

LETTER

Ecosystem allometry: the scaling of nutrient stocks and primary productivity across plant communities

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Abstract

A principal challenge in ecology is to integrate physiological function (e.g. photosynthesis) across a collection of individuals (e.g. plants of different species) to understand the functioning of the entire ensemble (e.g. primary productivity). The control that organism size exerts over physiological and ecological function suggests that allometry could be a powerful tool for scaling ecological processes across levels of organization. Here we use individual plant allometries to predict how nutrient content and productivity scale with total plant biomass (phytomass) in whole plant communities. As predicted by our model, net primary productivity as well as whole community nitrogen and phosphorus content all scale allometrically with phytomass across diverse plant communities, from tropical forest to arctic tundra. Importantly, productivity data deviate quantitatively from the theoretically derived prediction, and nutrient productivity (production per unit nutrient) of terrestrial plant communities decreases systematically with increasing total phytomass. These results are consistent with the existence of pronounced competitive size hierarchies. The previously undocumented generality of these ‘ecosystem allometries’ and their basis in the structure and function of individual plants will likely provide a useful quantitative framework for research linking plant traits to ecosystem processes.

Keywords

Community size distribution, ecological stoichiometry, functional diversity, macroecology, nitrogen, net primary productivity, phosphorus, plant allocation, vegetation biomass.

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INTRODUCTION

Relating traits of plant species to the structure and dynamics of whole communities and ecosystems is a critical challenge for both basic and applied ecology (Ehleringer & Field 1993; Lavorel & Garnier 2002; Chapin 2003; Diaz *et al.* 2004; Kerkhoff *et al.* 2005). Because many ecologically relevant plant traits vary in a coordinated fashion across environments, many changes in ecosystem structure and function in space and time are related to turnover of plant species and their respective characteristics (Diaz & Cabido 1997; Smith *et al.* 1997; Lavorel & Garnier 2002; Chapin 2003; Diaz *et al.* 2004).

Recently, many aspects of plant function and life history have been quantitatively related to traits of seeds (Westoby *et al.* 1996; Moles *et al.* 2005), leaves (Nielsen *et al.* 1996; Reich *et al.* 1997; Niinemets 2001; Wright *et al.* 2004) and whole plant stature (Enquist *et al.* 1998, 1999; Niklas &

Enquist 2001). These ‘major axes’ of functional variation (Westoby *et al.* 2002) suggest that geographical variation in plant functional traits (Yin 1993; Niinemets 2001; Wright *et al.* 2001; Moles & Westoby 2003; Reich & Oleksyn 2004; Kerkhoff *et al.* 2005) may inform large scale, dynamic ecosystem models (Moorcroft *et al.* 2001).

Here, we focus on the functional trait of plant size and its distribution within plant communities. Terrestrial plants vary over 10 orders of magnitude in mass, and a single individual of a large tree species may span much of this range over its lifetime. And plant size, whether indexed by mass, height or diameter, exerts a powerful and quantifiable influence on plant form, function and life history (Niklas 1994). Collectively, these quantitative size–function relationships are known as ‘allometry.’ From this perspective, the size distribution of individuals may be the single most informative characteristic of a community (Cyr & Pace 1993; Moorcroft *et al.* 2001; Enquist *et al.*

2003; Brown *et al.* 2004; Allen *et al.* 2005; Economo *et al.* 2005). We ask whether regularities in the size structure of plant communities and the size dependence of plant form and function can be used to make predictions about ecosystem structure and function and how they should vary with the size (i.e. the standing biomass) of the plant community.

Beginning with an approach based on plant size has two important advantages. First, despite considerable inter- and intraspecific variation in plant form and function, generalized allometric rules have been shown to apply across diverse plant species, with a high degree of predictive power (Enquist & Niklas 2002). Second, at least in relatively undisturbed forest communities, the size distribution of individual plants is quite regular, with many more small plants than large plants (Enquist & Niklas 2001; Niklas *et al.* 2003). Furthermore, the quantitative form of the relationship does not appear to change systematically with environmental conditions or species diversity. The generality of allometric rules and plant community size distributions allows us to develop and test predictions across communities without the detailed knowledge of community species composition and the distribution of other functional traits within communities.

Of course, focusing on community size distributions alone ignores potentially important differences among species along the other important functional axes. Variation in leaf-level properties, which reflect coordinated strategies of life history and resource capture (Reich *et al.* 1997; Niinemets 2001; Wright *et al.* 2004), is likely of particular importance. Comprehensive studies of trait distributions within communities and how they change along environmental gradients are an exciting research frontier in plant functional ecology (Wright *et al.* 2001; Ackerly *et al.* 2002; Walker & Langridge 2002; Ackerly 2004), but they await a more complete synthesis (Diaz *et al.* 2004; Wright *et al.* 2004). However, it is important to note that if quantitative generalities can be established concerning the distributions of functional traits across environments, a similar approach could incorporate variation along several of the 'major axes' of functional diversity.

AN ALLOMETRICALLY IDEAL PLANT COMMUNITY MODEL

For our purposes, a plant community is a collection of N individual plants of varied sizes and species that occupy a given area of ground. The fundamental assumption of this study is that all the individual plants in the community (regardless of species) follow a common set of allometric rules dictating their rates of production or growth (g), allocation of photosynthetic (l) and non-photosynthetic (s) biomass, and equilibrium density (n) based on theoretical models and empirical data (Table 1). These allometries all take the form $y = \beta_y m^{b_y}$, where y is the response function of interest (e.g. plant growth rate, leaf mass or plant density) and m is plant mass. The exponent, b_y , describes how function (y) changes with plant mass (m), while the allometric coefficient, β_y , which is the regression intercept on log-transformed data, sets the magnitude of the response function per unit plant mass.

The rules in Table 1 represent a minimal, internally consistent set of rules for an 'allometrically ideal' steady-state plant community, i.e. one in which growth and recruitment is exactly offset by mortality and total resource use is in equilibrium with the rate of resource supply (Enquist *et al.* 1998, 2003; Niklas & Enquist 2001; Enquist & Niklas 2002). The validity and generality of these 'rules' are subject to debate, and to some extent their applicability depends on the scale of the question. Our claim is that they comprise a useful starting point for scaling up from individual plants to whole communities and ecosystems. Variation in allometric rules among species and communities certainly exists (Coomes *et al.* 2003; Price & Enquist 2006). However, the broad empirical support for the scaling relations used here (Enquist *et al.* 1998, 2003; Niklas & Enquist 2001; Enquist & Niklas 2002) suggests that they represent the central tendencies across broad taxonomical and biogeographical domains. Thus, unless variation in scaling is systematically biased across communities, interspecific variation in the allometric rules should produce only unbiased residual variation from the predictions developed below.

Plant property (references)	Allometric function
Whole plant growth rate (g month ⁻¹) (Niklas & Enquist, 2001)	$g = \beta_g m^{3/4}$
Whole plant leaf mass (l) (Enquist & Niklas 2002)	$l = \beta_l m^{3/4} \propto g$
Whole plant non-photosynthetic mass (s) (Enquist & Niklas 2002)	$s = \beta_s m$
Plant density (n m ⁻²) (Enquist <i>et al.</i> 1998; Enquist & Niklas 2001)	$n = \beta_n m^{-3/4}$
Whole plant nutrient content (c) (this study)	$c = \beta_c m^{3/4} \propto l \propto g$

Table 1 Allometric 'rules' assumed in the plant community model

Growth rate and leaf mass both increase allometrically with plant mass, with an exponent of 3/4. Non-photosynthetic mass increases isometrically, i.e. with an exponent of 1. Conversely, plant density decreases allometrically as plant mass increases, with an exponent of -3/4.

We characterize the size distribution of the community by partitioning the individuals, regardless of species, into $K + 1$ discrete size classes, such that the k th size class contains n_k individuals (m^{-2}) of average mass m_k (g), and the size classes range from that of the smallest plants in the sampled community (where $k = 0$ and $m = m_0$) to that of the largest sampled plant (where $k = K$ and $m = m_K = M$). Mathematically, it is convenient to partition the size classes logarithmically, such that $m_k = m_0 e^{\varepsilon k}$, where ε is the grain, or (logarithmic) bin width, at which the size distribution is resolved. For a fixed value of ε , the ratio of plant masses from adjacent size classes is then constant ($m_k/m_{k+1} = e^{-\varepsilon}$), all size classes are related to the largest individual mass as $m_k = M e^{-\varepsilon(K-k)}$, and the number of classes increases with the sampled size range ($M - m_0$) as $K = \ln(M/m_0)/\varepsilon$. From these properties and the population density allometry ($n = \beta_n m^{-3/4}$, Table 1), it can be shown that $n_k = n_K (M/m_k)^{3/4}$, and the total biomass of a plant community ($M_{\text{tot}} = \sum_{k=0}^K n_k m_k$, in g m^{-2}), or total phytomass hereafter, is then,

$$\begin{aligned} M_{\text{tot}} &= n_K M e^{-\varepsilon K/4} \sum_{k=0}^K e^{\varepsilon k/4} \\ &= n_K M e^{-\varepsilon K/4} \left(\frac{1 - \exp(\varepsilon(K+1)/4)}{1 - e^{\varepsilon/4}} \right) = n_K M \Omega_K. \end{aligned} \quad (1)$$

Numerical simulations demonstrate that the function

$$\Omega_K \equiv e^{-\varepsilon K/4} \left(\frac{1 - \exp(\varepsilon(K+1)/4)}{1 - e^{\varepsilon/4}} \right)$$

becomes asymptotically proportional to

$$\frac{4}{\varepsilon} = \frac{4K}{\ln(M/m_0)}$$

as the number of size classes (K) increases (see Supplementary material). Thus, total phytomass is approximately proportional to the mass of the largest individuals in a community.

Based on this idealized community size structure and the assumed allometries, we wish to predict how aspects of ecosystem structure and function vary with total phytomass across plant communities. In particular, we focus on: (i) the net primary productivity (NPP) of the community; and (ii) the total plant nutrient stock or pool. Specifically, we examine the nitrogen (N) and phosphorus (P) content of plant communities because these two nutrients are most frequently limiting to production (Chapin *et al.* 1986; Güsewell 2004).

Assuming that NPP is an approximately constant fraction of gross production (Dewar 1996; Waring *et al.* 1998), it can be estimated as the summation of plant production across the size distribution of the community,

$$\text{NPP} \propto G_{\text{tot}} = \sum_{k=0}^K n_k g_k,$$

where $g_k = \beta_g m_k^{3/4}$ is the rate of biomass production of an individual in size class k (Table 1). Substituting the allometric relationships for n_k and g_k and using eqn 1, it can then be shown (see Supplementary material) that total production should vary with total phytomass as

$$G_{\text{tot}} = \beta_g n_K M^{3/4} = \beta_g n_K^{1/4} \left(\frac{M_{\text{tot}}}{\Omega_K} \right)^{3/4}. \quad (2)$$

Empirical data suggest that the value of the individual plant growth coefficient, β_g is independent of plant size ($\beta_g = 1.64 \text{ g g plant}^{-3/4} \text{ year}^{-1}$, 95% CI: 1.57–1.70) (Niklas & Enquist 2001). Also, because the density of individuals in the largest size class will usually be small, the term $n_K^{1/4}$ should not change dramatically with total phytomass. Thus, except for $\Omega_K^{-3/4}$ which increases sublogarithmically with the size range (i.e. as $\ln(M/m_0)^{3/4}$), total production should scale as approximately the 3/4 power of total phytomass. If the form of the individual allometries and the approximate constancy of β_g and $n_K^{1/4}$ holds across communities, a single scaling relationship should apply to diverse communities, from low phytomass grasslands and deserts to high-phytomass forests.

Predicting the nutrient content of the plant community requires another assumption concerning the allometry of individual plant nutrient content, i.e. how it changes with plant mass. Because nutrients are often a limiting resource, it is generally assumed that natural selection should result in efficient allocation of nutrients among plant organs (Hirose & Werger 1987; Gleeson & Tilman 1992; Dewar 1996). As a significant fraction of the plant body is metabolically inert sclerenchyma, nutrients invested these tissues would provide no metabolic return. Thus, we assume that whole plant nutrient content (c) reflects the metabolically active fraction of plant mass, which in turn should scale isometrically (i.e. in direct proportion) with total leaf mass: $c_k = \beta_c m_k^{3/4} \propto l$ (Niklas & Enquist 2001).

Under this assumption, the allometric coefficient β_c represents the nutrient content of metabolically active tissues (e.g. leaves) per unit mass, independent of plant size. Thus, while leaf nutrient content varies substantially across species, it should be largely invariant with respect to whole plant mass, which is consistent with both allometric theory and empirical surveys (West *et al.* 1999; Wright *et al.* 2004). That is, the leaves of small plants (or seedlings) should not be systematically higher or lower in nutrient content than those of larger individuals. At the extremes of plant size and development, this assumed invariance may break down (Koch *et al.* 2004). In contrast with leaves, because the mass of stems and roots increases approximately linearly with whole plant mass (Enquist & Niklas 2002), nutrient

'concentrations' in these organs should decrease with organ size as they become increasingly dominated by metabolically inert, nutrient poor tissue (Kerkhoff *et al.* 2005).

The allometric decrease in whole plant nutrient concentration is qualitatively consistent with several observations of decreased N and P concentration:

- (1) in heartwood relative to sapwood (Meerts 2002);
- (2) with increasing diameter in fine roots (Jackson *et al.* 1997);
- (3) with decreasing leaf : stem ratio in crops (Lemaire *et al.* 1992);
- (4) in the photosynthetic tissues of terrestrial vs. aquatic autotrophs (Cebrian 1999; Elser *et al.* 2000);
- (5) in the stems and roots of woody vs. herbaceous species (A. Kerkhoff, W. Fagan, J. Elser & B. Enquist, unpublished data).

Many elements, including N and P, also scale *within* leaves and other plant organs (Garten 1976; Wright *et al.* 2004; Niklas *et al.* 2005). Specifically, recent work has shown that leaf N scales as the 3/4 power of leaf P, $c_{\text{leaf}}^{\text{N}} \propto c_{\text{leaf}}^{\text{P}^{3/4}}$ (Wright *et al.* 2004; Niklas *et al.* 2005). Because the allometric coefficient β_c (but not the exponent) varies with leaf nutrient content, whole plant N and P content should both increase allometrically, with a common exponent of 3/4, but with intercepts (and residual variation) reflecting differences between the two nutrients. Furthermore, a common scaling exponent for the two nutrients implies that, in contrast with the leaf-level allometric scaling pattern, whole plant N and P should scale isometrically (i.e. $c_{\text{plant}}^{\text{N}} \propto c_{\text{plant}}^{\text{P}}$), and that whole plant N : P should not vary systematically with the size of a plant (Güsewell 2004).

Based on this assumed nutrient allometry, the nutrient content of entire plant communities ($C_{\text{tot}} = \sum_{k=0}^K n_k c_k$, in g nutrient m^{-2}) should scale isometrically with total production and thus share an analogous relationship with total phytomass (see Supplementary material):

$$C_{\text{tot}} = \beta_c n_K M^{3/4} = \beta_c n_K^{1/4} \left(\frac{M_{\text{tot}}}{\Omega_K} \right)^{3/4}. \quad (3)$$

Thus, by summing productivity and nutrient content over the size distribution of an allometrically idealized plant community, we arrive at four inter-related predictions:

- (1) Whole community nutrient content should scale as the 3/4 power of total phytomass ($C_{\text{tot}} \propto M_{\text{tot}}^{3/4}$).
- (2) Because N and P are assumed to share a common exponent: (i) in contrast with patterns at the leaf-level, N should scale isometrically with P (i.e. $C_{\text{tot}}^{\text{N}} \propto C_{\text{tot}}^{\text{P}}$) and (ii) the ratio of N : P should be invariant with respect to total phytomass ($C_{\text{tot}}^{\text{N}}/C_{\text{tot}}^{\text{P}} \propto M_{\text{tot}}^{3/4} M_{\text{tot}}^{-3/4} \propto M_{\text{tot}}^0$, see Güsewell 2004).
- (3) Whole community productivity (NPP) should also scale as the 3/4 power of total phytomass ($G_{\text{tot}} \propto M_{\text{tot}}^{3/4}$).

- (4) As a result of prediction numbers 1 and 3, productivity per standing unit of nutrient (so-called 'nutrient productivity', $\text{g g nutrient}^{-1} \text{ year}^{-1}$, Ågren 1988) should also be invariant with total phytomass ($G_{\text{tot}}/C_{\text{tot}} \propto M_{\text{tot}}^{3/4} M_{\text{tot}}^{-3/4} \propto M_{\text{tot}}^0$).

Note that deviation in any one of these predictions will result in deviations in at least one other prediction, i.e. they are not independent.

METHODS

We tested these predictions using data compiled from the literature detailing the phytomass, nutrient content and productivity of diverse plant communities ranging from tropical forest to arctic tundra. Total phytomass, annual NPP and vegetation nutrient (N and/or P) data were compiled from published sources. We limited ourselves to studies reporting total phytomass plus at least two of the other three variables together for the entire plant community (i.e. not just dominant species). Nutrient data were combined for all living vegetative components (i.e. roots, shoots, and leaves, but not litter or reproductive organs). Forested sites include several plantations as well as primary and secondary forests, but no fertilized or actively cultivated sites were included. Most studies included only above-ground biomass, nutrient content, and productivity, and the belowground component was only included when it was reported for all variables. The available data, drawn from 46 sites at 30 different locales, include tropical ($n = 13$), temperate ($n = 19$) forests (both deciduous and evergreen), tropical ($n = 2$) and temperate ($n = 2$) grasslands, Mediterranean ($n = 2$) and other ($n = 3$) shrublands, a savanna ($n = 1$), and Arctic tundras ($n = 4$). While North American and forested sites predominate, every continent except Antarctica is represented. All data and a complete list of citations are available online (see Supplementary material).

To estimate parameters of the scaling relationships between phytomass and nutrient content, NPP, and nutrient productivity, we utilize reduced major axis regression (RMA, a.k.a. model II or standardized major axis regression) on log-transformed variables. RMA minimizes residual variation in both variables (Isobe *et al.* 1990; Sokal & Rohlf 1995) and is more appropriate than ordinary least squares regression for describing functional relationships among variables when neither is clearly independent, as is the case here. To compare scaling relationships (i.e. the values of the exponents and coefficients) between the two nutrients, we used a recently developed likelihood ratio (LR) test analogous to analysis of covariance of ordinary least squares regression (Warton & Weber 2002). Where exponents were not significantly different (i.e. $P > 0.05$ in the LR test) we report the common slope estimate of the exponent based on both nutrients.

RESULTS

Data for both N and P content scale allometrically with total phytomass with exponents indistinguishable from one another and from the predicted $3/4$ (Fig. 1a, separate slope LR = 0.345, $n_P = 43$, $n_N = 40$, $P = 0.56$, common exponent: 0.76, 95% CI: 0.70–0.84). Thus, as predicted, and in contrast with the observed scaling at the leaf level, whole community N scaled isometrically with P (Fig. 1b, exponent: 0.98, 95% CI: 0.85–1.12) and N : P was invariant (i.e. uncorrelated) with total phytomass (Fig. 1c, $r = -0.083$, $n = 39$, $P = 0.61$). Productivity varies allometrically with total phytomass, but the exponent is significantly shallower than that predicted by the theory (Fig. 2a, $n = 42$, exponent: 0.46, 95% CI: 0.37–0.56). This, in turn, implies that nutrient productivity is not a constant but actually declines with increasing total phytomass. However, as the RMA regression exponents are not scaled by the correlation coefficients between variables (Isobe *et al.* 1990; Sokal & Rohlf 1995), there is no guarantee that the nutrient productivity exponent will be exactly $0.46 - 0.76 = -0.30$. Indeed, N and P share a common, negative nutrient productivity exponent [Fig. 2b, separate slope LR = 0.166, $n_P = 40$, $n_N = 38$, $P = 0.68$, common exponent: -0.50 , 95% CI: $-(0.59-0.42)$].

DISCUSSION

Regularities have been noted relating phytomass to productivity and nutrient stocks in crops and natural communities (Peters 1980; Shaver & Chapin 1991; Lemaire *et al.* 1992). However, to our knowledge, these ‘ecosystem allometries’ have never been shown to hold generally across such a

diverse array of plant communities, including temperate and tropical forests, shrublands, grasslands, and tundras, and over such a wide range of total phytomass.

The isometric scaling of ecosystem-level N and P content contrasts with the $3/4$ power scaling observed in leaves (Wright *et al.* 2004; Niklas *et al.* 2005), which implies that the ecosystem allometry is primarily driven by the allometric patterns of whole plant biomass allocation, with residual variation related to the nutrient content of metabolically active plant tissues in the community. The intercept values $\left[\left(\beta_c n_K^{1/4} \right) / \Omega_K^{3/4} \right]$ appear to be highly constrained across communities, with a value of 0.033 for N ($\text{gN m}^{-2} / M_{\text{tot}}^{0.76}$, 95% CI: 0.018–0.061) and 0.0028 for P ($\text{gP m}^{-2} / M_{\text{tot}}^{0.76}$, 95% CI: 0.0015–0.0053), when normalized to $M_{\text{tot}} = 1 \text{ g m}^{-2}$. Data on the geometric mean nutrient content of leaves (Wright *et al.* 2004) suggest that, on average, β_c should be ≈ 0.019 for N and 0.0011 for P. In turn, the other component of the intercept term $\left[n_K^{1/4} / \Omega_K^{3/4} \right]$, which is related to the range of plant sizes found in the community, is further constrained to a value on the order of 1–3, which is not unrealistic (see Supplementary material).

The relationship between the intercept and leaf nutrient content also implies that residual variation in the ecosystem-level nutrient allometry may be related to biogeographical gradients in leaf nutrient content (Reich & Oleksyn 2004; Kerkhoff *et al.* 2005). Based on an analysis of a subset of the data used here and species-level leaf data, Kerkhoff *et al.* (2005) suggest that the response of NPP to (principally latitudinal) gradients in growing season temperature might be mediated by inter-related changes in N : P and nutrient productivity. Here, we demonstrate that variation in nutrient productivity is due at least in part to

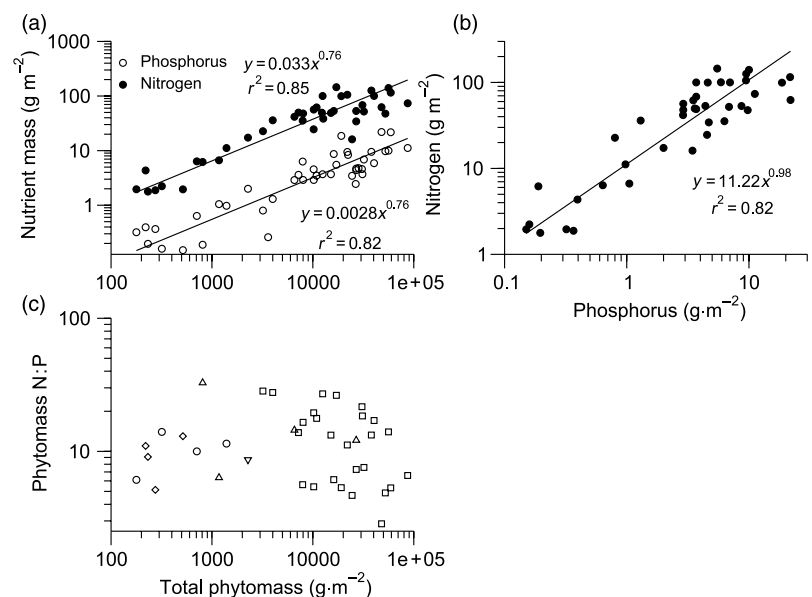


Figure 1 (a) The ecosystem allometry of nutrient content for nitrogen (N, filled circles) and phosphorus (P, open circles) in diverse plant communities. (b) Nitrogen scales approximately isometrically with P across communities. (c) Total phytomass N : P is invariant to three orders of magnitude change in total phytomass, across grasslands (diamonds), tundras (circles), shrublands (up, triangles), a savanna (down, triangle) and forests (squares).

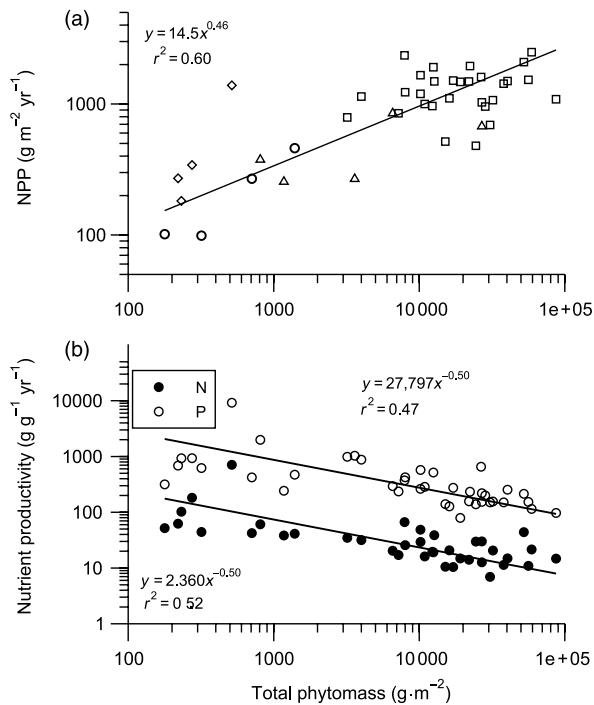


Figure 2 (a) Net primary productivity varies allometrically with total phytomass; symbols as in Fig. 1c. (b) Nutrient productivity decreases systematically with total phytomass for both N (filled circles) and P (open circles).

changes in community size structure and total phytomass. Disentangling these effects requires more detailed knowledge of (species abundance- and biomass-weighted) distributions of leaf N and P *within* plant communities and how they vary (or do not vary) *among* communities along the environmental gradients (Wright *et al.* 2001; Ackerly *et al.* 2002).

But why does the theory successfully predict nutrient content, where the assumptions are rather uncertain, yet overestimate the scaling of productivity, where the assumed individual allometries have much more empirical support? The intuitive idea that high-phytomass communities entail larger relative allocation to structural (non-metabolic) mass than to photosynthetic mass is already implicit in the model via the allometry of biomass partitioning (Table 1, Enquist & Niklas 2002). The term $\Omega_K^{-3/4}$, which was discounted above, would only increase the magnitude of the productivity exponent because it increases (albeit slowly) with the size range of the community, and it would theoretically apply to the nutrient allometry as well. On the other hand, systematic underestimation of productivity in high-biomass communities like forests (Clark *et al.* 2001) could generate a shallower scaling relationship than expected. However, the homoscedasticity of the data across the entire range of

phytomass (Fig. 2a) suggest that this sampling bias cannot fully explain our results.

Alternatively, the model assumptions may be incomplete. The broad theoretical and empirical support for the individual-level allometry of production (Niklas & Enquist 2001) suggests that the observed departure from the productivity prediction arises at the level of the plant community itself. In other words, allometric rates of production that have been observed to hold for individuals across *differing* environments may not approximate the allometric scaling of individuals *within* a local competitive size hierarchy (Keddy & Shipley 1989; Shipley & Keddy 1994; Keddy *et al.* 2002). Within a competitive size hierarchy, larger plants monopolize and exploit resources unavailable to smaller individuals. Such an asymmetry in resource competition (light limitation, resource preemption, etc.) will affect the realized return (productivity) on investment (biomass and nutrient stock).

Implicitly, the 'allometrically ideal' plant community model assumes that plants of all size classes have access to a common resource pool. In a local competitive size hierarchy, however, larger plants have access to larger soil nutrient and moisture pools, as well as less attenuated sunlight. Thus, if metabolically productive organs, e.g. leaves, represent a relatively fixed nutrient and material investment constrained in magnitude by plant size, a plant of a given size would likely realize a greater return on investment in a lower phytomass community, where it is near the top of the canopy, than in a higher phytomass community, in which it is subordinate to many larger individuals. Indeed, there are examples of small individuals in high-phytomass forests having a close to zero carbon balance as they 'wait' in the dark understory for an opening in the canopy (Dalling *et al.* 1999). This systematic decrease in the return on nutrient investment to smaller stature individuals with increasing total phytomass would depress productivity away from the predicted scaling relationship, without impacting the scaling of nutrient content, as observed in the data here. This hypothesis can be quantitatively incorporated into the allometric community model by introducing resource attenuation functions into the productivity summation (see eqns 1 and 2). Future work will explicitly elaborate on the effect of competitive size hierarchies and variation in the form of the size distribution on community-level processes.

We have shown that strong scaling regularities exist across physiognomically diverse plant communities (Figs 1 and 2), especially in nutrient content and nutrient productivity. The scaling exponents observed for N and P content match predictions from an allometrically idealized plant community model, and deviations from the predicted primary productivity and nutrient-productivity relationships are consistent with the presence of pronounced competitive

size hierarchies. Despite departures from the theoretical predictions in detail, the empirical data strongly suggest the existence of interlinked allometric constraints on individual plant resource use and population density, community phytomass and size structure, and the nutrient cycling and productivity of whole ecosystems (Cyr & Pace 1993; Enquist *et al.* 2003; Brown *et al.* 2004; Allen *et al.* 2005; Economo *et al.* 2005; Kerkhoff *et al.* 2005).

Regardless of their relation to theory, the presence of potentially global scaling rules for whole communities, in and of itself, has important implications for the modelling of coupled biogeochemical cycles in ecosystems. If these scaling relationships prove to be robust as more data accumulate, they will likely provide an important empirical test for global ecosystem simulations (Friedlingstein *et al.* 1999; Cramer *et al.* 2001; Moorcroft *et al.* 2001; Cowling & Field 2003), which are critical for predicting ecological responses to global change. In particular, the allometric (i.e. nonlinear) but predictable scaling of vegetation N and P with standing phytomass could be very useful in the validation of modelled or remotely sensed nutrient budgets.

Understanding the causes and consequences of plant functional diversity requires a more complete description of the fundamental trade-offs that underlie variation in plant strategies within and across communities (Westoby *et al.* 2002). The generality of allometric rules for production and biomass partitioning (Enquist *et al.* 1999; Enquist & Niklas 2001, 2002) suggest that whole plant size is one of the 'major axes' along which plant strategies vary. However, by focusing only on the single, albeit important, axis of plant size, we have ignored the many aspects of plant functional diversity that only emerge in light of a multivariate strategy space, incorporating variation in and trade-offs among multiple plant traits. At the same time, our findings support the premise that plant allometry provides a valuable tool for scaling from the distribution of plant traits to the dynamics of ecosystems, which is one of the keys to the development of a more predictive ecology (Enquist *et al.* 1998; Reich *et al.* 1999; Lavorel & Garnier 2002; Westoby *et al.* 2002; Diaz *et al.* 2004; Wright *et al.* 2004).

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SUPPLEMENTARY MATERIAL

The following supplementary material is available online for this article from <http://www.Blackwell-Synergy.com>:

Appendix S1 Derivation of eqs 1–3.

Appendix S2 Numerical results for the size distribution term Ω_K .

Appendix S3 Data on total phytomass, NPP, N and/or P content of ecosystems.

Figure S1 The size distribution term Ω_K as a function of the number of size classes in a community.

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