

Taxonomic, phylogenetic, and environmental trade-offs between leaf productivity and persistence

JIN-SHENG HE,^{1,2,5} XIANGPING WANG,¹ DAN F. B. FLYNN,^{1,3} LIANG WANG,¹ BERNHARD SCHMID,⁴
AND JINGYUN FANG¹

¹Department of Ecology, Peking University, Yi-Fu Building II, 5 Yiheyuan Road, Beijing 100871 China

²Shenzhen Graduate School, Peking University, Shenzhen 518055, China

³Department of Ecology, Evolution, and Environmental Biology, Columbia University, New York, New York 10027 USA

⁴Institute of Environmental Sciences, Zurich University, Winterthurerstrasse 190, CH-8057 Zürich, Switzerland

Abstract. Assessing the influence of climate, soil fertility, and species identity on leaf trait relationships is crucial for understanding the adaptations of plants to their environment and for interpreting leaf trait relationships across spatial scales. In a comparative field study of 171 plant species in 174 grassland sites across China, we examined the trade-offs, defined as negative covariance between two traits, between leaf persistence (leaf mass per area, LMA) and leaf productivity (mass-based photosynthetic rate, A_{mass} , N and P content, and photosynthetic N use efficiency, PNUE). We asked to which extent these trade-offs were influenced by: (1) variation among sites within species, decomposed into variation due to climatic and soil variables; (2) variation among species within sites, decomposed into variation among taxonomic, functional, or phylogenetic groups; and (3) the joint contribution of variation among species and sites. We used mixed-model analysis of covariance to partition bivariate relationships between leaf traits into trade-off components. We found significant mass-based persistence–productivity trade-offs of LMA– A_{mass} , LMA–N, LMA–P, and LMA–PNUE consistent with previous broadscale findings. Overall, (1) variation among sites within species explained 14–23%, (2) variation among species within sites explained 20–34%, and (3) the two together explained 42–63% of the total covariance between leaf traits. Interspecific trade-offs of LMA– A_{mass} , LMA–N, and LMA–P were stronger than inter-site ones. A relatively low amount of covariance was explained by climatic and soil variables. However, we found the trade-offs were stronger for LMA–N and LMA–P at higher precipitation and for LMA–PNUE at greater soil fertility, if displayed by major axis regression, which combined both intra- and interspecific variation. Residual trade-offs within species and sites were weak, suggesting that intraspecific, intra-site variation in physiology was less important than variation imposed by species identity or environmental differences among sites. Our results from grassland biomes add evidence for the fundamental nature of productivity–persistence trade-offs in plants. No individual factor emerged as the single major cause for these trade-offs. Rather, the total covariance between leaf traits was explained by a combination of factors, each contributing a range of explanatory power.

Key words: China; covariance partitioning; functional traits; grassland; Inner Mongolia; leaf trade-offs; taxonomic/phylogenetic constraints; Tibetan Plateau; Xinjiang.

INTRODUCTION

The value of a leaf to a plant is the contribution of the carbon fixed in photosynthesis. Because the lifetime carbon fixation by a single leaf depends on its productivity and persistence (Harper 1989, Kikuzawa and Lechowicz 2006), it is a central issue in physiological ecology to understand which factors influence the relationship between these two (Ackerly et al. 2000, Westoby et al. 2002). In particular, an unresolved key question is the extent to which the leaf productivity–persistence relationship is controlled by environmental

variation, including climatic and soil factors, or by interspecific variation.

A number of studies have demonstrated that bivariate scaling of plant leaf traits is relatively constant across biomes, plant life forms, and phylogeny (Poorter and Bergkotte 1992, Reich et al. 1997, Ackerly and Reich 1999, Garnier et al. 1999, Castro-Diez et al. 2000, Shipley and Lechowicz 2000, Wright et al. 2004, Wang 2007). In general, leaves with thicker lamina, higher tissue density, and longer life span have lower nutrient concentration and photosynthetic rate, representing a trade-off between leaf productivity and persistence (Reich et al. 1991, Diemer 1998). This trade-off has been characterized as a leaf economics syndrome or spectrum (Westoby et al. 2002, Wright et al. 2004). The scaling is of the nature of a power law function (assessed

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⁵ E-mail: jshe@pku.edu.cn

using log–log scaling) when examining pairwise relationships among traits. Although minor differences in slopes and intercepts of these log–log relationships exist, we have only rudimentary understanding of whether there are systematic patterns of variation in these relations or what the causes might be (Wright et al. 2005a).

In contrast to the mentioned relative constancy, there are also reports suggesting that the scaling rules may vary with climate (Reich et al. 1999, Wright et al. 2005b), plant life form (Tjoelker et al. 2005), or phylogeny (Kerkhoff et al. 2006). Up to now, not much was known about the potential causes of differences and controls of the scaling relationships (but see Shipley et al. 2006). One reason for the difficulty in assigning variation in the trade-off between leaf productivity and persistence to different causes is that previous large-scale studies typically used data aggregated from heterogeneous sources. In such cases, species composition overlaps little across sites, preventing researchers from being able to separate variation due to environmental differences from variation due to differences among species.

If we define a trade-off as negative covariance between leaf traits, it is possible to decompose this covariance into components (Kempthorne 1969:264–269). Thus, the influence of variation across different environments or among different species on the trade-off can be assessed. In the first case, the trade-off can be due to variation in leaf traits within species distributed across a range of environments. In the second case, the trade-off can be due to variation in leaf traits within environments (sites) among species. To the extent that the occurrence of species and environmental variation among sites are correlated, the two cases cannot be separated, which was the case in the abovementioned previous studies. Furthermore, in the present study where multiple species occurred at multiple sites, a residual component of covariance remains after accounting for the variation across environments and among species. This can be due to site \times species interactions or to variation in leaf traits within species within sites.

Here we present such analyses using a large data set collected from 2003 to 2004 across Chinese grasslands, ranging from the moist, temperate areas of eastern Inner Mongolia, to the desert and mountains of Xinjiang Autonomous Region, to the alpine grassland of the Tibetan Plateau (He et al. 2006a, 2008). We examine the trade-offs between leaf mass per area (LMA) as a measure of leaf persistence (Westoby et al. 2002) and mass-based photosynthetic rate and leaf N and P concentrations as measures of leaf productivity. The large range of environmental conditions and the large number of species allowed us to ask: (1) How are trade-offs influenced by variation among sites within species, in particular via climatic and soil variables? (2) How are trade-offs influenced by variation among species within sites, in particular variation among taxonomic or

phylogenetic groups? (3) How are trade-offs influenced by joint variation among sites and among species, i.e., changes in species compositions across sites? (4) Are there residual trade-offs within sites within species? In addition, we ask (5) whether trade-offs differ in slope with environmental variation, in particular with climatic and soil variables. This last question asks not how species and site data are arranged on any trade-off line, but rather how environmental factors influence the slope of the trade-off.

The answers to these questions will add new insight into the potential causes underlying the leaf economics syndrome (Wright et al. 2004) and bivariate scaling “laws” in plant ecology (Niklas 1994). In addition, Chinese grasslands differ in important aspects (dominance of low-stature perennial plants, low leaf phosphorus concentrations) from other grassland ecosystems (He et al. 2006b, 2008). These differences highlight the need for a more comprehensive examination of the patterns and the causes of the trade-off between productivity and persistence.

MATERIALS AND METHODS

Study site and plant species

This study was conducted across the Chinese grassland biomes, in the temperate grassland of the Inner Mongolia Plateau, the alpine grassland of the Tibetan Plateau, and the montane grassland in Xinjiang Autonomous Region. We sampled leaves of 171 abundant species (from 90 genera and 34 families of vascular plants) at 174 sites across the three grassland regions. The 171 species were grouped into three growth forms (56 grass, 78 herbaceous, and 37 woody species) and two nitrogen acquisition types (26 nitrogen-fixing legumes, 145 nonlegume species).

Descriptions of the study region, sampling protocol, leaf trait, and soil property measurements and the climate data used have been detailed previously (He et al. 2006b, 2008, Yang et al. 2008). In brief, field sampling and measurements were conducted in late July and early August of 2003 and 2004. Defining the occurrence of a species at a site as a population, the data set contained 429 populations (J.-S. He, *unpublished data*). For each population, we collected 5–10 samples from different individuals to measure the leaf traits. For species with insufficient biomass from single individuals, samples were pooled from several individuals. Since these data were collected by a single team using standardized collection protocols, this analysis avoids the difficulty of heterogeneous data in previous large-scale analyses of leaf traits (e.g., Wright et al. 2004).

In situ photosynthetic rates of current-season leaves were measured at saturating light ($1500 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ of photosynthetic photon flux density) with open-path gas exchange systems using red-blue light sources and CO_2 mixers (LI-6400; LI-COR, Lincoln, Nebraska, USA). The reference CO_2 concentration in the leaf cuvette was

maintained at 360 $\mu\text{mol CO}_2/\text{mol}$, and leaf cuvette temperature was maintained at 22°–25°C, depending on the external temperature. Leaf N concentration was assayed using an elemental analyzer (2400 II CHN Elemental Analyzer; Perkin-Elmer, Boston, Massachusetts, USA), total P concentration was measured by a molybdate/stannous chloride method (Kuo 1996) after $\text{H}_2\text{SO}_4\text{-H}_2\text{O}_2\text{-HF}$ digestion (Bowman 1988), and LMA was determined by dividing oven-dried (60°C) leaf mass by the corresponding leaf area measured in the field with a portable leaf area meter (AM200; ADC Bioscientific, Herts, UK). Photosynthetic nitrogen use efficiency (PNUE) was defined as photosynthetic capacity per unit leaf N.

Soil surveys were conducted at 163 of the 174 sites. Sampling procedures and measurement methods for soil bulk density (BD), soil total N (STN), and soil organic carbon (SOC) have been described elsewhere (Yang et al. 2008). Bulk density, STN, and SOC from 0–10 and 10–20 cm depths were used for the current study. Because BD, STN, and SOC were closely correlated, we used SOC as the measurement of soil fertility.

Data analysis

We used correlation networks to display the relationships between leaf traits and to examine the differences among growth forms (grass/herb/woody) and regions (Tibet/Inner Mongolia/Xinjiang). To examine how the trade-offs of leaf mass per area with mass-based photosynthetic rate ($\text{LMA}-A_{\text{mass}}$), $\text{LMA}-\text{N}$, $\text{LMA}-\text{P}$, and $\text{LMA}-\text{PNUE}$ were shaped by environmental variation among sites and by species identity, we drew scatter plots for the overall correlations of the population data, the correlations of site means, the correlations of species means, and the residual correlations of the population data (residuals after fitting sites and species). Note that mean correlations are approximations and that a partitioning of sums of products in a covariance analysis allows a more precise assessment of the influence of different factors such as site or species on the trade-off relationships (Kempthorne 1969, Falconer and Mackay 1996).

Here we use the term “analysis of covariance” in the sense of Kempthorne (1969) for a decomposition of sums of products, exactly analogous to the decomposition of sums of squares in an ANOVA. We used ordinary mixed-model analyses (Snedecor and Cochran 1980) for this partitioning of the total sums of squares into component sums of products for the above trade-off relationships. The F ratios of mean products (=sum of products/degree of freedom) were used to test significance. The sums of products were obtained using the following formula:

$$\text{SS}(X + Y) = \text{SS}(X) + \text{SS}(Y) + 2\text{SP}(X, Y)$$

where SS stands for a sum of squares, SP for a sum of products, X and Y for the traits of interest, and $X + Y$

for the sum of the two traits (Bell 1989). The explanatory terms in the analysis were “site” (random), decomposed into contrasts for “climate” (fixed, combining four climatic variables), “soil” (fixed, combining three soil variables), and remainder of “site” (random) and “species” (random), decomposed into contrasts for “functional groups” (fixed, combining growth form groups and nitrogen-fixing/non-nitrogen-fixing groups), “family” (random), “genus” (random, within family), and remainder of “species” (random, within family and genus). As alternatives for “family” and “genus,” we used also phylogenetic groupings of similar numbers of elements as “family” and “genus.” Due to the complexity of the design with the crossed and partially confounded main random terms “site” and “species,” we used ordinary mixed-model analysis. However, we also estimated covariance components for the random terms with restricted maximum-likelihood (REML) approaches, as implemented in GenStat software (Payne et al. 1993). In the ordinary mixed-model analysis, we fitted either “site” or “species” first to estimate the influence of these terms on the trade-offs alone (in the following referred to as “type I sum of products”) or corrected for the other (“type II sum of products”). We also fitted different sequences for the contrast terms within “site” but present only the sequence that we found most plausible.

Using ordinary rather than REML mixed-model analysis of covariance, we could obtain sums of products that were additive, allowing us to express the influence of each term on a trade-off by the percentage of the total sum of products it explained. This can be interpreted as the percentage of total covariance explained by the term, in the same way that a percentage sum of squares can be interpreted as the variance explained by the corresponding term. Thus, the type II sum of products for “site” (obtained by fitting “species” before “site”) explained the contribution of variation among sites within species to the trade-off (pure species effect), the type II sum of products for “species” (obtained by fitting “site” before “species”) explained the contribution of variation among species within sites, and the difference between the type I and type II sum of products for “site” (equal to the difference between the type I and type II sum of products for “species”) explained the shared contribution of variation among sites and species. The sum of these three items plus the residual sum of products added up to the total sum of products (Borcard et al. 1992, Schmid et al. 2002). These items were used to answer, in the given order, questions 1 to 4 posed in the *Introduction*.

The type I and type II sums of products for “site” and “species” were decomposed into the described contrasts, and the contributions of these contrasts to the total sum of products were calculated. This established the relative strength of environmental controls vs. species identity controls on the trade-offs between leaf traits. The “site” contrasts “climate” and “soil” were tested against the

remainder of the “site” term. The term “climate” contained the four climatic variables, i.e., mean annual temperature (MAT), mean annual precipitation (MAP), actual evapotranspiration (AET), and vapor pressure deficit (VPD); the term “soil” contained the three soil variables BD, SOC, and STN. The “species” contrasts were tested in the following way: “family” against “genus” (within “family”), “functional groups” and “genus” against the remainder of the “species” term, i.e., “species” within “family” within “genus” and within “functional groups.” In the alternative with “species” contrasts for phylogenetic groups (Appendix A), we tested our first-order groups (analogous to the “family” level) against the second-order groups (analogous to the “genus” level) and the functional groups and second-order groups against the remainder of the “species” term. The significance of the residual sum of squares was assessed by fitting the residuals of the two traits and correcting the residual degree of freedom for the number of fitted parameters.

Since taxonomic groupings may adequately represent the pattern of evolutionary relationships between species but not represent the rate of evolution, we constructed phylogenetic groupings for alternative interspecies contrasts. We identified the best available phylogenetic hypothesis for our species with the program Phylomatic (Webb et al. 2008) using a maximally resolved seed plant tree (Phylomatic tree version, R20040402) based on the Angiosperm Phylogeny Group supertree (Angiosperm Phylogeny Group 2003). The evolutionary history of the Poaceae, which represent only 10% of the species in our study (17/171) but >35% of all of our leaf trait data (155/429), is based on the Grass Phylogeny Working Group (Grass Phylogeny Working Group 2001). This tree includes no data on diversification within genera because little consensus exists for most cases. Branch lengths were based on the angiosperm-wide divergence dates for families (Wikström et al. 2001), interpolated using the branch length adjustment algorithm in the phylogenetic analysis package Phylocom (Webb et al. 2008). Rather than apply phylogenetically independent contrasts to these data to remove the phylogenetic signal, we created our phylogenetic groups by “cutting” the tree at a given divergence time. We created two contrasts, a first-order grouping cut at 25 million years before present ($n = 33$ groups; Appendix A) and a second-order grouping cut at 21 million years before present ($n = 88$ groups). We chose these ages because they resulted in roughly the same number of groups, and thus degrees of freedom, as the families and genera used in the taxonomic analysis. It should be noted as a caveat that our grouping procedure implied that all species within a group diverged from one another at the same time.

We also fitted bivariate relationships between leaf traits with standardized major axis (SMA) regression. The computer package SMATR was used to examine the differences in SMA slopes and intercepts among

groups (Falster et al. 2006). The effects of climate and soil on SMA relationships were analyzed using data pooled into different climate and soil organic carbon bands (Wright et al. 2005b). For all analyses, trait data were \log_{10} -transformed to increase homoscedasticity of residuals and to reflect allometric relationships between traits. The statistical analyses were calculated with the software products R (R Development Core Team 2007) and GenStat (11th edition; Payne et al. 1993) (see R and Genstat code in Appendix B).

RESULTS

Overall trade-offs

Across all species and sites, the leaf productivity traits area-based photosynthetic rate (A_{area}), A_{mass} , leaf N, leaf P, and PNUE were positively correlated with one another, and A_{mass} , leaf N, and leaf P were negatively correlated with leaf persistence, as measured by LMA (Fig. 1, Appendix C). Grass, herb, and woody growth forms all showed similar patterns of relationships. Furthermore, this pattern held true in the Tibetan Plateau alpine grasslands, Inner Mongolia temperate grasslands, and Xinjiang montane grasslands. In contrast, the relationship of LMA– A_{area} varied with biogeographic region.

The overall mass-based persistence–productivity trade-offs of LMA– A_{mass} , LMA–N, LMA–P, and LMA–PNUE were consistent with previous broadscale findings (Wright et al. 2004), but with lower coefficients of determination (Table 1, Fig. 2). In particular, the LMA–N relationship had identical slopes in this study and the global data set of Wright et al. (2004), confirming that this is a globally consistent pattern of a leaf trait correlation, even after removing the potentially confounding factor of large structural differences among biomes.

Mean and residual trade-offs between leaf traits

The mass-based persistence–productivity relationships became stronger when using site or species means, compared to the overall correlations discussed in *Overall trade-offs* (Table 2). The residual correlations for these mean values (i.e., the remaining variation after fitting site and species means) were weak ($r = -0.133$ to -0.268). As examples, the overall, mean, and residual correlations of LMA– A_{mass} and LMA–N are shown in Fig. 3.

Factors shaping the trade-offs

When “site” was fitted before “species” in the mixed-model analyses of covariance (Table 3), the contrasts “climate” and “soil” together explained 7.9–26.0% and the remaining variation among sites 51.7–57.6% of the total covariance in persistence–productivity relationships. Because these percentages were uncorrected for the term “species” (type I sums of products), they should be considered as maximum estimates. When “species” terms were introduced before “site” (Table 3), the

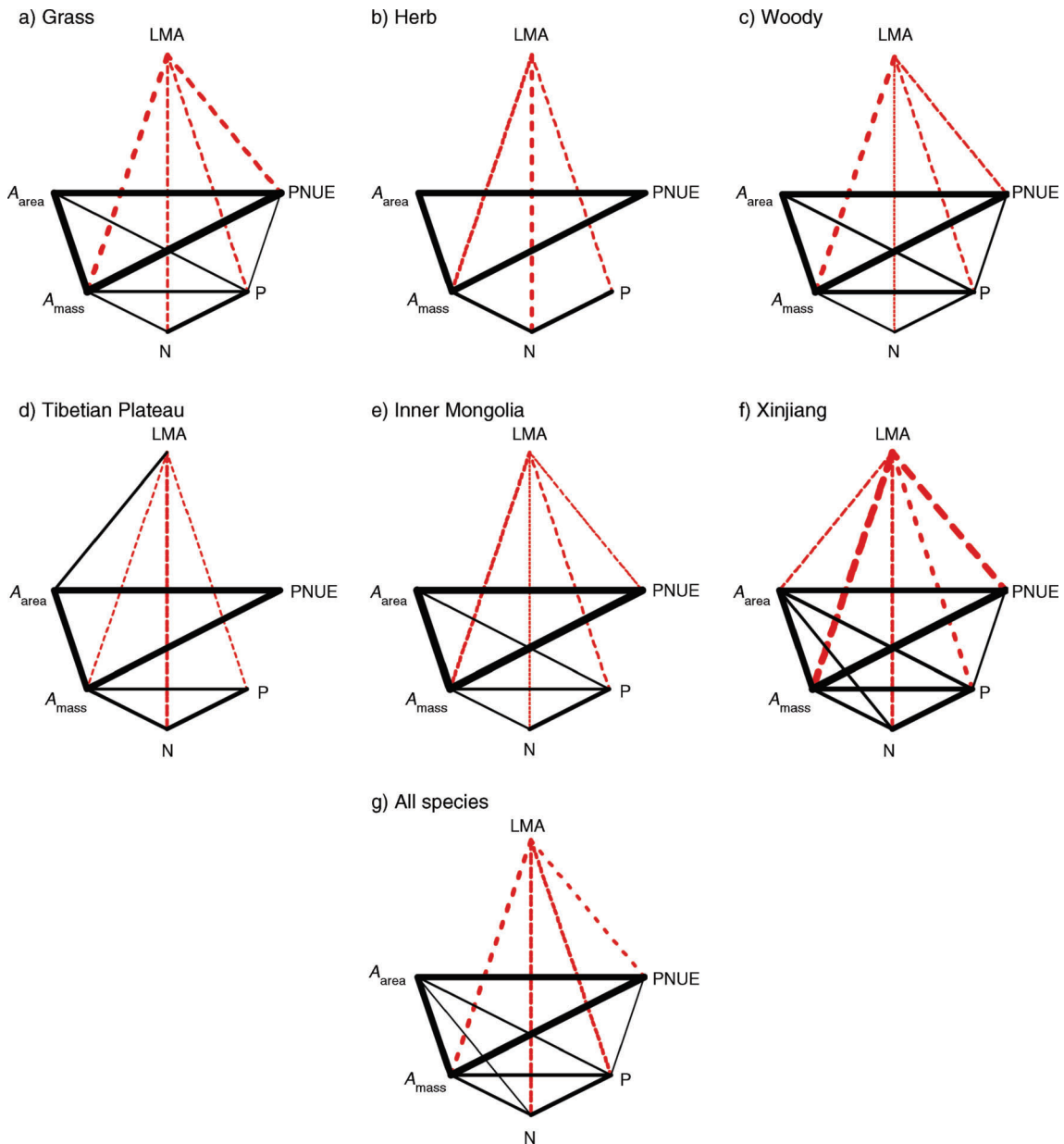


FIG. 1. Correlations between leaf traits for all species and species pooled into different groups in Chinese grassland biomes. Black/solid lines denote positive relationships, and red/dashed lines denote negative ones ($P \leq 0.01$). The width of each line is proportional to the correlation coefficient between the two connected variables. Leaf traits were \log_{10} -transformed prior to analysis. Leaf trait abbreviations are: LMA, leaf mass per area; A_{area} , area-based photosynthetic rate; A_{mass} , mass-based photosynthetic rate; N, nitrogen; P, phosphorus; and PNUE, photosynthetic nitrogen use efficiency.

corrected influences of climate and soil on covariance between leaf traits within species were $<4\%$, indicating that climatic and edaphic gradients had much weaker effects on trade-offs within species (type II sums of products) than among species (difference between type I and type II sums of products). The total contribution of “site” corrected for “species” to the trade-offs among leaf traits (question 1 in the *Introduction*) varied between 15.7% and 22.8% (“climate” + “soil” + “site” in Table 3; Fig. 4).

When “species” was fitted before “site” (Table 3), the contrast “functional groups” explained $\sim 6\text{--}17\%$ and the contrasts “family,” “genus,” and the remaining variation among species explained approximately 18–23%, 26–43%, 7–16% of covariance between leaf traits, respectively. Of these contrasts, only those for genus and species were significant. Replacing “family” and “genus” by phylogenetic terms (Appendix D), functional groups never explained a significant amount of variation, while second-order phylogenetic groups (approx-

TABLE 1. Comparison of leaf trait relationships between Chinese grassland species and the global data set of Wright et al. (2004).

Relationship and group	<i>n</i>	<i>R</i> ²	Slope	Intercept
LMA–<i>A</i>_{mass}				
Chinese grassland	336	0.31	–1.61	2.25
Global	763	0.50	–1.33	1.66
LMA–N				
Chinese grassland	413	0.17	–0.78†	2.90 ^A
Global	1949	0.57		2.79 ^B
LMA–P				
Chinese grassland	413	0.18	–0.92	2.01
Global	735	0.55	–1.22	2.50
LMA–PNUE				
Chinese grassland	339	0.17	–1.50	3.65
Global	705	0.21	–0.92	2.61

Notes: For each correlation, sample size (*n*), coefficient of determination (*R*²), *P* value, the standardized major axis (SMA) slope, and intercept are reported. Intercepts with different letters are statistically different at *P* < 0.05. All slopes are significantly different from zero (*P* < 0.001). Leaf trait abbreviations are: LMA, leaf mass per area; *A*_{mass}, mass-based photosynthetic rate; N, nitrogen; P, phosphorus; PNUE, photosynthetic nitrogen use efficiency.

† A common slope (CS) is given where the two slopes are not significantly different.

mate to genus-level differences) explained up to 40% of covariance (LMA–PNUE relationship). Correcting for “site” by inverting the sequence of fitting again (Table 3), the contrasts “functional groups,” “family,” “genus,” and remaining variation among “species” explained an average of 2%, 7%, 13%, and 6%, respectively. Using the phylogenetic instead of taxonomic terms, nearly identical results were obtained, with “functional groups,” first- and second-order phylogenetic groupings, and remaining variation among “species” explaining on average 2%, 7%, 10%, and 9% of the leaf trait covariation, respectively (Appendix D). The total contribution of “species” corrected for “site” to the trade-offs among leaf traits (question 2 in the *Introduction*) varied between 18.7% and 33.5% (“functional groups” + “family” + “genus” + “species” in Table 3; Fig. 4).

Using REML analysis of the covariance components allowed an alternative examination of how much each given random factor reduced the power of the fixed factors of “site” and “species” in explaining the trade-offs, but did not allow an examination of the shared site and species component. This analysis showed overall greater explanatory power assigned to pure site and pure species effects (14.1–42.1% and 21.5–64.7%, respectively) than the ordinary mixed-model analysis. For the LMA–*A*_{mass} and LMA–PNUE trade-offs, the effect of species corrected for site was much lower than that of species alone, while those for LMA–N and LMA–P were little affected by the site correction. See Appendix E for details.

Roughly half of the covariance (42.7–62.6%; Fig. 4) between leaf traits was explained by the shared influence

of species and sites due to their correlation in this comparative study (question 3 in the *Introduction*). In contrast to this shared influence, which could not further be separated into pure site (question 1) or pure species (question 2) effects, the residual sum of products was very small for all trade-off relationships, indicating that site × species interactions or variation within sites and species contributed very little to the total covariance of leaf traits (question 4; Fig. 4).

Modulation of the bivariate relationship by climate and soil fertility

Standardized major axis regressions (SMAs) fitted within temperature bands followed the same slope for all bivariate relationships, but they did differ in intercepts for LMA–*A*_{mass}, LMA–N, and LMA–PNUE, with higher intercepts at higher temperatures. Standardized major axis regressions fitted within precipitation bands differed in slope for LMA–N and LMA–P, with steeper negative slopes in zones of higher precipitation. Precipitation did not influence slope or intercept of LMA–*A*_{mass} or LMA–PNUE relationships. Standardized major axis regressions fitted within SOC bands differed in slope only for LMA–PNUE, but the intercept changed with SOC bands in LMA–*A*_{mass}, LMA–N, and LMA–P. Overall, the trade-offs were stronger for LMA–N and LMA–P at higher precipitation and for LMA–PNUE at greater soil fertility (question 5; Table 4).

DISCUSSION

Trade-offs exist for plants in balancing traits involved in resource uptake including carbon fixation and nutrient acquisition and traits that enable leaves to withstand stress and have longer life span (Mooney 1972, Chapin 1980, Givnish 1986, Reich et al. 1992, 1997, Wright et al. 2004). The unresolved question then is to what extent such trade-offs are driven by environmental variation or by variation among plant species. At the core of this question is whether trait values are variable within species, and so environmental conditions largely influence trait values, or whether species have rigid constraints on trait values, and it is through changes in species composition that trade-offs become apparent at the biogeographic scale.

In the present study, we use LMA rather than leaf life span (LL) as a measurement of leaf persistence. Higher LMA strongly correlates with longer LL (Niinemets 2001, Westoby et al. 2002). A number of studies have examined structural and anatomical traits in determining interspecific differences in LMA, which also lead to longer LL, including leaf dry matter concentration (Witkowski and Lamont 1991, Castro-Diez et al. 2000), leaf thickness (Witkowski and Lamont 1991), the proportion of vascular tissues (Garnier and Laurent 1994, Van Arendonk and Poorter 1994), and the proportion of cell wall components (Poorter and Bergkotte 1992).

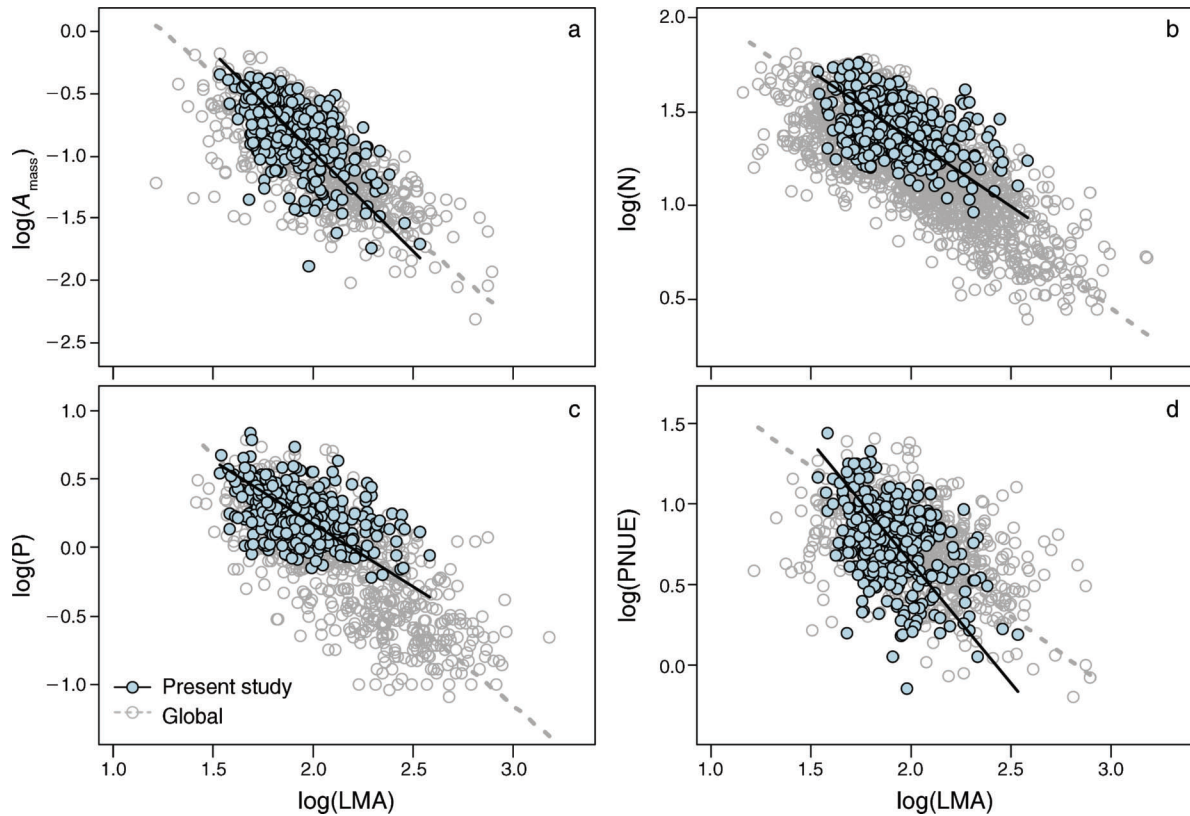


FIG. 2. Trade-offs between leaf mass per area (LMA) and mass-based photosynthetic rate (A_{mass}), N, P, and photosynthetic nitrogen use efficiency (PNUE) for Chinese grassland species in comparison with the global data set from Wright et al. (2004). See Table 1 for the differences in standardized major axis relationships between the two data sets. Data were log-transformed prior to analyses; units prior to transformation were: LMA, g/m^2 ; A_{mass} , $\mu\text{mol}\cdot\text{g}^{-1}\cdot\text{s}^{-1}$; N and P, mg/g ; PNUE, $\mu\text{mol}\cdot\text{g}^{-1}\cdot\text{s}^{-1}$.

The observed strong leaf persistence–productivity trade-offs were mostly due to environmental variation among sites and taxonomic variation among species, but not simply reflecting covariance between developmentally or physiologically interdependent traits within species and sites. This was shown by the stronger correlations based on site or species means than those using the raw data and by the weak residual correlations.

Relationships between leaf traits may arise by adaptive evolutionary processes, which lead to differences among species or among populations within species occurring under different environmental condi-

tions (Ackerly 2004, Lavorel et al. 2007). If the interspecific differences in these trait relationships are not readily interpreted as adaptations to current environmental conditions, then the trade-offs may be the result of evolutionary differentiation due to selective pressures no longer operating or to chance events. Here we label this interspecific component of trade-offs that is not due to environmental differences “phylogenetic.” If an adaptive interpretation is possible, e.g., because of a correlation with climatic or edaphic variables, then we label the component of trade-offs “differentiation,” which applies in particular to population differentiation

TABLE 2. Correlations between leaf traits at four levels: across sites and species (overall correlations at population level, overall); among sites (using site means); among species (using species means); and within sites, within species (using residuals of the traits after fitting site and species).

Leaf trait	Overall	Inter-site	Interspecific	Residual
LMA– A_{mass}	–0.558 ***	–0.662 ***	–0.667 ***	–0.268 ***
LMA–N	–0.416 ***	–0.443 ***	–0.455 ***	–0.235 ***
LMA–P	–0.418 ***	–0.448 ***	–0.441 ***	–0.133 **
LMA–PNUE	–0.417 ***	–0.549 ***	–0.532 ***	–0.184 ***

Notes: Leaf traits were \log_{10} -transformed prior to analysis. Leaf trait abbreviations are: LMA, leaf mass per area; A_{mass} , mass-based photosynthetic rate; N, nitrogen; P, phosphorus; PNUE, photosynthetic nitrogen use efficiency.
 ** $P < 0.01$; *** $P < 0.001$.

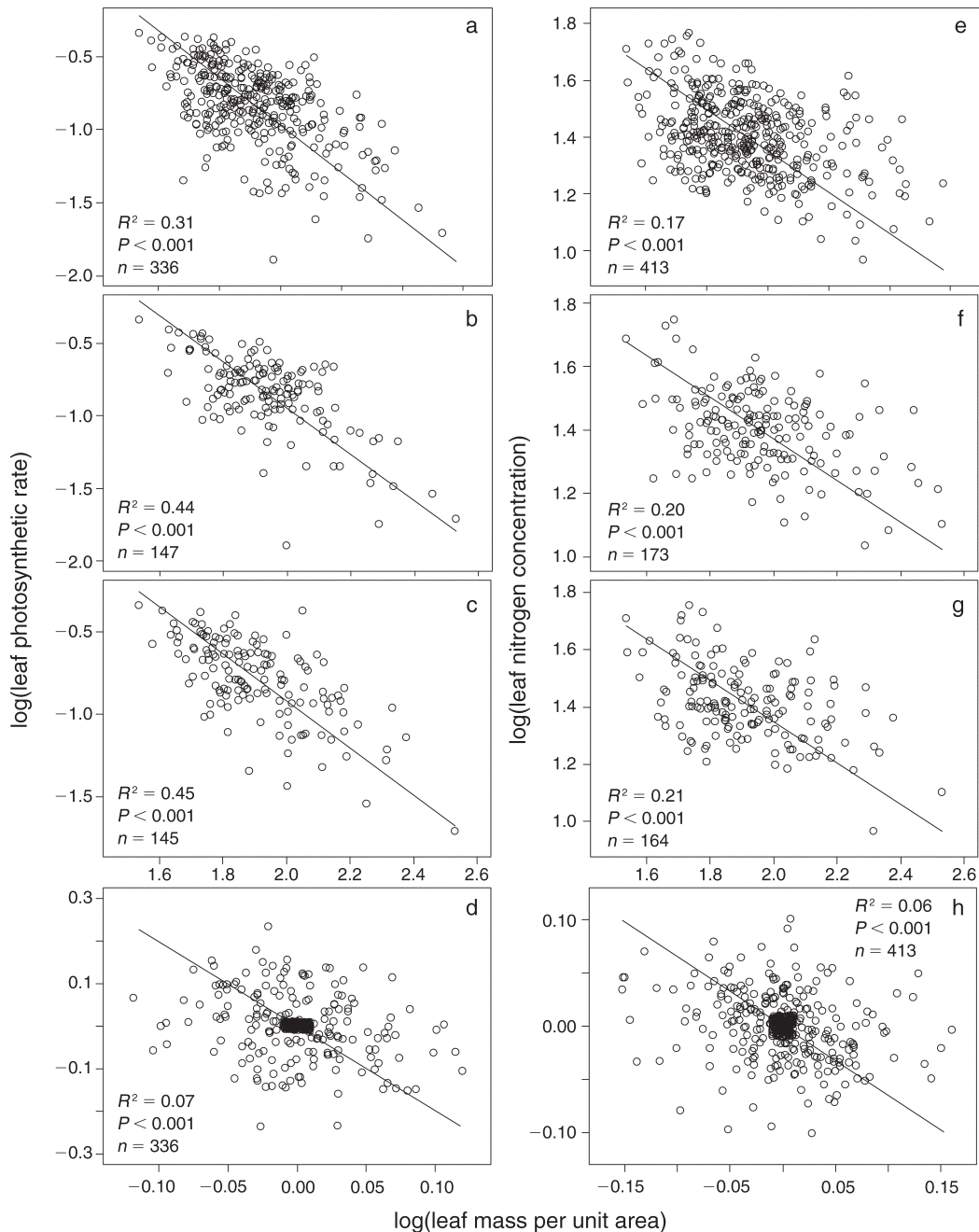


FIG. 3. Scatter plots showing the relationships between leaf mass per area and mass-based photosynthetic rate ($LMA-A_{\text{mass}}$) and between LMA and N at different levels of analysis: (a) and (e), overall correlations; (b) and (f), correlations of site means; (c) and (g), correlations of species means; (d) and (h), residual correlations (after fitting site and species). In panels (d) and (h), values around zero are slightly jittered to avoid too much overlap. Data were log-transformed prior to analyses; units prior to transformation were: LMA, g/m^2 ; A_{mass} , $\mu\text{mol}\cdot\text{g}^{-1}\cdot\text{s}^{-1}$; N, mg/g .

within species across sites. Under “phylogenetic,” we also subsume species with different ecological strategies such as growth form and nitrogen acquisition type, i.e., our functional groups.

To understand these interspecific differences in our study, we explored two avenues. First, we used a traditional approach, grouping species by genus and

family. However, this type of taxonomic nested analysis has been criticized for ignoring the pattern and rate of evolutionary diversification between such groups (Miles and Dunham 1993). An alternative approach would have been to use phylogenetically independent contrasts (Felsenstein 1985), but this approach would not have been suitable for our goals of partitioning the variation

TABLE 3. Summary of decomposition of covariance in a general linear model, using sums of products, for the effects of climate, soil fertility, other site effects, and taxonomic variation on leaf trait relationships: LMA- A_{mass} , LMA-N, LMA-P, and LMA-PNUE.

Effect	LMA- A_{mass}			LMA-N			LMA-P			LMA-PNUE			Error term
	df	%SP	Sig.	df	%SP	Sig.	df	%SP	Sig.	df	%SP	Sig.	
Site entered first													
Environmental variation among site													
Climate	4	13.87	***	4	13.44	***	4	5.79	**	4	18.12	***	site
Soil	3	5.95	**	3	-1.20	NS	3	2.12	NS	3	7.86	**	site
Site	122	51.71	***	148	52.33	***	148	57.57	***	123	53.79	***	residual
Taxonomic variation within site													
Functional group	3	0.25	NS	3	4.06	***	3	3.37	***	3	-0.34	NS	species
Family	25	6.18	NS	29	9.31	NS	29	8.54	NS	25	2.72	NS	genus
Genus	38	12.71	*	43	13.77	***	43	15.60	***	38	9.80	*	species
Species	45	7.97	***	58	6.35	***	58	4.63	***	45	6.53	***	residual
Residual covariance within sites and within species													
Residual	52	1.35	***	79	1.94	***	79	2.38	**	54	1.52	**	
Species entered first													
Taxonomic variation among species													
Functional group	3	7.37	NS	3	13.92	NS	3	17.19	NS	3	5.56	NS	species
Family	26	23.03	NS	30	21.70	NS	30	17.70	NS	26	19.25	NS	genus
Genus	41	38.23	***	45	26.50	***	45	32.60	***	41	43.29	***	species
Species	57	14.36	***	69	16.12	***	69	7.33	***	57	13.20	***	residual
Environmental variation within species													
Climate	4	1.05	NS	4	2.93	***	4	-0.94	NS	4	1.40	*	site
Soil	3	0.63	NS	3	0.77	NS	3	-0.99	NS	3	0.52	NS	site
Site	106	13.97	***	134	16.12	***	134	24.73	***	107	15.24	***	residual
Residual covariance within sites and within species													
Residual	52	1.35	***	79	1.94	***	79	2.38	**	54	1.52	**	

Notes: Features of taxonomic variation are functional groups [grasses/herbs/woody species and legumes/nonlegumes], family, genus, and species. Leaf trait abbreviations are: LMA, leaf mass per area; A_{mass} , mass-based photosynthetic rate; N, nitrogen; P, phosphorus; PNUE, photosynthetic nitrogen use efficiency. Explanatory terms are listed in the order of their entry into the model. The leaf traits were \log_{10} -transformed prior to analysis. Statistical abbreviations are: df, degree of freedom; %SP, percentage of total sum of products; Sig., significance. The significances of the residual mean sum of products term (residual covariance) were assessed by fitting the residuals of the two leaf traits against one another and correcting the residual df for the number of fitted parameters. Climatic variables (df = 4) are mean annual temperature, mean annual precipitation, actual evapotranspiration, and vapor pressure deficit. Soil variables (df = 3) are bulk density, soil organic carbon content, and soil total nitrogen content.

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$; NS, $P > 0.05$.

between environmental and interspecific effects. Therefore, we used an approach analogous to the taxonomic nested analysis, but with phylogenetic instead of taxonomic groupings. The results showed nearly identical patterns, demonstrating that the taxonomic classification in this case reflected the phylogenetic relationships quite well or that the rate of diversification was of little importance in these trade-offs. This result was supported by the REML analysis, which showed that phylogenetic groupings accounted for little of the explanatory power of species on the trade-offs (data not shown).

Analysis of covariance showed that correlations between species occurrences and sites (shared component) explained the largest part of the covariation in leaf persistence-productivity trade-offs in Chinese grassland species. On average, the covariation attributable to pure

species effects was always larger than the covariation attributable to pure site effects, of which only a very small amount could be attributed to climatic and soil variables. Combining the shared and pure species components, a maximum of more than three-quarters of the covariance could have reflected taxonomic and phylogenetic trade-offs among species. The cause of these trade-offs may have been differential selection in past environments, phylogenetic constraints, or differential genetic drift. Combining the shared and pure site components, a maximum of approximately two-thirds of the covariance could have reflected environmental trade-offs among sites. However, only a small part of these environmental trade-offs could have been caused by climatic or edaphic factors. Further causes for environmental trade-offs may have been unrecognized factors

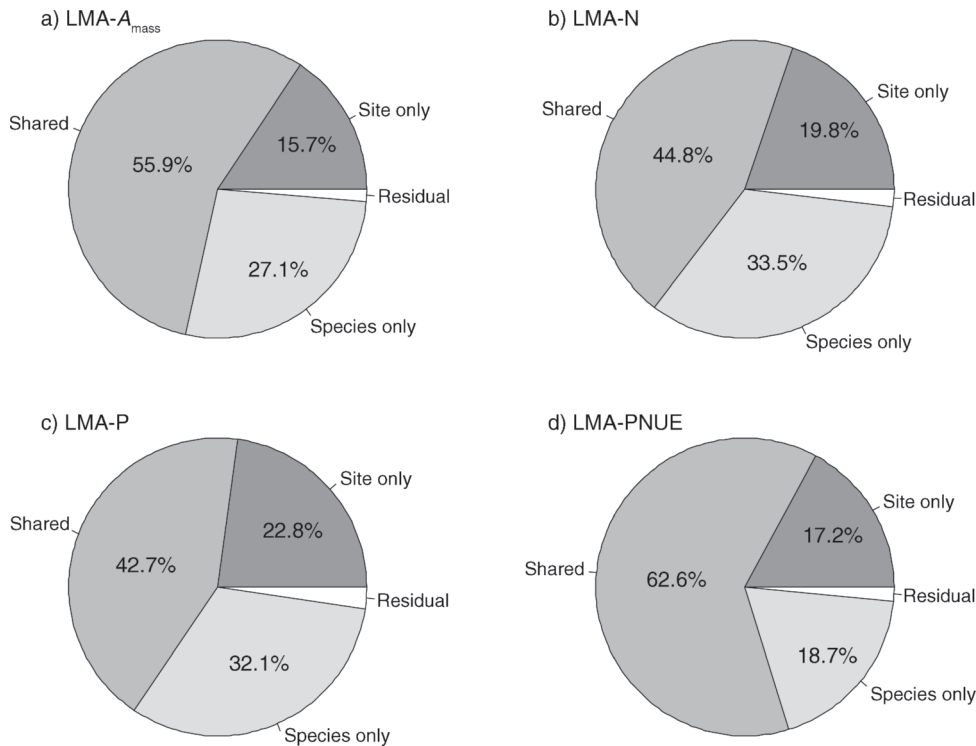


FIG. 4. Effects of species and site on bivariate leaf trait relationships, expressed as the percentage of the sum of products explained. The covariance was partitioned into four components by switching the order of site and species in the analysis of covariance (see Table 3): (1) covariance resulting from environmental variation among site within species (Site only); (2) covariance resulting from interspecific variation within sites (Species only); (3) shared covariance between site and species (Shared); (4) residual covariance within sites and within species (Residual).

such as grazing. The environmental trade-offs in our study could have been based on genetic variation or plasticity within species.

When we pooled species into different environmental classes, we found that temperature, precipitation, and soil fertility weakly altered the slopes and intercepts of standardized major axis regressions. For example, temperature did not influence the slopes of the trade-offs, but slightly increased the intercepts for LMA- A_{mass} and LMA-PNUE, indicating a shift to higher leaf productivity at a given leaf persistence under higher temperatures. The weakening of trade-offs with cooler temperatures, greater soil organic carbon, and greater precipitation may indicate relaxations in the persistence-productivity relationships under these conditions.

CONCLUSIONS

The analysis of trade-offs between plant traits is an important aspect of a trait-based approach to community ecology (Tilman 1990, Westoby and Wright 2006, Litchman et al. 2007). Trade-offs between key leaf traits related to persistence and productivity have been consistently observed, but determining to which extent these trade-offs reflect within-species adjustments to environmental conditions (question 1 in the *Introduc-*

tion) or variation among species unrelated to variation among sites (question 2) requires a data set in which the effects of variation among sites and variation among species can be separated from one another at least to some degree, rather than assigning it all to a shared component (question 3). Using such a data set from grassland plants across China allowed us to show for the first time that in addition to effects of the shared component on trade-offs, i.e., effects of changes of species occurrences across sites (explaining 42.7–62.6%), differences within species across sites (explaining 15.7–22.8%) and differences among species within sites (explaining 18.7–33.5%) significantly contribute to shaping trade-offs between plant leaf traits. The overall patterns of the investigated trade-off relating leaf persistence to leaf productivity (LMA- A_{mass} , LMA-N, LMA-P, and LMA-PNUE) matched previous broad-scale findings, suggesting that the different drivers identified here have convergent effects on the trade-off. In addition, we found that the trade-offs of LMA-N and LMA-P weaken with increasing precipitation and LMA-PNUE weaken with greater soil fertility. This may be due to relaxation of the physiological constraints on productivity-persistence relationships under these conditions.

TABLE 4. Comparison of leaf trait relationships for data pooled into three classes of mean annual precipitation (MAP), mean annual temperature (MAT), and soil organic carbon (SOC), using standardized major axis (SMA) regression.

Group	<i>n</i>	<i>R</i> ²	<i>P</i>	Slope	Intercept
LMA-<i>A</i>_{mass}					
MAP (mm)					
50–250	55	0.64	<0.001	–1.621†	2.293 ^A
250–450	161	0.21	<0.001		2.268 ^A
450–650	120	0.07	0.003		2.265 ^A
MAT (°C)					
–10 to –3	41	0.10	0.045	–1.608†	2.115 ^A
–3–4	261	0.28	<0.001		2.255 ^B
4–12	34	0.80	<0.001		2.327 ^C
SOC (%)					
0.085–0.50	24	0.63	<0.001	–1.621†	2.275 ^{AB}
0.50–2.95	123	0.41	<0.001		2.311 ^B
2.95–17.38	164	0.17	<0.001		2.221 ^A
LMA-P					
MAP (mm)					
50–250	88	0.32	<0.001	–0.792 ^B	1.815
250–450	195	0.12	<0.001	–1.038 ^A	2.221
450–650	130	0.09	0.001	–1.117 ^A	2.364
MAT (°C)					
–10 to –3	43	0.04	0.209	–0.935†	2.006 ^A
–3–4	304	0.15	<0.001		2.042 ^A
4–12	66	0.30	<0.001		2.060 ^A
SOC (%)					
0.085–0.50	39	0.18	0.008	–0.958†	2.195 ^C
0.50–2.95	155	0.27	<0.001		2.095 ^B
2.95–17.38	193	0.13	<0.001		2.045 ^A
LMA-N					
MAP (mm)					
50–250	88	0.22	<0.001	–0.603 ^b	2.571
250–450	195	0.06	0.001	–0.819 ^a	2.984
450–650	130	0.26	<0.001	–0.862 ^a	3.044
MAT (°C)					
–10 to –3	43	0.10	0.044	–0.736†	2.780 ^A
–3–4	304	0.18	<0.001		2.830 ^B
4–12	66	0.15	0.001		2.812 ^{AB}
SOC (%)					
0.085–0.50	39	0.33	<0.001	–0.747†	2.952 ^C
0.50–2.95	155	0.17	<0.001		2.863 ^B
2.95–17.38	193	0.19	<0.001		2.804 ^A
LMA-PNUE					
MAP (mm)					
50–250	57	0.53	<0.001	–1.529†	3.735 ^A
250–450	161	0.12	<0.001		3.681 ^A
450–650	121	0.00	0.673		3.685 ^A
MAT (°C)					
–10 to –3	41	0.04	0.199	–1.518†	3.530 ^A
–3–4	263	0.14	<0.001		3.675 ^B
4–12	35	0.60	<0.001		3.800 ^C
SOC (%)					
0.085–0.50	24	0.46	<0.001	–1.124 ^B	2.840
0.50–2.95	124	0.26	<0.001	–1.697 ^A	4.045
2.95–17.38	166	0.05	0.005	–1.393 ^{AB}	3.403

Notes: Soil organic carbon was classified using a log scale due to its lognormal distribution. For each relationship, sample size (*n*), coefficient of determination (*R*²), *P* value, the SMA slope, and the SMA intercept are reported. Leaf trait abbreviations are: LMA, leaf mass per area; *A*_{mass}, mass-based photosynthetic rate; N, nitrogen; P, phosphorus; PNUE, photosynthetic nitrogen use efficiency. Slopes and intercepts with different letters are statistically different at *P* ≤ 0.05.

† A common slope (CS) is given when the two slopes are not significantly different.

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APPENDIX A

Phylogenetic tree used for the 171 species in this study (*Ecological Archives* E090-197-A1).

APPENDIX B

R and Genstat code used in the analyses (*Ecological Archives* E090-197-A2).

APPENDIX C

Pearson correlations between leaf traits across all species within growth forms, and species from different regions (*Ecological Archives* E090-197-A3).

APPENDIX D

Summary of decomposition of covariance in the general linear model, using the sum of products for the effects of climate, soil fertility, other site effects, and phylogenetic variation on the relationships of $LMA-A_{mass}$, $LMA-N$, $LMA-P$, and $LMA-PNUE$ (*Ecological Archives* E090-197-A4).

APPENDIX E

Summary of covariance components for the random effects of site and species on leaf trait relationship, based on restricted maximum-likelihood analysis of covariance (*Ecological Archives* E090-197-A5).