LETTER

Decelerating growth in tropical forest trees

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Abstract

The impacts of global change on tropical forests remain poorly understood. We examined changes in tree growth rates over the past two decades for all species occurring in large (50-ha) forest dynamics plots in Panama and Malaysia. Stem growth rates declined significantly at both forests regardless of initial size or organizational level (species, community or stand). Decreasing growth rates were widespread, occurring in 24–71% of species at Barro Colorado Island, Panama (BCI) and in 58–95% of species at Pasoh, Malaysia (depending on the sizes of stems included). Changes in growth were not consistently associated with initial growth rate, adult stature, or wood density. Changes in growth were significantly associated with regional climate changes: at both sites growth was negatively correlated with annual mean daily minimum temperatures, and at BCI growth was positively correlated with annual precipitation and number of rainfree days (a measure of relative insolation). While the underlying cause(s) of decelerating growth is still unresolved, these patterns strongly contradict the hypothesized pantropical increase in tree growth rates caused by carbon fertilization. Decelerating tree growth will have important economic and environmental implications.

Keywords

Carbon cycling, carbon fertilization, climate change, forest dynamics, tree growth rates.

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INTRODUCTION

It is well documented that human activities are affecting environmental conditions world-wide. Given the high diversity as well as ecological and economical importance of lowland tropical rainforests it is critical that we understand their responses to these changes (Malhi & Phillips 2004; Wright 2005; Lewis 2006). Recent studies have reported that growth rates of tropical rainforests have accelerated over the past several decades (Laurance et al. 2004; Lewis et al. 2004b) consistent with the hypothesis of increased productivity caused by rising concentrations of atmospheric CO_2 and carbon fertilization (Melillo et al. 1993; Laurance et al. 2004; Lewis et al. 2004a; Lewis 2006). However, these studies have focused primarily on changes in stand-level growth rates (i.e. change in total basal area or biomass per unit area). One potential limitation of this approach is that stand-level growth rates provide little information about the dynamics of most species as changes may be driven by compositional shifts and/or the responses of just a few dominant species.

Laurance et al. (2004) investigated changes in tree dynamics at the genera-level in forest plots located near Manaus, Brazil, and found that the growth rates of most genera (87%) had increased over time. This increase was most pronounced in genera of large fast-growing canopy trees and was therefore considered a response to carbon fertilization. In contrast, in the only species-level study to date, Clark et al. (2003) looked at changes in the diameter growth of six canopy tree species at La Selva, Costa Rica, and found that annual growth rates decreased steadily over time in all species. Growth rates were negatively correlated with daily minimum temperatures and therefore the declines were attributed to increasing nighttime temperatures and the associated increases in respiratory costs relative to photosynthetic gains. However, this study tracked growth rates only within a single cohort of trees (i.e. new recruits were not incorporated; Clark et al. 2003) and thus decreased growth rates may alternatively be attributable to a decrease in the relative growth of larger trees. Clearly additional work is needed if we hope to understand how the dynamics of tropical trees respond to global anthropogenic disturbances such as rising concentrations of CO_2 and climate change (Clark 2004; Nelson 2005; Wright 2005). Understanding these responses will have important implications for the world's carbon

budget; for example, models show that accelerated stem growth may lead to persistent increases in carbon sequestration, potentially helping to offset emissions (Chambers *et al.* 2001).

Here we use long-term tree census data from New- and Old-World 50-ha tree plots [Barro Colorado Island, Panama (BCI), and Pasoh, Malaysia] to examine changes in relative basal area growth rates over the past several decades for various size classes of stems (saplings, poles, and canopy trees) at the species-, community- and stand-level. Species-level growth describes the mean growth across individuals within each species; community-level growth describes the mean relative growth across all species in the plot (i.e. species weighted equally); and stand-level growth rates are the relative change in total basal area (all stems combined regardless of species) caused by growth per hectare. Based on the species-specific growth rates, we then test if there are consistent differences between decelerating vs. non-decelerating species in several species traits related to life-history strategy including initial growth rate, adult stature, and wood density. Finally, using long-term meteorological data from BCI we test the relationship between the observed changes in community-wide growth rates and changes in temperature and precipitation.

METHODS

Study sites

This study was conducted using data from 50-ha Forest Dynamics Plots located on BCI and at Pasoh, Malaysia (Table 1). These plots differ greatly in their local weather regimes, soil characteristics, and history (Leigh *et al.* 2004; Manokaran *et al.* 2004). In both plots, all woody stems ≥ 10 mm dbh (excluding lianas) have been identified to species, mapped, tagged and measured to the nearest mm (but see below) in repeated censuses. The plot on BCI was initiated in 1981/1982 and has been recensused in 1985, 1990, 1995, 2000, and 2005. The plot at Pasoh was initiated in 1986 and has been recensused in 1990, 1995, and 2000 (Pasoh was recensused in 2005 but these data are currently unavailable). Both plots are administered

collaboratively with the Center for Tropical Forest Science which ensures strict standardization of methods.

Stand-level growth rates

In order to estimate stand-level growth rates at BCI and Pasoh, each plot was subdivided into 50 non-overlapping 1-ha (100 × 100 m) subplots. Relative stand-level growth rates (RGR_{stand}) were then calculated for each hectare subplot during each census period as:

$$RGR_{stand} = \frac{\ln(BA_t) - \ln(BA_0)}{t}$$

where BA is the total basal area of all trees in mm^2, regardless of species, that were alive and measurable at both the start (BA_0) and end (BA_t) of the census period annualized by the number of years (t, measured in days) between censuses. Changes in basal area due to mortality or recruitment are excluded. Estimates of RGR_{stand} were log-normally distributed and thus we used log transformed values for all analyses.

In the first two censuses at BCI and the first census at Pasoh the diameter of stems < 55 mm dbh were recorded at 5 mm increments (always rounded down). To account for this, the growth rates of these stems for the first two intervals at BCI and the first interval at Pasoh were based on diameter measurements rounded down to the nearest 5 mm (Condit *et al.* 2006). To correct for measurement errors, the maximum diameter growth rate was set to 75 mm $year^{-1}$. In addition, we assumed zero growth (i.e. $BA_0 = BA_t$) for any individuals in which the point of measurement (POM) changed between censuses (e.g. due to growth of buttresses) (Condit *et al.* 2006). POM corrections affected only a small percentage of individuals at BCI (0.3–6.7% depending on the census interval and size of stems included (Appendix S1), and no individuals at Pasoh. Still, we recalculated growth rates using several methods to estimate growth rates of trees for which POM changed (Appendix S1). Our results are robust to these corrections (Appendix S1). Here we only present results based on the correction method described above.

The rates of change in RGR_{stand} through time were determined by calculating the linear least-squares regression

Table 1 Characteristics of study plots

Site	Location(latitude, longitude)	Elevation (m)	Mean annual precipitation(mm)	No. of months with <100 mm precipitation	Number of species			
					Total*	Saplings†	Poles†	Trees†
BCI	9° 09′N, 79° 51′E	120–160	2551	3 – 4 (January – April)	320	242	219	217
Pasoh	2° 58′N, 102°18′E	80–104	1788	0 – 1 (January)	823	775	692	651

*Includes all species, even those present in only a single census.
†Includes only those species occurring in all censuses.

coefficient (β) of RGR_{stand} (log transformed) vs. date separately for each of the 50 subplots. The 95% confidence intervals (CIs) for the median β at BCI and Pasoh were determined through bootstrapping (5000 resamples) and compared with the null expectation of no consistent change (i.e. $\beta = 0$).

As growth rates are strongly related to tree size, we also calculated stand-level growth rates and the associated rates of change in growth rates separately for three different size classes of stems as defined by stem diameter at the start of each census period (saplings: 10–50 mm, poles: 50–100 mm, and trees: $\geq$ 100 mm dbh). This procedure allows a single stem to change (usually increase) size class through time. These size classes also facilitated comparisons with previous studies that have only included trees $\geq$ 100 mm dbh.

Community- and species-level growth rates

We calculated community-wide (RGR_{comm}) and species-specific ($RGR_{species}$) growth rates using Bayesian hierarchical modelling and Gibbs sampling for each of the three size classes defined above (Gelfand & Smith 1990; Clark 2003). Bayesian hierarchical modelling is advantageous in that it allows growth rates to be estimated for species too rare to be analyzed by standard techniques (Clark 2005). Bayesian models were constructed using non-informative priors (i.e. approximately uniform over all allowed values; distributional forms chosen for conjugacy) and assuming log-normal distributions of growth rates both within and across species using the protocols of Condit *et al.* (2006) but modified to generate estimates of basal area growth rates rather than diameter growth rates (but see below). We chose to estimate basal area growth rates to facilitate comparisons with previous studies and also because basal area is more closely related to important ecosystem functions such as carbon sequestration. As our models of RGR_{comm} and $RGR_{species}$ assumed a log-normal distribution they could not accept negative or zero growth measurements. Therefore in addition to setting the maximum diameter growth as 75 mm year^{-1}, we assumed a minimum diameter growth of 0.1 mm year^{-1}, which is less than half the detection threshold.

RGR_{comm} is the hyperparameter and is based on the posterior distribution of growth rates across species. Best estimates of RGR_{comm} and $RGR_{species}$ were the median of 10 000 Gibbs steps following an initial 1000-step burn-in period. Estimates for all parameters had strong convergence as determined through Geweke diagnostic tests (Geweke 1992). The 95% credible intervals around RGR_{comm} and $RGR_{species}$ were set as the 2.5 and 97.5% quantiles of Gibbs step estimates.

Once the growth rates were estimated, we determined the directions and rates of change in the parameters by calculating the linear least-squares regression coefficient

(β) of RGR_{comm} and $RGR_{species}$ (log transformed) vs. date at Pasoh and BCI ($RGR_{species}$ was calculated for each species that occurred in all censuses). We calculated the significance of β for each individual species through a stratified bootstrapping procedure: an estimate of the species-specific growth rate was sampled with replacement from the corresponding posterior distribution of $RGR_{species}$ for each of the census intervals and β was recalculated. This procedure was reiterated 1000 times to generate 95% CIs of β for each species incorporating intra-census variation. Likewise, the CIs for the rates of change in RGR_{comm} were determined by resampling from the posterior distributions of the community-wide growth rate parameter at each census period.

In order to ensure that our choice of growth rate parameters did not bias the results, we recalculated species growth rates at BCI using absolute basal area growth (i.e. Growth $= (BA_t - BA_0)/t$) and relative diameter growth (i.e. Growth $= (\ln(DBH_t) - \ln(DBH_0))/t$). We also recalculated the relative basal area growth for each species using non-Bayesian techniques incorporating negative growth measurements. Our conclusions were robust to both growth parameter and analytical method (Appendix S2).

Species traits

In order to determine if there was a relationship between species traits and changes in species-specific growth rates we compiled estimates of initial growth rate (i.e. the estimate of $RGR_{species}$ for each size class during the initial census period), adult stature (defined as the 95% quantile of diameter measurements for each species; King *et al.* 2006), and wood density (wood density is the oven-dry mass of a sample of wood divided by the green volume of the sample; Chave *et al.* 2005). Wood density values were extracted from data compiled by J. Chave (personal communication). Trait data were available for all species except in the case of wood density; species-specific wood density estimates were only available for 128 species at BCI and 291 species at Pasoh. These species traits are believed to be strong indicators of life-history and reproductive strategies (Wright *et al.* 2003; King *et al.* 2006).

For each of these traits we tested if the differences between species that declined significantly in their relative growth rates (i.e. β significantly < 0) vs. all other species were greater than random by comparing the difference in the median trait values for each group vs. the distribution of differences generated from 10 000 label permutation tests.

Climatic factors

In order to test if there was a relationship between changes in growth rates and regional climate changes, we correlated

RGR$_{comm}$ (log transformed) for each size-class of stems with climatic variables measured at BCI and averaged over the corresponding census periods. Climatic variables included total annual precipitation (mm), number of rainfree days, and yearly mean daily minimum, maximum and mean temperatures (°C; Fig. 1). Number of rainfree days was significantly positively correlated with annual radiation ($R = 0.25$) and PAR ($R = 0.29$) measured with a pyranometer and LiCor 190S, respectively. Climate data and corresponding metadata are available through http://striweb.si.edu/esp/physical_monitoring/download_bci.htm. Confidence intervals for the correlations were determined through stratified resampling of the posterior distributions of RGR$_{comm}$ for each census interval as described above.

All analyses were conducted in R 2.2.1 (http://www.R-project.org/) using modified functions available through Condit *et al.* (2006) and the Coda, CTFS, MASS, and MCMCpack packages (http://www.cran.r-project.org/doc/packages).

RESULTS

At the species level, growth rates decreased over time for the majority of species in both forests (Fig. 2;
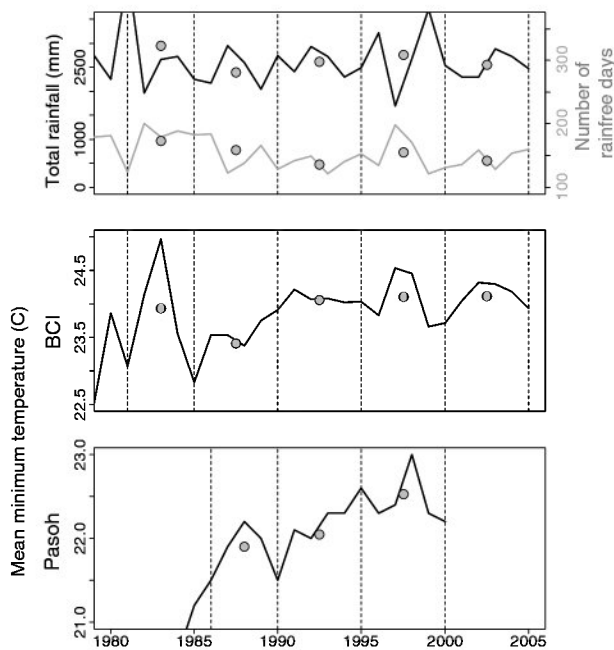

Figure 1 Patterns in precipitation (total annual rainfall and number of rainfree days per year) and mean daily minimum temperature at BCI (top two panels, respectively) and mean daily minimum temperature at Pasoh (bottom panel). Vertical lines indicate census years and points indicate the mean values per interval as used in the correlation analyses. Temperatures for Pasoh were recorded at the Felda Pasoh 2 station located *c.* 5 km southeast of the plot.

Appendix S3). At BCI, 242 species occurred as saplings in all censuses; 229 (95%) of these species decreased in relative growth rate over time and in 171 species (71%) the decrease was significant. In contrast, only three species (1%) had significantly accelerating growth rates. For poles, 219 species occurred in all censuses. Of these, 207 (95%) decreased in growth rate over time, 118 species (55%) significantly. No species had significantly accelerating growth rates. For the largest size class, there were 217 species that occurred in all censuses and 171 (79%) decreased in growth rate over time. In 52 species (24%) the decrease was significant and five species (2%) increased growth significantly (Fig. 2).

At Pasoh, 775 species occurred as saplings in all censuses, all of which decreased in relative growth rate over time. In 737 species (95%) the decrease was significant. For poles, 686 species occurred in all censuses. Again, nearly all species (685 = 99.9%) decreased in growth rate over time and 530 species (77%) decreased significantly in growth rates. For trees, there were 648 species that occurred in all censuses and 639 (99%) decreased in growth rate over time; in 374 species (58%) the decrease was significant. Nine species (1%) had accelerating growth, but in all cases the change was not statistically significant (Fig. 2).

Likewise, estimates of relative community-level growth rates (log transformed) decreased significantly over time for all three size classes of stems at both forests (BCI: saplings: $\beta = -0.030$; 95% CI $= -0.035$ to -0.025; poles: $\beta = -0.031$; 95% CI $= -0.036$ to -0.025; trees: $\beta = -0.014$; 95% CI $= -0.021$ to -0.007; Pasoh: saplings: $\beta = -0.076$; 95% CI $= -0.079$ to -0.073; poles: $\beta = -0.092$; 95% CI $= -0.098$ to -0.087; trees: $\beta = -0.079$; 95% CI $= -0.084$ to -0.072; Fig. 3a,b).

Finally, at the stand level, there were significant decreases in growth rates (log transformed) at both BCI and at Pasoh. This held true whether all sizes of stems were combined (BCI: $\beta = -0.014$; 95% CI $= -0.022$ to -0.007; Pasoh: $\beta = -0.048$; 95% CI $= -0.057$ to -0.041), as well as when each size class was analyzed individually (BCI: saplings: $\beta = -0.032$; 95% CI $= -0.040$ to -0.027; poles: $\beta = -0.026$; 95% CI $= -0.029$ to -0.018; trees: $\beta = -0.008$; 95% CI $= -0.018$ to -0.001; Pasoh: saplings: $\beta = -0.071$; 95% CI $= -0.083$ to -0.058; poles: $\beta = -0.083$; 95% CI $= -0.089$ to -0.074; trees: $\beta = -0.041$; 95% CI $= -0.050$ to $--0.032$; Fig. 3c,d).

At BCI, species with decelerating growth rates as saplings had significantly greater median wood density (+37.44%, $P < 0.0001$) as well as slower median initial growth rates (−4.87%, $P < 0.01$). At Pasoh, species with decelerating growth rates as trees had significantly faster initial growth rates (+1.05%, $P < 0.05$). All other differences in species traits between decelerating species and stable or accelerating species were not statistically distinguishable from random (Table 2).
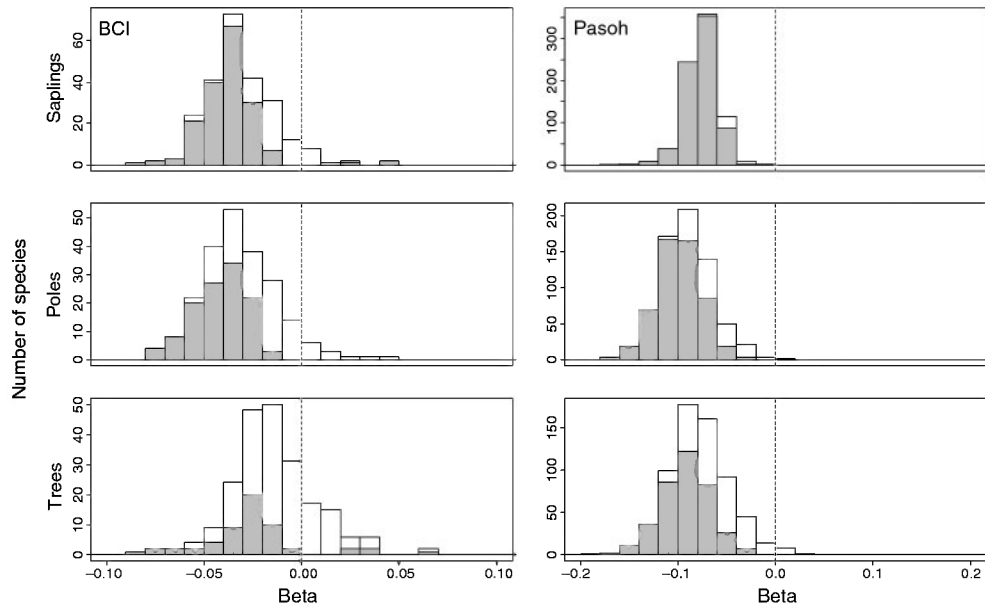
Figure 2 Histograms indicating the rates of change (β) in the species-level relative growth rates ($RGR_{species}$) for saplings, poles and trees at BCI (left panels) and Pasoh (right panels). Estimates are for all species occurring in all censuses. Shaded areas indicate species for which the change in RGR was significantly different from zero. Zero is indicated by the dotted vertical line.
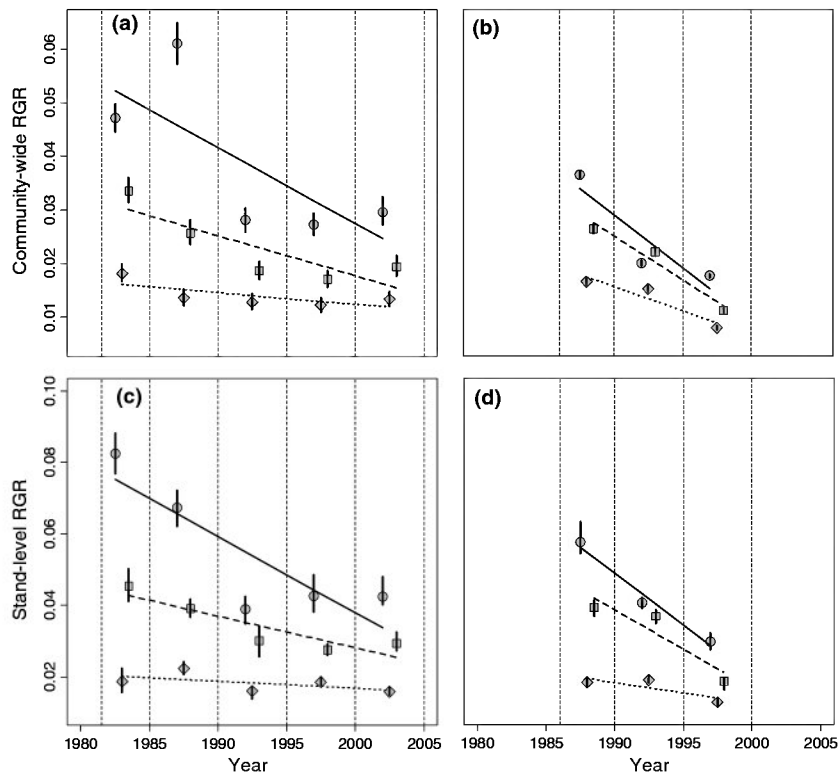

Figure 3 Estimates for stand- and community-level relative basal area growth rates (RGR_{stand} and RGR_{comm}) for saplings (circles, solid line), poles (squares, dashed line), and trees (diamonds, dotted line) at BCI (a and c) and Pasoh (b and d). Symbols indicate the median. Vertical bars indicate the 95% confidence intervals based on bootstrapping in (a) and (b) and the 95% credible intervals in (c) and (d). Lines depict the relationships between RGR and date. For all three size classes of stems and at both sites, growth rates decreased significantly over time (i.e. β significantly < 0). Vertical lines indicate census years. Symbols are offset horizontally to improve clarity.

Table 2 Percent differences in median trait values between species with significantly decreasing growth rates vs. all other species (positive values indicate that the trait value is greater in decreasing species) and two-tailed significance (*$P < 0.05$, **$P < 0.001$, ***$P < 0.0001$)

Trait	Saplings	Poles	Trees
BCI			
Initial growth rate	4.87 **	1.15	−4.79
Adult stature	−5.94	−4.89	0.15
Wood density	37.44 ***	6.36	9.39
Pasoh			
Initial growth rate	−0.80	−0.80	1.51 *
Adult stature	−0.46	−0.46	0.45
Wood density	2.96	7.67	4.88

The correlation coefficients between RGR_{comm} and climatic variables at BCI are presented in Table 3. Based on stratified resampling, relative basal area growth rates for saplings, poles, and trees all increased significantly with the mean number of rainfree days and total precipitation and decreased significantly at higher mean daily minimum temperatures (Table 3).

DISCUSSION

For the vast majority of tropical tree species at Pasoh and BCI, growth rates have decelerated dramatically and significantly over the past two decades. At the community-wide level, the change (β) translates into a 1.2–6.2% decrease in relative growth each year (for trees at BCI and poles at Pasoh, respectively). These results are consistent with the findings of Clark *et al.* (2003) who found steady decreases in the growth rates of focal tree species at

La Selva. However, our results contrast strongly with model-based predictions of forest productivity (Melillo *et al.* 1993; McKane *et al.* 1995), as well as with the empirical findings of Laurance *et al.* (2004) and Lewis *et al.* (2004a) that growth rates in Amazonian forests are accelerating at the genus and stand level, respectively.

In an attempt to identify the cause of the observed changes in growth rates, we tested for relationships between community-wide growth rates and climatic changes at BCI. For all stem size classes the strongest relationships were a significant increase in growth rates with increased frequency of rainfree days. This may be due to decreased cloudcover and increased light availability (Graham *et al.* 2003; Nemani *et al.* 2003) which is supported by the positive correlation between the number of rainfree days and insolation. There were also significant decreases in growth rates with decreased total precipitation and increased daily minimum temperatures. Climate data are not available from the Pasoh plot, but a nearby agricultural station (*c.* 5 km distant) recorded a steady increase in temperatures over the study period (Fig. 1) concurrent with the deceleration in growth rates (Table 3). Decreased growth at elevated temperatures is believed to be due to the increase in plant respiration relative to photosynthesis resulting in decreased net carbon assimilation (Amthor 2000; Clark *et al.* 2003; Clark 2004).

Several other alternative hypotheses might explain the dramatic decline of tree growth rates at BCI and Pasoh. Liana abundances have reportedly increased in many tropical forests (Phillips *et al.* 2002) including BCI where the production of liana leaves and flowers increased by > 50% between 1986 and 2002 (Wright *et al.* 2004; Wright & Calderon 2006). Lianas can overtop trees and thereby reduce the amount of light available for tree growth at all sizes. The role of lianas in tropical forest dynamics warrants additional attention.

Table 3 Correlation coefficients (and 95% confidence intervals) between the community-level relative growth rate estimates (RGR_{comm}; log transformed) and climatic factors (averaged over census periods) at BCI. The confidence intervals for bold values do not overlap zero.

Climatic factor	Saplings	Poles	Trees
BCI			
Temperature			
Daily minimum	**−0.61 (−0.70 to−0.49)**	**−0.47 (−0.60 to −0.32)**	**−0.31 (−0.89 to −0.27)**
Daily maximum	0.05 (−0.07 to 0.18)	0.18 (−0.02 to 0.35)	0.35 (−0.08 to 0.69)
Daily mean	**−0.12 (−0.24 to −0.01)**	0.03 (−0.12 to 0.20)	0.19 (−0.25 to 0.55)
Precipitation			
Total	**0.25 (0.13 to 0.38)**	**0.38 (0.23 to 0.53)**	**0.61 (0.19 to 0.86)**
No. of rainfree days	**0.84 (0.75 to 0.91)**	**0.82 (0.72 to 0.90)**	**0.90 (0.66 to 0.99)**
Pasoh			
Temperature			
Daily minimum	**−0.78 (−0.81 to−0.76)**	**−1.00 (−1.00 to −1.00)**	**−0.99 (−1.00 to −0.98)**
Daily maximum	**−0.50 (−0.54 to−0.47)**	**−0.94 (−0.96 to −0.92)**	**−0.97 (−0.98 to 0.95)**
Daily mean	**−0.75 (−0.78 to −0.72)**	**−1.00 (−1.00 to −1.00)**	**−1.00 (−1.00 to−0.99)**

Forest maturation may also result in stem thinning and decreased productivity as mean stem size increases along with competition for light and nutrients (Gower *et al.* 1996; Pregitzer & Euskirchen 2004). However, contrary to this hypothesis, mean successional status did not change over the study period at BCI and actually decreased significantly at Pasoh (K.J.F., unpublished data), indicating that neither site is undergoing recovery from past large-scale disturbances. This is in accord with the results of Piperno (1990) who found no evidence of anthropogenic disturbances in the BCI plot over the past 500 years. Furthermore, we still found significantly decelerating growth rates for the vast majority of species at both sites even when controlling for concurrent stand maturation (measured through changes in relative stem size distributions) through ANCOVA analyses (Appendix S4).

Other potential explanations for decelerating growth rates include global dimming (although satellite measurements indicate that for the tropics incoming solar radiation actually increased between 1983 and 2001; Pinker *et al.* 2005), changes in the pattern or timing of precipitation events (Condit *et al.* 1995; Tian *et al.* 1998; Asner *et al.* 2004; Rolim *et al.* 2005), edge effects (Ickes & Williamson 2000; Laurance 2000), and/or the impacts of human activities such as collecting, tree climbing and censusing on vegetation (Nelson 2005; but see Goldsmith *et al.* 2006).

While the cause(s) of decreasing tree growth rates is still poorly resolved, the patterns at BCI and Pasoh are most consistent with a decrease in productivity due to changes in regional climate including rising temperatures and increased cloudiness. These results provide strong evidence against the hypothesis of a pantropical increase in tree growth due to elevated resource availability caused by carbon fertilization and/or elevated nutrient deposition (Melillo *et al.* 1993; Lewis 2006). However, our results do not preclude a possible impact of CO_2 on tropical forest dynamics. At BCI, species with decreasing growth rates as saplings had significantly denser wood and slower initial growth rates than other species. This is in accord with the fertilization hypothesis which predicts differential responses between fast-growing pioneer species and slower-growing shade-tolerant species (Körner 2004; Laurance *et al.* 2004; Lewis *et al.* 2004a; Lewis 2006) and may indicate that rising CO_2 would accelerate tree growth in the absence of climate change. The overriding influence of regional climate change may help explain why the patterns reported here (and from Costa Rica) differ markedly with those from Amazonia; temperature increases over the past several decades have been more pronounced in Southeast Asia and Central America than through much of the Amazon basin, where some regions have actually experienced a net cooling since 1960 (Malhi & Wright 2004). Additional research from other regions is clearly needed to help untangle the complicated effects of global and regional environmental changes on tropical forest dynamics.

If widespread, decelerating tropical tree growth will have extremely important economic and environmental implications (Lewis 2006). Tropical forests are responsible for over a third of global primary productivity (Melillo *et al.* 1993) and provide many invaluable services including carbon sequestration and the production of timber and non-timber products. In addition, tropical forests are the basal resource for most terrestrial animal species. Decelerating growth rates may adversely affect these services, potentially leading to decreased economic yields and/or species extinctions. This is especially true in the face of increasing tree mortality as have been recorded at Pasoh (Condit *et al.* 2006), as well as through much of the Amazon (Lewis *et al.* 2004b; Phillips *et al.* 2004). An important caveat, however, is that changes in growth may not be indicative of overall changes in forest productivity. It is possible that trees are responding to changing environmental conditions through shifts in their allocation of photosynthate from stem growth to other pathways such as root growth, leaf production and/or reproduction (LaDeau & Clark 2001). For example, flower production has increased for trees at BCI over the past two decades (Wright & Calderon 2006). Therefore, it is still possible that total productivity has remained stable or even increased despite decelerated stem growth. Even under this scenario decreased growth could have important impacts on carbon sequestration/storage as the residence time of carbon in fine roots, leaves, flowers, or fruits is significantly shorter than in course woody tissue (Pregitzer *et al.* 1995).

Finally, we stress the potential for positive feedbacks to cause further declines in tropical forest growth rates. If decelerated stem growth results in slower rates of carbon uptake (Chambers *et al.* 2001; Vieira *et al.* 2005), the rise in atmospheric CO_2 concentrations could accelerate. This may in turn lead to even higher temperatures and lower net productivity. Another potential feedback might occur if reduced timber yields force loggers to compensate by enlarging the amount of area harvested, resulting in higher CO_2 emissions through deforestation and associated fires, as well as increased rates of habitat fragmentation/degradation and species extinctions.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Comparison of beta values generated using different POM correction methods.

Appendix S2 Comparison of beta values generated using different growth metrics at BCI.

Appendix S3 Species-level growth rate and beta estimates for BCI and Pasoh.

Appendix S4 ANCOVA testing changes in growth rates accounting for forest maturation.

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