RESEARCH PAPER

Plant allometry, stoichiometry and the temperature-dependence of primary productivity

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ABSTRACT

Aim While physical constraints influence terrestrial primary productivity, the extent to which geographical variation in productivity is influenced by physiological adaptations and changes in vegetation structure is unclear. Further, quantifying the effect of variability in species traits on ecosystems remains a critical research challenge. Here, we take a macroecological approach and ask if variation in the stoichiometric traits (C: N: P ratios) of plants and primary productivity across global-scale temperature gradients is consistent with a scaling model that integrates recent insights from the theories of metabolic scaling and ecological stoichiometry.

Location This study is global in scope, encompassing a wide variety of terrestrial plant communities.

Methods We first develop a scaling model that incorporates potentially adaptive variation in leaf and whole-plant nutrient content, kinetic aspects of photosynthesis and plant respiration, and the allometry of biomass partitioning and allocation. We then examine extensive data sets concerning the stoichiometry and productivity of diverse plant communities in light of the model.

Results Across diverse ecosystems, both foliar stoichiometry (N : P) and 'nitrogen productivity' (which depend on both community size structure and plant nutrient content) vary systematically across global scale temperature gradients. Primary productivity shows no relationship to temperature.

Main conclusions The model predicts that the observed patterns of variation in plant stoichiometry and nutrient productivity may offset the temperature dependence of primary production expected from the kinetics of photosynthesis alone. Our approach provides a quantitative framework for treating potentially adaptive functional variation across communities as a continuum and may thus inform studies of global change. More generally, our approach represents one of the first explicit combinations of ecological stoichiometry and metabolic scaling theories in the analysis of macroecological patterns.

Keywords

Ecosystems, global ecology, gradients, growth-rate hypothesis, macroecology, nutrient productivity, scaling.

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INTRODUCTION

Geographic variation in terrestrial primary productivity is influenced by physiological and environmental processes operating over a wide range of scales (Rosenzweig, 1968; Schlesinger, 1991; Ehleringer & Field, 1993; Schulze *et al.*, 1994; Geider *et al.*, 2001; Roy *et al.*, 2001). Because species respond individualistically to

spatiotemporal environmental variation, increasing interest has been focused on how productivity and other biogeochemical processes are influenced by variation in species-specific plant traits (Schimel *et al.*, 1996; Chapin *et al.*, 1997; Weiher *et al.*, 1999; Diaz & Cabido, 2001; Moorcroft *et al.*, 2001; Lavorel & Garnier, 2002; Chapin, 2003; Diaz *et al.*, 2004). For example, at the leaf level, nitrogen content is an important determinant of

photosynthetic capacity (Field & Mooney, 1986; Reich *et al.*, 1997), and interspecific variation in nitrogen content significantly influences whole canopy rates of production and biomass turnover (Vitousek, 1982; Webb *et al.*, 1983; Schlesinger, 1991; Baldocchi & Meyers, 1998; Cebrian, 1999; Sterner & Elser, 2002). Further, leaf nitrogen content is also correlated with a suite of other functional traits describing a 'fast–slow' continuum of plant life history strategies (Westoby *et al.*, 2002; Wright *et al.*, 2004). However, scaling from the functional traits and strategies of plants to ecosystem processes remains challenging (Ehleringer & Field, 1993; Moorcroft, 2003).

Over the past few decades, the study of terrestrial productivity has proceeded from relatively straightforward correlative methods (e.g. the 'Miami model'; Lieth, 1975) to increasingly sophisticated biogeochemical simulation models, including the latest generation of dynamic global vegetation models (DGVMs; see Melillo *et al.*, 1995; Cramer *et al.*, 2001; Adams *et al.*, 2004). DGVMs and other recent modelling approaches are concerned explicitly with the effects of transient changes in the composition of plant communities (Moorcroft *et al.*, 2001; Moorcroft, 2003). Often, these models represent the functional diversity of plant communities using varying numbers of discrete functional types (Bondeau *et al.*, 1999; Adams *et al.*, 2004). Thus, a better understanding of how biogeographical variation in plant traits affects patterns of primary productivity has important implications for the study of global change (Diaz & Cabido, 1997; Chapin, 2003).

Interestingly, a variety of productivity models, using very different parameterizations and input data, produce reasonable (and reasonably similar) geographical, seasonal and interannual patterns of primary productivity (Melillo *et al.*, 1995; Cramer *et al.*, 1999; Cramer *et al.*, 2001). However, a recent review of several terrestrial vegetation models (Adams *et al.*, 2004) demonstrates that, despite similarities in output, the approaches differ substantially in how they model the various components of net primary productivity. Differences in the underlying mechanics of the models do not indicate shortcomings in any particular approach, because each model was designed to address a different problem. However, this lack of consensus does demonstrate that, while generalized quantitative theory exists for many of the components of productivity (Thornley, 1970; Farquhar *et al.*, 1980; Amthor, 2000), these have not been integrated fully into a common modelling framework.

Here, we depart from such dynamical systems models and instead develop macroecological theory concerning the basis of broad-scale patterns of variation in plant functional traits, community structure and primary productivity. Although our study shares commonalities with earlier, correlative approaches to understanding global patterns of vegetation properties and primary productivity (Jordan, 1971; Lieth, 1975; Webb *et al.*, 1983; Neilson, 1995), we are guided specifically by recent theoretical advances linking the effects of plant size (Enquist *et al.*, 1999; Enquist & Niklas, 2002; Niklas & Enquist, 2002a; Ernest *et al.*, 2003a), stoichiometric composition (Reiners, 1986; Agren & Bosatta, 1996; Cebrian, 1999; Sterner & Elser, 2002; Agren, 2004) and environmental temperature (Gillooly *et al.*, 2001, 2002; Enquist *et al.*, 2003; Brown *et al.*, 2004) on productivity. Our goal is not

to introduce an alternative dynamical model of primary productivity. Instead, we ask whether broad-scale variation in plant stoichiometry, plant community structure and primary productivity are quantitatively consistent with this new integrative framework. If so, the developing theory gains empirical support and may serve as a basis for more detailed models linking plant strategies and functional traits to ecosystem-level processes (Schimel *et al.*, 1996; Diaz & Cabido, 2001; Moorcroft *et al.*, 2001; Lavorel & Garnier, 2002; Chapin, 2003). If not, it provides an opportunity to refine our assumptions and improve the theory.

METHODS

A scaling model of primary productivity

We derive a theory of steady state primary productivity in plant communities based on scaling up the productivity of individual plants. Fundamentally, our formulation is based on a classical model interrelating plant production, respiration and growth (Thornley, 1970; Penning de Vries, 1975; Amthor, 1984). The total (net) growth of a plant, G_T in $g \times time^{-1}$, is proportional to the cumulative balance of total photosynthetic assimilation (A_T, $g \times time^{-1}$) and maintenance respiration (R_m, $g \times time^{-1}$):

$$G_T = Y_G(A_T - R_m), \tag{1}$$

and the term Y_G (unitless) describes the realized growth yield from net mass gain (Amthor, 2000). More specifically, the growth yield is defined as $Y_G \equiv \dfrac{B_G}{B_G + R_G}$, where B_G is the rate at which photosynthetic products are assimilated into the functioning plant body via biosynthesis and R_G is the respiratory cost of that process, both in units of $g \times time^{-1}$ (Thornley, 1970).

To model the dependence of growth on plant size, stoichiometric composition and temperature we must model the dependencies of photosynthetic production, maintenance respiration and growth yield. Not all of these dependencies have been described fully, and interactions among them remain largely unexplored. Thus, the model derived below represents a reasoned hypothesis, rather than a definitive, synthetic statement.

Effects of plant size

Allometric theory predicts, and empirical data demonstrate, that both photosynthetic production and whole plant growth are directly proportional to leaf mass of individual plants:

$$G_T \propto A_T = \mu_L M_L, \tag{2}$$

where μ_L ($g \times g$ leaf$^{-1} \times time^{-1}$) is the leaf mass-specific photosynthetic production rate ($dM/M_L dt$), which is independent of whole plant mass (Niklas & Enquist, 2002a). Variability in the leaf mass-specific production μ_L probably reflects both environmental constraints and potentially adaptive taxon-specific differences in photosynthetic capacity (see below). Further, leaf mass varies allometrically with total plant mass, M_T, as $M_L = \beta_L M_T^{3/4}$

where the allometric coefficient β_L has units g leaf × g plant$^{-3/4}$. From the common allometric scaling of net growth and photosynthetic production, eqn 1 implies that both respiratory components must also scale as the 3/4 power of whole-plant mass, as predicted by allometric theory (Banavar *et al.*, 1999; West *et al.*, 1999) and observed across almost all organisms, i.e. $G_T \propto A_T \propto R_m \propto M_T^{3/4}$ (Ernest *et al.*, 2003b; Savage *et al.*, 2004). It also implies that growth yield should be independent of plant mass, $Y_G \propto M_T^0$.

Stoichiometric effects and interactions with plant size

Plant functioning is also greatly affected by stoichiometric composition, that is the relative concentrations of various macro- and micronutrients in plant tissues (Chapin *et al.*, 1986; Agren, 1988, 2004; Sterner & Elser, 2002). Here we focus in particular on nitrogen (N) and phosphorus (P), as they are the nutrients that most commonly limit plant growth and primary productivity (Chapin *et al.*, 1986; Agren, 1988, 2004; Gusewell, 2004). The role of N and P in the component processes of growth probably depends on the relative availability of the two resources as well as the underlying biochemistry (Chapin *et al.*, 1986; Agren, 1988, 2004; Sterner & Elser, 2002; Gusewell, 2004). Further, the effects of nutrient concentrations (i.e. dry mass fractions, g nutrient × g biomass^{-1}) on the terms of eqn 1 may be either independent of or colinear with the effects of whole plant mass (Elser *et al.*, 1996; Nielsen *et al.*, 1996; Cebrian, 1999). Distinguishing these two types of effects requires an explicit hypothesis about how whole-plant nutrient concentration, F_T, varies with whole-plant mass.

Whole-plant nutrient concentration depends on the fraction of biomass allocated to the principal plant organs, i.e. leaves, stems and roots, and their component nutrient concentrations. While foliar nutrient concentrations, F_L, vary considerably (~30–80-fold across species (Wright *et al.*, 2004), they are generally independent of whole-plant size. However, leaves make up a decreasing proportion of plant mass with increases in plant mass (M_T); specifically $M_L/M_T = \beta_L M_T^{-1/4}$ (Niklas & Enquist, 2002b). In contrast, stem and root mass (M_S and M_R, respectively) scale isometrically with whole-plant mass (i.e $M_S = \beta_S M_T$ and $M_R = \beta_R M_T$, so each makes up a relatively constant proportion of M_T, β_S and β_R (in g organ × g plant), respectively (Niklas & Enquist, 2002b). However, as plants increase in size, their stem and root systems are increasingly dominated by nutrient-poor, carbon-rich woody tissue. Here, we assume that the nutrient concentration of stems and roots reflects the metabolically active fraction of the organ masses, and will thus decrease as the −1/4 power of organ mass, i.e. the nutrient concentrations of roots and stems (F_R and F_S, respectively, in g nutrient × g organ) decrease as $F_R = f_R M_R^{-1/4} = \beta_R^{-1/4} M_T^{-1/4} f_R$ and $F_S = f_S M_S^{-1/4} = \beta_S^{-1/4} M_T^{-1/4} f_S$, where again M_T is whole-plant mass and the coefficients (f_S and f_R, in units of g nutrient × g organ$^{-3/4}$) describe maximum organ nutrient concentrations observed at some minimal organ mass, independent of whole-plant mass. Taken together with the allometries of biomass allocation (Niklas & Enquist, 2002b), these expressions yield a function relating whole plant nutrient concentration to whole plant mass:

$$F_T = \frac{1}{M_T}(F_L M_L + F_S M_S + F_R M_R) = (\beta_L F_L + \beta_S^{-1/4} f_S + \beta_R^{-1/4} f_R)M_T^{-1/4} \tag{3}$$

Based on eqn 3, at the whole-plant level, all three components of eqn 1, i.e. photosynthetic assimilation, respiration and net growth, should vary linearly with whole plant nutrient content (in g nutrient, $F_T M_T \propto M_T^{3/4}$), over a wide range of plant masses. Indeed, while maintenance respiration, R_m, is often considered a linear function of total plant mass, it is frequently better correlated with plant nitrogen content (Amthor, 1984, 2000). Similarly, the observation that whole-plant relative growth rate ($RGR = G_T/M_T \propto M_T^{-1/4}$, time^{-1}) varies linearly with nutrient concentration (Amthor, 1984, 2000; Agren, 1988; Agren & Bosatta, 1996; Nielsen *et al.*, 1996; Sterner & Elser, 2002) is consistent with our basic assumptions of plant allometric scaling of growth, respiration and nutrient content. Finally, if both N and P, with concentrations F_T^N and F_T^P, respectively, share a common scaling relationship, whole-plant N : P (unlike C : P or C : N) should be independent of plant mass, i.e. $F_T^N/F_T^P \propto M^0$ (Gusewell, 2004).

There are also other size-independent effects of plant stoichiometric composition, such as the dependence of photosynthetic capacity on foliar nitrogen concentration (Field & Mooney, 1986; Reich *et al.*, 1997). These size-independent effects can be incorporated into the allometric coefficients for the component processes of eqn 1. Here, we incorporate the effects of leaf nutrient concentration on photosynthetic production, because this relationship is both clearly independent of plant size and empirically well defined. As a corollary of the 'growth-rate hypothesis' (Elser *et al.*, 2003; Agren, 2004), we also put forward the hypothesis that growth yield, Y_G, depends importantly on whole plant N : P.

A generalized function relating leaf nutrient concentration to whole-plant production rates is (Agren & Bosatta, 1996; Sterner & Elser, 2002):

$$\mu_L = \phi_L F_L^N. \tag{4}$$

Here, μ_L is again the leaf mass-specific photosynthetic production rate and ϕ_L is the efficiency of leaves in using nitrogen to assimilate mass (i.e. the photosynthetic nitrogen use efficiency $PNUE = \mu_L/F_L^N$, g × g leaf N^{-1} × time^{-1}), which itself may change with nutrient concentration (Field & Mooney, 1986; Reich *et al.*, 1997; Sterner & Elser, 2002; Wright *et al.*, 2004). Equation 4 assumes balanced growth, i.e. $dP/Pdt = dN/Ndt = dM_T/M_Tdt$, which is biologically reasonable at the leaf level and consistent with the whole plant nutrient allometry of eqn 3.

Because eqn 4 applies to leaves independent of whole-plant mass, it can be inserted into eqn 2 to describe whole-plant photosynthetic production rate with plant mass and leaf nutrient concentration:

$$A_T = \beta_L \phi_L F_L^N M_T^{3/4}. \tag{5}$$

Further, we can incorporate the dependence of maintenance respiration on whole-plant nitrogen content (Amthor, 2000):

$$R_m = \phi_m F_T^N M_T. \tag{6}$$

Here, ϕ_m (units g × g nitrogen^{-1} × time^{-1}) expresses the maintenance costs realized at the whole-plant level per unit nitrogen content. This formulation reflects the strong dependence of maintenance respiration on the rate of protein turnover in metabolically active tissues (Amthor, 1984), under the assumption that the whole-plant protein pool is proportional to whole-plant nitrogen content.

While $A_T - R_m$ represents the net mass gain, the growth yield, Y_G depends on the rate of biosynthesis of new tissue and the respiratory cost of synthesis. Because protein synthesis is the basis of growth, and because ribosomes entail a substantial P investment (Sterner & Elser, 2002; Agren, 2004), we hypothesize that the biosynthetic component of growth-yield increases with whole-plant P, i.e. $B_G = c_B F_T^P M_T$. Similarly, because the respiratory cost of biosynthesis depends on the living mass it is proportional to whole plant N, i.e. $R_G = c_R F_T^N M_T$. The coefficients c_B and c_R are rate constants describing the biosynthesis per unit plant P (c_B units: g × g P^{-1} × time^{-1}) and the respiratory cost of biosynthesis per unit plant N (c_R units: g × g N^{-1} × time^{-1}). Substituting into the expression for Y_G above, the realized growth yield depends on whole plant N : P, independent of plant mass:

$$Y_G = c_G \frac{F_T^P}{F_T^N}, \tag{7}$$

where the coefficient is $c_G = \dfrac{c_B}{c_B \dfrac{F_T^P}{F_T^N} + c_R}$, with units of g N × g P^{-1},

also independent of whole-plant mass.

Substituting eqns 5–7 into eqn 1 yields an expression for whole-plant growth as a function of whole plant mass and tissue stoichiometry:

$$G_T = c_G \frac{F_T^P}{F_T^N}(\phi_L F_L^N \beta_L M_T^{3/4} - \phi_m F_T^N M_T). \tag{8a}$$

Consolidating whole-plant mass by using eqn 3 to express F_T^N and rearranging yields:

$$G_T = c_G \frac{F_T^P}{F_T^N}\left(F_L^N \beta_L M_T^{3/4} \phi_L \left(1 - \frac{\phi_m}{\phi_L}\left(1 + \frac{\beta_S^{-1/4} f_S^N + \beta_R^{-1/4} f_R^N}{F_L^N \beta_L}\right)\right)\right) \tag{8b}$$

Thus, this plant growth model, which integrates classic theory of production–respiration balance in plants (Amthor, 2000) with more recent allometric and stoichiometric insights, predicts that plant growth rate should increase as the 3/4-power of whole plant mass, as observed across unicellular and multicellular autotrophs (Niklas & Enquist, 2001). Growth rate should also increase with increased allocation to leaves (β_L), increased leaf N (F_L^N) and PNUE (ϕ_L); and it should decrease with increasing maintenance costs (ϕ_L), allocation of mass and nutrients to non-photosynthetic organs (i.e. $\beta_S^{-1/4} f_S^N + \beta_R^{-1/4} f_R^N$) and whole-plant N : P [i.e. it increases with $\dfrac{F_T^P}{F_T^N}$, in accordance with the 'growth rate hypothesis' (Sterner & Elser, 2002; Elser *et al.*, 2003; Agren, 2004)]. Of course, all these predictions assume that no other significant tradeoffs invalidate the model assumptions.

Kinetic effects of temperature

Finally, we incorporate the effects of environmental temperature on the components of eqn 1. Maintenance respiration generally responds exponentially to temperature (Amthor, 1984) and we assume a 'Boltzmann' response of the form $R_m \propto e^{\frac{-E_R}{kT}}$, where E_R is the activation energy (eV) of respiratory metabolism, k is Boltzmann's constant (8.6×10^{-5} eV × K^{-1}) and T is absolute temperature measured in Kelvins (K). Recently, it has been shown that such a temperature response, with an average activation energy of ~0.6 eV, may be common to many, if not all, organisms (Gillooly *et al.*, 2001, 2002; Enquist *et al.*, 2003; Ernest *et al.*, 2003b; Brown *et al.*, 2004). However, whether such a response is observed on longer timescales or across environments may be mediated by environmental temperature adaptation and acclimation (Conover & Schultz, 1995; Larigauderie & Korner, 1995; Dewar *et al.*, 1999; Enquist *et al.*, 2003; Gifford, 2003; Allen *et al.*, 2005).

While plant growth is driven by respiration, it is often limited by photosynthetic production. On a physiological level, net photosynthesis (C assimilation less photorespiration) generally responds hyperbolically to temperature, declining at high temperatures due either to the deactivation of component reactions or because of changes in the balance of assimilation and photorespiration (Cannell & Thornley, 1998; Leuning, 2002). However, across environments, photosynthetically optimal temperatures are generally correlated with the temperature range experienced by plants during the growing season (Larcher, 1995). Here, because our theory is meant to be broadly comparative, we ignore photosynthetic deactivation at high temperatures and also model the temperature as an exponential of the same form as for maintenance respiration. We also do not distinguish between the carboxylation and electron transport components of photosynthesis, and use the average activation energy value of the two processes drawn from a recent review (E_P~0.7 eV) (Leuning, 2002). Thus, we assume implicitly that (*i*) average growing season temperatures rarely exceed photosynthetic optima and (*ii*) that for modelling purposes, a generalized response ignoring potential interspecific differences is adequate. Analogous arguments have been made in models of metabolic rate for animals acclimated to different temperature ranges (Charnov & Gillooly, 2003; Savage, 2004).

Alternatives to the 'Boltzmann' temperature response proposed here range from simple hyperbolic functions (Cannell & Thornley, 1998; Thornley, 2002; Lenton & Huntingford, 2003) and modified exponentials incorporating deactivation (Leuning, 2002) to complex, detailed biochemical models (Farquhar *et al.*, 1980; Bernacchi *et al.*, 2003; Allen *et al.*, 2005). The principal qualitative difference is that, while the Boltzmann equation predicts a monotonic temperature increase over the biologically meaningful range of temperatures, the more complicated models predict a precipitous decrease above some optimal temperature. The aggregated time-scale of our model focuses on average growing season temperature (see below). Thus, we examine the response of productivity over a temperature range that is generally constrained relative to the physiological limits of photosynthesis.

Over much of this range (i.e. up to 25 or 30 °C) most models would predict some form of increasing function for photosynthesis (Adams *et al.*, 2004), so they largely represent alternatives of degree rather than direction. In any case, if the distinction is quantitatively important, it should be evident in decreased productivity response at extremely high growing season temperatures.

Including our exponential kinetic assumptions into eqn 8 completes the whole-plant growth model. The notation can be simplified significantly if we note, from eqn 3, that

$$\left(1 + \frac{\beta_S^{-1/4} f_S^N + \beta_R^{-1/4} f_R^N}{F_L^N \beta_L}\right) = \frac{F_T^N M_T}{F_L^N M_L},$$ which is simply the (unitless)

ratio of whole-plant to leaf nitrogen content, independent of whole-plant mass. Therefore,

$$G_T = c_G \frac{F_P^P}{F_P^P}\left(F_L^N \beta_L M_P^{3/4} e^{\frac{-E_P}{kT}} \phi_L \left(1 - \frac{\phi_m}{\phi_L} \frac{F_T^N M_T}{F_L^N M_L} e^{\frac{E_P - E_R}{kT}}\right)\right). \quad (9)$$

This model, generates many predictions of interest at the plant level, which will be evaluated in a separate work. Here, we use it as a basis for investigating broad-scale patterns of productivity and the nutrient economy of whole-plant communities. In the present context an important feature that greatly simplifies interpretation is the fact that, at least theoretically, the final term

in the model, $\left(1 - \frac{\phi_m}{\phi_L} \frac{F_T^N M_T}{F_L^N M_L} e^{\frac{E_P - E_R}{kT}}\right)$, or Φ_T hereafter, is unitless,

independent of plant mass, and nearly independent of temperature (because $E_P \cong E_R$). Thus it will not effect any subsequent predictions evaluated here. Because it represents losses due to maintenance respiration, the constrained nature of Φ_T is consistent with the observation that, at the whole-community level, respiration is a significantly constrained fraction of production (Waring *et al.*, 1998).

Aggregating to the plant community level

Annual total primary productivity (g × area⁻¹ × year⁻¹) in a plant community is influenced by the density of plants and their respective productivities, or growth rates G_T. Specifically, the total net primary productivity can be modelled as the sum of plant growth

over all individuals in the community, $G_{Tot} = \sum_{i=1}^{z} \alpha_i \left(\sum_{j=1}^{s_i} a_{ji} G_{T,ji}\right)$,

where the first summation is over all plants binned into Z size classes, regardless of species, and α_i is the proportion of total

community mass falling within size class i; that is, $\alpha_i \equiv \frac{m_i n_i}{M_{Tot}}$,

where m_i is the characteristic plant mass and n_i is the density of individuals (area⁻¹) of size class i, and M_{Tot} is total community plant biomass per unit area, called 'phytomass' hereafter. The second, nested summation describes functional variation across the s_i species in size class i, and a_{ji} is the relative abundance of species j in size class i. This model is similar to other recent models relating species-functional variation to productivity (Lavorel & Garnier, 2002). However, our model explicitly accounts for community size structure as well as species composition.

To estimate annual whole-community rates of production, we substitute the individual plant growth model (eqn 9) into the expression for net production and multiply by growing season length (l_S, measured in mo × y⁻¹) to yield a primary productivity equation

$$G_{Tot} = l_S \beta_L e^{\frac{-E_P}{kT_S}} M_{Tot} \sum_{i=1}^{z} \left(\alpha_i m_i^{-1/4} \sum_{j=1}^{s_i} c_{Gj} \frac{F_{Tj}^P}{F_{Tj}^N} \phi_{Lj} F_{Lj}^N \Phi_{Tj} a_{ji}\right). \quad (10)$$

Here, G_{Tot} is the annual rate of net primary production (mass × area⁻¹ × y⁻¹) and T_S is mean growing season temperature. The structure of eqn 10 describes a hierarchy of influences on net primary productivity, and effectively embodies our underlying assumptions. The terms that are (assumed to be) independent of plant mass and species identity appear as coefficients external to the summations. Those that are mass dependent, but independent of species identity (e.g. the community size distribution descriptor α_i) are within the first summation, while those that are species-specific but mass-independent (e.g. leaf N concentration F_L^N, all subscripted j) occur within the second, nested summation.

In order to have comparable measures of productivity across climatically diverse vegetative communities we divide eqn 3 through by l_S to find the production rate per month of the growing season, G_{Tot}^S. Further, because little information is available concerning the distribution of leaf functional traits within plant communities (Reich *et al.*, 1997; Wright *et al.*, 2001), we generalize the theory by using community-wide, abundance- and biomass-weighted averages of the species-specific traits, which yields:

$$G_{Tot}^S = \beta_L e^{\frac{-E_P}{kT_S}} M_{Tot} \left(c_G \frac{F_T^P}{F_T^N} \phi_L F_L^N \Phi_T\right) \sum_{i=1}^{z} (\alpha_i m_i^{-1/4}). \quad (11)$$

It is important to note that the term in angle brackets is the ensemble biomass- and abundance-weighted average of the product of all the terms, i.e. the mean of the product, and it is not simply equal to the product of the means. However, all else being equal, increasing the mean of one of the component terms cannot decrease the mean product. The exact form of the relationship between the mean of the product and the product of the means will depend on the covariance among the terms (Pasztor *et al.*, 2000; Savage, 2004).

A summation similar to that of eqn 10 can be used to derive the nutrient concentration of the entire plant community:

$$F_{Tot} = \left(\beta_L F_L + \beta_S^{-1/4} f_S + \beta_R^{-1/4} f_R\right)\left(\sum_{i=1}^{z} \alpha_i m_i^{-1/4}\right). \quad (12)$$

Here again, the angle brackets indicate biomass- and abundance-weighted averages for the nutrient concentration parameters. Further, it is useful to note that whole-community leaf mass per unit

ground area, L_{Tot}, can be described by $L_{Tot} = \beta_L M_{Tot} \sum_{i=1}^{z} \alpha_i m_i^{-1/4}$.

Taken together with eqn 11, these two expressions demonstrate that the theory derived here is consistent with several previously observed patterns in ecosystems.

First, as at the whole-plant level, community leaf mass is proportional to community-level rates of resource use, e.g. canopy transpiration (Webb *et al.*, 1983). At steady state, resource use will be in equilibrium with the rate of limiting resource supply. Therefore, our model implicitly entails the well-documented positive correlations of net productivity with leaf area index

(as LAI $\propto L_{Tot}$), evapotranspiration and site water balance (Rosenzweig, 1968; Lieth, 1975; Grier & Running, 1977; Webb *et al.*, 1983; Schlesinger, 1991; Neilson, 1995). Thus, we effectively assume that community size structure and total leaf mass (L_{Tot}) can be considered fixed by environmental factors that affect total community phytomass and its size distribution (e.g. water balance, disturbance regimes) independent of growing season temperature and leaf stoichiometry (Enquist *et al.*, 2003).

Secondly, the model is also consistent with the less-often noted correlation between leaf area index and canopy N concentration (Pierce *et al.*, 1994; Baldocchi & Meyers, 1998; Eamus & Prior, 2001; Green *et al.*, 2003). Because both are linearly dependent on the size distribution term $\sum_{i=1}^{z} \alpha_i m_i^{-1/4}$, our theory predicts that this correlation should hold even across plant communities that differ more substantially in size structure (Baldocchi & Meyers, 1998; Eamus & Prior, 2001). The relationship between LAI and total nitrogen has important implications for understanding variation in radiation use efficiency (Green *et al.*, 2003), which is another fundamental component of many vegetation productivity models (Haxeltine & Prentice, 1996; Landsberg & Waring, 1997; Gower *et al.*, 1999; Ruimy *et al.*, 1999; Goetz *et al.*, 2000). For simplicity, we ignore variation in radiation parameters (i.e. input, efficiency and canopy attenuation) in this preliminary model.

Theoretical predictions

In addition to being consistent with many existing plant community and ecosystem-level observations, the theory developed here (e.g. eqn 11) provides a quantitative framework for predicting how net primary productivity (G_{Tot}^S) should vary with changes in growing season temperature, community size structure and both foliar and phytomass nutrient concentrations and for establishing interdependencies among these potentially important determinants of primary productivity. For example, substituting the expression for L_{Tot} and rearranging terms, eq. (11) can be written as:

$$\ln(G_{Tot}^S) = \frac{-E_p}{1000k}\left(\frac{1000}{T_S}\right) + \ln\left(c_G \frac{F_T^P}{F_T^N} \phi_L F_L^N \Phi_T L_{Tot}\right). \tag{13}$$

Written in this form, our theory makes a clear link between variation in vegetation nutrient concentrations and other functional traits (in the second term) and the effect of temperature (in the first term) on primary productivity. Thus, the predicted relationship between productivity and temperature depends on covariation between temperature and the other plant parameters.

If we assume that none of the plant parameters vary with temperature and that productivity is limited by the kinetics of photosynthesis, the model predicts that plotting $\ln(G_{Tot}^S)$ vs. inverse temperature ($1000/T_S$, a so-called 'Arrhenius plot') should yield a linear relationship with a slope of $-E_p/1000k$, reflecting the activation energy of photosynthetic metabolism (Gillooly *et al.*, 2001). Under this restrictive assumption, the predicted slope should be $-E_p/1000k \approx -8$ K, all else being equal, with residual variation related to the other variables.

Alternatively, if the components of the second term increase systematically with temperature, the observed statistical relationship between net primary productivity and inverse temperature ($\ln(G_{Tot}^S)$ and $1000/T_S$) would be shallower. Thus, systematic changes in phytomass N : P, foliar nitrogen concentration or photosynthetic efficiency could modify the temperature dependence of primary productivity. While plant stoichiometry and other functional traits are known to vary across environments (Korner, 1989; Yin, 1993; Reich *et al.*, 1997; Wright *et al.*, 2001), until recently relatively few studies have addressed patterns of variation across global-scale gradients and across biomes (Jordan, 1971; McGroddy *et al.*, 2004; Reich & Oleksyn, 2004; Wright *et al.*, 2004). Variation in plant nutrient concentrations may simply reflect gradients in nutrient availability, or it may represent adaptation to contrasting environmental conditions, including temperature gradients (Korner, 1989; Yin, 1993; Conover & Schultz, 1995; Reich *et al.*, 1997; Woods *et al.*, 2003; McGroddy *et al.*, 2004; Reich & Oleksyn, 2004). The relative roles of these two alternatives and their influence on patterns of productivity remain important open questions.

It is important to note that we do not assume that temperature is the single best (or even a particularly good) predictor of global patterns of primary productivity. Because of its links to resource supply and LAI (Webb *et al.*, 1983; Chapin, 2003), productivity is better described statistically by variation in water balance and light availability than it is by temperature (Grier & Running, 1977; Neilson, 1995; Baldocchi & Meyers, 1998; Eamus & Prior, 2001). The relationship between total phytomass, LAI and primary productivity has been reviewed extensively elsewhere (Webb *et al.*, 1983; Neilson, 1995). Similarly, recently published data on leaf-level functional traits indicate that potential photosynthetic nitrogen use efficiency (i.e. ϕ_L) should vary modestly, if at all, with site temperature (Wright *et al.*, 2004). Thus, we focus here on the parameters that should vary largely independently of community size structure and assess whether or not the variation in the stoichiometric characteristics of leaves and whole plant communities along broad gradients in temperature is consistent with theoretical predictions. We examine extensive data compiled from the literature to detail how plant stoichiometry (on both a foliar and community phytomass basis) and productivity vary across latitudinal gradients in growing season temperature and duration. Because the variables are generally log-normally distributed, and to ease comparison with the predictions of eqn 13, we plot variables on a log scale as a function of $1000/T_S$, whenever reliable estimates of temperature are available.

Empirical data

We evaluated theoretical relationships among model parameters using several global-scale data compilations, with estimates of growing season length and temperature drawn from a recent, high-resolution global climatological study (New *et al.*, 2002). We detail each of the data compilations below. All data sets are available online either from the original data providers or as a supplement to the present work.

Foliar stoichiometry data

To assess the global distribution of foliar nutrient content and its covariance with temperature, we compiled an extensive database documenting the N : P stoichiometry of foliage collected under field conditions. Because we could often only estimate coarsely the geographical locations of many of the study sites (i.e. within 1–2 degrees) from published site descriptions, we use latitude as a surrogate for growing season temperature. Any observations that had only regional designation (e.g. China or Pacific Northwestern USA) were omitted from the analysis. Although the theory contains a foliar term only for nitrogen, we examined variation in both nutrients and their ratio, as stoichiometric variation at the leaf-level may reflect variation in the other plant organs as well (Gusewell, 2004; Kerkhoff *et al*. unpublished data). A total of 2216 observations were included, representing 1054 plant species in 175 plant families, including angiosperms, gymnosperms and pteridophytes spanning all major growth forms. Data are available as Appendix S1 in Supplementary materials, and a full citation list of data sources is available from the authors.

Global primary productivity data

We examined the temperature-dependence of primary productivity using a global compilation of above ground net primary production (ANPP) data for natural ecosystems (Olson *et al.*, 2001) compiled for the Global Primary Production Data Initiative (GPPDI). We used only data for natural ecosystems, i.e. no agricultural or plantation sites. We included both classes 'A' and 'B' data, which were distinguished based on the extensiveness of metadata. Separate analyses on the two classes do not affect our results. More information and the full data set are available online at www.daac.ornl.gov. The analysis included a total of 1599 sites representing 11 different vegetation types.

Estimation of growing season length

We estimated growing season length using monthly values for mean temperature, diurnal temperature range and mean precipitation (PPT) for each site were drawn from a global 10′ resolution gridded climatology (New *et al.*, 2002). Annual estimates from the gridded data were highly correlated with mean annual values of temperature and precipitation reported in the GPPDI database ($r^2 = 0.91$ and 0.71, respectively). We then used Thornthwaite's index of potential evapotranspiration (PET) to calculate a moisture index (MI = (PPT–PET)/PET) to describe site water balance on a monthly time-scale. A month was included in the growing season as long as it was not too cold (minimum T < 0 °C) or too dry (MI < −0.95). Mean growing season temperature was then estimated as the mean temperature across the months included in the growing season, while monthly NPP was estimated by dividing reported annual values by the estimated length of the growing season. The moisture index cut-off was chosen by calibrating the estimated season length against published phenology data for a seasonally dry chaparral site

(Gray & Schlesinger, 1981). Using only the minimum temperature criterion did not affect qualitatively any of our results.

Whole plant community data

Whenever available, we also compiled data on standing phytomass, NPP and vegetation nutrient (N and/or P) content of whole plant communities from published sources. Studies reporting all of the variables were relatively rare and thus our sample size is limited to 33 sites. Fortunately, the communities span a variety of environmental conditions and functional types, from arctic tundra to tropical forests. Nutrient data were combined for all living vegetative components (i.e. roots, shoots and leaves, but not litter or reproductive organs) and divided by the total vegetation biomass to get find whole-system nutrient concentrations. Here, we also examined variation in each nutrient separately, as well as their ratio. NPP was adjusted for growing season length, as described above. Finally, to assess the level of productivity returned per unit nutrient invested, we divided net productivity by the standing stock of each nutrient to find the so-called 'nutrient productivity' (Agren, 1988). Data are available as Appendix S2 in Supplementary materials, and a full citation list of data sources is available from the authors.

RESULTS

Leaf-level stoichiometry

In order to assess latitudinal variation in foliar nutrient content, we plotted values of leaf N, P and N : P (i.e. F_L^N, F_L^P, expressed as percentage dry mass and their ratio), averaged within 5-degree bands of absolute latitude. Assessed individually, neither foliar nitrogen nor phosphorus varied systematically with latitude (Fig. 1a, d.f. = 16, F = 0.50, 1.72 for N and P, respectively). However, N : P decreased systematically (Fig. 1b, d.f. = 16, F = 26.1). Thus, P concentration approximately doubled relative to N across 80° of latitude. Although foliar stoichiometry varied considerably at any given latitude, regression on the raw data demonstrated that the latitudinal decrease in N : P was not merely an artefact of the binning procedure (d.f. = 1401, F = 166.2, $P < 5 \times 10^{-35}$; see Appendix S3 in Supplementary material).

Community stoichiometry and nutrient productivity

As in the leaf-level analysis, phytomass N-concentration did not change systematically with temperature (d.f. = 31, F = 0.01, P = 0.9). However, phytomass P-concentration increased exponentially from warm to cold sites (d.f. = 32, F = 6.8, P = 0.01). Together, these patterns resulted in an exponential decrease in phytomass N : P with inverse growing season temperature (Fig. 2a, d.f. = 30, F = 10.1). Thus, colder sites had higher P concentrations relative to N than warmer sites. Further, in accord with model predictions, this variation in N : P was independent of total phytomass (Fig. 2b, d.f. = 28, F = 0.005). Counterintuitively, at the whole-community level, the nutrient productivity of both P and N (again in g × g nutrient^{-1} × mo^{-1}) actually increased exponentially with inverse growing season temperature,
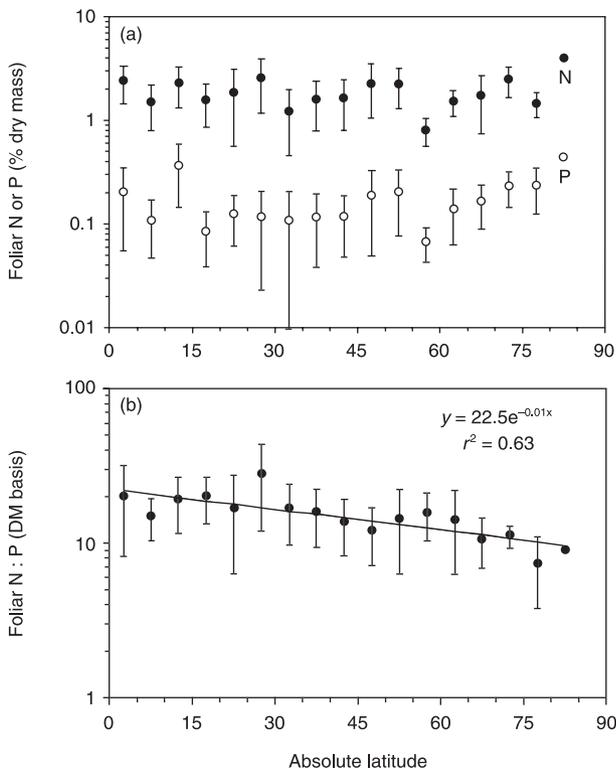
Figure 1 Latitudinal trends in components of foliar stoichiometry: (a) N concentration (black circles, 941 species) and P concentration (white circles, 842 species), both on a percentage dry mass basis; and (b) N : P (724 species). Means and standard deviations (bars) were calculated across all species in each 5-degree interval of absolute latitude. Solid line is OLS regression on log-transformed N: *P*-values. Mean foliar P-concentration approximately doubles relative to N with increasing latitude over the examined range.

i.e. colder communities exhibited more productivity per unit nutrient than warmer communities. While the change in P-productivity was modest (slope = 3.7, 95% CI = 0.1–7.3, d.f. = 33, F = 4.5, P = 0.04), the relationship between temperature-dependence of N-productivity was approximately the inverse of that expected for production, based on photosynthetic kinetics (Fig. 2c and 95% CI = 4.2–10.7, d.f. = 31, F = 22.2). Further, the increase in N-efficiency was correlated with a concomitant increase in phytomass P-concentration (Fig. 2d, d.f. = 28, F = 19.8). As in the more extensive data described below, these data exhibited no relationship between $\ln(G_{Tot}^{S})$ and $1000/T_S$ (d.f. = 35, F = 0.12, P = 0.7).

Temperature-invariance of primary productivity

The seasonally adjusted primary productivity data exhibited no significant relationship to mean growing season temperature across vegetation classes (Fig. 3, d.f. = 1,598, F = 1.05, P = 0.30 for all data pooled), and the productivity values for cold tundra and boreal sites overlapped completely with those of warm tropical forests. When we controlled for differences in total leaf mass (L_{Tot}) by examining the temperature response for each of the different vegetation classes, temperature rarely explained a meaningful fraction of the variation in ANPP (r^2 range 0.03–0.11), and the steepest negative slope (−0.06 K) was more than two orders of magnitude shallower than the predicted value of −8. Thus, while L_{Tot} affected productivity, it did not appear to be mediating the global-scale temperature response. Adjusting for latitudinal differences in day length yielded a significant exponential decrease in G_{Tot}^{S} with inverse temperature, but again the relationship had little explanatory power, and the slope was significantly shallower than the expected value of −8 (see Appendix S4 in Supplementary materials).

Figure 2 (a, b) Plant community phytomass N : P as a function of (a) inverse growing season temperature, and (b) total phytomass. The observed exponential change in N : P is driven by increases in P with decreasing temperature, and it is independent of total phytomass. (c, d) Changes in the N-efficiency of production as a function of both (c) inverse growing season temperature and (d) phytomass P-concentration. All lines are OLS regressions. The exponential increase in N-efficiency of production with decreasing temperature is of approximately the same magnitude (but opposite in sign) as the predicted kinetic response of photosynthesis.

Figure 3 Growing season above-ground net primary productivity, $\ln(G_{Tot}^S)$, plotted against inverse mean growing season temperature for ecosystems around the world. Adjusted for differences in growing season length, primary production shows no relationship with temperature. Forest designations are D: deciduous, E: evergreen, BL: broadleaf and NL: needle leaf.

DISCUSSION

Here, we have developed a theoretical model that incorporates insights from the theories of ecological stoichiometry and metabolic scaling into the classical theory of photosynthesis-respiration balance in plants. As described above, the theory is consistent with a wide variety of empirical patterns and quantitatively links plant community size structure, plant functional diversity and stoichiometry and ecosystem function. In this context, our empirical results demonstrate the potential importance of understanding broad-scale variation in plant stoichiometry for modelling patterns of primary productivity. The consistent relationship between both foliar and standing phytomass N : P and temperature (or latitude) indicates that assumption of independent effects of temperature and stoichiometry on productivity is clearly overly simplistic and should be discarded. Taken together, theory and data presented here suggest that systematic variation in N : P and N-productivity may approximately offset decreases in primary productivity due to decreased growing season temperatures.

For example, the negative relationship between inverse temperature and N : P (again, independent of standing phytomass) is predicted to have a compensatory effect because, from eqn 7, realized growth yield (Y_G) is an decreasing function of whole-plant N : P. Thus, as temperatures drop across environments, reductions in photosynthetic capacity due to low temperatures may be offset in part by increases in biosynthesis via increased P investment in ribosomes (per unit protein). The macroecological approach taken here does not address the underlying mechanisms of this hypothesis, but the empirical patterns are consistent.

As implied above, global-scale relationships between temperature (or latitude) and P-concentration and N : P ratio may reflect decreased P availability in the tropics, or an adaptive response of plants to colder, shorter growing seasons (Vitousek, 1984; Korner, 1989; McGroddy *et al.*, 2004; Reich & Oleksyn, 2004). These two alternatives can be reconciled by the 'growth rate hypothesis' (GRH) (Elser *et al.*, 2000; Sterner & Elser, 2002; Elser *et al.*, 2003;

Agren, 2004), which predicts that selection for rapid growth (i.e. high Y_G) increases tissue P-content disproportionately (and thus decreases N : P) due to increased allocation to P-rich ribosomes for protein synthesis. If cold, short growing seasons select for rapid growth, we would expect to see a dearth of P-poor species, even though P is still sometimes limiting. Conversely, where selection for rapid growth is less intense, P-limitation should show a strong signal in plant tissues. Although evaluation of the GRH for autotrophs is ongoing (Agren, 2004), our results highlight the more general importance of studies that link organism and ecosystem attributes in an explicitly evolutionary context.

The latitudinal variation in foliar stoichiometry documented here differs somewhat from a similar, recent study (Reich & Oleksyn, 2004). While the relationship they document between N : P and latitude is nearly identical to ours (Hedin, 2004), Reich and Oleksyn also find that both N and P decrease with latitude individually, which we did not find in our data. However, even where our results are similar (i.e. foliar N : P decreases with latitude), our interpretation differs substantially from the conclusions reached by Reich and Oleksyn. They contrast the 'soil substrate age hypothesis', which predicts decreasing N : P with latitude due to low P availability in the tropics, with the 'T physiology hypothesis', which predicts increasing N : P with latitude as a result of the P demands of fast growth in the tropics. Our interpretation above, based on the GRH, represents a third alternative that is more explicitly evolutionary in that it assumes that latitudinal variation in N : P is a adaptive response to *selection* on growth rate rather than a physiological response to the demands of growth rate *itself*. Distinguishing the relative influence of nutrient availability and adaptation on plant stoichiometry remains an important open question (Gusewell, 2004).

Perhaps our most striking empirical result is the precipitous nonintuitive increase in N-productivity with decreasing temperature and its correlation with phytomass P-concentration (Fig. 2). This result is surprising in light of the fact that corresponding leaf level traits of species appear to show no such trend (Wright

3 **Table 1** Index of mathematical symbols used in the paper, including a brief description and units, listed in order of appearance

Symbol	Description	Units
G_T	Plant growth rate	$g \times time^{-1}$
Y_G	Plant growth yield	unitless
A_T	Plant photosynthetic assimilation rate	$g \times time^{-1}$
R_m	Plant maintenance respiration rate	$g \times time^{-1}$
B_G	Plant biosynthesis rate	$g \times time^{-1}$
R_G	Plant respiratory cost of biosynthesis	$g \times time^{-1}$
μ_L	Leaf mass-specific photosynthetic assimilation rate	$g \times g\ leaf^{-1} \times time^{-1}$
M_L	Plant leaf mass	g leaf
β_L	Leaf mass allocation coefficient	$g\ leaf \times g\ plant^{-3/4}$
β_S, β_R	Stem, root mass allocation coefficients	$g\ organ \times g\ plant^{-3/4}$
F_L	Leaf nutrient concentration (N, P)	$g\ nutrient \times g\ leaf^{-1}$
F_S, F_R	Stem, root nutrient concentration (N, P)	$g\ nutrient \times g\ organ^{-1}$
f_S, f_R	Stem, root nutrient allocation coefficients (N, P)	$g\ nutrient \times g\ organ^{-3/4}$
F_T	Plant nutrient concentration (N, P)	$g\ nutrient \times g\ plant^{-1}$
ϕ_L	Leaf photosynthetic nitrogen use efficiency (PNUE)	$g \times g\ leaf\ N^{-1} \times time^{-1}$
ϕ_m	Plant maintenance respiration nitrogen use coefficient	$g \times g\ plant\ N^{-1} \times time^{-1}$
c_B	Plant biosynthesis phosphorus use coefficient	$g \times g\ plant\ P^{-1} \times time^{-1}$
c_R	Plant growth respiration nitrogen use coefficient	$g \times g\ plant\ N^{-1} \times time^{-1}$
c_G	Plant stoichiometric growth yield coefficient	$g\ plant\ N \times g\ plant\ P^{-1}$
E_R	Activation energy of respiratory metabolism	eV
T	Absolute temperature	K
E_p	Activation energy of photosynthesis	eV
k	Boltzmann's constant	$eV \times K^{-1}$
Φ_T	Plant aggregate maintenance cost factor	unitless
G_{Tot}	Community annual net primary productivity	$g \times area^{-1} \times year^{-1}$
M_{Tot}	Community total plant biomass (phytomass)	$g \times area^{-1}$
α_i	Community phytomass fraction in size class i	unitless
m_i	Plant characteristic mass in size class i	g plant
n_i	Plant density in size class i	$number \times area^{-1}$
a_{ji}	Relative abundance of species j in size class i	unitless
s_i	Species richness of size class i	species
l_S	Growing season length	months
G_{Tot}^{S}	Community seasonal net primary production	$g\ area^{-1} \times mo^{-1}$
T_S	Growing season temperature	K
L_{Tot}	Community total leaf mass	$g\ leaf \times area^{-1}$
F_{Tot}	Community nutrient concentration (N, P)	$g\ nutrient \times g\ phytomass$

et al., 2004). However, as described by eqns 11 and 12, at the community-level both productivity and nutrient content depend not only on species-specific leaf- or plant-level attributes, but also on the size distribution of individuals and the relative abundance of species in the community. Our findings here highlight the need to understand how these components of community structure and functional diversity change along broad environmental gradients.

The well-known relationship between mean annual temperature (MAT) and annual NPP (Lieth, 1975; Schlesinger, 1991) results largely from the correlation of MAT with season length (Bonan, 1993; Chapin, 2003). Nevertheless, the flatness of the temperature–monthly productivity relationship shown here is striking, as many ecosystem models predict significant, if modest, positive correlations between the two even after correcting for season length (Schloss *et al.*, 1999; Adams *et al.*, 2004). While the observed increases in both phytomass P-content and N-productivity are not predicted by our theory, they are again consistent with the notion that plant stoichiometry (and particularly P content) and community size structure may mediate the response of productivity to broad-scale temperature gradients. Indeed, the fact that the temperature response of N-productivity is almost exactly the inverse of that predicted from the kinetics of photosynthetic reactions suggests the interesting possibility that P-mediated increases in N-productivity may directly offset the temperature dependence of net primary productivity, producing the flat relationship. This conclusion is probably overly simplistic, as many other factors also mediate the response of NPP to temperature (Bonan, 1993). Nevertheless, the consistent patterns of variation documented here across a range of community types reinforce the importance of developing quantitative frameworks relating plant functional diversity and community structure to ecosystem function based on broad-scale, comparative investigations (Jordan, 1971; Lieth, 1975; Ehleringer & Field, 1993; Schulze *et al.*, 1994; Reich *et al.*, 1997; Diaz *et al.*, 2004). Because it treats

functional variation across communities continuously, rather than by using discrete functional types, the theory developed here may inform models of ecosystem response to climate change (Moorcroft *et al.*, 2001; Wright *et al.*, 2004).

The theoretical framework developed here is preliminary, based on a number of reasonable, but sometimes untested, assumptions. Its consistency with a wide variety of whole-plant and ecosystem-level patterns is encouraging, but it remains, like all scientific statements, subject to further revision and refinement. In particular, a better quantitative understanding of how community size structure and plant functional diversity vary along environmental gradients (Kleidon & Mooney, 2000; Lavorel & Garnier, 2002) would strengthen the predictive power of our approach. This same overall framework can potentially accommodate other important organismal and environmental factors, as well as more complicated submodels (e.g. of photosynthesis; see Allen *et al.*, 2005) for more detailed investigations. More generally, this work is one of the first explicit integrations of emerging theories of ecological stoichiometry (Sterner & Elser, 2002) and metabolic scaling (Brown *et al.*, 2004), and demonstrates their potential for analysing broad-scale patterns of characteristics of organisms and ecosystems (Chapin, 2003; Wright *et al.*, 2004).

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Supplementary material

The following material is available from
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Appendix S1. Leaf stoichiometry data.

Appendix S2. Whole community phytomass, nutrient, and productivity data.

Appendix S3. Additional leaf stoichiometry results

Appendix S4. Additional productivity results

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