META-ANALYSIS

A global study of relationships between leaf traits, climate and soil measures of nutrient fertility

Jenny C. Ordoñez[1]*, Peter M. van Bodegom[1], Jan-Philip M. Witte[1,2], Ian J. Wright[3], Peter B. Reich[4] and Rien Aerts[1]

[1]*Institute of Ecological Science, Department of Systems Ecology, de Boelelaan 1085, 1081 HV Amsterdam, The Netherlands,* [2]*KWR Watercycle Research Institute, PO Box 1072, 3430 BB Nieuwegein, The Netherlands,* [3]*Department of Biological Sciences, Macquarie University, Sydney, NSW 2109, Australia,* [4]*Department of Forest Resources, University of Minnesota, St Paul, MN 55108, USA*

ABSTRACT

Aim This first global quantification of the relationship between leaf traits and soil nutrient fertility reflects the trade-off between growth and nutrient conservation. The power of soils versus climate in predicting leaf trait values is assessed in bivariate and multivariate analyses and is compared with the distribution of growth forms (as a discrete classification of vegetation) across gradients of soil fertility and climate.

Location All continents except for Antarctica.

Methods Data on specific leaf area (SLA), leaf N concentration (LNC), leaf P concentration (LPC) and leaf N:P were collected for 474 species distributed across 99 sites (809 records), together with abiotic information from each study site. Individual and combined effects of soils and climate on leaf traits were quantified using maximum likelihood methods. Differences in occurrence of growth form across soil fertility and climate were determined by one-way ANOVA.

Results There was a consistent increase in SLA, LNC and LPC with increasing soil fertility. SLA was related to proxies of N supply, LNC to both soil total N and P and LPC was only related to proxies of P supply. Soil nutrient measures explained more variance in leaf traits among sites than climate in bivariate analysis. Multivariate analysis showed that climate interacted with soil nutrients for SLA and area-based LNC. Mass-based LNC and LPC were determined mostly by soil fertility, but soil P was highly correlated to precipitation. Relationships of leaf traits to soil nutrients were stronger than those of growth form versus soil nutrients. In contrast, climate determined distribution of growth form more strongly than it did leaf traits.

Main conclusions We provide the first global quantification of the trade-off between traits associated with growth and resource conservation 'strategies' in relation to soil fertility. Precipitation but not temperature affected this trade-off. Continuous leaf traits might be better predictors of plant responses to nutrient supply than growth form, but growth forms reflect important aspects of plant species distribution with climate.

Keywords

Ecosystem functioning, irradiance, leaf traits, N mineralization, potential evapotranspiration, rainfall, soil C:N, soil N, soil P, temperature.

*Correspondence: Jenny Ordoñez, Institute of Ecological Science, Department of Systems Ecology, de Boelelaan 1085, 1081 HV Amsterdam, The Netherlands.
E-mail: jenny.ordonez@ecology.falw.vu.nl*

INTRODUCTION

The availability of soil nutrients is one of the main factors determining the species composition of plant communities. At the same time, plants have species-specific impacts on soil nutrient availability through feedbacks on nutrient cycles. Despite the large variability of plant strategies within a site

(Poorter & De Jong, 1999; Fonseca *et al.*, 2000; Wright *et al.*, 2004), plants growing in nutrient-rich environments in general produce large amounts of nutrient-rich litter, which releases large amounts of nutrients and in turn sustain high levels of soil fertility. In contrast, plants in nutrient-poor environments produce small amounts of litter and conserve nutrients in long-lived and recalcitrant tissues, thus reinforcing the infertile environment

(Melillo *et al.*, 1982; Hobbie, 1992; Berendse, 1994; Crews *et al.*, 1995; Aerts & Chapin, 2000). It is important to note also that selection has led species to differ intrinsically in both responses to soil nutrition and in their impacts on soil nutrient supply (e.g. Hobbie, 1992; Berendse, 1994; Reich *et al.*, 2001; Booth *et al.*, 2005), and such effects can amplify or constrain the feedbacks described above. These patterns of plant responses and feedbacks on nutrient supply have been conceptualized in terms of a general trade-off between growth rate and nutrient conservation (Chapin, 1980; Reich *et al.*, 1992; Berendse, 1994; Aerts, 1999), itself integrated into well-known plant strategy models that characterize plant functioning according to axes of specialization (Grime, 1977; Westoby *et al.*, 2002). Experimental evidence for the global existence of such axes of specialization has appeared over the last decades through the analysis of leaf traits connected to this trade-off (Field & Mooney, 1986; Reich *et al.*, 1997; Diaz *et al.*, 2004; Wright *et al.*, 2004). These traits, i.e. specific leaf area (SLA), leaf nitrogen (LNC) and phosphorus (LPC) concentrations and leaf life span (LLS), have recently been denominated as the leaf economy traits (Wright *et al.*, 2004).

Although the plant–soil nutrient relationship has been studied extensively (see Chapin, (1980) and Aerts & Chapin, (2000) for reviews), quantification of the trait responses across various spatial scales is still limited (Lavorel & Garnier, 2002). Such quantitative knowledge is urgently needed to advance our understanding of ecosystem function (Chapin, 2003; Grime, 2006; McGill *et al.*, 2006) and is of paramount importance in the face of ongoing environmental changes. Predicting the effects of changes in nutrient availability on plant productivity is one of the highest uncertainties of future climate change predictions (Hungate *et al.*, 2003). For instance, global change is very likely to influence soil nutrient availability on relatively small time-scales (3–5 years) and plant species composition at longer time-scales (Rustad *et al.*, 2001; Aerts *et al.*, 2006).

Predictions about the effects of climate change on vegetation composition and nutrient cycling are carried out with vegetation and carbon balance models such as TEM, BIOME and LPJ (Melillo *et al.*, 1995; Pan *et al.*, 1998; Sitch *et al.*, 2003). In such models the vegetation continuum has been approached by using categorical variables to describe plant responses. For instance plant responses have been classified by biome, growth form and, the most widely used, plant functional type (PFT) (Gitay & Noble, 1998). Classification into relevant PFTs does allow repeatable mapping with traits, and trait trade-offs (Reich *et al.* 1997, 2007), but this approach has considerable limitations. One problem with PFTs and any other discrete classification is that they remain context dependent as they do not have a direct physiological basis (Gitay & Noble, 1998). A second major problem is that boundaries are forced, while functions may overlap (Wright *et al.*, 2005a). Moreover, it is questionable whether groupings defined under current climate will hold under changing conditions (Eviner & Chapin, 2003). Similar problems occur with discrete classifications of soil nutrient availability, like soil types or high versus low soil fertility (e.g. Wright *et al.*, 2001). Additionally, discrete classifications of nutrient availability complicate quantification of plant responses to nutrient supply

across global scales because the absolute magnitude of nutrient availability is not known.

An approach that follows naturally to overcome these problems is to link continuous plant traits to quantitative measures of soil nutrient availability. Until now, because of practical and logistical constraints, these studies mainly provided data on differences among only a few species or species from a limited geographical area (Vitousek *et al.*, 1995; Cunningham *et al.*, 1999; Poorter & De Jong, 1999; Fonseca *et al.*, 2000; Knops & Reinhart, 2000; Cavender-Bares *et al.*, 2004). Recent global data compilations have shed light on controls on nutrient cycling (Booth *et al.*, 2005), the convergence of plant functioning (Wright *et al.*, 2004), modulation of plant traits by climate (Wright *et al.*, 2005b) and patterns of leaf N and P in relation to climate and latitude (Reich & Oleksyn, 2004). These studies, together with previous research on local scales, have shown that climate and soils are among the important factors that control leaf traits. Nonetheless, relationships between plant traits and soil nutrient availability and combined effects of climate and soil on leaf traits are yet to be reliably quantified at global scales. Quantification of the continuous relationship of leaf traits to both climate and soils is of prime importance for the development of new modelling frameworks that could be used to study the effects of climate change.

The aim of this paper is to use quantitative and continuous leaf economy traits (from here onwards, 'leaf traits') in combination with soil nutrient availability and climate parameters measured at the same sites. Leaf traits, soil and climate variables were compiled from the authors' own work as well as from the literature. With the resulting dataset, we ask the following research questions. (1) Does the hypothesized positive relationship between leaf traits (SLA, leaf N and P) and soil fertility, that reflects the trade-off between fast growth and nutrient conservation, hold generally? (2) Are the relationships between different leaf traits and soil fertility stronger than between leaf traits and climate for the same set of species? (3) Do climate and soils have additional and/or interactive effects on different leaf traits, and if so, how strong are these effects? (4) Is the goodness of fit of relations between continuous leaf traits and either soil nutrient measures or climate higher than that for the relations of growth forms to soil or climate, as we hypothesized?

MATERIALS AND METHODS

Data selection

Data on leaf traits and soil fertility were collected from published studies in which both leaf traits and measures of soil fertility were obtained at the same site and within a time span of 2 years. This criterion proved to be strongly limiting for data selection: despite the wealth of studies on diverse aspects of plant trait variation, only a few studies report soil characteristics for the same locations. Nevertheless we considered this filter necessary to minimize errors caused by temporal and spatial variability in soil fertility. Only data from natural gradients and field studies (no crop fields or plantation forestry land) were selected, excluding

Table 1 Location, biomes and numbers of species within each growth form for studies included in this analysis.

Reference*	Country	Latitude	Biomes†	No. of sites	Growth forms‡ F	G	H	DS	ES	DT	ET	Soil data¶ Soil total N (%)	Soil C:N	Soil total P (mg kg⁻¹)	N mineraliz. (µg g⁻¹ year⁻¹)
1–6	United States	68.7	T	4		9		12	8			x	x		x
7	United States	19.5	ToRF, TF	10	4	2	2		17		13	x		x	
8, 9	Netherlands	52.4	Sh	8		24	8					x	x		x
10^f	New Zealand	−45.5	Sh, TF, BF	29		127	137					x			
11	France	43.9	TF	12		19	42		5			x	x		m
12	United States	68.6	T	2		4	2	4	4			x	x	x	x
13	India	25.3	W	2					10	54	26	x	x	x	m
14, 15	China	29.6	TF, BF	6					4	5	15	x	x		m
16	Estonia	58.6	TF	3				29	5	9		x	x		m
17	Australia	−12.7	G	4						18	6	x			
18	Venezuela	1.9	TSF	2					1		11	x	x	x	x
19	Brazil	−2.8	ToRF	13							91	x	x		m
20, 21	Australia	−33.6	TSF, W	4		1			61		20	x	x	x	m
Ranges of soil conditions												0.01–3	7–55	22–826	0–394
Total sites					2	56**	49**	9	30	14	36	97	54	22	56
Total species				99	4	186	200	45	115	86	182				

*For the list of references see Appendix S3.

†T = tundra, ToRF = tropical rain forest, TF = temperate forest, Sh = shrubland, BF = boreal forest, W = woodland, G = grassland, TSF = tropical seasonal forest.

‡F = ferns, G = grasses and sedges, H = herbs, DS = deciduous shrubs, ES = evergreen shrubs, DT = deciduous trees, ET = evergreen trees.

¶m = modelled N mineralization, x = data from the literature.

**Data on grasses and herbs reported by Craine & Lee (2003) = 29 sites was only included in the soil total N vs leaf traits and climate vs leaf traits relationships.

studies with short-term experimental manipulations in the field or in greenhouses.

The resulting dataset spans most world biomes (although deserts and temperate rain forests are not represented because of lack of adequate data), a wide range of soil nutrient conditions and all of the common higher-plant growth forms (Table 1). Even so, the growth forms grasses and herbs form a minority compared with trees and shrubs, and were predominantly sampled in New Zealand (Craine & Lee, 2003). This 'imbalance' is due to the limited number of available studies. The whole dataset encloses 474 species distributed across 99 sites (809 records).

Leaf traits

Leaf traits included in the analysis are generally known to be related to soil nutrient supply: Specific leaf area (SLA, m² kg⁻¹), leaf nitrogen concentration per mass (LNCmass mg g⁻¹), leaf phosphorus concentration per mass (LPCmass mg g⁻¹) and leaf N:P. Leaf traits like SLA, LNC and LPC are positively related to plant relative growth rates, leaf carbon assimilation rates and energy supply (Lambers & Poorter, 1992; Lavorel & Garnier, 2002; Niklas et al., 2005). Leaf nitrogen concentration and leaf phosphorus concentration on an area basis (LNCarea and LPCarea both in g m⁻²) were also included in the analysis. Leaf N:P is a common proxy for the type of nutrient limitation (Koerselman & Meuleman, 1996; Güsewell, 2004). Other plant traits previously shown to be related to soil nutrient supply, e.g. leaf life span and root traits, could not be included in the analysis because of insufficient data.

Specific leaf area (SLA) ranged between 2 and 41 m² kg⁻¹ across the dataset, LNCmass between 5 and 54 mg g⁻¹, LNCarea between 0.3 and 6.6 g m⁻², LPCmass between 0.1 and 6 mg g⁻¹, LPCarea between 0.02 and 4.74 g m⁻² and leaf N:P between 2.6 and 89. All leaf traits were correlated with each other (Appendix S1 in Supporting Information), consistent with patterns shown previously (Güsewell, 2004; Wright et al., 2004).

Soil fertility

Although a variety of measures can be used as proxies of soil fertility, there is little consistency across studies in this regard. Here we used some of the most commonly used measures: soil total N, soil C:N and soil total P, measured in the majority of cases for the upper 20 cm of soil (Table 1). These soil characteristics are proxies of the size of nutrient pools (soil total N and soil total P) and quality of the organic matter (soil C:N) (Heal et al., 1997). All soil nutrient measures were expressed on a mass basis, because of a lack of information on soil bulk density required to obtain area basis estimates. For correlations among the selected soil nutrients measures see Appendix S1.

Soil nutrient concentrations are only very rough approximations of nutrient supply to the vegetation, as most of the soil nutrient

stocks can be occluded in recalcitrant forms (Aerts & Chapin, 2000). Therefore, the net nitrogen mineralization rate was also used as a proxy of available N for plant uptake as it integrates both the nutrient pool potentially available for plant uptake and the controlling factors of nutrient cycling (soil temperature, moisture and soil texture). However, field data were available for relatively few of the sites in our dataset, so these data were complemented with data derived from a mineralization model based on CENTURY (Parton *et al.*, 1987). Although the model was run with weekly time steps, the effects of seasonality, temperature and moisture correction factors were calculated in monthly intervals using climate data extracted from the nearest meteorological stations and/or from a global 10 arcmin gridded dataset of mean monthly surface climate (New *et al.*, 2002). We used air temperature in place of soil temperature, given the paucity of data on soil temperature. Potential evapotranspiration was estimated with an empirical formula, based on temperature alone (Linacre, 1977). In the original CENTURY model, N mineralization is determined by the C:N ratios of three different pools representing active, slow and passive organic matter. In our model, this was simplified by estimating first the total amount of CO_2 released from the three pools and then estimating the total N conversion using the average soil C:N ratio. In this manner we implicitly assume that age structure of the soil organic matter of each soil was 'average'. N mineralization was corrected for microbial immobilization by assuming a constant C:N ratio of 9 for microbial biomass and a microbial yield of 0.3 g C biomass g^{-1} C consumed (Schimel, 1988). The model was tested with observed mineralization values from 35 sites, corresponding to 44 soil profiles using an ordinary least squares regression of observed on modelled values ($r^2 = 0.62$). The positive intercept of the regression ($B_0 = 20.95$ μg N g^{-1}soil $year^{-1}$) showed that the model tended to underestimate N mineralization. However, given that the slope of the model was close to 1 ($B_1 = 1.098$), the underestimation of the model was relatively constant across the observed values of N mineralization. Thus, although the model did not always provide a correct absolute measure of N supply, it was considered useful as a relative measure to allow comparisons among sites.

Climate

Site climate was described in terms of mean annual temperature (MAT, °C) and mean annual precipitation (MAP, mm $year^{-1}$), annual potential evapotranspiration (PET, mm $year^{-1}$) and irradiance (W m^{-2}). Mean annual temperature and precipitation were derived from publications cited in the source. Potential evapotranspiration was obtained from the 10-arcmin IWMI World Water Climate Atlas (http://www.iwmi.cgiar.org/WAtlas/). Irradiance was obtained from New *et al.* (1999) for all sites. For correlations among the selected climate variables, see Appendix S1.

Growth forms

The distribution of growth forms – grasses and sedges, herbs, evergreen trees, evergreen shrubs, deciduous trees, deciduous shrubs and ferns – was used as an example of a discrete classification

to contrast continuous leaf trait values in relation to soil fertility. These growth forms are straightforward to derive and are related to soil properties and nutrient cycling (Booth *et al.*, 2005). PFT classifications are generally based on similar morphological and life-history characteristics (Chapin *et al.*, 1996; Gitay & Noble, 1998). Where growth forms were not indicated in the original data sources, this information was extracted from various online databases of plant information (http://www.botany.hawaii.edu/; http://www.ctahr.hawaii.edu/ctahr2001/; http://efloras.org/; http://www.nzpcn.org.nz/; http://plants.usda.gov/).

Data analysis

All leaf trait and soil data were approximately log-normally distributed (right-skewed); hence they were log_{10} transformed prior to analyses in order to attain approximate normality and homogeneity of residuals. Of the climatic variables, only precipitation was log_{10}-transformed. Temperature, irradiance and PET showed approximately normal distributions.

Bivariate analysis of trait–soil and trait–climate relationships and multivariate analysis of the combined effects of soils and climate on leaf traits were quantified using linear mixed models with maximum likelihood (ML) methods, available in SPSS v.13.0. Soil, climate variables and their interactions were treated as fixed effects and site was treated as a random factor to account for the effects created by the non-independence of leaf trait observations at a site. Random effects are expressed as variances and can be compared with the error variance (analogous to a variance component analysis), but there is no equivalent to r^2. The lack of measures to estimate total explained variance (as in regression methods) is a limitation of the ML method.

Bivariate relationships were investigated using all available observations for each trait–soil and trait–climate combination. The fact that not all leaf traits and soil–climate parameters were measured simultaneously in all studies meant that for each trait–soil and trait–climate combination there was a different sample size for the analysis (see Fig. 1). Analogous to ANOVAs, the predictive power of soil versus climatic properties was compared in terms of *F*-values to account for differences in sample size. Multivariate analysis of the combined effects of soils and climate on leaf traits were made with sub-datasets composed of those records containing values for all selected leaf traits, soil data and climate. For multivariate analysis of SLA, LNCmass and LNCarea, we used a dataset with 425 observations and 46 sites with climate data and soil measures of N supply. For multivariate analysis of LPCmass, LPCarea and leaf N:P, we used a dataset with 243 observations and 22 sites with climate data and soil total N and soil total P as the only soil measures. We decided to use two different datasets, because of the differences in availability of information of measures on soil nitrogen and phosphorus supply (see Table 1). To avoid problems of collinearity among the independents, only variables with a Pearson coefficient lower than 0.5 (see Appendix S2) were included. All possible combinations of independents that fit this constraint were evaluated. Competing multivariate models to predict leaf traits were selected with the Akaike information criterion (AIC) as a goodness of fit measure:
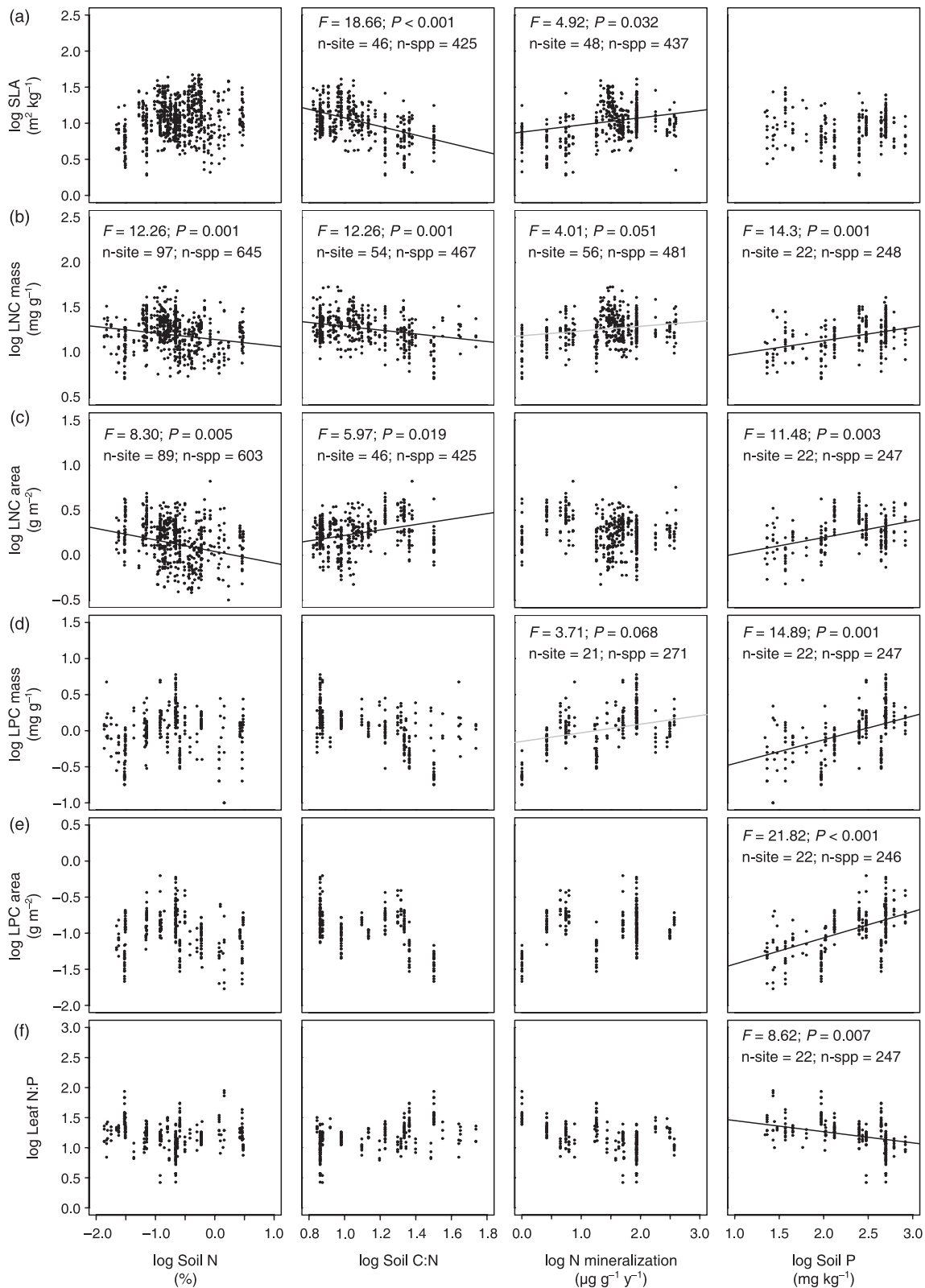
Figure 1 Relationships between leaf traits and soil nutrient measures for all species: (a) specific leaf area, SLA; (b) leaf N concentration on mass basis, LNCmass; (c) leaf N concentration on area basis, LNCarea; (d) leaf P concentration on mass basis, LPCmass; (e) leaf P concentration on area basis, LPCarea; (f) leaf N:P. Measures of nutrient fertility are: soil total N, soil N; soil C:N, soil N mineralization; soil total P, soil P. Lines in black were plotted for relationships with $P < 0.05$, lines in grey were plotted for relationships with $P < 0.1$. All leaf traits and soil nutrient measures were $\log_{10}$-transformed.

the lower the AIC value, the better the model. In addition, parameters can be assessed for possible exclusion from mixed models using *F*-values and chi-tests. All multivariate models are included in Appendix S2.

The relationships between growth form and soil fertility and growth form and climate were tested using one-way ANOVAs with growth form as a fixed factor. It was not possible to include a random term for sites in this analysis, because variation attributed to sites occurred together with the independent factor (growth form). Instead, given that each site has only one value for soil and climate variables, only one observation per growth form was selected for each site. In this manner we corrected for the majority of dependences of observations within sites that created, in this case, pseudo-replication. ANOVA methods were applied because ANOVA gives the same results as a mixed model with ML methods without a random term, while allowing for *post hoc* tests (in our study Tukey–Kramer; *P* < 0.05). Growth forms that occurred in fewer than five sites were not included in the analysis. *F*-values obtained from the ANOVA analysis for growth form versus soil nutrients and growth form versus climate were compared with those of the bivariate mixed models of leaf traits versus soil nutrients and leaf traits versus climate. In this manner we compared the explanatory power of growth form versus continuous leaf traits for predicting plant response to nutrient supply and climate.

RESULTS

Bivariate relationships of leaf traits versus soil fertility and versus climate

For all species pooled together there was a consistent and significant shift from species with low SLA, LNC and LPC at low soil fertility towards species with high SLA, LNC and LPC at high soil fertility (Fig. 1), although variability within sites was typically large. In line with our expectations, soil total N was not a good predictor of leaf trait variation: the relations of soil total N with SLA, LPC (mass and area basis) and leaf N:P were not significant, and those with LNCmass and LNCarea were in the opposite direction (with respect to high versus low fertility) to the other soil nutrient measures, including C:N. Therefore, we will not include soil total N in the following presentation, but will discuss these findings in the Discussion. In general, SLA and LNC (mass and area basis) were related to most soil nutrient measures (Fig. 1); positively to N mineralization and soil total P, and negatively to soil C:N (reflecting the increase in nutrient availability with decreasing soil C:N). Relationships of leaf N on an area basis were weaker than those on a mass basis. In contrast, leaf P(mass and area basis) and leaf N:P were only related to soil total P, and as expected, leaf P increased and N:P decreased with increasing soil P.

Across all bivariate analyses, soil nutrient measures on average explained more variance in individual leaf traits than climate. In the current dataset, SLA was not significantly related to any of the climatic parameters (Fig. 2). Leaf N was positively related on a mass basis to MAT and PET and on an area basis to PET. In contrast, leaf P was significantly related to all climatic parameters and in

the opposite direction (decreasing with MAT or PET) to leaf N; as a consequence N:P increased with MAT and MAP.

Multivariate relationships of leaf traits versus soil fertility and climate

From all available models (see Appendix S2), the best model for the prediction of variation in SLA included soil C:N, MAP and their two-way interaction. The significant interaction term of soil C:N × MAP had a positive sign indicating that as precipitation increases the slope of SLA on soil C:N becomes less negative (Table 2). For LNCmass the best model included soil total N, soil C:N and their two-way interaction. The significant interaction term of soil total N × soil C:N had a positive sign, indicating that as soil C:N increases the slope of LNCmass on soil total N becomes flatter. For LNCmass, none of the models including soils and climate had significant interaction terms, and from those without interactions the best model included soil C:N and irradiation (Appendix S2). For LNCarea the best model included soil C:N, MAP, irradiation and the three possible two-way interactions. All interaction terms were significant and were negative, showing that as MAP or irradiance increases, the slopes of LNCarea on soil C:N become flatter. Irradiation also moderated the response of LNCarea to MAP, making the response less pronounced at high irradiance (Table 2). For LPCmass, LPCarea and leaf N:P, all multivariate models were worse than the single model using soil total P only (results not shown).

Leaf traits versus growth forms

ANOVA analysis showed that of all soil nutrient proxies, only soil C:N was significantly related to the occurrence of the various growth forms (Fig. 3). On average, deciduous trees occurred at the lowest soil C:N and grasses corresponded to the highest soil C:N. The other growth forms – evergreen trees and shrubs, deciduous shrubs and herbs – were not different from each other and were intermediate to the others. In contrast, growth forms differed highly significantly in their mean value for all climatic properties (Fig. 4). On average, deciduous shrubs corresponded to low MAT, MAP, irradiance and PET, while evergreen and deciduous trees corresponded to warm climates with high MAP and irradiance. The other growth forms occurred at intermediate conditions and were not different from each other, although the ranking was fairly similar for all climatic parameters. The strength of the relationships of growth form to soil C:N (*F* = 3.34) was lower than that of leaf traits versus soil C:N. For climatic parameters, *F*-values of growth forms were almost always higher than those of leaf traits versus climate (with the exception of LPCarea).

DISCUSSION

Leaf traits related to soil fertility

In this first attempt to quantify relationships between leaf traits and soil fertility for multiple sites across continents and biomes,
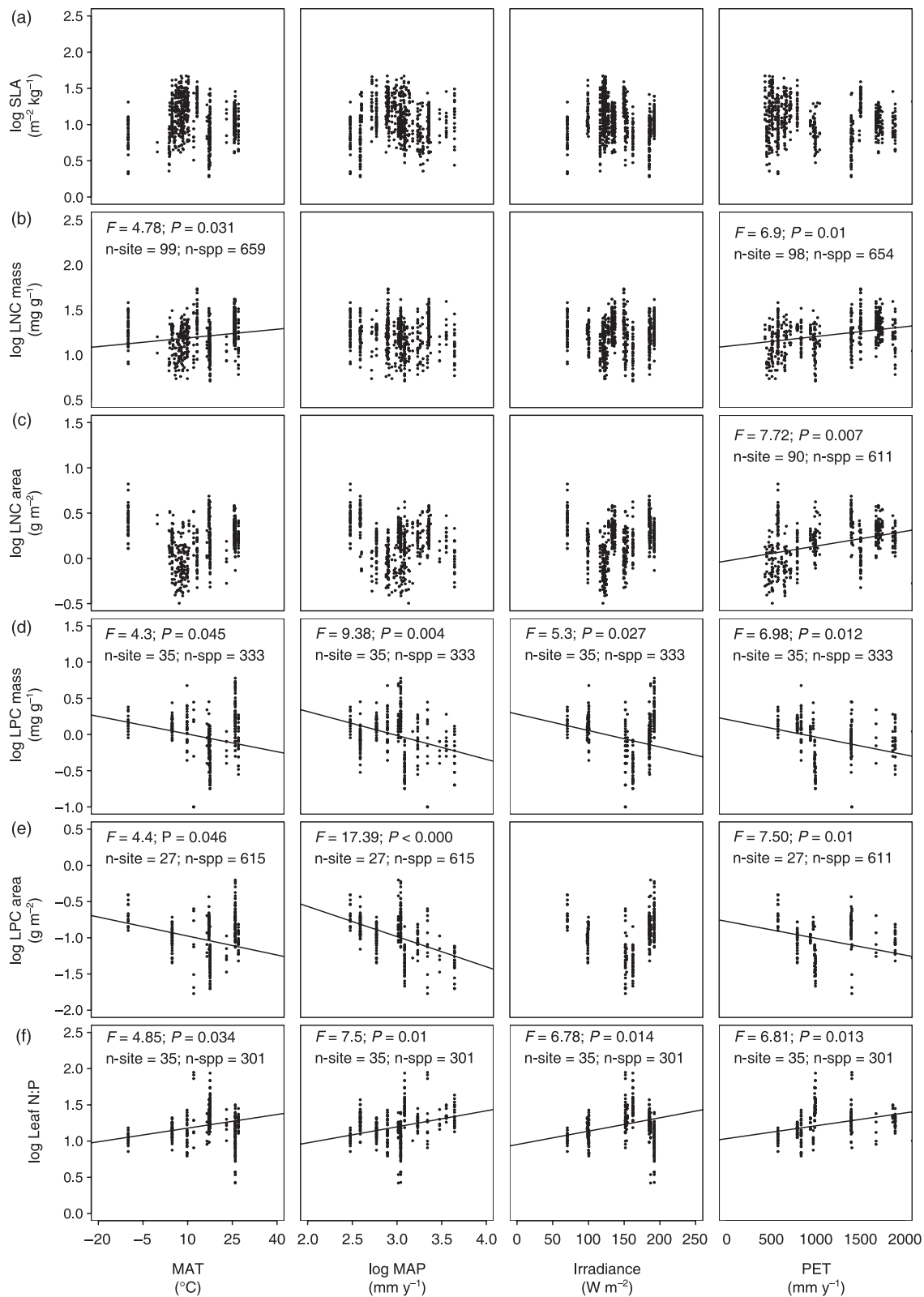
Figure 2 Relationships between leaf traits and climatic factors for all species: (a) specific leaf area, SLA; (b) leaf N concentration on mass basis, LNCmass; (c) leaf N concentration on area basis, LNCarea; (d) leaf P concentration on mass basis: LPCmass; (e) leaf P concentration on area basis: LPCarea; (f) leaf N:P. Climatic factors are: mean annual temperature, MAT; precipitation, MAP; irradiance; potential evapotranspiration, PET. Lines in black were plotted for relationships with $P < 0.05$. All leaf traits and MAP were $\log_{10}$-transformed.

Table 2 Summary of best multivariate models to predict specific leaf area, SLA (m² kg⁻¹); leaf N concentration on a mass basis, LNCmass (mg g⁻¹) and on an area basis, LNCarea (g m⁻²) for fixed effects of soils, climate and their significant interactions with the sign of the relationship (d), *F*-values (*F*) and probabilities (*P*). The ratio of the variance among sites explained by a model including fixed effects of climate and soil to a 'null' model with no fixed effects is included as an estimate of the variance explained by soil, climate and their interactions.

| Variables in the model		SLA			LNCmass			LNCarea		
		d†	F	*P*	d	F	*P*	d	F	*P*
Climate	Log MAP	–	18.54	***				+	57.09	***
	Irradiance				–			+	17.88	***
Soils	Log soil C:N	–	20.88	***	+	5.77	0.022	+	69.96	***
	Log soil total N				–	20.57	***			
Interactions	Log MAP × log soil C:N	+	15.83	***				–	34.15	***
	Log MAP × Irradiance							–	32.20	***
	Irradiance × log soil C:N							–	30.40	0.002
	Log soil C:N × soil total N				–	20.39	***			
Variance explained‡		%	*P*		%	*P*		%	*P*	
	Among-sites variance	59	***		61	***		78	***	

†Direction of the response. For models including interactions, single variables do not reflect the direction of a main effect but represent the direction of the slope when the other variables are zero. The sign of the interaction represents a conditional relationship showing the change in the slope of one of the variables when the other increases in one unit.

‡Null model includes no fixed effects and only the random effect of sites.

***$P < 0.001$.
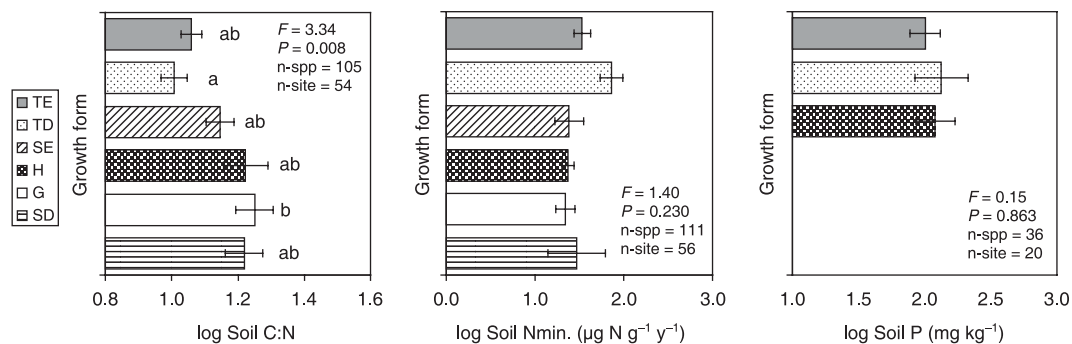
Figure 3 Distribution of growth forms in relation to soil nutrient measures. Different letters above bars indicate significant differences among growth forms, determined by a Tukey–Kramer *post hoc* test ($P < 0.05$). Growth forms: TD = deciduous trees, TE = evergreen trees, H = herbs, SD = deciduous shrubs, SE = evergreen shrubs, G = grasses. ANOVA results are indicated including numbers of species (n-spp) and sites (n-site). Nmin = N mineralization.
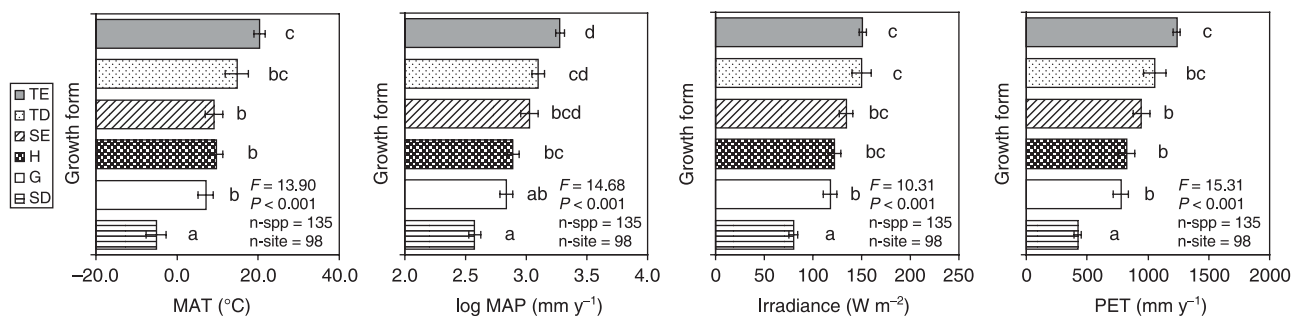
Figure 4 Distribution of growth forms in relation to climate. Different letters above bars indicate significant differences among growth forms, determined by a Tukey–Kramer *post hoc* test ($P < 0.05$). Growth forms: TD = deciduous trees, TE = evergreen trees, H = herbs, SD = deciduous shrubs, SE = evergreen shrubs, G = grasses. ANOVA results are indicated including numbers of species (n-spp) and sites (n-site). MAT = mean annual temperature, MAP = mean annual precipitation. PET = annual potential evapotranspiration.

we found several consistent, significant relationships. The quantified relationships fit the qualitative differences (particularly the degree of sclerophylly and evergreenness) observed by others among species originating from habitats differing in soil fertility (e.g. Beadle, 1954; Monk, 1966; Small, 1972; Aerts, 1990; Specht & Rundel, 1990). The ecological significance of sclerophylly and evergreenness in relation to nutrient supply has been described in the trade-off between plant growth and resource conservation (Chapin, 1980; Aerts, 1999; Aerts & Chapin, 2000). Plants with leaf traits that allow a fast use of nutrients and growth but for shorter times (Poorter & Garnier, 1999; Westoby *et al.*, 2002), like high SLA and high LNC, were found at high nutrient supply, while the reverse occurred at low nutrient supply where conservation of nutrients is arguably more important. In the present paper we have substantiated the claims made in previous studies by quantifying this trade-off across a wide variety of climatic regions and nutrient availabilities through the analysis of a large dataset.

Predicting leaf traits from soil and climate data

Bivariate relationships showed that SLA and leaf N (mass and area basis) were more tightly related to soil nutrient status than to climate, but not all proxies of soil fertility were equally good predictors of leaf traits. It has been reported frequently that low N fertility (van Arendonk *et al.*, 1997; Knops & Reinhart, 2000; Meziane & Shipley, 2001) as well as low P fertility (Specht & Rundel, 1990; McDonald *et al.*, 2003; Paoli, 2006) select for similar suites of leaf traits: low SLA, LNC, LPC (but see Cordell *et al.*, 2001, for contrasting results). In this study, however, SLA was responsive only to soil N (either soil C:N or N mineralization), while leaf P (mass and area basis) and leaf N:P were related only to soil P. Leaf N was the only leaf trait related to indicators of both N and P. This effect of soil P on leaf N seems determined by a tight coupling of leaf N and leaf P (Güsewell, 2004; Niklas *et al.*, 2005). In the current dataset it was not possible to include both soil total N and soil P in models to predict leaf N due to the paucity of data on soil P.

Results of multivariate analysis of SLA indicated a significant interaction of soil C:N with MAP, indicating that responses of SLA to soil N availability are modified by climate interactions. Other interactions between climate and soil were non-significant for SLA. This contrasts with results of Wright *et al.* (2005b), in which irradiance was the strongest climatic variable modulating SLA. In all possible models, climate only had a modest effect on LNCmass, coinciding with results by Wright *et al.* (2005b) and Reich *et al.* (2007) where effects of climate on LNCmass were weaker than those on SLA. This was also reflected in the multivariate analysis in which leaf N was only related to N availability. LNCarea combines information from LNCmass and SLA which was reflected in the results of the multivariate analysis.

In addition to measures of P availability, leaf P (mass and area basis) and leaf N:P were related to all climatic variables, particularly to MAP. These results agree with patterns found by Reich & Oleksyn (2004). Soil P and MAP were correlated, which may reflect the occurrence of poor leached soils in areas with high precipitation. Given that all climatic variables were correlated, it

seems that detected effects of climate variables other than MAP acted indirectly on leaf P. This convergence of effects of climate and soils on leaf P was also evident from multivariate analysis in which adding climatic variables (MAT, irradiance or PET) made models worse. Patterns of leaf N:P reflect the fact that leaf N:P is determined largely by leaf P (Güsewell, 2004; Reich & Oleksyn, 2004).

Leaf trait variability

Even though the relationships discussed above were statistically significant, the soil–trait relationships still showed considerable scatter around the fitted lines. Within-site variability was the largest source of variability. Results from the mixed models showed that from the total variability that was not captured by soil and climate parameters, on average 58% of the variance in SLA, 73–57% for LNC(area–mass), 48–43% for LPC(area–mass) and 55% for leaf N:P was due to within-site variability, the rest of the variability was due to unquantified differences among sites. Similar high variability in leaf trait versus environment relationships have been reported before (Poorter & De Jong, 1999; Fonseca *et al.*, 2000; Wright *et al.*, 2004; Wright *et al.*, 2005b). The broad spread of trait values observed within individual sites could have various causes: disturbance (Grime, 2006), unquantified microsite variability, alternative optimal evolutionary solutions for the same environmental challenges and game theoretical or frequency-dependent processes (Westoby & Wright, 2006). To estimate the relative filtering capacity of soils and climate, the proportion of variance among sites explained in a model including the effects of climate and/or soil can be compared with a 'null' model without these effects. In this study, soil C:N alone explained up to 32–34% of the variability in SLA among sites, soil C:N and soil total N explained up to 61% for LNCmass. Climate alone explained very little variance in SLA and LNC (between 0.5% and 5.5%). Climate and soils combined on the other hand could explain up to 59% of the variability among sites for SLA and 78% for LNCarea (best multivariate mixed models). Soil P alone explained 48% of the variability in LPCmass and 43% in leaf N:P. Of the climate variables, only MAP was important, explaining 7–11% for LPCmass and leaf N:P and up to 44% for LPCarea. Soil P and MAP were not combined due to high collinearity. Thus, among sites, soils showed the strongest filtering capacity on traits. The strength of climate acted through interactions with soils and varied from trait to trait. Future inclusions of other factors such as disturbance frequencies and land-use history may further decrease unexplained variance among sites. Finally, an important aspect of the leaf trait variability was the amplitude, which was similar across the whole range of soil fertility. This implies that the range in trait value possibilities was similar in each environment, independent on how favourable or harsh the environment was.

Leaf traits versus growth forms

Soils under grasses and woody species have been found to differ significantly in C:N ratios and N mineralization rates (Reich

et al., 2001; Booth *et al.*, 2005). In the present study, soils under grasses and herbs also tended to have higher C:N ratios, but the differences from other growth forms were not strong and were insignificant for N mineralization. These weak differences among growth forms in relation to soil fertility contrasted with the strength of the correlations among leaf traits and soils. Together, this might imply that to characterize plant responses to soil fertility continuous leaf traits might perform better than growth form. In contrast, growth forms were strongly affected by climate (and more so than continuous leaf traits). These offsets according to growth form abundance in combination with the fact the different growth forms have different trait values (Wright *et al.*, 2005a; Reich *et al.*, 2007) may explain the low explanatory power of precipitation, MAP and PET in predicting trait values. Shifts according to growth forms did not interfere with soil–trait relationships, due to the minor effects of soil fertility indicators on distribution of growth form.

Importance of reporting adequate site information

Soil total N is the most commonly used proxy of N supply. Nevertheless, soil total N had weaker relationships with leaf traits than soil C:N, N mineralization or soil P; and in two instances had opposite patterns with leaf traits compared with those of the other soil nutrient measures. These results show the inadequacy of soil total N, when used alone, to characterize nutrient supply in relation to plant functioning. Soil total N gives an indication of the size of the soil N pool, but not how much of this pool is actually available for plant uptake (Vitousek & Howarth, 1991). Routinely measuring soil C together with soil total N will help to make better inferences about plant–soil interactions, because soil C:N provides more information about the potential to mineralize or immobilize nutrients. In addition, soil C:N is a critical parameter to estimate N mineralization in existing decomposition models. Although soil total P is not directly related to actual P availability (Hinsinger, 2001), it still seemed to be a robust indicator of P fertility and was related to both leaf N and leaf P. Paucity of information on soil P hindered the use of a multiple regression approach to separate partial effects of soil N and P on leaf traits. The information generated in this study stresses the importance of reporting soil information in ecological studies involving leaf traits. This is critical for expanding the current analysis and including other plant traits related to soil nutrient availability.

CONCLUSIONS

This is the first attempt, to our knowledge, to quantitatively relate leaf traits to soil fertility on a global scale. Firstly, our study has quantified and therefore corroborated the general trade-off between leaf traits associated with fast growth and resource conservation 'strategies' in relation to soil fertility. Secondly, in this study, not all environmental factors were equally good predictors of leaf traits. SLA tended to be more related to N supply and MAP. Leaf N concentration was related to both soil C:N and soil total P. Leaf P concentration and leaf N:P were related to soil total P alone (and to climate variables affecting global soil P

distribution). Thirdly, continuous leaf traits are better correlated to soil resources than to growth form, but growth forms reflect important aspects of plant distribution with climate. Finally, within-site variance in the relationships of leaf traits to soils and climate remains the highest source of variability. It is critical to understand which factors determine this trait variability and the coexistence and selection of trait values across a range of abiotic conditions.

REFERENCES

Aerts, R. (1990) Nutrient use efficiency in evergreen and deciduous species from heathlands. *Oecologia*, **84**, 391–397.

Aerts, R. (1999) Interspecific competition in natural plant communities: mechanisms, trade-offs and plant-soil feedbacks. *Journal of Experimental Botany*, **50**, 29–37.

Aerts, R. & Chapin, F.S. III (2000) The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *Advances in Ecological Research*, **30**, 1–67.

Aerts, R., Cornelissen, J.H.C. & Dorrepaal, E. (2006) Plant performance in a warmer world: general responses of plants from cold, northern biomes and the importance of winter and spring events. *Plant Ecology*, **182**, 65–77.

van Arendonk, J., Niemann, G.J., Boon, J.J. & Lambers, H. (1997) Effects of nitrogen supply on the anatomy and chemical composition of leaves of four grass species belonging to the genus *Poa*, as determined by image-processing analysis and pyrolysis-mass spectrometry. *Plant Cell and Environment*, **20**, 881–897.

Beadle, N.C.W. (1954) Soil phosphate and the delimitation of plant communities in eastern Australia. *Ecology*, **35**, 370–375.

Berendse, F. (1994) Litter decomposability – a neglected component of plant fitness. *Journal of Ecology*, **82**, 187–190.

Booth, M.S., Stark, J.M. & Rastetter, E. (2005) Controls on nitrogen cycling in terrestrial ecosystems: a synthetic analysis of literature data. *Ecological Monographs*, **75**, 139–157.

Cavender-Bares, J., Kitajima, K. & Bazzaz, F.A. (2004) Multiple trait associations in relation to habitat differentiation among 17 Floridian oak species. *Ecological Monographs*, **74**, 635–662.

Chapin, F.S. III (1980) The mineral-nutrition of wild plants. *Annual Review of Ecology and Systematics*, **11**, 233–260.

Chapin, F.S. III (2003) Effects of plant traits on ecosystem and regional processes: a conceptual framework for predicting the consequences of global change. *Annals of Botany*, **91**, 455–463.

Chapin, F.S. III, Bret-Harte, M.S., Hobbie, S.E. & Zhong, H.L. (1996) Plant functional types as predictors of transient responses of arctic vegetation to global change. *Journal of Vegetation Science*, **7**, 347–358.

Cordell, S., Goldstein, G., Meinzer, F.C. & Vitousek, P.M. (2001) Morphological and physiological adjustment to N and P fertilization in nutrient-limited *Metrosideros polymorpha* canopy trees in Hawaii. *Tree Physiology*, **21**, 43–50.

Craine, J.M. & Lee, W.G. (2003) Covariation in leaf and root traits for native and non-native grasses along an altitudinal gradient in New Zealand. *Oecologia*, **134**, 471–478.

Crews, T.E., Kitayama, K., Fownes, J.H., Riley, R.H., Herbert, D.A., Mueller-Dombois, D. & Vitousek, P.M. (1995) Changes in soil phosphorus fractions and ecosystem dynamics across a long chronosequence in Hawaii. *Ecology*, **76**, 1407–1424.

Cunningham, S.A., Summerhayes, B. & Westoby, M. (1999) Evolutionary divergences in leaf structure and chemistry, comparing rainfall and soil nutrient gradients. *Ecological Monographs*, **69**, 569–588.

Diaz, S., Hodgson, J.G., Thompson, K., Cabido, M., Cornelissen, J.H.C., Jalili, A., Montserrat-Martí, G., Grime, J.P., Zarrinkamar, F., Asri, Y., Band, S.R., Basconcelo, S., Castro-Díez, P., Funes, G., Hamzehee, B., Khoshnevi, M., Pérez-Harguindeguy, N., Pérez-Rontomé, M.C., Shirvany, F.A., Vendramini, F., Yazdani, S., Abbas-Azimi, R., Bogaard, A., Boustani, S., Charles, M., Dehghan, M., de Torres-Espuny, L., Falczuk, V., Guerrero-Campo, J., Hynd, A., Jones, G., Kowsary, E., Kazemi-Saeed, F., Maestro-Martínez, M., Romo-Díez, S., Shaw, A., Siavash, B., Villar-Salvador, P. & Zak, M.R. (2004) The plant traits that drive ecosystems: evidence from three continents. *Journal of Vegetation Science*, **15**, 295–304.

Eviner, T.E. & Chapin, F.S. III (2003) Functional matrix: a conceptual framework for predicting multiple plant effects on ecosystem processes. *Annual Review of Ecology, Evolution and Systematics*, **34**, 455–485.

Field, C.B. & Mooney, H.A. (1986) The photosynthesis-nitrogen relationship in wild plants. *On the economy of plant form and function* (ed. by T.J. Givnish), pp. 25–49. Cambridge University Press, Cambridge.

Fonseca, C.R., Overton, J.M., Collins, B. & Westoby, M. (2000) Shifts in trait-combinations along rainfall and phosphorus gradients. *Journal of Ecology*, **88**, 964–977.

Gitay, H. & Noble, I.R. (1998) What are functional types and how should we seek them? *Plant functional types: their relevance to ecosystem properties and global change* (ed. by T.M. Smith, H.H. Shugart and F.I. Woodward), pp. 3–19. Cambridge University Press, Cambridge, UK.

Grime, J.P. (1977) Evidence of the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist*, **111**, 1169–1194.

Grime, J.P. (2006) Trait convergence and trait divergence in herbaceous plant communities: mechanisms and consequences. *Journal of Vegetation Science*, **17**, 255–260.

Güsewell, S. (2004) N:P ratios in terrestrial plants: variation and functional significance. *New Phytologist*, **164**, 243–266.

Heal, O.W., Anderson, J.M. & Swift, M.J. (1997) Plant litter quality and decomposition: an historical overview. *Driven by nature* (ed. by G. Cadisch and K.E. Giller), pp. 3–30. CAB International, Wallingford, UK.

Hinsinger, P. (2001) Bioavailability of soil inorganic P in the rhizosphere as affected by root-induced chemical changes: a review. *Plant and Soil*, **237**, 173–195.

Hobbie, S.E. (1992) Effects of plant species on nutrient cycling. *Trends in Ecology and Evolution*, **7**, 336–339.

Hungate, B.A., Dukes, J.S., Shaw, M.R., Luo, Y.Q. & Field, C.B. (2003) Nitrogen and climate change. *Science*, **302**, 1512–1513.

Knops, J.M.H. & Reinhart, K. (2000) Specific leaf area along a nitrogen fertilization gradient. *American Midland Naturalist*, **144**, 265–272.

Koerselman, W. & Meuleman, A.F.M. (1996) The vegetation N:P ratio: a new tool to detect the nature of nutrient limitation. *Journal of Applied Ecology*, **33**, 1441–1450.

Lambers, H. & Poorter, H. (1992) Inherent variation in growth rate between higher plants: a search for physiological causes and consequences. *Advances in Ecological Research*, **23**, 187–261.

Lavorel, S. & Garnier, E. (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology*, **16**, 545–556.

Linacre, E.T. (1977) Simple formula for estimating evaporation rates in various climates, using temperature data alone. *Agricultural Meteorology*, **18**, 409–424.

McDonald, P.G., Fonseca, C.R., Overton, J.M. & Westoby, M. (2003) Leaf-size divergence along rainfall and soil-nutrient gradients: is the method of size reduction common among clades? *Functional Ecology*, **17**, 50–57.

McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. (2006) Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution*, **21**, 178–185.

Melillo, J.M., Aber, J.D. & Muratore, J.F. (1982) Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology*, **63**, 621–626.

Melillo, J.M., Borchers, J., Chaney, J., Fisher, H., Fox, S., Haxeltine, A., Janetos, A., Kicklighter, D.W., Kittel, T.G.F., Mcguire, A.D., Mckeown, R., Neilson, R., Nemani, R., Ojima, D.S., Painter, T., Pan, Y., Parton, W.J., Pierce, L., Pitelka, L., Prentice, C., Rizzo, B., Rosenbloom, N.A., Running, S., Schimel, D.S., Sitch, S., Smith, T. & Woodward, I. (1995) Vegetation/Ecosystem Modeling and Analysis Project – comparing biogeography and biogeochemistry models in a continental-scale study of terrestrial ecosystem responses to

climate-change and CO_2 doubling. *Global Biogeochemical Cycles*, **9**, 407–437.

Meziane, D. & Shipley, B. (2001) Direct and indirect relationships between specific leaf area, leaf nitrogen and leaf gas exchange. Effects of irradiance and nutrient supply. *Annals of Botany*, **88**, 915–927.

Monk, C.D. (1966) An ecological significance of evergreenness. *Ecology*, **47**, 504–505.

New, M., Hulme, M. & Jones, P. (1999) Representing twentieth-century space-time climate variability. Part I: Development of a 1961–90 mean monthly terrestrial climatology. *Journal of Climate*, **12**, 829–856.

New, M., Lister, D., Hulme, M. & Makin, I. (2002) A high-resolution dataset of surface climate over global land areas. *Climate Research*, **21**, 1–25.

Niklas, K.J., Owens, T., Reich, P.B. & Cobb, E.D. (2005) Nitrogen/phosphorus leaf stoichiometry and the scaling of plant growth. *Ecology Letters*, **8**, 636–642.

Pan, Y.D., Melillo, J.M., McGuire, A.D., Kicklighter, D.W., Pitelka, L.F., Hibbard, K., Pierce, L.L., Running, S.W., Ojima, D.S., Parton, W.J. & Schimel, D.S. (1998) Modeled responses of terrestrial ecosystems to elevated atmospheric CO_2: a comparison of simulations by the biogeochemistry models of the Vegetation/Ecosystem Modeling and Analysis Project (VEMAP). *Oecologia*, **114**, 389–404.

Paoli, G.D. (2006) Divergent leaf traits among congeneric tropical trees with contrasting habitat associations on Borneo. *Journal of Tropical Ecology*, **22**, 397–408.

Parton, W.J., Schimel, D.S., Cole, C.V. & Ojima, D.S. (1987) Analysis of factors controlling soil organic-matter levels in great-plains grasslands. *Soil Science Society of America Journal*, **51**, 1173–1179.

Poorter, H. & De Jong, R. (1999) A comparison of specific leaf area, chemical composition and leaf construction costs of field plants from **15** habitats differing in productivity. *New Phytologist*, **143**, 163–176.

Poorter, H. & Garnier, E. (1999) Ecological significance of inherent variation in relative growth rate and its components. *Handbook of functional plant ecology* (ed. by F.I. Pugnaire and F. Valladares), pp. 81–120. Marcel Dekker, Inc., New York.

Reich, P.B. & Oleksyn, J. (2004) Global patterns of plant leaf N and P in relation to temperature and latitude. *Proceedings of the National Academy of Sciences USA*, **101**, 11001–11006.

Reich, P.B., Walters, M.B. & Ellsworth, D.S. (1992) Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecological Monographs*, **62**, 365–392.

Reich, P.B., Walters, M.B. & Ellsworth, D.S. (1997) From tropics to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Sciences USA*, **94**, 13730–13734.

Reich, P.B., Peterson, D.W., Wedin, D.A. & Wrage, K. (2001) Fire and vegetation effects on productivity and nitrogen cycling across a forest-grassland continuum. *Ecology*, **82**, 1703–1719.

Reich, P.B., Wright, I.J. & Lusk, C.H. (2007) Predicting leaf functional traits from simple plant and climate attributes using the GLOPNET global dataset. *Ecological Applications*, **17**, 1982–1988.

Rustad, L.E., Campbell, J.L., Marion, G.M., Norby, R.J., Mitchell, M.J., Hartley, A.E., Cornelissen, J.H.C. & Gurevitch, J. (2001) A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia*, **126**, 543–562.

Schimel, D.S. (1988) Calculation of microbial-growth efficiency from 15N immobilization. *Biogeochemistry*, **6**, 239–243.

Sitch, S., Smith, B., Prentice, I.C., Arneth, A., Bondeau, A., Cramer, W., Kaplan, J.O., Levis, S., Lucht, W., Sykes, M.T., Thonicke, K. & Venevsky, S. (2003) Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Global Change Biology*, **9**, 161–185.

Small, E. (1972) Photosynthetic rates in relation to nitrogen recycling as an adaptation to nutrient deficiency in peat bog plants. *Canadian Journal of Botany*, **50**, 2227–2233.

Specht, R.L. & Rundel, P.W. (1990) Sclerophylly and foliar nutrient status of mediterranean-climate plant-communities in southern Australia. *Australian Journal of Botany*, **38**, 459–474.

Vitousek, P.M. & Howarth, R.W. (1991) Nitrogen limitation on land and in the sea – how can it occur. *Biogeochemistry*, **13**, 87–115.

Vitousek, P.M., Turner, D.R. & Kitayama, K. (1995) Foliar nutrients during long-term soil development in Hawaiian montane rain forest. *Ecology*, **76**, 712–720.

Westoby, M. & Wright, I.J. (2006) Land-plant ecology on the basis of functional traits. *Trends in Ecology and Evolution*, **21**, 261–268.

Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A. & Wright, I.J. (2002) Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics*, **33**, 125–159.

Wright, I.J., Reich, P.B. & Westoby, M. (2001) Strategy shifts in leaf physiology, structure and nutrient content between species of high- and low-rainfall and high- and low-nutrient habitats. *Functional Ecology*, **15**, 423–434.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, J., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.L., Niinemets, U., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J. & Villar, R. (2004) The worldwide leaf economics spectrum. *Nature*, **428**, 821–827.

Wright, I.J., Reich, P.B., Cornelissen, J.H.C., Falster, D.S., Garnier, E., Hikosaka, K., Lamont, B.B., Lee, W., Oleksyn, J., Osada, N., Poorter, H., Villar, R., Warton, D.I. & Westoby, M. (2005a) Assessing the generality of global leaf trait relationships. *New Phytologist*, **166**, 485–496.

Wright, I.J., Reich, P.B., Cornelissen, J.H.C., Falster, D.S., Groom, P.K., Hikosaka, K., Lee, W., Lusk, C.H., Niinemets, U., Oleksyn, J., Osada, N., Poorter, H., Warton, D.I. & Westoby, M. (2005b) Modulation of leaf economic traits and trait relationships by climate. *Global Ecology and Biogeography*, **14**, 411–421.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Pearson correlations for traits and for selected soil and climate variables.

Appendix S2 Mixed models: multivariate analysis of leaf traits versus soils and climate.

Appendix S3 List of references from which trait and soil data was obtained.

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.

BIOSKETCHES

Jenny Ordonez is a PhD candidate in the Systems Ecology Department at the Vrije Universiteit Amsterdam. Her research interests focus on plant adaptation to nutrient fertility gradients, nutrient cycling, plant-mediated feedbacks on nutrient cycles and modelling.

Peter van Bodegom's main research interests focus on plant trait–biogeochemistry interactions through dedicated experiments in the laboratory and on mesocosms, the execution of meta-analyses and the development of process-based models.

Jan-Philip Witte specializes in the relationship between groundwater and vegetation biodiversity, with an emphasis on modelling the ecological effects of water management.

Ian Wright is a Research Fellow at the Department of Biological Sciences of Macquarie University. His research works towards identifying major dimensions of strategic variation among species and understanding the adaptations of plants to site factors such as climate and soil nutrients (http://www.bio.mq.edu.au/ecology/wright/wright.htm).

Peter Reich's work focuses on ecology, global change and the sustainability of managed and unmanaged terrestrial ecosystems. This includes experimental field studies of the effects of global change on grasslands and forests as well as the development of synthetic databases and analyses at local to global scales.

Rien Aerts research interests address the effects of climate change on ecosystem biogeochemistry, with a special interest in litter decomposition.

Editor: Martin Sykes