

LETTER

Testing metabolic ecology theory for allometric scaling of tree size, growth and mortality in tropical forests

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Abstract

The theory of metabolic ecology predicts specific relationships among tree stem diameter, biomass, height, growth and mortality. As demographic rates are important to estimates of carbon fluxes in forests, this theory might offer important insights into the global carbon budget, and deserves careful assessment. We assembled data from 10 old-growth tropical forests encompassing censuses of 367 ha and > 1.7 million trees to test the theory's predictions. We also developed a set of alternative predictions that retained some assumptions of metabolic ecology while also considering how availability of a key limiting resource, light, changes with tree size. Our results show that there are no universal scaling relationships of growth or mortality with size among trees in tropical forests. Observed patterns were consistent with our alternative model in the one site where we had the data necessary to evaluate it, and were inconsistent with the predictions of metabolic ecology in all forests.

Keywords

Asymmetric competition, demographic rates, forest dynamics, light availability, metabolic theory of ecology, resource competition theory, tree allometry.

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INTRODUCTION

Tree growth and mortality rates vary widely among tropical forests worldwide (Baker *et al.* 2003; Phillips *et al.* 2004), yet relationships of tree growth and mortality rates to tree diameter show fundamental similarities that suggest general underlying principles (Coomes *et al.* 2003). Recently, the theory of metabolic ecology has generated specific predictions about the functional form of these relationships (Enquist *et al.* 1999; Brown *et al.* 2004). Such a general theory could potentially advance fundamental understanding of forest structure and dynamics, and also provide a basis for predicting future changes in associated carbon pools and fluxes (Phillips *et al.* 1998; Clark *et al.* 2001).

The metabolic theory of ecology strives to apply basic principles of physics, chemistry and biology to explain the physiology and performance of individual organisms and thereby the structure of populations, communities and ecosystems (West *et al.* 1997; Brown *et al.* 2004). West *et al.* (1997) pioneered these efforts with predictions for the scaling of metabolic rates (in plants, gross photosynthetic rates) with body mass based on the scaling of resource uptake and redistribution within optimized networks (e.g. arteries and xylem). West *et al.* (1999) derived additional predictions for

the scaling of height, biomass, diameter and leaf area in plants. In combination with assumptions relating growth and mortality to metabolic rate, Enquist *et al.* (1999) and Brown *et al.* (2004) extend these to make further predictions for the scaling of plant growth and mortality respectively.

There is considerable debate about the validity and consistency of the underlying assumptions of metabolic ecology (e.g. Dodds *et al.* 2001; Kozłowski & Konarzewski 2004; Meinzer *et al.* 2005). For trees in particular, we suggest that the scaling of metabolic rates with size will depend not only on the potential for resource uptake and redistribution that is central to metabolic ecology theory, but also on availability of these resources. Small plants in the shaded understory of forests are much farther from their maximum potential metabolic rates than the canopy trees that overtop them. Light is a limiting resource for plant growth in tropical forests (Chazdon & Pearcy 1986; King 1994; Graham *et al.* 2003), and competition for light is strongly size asymmetric (Weiner 1990). In addition, site-specific mortality factors might affect some size classes more than others and thus change the scaling of mortality with size. For example, hurricanes induce more mortality among large trees (Zimmerman *et al.* 1994), while fires and large mammals cause more mortality among small trees (Ickes *et al.* 2005;

Sukumar *et al.* 2005). The scaling of growth with size is also expected to vary ontogenetically because of changes in relative expenditure on maintenance and reproduction (Kooijman 2000), as considered in some theoretical work on metabolic ecology (West *et al.* 2001).

Large-scale empirical patterns appear broadly consistent with the predictions of metabolic ecology theory (Brown *et al.* 2004), although substantial deviations have been found, especially (but not exclusively) when patterns are examined over smaller ranges of body size within particular taxonomic groups or ecosystems (Tilman *et al.* 2004). The predictions for the scaling of leaf mass with stem diameter and total plant biomass have both been supported (Niklas & Enquist 2001; Enquist & Niklas 2002), while the prediction for plant height with biomass has not (Niklas & Enquist 2001). There appears to be considerable variability in the scaling of plant biomass with stem diameter (Li *et al.* 2005), with average scaling values inconsistent with theoretical predictions (Enquist *et al.* 1998). Nonetheless, both Niklas & Enquist (2001) and Ernest *et al.* (2003) found that biomass growth (or production) scaled with biomass as predicted. Further, Enquist *et al.* (1999) were unable to reject the predicted scaling of tree diameter growth with diameter in their species-specific analyses for 40 of 45 species, although the power of their analyses was severely limited by sample size (for three of four species for which there were data on more than 100 individuals, the predictions were rejected). To our knowledge, no studies have yet tested the relatively new prediction for the scaling of mortality rates in plants (Brown *et al.* 2004). Given its potential to expand our understanding of plant communities, metabolic ecology theory merits thorough investigation of all its predictions.

Here we first summarize the predictions of metabolic ecology for the scaling of plant diameter, height, biomass, growth and mortality rates and the logic underlying and linking these predictions. We then examine how the predictions for growth and mortality change if we incorporate the scaling of resource availability as well as resource uptake ability with tree size, and if we use empirically observed allometric relationships rather than theoretically predicted ones as starting points. We use data on light availability and on tree diameter, height and biomass to test metabolic ecology predictions for tree allometry in one tropical forest and to parameterize the alternative, empirically based model. We evaluate both sets of predictions for growth and mortality using data for over 1.7 million trees in 10 tropical forests around the world.

PREDICTIONS FROM METABOLIC ECOLOGY THEORY

The foundations of metabolic ecology theory for plants, as detailed in West *et al.* (1997, 1999), are as follows:

M1 – Assumption: A plant's gross photosynthetic rate (its metabolic rate) is determined by its potential rates of resource uptake across its surface and resource redistribution through its body.

M2 – Assumption: The branching networks distributing resources through plants have a self-similar, fractal structure, a fixed smallest branch size, and are organized to minimize the energy required to distribute resources.

Implicit in M1 is the following assumption:

M3 – Implicit Assumption: A plant's access to resources does not limit its gross photosynthetic rate, or else scales with plant size in the same way potential rates of resource uptake and redistribution scale with plant size.

West *et al.* (1997, 1999) and Enquist & Niklas (2002) use these assumptions to derive predictions for the scaling of biomass, stem diameter, photosynthetic rates, height and leaf allocation:

M4 – Prediction: A plant's trunk diameter, D scales with its biomass, M as $M^{3/8}$ (thus $M \propto D^{8/3}$).

M5 – Prediction: A plant's height, H scales with its biomass as $M^{1/4}$ and thus with $D^{2/3}$.

M6 – Prediction: A plant's leaf number and leaf mass, L scale with $M^{3/4}$, and thus with D^2 .

M7 – Prediction: A plant's gross photosynthetic rate scales with $M^{3/4}$, and thus with D^2 and L .

Enquist *et al.* (1999) further assume

M8 – Assumption: A plant's biomass growth rate is proportional to its gross photosynthetic rate (its metabolic rate).

This allows growth to be related to biomass and diameter:

M9 – Prediction: A plant's biomass growth rate scales with $M^{3/4}$, and its diameter growth rate with $D^{1/3}$ (based on M4, M7 and M8).

Brown *et al.* (2004) make an analogous assumption for mortality:

M10 – Assumption: An individual's mortality rate is proportional to its mass-specific metabolic rate (its metabolic rate divided by its mass).

This leads to a prediction for the scaling of mortality with biomass, which we extend to a prediction for scaling with diameter:

M11 – Prediction: An individual's mortality rate scales with $M^{-1/4}$ and thus with $D^{-2/3}$ (based on M4, M7 and M10).

The assumptions about the scaling of growth and mortality with photosynthesis result in a further prediction for the

relationship between the growth and mortality exponents (though never to our knowledge stated in previous papers):

M12 – Prediction: The difference between the scaling exponent for diameter growth with diameter and the scaling exponent for mortality with diameter is 1 (based on M8 and M10).

Note that this prediction does not rely upon the specific photosynthesis scaling assumption (M7).

ALTERNATIVE PREDICTIONS INCORPORATING RESOURCE COMPETITION

Consider the alternative foundation:

A1 – Assumption: A plant's gross photosynthetic rate is determined by both its access to resources and its potential rate of resource uptake.

A2 – Assumption: The most important resource for determining the scaling of photosynthetic rates with size among trees within forests is light; a forest tree's gross photosynthetic rate is proportional to its crown area times the light reaching its crown.

Instead of deriving the relationships of tree size with crown area and light from first principles, we use empirically observed relationships. Thus, our alternative is necessarily less general than pure metabolic ecology theory. For consistency with metabolic ecology theory, we represent the scaling of stem diameter, tree height, crown area, biomass, and resource availability as power functions, but with empirically fitted exponents S_L , S_M , S_H , S_C :

A3 – Assumption: Within a forest, a tree's light availability scales with its height, H as H^{S_L} .

A4 – Assumption: A tree's biomass scales with D^{S_M} .

A5 – Assumption: A tree's height scales with D^{S_H} .

A6 – Assumption: A tree's crown area scales with D^{S_C} .

The combination of these assumptions leads to a power-function prediction for photosynthesis:

A7 – Prediction: A tree's gross photosynthetic rate scales with $D^{S_C+S_H+S_L}$ (based on A2–A6).

Because they incorporate power functions, these assumptions and predictions (A3–A7) are equivalent to the predictions of metabolic ecology (M3–M7) if we think of crown area as equivalent to leaf mass or leaf area, and if the predictions of metabolic ecology prove correct such that $S_L = 0$, $S_M = 8/3$, $S_H = 2/3$ and $S_C = 2$.

In practice, we expect to see a shift in the relationship between light availability and height when trees grow out of the understory (where there is a strong vertical gradient in light availability) into the canopy (where all trees have some

access to full sun). We expect a parallel shift in the relationships of height and biomass with diameter as height asymptotes in canopy individuals. We also expect the allometric and resource scaling exponents to vary among sites with soil, climate, tree species composition, and other factors, resulting in parallel variation in the scaling of photosynthetic rates.

If we retain the metabolic ecology assumption that biomass growth is proportional to gross photosynthesis (A8 = M8), then our prediction for the scaling of photosynthesis translates into predictions for the scaling of growth:

A9 – Prediction: A tree's biomass growth rate scales with $D^{S_C+S_H+S_L}$ and its diameter growth rate scales with $D^{S_C+S_H+S_L-S_M+1}$ (based on A4, A7 and A8, because

$$\frac{dD}{dt} = \frac{dM/dt}{dM/dD} \propto \frac{D^{S_C+S_H+S_L}}{D^{S_M-1}} = D^{S_C+S_H+S_L-S_M+1}.$$

Similarly, if we retain the metabolic ecology assumption that mortality is proportional to the mass-specific metabolic rate (A10 = M10), we arrive at a prediction for mortality.

A11 – Prediction: A tree's mortality rate scales with $D^{S_C+S_H+S_L-S_M}$ (A7 and A10).

As before, no matter what the precise scaling of photosynthetic rates with size (A7), A8 and A10 lead to A12 = M12, a constant relationship between growth and mortality scaling exponents.

We expect considerable deviations from the hypothesized relationship of photosynthesis and mortality (A10) and thus between mortality and size (A11) because mortality depends not only on vulnerability (which is encapsulated in these resource-based predictions), but also on risks, which are likely to scale unpredictably. We also expect size-dependent changes in relative allocation to maintenance, defence, growth and reproduction to cause further deviations in the scaling of both mortality and growth with photosynthesis and size (A8–A12). Nonetheless, comparison with empirical data will allow us to see whether changes to assumptions about the scaling of photosynthetic rates (A1–A7) to incorporate resource availability lead to improvements in the predictions of the scaling of tree growth and mortality rates (A9 and A11) over the predictions of pure metabolic ecology (M9 and M11). We note that our alternative is conceptually similar to previous efforts, mostly in agriculture and forestry, that have predicted biomass accumulation as the product of light interception and light use efficiency (Kirschbaum *et al.* 1994; Sands 1996; Waring & Running 1998).

Here we fit the power-function relationships assumed in A3–A6 to data on light availability below the canopy and on tree allometry for small (below canopy) and large (canopy)

individuals for the one site in which we have appropriate data – Barro Colorado, Panama. We then use the resulting fitted parameters to predict the corresponding scaling exponents for diameter growth (A9) and mortality (A11) for below-canopy individuals at this site.

MATERIALS AND METHODS

Study sites and data sets

Our study sites are 10 large plots (25–52 ha each) in old-growth tropical forests around the world (see Table 1 and Losos & Leigh 2004). All plots were censused two or more times at \approx 5-year intervals using the standard methods of the Center for Tropical Forest Science (Condit 1998): all free-standing woody plants with a stem diameter \geq 1 cm (at 1.3 m above the ground) were mapped, tagged, identified to species, and measured in diameter (with a precision of 0.1 cm – we excluded early censuses in which small stems were measured only to the nearest 0.5 cm). We examined growth and mortality over one census interval (two censuses) at seven sites, and over two successive census intervals (three censuses) at three sites. We excluded data for individuals whose diameters were recorded as 1.0 cm to avoid inconsistencies in the definitions of this smallest size classes. (In some cases, any stem between 0.95 and 1.05 cm was recorded as a 1.0-cm stem, while in others only stems between 1.00 and 1.05 cm were thus recorded.)

Data on light availability and on diameter, height and crown area allometries were collected at one of these sites, Barro Colorado, Panama. Biomass-diameter data were from a pantropical compilation (Chave *et al.* 2005).

Light availability and tree size allometry

Canopy openness was measured in Barro Colorado on a 5-m grid over 50 ha (Hubbell *et al.* 1999). At each point, a technician assessed the presence or absence of vegetation in the following height intervals: 2–5, 5–10, 10–20, 20–30 and $>$ 30 m. The canopy openness at the bottom of each height interval was then calculated as the fraction of sampled locations that have no vegetation above that height. Our measure of light availability at a given height is thus the probability that a point at that height is not shaded by vegetation directly above. A linear regression of log-transformed data was performed in each year to obtain power functions relating canopy openness to height, and parameters were averaged across years. CIs were obtained from 1000 bootstraps, which were carried out across 50 \times 50-m subplots due to spatial autocorrelation.

Tree heights were measured on 9042 individuals of 223 woody dicot species in the Barro Colorado Nature Monument (Bohlman & O'Brien 2006 and S.J. Wright, H.C. Muller-Landau, P. Spiro, S.C. Thomas, R. Condit, unpublished data). Eight crown radii per tree were measured for 849 individuals of 78 species at the same site, and crown area was calculated as pi times the square of the mean radius (Bohlman & O'Brien 2006). For both tree heights and crown area, systematic correction factors were applied to account for measurement differences among investigators and normalize all measurements to the most accurate methods used: laser rangefinder measurements (Bohlman & O'Brien 2006). Individual tree above-ground biomass and diameter data for 1504 individuals from moist tropical

Table 1 The 10 tropical forest dynamics plots used in this study and their site characteristics

Site	Plot area (ha)	Elevation (m a.s.l.)	Rainfall (mm)	Dry season (months)	T_{\max} (°C)	T_{\min} (°C)
Sinharaja Wilderness Area, Sri Lanka	25	500	5016	0	24.7	20.4
La Planada Nature Reserve, Colombia	25	1845	4415	0	23.8	12.9
Yasuni National Park, Ecuador	25	230	3081	0	30.9	21.0
Lambir Hills National Park, Sarawak, Malaysia	52	175	2664	0	30.3	22.9
Pasoh Forest Reserve, Malaysia	50	80	1788	1	33.2	22.7
Barro Colorado Nature Monument, Panama	50	140	2551	3	31.1	23.2
Edoro study area, Ituri Forest, Congo	20*	775	1785	3	25.5	17.9
Lenda study area, Ituri Forest, Congo	20*	775	1674	4	27.8	18.3
Huai Kha Khaeng Wildlife Sanctuary, Thailand	50	595	1476	6	30.4	17.7
Mudumalai Wildlife Sanctuary, India	50	1050	1250	4	28.2	17.3

Rainfall is the average annual total; dry season length is the number of calendar months with average rainfall $<$ 100 mm. T_{\max} and T_{\min} are the average daily maximum and minimum temperatures respectively. Climate data for Yasuni are from S.J. Wright (personal communication); all other data are from Losos & Leigh (2004). Plots are ordered by increasing dryness.

*The two Congo sites each consist of two 10-ha plots (the Edoro study area consists mainly of mixed forest, and the Lenda study area mainly of monodominant forest); all other sites are one contiguous rectangle or square.

forests were from a pan-tropical compilation (Chave *et al.* 2005). Power functions relating tree height, crown area and biomass to stem diameter were fit using ordinary least-squared regression on log-transformed data. Separate fits were carried out for individuals < 20-cm diameter only (henceforth small individuals), and individuals ≥ 20 cm in diameter only (large individuals), and all individuals combined.

To obtain CI for the predictions of the growth and mortality exponents based on allometric and resource scaling exponents (A9 and A11), we bootstrapped 1000 times over the error distributions of the allometric and resource scaling exponents that went into the calculation.

Growth

To investigate the scaling of growth with size within each site, we first calculated mean absolute diameter growth rates (cm year^{-1}) and mean initial diameters for each diameter class, with classes chosen to be approximately evenly distributed on a log(diameter) scale (see Appendix S1). Subsequent analyses were based on mean diameter growth rates within size classes rather than growth rates of individual trees to avoid undue influence of the many small individuals. In calculating mean growth rates within each size class, we excluded individuals whose stems were measured at different heights in the two censuses (due to changes in the height of buttresses).

We estimated the power function relating diameter growth rate, $g(D)$, and diameter,

$$g(D) = \frac{dD}{dt} = rD^c \quad (1)$$

that was most consistent with the change in mean diameter growth rates among size classes. Because growth is a function of size and size changes continuously as growth occurs, a power-function relationship for continuous growth rate (eqn 1) implies that the expected diameter at time t of an individual with initial diameter D_0 is

$$D_t = [D_0^{1-c} + r(1-c)t]^{1/(1-c)} \quad (2)$$

(see Appendix S1). We estimated the parameters r and c by minimizing the sum of squared differences between the log of mean observed growth and the log of growth expected given the mean initial diameter (eqn 2).

The growth scaling parameters (r and c) were estimated separately for each site and intercensus interval, and for three different size ranges: all sizes combined, small individuals (< 20-cm diameter) only, and large individuals (≥ 20 -cm diameter) only. In each case, 95% CI on the parameters were obtained by bootstrapping across 50×50 -m subplots.

Mortality

Size-specific mortality rates were calculated for the same diameter classes and census intervals used for the growth analyses. In calculating mortality rates within each diameter class, we counted as dead those few individuals that were lost from the census because their new diameters were below the 1 cm census threshold (due to major stem breaks).

We then estimated the power-function relating mortality rate, $m(D)$, and diameter,

$$m(D) = aD^b \quad (3)$$

that was most consistent with the change in mortality rate among size classes. Because mortality changes continuously as growth occurs, power functions for growth and mortality (eqns 1 and 3) imply that the survival probability during a census interval t of an individual that starts with diameter D_0 is $\exp(-\mu)$ where

$$\mu = \frac{a}{r(1-c+b)} \left[(D_0^{1-c} + r(1-c)t)^{1-c+b/(1-c)} - D_0^{1-c+b} \right] \quad (4)$$

(see Appendix S1). We estimated the parameters a and b by minimizing the sum of squared differences between the log of the observed mortality rate and the log of the mortality rate expected given mean initial diameter and the fitted growth parameters (eqn 4). As for growth, mortality parameters were estimated separately for each study site and intercensus interval, and for size ranges including all individuals, small individuals and large individuals.

RESULTS

Size allometry and light availability

Canopy openness increased almost 100-fold between 1- and 30-m height, and the best power-function fit to this increase had an exponent of 1.64 (Fig. 1a, Table 2). The relationships between stem diameter and tree height, crown area and above-ground biomass were all approximately power functions (Fig. 1b–d). However, height asymptotes and crown area and biomass both increase less steeply at larger diameters; thus, the exponents of best-fit power functions for large individuals are smaller than those for small individuals (Table 2). Consistent with the findings of Chave *et al.* (2005) that tree biomass is proportional to height times the square of diameter in tropical moist forests, the exponents relating tree biomass to stem diameter are equal to 2 plus the exponents relating tree height to stem diameter (Table 2).

Metabolic ecology assumptions and predictions were inconsistent with the observed patterns. The strong gradient in light availability with size combined with previous research showing that light is a strongly limiting resource

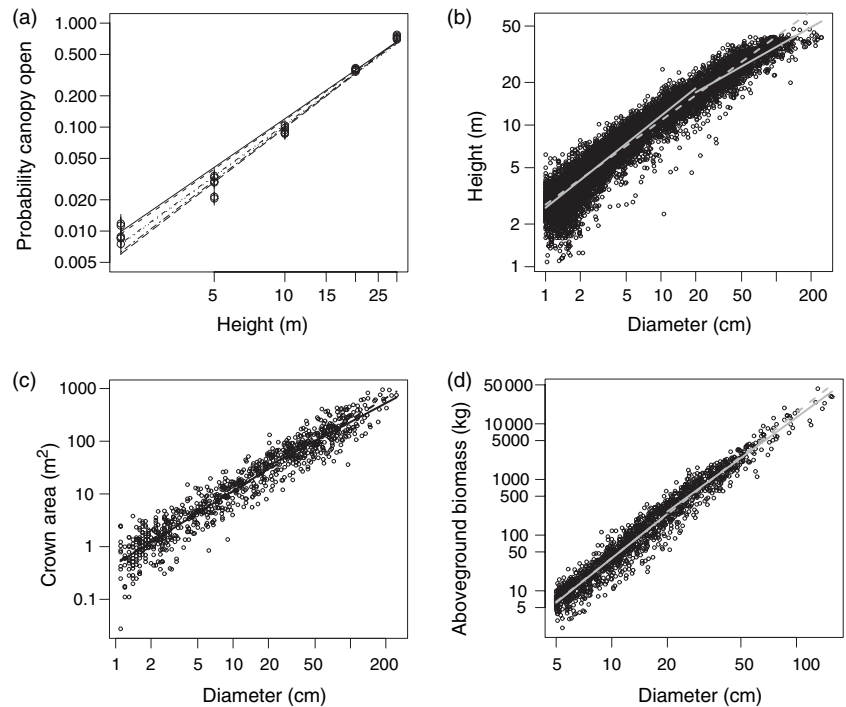


Figure 1 Data and fitted power functions on the relationships of (a) canopy openness with height above ground, (b) tree height with stem diameter, and (c) tree crown area with stem diameter, for Barro Colorado Island, Panama; and of (d) tree above-ground biomass with stem diameter in wet tropical forests worldwide (Chave *et al.* 2005). In (a), different symbols and line types denote data and fits for different years. In (b–d), dashed lines show power-function fits to the full data sets; solid lines show separate fits to small (< 20-cm diameter) and large (\geq 20-cm diameter) individuals. The fitted parameters are given in Table 2.

for tropical tree growth (Chazdon & Pearcy 1986; King 1994; Graham *et al.* 2003) provides clear evidence against the implied assumption that resource availability is not limiting or is similar across sizes (M2). The observed scaling exponents relating height and biomass to diameter were significantly lower than those predicted by metabolic ecology (M4 and M5). However, the biomass exponent for small individuals alone (2.65) was not significantly different from the predicted $8/3$ and the observed height exponent for small individuals (0.649) was close to the predicted $2/3$ (although still significantly lower). In contrast, the scaling exponents for large individuals were much lower than predicted, indicating that the metabolic ecology predictions work better for individuals that have not yet reached the canopy than for those within the canopy.

Growth

Growth rate consistently increased with diameter for small individuals in all closed canopy forests (Fig. 2a–g), but not in the two relatively open canopy sites – Huai Kha Khaeng and Mudumalai (Fig. 2h,i). The rate of increase in growth rate with diameter tended to decrease at larger sizes in closed-canopy sites, as reflected in smaller exponents of the power-function fits for larger individuals – significantly smaller in five of eight sites (Table 3). In the open-canopy sites, this pattern reversed, with larger exponents in larger size classes (significant at Huai Kha Khaeng and in one census at Mudumalai; Table 3). In the closed-canopy sites, power functions were reasonably good fits to growth in

small individuals, but performed less well for large individuals. All sites showed slightly S-shaped log–log growth–diameter relationships. Overall, patterns in growth with size at closed-canopy sites were qualitatively similar but significantly different in their slopes and intercepts (Table 3, Table S1).

The scaling of growth was clearly inconsistent with metabolic theory predictions. The observed exponents were significantly different from $1/3$, the value predicted by the theory (M9), at nine of 10 sites (Table 3). The only site in which the CI for growth encompassed $1/3$ was La Planada, which is exceptional in being a montane site (1845-m elevation). When only small individuals were considered, the fitted growth exponent was significantly different from $1/3$ at all census intervals at all 10 sites, while among large individuals the exponent was closer to $1/3$, although still significantly different at half the sites despite large CI.

In contrast, growth scaling was consistent with our alternative prediction incorporating the scaling of resource availability among small individuals at the only site where we could test it. The growth exponents for small individuals in Barro Colorado, Panama, in both census intervals (0.78 and 0.67) were close to, and not significantly different from, our prediction based on the observed scaling of tree height, crown area and light availability (0.81, Table 1).

Mortality

Mortality was less strongly size-dependent than growth, and changes in mortality with diameter were more variable

Table 2 Results of the resource availability and tree allometry analyses

Relationship	Data set	<i>n</i>	Exponent (95% CI)	<i>r</i> ²	Source
Observed canopy openness vs. height	5 m ≤ height ≤ 30 m (below canopy)	6 × 20 000	$\beta_L = 1.64$ (1.57–1.72)	0.989	Annual measurements at 20 000 points spaced 5 m apart on Barro Colorado, Panama between 1990 and 1996, excluding 1994 (Condit and Hubbell)
		All	$\beta_H = 0.593$ (0.59–0.597)	0.919	
		Small	$\beta_H = 0.649$ (0.642–0.655)	0.849	
Observed tree height vs. stem diameter	All Small Large	9043	$\beta_H = 0.460$ (0.443–0.477)	0.651	Measurements on trees from Barro Colorado, Panama (Wright, Muller-Landau, Spiro, O'Brien, Bohlman, Thomas, Condit)
		Small	$\beta_C = 1.36$ (1.33–1.39)	0.920	
		Large	$\beta_C = 1.39$ (1.33–1.45)	0.791	
Observed crown area vs. stem diameter	All Small Large	850	$\beta_C = 1.19$ (1.09–1.29)	0.637	Measurements on trees from Barro Colorado, Panama (Spiro, O'Brien, Bohlman, Condit)
		Small	$\beta_M = 2.61$ (2.58–2.64)	0.948	
		Large	$\beta_M = 2.65$ (2.58–2.72)	0.857	
Observed tree biomass vs. stem diameter	All Small Large	1504	$\beta_M = 2.42$ (2.38–2.47)	0.862	Data from moist tropical forests worldwide (Chave <i>et al.</i> 2005)
		Small	$\beta_C + \beta_H \beta_L - \beta_M + 1 = 0.807$ (0.712–0.9.13)		
		Large	$\beta_C + \beta_H \beta_L - \beta_M = -0.193$ (–0.288 to –0.087)		
Predicted diameter growth vs. stem diameter	Small, below canopy individuals				Prediction A9
Predicted mortality vs. stem diameter	Small, below canopy individuals				Prediction A11

For tree allometry, separate fits were performed for data sets including all individuals, small individuals (< 20 cm in stem diameter), and large individuals (≥ 20 cm in stem diameter); *n* is the number of points measured in the case of canopy openness, and the number of trees otherwise. CI on the fits are based on 1000 bootstraps, carried out over 50 × 50-m subplots for canopy openness and over trees for the allometric relationships. CI on the predicted relationships are based on bootstrapping over draws from the error distribution of the fitted parameters.

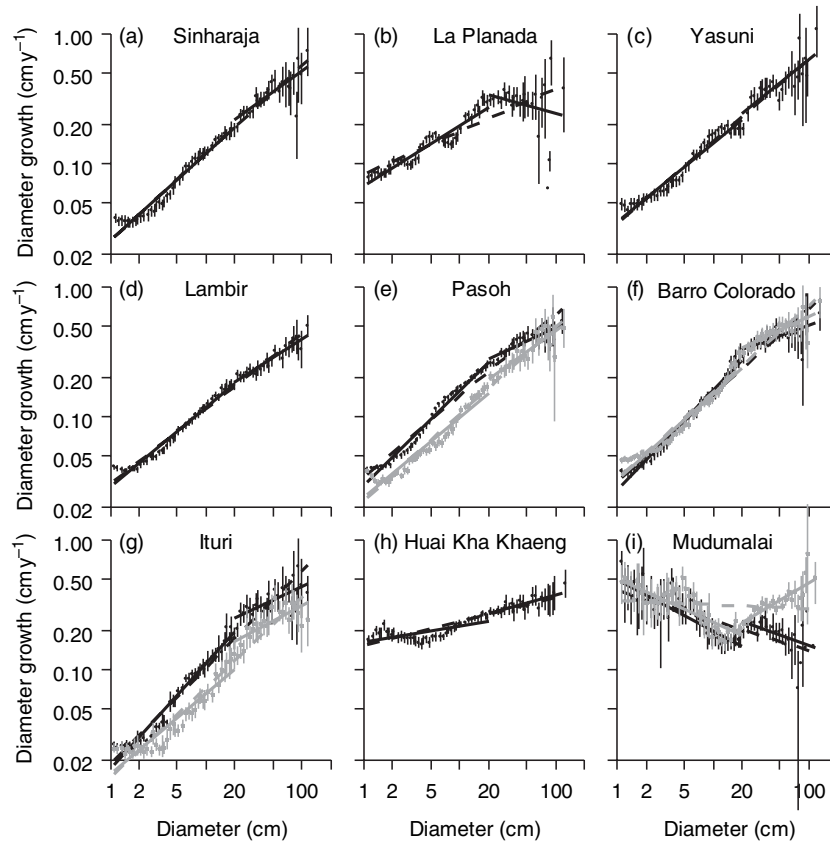


Figure 2 Mean absolute diameter growth rates as a function of diameter for all trees in 10 tropical forests. Vertical lines show 95% CI based on bootstrapping over 50×50 -m subplots. Thick dashed lines show power-function fits to the full data sets; thick solid lines show separate fits to small (< 20 -cm diameter) and large (≥ 20 -cm diameter) individuals. When there are two intercensus intervals at the same site, the earlier one is shown in black and the later one in grey. In the case of the Ituri site in the Congo, the results for the Egoro study area are in black and those for the Lenda study area are in grey. Sites are ordered by increasing dryness. The fitted parameters are given in Table 3.

among sites (Fig. 3). Among small individuals, mortality decreased as diameter increased in all 10 tropical forests; however, among large individuals, it variously continued to decrease as diameter increased, ceased to change significantly with diameter or increased with diameter. These changes were reflected in changes in the exponents relating mortality to diameter, which were larger for large individuals than for small individuals at nine of 10 sites, with significant differences at eight sites. Among large individuals, mortality exponents were not significantly different from zero in five of 10 sites, were significantly positive at three sites, and significantly negative at two sites (Table 3). In general, mortality patterns were less well approximated by power functions than were growth patterns, even among small individuals or large individuals alone.

The scaling of mortality rates with diameter was clearly inconsistent with metabolic ecology predictions at all sites, while consistent with our resource scaling alternative where it could be evaluated. Specifically, the exponents relating mortality to diameter for all individuals combined and for

small individuals alone were significantly different from the $-2/3$ value predicted by metabolic theory (M11): the exponents were significantly smaller at the driest site Mudumalai, and significantly larger at all other sites (Table 3). The values of the mortality exponent for small individuals in Panama in both census intervals (-0.33 and -0.26) were much closer to, and not significantly different from, the prediction for this site based on the scaling of resource availability (-0.19).

DISCUSSION

Assessing metabolic ecology theory for tropical forests

The predictions of metabolic ecology theory regarding the scaling of height, biomass, diameter growth and mortality with tree diameter were all rejected for tropical forests. Given that our alternative predictions based on the scaling of resource availability were closer to the observed values and were not rejected, we conclude that the implicit

Table 3 Results of power-function fits of absolute diameter growth rates and mortality rates to tree diameter in 10 tropical forests

Site	Census interval	Data set	N_{grow}	N_{mort}	Growth exponent (a)	Mortality exponent (b)	Difference in exponents ($c - b$)
Sinharaja	1995–2000	All	170 955	195 627	0.679 (0.643 to 0.706)*	0.125 (0.043 to 0.175)*	0.554 (0.48 to 0.627)*
		Small	164 889	188 555	0.687 (0.651 to 0.721)*	-0.195 (-0.249 to -0.152)*	0.882 (0.8220 to 0.941)*
		Large	6066	7072	0.539 (0.347 to 0.658)*	0.726 (0.367 to 0.959)*	-0.187 (-0.521 to 0.147)*
La Planada	1997–2003	All	76 610	108 751	0.344 (0.302 to 0.407)	-0.400 (-0.500 to -0.358)*	0.744 (0.655 to 0.832)*
		Small	72 760	104 107	0.488 (0.462 to 0.514)*	-0.558 (-0.596 to -0.522)*	1.045 (1 to 1.091)*
		large	3850	4644	-0.205 (-0.452 to 0.122)*	0.399 (-0.329 to 0.804)*	-0.603 (-1.238 to 0.032)*
Yasuni	1997–2004	All	115 827	146 941	0.645 (0.607 to 0.670)*	-0.024 (-0.120 to 0.018)*	0.669 (0.592 to 0.745)*
		Small	111 441	141 461	0.613 (0.583 to 0.644)*	-0.335 (-0.380 to -0.289)*	0.949 (0.894 to 1.003)
		large	4386	5480	0.618 (0.428 to 0.746)*	0.537 (0.046 to 0.853)*	0.081 (-0.353 to 0.514)*
Lambir	1992–1997	All	305 712	335 457	0.584 (0.567 to 0.600)*	-0.213 (-0.269 to -0.161)*	0.797 (0.741 to 0.854)*
		Small	294 450	323 502	0.620 (0.596 to 0.645)*	-0.189 (-0.227 to -0.158)*	0.809 (0.766 to 0.852)*
		Large	11 262	11 955	0.483 (0.395 to 0.557)*	-0.462 (-0.744 to -0.138)	0.945 (0.631 to 1.258)
Pasoh	1990–1995	All	275 766	315 665	0.640 (0.621 to 0.657)*	-0.103 (-0.159 to -0.063)*	0.743 (0.692 to 0.794)*
		Small	267 926	306 925	0.747 (0.733 to 0.763)*	-0.320 (-0.353 to -0.293)*	1.067 (1.034 to 1.101)*
		Large	7840	8740	0.360 (0.265 to 0.438)	-0.038 (-0.333 to 0.205)*	0.397 (0.115 to 0.68)*
	1995–2000	All	263 845	310 004	0.677 (0.644 to 0.699)*	-0.079 (-0.143 to -0.047)*	0.756 (0.701 to 0.811)*
		Small	256 001	300 929	0.636 (0.615 to 0.658)*	-0.303 (-0.334 to -0.277)*	0.94 (0.904 to 0.975)*
		Large	7844	9075	0.554 (0.365 to 0.664)*	0.295 (-0.023 to 0.479)*	0.259 (-0.033 to 0.551)*
	1990–1995	All	192 091	235 745	0.680 (0.652 to 0.701)*	-0.216 (-0.280 to -0.175)*	0.897 (0.839 to 0.954)*
		Small	186 080	227 990	0.776 (0.751 to 0.799)*	-0.329 (-0.365 to -0.297)*	1.105 (1.064 to 1.147)*
		Large	6011	7755	0.275 (0.128 to 0.39)	-0.193 (-0.541 to 0.046)*	0.468 (0.146 to 0.789)*
1995–2000	All	182 607	221 136	0.674 (0.651 to 0.692)*	-0.217 (-0.278 to -0.177)*	0.891 (0.837 to 0.945)*	
	Small	175 866	213 315	0.673 (0.652 to 0.695)*	-0.264 (-0.298 to -0.231)*	0.937 (0.898 to 0.976)*	
	Large	6741	7821	0.357 (0.23 to 0.452)	-0.171 (-0.488 to 0.066)*	0.528 (0.229 to 0.826)*	
Ituri-Edoro	1995–2000	All	136 613	152 827	0.751 (0.719 to 0.771)*	-0.017 (-0.096 to 0.029)*	0.768 (0.701 to 0.836)*
		Small	134 302	150 284	0.817 (0.782 to 0.848)*	-0.197 (-0.281 to -0.144)*	1.015 (0.939 to 1.091)
		Large	2311	2543	0.351 (0.165 to 0.478)	0.770 (0.499 to 1.224)*	-0.418 (-0.813 to -0.023)*
Ituri-Lenda	1995–2000	All	114 849	127 684	0.705 (0.671 to 0.727)*	-0.236 (-0.328 to -0.171)*	0.941 (0.857 to 1.025)
		Small	112 029	124 711	0.625 (0.582 to 0.668)*	-0.38 (-0.484 to -0.316)*	1.005 (0.91 to 1.099)
		Large	2820	2973	0.401 (0.247 to 0.528)	0.290 (-0.024 to 0.876)*	0.111 (-0.36 to 0.583)*
Huai Kha Khaeng	1993–1999	All	52 949	75 573	0.202 (0.179 to 0.222)*	-0.591 (-0.635 to -0.523)*	0.792 (0.732 to 0.852)*
		Small	45 499	67 021	0.135 (0.108 to 0.162)*	-0.926 (-0.974 to -0.881)*	1.062 (1.008 to 1.116)*
		Large	7450	8552	0.213 (0.127 to 0.295)*	-0.666 (-0.823 to -0.242)	0.879 (0.577 to 1.181)
Mudumalai	1992–1996	All	13 665	17 479	-0.259 (-0.377 to -0.194)*	-1.175 (-1.319 to -1.111)*	0.916 (0.777 to 1.054)
		Small	5443	8494	-0.485 (-0.598 to -0.367)*	-1.027 (-1.144 to -0.922)*	0.541 (0.381 to 0.701)*
		Large	8222	8985	-0.268 (-0.842 to 0.001)*	0.015 (-0.604 to 0.479)*	-0.283 (-0.969 to 0.403)*
	1996–2000	All	13 556	15 284	-0.032 (-0.076 to 0.004)*	-0.901 (-1.064 to -0.793)*	0.869 (0.727 to 1.01)
		Small	5094	6374	-0.422 (-0.495 to -0.34)*	-0.805 (-0.936 to -0.612)	0.383 (0.204 to 0.562)*
		Large	8462	8910	0.442 (0.250 to 0.572)	0.144 (-0.577 to 0.606)*	0.298 (-0.315 to 0.912)*

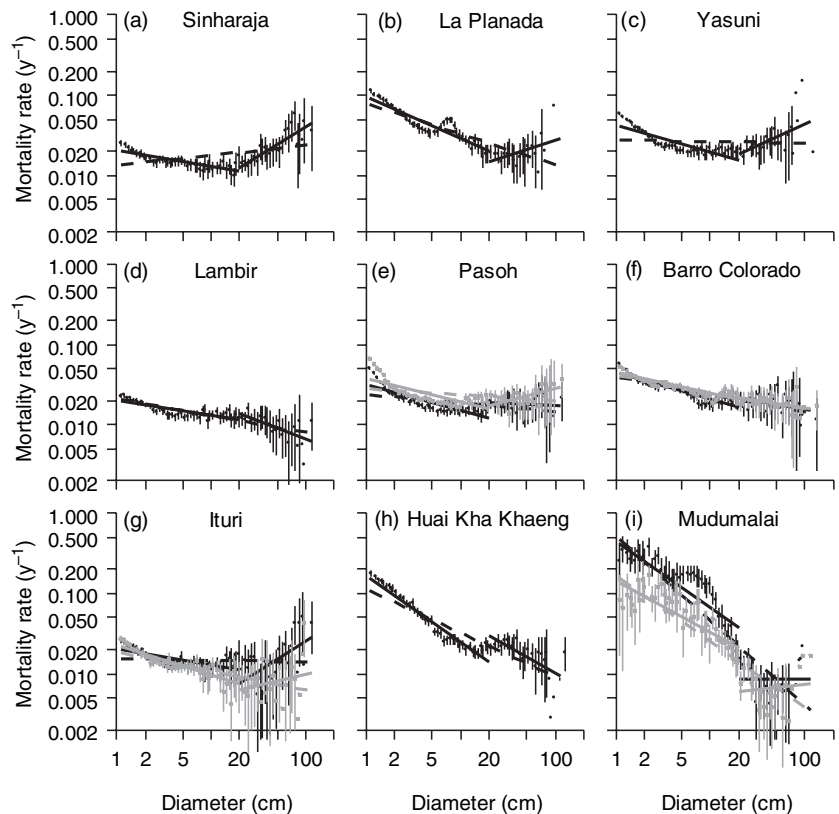
Separate fits were performed for data sets including all individuals, small individuals (< 20-cm diameter), and large individuals (\geq 20-cm diameter). N_{grow} and N_{mort} are the numbers of individuals included in the growth and mortality fits respectively. CI (95%) on the fitted exponents are based on 1000 bootstraps over 50×50 -m subplots.

*Indicates values that are significantly different from the predictions of metabolic ecology theory (1/3 for the growth exponent, -2/3 for the mortality exponent, 1 for the difference in exponents). When the exponents for small and large stems are significantly different, those estimates are boldface; when they are not significantly different, the estimate for all stems is in boldface. Plots are ordered in increasing dryness (Table 1).

assumption of metabolic ecology that the scaling of gross photosynthetic rates depends only on the scaling of the potential for resource capture and redistribution (M3) is faulty. Photosynthesis of tropical trees is commonly limited by light availability (Chazdon & Pearcy 1986; Pearcy *et al.* 1994; Graham *et al.* 2003), and competition for light among terrestrial plants is strongly size asymmetric (Weiner 1990). This asymmetry and the resulting changes in light availability with size need to be considered in order to understand the

scaling of gross photosynthetic rate with plant size in closed canopy forests. The scaling predicted by metabolic ecology may yet prove a good approximation for individual trees grown in the absence of competition, and in systems in which high mortality severely reduces competition. However, it cannot begin to explain variation in growth rates found over the eight orders of magnitude variation in individual biomass between understory saplings and canopy trees within a forest.

Figure 3 Mean mortality rates as a function of diameter for all trees in 10 tropical forests. Vertical lines show 95% CI based on bootstrapping over 50×50 -m subplots. Thick dashed lines show power-function fits to the full data sets; thick solid lines show separate fits to small (< 20 -cm diameter) and large (≥ 20 -cm diameter) individuals. When there are two intercensal intervals at the same site, the earlier one is shown in black and the later one in grey. In the case of the Ituri site in the Congo, the results for the Egoro study area are in black and those for the Lenda study area are in grey. Sites are ordered by increasing dryness. The fitted parameters are given in Table 3.



Taken together, the results suggest that one or both of the assumptions that tree growth and mortality rates scale with gross and mass-specific photosynthetic rates, respectively (M9 and M11), must also be rejected for the forest as a whole, although they may be appropriate for understory individuals. No matter what the scaling of photosynthetic rates with size, this combination of assumptions means that the difference between the exponents of growth and mortality ($c - b$) should be exactly one (M12). For all trees combined and especially for large individuals alone, the difference between the growth and mortality exponents was significantly > 1 in all but one closed-canopy forest (Ituri-Lenda, Table 3). Thus, there does not exist any scaling of photosynthesis with size that can reconcile these patterns with the assumptions that tree growth and mortality rates scale with gross and mass-specific photosynthetic rates respectively. We hypothesize that these deviations result mainly from strong size dependence of some mortality threats independent of resource availability and photosynthetic rates (Coomes *et al.* 2003). Size-dependent changes in allocation to reproduction may also contribute to this pattern (Thomas 1996; Wright *et al.* 2005). Among small individuals in closed-canopy forests, in contrast, the difference between growth and mortality exponents is generally close to 1, although still significantly different from one for most sites (Table 3). This suggests that for

trees in the understory, growth and mortality may scale with photosynthesis approximately as hypothesized in metabolic ecology theory; this idea is further supported by the success of our alternative predictions for below-canopy individuals that incorporate these assumptions regarding the relationship of growth and mortality to photosynthesis, while changing assumptions regarding how photosynthesis scales with size.

Both basic metabolic ecology theory and the variation upon it that we present here treat all individuals within the forest as identical in terms of demographic parameters and underlying physiological processes. These theories thus ignore ontogenetic and interspecific variation, and essentially average over it in making their predictions. Explicit consideration of known size-dependent changes in maintenance costs could lead to better predictions for biomass growth (Kooijman 2000). Several authors have already begun to consider how ontogenetic changes in maintenance costs might be incorporated into metabolic ecology theory (West *et al.* 2001); what we need now is a synthesis that considers interspecific as well as intraspecific variation in maintenance with size. There is abundant evidence that tropical tree species show large differences in stem allometry (O'Brien *et al.* 1995), photosynthesis (Kitajima 1994) and wood density (Muller-Landau 2004), as well as in ontogenetic variation in physiology and allometry (Poorter *et al.*

2003; Bohlman & O'Brien 2006). Thus, it is not surprising that there is considerable interspecific variation in demographic rates (Condit *et al.* 1993, 1995). It is likely that both interspecific differences and ontogenetic changes within a given species are important influences on the observed size-dependent patterns in growth and mortality for the forest as a whole, and that a complete understanding of patterns within and across sites will eventually require explicit consideration of such variability.

Significance and future directions

The results presented here indicate that, despite qualitative similarities in some patterns, there are no universal scaling relationships of photosynthetic rates, growth rates, or mortality rates with size among trees in forests. Instead, there are significant quantitative differences in the allometric scaling of demographic rates among forests, differences that our work suggests are related proximally to among-site variation in tree allometries and the scaling of light availability. Of course, the scaling of light availability within forests itself depends on the tree size distribution (Denslow & Guzman 2000; Montgomery & Chazdon 2001), which can be derived from the growth and mortality functions in old-growth forests (Kohyama *et al.* 2003). Likewise, the height and crown allometries of trees reflect plastic responses to resource availability as well as ecological sorting and natural selection of species for success within the local resource competition environment (Iwasa *et al.* 1985; King & Maindonald 1999; Poorter *et al.* 2003; Kitajima *et al.* 2005). Ultimately, we would like to not only explain size distributions in terms of growth and mortality, and growth and mortality in terms of allometries and light, but also all of these patterns simultaneously from more fundamental physiological and physical characteristics of trees and sites.

We hypothesize that the key factor for understanding variation in demographic rates among forests is the degree to which large individuals can monopolize resources versus the degree to which their abundance and resource monopolization are limited by other factors such as lethal disturbances (Coomes *et al.* 2003) or relatively more symmetric resource competition (Stoll *et al.* 2002). Among-site variation in growth and mortality is greatest between closed and open canopy forests. In open canopy forests, the abundance of large trees is below its theoretical maximum – in the two forests here because of the effects of fire and elephants on the recruitment and mortality rates of large trees (Sukumar *et al.* 2005). Where the densities of large trees are limited and canopies are consequently more open, competition for resources is likely to be relatively more symmetric as small individuals have more access to resources. Major disturbances, such as fires and cyclones,

that are important causes of large tree mortality and thus of canopy openings in many forests occur over large areas at long time intervals. Thus, it will take many years to accumulate enough data to understand the frequencies of such disturbances and accurately estimate long-term average mortality and growth rates as a function of size.

A mechanistic explanation for size-dependent patterns of tree growth and mortality is not only a fundamental challenge in forest ecology, but also a problem of considerable applied significance. Given the large role of tropical forests in the global carbon cycle, it is important to understand how increases or decreases in tree photosynthetic rates because of carbon fertilization, nitrogen deposition, increased temperature or other global forcings might ultimately affect forest dynamics, and thereby net carbon fluxes (Cramer *et al.* 2004; Wright 2005). A better mechanistic understanding of the processes governing tree growth and mortality rates and their changes with tree size will shed light not only on geographical variation in these patterns today, but on how future forests are likely to change.

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SUPPLEMENTARY MATERIAL

The following material is available online at <http://www.Blackwell-Synergy.com>:

Appendix S1 Details of the growth and mortality fits.

Table S1 Intercepts of the growth and mortality fits.

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