Tropical rain forest tree growth and atmospheric carbon dynamics linked to interannual temperature variation during 1984–2000

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During 1984–2000, canopy tree growth in old-growth tropical rain forest at La Selva, Costa Rica, varied >2-fold among years. The trees' annual diameter increments in this 16-yr period were negatively correlated with annual means of daily minimum temperatures. The tree growth variations also negatively covaried with the net carbon exchange of the terrestrial tropics as a whole, as inferred from nearly pole-to-pole measurements of atmospheric carbon dioxide (CO_2) interpreted by an inverse tracer–transport model. Strong reductions in tree growth and large inferred tropical releases of CO_2 to the atmosphere occurred during the record-hot 1997–1998 El Niño. These and other recent findings are consistent with decreased net primary production in tropical forests in the warmer years of the last two decades. As has been projected by recent process model studies, such a sensitivity of tropical forest productivity to on-going climate change would accelerate the rate of atmospheric CO_2 accumulation.

Although human activities are rapidly increasing atmospheric levels of the greenhouse gas CO_2 (1), understanding of the global carbon budget and how it is affected by climatic change remains approximate and evolving (2). Current knowledge of plant function, however, raises the likelihood that continued warming will alter the net carbon balance of global vegetation (3, 4). Plant respiration increases exponentially with increasing temperature, whereas photosynthetic rates increase to a temperature optimum and then decline (5). At the ecosystem level, the balance between these two processes determines net primary production (NPP). Decreasing terrestrial NPP with rising temperatures would constitute a biotic positive feedback to the increase in atmospheric CO_2 (3, 4).

Tropical rain forests, among the warmest terrestrial ecosystems, might be expected to be among the first to show negative temperature responses (6). Because these forests account for a third of global terrestrial NPP (7), any such responses could strongly affect atmospheric CO_2 levels. Studies at the leaf (8, 9) and stand level (10, 11) in this biome already suggest reduced carbon uptake with even small temperature increases. Measured respiration rates of tree boles in one tropical rain forest show an 8% increase with a 1°C temperature rise (12); compared with that of boles, the respiration of other plant parts tends to be even more sensitive to temperature changes (13). In addition, carbon losses by tropical trees in the form of volatile organic compounds increase exponentially over current temperature ranges (8, 9). Quantifying responses of these processes at the ecosystem level, however, remains elusive because of limitations of both data and methods (14, 15). Estimating forest carbon exchange with eddy covariance techniques has been found to be problematic for tropical forests, because of the prevalent still-air conditions at night (>80% of nights; ref. 11). In addition, short-term data may be poor indicators of longer-term trends, given the possibilities of critical thresholds, acclimation, and substrate limitation (6, 16).

One line of evidence for projecting the future performance of tropical rain forests is how they have responded to the substantial interannual climatic variation in recent decades. We demonstrate a correspondence between two such long-term data sets, measurements of annual tree growth in an old-growth tropical rain forest and the net CO_2 exchange between the terrestrial tropics and the atmosphere, as inferred from atmospheric data. We then show that both records indicate a strong negative relationship between annual temperatures and tropical forest productivity.

Methods

Tree Growth. To determine tree growth patterns in old-growth rain forest at the La Selva Biological Station, Costa Rica (10°26′N, 84°00′W, elevation 37–150 m, 4 m rainfall yr^{-1}; ref. 17), the bole diameter of adult trees of six canopy species (Table 1) was measured every year since 1984 as part of a comparative study of tree life histories (18). The study samples of the six species consisted of all individuals found in searches of 216 hectares (ha) of upland forest. Trees were measured in the same sequence each year, January–June; measurement years were thus defined as April 1 (Yr 1) to March 31 (Yr 2). Bole measurements were strongly quality-controlled (19). The 16-yr records of annual diameter increments (Tables 4 and 5, which are published as supporting information on the PNAS web site, www.pnas.org) were detrended for trees that grew through a diameter range for which our larger data set (ref. 18; D.B.C. and D.A.C., unpublished data) showed a significant relationship between diameter and annual increment (17–42% of the trees, depending on species).

To our knowledge, this is the only long-term record of annual tree growth that has been documented for tropical rain forest. The published long-term studies of tropical rain forest tree growth (cited in ref. 19) are based on remeasuring the bole at multiyear rather than yearly intervals; in one 10-yr study involving annual measurements, the data were aggregated over multiple years because of data quality problems at the annual scale (20).

Local Climatic Data. On-site meteorological data (see Tables 4 and 5) include daily rainfall through the study period, daily irradiance (pyranometer) for 1992–2000, and automated daily maximum and minimum temperatures for 1992–2000. The temperature record was extended back to 1984 by regressing the automated La Selva data against those of a nearby surface station (MOLA 1, 10°35′N, 83°77′W, elevation 70 m; 21) for maximum and minimum temperature (Pearson's *r*: 0.82 and 0.85, respectively; $P < 0.001$, both cases).

Global and Tropical Net CO_2 Fluxes. The global net CO_2 exchange flux between the atmosphere and the earth's surface was first estimated (22) by a deconvolution procedure that takes account of observations of the concentration and $^{13}C/^{12}C$ isotopic ratio

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Table 1. Interannual variation in diameter increments of adults (≥30 cm diameter, thus canopy level) of six canopy tree species in lowland rain forest at La Selva, Costa Rica, 1984–2000

Species [family]	N	16-yr range of annual means, mm/yr	P*
Minquartia guianensis Aubl. [Olacaceae]	37	0.9–3.4	<0.0001
Lecythis ampla Miers [Lecythidaceae]	22	2.1–7.0	<0.0001
Dipteryx panamensis (Pittier) Record & Mell [Papilionaceae]	41	4.1–6.6	<0.0001
Hyeronima alchorneoides Allemão [Euphorbiaceae]	12	4.7–8.7	0.06
Balizia elegans Ducke [Mimosaceae]	46	4.6–9.3	<0.0001
Hymenolobium mesoamericanum Lima [Papilionaceae]	6	6.2–14.1	0.003

*Probability is from a Friedman two-way analysis of a species' diameter increments among years, controlling for individuals within a species.

of CO_2 at nine stations from the Arctic to the South Pole. In this procedure, terrestrial and oceanic exchange fluxes were distinguished by their differing effects on the isotopic ratio of atmospheric CO_2. An industrial flux, owing mainly to combustion of fossil fuels, was calculated directly from international statistical data. The resulting global terrestrial flux, although mainly reflecting changes in NPP and heterotrophic respiration, also includes net fluxes from rivers (23) and the effects of land-use changes (agriculture, deforestation, burning, regrowth).

Secondly, the net CO_2 flux from the terrestrial tropics was distinguished from the global mean biospheric flux by an inverse procedure (24) involving a three-dimensional atmospheric tracer transport model. This model, TM2 (25), with 1986 observed winds, was used to predict atmospheric CO_2 concentration responses at the nine stations from simulated zonal CO_2 sources.

Corresponding $^{13}C/^{12}C$ responses were also predicted, taking account of carbon isotopic fractionation (26), assumed to be time-invariant. The responses, weighted by the variances of the observations and linearly combined, were constrained to sum to the global flux estimates and also to give an optimal least-squares fit to annual averages of atmospheric CO_2 and $^{13}C/^{12}C$ at the nine stations.

The inverse model specified four biospheric and three oceanic regional sources corresponding to tropical, temperate and boreal zones (24). The inverse calculation was sensitive to atmospheric data from three tropical stations (Cape Kumukahi, Hawaii: 19.5°N,154.8°W; Christmas Island: 2.0°N, 157.3°W; Samoa: 14.2°S,170.6°W) and two stations bracketing the tropics: La Jolla, California (32.9°N, 117.3°W) and Raoul Island (29.2°S, 177.9°W). The standard error in the tropical terrestrial flux, attributed to random error in the observations, was 0.64 petagrams (1 Pg = 10^{15} g) carbon (C)·yr^{-1}. Potential sources of systematic error were investigated by sensitivity tests for atmospheric transport, specification of isotopic processes, method of inverse calculation, and configurations of the source components and the observational network (27). The timing of peaks and troughs of the inferred tropical terrestrial CO_2 flux changed very little in all tests. The range of the interannual variation also changed little, with the following exceptions. The range was ≈20% larger when the TM3 transport model and 1998 winds were used in place of the TM2 model with 1986 winds, ≈15% larger when the inverse calculation was made time-dependent to account for the distribution of an annual CO_2 pulse over 4 yr, instead of 1 yr, and reduced by 10–30% if the low discrimination of C_4 plants relative to that of C_3 plants was ignored. Also, the large increase in flux from 1991–1998 was reduced by ≈35% when $^{13}C/^{12}C$ data were ignored and ocean fluxes held nearly invariant.

Results

Tree Growth Variation. Tree bole growth in the La Selva forest varied strongly over the 16 yr (Fig. 1). For the six study species, mean diameter increment in the year of greatest growth was 61%
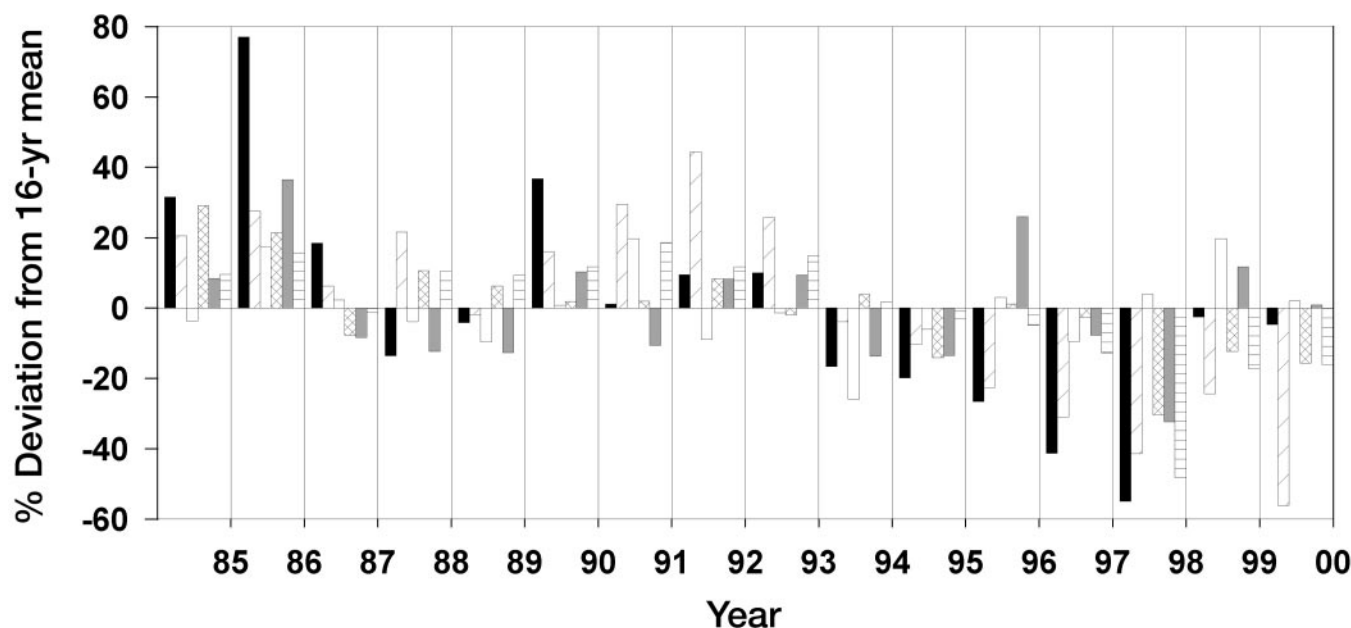
Fig. 1. Interannual variation in tree growth in old-growth lowland rain forest at La Selva, Costa Rica. Bars show the annual mean growth deviations of adult trees of six canopy species (left to right in each year: Mg, La, Dp, Ha, Be, and Hm; see Table 1 for species names and sample sizes); growth deviations are calculated as the percent departure of the species' mean annual diameter increment, from that species' 16-yr mean annual increment. *x* axis: yr 2 of measurement years.

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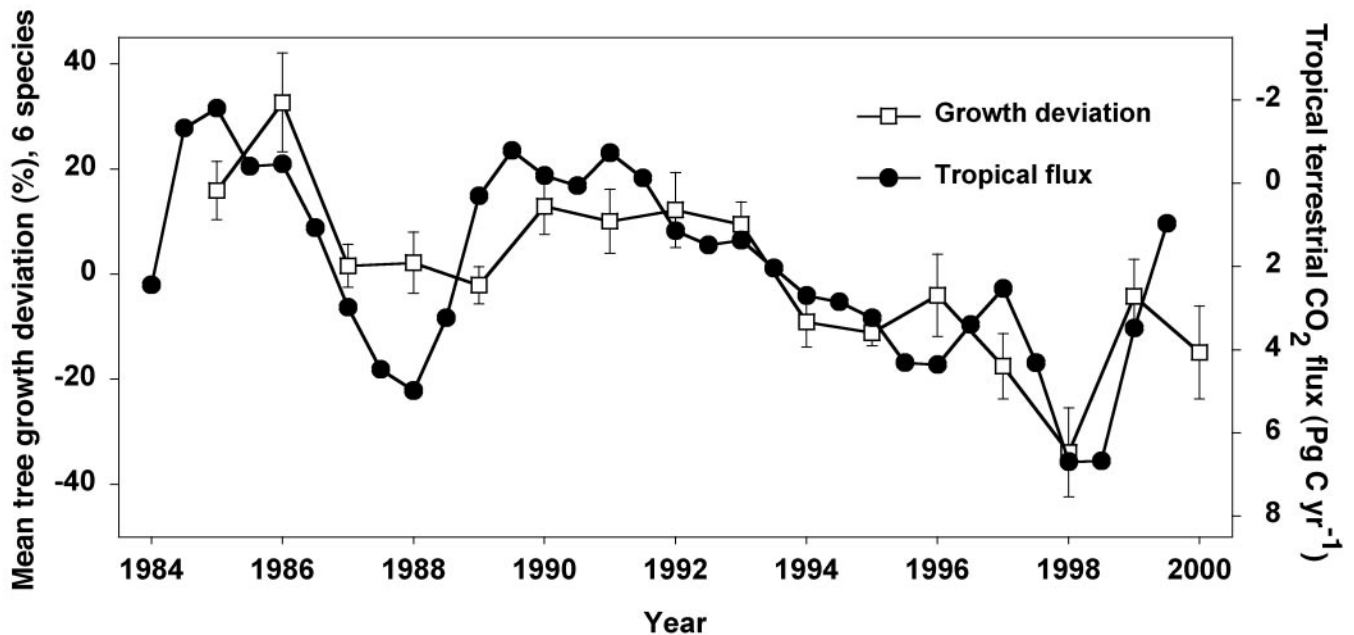
Fig. 2. The relation between the annual mean tree growth deviation (±1 SE) at La Selva, Costa Rica, averaged over the six species, and the net CO_2 flux from the terrestrial tropics (note inverted y axis), as inferred from an inverse model calculation [ref. 24; annual means centered on January 1 and June 1 each year; positive values (lower part of the y axis) indicate net flux to the atmosphere]. Pearson's $r = -0.77$, $n = 15$ yr, $P < 0.001$ for the correlation between annual fluxes (centered on January 1) and annual mean growth deviations for the six tree species (centered on October 1, previous year). x axis: yr 2 of tree measurement years.

to 278% (mean = 148%) greater than in the year of least growth (Table 1). The temporal coherence of growth patterns among conspecific trees (Table 1) was mirrored by highly significant temporal coherence among species (Friedman analysis of mean growth deviations among years, controlling for tree species: $P = 0.001$, df = 15), despite differences in details of their annual growth variation (Fig. 1). In the measurement year 1985/1986, all six species showed above-average mean diameter increments. After 1993, growth was notably depressed, with record low mean increments in 1997/1998. Relatively poor growth also occurred in 1987–1989.

Correlation, Tree Growth and Tropical CO_2 Fluxes. The inversion model analysis (24) indicated substantial interannual variation in global net CO_2 exchange with the atmosphere. The largest peaks in this flux occurred in the strong El Niño events of 1987/1988 and 1997/1998. The tropical region (23.5°N to 23.5°S) dominated the terrestrial biospheric component of the global flux (28). Interannual variations in the net CO_2 flux from tropical land regions, though not as large as in our study, have also been inferred in two inversion studies based on atmospheric observations independent of ours (29, 30). In our analysis, the terrestrial tropics were inferred to vary among years from a net sink of -1.8 to a net source of $6.7\,\mathrm{Pg\,C\cdot yr^{-1}}$. There is a highly significant negative correlation (Fig. 2) between this estimated tropical terrestrial CO_2 flux and the interannual variation in tree growth at La Selva.

In the inverse calculation, it was assumed that isotopic fractionation during photosynthesis did not vary interannually; however, plants may in fact discriminate less against the heavy isotope ^{13}C during years of climatic stress (31). A second inversion calculation of the tropical terrestrial CO_2 flux was therefore performed, ignoring $^{13}C/^{12}C$ data (27). The fluctuations in the resulting flux, based solely on observed CO_2 concentrations, retained the overall temporal pattern of the original, but with substantially reduced peaks. Because it is unknown whether isotopic discrimination associated with photosynthesis by tropical plants varied over this period, it is not possible to determine which inversion calculation is

more nearly correct. The tropical terrestrial fluxes from both calculations, however, correlate strongly with the La Selva tree growth record (original inversion: Fig. 2; second inversion: Pearson's $r = -0.68$, $P < 0.005$, df = 15).

Relations with Temperature. The annual tree growth deviations, averaged over the six species, were highly significantly negatively correlated with current-year means for daily minimum temperature at La Selva (Table 2). Mean annual growth averaged over the two coolest measurement years, 1984/1985 and 1985/1986, was 81% greater than in the record-hot 1997/1998 measurement year; intermediate growth occurred in years of intermediate temperatures (Fig. 3).

Table 2. Correlations (Pearson's r) between the mean annual tree growth deviations (averaged over the six species) and annual climatic factors at La Selva, Costa Rica, 1984–2000

Climatic factor	Correlation	P^*
Daily minimum temperature[†]	**−0.68**	**0.002**
Daily maximum temperature[†]	−0.10	0.36
Daily mean temperature[‡]	**−0.59**	**0.007**
Total annual rainfall	**−0.55**	**0.03**
Total annual irradiance[§]	+0.12	0.39
Partial correlations		
Mean minimum temperature, controlling for annual rainfall	**−0.52**	**0.02**
Annual rainfall, controlling for mean minimum temperature	−0.21	0.46

*Cases with $P \leq 0.05$ are in bold; for temperature, one-tailed probability for negative correlations with growth deviations; for rainfall, two-tailed probabilities; for annual irradiance, one-tailed probability for positive correlations.
[†]Yearly mean of daily (maximum or minimum) values.
[‡]Yearly mean of daily mean temperatures, calculated as [(daily maximum temperature + daily minimum temperature)/2].
[§]Annual irradiance is for each of the 8 yr in the period from 1992/1993 to 1999/2000.
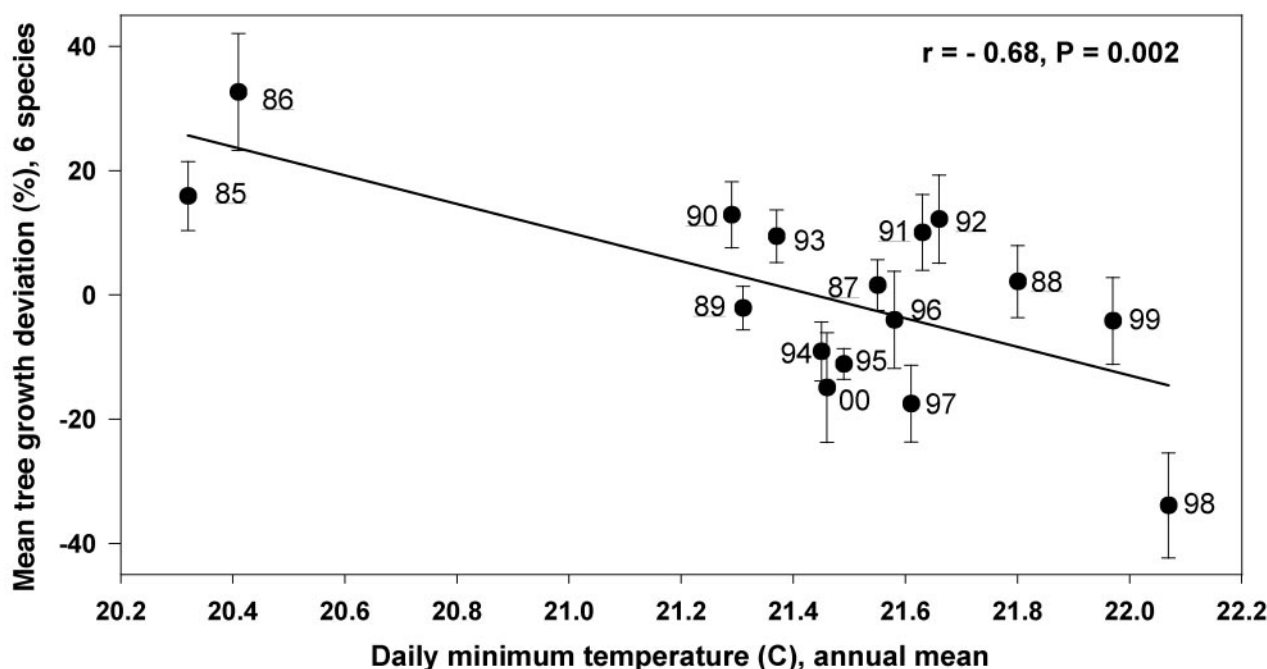
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Fig. 3. The relation between the annual diameter growth of six canopy tree species (mean of the six species' growth deviations in each year ± 1 SE) and annual means of daily minimum temperatures at La Selva, Costa Rica. Data labels: yr 2 of tree measurement years (nonunderlined, La Selva automated temperature data; underlined, data calculated by regression from a nearby surface station; ref. 21).

For all six species, the correlation between annual growth deviations and annual means for minimum temperature was negative, and four of the six correlations were significant ($P = 0.0005$, 0.0005, 0.01, 0.02, 0.06, 0.48). These correlations, most of which strongly decreased with lags of 1 and 2 yr, are notable given both the small interannual range in the mean of daily minimum temperatures during this period (1.75°C) and the complex responses of tree growth to multiple biotic and climatic factors. The annual means of daily maximum temperatures at La Selva varied over a smaller range (1.08°C) and were not significantly correlated with the growth of any species. Annual rainfall was strongly positively correlated with annual means of daily minimum temperature during this period, and the tree growth deviations were thus also negatively correlated with rainfall; however, a partial correlation controlling for minimum temperature was not significant (Table 2). There is no indication that the relation between tree growth and minimum temperature was an indirect effect of light limitation. Although warmer nights might be expected to be linked to greater daytime cloud cover, there is only a very weak negative correlation between minimum temperatures and irradiance at La Selva ($r^2 = 0.03$, 0.02, and 0.14 at daily, monthly, and annual time steps, respectively). Although tree growth rates varied highly significantly during the 8-yr period when irradiance was measured (Friedman $P < 0.001$), they were not correlated with the 35% range in irradiance among years. They were, however, negatively correlated with the annual means for minimum temperature ($r = -0.59$, $P = 0.06$), which varied by only 0.7°C for the same 8 yr.

The variations in tree growth and temperature at La Selva during 1984–2000 are mirrored in variations for the tropics as a whole. Annual means of both daily mean and daily minimum temperature at La Selva were strongly correlated with mean annual temperatures for the global terrestrial tropics (28) over this period ($r = 0.86$ and 0.74, respectively; df = 16, $P \leq 0.001$, both cases), and the inferred pantropical terrestrial CO_2 flux was also highly significantly correlated with the mean tropical land temperatures ($r = +0.83$, $P < 0.001$, at 0 time lag). The peak values of this flux occurred at the times of warmest temperatures for the tropical belt as a whole,

most of which were during strong El Niño events (28). When averaged decadally, the tropical terrestrial net CO_2 flux increased from a 0.9 Pg C·yr^{-1} source in the 1980s to a 2.6 Pg C·yr^{-1} source in the 1990s; the estimated total global land flux, however, became a greater sink (-0.2 to -0.8 Pg C·yr^{-1}) due to increased carbon uptake by the temperate and boreal zones (28).

Discussion

The large interannual growth variation during 1984–2000 that we found for six canopy tree species at La Selva was strongly negatively correlated with interyear temperature differences. These interannual growth patterns can be reasonably taken as representative of the forest as a whole. Although only six of La Selva's >300 tree species (17), our study group spans five plant families and a broad range of life history types (19) and growth rates (Table 1). The temporally concordant growth variations of these trees thus indicate large interyear variations in forest-wide aboveground biomass increment, a major component of NPP. Furthermore, such diameter increment anomalies are considered sensitive indicators of overall tree carbon balance because of a low priority for carbon allocation to wood production (32, 33).

The strong correlation between the long-term tree growth patterns and the inferred tropical terrestrial CO_2 fluxes (Fig. 2) is the first instance of a correspondence between findings from an inversion model based on atmospheric gas samples, and long-term ground-based measurements of forest productivity. This inversion study (24) is the first analysis of interannual zonal CO_2 fluxes to be based on a long-term series of both CO_2 concentrations and the $^{13}C/^{12}C$ isotopic ratio of CO_2 at stations from the Arctic to the South Pole. The relation between these data sets suggests that the interannual variation in rates of atmospheric CO_2 accumulation involves a major signal from annual variation in tropical forest productivity.

Such a signal from the terrestrial tropics has been found for various time periods since 1970 in simulations based on three global biospheric process models (34–36) forced by observed climatic variations. The simulated interannual variations in the net CO_2 flux

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Table 3. Potential impacts of small changes in photosynthesis and respiration on net carbon fluxes from tropical forests (see text)

Scenario	Global flux from tropical forests, Pg C·yr^{-1}
Baseline	
Photosynthesis	−43.8
Plant respiration	+21.9
Heterotrophic respiration	+21.9
Net flux	0.0
Photosynthesis decreased 5%, plant respiration increased 10%	
Photosynthesis	−41.6
Plant respiration	+24.1
Heterotrophic respiration	+21.9
Net flux	+4.4

Positive fluxes indicate emission from forests to the atmosphere; negative fluxes indicate uptake from the atmosphere.

from global land regions were dominated by negative responses of NPP in tropical evergreen forests to temperature. This simulated tropical forest production was strongly correlated with previous inversion model estimates of the terrestrial CO_2 flux at the global scale (37). Four modeling studies (38–41) that coupled climate change scenarios to global biosphere process models have projected decreasing NPP and carbon storage in tropical forests with rising temperatures. Three independent modeling approaches (36, 42, 43) found an explicit link between the El Niño cycle and tropical forest productivity; substantial decreases in tropical forest NPP were projected to occur in strong El Niño events.

Other recent research findings point to decreased tropical forest productivity at higher temperatures. A carbon flux model developed from eddy covariance measurements in an Amazonian forest indicated strong negative effects on net ecosystem carbon uptake from even small temperature increases (10). In three recent studies (44–46), NDVI, a satellite-derived measure of vegetation greenness, was found to be reduced in tropical ecosystems in warmer years. Annual bole measurements of all trees in 18 0.5-hectare forest plots during October 1997 to September 2000 at La Selva (D.B.C., D.A.C., and S. F. Oberbauer, unpublished data) indicated that the aboveground forest biomass increment was 39% lower in the record-hot 1997/1998 measurement year than in the two cooler years that followed; eddy covariance estimates of net CO_2 flux for these 3 yr indicated similar strong interannual changes in daily carbon uptake by the La Selva old-growth forest (ref. 11; H. W. Loescher, S. F. Oberbauer, H. Gholz, unpublished data).

The net CO_2 fluxes estimated by the inverse calculation (24) for the terrestrial tropics are substantial, especially for the 1987/1988 and 1997/1998 El Niño events (Fig. 2). Such net fluxes from this region are, however, distinctly plausible. Even small shifts in the balance between photosynthesis (P) and plant respiration (R_a) in tropical forests will result in large CO_2 emissions or uptake. To illustrate this possibility (Table 3), we use a recent estimate of global tropical-forest NPP (21.9 Pg C·yr^{-1}; 47) and assume a baseline scenario in which NPP and R_a are each 50% of P, and where

heterotrophic respiration (R_h) equals NPP. If, then, in warmer years P should decrease by 5% and R_a increase by 10%, tropical forest NPP would decline by 4.4 Pg C·yr^{-1}, producing a source of this magnitude to the atmosphere. Total tropical emissions would be even greater if there were similar temperature responses from tropical savannas or grasslands, if R_h also increased, or if emissions from tropical deforestation were enhanced due to increased tropical forest fires. An example of the last possibility is the burning of Indonesian peat swamp forests in the 1997/1998 El Niño, estimated to have produced carbon emissions of 0.8–2.6 Pg C (48).

The negative correlations that we find between annual tree growth and minimum temperatures at La Selva, and between the net CO_2 fluxes inferred for the terrestrial tropics by inverse calculation and global tropical land temperatures (28), are both consistent with the hypothesis that tropical forest NPP is already being reduced in warmer years. The La Selva data (Fig. 1) indicate a major depression of tree growth in the 1990s, the warmest decade globally in the instrumental record (1). Precipitation trends in the terrestrial tropics also need to be considered, however. During the last two decades, rainfall has been negatively correlated with mean temperatures for the global tropical land region; the strong El Niño events brought both record-high temperatures and rainfall minima (28). Temperature stress and moisture stress are thus likely to act together to decrease NPP in the more seasonal tropical moist forests, as projected by recent model simulations (38–41, 43). For such forests, this linkage will make it difficult to quantify on-going ecosystem responses to temperature alone. La Selva, a tropical wet forest where drought is minimal and not coupled to temperature, is particularly suited for detecting temperature responses in the absence of drought stress.

In this study we found very large interannual variations in two long-term records spanning the period 1984–2000: a 90% difference between mean tree growth at La Selva in the years of maximal and minimal growth, and an 8.5 Pg C·yr^{-1} range in inferred annual net CO_2 exchange by the terrestrial tropics between the years of greatest uptake and of greatest emission. The two records were strongly negatively correlated, and both covaried highly significantly with annual temperatures. As summarized above, data consistent with these relationships have been produced by other recent studies based on model simulations, satellite observations, and ground measurements. Together these findings suggest a remarkable sensitivity of the net carbon balance of tropical rain forests to increasing temperature, and thus indicate the potential for these forests to produce a large positive feedback to on-going atmospheric CO_2 accumulation. Such a feedback in future years would accelerate global warming.

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