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

Andrew J. Kerkhoff1,*, Brian J. Enquist1, James J. Elser2 and William F. Fagan3

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 depends 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.

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 individually 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; Mooshcroft 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 × time\(^{-1} \), is proportional to the cumulative balance of total photosynthetic assimilation (\( A_t \), g × time\(^{-1} \)) and maintenance respiration (\( R_m \), g × time\(^{-1} \)):

\[
G_t = Y_c (A_t - R_m),
\]

and the term \( Y_c \) (unitless) describes the realized growth yield from net mass gain (Amthor, 2000). More specifically, the growth yield is defined as \( Y_c = \frac{B_G}{B_G + R_G} \), 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 × 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. A summary of all model terms is provided below (Table 1).

**Effects of plant size**

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

\[
G_t \propto A_t = \mu_L M_L,
\]

where \( \mu_L \) (g × g leaf\(^{-1} \) × time\(^{-1} \)) is the leaf mass-specific photosynthetic production rate (dM/dM/dt), which is independent of whole plant mass (Niklas & Enquist, 2002a). Variability in the leaf mass-specific production \( \mu_L \) probably reflects both environmental constraints and potentially adaptive taxon–specific differences in photosynthetic capacity (see below). Further, leaf mass
Plant allometry, stoichiometry and productivity

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

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
<th>Units</th>
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<tbody>
<tr>
<td>$G_r$</td>
<td>Plant growth rate</td>
<td>g × time$^{-1}$</td>
</tr>
<tr>
<td>$Y_c$</td>
<td>Plant growth yield</td>
<td>unitless</td>
</tr>
<tr>
<td>$A_r$</td>
<td>Plant photosynthetic assimilation rate</td>
<td>g × time$^{-1}$</td>
</tr>
<tr>
<td>$R_m$</td>
<td>Plant maintenance respiration rate</td>
<td>g × time$^{-1}$</td>
</tr>
<tr>
<td>$R_b$</td>
<td>Plant biosynthesis rate</td>
<td>g × time$^{-1}$</td>
</tr>
<tr>
<td>$R_c$</td>
<td>Plant respiratory cost of biosynthesis</td>
<td>g × time$^{-1}$</td>
</tr>
<tr>
<td>$\mu$</td>
<td>Leaf mass-specific photosynthetic assimilation rate</td>
<td>g × g leaf$^{-1}$ × time$^{-1}$</td>
</tr>
<tr>
<td>$M_l$</td>
<td>Plant leaf mass</td>
<td>g leaf</td>
</tr>
<tr>
<td>$\beta_l$</td>
<td>Leaf mass allocation coefficient</td>
<td>g leaf × g plant$^{-3/4}$</td>
</tr>
<tr>
<td>$\beta_0, \beta_x$</td>
<td>Stem, root mass allocation coefficients</td>
<td>g organ × g plant$^{-3/4}$</td>
</tr>
<tr>
<td>$F_1$</td>
<td>Leaf nutrient concentration (N, P)</td>
<td>g nutrient × g leaf$^{-1}$</td>
</tr>
<tr>
<td>$F_p, F_x$</td>
<td>Stem, root nutrient concentration (N, P)</td>
<td>g nutrient × g organ$^{-3/4}$</td>
</tr>
<tr>
<td>$f_{p0, f_x}$</td>
<td>Stem, root nutrient allocation coefficients (N, P)</td>
<td>g nutrient × g organ$^{-3/4}$</td>
</tr>
<tr>
<td>$\Phi_l$</td>
<td>Leaf photosynthetic nitrogen use efficiency (PNUE)</td>
<td>g × g g leaf N$^{-1}$ × time$^{-1}$</td>
</tr>
<tr>
<td>$\Phi_n$</td>
<td>Plant maintenance respiration nitrogen use coefficient</td>
<td>g × g plant N$^{-1}$ × time$^{-1}$</td>
</tr>
<tr>
<td>$c_n$</td>
<td>Plant biosynthesis phosphorus use coefficient</td>
<td>g × g plant P$^{-1}$ × time$^{-1}$</td>
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<tr>
<td>$c_x$</td>
<td>Plant growth respiration nitrogen use coefficient</td>
<td>g × g plant N$^{-1}$ × time$^{-1}$</td>
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<tr>
<td>$c_i$</td>
<td>Plant stoichiometric growth yield coefficient</td>
<td>g plant N × g plant P$^{-1}$</td>
</tr>
<tr>
<td>$E_A$</td>
<td>Activation energy of respiratory metabolism</td>
<td>eV</td>
</tr>
<tr>
<td>$T$</td>
<td>Absolute temperature</td>
<td>K</td>
</tr>
<tr>
<td>$E_P$</td>
<td>Activation energy of photosynthesis</td>
<td>eV</td>
</tr>
<tr>
<td>$k$</td>
<td>Boltzmann’s constant</td>
<td>eV × K$^{-1}$</td>
</tr>
<tr>
<td>$\Phi_r$</td>
<td>Plant aggregate maintenance cost factor</td>
<td>unitless</td>
</tr>
<tr>
<td>$G_{net}$</td>
<td>Community annual net primary productivity</td>
<td>g × area$^{-1}$ × year$^{-1}$</td>
</tr>
<tr>
<td>$M_{st}$</td>
<td>Community total plant biomass (phytomass)</td>
<td>g × area$^{-1}$</td>
</tr>
<tr>
<td>$\alpha_i$</td>
<td>Community phytomass fraction in size class i</td>
<td>unitless</td>
</tr>
<tr>
<td>$m_i$</td>
<td>Plant characteristic mass in size class i</td>
<td>g plant</td>
</tr>
<tr>
<td>$n_i$</td>
<td>Plant density in size class i</td>
<td>number × area$^{-1}$</td>
</tr>
<tr>
<td>$a_j$</td>
<td>Relative abundance of species j in size class i</td>
<td>unitless</td>
</tr>
<tr>
<td>$s_i$</td>
<td>Species richness of size class i</td>
<td>species</td>
</tr>
<tr>
<td>$L_i$</td>
<td>Growing season length</td>
<td>months</td>
</tr>
<tr>
<td>$G_{season}$</td>
<td>Community seasonal net primary production</td>
<td>g area$^{-1}$ × mo$^{-1}$</td>
</tr>
<tr>
<td>$T_s$</td>
<td>Growing season temperature</td>
<td>K</td>
</tr>
<tr>
<td>$L_{tot}$</td>
<td>Community total leaf mass</td>
<td>g leaf × area$^{-2}$</td>
</tr>
<tr>
<td>$F_{nut}$</td>
<td>Community nutrient concentration (N, P)</td>
<td>g nutrient × g phytomass</td>
</tr>
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varies allometrically with total plant mass, $M_p$, as $M_i = \beta_i M_p^{3/4}$ where the allometric coefficient $\beta_i$ 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. $G_r \propto A_r \propto R_m \propto M_p^{3/4}$ (Ernest et al., 2003; Savage et al., 2004). It also implies that growth yield should be independent of plant mass, $Y_c \propto M_p^{0}$.

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, $F_{nut}$, 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 $M_L/M_T = \beta_M M_T^{-1/4}$ (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 $M_T$, $\beta_S$ and $\beta_R$ (in g organ $\times$ 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 ($F_S$ and $F_R$, respectively, in g nutrient $\times$ g organ) decrease as $F_S = f_S M_R^{-1/4} = \beta_R^{-1/4} M_T^{-1/4} f_S$ and $F_R = f_R M_S^{-1/4} = \beta_S^{-1/4} M_T^{-1/4} f_R$, where again $M_T$ is whole-plant mass and the coefficients ($f_S$ and $f_R$, in units of g nutrient $\times$ g organ $^{-1/4}$) 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:

$$F_i = \frac{1}{M_T} (F_T M_T + F_S M_S + F_R M_R) = (\beta_T F_T + \beta_S^{-1/4} f_S + \beta_R^{-1/4} f_R) M_T^{-1/4}$$

(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, $F_T M_T = M_T^{34}$), 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):

$$\mu_T = \phi_T F_T^{N^*}.$$  (4)

Here, $\mu_T$ is again the leaf mass-specific photosynthetic production rate and $\phi_T$ is the efficiency of leaves in using nitrogen to assimilate mass (i.e. the photosynthetic nitrogen use efficiency $PNUE = \mu_T/F_T^N$, g $\times$ g leaf N$^{-1}$ $\times$ 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. $dP/dt = dN/dt = dM_T/dt$, 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:

$$A_T = \beta_T \phi_T F_T^{N^*} M_T^{3/4}.$$  (5)

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

$$R_m = \phi_m F_T^N M_T.$$  (6)

Here, $\phi_m$ (units g $\times$ g nitrogen$^{-1}$ $\times$ 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. $B_c = c_p F_T^P M_T$. Similarly, because the respiratory cost of biosynthesis depends on the living mass it is proportional to whole plant N, i.e. $R_c = c_p F_T^N M_T$. The coefficients $c_p$ and $c_p$ are rate constants describing the biosynthesis per unit plant N ($c_P$ units: g $\times$ g P$^{-1}$ $\times$ time$^{-1}$) and the respiratory cost of biosynthesis per unit plant N ($c_p$ units: g $\times$ g N$^{-1}$ $\times$ time$^{-1}$). Substituting into the expression for $Y_G$ above, the realized growth yield depends on whole plant N : P, independent of plant mass:

$$Y_G = c_P F_T^P,$$  (7)

where the coefficient is $c_P = \frac{c_p}{c_p F_T^P + c_R}$, with units of g N $\times$ 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:

$$G_T = c_P F_T^P (\phi_T F_T^{N^*} M_T^{3/4} - \phi_m F_T^N M_T).$$  (8a)
Consolidating whole-plant mass by using eqn 3 to express $F_T^N$ and rearranging yields:

$$G_T = \frac{F_T^p}{F_T} \left( F_T^N \beta_L M_T^{1/4} \phi_L \left( 1 - \frac{\phi_m}{\phi_L} \left( \frac{1 + \frac{\beta_L}{\beta_P} F_T^N + \frac{\beta_P}{\beta_L} F_T^N}{F_T^p \beta_L} \right) \right) \right).$$

(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 ($\beta_L$), increased leaf N ($F_T^N$) and PNU (\phi_L); and it should decrease with increasing maintenance costs ($\phi_L$), allocation of mass and nutrients to non-photosynthetic organs (i.e. $\beta_L F_T^N + \beta_P F_T^N$) and whole-plant N : P [i.e. it increases with $\frac{F_T^p}{F_T}$, 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 $R_m \propto e^{\frac{-E}{T}}$, where $E_R$ is the activation energy (eV) of respiratory metabolism, $k$ is Boltzmann’s constant ($8.6 \times 10^{-5} \text{ eV} \times \text{K}^{-1}$) 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 different 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 ($E_R \approx 0.7 \text{ eV}$) (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 exponential functions 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

$$\left( 1 + \frac{\beta_L}{\beta_P} F_T^N + \frac{\beta_P}{\beta_L} F_T^N \right) = \left( \frac{F_T^N}{F_T^p} \beta_L M_T^{1/4} \right),$$

which is simply the (unitless) ratio of whole-plant to leaf nitrogen content, independent of whole-plant mass. Therefore,

$$G_T = \frac{F_T^p}{F_T} \left( F_T^N \beta_L M_T^{1/4} e^{\frac{-E}{T}} \phi_L \left( 1 - \frac{\phi_m}{\phi_L} \left( \frac{\phi_m F_T^N M_T^{1/4} e^{\frac{-E}{T}}}{\phi_L F_T^p M_T^{1/4}} \right) \right) \right).$$

(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, $\left( 1 - \frac{\phi_m}{\phi_L} \frac{F_T^N M_T^{1/4} e^{\frac{-E}{T}}}{\phi_L F_T^p M_T^{1/4}} \right)$, or $\Phi$, hereafter, is unitless, independent of plant mass, and nearly independent of temperature (because $E_R \equiv E_R$). Thus it will not affect any subsequent predictions evaluated here. Because it represents losses due to maintenance respiration, the constrained nature of $\Phi$, 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 \((g \times \text{area}^{-1} \times \text{year}^{-1})\) 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, 
\[
G_{\text{tot}} = \sum_{i=1}^{s} \alpha_i \left( \sum_{j=1}^{z} a_{ij} G_{T_{ij}} \right),
\]
where the first summation is over all plants binned into \(Z\) size classes, regardless of species, and \(\alpha_i\) is the proportion of total community mass falling within size class \(i\); that is, 
\[
\alpha_i = \frac{m_i n_i}{M_{\text{tot}}},
\]
where \(m_i\) is the characteristic plant mass and \(n_i\) is the density of individuals (area\(^{-1}\)) of size class \(i\), and \(M_{\text{tot}}\) is total community plant biomass per unit area, called ‘phytomass’ hereafter. The second, nested summation describes functional variation across the \(s\) species in size class \(i\), and \(a_{ij}\) 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 \(\times\) \(y^{-1}\)) to yield a primary productivity equation
\[
G_{\text{tot}} l_s = \beta_i \left( \sum_{j=1}^{z} \alpha_i m_i^{1/4} \right) \sum_{j=1}^{z} \left( \sum_{i=1}^{s} a_{ij} \frac{F_{ij}}{F_{14}} \Phi_s \Phi_{y} \right).
\]

Here, \(G_{\text{tot}} l_s\) is the annual rate of net primary production (mass \(\times\) area\(^{-1}\) \(\times\) \(y^{-1}\)) 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 \(\alpha_i\)) are within the first summation, while those that are species-specific but mass-independent (e.g. leaf N concentration \(F_{14}\)) 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, \(G_{\text{tot}}^S\). 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:
\[
G_{\text{tot}}^S = \beta_i \left( \frac{F_{14}}{F_{ij}} \right) M_{\text{tot}} \left\{ \sum_{j=1}^{z} \left( \sum_{i=1}^{s} a_{ij} \frac{F_{ij}}{F_{14}} \Phi_s \Phi_{y} \right) \right\} \sum_{i=1}^{s} \left( \alpha_i m_i^{1/4} \right).
\]

It is important to note that the term in angled 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:
\[
F_{\text{tot}} = \left( \beta_i \left( \frac{F_{ij}}{F_{14}} \right) + \beta_1^{1/4} \left( f_s \right) + \beta_2^{1/4} \left( f_y \right) \right) \left( \sum_{i=1}^{s} \alpha_i m_i^{1/4} \right).
\]

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, \(L_{\text{tot}}\), can be described by \(L_{\text{tot}} = \beta_i M_{\text{tot}} \sum_{i=1}^{s} \alpha_i m_i^{1/4}\).

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 \(\propto L_{\text{tot}}\)), 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 \(L_{\text{tot}}\) 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 \(\sum_{i=1}^{s} \alpha_i m_i^{1/4}\), 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 \(G_{\text{tot}}^S\) 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:

$$\ln(G_{tot}^S) = \frac{-E_P}{1000k} \left( \frac{1000}{T_s} \right) + \ln \left( \frac{c_0}{E_P^S} \frac{P}{E_T^S} \phi_L P_N N_T \right).$$  \hspace{1cm} (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 $\left(1000/T_s\right)$, 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. $\phi_L$) 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 was 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 (GPPD). 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 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.
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 $T < 0\,^\circ C$) 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 qualitatively affect 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

**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.

**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.
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. \( F^N_{L}, F^P_{L} \), expressed as percentage dry mass and their ratio), averaged within 5-degree bands of absolute latitude. Assessed individually, neither foliar 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, 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 \( \ln(G^N_{GTo}) \) and 1000/T (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 (\( L_{lw} \)) 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 \( L_{lw} \) 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 \( G^N_{GTo} \) 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).

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 $Y_p$) 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 an 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 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

![Figure 3](https://example.com/figure3.png)
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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REFERENCES


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Supplementary Material

The following material is available from http://www.blackwell-synergy.com/loi/geb
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