Assessing the generality of global leaf trait relationships

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Summary

• Global-scale quantification of relationships between plant traits gives insight into the evolution of the world's vegetation, and is crucial for parameterizing vegetation–climate models.

• A database was compiled, comprising data for hundreds to thousands of species for the core 'leaf economics' traits leaf lifespan, leaf mass per area, photosynthetic capacity, dark respiration, and leaf nitrogen and phosphorus concentrations, as well as leaf potassium, photosynthetic N-use efficiency (PNUE), and leaf N : P ratio.

• While mean trait values differed between plant functional types, the range found within groups was often larger than differences among them. Future vegetation–climate models could incorporate this knowledge.

• The core leaf traits were intercorrelated, both globally and within plant functional types, forming a 'leaf economics spectrum'. While these relationships are very general, they are not universal, as significant heterogeneity exists between relationships fitted to individual sites. Much, but not all, heterogeneity can be explained by variation in sample size alone. PNUE can also be considered as part of this trait spectrum, whereas leaf K and N : P ratios are only loosely related.

Key words: leaf economics, nutrient stoichiometry, photosynthesis, plant functional types, respiration.

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Introduction

There are ≈250 000 vascular plant species, yet all face the same basic challenges: they must obtain sufficient water, nutrients and light to drive carbon fixation, and make enough carbon profit to ensure continuity to future generations. Over the past two decades, plant ecologists and physiologists have become increasingly concerned with quantifying correlations between key leaf traits, and between leaf traits and climate (Field & Mooney, 1986; Reich *et al.*, 1992; Schulze *et al.*, 1994; Körner, 1995; Grime *et al.*, 1997; Reich *et al.*, 1997; Niinemets, 2001; Wright & Westoby, 2002). This can be seen as part of a broader push to identify and understand the major dimensions of trait variation among the vegetation of the world (Weiher *et al.*, 1999; Westoby *et al.*, 2002; Diaz *et al.*, 2004). Recent models concerning shifts in vegetation with climate and land-use change have begun to make use of information from studies such as that of Reich *et al.* (1997), in order to model fluxes

and pools of carbon and nitrogen (Moorcroft *et al.*, 2001; Bonan *et al.*, 2002; Kaplan *et al.*, 2003). Reliable large-scale quantification of leaf trait relationships will help to improve these models, as well as increasing our understanding of plant evolution.

With these aims in mind, we have compiled leaf trait data from >2500 vascular plant species, from 175 sites around the world. Recently we showed that nearly three-quarters of the global variation in six key leaf traits (leaf mass per area, LMA; leaf lifespan, LL; leaf N per unit mass, N_{mass}; photosynthetic capacity per unit leaf mass, A_{mass}; leaf dark respiration rate per unit mass, Rd_{mass}; leaf P concentration per unit mass, P_{mass}) is captured by a single axis through multidimensional trait space. This 'leaf economics spectrum' (Wright *et al.*, 2004) runs from species with the potential for quick returns on investments of nutrients and dry mass in leaves to those with a slower potential rate of return. At the quick-return end are species with high leaf nutrient concentrations, high rates of photosynthesis and respiration, short leaf lifespan and low dry-mass investment per leaf area. At the slow-return end are species with long LL, expensive high-LMA leaf construction, low nutrient concentrations, and low rates of photosynthesis and respiration. Importantly, the directionality of trait correlations along the primary axis of this spectrum was shown to operate similarly across species pooled by growth form, functional group or major biome, indicating a very general and predictable interdependence of these key leaf traits (Wright *et al.*, 2004).

Here we present a number of complementary analyses concerning variation in leaf traits and trait relationships from the GLOPNET database. We extend our analyses of leaf trait relationships to include the macronutrient potassium (data for 251 species), as well as to photosynthetic N-use efficiency (PNUE, 710 species) and leaf N : P ratios (745 species). First we describe the patterning of leaf traits according to growth form and common plant functional types (PFTs, e.g. deciduous vs evergreen species). Second, we quantify pairwise trait relationships among these species groupings, providing a set of regression equations for use in modelling exercises. Third, we assess the extent to which leaf K, PNUE and N : P ratios are associated with traits making up the leaf economics spectrum. Finally, we examine the extent to which differences in leaf trait relationships fitted to individual sites can be explained by variation in sample size or the range of trait variation at sites, as opposed to, say, indicating that fundamentally different trait relationships occur among different sets of co-occurring species (Reich, 1993; Diemer, 1998).

This study represents the first attempt simultaneously to assess the relationship of leaf K to several leaf economic traits for a large data set of field-grown plants, at a broad geographic scale. Leaf K data were compiled from 16 sites, representing a variety of different vegetation types from eight countries (Canada, England, Germany, Malaysia, New Zealand, Sri Lanka, USA, Venezuela). The majority of the data were for trees and shrubs (229 species), with the remaining species being ferns, grasses, herbs (five species each) or vines (seven species). Previous surveys have looked only at the relationship of leaf K with other leaf nutrients (Garten, 1976; Garten, 1978; Thompson *et al.*, 1997), or where correlations between leaf K and a wide range of other plant traits were assessed, the study was restricted to common species from the British Isles (Grime *et al.*, 1997).

PNUE is defined as the ratio of photosynthetic capacity to leaf N. Understanding how different plant groups vary in PNUE, and how PNUE relates to other plant traits, gives us further insight into the role of leaf N in plant economics (Pons *et al.*, 1994; Poorter & Evans, 1998). Again, our database represents the largest compilation of PNUE data to date, allowing us to assess the extent to which PNUE varies along the leaf economics spectrum at a very broad scale. Previous work has shown that species at the slow-return end of the spectrum (as evidenced by having a long LL) tend to have lower PNUE (Reich *et al.*, 1992). Here we assess the generality of that result.

There has been a recent resurgence of interest in nutrient stoichiometry in biology, particularly that between N, P and C. Leaf N : P ratios may influence plant–herbivore interactions in food webs (Sterner & Elser, 2002), as well as indicating soil N or P limitation to plant growth (Koerselman & Meuleman, 1996; Aerts & Chapin, 2000; Tessier & Raynal, 2003; Güsewell, 2004). On average, leaf N : P ratios increase from the poles towards the equator, presumably related to latitudinal trends in temperature and biogeographical gradients in soil substrate age (McGroddy *et al.*, 2004; Reich & Oleksyn, 2004). In organisms lacking major mineral storage of P (as in vacuoles or bones), the potential for rapid growth tends to be correlated with low biomass C : P and N : P ratios. This is thought to reflect increased allocation to P-rich ribosomal RNA, as rapid protein synthesis by ribosomes is required to support fast growth (Elser *et al.*, 2000; Sterner & Elser, 2002). In a broad survey of (mostly) aquatic and terrestrial plant species (Nielsen *et al.*, 1996), growth rate was correlated with both the N and P concentration of the photosynthetic tissue, and N : P ratios tended to be lower in faster-growing species. But is this generally true for higher plants? Higher plants with inherently fast growth tend to have low LMA and LL, and high A_{mass} (Lambers & Poorter, 1992; Reich *et al.*, 1992; Grime *et al.*, 1997). Consequently, we quantified how leaf N : P ratios were correlated with these other leaf traits in order to assess the extent to which recent concepts of 'ecological stoichiometry' (Elser *et al.*, 2000; Sterner & Elser, 2002) apply to higher plants, particularly to shrubs and trees (717 of the 745 species for which we could calculate leaf N : P ratios).

Materials and Methods

Leaf trait data were compiled from both published and unpublished sources. A data set was considered suitable provided it

contained data for at least two of the leaf traits for a minimum of four co-occurring species. The total data set represented 175 sites and contained 2548 species/site combinations, consisting of 2021 different species, with 341 occurring at more than one site. This coverage of traits, species and sites is substantially larger than previous data compilations, extends to all vegetated continents, and represents a wide range of vegetation types, including arctic tundra, boreal, temperate and tropical forests, grasslands, shrublands, woodlands and desert. The data set (available on request from the lead author) includes broad- and needle-leaved trees and shrubs, herbs, grasses, ferns, geophytes and epiphytes. Site elevation ranges from below sea level (Death Valley, USA) to ≈4800 m. Mean annual temperature ranges from −16 to 27.5°C; mean annual rainfall ranges from 133 to 5300 mm yr^{-1}. This covers most of the range of mean annual temperature–rainfall space in which higher plants are found (Whittaker, 1975). Still, some large geographic regions are poorly represented in the data set, in particular Russia, China, north and central Africa, and the Middle East.

Mean trait values were calculated for each species at a site. Here, photosynthetic 'capacity' refers to photosynthetic rates measured on young but fully expanded leaves, under high light and low water stress, and at ambient CO_2 concentration. Where photosynthetic capacity or leaf N was reported on an area basis, the traits were converted to a mass basis using LMA, or *vice versa* when reported on a mass basis only. Where traits were reported separately for sun leaves and shade leaves, sun-leaf data were used. Where data were presented separately for recently matured and for old leaves, data for recently matured leaves were used.

Data analysis

All leaf traits were log-transformed before analyses as their distributions were strongly right-skewed. Group means for the various leaf traits and species groupings (growth forms, PFTs) were compared by *t*-test for two-group tests, or by ANOVA followed by multiple comparison tests where more than two groups were compared (Games–Howell tests where variances were deemed heterogeneous with Levene's test; Tukey's tests where variances were deemed homogeneous). The strength of bivariate trait relationships was quantified with standard correlation and ordinary least-squares regression statistics in conjunction with standardized major axis slopes (SMAs, also known as reduced major axis slopes). An SMA fit is the line along the longest axis of a data cloud, fit by minimizing sums of squares in X and Y dimensions simultaneously. It gives the slope of the first component from a principal components analysis calculated from a correlation matrix; that is, the line is a summary in the sense that a single dimension is used to describe two-dimensional data. SMA slope-fitting is commonly required for allometric studies (Niklas, 1994). However, for *predicting* one trait from another, ordinary least-squares regression should be used (Sokal & Rohlf, 1995). The regression equations given in online Appendix 2 use this method. SMA slopes can be calculated from these equations simply by dividing the ordinary least-squares slope by the relevant correlation r value. In the Results section, where variation in trait relationships between sites is examined, we look at heterogeneity in both correlation r values and SMA slopes.

SMA routines were run using a DOS-based computer package (s)MATR (Falster *et al.*, 2003). In this program heterogeneity between SMA slopes is tested via a permutation test. Where deemed nonheterogeneous, a common SMA slope is estimated using a likelihood-ratio method (Warton & Weber, 2002). Differences in SMA elevation (intercept) can then be tested with the SMA analogue of standard ANCOVA, i.e. by ANOVA on Y', where Y' is the set of Y values for each group of data transformed by the common slope (Wright *et al.*, 2001). Heterogeneity among correlation coefficients calculated for trait relationships fitted to individual sites was assessed by the standard procedure for this test, whereby the weighted sums of squares of the z values corresponding to the correlation coefficients are subjected to a χ^2 test (Sokal & Rohlf, 1995).

Results

Leaf traits are patterned according to growth form and plant functional type

Across the data set, each leaf trait varied across one to two orders of magnitude, and was patterned according to growth form. On average, grasses and herbs had shorter leaf lifespan, lower LMA, and lower leaf N concentration per unit area (N_{area}), and higher A_{mass}, photosynthetic capacity per unit area (A_{area}), Rd_{mass} and PNUE than either trees or shrubs (all comparisons, $P < 0.002$; Fig. 1). But, importantly, trees and shrubs covered almost the entire observed range of each trait. That is, while broad differences in trait means certainly existed, trait space was not divided neatly between growth forms.

Common PFTs showed patterns similar to growth forms. N_2-fixing species had higher mean N_{mass} and N_{area} than nonfixing species (*t*-tests run within herbs, shrubs and trees, or with growth forms pooled, all $P < 0.001$; Fig. 2a,b), yet the range of leaf N was larger in the nonfixing plants, and extended up to similar N values in both groups. Evergreen woody species had longer mean LL and higher mean LMA than deciduous woody species, yet evergreens extended to leaf lifespans almost as short as for the shortest-LL deciduous species, and to similarly low LMA (Fig. 2c,d). Considering evergreen trees only, angiosperms had higher average N_{mass}, A_{mass}, A_{area}, Rd_{mass} and PNUE, but lower LMA, N_{area} and leaf lifespan than gymnosperms (*t*-tests, all $P < 0.015$). Again, while the differences in trait means were sometimes quite large (e.g. mean A_{mass} and PNUE were twice as high for angiosperms as for gymnosperms), there was considerable overlap between the trait ranges among these groups.

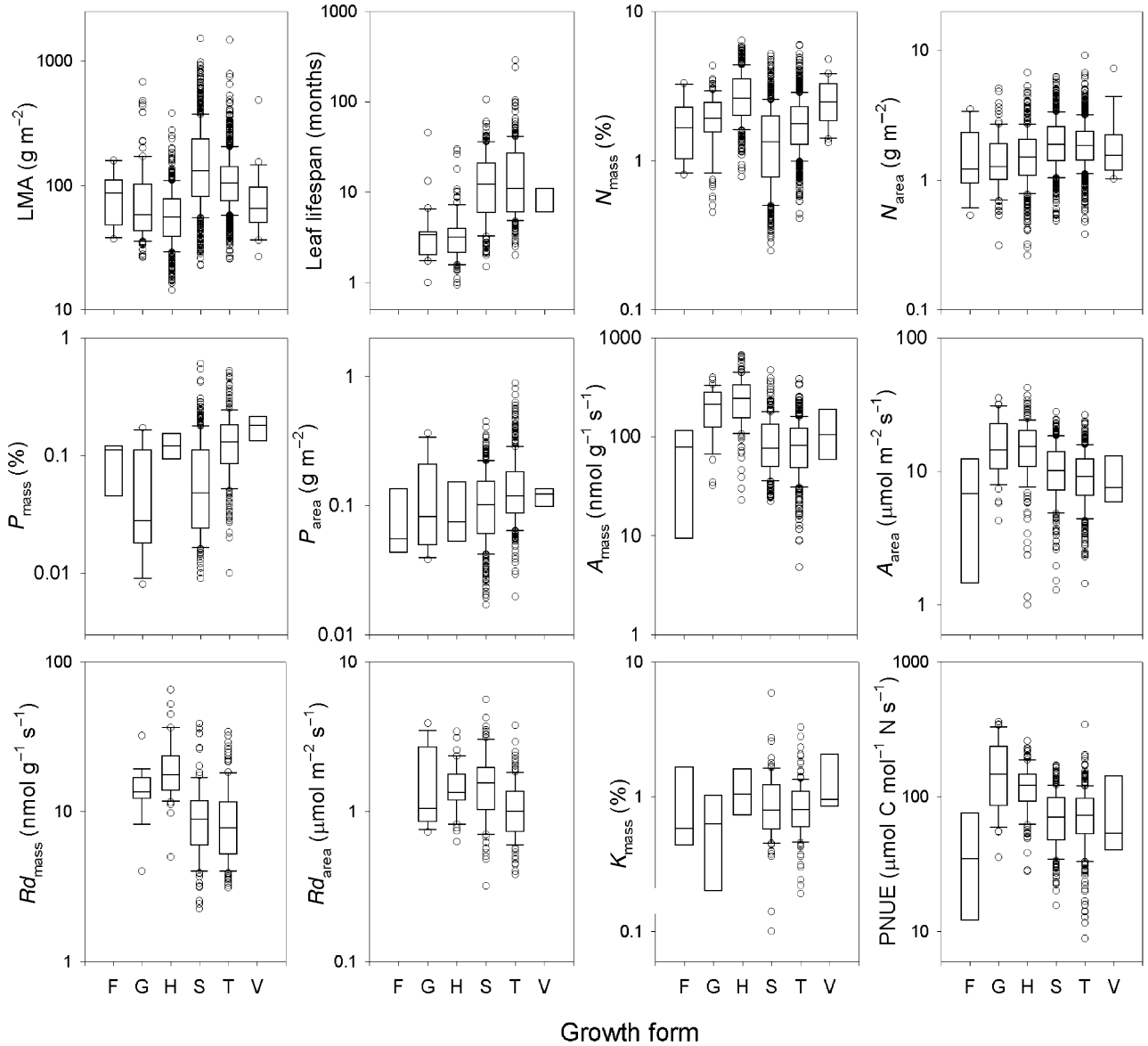

Fig. 1 Box plots of the leaf traits, with species grouped by growth form (F, ferns and fern allies; G, grasses and sedges; H, herbs and geophytes; S, shrubs; T, trees; V, vines and lianas). The central box in each box plot shows the interquartile range and median; whiskers indicate the 10th and 90th percentiles. No whiskers are shown for groups with <10 species.

Trait relationships across all species vs within growth forms

Across all species N_{mass}, P_{mass}, A_{mass} and Rd_{mass} were positively correlated with one another, and negatively correlated with LMA and leaf lifespan, with the same pattern of trait correlations generally true of data subsets defined by growth form (online Appendices 1 and 2). There were too few data to quantify trait relationships reliably for ferns, epiphytes or vines, and relatively few data for trait pairs such as P_{mass} and Rd_{mass} in herbs or grasses. Relationships among area-basis formulations of photosynthetic capacity, dark respiration rate and leaf nutrient concentrations were generally weaker than among mass-based traits, as were their relationships with LMA and LL (Appendix 2). This was generally true within growth forms also. One trait pair exhibiting a notably different pattern across all species compared to within most data subsets was A_{area} and LMA. These traits were unrelated across the data set as a whole (r^2 = 0.003, P = 0.159), but were positively associated within each of grasses, herbs, shrubs and deciduous trees (Appendix 2).

Leaf K shows generally weaker trait relationships than N and P

P_{mass} and K_{mass} (leaf K concentration per unit mass) (r^2 = 0.27; Fig. 3a) were considerably more weakly correlated

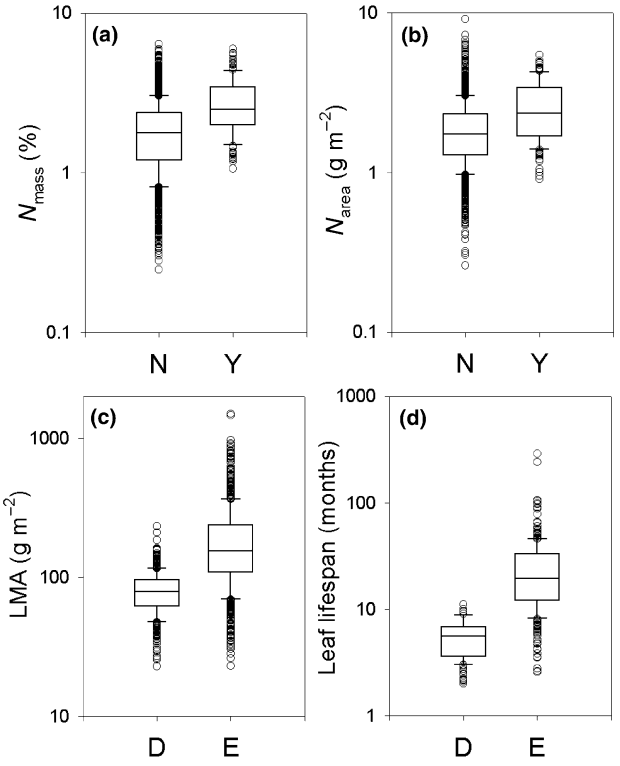

Fig. 2 (a,b) Box plots of N_{mass} and N_{area} with species divided into those that fix nitrogen (*Y*) and those that do not (*N*). Fifth and 95th percentiles for each box plot: N_{mass}, *Y* (1.3, 4.8%), *N* (0.6, 3.6%); N_{area}, *Y* (1.3, 4.5 g m^{-2}), *N* (0.8, 3.5 g m^{-2}). (c,d) Box plots of LL and LMA for trees and shrubs, with species divided into those known to be deciduous (D) and evergreen (E). Fifth and 95th percentiles for each boxplot: LMA, D (40, 128 g m^{-2}), E (55, 485 g m^{-2}); LL, D (2.5, 9.5 months), E (6.2, 60 months).

than were N_{mass} and P_{mass} ($r^2 = 0.73$). The relationship between N_{mass} and K_{mass} was weaker again ($r^2 = 0.19$; Fig. 3c). These relationships were tighter on a per area than on a per mass basis (Fig. 3b,d), in this case being of similar strength to the relationship between N_{area} and leaf P concentration per unit area (P_{area}) ($r^2 = 0.35$). K_{mass} and N_{mass} were significantly positively correlated ($P < 0.05$) at six of 16 individual sites, and showed no relationship at the others. K_{mass} and P_{mass} were at least marginally positively correlated ($P < 0.10$) at six of 16 sites, marginally negatively associated at one, and showed no relationship at the other sites. By comparison, N_{mass} and P_{mass} were at least marginally positively correlated ($P < 0.10$) at 29 of 59 sites, negatively correlated at one, and showed no relationship at the other sites.

In general, K_{mass} showed weaker relationships with other leaf traits than did N_{mass} or P_{mass}. K_{mass} was only weakly and negatively correlated with LMA ($r^2 = 0.07$, $n = 240$, $P < 0.0001$) and LL ($r^2 = 0.11$, $n = 52$, $P = 0.016$), and showed no significant relationship with A_{mass} ($r^2 = 0.04$, $n = 64$, $P = 0.115$). Variation in leaf K concentration per unit area (K_{area}) was unrelated to that in either LL or A_{area} (both $P > 0.3$), but was driven strongly by variation in LMA ($r^2 = 0.40$, $P < 0.0001$). K_{mass} and LMA were at least marginally negatively correlated at four of 15 sites; elsewhere they showed no relationship. K_{mass} and LL were negatively correlated at two of four sites, and unrelated at the other two. K_{mass} and A_{mass} were at least marginally correlated at three of six sites, and unrelated at the other three sites.

Photosynthetic N-use efficiency

A_{mass} scaled with N_{mass} with an SMA slope steeper than 1 (Appendix 1), indicating that the ratio of A_{mass} to N_{mass} (PNUE) increases towards the high A_{mass}, high N_{mass} end of the trait relationship. High PNUE was also associated with short LL ($r^2 = 0.34$, $n = 498$) and low LMA ($r^2 = 0.22$, $n = 702$), that is, PNUE tended to be higher for species at the 'quick-return' end of the leaf economics spectrum. Species groups could have high mean PNUE because they occur further up the A_{mass}–N_{mass} relationship (the slope being >1), or because they have similar A_{mass}–N_{mass} slopes to groups with lower PNUE, but higher *Y* intercepts. The differences between growth forms in mean PNUE (Fig. 1) were associated with both these sources of variation. Grasses and herbs tended to have both higher mean A_{mass} and N_{mass} than shrubs and trees, as well as higher A_{mass} at a given N_{mass} (and statistically indistinguishable SMA slopes; $P = 0.153$). At the grand mean of N_{mass} (1.8%), mean A_{mass} was 176, 109, 88 and 93 nmol g^{-1} s^{-1} for grasses, herbs, shrubs and trees, respectively (= PNUE of 247, 153, 123 and 130 μmol C mol^{-1} N s^{-1}).

N : P stoichiometry

The ratio of leaf N_{mass} to P_{mass} was approximately log-normally distributed, varying between 2.6 and 89, with a geometric mean of 16. The mean N : P ratio of tree leaves was lower than for shrubs (13.5 vs 18.8, *t*-test $P < 0.0001$), and lower for deciduous woody species than for evergreens (considering trees and shrubs separately, or with both growth forms pooled; *t*-tests all $P < 0.002$). Few data were available for ferns, grasses, herbs or vines.

Across all species, N : P ratio was positively correlated with both LMA ($r^2 = 0.14$, $P < 0.0001$, $n = 733$) and leaf lifespan ($r^2 = 0.05$, $P = 0.001$, $n = 207$), but unrelated to A_{mass} ($P = 0.26$, $n = 212$). This last result was strongly influenced by four outlying points, all with both a low A_{mass} and a low N : P ratio (two semiarid zone conifers from Nevada; one semiarid zone stem-photosynthesizing tree from eastern Australia; one fern from Hawaii). With these species removed, N : P ratio and A_{mass} were weakly, negatively correlated ($r^2 = 0.04$, $P = 0.003$). Considering individual sites, N : P ratio and LMA showed no relationship at 50 of 56 sites. Of the remaining six sites, they were positively correlated at four and negatively at two (at least marginally, i.e. $P < 0.10$). N : P

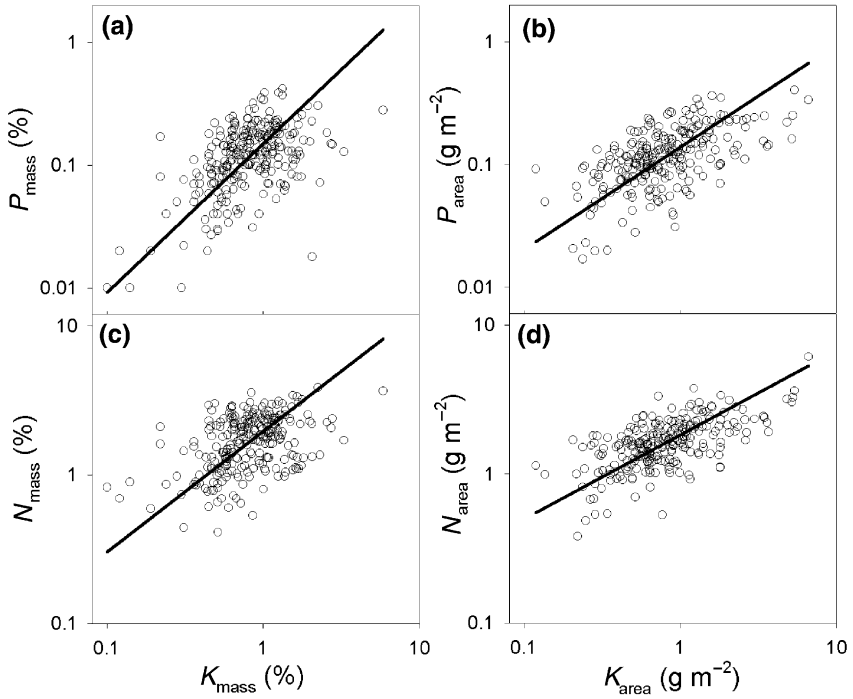

Fig. 3 Relationships between leaf N, P and K, on a per mass and per area basis. (a) P_{mass} vs K_{mass}. SMA slope = 1.21 (95% CI 1.09, 1.35), $r^2 = 0.27$, $n = 251$. (b) P_{area} vs K_{area}. SMA slope = 0.83 (95% CI 0.75, 0.93), $r^2 = 0.34$, $n = 240$. (c) N_{mass} vs K_{mass}. SMA slope = 0.81 (95% CI 0.72, 0.91), $r^2 = 0.19$, $n = 250$. (d) N_{area} vs K_{area}. SMA slope = 0.57 (95% CI 0.51, 0.63), $r^2 = 0.39$, $n = 240$.

ratio and LL were unrelated at 12 of 16 sites, positively correlated at three, and negatively at one (at least marginally). A_{mass} and N : P ratio were unrelated at 15 of 17 sites, and positively or negatively correlated at one site apiece.

Patterning of trait relationships with sample size

In this section we focus on variation among sites in relationships between the core leaf economic traits (LMA, LL, N_{mass}, P_{mass}, A_{mass}, Rd_{mass}). Trait relationships fitted for individual sites varied considerably, both in SMA slope and in correlation strength. There was strong patterning of this variation according to the range of trait variation at each site (first and last columns of panels, Fig. 4) and to sample size (second column, Fig. 4), yielding a series of striking 'funnel graphs'. That is, with increasing trait variation or sample size, SMA and correlation *r* values converged towards values close to those observed across all species (solid lines, Fig. 4). For example, taking a trait pair such as N_{mass} and LMA, a wide range of correlation *r* values or SMA slopes was observed in data sets consisting of <10 species or with more than fivefold variation in LMA (bottom row of panels, Fig. 4). But in just about all data sets that were larger or more variable than this, very similar estimates of relationship strength and slope were obtained. For this trait pair, as for the others, there tended to be more trait variation between species at sites where more species had been sampled (third column of panels, Fig. 4).

Testing for heterogeneity among SMAs and correlation *r* values for each trait pair allows one to ask whether the scatter seen in the funnel graphs indicates the existence of fundamentally different relationships at some sites, vs the alternative explanation that the scatter has arisen by chance alone (e.g. caused by variation in sample size). For most of the bivariate trait relationships considered, there was significant heterogeneity among both the SMAs and correlation *r* values (all $P < 0.015$). P_{mass} and Rd_{mass} (data for four sites only) were the only trait pair for which neither the SMAs nor correlation *r* values were heterogeneous (both $P > 0.29$). Sites with SMA or *r* values lying furthest away from the convergence value in each graph (solid horizontal lines in Fig. 4) were identified to see whether they had features in common, such as representing particular vegetation types. No such factors were identified beyond the generally small sample sizes (or low range of trait variation) lying behind these points.

Discussion

Should leaf K be considered part of the leaf economics spectrum?

The question of whether leaf K should be considered part of the leaf economics spectrum can be broken down into two subquestions. First, to what extent is variation in K correlated with leaf N and leaf P? Second, how tightly is K correlated with the nonnutrient leaf economics traits LMA, LL and A_{mass}? For the first question we found that, especially on a mass basis, leaf P and K were considerably more weakly correlated than were N and P, with the relationship between N and K being weaker again. Similar results have been found

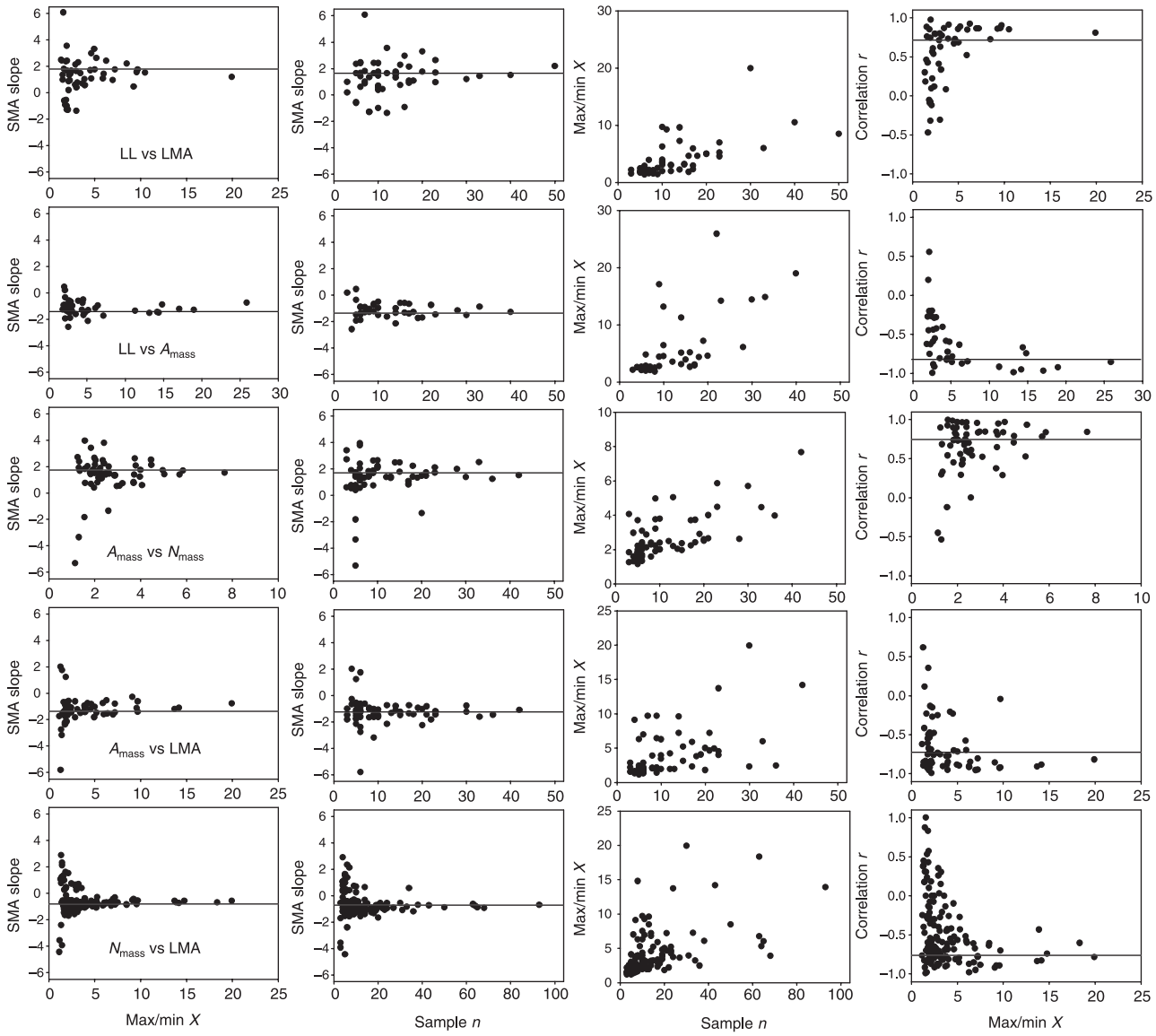

Fig. 4 Patterning of strength and slope of trait relationships fitted within individual sites in relation to the range of trait variation and sample size at the study sites. Data for five of the bivariate trait relationships are shown. Solid horizontal lines indicate the SMA or correlation *r* value seen for the all-species relationships. First column: funnel graphs of SMA slopes fitted to each site vs the range of trait variation in the *X* variable of each trait relationship. A similar pattern of funnelling was seen whether trait variation in either the *X* or *Y* variable (not shown) was plotted. Second column: funnel graphs of SMA slopes fitted to each site vs sample size (minimum $n = 5$). Third column: range of trait variation in the *X* variable vs sample size. A similar pattern was seen whether trait variation in either the *X* or *Y* variable (not shown) was plotted. Fourth column: funnel graphs of correlation *r* values fitted to each site vs the range of trait variation in the *X* variable of each trait relationship. A similar pattern of funnelling was seen whether trait variation in either the *X* or *Y* variable (not shown) was plotted.

in previous studies. Both Thompson *et al.* (1997) (83 mostly herbaceous species from central England) and Cornelissen *et al.* (1997) (seedlings of 81 European woody species grown under controlled conditions with ample water and nutrients) found that the correlation between N_{mass} and P_{mass} was clearly stronger than that between P_{mass} and K_{mass} or between N_{mass} and K_{mass}, although the relationships involving K_{mass} were still highly significant. In two surveys of leaf elements across a broad range of plant types, leaf N_{mass} and P_{mass} were tightly correlated, whereas K_{mass} was either unrelated to N_{mass} or P_{mass} (Garten, 1976, 54 species); or related to P_{mass} only (and then only marginally so; Garten, 1978, 110 species). In both these studies approximately half the species were terrestrial vascular plants, the remainder being predominantly vascular and nonvascular aquatic plants (note that there was considerable species overlap between the two studies).

In a principal components analysis of his 1978 data set, Garten (1978) extracted and interpreted three axes on the

basis of biochemical functions of elements in cells. The first axis, PCA1, was a 'nucleic acid-protein set' correlated with concentrations of P, N, Cu, S and Fe. PCA2 was a 'structural and photosynthetic set' correlated with concentrations of Mg, Ca, K, Zn, Mn and N. PCA3 was an 'enzymatic set' correlated with concentrations of Mn, K and Mg. We ran a similar analysis on the data of Thompson *et al.* (1997) (principal components extracted from the correlation matrix of $\log_{10}$-transformed data), finding a pattern congruent with Garten's, with the first axis largely representing variation in N and P; the second Ca, Mg and K; and the third Mn (details not shown).

Whereas the major pools of N and P in leaves are in cellular constituents such as proteins, ribosomes and nucleic acids, K is primarily found in cell sap as a dissolved ion (Larcher, 2003). Potassium is important as an activator of many enzymes that are essential for photosynthesis and respiration, as an important contributor to the osmotic potential of cells, and in stomatal control (Salisbury & Ross, 1991). Leaf calcium is found in cell walls; Mg is central to chlorophyll and helps maintain ribosome structure; Mn plays a role in maintaining the structure of chloroplast membranes; and both Mn and Mg also act as activators of enzymes (Garten, 1978; Salisbury & Ross, 1991). Collectively, the studies cited above suggest that, while K concentration may be broadly correlated with the concentration of N and P in leaves, it is at least as tightly associated with elements such as Ca and Mg, if not more so. To some extent this appears to reflect the different roles these groups of elements play in leaves.

Few studies have quantified the strength of association between leaf K and plant traits other than tissue nutrient concentrations. Here, we found that K_{mass} showed clearly weaker relationships with LMA, LL and A_{mass} than did either N_{mass} or P_{mass}; indeed the A_{mass}–K_{mass} relationship was nonsignificant across all species (although the traits were positively correlated at three of the six individual sites). Considering the individual sets of site-based data that constituted our data set, none of the relationships between K_{mass} and LMA and LL went the 'wrong' way (i.e. opposite in sign to the all-species relationship), but compelling evidence for general relationships between K and these other leaf traits was lacking. Among the seedlings studied by Cornelissen *et al.* (1997), the strength of association with both LMA and seedling maximum RGR decreased in the order N_{mass}, P_{mass} then K_{mass}, but all these relationships were highly significant ($P < 0.001$), and the trend towards weaker relationships involving K_{mass} was much less obvious than in our field-based data set.

In conclusion, leaf K cannot be considered as one of the core traits making up the leaf economics spectrum, although it is still loosely associated with it. Here we have considered just leaf traits. In the landmark study of Grime *et al.* (1997), 43 common species from the British Isles were screened for a diverse array of 67 traits. Pairwise correlations among the traits were not reported; rather, a variety of data-reduction analyses were run. These analyses indicated that the primary axis of trait variation was made up of leaf nutrient concentrations (N, P, K, Ca, Mg), life history (ephemeral, annual, perennial), root and shoot foraging ability, specific leaf area (SLA), LL, leaf strength, leaf palatability and litter decomposition rate. In essence, this axis describes the capacity of species to take advantage of favourable growth opportunities (Grime, 1977; Grime *et al.*, 1997). The leaf economics spectrum is thus a major part of this axis.

Photosynthetic N-use efficiency

By contrast with leaf K, PNUE was quite tightly related to the core leaf economic traits. This adds further generality to the finding from a previous data compilation where PNUE was shown to be negatively correlated with leaf lifespan (Reich *et al.*, 1992). At least three factors could contribute to species with high LMA (thicker or denser leaf tissue, or both) having lower photosynthetic capacity at a given leaf N (Reich *et al.*, 1998). First, the path of CO_2 diffusion may be more tortuous, that is, they suffer a higher degree of diffusional limitation to photosynthesis (Parkhurst, 1994; Enriquez *et al.*, 1996). Second, a lower fraction of light may be transmitted through the leaf, that is, photosynthesis may be relatively more light-limited (Green & Kruger, 2001). Third, leaf N may be partitioned differently in high-LMA species, with a greater fraction occurring in non-photosynthetic components (Hikosaka *et al.*, 1998; Poorter & Evans, 1998; Hikosaka & Hirose, 2000). These prospective explanations are not mutually exclusive. But in our view the third point, in particular, warrants further systematic investigation across the vegetation of the world.

Leaf N : P ratios

Across all species, leaf N : P ratios were positively correlated with LL and LMA, and negatively correlated with A_{mass}. These trends are consistent with what would be expected if low N : P ratios are characteristic of species with fast growth rates (Elser *et al.*, 2000; Sterner & Elser, 2002). However, the relationships had only low explanatory power (all $r^2 < 0.14$). Within individual sites, the relationships between N : P ratio and these other leaf traits were nonsignificant in the majority of cases (75% to 89% of the time, depending on the trait pair). Thus, across this broad sample of species, variation in leaf N : P ratio can be considered as only very weakly associated with the leaf economics spectrum. Yet in a variety of organisms, particularly those with small body size, the potential for rapid growth tends to be quite tightly correlated with tissue N : P ratios (Elser *et al.*, 2000; Sterner & Elser, 2002). Possible factors contributing to this apparent discrepancy include the following.

(i) Terrestrial plants, particularly woody species, have a much greater proportion of biomass tied up in 'nonproductive' tissues, such as stems, with rather different N : P ratios to leaves. Our database of leaf N : P ratios was strongly dominated by woody species.

(ii) Differential partitioning of leaf N and P among species may cloud any underlying link between growth rate and N : P ratio. Rather than measuring total P, perhaps we should be measuring just the inorganic P pool? Rather than studying total N, perhaps we should be studying just organic N or protein N? As pointed out above, the degree to which species and species groups vary in within-leaf partitioning of key elements warrants further investigation.

(iii) Traits such as LL, LMA and A_{mass} are only approximate indices of growth rate. This appears to be the weakest argument of the three. In a number of vegetation types, LMA and LL are quite tightly correlated with the amount of above-ground net primary production per unit foliage biomass (Reich *et al.*, 1992; Gower *et al.*, 1993; Garnier *et al.*, 2004) and, at least in seedlings, LMA is a strong predictor of potential RGR (Lambers & Poorter, 1992). Furthermore, several leaf economic traits contribute strongly to the primary axis of strategic variation identified by Grime (1977) and Grime *et al.* (1997), this axis describing the capacity of species for rapid growth when growing under favourable conditions.

Relationships between leaf trait data and ecosystem properties

Leaf traits such as LMA (or its inverse, SLA), LL, N_{mass} and dark respiration rates are used as input parameters in many global vegetation models (Friend *et al.*, 1997; Moorcroft *et al.*, 2001; Bonan *et al.*, 2002; Bonan *et al.*, 2003; Kaplan *et al.*, 2003; Sitch *et al.*, 2003). Models such as the LPJ model (Sitch *et al.*, 2003) and the ecosystem demography model (Moorcroft *et al.*, 2001) make use of published relationships between traits such as LL, SLA and N_{mass} (Reich *et al.*, 1997) for parameterization. The degree of accuracy in parameterizing these kinds of model can substantially affect the reliability of model output. For example, output from the BIOME–BGC terrestrial ecosystem model is particularly sensitive to the choice of SLA assigned to each PFT (White *et al.*, 2000). Here, leaf traits were patterned by growth form and PFT, echoing previous results from smaller studies (Diaz & Cabido, 1997; Aerts & Chapin, 2000; Reich *et al.*, 2003). An important conclusion from our study is that, despite mean trait differences between species groups, the overlap in trait ranges are sufficiently large that considerable caution should be exercised when assigning average trait values to growth forms or PFTs for use in global vegetation models.

One possible way forward would be to describe different vegetation types in models with frequency distributions of individual traits (e.g. SLA) rather than with frequency distributions of PFTs, with each PFT assigned a given set of fixed trait values (Moorcroft *et al.*, 2001; Bonan *et al.*, 2002; Kaplan *et al.*, 2003). This does not mean that trait values would be needed for every species at a site, but the trait frequency distributions would need to be weighted by the relative abundance of the constituent species, and values would be needed for the more common species. In a recent study concerning a successional sequence of post-agricultural sites in France (Garnier *et al.*, 2004), above-ground production efficiency (above-ground net primary production/foliage biomass), litter decomposition rate, and soil N and C concentrations were all tightly correlated with community-mean SLA, N_{mass} and leaf dry matter concentration (ratio of dry mass to fresh mass). Community-mean trait values were weighted by species abundance. Remarkably, the correlations were almost as tight when trait means were calculated from just the two most dominant species at each site, rather than from the whole set. The biggest differences were seen in correlations involving litter decomposition rate, being tighter using the community-mean trait values. Across a variety of forest sites, canopy-mean leaf lifespan and LMA have also been shown to be negatively correlated with above-ground production efficiency, as well as being positively correlated with the total foliage mass or area per unit ground area (Reich *et al.*, 1992; Gower *et al.*, 1993; Pierce *et al.*, 1994). The high foliage mass of species with long leaf lifespans appeared to compensate for low production per unit foliage mass, as above-ground net primary production of forest stands was not related to leaf lifespan (Reich *et al.*, 1992; Gower *et al.*, 1993). Similarly, above-ground net primary production was not correlated with SLA, N_{mass} or leaf dry matter concentration in the French study (Garnier *et al.*, 2004).

Sample size and funnel graphs

Funnel graphs are sometimes used for meta-analysis of experimental studies in order to identify whether, with increasing sample size, the effect size (e.g. correlation strength) converges towards an average value (the 'true' effect size), and to detect bias caused by the selective nonreporting of nonsignificant or counterintuitive results (Devlin *et al.*, 1997; Egger *et al.*, 1997; Palmer, 2002). Here, however, we were not searching for the 'true' effect size, so much as asking whether the heterogeneity between results from different studies could be explained by sample size alone, as opposed to reflecting truly different trait relationships among different sets of coexisting species. That is, we used this technique to assess the generality of the trait relationships seen across the larger data set. The tests for heterogeneity among SMA slopes and correlation coefficients suggested that there was indeed real heterogeneity among the results. So what factors may contribute to heterogeneity, over and above that expected on the basis of variable sample size alone?

Different mixes of growth forms or functional types occurring at different sites could contribute to among-site heterogeneity: for all trait pairs there was variation in both relationship slope and correlation strength with growth form of PFT (Appendix 2). Still, even when our analyses were restricted to more homogeneous groups, such as evergreen trees only, there was still heterogeneity among the SMAs fitted to individual sites (data not shown). What other factors might also be at play?

Abiotic site factors may be important. For example, some key trait relationships are modulated by climatic factors: considered across all species, both LL–LMA and A_{mass}–N_{mass} relationships become less steep with increasing site temperature, potential evapotranspiration or irradiance (Wright *et al.*, 2004; I.J.W. and co-workers, unpublished data). Trait relationships may also be modified by soil nutrients (Wright *et al.*, 2001; Niinemets & Kull, 2003). Differences in the methods used to measure leaf traits may be another factor. In recognition of this fact, there has been increased effort in recent times to encourage researchers to employ standard protocols (Garnier *et al.*, 2001; Cornelissen *et al.*, 2003). Other possibilities include variation associated with limiting species sampling to within restricted clades (e.g. where the range of trait variation may be low), and differences in leaf trait relationships associated with the degree of light exposure experienced by plants.

Conclusions: looking forward

The main conclusions emerging from these analyses were as follows.

(i) Despite mean trait differences between species groups for core leaf economic traits (LMA, LL, N_{mass}, P_{mass}, A_{mass}, Rd_{mass}), the overlap in trait ranges was sufficiently large that considerable caution should be exercised when assigning average trait values to growth forms or PFTs.

(ii) These core traits were intercorrelated, both globally and within growth forms and PFTs; together the traits can be considered as forming a 'leaf economics spectrum' (Wright *et al.*, 2004). Whereas PNUE can also be considered as part of this trait spectrum, the same cannot be said for leaf K or for leaf N : P ratios. At this stage it is not clear that recent ideas on ecological stoichiometry (Sterner & Elser, 2002) can be applied to terrestrial, woody vegetation.

(iii) Much of the scatter among trait relationships fitted to individual sites reflects variation in sample size and differences in the range of trait variation between studies. Still, there was more scatter than expected by chance alone, suggesting that, while these trait relationships can indeed be considered very general, they are not necessarily universal.

In this project we have brought together unpublished leaf trait data with much of the data that is scattered through the literature. For traits such as LMA, we now have data for almost 1% of vascular plant species. For other traits and growth forms, the sampling is less comprehensive. For example, we know far less about how respiration varies among species than about photosynthetic rates, and we know considerably less about leaf P than about leaf N concentrations, especially for herbs, grasses, ferns and vines, and we have few data for cryptograms, despite the fact that mosses and lichens are extremely important in cool and cold biomes. The addition of data such as these to global trait compilations would increase their generality considerably.

Our ability to model vegetation shifts with climate and land-use change has been, and will continue to be, enhanced by formulating solid generalizations about key structural and physiological leaf traits at world scale. However, linking this sort of information to data from other scales remains a significant challenge. In particular, linking leaf-level information with multi-species data sets concerning root, canopy and whole-plant traits would be valuable, as would matching data with information on the relative abundance of species, and with ecosystem properties such as rates of nutrient cycling through communities (Garnier *et al.*, 2004). Incorporating this sort of knowledge into future vegetation–climate models would indeed represent an exciting challenge.

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Supplementary material

The following material is available as supplementary material at http://www.blackwellpublishing.com/products/journals/suppmat/NPH/NPH1349/NPH1349sm.htm

Appendix 1

Matrix of scatterplots for six key leaf traits.

Appendix 2

Details of OLS regression relationships among the leaf traits.