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TEMPERATURE INFLUENCES CARBON ACCUMULATION IN MOIST TROPICAL FORESTS

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Abstract. Evergreen broad-leaved tropical forests can have high rates of productivity and large accumulations of carbon in plant biomass and soils. They can therefore play an important role in the global carbon cycle, influencing atmospheric CO₂ concentrations if climate warms. We applied meta-analyses to published data to evaluate the apparent effects of temperature on carbon fluxes and storages in mature, moist tropical evergreen forest ecosystems. Among forests, litter production, tree growth, and belowground carbon allocation all increased significantly with site mean annual temperature (MAT); total net primary productivity (NPP) increased by an estimated 0.2–0.7 Mg C·ha⁻¹·yr⁻¹·°C⁻¹. Temperature had no discernible effect on the turnover rate of aboveground forest biomass, which averaged 0.014 yr⁻¹ among sites. Consistent with these findings, forest biomass increased with site MAT at a rate of 5–13 Mg C·ha⁻¹·°C⁻¹. Despite greater productivity in warmer forests, soil organic matter accumulations decreased with site MAT, with a slope of –8 Mg C·ha⁻¹·°C⁻¹, indicating that decomposition rates of soil organic matter increased with MAT faster than did rates of NPP. Turnover rates of surface litter also increased with temperature among forests. We found no detectable effect of temperature on total carbon storage among moist tropical evergreen forests, but rather a shift in ecosystem structure, from low-biomass forests with relatively large accumulations of detritus in cooler sites, to large-biomass forests with relatively smaller detrital stocks in warmer locations. These results imply that, in a warmer climate, conservation of forest biomass will be critical to the maintenance of carbon stocks in moist tropical forests.

Key words: *belowground carbon allocation; carbon cycle; carbon turnover; decomposition; forest biomass; forest productivity; global warming; mean annual temperature; meta-analysis; net primary productivity; soil organic matter; tropical evergreen forests.*

INTRODUCTION

Increasing atmospheric CO₂ concentrations (Keeling et al. 1989) are predicted to increase temperatures and cause other environmental changes (Overpeck et al. 1990, Bazzaz 1998). Temperature influences rates of plant photosynthesis and respiration (Berry and Björkman 1980), litter decomposition and microbial activity (Swift et al. 1979), and other biologically mediated processes affecting the immobilization and release of

CO₂. Thus, global warming is expected to alter terrestrial carbon pools and feed back to further increase atmospheric CO₂ levels (Jenkinson et al. 1991, Schimel et al. 1994, Trumbore et al. 1996).

The tropics play a particularly important role in the terrestrial carbon budget. They contain >40% of the world's forest biomass (Dixon et al. 1994, FAO 2001) and soil carbon (Jobbágy and Jackson 2000). Warming-induced changes in carbon storage within tropical forests have significant potential to alter atmospheric CO₂ concentrations and future warming potentials (Townsend et al. 1995). Although the warming predicted for tropical regions is less than is expected at higher lat-

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itudes (Houghton et al. 2001), there is evidence that tropical forest regions already are warming (Malhi and Wright 2004), and even slight warming may be important where temperatures are already high (Townsend et al. 1992, Meir et al. 1996). However, the net effects of temperature on CO₂ uptake by and release from tropical forest ecosystems remain unclear.

Along elevational gradients on windward Mauna Loa, Hawai'i, aboveground net primary productivity (ANPP) increased linearly with temperature (Raich et al. 1997); litter decay rates increased with temperature (Vitousek et al. 1994, 1995); and soil carbon accumulations were large at an old, high-elevation site where ANPP and temperatures were low (Raich et al. 1997). Similar results were obtained from studies on two substrates on Mount Kinabalu, Malaysia (Kitayama and Aiba 2002a, b). Extensive modeling of the Mauna Loa elevational gradient using CENTURY (Metherell et al. 1993) provided a means of disentangling the effects of temperature on ecosystem processes from those of other factors, and supported a substantial direct effect of temperature on net primary productivity (NPP) and decomposition (Raich et al. 2000).

Based on these studies, we propose several specific hypotheses that describe the effects of temperature on carbon stocks and cycling rates among mature tropical evergreen forests. First, tropical forest productivity correlates positively with mean annual temperature (MAT) (H1). Second, forest biomass turnover rates (i.e., productivity/mass) do not vary systematically with MAT (H2). Third, forest biomass and MAT are positively correlated (H3), as a consequence of hypotheses 1 and 2. Fourth, detritus decay rates increase with increasing forest MAT (H4). Fifth, as a result of hypotheses 1 and 4, detrital carbon pools do not vary significantly with temperature (H5). Below we evaluate each of these hypotheses by testing the null hypothesis of no relationship between an ecosystem attribute and temperature.

Biogeochemical models that simulate the responses of terrestrial ecosystems to global changes differ in many respects, but predictions of temperature-driven changes in tropical forest carbon stocks, and resulting effects on atmospheric CO₂ pools, are largely the result of a few basic assumptions (Fig. 1). These include relationships describing temperature effects on net CO₂ uptake by plants (H1) and biomass turnover rates (H2), which control live-plant carbon pools (H3); and on detritus production (H1) and decay rates (H4), which control detrital (including soil) carbon stocks (H5). The objective of this paper is to test these hypotheses based on available published information from studies of natural, relatively undisturbed, mature moist broadleaved tropical evergreen forests. We also ask "Do total ecosystem carbon stocks in moist tropical forest ecosystems vary predictably with temperature?" Any net changes in total organic C storage within tropical for-

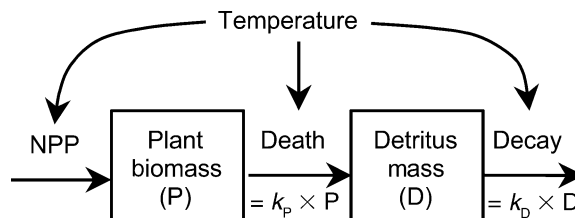


FIG. 1. Conceptual model of the potential effects of temperature on carbon storage in moist tropical forests. By influencing carbon fluxes, temperature may influence carbon stocks in living plants and detritus. The variables k_p and k_d refer to the turnover rates of plant biomass and detritus, respectively.

ests would be expected to influence atmospheric CO₂ levels and, thus, future warming potentials.

METHODS

Data compilation

To test these hypotheses we compiled data sets (Appendices A–E) that contain previously published measurements of carbon fluxes and stocks within intact tropical evergreen forests, and associated information on site mean annual temperatures (MAT, °C). Throughout we assumed that plant biomass and plant detritus were 48% C and that soil organic matter (SOM) was 58% C.

One of the difficulties in comparing data from tropical forests of the world is that great diversity of climates, soils, nutrient deposition rates, topographies, biota, and disturbance histories among sites may mask any effects of temperature. For this reason we limited our analyses to sites specifically described as being relatively mature forests free of recent large-scale disturbances, and not significantly modified by human activities. The single exception was our inclusion of two studies that compared soil C stocks among elevations (i.e., Colombia and Congo in Fig. 3), but did not provide detailed vegetation descriptions for each location. Seasonally flooded and swamp forests were excluded from all data sets. We minimized the potentially confounding effects of site seasonality on our analyses by including only tropical evergreen forest environments having <3 consecutive months of <50 mm/mo precipitation on average. This definition encompasses most of the world's natural tropical evergreen forests, but excludes deep-rooted evergreen forests in locations with distinct dry seasons (e.g., Nepstad et al. 1994).

Total net primary productivity (NPP) has been quantified in few moist tropical forests, with information on herbivory rates and belowground production being particularly sparse (Clark et al. 2001). To test H1 we collated available measurements of fine litter production, tree growth, and belowground carbon allocation. Collated data on fine litter production rates (Appendix A) included only sites where litterfall was collected from multiple traps for ≥ 1.0 year. Measurements of

aboveground biomass increment (ABI, the total biomass increment of all live trees within a plot; Appendix B) were derived from plot-level studies where all trees within plots were remeasured through time at annual or shorter time intervals, and where growth was quantified in terms of biomass. We also compared total forest ANPP data from three elevational transects through mature tropical forests, two on Mt. Kinabalu ($n = 4$ sites per transect; Kitayama and Aiba 2002a) and one in Puerto Rico ($n = 3$ sites; Weaver and Murphy 1990).

Robust measurements of belowground NPP in tropical forests are lacking. We used the soil carbon budgeting approach (Raich and Nadelhoffer 1989, Nadelhoffer et al. 1998, Giardina and Ryan 2002) to estimate total carbon fluxes to roots, i.e., belowground carbon allocation (BCA), which includes both belowground net primary productivity (BNPP) and root respiration. We estimated BCA as the difference between annual soil respiration and litterfall rates (Appendix C), under the assumption of no substantial annual changes in belowground carbon stocks.

To test H2, the relationship between temperature and forest biomass turnover rates, we calculated biomass turnover rate (k_p in Fig. 1) as ABI (megagrams per hectare per year) divided by mean aboveground forest biomass (megagrams per hectare), based on data from tree growth-monitoring plots (Appendix B). This calculation describes the rate of turnover of live-tree wood. We were unable to include root estimates due to lack of data.

Forest biomass varies in response to many factors (e.g., Cannell 1984, Brown and Lugo 1992). To identify the effects of temperature (H3) we collated available data from studies that measured the biomass of mature forests along elevational gradients within the wet tropics. Within such transects, state factors (sensu Jenny 1980) vary less than they do among tropical forests of the world, allowing the effects of temperature to be more evident. Few rigorous measurements of total root biomass in tropical forests exist (e.g., Sanford and Cuevas 1996), so our analysis is based on aboveground data only. In some cases only aboveground tree biomass was reported, but almost all of the live biomass in tropical forests is in trees (Brown and Lugo 1992, Nascimento and Laurance 2002).

Detritus production rate ("Death" in Fig. 1) is herein assumed to be approximately equal to NPP, which is determined based on measurements of both growth and detritus production. Rates of net biomass accumulation vary among tropical humid forests, but generally are small: $\sim 0.3 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ in the Neotropics (Clark 2002); $< 1 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ in Amazonia (Phillips et al. 1998, Chambers et al. 2004); and no significant accumulation in the Paleotropics (Phillips et al. 1998). These low rates of net biomass accumulation do not meaningfully impact any of our analyses or conclusions.

Detrital carbon pools in tropical evergreen forests include surface litter, standing and fallen coarse woody debris, and soil organic matter, with the latter being the largest. We assembled data from studies that compared total soil organic carbon (SOC) stocks among elevations within tropical evergreen forest environments, where sampling extended across $> 500 \text{ m}$ elevation, sometimes including disturbed sites (i.e., in Colombia and possibly Congo). We did not include data from transects located on hydromorphic soils, because soil saturation strongly influences SOC accumulation rates (Schlesinger 1997, Schuur et al. 2001). Data from throughout Costa Rica (Holdridge et al. 1971) were derived from soil profile descriptions; missing bulk density data were estimated based on the relationship between soil bulk density, soil texture, and SOM content. To test the relationship between SOC mass and temperature (H5), we estimated elevation-specific temperatures from climate data provided by the study authors. For sites in Colombia (Alexander and Pichott 1979) and Thailand (Yoda and Kira 1969) we assumed a lapse rate of $-0.006^\circ\text{C}/\text{m}$.

Data on mean annual surface litter mass were compiled from sites that included information on fine litter production rates (Appendix D). We calculated litter turnover rates (k_L , yr^{-1}) from litterfall/mean litter mass (e.g., Anderson and Swift 1983). This approach for defining k_L provides specific information on the mean annual turnover rate of the surface fine litter in intact forests. We also collated data on the mass of coarse woody debris present in tropical evergreen forests, including both standing dead trees and surface woody debris whenever possible.

Finally, to evaluate trends in total ecosystem carbon storage among forests, we summarized data from 22 mature tropical evergreen forest sites where total biomass and carbon storage, including root biomass and total soil carbon to 1 m depth, were determined (Appendix E). Coarse woody debris (CWD) was measured in only nine of those sites, and did not correlate with site MAT. There are no reported or apparent correlations between accumulations of CWD and climatic factors among tropical evergreen forests. To estimate total detrital carbon stocks in the 13 sites lacking CWD data, we estimated CWD mass as 10% of aboveground tree biomass (Delaney et al. 1998). Sampling depths for measurements of SOC stocks varied among sites; we included data for the entire soil profile to 1.0 m depth whenever possible (see footnotes to Appendix E).

Data analysis

The appendices contain two types of data: spatially extensive data that include measurements from forests throughout the tropics, and data collected from elevational gradients within specific locations. In the geographically extensive data sets, each stand (datum) was treated as a single measurement of carbon flux or stock on a temperature gradient; MAT varied among sites

due to differences in latitude and elevation. To evaluate our hypotheses, we applied linear regression to test for relationships between MAT (independent variable) and carbon stock or flux (null hypothesis: slope = 0).

Data from elevational gradients were evaluated using meta-analysis (MetaWin; Rosenberg et al. 2000). We first applied linear regression to estimate slopes of relationships between MAT and ecosystem attributes for each transect. The variance-weighted mean effect among all transects was determined based from the transect-specific slopes, weighted by their standard errors (e.g., Gurevitch and Hedges 1999, Rosenberg et al. 2000). The heterogeneity of variance among transects was significant, so we used bootstrapping procedures to calculate 95% confidence intervals around the mean effect (Adams et al. 1997), for comparison with the null hypothesis (i.e., slope = 0). Concordant results were obtained using unweighted means; for brevity, only variance-weighted means are presented.

RESULTS

Among moist tropical evergreen forests, litterfall increased with MAT ($^{\circ}\text{C}$) with a slope of $0.10 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}\cdot^{\circ}\text{C}^{-1}$ ($n = 79$, 95% CL = 0.06, 0.13, $P < 0.0001$; Fig. 2A). Meta-analysis of data from five elevational transects also showed that aboveground litter production increased with site MAT, by an average of $0.26 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}\cdot^{\circ}\text{C}^{-1}$ (95% CL = 0.16, 0.45; Fig. 2B). This is consistent with the findings of Silver (1998), who conducted a similar analysis based on unweighted means. Mean annual aboveground tree biomass increment (ABI) also increased significantly with MAT, with a slope of $0.10 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}\cdot^{\circ}\text{C}^{-1}$ ($n = 22$, 95% CL = 0.04, 0.17, $P < 0.003$; Fig. 2C). Consistent with these findings, total forest ANPP increased with MAT among elevational gradients, with a mean effect of $0.66 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}\cdot^{\circ}\text{C}^{-1}$ (meta-analysis, $n = 3$, 95% CL = 0.40, 0.73, $P < 0.05$). Belowground carbon allocation also increased with site MAT among forests, with a slope of $0.27 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}\cdot^{\circ}\text{C}^{-1}$ ($n = 26$, 95% CL = 0.10, 0.44; $P < 0.004$; Fig. 2D). Thus, tropical evergreen forests allocated more photosynthetically derived carbon to their root systems when growing in warmer environments.

Among elevational transects, aboveground forest biomass increased significantly with site MAT, at an average of $13.2 \text{ Mg C}\cdot\text{ha}^{-1}\cdot^{\circ}\text{C}^{-1}$ (meta-analysis, $n = 4$, 95% CL = 7.9, 17.7; Fig. 2E). Among tropical forests (Appendix B) aboveground forest biomass increased with MAT, with a slope of $7.5 \text{ Mg C}\cdot\text{ha}^{-1}\cdot^{\circ}\text{C}^{-1}$ (linear regression, $n = 22$, 95% CL = 3.2, 11.8, $P < 0.0002$; Fig. 2F). These were not wholly independent tests, however; nine of the 22 sites in Fig. 2F were located along elevational gradients included in Fig. 2E. Aboveground biomass (i.e., wood) turnover rates averaged 0.014 yr^{-1} (CL = 0.10, 0.17) among forests, and did not vary with temperature (linear regression, $n = 22$, $P = 0.70$; Fig. 2G).

Soil surveys along elevational gradients in the wet tropics document higher soil carbon pools at higher elevations (Fig. 3), with the exception of the ultrabasic soils on Mt. Kinabalu (Kitayama and Aiba 2002a, b). Meta-analysis of data from six locations (Fig. 3) showed that SOC stocks declined significantly with increasing MAT, by an average of $-7.8 \text{ Mg C}\cdot\text{ha}^{-1}\cdot^{\circ}\text{C}^{-1}$ (95% CL = -23.4 , -1.5). Surface fine litter mass also declined with increasing site MAT, at $-0.052 \text{ Mg C}\cdot\text{ha}^{-1}\cdot^{\circ}\text{C}^{-1}$ (linear regression, $n = 32$, slope < 0 , 95% CL = -0.11 , 0.00 , $P = 0.061$; Fig. 2I). These results are consistent with trends in surface-litter decay rates (k_L , yr^{-1}), which increased by an average of $0.12 \text{ yr}^{-1}\cdot^{\circ}\text{C}^{-1}$ (linear regression, $n = 32$, 95% CL = 0.06, 0.18, $P < 0.0003$; Fig. 2H). Variability in litter turnover rates was high among the warmer forests (Fig. 2H), but the positive relationship between k_L and MAT held true when only sites with MAT $\leq 25^{\circ}\text{C}$ were included ($n = 22$, $P < 10^{-5}$), and when $\ln(k_L)$ was used as the dependent variable ($n = 32$, $P < 10^{-6}$). Total dead wood mass averaged 14.7 Mg C/ha (95% CL = 11.2, 18.1) among forests, and did not vary with MAT (linear regression, $n = 16$, $P = 0.80$; Fig. 2J). There were insufficient data to allow us to test the relationship between site MAT and the decay rates of coarse woody debris or SOM.

Among 22 forests with total organic matter inventories (Appendix E), mean annual temperatures ranged from 10° to 27°C , total plant biomass ranged from 22 to 322 Mg C/ha, and SOC accumulations ranged from 62 to 600 Mg/ha. Consistent with our previous results, total plant biomass (including roots) increased with site MAT (linear regression, slope = $5.2 \text{ Mg C}\cdot\text{ha}^{-1}\cdot^{\circ}\text{C}^{-1}$, 95% CL = 0.8, 9.7, $P < 0.025$), and total SOC declined with increasing site MAT (slope = $-7.2 \text{ Mg C}\cdot\text{ha}^{-1}\cdot^{\circ}\text{C}^{-1}$, 95% CL = -15.9 , 1.4 , $P = 0.095$). Total ecosystem carbon stocks, including both live and dead organic materials, did not vary with temperature (linear regression, $P = 0.78$; Fig. 4A).

DISCUSSION

Observational studies are not experiments, and comparisons among different sites are notorious for their inability to control for all factors other than the factor of interest, in this case temperature. However, comparisons among intact mature forest ecosystems in different temperature environments provide the best available evidence for understanding the long-term, whole-ecosystem responses of those forests to prevailing atmospheric temperatures.

We hypothesized that among intact mature moist tropical evergreen forests: productivity increases with site mean annual temperature (H1); forest biomass turnover rates do not vary systematically with MAT (H2); forest biomass increases with increasing MAT (H3); detritus decay rates increase with increasing MAT (H4); and that total detritus mass does not vary systematically with site MAT (H5). Our analyses sup-

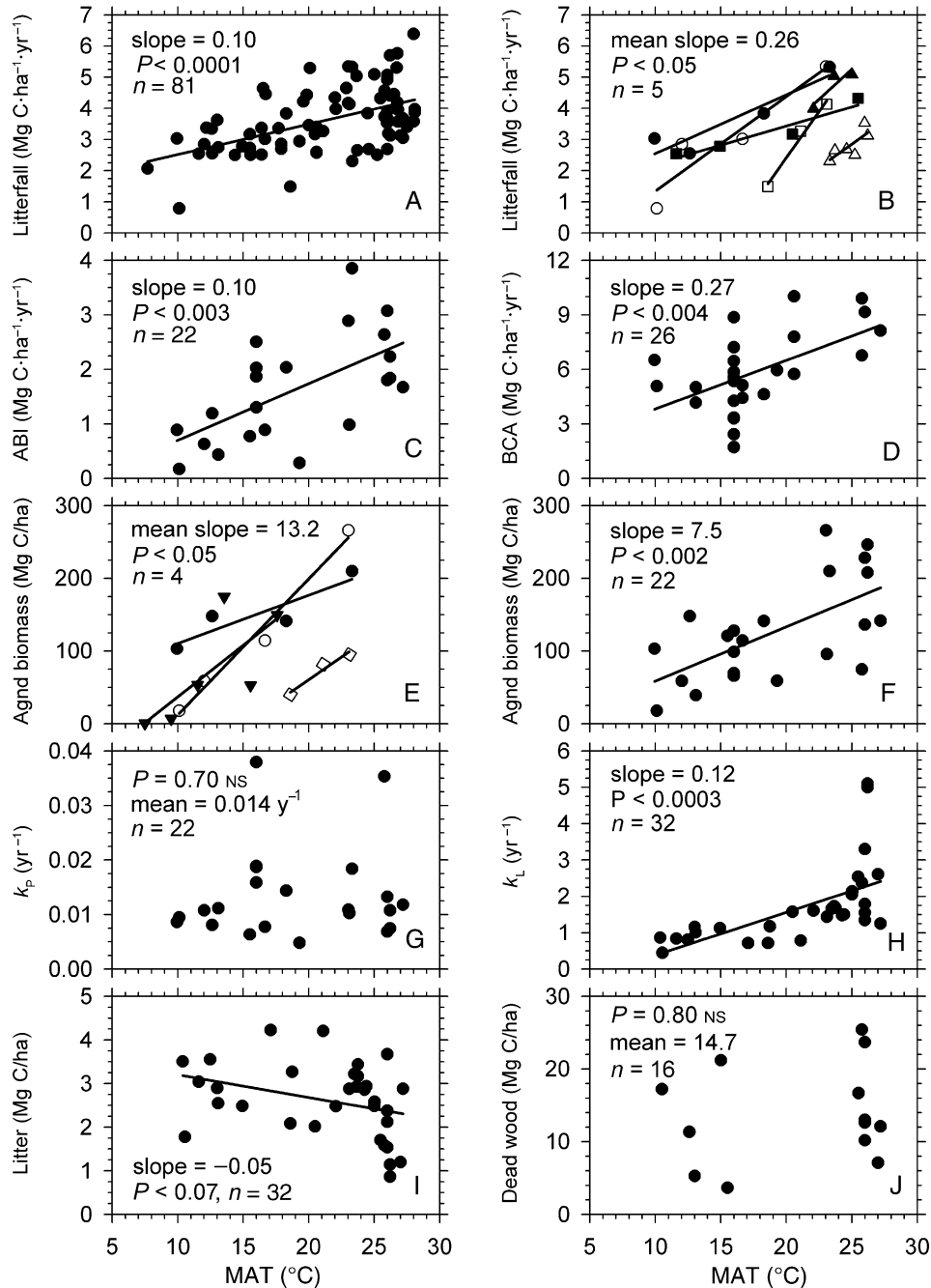


FIG. 2. Ecosystem attributes, in units of carbon, in relation to site mean annual temperature (MAT) in mature moist tropical evergreen forests (ns, no significant relationship). (A) Fine-litter production increased significantly with MAT (Appendix A). (B) Litterfall increased significantly with MAT among six individual elevational transects; variance-weighted mean effect = $0.26 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}\cdot\text{C}^{-1}$ (Appendix A). (C) Mean annual aboveground biomass increment (ABI) increased significantly with MAT (Appendix B). (D) Belowground carbon allocation (BCA) increased significantly with MAT (Appendix C). (E) Aboveground (Agnd) plant biomass among individual elevational transects increased significantly with MAT; variance-weighted mean effect = $13.2 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{C}^{-1}$. (F) Aboveground plant biomass increased significantly with MAT among forest growth-monitoring plots (Appendix B). (G) Turnover rates of plant biomass (k_p ; Fig. 1) did not vary systematically with MAT (Appendix B). (H) Surface fine-litter decay rates (k_L) increased significantly with MAT among tropical evergreen forests (Appendix D). (I) Surface litter mass declined with site MAT (Appendix D). (J) There was no relationship between the mass of coarse woody debris and site MAT. Data are from Appendix E and from Uhl and Jordan (1984), Delaney et al. (1997, 1998), Puig and Delobelle (1988), Saldarriaga et al. (1988), and Hughes et al. (2000). For (B) and (E), data are from sedimentary (solid circles) and ultrabasic (open circles) substrates, Mt. Kinabalu (Kitayama and Aiba 2002a); Volcán Barva, Costa Rica (solid square; Heaney and Proctor 1989); Luquillo Mountains, Puerto Rico (open square; Weaver and Murphy 1990); Bukit Belalong, Brunei (solid triangle; Pendry and Proctor 1996); Gunung Silam, Malaysia (open triangle; Proctor et al. 1989); and old 'a'a lava substrates, Mauna Loa (inverted solid triangle; Aplet and Vitousek 1994).

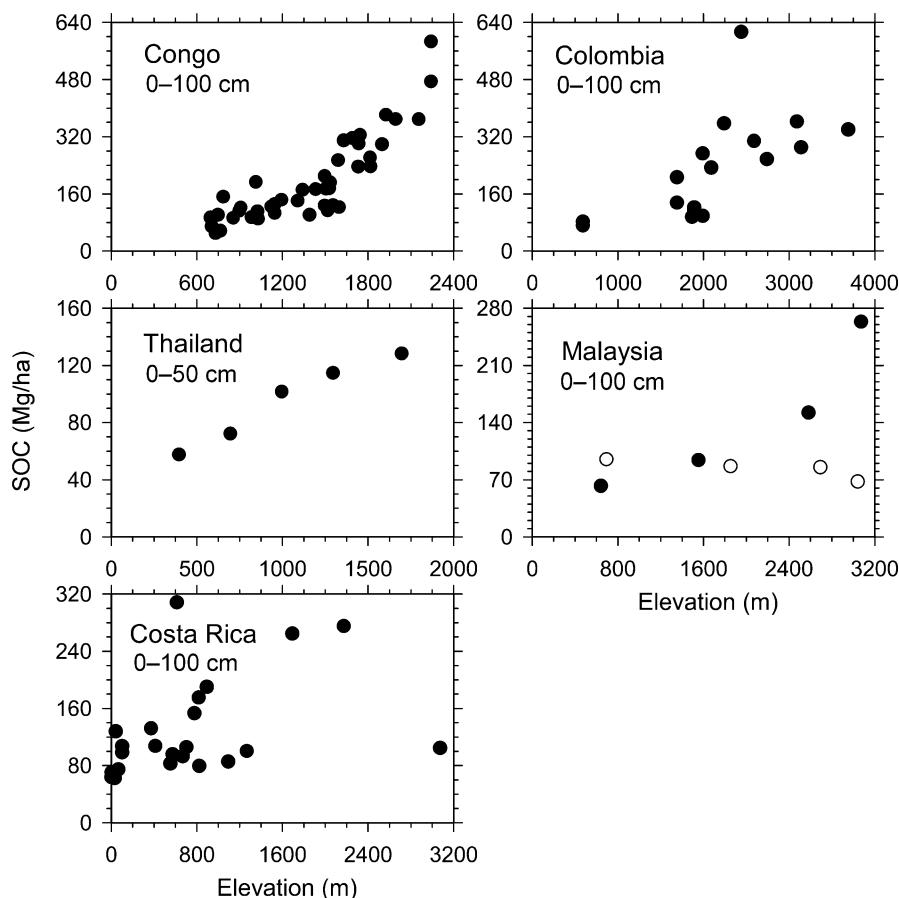


FIG. 3. Soil organic carbon (SOC) pools generally increase at higher elevations in wet tropical regions. Surface litter stocks are excluded from all figures. Sites are in Kivu Mountains, Democratic Republic of the Congo (derived from Pérot 1959; Fig. 3 [reprinted with permission from Blackwell Publishing, Ltd.]); Colombia (Alexander and Pichott 1979); Khao Luang, Thailand, exclusive of the summit, which was not forested (Yoda and Kira 1969); Mt. Kinabalu, Sabah, Malaysia (Kitayama and Aiba 2002a, b; open symbols are ultrabasic substrates; solid symbols are sedimentary substrates); and Costa Rica, which includes intact moist, wet, and rain forests throughout the country, excluding flooded and highly disturbed sites (Holdridge et al. 1971).

ported the first four of these hypotheses, but were inconsistent with H5.

Our analysis differs in three principal ways from previous studies describing environmental controls over productivity and organic matter stocks in tropical forests (e.g., Brown and Lugo 1982, Silver 1998, Clark et al. 2001). First, we evaluated the influence of a single variable, temperature, on C-cycling processes from a whole-ecosystem mass-balance perspective (Fig. 1). Second, we focused our analysis on mature evergreen broad-leaved tropical forests without significant dry seasons, thus minimizing any confounding effects of forest age, successional status, moisture limitations, or canopy deciduousness. Third, we used available data to quantify the rate of change in forest ecosystem attributes with respect to among-site variations in mean annual temperature, rather than to estimate mean values for the tropical forest biome, at specific temperatures, or within individual life zones.

Our focus on temperature does not minimize the importance of other factors that influence carbon accumulation and cycling within tropical forests (e.g., Vitousek and Sanford 1986, Waide et al. 1998, Raich et al. 2000). In summaries of data from many forests, variations in these other factors diminish the likelihood of identifying significant relationships with temperature, that is, they increase likelihood of Type II statistical errors. Therefore, significant relationships that we did identify are quite likely to be robust. On the other hand, if any factor consistently covaries with temperature, then our results might be confounded.

Elevation as a temperature gradient

Changes in elevation within forested regions are accompanied by variations in climate (e.g., Friend and Woodward 1990, Juvik and Nullet 1994) and in other important state factors (e.g., Vitousek et al. 1995, 2003). Rainfall, solar radiation, nutrient input rates,

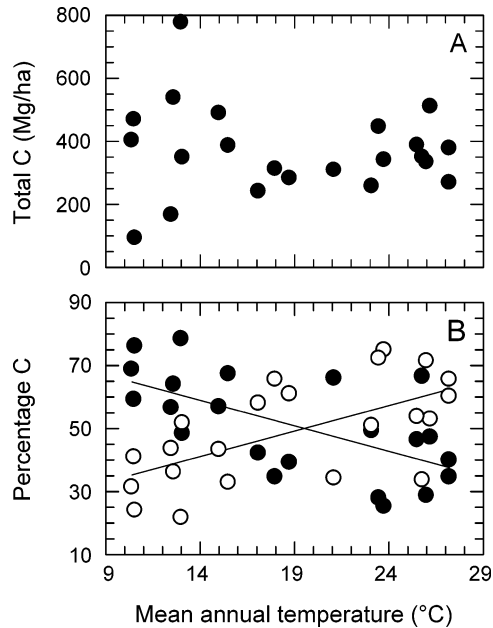


FIG. 4. (A) Total carbon present in vegetation, soils, and aboveground detritus in moist tropical evergreen forests does not correlate with site MAT ($n = 22$, $P = 0.72$). (B) The relative amounts of carbon present in live biomass (open circles) and detritus (solid circles) vary significantly with site MAT among moist tropical evergreen forests. Lines show the least-squares linear relationships between each variable and mean annual temperature ($n = 22$, adjusted $R^2 = 0.36$, $P = 0.002$; data in Appendix E).

soil parent materials, and other factors vary among sites, but none of these vary predictably and monotonically with either temperature or elevation (see Raich et al. 1997, 2000, Kitayama and Aiba 2002a). Among-forest variations in such factors may diminish the sensitivity of our analyses, but they do not explain the consistent trends in ecosystem properties with increasing elevation that we document, and relate to temperature.

Temperature and atmospheric pressure do covary (both decrease as elevation increases) suggesting that changes in atmospheric pressure could explain the elevational trends documented herein. Declining pressure does not alter the molar ratio of CO_2 in the atmosphere, but does cause a decline in the partial pressure of atmospheric CO_2 , which could diminish photosynthesis rates at higher elevations (e.g., Gale 1972, 2004, Friend and Woodward 1990). However, increases in the diffusivity of CO_2 partially offset decreases in CO_2 partial pressure, and concomitant declines in O_2 partial pressures lead to lower rates of photorespiration in C_3 plants at high elevations (Terashima et al. 1995, Sakata and Yokoi 2002). Overall differences in leaf photosynthetic capacity among high- and low-elevation plants are small (e.g., Körner and Diemer 1987, Cordell et al. 1999). If suppression of photosynthesis occurs at high elevations, it is likely caused by limited internal CO_2

diffusion rates (Vitousek et al. 1990, Terashima et al. 1995), by lower temperatures (Berry and Björkman 1980, Friend and Woodward 1990, Terashima et al. 1995), or by reduced sink strength (Körner 2003), not by lower CO_2 partial pressures. There also is no convincing evidence that changes in atmospheric pressure lead to changes in plant tissue chemistry that would cause decomposition rates to decline at higher elevations. Indeed, high-elevation plants sometimes have high nutrient contents (Körner 1989). We therefore argue that elevational gradients provide a useful basis for identifying temperature's effects on forest carbon-cycling processes.

Temperature and tropical forest biomass

The biomass of a forest reflects the balance between the production of new biomass (NPP) and the production of detritus (Fig. 1): both faster rates of forest productivity (NPP) and slower biomass turnover rates act to increase forest biomass. Forest ANPP along elevational transects increased by an average of $0.7 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}\cdot\text{C}^{-1}$. Aboveground litter production and aboveground tree biomass increment both increased significantly with MAT (Fig. 2A–C), with their sum effect being $0.2\text{--}0.4 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}\cdot\text{C}^{-1}$. We thus estimate the effect of temperature on ANPP to be $0.2\text{--}0.7 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}\cdot\text{C}^{-1}$ (Table 1). This effect was mirrored by a significant positive relationship between MAT and belowground carbon allocation (Fig. 2D). Belowground carbon allocation includes both rhizosphere respiration and root (belowground) net primary production (BNPP). We have no direct evidence of the actual contribution of BNPP to total BCA (i.e., of BNPP/BCA) or how it varies with temperature among forests. However, the ratio between biomass production and total carbon use (i.e., carbon use efficiency, CUE) is relatively uniform among mature forest ecosystems (Waring et al. 1998, Medlyn and Dewar 1999, Gifford 2003). In a recent review, C. M. Litton, J. W. Raich, and M. G. Ryan (*unpublished manuscript*) found that belowground carbon use efficiency (BNPP/BCA) averaged 0.41 among forests ($n = 25$, $r^2 = 0.57$), which is lower than previous estimates. Assuming that BNPP/BCA = 0.41, then BNPP in moist tropical evergreen forests varied with site MAT by an average of $0.11 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}\cdot\text{C}^{-1}$, and total NPP varied by $0.3\text{--}0.8 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}\cdot\text{C}^{-1}$ (Table 1).

There was no significant relationship between MAT and the turnover rate of forest biomass (k_p in Fig. 1), which averaged 0.014 yr^{-1} (Fig. 2G). Given a positive relationship between temperature and forest NPP, but no relationship between temperature and k_p , forest biomass should also increase with MAT among forests. The available data confirm this: aboveground forest biomass increased by $7.5\text{--}13.2 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{C}^{-1}$ and total biomass increased by $5.2 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{C}^{-1}$ (Table 1). Whittaker and Likens (1973) showed that mature forest biomass increased with productivity among forests of

TABLE 1. Variation in carbon cycling rates and storages among mature moist tropical evergreen forests, in relation to mean annual temperature (MAT).

Variable	Temperature effect	Source	Probability
$\Delta\text{NPP}/\Delta\text{MAT}$ (Mg C·ha ⁻¹ ·y ⁻¹ ·°C ⁻¹)			
Litterfall	0.10 (0.06, 0.13)	Fig. 2A	<0.0001
Litterfall	0.26 (0.16, 0.45)	Fig. 2B	<0.05
ABI	0.10 (0.04, 0.17)	Fig. 2C	<0.003
ANPP	0.66 (0.40, 0.73)	meta-analysis	<0.05
ANPP (range)	0.20, 0.66	range of above results	
BCA	0.27 (0.10, 0.44)	Fig. 2D	<0.004
BNPP (estimate)	0.11	= 41% of BCA†	
NPP (range)	0.31, 0.77	= ANPP + BNPP	
$\Delta\text{Plant biomass}/\Delta\text{MAT}$ (Mg C·ha ⁻¹ ·°C ⁻¹)			
Aboveground	13.2 (7.9, 17.7)	Fig. 2E	<0.05
Aboveground	7.5 (3.2, 11.8)	Fig. 2F	<0.002
Total	5.2 (0.8, 9.7)	Appendix E	<0.025
$\Delta k_p/\Delta\text{MAT}$ (y ⁻¹ ·°C ⁻¹)			
Aboveground k_p	0 (-0.001, 0.001)	Fig. 2G	0.70
$\Delta\text{Detritus}/\Delta\text{MAT}$ (Mg C·ha ⁻¹ ·°C ⁻¹)			
SOC	-7.8 (-23.4, -1.5)	Fig. 3	<0.05
SOC	-7.2 (-15.9, 1.4)	Appendix E	<0.10
Surface fine litter	-0.05 (-0.11, 0.00)	Fig. 2I	0.06
Coarse woody debris	0 (-0.5, 0.6)	Fig. 2J	0.80
Total	-8	= sum of above estimates	
$\Delta k_D/\Delta\text{MAT}$ (y ⁻¹ ·°C ⁻¹)			
k_L	0.12 (0.06, 0.18)	Fig. 2H	<0.0003
k_{SOC}	>0	†	
k_D	>0	from above	
$\Delta\text{C}/\Delta\text{MAT}$ (Mg C·ha ⁻¹ ·°C ⁻¹)			
Total carbon	0 (-12.0, 9.2)	Fig. 4A	0.78

Notes: Variables reflect state variables and fluxes in reference Fig. 1. Values under "Temperature effect" represent the mean rate of change (95% CL) of the specified variable with respect to a +1°C difference in site MAT. Abbreviations refer to aboveground biomass increment (ABI), belowground carbon allocation (BCA), net primary productivity (NPP), aboveground NPP (ANPP), belowground NPP (BNPP), soil organic carbon (SOC), and turnover rates of aboveground tree biomass (k_p), detritus (k_D), surface litter (k_L), and soil organic carbon (k_{SOC}). Rows in bold font represent summary results.

† See Discussion: Temperature and tropical forest biomass.

‡ See Discussion: Temperature and tropical forest detritus.

the world. Our data support this trend, and suggest that it may be explained by a positive effect of temperature on forest productivity coupled with no relationship between temperature and forest-biomass turnover rates.

Temperature and tropical forest detritus

A similar logic applies to detritus stocks: given greater NPP at warmer temperatures, almost all of which reflects equivalent detritus production, warmer forests should contain more detrital carbon than do cooler forests. The opposite was true: SOC stocks decreased with increasing temperature (Table 1). Thus, soil organic matter decay rates must increase with increasing MAT. This conclusion is consistent with studies demonstrating that litter decomposes faster at higher temperatures among moist tropical forests (e.g., Fig. 2H; Vitousek et al. 1994, Silver 1998, Kitayama and Aiba 2002a).

Soils are the major site of detritus accumulation in most tropical forests (Delaney et al. 1997, and data in Appendix E), and are a focus of debate concerning how environmental changes may alter the atmospheric carbon balance (e.g., Trumbore 1997, Cox et al. 2000, Davidson et al. 2000). It is difficult to reconcile in-

creasing rates of detritus production with decreasing soil carbon pools along temperature gradients, unless SOC turnover rates increase with increasing temperature faster than do rates of NPP. Thus, our analyses contradict the argument of Giardina and Ryan (2000), that the turnover times (1/decay rates) of mineral-soil carbon are not sensitive to temperature. We cannot, based on our analyses, rule out the existence of a SOC pool or pools that are insensitive to temperature, but total soil carbon stocks within the surface meter of soil are lower at warmer temperatures (Fig. 3) despite that organic matter production is higher (Fig. 2).

Temperature and carbon storage in moist tropical evergreen forests

Results of our analyses are consistent with the hypothesis that warmer temperatures stimulate faster mineralization of SOC to CO₂, potentially providing a positive feedback to global warming (e.g., Schleser 1982). However, observed decreases of ~8 Mg C·ha⁻¹·°C⁻¹ in detrital carbon stocks were counterbalanced by increases in living vegetation that averaged 5–13 Mg C·ha⁻¹·°C⁻¹ (Table 1). Total carbon stocks in mature

evergreen moist tropical forests did not vary with temperature ($P = 0.78$; Fig. 4A, Appendix E), suggesting no net impact of changing atmospheric temperature on total carbon storage in these forests. There was, however, a fundamental change in carbon stocks among forests: most of the carbon in lowland tropical forests is in living trees; most of the carbon in montane forests is in soils (Fig. 4B). This finding is consistent with studies on Mount Kinabalu (Kitayama and Aiba 2002b), but applies more generally. It is widely recognized that montane and lowland tropical forests differ from one another (e.g., Richards 1952, Whitmore 1975), and the reasons for these differences have long been discussed (e.g., Leigh 1975, Grubb 1977, Vitousek and Sanford 1986). Our analyses do not preclude a role for other factors, but do suggest that the effects of temperature on forest growth and detritus decay are important in driving variations in the structure of tropical forests along elevational gradients.

Implications of warming in the tropics

The forests we included in our analyses cover $\sim 11 \times 10^6$ km², or $\sim 8\%$ of Earth's land surface, ca. 2000 (Hansen et al. 2000, FAO 2001). Mean carbon stocks in tropical and subtropical forests include 121 Mg C/ha in vegetation and 123 Mg C/ha in the surface 1 m of soil (Dixon et al. 1994). Our analyses (Table 1) suggest that a 1°C increase in MAT could result in the eventual net transfer of ~ 8 Pg of soil organic carbon from moist evergreen tropical forests to the atmosphere, but that this could be offset by an equivalent increase in forest biomass, as pointed out by Kitayama and Aiba (2002a). Such an offset is unlikely, however. Tropical deforestation averaged 14.2×10^6 ha/yr from 1990 to 2000, and the remaining forests are becoming increasingly degraded. Forest fragmentation, logging within forests, and fires have all contributed to a decline in the biomass of standing forests in recent years (Laurance et al. 1997, Nepstad et al. 1999, FAO 2001). As much as 60% of the tropical forestland area has already been disturbed by humans, and has less-than-potential biomass (Houghton et al. 1993). Our results indicate that tropical evergreen forests subject to warming are likely to lose soil C: warming-induced increases in forest biomass are unlikely to compensate.

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APPENDIX A

Published measurements of aboveground fine litter production (litterfall) in mature moist broad-leaved evergreen tropical forests (*Ecological Archives* E087-002-A1).

APPENDIX B

Data for aboveground tree biomass, growth (i.e., biomass increment), and fine litter production in mature moist broad-leaved evergreen tropical forests (*Ecological Archives* E087-002-A2).

APPENDIX C

Measured rates of aboveground fine litter production and total soil respiration in mature moist broad-leaved evergreen tropical forests (*Ecological Archives* E087-002-A3).

APPENDIX D

Aboveground fine litter production rates and surface fine litter accumulations in mature moist broad-leaved evergreen tropical forests (*Ecological Archives* E087-002-A4).

APPENDIX E

Data on carbon storage in mature moist broad-leaved evergreen tropical forests (*Ecological Archives* E087-002-A5).

APPENDIX F

The references cited in the appendices (*Ecological Archives* E087-002-A6).