

LETTER

Temperature-dependence of biomass accumulation rates during secondary succession

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Abstract

Rates of ecosystem recovery following disturbance affect many ecological processes, including carbon cycling in the biosphere. Here, we present a model that predicts the temperature dependence of the biomass accumulation rate following disturbances in forests. Model predictions are derived based on allometric and biochemical principles that govern plant energetics and are tested using a global database of 91 studies of secondary succession compiled from the literature. The rate of biomass accumulation during secondary succession increases with average growing season temperature as predicted based on the biochemical kinetics of photosynthesis in chloroplasts. In addition, the rate of biomass accumulation is greater in angiosperm-dominated communities than in gymnosperm-dominated ones and greater in plantations than in naturally regenerating stands. By linking the temperature-dependence of photosynthesis to the rate of whole-ecosystem biomass accumulation during secondary succession, our model and results provide one example of how emergent, ecosystem-level rate processes can be predicted based on the kinetics of individual metabolic rate.

Keywords

Aggrading ecosystem, angiosperm, carbon cycle, disturbance, ecosystem development, gymnosperm, metabolic theory, resilience, scaling, secondary forest.

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INTRODUCTION

Understanding the effects of temperature on ecological rates – particularly those involved in the global carbon cycle – is important in light of current trends in global climate and land use. One phenomenon of interest is the rate of ecosystem recovery following disturbance. This process, referred to as secondary succession, entails wholesale reorganization of the ecosystem with respect to species composition (e.g. Odum 1969; Pickett 1982), nutrient cycling (e.g. Vitousek & Reiners 1975; Bormann & Likens 1979), community energetics (e.g. Odum 1969; Litvak *et al.* 2003), and – perhaps most importantly – biomass storage (e.g. Odum 1969). The accumulating biomass serves as a net sink for carbon, so forest regrowth plays a key role in the global carbon balance (e.g. Odum 1969; Fearnside & Guimarães 1996; Houghton *et al.* 1999; Caspersen *et al.* 2000; Prentice *et al.* 2001; Schimel *et al.* 2001). However, the role of secondary succession in global biogeochemical cycles remains a major source of uncertainty in terrestrial ecosystem models (e.g. Schimel *et al.* 2001; Houghton

2003, 2005). Additionally, ecosystem recovery rates have a bearing on conservation efforts through their effects on landscape composition (e.g. Turner *et al.* 1993) and meta-population dynamics (e.g. Hastings 2003) that result from species' differential use of successional series (e.g. Pickett 1982).

Surprisingly, few studies have evaluated how global gradients in climate influence rates of biomass accumulation in forests during the course of secondary succession. Furthermore, studies have typically evaluated climatic effects on succession using indirect climate proxies such as the 'temperature summation' (i.e. the product of stand age, growing season temperature and growing season length; O'Neill & DeAngelis 1981; Johnson *et al.* 2000; Zarin *et al.* 2001). The direct effects of temperature on rates of biomass accumulation have yet to be specifically investigated for forests undergoing secondary succession (although temperature effects on ecosystems undergoing primary succession have been studied; see Aplet & Vitousek 1994; Aplet *et al.* 1998). Brown & Lugo (1982) found that biomass accumulates more rapidly in tropical than in temperate

forests and that, within tropical forests, biomass accumulates more rapidly at 'moist' sites (i.e. sites receiving *c.* 1500–3000 mm year⁻¹) than at sites receiving more or less rainfall. The rate of biomass accumulation during secondary succession has also been related to type and intensity of disturbance (e.g. Uhl *et al.* 1988; Brown & Lugo 1990; Mou *et al.* 1993; Fearnside & Guimarães 1996; Hughes *et al.* 1999; Steininger 2000), nutrient availability (e.g. Vitousek *et al.* 1989; Gehring *et al.* 1999; Davidson *et al.* 2004; see also Vitousek 2004 for primary succession), soil texture (i.e. water holding capacity; Odum 1960; Johnson *et al.* 2000; Zarin *et al.* 2001), and physiological traits of dominant plant species (e.g. Johnson *et al.* 2000).

Here, we investigate how global gradients in temperature influence rates of biomass accumulation during secondary succession in forests. To do so, we first derive a model that quantifies the storage and flux of materials in ecosystems based on individual metabolic rate (e.g. Brown *et al.* 2004; Allen *et al.* 2005), which is governed largely by body size and temperature (e.g. Gillooly *et al.* 2001; Brown *et al.* 2004). We then test model predictions using a global compilation of data for ecosystems in the relatively early stages of secondary succession during which biomass is accumulating rapidly.

MODEL DEVELOPMENT

In order to predict the rate of biomass accumulation during secondary succession based on individual energetics, we derive a model that quantifies how the size- and temperature-dependence of individual-level photosynthesis (eqn 1) controls the size- and temperature-dependence of ecosystem-level gross primary production (eqn 2) and the resulting temperature-dependence of biomass accumulation during secondary succession (eqns 3–5).

Size- and temperature-dependence of individual-level photosynthesis

The gross rate of photosynthesis by an individual, P_i (g daylight h⁻¹), increases with mass, M_i (g), and temperature, T (K), according to the following relation (Allen *et al.* 2005):

$$P_i = p_o M_i^{3/4} e^{-E_p/kT} \quad (1)$$

Here, p_o is a normalization constant independent of temperature (g^{1/4} daylight h⁻¹), k is Boltzmann's constant ($k = 8.62 \times 10^{-5}$ eV/K), and E_p is an effective activation energy that characterizes the overall effect of temperature on photosynthesis over the temperature range 0–30 °C (*c.* 0.32 eV; Allen *et al.* 2005). The temperature term of eqn 1 approximates a more complicated function (Farquhar *et al.*

1980; Bernacchi *et al.* 2001) by assuming that the Rubisco carboxylation step in C₃ photosynthesis is approximately limiting or co-limiting to photosynthetic rate across geographic gradients in temperature, in agreement with empirical data (Allen *et al.* 2005). The scaling of P_i with M_i is driven by the $M_i^{3/4}$ -scaling of total leaf mass in relation to total plant mass (West *et al.* 1999; Enquist & Niklas 2002). The mass- and temperature-independent normalization constant, p_o , is influenced by the leaf-level photosynthetic capacity, which is largely determined by the density of N-rich chloroplasts in leaves, and which is therefore directly related to leaf-level nutrient concentrations (e.g. Field & Mooney 1986). We return to the issue of resource availability below.

Size- and temperature-dependence of ecosystem-level gross primary production

During daylight hours of the growing season, when temperatures exceed 0 °C, the gross rate of primary production, G (g m⁻² daylight h⁻¹), in an ecosystem comprised of J plants in an area of size A (m²), is equal to the sum of the individual photosynthetic rates from eqn 1:

$$G = \left(\frac{1}{A}\right) \sum_{i=1}^J P_i = p_o \left(\frac{J}{A}\right) \langle M^{3/4} \rangle_J e^{-E_p/kT} = g_o e^{-E_p/kT}. \quad (2)$$

Here, the normalization constant

$$g_o = p_o \left(\frac{J}{A}\right) \langle M^{3/4} \rangle_J,$$

where $\langle M^{3/4} \rangle_J$ is an average for plant size ($= (1/J) \sum_{i=1}^J M_i^{3/4}$) (Allen *et al.* 2005). We would expect g_o to be largely independent of average plant size for three reasons. First, previous work has explicitly demonstrated that $(J/A) \propto 1/\langle M^{3/4} \rangle_J$, which implies that g_o is independent of the average plant size (Enquist *et al.* 1998, 2003). Second, total foliage biomass, which drives ecosystem-level rates of gross primary production, generally plateaus rapidly relative to woody biomass (e.g. Post 1970; Aber 1979; Bormann & Likens 1979; Brown & Lugo 1982; Uhl & Jordan 1984; Crowell & Freedman 1994). And third, because we deal with only relatively mesic forests, individual plant size, characterized by $\langle M^{3/4} \rangle_J$, is unlikely to show substantial variation among the sites we analyse. For these three reasons, we assume that plant size is not a primary driver of ecosystem-level production during forest succession.

The availability of water and/or nutrients may constrain the total photosynthetic capacity of the ecosystem (characterized by g_o) through its effects on leaf-level photosynthetic capacity (encompassed in p_o ; eqn 1) and/

or plant density (J/A ; eqn 2; e.g. Harrington *et al.* 2001). It is possible to directly test the effect of precipitation on g_o ; however, it is not yet clear whether overall effects of nutrients on the rates of photosynthesis differ across latitudes (e.g. Aber & Melillo 2001). Currently, it appears that nitrogen tends to limit terrestrial primary production in temperate ecosystems (e.g. Vitousek & Howarth 1991), whereas phosphorus tends to limit it in tropical ecosystems (e.g. Vitousek & Sanford 1986; Menge 2003; Vitousek 2004), although results are mixed. With respect to nitrogen, global patterns in leaf stoichiometry – which generally reflects nutrient limitation in the environment (e.g. Vitousek 2004; Han *et al.* 2005) – suggest that nitrogen availability does not vary substantially across geographic gradients in temperature (e.g. Reich & Oleksyn 2004; Han *et al.* 2005; Reich 2005). For the purposes of this model, we assume that nutrient limitation does not systematically affect g_o across the latitudinal temperature gradient. Violation of this assumption would cause the observed temperature dependence to differ from the predicted value (eqn 2); for example, if resource availability were to systematically decrease towards warm tropical habitats, the observed temperature dependence would be weaker than predicted.

Temperature-dependence of biomass accumulation during secondary succession

The rate of accumulation of above- plus below-ground plant biomass during secondary succession, r_{ba} ($\text{g m}^{-2} \text{ day}^{-1}$), is always less than the rate of gross primary production because a substantial fraction of the photosynthate fixed by plants is lost from the plant biomass pool through respiration (R) and aboveground litterfall/below-ground root turnover (L). Thus, r_{ba} represents the net productivity of plants minus the litterfall/root turnover:

$$r_{ba} = G - R - L = G - (1 - \varepsilon)G - (1 - \delta)\varepsilon G = \delta\varepsilon G, \quad (3)$$

where $R = (1 - \varepsilon)G$, $L = (1 - \delta)\varepsilon G$, and ε and δ represent the carbon use efficiency and the fraction of net production contributing to perennating tissues, respectively, which theory and data indicate are both relatively independent of plant size and environmental temperature (O'Neill & DeAngelis 1981; Enquist *et al.* 1998; Waring *et al.* 1998; Dewar *et al.* 1999; Gifford 2003; Allen *et al.* 2005). During early stages of secondary succession, the rate of biomass accumulation is therefore predicted to show the following relationship to average growing season temperature, T_{gs} :

$$r_{ba} = \delta\varepsilon G = \delta\varepsilon g_o e^{-E_p/kT_{gs}}. \quad (4)$$

Furthermore, because the fraction of total biomass that is aboveground, α , is approximately independent of plant size (Enquist & Niklas 2002) and environmental temperature

(Cairns *et al.* 1997), the rate of aboveground biomass accumulation (r_{aba}) is predicted to vary as:

$$r_{aba} = \alpha r_{ba} = \alpha \delta\varepsilon g_o e^{-E_p/kT_{gs}}. \quad (5)$$

Thus, rates of total and aboveground biomass accumulation (r_{ba} and r_{aba} respectively) are both predicted to show the same temperature- and resource-dependence as gross ecosystem-level photosynthesis (eqn 2) during early stages of secondary succession.

MODEL PREDICTIONS

Equations 4 and 5 can be rewritten in forms that can be evaluated using the global database compiled for this study:

$$\ln r_{ba} = -E_p \left(\frac{1}{kT_{gs}} \right) + \ln C \quad (6a)$$

and

$$\ln r_{aba} = -E_p \left(\frac{1}{kT_{gs}} \right) + \ln(\alpha C), \quad (6b)$$

where $C = \delta\varepsilon g_o$. Equation 6 yields the following testable predictions.

Temperature-dependence of $\ln r_{ba}$ and $\ln r_{aba}$

These should both exhibit the same, approximately linear relationship to inverse growing season temperature, $1/kT_{gs}$, with a slope of $-E_p \approx -0.32 \text{ eV}$, which reflects the kinetic effects of temperature on Rubisco carboxylation in chloroplasts (Allen *et al.* 2005). Support for this prediction would corroborate our model assumption that the normalization constant in eqns 2, 4 and 5 (g_o) is largely independent of geographic gradients in temperature.

Resource-dependence of r_{ba} and r_{aba}

$\ln C$ should be lower in nutrient- or water-limited ecosystems than in ecosystems where there is an abundant supply of these material resources. This reflects the effects of resource limitation on ecosystem gross primary production (characterized by g_o), which is in turn governed by the photosynthetic capacities of individual plants (characterized by p_o) and total plant abundance per unit area (characterized by J/A).

Relationship between r_{ba} and r_{aba}

The intercepts of the models for r_{ba} and r_{aba} should differ by only a constant multiplier, α , that directly reflects individual-level biomass allocation to above- vs. below-ground biomass components. An important caveat is that the above predictions are made for succession in ecosystems

dominated by the same life form, such as the forests dominated by trees in our data set. They do not apply straightforwardly across ecosystem types such as forests and grasslands, where the dominant plants may differ dramatically in their allocation to above- vs. below-ground biomass, and therefore in α .

METHODS

We compiled data (Appendix 1) on aboveground and/or total biomass accumulation ($n = 87$ and 31 respectively) during secondary succession in forested ecosystems from published studies conducted in 64 locations worldwide (Fig. 1). Study methods included both long-term monitoring of permanent plots (*c.* 30% of studies) and the use of chronosequences, which substitute space for time by comparing multiple sites in different stages of succession. Community types were categorized as gymnosperm-dominated/mixed (combined because their rates were statistically similar, $P = 0.71$; $n = 30$) or angiosperm-dominated ($n = 61$). Tree plantations in which no fertilization, watering, or weeding treatments were performed were also included ($n = 20$). Regrowth occurred after a variety of stand-clearing disturbances, which we categorized as either 'basic' (e.g. fire; $n = 53$) or 'prolonged/intense' (e.g. agriculture/'old fields', ranching; $n = 27$) following the classification scheme of Vitousek *et al.* (1989).

Rates of dry biomass accumulation, r_{ba} and r_{aba} , were calculated separately for each successional sequence. We define these rates as the slopes of the regression of biomass (g m^{-2}) vs. time during the portion of succession when these relationships are approximately linear, i.e. before biomass plateaus. While no single rate can characterize the entire course of succession, this represents an average rate for the phase of ecosystem development during which biomass is accumulating most rapidly. Rates were calculated in two ways: (i) by forcing regression lines through the origin ('origin intercept'), which enforces the assumption that no live biomass exists initially, but may underestimate

rate if biomass accumulation gets a slow start; and (ii) by allowing the intercept to vary ('free intercept'), which accounts for any initial lag in biomass accumulation rate but may underestimate rate if the calculated intercept is positive. Under the free intercept model, we excluded studies for which the r_{aba} calculation had a Type I error probability $P > 0.1$, an intercept > 0 with probability $P > 0.1$, and/or a value $\leq 75\%$ of the rate calculated using the origin intercept model. For both types of regressions, the fitted model used to calculate r_{aba} and r_{ba} generally had high explanatory power (origin intercept – r_{aba} : $n = 87$, all $P < 0.1$, average $R^2 = 0.962$; r_{ba} : $n = 31$, all $P < 0.1$, average $R^2 = 0.979$; free intercept – r_{aba} : $n = 65$, all $P < 0.1$, average $R^2 = 0.920$; r_{ba} : $n = 21$, 19 $P < 0.1$, average $R^2 = 0.958$; Appendix 1). Biomass accumulation rates were expressed in terms of daylight growing season hours ($\text{g m}^{-2} \text{h}^{-1}$) because photosynthesis only occurs during daylight hours, and because average day length during the growing season varies systematically with latitude (Allen *et al.* 2005).

Average growing season temperature was estimated using the database of Legates & Willmott (1990a). The growing season was defined as the months with average air temperature > 0 °C, and average growing season temperature, T_{gs} , was calculated as the average of the monthly average air temperatures for all growing season months (range for T_{gs} : 8–27 °C). The number of daylight hours during the growing season was calculated using the model of Forsythe *et al.* (1995). Average annual precipitation data was obtained from the original publication or from the global database of Legates & Willmott (1990b) (range: 213–3920 mm year^{-1}). Productivity of ecosystems receiving precipitation of $\geq 2000 \text{ mm year}^{-1}$ does not appear to be strongly affected by precipitation (e.g. Lieth 1973; Schuur 2003; Huxman *et al.* 2004); therefore, we used $2000 \text{ mm year}^{-1}$ as a maximum value (representing all precipitation values $\geq 2000 \text{ mm year}^{-1}$) to ensure that the effects of precipitation we tested were only over the range of values where precipitation may limit r_{ba} and r_{aba} through its effects on $\ln C$ (eqn 6). To assess potential effects of

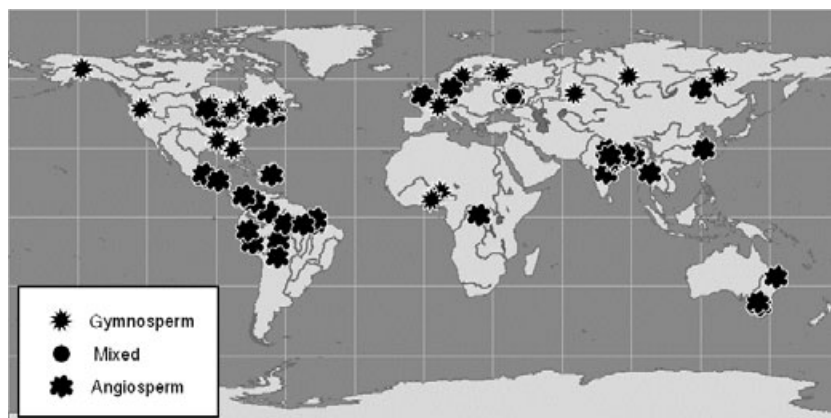


Figure 1 Rates of biomass accumulation during secondary succession were obtained from 64 locations worldwide. Some sites include multiple successional sequences. Symbols vary according to dominant vegetation type.

resources other than precipitation on $\ln C$, we evaluated the effects attributable to site type (naturally regenerating vs. plantation), vegetation type (gymnosperm-dominated/mixed vs. angiosperm-dominated), and disturbance intensity (standard vs. prolonged/intense).

In order to assess the combined effects of these variables and test the predictions of eqn 6, we performed an ANCOVA using S-Plus 2000 (Lucent Technologies, Inc., Murry Hill, NJ, USA) on the combined dataset of r_{ba} and r_{aba} values. This allowed us simultaneously to estimate the following: (i) the overall effect of growing season temperature, $1/kT_{gs}$, on biomass accumulation rate (characterized by the slope $-E_p$); (ii) the separate effects of vegetation type (gymnosperm-dominated/mixed vs. angiosperm-dominated), site type (naturally regenerating vs. plantation), disturbance intensity (standard vs. prolonged/intense), and precipitation on the intercept $\ln C$; and (iii) the logarithm of the aboveground biomass fraction, $\ln \alpha$. Our ANCOVA analysis explicitly assumed that $r_{aba} = \alpha r_{ba}$ (eqn 5). Prior to performing ANCOVA, we validated this assumption by performing univariate regressions on the subset of studies from which we were able to derive paired estimates of r_{ba} and r_{aba} ($n = 27$ and 17 for fixed and free intercepts, respectively). The magnitude of $\ln \alpha$ showed no significant relationship to temperature, vegetation type, or site type in the three univariate tests (all $P > 0.05$, details not presented), thereby validating our model assumption and our ANCOVA analysis. Precipitation and disturbance type were excluded from the final multi-predictor model for r_{ba} and r_{aba} because they were neither significant when included in multi-predictor models nor correlated with the models' residuals.

RESULTS

On a global scale, the annual rate at which aboveground plant biomass accumulates during secondary succession ($\text{g m}^{-2} \text{ year}^{-1}$) increases about four-fold from boreal to tropical forests (Fig. 2). When these data are expressed in terms of daylight hours during the growing season ($\text{g m}^{-2} \text{ h}^{-1}$), the relationship between the biomass accumulation rate and average growing season temperature is approximately exponential (Fig. 3a), as predicted (eqns 4 and 5). Additionally, the logarithm of biomass accumulation rate is linearly related to the inverse of average growing season temperature, $1/kT_{gs}$, with a slope close to the predicted (eqn 6) value of $E_p = -0.32 \text{ eV}$ ($\bar{x} = -0.35$; 95% CI: -0.45 to -0.25 for origin intercept; $\bar{x} = -0.36$; 95% CI: -0.47 to -0.26 for free intercept; Table 1; Fig. 3b). Excluding the 28 sites at tropical latitudes (23.5° S – 23.5° N) from our analysis had essentially no effect on the estimate for E_p ($\bar{x} = -0.30$, 95% CI: -0.49 to -0.12 , $P = 0.002$ for origin intercept; $\bar{x} = -0.36$, 95% CI: -0.53 to -0.19 , $P < 0.001$ for free intercept). This suggests that overall

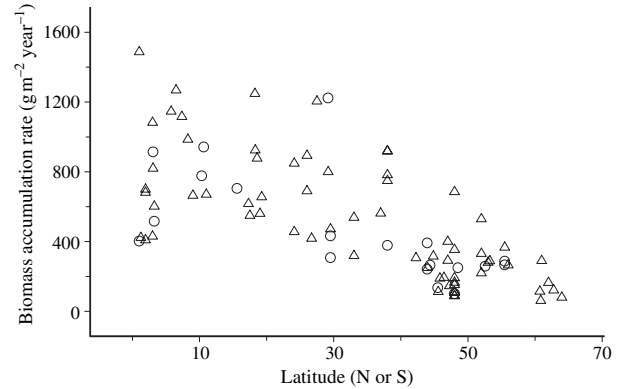


Figure 2 The annual rate of aboveground biomass accumulation (r_{aba} ; $\text{g m}^{-2} \text{ year}^{-1}$; calculated with origin intercept) in successional forests increases from the poles to the tropics. Southern latitudes are represented by circles, northern by triangles.

nutrient limitation (whether N or P) does not cause substantial differences in rates of primary production during secondary succession between temperate and tropical regions.

For the combined temperate–tropical dataset, our estimated value for the aboveground biomass fraction ($\alpha = e^{-0.18} = 0.83$; 95% CI: 0.76 – 0.91 ; Table 1; Fig. 4a) is somewhat higher than the value of 0.721 ± 0.004 reported by Enquist & Niklas (2002), perhaps due to differences in belowground biomass sampling methodologies in the studies compiled here. On average, the rate of biomass accumulation in angiosperm-dominated stands is 1.17 times higher ($=e^{0.16}$; Table 1) than that of gymnosperm-dominated or mixed stands (Fig. 4b), and that of plantations is 1.22 times higher ($=e^{0.20}$; Table 1) than that of naturally regenerating sites (Fig. 4c). Note that these values pertain to biomass accumulation rates calculated by forcing the fitted line through the origin (i.e. origin intercept method); we obtained very similar values when the intercept was not forced through the origin (i.e. free intercept method; Table 1). Overall, both models are highly significant ($F_{4,86} = 35.7$, $P < 0.0001$ for origin intercept; $F_{4,64} = 33.95$, $P < 0.0001$ for free intercept) and explain 62% (origin intercept) and 69% (free intercept) of the variation in biomass accumulation rates. Neither precipitation nor disturbance type were significant predictors in the models (precipitation: both $F < 1.05$, $P > 0.3$; disturbance: both $F < 0.9$, $P > 0.4$). Including precipitation in our multi-predictor model brought values of $-E_p$ slightly closer to the predicted value of -0.32 eV ($\bar{x} = -0.31$; 95% CI: -0.44 to -0.18 for origin intercept; $\bar{x} = -0.34$; 95% CI: -0.49 to -0.19 for free intercept) and did not reduce the explanatory power of temperature ($F = 100.85$ for origin intercept; $F = 92.23$ for free intercept).

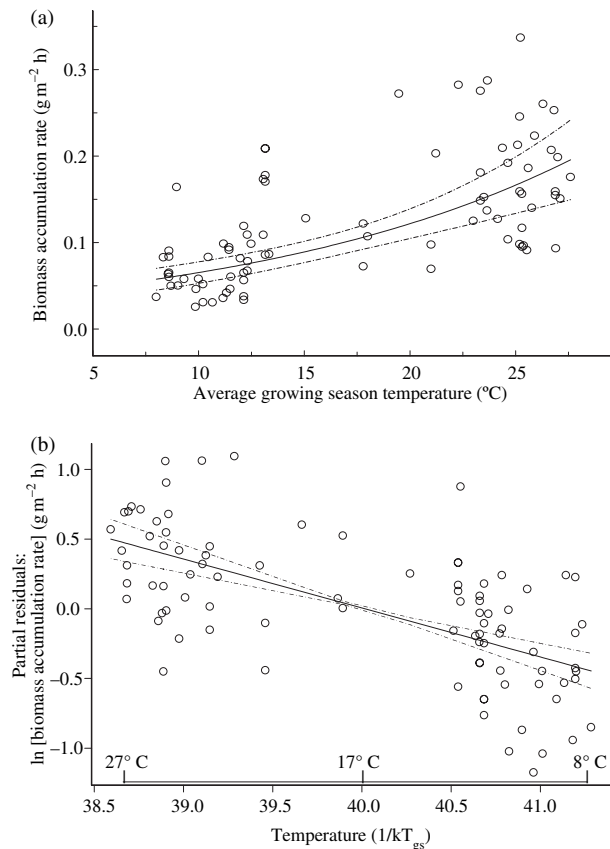


Figure 3 Effects of temperature on biomass accumulation rate. (a) Rates of aboveground biomass accumulation (r_{aba} ; g m^{-2} daylight-growing-season- h^{-1} ; calculated with origin intercept) as a function of average growing season temperature ($^{\circ}\text{C}$). The fit exponential curve relates r_{aba} to average growing season temperature and does not represent the complete model (Table 1). (b) Partial residual plot showing biomass accumulation rate ($\ln r_{\text{ba}}$ or $\ln r_{\text{aba}}$; calculated with origin intercept) – corrected for effects of aboveground vs. total biomass, site type, and vegetation type – as a function of inverse temperature ($1/kT_{\text{gs}}$; slope of $-E_p$). Plotted are $r_i + b_k x_{ik}$ vs. x_{ik} , where r_i is the ordinary residual for observation i , x_{ik} is corresponding observation of variable k , and b_k is the regression coefficient estimate for variable k . The corresponding model is presented in Table 1 ('origin intercept'). Dashed lines represent the 95% confidence bounds for the mean (solid line).

DISCUSSION

Our model and results demonstrate how rates of biomass accumulation – an emergent, ecosystem-level phenomenon – can be predicted based on the kinetics of individual- and molecular/cellular-level metabolic processes. After accounting for latitudinal variation in length of the growing season and day length, biomass accumulation during secondary succession exhibits the temperature dependence predicted based on the kinetics of photosynthesis in chloroplasts

($E_p \approx 0.32$ eV, eqn 1; Fig. 3). This temperature-dependence agrees qualitatively with previous work showing that growing season temperature should be incorporated into secondary forest biomass predictions (O'Neill & DeAngelis 1981; Johnson *et al.* 2000; Zarin *et al.* 2001), and is similar to that observed for terrestrial net primary production (e.g. Lieth 1973; Field *et al.* 1998; Schuur 2003; Allen *et al.* 2005).

The close match between our observed value of E_p and that of leaf-level photosynthesis and net primary production of steady-state forests (Allen *et al.* 2005) reinforces our model assumption that the intrinsic capacity of ecosystems to fix carbon, characterized by g_o , is invariant of global gradients in temperature and that constraints of resource limitation on rates of secondary succession show no systematic changes with latitude. While – as discussed earlier – leaf-level nitrogen exhibits no significant latitudinal pattern, leaf-level phosphorus declines towards the warm tropics, consistent with the hypothesis that many tropical ecosystems are more strongly limited by phosphorus than by nitrogen (e.g. Vitousek & Sanford 1986; Menge 2003; Vitousek 2004). Despite this, the temperature dependence we observe for secondary succession (Fig. 3) is essentially identical whether or not tropical sites are included in our analysis, indicating that g_o does not differ substantially between temperate and tropical sites.

Despite the apparent lack of a detectable latitudinal gradient in nutrient limitation, our results still indicate that smaller-scale variation in nutrient and water availability strongly influences biomass accumulation rates during secondary succession, as shown in previous work (e.g. Brown & Lugo 1982; Gehring *et al.* 1999; Davidson *et al.* 2004). Within forests, rates of biomass accumulation are higher in angiosperm-dominated communities than in gymnosperm/mixed communities (Fig. 4b), and higher in plantations than in naturally regenerating forests (Fig. 4c). These observed differences may be primarily due to resource availability-driven differences in leaf-level photosynthetic capacity and/or plant density. Angiosperms tend to have higher leaf nitrogen concentrations than gymnosperms (Reich & Oleksyn 2004), to grow in moister environments (this difference is significant in our data set at $P < 0.001$), and to exhibit higher rates of net primary productivity (Zheng *et al.* 2003). Plantations may have higher rates than naturally regenerating sites because humans tend to choose the most fertile land for cultivation (Hall *et al.* 1995). Surprisingly, the previously demonstrated effect of disturbance on secondary succession (e.g. Uhl *et al.* 1988; Brown & Lugo 1990; Mou *et al.* 1993; Fearnside & Guimarães 1996; Hughes *et al.* 1999; Steininger 2000) is not apparent in our data set; succession rates of sites that had experienced a prolonged or intense disturbance did not differ significantly from those of sites that had been less severely disturbed.

Table 1 Multi-predictor models for rates of biomass accumulation during secondary succession (r_{ba} and r_{aba} ; g m^{-2} daylight-growing-season- h^{-1}). The effects of growing season temperature (T_{gs}) are quantified by the effective activation energy, E_p (eV), which characterizes the overall effects of temperature on photosynthesis over the temperature range 0–30 °C (Allen *et al.* 2005). Statistical significance of individual variables was assessed using Type III analysis of variance because the hypothesized effects of the variables are independent of their order of introduction into the model (Hays 1994). The overall models are highly significant (origin intercept: $F_{4,86} = 35.7$, $P < 0.0001$, $R^2 = 0.62$; free intercept: $F_{4,64} = 33.95$, $P < 0.0001$, $R^2 = 0.68$).

	Origin intercept			Free intercept		
	Value \pm SE	<i>F</i>	<i>P</i> -value	Value \pm SE	<i>F</i>	<i>P</i> -value
Temperature ($1/kT_{gs}$): $-E_p$ (eV)	-0.35 ± 0.05	100.79	< 0.001	-0.36 ± 0.05	93.93	< 0.001
Aboveground biomass allocation (α): $-\ln \alpha$	0.18 ± 0.04	16.77	< 0.001	0.19 ± 0.05	15.46	< 0.001
<i>C</i> Differences: vegetation type: $\ln(C_{angiosperm}/C_{gymnosperm-mixed})$	0.16 ± 0.05	7.53	0.007	0.21 ± 0.05	11.16	0.001
<i>C</i> Differences: site type: $\ln(C_{plantation}/C_{natural})$	0.20 ± 0.05	17.65	< 0.001	0.23 ± 0.06	15.79	< 0.001
Overall intercept (<i>C</i>): $\ln(C)$ ($\text{g m}^{-2} \text{h}^{-1}$)	11.98 ± 1.99		< 0.001	12.52 ± 2.14		< 0.001

While an effect of precipitation on the rate of biomass accumulation was expected based on studies of net primary productivity (e.g. Lieth 1973; Sala *et al.* 1988; Field *et al.* 1998; Knapp & Smith 2001; Schuur 2003; Huxman *et al.* 2004), it is not significant in our data set. In part, this undoubtedly reflects the fact that our analysis is restricted to forest ecosystems, which generally experience less water limitation than do other terrestrial biomes such as grasslands and deserts. This – together with the still unclear role of nutrients – underscores the need for a better understanding of the roles of water and nutrient availability on the rate of biomass accumulation during secondary succession.

Our model makes five simplifying assumptions that may limit the precision with which it can predict the behaviour of real ecosystems. First, our model is based on the allometry-derived prediction that ecosystem productivity does not depend on the size of dominant plants (eqn 2; Enquist *et al.* 1998, 2003). While we view this prediction as being well supported by data, models upon which it is based have been the subject of some controversy (e.g. Enquist *et al.* 1998, 2003; West *et al.* 1999; Glazier 2005; Reich *et al.* 2006). Second, the approximation for the temperature dependence of photosynthesis (eqn 1; Allen *et al.* 2005) assumes that the Rubisco carboxylation step of photosynthesis – as opposed to the light-dependent reactions – is approximately limiting or co-limiting to photosynthetic rate (Woodward 1995). While this approximation does not necessarily apply to diurnal and/or seasonal fluctuations in photosynthesis at individual sites, it does appear reasonable for making comparisons among terrestrial ecosystems (Woodward 1995; Allen *et al.* 2005). Third, we assume that the carbon use efficiency (ϵ ; eqn 3) and biomass allocation (δ ; eqn 3 and α , eqn 5) are independent of temperature and/or plant size. Obviously, these parameters do vary across species with differing ecological strategies (e.g. Lambers *et al.* 1998), but such variation should not effect global-scale compari-

sons among ecosystems provided that these parameters show no systematic variation at broad spatial scales. Fourth, we assume that total rates of metabolism and biomass accumulation by the plant community are limited by total leaf-level photosynthesis and not by total leaf area. This assumption is likely violated during the first few months to years of succession when plant cover is low and the community is not yet able to use all available resources (e.g. Vitousek & Reiners 1975; Bormann & Likens 1979). However, this initial lag in biomass accumulation rate does not appear to have much effect on our results, as is shown when we account for it by using ‘free origin’ rate calculations (Table 1). Finally, we do not account for the decrease in r_{ba} that occurs toward the end of succession as individual plants approach their size limits, net biomass accumulation declines to zero or becomes negative, and ecosystems approach steady-state (Bormann & Likens 1979; Janisch & Harmon 2002; Litvak *et al.* 2003). Sites at this stage of succession were specifically excluded from our analysis.

While our model is not intended to describe rates of biomass accumulation during the very early or late stages of succession, it should be useful for characterizing broad-scale patterns in the temperature-dependence of succession rates over most of the ‘aggrading’ (Bormann & Likens 1979) phase of ecosystem development. The inevitable deviation of real systems from this deliberately simplified model contributes to the observed variation. While our model does not predict or account for all of the observed variation, it provides a theoretical baseline that can be used to assess the influence of the many other factors affecting biomass accumulation rates, and it could be refined to explicitly incorporate such effects.

Our model and results demonstrate that biomass accumulation rates of successional ecosystems increase with temperature, which implies that global warming could speed the rate at which these ecosystems sequester carbon.

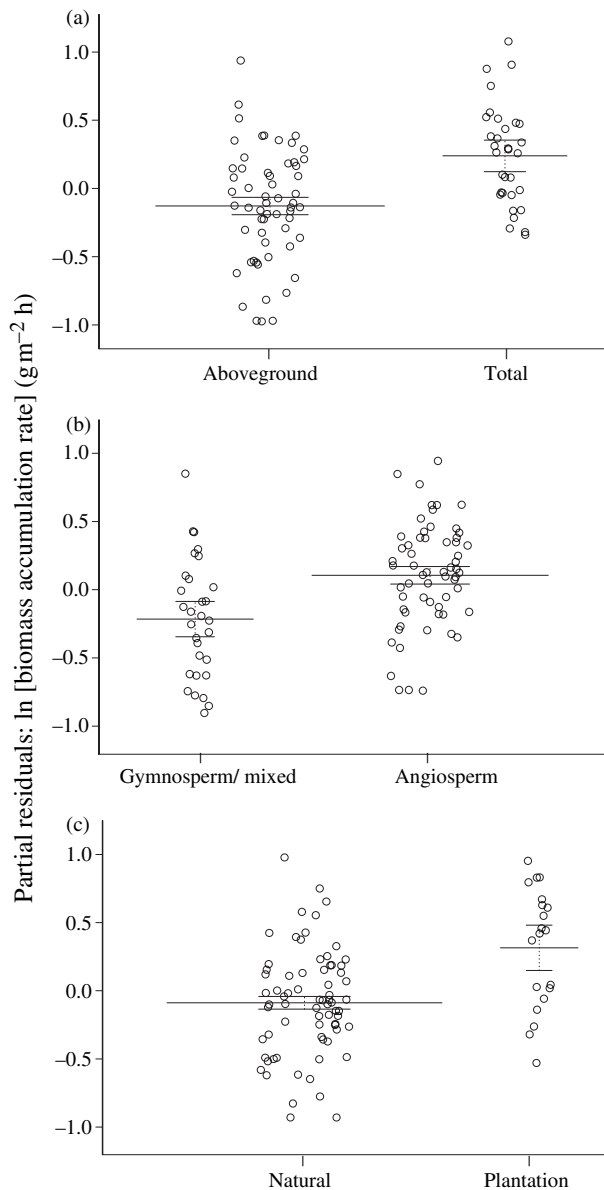


Figure 4 Partial residual plots showing how the rate of biomass accumulation is affected by (a) aboveground vs. total biomass ($\ln \alpha$, where α is the fraction of biomass aboveground), (b) vegetation type (gymnosperm-dominated/mixed vs. angiosperm-dominated, manifested as differences in $\ln C$), and (c) site type (naturally regenerating vs. plantation, manifested as differences in $\ln C$). Plotted are $r_i + b_k x_{ik}$ vs. x_{ik} , where r_i is the ordinary residual for observation i , x_{ik} is corresponding observation of variable k , and b_k is the regression coefficient estimate for variable k . Outer lines represent the 95% confidence bounds for the mean. The corresponding model is presented in Table 1 ('origin intercept').

However, with respect to global change, three other factors must be considered. First, any temperature driven increase in rates of carbon accumulation during succession could

be offset by increased rates of carbon release through decomposition, which has a stronger temperature dependence ($E \approx 0.65$; Allen *et al.* 2005). Second, the predicted temperature response (E_p ; eqn 1) assumes near-ambient atmospheric CO₂ concentrations (Allen *et al.* 2005). Theoretically, increasing atmospheric CO₂ levels is predicted to increase the temperature dependence of gross C₃ photosynthesis by reducing photorespiration (Farquhar *et al.* 1980). For example, at atmospheric CO₂ concentrations of 540 and 970 p.p.m. (IPCC predicted range for the year 2100; Morita *et al.* 2001), the effective activation energy E_p would increase to *c.* 0.38 and 0.47 eV, respectively (calculated using the method of Allen *et al.* 2005). Thus, the difference between the temperature-dependence of photosynthesis and respiration, which strongly influences geographic gradients in labile soil carbon storage (Allen *et al.* 2005), may be reduced. Third, because global change may result in transient dynamics that are not well described by models based upon current conditions (Pastor & Post 1993), our model must be applied with caution.

In conclusion, our model demonstrates that the temperature-dependence of biomass accumulation in successional ecosystems can be predicted based on the temperature-dependence of photosynthesis, thereby linking individual physiology to a dynamic, whole-ecosystem process. This should be helpful for better understanding the implications of climate change and deforestation for carbon cycling at the global scale.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available online from www.Blackwell-Synergy.com:

Appendix S1 Data on climate, forest types, biomass accumulation rates and their statistical quality, and data sources.

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