vol. 168, no. 4 the american naturalist october 2006

E-Article

Phylogenetic and Growth Form Variation in the Scaling of Nitrogen and Phosphorus in the Seed Plants

Andrew J. Kerkhoff,[1,*] William F. Fagan,[2,†] James J. Elser,[3,‡] and Brian J. Enquist[1,§]

1. Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721;
2. Department of Biology, University of Maryland, College Park, Maryland 20742;
3. School of Biological Sciences, Arizona State University, Tempe, Arizona 85287

Submitted August 2, 2005; Accepted April 26, 2006; Electronically published September 6, 2006

abstract: Plant biomass and nutrient allocation explicitly links the evolved strategies of plant species to the material and energy cycles of ecosystems. Allocation of nitrogen (N) and phosphorus (P) is of particular interest because N and P play pivotal roles in many aspects of plant biology, and their availability frequently limits plant growth. Here we present a comparative scaling analysis of a global data compilation detailing the N and P contents of leaves, stems, roots, and reproductive structures of 1,287 species in 152 seed plant families. We find that P and N contents (as well as N : P) are generally highly correlated both within and across organs and that differences exist between woody and herbaceous taxa. Between plant organs, the quantitative form of the scaling relationship changes systematically, depending on whether the organs considered are primarily structural (i.e., stems, roots) or metabolically active (i.e., leaves, reproductive structures). While we find significant phylogenetic signals in the data, similar scaling relationships occur in independently evolving plant lineages, which implies that both the contingencies of evolutionary history and some degree of environmental convergence have led to a common set of rules that constrain the partitioning of nutrients among plant organs.

Keywords: ecological stoichiometry, plant functional traits, independent contrasts, trait conservatism, convergence, macroecology.

* Present address: Departments of Biology and Mathematics, Kenyon College, Gambier, Ohio 43022; e-mail: kerkhoffa@kenyon.edu.

† E-mail: bfagan@glue.umd.edu.

‡ E-mail: j.elser@asu.edu.

§ E-mail: benquist@u.arizona.edu.

Patterns of allocation have long been of central interest in studies examining the evolution of plant functional traits and life histories as well as the structure and function of ecosystems (Grime 1979; Chapin et al. 1986; Bazzaz and Grace 1997; Aerts and Chapin 2000; Westoby et al. 2002). Functional variation among plant species can largely be described by differences in allocation among major plant organs (leaves, stems, roots, and reproductive structures) as well as overall differences in plant size (Grime 1979; Tilman 1988; Weiher et al. 1999; Westoby et al. 2002; Wright et al. 2004). Allocation involves both biomass partitioning (Enquist and Niklas 2002) and the composition, morphology, and structure of plant organs (Bazzaz and Grace 1997). In seeds, roots, and leaves, nutrient content is related to organ function (e.g., leaf photosynthesis, respiration, seedling establishment), rates of organ growth and turnover, and plant life-history strategies (Grime 1979; Field and Mooney 1986; Jackson et al. 1997; Milberg and Lamont 1997; Wright et al. 2004). Thus, more complete knowledge of the partitioning of nutrients among plant organs is critical to evolutionary explanations of plant functional diversity, the development of accurate nutrient budgets from sparse and costly data, and the parameterization of models of global ecosystem function (Cebrian 1999; Friedlingstein et al. 1999; Moorcroft et al. 2001; Lavorel and Garnier 2002; Westoby et al. 2002; Chapin 2003; Diaz et al. 2004; Güsewell 2004).

The balance of nitrogen (N) and phosphorus (P) in plant tissues is of particular interest because these elements play a pivotal role in many aspects of plant biology, and their availability frequently limits plant growth (Lisanti et al. 1971; Vitousek 1982; Chapin et al. 1986; Ågren 1988; Güsewell 2004). The N : P stoichiometry of plant tissues may reflect important biochemical constraints on relative investments in proteins (which are particularly N rich) and the ribosomal RNA used to generate them, which is a large, metabolically important sink for P (Sterner and Elser 2002; Ågren 2004). This strong interaction likely leads to the coordinated patterns of variation in N and P observed in leaves across plant species (Güsewell 2004; Wright et al. 2004; Niklas et al. 2005). Further, N and P

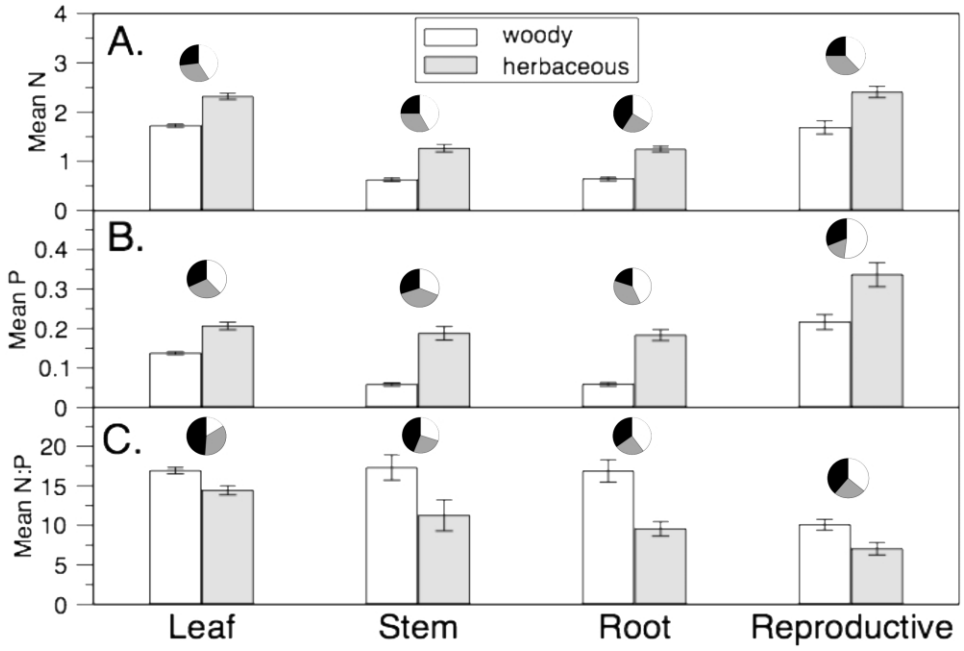

Figure 1: Growth form (woody vs. herbaceous) comparisons of N content (*A*), P content (*B*), and N : P (*C*) of leaves, stems, roots, and reproductive structures. Error bars are standard errors. For all plant organs, all differences are significant (*t*-tests, $P \ll .05$). Individual pie charts show the taxonomic partitioning of trait variation at the family (*white*), genus (*gray*), and species (residual; *black*) levels (nested ANOVAs; see app. A).

contents are important determinants of both the consumption of living tissues by herbivores and the decomposition of senesced litter (Mattson 1980; Melillo et al. 1982; Cebrian 1999; Elser et al. 2000*b*). Thus, plant P and N contents critically influence the material and energy cycles of whole ecosystems (De Angelis 1980; Vitousek 1982; Vogt et al. 1986; Silver 1994; Ågren and Bosatta 1996; Koerselman and Meuleman 1996; Chapin et al. 1997; Sterner and Elser 2002; Kerkhoff et al. 2005).

Plant nutrient concentrations are influenced by site-specific nutrient availability as well as species-specific differences in growth form, physiology, and life history (Chapin et al. 1986; Aerts and Chapin 2000). The relationship between plant nutrient content and resource availability, especially within species, is supported by a number of experimental (i.e., fertilization) and observational (i.e., gradient) studies (Olff 1992; Knops and Koenig 1997; Thompson et al. 1997; Vitousek 1998). Moreover, three recent studies have documented a broad latitudinal gradient in leaf (and forest litter) N : P, which may reflect very broad gradients in nutrient availability (McGroddy et al. 2004; Reich and Oleksyn 2004; Kerkhoff et al. 2005). However, this same pattern is also consistent with an adaptive explanation based on a latitudinal gradient in selection on growth rate driven by changes in growing season length (Kerkhoff et al. 2005).

At the same time, variation in nutrient content among species and growth forms within a community appears similar in magnitude to variation observed across pronounced gradients in nutrient availability (McJannet et al. 1995; Thompson et al. 1997; Wright et al. 2001; Güsewell and Koerselman 2002; Hobbie and Gough 2002; Bowman et al. 2003). Further, recent studies have shown that significant fractions of variation in plant nutrient content can be explained by taxonomic (Thompson et al. 1997) or phylogenetic (Broadley et al. 2004) affiliation, which suggests that nutrient content does not simply track nutrient availability and may be considered a meaningful species-level trait, as we treat it here.

Several comprehensive surveys have demonstrated consistent correlations in plant tissue N and P content (as well as other elements) across species (Woodwell et al. 1975; Garten 1976; Duarte 1992; McJannet et al. 1995; Thompson et al. 1997; Broadley et al. 2004; Wright et al. 2004). However, most studies have focused solely on photosynthetic tissues, and until recently, none have considered relationships among plant organs, as we do here (but see Craine et al. 2005 for an example in grasses). Further, only two studies have investigated phylogenetic components of these relationships (Thompson et al. 1997; Broadley et al. 2004).

Despite the stoichiometric regularities observed within

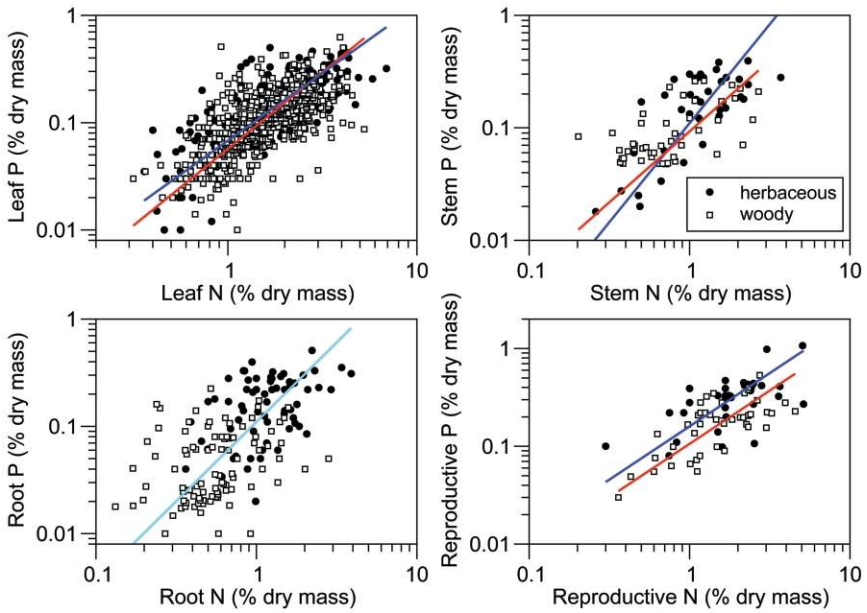

Figure 2: Scaling of P content as a function of N content (both percent dry mass) within leaves, stems, roots, and reproductive structures. All lines are significant RMA regressions (likelihood ratio tests, $P < .05$). Where two lines are present, the regression for herbaceous species (*red*) differed significantly from that of woody species (*blue*) in either slope or intercept. A single cyan line indicates no significant difference in scaling between growth forms.

plant organs, predicting how nutrient content should covary between plant organs is potentially complicated by the distinctively modular construction of land plants (Preston and Ackerly 2004). The continuum of possible outcomes depends on the degrees of correlated evolution and functional integration among the stoichiometric characteristics of plant organs. At one extreme, neither correlated evolution nor functional integration applies, and the nutrient content of different organs in the same plant species can vary independently in response to various ecological and evolutionary factors, regardless of functional type and phylogenetic affiliation. This "independent organ" scenario gains some support from the fact that the nutrient content of plant organs varies significantly not only among individuals but even within an individual plant. For example, foliar N concentration varies with position in a plant's canopy and with leaf age (Schimel et al. 1991; Schieving et al. 1992; Hirose and Werger 1994). However, intraindividual variation tends to be small compared with that observed between species even in a local community.

Alternatively, the nutrient content of one organ may be highly constrained by the evolutionary history and physiological interactions it shares with other organs. The consistent correlation between N and P content in leaf and shoot tissues observed across species (Garten 1976; Duarte 1992; Thompson et al. 1997; Broadley et al. 2004; Wright et al. 2004) by itself suggests strong coordination of nutrient stoichiometry. Likewise, well-documented correlations in size among organs (e.g., "Corner's Rules"; Corner 1949; Ackerly and Donoghue 1998) suggest that separate organs are not strictly independent.

In this study, we ask whether general relationships exist that describe the partitioning of N and P both within and among the major organs of terrestrial seed plants and, further, whether these relationships are generalizable across diverse plant lineages and growth forms. Specifically, we ask four questions. First, do N and P contents vary in a coordinated fashion across species within and among the major plant organs? Second, does the degree of correlation or the form of the relationships differ between the two nutrients or among organs? Third, do tissue nutrient contents differ significantly between woody and herbaceous taxa, and if so, do the observed scaling relationships differ between these two growth forms? Fourth, if there is a phylogenetic signal in the nutrient content of plants, to what extent do the observed relationships simply reflect a shared phylogenetic history?

To address these questions, we take a comparative approach (Duarte et al. 1995) and examine nutrient concentrations in leaves, stems, roots, and reproductive structures, using a global compilation of published seed plant

Table 1: Summary of reduced major axis (RMA) regression results for pooled woody and herbaceous species

	Species-level data						PICs			
	b_{RMA}	95% CI	a_{RMA}	95% CI	r^2	N_{spp}	b_{PIC}	95% CI_{PIC}	r^2	N_{node}
Regression P vs. N:										
Leaves	**1.38**	1.31–1.45	.06	.06–.06	.49	790	**1.31**	1.19–1.43	.38	288
Woody	**1.43**	1.35–1.52	.06	.06–.06	.44	585	**1.30**	1.17–1.46	.33	212
Herbaceous	**1.26**	1.14–1.38	.07	.06–.07	.57	205	**1.21**	1.04–1.40	.51	92
Stems	**1.42**	1.28–1.56	.11	.09–.12	.52	191	**1.47**	1.31–1.63	.67	110
Woody	**1.76**	1.44–2.08	.11	.09–.14	.35	150	**1.20**	1.04–1.38	.56	86
Herbaceous	**1.26**	1.10–1.43	.09	.08–.11	.67	41	**1.78**	1.46–2.16	.76	26
Roots	**1.49**	1.29–1.67	.11	.10–.13	.34	161	**1.53**	1.30–1.79	.39	94
Reproductive	1.19	.99–1.39	.12	.10–.14	.44	79	1.06	.86–1.31	.50	44
Woody	1.09	.92–1.29	.11	.09–.12	.49	45	1.21	.91–1.61	.49	26
Herbaceous	1.09	.92–1.29	.16	.12–.19	.35	34	.96	.69–1.33	.47	21
Stems vs. leaves:										
N	**1.49**	1.34–1.64	.24	.22–.28	.48	202	**1.37**	1.16–1.61	.28	104
Woody	**1.38**	1.23–1.54	.24	.22–.28	.20	128	**1.48**	1.20–1.83	.15	73
Herbaceous	**1.38**	1.23–1.54	.30	.25–.36	.51	74	**1.34**	1.09–1.64	.64	35
P	**1.49**	1.32–1.67	1.22	.83–1.80	.39	176	**1.60**	1.36–1.89	.31	103
Woody	**1.39**	1.23–1.57	.91	.61–1.36	.22	145	**1.54**	1.24–1.90	.04	73
Herbaceous	**1.39**	1.23–1.57	1.32	.92–1.89	.62	31	**1.75**	1.35–2.26	.64	35
N : P	**1.30**	1.14–1.46	.35	.23–.54	.43	149	**1.33**	1.13–1.57	.40	89
Roots vs. leaves:										
N	**1.35**	1.19–1.51	.31	.27–.36	.38	173	1.06	.87–1.30	.07	93
Woody	**1.33**	1.07–1.59	.26	.23–.31	.21	87	**1.30**	1.01–1.66	.16	54
Herbaceous	1.00	.82–1.17	.50	.42–.60	.32	86			NS	44
P	**1.52**	1.32–1.71	1.46	.95–2.25	.47	123	**1.50**	1.25–1.79	.37	78
Woody	**1.38**	1.19–1.61	.99	.61–1.60	.33	85	**1.67**	1.35–2.06	.40	54
Herbaceous	**1.38**	1.19–1.61	1.40	.93–2.10	.29	38			NS	26
N : P	**1.46**	1.25–1.68	.24	.14–.43	.35	117	**1.36**	1.14–1.62	.40	75
Woody	**1.77**	1.43–2.11	.09	.04–.24	.30	82	**1.53**	1.23–1.92	.35	52
Herbaceous	**1.26**	.95–1.58	.49	.24–1.04	.38	35	1.21	.85–1.73	.23	25
Reproductive vs. leaves:										
N	1.09	.96–1.21	.82	.73–.92	.62	113	.91	.75–1.10	.54	53
P	.94	.75–1.14	1.27	.86–1.87	.30	67	**.72**	.54–.96	.21	40
N : P	**.83**	.66–.99	.97	.64–1.46	.39	62	.78	.58–1.05	.19	37
Roots vs. stems:										
N	1.05	.95–1.14	1.04	.96–1.11	.71	146	.89	.75–1.05	.45	80
P	1.17	1.00–1.33	1.80	1.06–3.04	.52	96	**1.21**	1.05–1.40	.64	65
N : P	1.29	1.08–1.51	.50	.29–.86	.37	91			NS	
Reproductive vs. stems:										
N	**.85**	.74–.97	2.17	2.01–2.34	.62	85	**.75**	.60–.94	.49	40
P	**.79**	.60–.99	1.41	.87–2.29	.49	37	**.67**	.48–.94	.40	22
N : P	**.68**	.53–.83	1.88	1.33–2.63	.61	34	**.63**	.49–.80	.69	22
Reproductive vs. roots:										
N	**.85**	.72–.99	2.07	1.89–2.27	.41	95	**.70**	.56–.86	.46	48
P	**.73**	.51–.94	1.05	.64–1.70	.26	37	**.63**	.44–.88	.24	26
N : P					NS	35	**.46**	.34–.65	.39	26

Note: PIC = phylogenetically independent contrast, CI = confidence interval. Unless designated not significant (NS), all regressions were highly significant ($P \ll .05$). Exponent estimates in bold are significantly >1 or <1, indicating anisometric scaling of the two traits.

data representing a total of 1,287 species in 152 families. As in the case of allometry (Niklas 1994), comparative scaling approaches have been very productive in documenting generalities and trade-offs in plant function and their effect on ecosystem processes (Nielsen et al. 1996; Reich et al. 1997; Cebrian 1999; Wright et al. 2004), and the fuller incorporation of phylogenetic information into such analyses promises stronger links between evolutionary and ecological perspectives on plant communities (Ackerly and Reich 1999; Cavender-Bares et al. 2004).

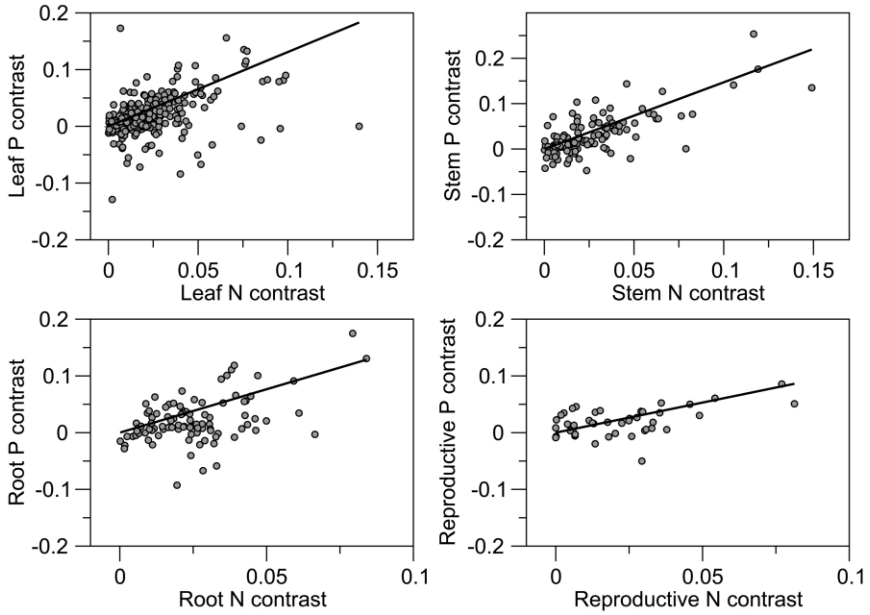

Figure 3: Scaling of P content as a function of N content within each organ type, assessed as PICs (difference in log percent dry mass). All RMA regressions are significant (likelihood ratio tests, $P < .05$).

Methods

Data Compilation

Data were compiled from published studies examining plants in the field, that is, excluding agricultural and greenhouse studies. Sites spanned from Signy Island in the maritime Antarctic (60°S) to Franz Josef Land (81°N) and included arctic, boreal, temperate, desert, and tropical locales. Previous work (Elser et al. 2000*b*; Kerkhoff et al. 2005) has examined broad patterns of variation in foliar C : N : P stoichiometry in this database. Here, we focus on N and P in all plant tissues and use the raw values from the source literature, which were generally reported as percent dry weight. Across the 497 primary and secondary sources, researchers sampled and classified plant tissues in a very heterogeneous fashion. In general, published sources reported only mean values, and few species were compiled from more than a handful of sites, so it is impossible to make meaningful estimates of variation within species for the entire database. This sort of macroecological approach reinforces the importance of publishing estimates of variability as well as average values.

For this study, we grouped measurements into four organ classes: leaves, stems, roots, and reproductive structures. "Leaves" includes only data reported for fresh foliage, that is, no litter. "Stems" includes data reported as stems, branches, twigs, bark, or trunk. Note that while stems may include photosynthetic tissue, data reported for "shoots" were excluded from the analysis because they represent a combination of leaf and stem. "Roots" includes data reported as fine and coarse roots, rhizomes, and all other belowground structures. "Reproductive structures" includes flowers, fruits, and seeds. While this crude classification lumps tissues that may vary greatly in structure and function (e.g., rhizomes and coarse roots), it maximizes our ability to compare tissue nutrient content across species and organ classes. In all cases, when multiple values occurred for a given class of organ for a single species, we used the average of the reported values between studies, across sites, and across the various reported tissue types (e.g., trunk and bark for a single species would be averaged as stem). All taxa were also classified as either woody or herbaceous on the basis of descriptions from the original studies or other sources. Available sample sizes and their phylogenetic breadth varied among the analyses described below, but most analyses captured a great deal of seed plant diversity (table A1). The raw data are available in appendix C, and a complete list of data sources is available from the authors.

The phylogenetic affiliation of each taxon was incorporated into the database using the most recent consensus tree for seed plants (APG II 2003; Davies et al. 2004). We used the online software Phylomatic (http://www.phylodiversity.net/phylomatic) to construct a supertree for all of the taxa in the database (Webb and Donoghue 2005). Although the backbone of the consensus seed

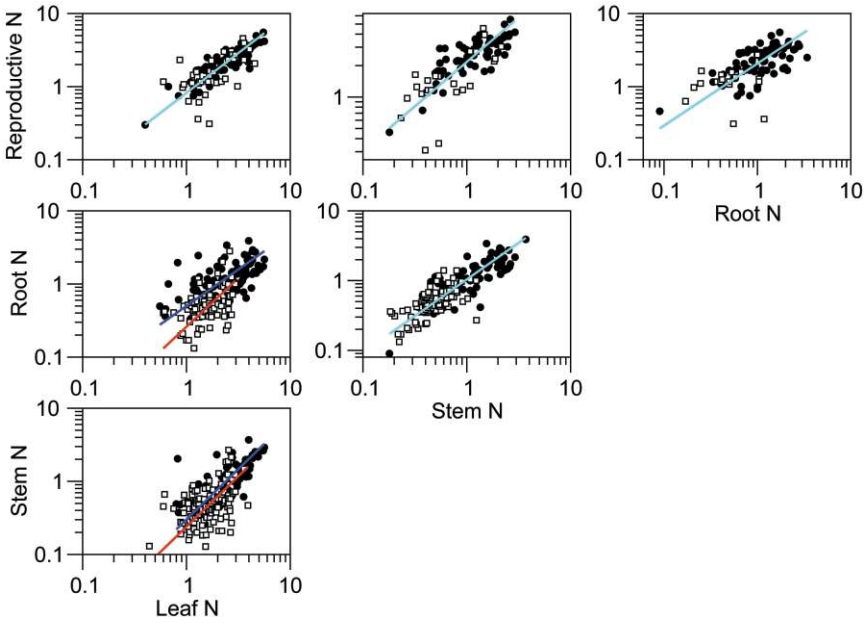

Figure 4: Scatterplot matrix showing the scaling of N content between organ types (percent dry mass). Separate lines are used for woody (*red*) and herbaceous (*blue*) taxa only where slopes or intercepts were significantly different (likelihood ratio tests, $P < .05$). A single cyan line is used otherwise. All RMA regressions are significant (likelihood ratio tests, $P < .05$). Symbols as in figure 2.

plant tree has been quite stable recently, all genera and families, and even many orders, are not resolved in the supertree. Thus, polytomies proliferate toward the tips of the tree, and the phylogenetic approaches employed here (see below) are necessarily coarse grained. Given the taxonomically broad but patchy nature of the available data, this approach is conservative. That is, our results will not be unduly influenced by the inclusion of idiosyncratically available data concerning intrafamilial and intrageneric relationships for specific, well-resolved clades. Thus, data were included for all samples determined to at least the familial level.

Scaling Analyses

We take a scaling approach to these questions, similar to studies of the plant allometry (Niklas 1994). However, here we are addressing plant composition rather than size, and the four questions outlined above entail two separate but not independent scaling components: (1) within organs and between nutrients, for example, the scaling of P versus N within leaves (Wright et al. 2004); and (2) within a nutrient across plant organs, for example, the scaling of stem N with leaf N. We also examined the covariation in N : P across organs to assess interactions between the two nutrients. However, because the scaling of N : P necessarily depends on the scaling of N and P within and among organs, we focus primarily on the raw nutrient content data.

As with many biological traits, nutrient concentrations tend to be log normally distributed (Wright et al. 2004), which implies that it is more meaningful to examine their relationships in terms of magnitude rather than their arithmetic quantities per se (Gingerich 2000). As in allometry, magnitude relationships take the form of a power law between two variables of interest, $Y = aX^b$, where the exponent b is the regression slope on log-transformed data and the coefficient a is the intercept or "elevation" of the line. In our case, variation (or invariance) in the observed values of the exponents is very informative concerning the relative allocation of nutrients to various plant organs. For example, the fact that the exponent of the relationship describing leaf P as a function of leaf N is >1 indicates that, on average, as leaf N increases, leaf N : P will decline because P increases faster than linearly with N (Wright et al. 2004), which is potentially important for understanding the effect of leaf N : P on plant growth rate (Ågren 2004; Niklas et al. 2005), interspecific competition and community structure (Wedin and Tilman 1993), and ecosystem function (Ågren and Bosatta 1996; Kerkhoff et al. 2005).

To examine correlations among organs and between nutrients, we used model II regression (also known as reduced major axis [RMA]) on log-transformed values of N, P, and their ratio N : P. Reduced major axis characterizes

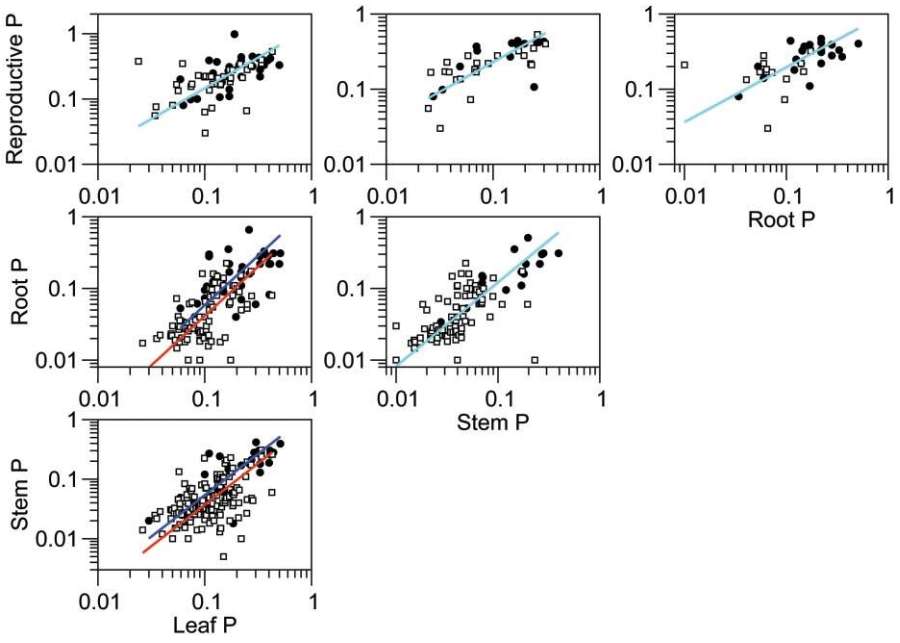

Figure 5: Scatterplot matrix showing the scaling of P content between organ types (percent dry mass). Separate lines are used for woody (*red*) and herbaceous (*blue*) taxa only where slopes or intercepts were significantly different (likelihood ratio tests, $P < .05$). A single cyan line is used otherwise. All RMA regressions are significant (likelihood ratio tests, $P < .05$).

the functional relationship by minimizing the residuals in both the variables. This choice is more appropriate than model I regression (ordinary least squares [OLS]) because comparable errors likely exist in all measurements and because none of the nutrients or organs have a priori precedence as "driving" the observed relationships (Niklas 1994; Sokal and Rohlf 1995). For clarity of presentation, we assigned the *X* variable arbitrarily but consistently, always showing P as a function of N within organs and assigning the organs in the following order: leaf, stem, root, reproductive. Switching axes assignment does not affect any diagnostic results.

The Effects of Functional Type

Interspecific scaling relationships such as those used here may be confounded by the sorting of species into taxonomic or functional groups (e.g., growth forms) that exhibit distinct within-group scaling relationships (Niklas 1994; Wright et al. 2001; Enquist and Niklas 2002; Preston and Ackerly 2004). Within each organ type, we used *t*-tests to establish significant differences in mean trait values between woody and herbaceous taxa. To test for significant differences in stoichiometric scaling between woody and herbaceous taxa, we compared regression slopes and intercepts between the two growth forms using a likelihood ratio technique that provides significance tests analogous to an ANCOVA for RMA models (Wright et al. 2001; Warton and Weber 2002). We tested sequentially for (1) significant (i.e., $\alpha < 0.05$) differences in regression slope (i.e., the exponent, *b*) and then (2) significant differences in regression elevation, given a common slope (i.e., the coefficient, *a*).

Phylogenetic Analyses

We looked for phylogenetic signals both in individual nutrient characters and in each of the RMA regression relations described above by calculating phylogenetically independent contrasts (PICs; Felsenstein 1985), using the analysis of traits (AOT) component of the software package Phylocom (Ackerly 2004*a*, 2004*b*; Webb et al. 2005). All contrasts were calculated on log-transformed values and standardized by branch lengths, which were based on fossil-estimated node ages (Wikstrom et al. 2001). The position of undated nodes was estimated as the midpoint between their nearest dated neighbors. While this dating procedure is very coarse, the results of most PIC analyses have been shown to be robust to different branch length distributions (Ackerly 2000). Although this standardization procedure sometimes left weak trends between contrast SD and absolute contrast value (Garland et al. 1992), using log-transformed nodal ages as an alternative standardization did not significantly affect our results (app.

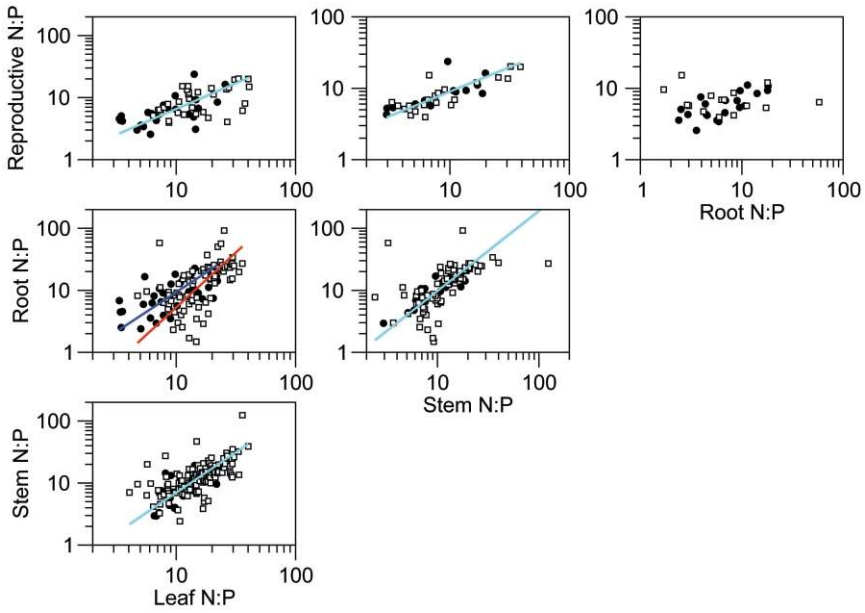

Figure 6: Scatterplot matrix showing the scaling of N : P between organ types. The regression for reproductive N : P as a function of root N : P was not significant for both the pooled data and the separate growth forms. All other RMA regressions are significant (likelihood ratio tests, $P < .05$). Symbols and lines as in previous figures.

B); all results presented below are for the original, node age standardization. Polytomies were resolved by contrasting the mean of the upper two quantiles of the descendant node trait values with that of the lower two quantiles (Pagel 1992).

For each analysis, the phylogenetic tree was constructed using Phylomatic. For individual traits, Phylocom AOT assesses the strength of the phylogenetic signal by averaging the SD of the descendant trait means across all evolutionary divergences in the tree. This is similar to evaluating the mean or variance of contrast values across the tree (Blomberg and Garland 2002), but use of the divergence SD is more amenable to the presence of polytomies, as in our analysis (Ackerly 2004*b*). Using this index, stronger phylogenetic signals (i.e., strong similarity between closely related taxa) will result in low values of the divergence SD. To make inferences about the significance of the signal, the observed data were compared to the distribution drawn from 999 Monte Carlo simulations that randomized the trait value across the tips of the tree, on the basis of a one-tailed alternative that the observed data show more similarity (lower divergence SD) than the randomizations. We also reevaluated all trait-by-trait regressions using PICs. Because PICs are calculated on the basis of nonnegative *X*-axis contrasts, we forced the RMA regressions on PICs through the origin.

Because the seed plant supertree was not resolved below the family level, we augmented the phylogenetic analyses with taxonomically based nested ANOVA models of each trait and for each of the pairwise regressions described above to partition the variance among the nested taxonomic levels, from species up to family (Niklas 1994; Pinheiro and Bates 2000). Significance of the variance components was established using a likelihood ratio test to see whether sequentially adding family and then genus significantly improved the model. In the case of the pairwise regressions, such an analysis tests for taxonomic structure in the residual variation. Thus, if the variance observed across species within genera consistently dwarfs that observed among families, the phylogenetic signal in the individual traits or their interrelationships must be relatively weak, at least toward the tips of the phylogeny. We note that, unlike our RMA analyses, using a nested ANOVA approach entails treating the *X* variable as truly "independent" in the pairwise regressions. However, *F*-tests from OLS regressions are routinely used to assess the significance of RMA regressions (Niklas 1994; Sokal and Rohlf 1995). All statistical analyses were performed using the R statistical platform.

Phylogenetic and growth form effects may be convolved, because growth form itself likely carries a phylogenetic signal. To assess this possibility, we first tested for a phylogenetic signal in the woody/herbaceous growth form distinction. Second, we repeated our comparison of tissue

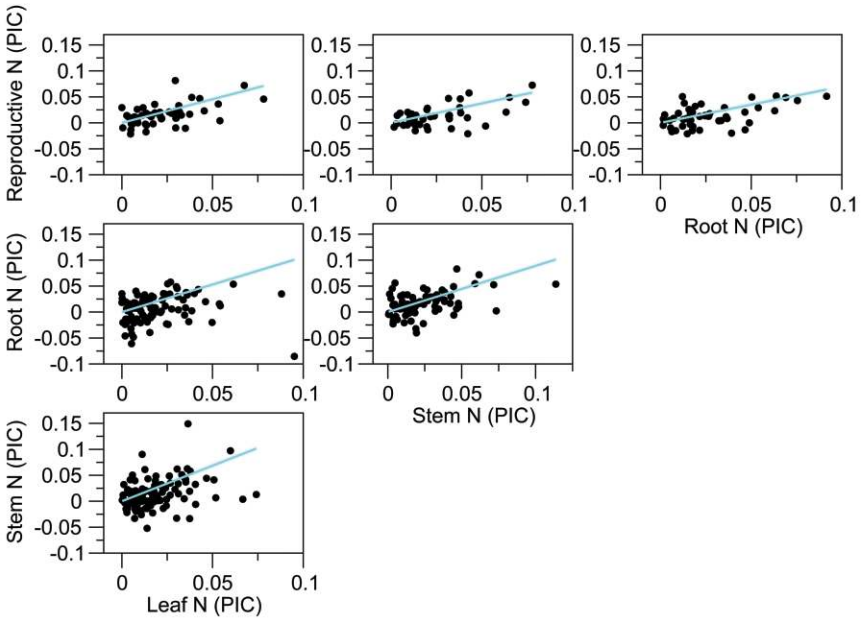

Figure 7: Scatterplot matrix showing the scaling of contrasts in N content (difference in log percent dry mass) between organ types. All RMA regressions are significant (likelihood ratio tests, $P < .05$).

nutrient content of woody and herbaceous taxa based on PICs. For each phylogenetic branching that entailed both woody and herbaceous descendant lineage, we compiled tissue nutrient contrasts. On the basis of the number of positive versus negative contrasts, the null hypothesis of no directional difference between woody and herbaceous descendant lineages was tested with an exact binomial test against the alternative that woody lineages had lower nutrient content and higher N : P. The one-sided alternative was based on our initial, species-level results (see below). Finally, wherever analyses of the species-level regressions showed significant differences between functional types, we repeated all of the contrast-based analyses separately for woody and herbaceous species. However, we note that decreases in phylogenetic breadth and sample size lower the power of these contrast analyses.

Results

Single Traits

In leaves, stems, roots, and reproductive structures, mean nutrient content was consistently higher and mean N : P consistently lower in herbaceous taxa than in woody taxa, on the basis of the species data (fig. 1; *t*-tests, all $P \ll .05$). While the contrast analysis generally mirrored the species-level result (table A2), contrast differences were not significant for stem N ($P = .11$) and reproductive N ($P = .06$), on the basis of the tree tip randomizations. Growth form also showed a significant phylogenetic signal ($P \ll .05$).

The tissue nutrient contents themselves all exhibited a highly significant phylogenetic signal (table A3). Likewise, in the taxonomically nested ANOVA, significant components of total trait variation resided at the family and, in most cases, generic levels, and these higher-level taxonomic components were similar in magnitude to the residual, species-level variation (fig. 1; table A3).

P versus N Scaling, within Organs

Across species, N and P content were highly correlated within leaves, stems, roots, and reproductive structures (fig. 2). In the three nonreproductive organs, P content increased faster than linearly with N content; that is, exponent (b) values were significantly >1 (table 1). In roots, despite differences in mean nutrient content (fig. 1), woody and herbaceous species shared a common scaling relationship. In leaves and stems, the two growth forms exhibited significantly different regression slopes, and in both cases, P increased more quickly with N in woody species than in herbaceous species (fig. 2; table 1). However, in both cases, exponent values were still >1 for both herbaceous and woody species considered separately. Although the P-N scaling relationship in reproductive structures did not differ significantly from isometry, elevations

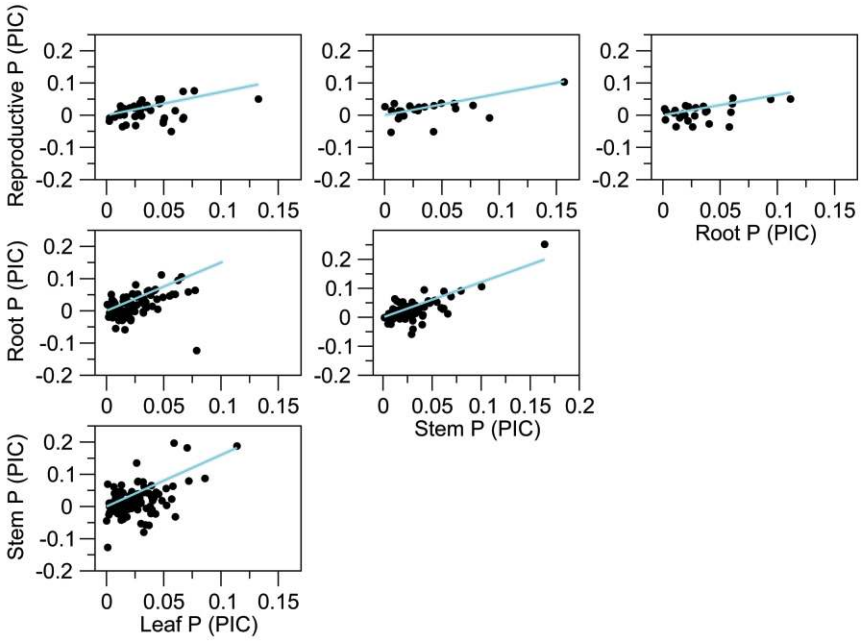

Figure 8: Scatterplot matrix showing the scaling of contrasts in P content (difference in log percent dry mass) between organ types. All RMA regressions are significant (likelihood ratio tests, $P < .05$).

differed between functional groups. Specifically, for a given N content, herbaceous taxa contained significantly more P than woody taxa (fig. 2; table 1).

Using PICs, the P-N scaling relationships remained significant in all four organ types (fig. 3; table 1). Further, correlation coefficients and exponent values for the PIC regressions were similar to those observed in the analyses of the species data (table 1). In leaves, stems, and roots, significant variance components were found at both the generic and family levels, while family, but not genus, identity accounted for a significant fraction of the observed variation in P-N scaling in reproductive structures (table A4). As in the case of the individual traits, the higher-level variance components were similar in magnitude to the residual, species-level variance.

When PICs were analyzed separately for the two functional groups, P-N scaling remained significant. As in the raw data, P content of leaves and stems scaled faster than linearly with N (i.e., $b > 1$) in both woody and herbaceous species, while the exponent for reproductive structures was not significantly different from 1 (table 1).

Stoichiometric Scaling across Organs

Nutrient content was significantly correlated across all pairwise organ combinations for both N (fig. 4) and P (fig. 5). In the case of reproductive versus leaf and root versus stem, the scaling of nutrient content across organs was indistinguishable from isometry (i.e., $b = 1$; table 1). When reproductive nutrient content was examined as a function of stem or root nutrient contents, the estimates of the exponents were slightly (but significantly) <1 (table 1), suggesting that reproductive nutrient content rises slower than linearly with the nutrient content of stems and roots. Conversely, exponents deviated above 1 when the nutrient contents of stems and roots were examined as a function of leaf nutrient content (table 1).

These same cases (i.e., stem vs. leaf and root vs. leaf) were also the only relationships that showed significant differences between growth forms (figs. 4, 5; table 1). In the case of root N versus leaf N, woody and herbaceous taxa had significantly different slopes (fig. 4), and within growth form, only woody species retained an exponent significantly >1 (table 1). For root P versus leaf P as well as stem versus leaf relationships for both nutrients, woody and herbaceous species shared a common exponent, but herbaceous plants exhibited significantly greater root and stem nutrient content for a given leaf nutrient content (i.e., a higher intercept) than did woody plants (table 1).

Among organs, results for N : P were similar to those for the single nutrients. The N : P was significantly correlated across all pairwise organ combinations except in the case of reproductive N : P versus root N : P (fig. 6). Like N and P content, N : P also exhibited exponents >1

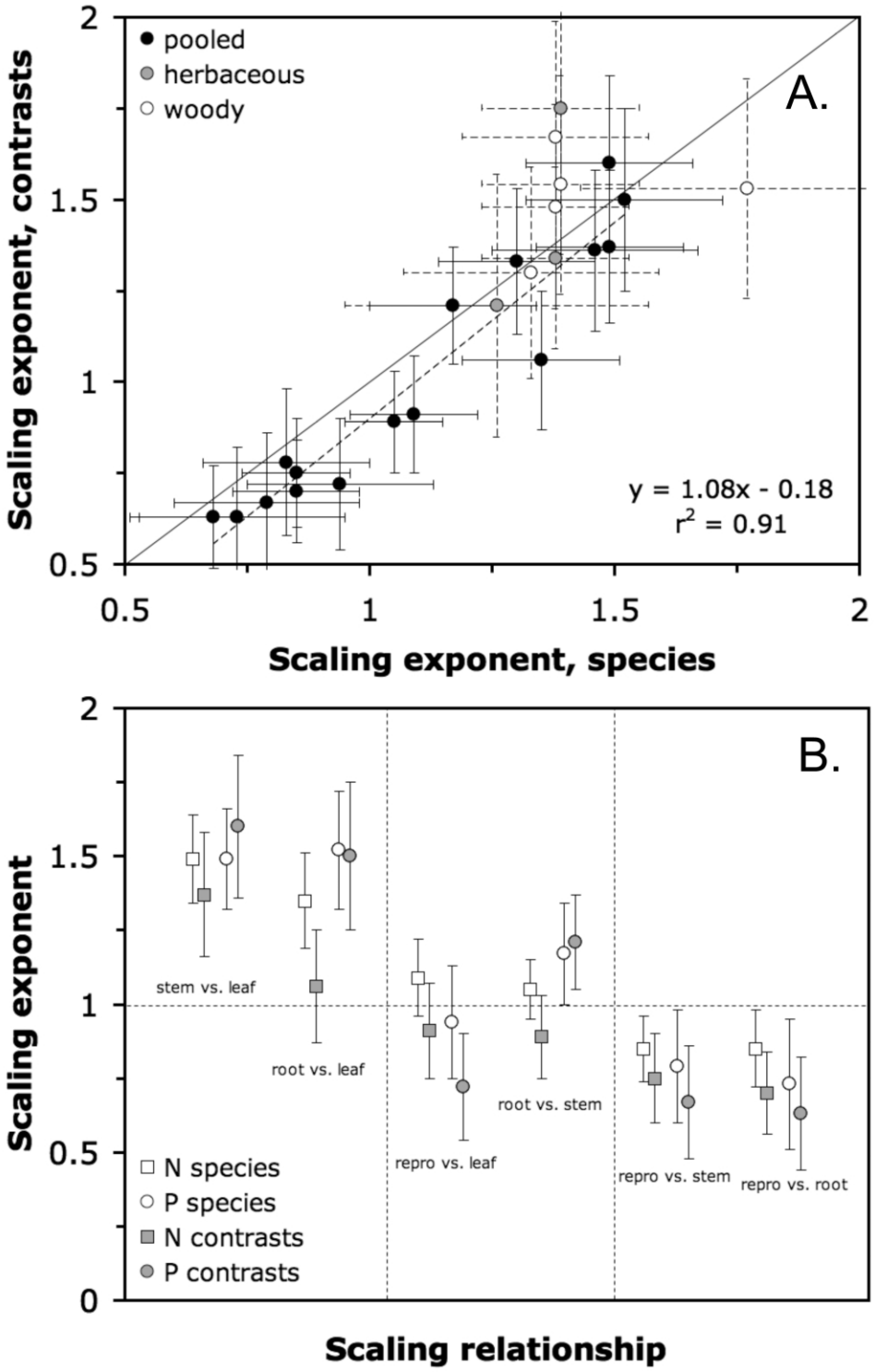

Figure 9: Comparison of exponent values (regression slopes) for species-level and phylogenetically adjusted scaling relationships. *A*, Contrast exponent as a function of species data exponent. The solid line is 1 : 1, and the dashed line and the equation describe an OLS regression on the pooled data predicting the PIC exponent from the species-level exponent. *B*, Grouping of RMA exponent values for sets of interorgan scaling relationships. The horizontal dashed line shows a slope value of 1 for reference. Three groups are delineated by the vertical dashed lines, depending on whether their exponents are >1, ≈1, or <1. In both panels, error bars are the 95% confidence intervals on the regression slope estimates.

when stems and roots were examined as a function of leaves; scaling was isometric in all other comparisons (table 1). Woody and herbaceous species had significantly different slopes in the case of root N : P versus leaf N : P, and as in the case of N, the exponent for woody plants remained above 1, while that of herbs was indistinguishable from 1 (table 1).

In the PIC regressions, all pairwise relationships remained significant for N (fig. 7) and P (fig. 8) as well as their ratio (table 1). As in the P-N scaling analyses, both exponent estimates and correlation coefficients were similar to those of the raw data in most cases (table 1), though in the case of root N versus leaf N, the correlation coefficient and exponent both decreased substantially after phylogenetic correction. Notably, for both N and P, exponents remained >1 for stem or root versus leaf and <1 for reproductive versus stem or root. In the taxonomically nested ANOVAs, family contained a significant fraction of the residual variation in 11 of the 18 pairwise analyses, while genus was a significant variance component in only five cases (table A4).

When PIC analyses were conducted separately for woody and herbaceous species, results remained significant except for the root versus leaf relationships in herbaceous taxa. In all significant relationships, the exponent estimates remained similar to those of the raw data for the two functional types (table 1). However, in many cases the degree of correlation decreased substantially, especially for woody species (table A3).

Several patterns emerged across analyses. Across all of the examined scaling relationships, exponent estimates from the PIC analyses were comparable to and highly correlated with those from the raw, species-level data (fig. 9*A*). Performing separate analyses on each growth form led to somewhat noisier yet consistent results (fig. 9*A*). For any given relationship between organs, exponent estimates were also similar for the two nutrients, whether examined as species or as PICs (fig. 9*B*). Further, with few exceptions, for a given relationship between organs, exponent estimates were consistently either >1 (stem or root vs. leaf), <1 (reproductive vs. stem or root), or indistinguishable from 1 (reproductive vs. leaf, root vs. stem; fig. 9*B*).

Discussion

This study is the first that we know of to demonstrate that the patterns of functional trait coordination similar to those widely documented for plant leaves (Reich et al. 1999; Wright et al. 2004) also apply both within and between the other major plant organs. We also show significant phylogenetic signals in the nutrient content of plant organs and in their patterns of covariation, again similar to patterns in leaves (Ackerly and Reich 1999). Despite this consistent phylogenetic signal, not only do the trait correlations persist after adjusting for phylogenetic relatedness, but also they retain similar values of the scaling exponents, which suggests that the form of the scaling relationships is not simply an artifact of common descent. Although woody and herbaceous taxa differed on average in nutrient content, in most cases they exhibited statistically indistinguishable scaling relationships both within and across organs. Especially in light of the methodological, taxonomic, environmental, and geographic heterogeneity of the studies surveyed, the remarkable consistency of the observed patterns may signal the existence of very general constraints or allocation rules governing the partitioning of nutrients among organs of seed plants.

Within organs, N and P content were always correlated, and in the three nonreproductive organs, the relationships observed here were quantitatively similar to previously observed relationship in leaves (Wright et al. 2004), with P rising faster than linearly with N. Thus, the nonreproductive plant organs of more nutrient-rich species will, on average, show a decrease in N : P. In contrast, the N : P ratio of reproductive structures should be relatively constant, independent of overall nutrient content.

Across organs, nutrient content was also consistently correlated. In both N and P, growth form differences were significant only for stem or root versus leaf nutrient content. However, these relationships were generally anisometric even within growth forms. The observed differences between woody and herbaceous species may indicate the importance of overall plant size for understanding patterns of stoichiometric coordination like those observed here. The nutrient content of leaves and reproductive structures is known to not vary strongly with plant size within species. However, nutrient content in stems and roots may change systematically with the size of the organ, both ontogenetically and across species, as nutrients become increasingly "diluted" by metabolically inactive, carbon-rich, nutrient-poor, structural components of large (woody) plants. Indeed, differences between woody and herbaceous taxa were more pronounced for stems and roots than for leaves and reproductive structures.

Our results suggest an intuitive grouping of plant organs into two groups that we might term "structural" (stems and roots) versus "metabolic" (leaves and reproductive structures). Of course, fine roots would belong to the latter group, but here they appear to be swamped by the more massive structural component, and much of the available data is for coarse roots. Within-group scaling (i.e., root vs. stem and reproductive vs. leaf) tends to yield isometric relationships, whereas between-group scaling (i.e., stem or root vs. leaf and reproductive vs. stem or root) tends to be anisometric (fig. 9*B*).

It is particularly interesting that an increase in leaf nutrient content is accompanied by an even larger increase in the nutrient content of stems and roots, even though these "structural" organs are generally more nutrient poor. The separate analyses on the two growth forms suggest that this nonlinearity is not simply due to the increased nutrient content of herbaceous taxa and thus cannot simply be explained by differences in plant size and growth form. Instead, it implies that nutrient-rich leaves, which generally exhibit high metabolic and photosynthetic activity, require relatively higher nutrient investments in stem tissue. One possibility is that higher nutrient content in stems and roots may represent high rates of nutrient recycling in the phloem, which is associated with increased photosynthate export and phloem loading (Marschner et al. 1997).

Across the seed plants, the nutrient contents of plant organs exhibit a significant phylogenetic signal. However, gauging the relative strength of this phylogenetic signal across analyses and across phylogenetic trees is difficult (Blomberg and Garland 2002), especially using a coarsely dated and partially resolved supertree, as we do here. The consistently highly significant results in the phylogenetic randomizations suggest that for all of the traits considered here, related taxa are more similar than expected by chance. However, genus and species, which were not well resolved in the phylogeny, account for a substantial fraction of the variation in any particular trait (63.4% $\pm$ 9.2%, mean $\pm$ SD; see table A3) or scaling relationship (75.7% $\pm$ 12.7%; see table A4). At the same time, in the contrast analyses, almost all of the relationships remain virtually unchanged. Together, these results indicate that although there is a significant phylogenetic signal, the observed patterns are not simply the by-product of shared ancestry. That is, the same nutrient relationships appear to be maintained in independently evolving lineages of terrestrial plants. This, in turn, implies that the terrestrial environment has selected for some degree of convergence toward a common set of rules (i.e., adaptive and/or physicochemical constraints) that govern the partitioning of nutrients among plant organs.

Our findings support the notion that nutrients and their stoichiometric ratios provide a valuable means for linking ecological and evolutionary perspectives on organisms and their environment (Elser et al. 2000*a*; Kay et al. 2005). Furthermore, the regular relationships within and among organs and the effect of growth form suggest that plant N : P stoichiometry represents part of a complex, multivariate aspect of phenotype that responds to selection in a coordinated fashion. In the case of the seed plants, which provide most of the material and energetic basis for terrestrial food webs, this link between evolutionary and ecological processes is particularly important. From the perspective of ecosystem science, the scaling relationships shown here add to a growing set of empirical and theoretical "rules" for parameterizing the vegetative components of biogeochemical models to better incorporate both between- and within-community functional diversity (Jackson et al. 1997; Reich et al. 1997; Enquist and Niklas 2002; Moorcroft 2003; Wright et al. 2004). Moreover, the phylogenetic signal we have found for plant nutrient allocation and stoichiometry reinforces the proposition that the evolved strategies of land plants have important ecosystem-level implications (Cebrian 1999; Lavorel and Garnier 2002; Chapin 2003; Diaz et al. 2004; Kerkhoff et al. 2005).

For example, changes in community composition due to anthropogenic N deposition are mediated in part by species functional traits (Suding et al. 2005), and changes in functional diversity in turn affect ecosystem processes (Reich et al. 2004). Because plant nutrient content is correlated with other functional traits (Jackson et al. 1997; Reich et al. 1997), compositional changes could result in directional shifts in, for example, foliar or root N content. Thus, our results suggest that compositional changes will be accompanied by coordinated, predictable changes in the nutrient content and stoichiometry of leaves, roots, stems, and even reproductive structures. For instance, increased dominance by species with high leaf N would likely entail increases in stem and root N (fig. 4) as well as decreases in overall N : P ratio (fig. 2; table 1) due to the nonlinear scaling of N and P within and across organs. The documented scaling relationships probably exhibit too much residual variation to make reliable predictions in any particular, local case. However, the generality of the patterns and the fact that they apply across multiple independently evolving lineages of land plants could prove very useful for modeling continental to global responses to N deposition, which depend in part on the C : N ratio of plant organs in different communities (Norby 1998).

The relationship between biogeochemical and biogeographic processes is both dynamical and complex (Foley et al. 1996; Kleidon and Mooney 2000; Cowling 2001; Chapin 2003). In response to environmental change in space and time, plants disperse, evolve, and organize into highly structured, functionally diverse communities. In turn, the ecological and evolutionary dynamics of plant communities strongly influence the flux and transformation of materials and energy, feeding back onto the environment. In terms of N and P, our results suggest that, despite some systematic differences between growth forms, both shared evolutionary history and convergence significantly constrain the covariation of nutrient content of both structural and metabolically active plant organs. While significant variation remains, the resulting relationships appear both highly generalized (i.e., they apply over

broad phylogenetic and biogeographic domains) and often nonlinear (anisometric). Further studies of the evolutionary basis and biogeochemical implications of continuous variation and plant form and function are an important step toward making ecology a more predictive, synthetic science.

Acknowledgments

We are most thankful for the hard work of field researchers who collected the data compiled here. This work would be impossible without them. We are also grateful to L. Crumbacher and C. Soykan for their work on the plant stoichiometry database and to D. Ackerly, N. Swenson, D. Warton, and C. Webb for software and analytical assistance. A.J.K. and B.J.E. were supported by funds from the National Science Foundation and the U.S. Department of Energy, and A.J.K. was supported by the Kenyon College Howard Hughes Medical Institute Bio-Mathematics program. I. Wright and two anonymous reviewers provided challenging and helpful comments on earlier versions of this manuscript.

APPENDIX A

Supplementary Tables

Table A1: Summary of the phylogenetic breadth of sampling for each regression analysis

Regression	Major clades						Species total
	Coniferales	Monocots	"Magnoliids"	"Basal eudicots"	Rosids	Asterids	
P vs. N:							
Leaves	42	106	18	33	379	182	790
Stems	13	25	9	3	84	37	192
Roots	7	36	3	7	56	38	161
Reproductive	2	20	3	2	33	11	79
Stems vs. leaves:							
N	13	15	6	3	88	64	202
P	13	17	6	3	94	36	176
Roots vs. leaves:							
N	7	23	3	5	63	57	173
P	7	23	3	5	50	26	123
Stems vs. roots:							
N	7	8	3	3	56	58	146
P	7	9	3	3	44	25	96
Reproductive vs. leaves:							
N	2	18	0	2	38	41	113
P	2	20	0	2	28	10	67
Reproductive vs. stems:							
N	2	9	0	0	34	40	85
P	2	10	0	0	18	7	37
Reproductive vs. roots:							
N	2	11	0	2	25	45	95
P	2	12	0	1	11	7	37

Note: Entries are the number of taxa in each major clade used in each analysis. Note that because of the presence of taxa from other clades, the rows do not always sum to the species totals. For this summary, "Magnoliids" includes taxa in the Chloranthales, and "Basal eudicots" is made up of taxa in the Ranunculales, Proteales, and other eudicots whose divergence is basal to the so-called core eudicots.

Table A2: Comparison of tissue nutrient content of woody and herbaceous taxa, based on phylogenetically independent contrasts (PICs)

Trait	Nodes	PIC > 0	*P*
Leaf:			
N	49 (33)	11 (9)	.00007 (.006)
P	50 (34)	12 (11)	.0005 (.03)
N : P	46 (31)	30 (20)	.03 (.07)
Stem:			
N	15 (10)	4 (4)	.06 (.38)
P	17 (12)	1 (1)	.0001 (.003)
N : P	14 (9)	12 (8)	.006 (.02)
Root:			
N	18 (14)	3 (3)	.004 (.03)
P	18 (13)	1 (1)	.00007 (.001)
N : P	16 (12)	15 (11)	.0003 (.003)
Reproductive:			
N	11 (6)	3 (2)	.11 (.34)
P	9 (4)	1 (0)	.02 (.06)
N : P	9 (4)	8 (4)	.02 (.06)

Note: Because growth form is a binary trait (woody vs. herbaceous), contrasts can be compared only for the subset of nodes where contrasting growth forms occur on at least two descendant nodes, and these must be defined iteratively from the tips toward the root of the phylogenetic tree. This subset of nodes can be further subdivided into "sister taxa" nodes and "paraphyletic" nodes. Sister taxa nodes branch into daughter clades that are uniformly woody or herbaceous; that is, the character states are not mixed. Paraphyletic nodes are those that contain contrasting but not uniform daughter clades, once the descendant nodes that have already contributed to the analysis have been "pruned." In all tests, contrasts were calculated by subtracting the mean (log-transformed) nutrient content of the herbaceous lineage from that of the woody lineage, weighted by the estimated phylogenetic branch length. The null hypothesis of no directional difference between woody and herbaceous descendant lineages was tested with an exact binomial test against the alternative that woody lineages had lower nutrient content and higher N : P. In the table, we present results for both paraphyletic and sister taxa contrasts together, with sister taxa contrasts alone in parentheses.

Table A3: Phylogenetic signal and taxonomic partitioning of variance in stoichiometric traits

	Phylogenetic signal		Nested variance components		
Organ	Divergence SD	*P*	Family	Genus	Species (residual)
Leaf:					
N	**.12** (326)	.001	**.41** (134)	**.32** (563)	.28 (973)
P	**.18** (330)	.001	**.38** (135)	**.30** (566)	.32 (975)
N : P	**.13** (288)	.001	**.16** (125)	**.35** (466)	.49 (790)
Stem:					
N	**.16** (124)	.001	**.42** (64)	**.33** (158)	.25 (247)
P	**.26** (128)	.001	**.31** (69)	**.39** (146)	.30 (228)
N : P	**.16** (109)	.001	**.30** (62)	**.26** (124)	.44 (192)
Root:					
N	**.15** (116)	.001	**.34** (60)	**.25** (150)	.41 (229)
P	**.24** (98)	.001	**.43** (60)	**.37** (119)	.20 (169)
N : P	**.19** (94)	.001	**.40** (58)	**.25** (112)	.35 (161)
Reproductive:					
N	**.14** (65)	.001	**.38** (39)	**.37** (101)	.25 (138)
P	**.19** (52)	.02	**.52** (39)	.17 (83)	.31 (101)
N : P	**.14** (44)	.02	**.36** (34)	.25 (65)	.38 (79)

Note: Numbers in bold indicate the statistical significance ($P < .05$). For phylogenetic signal, the divergence SD was compared with 999 simulations randomizing trait values across taxa. The contribution of family and genus in explaining variation in organ nutrient content was assessed using a likelihood ratio test. Because species-level variability is residual, its significance cannot be assessed. Numbers in parentheses are the number of nodes or taxonomic units used in each analysis.

Table A4: Fractional partitioning of residual variance in nutrient relationships within and among organs and across species, genera, and families

Regression	Family	Genus	Species (residual)
P vs. N:			
Leaves	**.17** (125)	**.35** (466)	.48 (790)
Stems	**.30** (62)	**.26** (124)	.44 (192)
Roots	**.41** (58)	**.26** (112)	.33 (161)
Reproductive	**.37** (34)	.28 (65)	.35 (79)
Stems vs. leaves:			
N	**.25** (56)	**.26** (134)	.49 (202)
P	.06 (59)	**.49** (120)	.44 (176)
N : P	**.10** (53)	.00 (102)	.90 (149)
Roots vs. leaves:			
N	**.38** (48)	.14 (115)	.48 (173)
P	**.36** (47)	.00 (87)	.64 (123)
N : P	**.21** (45)	**.32** (81)	.47 (117)
Reproductive vs. leaves:			
N	**.24** (29)	**.38** (83)	.38 (113)
P	.00 (27)	.59 (54)	.41 (67)
N : P	.11 (26)	.00 (50)	.89 (62)
Stems vs. roots:			
N	**.20** (46)	.03 (100)	.76 (146)
P	**.27** (46)	.20 (71)	.53 (96)
N : P	**.18** (43)	**.48** (66)	.34 (91)
Reproductive vs. stems:			
N	**.32** (22)	.00 (61)	.68 (85)
P	.12 (16)	.00 (30)	.88 (37)
N : P	.00 (16)	.00 (28)	.89 (34)
Reproductive vs. roots:			
N	**.49** (26)	.24 (69)	.27 (95)
P	.30 (19)	.19 (33)	.51 (37)
N : P	.38 (19)	.00 (31)	.62 (35)

Note: Numbers in bold indicate the statistical significance (likelihood ratio test, $P < .05$) of family and genus in each analysis. Because data are species means, species-level variance is residual, and significance is not assessed. Numbers in parentheses are the number of each taxonomic unit in each analysis.

APPENDIX B

Comments on Branch Length Standardization

Contrasts were originally standardized on the basis of branch lengths estimated from fossil dates (Wikstrom et al. 2001). In some cases, the current standardization left weak trends between contrast SD and absolute contrast value (Garland's method for evaluating standardization [Garland et al. 1992]). Specifically, we sometimes observed a "triangular" relationship between node SD and contrast value, with low SD having a wider range of contrast values decreasing to uniformly low contrasts at high SD. However, this pattern was not consistent over all analyses, and contrasts occasionally exhibited other slight trends (usually negative) with increasing SD. In other cases, the original standardization left no trend, indicating sufficient standardization.

According to Garland et al. (1992) and Diaz-Uriarte and Garland (1998), the triangle pattern indicates that log transformation may be appropriate, while negative trends might indicate a power transformation. However, to preserve our ability to compare PIC exponents to species data exponents, we sought to avoid separate transformations of different sets of contrasts; such ad hoc transformations can change the scale of slope estimates in such a way as to make comparisons to the species-level analyses impossible (Garland et al. 1992; Diaz-Uriarte and Garland 1998).

Because the log transformation was most frequently indicated, we repeated all phylogenetic regressions using that transformation. We found that restandardizing the contrasts using log branch lengths did not strongly affect any of our results. In particular, the RMA slopes from the two procedures (our primary concern here) change by only 5% on average, and slopes are highly correlated across the two analyses (fig. B1). Additionally, in no case was there a reversal of statistical inference; that is, no significant relationship became insignificant, and no insignificant relationship became significant as a result of branch length transformation.

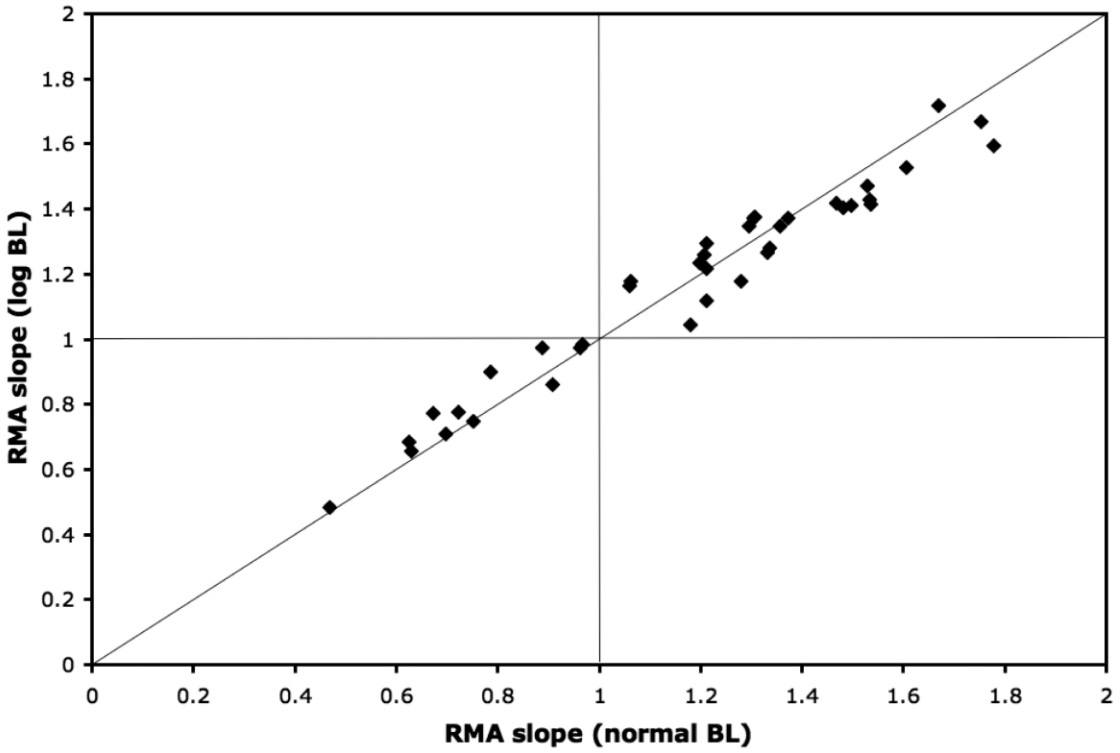

Figure B1: Effect of log transformation of phylogenetic branch lengths (BL) on scaling exponents. Diagonal line is 1 : 1.

APPENDIX C

Species-Level Data

The species-level data are available in a zip archive as both an Excel file and a tab-delineated ASCII file.

Literature Cited

Ackerly, D. D. 2000. Taxon sampling, correlated evolution, and independent contrasts. Evolution 54:1480–1492.

———. 2004*a*. Adaptation, niche conservatism, and convergence: comparative studies of leaf evolution in the California chaparral. American Naturalist 163:654–671.

———. 2004*b*. Analysis of traits (AOT) manual. Version 3.0. A module of Phylocom. http://www.phylodiversity.net/phylocom.

Ackerly, D. D., and M. J. Donoghue. 1998. Leaf size, sapling allometry, and Corner's rules: phylogeny and correlated evolution in maples (Acer). American Naturalist 152:767–791.

Ackerly, D. D., and P. B. Reich. 1999. Convergence and correlations among leaf size and function in seed plants: a comparative test using independent contrasts. American Journal of Botany 86:1272–1281.

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

Ågren, G. I. 1988. Ideal nutrient productivities and nutrient proportions in plant growth. Plant Cell and Environment 11:613–620.

———. 2004. The C : N : P stoichiometry of autotrophs: theory and observations. Ecology Letters 7:185–191.

Ågren, G. I., and E. Bosatta. 1996. Theoretical ecosystem ecology: understanding nutrient cycles. Cambridge University Press, Cambridge.

APG II (Angiosperm Phylogeny Group). 2003. An update of the Angiosperm Phylogeny Group classification for the orders and

families of flowering plants: APG II. Botanical Journal of the Linnean Society 141:399–436.

Bazzaz, F. A., and J. Grace. 1997. Plant resource allocation. Academic Press, San Diego, CA.

Blomberg, S. P., and T. Garland. 2002. Tempo and mode in evolution: phylogenetic inertia, adaptation and comparative methods. Journal of Evolutionary Biology 15:899–910.

Bowman, W. D., L. Bahnj, and M. Damm. 2003. Alpine landscape variation in foliar nitrogen and phosphorus concentrations and the relation to soil nitrogen and phosphorus availability. Arctic Antarctic and Alpine Research 35:144–149.

Broadley, M. R., H. C. Bowen, H. L. Cotterill, J. P. Hammond, M. C. Meacham, A. Mead, and P. J. White. 2004. Phylogenetic variation in the shoot mineral concentration of angiosperms. Journal of Experimental Botany 55:321–336.

Cavender-Bares, J., D. D. Ackerly, D. A. Baum, and F. A. Bazzaz. 2004. Phylogenetic overdispersion in Floridian oak communities. American Naturalist 163:823–843.

Cebrian, J. 1999. Patterns in the fate of production in plant communities. American Naturalist 154:449–468.

Chapin, F. S. 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., P. M. Vitousek, and K. Vancleve. 1986. The nature of nutrient limitation in plant communities. American Naturalist 127:48–58.

Chapin, F. S., B. H. Walker, R. J. Hobbs, D. U. Hooper, J. H. Lawton, O. E. Sala, and D. Tilman. 1997. Biotic control over the functioning of ecosystems. Science 277:500–504.

Corner, E. J. H. 1949. The Durian theory or the origin of the modern tree. Annals of Botany 13:367–414.

Cowling, S. A. 2001. Plant carbon balance evolutionary innovation and extinction in land plants. Global Change Biology 7:231–239.

Craine, J. M., W. G. Lee, W. J. Bond, R. J. Williams, and L. C. Johnson. 2005. Environmental constraints on a global relationship among leaf and root traits of grasses. Ecology 86:12–19.

Davies, T. J., T. G. Barraclough, M. W. Chase, P. S. Soltis, D. E. Soltis, and V. Savolainen. 2004. Darwin's abominable mystery: insights from a supertree of the angiosperms. Proceedings of the National Academy of Sciences of the USA 101:1904–1909.

De Angelis, D. L. 1980. Energy-flow, nutrient cycling, and ecosystem resilience. Ecology 61:764–771.

Diaz, S., J. G. Hodgson, K. Thompson, M. Cabido, J. H. C. Cornelissen, A. Jalili, G. Montserrat-Marti, et al. 2004. The plant traits that drive ecosystems: evidence from three continents. Journal of Vegetation Science 15:295–304.

Diaz-Uriarte, R., and T. Garland. 1998. Effects of branch length errors on the performance of phylogenetically independent contrasts. Systematic Biology 47:654–672.

Duarte, C. M. 1992. Nutrient concentration of aquatic plants: patterns across species. Limnology and Oceanography 37:882–889.

Duarte, C. M., K. Sand-Jensen, S. L. Nielsen, S. Enriquez, and S. Agusti. 1995. Comparative functional plant ecology: rationale and potentials. Trends in Ecology & Evolution 10:418–421.

Elser, J. J., R. W. Sterner, E. Gorokhova, W. F. Fagan, T. A. Markow, J. B. Cotner, J. F. Harrison, S. Hobbie, G. Odell, and L. J. Weider. 2000*a*. Biological stoichiometry from genes to ecosystems. Ecology Letters 3:540–550.

Elser, J. J., W. F. Fagan, R. F. Denno, D. R. Dobberfuhl, A. Folarin, A. Huberty, S. Interlandi, et al. 2000*b*. Nutritional constraints in terrestrial and freshwater food webs. Nature 408:578–580.

Enquist, B. J., and K. J. Niklas. 2002. Global allocation rules for patterns of biomass partitioning in seed plants. Science 295:1517–1520.

Felsenstein, J. 1985. Phylogenies and the comparative method. American Naturalist 125:1–15.

Field, C., and H. A. Mooney. 1986. The photosynthesis-nitrogen relationship in wild plants. Pages 25–55 *in* T. J. Givnish, ed. On the economy of plant form and function. Cambridge University Press, Cambridge.

Foley, J. A., I. C. Prentice, N. Ramankutty, S. Levis, D. Pollard, S. Sitch, and A. Haxeltine. 1996. An integrated biosphere model of land surface processes, terrestrial carbon balance, and vegetation dynamics. Global Biogeochemical Cycles 10:603–628.

Friedlingstein, P., G. Joel, C. B. Field, and I. Y. Fung. 1999. Toward an allocation scheme for global terrestrial carbon models. Global Change Biology 5:755–770.

Garland, T., P. H. Harvey, and A. R. Ives. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. Systematic Biology 41:18–32.

Garten, C. T. 1976. Correlations between concentrations of elements in plants. Nature 261:686–688.

Gingerich, P. D. 2000. Arithmetic or geometric normality of biological variation: an empirical test of theory. Journal of Theoretical Biology 204:201–221.

Grime, J. P. 1979. Plant strategies and vegetation processes. Wiley, Chichester.

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

Güsewell, S., and M. Koerselman. 2002. Variation in nitrogen and phosphorus concentrations of wetland plants. Perspectives in Plant Ecology Evolution and Systematics 5:37–61.

Hirose, T., and M. J. A. Werger. 1994. Photosynthetic capacity and nitrogen partitioning among species in the canopy of a herbaceous plant community. Oecologia (Berlin) 100:203–212.

Hobbie, S. E., and L. Gough. 2002. Foliar and soil nutrients in tundra on glacial landscapes of contrasting ages in northern Alaska. Oecologia (Berlin) 131:453–462.

Jackson, R. B., H. A. Mooney, and E. D. Schulze. 1997. A global budget for fine root biomass surface area and nutrient contents. Proceedings of the National Academy of Sciences of the USA 94: 7362–7366.

Kay, A. D., I. W. Ashton, E. Gorokhova, A. J. Kerkhoff, A. Liess, and E. Litchman. 2005. Toward a stoichiometric framework for evolutionary biology. Oikos 109:6–17.

Kerkhoff, A. J., B. J. Enquist, J. J. Elser, and W. F. Fagan. 2005. Plant allometry, stoichiometry and the temperature-dependence of primary productivity. Global Ecology and Biogeography 14:585–598.

Kleidon, A., and H. A. Mooney. 2000. A global distribution of biodiversity inferred from climatic constraints: results from a process-based modelling study. Global Change Biology 6:507–523.

Knops, J. M. H., and W. D. Koenig. 1997. Site fertility and leaf nutrients of sympatric evergreen and deciduous species of *Quercus* in central coastal California. Plant Ecology 130:121–131.

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

Lavorel, S., and E. Garnier. 2002. Predicting changes in community

composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Functional Ecology 16:545–556.
Lisanti, L. E., C. Testini, and M. Polemio. 1971. Nitrogen-phosphorus interaction in plants. Agrochimica 16:53–61.
Marschner, H., E. A. Kirkby, and C. Engels. 1997. Importance of cycling and recycling of mineral nutrients within plants for growth and development. Botanica Acta 110:265–273.
Mattson, W. J. 1980. Herbivory in relation to plant nitrogen content. Annual Review of Ecology and Systematics 11:119–161.
McGroddy, M. E., T. Daufresne, and L. O. Hedin. 2004. Scaling of C : N : P stoichiometry in forest ecosystems worldwide: implications of terrestrial Redfield-type ratios. Ecology 85:2390–2401.
McJannet, C. L., P. A. Keddy, and F. R. Pick. 1995. Nitrogen and phosphorus tissue concentrations in 41 wetland plants: a comparison across habitats and functional groups. Functional Ecology 9:231–238.
Melillo, J. M., J. D. Aber, and J. F. Muratore. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology 63:621–626.
Milberg, P., and B. B. Lamont. 1997. Seed/cotyledon size and nutrient content play a major role in early performance of species on nutrient-poor soils. New Phytologist 137:665–672.
Moorcroft, P. R. 2003. Recent advances in ecosystem-atmosphere interactions: an ecological perspective. Proceedings of the Royal Society B: Biological Sciences 270:1215–1227.
Moorcroft, P. R., G. C. Hurtt, and S. W. Pacala. 2001. A method for scaling vegetation dynamics: the ecosystem demography model (ED). Ecological Monographs 71:557–585.
Nielsen, S. L., S. Enriquez, C. M. Duarte, and K. Sand-Jensen. 1996. Scaling maximum growth rates across photosynthetic organisms. Functional Ecology 10:167–175.
Niklas, K. J. 1994. Plant allometry: the scaling of form and process. University of Chicago Press, Chicago.
Niklas, K. J., T. Owens, P. B. Reich, and E. D. Cobb. 2005. Nitrogen/phosphorus leaf stoichiometry and the scaling of plant growth. Ecology Letters 8:636–642.
Norby, R. J. 1998. Nitrogen deposition: a component of global change analyses. New Phytologist 139:189–200.
Olff, H. 1992. Effects of light and nutrient availability on dry-matter and N-allocation in 6 successional grassland species: testing for resource ratio effects. Oecologia (Berlin) 89:412–421.
Pagel, M. D. 1992. A method for the analysis of comparative data. Journal of Theoretical Biology 156:431–442.
Pinheiro, J. C., and D. M. Bates. 2000. Mixed effects models in S and S-PLUS: statistics and computing. Springer, New York.
Preston, K. A., and D. D. Ackerly. 2004. The evolution of allometry in modular organisms. Pages 80–106 *in* M. Pigliucci and K. A. Preston, eds. Phenotypic integration: studying ecology and evolution of complex phenotypes. Oxford University Press, Oxford.
Reich, P. B., and J. Oleksyn. 2004. Global patterns of plant leaf N and P in relation to temperature and latitude. Proceedings of the National Academy of Sciences of the USA 101:11001–11006.
Reich, P. B., M. B. Walters, and D. S. Ellsworth. 1997. From tropics to tundra: global convergence in plant functioning. Proceedings of the National Academy of Sciences of the USA 94:13730–13734.
Reich, P. B., D. S. Ellsworth, M. B. Walters, J. M. Vose, C. Gresham, J. C. Volin, and W. D. Bowman. 1999. Generality of leaf trait relationships: a test across six biomes. Ecology 80:1955–1969.
Reich, P. B., D. Tilman, S. Naeem, D. S. Ellsworth, J. Knops, J. Craine, D. Wedin, and J. Trost. 2004. Species and functional group diversity independently influence biomass accumulation and its response to CO_2 and N. Proceedings of the National Academy of Sciences of the USA 101:10101–10106.
Schieving, F., T. L. Pons, M. J. A. Werger, and T. Hirose. 1992. The vertical distribution of nitrogen and photosynthetic activity at different plant densities in *Carex acutiformis*. Plant and Soil 142:9–17.
Schimel, D. S., T. G. F. Kittel, A. K. Knapp, T. R. Seastedt, W. J. Parton, and V. B. Brown. 1991. Physiological interactions along resource gradients in a tallgrass prairie. Ecology 72:672–684.
Silver, W. L. 1994. Is nutrient availability related to plant nutrient use in humid tropical forests? Oecologia (Berlin) 98:336–343.
Sokal, R. R., and F. J. Rohlf. 1995. Biometry: the principles and practice of statistics in biological research. W. H. Freeman, New York.
Sterner, R. W., and J. J. Elser. 2002. Ecological stoichiometry: the biology of elements from molecules to the biosphere. Princeton University Press, Princeton, NJ.
Suding, K. N., S. L. Collins, L. Gough, C. Clark, E. E. Cleland, K. L. Gross, D. G. Milchunas, and S. Pennings. 2005. Functional- and abundance-based mechanisms explain diversity loss due to N fertilization. Proceedings of the National Academy of Sciences of the USA 102:4387–4392, doi:10.1073/pnas.0408648102.
Thompson, K., J. A. Parkinson, S. R. Band, and R. E. Spencer. 1997. A comparative study of leaf nutrient concentrations in a regional herbaceous flora. New Phytologist 136:679–689.
Tilman, D. 1988. Plant strategies and the dynamics and structure of plant communities. Monographs in Population Biology. Vol. 26. Princeton University Press, Princeton, NJ.
Vitousek, P. 1982. Nutrient cycling and nutrient use efficiency. American Naturalist 119:553–572.
———. 1998. Foliar and litter nutrients, nutrient resorption, and decomposition in Hawaiian *Metrosideros polymorpha*. Ecosystems 1:401–407.
Vogt, K. A., C. C. Grier, and D. J. Vogt. 1986. Production, turnover, and nutrient dynamics of aboveground and belowground detritus of world forests. Advances in Ecological Research 15:303–377.
Warton, D. I., and N. C. Weber. 2002. Common slope tests for bivariate errors-in-variables models. Biometrical Journal 44:161–174.
Webb, C. O., and M. J. Donoghue. 2005. Phylomatic: tree assembly for applied phylogenetics. Molecular Ecology Notes 5:181–183.
Webb, C. O., D. D. Ackerly, and S. W. Kembel. 2005. Phylocom: software for the analysis of community phylogenetic structure and character evolution. Version 3.34. http://www.phylodiversity.net/phylocom.
Wedin, D., and D. Tilman. 1993. Competition among grasses along a nitrogen gradient: initial conditions and mechanisms of competition. Ecological Monographs 63:199–229.
Weiher, E., A. Van der Werf, K. Thompson, M. Roderick, E. Garnier, and O. Eriksson. 1999. Challenging Theophrastus: a common core list of plant traits for functional ecology. Journal of Vegetation Science 10:609–620.
Westoby, M., D. S. Falster, A. T. Moles, P. A. Vesk, and I. J. Wright. 2002. Plant ecological strategies: some leading dimensions of variation between species. Annual Review of Ecology and Systematics 33:125–159.
Wikstrom, N., V. Savolainen, and M. W. Chase. 2001. Evolution of the angiosperms: calibrating the family tree. Proceedings of the Royal Society B: Biological Sciences 268:2211–2220.

Woodwell, G. M., R. H. Whittaker, and R. A. Houghton. 1975. Nutrient concentrations in plants in Brookhaven oak-pine forest. Ecology 56:318–332.

Wright, I. J., P. B. Reich, and M. Westoby. 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., P. B. Reich, M. Westoby, D. D. Ackerly, Z. Baruch, F. Bongers, J. Cavender-Bares, et al. 2004. The worldwide leaf economics spectrum. Nature 428:821–827.

Associate Editor: James P. Grover
Editor: Jonathan B. Losos