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Title: Idiosyncrasy and predictability in intraspecific trait-climate relationships of grasses

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Abstract

Many plant species can exhibit remarkable variation in leaf characteristics, depending on their abiotic and biotic environment. Environmental changes therefore have the potential to alter leaf traits, which in turn scale up to influence ecosystem processes including net primary productivity, susceptibility to fire and palatability to herbivores. It is not well understood how consistent trait-environment relationships are among species, across sites and over time. This presents a fundamental challenge for functional ecology, since no study can measure all relevant species in all places at all times. Thus, understanding the limits of transferability is critical.

We collected leaf trait measurements on 13 species of grass (family: Poaceae) across 11 sites and five years (n = 3091 individuals). Sites were arrayed along a spatial precipitation gradient in coastal northern California (annual precipitation of 590 to 1350 mm) with substantial inter-annual precipitation variability (from 60% below the 30-year average to 100% above average). Temporal and spatial linear relationships between precipitation and specific leaf area (SLA) appear at first idiosyncratic, with each species sometimes displaying positive and sometimes negative responses. However, this variation arises from sampling different portions of an underlying hump-shaped relationship, which was shared across most species. This hump-shaped relationship was driven primarily by changes in leaf tissue density. These results suggest the potential for transferability among species, as well as between space and time, as long as the gradients are sufficiently long to capture the non-linear response. Future work could explore the physiological basis of the non-linear SLA response, including the possibility that distinct physiological mechanisms are operating at the two extremes of the gradient.

Introduction

Functional traits can shed light on plant ecological strategies and responses to environmental change (Suding et al. 2008; Diaz et al. 2016). As Earth's climate changes, it is important to understand how plant traits might respond, as shifts in the functional attributes of plant communities can impact ecosystem processes (Lavorel and Garnier, 2002). Leaf traits are often a focus of study, given their critical role in gas exchange and light capture (Wright et al. 2004, Ordoñez et al. 2009), as well as interactions with several ecosystem processes including forage palatability (Pontes et al. 2007) and fire intensity (Simpson et al. 2016). Specific leaf area (SLA), the ratio of a leaf's surface area to dry mass can characterize the resource-use economics of a leaf, particularly with regards to carbon and light capture (Westoby 1998, Wright et al. 2004, Diaz et al. 2016). Plants with low SLA values are considered "conservative", displaying low relative growth rates, greater longevity, and low leaf tissue nitrogen and phosphorous concentrations (Wright and Westoby 1999, Wright et al. 2004, Shipley 2006, Diaz et al. 2016). Accordingly, plants with low SLA are often associated with nutrient poor (Ordoñez et al. 2009) and sometimes dry environments (Wright et al. 2005, Dwyer et al. 2014), though relationships with precipitation are often weak (e.g. Maire et al. 2015, Bruelheide et al 2018). In grasslands, ecosystem productivity often shows large inter-annual variation (Lauenroth and Sala 1992, Zhang et al. 2014) associated with precipitation variation. Changes in community-level variation in SLA is potentially an important driver of these responses (Griffin-Nolan et al. 2019). Thus, understanding how SLA responds to climate variation could improve predictions of grassland responses to climate change.

It is infeasible to directly quantify responses for all species in all regions to all potentially important environmental drivers. An appeal of trait-based ecology is the premise that, by focusing on functional characteristics of organs shared across many plant species, it will be possible to make general predictions and transfer inferences across domains (McGill et al. 2006). However, the constraints on this transferability are poorly delineated. For example, if wetter regions tend to have tree communities with higher average SLA, do wetter years also tend to have higher-SLA communities (Sandel 2019)? Do intraspecific shifts in traits along an environmental gradient mirror among-species turnover, such that sites with taller species also tend to have taller individuals of a species (Lepš et al. 2011)? Most evidence for the form of trait-environment relationships is derived from interspecific trait variation along spatial environmental gradients (Moles et al. 2009; Sandel et al. 2016, Bruelheide et al. 2018, Šímová et al. 2018, Sandel and Low 2019), yet in a global change context the goal is often to predict a change through time (e.g. Gaüzère et al. 2020, Pansini et al. 2021, Rubio-Rios et al. 2022). This requires a space-for-time substitution, which may or may not be reliable (Pickett 1989, Johnson and Myanishi 2008, De Lombaerde et al. 2018, Blois et al., 2013, Damgaard 2019). For example, warming-induced shifts in community trait values in tundra ecosystems often lagged behind the predictions made from spatial relationships between plant traits and temperature (Bjorkman et al. 2018).

Furthermore, many of the known trait-climate relationships are based on measurements across species, ignoring significant intraspecific trait variability and potentially misrepresenting a species' fitness in a particular environment (Siefert et al. 2015; Sandel et al. 2021; Westerband et al. 2021). Thus, we currently lack an understanding of whether intraspecific trait-climate relationships are consistent across space and time (Lang et al. 2019) and some early studies have struggled to identify consistent patterns (e.g. Albert et al. 2010, Roybal and Butterfield 2019). In at least some cases, intraspecific trait shifts are opposite to those associated with community turnover. For example, in communities consisting of species with typically high stem dry matter content (LDMC), individuals tended to have lower-than-average SDMC (Leps et al. 2011). Leaf nitrogen and phosphorous concentrations have shown similar negative covariation between inter- and intraspecific variation (Kichenin et al. 2013).

Our goal is to assess the transferability of intraspecific trait-climate relationships across space, time and among species. We examine intraspecific shifts in SLA and associated leaf traits (e.g., leaf thickness and tissue density) for 13 grass species along a precipitation gradient across 11 grassland sites in the San Francisco Bay Area of California for 5 years. We focus on SLA as it shows substantial intraspecific variation (Shipley and Almeida-Cortez, 2003; Sandel et al. 2021, Griffin-Nolan and Sandel 2023) and is sensitive to precipitation variability (Wellstein et al., 2017). While positive and negative intraspecific precipitation-SLA relationships are roughly balanced globally (Griffin-Nolan and Sandel 2023), the first year of data from this project revealed consistently negative intraspecific spatial precipitation-SLA relationships, opposite to the interspecific pattern and possibly due to changing trait covariance with precipitation (Sandel and Low 2019). Here, we ask whether these relationships remain consistent across years of widely varying precipitation, whether wetter years within a site are also associated with lower SLA values, and whether these relationships are consistent across species. If inconsistencies are detected, we further hypothesize that they may be segments of one non-linear relationship between traits and climate (Albert et al. 2010). Finally, we assess the relative importance of changes in leaf thickness and leaf tissue density in driving changes in SLA, considering that uncoordinated shifts in these traits could lead to opposite responses of SLA at the two ends of the precipitation gradient.

Materials and Methods

Site Characteristics

Grasslands in the San Francisco Bay Area are characterized by a Mediterranean climate, with warm, dry summers and cool, wet winters. Growth occurs during the wet season, with most grass species reaching reproductive maturity in April or May. We selected 11 sites (Figure 1, Table S1) to collect trait data across five years (2017-2021), although not all sites were sampled in all years. Sampling was particularly limited during the 2020 field season because of COVID-19. The sites include eight Marin County Parks, here divided into three “regions”: the Tiburon Peninsula (Old Saint Hilary’s, Ring Mountain), Central Marin (Loma Alta, French Ranch, Terra Linda/Sleepy Hollow Divide, Lucas Valley) and Northern Marin (Verissimo Hills and Mount Burdell), one University of California Natural Reserve (Blue Oak Ranch Reserve), one National Seashore (Point Reyes), and one site held by the Peninsula Open Space Trust (Wavecrest). The San Francisco Bay Area has very strong gradients in annual precipitation, which are well captured by these sites. Based on downscaled climate estimates from PRISM (see details below), the driest site, Blue Oak Ranch Reserve, receives about 590 mm of precipitation per year. The wettest, Lucas Valley, receives about 1350 mm per year. The wettest year in the study (2017) received 60-100% more rainfall than average across the sites, while the driest year (2021) received 60-70% less than average (Figure 2, Table S1). Precipitation is a strong positive predictor of net primary productivity within California annual grasslands (Alexander et al. 2023).

Trait Measurements

We measured leaf traits of grasses in late April through early June, near the end of their growing season. We established an average of 5 plots (5x5 m) in each site in each year. For every grass species present in a plot, we collected trait measurements from an average of 4 individuals. New plots were established each year to avoid resampling the same individuals. Plots within a sampling site were separated by a median distance of 465 m, with an inter-quartile range of 152 to 1023 m.

From each individual, we collected the highest fully expanded, undamaged, green leaf along the stem and measured its thickness using a caliper. We immediately photographed the leaf against a white background with a scale bar, using a sheet of plexiglass if necessary to hold the leaf flat. The leaves were placed in individually labeled coin envelopes and returned to the lab, where we dried them at 55-60 °C for at least 48 hours and then weighed them. We determined leaf area (in cm^2) from each image using ImageJ software (https://imagej.nih.gov/ij/). We calculated SLA as the ratio of leaf area to dry mass (cm^2/g). Finally, we estimated leaf volume as leaf surface area x leaf thickness (cm^3), and calculated leaf tissue density as leaf dry mass/leaf volume (g/cm^3).

In total, we collected trait measurements for 3517 individuals of 33 species across 136 sampling plots. For our analysis, we focus on those species that were sampled from at least 20 plots, leading to a sample size of 13 species and 3091 total individuals. Each of these species occurred at a minimum of 7 of our sites.

To describe recent and long-term precipitation patterns at each sampling plot, we used PRISM monthly climate data (PRISM Climate Group, 2021). Most plots were not located near weather stations, but the resolution of the PRISM dataset (800 m for 30-year normals) allowed us to capture the fine-scale variation in climate among plots. For each sampling plot, we extracted the long-term (30-year) mean annual precipitation (P) as well as the total precipitation during the 12 months preceding sampling (P_1). We used this 12-month window to capture the short California growing season as well as any rare precipitation events that may have affected plant trait expression.

Analysis

We fit Bayesian hierarchical models to relate SLA to P_1. To improve the convergence of the Markov chain Monte Carlo (MCMC) sampler, we performed two initial processing steps. First, we standardized each SLA measurement against its species mean by subtracting the species mean value (all on a log scale), calling these values deltaSLA. Second, we scaled these deltaSLA values and $P_1$to a mean of 0 and variance of 1.

One model was fit to describe spatial relationships, in which a different slope and intercept was estimated for each species in each year. Another model described temporal relationships, with different slopes and intercepts for each species in each sampling region. We used five regions (Blue Oak Ranch, Tiburon Peninsula, Central Marin, Northern Marin and Point Reyes) for the temporal model and four years for the spatial model. One region, Wavecrest, was sampled in only one year, and therefore not usable to establish relationships through time. Similarly, sampling in 2020 was limited to just two sites, so we did not consider spatial relationships in that year. These models describe, for each species, whether 1) wet sites within a year produce different trait values than dry sites (spatial relationships), and 2) wet years within a region produce different trait values than dry years (temporal relationships). We were interested in the consistency of temporal relationships across space, spatial relationships through time, and temporal vs spatial relationships.

The above approach allows us to compare model coefficients to assess consistency, but we also wanted to assess the transferability of model predictions across regions, years and species. We randomly selected two combinations of region, year and species that differed in only one respect (e.g. *Bromus hordeaceus* in Blue Oak Ranch in 2021 and *Bromus hordeaceus* in Blue Oak Ranch in 2017). We then used the estimated model coefficients for the first combination to predict trait values for both combinations. We computed the predicted-observed Pearson correlations in both cases, with the ratio of these correlations serving as an indication of the extent to which predictions can be transferred. We repeated this process 1000 times changing only year, 1000 times changing only the region, and 1000 times changing only the species. Finally, we used the same procedure to assess a space-for-time substitution – using the estimated model coefficients for one species in one year across sites to predict its dynamics at one site through time (e.g. *Bromus hordeaceus* in 2018 to predict *Bromus hordeaceus* through time at Blue Oak Ranch).

The model fitting and assessment of transferability were then repeated for models that included both $P_1$and its quadratic term P_1^2. To simulate a common application of a space-for-time substitution, we also examined quadratic terms in models fit only with data from 2017, 2018, 2019 and 2021. The idea was to examine whether data from one year could be enough to accurately estimate a non-linear relationship that might be apparent in a longer time-series.

Finally, we explored precipitation-trait relationships for other traits related to SLA: leaf surface area, thickness, tissue density and dry mass. In each case, we fit one overall spatial-temporal hierarchical model including both species-by-region and species-by-year interactions.

We fit all models using the *brms* package (Bürkner 2017,2018, 2021) in R v4.1.2 (R Core Team 2021). For each model, we ran 2 chains for the MCMC sampler, each with 5000 iterations after a 2500 iteration burn-in. Convergence metrics were adequate, including R-hat values very close to 1 (maximum 1.01) and bulk effective sample sizes larger than 1000 for all estimated parameters. In the following text and figures, we present the mean value of the posterior distribution for these parameters.

Results

The overall main effects of P_1 on deltaSLA were similar in the spatial and temporal models (mean estimate and 95% credible interval were 0.16 (-0.01,0.33) and 0.22 (0.06,0.40), respectively). However, the linear slopes of trait-precipitation relationships were not consistent within or among species, regions or years. For example, SLA of *Bromus hordeaceus* responded positively, negatively, or weakly to precipitation depending on the year (Figure 3A) or region (Figure 3B). Spatial relationships were highly variable among years. For example, in 2017, all species showed negative spatial precipitation-SLA relationships, while in 2019 most (11/13) were positive (Figure 3C). Considering temporal relationships, wetter years were associated with higher SLA values for nearly all species in Point Reyes and the Tiburon Peninsula, while in Central Marin, all but one species had lower SLA in wetter years (Figure 3D). Every species showed both negative and positive P_1 slope estimates among years in the spatial model. The same was true among regions for temporal P_1 slope estimates, with one exception (*Briza minor*, with only positive slope estimates).

Accordingly, transferability was low for these models, particularly across space and time. The median correlation between predicted and observed deltaSLA values for a particular species, region and year was about 0.24. Transferring a prediction to another region (for the same species and year) reduced the median correlation to -0.06, while transferring to another year (for the same species and region) reduced it to -0.07. Thus, these transfers are slightly worse than a random guess. Transferring to another species (in the same region and year) produced a less pronounced reduction in predictive performance, reducing the correlation to 0.16. The space-for-time substitution was poor, with a median correlation of 0.06. Thus, a linear relationship fit in one region was essentially useless to predict patterns in another region, and the same was true for years.

Across the complete dataset, the quadratic effect of P_1 on SLA was strongly supported in the models, and reliably negative (spatial model coefficient: -0.36, CI: (-0.51, -0.20), temporal model coefficient -0.43, CI: (-0.58, -0.27)). The overall estimated equation from spatial models was $\text{deltaSLA} = 0.37 + 0.28\,P_1 - 0.36\,P_1^2$. For the temporal model it was $\text{deltaSLA} = 0.38 + 0.14\,P_1 - 0.43\,P_1^2$. Back-transforming to original precipitation values, the spatial model estimates maximum SLA values at 1.4 m of rainfall, while the temporal model estimates the maximum slightly lower, at 1.25 m. Across species, years and regions, the quadratic terms were nearly uniformly negative, and their 95% credible intervals often did not include 0 (Figure 4). In any of the four individual years, however, there was weak support for a quadratic term in the model. Of the four years, only the wettest year (2017) showed clear evidence for a negative quadratic relationship (estimated quadratic term -1.01, 95% credible interval: (-1.51, -0.53)). In one of the dry years (2018) it was positive (7.77, CI from (2.72 to 12.90)), and in both 2021 (very dry) and 2019 (wet) the estimates were close to zero, with credible intervals including zero. Therefore, in the complete data set a clear and consistent hump-shaped relationship appeared across many species, but this was not readily detectable in most single years.

The quadratic term also substantially improved transferability, particularly among regions and years. The median correlation between predicted and observed deltaSLA values for a given species, region and year was 0.30. Transferring predictions to another region (maintaining the species and year) reduced this correlation by 23%, transferring to another year (maintaining species and region) reduced it by 57% and transferring to another species (maintaining region and year) reduced it by 20%. A space-for-time transfer reduced the correlation by 23%. Thus, there was always some loss of predictive power when transferring across domains, but this loss was fairly small across space, across taxa and from space to time. However, transferring across years produced a much weaker prediction.

The pattern in leaf area largely mirrored that for SLA, while leaf dry mass is essentially invariant with respect to P_1 (Table 1, Figure 5). Thus, the same mass produces variable leaf areas depending on precipitation This difference in area return per mass invested appears to be driven primarily by changes in leaf tissue density rather than thickness, as density showed responses very much the opposite of the SLA response (Figure 5). Consistent with an important role for density, variation in density was overall much more strongly related to SLA than was thickness (median within-species r = -0.80 for density, r = -0.08 for thickness).

Discussion

Consistency of trait-climate relationships

We explored the spatial and temporal relationships between SLA and precipitation within grass species to determine the consistency and transferability of trait-climate relationships. Overall, we make the following three conclusions: (1) linear precipitation-SLA relationships are inconsistent among species, regions and years, (2) this idiosyncrasy could be resolved by postulating an underlying non-linear relationship (approximated piece-wise by subsets of the data) which is undetectable from single years of data, and (3) when the range of precipitation values is sufficient to detect the unifying nonlinear relationship, a fairly consistent negative hump-shaped relationship does appear. This closely matches the expectation presented by Albert et al. (2010) in their attempt to explain idiosyncratic intraspecific trait patterns among species.

Like previous studies on grasses that assessed linear relationships between climate and traits within species, we found very inconsistent relationships (Roybal and Butterfield 2019, Sandel et al. 2021, Weemstra et al. 2021). This has led to some skepticism that these relationships could be understood in a general way. Albert et al. (2010) recognized this problem, and proposed a conceptual model unifying divergent responses according to the position along a species' niche axis. Because one region or year often did not encompass enough precipitation variability to reveal the nonlinearity, individual spatial and temporal relationships between precipitation and SLA often appeared approximately linear. And, because these linear approximations are pieces of a hump-shaped function, their slopes often differed not just in magnitude but in sign. Thus, the patterns among years or regions can appear idiosyncratic, despite being pieces of one nonlinear function.

Given the inadequacies of the linear models, it might seem that it would be easy to detect a unifying non-linear relationship. However, among the four years we modeled, the hump-shaped relationship between P_1 and SLA was only detectable in 2017. In other years, the estimated curvature was either weak or in the opposite direction. Were we to have conducted the study in just one of those years, any resulting space-for-time substitution would be weak. Furthermore, our own previous analysis of the 2017 data (Sandel and Low 2019) was solely based on linear relationships between precipitation and SLA, which seemed at the time to fit the data adequately. The lesson we take from this is that a unifying non-linear relationship may be very difficult to detect in just one year of study.

However, with our multi-year data, predictions from the quadratic model were transferable among regions, years and species, with less loss in explanatory power. By virtue of the similar estimated equations for temporal and spatial patterns, spatial predictions were also transferable to temporal dynamics. Thus, our results emphasize the importance of carefully considering the extent of the spatial gradient, and whether it is sufficient to encompass the expected climatic changes through time. In this case, despite large spatial variability in precipitation, the interannual variation was even larger (Figure 2). Thus, several years of spatial data with varying climate conditions is likely needed to establish a robust space-for-time substitution, at least when the underlying function is nonlinear.

It is common to detect evidence of some degree of non-equilibrium in evaluations of space-for-time substitutions (Sandel et al. 2010, Blois et al. 2013, Svenning and Sandel 2013, Sandel 2019, Gaüzère et al. 2020). Perfect spatial-temporal equilibrium in trait-climate relationships implies that the function linking the two is equivalent regardless of whether the relationship is computed across space or through time. However, a large number of processes can disturb this equilibrium, including lagged responses to environmental change and non-climatic influences on trait values (Svenning and Sandel 2013). Here, we found largely congruent spatial and temporal responses, suggesting strong trait-climate equilibrium. This may be because, unlike most previous studies, we are focused on intraspecific trait variation rather than aggregate community metrics such as the community-weighted mean. Individual-level shifts in trait expression may be fairly rapid in response to variation in precipitation over the previous growing season, leading to weak lags and therefore strong equilibrium. Our focus on recent (12-month antecedent) precipitation, rather than long term averages as is most typical (e.g. Wright et al. 2005), also likely contributed to the stronger equilibrium we observed. Further, many of the species considered here are annuals, increasing the potential for rapid responses. Individual plants often respond to climate on short timescales (e.g., months to years). Legacies of antecedent precipitation can have a strong influence on both plant traits and ecosystem functioning (Sala et al. 2012). Understanding plant responses to recent climate may explain potential inconsistencies in space-for-time substitutions as plant responses to extreme wet or dry years are likely to differ from expectations based on spatial variation in mean climate.

Implications for plant functional ecology

Our finding of a hump-shaped relationship between precipitation and SLA within species was somewhat surprising. Most previous research has found that SLA is generally lower in drier areas and years as plants reduce their potential area for evapotranspiration, produce hardier drought tolerant leaves, or both. Given that drought negatively influences SLA of grasses (Wellstein et al. 2017) and that increased competition and shading (as expected in wetter years with higher NPP) tend to increase SLA (Poorter et al. 2009, Bennett et al. 2016) the decline in SLA we observed at higher precipitation was puzzling. We investigated this further by exploring mechanisms of SLA variation and found that it was primarily driven by changes in leaf tissue density. In other words, as precipitation increased in wet sites/years, SLA decreased as leaves became denser. Increased leaf tissue density could result from greater cell wall fraction (vs. cytoplasm) (Poorter et al. 2009) or increased vein density (Alanso-Forn et al. 2020, reviewed in Sancho-Knapik et al. 2020). Additionally, reduced tissue density with little change to thickness may indicate that plants are producing leaves with more densely packed cells and/or smaller air spaces (Castro-Díez et al. 2000), which are already reduced in grasses compared to dicots (Byott 1976). In turn, the percent airspace in leaf tissue is negatively correlated with area-based photosynthetic rates for some species (Chazdon and Kaufmann 1993). While we did not investigate microanatomy of leaves, it is possible that such mechanisms may be driving the nonlinear effect of precipitation on SLA. For example, enhanced ecosystem productivity on the wet end of a species' range could increase herbivory activity, prompting greater resource investment in cell wall material and thus increased tissue density (Xing et al. 2021). In drier regions, however, species may increase tissue density via increased vein density as an adaptation to drought (Sack and Scoffoni, 2013). Further investigations into the microanatomy of these species is required to determine the exact physiological mechanisms.

Two previous studies of regional or global trait-climate relationships in grasses have found weak effects of precipitation on interspecific SLA patterns (Forrestel et al. 2017, Jardine et al. 2020). However, one study (Sandel et al. 2016, the largest of these in terms of species coverage) did reveal hump-shaped relationships between annual precipitation and community mean SLA at continental to global scales, with maximum SLA values expected around 1.0 to 1.5 m of annual precipitation. This may suggest some shared mechanism promoting maximal SLA in grasses around 1.0 m of annual rainfall at both inter- and intraspecific levels, but more work is needed to determine if this is robust. In particular, our study examined only C3 species, and it might be expected that C4 grasses (by virtue of their higher water use efficiencies) might experience a maximum SLA at a lower precipitation value; however, SLA of grass species do not generally vary by photosynthetic pathway, nor do intraspecific precipitation-SLA relationships (Griffin-Nolan et al. 2023). It will also be valuable to extend these results beyond grasses, to other herbaceous plants and trees, which can exhibit different trait-climate relationships (e.g. Reich and Oleksyn 2004, Šímová et al. 2018). In particular, the traits of species with long-lived leaves may not track recent precipitation as strongly as annual grasses, which would likely cause greater mismatch between spatial and temporal trait-environment relationships.

The strength and direction of trait-climate relationships shown here should be viewed cautiously considering we did not assess additional traits which may influence the response of SLA to precipitation. For example, rooting depth and associated root traits (e.g., root diameter, specific root length) are known to influence plant responses to precipitation (Garbowski et al. 2020). Hypotheses on how SLA will respond to precipitation assume the plants are experiencing lower soil moisture and greater water stress in more arid sites. Deep-rooted species with large root diameters are an exception to this assumption as they can access groundwater stores (Ding et al. 2021); however, grasses are generally shallow rooted and access water in upper soil layers (Nippert and Knapp 2007). Additionally, our predictions about how precipitation may impact SLA depends on a species biomass allocation to total leaf biomass production (Poorter and Remkes 1990). While we would expect plants to reduce SLA in drier conditions to limit evaporative leaf surface area, some plants may accomplish this through reduced allocation to leaf biomass in general (Eziz et al. 2017), and this can be independent of changes to SLA. Interestingly, low SLA species can sometimes have denser canopies as their leaves have longer lifespans and thus accumulate over time (Wright et al. 2019); thus, our predictions also depend on a plant's lifespan. Finally, our sampling covers a limited geographical scope; therefore, we call for more expansive temporal and spatial trait datasets to make general conclusions about spatiotemporal trait-climate relationships for grasses.

It is particularly important to understand the drivers of SLA variation for grasses as the traits of these species contribute to net primary production, grazing dynamics, fire regimes, and carbon sequestration. Relative growth rate of herbaceous plants is strongly determined by SLA (~64% interspecific variation in RGR is attributed to SLA; Poorter and Van der Werf 1998) which suggests shifts in SLA with climate will also impact productivity. This is important for understanding fire regimes in California grasslands as grass flammability is linked to biomass production in addition to vegetation moisture content (Simpson et al. 2016). Additionally, species with higher SLA are often more flammable, particularly exotic grasses which are common to California (Murray et al. 2013).

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Author contributions

BS conceived the study and led the data collection. BS and RJG-N designed the analysis, BS conducted the analysis, and both authors wrote the manuscript.

Conflict of Interest Statement

The authors declare no conflicts of interest.

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Table 1: Regression coefficients (mean of posterior distribution) and 95% credible intervals linking precipitation with five traits, derived from overall quadratic models including species-by-region and species-by-year interactions.

	P_1		P_1^2	
Trait	Estimate	Credible int.	Estimate	Credible int.
SLA	0.25	(0.11,0.39)	-0.38	(-0.57,-0.18)
Thickness	-0.09	(-0.19,0.01)	-0.10	(-0.23,0.02)
Density	-0.11	(-0.24,0.02)	0.35	(0.17,0.51)
Area	0.05	(-0.12,0.25)	-0.20	(-0.38,0.04)
Mass	0.00	(-0.18,0.18)	-0.01	(-0.19,0.19)

Figure captions

Figure 1: Sampling locations and illustration of spatial and temporal relationships. (A) Each symbol represents a sampling location, divided into 6 main regions and sampled in one of 5 years. The background map indicates topography. The zoom-in shows the distribution of sampling locations at one site: Blue Oak Ranch. (B) and (C) illustrate examples of spatial and temporal relationships. In (B), the spatial relationship between precipitation and SLA is shown for one year (2021) for Bromus hordeaceus. In (C), the temporal relationship is shown for one site (Blue Oak Ranch). Symbols and colors as in (A).

Figure 2: Monthly rainfall totals across the five years within the five study regions (A) and their deviation from the 30-year monthly averages for each site (B).

Figure 3: Spatial and temporal relationships between SLA and precipitation over the previous 12 months. Top row: example for one species, Bromus hordeaceus. Each point represents a sampling location in a year, grouped either by the year of sampling (A) or by the sampling region (B). Thus, (A) shows the spatial relationships estimated in each year, while (B) shows the relationships through time in each region. Parameters for the fitted curves are the means of the posterior distribution. The bottom row visualizes the distribution of spatial (C) and temporal (D) precipitation-SLA estimated regression coefficients across species as violin plots. Coefficients for 2020 are missing because of limited data collection that year. The numbers at the top and bottom indicate the number of species with positive or negative posterior means, with the number in parentheses indicating the number for which the 95% credible interval does not include 0.

Figure 4: Summary of quadratic model fits. Panels A and B show the distribution of coefficients for the P_1^2 term across species in each year or sampling region, respectively. Counts at the bottom indicate the number of species within that region or year for which the quadratic term was negative, while the number in parentheses indicates the number of species for which the credible interval did not include 0. Counts at the top are the same for positive responses. Panels C and D show the resulting fitted curves for each species in each year (C) or sampling region (D). Colors in (C) and (D) correspond with (A) and (B), respectively.

Figure 5: Relationships between P_1 and delta trait values for four leaf traits, specific leaf area (SLA, A), leaf thickness (B), leaf tissue density (C) and leaf surface area (D). Fitted curves represent main effects from quadratic models. Symbols and colors as in Figure 1, dashed lines indicate relationships for which the credible interval overlaps 0.