

Adaptive differences in plant physiology and ecosystem paradoxes: insights from metabolic scaling theory

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Abstract

The link between variation in species-specific plant traits, larger scale patterns of productivity, and other ecosystem processes is an important focus for global change research. Understanding such linkages requires synthesis of evolutionary, biogeographic, and biogeochemical approaches to ecological research. Recent observations reveal several apparently paradoxical patterns across ecosystems. When compared with warmer low latitudes, ecosystems from cold northerly latitudes are described by (1) a *greater temperature normalized instantaneous flux of CO₂ and energy*; and (2) *similar annual values of gross primary production (GPP), and possibly net primary production*. Recently, several authors attributed constancy in GPP to historical and abiotic factors.

Here, we show that metabolic scaling theory can be used to provide an alternative ‘biotically driven’ hypothesis. The model provides a baseline for understanding how potentially adaptive variation in plant size and traits associated with metabolism and biomass production in differing biomes can influence whole-ecosystem processes. The implication is that one cannot extrapolate leaf/lab/forest level functional responses to the globe without considering evolutionary and geographic variation in traits associated with metabolism. We test one key implication of this model – that directional and adaptive changes in metabolic and stoichiometric traits of autotrophs may mediate patterns of plant growth across broad temperature gradients.

In support of our model, on average, mass-corrected whole-plant growth rates are not related to differences in growing season temperature or latitude. Further, we show how these changes in autotrophic physiology and nutrient content across gradients may have important implications for understanding: (i) the origin of paradoxical ecosystem behavior; (ii) the potential efficiency of whole-ecosystem carbon dynamics as measured by the quotient of system capacities for respiration, *R*, and assimilation, *A*; and (iii) the origin of several ‘ecosystem constants’ – attributes of ecological systems that apparently do not vary with temperature (and thus with latitude). Together, these results highlight the potential critical importance of community ecology and functional evolutionary/physiological ecology for understanding the role of the biosphere within the integrated earth system.

Keywords: allometry, ecosystem constants, functional traits, growth efficiency, invariants, latitudinal gradient, net primary production, scaling, stoichiometry, temperature response

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Introduction

Our understanding of the role that organisms play in influencing global material and energy cycles is in part

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constrained by a lack of knowledge of the relative influences of both abiotic and biotic features of the integrated earth environmental system (Osmond *et al.*, 2004). It is clear, however, that the performance of autotrophs is critical in influencing ecosystem processing and dynamics. For example, autotrophic respiration plays a substantial role in governing ecosystem carbon balance (Field *et al.*, 1992; Ryan *et al.*, 1995).

Integration of basic biochemistry and biophysics of photosynthesis, whole-plant responses to regional and global climate, and ecology are essential for developing a predictive understanding of ecosystem flux (Geider *et al.*, 2001). Therefore, accurate modeling of the response of autotrophic respiration and overall carbon balance to differing climate regimes is essential to predict the impacts of the traits that influence plant metabolism on global carbon budgets.

The overall message from autecological studies is that physiological and life-history traits of plants vary in accord with changes in climate and edaphic regimes. Since the pioneering work of Clausen, Keck and Hiesey (Clausen *et al.*, 1940) botanists have amassed a large list of examples of how differing environments select for unique life histories and physiological traits (Mooney & Billings, 1961; Klikoff, 1966; Strain, 1966; McNaughton, 1967). Differences in local climate and abiotic regimes can also act as a filter 'selecting' those combinations of organismal traits that ensure that the organism maintains a positive carbon and energy balance (Criddle *et al.*, 1994; Weiher & Keddy, 1995; McGill *et al.*, 2006). Thus, as a result of acclimatization and environmental selection of traits, differing ecosystems tend to be characterized by plants with unique physiological and life-history adaptations for that specific environment (Schimper, 1903; Shields, 1950; Mooney, 1977; Reich *et al.*, 1999; Fonseca *et al.*, 2000; Kleidon & Mooney, 2000; Schippers *et al.*, 2001; Wright *et al.*, 2001; Nicotra *et al.*, 2002). Although evidence for physiological and life-history adaptation is abundant, relatively little is known about the importance of local adaptations in influencing ecosystem processes across broad scale gradients.

Can adaptive and directional shifts in functional traits influence ecosystem processes?

Patterns of plant trait variation due to both species replacements and within-species variation across resource and environmental gradients (light, water, nutrients, and temperature) are thought to reflect local adaptation (Reich *et al.*, 2003). For example, within species, there is a rich literature on acclimation, the adaptive adjustments of physiology to temperature and other environmental factors (see Criddle *et al.*, 1994; Atkin & Tjoelker, 2003; Talts *et al.*, 2004; Atkin *et al.*, 2005; Galmés *et al.*, 2005). Between species inhabiting differing environments, the optimal temperatures for photosynthesis and overall optimal growth are generally correlated with the temperature range experienced by plants during the growing season (Amthor, 1989; Larcher, 1995; Cunningham *et al.*, 1999; Saxe *et al.*, 2001). Cold adapted plants tend to have physiological adaptations associated with the rate of metabolism. For exam-

ple, they tend to have *higher* rates of cellular respiration and carbon assimilation at a given temperature than plants grown in warm environments (Will, 2000; Galmés *et al.*, 2005; but see Wright *et al.*, 2006). Changes in respiration often reflects (i) an increase in the potential rates of respiratory activity per unit mitochondrial volume (Klikoff, 1966; Miroslavov & Kravkina, 1991) in addition to; (ii) a change in the proteins and efficiency of terminal oxidase (Ribas Carbo *et al.*, 2000; Kurimoto *et al.*, 2004); and (iii) an overall altering of the temperature dependence of metabolism by changes in biochemical activation energies as measured by the Arrhenius temperature coefficient (Criddle *et al.*, 1994). In common garden experiments, plant respiration rates are generally higher for plants originating colder sites (Mooney, 1963; Criddle *et al.*, 1994; Oleksyn *et al.*, 1998). Acclimation of respiration and photosynthesis strongly suggests that factors other than reaction kinetics regulate plant flux. In addition to changes in rates of carbon fluxes associated with respiration and photosynthesis the efficiency of carbon use (the ratio of organismal net primary production divided by gross primary production (NPP/GPP), a measure of what fraction of total carbon assimilated becomes incorporated into biomass) may also vary across plants across temperature gradients (Chambers *et al.*, 2004).

Despite the many examples of physiological adaptation and geographic variation in functional groups, it is still not clear if such evolutionary and ecological changes in organismal traits systematically alter large-scale ecosystem processes (Ackerly & Monson, 2003). Further, what specific adaptive differences in plant traits could modify ecosystem processes? Recent analyses suggest that adaptive variation in traits that influence plant metabolism can have substantial impact on the carbon balance of ecosystems (Luo *et al.*, 2001; Kerkhoff *et al.*, 2005; Wythers *et al.*, 2005). Here, we ask whether plant physiological adaptation can mediate the influence of abiotic drivers on ecosystem processes such as primary production or nutrient cycling across the globe. We build upon a growing awareness of the importance of functional traits (see McGill *et al.*, 2006) by mechanistically emphasizing the fundamental role of potential variation in organismal physiology, instead of climate alone, in influencing variability in ecosystem fluxes (Kerkhoff *et al.*, 2005).

This paper has three objectives:

1. We first highlight a prominent yet paradoxical cross-ecosystem finding that relates environmental temperature and ecosystem energetics. We show how this pattern has important implications for understanding the response of the biosphere to aspects of global change. To account for this pattern we review

a novel model for scaling organismal metabolism from cells to ecosystems that builds upon metabolic scaling theory (West *et al.*, 1997; Enquist *et al.*, 1998, 2003; Brown *et al.*, 2004; Kerkhoff *et al.*, 2005).

2. Next, we show that a trait-based elaboration of metabolic scaling theory specifies how directional shifts in plant traits across latitudinal/temperature gradients can influence ecosystem behavior. In particular, recent work by Kerkhoff *et al.* (2005) highlights the importance of plant tissue nutrient stoichiometry and growth efficiency. We provide empirical evidence showing that the growth rates of trees (adjusted for average mass) does not appear to vary significantly and systematically in response to a broad temperature gradient. This result is consistent with the Kerkhoff *et al.* (2005) model indicating that variation in traits associated with organismal growth and metabolism, due to selection for increased growth rates in cold environments, can in turn yield the 'paradoxical responses' of whole-ecosystems mentioned above.
3. Finally, we explore the implications of an approximate invariance in growth rate with latitude/temperature for autotrophic respiration and net ecosystem primary production. Specifically, we show that the ratio between ecosystem capacities for respiration and net assimilation is invariant with respect to a temperature gradient, providing one of several 'ecosystem invariants.'

Latitude, temperature, and paradoxical patterns of ecosystem flux and production constants

A physical explanation for large-scale variability in ecosystem flux along temperature and latitudinal gradients

Temperature is fundamental in influencing the kinetics of biochemical reactions. In general, rates of biologically mediated conversions are tightly linked to changes in temperature (Johnson *et al.*, 1974; Lloyd & Taylor, 1994). It is widely thought that increases in global temperature will bring about increases in the metabolic activity of organisms within terrestrial ecosystems. Recently, however, utilizing a network of CO₂ and H₂O flux monitoring stations across Europe (EUROFLUX), Valentini *et al.* (2000) found no trend in *annual* ecosystem GPP across European latitudes north of the Mediterranean. Further, a recent analysis by Kerkhoff *et al.* (2005) showed that variation in *instantaneous rates* of net primary productivity, showed little to no variation with latitude and growing season temperature. These results are surprising as they run counter to the prominent paradigm that

cold, high latitude ecosystems are less productive than warmer, lower latitude ecosystems (Lieth, 1975).

Valentini *et al.* (2000) hypothesized that the apparent constancy in GPP was not due to functional trait or diversity differences between sites but instead due to the relatively high abundance of soil carbon and recent warming of northerly latitudes. However, others have suggested that there are no clear trends of decreasing soil carbon with increasing mean annual temperature (Thornley & Cannell, 2001). In contrast, Kerkhoff *et al.* (2005) hypothesized that the relative constancy of instantaneous rates of NPP with temperature was due to possibly adaptive differences in growth rates across temperature gradients.

An alternative hypothesis: the three A's – Acclimation, Adaptation, Assembly – can negate physical drivers of ecosystem flux and production

The findings of Giardina & Ryan (2000) (Liski *et al.*, 1999) and Baldocchi *et al.* (2001) may offer another insight into the relative insensitivity of GPP and annual NPP (ANPP) with latitude noted by Valentini *et al.* (2000) and Kerkhoff *et al.* (2005). Giardina & Ryan (2000) found that soil decomposition rates across a global-scale gradient in mean annual temperature were remarkably constant. Baldocchi *et al.* (2001) noted that the temperature optimum for ecosystem photosynthesis appeared to change with mean growing season temperature. Similar to findings from comparative ecophysiology of leaves (Niinemets *et al.*, 1999), 'cold' ecosystems seemed to have lower temperature optima for photosynthesis and 'warm' ecosystems had higher temperature optima (Fig. 1). The findings from Baldocchi *et al.* suggest that photoautotrophic processes may systematically vary across broad gradients. However, the specific mechanisms behind such shifts in the optimum temperature for ecosystem photosynthesis are not clear. If, as proposed for autotrophs, whole-ecosystem respiration acclimates to ecosystem photosynthate supply (i.e. primary production; Dewar *et al.*, 1999), then the temperature response of whole-ecosystem carbon flux and biomass production will likely also be altered.

Building upon the findings of Valentini *et al.* (2000) and Giardina & Ryan (2000), Enquist *et al.* (2003) used data from FLUXNET (<http://daac.ornl.gov/FLUXNET/>) to document a related pattern of ecosystem invariance. Across a variety of arid and mesic sites in both Europe and North America, CO₂ and energy flux was characterized by a similar exponential functional response with temperature the Boltzmann or Van't Hoff reaction rate rule (Gillooly *et al.*, 2001). However, when the total annual ecosystem respiration was plotted as a function of annual temperature *no* significant relation-

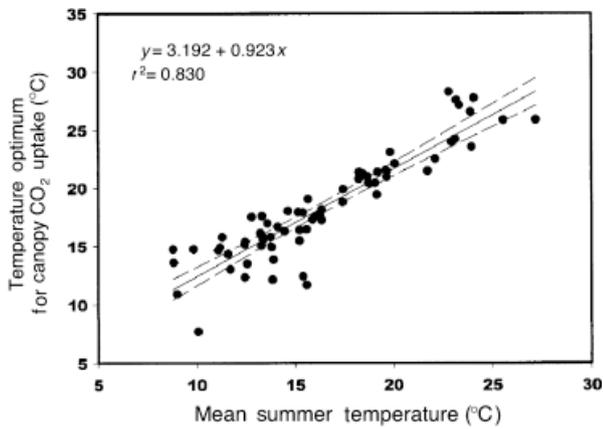


Fig. 1 Data from Baldocchi *et al.* (2001) (Fig. 9) showing a change in the temperature optimum for CO₂ uptake and the mean summer temperature for several sites in the FLUXNET dataset. The positive correlation indicates that the photosynthetic temperature response curves of entire ecosystems varies in direct proportion to the mean growing season temperature experienced by that ecosystem. 'Cold ecosystems' have lower optimal temperatures for optimum photosynthesis than 'warm ecosystems.' The slope of the line is close to 1.0 indicating that the ecosystem response in optimal photosynthesis temperature is closely matches a change in growing season temperature.

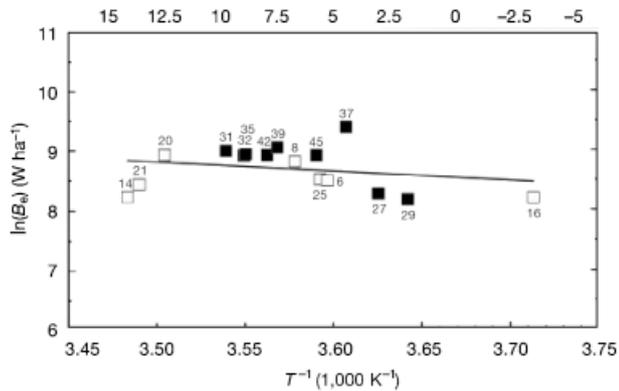


Fig. 2 Relationship between the annual night-time CO₂ flux (average rate per second) and the average annual night-time temperature for several FLUXNET sites. Data from Enquist *et al.* (2003). Temperature, T , is plotted as inverse temperature as measures in kelvins (K). The differing symbol numbers refer to different sites as originally listed in Enquist *et al.* (2003). The solid symbols are for European sites and the open symbols are for North American sites. Numbers on the upper x-axis are temperature in degrees C.

ship was found (Fig. 2). More importantly, they found that when the *instantaneous* rates of ecosystem respiration were standardized for a given temperature, colder and higher latitude ecosystems actually exchanged CO₂ and energy at three- to sixfold greater rates than warmer low latitude ecosystems. Figure 3 shows a positive

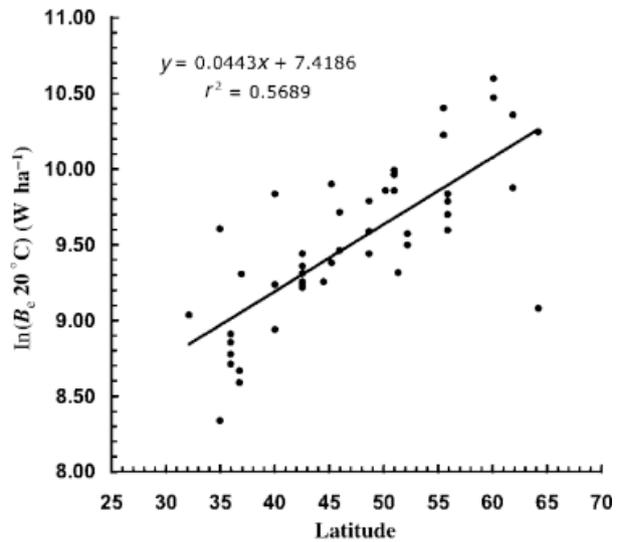


Fig. 3 Increase in the temperature normalized (at 20 °C) *instantaneous* nightly ecosystem energy flux (B_e) with latitude. Note, temperature normalized data are natural log transformed. The positive correlation indicates that at a given temperature, high latitude sites flux energy and carbon at greater rates than low latitude sites. Sites include all of the site years listed in Enquist *et al.* (2003). The dataset is dominated by forest ecosystems although there are a few grassland and arid sites included.

correlation between temperature-standardized flux (at 20 °C) and latitude for all sites used in the analysis ($r^2 = 0.569$, $n = 46$, $F = 58.06$, $P < 0.0001$ data from Enquist *et al.*, 2003). Enquist *et al.* concluded that taking the annualized and instantaneous findings together illustrates a paradox – why should it be that (i) there are no significant differences in annual fluxes across diverse ecosystems yet (ii) instantaneous fluxes of colder sites are much greater than warmer sites?

Enquist *et al.* (2003) provided a mechanistic model to account for the observed temperature response function of ecosystem respiration. Based on this model, they outlined several hypotheses to explain the increase in *instantaneous* rates of respiration at a standardized temperature *and* the approximate constancy in total annual respiration across latitude. One possibility proposed by Enquist *et al.* is the organismal-centered hypothesis that focuses on the importance of local adaptations or acclimation of cellular metabolism (b_0 in the model of Enquist *et al.*, 2003) and turnover in the presence and relative abundance of species.

Below, we revisit the Enquist *et al.* (2003) model to assess the hypothesis that the approximate invariance of annual ecosystem flux and the increase in the rates of instantaneous flux *across sites* (with temperature or latitude) results from adaptive changes in organismal metabolism across broad gradients. Focusing more specifically on the autotrophic community alone, we utilize

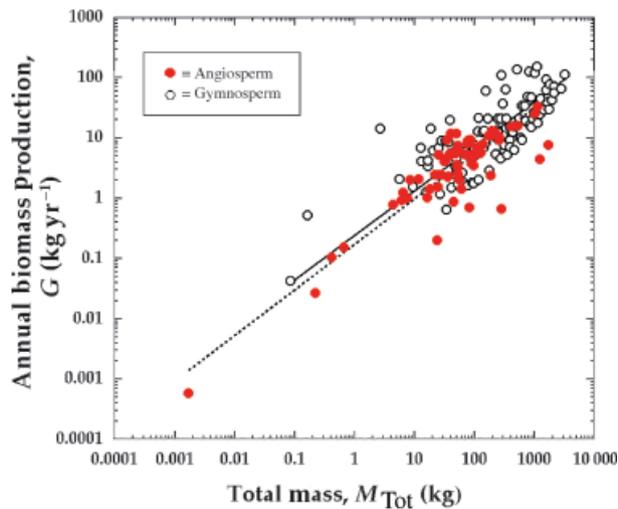


Fig. 4 Allometric relationship between total plant biomass and the annual rate of biomass production. Open symbols are angiosperms and filled symbols are conifers. The slope of the fitted relationship for both taxa are indistinguishable from each other and from the predicted value of 3/4 (angiosperms $\alpha_{\text{RMA}} = 0.755$, 95% CI = 0.803–0.707, $\beta_{\text{RMA}} = -1.09$, 95% CI = -0.987 to -1.20, $r^2 = 0.839$, $F = 891.18$, $n = 173$, $P < 0.0001$; gymnosperms $\alpha_{\text{RMA}} = 0.748$, 95% CI = 0.801–0.695, $\beta_{\text{RMA}} = -0.658$, 95% CI = -0.557 to -0.758, $r^2 = 0.860$, $F = 719.18$, $n = 119$, $P < 0.0001$). Data from Cannell (1982), see Enquist (2003) for details.

a recently modified version of this model (Kerkhoff *et al.*, 2005) to argue that the above paradoxical variation in ecosystem fluxes primarily reflects local adaptations to cooler temperatures and shorter growing seasons that involve how stoichiometric changes influences plant metabolism and the efficiency of biomass production.

A general model for scaling organismal metabolisms from cells to ecosystems

Enquist *et al.* (2003) utilized metabolic scaling theory (West *et al.*, 1997; Enquist *et al.*, 1998; Brown *et al.*, 2004) to derive a general equation for how temperature and plant size will influence ecosystem flux. Metabolic scaling theory builds upon the approach advocated by Harte (2002). Specifically, we take ‘a Fermi approach’ (or a zeroth-order model *a la* West *et al.*, 1997), in that our goal is to construct the simplest model possible that captures the essence of the problem (Harte, 2002). Thus, as discussed below, the model provides a baseline by which to incorporate more detail of organismal physiology, ecology, and evolution.

With a good deal of empirical support, metabolic scaling theory claims that most variation in the metabolic rates (i.e. respiration rates) of individuals, B_i , can be quantified based on the combined effects of two variables, body size, M_i (West *et al.*, 1997), and absolute

temperature, T in kelvin (K) (Gillooly *et al.*, 2001), using the general model for metabolic scaling:

$$B_i = b_0 e^{-E/kT} M_i^{3/4}, \quad (1)$$

where b_0 is a normalization constant (units of Watts $\times M^{-3/4}$) and is independent of body size and temperature. The value of b_0 can be shown to be a function of the average metabolic rate of a cell, B_c , and the average mass of a cell, M_c , so that $b_0 = (B_c/M_c)M^{1/4}$ (McCarthy & Enquist, 2005). Importantly, potential variation in b_0 then must reflect variation in the mass weighted metabolic intensity of a cell.

The 3/4 power scaling exponent reflects the constraints on optimal transport of resources to individual cells through fractal-like distribution networks (West *et al.*, 1997) and is expected to hold over most of the size ranges of plants and animals. The Van’t Hoff/Boltzmann factor, $e^{-E/kT}$, describes the temperature dependence of metabolic rate, where E is the average activation energy of metabolism and k is Boltzmann’s constant ($= 8.62 \times 10^{-5} \text{ eV K}^{-1}$) (Gillooly *et al.*, 2001). Previous work has indicated that the normalization constant, b_0 , and the activation energy, E , are approximately constant for plants and microbes and approximates 0.6 eV (Gillooly *et al.*, 2001, 2002) the two groups which comprise the majority of biomass in terrestrial ecosystems.

A global dataset of biomass production (which is assumed to be proportional to metabolic rate (Niklas & Enquist, 2001)) supports the 3/4 exponent given in Eqn (1). Recent work has indicated that the exponent for the scaling of metabolism for very small plants early in ontogeny (seedlings) scales with an exponent closer to 1.0 (Reich *et al.*, 2006). Some have argued that this ‘seedling specific’ finding challenges the generality of metabolic scaling theory (Hedin, 2006; Reich *et al.*, 2006). However, these conclusions are based on an inaccurate reading of metabolic theory. For seedlings, deviation from the 3/4 exponent is actually predicted by metabolic theory (West *et al.*, 1999) see also (Savage *et al.*, 2004) as biomechanical constraints that influence branching morphology differ during this important life stage. Figure 4 shows that variation in annual biomass production of both angiosperms and conifers scales allometrically with the total plant mass (roots, stems, leaves), M_{tot} of the plant. In agreement with metabolic scaling theory (West *et al.*, 1997) the fitted exponent is indistinguishable from the predicted value of 3/4 given in Eqn (1). Interestingly, the allometric functions that describes biomass production in conifers and angiosperms are indistinguishable from each other. Note, in this graph, data are ‘average individuals’ from a global collection of stand production studies ranging from the tropics to the high latitude Boreal forests (Enquist, 2003). Thus, growing season temperature is not controlled for.

Table 1 Key parameters of scaling model reviewed in the main text (from Enquist *et al.*, 2003; Kerkhoff *et al.*, 2005). Each parameter is provided with a descriptions, units, and key assumptions

Parameter	Description	Units	Assumption
v	Rate of limiting resource supply	mass area ⁻² time ⁻¹	1
R_e	Respiration rate of an ecosystem	W area ⁻²	–
B	Organismal metabolic rate	W	–
Q	Organismal rate of resource use	mass	–
M	Organismal mass	mass	–
G	Organismal growth rate	mass time ⁻¹	–
E	Activation energy for metabolism	eV	1
k	Boltzmann's constant	eV K ⁻¹	1
T	Temperature	Measured in kelvins (K)	–
b_0	Allometric normalization constant for metabolism = B/M . This is a measure of metabolic intensity per unit mass	W mass ^{-3/4}	1
c_G	Allometric normalization constant for growth rate, $c_G = c_b(b_0)$	mass ^{1/4} time ⁻¹	1
c_b	Allometric growth efficiency (note this variable is also proportional to the carbon use efficiency)	mass W ⁻¹ time ⁻¹	–
c_A	Allometric assimilation constant reflecting intensity of carbon assimilation rates	mass ^{1/4} time ⁻¹	–
c_R	Allometric respiration constant reflecting intensity of the rate of respiration	mass ^{1/4} time ⁻¹	–
i	Specific species	–	–
n	Number of size classes in plant community	–	–
j	Specific size class	–	–
N	Population density	number area ⁻²	–
m_j	Average mass of individuals within size class j	mass	–
M_c^{Tot}	Total standing biomass	mass	–
C	See Eqns (3 and 4)	–	–
α_i	Proportion of total community mass falling within size class i , which has a characteristic plant mass of m_i	$\alpha_j \equiv \frac{m_j n_j}{M_c^{\text{Tot}}}$	2
NPP_{Tot}	Instantaneous rate of net primary production	mass area ⁻¹ time ⁻¹	–
l_s	Length of growing season	time	–
ANPP	Annualized generalized primary productivity	mass area ⁻¹ year ⁻¹	–
M_{Tot}	Total autotrophic biomass	mass area ⁻²	1
T_S	Mean growing season temperature	Measured in kelvins (K)	1
F_{Tj}^N	Whole-plant nitrogen concentration	mass	3
F_{Tj}^P	Whole-plant phosphorus concentration	mass	3
ϕ_{Tj}	The photosynthetic nutrient use efficiency	g g leaf N ⁻¹ time ⁻¹	3
a_{ij}	Relative abundance of species j in size class i	–	3
c_{sj}	= $c_B/(c_B(F_{Tj}^N/F_T^P) + c_R)$ where c_R and c_B are rate constants describing the biosynthesis per unit plant P and the respiratory cost of biosynthesis per unit plant N	$c_B = \text{g g P}^{-1} \text{ time}^{-1}$ $c_R = \text{g g N}^{-1} \text{ time}^{-1}$	3
L	Subscript meaning parameter specific of leaves	–	–
A_T	Whole-organismal assimilation rate	W or mass time ⁻¹	–
R_T	Whole-organismal respiration rate	W or mass time ⁻¹	–

Assumption #1 = assumed to be independent of plant mass and species identity; #2 = assumed to be mass dependent, but independent of species identity; #3 = key autotrophic traits that are assumed to be species specific but mass independent. See text for additional details.

A baseline 'allometrically ideal' and zero-sum ecosystem model

Enquist *et al.* (2003) built on the general model Eqn (1) (all parameters summarized and presented are shown in Table 1 for each equation listed in the text) to account

for intrasite variation in rates of ecosystem respiration across the globe. They assumed that for a given site organisms grow and fill physical space so that rates of resource use by all individuals, Q_{Tot} is proportional to v , the approximate rate of limiting resource supply (water, nutrients, carbon, etc.) when evaluated per unit

area per unit time. This assumption implies that autotrophic resource use in the system follows a zero-sum dynamic where decreases in resource use by a given species is matched by an increase in resource use by another species. Therefore, ecosystem respiration, R_T , is equal to the sum of metabolic rates, B_i , for all individuals, i :

$$v \propto Q_{\text{Tot}} \propto R_T = \sum_i B_i. \quad (2)$$

To account for the allometric dependency of R_T , the summation of B_i is completed across n discrete body size classes, indexed by j , from the smallest sizes (m_1) to the largest sizes (m_n). Here, m_j is the average mass within a given size class. Whole-system metabolism is the summation across all size classes, B_j , and their associated total population density, N_j , so that $R_T \approx \sum_{j=1}^n [(B_j)(N_j)]$. The total biomass contained within a given j th size class bin, $M_j^{\text{Tot}} = m_j N_j$ and the density of individuals per bin is $N_j = M_j^{\text{Tot}}/m_j$.

From Eqn (1) one can derive the general form of the ecosystem respiration equation

$$Q_{\text{Tot}} \propto B_e = e^{-E/kT} b_0 \left[M_e^{\text{Tot}} \left(\sum_{j=1}^n \alpha_j m_j^{-1/4} \right) \right], \quad (3)$$

where α_j is the proportion of total community mass falling within size class j . Specifically, $\alpha_j \equiv m_j N_j / M_{\text{Tot}}^e$ and M_{Tot}^e is the total ecosystem biomass per unit area. The term $\left(\sum_{j=1}^n \alpha_j m_j^{-1/4} \right)$ can be treated as a constant, C , and represents the allometric dependency of the community size distribution. Empirical data and allometric theory suggest that $Q_{\text{Tot}} \approx R_T \approx C \propto v$ independent of the standing biomass, M_e^{Tot} (Enquist *et al.*, 1998; Enquist & Niklas, 2001). Under the steady-state assumption, $Q_{\text{Tot}} \approx R_T \approx C \propto v$. As a result, variation in v must then influence the nature of the size distribution within a given ecosystem through variation in M_e^{Tot} , the density of individuals of a given size ($m_j N_j$), and the maximum (m_n) and/or minimum sizes (m_1) of organisms. In other words, the local ecology of organisms must be constrained by the abiotic environment within the context of different combinations of these metabolic/organism size features.

Equation (3) can be rearranged into the following form:

$$\ln(Q_{\text{Tot}}) \propto \ln(B_e) = \frac{-E}{1000k} \left(\frac{1000}{T} \right) + \ln[(b_0)(C)], \quad (4)$$

where again, $C \propto v$. Equation (4) is similar in form to an Arrhenius plot for calculating activation energies for biochemical reactions (Nobel, 1983). Here, however, values of E represent the average activation energy for metabolism across plants, animals, and microbes found within a given assemblage.

As outlined by Enquist *et al.* (2003) using average values for the activation energy of metabolism yields an important prediction. Plotting the inverse of temperature (measured in kelvins, K) against the natural log of ecosystem respiration should yield a straight line with a slope of approximately -7.5 . Analysis of night-time respiration across numerous sites within FLUXNET provided support for this prediction. However, as discussed above, the intensity of instantaneous ecosystem flux (the height of the exponential function) varied (see Fig. 2a in Enquist *et al.*, 2003 and Fig. 3) and there was no relationship between mean annual temperature and total annual ecosystem flux (Fig. 2). Further analyses of community structure and biomass trends indicated that across forest communities there is little to no relationship with the number of individuals per unit area and total biomass across latitude (Enquist & Niklas, 2001). In other words, the term C in Eqn (4) is likely to not vary across latitude and temperature gradients. Thus, the observed paradoxical patterns in Figs 1–3 might then be related to directional changes in the term b_0 in Eqn (4).

Below, we review an extension of the above theory that elaborates on autotrophic traits that influence the physiology behind the metabolic normalization parameter b_0 (see Eqn (1)). For heterotrophic metabolism, there is already a small but growing literature that suggests that the value of b_0 varies with latitude. Recent compilations show that in both mammals and birds high latitude species tend to have higher values of b_0 than low latitude species (Lovegrove, 2000; Anderson & Jetz, 2005). We hypothesize that increases in b_0 with latitude reflects selection for traits that can deal with short growing seasons and cold temperatures. We show how in plants, b_0 , and a new variable, the efficiency of biomass production, are both likely key parameters that may account for the invariance of ecosystem flux and production across temperature and latitudinal gradients.

Including importance of plant traits on metabolic growth efficiency and plant biomass production into the general scaling model

Here, we elaborate on Eqn (4) to more accurately gauge the role of plant traits on annual whole-community rates of production. On a physiological level, net photosynthesis (carbon assimilation less photorespiration) generally responds hyperbolically to temperature, declining at high temperatures due to the deactivation of component reactions, denaturing of primary carboxylation enzymes, or changes in the balance between assimilation and photorespiration (Cannell & Thornley, 1998; Leuning, 2002).

This elaborated model explicitly accounts for community size structure, as well as functional trait variation. We focus on traits associated with autotrophs by expanding the parameters C and b_0 Eqn (3) of Enquist *et al.* (2003). As shown by Fig. 4, and assuming a Boltzmann temperature response, net annual rate of autotrophic biomass production, G , scale allometrically as

$$G = c_G e^{E_P/kT_s} M^{3/4}. \quad (5)$$

Here, the allometric coefficient c_G (with units of $\text{mass}^{1/4} \text{ time}^{-1}$) indexes the mass-specific intensity of cellular metabolism into whole-organismal biomass production, G , and the value of E_P is the activation energy for photosynthesis and T_s is the average growing season temperature (Kerkhoff *et al.*, 2005). Photosynthesis displays a more complex temperature response. Although Kerkhoff *et al.* (2005) use an average activation energy for photosynthetic reactions $\sim 0.7 \text{ eV}$ (Leuning, 2002), work based on Rubisco limitation of C3 photosynthesis hypothesizes that across broad temperature gradients a Boltzmann-like response with an effective activation energy of 0.37 may exist for photosynthetically limited metabolism (Allen *et al.*, 2005).

We assume that c_G and the mass normalized intensity of cellular respiration, b_0 (as highlighted in Eqns (3) and (4)), can be related by a metabolic efficiency term, c_b , that may or may not differ across taxa and environments so that

$$c_G = c_b(b_0), \quad (6)$$

where c_b is an important physiological attribute of organisms as it indexes the efficiency of biomass production (biomass produced per unit energy per unit time), specifically, $c_b = c_G/b_0$ (units = $\text{mass W}^{-1} \text{ time}^{-1}$). The value of c_b is effectively a measure of growth efficiency and is proportional to whole-plant carbon use efficiency (CUE) of plant physiology (Gifford, 2003).

$$G = c_b(b_0) e^{-E_P/kT_s} M^{3/4}. \quad (7)$$

Here, we assume that biomass production will be described by the Boltzmann term, e^{-E_P/kT_s} , across biologically meaningful temperatures (typically 0°C through 50°C). The rate of net primary production, NPP_{Tot} which includes both above and below ground biomass production, can be modeled as the sum of plant growth over all individuals in the community,

$$\begin{aligned} \text{NPP}_{\text{Tot}} &= \sum_{i=1}^n \alpha_i \left(\sum_{j=1}^S a_{ji} G_{ji} \right) \\ &= \sum_{i=1}^n \alpha_i \left(\sum_{j=1}^S a_{ji} \left(c_{G_{ji}} M_{ji}^{3/4} \right) \right), \end{aligned} \quad (8)$$

where the first summation is over all plants binned into n size classes, regardless of species, α_i is the proportion of total community mass falling within size class i , which has a characteristic plant mass of m_i . The second, nested summation describes functional variation in metabolic traits and abundances across the S_i species in size class i , where a_{ji} is the relative abundance of species j in size class i . It is important to note, the second summation is influenced by the value of c_G which in turn reflects possible variation in the metabolic intensity of cells, b_0 , or the efficiency of growth, c_b .

Equation (8) is similar to other recent models relating species functional variation to productivity (Lavorel & Garnier, 2002). However, the elaborated model explicitly accounts for community size structure, as well as functional trait and possible metabolic variation due to differences in c_G , species composition, and species abundance. Because carbon uptake occurs in the context of a resource or temperature limited timeframe (e.g. a growing season), we partition the effect of temperature on total annual production (ANPP_{Tot}), into the growing season, of length l_s , and the mean growing season temperature, T_s , in Eqn (6) yielding

$$\text{ANPP}_{\text{Tot}} = l_s e^{-E_P/kT_s} M_{\text{Tot}} \sum_{i=1}^n \left(\alpha_i m_i^{-1/4} \sum_{j=1}^{S_i} c_{G_{ji}} a_{ji} \right). \quad (9)$$

Here, c_{G_j} is the allometric growth normalization of species j , which may be influenced by a variety of physiological and life-history traits (e.g. specific leaf area or SLA, nutrient stoichiometry, tissue density, growth form, see below). We can simplify the theory by taking community-wide abundance – and biomass weighted averages of the species-specific growth rate where $\langle c_g \rangle \approx \sum_{j=1}^{S_i} c_{G_j} \alpha_{ji}$. Again, given the resource steady state or zero-sum assumption from above, the first summation can be treated as an approximate constant where $M_{\text{Tot}} \sum_{i=1}^n \left(\alpha_i m_i^{-1/4} \right) = C$, where C approximates the rate of limiting resource supply $C \approx v$, then we have,

$$\text{ANPP}_{\text{Tot}} = e^{-E_P/kT_s} l_s \langle c_g \rangle C. \quad (10)$$

Similar to Eqn (4) above, taking the logarithm of each side reveals

$$\ln(\text{ANPP}_{\text{Tot}}) = \frac{-E_P}{1000k} \left(\frac{1000}{T_s} \right) + \ln[\langle c_g \rangle (l_s)(C)]. \quad (11)$$

A more explicit scaling model that includes functional traits or c_G : The Kerkhoff et al. (2005) model

What sort of plant traits could influence such an increase in cold temperature function? Kerkhoff *et al.* (2005) provide a stoichiometric hypothesis that breaks

down the important physiological variable, c_G , into assimilation, growth, and maintenance respiration. They substitute an individual plant growth model that specifies the traits that could influence interspecific and intersite differences in plant growth that mediate ecosystem temperature responses. Specifically, they focus on how stoichiometric differences in plant tissue influences physiological efficiencies and growth rate. They include the following key parameters:

- (i) total whole-plant nitrogen and phosphorus concentration, F_{Tj}^N and F_{Tj}^P , of species j ;
- (ii) the photosynthetic nutrient use efficiency Φ_p that reflects the ability of plants at using nitrogen to assimilate carbon into biomass (i.e. $\text{PUNE} = \alpha_L / F_L^N$, $\text{g g leaf N}^{-1} \text{ time}^{-1}$);
- (iii) the cost of biosynthesis per unit nutrient or c_{gj} which is equivalent to $c_B / (c_B(F_T^N / F_T^P) + c_R)$ where c_R and c_B are rate constants describing the biosynthesis per unit plant P (c_B units: $\text{g g P}^{-1} \text{ time}^{-1}$) and the respiratory cost of biosynthesis per unit plant N (c_R units: $\text{g g N}^{-1} \text{ time}^{-1}$);
- (iv) the whole-plant community leaf mass per unit ground area L_{Tot}

Specifically, Kerkhoff *et al.* modify Eqn (8) to give

$$\ln(\text{ANPP}) = \frac{-E_P}{1000k} \left(\frac{1000}{T_s} \right) + \ln \left\{ l_s \left\langle c_g \frac{F_p^P}{F_p^N} \phi_L F_L^N \Phi_p \right\rangle L_{\text{Tot}} \right\}, \quad (12)$$

where community-wide, abundance- and biomass-weighted averages of the species-specific traits, $\langle c_g (F_p^P / F_p^N) \phi_L F_L^N \Phi_p \rangle$ approximates the value of c_G in Eqns (5, 6 and 10) and in Eqn (11). Equation (12) is similar in form to Eqn (5). However, the right-hand side of Eqn (12) explicitly includes the role of potential variability in plant tissue stoichiometry and the biochemical efficiency of biomass production per unit nutrient mass. Written in this form, the 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. Note, these key parameters are species specific and potentially site specific. Thus, directional changes in any of the parameters (due to adaptation and/or species replacements), along physical gradients, such as temperature, will influence ecosystem flux and production.

Kerkhoff *et al.* utilize a global stoichiometry and ecosystem NPP dataset to assess how autotrophic stoichiometric traits systematically vary across latitude and temperature gradients. The term $(c_g (F_p^P / F_p^N) \phi_L F_L^N \Phi_p)$ reflects the influence of plant nutrient concentration on

rates of production is effectively equal to the value of c_G and is then, according to Eqn (6), also proportional to the product of the intensity of cellular metabolism, b_0 and growth efficiency c_b (see Eqns (6) and (7)). Kerkhoff *et al.* show that the magnitude of this term likely changes dramatically across temperature (and hence latitude) gradients. Similar changes in autotrophic stoichiometric content has also been found in three additional recent studies (McGroddy *et al.*, 2004; Reich & Oleksyn, 2004; Han *et al.*, 2005). Kerkhoff *et al.* (see also Hedin, 2004) show that vegetation N:P and N-productivity Φ_p increase with growing season temperature. Importantly, empirical data show that the temperature response of N-productivity, Φ_p , is: (1) almost exactly the inverse of that predicted from the kinetics of photosynthetic reactions with an E_P of 0.7; and (2) increases with phosphorus content of plant tissue (Kerkhoff *et al.*, 2005). That is, the value of Φ_p appears to increase exponentially with temperature in a fashion that negates the change in environmental temperature on instantaneous rates.

A critical prediction of the Kerkhoff et al. (2005) model

The finding that plant tissue stoichiometry and the efficiency of biomass production changes along temperature gradients suggests the following hypothesis: If plant density and size does not vary across temperature gradients then the observed values of phosphorus-mediated increases in nitrogen-productivity of autotrophs can directly offset (i) the temperature dependence of net primary productivity and (ii) likely lead to an increase in temperature normalized ecosystem flux. Indeed, in accord with their model, Kerkhoff *et al.* show that there is no significant relationship between *instantaneous* rates of NPP across and average growing season temperature. The elaborated model of Kerkhoff *et al.* and empirical data on nutrient content and nutrient productivity, Φ_p , suggests that the flat response of annual ecosystem respiration with temperature across sites (discussed above), the increase in temperature normalized *instantaneous* rates of flux (Fig. 3), and the approximately flat relationship between ANPP and growing season temperature may be driven by the turnover of species with varied physiological attributes across sites.

A critical prediction of the Kerkhoff *et al.* model is that: *mass corrected instantaneous growth rates of individual autotrophs should also be insensitive to growing season temperature.* Support of this prediction would be consistent with the hypothesis that changes in organismal traits influence large-scale variation in ecosystem production and flux along temperature gradients. In this case, changes in autotrophic nutrient stoichiometry and

growth efficiency along temperature (latitude) gradients are hypothesized to influence ecosystem rates of production and carbon flux. In order to test this prediction, we ask whether the instantaneous rate of biomass production of plants show a temperature response across sites? If no temperature response, or a much shallower response, is observed this would be consistent with the hypothesis that physiological differences in organisms within each site compensate for the change in environmental temperature.

Testing the prediction – organismal instantaneous rates of production are independent of latitude and temperature

Latitudinal variation in annual rates of biomass production?

Annual growth rates for trees across a broad temperature gradient were taken from the a global plant production and biomass database that consists of data from Cannell (1982) and Niklas & Enquist (2004). The Cannell dataset is standardized to 1.0 ha and contains plant density, total basal stem diameter, standing biomass and annual production rates of stem, litterfall, bark, foliage, roots and fruits, as well as latitude, elevation and age of dominant species. Annual NPP data ($ANPP_{Tot}$) calculated on a per individual basis (G) includes above and below ground production. Data used for analyzing biomass production were generally from even-aged conspecific stands and production was often an average of several years. Some have highlighted that there are limitations in the type of methodology utilized – including likely underestimations in root biomass (Clark *et al.*, 2001a,b) see also (Enquist & Niklas, 2002). Nevertheless, the Cannell dataset represents one of the best standardized global datasets on terrestrial plant production available.

From the Cannell database we calculated the average annual rate of biomass production per plant. Average individual biomass and production values were calculated by dividing the total stand organ mass and organ production by the number of individuals in the plot (Enquist & Niklas, 2002; Niklas & Enquist, 2002). This average rate of biomass production per individual enables us to assess the impact of latitude and temperature on plant growth rates. The averaging of individual production data reduces the variance in the estimated rates of production, but the geographic and taxonomic breadth of the data trades-off against this limitation.

As shown in Eqn (1) and Fig. 4, size is a dominant controller of biomass production. In order to remove the effect of size we corrected *annualized* tree growth rates for tree mass by dividing annual growth rate through

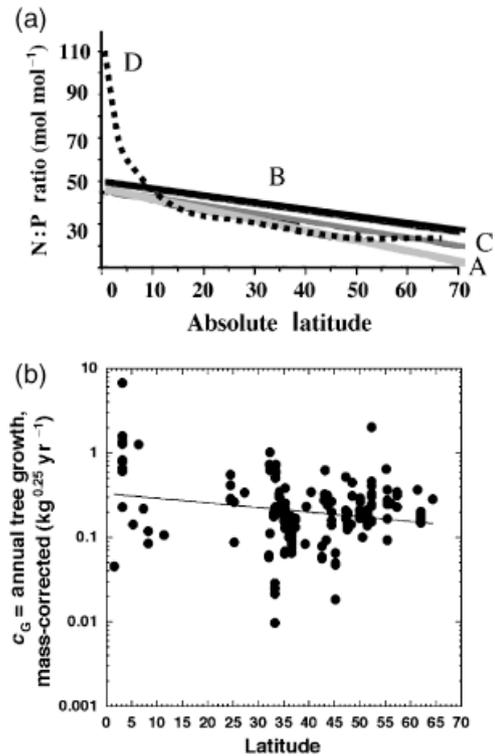


Fig. 5 (a) From Hedin (2004), showing the latitudinal shift in plant tissue N:P ratio light grey line A from Reich & Oleksyn (2004), black line B from Kerkhoff *et al.* (2005), dark grey line C and dashed line D from McGroddy *et al.* (b) Mass corrected rates of annual biomass production for individual trees (kg yr^{-1}) across the Latitudinal Gradient. Data from Cannell (1982) and are the same as the data presented in Fig. 4. Correcting for the individual allometric rate of biomass production (shown in Fig. 4) is the value of the allometric constant c_G in Eqns (5, 6 and 10). Variation in this value reveals that latitude explains little in the variation in annualized rates of biomass production. Although the relationship is significant (see main text), the r^2 value is less than 0.01 indicating that for trees of similar sizes, individuals growing in cold northerly latitudes produce approximately similar amounts of biomass in a year as individuals growing in warmer latitudes.

by tree mass raised to the $3/4$ power. In doing so, we then calculate the mass corrected the growth rate, c_G , in Eqn (5) ($c_G = G/M^{3/4}$). Plotting the mass-corrected annualized rate of growth or c_G , for each species as a function of latitude (Fig. 5) reveals that latitude explains little in the variation in annualized rates of mass corrected biomass production. Although the relationship is significant (natural logarithmic transformation of growth values, $P < 0.001$), the r^2 value is less than 0.01 indicating that latitude explains remarkably little variation in growth rates ($r^2 = 0.045$, $n = 178$, $F = 8.26$). These results indicate that for trees of similar size, individuals growing in cold northerly latitudes produce approximately similar amounts of biomass in a year as indivi-

duals growing in warmer latitudes. This pattern is consistent with past speculation and preliminary data on global variability in tree growth (Jordan, 1971).

Calculating instantaneous rates of growth: correcting for growing season length

In order to assess the Kerkhoff *et al.* model, a growing season length correction and instantaneous growth rates are required as annualized growth rates are confounded by the influence of growing season length. For each site within the Cannell database, taking the latitude and longitude of each site, we estimated growing season length using monthly values for mean temperature, diurnal temperature range, and mean precipitation (PPT) drawn from a global 10' resolution gridded climatology (New *et al.*, 2002). Temperature and precipitation data for each site in Cannell were extracted using Arcview geographical information system (GIS). 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 timescale. Months were included in the growing season only if they were not too cold (minimum temperature >0) or too dry (MI ≥ 0.95). Because we assume that metabolism is photosynthetically limited, and because the kinetic effects of temperature are more instantaneous in nature, we calculated mass-corrected growth rates per daylight hour during the growing season, based on site latitude. Additional details of the calculation of growing season length are given in Kerkhoff *et al.* (2005).

Our analyses show that a more *instantaneous* measure of tree growth rate (g h⁻¹) shows a weak relationship with mean growing season temperature (Fig. 6). For all plants, without correcting for plant size, there is no relationship between annual growth rate and mean growing season temperature ($r^2 = 0.0019$, $n = 266$, $F = 0.5165$, $SE = 1.49$, $P = 0.4729$). After correcting for tree mass, the fitted regression for mass corrected growth for all trees, explains very little of the variation in mass corrected growth ($r^2 = 0.0213$, $n = 210$, $SE = 0.604$, $F = 4.53$, $P = 0.034$) but indicates that there is a slight but significant negative slope (slope = -2.38, 95% CI = -0.176 to -4.596). This relationship lends some support to an alternative photosynthetic model that predicts a shallower slope (Allen *et al.*, 2005), but growing season temperature explains almost none of the variation in growth. Separating these trees into angiosperms and conifers reveals that for conifers, there is no relationship between mass corrected hourly growth rate and mean growing season temperature ($r^2 = 0.003$, $n = 140$, $F = 0.422$, $SE = 0.611$, $P = 0.5169$).

Similarly, for angiosperms ($r^2 = 0.0479$, $n = 70$, $F = 3.42$, $SE = 0.579$, $P = 0.068$) the slope, -2.697, is also statistically indistinguishable from zero. In all cases, growing season temperature explains little to no variation in plant growth (Fig. 6). The slopes for all relationships are significantly less than -7.5, the value predicted from the metabolic model.

Implications: directional variability in plant metabolic and growth traits imply additional ecosystem invariants

The finding of approximate invariance in plant growth rate with temperature (and thus, latitude) has important implications for other ecosystem measures. Across sites, the net rate of organismal biomass production, G , scales allometrically as $G = c_G M^{3/4}$. Note, that the allometric growth constant c_G , which is the mass-normalized growth rate, is the intercept value for the fitted regression line through Figs 5 and 7. If, as implied by Figs 5 and 7, $G = c_G M^{3/4}$ holds across differing temperature regimes, then the constant c_G is insensitive to temperature variation. Again, Kerkhoff *et al.* hypothesize that constancy in c_G may be due to directional changes in tissue stoichiometry and biochemical efficiency of production across temperature gradients (i.e. the variables b_0 and/or c_b in Eqns (6 and 7)).

The apparent generality of $G = c_G M^{3/4}$, especially for larger shrubs and trees (West *et al.*, 1999) allows one to begin to assess the implications of organismal traits (specifically, traits of autotrophs) that then in turn influence variability in autotrophic carbon assimilation, A , and respiration, R , rates. Autotrophic net-carbon growth rate, G_C , a necessary component of net biomass growth (G), is equal to the whole-plant carbon assimilation rate A_T minus the whole-plant respiration rate, R_T (where R_T is equal to the whole-plant metabolic rate B). Here, R_T reflects both maintenance and growth respiration. Thus, we do not explicitly include the specific subcomponents of plant respiration (Thornley & Cannell, 2000). Substituting the allometric relationships predicted from metabolic scaling theory (West *et al.*, 1997), and *within site* temperature dependency for A_T and R_T , we have

$$G_C = A_T - R_T = \left(c_A e^{-E_A/kT} M^{3/4} \right) - \left(c_R e^{-E/kT} M^{3/4} \right), \quad (13)$$

where c_A and c_R are the assimilation and respiration constants, respectively, with units of c_A and c_R being equal to carbon mass^{1/4} × time⁻¹. Note, c_R just reflects the metabolic constant b_0 but with mass units instead of energy units. Further, E_A and E represents the activation energies for carbon assimilation and respiration, respec-

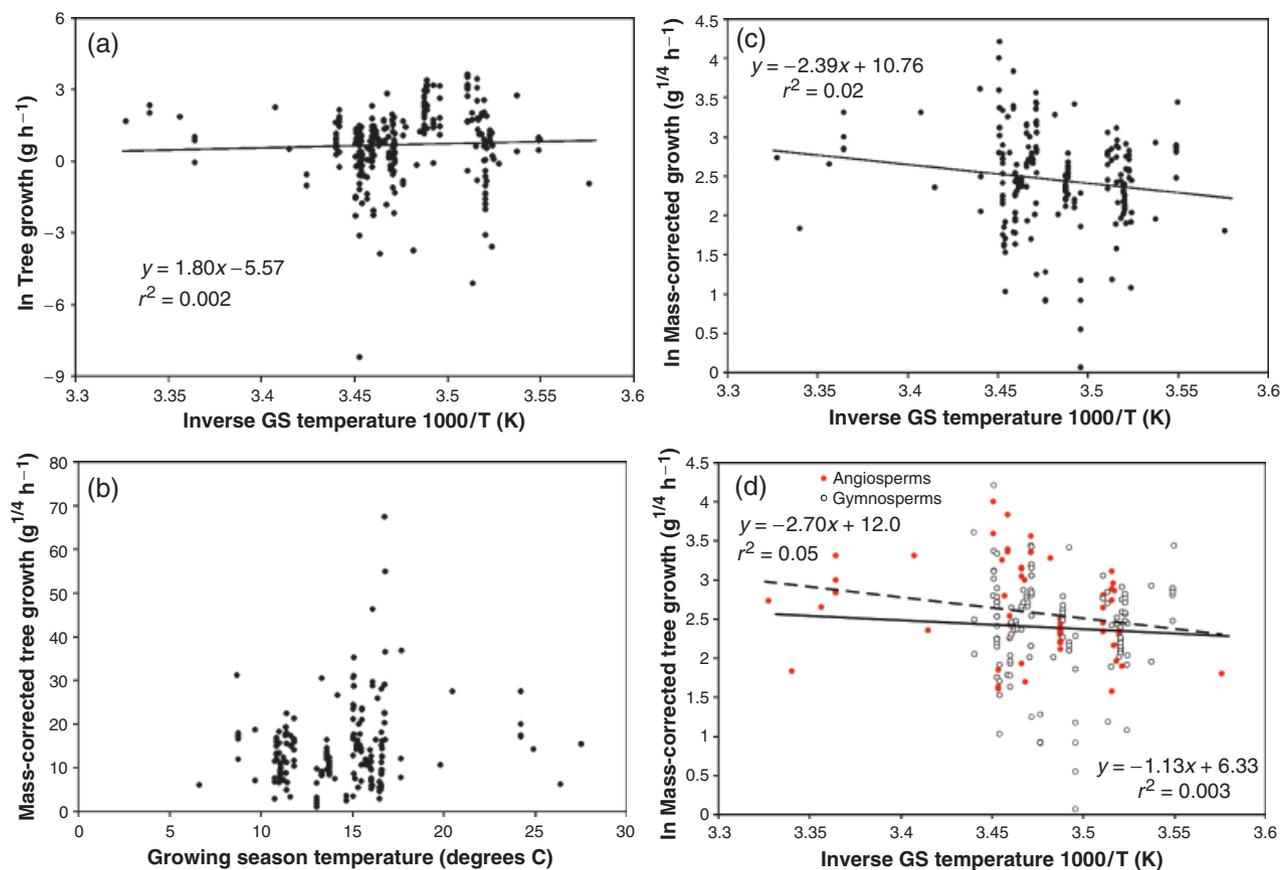


Fig. 6 (a) The same graph as shown in Fig. 5 but individual growth rates are corrected for growing season length where individual tree growth, with units of kg h^{-1} (log scale). The value of c_G is then plotted as a function of inverse growing season temperature in kelvins (K). Here, growth is *not* mass corrected for the individual allometric rate of biomass production. There is no significant relationship between temperature and whole-plant growth rate during the growing season; (b) relationship between mass corrected growth rate ($G = dM/dt$, where $[(dM/dt)/M^{3/4}] = c_G$) and mean growing season temperature ($^{\circ}\text{C}$); (c) relationship between mass corrected growth rate and the inverse of growing season temperature. These growth data are the same graph as shown in Fig. 5 but here, individual rates of biomass production are both mass corrected *and* corrected for the length of the growing season. The y -axis is the allometric normalization parameter c_G (see text for details) where the units of $c_G = \text{kg}^{0.25} \text{h}^{-1}$, (log scale); and (d) same data as in (c) but data are broken out by gymnosperms and angiosperms. In general, temperature explains little to no variation in plant growth rates (see text for details).

tively. Therefore, the value of c_G can now be defined as $c_G \equiv c_A - c_R$ (see Eqn (5)). If a plant is actively growing then $(c_A e^{-E_A/kT} M^{3/4}) > (c_R e^{-E_R/kT} M^{3/4})$.

For the entire plant community, the net carbon production ($\text{NPP}_{\text{carbon}}$), is equal to summing the net growth rates of all individuals, j , within the community. Summing growth across all size classes, similar to above, yields

$$\begin{aligned} \text{NPP}_{\text{carbon}} &= \sum_{j=1}^n [(A_{Tj} - R_{Tj})(N_j)] \\ &= \left[(c_{A_j} e^{-E_{A_j}/kT} M_j^{3/4}) - (c_{R_j} e^{-E_{R_j}/kT} M_j^{3/4}) \right] (N_j). \end{aligned} \quad (14)$$

Thus, knowing variability in whole-ecosystem rates of net carbon production, $\text{NPP}_{\text{carbon}}$, across sites also

must reflect variability in A_T and R_T across species. However, do autotrophic values of A_T and R_T change directionally across temperature and latitudinal gradients? As mentioned in the Introduction, there is a literature claiming adaptive changes in both organismal respiration (see also Fig. 4) and photosynthetic rates (see also Fig. 2) across broad temperature gradients. Unfortunately, measurements of A_T are difficult to obtain as daytime net carbon exchange rates, A_e (what is usually measured and reported in the literature) comprise of both assimilation and respiration rates. However, if measures of A_e are directly proportional to A_T then we can assess the general predictions made by Eqn (13).

Analyzing an extensive dataset presented by Buchmann & Schulze (1999) who report A_e (but not A_T) and

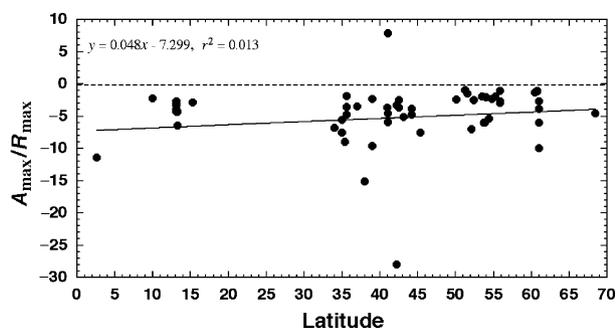


Fig. 7 Ratio of maximum ecosystem CO₂ assimilation rates (A_e^{\max}) during the day ($\text{mmol m}^{-2} \text{s}^{-1}$) and maximum night-time respiration rates (R_e^{\max}) ($\text{mmol m}^{-2} \text{s}^{-1}$). Data from Buchmann & Schulze (1999). Sites include grasslands, savannas and forests. The value is a dimensionless number that does not vary across latitude indicating that despite differences in growing season temperatures and species composition the ratio is an approximate constant. The mean fitted average value across sites is a dimensionless number with a value of -7.299 . If the values of c_A and b_0 both vary in direct proportion to one another across temperature and latitudinal gradients then their ratio, as indicated by Eqn (14), is a constant indicating that (i) respiratory physiology and photosynthetic physiologies are tightly coupled to one another; and (ii) this coupling does not seem to vary despite apparent differences in adaptations to differences in growing season temperature across major biomes or major phylogenetic differences between autotrophs (see text for details)

R_T (as measured as night time respiration) suggests that the quotient of A_T and R_T may also be insensitive to broad-scale temperature gradients. For most sites Buchmann and Schultze report a mean maximum value for instantaneous rates of net assimilation, A_e^{\max} , and night-time respiration R_e^{\max} . This dataset includes terrestrial flux data from 139 studies (ranging from tropical and boreal forests, and includes grassland and savannas (Buchmann & Schulze, 1999). These surface flux values represent the operation of both autotrophs and heterotrophs. Again, here, we assume that A_e^{\max} is directly proportional to A_e .

Assuming autotrophic values of assimilation, A_T , and respiration, R_T , across sites are approximately proportional to whole-ecosystem values of A_e^{\max} and R_e^{\max} then several interesting results emerge. Our analysis of this dataset shows no relationship between absolute latitude and net maximum ecosystem surface carbon assimilation capacity (A_e^{\max} , $\text{mmol m}^{-2} \text{s}^{-1}$; $r^2 = 0.030$, $n = 77$, $F = 2.29$, $P = 0.1344$), net ecosystem surface respiration capacity (R_e^{\max} , $\text{mmol m}^{-2} \text{s}^{-1}$; $r^2 = 0.0044$, $n = 57$, $F = 0.2483$, $P = 0.6202$). Interestingly, even variability in net surface evapotranspiration capacity (mm day^{-1} ; R_{smax} $r^2 = 0.0288$, $n = 32$, $F = 0.8902$, $P = 0.3530$) is not related to latitude. Presumably, if both A_e^{\max} and R_e^{\max} are not related to latitude, then mean annual growing

season temperature also does not explain much variability in A_e^{\max} and R_e^{\max} .

Together, these findings indicate that ecosystems are likely to be characterized by another approximate constant across broad environmental gradients. The constancy of ecosystem assimilation (ANPP) and respiration (GPP) with latitude (and presumably temperature) indicates that the ratio, A_e^{\max}/R_e^{\max} and thus, the autotrophic ratio, A_T/R_T , will also be an approximate constant dimensionless number where

$$\frac{A_e^{\max}}{R_e^{\max}} \propto \frac{A_T}{R_T} \propto \frac{(c_A e^{-E_A/kT} M^{3/4})}{(c_R e^{-E/kT} M^{3/4})} = \frac{c_A}{c_R}. \quad (15)$$

Here, the Boltzmann term and the mass term in the numerator and denominator cancel out leaving the ratio c_A/c_R . However, in the Kerkhoff *et al.* model, both c_A and b_0 (remember that c_R reflects the term b_0 but with different units) can vary (because of changes in c_G) due to traits that influence growth efficiency and/or metabolic intensity but are independent of mass. The question then arises, how are the values of c_A and c_R related to one another across differing environments, especially differences in growing season temperature and latitude? Figures 4 and 7 suggest that c_G (where again $c_G = c_A - c_R$ see Eqn (5) above) does not appreciably vary across latitude and growing season temperature.

If the values of c_A and b_0 both vary in direct proportion to one another across temperature and latitudinal gradients (as suggested by our results) then their ratio should reveal an approximately constant number – indicating that respiratory physiology and photosynthetic physiologies are tightly coupled to one another. Indeed, this is what we see. Plotting the ratio of A_e^{\max}/R_e^{\max} , as reported in Buchmann & Schultze (1999), across latitudes reveals a flat line (Fig. 7; $r^2 = 0.0127$, $n = 57$, $F = 0.7079$, $P = 0.404$). Fitting a standard least squares linear regression through the data shows that the intercept of the line is the average value of A_e^{\max}/R_e^{\max} (Fig. 8). The value for this dimensionless constant is -7.29 (95% CI = -2.19 to -12.40) and it is significantly different from zero ($P = 0.0059$). This number indicates that, on average, across sites that differ dramatically in their average annual temperature, in terms of net flux capacity, for every carbon atom that can be respired approximately 7 ± 5 carbon atoms can be assimilated from the atmosphere (see also findings of (Amthor, 2000; Saxe *et al.*, 2001).

Although there is variability in the numeric value of the ratio, remarkably, this number appears to be insensitive fundamental aspects of climate and physiognomy of these sites that range greatly in temperature and precipitation (grasslands, to savannas to forests). Variability in the value of (A_e^{\max}/R_e^{\max}) is not explained by

ecosystem age ($r^2 = 0.027$, $n = 20$, $F = 0.48$, $P = 0.489$, sites ranged from ecosystems 5.5 years since disturbance to 300 years since disturbance), the leaf area index of the site, or LAI (measured as leaf area per unit ground area; $r^2 = 0.029$, $n = 49$, $F = 1.40$, $P = 0.243$, sites range in LAI from 0.2 to almost 8) or the vegetation height ($r^2 = 0.0002$, $n = 40$, $F = 0.0063$, $P = 0.937$, sites ranging in height from 0.2 m to almost 30 m). The observation of approximate constancy with latitude is important given that the biomes represented in the dataset also differ dramatically in their values of NPP and standing biomass.

Does the ecosystem ratio of (A_e^{\max}/R_e^{\max}) approximate the autotrophic leaf ratio (A_T/R_T)

If, as assumed in our model, the constancy in (A_e^{\max}/R_e^{\max}) reflects physiological processes at the leaf level then the leaf-level value of (A_T/R_T) should be similar to the ecosystem value. Detailed temperature response of both the whole-ecosystem and the autotrophic component are difficult to obtain. However, data from, Niwot Ridge, a high alpine ecosystem (Huxman *et al.*, 2003), not represented in the Buchmann and Schultze data set, allows us to assess our assumption that the observed ecosystem value of (A_e^{\max}/R_e^{\max}) approximates the autotrophic ratio (A_T/R_T). Across the growing season, using branch-scale measurements of gas exchange for three conifer species under saturating light and optimal temperature revealed an average photosynthesis-to-respiration ratio (A_T/R_T) of -7.53 ± 1.29 . This autotrophic value is indistinguishable from the observed average of (-7.29) observed across ecosystems (Fig. 8). At the same site, for the ecosystem scale, the temperature response of A_e^{\max} and R_e^{\max} (reported as NEE and R_e), shows a maximum ratio of around -6.1 at about $8-10^\circ\text{C}$ for two different years. When evaluating maximum values of A_e^{\max} and R_e^{\max} on days of maximum flux within a season (DOY 145 for 1999; DOY 131 for 2000), we find: -6.98 (1999) and -7.32 (2000). Thus, detailed data from one site is consistent with the assumption that (A_e^{\max}/R_e^{\max}) does approximate (A_T/R_T) as codified in Eqns (13 and 15).

Conclusions

Understanding how organisms in terrestrial ecosystems influence large-scale biogeochemical cycles is a focal point of many research programs. For example, how changes in vegetation composition on a landscape mechanistically influence different aspects of the water cycle, such as streamflow, is an active area of science (Zhang *et al.*, 2001; Huxman *et al.*, 2005; Wilcox *et al.*, 2005). Likewise, a number of researchers are interested

in understanding how shifts in vegetation may influence carbon sequestration from the atmosphere or loss from long-term soil carbon pools (Archer *et al.*, 2001; Pacala *et al.*, 2001; Jackson *et al.*, 2002). Underlying each of these questions is the influence of species traits, and their combination in communities, that translate variation in salient features of the environment into biological activity. It is interesting to note, however, that ecologists and physiologists have long viewed Darwinian selection and adaptation as a local and individualistic phenomena with little discussion of the implications for ecosystem processes (Hedin, 2004). Our approach has explicitly focused on how local adaptation, specific plant traits, and ecology can influence ecosystem processes.

Using a theoretical framework outlined by metabolic scaling theory (Enquist *et al.*, 2003; Kerkhoff *et al.*, 2005), we focused on understanding the paradoxical (1) invariance of GPP and annualized ecosystem respiration across latitude and (2) the increase in ecosystem temperature normalized respiration rate with latitude. It is important to emphasize that Metabolic Scaling Theory does not 'predict' that ecosystem level temperature responses will be approximately flat or constant across temperature gradients. The theory does, however, show that *if* traits that influence the value of b_0 and/or c_G in Eqns (5) and (6) vary inversely with temperature between sites *and both* the number of plants per unit area and the average plant size does not vary *then* the theory does show that temperature will likely not be a major controller of ecosystem fluxes.

Analyses of global datasets reveal that mass-corrected instantaneous measures of woody plant biomass production are insensitive to growing season temperature. This observation supports a critical prediction of the theory developed by Enquist *et al.* (2003) and Kerkhoff *et al.* (2005) that a systematic change in b_0 and/or c_b with latitude can then yield a much weaker to constant temperature response of annual ecosystem net production and annual flux across latitude and possibly an increase in the temperature normalized ecosystem respiration. In other words, adaptive changes in physiology can trump and even outweigh large-scale variability in the abiotic environment. The end result is photoautotrophic behavior can influence the magnitude and variability in ecosystem processes. Thus, differences in local ecology (specifically, the distribution of organismal traits within communities) appear to account for latitudinal patterns of ecosystem production and flux. Combined with the findings of Kerkhoff *et al.* (2005), our results are consistent with the hypothesis that directional changes in organismal traits associated with metabolism and/or growth efficiency (b_0 and c_b , respectively, see Eqns (5-7)), along broad

climatic gradients, can negate the effects of abiotic variability along that gradient.

Our model is a deliberate oversimplification of whole-plant and whole-ecosystem growth and respiration. Empirical studies have shown that the link between the response of growth and the response of net carbon assimilation to temperature in a plant is not direct (Körner, 1991). This is mainly because plant growth is the end result of many processes, such as proportional partitioning of metabolic production to plant organs, respiration in leaves, stems and roots, photosynthesis and stomatal conductance, (each with a potentially different optimum temperature) (Körner, 1991; Pereira, 1994). Here, we have not explicitly discussed these potentially more involved attributes of growth (but see Niklas & Enquist, 2002; Kerkhoff *et al.*, 2005). Nevertheless, our model highlights how specific traits associated with whole-plant respiration rate and the efficiency of biomass production *alone* can account for the paradoxical patterns of ecosystem respiration and net production with latitude.

In a prominent review of possible mechanisms to account for the invariance of annual respiration and production across temperature gradients (Grace & Rayment, 2000), an adaptive or 'biotically driven' explanation was not mentioned. The hypothesis evaluated in this current paper focuses on the importance of adaptive responses of organisms in influencing the paradoxical patterns of ecosystem flux with latitude. Although the mechanisms listed by other authors (Giardina & Ryan, 2000; Grace & Rayment, 2000; Thornley & Cannell, 2001) are still potentially important, we have provided empirical evidence and a theoretical framework that suggests that adaptive responses of organismal metabolism and growth, across broad scale temperature and latitudinal gradients, can also significantly influence ecosystem flux and production.

Interestingly, our findings highlight the possibilities of several 'ecosystem invariants'. We have shown that mass corrected rates of autotrophic biomass production, or c_G (where $G/M^{3/4} = c_G$), the ecosystem ratio of (A_e^{\max}/R_e^{\max}) , and likely the organismal-level ratio of (A_T/R_T) are invariant with respect to latitude and growing season temperature. These 'ecosystem constants' appear to hold across diverse biomes. Naturally, these 'invariants' appear to be average values with scatter about their values. Nevertheless, the finding that some attributes of ecosystem functioning appear to not vary with changes in organismal composition is potentially insightful.

The constancy observed in Fig. 7 is supportive of recent comments by Cannell & Thornley (2000). Specifically, they state that '*ratios between rates of photosynthesis and respiration ... are expected to vary within a limited*

range ... because of the coupling between respiration and C substrate supply. Realistic models should reflect this inherent constraint as an unforced outcome of the dependence of respiration on C substrate concentrations.' (Cannell & Thornley, 2000). What is intriguing about our finding is that the invariance of the ratio indicates that the outcome of the dependence of whole-plant respiration on carbon substrate concentrations does not appear to be influenced by apparent differences in adaptations to differences in growing season temperature across major biomes or major phylogenetic differences between autotrophs (e.g. ecosystems dominated by monocots, conifers, and angiosperm trees). A recent review of available data also seems to suggest that temperature-mediated differences in dark leaf respiration are closely linked to concomitant differences in leaf photosynthesis (Atkin *et al.*, 2005). A constancy of (A_e^{\max}/R_e^{\max}) across temperature gradients suggests that (1) the sorting of species along environmental gradients and possible thermal acclimation strongly implies a tight coupling of A_e^{\max} and as a result (2) that plant community assembly and organization can be equated with carbon balance at the physiological and ecosystem scale.

There has been recent discussions in the literature regarding (i) the discovery of additional ecosystem 'constants' not reported here; and (ii) the underlying mechanisms behind apparent constancy in ecosystem functioning (Waring *et al.*, 1998; Brown *et al.*, 2001; Enquist & Niklas, 2001; Ernest & Brown, 2001; Ernest *et al.*, 2003; Huxman *et al.*, 2004). These studies have shown how species replacements and community dynamics appear to be organized in a way that the end result is the convergence of many ecosystem attributes to similar values or states (biomass production, exchange of energy, etc.). For example, over a wide range of biomes, receiving precipitation of between 50 and 3000 mm yr⁻¹, there is a convergence to similar maximum rain-use efficiencies of biomass production during historically dry periods (Huxman *et al.*, 2004). Thus, similar to the illustration of temperature effects on production in the current paper, despite differences in physiognomy, diversity, climate, and cumulative annual water consumption, rain-use efficiencies across biomes remain similar.

Given our findings it is important to highlight that it is *still* paradoxical that organisms at high latitudes and possibly high elevations have higher values of cellular metabolism, b_0 , and/or growth efficiency, c_b , than lower latitude organisms. Why should it be that natural selection has not produced phenotypes that maximize their temperature response everywhere? Our answer is speculative but based on natural selection.

We speculate that a latitudinal gradient in organismal values of cellular respiration and or the efficiency of

converting metabolism into growth (i.e. b_0 and/or c_b , respectively), reflects directional selection for increased growth rates in cold environments and a lack of stabilizing selection on growth rate, at lower latitudes and elevations. This hypothesis assumes that in colder environments there is strong selection for up-regulation of metabolism (see also Criddle *et al.*, 1994). Across all autotrophs, if there is a maximum limit for the species specific values of b_0 and/or c_b then this hypothesis predicts that (i) at lower latitudes and altitudes a lack of stabilizing selection has resulted in a higher variance in these variables and (ii) at higher latitudes and altitudes strong stabilizing selection has favored higher values and less variance in b_0 and or c_b .

Although we are not aware of any autotrophic dataset precise enough to test this hypothesis, a recent analysis of heterotrophic values of b_0 in endotherms (mammals and birds) – a component of whole-ecosystem respiration – does appear to support this hypothesis (Anderson & Jetz, 2005). Our findings of approximate invariance of growth rates with temperature suggests that respiration rates and/or growth efficiencies are higher for plants inhabiting colder environments. If correct, then: (1) higher values of b_0 could account for the increased in ecosystem temperature normalized respiration as reported by Enquist *et al.* (2003) (see also Fig. 3) and (2) a change in b_0 and/or c_b could account for the approximate invariance in NPP with temperature as reported by Kerkhoff *et al.* (2005). There is some degree of support for a directional change in autotrophic values of b_0 with broad scale temperature gradients. As discussed above, there are several studies that suggest that high altitude and latitude species may have proportionally higher rates of respiration than low latitude and lowland species (see Introduction above but see Wright *et al.*, 2006). There is also indication that cold acclimation and general cold adaptation may involve a change in metabolic efficiencies, c_b (Kurimoto *et al.*, 2004). A systematic increase of the allometric growth efficiency, c_b , with temperature or latitude is consistent with preliminary data that suggests that CUE, where $CUE \propto c_b$, is highest for high latitude plants and the lowest for tropical species (Amthor, 2000; Chambers *et al.*, 2004). Nevertheless, while our study and the literature appear to be consistent with our hypothesis much more work is needed in order to properly assess this 'biotically driven hypothesis.' For example, it is unclear if there are broad scale geographic patterns in autotrophic values of b_0 and c_b . Our approach indicates that future studies need to quantify the biogeographic and macroecological nature of plant physiology (see also Reich, 2005) – specifically, both the values of b_0 and c_b – across broad scale temperature and geographic gradients. Doing so

will more accurately inform global change and modeling studies.

Together, our results, in conjunction with these studies, suggest that patterns of species replacements along gradients must be such that some aspects of ecosystem organization do not appreciably change or change in a manner in which to cause compensatory functional dynamics at the ecosystem scale. In addition, approximate constancy at the ecosystem level highlights the importance of the need to understand the mechanistic basis for species organization and replacement in communities (Ernest & Brown, 2001), along with the ecological implications of physiological acclimation and species adaptation in setting the stage for ecosystem response to global change. The search for the processes that influence ecosystem homeostasis and the link between the distribution of traits within a given locality will prove a ripe area of investigation.

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References

- Ackerly DD, Monson RK (2003) Waking the sleeping giant: the evolutionary foundations of plant function. *International Journal of Plant Sciences*, **164**, S1–S6.
- Allen AP, Gillooly JF, Brown JH (2005) Linking the global carbon cycle to individual metabolism. *Functional Ecology*, **19**, 202–213.
- Amthor JS (1989) *Respiration and Crop Productivity*. Springer-Verlag, New York.
- Amthor JS (2000) The McCree–de Wit–Penning de Cries–Thornley respiration paradigms: 30 years later. *Annals of Botany*, **86**, 1–20.
- Anderson KJ, Jetz W (2005) The broad-scale ecology of energy expenditure of endotherms. *Ecology Letters*, **8**, 310–318.
- Archer S, Boutton TW, Hibbard KA (2001) Trees in grasslands: biogeochemical consequences of woody plant expansion. In: *Global Biogeochemical Cycles in the Climate System* (eds Schulze

- ED, Harrison SP, Heimann M, Holland EA, Lloyd JJ, Prentice IC, Schimel D), pp. 115–138. Academic Press, Durham, NC.
- Atkin OK, Bruhn D, Hurry VM *et al.* (2005) The hot and the cold: unravelling the variable response of plant respiration to temperature. *Functional Plant Ecology*, **32**, 87–105.
- Atkin OK, Tjoelker MG (2003) Thermal acclimation and the dynamic response of plant respiration to temperature. *Trends in Plant Science*, **8**, 343–351.
- Baldocchi D, Falge E, Gu LH *et al.* (2001) FLUXNET: a new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapor, and energy flux densities. *Bulletin of the American Meteorological Society*, **82**, 2415–2434.
- Brown JH, Ernest SKM, Parody JM *et al.* (2001) Regulation of diversity: maintenance of species richness in changing environments. *Oecologia*, **126**, 321–332.
- Brown JH, Gillooly JF, Allen AP *et al.* (2004) Toward a metabolic theory of ecology. *Ecology*, **85**, 1771–1789.
- Buchmann N, Schulze ED (1999) Net CO₂ and H₂O fluxes of terrestrial ecosystems. *Global Biogeochemical Cycles*, **13**, 751–760.
- Cannell MGR (1982) *World Forest Biomass and Primary Production Data*. Academic Press, New York.
- Cannell MGR, Thornley JHM (1998) Temperature and CO₂ responses of leaf and canopy photosynthesis: a clarification. *Annals of Botany*, **82**, 883–892.
- Cannell MGR, Thornley JHM (2000) Modelling the components of plant respiration: some guiding principles. *Annals of Botany*, **85**, 45–54.
- Chambers JC, Tribuzy ES, Toledo LC *et al.* (2004) Respiration from a tropical forest ecosystem: partitioning of sources and low carbon use efficiency. *Ecological Applications*, **14**, S72–S88.
- Clark DS, Brown S, Kicklighter DW *et al.* (2001a) Measuring net primary production in forests: concepts and field methods. *Ecological Applications*, **11**, 356–370.
- Clark DS, Brown S, Kicklighter DW *et al.* (2001b) Net primary productivity in tropical forests: an evaluation and synthesis of existing field data. *Ecological Applications*, **11**, 371–384.
- Clausen J, Keck DD, Hiesey WM (1940) *Experimental Studies on the Nature of Species I. The Effect of Varied Environments on North American Plants*. Carnegie Institution of Washington, Washington, DC.
- Criddle RS, Hopkin MS, McArthur ED *et al.* (1994) Plant distribution and the temperature coefficient of metabolism. *Plant, Cell and Environment*, **17**, 233–243.
- Cunningham SA, Summerhayes B, Westoby M (1999) Evolutionary divergences in leaf structure and chemistry, comparing rainfall and soil nutrient gradients. *Ecological Monographs*, **69**, 569–588.
- Dewar RC, Medlyn BE, McMurtrie RE (1999) Acclimation of respiration/photosynthesis ratio to temperature: insights form a model. *Global Change Biology*, **5**, 615–622.
- Enquist BJ (2003) Scaling the macroecological and evolutionary implications of size and metabolism within and across plant taxa. In: *Macroecology: Concepts and Consequences* (eds Blackburn T, Gaston KJ), pp. 321–341. Cambridge University Press, UK.
- Enquist BJ, Brown JH, West GB (1998) Allometric scaling of plant energetics and population density. *Nature*, **395**, 163–165.
- Enquist BJ, Economo EP, Huxman TE *et al.* (2003) Scaling metabolism from organisms to ecosystems. *Nature*, **423**, 639–642.
- Enquist BJ, Haskell JP, Tiffney BH (2002) General patterns of taxonomic and biomass partitioning in extant and fossil plant communities. *Nature*, **419**, 610–613.
- Enquist BJ, Niklas KJ (2001) Invariant scaling relations across tree-dominated communities. *Nature*, **410**, 655–660.
- Enquist BJ, Niklas KJ (2002) Global allocation rules for patterns of biomass partitioning in seed plants. *Science*, **295**, 1517–1520.
- Ernest SKM, Brown JH (2001) Homeostasis and compensation: the role of species and resources in ecosystem stability. *Ecology*, **82**, 2118–2132.
- Ernest SKM, Enquist BJ, Brown JH *et al.* (2003) Thermodynamic and metabolic effects on the scaling of production and population energy use. *Ecology Letters*, **6**, 990–995.
- Field C, Chapin FS, Matson PA *et al.* (1992) Responses of terrestrial ecosystems to the changing atmosphere: a resource-based approach. *Annual Review of Ecology and Systematics*, **23**, 201–235.
- Fonseca CR, Overton JM, Collins B *et al.* (2000) Shifts in trait-combinations along rainfall and phosphorus gradients. *Journal of Ecology*, **88**, 964–977.
- Galmés J, Flexas J, Keys AJ *et al.* (2005) Rubisco specificity factor tends to be larger in plant species from drier habitats and in species with persistent leaves. *Plant, Cell and Environment*, **28**, 571–579.
- Geider RJ, Delucia EH, Falkowski PG *et al.* (2001) Primary productivity of planet earth: biological determinants and physical constraints in terrestrial and aquatic habitats. *Global Change Biology*, **7**, 849–882.
- Giardina CP, Ryan MG (2000) Evidence that decomposition rates of organic carbon in mineral soil do not vary with temperature. *Nature*, **404**, 858–861.
- Gifford RM (2003) Plant respiration in productivity models: conceptualisation, representation and issues for global terrestrial carbon-cycle research. *Functional Plant Biology*, **30**, 171–186.
- Gillooly JF, Brown JH, West GB *et al.* (2001) Effects of size and temperature on metabolic rate. *Science*, **293**, 2248–2251.
- Gillooly JF, Charnov EL, West GB *et al.* (2002) Effects of size and temperature on developmental time. *Nature*, **417**, 70–73.
- Grace J, Rayment M (2000) Respiration in the balance. *Nature*, **404**, 819–919.
- Han W, Fang J, Guo D (2005) Leaf N and P stoichiometry across 753 terrestrial plant species in China. *New Phytologist*, **168**, 377–385.
- Harte J (2002) Towards a synthesis of the Newtonian and Darwinian world views. *Physics Today*, **55**, 29–37.
- Hedin LO (2004) Global organization of terrestrial plant–nutrient interactions. *Proceedings of the National Academy of Sciences of the USA*, **101**, 10849–10850.
- Hedin LO (2006) Plants on a different scale. *Nature*, **439**, 399–400.
- Huxman TE, Smith MD, Fay PA *et al.* (2004) Convergence across biomes to a common rain-use efficiency. *Nature*, **429**, 651–654.
- Huxman TE, Turnipseed AA, Sparks JP *et al.* (2003) Temperature as a control over ecosystem CO₂ fluxes in a high-elevation, subalpine forest. *Oecologia*, **134**, 537–546.
- Huxman TE, Wilcox BP, Scott RL *et al.* (2005) Ecohydrological implications of woody plant encroachment. *Ecology*, **86**, 308–319.

- Jackson RB, Banner JL, Jobbagy EG *et al.* (2002) Ecosystem carbon loss with woody plant invasion of grasslands. *Nature*, **418**, 623–636.
- Johnson FH, Eyring H, Stover BJ (1974) *The Theory of Rate Processes in Biology and Medicine*. John Wiley & Sons, New York, NY.
- Jordan CF (1971) A world pattern in plant energetics. *American Scientist*, **59**, 425–428.
- Kerkhoff AJ, Enquist BJ, Fagan WF *et al.* (2005) Plant allometry, ecological stoichiometry, and the temperature-dependence of terrestrial primary production. *Global Ecology and Biogeography*, **4**, 585–598.
- Kleidon A, Mooney HA (2000) A global distribution of biodiversity inferred from climatic constraints: results from a process-based modelling study. *Global Change Biology*, **6**, 507–523.
- Klikoff LC (1966) Temperature dependence of the oxidative rates of mitochondria in *Danthonia intermedia*, *Penstemon davidsonii*, and *Sitanion hystrix*. *Nature*, **212**, 529–530.
- Körner C (1991) Some often overlooked plant characteristics as determinants of plant growth: a reconsideration. *Functional Ecology*, **5**, 162–173.
- Kurimoto K, Millar AH, Lambers H *et al.* (2004) Maintenance of growth rate at low temperature in rice and wheat cultivars with a high degree of respiratory homeostasis is associated with a high efficiency of respiratory ATP production. *Plant and Cell Physiology*, **45**, 1015–1022.
- Larcher W (1995) *Physiological Plant Ecology*, 3rd edn. Springer-Verlag, Berlin.
- Lavorel S, Garnier E (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology*, **16**, 545–556.
- Leuning R (2002) Temperature dependence of two parameters in a photosynthesis model. *Plant, Cell and Environment*, **25**, 1205–1210.
- Lieth H (1975) Modeling the primary productivity of the world. In: *Primary Productivity and the Biosphere* (eds Lieth H, Whitaker RH), pp. 237–263. Springer-Verlag, New York.
- Liski J, Ilvesniemi H, Makela A *et al.* (1999) CO₂ emissions from soil in response to climatic warming are overestimated – the decomposition of old soil organic matter is tolerant of temperature. *Ambio*, **28**, 171–174.
- Lloyd J, Taylor JA (1994) On the temperature dependence of soil respiration. *Functional Ecology*, **8**, 315–323.
- Lovegrove BG (2000) The zoogeography of mammalian basal metabolic rate. *American Naturalist*, **156**, 201–219.
- Luo Y, Wan S, Hui D *et al.* (2001) Acclimatization of soil respiration to warming in a tall grass prairie. *Nature*, **413**, 622–625.
- McCarthy MC, Enquist BJ (2005) Organismal size, metabolism and the evolution of complexity in metazoans. *Evolutionary Ecology Research*, **7**, 681–696.
- McGill B, Enquist BJ, Weiher E *et al.* (2006) Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution*, **21**, 178–185.
- McGroddy ME, Daufresne T, Hedin LO *et al.* (2004) Scaling of C : N : P stoichiometry in forests worldwide: implications of terrestrial redfield-type ratios. *Ecology*, **85**, 2390–2401.
- McNaughton SJ (1967) Photosynthetic system II. Racial differentiation in *Typha latifolia*. *Science*, **156**, 1363.
- Miroslavov EA, Kravkina IM (1991) Comparative analysis of chloroplasts and mitochondria in leaf chlorenchyma from mountain plants grown at different altitudes. *Annals of Botany*, **195**–200.
- Mooney H (1963) Physiological ecology of coastal, sub-alpine, and alpine populations of *Polygonum bistortoides*. *Ecology*, **44**, 812–816.
- Mooney H (ed.) (1977) *Convergent Evolution in Chile and California: Mediterranean Climate Ecosystems*. Dowden, Hutchinson and Ross, Stroudsburg, PA.
- Mooney HA, Billings WD (1961) Comparative physiological ecology of arctic and alpine populations of *Oxyria digyna*. *Ecological Monographs*, **31**, 1–29.
- New M, Lister D, Hulme M *et al.* (2002) A high-resolution data set of surface climate over global land areas. *Climate Research*, **21**, 1–25.
- Nicotra AB, Babicka N, Westoby M (2002) Seedling root anatomy and morphology: an examination of ecological differentiation with rainfall using phylogenetically independent contrasts. *Oecologia*, **130**, 136–145.
- Niinemets U, Oja V, Kull O (1999) Shape of leaf photosynthetic electron transport versus temperature response curve is not constant along canopy light gradients in temperate deciduous trees. *Plant, Cell and Environment*, **22**, 1497–1513.
- Niklas KJ, Enquist BJ (2001) Invariant scaling relationships for interspecific plant biomass production rates and body size. *Proceedings of the National Academy of Sciences of the USA*, **98**, 2922–2927.
- Niklas KJ, Enquist BJ (2002) On the vegetative biomass partitioning of seed plant leaves, stems, and roots. *American Naturalist*, **159**, 482–497.
- Niklas KJ, Enquist BJ (2004) *Biomass Allocation and Growth Data of Seeded Plants*. Data set. Available online from Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, TN, USA [http://www.daac.ornl.gov].
- Nobel PS (1983) *Biophysical Plant Physiology and Ecology*. Freeman, San Francisco.
- Oleksyn J, Modrzyński J, Tjoelker MG *et al.* (1998) Growth and physiology of *Picea abies* populations from elevational transects: common garden evidence for altitudinal ecotypes and cold adaptation. *Functional Ecology*, **12**, 573–590.
- Osmond B, Ananyev G, Berry J *et al.* (2004) Changing the way we think about global change research: scaling up in experimental ecosystem science. *Global Change Biology*, **10**, 393–407.
- Pacala SW, Hurtt GC, Baker D *et al.* (2001) Consistent land- and atmosphere-based U.S. carbon sink estimates. *Science*, **292**, 2316–2319.
- Pereira JS (1994) Gas exchange and growth. In: *Ecophysiology of photosynthesis*. (ed. Caldwell E-DSaMM), pp. 147–181. Springer-Verlag, London.
- Reich PB (2005) Global biogeography of plant chemistry: filling in the blanks. *New Phytologist*, **168**, 263–266.
- Reich PB, Ellsworth DS, Walters MB *et al.* (1999) Generality of leaf trait relationships: a test across six biomes. *Ecology*, **80**, 1955–1969.

- Reich PB, Oleksyn J (2004) Global patterns of plant leaf N and P in relation to temperature and latitude. *Proceedings of the National Academy of Sciences of the USA*, **101**, 11001–11006.
- Reich PB, Tjoelker MG, Machado JL *et al.* (2006) Universal scaling of respiratory metabolism, size and nitrogen in plants. *Nature*, **439**, 457–461.
- Reich PB, Wright IJ, Cavender-Bares J *et al.* (2003) The evolution of plant functional variation: traits, spectra, and strategies. *International Journal of Plant Sciences*, **164**, S143–S164.
- Ribas Carbo M, Aroca R, Gonzalez Meler MA *et al.* (2000) The electron partitioning between the cytochrome and alternative respiratory pathways during chilling recovery in two cultivars of maize differing in chilling sensitivity. *Plant Physiology*, **122**, 199–204.
- Ryan MG, Gower ST, Hubbard RM *et al.* (1995) Woody tissue maintenance respiration of four conifers in contrasting climates. *Oecologia*, **101**, 133–140.
- Savage VM, Gillooly JF, Woodruff WH *et al.* (2004) The predominance of quarter-power scaling in biology. *Functional Ecology*, **18**, 257–282.
- Saxe H, Cannell MGR, Johnsen O *et al.* (2001) Tree and forest functioning in response to global warming. *New Phytologist*, **149**, 369–400.
- Schimper AFW (1903) *Plant-Geography Upon a Physiological Basis*. Clarendon, Oxford, UK.
- Schippers P, van Groenendael JM, Vleeshouwers LM *et al.* (2001) Herbaceous plant strategies in disturbed habitats. *Oikos*, **95**, 198–210.
- Shields LM (1950) Leaf xeromorphology as related to physiological and structural influences. *Botanical Review*, **16**, 399–447.
- Strain BR VCC (1966) Effect of past and prevailing temperatures on the carbon dioxide exchange capacities of some woody desert perennials. *Ecology*, **47**, 1043–1045.
- Talts P, Parnik T, Gardstrom P *et al.* (2004) Respiratory acclimation in *Arabidopsis thaliana* leaves at low temperature. *Journal of Plant Physiology*, **161**, 573–579.
- Thornley JHM, Cannell MGR (2000) Modelling the components of plant respiration: representation and realism. *Annals of Botany*, **85**, 55–67.
- Thornley JHM, Cannell MGR (2001) Soil carbon storage response to temperature: an hypothesis. *Annals of Botany*, **87**, 591–598.
- Valentini R, Matteucci G, Dolman AJ *et al.* (2000) Respiration as the main determinant of carbon balance in European forests. *Nature*, **404**, 861–865.
- Waring RH, Landsberg JJ, Williams M (1998) Net primary production of forests: a constant fraction of gross primary production? *Tree Physiology*, **18**, 129–134.
- Weiher E, Keddy PA (1995) Assembly rules, null models, and trait dispersion: new questions from old patterns. *Oikos*, **74**, 159–164.
- West GB, Brown JH, Enquist BJ (1997) A general model for the origin of allometric scaling laws in biology. *Science*, **276**, 122–126.
- West GB, Brown JH, Enquist BJ (1999) A general model for the structure and allometry of plant vascular systems. *Nature*, **400**, 664–667.
- Wilcox BP, Owens MK, Knight RW *et al.* (2005) Do woody plants affect streamflow on semiarid Karst rangelands? *Ecological Applications*, **15**, 127–136.
- Will R (2000) Effect of different daytime and night-time temperature regimes on the foliar respiration of *Pinus taeda*: predicting the effect of variable temperature on acclimation. *Journal of Experimental Botany*, **51**, 1733–1739.
- Wright IJ, Reich PB, Atkin OK *et al.* (2006) Irradiance, temperature and rainfall influence leaf dark respiration in woody plants: evidence from comparisons across 20 sites. *Plant, Cell and Environment*, **169**, 309–319.
- Wright IJ, Reich PB, Westoby M (2001) Strategy shifts in leaf physiology, structure and nutrient content between species of high- and low-rainfall and high- and low-nutrient habitats. *Functional Ecology*, **15**, 423–434.
- Wythers KR, Reich PB, Tjoelker MG *et al.* (2005) Foliar respiration acclimation to temperature and temperature variable Q(10) alter ecosystem carbon balance. *Global Change Biology*, **11**, 435–449.
- Zhang L, Dawes WR, Walker GR (2001) Response of mean annual evapotranspiration to vegetation changes at catchment scale. *Water Resources Research*, **37**, 701–708.