

Relative effects of phylogeny, biological characters and environments on leaf traits in shrub biomes across central Inner Mongolia, China

Chao Liu¹, Xiangping Wang^{1,*}, Xian Wu¹, Shuang Dai¹, Jin-Sheng He² and Weilun Yin^{1,*}

¹ The Key Laboratory of Silviculture and Conservation of the Ministry of Education, and the National Engineering Laboratory for Forest Genetics and Tree Breeding, Beijing Forestry University, Beijing 100083, China

² Department of Ecology, College of Environmental Sciences, and Key Laboratory for Earth Surface Processes of the Ministry of Education, Peking University, Beijing 100871, China

*Correspondence address. College of Forestry, Beijing Forestry University, 35 East Qinghua Road, Haidian, Beijing 100083, China. Tel: +86-10-6233-6985; Fax: +86-10-6233-6400; E-mail: wangxiangping@bjfu.edu.cn, yinwl@bjfu.edu.cn

Abstract

Aims

Understanding the drivers for leaf traits is critical to improving our predictions on ecosystems' responses to global changes. Geographic patterns of leaf traits are shaped by phylogenetic, biological and environmental factors simultaneously. However, till now few studies have examined how these factors influenced leaf traits together, and how their effects differed at the within- and among-site levels.

Methods

We sampled leaf traits from a 1100 km shrub-biome transect across central Inner-Mongolia, including leaf mass per area (LMA), mass-based photosynthetic rate, nitrogen (N) and phosphorus (P) concentrations. We examined the effects of phylogenetic, biological (height and growth rate) and environmental (climate and soil) factors on leaf traits with mixed-model analyses of variance. Variation partitioning method was used to separate the joint and independent effects of these three types of factors.

Important Findings

(i) Climate and soil fertility (total or available nutrient concentrations) together explained 11.4–41.4% of among-site variations, with remarkable difference among traits. (ii) Height and height growth rate together explained 0.4–31.9% of trait variations

(mostly among-site variations). Our results could only weakly support the ability of leaf traits as predictors for whole-plant growth. (iii) LMA was negatively related to height, which was consistent with the resource-use strategy hypothesis but inconsistent with the hypotheses proposed for coexisting trees, suggesting that the LMA–height relationship is shaped by rather different mechanisms between the within- and among-communities levels. (iv) The variation partitioning analysis showed that, the relationships between leaf traits and biological characters largely reflected the differences in both leaf traits and biological characters among species that occupying different sites. The relative importance of phylogenetic, biological and environmental factors differed remarkably among leaf traits, between the within- and among-communities levels, and between different biomes. (v) Our results strongly suggest the necessity of examining the three types of factors simultaneously, and at both the within- and among-communities levels, for a better understanding of the drivers for leaf traits patterns.

Keywords: leaf trait • phylogeny • height • growth rate • soil fertility • climate

Received: 21 February 2012 Revised: 26 July 2012

Accepted: 7 August 2012

INTRODUCTION

Understanding the drivers for leaf traits variations is critical for improving our predictions on ecosystems' responses to global changes (Garnier et al. 2007; Reich et al. 2007; Wright et al. 2005). In recent years, some leaf traits that are key components of the 'leaf economics spectrum' (Wright et al. 2004) have received special attentions, including leaf area per mass (LMA), photosynthetic rate (A_{mass}), leaf nitrogen (N_{mass}) and phosphorous (P_{mass}) concentrations on mass basis. These key leaf traits reflect the fundamental trade-off between leaf productivity and persistence, and thus are critical for the carbon budget of plants (He et al. 2009). A number of studies have analyzed the potential factors that modulated the geographic patterns of key leaf traits. These studies differed remarkably in spatial scales and in the species, ecosystems and regions examined. However, they found a consistent pattern that leaf traits were modestly controlled by climate, and that as much variability in leaf traits were observed within-site as observed among-site (e.g. Elser et al. 2010; He et al. 2010; Ordóñez et al. 2009; Reich et al. 2007; Wright et al. 2004). Understanding why leaf traits showed great variations both within- and among-communities is not only important to improving our ability to predict the geographic patterns of key leaf traits (to parameterize ecosystem models; Reich et al. 2007), but also critical to understanding some fundamental questions such as the relative influences of environments vs. ecological strategies on leaf traits (Elser et al. 2010).

Previous studies have suggested that the geographic patterns of leaf traits are shaped by different factors simultaneously. Climatic and soil fertility gradients are critical in shaping the among-site variations of leaf traits (despite that their direct influences may be modest, e.g. Han et al. 2005; Ordóñez et al. 2009; Wright et al. 2005). At the same time, some factors seemed to be related to both the within- and among-site leaf traits variations, e.g. phylogeny (He et al. 2010; Reich et al. 2003), growth rate (Elser et al. 2010; Reich et al. 1997) and plant stature (Westoby et al. 2002). However, few studies have examined how phylogenetic, biological (height and growth rate) and environmental factors influenced leaf traits jointly and independently, and how their effects differed at the within- and among-community levels. In this analysis, we used leaf trait data sampled from a 1100-km shrub biome transect to examine the relative effects of these different factors.

1 **Phylogeny.** Recent studies have increasingly suggested that phylogenetic history may be critical in shaping leaf trait patterns (Ackerly 2004a; He et al. 2010; Reich et al. 2003). The species composition shift with environments is an important source of among-site leaf trait variations (He et al. 2008, 2010), and the differences in traits for species that occur in different environments may be a result of niche conservatism (Ackerly et al. 2006; Reich et al. 2003). For the within-site leaf traits variations, phylogeny is also a

powerful predictor (He et al. 2010), which may be a result of phylogeny-related community assembly processes (Ackerly et al. 2006; Prinzing et al. 2008).

- 2 **Plant height.** Height is one of the key dimensions of plant ecological strategies (Westoby et al. 2002). Within forest communities, it is widely observed that leaf traits changed remarkably with height, which is suggested to be related to two mechanisms (e.g. Cavaleri et al. 2010; Ryan et al. 2006): (i) the difficulty in water transportation increased with tree height (*the hydrostatic hypothesis*); (ii) the light availability increased with height (*the light gradient hypothesis*). The two hypotheses were proposed to explain the different relationships between photosynthetic rate (and other leaf traits) and tree height observed in different studies. Nevertheless, both mechanisms lead to a positive relationship between LMA and tree height (Cavaleri et al. 2010; Poorter et al. 2009; Ryan et al. 2006). Leaf traits have seldom been related to plant height at a large scale, except for a few analyses using maximum height which suggested that LMA and height were largely not related (Díaz et al. 2004; Wright et al. 2007). To examine whether these previous findings could be observed in shrub biomes, we tested the ability of plant height in explaining the within- and among-site variations of leaf traits.
- 3 **Growth rate.** Leaf traits differ remarkably between species with different growth strategies. Fast growing species are generally characterized by short leaf lifespan, low LMA, high leaf nitrogen (N) and phosphorous (P) concentrations, and high photosynthetic capacity. On the other hand, slow growing species generally revealed an opposite pattern (Poorter and Bergkotte 1992; Reich et al. 1992, 1997). Accordingly, previous studies have also found a strong relationship between leaf traits and individual growth rate (e.g. Reich et al. 1992, 1997). However, this close relationship was mostly reported for seedlings and saplings or for herbaceous species, and has rarely been tested directly in natural woody communities (Poorter and Bongers 2006). Both growth rate and leaf traits will change along climatic gradients (e.g. Reich et al. 1997). At the same time, both of them also differ remarkably among species within a same community (Poorter and Bongers 2006; Wright et al. 2010). Consequently, we tested the hypothesis that both the within- and among-site variations of leaf traits could be well explained by different growth rate (i.e. difference in fast vs. slow growth strategy). Previous studies on woody seedlings or herbaceous species generally used biomass growth rate. However, measuring biomass growth rate is hard for our study on woody communities across great distance. Thus we used height growth rate, which was strongly related with biomass growth rate, as a surrogate (e.g. Poorter and Bongers 2006).
- 4 **Climate and soil fertility.** Recently, the role of soil fertility has received new attentions because leaf traits were widely observed to be only modestly modulated by climate (e.g. Elser et al. 2010; Han et al. 2005; Reich et al. 2007;

Wright *et al.* 2004, 2005). A few studies at a large scale suggested that the influence of soil fertility was similarly weak as climate (e.g. Chen *et al.* 2012; Ordonez *et al.* 2009; He *et al.* 2010). However, most of these analyses used soil total N and P concentrations as indicators of soil fertility. It can be argued that the effect of soil fertility might be underestimated because total N and P were not direct measures of nutrients that were available for plants growth. Studies on the relations between leaf traits and soil at different spatial scales are still limited (Ordonez *et al.* 2009), thus this possibility should be tested carefully to better understand the relative effects of abiotic gradients and biotic factors on leaf traits. In this analysis, we used both available and total N and P content data to further examine this question.

These factors are not mutually exclusive and may work together to influence leaf traits. For instance, the effect of phylogeny on leaf traits may have included some effects of environmental differences among sites (He *et al.* 2009), and partly because different species and phylogenetic groups differ in growth rate, stature and other biological characters (Elser *et al.* 2010). Consequently, we partitioned their effects into pure and shared components, to examine how phylogeny, biological characters (height and growth rate) and environments affected leaf traits independently and jointly.

MATERIALS AND METHODS

Study sites and shrub species

We sampled 33 shrub biomes plots in August 2009 along a transect across the central Inner Mongolia plateau in north China. The transect spanned longitudes from 105.0 to 116.6°E and latitudes from 37.4 to 44.0°N, with a distance of *ca.* 1100 km. Located in the transitional zone from semi-arid to arid climate in north China, the transect covered an annual precipitation range of 113–427 mm, and a mean annual temperature range between 0.82 and 9.64°C. As a result of great climatic gradients, the shrub communities differed significantly in species composition. In the east part of the transect, the shrub biomes were generally composed of mesophyte (e.g. *Salix* spp., *Prunus sibirica* L.), mesoxerophyte species (e.g. *Elaeagnus angustifolia* L. and *Prunus pedunculata* Pall.) or xerophyte species (e.g. *Caragana* spp.). Although in the western part the shrub communities were generally composed of superxerophyte species (e.g. *Reaumuria soongorica* (Pall.) Maxim., *Caragana brachypoda* Pojark., *Zygophyllum xanthoxylon* (Bunge) Maxim.), which were characterized of desert habitat, xerophyte species also were frequently observed (e.g. *Caragana* spp., *Hedysarum fruticosum* var. *laeve* (Maxim.) H. C. Fu, *Artemisia ordosica* Krasch. and *Artemisia sphaerocephala* Krasch.).

Sampling and measurements

A total of 373 individuals for 44 shrub species (27 genera and 16 families) were sampled from the 33 plots (10 × 10 m). For each species sampled in a plot, three individuals with mean

sizes which were not shaded by other plants were chosen for measurements.

For each individual, fully expanded new leaves were selected to measure *in situ* photosynthetic rates and then sampled for laboratory analyses. The field measurements and sampling were conducted using the protocol described in He *et al.* (2009). Briefly, leaf photosynthetic rates were measured at saturating light (1500 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ of photosynthetic photon flux density) with an open path gas-exchange systems using red-blue light sources and CO₂ mixers (LI-6400; Li-Cor Inc., Lincoln, NE, USA). The reference CO₂ concentration in the leaf cuvette was maintained at 360 $\mu\text{mol CO}_2\cdot\text{mol}^{-1}$, and leaf cuvette temperature was maintained at 22–25°C, depending on the external temperature. For each individual, photosynthetic rates were measured for three or two leaves and the mean value was used for the individual. Then a sample of leaves was collected from the same individual for the measurements of LMA and nutrient concentrations. Leaf area was measured *in situ* with a portable leaf area meter (AM300; ADC Bioscientific, Herts, UK). Leaf samples were then dried for 72 h at 60°C in laboratory for measurements of dry mass to calculate LMA. Leaf N concentration was assayed using an elemental analyzer (2400 II CHNS; Perkin-Elmer, Boston, MA, USA) with a combustion temperature of 950°C and a reduction temperature of 640°C, while P concentration was measured by the molybdate/ascorbic acid method after H₂SO₄-H₂O₂ digestion (Jones 2001).

Plant height and current-year height growth were measured for the same individuals used for leaf sampling. Height growth rate was measured as the vertical length of the current-year shoot on the top of the main stem. For individuals with no obvious main stems, measurements were conducted on the three highest stems and then the three values were averaged. We used absolute instead of relative height growth rate in the final data analyses. This is because relative height growth rate is strongly affected by the size and age of woody plant (Reich *et al.* 1992). Consequently, it was generally used in studies on seedlings, but not appropriate for woody plants with markedly different sizes (ages) in natural communities (Poorter and Bongers 2006; Reich *et al.* 1992). Our data also showed that absolute and relative height growth rates showed opposite relationships with leaf traits (e.g. their correlations with LMA was –0.38 and 0.32, respectively), with the results of relative growth rate clearly not appropriate (LMA should be negatively related to productivity, see Garnier *et al.* 2004; Reich *et al.* 1997).

In each plot, soil samples at the 0–10 and 10–20 cm depths were collected from three soil profiles at the center and two corners of the plot, and the soil samples from the same depth were mixed. Soil organic carbon (SOC), soil total N (STN) and total P (STP) were sampled and measured using the same protocol as in He *et al.* (2009) and thus not detailed here. Soil available nitrogen (SAN), which consist of NO₃-N (nitrate) and NH₄-N (ammonium), were extracted *in situ* from 10 g soil with 50 ml 1 M KCl for 60 min following the procedures described

in [Baumann *et al.* \(2009\)](#). Each extraction was conserved with 2 ml HCl (30%) before laboratory assays. Soil available phosphorus (SAP) were extracted from 2.5 g air-dried soil sample with 50 ml 0.5 M NaHCO₃ solution ([Jones 2001](#)). The extractions for NO₃-N, NH₄-N and SAP assays were measured photometrically (EasyChem Plus, SYSTEA, Italy). For each soil variable, measured values for the two depths of a plot was averaged.

Phylogenetic groups and climate data

To examine the effect of phylogeny on leaf traits, we developed a phylogenetic tree for the 44 species in this study ([Figure A1](#)). The tree topology was built with the online program of Phylomatic 2 ([Webb *et al.* 2008](#), <http://phylodiversity.net/phylomatic/>), using the 'Maximally resolved seed plant tree (version R20091110)' based on the supertree of the Angiosperm Phylogeny Group III ([APG III 2009](#)). The branch lengths were determined using the BLADJ program ([Webb *et al.* 2008](#)), with the nodes ages available in [Wikström *et al.* \(2001\)](#) fixed. The remaining branch lengths were adjusted by spacing undated nodes in the tree evenly between dated nodes to minimize variance in branch lengths (for details, see [Webb *et al.* 2008](#)). The phylogenetic relationships within families was not available for our species in the Phylomatic database, and the Phylomatic program treated genera as polytomies within their families while species were treated as polytomies within their genera. Thus different genera within a family (and species within a genus) were assigned the same branch length by BLADJ ([Figure A1](#)). This hypothesis of polytomy adopted by Phylomatic was commonly accepted by ecological studies, when the within-family phylogenetic information was absent (e.g. [He *et al.* 2009](#); [Kembel and Hubbell 2006](#); [Kerckhoff *et al.* 2006](#)). The phylogenetic trees thus created by the Phylomatic and BLADJ programs are widely recognized and used in ecological studies, and have led to many important findings not only in community ecology (e.g. [Kembel and Hubbell 2006](#); [Letcher 2012](#)), but also for studies on plant functional traits (e.g. [He *et al.* 2009, 2010](#); [Kerckhoff *et al.* 2006](#)).

We created phylogenetic divisions ([Figure A1](#)) by 'cutting' the phylogenetic tree at 60 and 30 million years ago (Mya). This procedure is similar as in cluster analysis, where the clusters are created by cutting the tree at a certain distance. The phylogenetic divisions thus created were then used as category variables in general linear models, just as using family (or genus) as category variable to explain leaf traits (e.g. [He *et al.* 2006, 2010](#)). We chose the 60 and 30 Mya because they resulted in roughly the same numbers of divisions (16 and 26, respectively) as the family (16) or genus number (27) of our species ([He *et al.* 2009](#)). In contrast to the commonly used method of phylogenetically independent contrasts, this method has a great advantage in that the effect of phylogeny on leaf traits could be quantified as the percentage of variations explained by ancient lineages formed at different times in the evolutionary history. Consequently, the relative effects of phylogenetic, abiotic and biological factors on leaf traits

could be compared. At the same time, because the degrees of freedoms of the phylogenetic variables were similar as that of taxonomic groups, this method also provided a good opportunity to compare the effects of phylogenetic and taxonomic groups on leaf traits ([He *et al.* 2009, 2010](#)).

For each plot, monthly mean temperature and precipitation (means over 1950–2000) were extracted from a global climate database according to the geographical coordinates of the plots ([Hijmans *et al.* 2005](#)). Four climatic indices were calculated using these monthly climatic data, including mean annual temperature (MAT) and precipitation (MAP), annual potential evapotranspiration (PET) and water deficit (WD). WD is calculated as the difference between PET and annual actual evapotranspiration ([Thorntwaite 1948](#)). PET and WD together explained similar variations in leaf traits as MAT and MAP together, and consequently we presented only the results of MAT and MAP because they were the most commonly used indices in previous studies.

Statistic analyses

Four key leaf traits were selected in this analysis (see INTRODUCTION section): LMA, A_{mass} , N_{mass} and P_{mass} . We examined the effects of three types of factors on leaf traits: (i) environmental variations among-site: including climate, soil fertility and site (i.e. the plots); (ii) biological characters: plant height and absolute height growth rate; (iii) phylogenetic divisions: including the 60 and 30 Mya divisions, and species. Leaf traits, STP and SAP, height and growth rate were log transformed prior to data analyses to increase the normality and homoscedasticity of residuals ([He *et al.* 2009](#)). Climatic variables and other soil variables were remained untransformed.

We used general linear models (GLMs) and mixed-model analyses of variance (ANOVA) to examine the effects of different factors on leaf traits ([Balvanera *et al.* 2006](#); [He *et al.* 2009](#); [Schmid *et al.* 2002](#)). We conducted GLM analyses at two levels: the among- and within-site level, and the within-site level. (i) We first explained leaf trait data directly with different factors. It should be noted that all the species in a plot have the same value for a climatic or soil variable, but have different values for a biological or phylogenetic variable. Consequently, the percentages of sum of squares (%SSs) explained by climatic or soil variables were variations among-site, while the %SSs for other variables were variations among- and within-site. (ii) We entered the 'site' term into GLMs before biological characters or phylogenetic groups. In this situation the %SSs explained by biotic or phylogenetic variables were variations within-site ([He *et al.* 2009](#); [Wang *et al.* 2009](#)). In these analyses, climatic and soil variables were nested within site, and thus climatic and soil variables were treated as fixed factors while site as random effect in mixed-model ANOVA (for details, see [He *et al.* 2009](#); [Schmid *et al.* 2002](#)). Similarly, the phylogenetic divisions were also nested. Thus for the 60 Mya phylogenetic division, the 30 Mya division was used as the random effect; while for the 30 Mya division, the species term was treated as the random effect.

To examine how the three types of factors work together to influence leaf traits, we partitioned the leaf trait variations into different components (Borcard *et al.* 1992; Heikkinen *et al.* 2005): (i) *a*, *b* and *c*—the independent effects of environmental variations among-site ('Site' in Fig. 1), biological characters ('BIO') and phylogenetic differences among species ('Species'), respectively; (ii) *d*, *e* and *f*—the shared effects between Site and BIO, between Species and Site, and between Species and BIO, respectively; (iii) *g*—the shared effects of Site, Species and BIO together; (iv) Unexplained variations. The pure effects (*a*, *b* and *c*) were the %SSs explained by a factor (e.g. Site) when it entered GLM after other variables, consequently the significances of *a*, *b* and *c* could be evaluated by *F* test. The shared effects (*d*–*g*), however, were obtained by subtracting the %SSs explained by different GLMs which included different variables (for details, see Heikkinen *et al.* 2005), and thus the significances could not be tested (Fig. 1).

All statistical analyses were performed with R 2.10 (R Development Core Team 2007).

RESULTS

Effects of climate and soil fertility on among-site leaf trait variations

Leaf traits showed great variations in this study (Table 1), with a range similar as those reported for grasslands across China (He *et al.* 2010). LMA increased with decreasing MAP while A_{mass} and P_{mass} showed a reversed pattern ($P < 0.05$ level, Table 2). Leaf traits were far more closely related with MAP than MAT except for N_{mass} . For instance, MAP explained 34.6% of variations in LMA while MAT accounted for only 6.0%.

LMA was negatively related to SOC and STN. On the other hand, A_{mass} was positively related to SOC, STN, and STP ($P < 0.05$), and N_{mass} and P_{mass} was positively related to STN and SAN, respectively. However, the positive relationships between leaf productivity (A_{mass} , N_{mass} and P_{mass}) and soil fertility were generally very weak ($R^2 \leq 0.08$), no matter soil N and P were measured as total N and P or as available N and P contents (Table 2, Fig. 2).

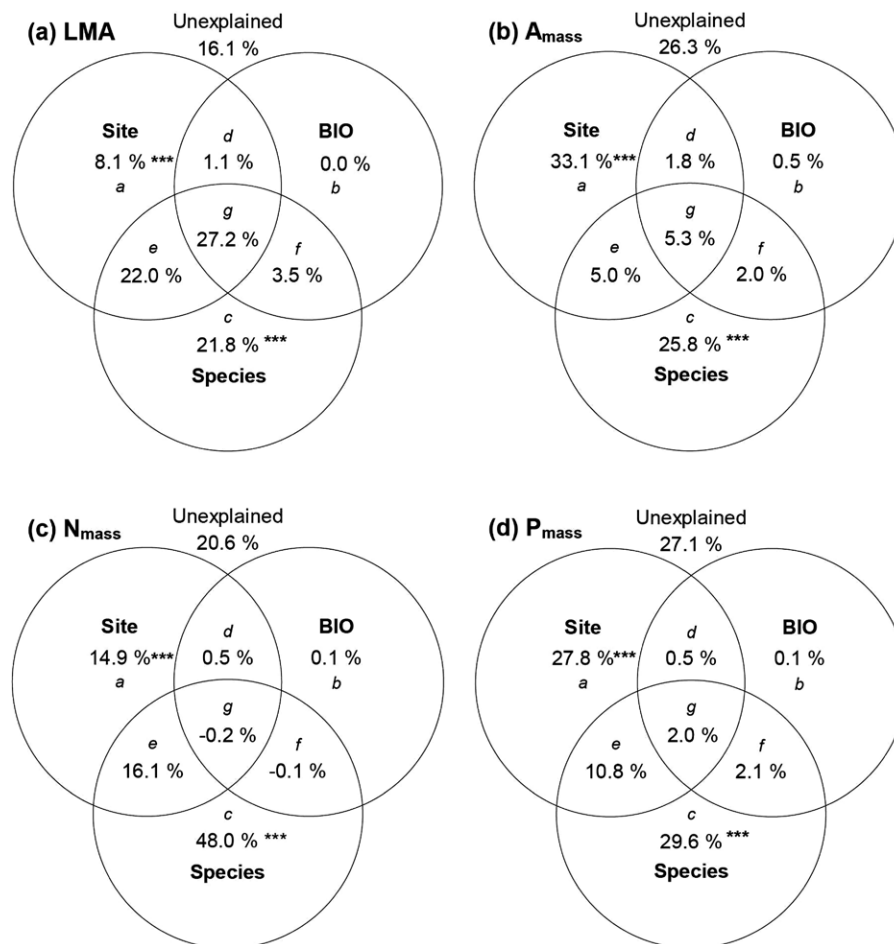


Figure 1: Variation partitioning for leaf traits in terms of the percent of variations explained by three types of factors: Site (environmental variations among-site), Species (phylogenetic differences among species), BIO (biological characters, i.e. height and height growth rate), and unexplained variations. *a*, *b* and *c* are the pure effects of Site, Species and BIO, respectively; *d*, *e*, *f* and *g* are shared effects of them. The significances of *a*, *b* and *c* were evaluated with *F* test, while *d*, *e*, *f* and *g* were not tested (see MATERIALS AND METHODS section). *** $P < 0.001$.

Table 1: Statistic description of leaf traits in this study

	Units	<i>n</i>	Mean	Median	s.d.	Min	Max
LMA	g m ⁻²	300	121.33	109.40	45.07	53.58	366.44
<i>A</i> _{mass}	μmol g ⁻¹ s ⁻¹	231	0.13	0.11	0.09	0.01	0.45
<i>N</i> _{mass}	mg g ⁻¹	366	24.17	23.04	6.93	8.47	44.46
<i>P</i> _{mass}	mg g ⁻¹	358	1.77	1.70	0.58	0.69	4.83

Abbreviations: *n*, sample size; s.d., standard deviation; LMA, leaf mass per area; *A*_{mass}, *N*_{mass} and *P*_{mass}, photosynthetic capacity, nitrogen and phosphorus concentration on mass basis, respectively.

Climate (MAT and MAP together) generally showed significant effect on leaf traits, and explained 6.6–34.6% of variations when entered the GLMs before soil variables (Table 3). Soil fertility (SOC, SAN and SAP together) also showed significant effect for LMA and *P*_{mass} at *P* < 0.05, and explained 6.0–22.8% of variances when entering GLMs the first. The effect of soil fertility was generally much lower when entering GLMs after climatic variables, suggesting collinearity between climatic and soil variables. The results in Table 3 were based on soil available N and P. If soil total N and P were used for analyses instead (Table A1), the effects of soil fertility were similarly weak.

Table 2: The percentage of sum of squares (%SS) in leaf traits explained by single climatic or soil variables

%SS	LMA	<i>A</i> _{mass}	<i>N</i> _{mass}	<i>P</i> _{mass}
Climate				
MAT (°C)	6.02 [#]	-1.74	-10.42 ^{***}	-2.81
MAP (mm)	-34.59 ^{***}	10.80 [*]	3.04 [#]	6.20 [*]
Soil fertility				
SOC (mg g ⁻¹)	-21.38 ^{***}	8.45 [*]	2.54	-0.00
STN (mg g ⁻¹)	-13.35 ^{**}	8.20 [*]	3.94 [*]	-0.01
STP (mg g ⁻¹)	-2.08	8.45 [*]	1.18	-0.01
SAN (mg g ⁻¹)	0.96	-4.65	1.16	5.91 [*]
SAP (mg g ⁻¹)	-2.39	6.58 [#]	0.41	2.84

The significances were tested by treating climatic or soil variables as fixed factors while site as random effect (see MATERIALS AND METHODS section, the ‘site’ term was not reported for simplicity). The sign of ‘-’ denotes a negative relationship while others are positive relations. Abbreviations: MAT and MAP, mean annual temperature and precipitation, respectively; SOC, soil organic carbon content; STN and STP, soil total nitrogen and phosphorus content; SAN and SAP, soil available nitrogen and phosphorus content, respectively; ^{***}*P* < 0.001, ^{**}*P* < 0.01, ^{*}*P* < 0.05, [#]*P* < 0.1. Leaf traits, STP and SAP were log transformed prior to analysis.

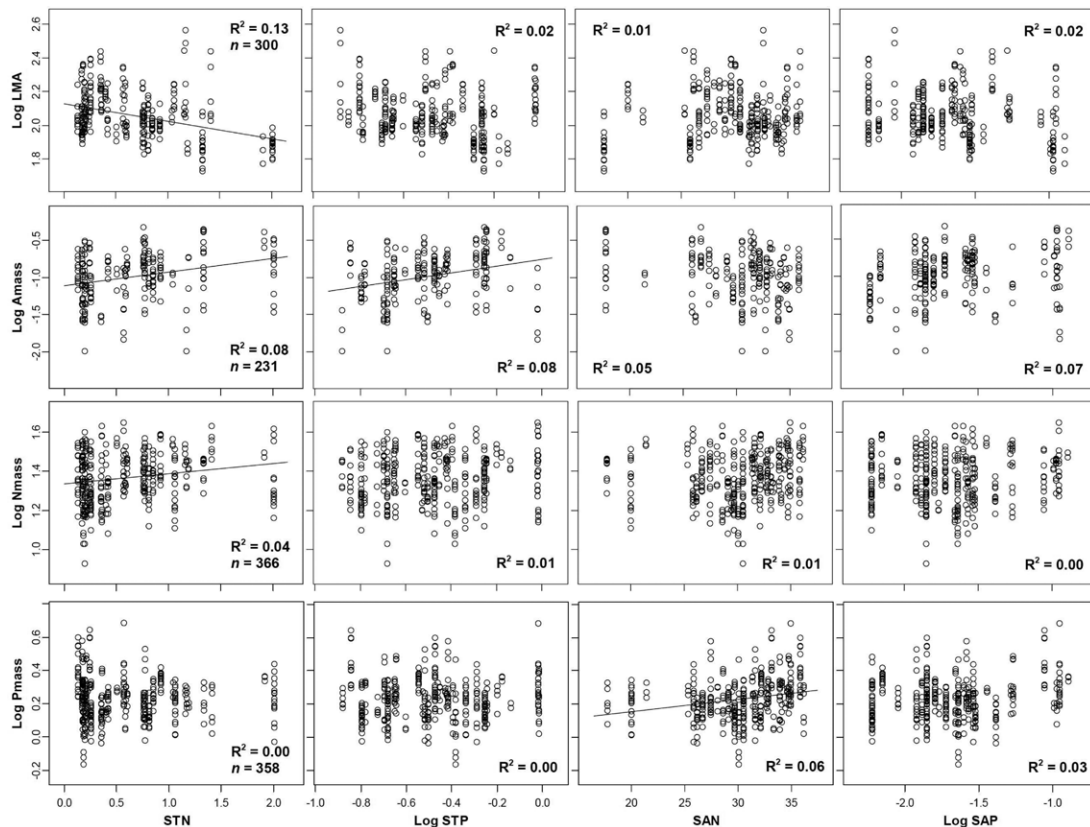


Figure 2: Relationships between leaf mass per area (LMA), mass-based photosynthetic rate (*A*_{mass}), nitrogen (*N*_{mass}), and phosphorus concentration (*P*_{mass}) with soil total nitrogen (STN), soil total phosphorus (STP), soil available nitrogen (SAN), and soil available phosphorus (SAP). Regression lines are shown for relationships that were significant at *P* < 0.05 (for significance, see Table 1).

Table 3: Summary for the effects of environments on among-site variations of leaf traits, including: climate, soil fertility and the remaining variations among site (the site term)

	LMA			A_{mass}			N_{mass}			P_{mass}			Error term
	df	%SS	<i>P</i>	df	%SS	<i>P</i>	df	%SS	<i>P</i>	df	%SS	<i>P</i>	
Climate first													
Climate factors pooled	2	34.59	0.000	2	10.81	0.044	2	10.55	0.003	2	6.59	0.051	Site
<i>MAT</i>	<i>1</i>	<i>6.02</i>	<i>0.006</i>	<i>1</i>	<i>1.74</i>	<i>0.290</i>	<i>1</i>	<i>10.42</i>	<i>0.001</i>	<i>1</i>	<i>2.81</i>	<i>0.103</i>	<i>Site</i>
<i>MAP</i>	<i>1</i>	<i>28.57</i>	<i>0.000</i>	<i>1</i>	<i>9.06</i>	<i>0.022</i>	<i>1</i>	<i>0.13</i>	<i>0.681</i>	<i>1</i>	<i>3.78</i>	<i>0.061</i>	<i>Site</i>
Soil variables pooled	3	6.84	0.030	3	4.90	0.370	3	0.85	0.764	3	7.88	0.069	Site
<i>SOC</i>	<i>1</i>	<i>5.69</i>	<i>0.007</i>	<i>1</i>	<i>2.85</i>	<i>0.180</i>	<i>1</i>	<i>0.17</i>	<i>0.638</i>	<i>1</i>	<i>2.72</i>	<i>0.109</i>	<i>Site</i>
<i>SAN</i>	<i>1</i>	<i>0.53</i>	<i>0.378</i>	<i>1</i>	<i>0.88</i>	<i>0.448</i>	<i>1</i>	<i>0.01</i>	<i>0.904</i>	<i>1</i>	<i>1.29</i>	<i>0.264</i>	<i>Site</i>
<i>SAP</i>	<i>1</i>	<i>0.63</i>	<i>0.337</i>	<i>1</i>	<i>1.17</i>	<i>0.385</i>	<i>1</i>	<i>0.68</i>	<i>0.346</i>	<i>1</i>	<i>3.87</i>	<i>0.058</i>	<i>Site</i>
Soil first													
Soil variables pooled	3	22.78	0.000	3	10.74	0.096	3	6.03	0.063	3	9.91	0.034	Site
<i>SOC</i>	<i>1</i>	<i>21.38</i>	<i>0.000</i>	<i>1</i>	<i>8.45</i>	<i>0.027</i>	<i>1</i>	<i>2.54</i>	<i>0.074</i>	<i>1</i>	<i>0.00</i>	<i>0.950</i>	<i>Site</i>
<i>SAN</i>	<i>1</i>	<i>1.40</i>	<i>0.156</i>	<i>1</i>	<i>0.55</i>	<i>0.548</i>	<i>1</i>	<i>3.40</i>	<i>0.041</i>	<i>1</i>	<i>6.64</i>	<i>0.015</i>	<i>Site</i>
<i>SAP</i>	<i>1</i>	<i>0.00</i>	<i>0.996</i>	<i>1</i>	<i>1.74</i>	<i>0.291</i>	<i>1</i>	<i>0.09</i>	<i>0.724</i>	<i>1</i>	<i>3.26</i>	<i>0.080</i>	<i>Site</i>
Climate factors pooled	2	18.65	0.000	2	4.97	0.211	2	5.37	0.040	2	4.56	0.119	Site
<i>MAT</i>	<i>1</i>	<i>1.04</i>	<i>0.220</i>	<i>1</i>	<i>0.57</i>	<i>0.542</i>	<i>1</i>	<i>5.25</i>	<i>0.013</i>	<i>1</i>	<i>1.57</i>	<i>0.219</i>	<i>Site</i>
<i>MAP</i>	<i>1</i>	<i>17.61</i>	<i>0.000</i>	<i>1</i>	<i>4.40</i>	<i>0.100</i>	<i>1</i>	<i>0.11</i>	<i>0.697</i>	<i>1</i>	<i>3.00</i>	<i>0.093</i>	<i>Site</i>
Site	26	17.08	0.000	20	29.55	0.000	27	19.89	0.000	27	26.69	0.000	Residuals
Residuals	268	41.49		205	54.74		333	68.70		325	58.84		

For climatic (*MAT* and *MAP*) and soil variables (*SOC*, *SAN* and *SAP*), we reported both the pooled effects of climatic (soil) variables, and the effect of each variable itself (italicized). The significances of climatic and soil variables were tested by treating site as random effect (see the error term). We also change the order of climate and soil entering the models to examine their effects in common. Leaf traits and *SAP* were log transformed prior to analysis. Abbreviations: df, Degree of freedom; %SS, percentage of sum of squares explained.

The influences of biological characters

LMA was negatively related with plant height and height growth rate, while A_{mass} and P_{mass} showed a positive correlation (Fig. 3). At the among- and within-site level, growth rate and height together explained 31.9% of variations in LMA, 9.7% in A_{mass} and 4.7% in P_{mass} (Table 4). Height was more powerful in explaining LMA and A_{mass} (8.1–31.9%) than growth rate, while growth rate had a stronger effect on P_{mass} (4.3%) than plant height. These results suggested that, the influences of biological characters differed remarkably among leaf traits.

For the within-site leaf traits variations, the explanatory power of height, height growth rate and the two factors together were very weak (<3.7%) (Table 4). This suggests that height and growth rate were much more powerful in explaining among-site instead of within-site variations.

The effect of phylogeny

At the among- and within-site level, the 60 Mya division explained 52.9% and 42.3% of variations, respectively, for LMA and N_{mass} ($P < 0.05$), but did not show significant effect for A_{mass} and P_{mass} . The 30 Mya division was not significant in explaining the variations within the 60 Mya division, except for P_{mass} . On the other hand, the species term shows significant effect for all traits and explains 6.7–16.4% of traits variations within the 30 Mya division.

At the within-site level, the 60 and 30 Mya division show significant effect only for N_{mass} and A_{mass} , respectively. The species term, however, was significant for most traits (except A_{mass}).

The phylogenetic divisions together (60 Mya + 30 Mya + species) explained an average of 55.3% of variations at the among- and within-site level while 33.2% of variations at the within-site level, which was far more powerful than either climate and soil, or growth rate and height together (Tables 3 and 4), suggesting the critical effect of phylogeny on leaf traits.

When the phylogenetic divisions in Table 5 were replaced with taxonomic groups (Table A2), the explanatory powers of family and genus were largely similar as the 60 and 30 Mya divisions, respectively. This confirmed previous findings that taxonomic classification could roughly be used as an approximation of phylogenetic relationships, when the latter was not available (He *et al.* 2009, 2010).

Variation partitioning among three types of factors

The environmental differences among sites, biological characters and phylogenetic differences among species together explained 72.9–83.9% (100% minus unexplained) of variations in leaf traits (averaged 77.5%, Fig. 1). In these explained variations, the pure effect of species (c ; Fig. 1) was among the largest fractions for all the traits (21.8–48.0%), and the

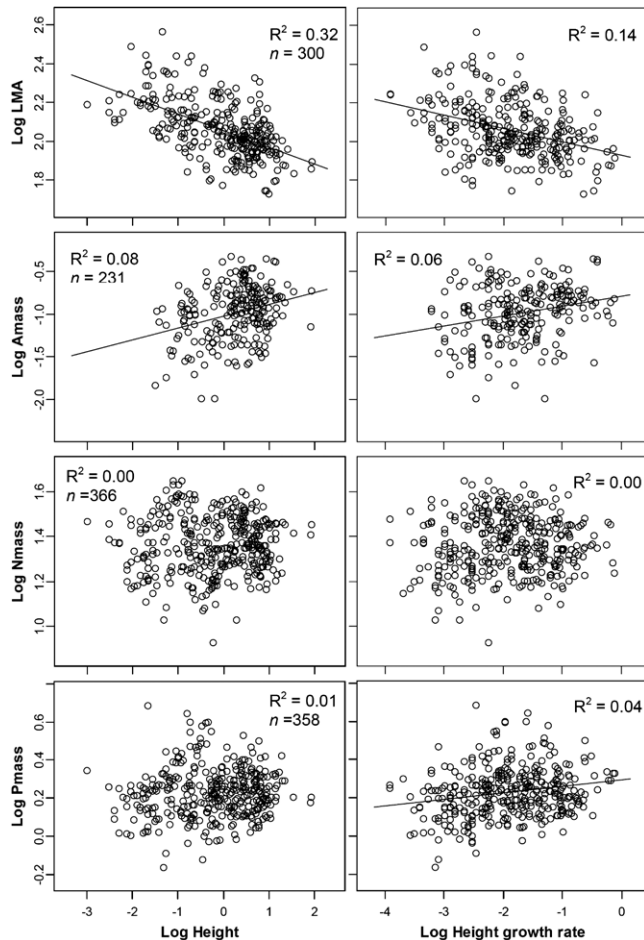


Figure 3: Relationships between leaf mass per area (LMA), mass-based photosynthetic rate (A_{mass}), nitrogen (N_{mass}), and phosphorus concentration (P_{mass}) with plant height and height growth rate. Regression lines are shown for relationships that were significant at $P < 0.05$.

pure effect of site (a) was also an important fraction for A_{mass} (33.1%), P_{mass} (27.8%) and N_{mass} (14.9%). The pure effects of both species and site were highly significant ($P < 0.001$) for all traits, while the pure effect of biological characters (b) was very small (<0.5%) and not significant.

The shared effect between site and species (e) accounted for 10.8–22.0% of variations in LMA, N_{mass} and P_{mass} , while the shared effect of site, species and biological characters (g) was the largest component for LMA. Other shared effects were generally weak and accounted for <5.3% of variances in leaf traits (Fig. 1).

DISCUSSION

Effects of climate and soil fertility on among-site leaf traits variations

Our results on the climatic and soil factors were generally consistent with previous studies. (i) For leaf productivity (A_{mass} , N_{mass} and P_{mass}), a large proportion of variations were remained unexplained by climate and soil fertility (>84.3%, Table 3), confirming that the effects of both climate and soil were only

Table 4: The percentage of sum of squares (%SS) in leaf traits explained by biological characters at two levels: the among- and within-site level, and the within-site level

%SS	LMA	A_{mass}	N_{mass}	P_{mass}
Among- and within- site level				
Height (m)	31.89***	8.08***	0.13	0.75
Height growth rate (m/yr)	14.12***	5.81***	0.38	4.33***
Height + growth rate	31.92***	9.71***	0.38	4.69***
Within-site level				
Height (m)	3.11***	1.74*	0.05	0.26
Height growth rate (m/yr)	0.03	1.41*	0.05	1.39**
Height + growth rate	3.56***	2.59**	0.08	2.17**

The within-site level was analyzed by entering the ‘site’ term into general linear models before biological variables (for the %SSs of site, see Table 5). *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$. All variables were log transformed prior to analysis.

modest (Chen et al. 2012; He et al. 2010; Ordonez et al. 2009; Wright et al. 2005). (ii) LMA was high at arid and infertile sites while leaf productivity were low (Table 2, Fig. 2), supporting the hypothesis that there is a basic biophysical and evolutionary trade-off between fast growth and resource conservation strategy (e.g. Reich et al. 2003). However, our analysis differed from previous studies in that: the effect of climate or soil on LMA was not weak at all, and they together explained 41.4% of variations for LMA (Table 3). This suggests that the environmental modulation of leaf traits can differ markedly among leaf traits.

Testing the effect of soil fertility is crucial for understanding the role of environmental gradients in shaping geographic patterns of leaf traits (see INTRODUCTION section). In this analysis, we used both available and total nutrient concentrations of soil, and showed that soil fertility explained only a small amount of variances in addition to climate (0.85–7.88%, Table 3). Consequently, our results strongly support the idea that soil fertility can not be the ‘missing link’ to explain the large amount of variations unexplained by climate (He et al. 2010). The weak effect of soil has been repeatedly reported at global (Ordonez et al. 2009), national (Chen et al. 2012; He et al. 2010) and regional scales (this study). This consistent conclusion across spatial scales suggests that factors other than environmental gradients, e.g. phylogeny and biological characters (Elser et al. 2010; He et al. 2010), may have far more important influence on leaf traits and should receive much more attentions in future studies.

Leaf traits in relation to plant growth

The relationship between leaf traits and growth rate is not only important in examining species life history strategies (Poorter and Bongers 2006; Wright et al. 2010), but also critical in scaling up leaf traits to individual and ecosystem performance (Garnier et al. 2004; Reich et al. 1997). However, actually this relationship has rarely been tested directly in natural communities (Poorter and Bongers 2006). As far as we know, relating leaf traits and growth rate in shrub biomes at a regional scale has seldom been reported.

Table 5: The effects of phylogenetic divisions on leaf traits at two levels: the among- and within-site level, and the within-site level

	LMA			A_{mass}			N_{mass}			P_{mass}			Error term
	df	%SS	<i>P</i>	df	%SS	<i>P</i>	df	%SS	<i>P</i>	df	%SS	<i>P</i>	
Among- and within-site level													
60 Mya	13	52.86	0.017	11	22.06	0.508	15	42.49	0.033	14	24.85	0.277	30 Mya
30 Mya	7	5.35	0.707	5	9.44	0.108	10	8.76	0.325	10	12.16	0.020	Species
Species	14	16.39	0.000	9	6.74	0.010	18	12.59	0.000	18	7.24	0.002	Residuals
Residuals	265	25.40		205	61.76		322	36.16		315	55.75		
Within-site level													
Site	31	58.51	0.000	25	45.26	0.000	32	31.30	0.000	32	41.16	0.000	Residuals
60 Mya	13	13.87	0.105	11	20.61	0.316	15	37.45	0.004	14	16.45	0.260	30 Mya
30 Mya	7	2.87	0.730	5	5.87	0.005	10	4.42	0.295	10	7.80	0.115	Species
Species	13	8.59	0.000	9	1.41	0.401	18	6.06	0.000	18	7.41	0.000	Residuals
Residuals	235	16.16		180	26.85		290	20.77		283	27.19		

The phylogenetic divisions included three nested terms: the 60 Mya division, the 30 Mya division, and species (see [Figure A1](#)). The significances of the explanatory terms were tested by treating appropriate error terms as random effect. Leaf traits were log transformed prior to analysis.

The present analysis showed that A_{mass} and P_{mass} was positively related with height growth rate, while LMA showed a negative relationship ([Fig. 3](#)). This result is consistent with the growth rate hypothesis that P content is driven by rapid growth, which requires increased allocation to P-rich ribosomal RNA ([Elser *et al.* 2003, 2010](#)). However, growth rate explained only a small proportion of leaf traits variations (<14.1%, [Table 4](#)), and the effect at the within-site level was very weak (<1.4%). Thus our hypothesis that both the within- and among-site traits variations could be well explained by growth rate was not supported.

Our results could only weakly support the ability of leaf traits as predictors for whole-plant growth ([Reich *et al.* 1992, 1997](#)). Previous studies that found a strong relationship between leaf traits and individual growth rate were generally conducted for seedlings and saplings, and typically under experimental environments (see [Poorter and Bongers 2006](#)). However, woody plant growth rates are also strongly influenced by other factors, such as plant size and age ([Reich *et al.* 1992](#)). Recent studies in tropical forests also showed that that leaf traits were only weakly related to height or diameter growth rate. Instead, they found that woody density seemed to be a better predictor of tree growth and survival ([Poorter and Bongers 2006; Poorter *et al.* 2008; Wright *et al.* 2010](#)). In line with these studies, our results suggest that leaf traits themselves may have only limited use in discriminating fast vs. slow growth strategies in natural woody communities, at least at the within-site level ([Table 4](#)). Instead, a combination of leaf traits and other functional traits (e.g. height, woody density and seed mass) may be more useful ([Ackerly 2004b; Falster and Westoby 2005; Westoby *et al.* 2002](#)).

The relationship between leaf traits and plant height

How leaf traits are associated with plant stature over large distances has rarely been reported (but see [Díaz *et al.* 2004; Wright *et al.* 2007](#)). A positive relationship between LMA and height is not only widely observed for trees within-communities (see INTRODUCTION section), but also reported for herb

communities at the within-site level ([Anten and Hirose 2003; Poorter *et al.* 2009](#)). However, in our analysis at the regional scale LMA was negatively related to shrub height ([Fig. 3](#)), and this negative relationship can be well explained by resource-use strategy ([Reich *et al.* 2003](#)). (i) Considering the role of selection pressure: in unfavorable environments, natural selection will favor those species with the traits that can reserve the resources for survival (i.e. low tissue turnover rate and high LMA), instead of the traits to be more competitive (growing higher and faster; [Reich *et al.* 2003](#)). (ii) Considering the ecological plasticity within a species: growing fast and high is not permitted by the resource-poor environments ([Ryan *et al.* 2006; Wang *et al.* 2006](#)), and high LMA is well known to be a physiological acclimation to unfavorable environments ([Reich *et al.* 2003](#)). Both mechanisms predict a negative relationship between LMA and plant height across environmental gradients. The first mechanism seems to be more powerful in the present study, because in [Fig. 1a](#) the component *g* (27.2%, i.e. the effect of height on LMA that was shared with the effect of species shift with sites) were much larger than component *d* (1.1%, i.e. the effect of height on the within-species and among-site variations of LMA). Consequently, our results suggest that leaf trait–height relationships across sites are shaped by rather different mechanism as those reported for coexisting trees.

Previous studies generally suggested that LMA and maximum plant height are orthogonal (i.e. not correlated) axes of ecological strategies ([Díaz *et al.* 2004; Westoby *et al.* 2002; Wright *et al.* 2007](#)). However, our result suggests that the among-site height changes seem to be controlled by the same mechanisms that shape the leaf economics spectrum. Our result is also supported by an analysis using maximum height ([Ackerly and Cornwell 2007](#)). In their study on woodland and shrub communities, LMA and maximum height were also not significantly correlated. However, when LMA and height values were partitioned into α (within-site) and β (among-site) components, they were closely related and the relationship was negative at the among-site level while positive at the within-site level.

These two contrast relationships are, respectively, consistent with our results across sites (Fig. 3), and previous studies at the within-site level (Cavaleri et al. 2010; Poorter et al. 2009). Thus we suspect that those findings that LMA and maximum height are largely not related at a large scale (Díaz et al. 2004; Wright et al. 2007) may be caused by the opposite LMA–height relationships at the within- and among-site levels. We suggest future studies to collect data in other biomes to test this hypothesis.

The relative effects of phylogeny, biological characters and environments

From our results, it was clear that phylogeny (the two divisions and species together) explained far more variances in leaf traits than either climate and soil fertility, or height and growth rate together (Tables 3–5), suggesting the critical role of phylogeny in shaping leaf trait patterns. We also show that, the effects of phylogenetic divisions differed markedly not only among leaf traits, but also between the within- and among-site levels (Table 5). For instance, the ancient lineages at 60 million years ago accounted for >66% of the total effects of phylogeny on LMA and N_{mass} at the among- and within-site level, confirming that some leaf traits are rather conservative during the evolutionary history (see also Ackerly 2004a; Ackerly et al. 2006). However, for A_{mass} and P_{mass} the 60 Mya division did not show significant effect at both the two spatial levels we examined, while the other two phylogenetic divisions were significant, suggesting that A_{mass} and P_{mass} may be less affected by niche conservatism. This finding is also consistent with the results of variation partitioning (Fig. 1), which suggest that P_{mass} and A_{mass} seem to be more plastic across abiotic gradients than N_{mass} and LMA (see below).

Similar to our results, other studies have also found strong influences of taxonomic or phylogenetic groups on geographic patterns of leaf traits (e.g. He et al. 2008, 2010). However, these strong phylogeny effects may have included some effects of the environment and biological characters (see INTRODUCTION section). In this analysis, we quantified the joint and independent effects of these factors for the first time (Fig. 1). We show that 14.2–53.9% of leaf trait variations were due to shared influences of species, site and biological characters (components d – g), which differed greatly among traits.

Through the variation partitioning of the three types of factors, our results revealed some patterns that were not noticed by previous studies (Fig. 1). For instance, differences in biological characters among species were generally used to explain the great variations of leaf traits within forest and herb communities (e.g. Cavaleri et al. 2010; Elser et al. 2010; He et al. 2010). However, we showed that in shrub biomes most of the within-site variations were not caused by this effect (component f , < 3.5%), but were mainly caused by the pure effect of phylogenetic differences among species (c). Instead, an interesting finding of our study is that the influences of biological characters on LMA, A_{mass} and P_{mass} were mainly a result that different species differed in both leaf traits and biological characters, because most effects of biological characters were shared among species (g + f). Our results further suggest that the relationships between biological characters and LMA and

A_{mass} (Fig. 3) are strongly shaped by species shift across site (g) as a result of abiotic gradients, and only weakly driven by differences among coexisting species (f). It is also interesting that the total effect of biological characters was much larger for LMA than other traits (Fig. 1). Whether this suggests that biological characters influence leaf productivity only indirectly (e.g. through LMA) deserves further examinations. In our study, a large proportion (c and e) of the effect of phylogenetic differences among species could not be attributed to differences in biological characters, for both the within- and among-communities variations of leaf traits. This result further supports the critical role of phylogenetic history on leaf traits.

Recent studies on woody plants have suggested that N_{mass} was more controlled by taxonomic or functional groups, while P_{mass} was affected by environments and functional groups together (Chen et al. 2012; Townsend et al. 2007). Our results are consistent with their findings (Fig. 1): the pure species effect (c) was by far the largest fraction for N_{mass} , while the pure effects of site (a) and species (c) were both important for P_{mass} and A_{mass} . In addition, our results further reveal that the among-site variations of P_{mass} and A_{mass} are mainly caused by variations within species (a + d), while the variations caused by species shift with site (e + g) played a second role. This means that the within-species physiological plasticity along abiotic gradients was much stronger for P_{mass} and A_{mass} (than for N_{mass} and LMA). We suggest that this difference is one of the reasons why P_{mass} was found to be more closely related to environments than N_{mass} for woody species (e.g. Chen et al. 2012; Elser et al. 2010).

Fig. 1 clearly showed that the independent and joint effects of species and site differed remarkably among leaf traits. This is different from a recent study on Chinese grassland which partitioned the effects of species and site (He et al. 2010). In their analyses (Table A3), the pure and shared effects of species and site did not differ much among leaf traits. Further, their results showed that the variations among-site and among-species (e + g) was the largest fraction for most traits (this is the case only for LMA in our study), and P_{mass} and A_{mass} also did not differ clearly from other traits in the physiological plasticity within species across site (a + d). Why grassland and shrub biomes showed these remarkable differences is interesting and careful comparative studies are needed to explore the underlying mechanisms.

CONCLUSIONS

The present analysis revealed that the relative importance of phylogeny, biological characters and environments differed remarkably among leaf traits, between the within- and among-site levels, and among different biomes (Tables 3–5, Fig. 1). Our results strongly suggest the necessity of examining phylogenetic, biological and environmental factors simultaneously (which has seldom been conducted before). We also suggest future studies to explore the different effects of phylogenetic and biological factors between the within- and among-communities levels, because the mechanisms regulating leaf traits patterns may be completely different at the two levels (Figs. 1 and 3; Ackerly and Cornwell 2007; Ackerly et al. 2006) and may be critical for a better understanding of the drivers of leaf trait variation.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Plant Ecology* online.

ACKNOWLEDGEMENTS

This work was supported by the National Key Technologies R & D Program (2011BAD38B01) and the Research Funds for Doctoral Education in Universities of China (20090014120002), and the Strategic Priority Research Program - Climate Change: Carbon Budget and Related Issues' of the Chinese Academy of Sciences (#XDA05050300). Many thanks are due to Prof. H. Qian for constructive comments on the manuscript, and Prof. C.Z. Liang and W.H. Ma for help in species identification, and M. Wang and L.B. Zeng and others for participation in the field work.

REFERENCES

- Ackerly DD (2004a) Adaptation, niche conservatism, and convergence: comparative studies of leaf evolution in the California chaparral. *Am Nat* **163**:654–71.
- Ackerly DD (2004b) Functional strategies of chaparral shrubs in relation to seasonal water deficit and disturbance. *Ecol Monogr* **74**:25–44.
- Ackerly DD, Cornwell WK (2007) A trait-based approach to community assembly: partitioning of species trait values into within- and among-community components. *Ecol Lett* **10**:135–45.
- Ackerly DD, Schwillk DW, Webb CO (2006) Niche evolution and adaptive radiation: testing the order of trait divergence. *Ecology* **87**:S50–61.
- APG III (2009) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Bot J Linn Soc* **161**:105–21.
- Anten NPR, Hirose T (2003) Shoot structure, leaf physiology, and daily carbon gain of plant species in a tallgrass meadow. *Ecology* **84**:955–68.
- Balvanera P, Pfisterer AB, Buchmann N, *et al.* (2006) Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecol Lett* **9**:1–11.
- Baumann F, He J-S, Schmidt K, *et al.* (2009) Pedogenesis, permafrost, and soil moisture as controlling factors for soil nitrogen and carbon contents across the Tibetan Plateau. *Glob Change Biol* **15**:3001–17.
- Borcard D, Legendre P, Drapeau P (1992) Partialling out the spatial component of ecological variation. *Ecology* **73**:1045–55.
- Cavaleri MA, Oberbauer SF, Clark DB, *et al.* (2010) Height is more important than light in determining leaf morphology in a tropical forest. *Ecology* **91**:1730–9.
- Chen Y, Han W, Tang L, *et al.* (2012) Leaf nitrogen and phosphorus concentrations of woody plants differ in responses to climate, soil and plant growth form. *Ecography* (in press) doi: 10.1111/j.1600-0587.2011.06833.x.
- Díaz S, Hodgson JG, Thompson K, *et al.* (2004) The plant traits that drive ecosystems: evidence from three continents. *J Veg Sci* **15**:295–304.
- Elser JJ, Acharya K, Kyle M, *et al.* (2003) Growth rate–stoichiometry couplings in diverse biota. *Ecol Lett* **6**:936–43.
- Elser JJ, Fagan WF, Kerkhoff AJ, *et al.* (2010) Biological stoichiometry of plant production: metabolism, scaling and ecological response to global change. *New Phytol* **186**:593–608.
- Falster DS, Westoby M (2005) Alternative height strategies among 45 dicot rain forest species from tropical Queensland, Australia. *J Ecol* **93**:521–35.
- Garnier E, Cortez J, Billes G, *et al.* (2004) Plant functional markers capture ecosystem properties during secondary succession. *Ecology* **85**:2630–7.
- Garnier E, Lavorel S, Ansquer P, *et al.* (2007) Assessing the effects of land-use change on plant traits, communities and ecosystem functioning in grasslands: a standardized methodology and lessons from an application to 11 European sites. *Ann Bot* **99**:967–85.
- Han W, Fang J, Guo D, *et al.* (2005) Leaf nitrogen and phosphorus stoichiometry across 753 terrestrial plant species in China. *New Phytol* **168**:377–85.
- He J-S, Wang L, Flynn DFB, *et al.* (2008) Leaf nitrogen: phosphorus stoichiometry across Chinese grassland biomes. *Oecologia* **155**:301–10.
- He J-S, Wang XP, Flynn DFB, *et al.* (2009) Taxonomic, phylogenetic and environmental tradeoffs between leaf productivity and persistence. *Ecology* **90**:2779–91.
- He J-S, Wang XP, Schmid B, *et al.* (2010) Taxonomic identity, phylogeny, climate and soil fertility as drivers of leaf traits across Chinese grassland biomes. *J Plant Res* **123**:551–61.
- He J-S, Wang ZH, Wang XP, *et al.* (2006) A test of the generality of leaf trait relationships on the Tibetan Plateau. *New Phytol* **170**:835–48.
- Heikkinen RK, Luoto M, Kuussaari M, *et al.* (2005) New insights into butterfly–environment relationships using partitioning methods. *Proc R Soc B: Biol Sci* **272**:2203–10.
- Hijmans RJ, Cameron SE, Parra JL, *et al.* (2005) Very high resolution interpolated climate surfaces for global land areas. *Int J Climatol* **25**:1965–78.
- Jones JB (2001) *Laboratory Guide for Conducting Soil Tests and Plant Analysis*. New York: CRC Press.
- Kemmel SW, Hubbell SP (2006) The phylogenetic structure of a neotropical forest tree community. *Ecology* **87**:86–99.
- Kerkhoff AJ, Fagan WF, Elser JJ, *et al.* (2006) Phylogenetic and growth form variation in the scaling of nitrogen and phosphorus in the seed plants. *Am Nat* **168**:E103–22.
- Letcher S (2012) Phylogenetic structure of angiosperm communities during tropical forest succession. *Proc R Soc B: Biol Sci* **277**:97–104.
- Ordonez JC, Bodegom PMv, Witte J-PM, *et al.* (2009) A global study of relationships between leaf traits, climate and soil measures of nutrient fertility. *Glob Ecol Biogeogr* **18**:137–49.
- Poorter H, Bergkotte M (1992) Chemical composition of 24 wild species differing in relative growth rate. *Plant, Cell Environ* **15**:221–9.
- Poorter H, Niinemets ü, Poorter L, *et al.* (2009) Causes and consequences of variation in leaf mass per area (LMA): A meta-analysis. *New Phytol* **182**:565–88.
- Poorter L, Bongers F (2006) Leaf traits are good predictors of plant performance across 53 rain forest species. *Ecology* **87**:1733–43.
- Poorter L, Wright SJ, Paz H, *et al.* (2008) Are functional traits good predictors of demographic rates? Evidence from five neotropical forests. *Ecology* **89**:1908–20.
- Prinzing A, Reiffers R, Braakhekke WG, *et al.* (2008) Less lineages – more trait variation: phylogenetically clustered plant communities are functionally more diverse. *Ecol Lett* **11**:809–19.
- R Development Core Team (2007) *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.

- Reich PB, Walters MB, Ellsworth DS (1992) Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecol Monogr* **62**:365–92.
- Reich PB, Walters MB, Ellsworth DS (1997) From tropics to tundra: global convergence in plant functioning. *Proc Natl Acad Sci USA* **94**:13730–4.
- Reich PB, Wright IJ, Cavender-Bares J, *et al.* (2003) The evolution of plant functional variation: traits, spectra, and strategies. *Int J Plant Sci* **164**:S143–64.
- Reich PB, Wright IJ, Lusk CH (2007) Predicting leaf physiology from simple plant and climate attributes: A global GLOPNET analysis. *Ecol Appl* **17**:1982–8.
- Ryan MG, Phillips N, Bond BJ (2006) The hydraulic limitation hypothesis revisited. *Plant, Cell Environ* **29**:367–81.
- Schmid B, Hector A, Huston MA, *et al.* (2002) The design and analysis of biodiversity experiments. In Loreau M, Naeem S, Inchausti P (eds). *Biodiversity and Ecosystem Functioning: Synthesis and Perspectives*. Oxford, New York: Oxford University Press, 66–75.
- Thornthwaite CW (1948) An approach toward a rational classification of climate. *Geogr Rev* **38**:57–94.
- Townsend AR, Cleveland CC, Asner GP, *et al.* (2007) Controls over foliar N: P ratios in tropical rain forests. *Ecology* **88**:107–18.
- Wang XP, Fang JY, Sanders NJ, *et al.* (2009) Relative importance of climate vs. local factors in shaping the regional patterns of forest plant richness across Northeast China. *Ecography* **32**:133–42.
- Wang XP, Fang JY, Tang ZY, *et al.* (2006) Climatic control of primary forest structure and DBH-height allometry in Northeast China. *For Ecol Manage* **234**:264–74.
- Webb C, Ackerly D, Kembel SW (2008) Phylocom: software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics* **24**:2098–100.
- Webb C, Ackerly D, Kembel S (2009) Phylocom: software for the analysis of phylogenetic community structure and character evolution (with phylomatic and ecovolve) - user's manual version 4.1. <http://phylodiversity.net/phylocom/>.
- Westoby M, Falster DS, Moles AT, *et al.* (2002) Plant ecological strategies: some leading dimensions of variation between species. *Annu Rev Ecol Syst* **2002**:125–59.
- Wikström N, Savolainen V, Chase MW (2001) Evolution of the angiosperms: calibrating the family tree. *Proc R Soc Lond B: Biol Sci* **268**:2211–20.
- Wright IJ, Ackerly DD, Bongers F, *et al.* (2007) Relationships among ecologically important dimensions of plant trait variation in seven neotropical forests. *Ann Bot* **99**:1003.
- Wright IJ, Reich PB, Cornelissen JHC, *et al.* (2005) Modulation of leaf economic traits and trait relationships by climate. *Glob Ecol Biogeogr* **14**:411–21.
- Wright IJ, Reich PB, Westoby M, *et al.* (2004) The worldwide leaf economics spectrum. *Nature* **428**:821–7.
- Wright SJ, Kitajima K, Kraft NJB, *et al.* (2010) Functional traits and the growth-mortality trade-off in tropical trees. *Ecology* **91**:3664–74.