use efficient (Wright et al. 2001). Therefore, the positive effect of temperature on SLA observed elsewhere (Sandel et al. 2021) may only apply to water-use efficient species that can afford to invest in higher SLA and thus greater carbon assimilation as temperature increases, while species with low Nmass decrease SLA to reduce water loss via transpiration. We also observed a positive relationship between mean Nmass and SLA-P_{warm} slope coefficients, which suggests acquisitive species produce leaves with higher SLA in regions with high summer precipitation (Fig. S3). However, this same slope coefficient was negatively correlated with a species' mean SLA, suggesting the oft cited positive effect of precipitation on SLA may be restricted to species with on average low SLA, at least for grasses. Finally, species with on average low Nmass or high SLA increased Nmass in regions with high T_{warm} and low T_{cold} (Fig. S3), implying species with high potential for evapotranspiration (high SLA) or low average water use efficiency (low Nmass) may increase Nmass to compensate for an inefficient water use strategies in temperate regions with hot summers and cold winters. This suggests functionally similar responses are achieved through either high SLA or low Nmass, which is intriguing given the positive correlation of these traits among species (Fig. 3).

We found fewer significant effects of plant height on intraspecific trait-climate coefficients. Notably, taller species grew taller and produced leaves with lower Nmass in regions with greater precipitation seasonality (Fig. 5 c and f). Plant height is indicative of both competitive vigor and biomass production in grasses (Westoby 1998; Cornelissen et al. 2003; Chieppa et al. 2020). Therefore, this result suggests competitive grass species become even more competitive, but perhaps less water-use efficient in regions with high variation in precipitation, such as desert ecosystems. It is unclear what drives this pattern; however, tall plants often have thicker roots (Garbowski et al. 2021) which may allow them to acquire more water and invest less in their N-based water use efficiency in climatically variable environments.

Annual and perennial plants differed from one another in their resource use strategies and leaf economics (Fig. 3). On average, annual grasses were more acquisitive given the need for them to complete their lifecycle within one growing season. As such, we hypothesized these two functional groups would differ in their trait responses to climate. Indeed, we found the traits of annuals and perennials often responded to climate in an opposite manner, which likely explains why we observed both positive and negative trait-climate coefficients (Fig. 4). Compared to perennials, annual grasses grew taller in regions with low climate seasonality (Fig. 5) suggesting consistent resource availability is conducive to growth for these acquisitive species. Additionally, annuals grew taller in regions with relatively wet summers and/or warm dry winters, again indicative of an annual strategy benefiting from optimal growing seasons. We also found that annual species produced leaves with lower Nmass in regions with high precipitation seasonality (Fig. 5). Given that annuals were shorter in such environments, investing in less N-rich leaves may simply be indicative of their slower growth rates. Finally, annual grasses produced leaves with lower SLA in regions with high summer temperature (i.e., more negative

SLA-T_{warm} slope coefficients than perennials; Fig. S3) and/or low precipitation seasonality (Fig. 5). Reducing SLA in regions with high evaporative demand is likely a mechanism to reduce water loss (Dwyer et al. 2014), which we'd expect for both annuals and perennials, although SLA of perennials was less responsive to summer temperature. While we cannot be sure of the mechanism behind all of these trends, it is clear that the lifespan of grasses has a strong influence on how its traits respond to climate.

We also hypothesized that the traits of C_4 grasses would respond to climate differently than C_3 grasses. The carbon concentrating mechanism of C_4 photosynthesis means C_4 grasses can achieve higher water use efficiency than C_3 plants, particularly at warm temperatures (Still et al. 2003), which is likely to impact how species respond morphologically to climate. However, photosynthetic pathway was not a significant predictor in any of our PGLS models. The C_4 photosynthetic pathway has evolved multiple times across the grass family, but still shows very strong phylogenetic signal (Sage 2004). Thus, it may be difficult to separate the role of the photosynthetic pathway with other similarities due to shared descent.

Earth's climate is rapidly changing and there is an urgent need to understand how plant species will respond. Intraspecific relationships between plant traits and climate can benchmark predictions of how individuals of a species may respond to environmental change. While many of the species-specific trait-climate relationships we explored were not significant, variation in trait-climate sensitivity (i.e., slope coefficients) across species was explained by a species' typical form and function (e.g., SLA, Height, leaf Nmass, and lifespan). The results here provide evidence for the hypothesis that the location of a species within the global spectrum of plant form and function influences the direction and slope of its intraspecific trait-climate relationship.

However, independent studies beyond grasses are still needed to confirm and generalize these results.

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Table 1. The number of slope coefficients from individual simultaneous autoregressive models that were positive or negative. The number of slope coefficients that were significantly different from zero ($p < 0.05$) are shown in parentheses. MAP = mean annual precipitation; MAT = mean annual temperature; PS = precipitation seasonality; TS = temperature seasonality; SLA = specific leaf area; Nmass = mass-based leaf nitrogen content; Height = plant height.

	SLA				**Nmass**				**Height**			
	MAP	**MAT**	**PS**	**TS**	**MAP**	**MAT**	**PS**	**TS**	**MAP**	**MAT**	**PS**	**TS**
# Positive	60 (20)	55 (20)	58 (19)	47 (16)	31 (15)	28 (11)	34 (13)	27 (12)	38 (15)	37 (17)	33 (16)	36 (15)
# Negative	49 (22)	54 (15)	51 (22)	62 (24)	30 (10)	33 (11)	27 (11)	34 (11)	28 (12)	29 (12)	33 (15)	30 (26)
Total	109 (42)	109 (35)	109 (41)	109 (40)	61 (25)	61 (22)	61 (24)	61 (23)	66 (27)	66 (29)	66 (31)	66 (41)

Figure Descriptions

Figure 1. Hypothetical framework describing how a species' typical form and function may influence its intraspecific trait sensitivity to climate. The central PCA depicts a partial projection of the global spectrum of plant form and function *sensu* Diaz et al. (2016) using only the traits involved in the present study. The solid arrows depict the direction and weighting of vectors describing three traits: leaf mass per area (LMA; the inverse of SLA), leaf nitrogen content (Nmass) and plant height (H). The colored clouds represent high (red) and low (yellow) probability of species occurrence in the trait space, with contour lines indicating 0.5, 0.95 and 0.99 quantiles. The mean traits of the 122 grass species included in this analysis are overlaid on the PCA as larger points colored by annual (orange) or perennial lifespan (white). These species are well distributed within the herbaceous plant trait space (lower left cloud). While each point represents the mean traits for a single grass species, there is known intraspecific variation to that mean, which may be driven by climate. Depicted on the left and right are hypothetical intra-specific relationships between height and precipitation for two species of similar mean height but drastically different leaf economic strategies. Each point in these relationships represents an individual of that species along a spatial gradient of precipitation. We hypothesize that individuals of more acquisitive species (left panel) should be able to acquire resources more efficiently than conservative species (right panel) and thus grow larger where resources are more plentiful. The PCA was created using the PhenoSpace shiny application (Segrestin et al. 2021).

Figure 2. Global distribution of grass trait measurements for (A) specific leaf area (SLA), (B) mass-based leaf nitrogen content (Nmass), and (C) maximum plant height. For clarity, data are binned with the density of measurements depicted as a gradient from low (purple) to high

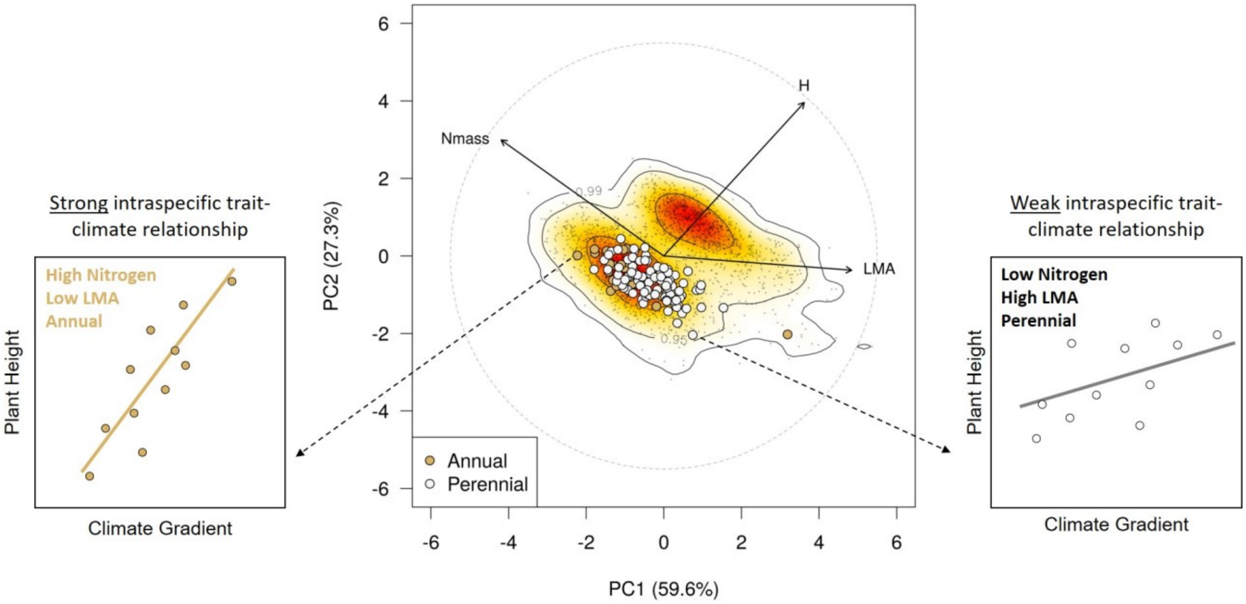
(yellow). The number of measurements and species covered varied by trait with 2648 measurements of SLA for 109 species, 1359 measurements of Nmass for 61 species, and 1439 measurements of plant height 66 species. (D) Our measurements span the major terrestrial biomes, as defined by mean annual temperature and precipitation, but are concentrated in grasslands and shrublands. The Whittaker plot of biomes was produced using the *plotbiomes* package (Stefan and Levin 2018).

Figure 3. Standard major axis (SMA) regressions between the log-transformed continuous traits of interest: specific leaf area (SLA), mass-based leaf nitrogen content (Nmass), and maximum plant height (panels A, D, and G). The black lines in panels A and G are the significant SMA regression relationships and grey bands depict bootstrapped 95% confidence intervals around these relationships. We did not observe a significant correlation between height and SLA (panel D) so no line is shown. Mean trait values (± standard errors) for perennial and annual as well as C_3 and C_4 grasses are shown in panels to the right along with p-values if significant differences were observed.

Figure 4. Boxplots showing the distribution of the slope coefficients from simultaneous autoregressive (SAR) models of the form: Trait ~ MAP + MAT + PS + TS. The trait-climate slope coefficients from these models are grouped in panels based on the climate of interest and color coded based on the trait. On average, each trait-climate SAR slope coefficients is not significantly different from zero (Bonferroni adj p-values). This is driven by both statistically significant positive and negative responses to climate across species (Table 1).

Figure 5. The effect of a species' mean traits on its intraspecific trait responses to climate. Shown are partial residual plots (or just means ± SE for categorical traits) for significant predictors of intraspecific trait-climate slope coefficients including: Height-climate slope coefficients (A-E; in blue), Nmass-climate slope coefficients (F-G; in yellow), and SLA-climate slope coefficients (H-K; in grey). The slope coefficients (on the y-axis in each panel) are the response variables in the phylogenetic generalized least squares regression models shown in Table S1, S2, and S3. Grey bands represent the 95% confidence interval for the partial residual plots.

Figure 1



Strong intraspecific trait-climate relationship
High Nitrogen
Low LMA
Annual
Plant Height
Climate Gradient
H
Nmass
LMA
0.99
0.95
PC2 (27.3%)
PC1 (59.6%)
6
4
2
0
-2
-4
-6
Annual
Perennial
Weak intraspecific trait-climate relationship
Low Nitrogen
High LMA
Perennial
Plant Height
Climate Gradient

Figure 2

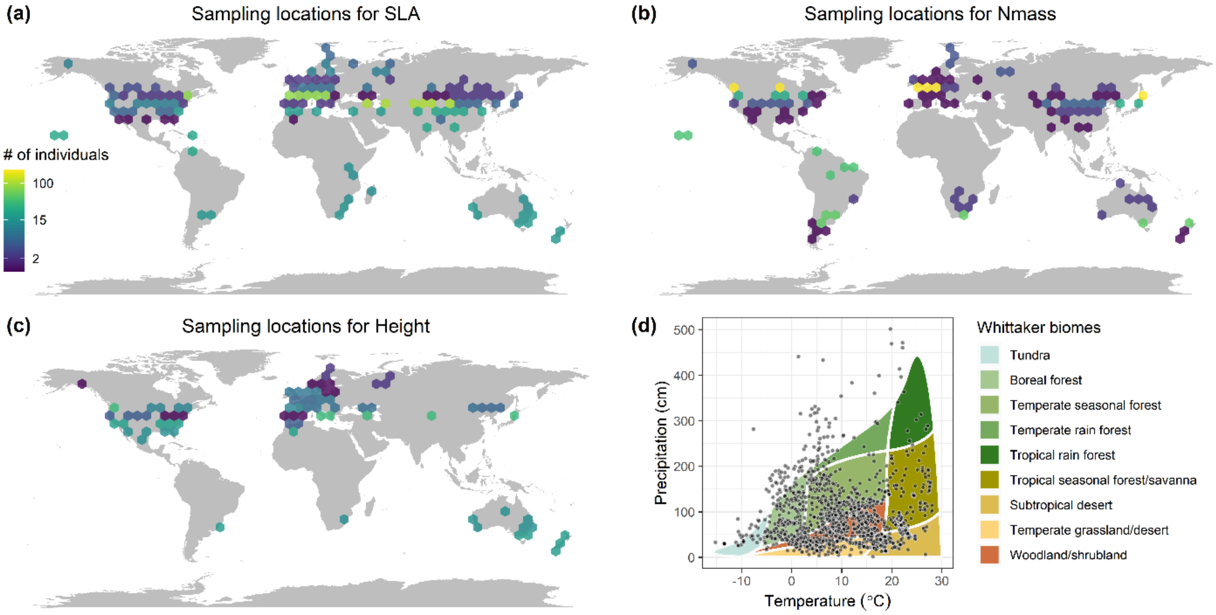

(a)
Sampling locations for SLA
# of individuals
100
15
2
(b)
Sampling locations for Nmass
(c)
Sampling locations for Height
(d)
500
400
300
200
100
0
Precipitation (cm)
-10
0
10
20
30
Temperature (°C)
Whittaker biomes
Tundra
Boreal forest
Temperate seasonal forest
Temperate rain forest
Tropical rain forest
Tropical seasonal forest/savanna
Subtropical desert
Temperate grassland/desert
Woodland/shrubland

Figure 3

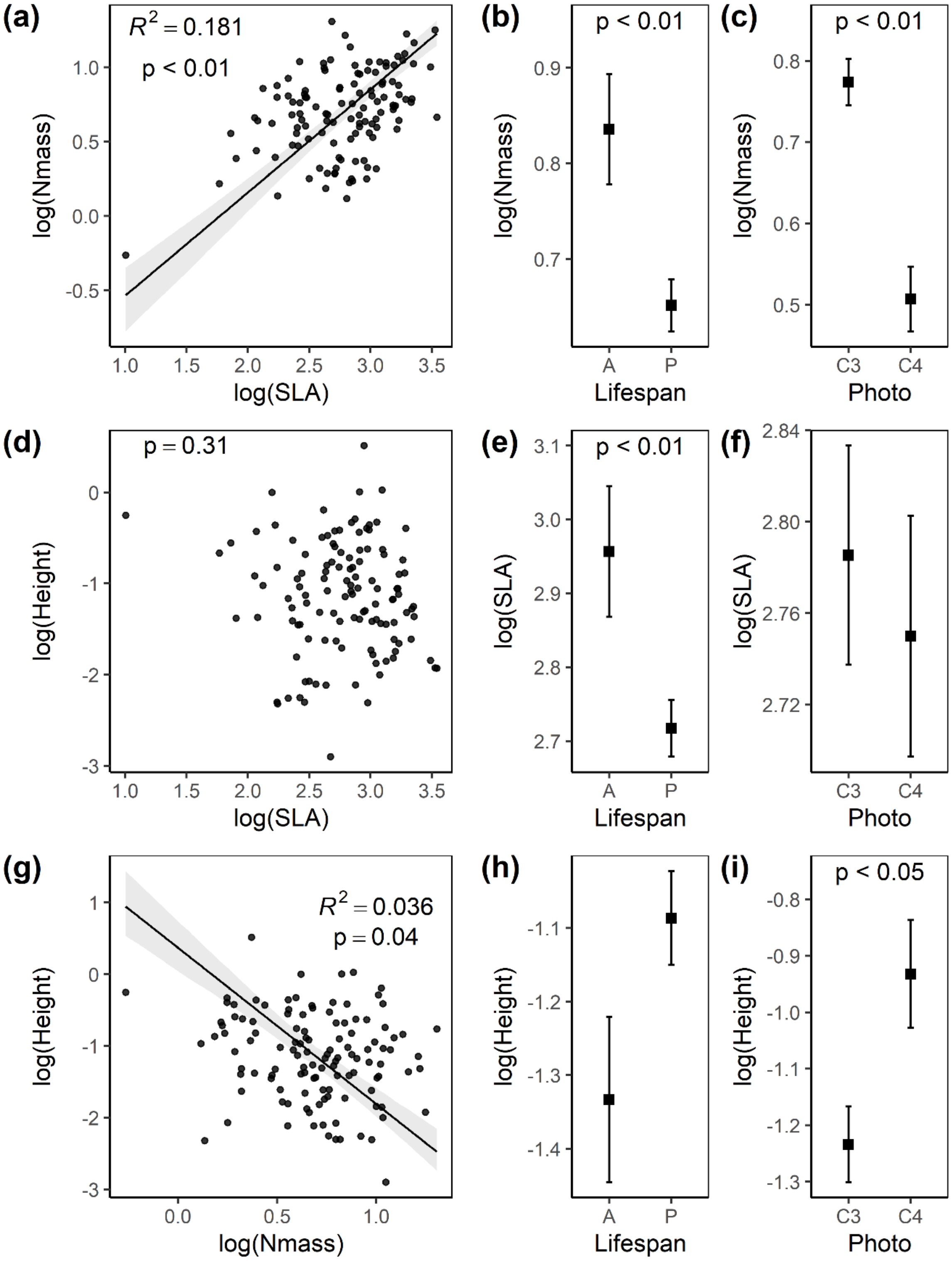

(a)
$R^2 = 0.181$
p < 0.01
log(Nmass)
1.0
0.5
0.0
-0.5
1.0
1.5
2.0
2.5
3.0
3.5
log(SLA)
(b)
p < 0.01
log(Nmass)
0.9
0.8
0.7
A
P
Lifespan
(c)
p < 0.01
log(Nmass)
0.8
0.7
0.6
0.5
C3
C4
Photo
(d)
p = 0.31
log(Height)
0
-1
-2
-3
1.0
1.5
2.0
2.5
3.0
3.5
log(SLA)
(e)
p < 0.01
log(SLA)
3.1
3.0
2.9
2.8
2.7
A
P
Lifespan
(f)
log(SLA)
2.84
2.80
2.76
2.72
C3
C4
Photo
(g)
$R^2 = 0.036$
p = 0.04
log(Height)
1
0
-1
-2
-3
0.0
0.5
1.0
log(Nmass)
(h)
log(Height)
-1.1
-1.2
-1.3
-1.4
A
P
Lifespan
(i)
p < 0.05
log(Height)
-0.8
-0.9
-1.0
-1.1
-1.2
-1.3
C3
C4
Photo

Figure 4

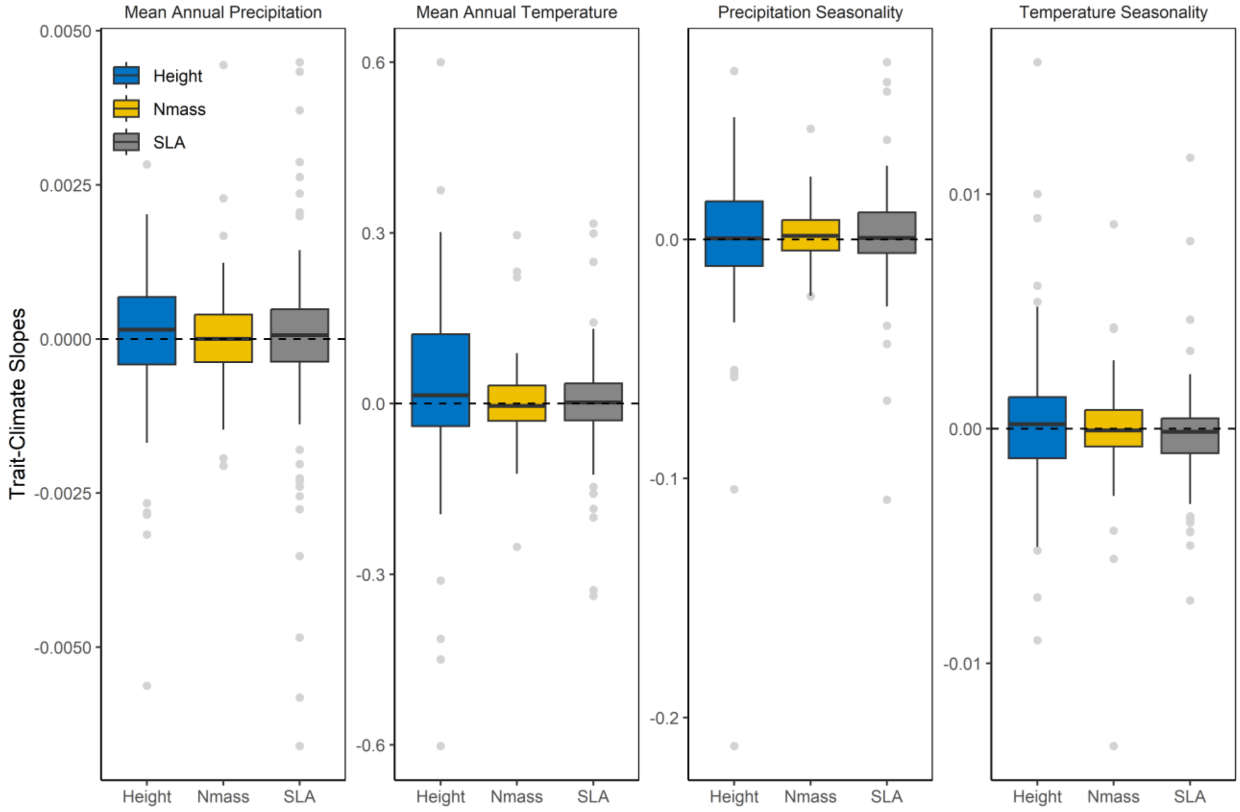
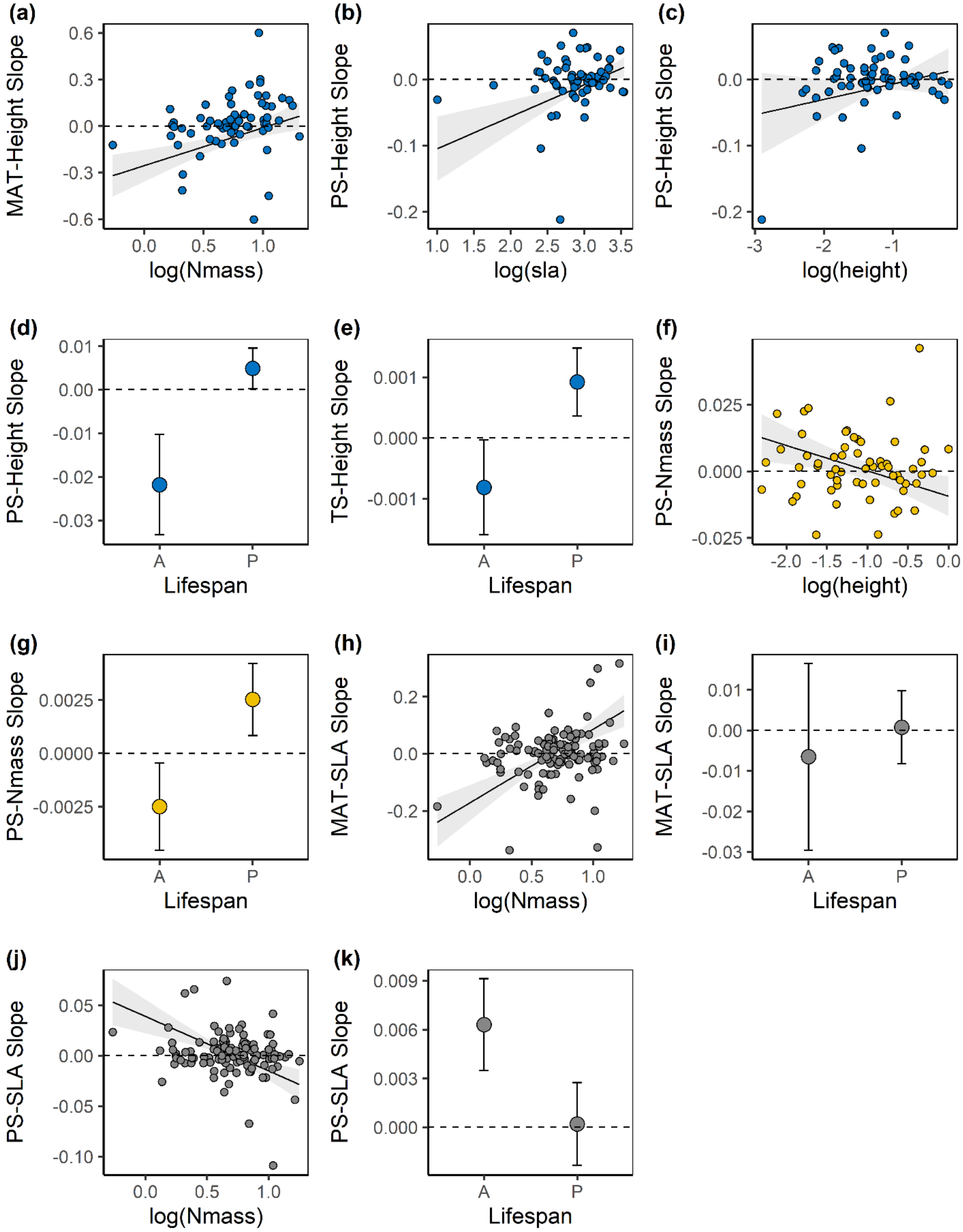

Mean Annual Precipitation
Mean Annual Temperature
Precipitation Seasonality
Temperature Seasonality
Trait-Climate Slopes
Height
Nmass
SLA
0.0050
0.0025
0.0000
-0.0025
-0.0050
0.6
0.3
0.0
-0.3
-0.6
0.0
-0.1
-0.2
0.01
0.00
-0.01
Height
Nmass
SLA

Figure 5


(a)
MAT-Height Slope
0.6
0.3
0.0
-0.3
-0.6
0.0
0.5
1.0
log(Nmass)
(b)
PS-Height Slope
0.0
-0.1
-0.2
1.0
1.5
2.0
2.5
3.0
3.5
log(sla)
(c)
PS-Height Slope
0.0
-0.1
-0.2
-3
-2
-1
log(height)
(d)
PS-Height Slope
0.01
0.00
-0.01
-0.02
-0.03
A
P
Lifespan
(e)
TS-Height Slope
0.001
0.000
-0.001
A
P
Lifespan
(f)
PS-Nmass Slope
0.025
0.000
-0.025
-2.0
-1.5
-1.0
-0.5
0.0
log(height)
(g)
PS-Nmass Slope
0.0025
0.0000
-0.0025
A
P
Lifespan
(h)
MAT-SLA Slope
0.2
0.0
-0.2
0.0
0.5
1.0
log(Nmass)
(i)
MAT-SLA Slope
0.01
0.00
-0.01
-0.02
-0.03
A
P
Lifespan
(j)
PS-SLA Slope
0.05
0.00
-0.05
-0.10
0.0
0.5
1.0
log(Nmass)
(k)
PS-SLA Slope
0.009
0.006
0.003
0.000
A
P
Lifespan