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.


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 metapopulation 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; Steiming 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; Zarint 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 how 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):

\[
P_i = \rho_o M_i^{3/4} e^{-E_p/\kappa T}
\]

Here, \(\rho_o\) is a normalization constant independent of temperature (g\(^{1/4}\) daylight h\(^{-1}\)), \(\kappa\) is Boltzmann’s constant (8.62 \times 10^{-5} \text{ 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 C\(_3\) 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, \(\rho_o\), 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 \(A\) (m\(^2\)), is equal to the sum of the individual photosynthetic rates from eqn 1:

\[
G = \left( \frac{1}{A} \right) \sum_{i=1}^{j} P_i = \rho_o \left( \frac{1}{A} \right) \left( \frac{M_i^{3/4}}{j} \right) e^{-E_p/\kappa T} = g_o e^{-E_p/\kappa T}.
\]

Here, the normalization constant

\[
g_o = \rho_o \left( \frac{1}{A} \right) \left( \frac{M_i^{3/4}}{j} \right),
\]

where \(\left( M_i^{3/4} / j \right)\) is an average for plant size \(\left( = (1/j) \sum_{i=1}^{j} M_i^{3/4} \right)\) (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 \((1/j) \approx 1 / (M_i^{3/4})\) 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; Crowl & Freedman 1994). And third, because we deal with only relatively mesic forests, individual plant size, characterized by \(\left( M_i^{3/4} / j \right)\), 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 \(\rho_o\); 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, $n_{ba}$ (g m$^{-2}$ day$^{-1}$), is always less than the rate of gross primary production because a substantial fraction of the photosynthesis fixed by plants is lost from the plant biomass pool through respiration ($R$) and aboveground litterfall/belowground root turnover ($L$). Thus, $n_{ba}$ represents the net productivity of plants minus the litterfall/root turnover:

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

where $R = (1 - \varepsilon)G$, $L = (1 - \delta)\varepsilon G$, and $\varepsilon$ and $\delta$ 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, $T_{gs}$:

$$n_{ba} = \delta \varepsilon G = \delta g_o e^{-E_p/kT_{gs}}.$$

Furthermore, because the fraction of total biomass that is aboveground, $x_a$, 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:

$$r_{aba} = x_a n_{ba} = x_a \delta g_o e^{-E_p/kT_{gs}}.$$

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:

$$\ln n_{ba} = -E_p \left( \frac{1}{kT_{gs}} \right) + \ln C.$$

and

$$\ln r_{aba} = -E_p \left( \frac{1}{kT_{gs}} \right) + \ln(zC),$$

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

**Temperature-dependence of $\ln n_{ba}$ 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 $-E_p = -0.32$ 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 $r_{aba}$**

In $C$ 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 $n_{ba}$ and $r_{aba}$ should differ by only a constant multiplier, $z$, 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 $z$.

**METHODS**

We compiled data (Appendix 1) on aboveground and/or total biomass accumulation ($n = 87$ and $n = 31$ 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, $n_a$ 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 $n_a$ generally had high explanatory power (origin intercept – $r_{aba}$: $n = 87$, all $P < 0.1$, average $R^2 = 0.962$; $n_a$: $n = 31$, all $P < 0.1$, average $R^2 = 0.979$; free intercept – $r_{aba}$: $n = 65$, all $P < 0.1$, average $R^2 = 0.920$; $n_a$: $n = 21, 19$ $P < 0.1$, average $R^2 = 0.958$; Appendix 1). Biomass accumulation rates were expressed in terms of daylight growing season hours (g m$^{-2}$ 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 $>0 \, ^\circ C$, 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 $^\circ C$). The number of daylight hours during the growing season was calculated using the model of Fro侵th 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 $\geq 2000$ 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 mm year$^{-1}$ as a maximum value (representing all precipitation values $\geq 2000$ mm year$^{-1}$) to ensure that the effects of precipitation we tested were only over the range of values where precipitation may limit $n_a$ 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.](image-url)
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 $n_0$ 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 $n_0$ 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 $n_0$ 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 (g m$^{-2}$ 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 (g m$^{-2}$ 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 $E_p = -0.32$ eV ($\tilde{x} = -0.35$; 95% CI: $-0.45$ to $-0.25$ for origin intercept; $\tilde{x} = -0.36$; 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 $E_p$ ($\tilde{x} = -0.30$, 95% CI: $-0.49$ to $-0.12$, $P = 0.002$ for origin intercept; $\tilde{x} = -0.36$, 95% CI: $-0.53$ to $-0.19$, $P < 0.001$ for free intercept). This suggests that overall 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 ($\alpha = e^{-0.18}$; 95% CI: 0.36–0.91; Table 1; Fig. 4a) is somewhat higher than the value of $0.721 \pm 0.004$ 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 ($\tilde{x} = -0.31$; 95% CI: $-0.44$ to $-0.18$ for origin intercept; $\tilde{x} = -0.34$; 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).
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 \((E_g = 0.32 \text{ eV}, \text{ eqn 1}; \text{ Fig. 3})\). 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 \(E_g\) 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.
Introduction into the model (Hays 1994). The overall models are highly significant (origin intercept: \(F_{\text{p},\text{interaction}} = 39.6, P < 0.0001, R^2 = 0.62\); free intercept: \(F_{\text{p},\text{free}} = 33.95, P < 0.0001, R^2 = 0.68\)).

<table>
<thead>
<tr>
<th>Origin intercept</th>
<th>Free intercept</th>
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<tr>
<td>Value ± SE</td>
<td>(F)</td>
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<tr>
<td>Temperature ((kT_p)): (-E_p) (eV)</td>
<td>(-0.35 ± 0.05)</td>
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<tr>
<td>Aboveground biomass allocation (\alpha): (-\ln \alpha)</td>
<td>0.18 ± 0.04</td>
</tr>
<tr>
<td>(\ln (C_{\text{angiosperm}}/C_{\text{gymnosperm-mixed}}))</td>
<td>0.16 ± 0.05</td>
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<tr>
<td>(\ln (C_{\text{plantation}}/C_{\text{natural}}))</td>
<td>0.20 ± 0.05</td>
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<tr>
<td>Overall intercept ((C)): (\ln (C)) ((g \text{ m}^{-2} \text{ h}^{-1}))</td>
<td>11.98 ± 1.99</td>
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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 \((\varepsilon); \text{eqn 3})\) and biomass allocation \((\delta; \text{eqn 3 and } \alpha, \text{eqn 5})\) 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 comparisons 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 \(n_a\) 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.

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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 ($E = 0.65$; Allen et al. 2005). Second, the predicted temperature response ($E_p$, eqn 1) assumes near-ambient atmospheric CO$_2$ concentrations (Allen et al. 2005). Theoretically, increasing atmospheric CO$_2$ levels is predicted to increase the temperature dependence of gross C$_3$ photosynthesis by reducing photorespiration (Farquhar et al. 1980). For example, at atmospheric CO$_2$ 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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REFERENCES


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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