Annual wood production in a tropical rain forest in NE Costa Rica linked to climatic variation but not to increasing CO_2

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Abstract

Increased atmospheric [CO_2] could theoretically lead to increased forest productivity ('CO_2 fertilization'). This mechanism was hypothesized as a possible explanation for biomass increases reported from tropical forests in the last 30 + years. We used unique long-term records of annually measured stands (eighteen 0.5 ha plots, 10 years) and focal tree species (six species, 24 years) to assess the effects of rainfall, temperature, and atmospheric [CO_2] on annual wood production in a neotropical rain forest. Our study area was a meso-scale section (600 ha) of old-growth Tropical Wet Forest in NE Costa Rica. Using the repeated remeasurements we directly assessed the relative effects of inter-annual climatic variation and increasing atmospheric [CO_2] on wood production. A remarkably simple two-factor model explained 91% of the interannual variance in stand-level tree growth; the statistically independent factors were total dry season rainfall (positive effect, $r^2 = 0.85$) and night-time temperature (negative effect, $r^2 = 0.42$). Stand-level tree mortality increased significantly with night-time temperature. After accounting for dry season rainfall and night-time temperature, there was no effect of annual [CO_2] on tree growth in either the stand or focal species data. Tree growth in this Tropical Wet Forest was surprisingly sensitive to the current range of dry season conditions and to variations in mean annual night-time temperature of 1–2°. Our results suggest that wood production in the lowland rainforests of NE Costa Rica (and by extension in other tropical regions) may be severely reduced in future climates that are only slightly drier and/or warmer.

Keywords: climate, CO_2 fertilization, Costa Rica, drought, global climate change, La Selva, rainfall, temperature, tropical rain forest, tropical tree growth

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Introduction

Indeed, a harsh, but not entirely unwarranted, view would be that our current understanding of biosphere-atmosphere feedbacks is a collection of interesting, but largely untested, hypotheses for the future state of terrestrial ecosystems and climate Moorcroft (2006).

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The amount of accumulated anthropogenic CO_2 emissions that would severely perturb global carbon cycle processes is highly uncertain (Medvigy et al., 2009). Reducing this uncertainty will require a quantitative understanding of the current and future feedbacks from terrestrial ecosystems in response to changing climate and atmospheric CO_2 levels (Jones et al., 2006; Canadell et al., 2007; Denman et al., 2007; Matthews et al., 2007; Heimann & Reichstein, 2008). The world's tropical forests are of particular importance in this regard, because they store a large fraction of terrestrial carbon in their vegetation and soils (Dixon et al., 1994) and are estimated to account for 35% of global net primary productivity (Saugier et al., 2001).

Multiple lines of evidence suggest that tropical forests may be nearing thresholds for marked negative effects of increasing temperatures on forest productivity:

(1) Short-term leaf-level measurements in multiple tropical forest regions indicate reduced net carbon assimilation at higher current daytime temperatures (Tribuzy, 2005; Doughty & Goulden, 2008 and included references);

(2) Eddy-covariance studies from above-canopy towers in Brazil and Costa Rica found reduced net forest carbon uptake in the warmest daytime periods (Loescher *et al.*, 2003; Goulden *et al.*, 2004; Doughty & Goulden, 2008); and

(3) Repeat measurements of tree growth in three tropical forests showed negative correlations between tree growth in successive periods and temperature metrics from these periods (six canopy tree species, La Selva, Costa Rica, sixteen 1-year intervals, Clark *et al.*, 2003; forest-level growth, three [Pasoh, Malaysia] and five [Barro Colorado I., Panama] 3–5-year intervals, Feeley *et al.*, 2007).

In addition, severe drought stress led to major reductions in forest productivity in a multiyear forest drydown experiment in Brazilian Amazonia (Brando *et al.*, 2008). Elevated tree mortality and lower tree growth have been reported from all tropical regions in extreme El Niño events, which brought record pantropical temperatures and severe drought to many areas (reviewed in Clark, 2004; McDowell *et al.*, 2008).

During the 1980s and 1990s, anomalous strong CO_2 emissions from the land tropics were inferred to have occurred in years of elevated tropical temperatures and reduced tropical rainfall (Adams & Piovesan, 2005; Baker *et al.*, 2006; Denman *et al.*, 2007). These tropical emissions were tightly negatively correlated with the interannual variation in tree growth rates in a Costa Rican forest during 1984–2000 (Clark *et al.*, 2003). These links suggest that a significant fraction of the anomalous tropical carbon emissions derives from shifts in tropical forest carbon balance in response to interyear variation in temperatures and/or rainfall.

In contrast, a directional increase in forest wood productivity due to 'CO$_2$ fertilization' (Körner, 2006; Huang *et al.*, 2007) has been hypothesized to underlie increases in aboveground biomass reported for a series of Amazonian forest plots over the same decades (Phillips *et al.*, 2008). A similar increase has been reported for African rainforests (Lewis *et al.*, 2009). However, other studies have found either no biomass change in recent decades (Laurance *et al.*, 2004; Chave *et al.*, 2008) or evidence suggesting that local biomass increases reflect recovery from past disturbances (Chave *et al.*, 2008; Fisher *et al.*, 2008).

Vegetation process models suggest future negative impacts on tropical forest net primary productivity (NPP) from drought and temperature, and strong positive effects from CO_2 fertilization (Cramer *et al.*, 2001; Cox *et al.*, 2004; Berthelot *et al.*, 2005; Denman *et al.*, 2007; Matthews *et al.*, 2007; Hickler *et al.*, 2008; Lloyd & Farquhar, 2008) and from periods of increasing insolation (Nemani *et al.* 2003).

The field data needed for evaluating these conflicting hypotheses and for refining the process models (Jones *et al.*, 2006; Matthews, 2007; Matthews *et al.*, 2007; Heimann & Reichstein, 2008) remain limited (see introductory quote). Because there are no reliable annual tree-ring chronologies for most of the moist/wet tropics, growth analyses must be based on direct measurements. Nearly all long-term records of tropical forest performance are based on fewer than six remeasurements at a site, usually separated by intervals of ≥ 5 years (reviewed in Clark, 2007; Rolim *et al.*, 2004 is a notable exception). The small number of measurement intervals and the multiyear period between remeasurements makes it difficult or impossible to identify the forests' responses to environmental drivers, particularly the effects of interannual climatic variation. One approach to this problem has been to unite data from many sites monitored for different periods and each with only a few remeasurements (cf. Phillips *et al.*, 1998; Baker *et al.*, 2004; Lewis *et al.*, 2009). Such meta-analyses do not resolve uncertainties regarding the magnitude of annual climatic impacts at each site, but could potentially reveal long-term trends if the data sets are internally consistent in methods, and if the plots are unbiased samples of the different forests (Clark, 2007; Fisher *et al.*, 2008).

Here we use a very different approach: a direct assessment of how interyear variation in temperatures, drought intensity, and atmospheric CO_2 levels have affected the performance of one old-growth tropical rain forest landscape over recent decades. We take two independent records of tree growth at this site, both based on annual remeasurements, and analyze their relation to annual climatic variation. After statistically accounting for the effects of local interannual climatic variation on tree growth, we then test for relations between tree growth and atmospheric [CO$_2$]. One data series is based on stand-level measurements (all species, all individuals) and the other on samples of canopy-sized individuals of six focal canopy tree species. The data sets span 10 and 24 years, respectively, and thus sample a broad range of annual climatic conditions. The 24-year record spans much of the same period covered by one of the composite (across-plot) studies that led to the CO$_2$ fertilization hypothesis (also 24 years, Baker *et al.*, 2004). These two decadal-scale series of annual measurements make possible the first

direct test of the CO_2 hypothesis for a tropical rain forest landscape.

Our analyses show that, for this old-growth forest in NE Costa Rica, the current levels of variation in seasonal rainfall and in temperatures have immediate and substantial impacts on forest wood production and on tree mortality. In contrast, after accounting for local rainfall and temperature, we found no detectable effect on tree growth from the increase in atmospheric $[CO_2]$ over the last 10–24 years. If these findings apply to forests across the biome, and if trees cannot acclimate to warmer and drier conditions, our results suggest that major changes in the structure and function of tropical wet forests are likely as global climate change progresses in the coming decades.

Materials and methods

Study site and meteorological data

The study site is an approximately 600 ha area of old-growth tropical wet forest at the La Selva Biological Station, Costa Rica. The 3×2 km study area is embedded within an area of ca. 100 000 ha of continuous forest made up of national parks, national forests and private reserves (La Selva GIS coverages). Annual rainfall over the study period (1983–2006) averaged 4142 mm, while mean annual temperature averaged 25.0 °C (1992–2006 automated temperature recorder half-hour means, Organization for Tropical Studies, unpublished results). There is a regular 'dry season' from approximately January–April, although long-term mean rainfall exceeds 160 mm for each of these months (supporting information Table S1). At this site there is no consistent relation between temperature, dry season rainfall, and ENSO status (Table S2).

Because solar radiation data did not cover the entire 24-year study period and also periodically involved serious quality-control issues, we estimated daily radiation for the entire period from measurements of daily maximum and minimum temperature and daily rainfall using a model derived from the first 60 days of readings for all newly installed pyranometers used at the site ($N = 7$, 1992–2006):

$$\begin{aligned}
&\text{Ln(total daily radiation, MJ day}^{-1}) \\
&= -0.482 + (0.157 \times \text{daily maximum temperature}) \\
&\quad - (0.084 \times \text{daily minimum temperature}) \\
&\quad - (0.002 \times \text{daily rainfall}), r^2 = 0.80, N = 337 \text{ days.}
\end{aligned}$$

For the 10-year period of stand-level tree diameter measurements in the forest plots (1997–2007), and for 15 years of the 24-year focal-species study, temperature data were available from an automated station at La Selva. Maximum and minimum temperatures from 1983 to 1992 were based on a regression of data from the La Selva automated station and a nearby manual station (MOLA 1, 10°35′N, 83°77′W, elevation 70 m, Pearson's $r^2 = 0.67$ and 0.72, respectively, $P < 0.001$, $N = 1701$, 1698). Daily climate data were summarized over the measurement years: 1 October, Year 1–30 September, Year 2 in the forest inventory analyses (October 1997–September 2007), and 1 April, Year 1–30 March, Year 2 in the focal species analyses (April 1983–March 2007).

For annual metrics of temperature we used each year's average of all days' minimum, maximum, and mean air temperatures. This allowed us to use comparable temperature metrics for the entire 24-year record, including the period not covered by the automated weather station. For simplicity we refer to the annual mean of daily minimum temperatures as 'night-time temperature'; annual means for daily minimum temperature are highly correlated with annual means for night-time (18:00-06:00 hours) temperatures ($r^2 = 0.99$, 1997–2007, OTS temperature data). Similarly, we refer to the annual means of daily maximum temperature, daily daytime (06:00–18:00 hours) temperature, and of 24 h average temperature as 'maximum temperature,' 'daytime temperature,' and 'mean temperature,' respectively.

Potential evapotranspiration was calculated as $\text{PET} = aR_a (\text{TD})^{1/2}(T_a + 17.8)$, where $a = 0.0023$ is a constant, R_a is the extraterrestrial radiation expressed in equivalent evaporation units, TD is the difference between maximum and minimum daily temperature, and T_a is mean air temperature (Xu & Singh, 2002). In the forest plots volumetric soil moisture in the top 30 cm of soil was measured biweekly with a Campbell Scientific CS615 probe (Frequency Domain Reflectometry sensor) permanently installed in the center of each plot.

Atmospheric CO_2 data

We averaged the monthly data from the Mauna Loa, Hawaii observatory (http://scrippsco2.ucsd.edu, μmol mol^{-1}, ppm) over each measurement year in the two studies. No closer CO_2 observatory covered our entire study interval (1983–2007). However, the strong correlation between the annual means from Mauna Loa and the much closer Key West NOAA data set ($r^2 = 0.998$, $N = 26$ years, 1977–2002) indicates that annual-scale Mauna Loa data are excellent proxies for local annual CO_2 levels.

Forest inventory plots

Our stand-level tree-growth data come from eighteen 0.5 ha plots that were sited in old-growth forest using a

stratified random design based on soil fertility and slope (Clark & Clark, 2000). Beginning in September 1997 and annually thereafter, all woody stems with diameter ≥ 10 cm ($\bar{x} = 4375$ trees, palms and lianas of > 200 species yr^{-1}) were mapped, identified, and measured with a fabric diameter tape for stem diameter at breast height or above basal irregularities such as buttresses. We annually assessed precision of diameter measurements by remeasuring ca. 80 stems after an interval of at least 1 day; 76.9% of remeasurements were identical, and 99.1% were within 1 mm ($N = 873$). Complete data on annual plot-level performance and weather variables are given in Table S3. Because diameter growth was the directly measured variable, we report mainly those analyses. However, the results for basal area increment and allometrically derived estimated aboveground biomass increment (using the tropical wet forest allometry of Brown, 1997) were virtually identical (examples shown in Table 1), so we use 'wood production' and 'mean annual diameter growth' synonymously.

Focal species measurements

Canopy-level individuals ($\geq$ 30 cm diameter, Clark & Clark, 1992) of six focal species (Table S2) were located using transects and extensive additional searches within an approximately 220 ha section of the study area (Clark *et al.*, 1998, Fig. 2). The diameter ($\pm$ 1 mm) of each tree was measured annually with a fabric diameter tape (Clark & Clark, 2006). Trees were measured in the same temporal sequence between January and June each year from 1983 to 2007. Because every year some trees died and new individuals recruited from lower size classes and/or were added to the sample, the individuals in each species' sample of measured trees varied considerably among years; overall, only 22% of the individuals in the final annual interval were also measured in the first. The size distribution of the first and last samples did not differ for any species (analyses not shown). Because the individuals in a species' sample changed each year with no temporal trend in diameter distributions, we did not detrend the increment data for ontogenetic changes in growth rate (in contrast to analyses in Clark *et al.*, 2003).

Median sample size per species per year was 43 trees, and median total sample size per year was 354 trees. Because the species' mean diameter increments differed by a factor of 5, we calculated the normal deviate for each species' yearly growth to put the species' diameter growths on the same absolute scale; we then averaged these normal deviates for all six species each year to get annual mean normalized diameter growth. Detailed methods descriptions, complete field data, and full

documentation for years 1–18 are published on-line (Clark & Clark, 2006). Species-level increment data, sample sizes, and annual climate data are given in Table S2.

This approach differs substantially in data and methods from a previous study on temperature–growth relations (Clark *et al.*, 2003). That analysis was based on following the same individuals (species-level cohorts) through time (164 individuals remeasured 2624 times over 16 years), with trees' increment-series detrended for species-level changes of growth with size. Here we report analyses based on all individuals alive each year in the size class analyzed (7755 remeasurements on 487 individuals taken over 24 years).

Monthly tree growth

From February 2006 to December 2008 we measured monthly stem growth in a 20×40 m plot in old growth on upland oxisols for all stems > 10 cm diameter using stainless steel dendrometer bands with etched vernier scales (Felkera & Diaz-de Leon, 2005). We allowed a 3-month period for the bands to stabilize, and here report the average monthly diameter increment read to the nearest 0.25 mm for the 28 individual dicot trees for which there were complete records from May 2006 to December 2008.

Results

Climatic effects on stand-level growth (wood production)

Over the 10-year period, annual stand-level tree growth (all stems ≥ 10 cm diameter, all species) was strongly positively related to dry season rainfall (Fig. 1, $r^2 = 0.85$). The 1998 dry season had only half the rainfall as the next-driest dry season. While this is not an unusual event on the decadal scale (Table S1), we analyzed the effect of not including this year or of considering only certain sequences of years to determine if the strong association between annual wood production and dry season rainfall was related to observing a particular sequence of years. The rainfall–productivity relation was consistent throughout the decade and did not depend on observing any 1 year. All 15 possible sequences of 6 years or more showed a significant positive correlation ($P_{\text{two-tail}} < 0.05$) between total dry season rainfall and annual wood production. Furthermore the 10 sequences of 6–9 years omitting the driest year, in addition to being significant with $r^2 \geq 0.77$, had 798–1431 mm of dry season rainfall. The decade of this study was also not unusual in rainfall compared with recent decades, because 88% of the dry season rainfall totals in the 40

Table 1 Correlations of tree growth and climatic factors

	Factor 1	Factor 2	r	$P_{(1,2)}$	df	Variable controlled
Forest plots						
All stems	Growth	Dry rain	**0.92**	**0.0002**$_{(2)}$	8	–
	Basal area increment	Dry rain	**0.90**	**0.0002**$_{(2)}$	8	–
	Biomass increment	Dry rain	**0.89**	**0.0001**$_{(2)}$	8	–
	Growth	MinT	**−0.65**	**0.022**$_{(1)}$	8	–
	Basal area increment	MinT	**−0.68**	**0.016**$_{(1)}$	8	–
	Biomass increment	MinT	**−0.68**	**0.016**$_{(1)}$	8	–
	Growth	MaxT	−0.41	ns$_{(1)}$	8	–
	Growth	MeanT	**−0.62**	**0.027**$_{(1)}$	8	–
	Growth	Annual rain	0.43	ns$_{(2)}$	8	–
	Growth	Light	−0.29	ns$_{(2)}$	8	–
	Growth	CO_2	0.23	ns$_{(1)}$	8	–
	Growth	MinT	**−0.62**	**<0.05**$_{(1)}$	7	Dry rain
	Growth	Dry rain	**0.92**	**<0.001**$_{(2)}$	7	MinT
	Growth	Year	0.22	ns$_{(2)}$	8	–
	Growth	Dry soil	**0.74**	**<0.05**$_{(2)}$	8	–
	Mortality	MinT	**0.56**	**0.045**$_{(1)}$	8	–
	Mortality	Dry rain	−0.32	ns$_{(2)}$	8	–
	Mortality	Year	−0.60	ns$_{(2)}$	7	MinT
Sub-canopy	Growth	MinT	**−0.66**	**0.018**$_{(1)}$	8	–
	Growth	Dry rain	**0.94**	**0.0001**$_{(2)}$	8	–
Canopy	Growth	MinT	**−0.65**	**0.022**$_{(1)}$	8	–
	Growth	Dry rain	**0.84**	**0.002**$_{(2)}$	8	–
Focal species	Growth	MinT	**−0.55**	**0.003**$_{(1)}$	22	–
	Growth	MaxT	−0.23	ns$_{(1)}$	22	–
	Growth	MeanT	−0.28	ns$_{(1)}$	13	–
	Growth	Light	0.02	ns$_{(2)}$	22	–
	Growth	Annual rain	−0.31	ns$_{(2)}$	22	
	Growth	CO_2	−0.36	ns$_{(1)}$	22	
	Growth	CO_2	0.03	ns$_{(1)}$	21	MinT
	Growth	Year	**−0.37**	**0.04**$_{(1)}$	22	
	Growth	Year	0.02	ns$_{(1)}$	21	MinT
	Growth	MinT	**−0.45**	**0.025**$_{(1)}$	21	CO_2
	Growth	MinT	**−0.44**	**0.025**$_{(1)}$	21	Year

Pearson's correlation (r) between climatic factors or year, and annual mean diameter increment (growth) and annual exponential mortality rate (mortality, Sheil *et al.*, 1995). Forest plot data are for all stems ≥10 cm diameter in eighteen 0.5 ha forest inventory plots (10 years). Basal area increment and biomass increment are the summed annual increases in basal area and estimated aboveground biomass of all surviving trees. For the six focal species, growth is the mean normalized deviate of diameter increment for all live canopy-level (≥30 cm diameter) trees of all species (24 years). Climate variables are annual means of daily minimum, mean, and maximum air temperatures [MinT (night-time), MeanT, MaxT (daytime)]; annual means of estimated daily radiation (light, see ''Materials and methods''); annual rainfall (annual rain), annual atmospheric CO_2 (CO_2), dry season rainfall (Dry rain), and mean monthly dry season volumetric soil moistures (Dry soil). Subcanopy: all trees 10– ≤30 cm diameter; canopy: all trees >30 cm diameter. Subscripts on probabilities indicate if the test was *a priori* one- or two-tailed, bolded values are significant. 'Variable controlled' is the third variable accounted for in partial correlations.

years before this study fall in the range observed during study period (Table S1).

These analyses demonstrate a constraint on wood production by dry season total rainfall at rainfall levels well above any previously known to be limiting for tropical rain forest productivity. To examine temporal periods over which the effects of precipitation on diameter growth operate, we calculated the correlation between recent rainfall (total rainfall over 15, 30, 45, 60, 75, 90, and 115 days before measurement) and tree growth using monthly band dendrometer data. We analyzed this correlation for the dry season months (Fig. 2) separately as well as the entire 32-month data set. The correlation peaked with rainfall totals in the 60 days before diameter measurement ($r^2 = 0.82$, $N = 8$ dry season months), and averaged twice as high at the

different lags for the dry season months compared with the entire data set (mean r^2 0.56 and 0.28, respectively). The effects of 60-day periods with ca. 110 mm rainfall on stem growth were particularly notable (Fig. 2).

Annual stand-level tree growth was negatively related to night-time temperature ($r = -.65$, $P_{one-tail} = 0.02$), even
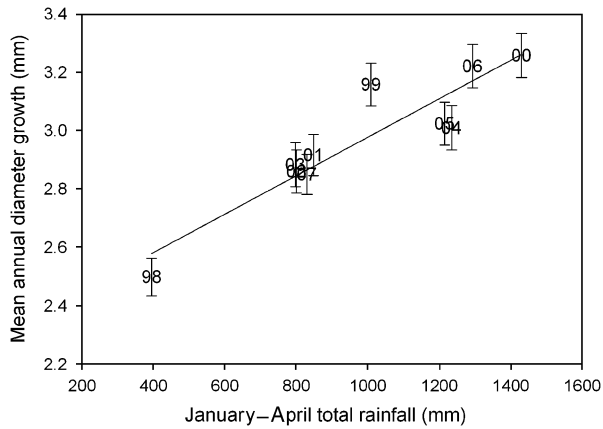

Fig. 1 Whole-forest (stand-level) wood production in eighteen 0.5 ha forest inventory plots decreased in years of drier dry seasons ($r^2 = 0.85$, $P_{two-tail} = 0.0002$, $N = 10$ years). Note that even in the 'driest' dry season, mean monthly rainfall was ≥ 100 mm. Data points are all-stem means of annual diameter increment, error bars are ± 1 SEM; labels indicate Year 2 of each measurement year (1 October–30 September).

though this temperature metric varied $<1\,°C$ over the 10 years (Fig. 3). Annual diameter growth also declined with higher mean temperature, but was not significantly correlated with annual means of atmospheric $[CO_2]$, maximum temperature, estimated annual irradiance or total rainfall (Table 1). Stand-level tree mortality increased significantly with higher night-time temperatures (Table 1).

The correlations between annual climatic factors and tree growth were very similar for sub-canopy and canopy-level trees (Table 1). For the forest plots, the climate–growth correlations were strongest with climate of the current year, and there were no significant relations between wood production and any aspect of climate lagged 1 year. Mortality, however, was correlated with prior-year dry season intensity (mortality × prior dry season rainfall, $r = -0.69$, $P_{one-tail} < 0.025$).

These data show a tight linkage of annual wood production at La Selva to current ranges of dry season intensity and annual temperature. We used multiple-regression models to examine the combined effects of dry season rainfall, night-time temperature, mean dry season soil moisture, annual radiation and $[CO_2]$ on annual stand-level diameter increment. The best single-factor model incorporated dry season rainfall ($r^2 = 0.85$, Table 1). The best two-factor model ($r^2 = 0.91$) incorporated dry season rainfall and night-time temperature (temperature effect $P_{one-tail} < 0.04$). We found no

Fig. 2 Drier bimonthly periods are associated with reduced tree diameter growth in a tropical wet forest. Black circles and left axis: mean monthly diameter increment (+ 1 SEM) for 28 dicot trees in a 20 × 40 m plot on upland oxisols at La Selva. Bars and right axis: total rainfall in the 60 days preceding measurement, white bars corresponding to the dry season months (January–April, cf. Fig. 1).
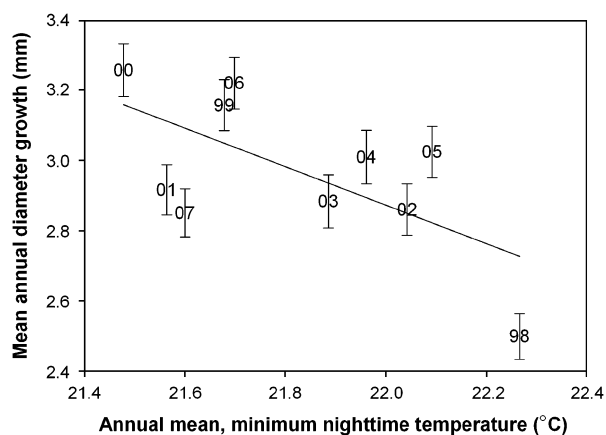
Fig. 3 Annual tree diameter growth decreased in hotter years. Over a 10-year period, annual diameter measurements of all live woody stems (trees, palms, lianas) $\geq 10\,cm$ diameter in eighteen 0.5 ha old-growth forest inventory plots ($\bar{x} = 4375$ individuals yr^{-1}) showed reduced aboveground wood production (= stand-level mean diameter increments) with higher night-time temperature (annual means of daily minimum temperature; $r^2 = 0.42$, $P_{\text{one-tail}} = 0.022$, $N = 10$ years). Labels indicate Year 2 of each measurement year (1 October–30 September), error bars are $\pm 1\,\text{SEM}$.

three-factor model where all factors were significant. The effects of night-time temperature and dry season intensity on annual stand-level wood production were statistically independent (Table 1, partial correlations).

The small range of diameter growth values in Figs 1 and 3 in fact corresponds to substantial variation in annual wood production. Estimated aboveground biomass increment varied $0.7\,\text{Mg}\,\text{C}\,\text{ha}^{-1}\,\text{yr}^{-1}$ between the most favorable years for growth (2006, wet dry season, cool nights) and the worst (1998, dry dry season, warm nights) (Table S3). This represents a variation of 33% relative to the decadal mean of $2.2\,\text{Mg}\,\text{C}\,\text{ha}^{-1}\,\text{yr}^{-1}$ (Table S3) under current climate conditions. The corresponding variation in basal area addition was virtually identical (31% of decadal means, data in Table S3).

Climatic effects on species-level tree growth

We also assessed the relation between night-time temperatures and annual tree-growth in the much longer study (1983–2007) of canopy-level individuals of six focal tree species (Table S2). During this 24-year period, night-time temperature increased significantly (temperature x year $r = 0.70$, $P_{\text{one-tail}} < 0.001$). The focal species' mean annual growth was negatively correlated with night-time temperature (Fig. 4a, Table 1), even though the total interannual range of this temperature metric was $<2\,°C$. Maximum growth occurred in the coolest years (the early 1980s), and the lowest growth

occurred in the hottest year (the negative relation was still highly significant omitting the hottest year, $r = -0.48$, $P_{\text{one-tail}} = 0.01$). There was a marginally significant correlation between annual diameter growth and night-time temperatures 2 years prior, but the correlation was considerably weaker than with current year night-time temperatures ($r = -0.34$ vs. -0.55). Mean annual diameter increments were not significantly related to annual maximum or mean temperature, or to total annual rainfall or estimated annual radiation (Table 1).

Contrary to the CO_2 fertilization hypothesis, tree growth decreased with increasing atmospheric $[CO_2]$. The effect however was entirely attributable to night-time temperatures; once night-time temperature was accounted for, there was no significant correlation between atmospheric $[CO_2]$ and growth (Table 1). There was also no indication of any temporal pattern in the relation of the residuals from the tree growth $\times$ night-time temperature regression to $[CO_2]$ over the 24-year period (Fig. 4b).

Although tree growth declined over time, the relation was not significant when night-time temperature was accounted for (Table 1). Similarly, the interyear growth variation was not attributable to size effects within the species' samples, because tree-size distributions of the samples did not change over time in spite of considerable within-species death and recruitment (see 'Materials and methods'). Because individuals in the focal-species study were censused throughout the annual dry season, dry season effects could not be tested.

Discussion

Dry season and temperature effects on wood production and tree mortality

The strong relation between dry season rainfall and annual stand-level wood production was unanticipated for this evergreen forest. Although drought stress effects on growth are well known for tropical forests with substantially lower annual rainfall and marked dry seasons, dry season intensity has not previously been known to affect productivity even in considerably drier tropical forests (cf. Hutyra *et al.*, 2007, 1920 mm annually). In this tropical wet forest annual rainfall averages 4.3 m (49 year record), and mean monthly rainfall in each of the four dry season months (January–April) exceeds 100 mm (Table S1), the commonly assumed threshold for drought stress in tropical forests. For the 10 dry seasons of the stand-level study analyzed here, seasonal water balance (total precipitation minus Potential EvapoTranspiration) was $\geq 250\,mm$ in all years but 1998, when it was $-140\,mm$. During the driest
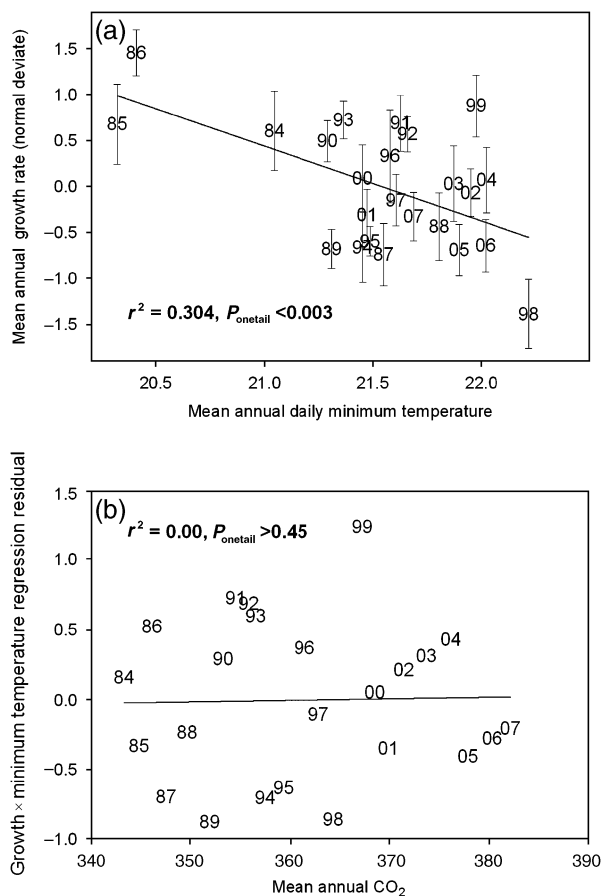
Fig. 4 (a) Focal species diameter growth decreased with higher night-time temperatures (annual means of daily minimum temperature). For six focal tree species at the study site, long-term annual measurements of canopy-level individuals ($>30\,cm$ diameter; median = 318 trees yr^{-1}) demonstrate a negative relation between annual diameter increments and night-time temperatures over the last 24 years ($r^2 = 0.30$, $P_{one-tail} = 0.003$). Growth data are the annual means of the normal deviates of the six species' diameter growth rates. Labels indicate Year 2 of each measurement year (1 April–31 March), bars are $\pm 1\,SEM$. (b) After accounting for night-time temperature, increasing $[CO_2]$ had no effect on tree growth. There is no temporal pattern in the residuals from the night-time temperature × tree growth regression and $[CO_2]$. Labels indicate Year 2 of each measurement year (1 April–31 March).

dry season of the 10-year record (1998, Fig. 1), in only one of the 4 months rainfall was below 100 mm. In addition a similarly dry dry season month occurred in 3 of the other 9 years, including that of greatest wood production (2000; Fig. 1).

The band dendrometer data show that the common assumption of a water limitation boundary at around 100 mm per month is probably incomplete. Both Fig. 2 and the significant correlations of monthly stem growth with total rainfall over a much broader range of rainfall conditions suggest that water limitations on wood production occur at considerably higher monthly rainfall levels. In this study the strongest relation between monthly diameter growth was with the two prior months of rainfall. Two-month periods similar to the two driest 60-day periods shown on Fig. 2 ($<200\,mm$) are regular occurrences in this forest's current climate; over the last 45 years there have been 13 such periods in nine different years. This means that a canopy tree will undergo drought stress sufficient to severely decrease diameter growth at least several dozen times in its lifetime. Overall these results indicate that relatively short periods of low rainfall are sufficient to reduce stand wood production, even in very wet tropical forests. These reductions are substantial; $>20\%$ less wood is produced in years with dry dry seasons compared with wetter years (Figs 1 and 2). More attention should be given to the effects of such periods, which could increase significantly even with little change in annual total precipitation (Jentsch *et al.*, 2007).

The physiological mechanisms underlying the negative relation between annual wood production and dry season intensity are as yet undetermined. It is likely that the strong stand-level response reflects links between dry season rainfall and several intercorrelated factors known to directly affect plant carbon balance. Over the study period, the dry season rainfall totals were significantly related to dry season means for volumetric soil moisture (+), incoming radiation (−), and daytime and night-time temperatures (−) (analyses not shown). There was no evidence of dry season light limitation of annual wood production; dry season radiation decreased with increasing dry season rainfall (analyses not shown). We assessed many single- and multiple-factor models relating tree growth to climate factors, but found no combination of factors excluding dry season rainfall that explained as high a percentage of the variance as dry season rainfall by itself.

It is also possible that the very strong relation of woody productivity to dry season rainfall is related to some unmeasured factor(s) that is itself related to rainfall, for example atmospheric conditions like the relation of diffuse to total radiation, or to changed allocation patterns. One factor could be a significant dry season decrease in leaf area index (LAI) of canopy trees (cf. Nepstad *et al.*, 2002) perhaps preceding new leaf production. However, the canopy at La Selva is largely evergreen (Hartshorn & Hammel, 1994), with only a few emergent species that are seasonally deciduous. The only quantitative data comparing directly measured LAI during dry and wet seasons found no interseasonal differences (Clark *et al.*, 2008), but these data were not sufficient to rule out potentially

significant seasonal variation in the highest and most productive layers of LAI (Doughty & Goulden, 2008).

Our current working hypothesis is that several factors, each related to dry season rainfall, interact to drive wood production. Our results show that annual wood production closely tracks both annual and seasonal climatic patterns. These annual landscape-scale responses can be interpreted as emergent phenomena based on physiological processes at much shorter time scales. Determining what these physiological mechanisms are, and the temporal scale over which they operate, will require process-level studies at subannual time scales (e.g., eddy covariance, sap-flow, fine-root production and respiration, quantitative stand-level phenology). These much shorter-term studies will help quantify relations between different eco-physiological process, climatic variation and wood production, and will hopefully serve as the basis for improved models of tropical forest performance. An indication of the need for this improved mechanistic understanding is that no model of tropical rain forest woody productivity that we are aware of predicts the strong and generalized relation of woody production to the range of dry season conditions observed in this decadal study. Long-term, well-replicated field data series such as those analyzed here provide the key results necessary to assess the realism and accuracy of these new models.

Both data series suggest that today's higher temperatures are already having a negative impact on the annual balance between gross primary productivity (photosynthesis) and forest-level plant respiration in this tropical rain forest. The physiological mechanisms for the highly significant reductions in both forest-level and species-level wood production with increasing night-time temperatures have not yet been identified. However, the fact that the 10- and 24-year growth series are more strongly correlated with night-time temperatures than with maximum temperatures is consistent with negative impacts of enhanced night-time respiration on tree growth. Respiration Q_{10} values for foliage and wood (stems/branches) at this site are ≥ 2 (Ryan *et al.*, 1994; Cavaleri *et al.*, 2008).

Although we did not detect significant negative effects of maximum temperatures on annual growth, they may soon contribute to NPP reductions in this forest. With hotter daytime temperatures in the coming years, canopy leaves will experience an increasing percentage of daytime leaf temperatures above their photosynthetic optima (26–34 °C; Clark, 2004; Tribuzy, 2005; Doughty & Goulden, 2008). Eddy covariance studies at this site (Loescher *et al.*, 2003) have already shown reductions in net forest carbon uptake at the high end of the current range of daytime air temperatures (>25 °C). Negative effects of temperature on photosynthesis are likely to be most intense for the topmost and most productive layer of canopy leaves (Doughty & Goulden, 2008).

Across the tropical rain forest biome, mean annual temperatures have risen 0.26 °C per decade over the last 30 years, and rainfall patterns have changed in some parts of the tropics (Malhi & Wright, 2005). The findings presented here indicate that trees in this Costa Rican lowland rain forest respond quickly (≤ 2 years, Table 1) to current levels of interannual variation in dry season intensity and temperature, with substantial impacts on forest performance. If these responses continue under future climates, these data suggest that there will be major changes in the structure and functioning of this forest with even moderate additional drying and/or warming.

We projected future forest performance at our site based on the regressions of growth and mortality on night-time temperature from the 10-year stand-level record (Table S3), and incorporating a 3 °C temperature increase as predicted by the IPCC A1B scenario (Alley *et al.*, 2007). If the same relations between night-time temperature, tree growth, and mortality hold with a 3 °C increase, annual tree mortality in the La Selva forest would increase from 2.6% to 6.9%, while annual wood production would decrease 56%. These changes would obviously have very large impacts on the current biological and physical structure of this forest as well as on virtually all aspects of forest function. Given the demographic, physiological, and morphological diversity of trees, palms, and lianas in tropical forests, inevitably some species will respond better than others to increased temperatures. A period of decline for temperature-sensitive species and of increase for more heat-tolerant species appears highly likely (Matthews *et al.*, 2007; Colwell *et al.*, 2008). The strong sensitivity of wood production to dry season intensity shown here further suggests that any decreases in dry season rainfall could compound the independent effects of higher temperatures.

The CO_2 fertilization hypothesis: not supported

The on-going increase in atmospheric [CO_2] has been hypothesized to have increased tropical forest above-ground biomass by enhancing primary production in tropical forests over recent decades (Lloyd & Farquhar, 2008; Phillips *et al.*, 2008; Lewis *et al.*, 2009). Contrary to this hypothesis, neither long-term record of annual wood production at La Selva was related to the annual atmospheric CO_2 concentrations over the multidecadal study period (Table 1), and there was no suggestion of the emergence of any temporal trend (Fig. 4b). Perhaps this should not be surprising, because the Mauna Loa record (P. Tans, NOAA/ESRL; www.esrl.noaa.gov/gmd/ccgg/trends/) indicates an increase of only 12% in atmospheric

[CO_2] ($x = 342.8$–383.6 ppm) over the 1983–2007 interval of the focal-species study. However, this 24-year period in fact corresponds very closely in duration and in calendar years to the interval over which increased tropical rain forest biomass has been reported (Phillips *et al.*, 2008).

Because our analyses are based on good spatial and temporal replication (an annual average of 323 individuals distributed over a 220 ha landscape, 24 remeasurements), they provide the most powerful test to date of the CO_2 fertilization hypothesis for a single tropical rain forest site. The results show no sign of a CO_2 fertilization effect. Failure to accept the fertilization hypothesis at any given site does not by itself mean that the hypothesis will fail at other tropical forest sites, or that such fertilization will not be revealed with additional remeasurements at our study site. However, if CO_2 enhancement of tropical forest woody productivity has been affecting the tropical forest biome in the last decades, then it should ultimately be detectable in single-site studies such as this one. Definitive acceptance or rejection of this global hypothesis will require single-site time series from additional tropical forests. These studies should have enough remeasurements to statistically isolate the effects of interannual climate effects; unfortunately, the norm for long-term studies of tropical forest growth has been multiyear census intervals, with data series from each forest site so far spanning only a handful of remeasurements (mean number of remeasurements to 2007 for published plot studies = 2.6; Clark, 2007). Alternatively, growth enhancement may be detectable if a time series is long enough so that interannual variation is less than the directional change attributable to increasing atmospheric [CO_2]. Our results show, however, that there is substantial interannual variance in growth rate, so that it may take a number of remeasurements at super-annual intervals to submerge this interannual variance (compare in Fig. 1 the 1998–2002 interval, for example with 1999–2003). At our study site, even with the 24-year annual measurement series and highly quality-controlled methods, there is no suggestion of CO_2 fertilization to date.

Our data also do not support two other current hypotheses about environmental drivers of tropical forest productivity. Increased insolation has been proposed to increase primary production in this biome (Nemani *et al.*, 2003; Wright, 2005), while elevated levels of annual rainfall have been hypothesized to decrease it (Schuur, 2003). In this study neither annual insolation nor annual rainfall was significantly correlated with annual stand-level wood production (Table 1).

Rescue by acclimation?

The findings from this study, together with accumulating lines of evidence from other tropical forest sites,

suggest that drier and warmer climates will decrease wood production and increase tree mortality rates in many tropical rain forests. However, current forest sensitivities to drought and temperature could conceivably be reduced or eliminated in future climates through physiological acclimation. It has been suggested that '. . . there is no reason to believe that tropical trees should not be able to acclimate their respiration to increasing temperatures,' or if not, then respiratory losses could be '..more than offset' by the positive effects of increased [CO_2] (Lloyd & Farquhar, 2008).

The contrast between the predictions based on the sensitivity of tree growth to temperature seen in our results (Figs 3 and 4) and a 'rescue by acclimation' scenario is illustrated in Fig. 5. If the current relation between night-time temperature and tree growth is maintained in future climates, future measurements of wood production will fall along the extension of the current regression line into the yet-unexperienced range of hotter environments (represented by the dotted line in Fig. 5). If, however, substantial temperature acclimation occurs, future data points will fall above the current empirical regression line, or in other words, equal levels of tree growth will occur at higher temperatures than they do today (represented by the arrows in Fig. 5).

Fortunately it could be 'relatively' straightforward to distinguish between these two possibilities. Based on the current 10-interval stand-level record from La Selva
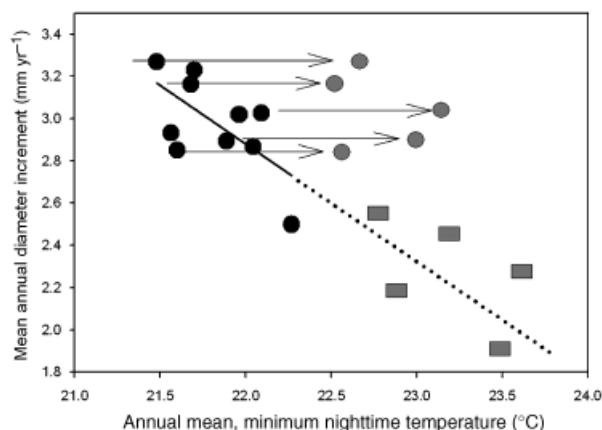

Fig. 5 Diagrammatic representation of two possible responses of tropical tree growth to rising temperature. The black circles and solid regression line represent the observed response of stand-level tree growth in the forest inventory plots to night-time temperature from 1997 to 2007 (Fig. 2 replotted). The gray circles represent 100% acclimation of growth to increased temperature, i.e., the same diameter growth as current observations but at higher temperatures. The gray rectangles represent the case where tree growth at higher temperatures follows the relation predicted by the current regression (dotted line): lower growth with increasing night-time temperature.

(df = 8), the negative correlation between stand-level wood production and yearly night-time temperatures is significant at $P_{\text{one-tail}} < 0.025$. If the current degree of association between these variables ($r = -0.65$) continues through the next 5 years (Fig. 5, gray boxes), the P value would decrease to < 0.005 ($N = 15$ years, df = 13). Alternatively, with temperature acclimation the current relation could degrade relatively quickly with additional data (Fig. 5, gray circles). The same basic argument applies to the other current hypotheses concerning climatic/atmospheric drivers of tropical forest structure and function. Extending any tropical data series of these lengths with 5–10 additional remeasurements will provide a substantial increase in statistical power.

Globally, tropical forests will continue to warm substantially (Denman *et al.*, 2007) and mean temperatures by the end of the century will likely exceed the most extreme seasonal temperatures of the 20th century (Battisti & Naylor, 2009). Many models also predict substantial drying for much of the tropics (Alley *et al.*, 2007; Malhi *et al.*, 2009). Our long-term observations from one Costa Rican rain forest, combined with multiple lines of evidence from other tropical forest regions, suggest that even modest levels of warming and drying would both have significant negative impacts on wood productivity in wet forests of this biome. Unless rapid acclimation occurs, lower growth rates, higher death rates, species substitutions, and even biome shifts all appear likely (Colwell *et al.*, 2008). If similar effects of both higher temperatures and increased dry season intensity are confirmed in other sites, current models of the global carbon cycle will need to be modified to better represent these potentially strong positive feedbacks from tropical forests to the rate of global warming.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Rainfall and temperature data at the study site, 1958–2007.
Table S2. Growth data and climate data for focal species.
Table S3. Growth and climate data for the forest inventory plots.

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