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Field-quantified responses of tropical rainforest aboveground productivity to increasing CO₂ and climatic stress, 1997–2009

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[1] A directional change in tropical-forest productivity, a large component in the global carbon budget, would affect the rate of increase in atmospheric carbon dioxide ([CO₂]). One current hypothesis is that “CO₂ fertilization” has been increasing tropical forest productivity. Some lines of evidence instead suggest climate-driven productivity declines. Relevant direct field observations remain extremely limited for this biome. Using a unique long-term record of annual field measurements, we assessed annual aboveground net primary productivity (ANPP) and its relation to climatic factors and [CO₂] in a neotropical rainforest through 1997–2009. Over this 12 year period, annual productivity did not increase, as would be expected with a dominant CO₂ fertilization effect. Instead, the negative responses of ANPP components to climatic stress far exceeded the small positive responses associated with increasing [CO₂]. Annual aboveground biomass production was well explained (73%) by the independent negative effects of increasing minimum temperatures and greater dry-season water stress. The long-term records enable a first field-based estimate of the [CO₂] response of tropical forest ANPP: 5.24 g m⁻² yr⁻¹ yr⁻¹ (the summed [CO₂]-associated increases in two of the four production components; the largest component, leaf litterfall, showed no [CO₂] association). If confirmed by longer data series, such a small response from a fertile tropical rainforest would indicate that current global models overestimate the benefits from CO₂ fertilization for this biome, where most forests’ poorer nutrient status more strongly constrains productivity responses to increasing [CO₂]. Given the rapidly intensifying warming across tropical regions, tropical forest productivity could sharply decline through coming decades.

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1. Introduction

... the timing and magnitude of any projections of tropical forest cover will depend strongly on modelled response to higher temperatures, elevated CO₂ concentrations and changes in precipitation regimes. Physiological processes, rather than differences amongst climate projections, dominate uncertainties in the amount of future carbon accumulation in undisturbed tropical forests... [Huntingford *et al.*, 2013].

In the absence of sufficient data to constrain the high temperature plant responses, particularly in tropical ecosystems..., the under-constrained response of terrestrial carbon cycling will remain a leading order uncertainty for future projections of atmospheric CO₂ concentrations. [Booth *et al.*, 2012].

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[2] Tropical forest net primary productivity (NPP: photosynthetic carbon [C] uptake minus plant respiratory C losses), a large but poorly understood contributor to the C balance of the land tropics [Clark *et al.*, 2001a; Denman *et al.*, 2007; Huston and Wolverton, 2009; Davidson *et al.*, 2012; Booth *et al.*, 2012], plays a major role in the global C budget [Clark *et al.*, 2003; Denman *et al.*, 2007]. A directional increase or decrease in tropical forest NPP would respectively slow or speed up the rise in atmospheric carbon dioxide levels ([CO₂]) [Clark *et al.*, 2003; Adams and Piovesan, 2005; Denman *et al.*, 2007; Booth *et al.*, 2012] while also changing the energy base for the biome’s exceptional biodiversity. One current hypothesis, based on theoretical expectations and observations of increased biomass stocks in forest plots, is that tropical forest NPP has been increasing, possibly due to “CO₂ fertilization” [Lloyd and Farquhar, 2008; Lewis *et al.*, 2009a; but see Silva and Anand, 2013; Chave *et al.*, 2008; Clark *et al.*, 2010; Wright, 2012]. Other lines of evidence (see below) instead highlight recent negative climatic effects. Contrasting projections for this biome by different dynamic vegetation models reflect persistent uncertainty about these forests’ responses to climatic factors and to increasing [CO₂] [Galbraith *et al.*, 2010; Cox *et al.*, 2013; Huntingford *et al.*, 2013].

[3] The accumulating evidence points to negative impacts on tropical forest NPP from current levels of climatic

stressors. The close parallel between tropical temperatures and annual $[\text{CO}_2]$ changes during 1960–2003 (after factoring out anthropogenic inputs) [Adams and Piovesan, 2005; Cox *et al.*, 2013] suggests that global tropical NPP decreased in the warmer years of recent decades. Tropical NPP reductions in 2000–2009 due to high temperatures and associated water stress were inferred in analyses based on remote-sensed data and modeling [Zhao and Running, 2010]. Recent field studies in tropical forests have linked higher temperatures and/or greater water stress to reduced forest- and leaf-level net C uptake [Loescher *et al.*, 2003; Goulden *et al.*, 2004; Tribuzy, 2005; Doughty and Goulden, 2008; Vourlitis *et al.*, 2011], reduced tree growth [Clark *et al.*, 2003, 2010; Brando *et al.*, 2008; da Costa *et al.*, 2010; Gliniars *et al.*, 2013; Silva and Anand, 2013], and increased tree mortality [Phillips *et al.*, 2009; Clark *et al.*, 2010; da Costa *et al.*, 2010].

[4] Until now, the biome has lacked the long field data series required for quantifying the trend and environmental responses of tropical forest NPP [Clark and Clark, 2010]. Long-term local climatic and soil moisture records are rare [Fung *et al.*, 2005; Phillips *et al.*, 2009; Clark and Clark, 2010], and productivity data are typically restricted to single NPP components, from single plots, and based on short periods or few re-measurements [Clark *et al.*, 2001b; Aragão *et al.*, 2009; Huston and Wolverton, 2009].

[5] In an old-growth lowland tropical rainforest (La Selva, Costa Rica), we field-measured annual aboveground net primary productivity (ANPP* [Clark *et al.*, 2001a]: fine litterfall [reproductive, twig, and leaf litterfall] + estimated aboveground biomass increment) through the period 1997–2009 and assessed its relation to annual $[\text{CO}_2]$ and local climatic variation. These long field data series (12 yearly data points) for all ANPP* components make possible the first assessment of the directional trend and climatic and $[\text{CO}_2]$ responses of annual ANPP* in a tropical forest (our prior analyses of earlier data from this long-term study [Clark *et al.*, 2010] were restricted to a single ANPP* component). In the present study we show that ANPP* did not increase over this 12 year period, contrary to what would be expected with a dominant CO_2 fertilization effect [Lloyd and Farquhar, 2008; Lewis *et al.*, 2009a]. Only two of the four ANPP* components showed evidence consistent with a (small) benefit from increasing $[\text{CO}_2]$. The strong negative impacts from recent levels of two climatic stressors, high temperatures and periods of high vapor pressure deficit (VPD), instead raise the possibility of a progressive decline in tropical forest productivity as these stressors rapidly intensify across tropical regions [Diffenbaugh and Scherer, 2011].

2. Materials and Methods

2.1. Study Site and Plot Network

[6] The study site is an approximately 500 ha area of old-growth lowland tropical rainforest at the La Selva Biological Station (NE Costa Rica, $10^\circ 26' \text{N}$, $83^\circ 59' \text{W}$, elevation range 37–150 m). La Selva is the NW terminus of approximately 100,000 ha of continuous forest (national park, national forests, and private reserves). The La Selva forest is classified as Tropical Wet Forest in the Holdridge Life Zone system [Hartshorn, 1983]. Over the study period, annual rainfall at La Selva averaged 4537 mm and the mean

annual temperature was 25.1°C (annual climatic data are given in Table S1 in the supporting information). Rainfall varies seasonally at La Selva, with notably lower rainfall in the four months January–April, based on the long-term averages [Sanford *et al.*, 1994]. We refer to this period as the annual “dry season”; however, the long-term mean rainfall for each of these 4 months exceeds 175 mm (<http://www.ots.ac.cr/meteoro/default.php?pestacion=2>). Overlying volcanically derived soils, La Selva is at the high-fertility end of the fertility range spanned by lowland neotropical forests [Powers *et al.*, 2005].

[7] The ANPP* measurements were carried out in the CARBONO Project (<http://www.ots.ac.cr/carbonoproject>) plots. This network of 18 0.5 ha plots (Figure S1) was designed to sample old-growth forest with replication on each of the three dominant edaphic conditions in the upland forest landscape (younger oxisol terrace, older oxisol plateau, and older oxisol slope; six plots each). La Selva’s geographic information system coverages (soils, digital elevation model) were used to site the plots across the landscape in an unbiased, random-block design [Clark and Clark, 2000].

2.2. ANPP* Methods

[8] From October 1997 to September 2009, we measured ANPP* in all 18 plots (the annual plot-level production data are given in Table S2). ANPP*, the estimate of annual aboveground NPP based on best practice field measurements [Clark *et al.*, 2001a; Huston and Wolverton, 2009] represents a large but unknown fraction of total NPP. It omits several aboveground components as well as all belowground NPP (which is potentially large and time varying), due to intractable methods challenges for yearly monitoring (see Figure S2).

[9] Fine litterfall (leaves, twigs < 1 cm in diameter, reproductive material) was collected biweekly beginning in October 1997. In each plot, fine litterfall was collected from nine 0.25 m^2 standing litterfall traps (height 0.80 m) and nine 0.25 m^2 ground-level traps for large litter items (largest dimension > 50 cm; e.g., palm fronds), which are poorly sampled by standing basket traps [Villela and Proctor, 2002]. The traps were set out across all plots at predetermined coordinates in a standardized regular array. If a tree or large branch subsequently fell onto a trap location, the trap was shifted horizontally the minimal distance needed to allow unimpeded litter collection. The standing traps were maintained and re-leveled if necessary at each biweekly collection. When a trap was compromised during a given collection period by blockage or trap damage (e.g., from tree or branch fall or animals), its contents were discarded and the plot-level litterfall rate for that collection was based on the reduced sampling area. For each biweekly collection, samples from all litter traps in a plot were combined, sorted by fine-litter category, and oven dried to constant mass at 65°C . Annual fine litterfall for each plot was the summed litterfall from the 26 collections in each measurement year (1 October, year 1, to 30 September, year 2).

[10] All live woody stems of ≥ 10 cm diameter (trees, palms, lianas; > 200 species per year) were mapped and identified at plot installation and then censused annually in September–November for recruits, mortality, and growth, beginning in September 1997. In each annual census, the diameter of all live woody stems of diameter ≥ 10 cm in each plot was measured with a fabric diameter tape at a permanently marked point of measurement (POM; 10 cm

below an aluminum nail in the bole) at 130 cm height above the ground or above any buttresses or stem irregularities; measurements at the higher POMs were made using one to four 3 m tall portable ladders [cf. Clark, 2002]. Tape replacements during each census were based on regular (every hectare) tape calibrations against a metal meter stick. Each year the precision of the diameter measurements was quantified by re-measuring approximately 80 stems after an interval of at least 1 day (for years 1–10, 77% of re-measurements were identical and 99% were within 1 mm [Clark *et al.*, 2010]). Plots were measured in the same sequence every year. In a year when a tree's POM was judged to be threatened by upward “buttress-creep” or other encroaching irregularities, double measurements were taken (at the original POM and at a new POM higher on the bole) to maintain continuity of the tree's increment record. The diameter measurement protocols and data quality-control were as further detailed by Clark and Clark [2006]. Each year, the aboveground biomass of each live woody stem ≥ 10 cm in diameter was estimated from its diameter using the Tropical Wet Forest biomass allometric equation of Brown [1997], which was based on 175 harvested trees, 100 of which were harvested < 30 km from La Selva. Each tree's estimated annual aboveground biomass increment was calculated as the difference between successive annual biomass estimates and then annualized (multiplied by $[365/(\text{actual days between measurements})]$). The Brown [1997] allometry produces an estimate of landscape-level aboveground biomass increment at La Selva within 8% of that calculated with an alternative tropical wet forest allometry [Chave *et al.*, 2005] that incorporates species- or genus-level wood densities for all stems (for this comparison, we used the most local wood-density data available for each species from a large global tropical compilation [Zanne *et al.*, 2009] and other sources; $r^2 = 0.94$ between the two allometric biomass estimates for each tree, Figure S3). For trees with a POM change(s) during the 12 year period, subsequent yearly estimates for biomass and biomass increment were based on the tree's last diameter measurement at the original POM, augmented by the subsequent annual diameter increments; this calculation prevents progressive biomass underestimation when the POM is moved up the bole, where diameter may be reduced by bole taper. Each year's plot-level estimate of aboveground biomass increment (henceforth “wood production”) was calculated as the sum of the estimated annual increments in aboveground biomass by all surviving woody stems ≥ 10 cm in diameter in the plot, with a further adjustment for recruits (new stems ≥ 10 cm in diameter that year in the plot). The annual biomass increment of each recruit in their first year of inclusion was calculated as their end-of-year estimated aboveground biomass minus that of a 10 cm diameter tree [Clark *et al.*, 2001a].

2.3. Meteorological and [CO₂] Data and the Derived Annual Metrics

[11] Local meteorological records covering the entire study period were from the La Selva weather station, a ground-based automated system recording both 30 min and daily data from sensors for air temperature and relative humidity, rainfall (tipping-bucket), and total radiation (pyranometer), with parallel manual data for daily rainfall (pluviometer) and daily maximum and minimum air temperature (maximum and minimum thermometers supplied and calibrated by the Instituto Meteorológico de Costa Rica). Data screening (D. A. Clark)

consisted of between-record cross-checks (30 min versus daily data, automated versus manual data, comparison with parallel above-canopy data from one or more above-canopy towers at La Selva). Cross-sensor regressions were used to replace questionable data and fill data gaps, producing complete daily records for the 12 years (downloadable documented files at <http://www.ots.ac.cr/meteoro/default.php?pestacion=2>). In addition, we monitored volumetric soil moisture at 0–30 cm depth in each of the 18 plots with a Campbell CS615 frequency domain reflectometry sensor buried vertically in the center of each plot; sensors were read biweekly beginning March 1998, with some limited data gaps during the 12 year period. From these data, annual climatic metrics (Tables 1 and S1) were calculated based on each 12 month ANPP* measurement year (1 October, year 1, to 30 September, year 2) and on the included 4 month “dry season”(January–April).

2.4. Data Analysis

[12] We tested for trends and responses of landscape-scale ANPP* using the program JMP 8.0 (SAS Institute). Interyear variation in productivity metrics was first assessed based on the plot-level data (Figure S4), in tests controlling for the repeated measures from individual plots (Friedman two-way nonparametric tests and one-way repeated measures analysis of variance with the Univar G-G correction, testing the 18 plot-level values each year for a year effect). Given the significant interyear variation (see section 3.4), we then tested each landscape-scale productivity metric (annual means of data from the 18 plots for total ANPP* and each of its four components) for directional change and for climatic/[CO₂] responses. We used simple linear regression with a priori predictions of effect direction for all factors but year (positive effect assumed for light, water, [CO₂]; negative effect assumed for temperature).

[13] Based on analysis of cross correlations among all climatic metrics to identify the most informative factors, a subset was selected of 16 annual metrics related to temperature, light, and water limitation, the climatic drivers expected to most influence tropical forest productivity [Nemani *et al.*, 2003; Doughty and Goulden, 2008; Lewis *et al.*, 2009a; Way and Oren, 2010; Zhao and Running, 2010]. Two metrics involved air temperatures above 28°C, above which leaf- and ecosystem-level C uptakes have been found to decline in tropical forests [Loescher *et al.*, 2003; Goulden *et al.*, 2004; Tribuzy, 2005; Doughty and Goulden, 2008; Vourlitis *et al.*, 2011]. We also included mean temperature because of its widespread use in dynamic vegetation models. The 16 selected annual climatic metrics, plus the annual means for atmospheric [CO₂] (annualized from monthly atmospheric [CO₂] from the Mauna Loa record, <http://scrippsco2.ucsd.edu>), constituted the standard set of 17 factors (Table 1) used to evaluate environmental responses of annual ANPP* and its components. The annual values of these factors are given in Table S1.

[14] We tested each productivity metric for a significant relationship with each of the 17 environmental metrics (simple linear regression). We further used two-factor linear least squares models to enable detection of independent effects from pairs of significant drivers with opposing effects and/or contrasting patterns of interannual variation. In such cases, each factor's individual effect could be missed or diluted in simple one-factor tests due to the uncontrolled for effects of a second important driver. Because maximum and minimum temperatures can differentially affect plant

Table 1. The Climatic and [CO₂] Metrics Assessed for Relationships With Annual ANPP*

| Factor | Definition | Maximum | Minimum | Range/Mean |
|--------------------------------------|--|------------|------------|------------|
| <i>Temperature</i> | | | | |
| 1. Daily mean T | Annual mean of daily mean air temperature | 25.55°C | 24.58°C | 4% |
| 2. Daily maximum T | Annual mean of daily maximum air temperature | 31.93°C | 30.15°C | 6% |
| 3. Daily minimum T | Annual mean of daily minimum air temperature | 22.27°C | 21.34°C | 4% |
| 4. Daily daytime T | Annual mean of hourly mean air temperature from 0600–1800 h | 27.65°C | 26.50°C | 4% |
| 5. Daily nighttime T | Annual mean of hourly mean air temperature from 1800–0600 h | 23.48°C | 22.62°C | 4% |
| 6. Daily Tsum >28°C | Annual mean, daily Σ (mean hourly temperature – 28°C), for daytime hours (0600–1800) with mean air temperature > 28°C | 15.65°C | 7.92°C | 67% |
| 7. Dry season Tsum >28°C | Jan–Apr mean, daily Σ (mean hourly temperature – 28°C), for daytime hours (0600–1800) with mean air temperature > 28°C | 14.43°C | 6.62°C | 72% |
| <i>Light</i> | | | | |
| 8. Daily radiation | Annual mean of daily total radiation (pyranometer) | 15.52 MJ/d | 13.01 MJ/d | 18% |
| 9. Dry-season daily radiation | Jan.–Apr. mean of daily total radiation (pyranometer) | 16.47 MJ/d | 13.59 MJ/d | 19% |
| <i>Water</i> | | | | |
| 10. Annual rainfall | Total 12 month rainfall | 6550 mm | 3282 mm | 72% |
| 11. Dry-season rainfall | Total rainfall during Jan.–Apr. | 1431 mm | 396 mm | 104% |
| 12. Dry-season soil moisture deficit | Σ [(biweekly volumetric soil moisture at 0–30 cm depth) - 43%, the upper limit of the lowest decile of all readings], for the across-plot means of all biweekly readings in Jan.–Apr. that were below 43% | 0.0% | –24.0% | 336% |
| 13. Daily minimum RH | Annual mean of the lowest daily hourly mean for relative humidity (%) | 78.64% | 61.15% | 24% |
| 14. Daily mean VPD | Annual mean of daily average vapor pressure deficit, based on hourly means for air temperature and RH (0600–1800 h) | 1.01 kPa | 0.43 kPa | 94% |
| 15. Annual high VPD | Annual mean of the daily proportion of the 12 daytime hrs (0600–1800) with mean hourly vapor pressure deficit > 1 kPa | 0.46 | 0.17 | 112% |
| 16. Dry-season high VPD | Jan–Apr mean of daily proportion of the 12 daytime hours (0600–1800) with mean hourly vapor pressure deficit > 1 kPa | 0.55 | 0.19 | 110% |
| <i>CO₂</i> | | | | |
| 17. Atmospheric [CO ₂] | Mean of the 12 monthly means of Mauna Loa [CO ₂] | 386.9 ppmv | 365.7 ppmv | 6% |

productivity [cf. *Welch et al.*, 2010], a two-factor model combined them. To test for [CO₂] mitigation of physiological stress, two-factor models combined [CO₂] with temperature and water metrics. A standard set of 82 two-factor models (Table S3) was used to test for climatic/[CO₂] responses of landscape-scale ANPP* and its components.

[15] Because of the large number of tests, the threshold significance level for a predictive model was set at $P_{1\text{-tail}} \leq 0.02$ for one-factor models and at $P_{1\text{-tail}} \leq 0.01$ for both factors in two-factor models (a two-factor model was considered significant when both factors were significant at this level in the model). These arbitrary thresholds compromise between the highly conservative threshold resulting from the Bonferroni correction ($P_{1\text{-tail}} \leq 0.001$ required for significance in the 18 single-factor tests [climatic factors/[CO₂]/year]; $P_{1\text{-tail}} \leq 0.0003$ required for significance in the 82 two-factor tests), which increases the likelihood of missing a true relation, and a too-liberal significance level, which increases the likelihood of accepting spurious relationships, a risk that increases with the number of tests (one or more models, particularly those with marginal P values, could by chance indicate a relation that does not actually exist). The model results serve both (1) to identify those factors with no detectable effect on annual productivity and (2) to reveal the likely environmental contributors to the observed interannual changes in productivity.

3. Results

3.1. Assessing Forest Productivity: Single Plots Versus the Landscape

[16] The observations of annual productivity were sensitive to spatial scale and replication. While the interyear range in

landscape-scale ANPP* (annual across-plot means from the eighteen 0.5 ha plots; Figure 1) was only 1.38 Mg ha^{−1} yr^{−1} (10.3% of the 12 year mean), annual ANPP* varied more than 100% (range: 8.72–19.94 Mg ha^{−1} yr^{−1}; Figure S4) at the level of individual plots. Similarly, the contributions to total ANPP* from individual components varied far less at the landscape scale (Figure 1) than they did at the scale of individual plots (Figure 2). Wood production, for example, constituted as little as 18% and as much as 48% of annual ANPP*

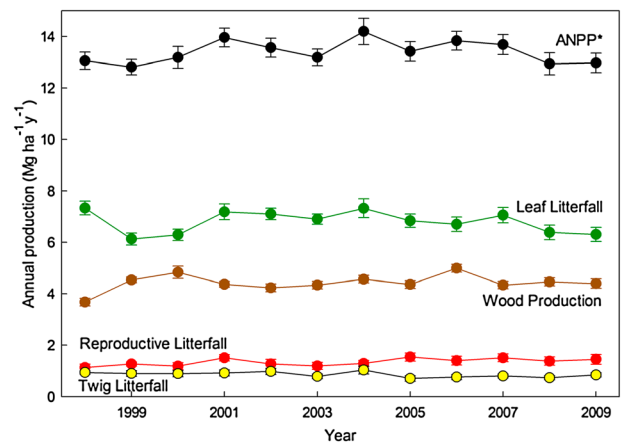


Figure 1. Landscape-scale ANPP* and its four components at La Selva, Costa Rica, over the 12 year study period. x axis: year 2 of each measurement year (1 October, year 1, to 30 September, year 2). Error bars indicate ± 1 SEM for each annual cross-plot mean ($N = 18$ plots).

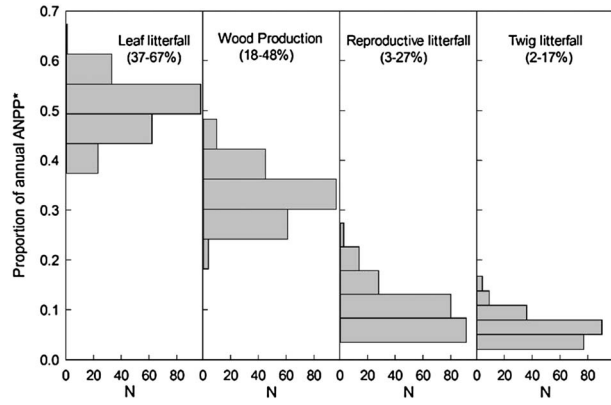


Figure 2. Contributions to ANPP* from its four constituents at the level of individual plots. The plot-level constituents (proportion of annual ANPP*; 18 plots in each of 12 years, $N=216$ plot years; data in Table S2) varied strongly, spanning a much wider range than seen among years at the landscape scale (Figure 1).

in given years at the plot level; the other three components showed similarly wide variation among individual plots (Figure 2). Our analyses of trends and climatic/[CO₂] responses are therefore all at the landscape scale.

3.2. ANPP* Composition

[17] Short-lived tissues (leaf, twig, and reproductive litterfall) together dominated landscape-scale ANPP* in all years (Figures 1 and 2), as also seen in 32 other tropical forests with short-term data for all ANPP* components [Clark *et al.*, 2001b; Malhi *et al.*, 2004; Aragão *et al.*, 2009; Huston and Wolverton, 2009; Girardin *et al.*, 2010]; the Indonesian lowland forests studied by Paoli and Curran [2007] are an exception. As found across tropical forests [Clark *et al.*, 2001b; Chave *et al.*, 2010], fine litterfall was predominantly leaves (73–78%). Wood production comprised 28–37% of landscape-scale ANPP* (Figure 1).

3.3. Interannual Environmental Variation

[18] The years of the study period spanned diverse climatic conditions (Tables 1 and S1). They included a strong El Niño (1997–1998), the protracted 1998–2000 La Niña, and two record-hot years (1998, 2005). Although daily minimum temperatures have strongly increased since 1983 at La Selva (D. A. Clark, unpublished data), within our 12 year study period the annual means for daily minimum, maximum, and mean air temperature all showed no significant trend. At La Selva, the last 2 years (2007/2008 and 2008/2009) were notably cooler than several earlier years in the study period (Table S1), as they were across the global land tropics (<http://data.giss.nasa.gov/gistemp/>). Factors related to water limitation varied strongly through the study period, with a more than threefold range in dry-season (January–April) rainfall and soil moisture deficit and a more than twofold range in metrics based on annual and dry-season VPD. In the last 3 years (2006/2007–2008/2009) annual means for daytime VPD metrics at La Selva (Table S1) were higher, and annual means for actual vapor pressure were lower (D.A. Clark, unpublished data), than in the earlier 9 years. Over the 12 year period, [CO₂] increased from 366 to 387 ppmv.

3.4. Interannual Variation in Forest Productivity

[19] The annual data from the 18 plots (Figure S4 and Table S2) indicated significant interannual variation through the study period for total ANPP* and for each of its four components on this tropical forest landscape (Friedman test: $P < 0.001$ [ANPP*, leaf litterfall, wood production, twig litterfall], $P < 0.01$ [reproductive litterfall]; repeated measures analysis of variance: $P < 0.001$ [leaf litterfall, wood production,], $P < 0.01$ [ANPP*], and $P < 0.05$ [twig litterfall, reproductive litterfall]).

[20] Strikingly, the four components of landscape-scale ANPP* varied individually through the study period (Figure 1). There were no significant correlations between components across the 12 years (Pearson's r , six pairwise tests of d.f. = 12, $P_{2\text{-tail}} = 0.09\text{--}0.97$).

Table 2. The Significant 1- and 2-Factor Models of the Interyear Variation in ANPP* at La Selva, Costa Rica During 1997–2009

| Production Model | Model r^2 | Factor ^a | Sign of Effect | $P_{1\text{-tail}}$, factor | N (years) |
|--|-------------|--------------------------------------|----------------|------------------------------|-----------|
| <i>Wood Production</i> | | | | | |
| (1) | 0.73 | (1) Daily minimum T | - | 0.0006 | 12 |
| (2) | 0.71 | (2) Dry-season high VPD | - | 0.003 | |
| | | (1) Daily minimum T | - | 0.005 | 10 |
| | | (2) Dry-season soil-moisture deficit | - | 0.01 | |
| (3) | 0.63 | Dry-season rainfall | + | 0.001 | 12 |
| (4) | 0.36 | Daily mean T | - | 0.02 | 12 |
| (5) | 0.35 | Daily minimum T | - | 0.02 | 12 |
| <i>Leaf Litterfall (No Significant Models)</i> | | | | | |
| <i>Twig Litterfall</i> | | | | | |
| (6) | 0.48 | Daily maximum T | - | 0.006 | 12 |
| (7) | 0.40 | T sum > 28°C | - | 0.01 | 12 |
| <i>Reproductive Litterfall</i> | | | | | |
| (8) | 0.40 | Atmospheric [CO ₂] | + | 0.01 | 12 |
| <i>ANPP* (No Significant Models)</i> | | | | | |

^aFactor definitions are given in Table 1.

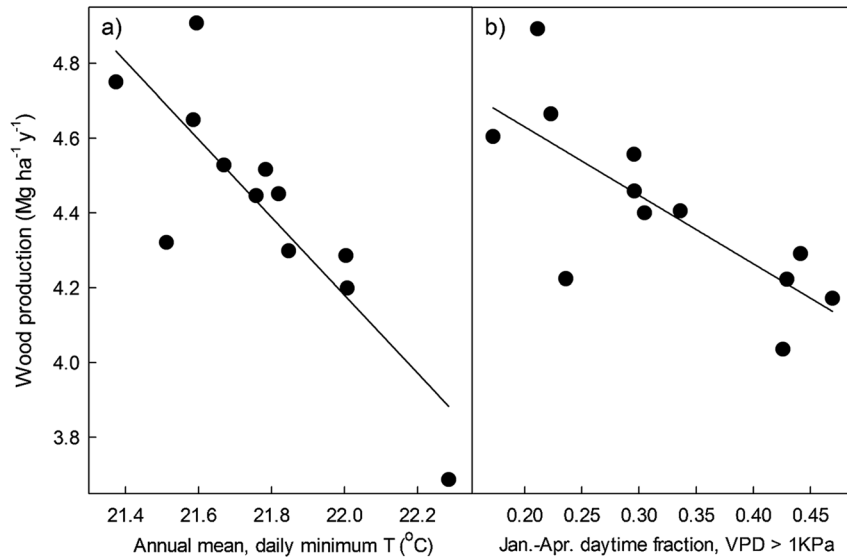


Figure 3. The strongest two-factor model of annual wood production (Model 1, Table 2), indicating marked reductions in annual wood production with both (a) higher minimum temperatures and (b) greater dry-season VPD. These partial regression plots indicate the effect of each factor on wood production, when controlling for the variation in the second factor: annual mean of daily minimum temperatures, $P_{1\text{-tail}} = 0.0006$; the proportion of dry-season daytime hours with high VPD, $P_{1\text{-tail}} = 0.003$.

3.5. Long-Term Productivity Trends

[21] Landscape-scale ANPP* in this forest showed no directional change over the 12 year period (annual ANPP* versus year, Pearson's $r = 0.10$, d.f. = 12, $P_{2\text{-tail}} = 0.75$). Three of the four ANPP* components similarly showed no long-term trend (leaf litterfall versus year: Pearson's $r = -0.19$, d.f. = 12, $P_{2\text{-tail}} = 0.56$; wood production versus year: Pearson's $r = 0.29$, d.f. = 12, $P_{2\text{-tail}} = 0.36$; twig litterfall versus year: Pearson's $r = -0.55$, d.f. = 12, $P_{2\text{-tail}} = 0.06$). For only one minor ANPP* component, reproductive litterfall, was the 12 year data series consistent with directional change (an increase; Pearson's $r = 0.64$, d.f. = 12, $P_{2\text{-tail}} = 0.02$).

3.6. Climatic and [CO₂] Responses of Annual Productivity

[22] The significant models linking the interannual variation in landscape-scale productivity to environmental factors (see section 2.4) are presented in Table 2. They indicate individualistic climatic and [CO₂] responses from the different constituents of annual ANPP*. Temperature, water limitation, and [CO₂] all appeared as a significant driver in one or more models. Notably, annual radiation metrics did not contribute to any significant model.

[23] For the production of long-lived tissues (wood production), the significant climatic models (Table 2) were all related to two classes of stressors: higher temperatures and water limitation. The interyear variation in wood production was well explained by two 2-factor models ($r^2 = 73\%$ and 71% , respectively) that identified independent negative effects of higher year-round minimum temperatures and either of two aspects of dry-season water limitation: increased prevalence of high-VPD conditions (Model 1: Figure 3) or greater soil moisture deficit (Model 2: Figure S5). The latter model was based on 10 (not 12) years of data due to gaps in

the soil moisture record, and, perhaps due to the shorter data series, the factor-level probabilities were notably greater than those of Model 1.

[24] In contrast, for the short-lived constituents of ANPP* (leaf, twig, and reproductive litterfall), no significant model was based on a metric related to water stress (Table 2). Two significant models indicated negative temperature impacts on annual twig litterfall, but from higher daytime, rather than nighttime, temperatures (Table 2). For annual leaf litterfall, the largest ANPP* component, lower values in four of the cooler years (Figure 4) produced a weak increase with minimum temperatures (but nonsignificant, given the a priori expectation of a negative relationship; for a two-tailed expectation, P would have been 0.029).

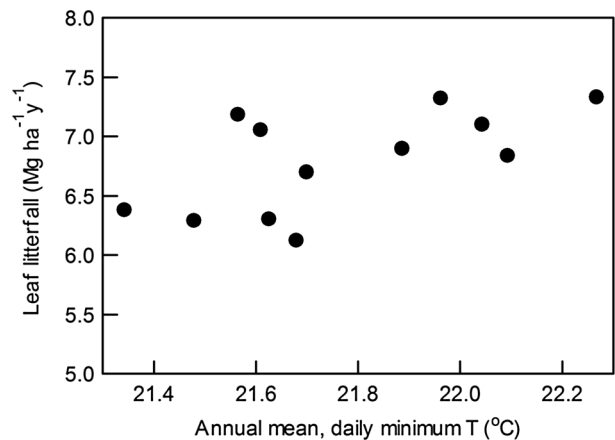


Figure 4. The relation of annual leaf litterfall to yearly means of daily minimum temperatures through the 12 year period 1997–2009.

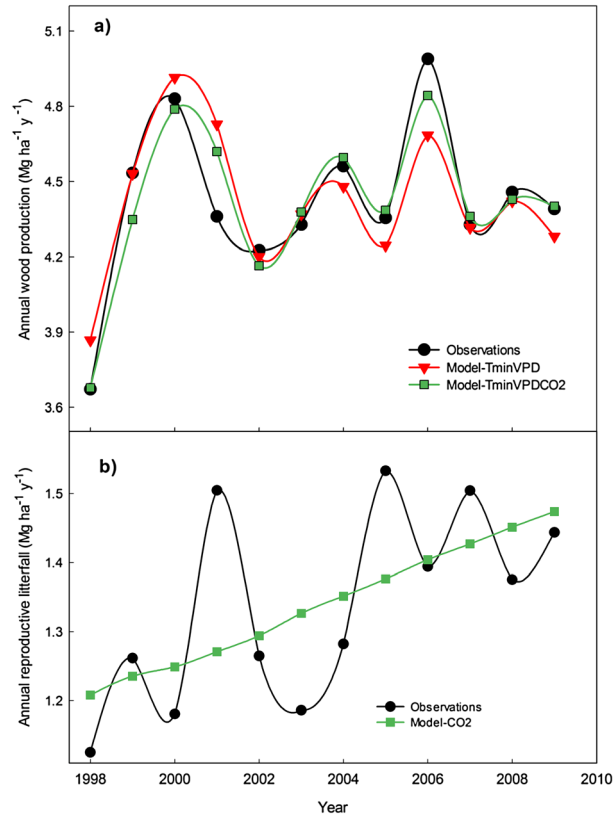


Figure 5. Observed and modeled interyear variation in the two $[\text{CO}_2]$ -associated ANPP* components: (a) wood production (*TminVPD*: Model 1, Table 2; *TminVPDCO2*: $[\text{CO}_2]$ added to Model 1 as a third factor; see text) and (b) reproductive litterfall (CO_2 : Model 8, Table 2). The x axes as in Figure 1.

[25] To assess the relationship of annual production with increasing $[\text{CO}_2]$, we evaluated for each productivity metric (1) a linear regression on annual $[\text{CO}_2]$ and (2) 16 two-factor models that combined annual $[\text{CO}_2]$ with each of the 16 climatic metrics (Table 1). Wood production, leaf litterfall, and twig litterfall all showed no significant association with annual $[\text{CO}_2]$ in these models. When, however, $[\text{CO}_2]$ was added as a third factor to the strongest climatic model for annual wood production (Model 1, Table 2), the model r^2 rose to 0.88 and the negative relationships with minimum temperatures and dry-season VPD both notably sharpened (to $P_{1\text{-tail}} = 0.00015$; see Figures S6 and S7 for full statistical output). With 95% confidence intervals, the modeled declines in annual wood production were $0.949 \pm 0.367 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ per degree C increase in annual means of daily minimum temperatures, and $0.026 \pm 0.010 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ per additional percent of the dry-season daytime period with hourly VPD averaging $> 1 \text{ kPa}$. With both climatic factors controlled for, this model indicated a highly significant increase in annual wood production with increased annual $[\text{CO}_2]$ ($0.021 \pm 0.015 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ per additional ppmv of annual $[\text{CO}_2]$; $P_{1\text{-tail}} = 0.006$). The already good fit of Model 1 to the observed interyear changes in wood production was notably improved by the incorporation of $[\text{CO}_2]$ as a third factor (Figure 5a). In the case of reproductive litterfall, simple linear regression indicated a production increase of $0.012 \pm 0.011 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ per ppmv of annual $[\text{CO}_2]$ over the 12 years (Model 8, Table 2), but with a poor fit to the actual interannual variation (Figure 5b). For both production components, the $[\text{CO}_2]$

association weakened or disappeared when the model was based on shorter data series (Table 3). Over the total 12 year study period, total ANPP* showed no hint of an association with annual $[\text{CO}_2]$ (simple linear regression: d.f. = 12, $r^2 = 0.01$, $P_{1\text{-tail}} = 0.40$).

Table 3. The Effect of Data Series Length (N, Annual Re-Measurements) on Factor Significance (P) in the Two Models Indicating a $[\text{CO}_2]$ Response

| Production Metric | Factor | Sign of Effect ^a | P , Factor ^b | | |
|--------------------------------------|---------------------------|-----------------------------|---------------------------|----------|----------|
| | | | 8 Years | 10 Years | 12 Years |
| Wood Production ^c | 1) Daily minimum T | - | 0.02 | 0.001 | 0.00015 |
| | 2) Dry-season high VPD | - | 0.18 | 0.003 | 0.00015 |
| | 3) Annual $[\text{CO}_2]$ | + | 0.29 | 0.02 | 0.006 |
| Reproductive Litterfall ^d | 1) Annual $[\text{CO}_2]$ | + | 0.09 | 0.02 | 0.01 |

^aIn each case, the sign of the factor parameter was unchanged by data-series length.

^bOne-tail probability associated with the factor in the model.

^cProbabilities from the three-factor model (see section 3.6) are for each factor when controlling for the effects of the other two.

^dProbabilities from simple linear regression (Table 2, Model 8).

4. Discussion

4.1. Overview

[26] This study provides the first quantitative evaluation of the climatic/[CO₂] responses and long-term trend of tropical forest annual aboveground NPP based on direct field measurements of multiple NPP components at the landscape scale. It was made possible by La Selva's long data series for local climate, soil moisture, and annual ANPP* across a large old-growth tropical rainforest landscape. As emphasized by researchers working with global process models [Booth *et al.*, 2012; Huntingford *et al.*, 2013], such observations from this key biome are needed to help reduce large current uncertainties concerning future global climate and the fate of these extremely biodiverse ecosystems.

4.2. Impacts From Current Levels of Climatic Stress

[27] In this lowland tropical rainforest, large negative effects on the annual production of new aboveground biomass (wood production) were produced by two independently important classes of climatic stressors: higher temperatures and greater levels of dry-season water limitation (Figures 3 and S5). The marked interyear changes in this major ANPP* component during the 12 year study period were well explained ($r^2 = 0.73$; Figure 5a) by the joint effects of annual changes in both the annual means of daily minimum temperatures and the prevalence of high-VPD conditions during the dry season. Notably small ranges of both stressors were associated with large drops in wood production (Figure 3). Annual wood production decreased 22% with an increase of 1°C in the annual mean of daily minimum temperatures, and it dropped 13% as the prevalence of high-VPD (>1 kPa) conditions in the dry season increased from 17% to 47% of daytime hours. The ANPP* field data series from this old-growth tropical rainforest landscape thus provide direct support for inferences made in three recent studies based on remote-sensing and eddy-covariance data [Zhao and Running, 2010; Toomey *et al.*, 2011; Vourlitis *et al.*, 2011]. In these studies, inferred negative impacts on tropical forests (reduced photosynthesis, reduced NPP, or increased tree mortality) were attributed to the joint, independent effects of higher recent temperatures and increased VPD.

[28] These analyses based on the 12 year record have produced a more process-level understanding of the negative effects on wood production from water limitation than emerged from our earlier analysis [Clark *et al.*, 2010]. In that earlier study, dry-season (January–April) rainfall was found to be highly predictive of annual wood production (simple linear regression, $r^2 = 0.85$, $P_{1\text{-tail}} = 0.0001$, d.f. = 10). With a further 2 years, the simple linear regression between this climatic metric and annual wood production, while still highly significant, has less explanatory power ($r^2 = 0.63$; Table 2, Model 3). Instead, our analyses based on the longer record now reveal highly significant negative effects of two other water-based metrics, dry-season high VPD and dry-season soil moisture deficit (Table 2, Models 1 and 2), both of which are more directly interpretable in ecophysiological terms than is dry-season rainfall.

[29] Notably different climatic responses were shown by the short-lived ANPP* components at La Selva (Table 2). No significant model indicated water limitation as a driver of the observed interyear variation (Figure 1) in leaf litterfall, twig

litterfall, or reproductive litterfall. Reproductive litterfall also showed no response to the interannual temperature changes. Negative effects of higher temperatures were evident for twig litterfall, but for daytime, rather than nighttime, temperatures (Table 2). For leaf litterfall, the largest ANPP* component (Figure 1), reduced litterfall in four of the cooler years produced a (nonsignificant) positive relationship with annual means of daily minimum temperature (Figure 4).

[30] Because all the short-lived ANPP* components are surrogates rather than direct measures of current-year production, additional processes need to be considered [Clark *et al.*, 2001a]. Reproductive litterfall strongly underestimates actual reproductive production in tropical forests because of the heavy consumption of fruits and seeds by animals [Clark *et al.*, 2001a; Parrado-Rosselli *et al.*, 2006]. Interannual variation in the proportion of the year's seeds and fruits that is consumed and thus does not fall into the litterfall traps would produce additional noise for this ANPP* component. Similarly, in tropical lowland forests the biomass of dead twigs can be substantially reduced by pre-collection (on-branch) decomposition and/or resorption before the twigs fall into litterfall traps (e.g., 40% biomass reduction for twigs 0.5–1.0 cm in diameter [Edwards, 1977]). Tropical forest leaf litterfall may be an unreliable indicator of current-year production due to multiple factors: (1) significant pre-collection losses from both herbivory and decomposition; (2) the multiyear life spans of some subclasses of leaves (intensified leaf-shedding in a stressful dry season could involve leaves produced in multiple years); and (3) possible interyear variation in these factors [Clark *et al.*, 2001a]. These biotic processes clearly complicate efforts to measure the climatic and [CO₂] responses of annual production for these short-lived tissues in tropical forests. Quantifying the impacts of these unmeasured processes on the short-lived ANPP* components unfortunately remains intractable due to the lack of stand-level field data on these processes and their interannual variation.

[31] Several process-level inferences about C cycling in this forest nevertheless emerge from our findings.

[32] 1. A plausible interpretation of the strong negative association of wood production with the annual means of daily minimum temperature (as also found in two prior La Selva studies [Clark *et al.*, 2003, 2010]) is that the temperature sensitivity of nighttime plant respiration in this forest is a key current controller of stand-level aboveground biomass production. A notable feature of this negative temperature response by annual wood production at La Selva has been its constancy since 1984 [Clark *et al.*, 2003, 2010; present study], suggesting a lack of temperature acclimation by plant respiration in this forest through three recent decades.

[33] 2. The independent negative effect of dry-season high-VPD conditions implicates reductions in dry-season photosynthesis due to stomatal closure as a second important controller of annual biomass production.

[34] 3. In contrast, the negative associations between annual twig litterfall and higher daytime temperatures (Models 6 and 7, Table 2) suggest enhancement of pre-collection (on-branch) decomposition, rather than a climatic effect on production. Supporting this inference is the lack of association between high daytime temperatures and wood production, a climatically sensitive ANPP* component.

[35] 4. The possible temperature response of leaf litterfall merits a closer look. While lower leaf litterfall occurred in

four cooler years, in the remaining 8 years, leaf litterfall varied little while spanning most of the observed temperatures (Figure 4). A longer data series may resolve whether leaf litterfall consistently increases over this temperature range, or whether the 12 year pattern was a chance result of unmeasured biotic processes.

[36] 5. Solar radiation, a factor that has been hypothesized to drive annual productivity in tropical forests [e.g., *Clark and Clark*, 1994; *Nemani et al.*, 2003; *Wright and Calderon*, 2006; *Lloyd and Farquhar*, 2008], was unrelated to the interannual changes (Table 2) in any component of aboveground production; although leaf- and forest-level C exchange in these forests is highly responsive to high-frequency variation in light (e.g., at 30 min. intervals) [*Loescher et al.* 2003], the interyear variation in solar radiation at La Selva appears to not affect annual production.

[37] Given the individualistic responses shown by ANPP* components over the 12 year study period, it is not surprising that no climatic models (Table 2) explained the interyear changes in total ANPP* (Figure 1). Together these findings argue for a more nuanced representation of the climatic responses of tropical forest NPP in dynamic vegetation models. Process-model parameterization and validation of modeled NPP processes for this biome should not be based on field data for a single NPP component.

4.3. The [CO₂] Response of Forest Productivity

[38] The 12 year La Selva records for total ANPP* and for leaf and twig litterfall showed no evidence of a [CO₂] fertilization effect (see section 3.6). The data for the remaining two components, however, were consistent with stimulation by increasing [CO₂]. Although wood production was not associated with annual [CO₂] in the one- and two-factor models (as also found in the prior analyses [*Clark et al.*, 2010]), a highly significant [CO₂] response ($P_{1\text{-tail}} = 0.006$) was indicated by a three-factor model simultaneously controlling for the variation in annual means of minimum temperatures, in dry-season high VPD and in annual [CO₂]. This simple model explained 88% of the marked interyear changes in wood production during the study period (Figure 5a). The significant regression for reproductive litterfall (Figure 5b) was also consistent with a positive response to increasing [CO₂].

[39] Multiple caveats pertain to these relationships, however. To promote detection of forest responses, we set larger threshold probability values than prescribed by commonly used but conservative statistical standards (see section 2.4). Secondly, identifying the underlying cause of a directional response is difficult when more than one potential driver is monotonically increasing. The positive associations with annual [CO₂] shown by wood production and reproductive litterfall could instead stem from multiyear forest demographic changes, such as recovery from the impacts of the record-hot El Niño in year 1 (counter evidence, however, is the progressive increase in the significance of the [CO₂] responses with increasing length of data series; Table 3). The negative findings for two ANPP* components, while statistically robust given the liberal significance levels, might have resulted from noise produced by interyear changes in unmeasured biotic processes such as herbivory or decomposition (see above). As the data series lengthen in this ongoing study, some of these sources of uncertainty around the degree of [CO₂] response by ANPP* and its components

should be reduced or eliminated. Alternatively, however, one of the two ANPP* components showing no [CO₂] association, leaf litterfall, may be inherently unresponsive to increasing [CO₂]. The law of diminishing returns may preclude additional leaf production beyond that attained with canopy closure. Since leaf production dominates tropical forest ANPP, its lack of response would greatly reduce the [CO₂] response of total ANPP in this biome.

[40] These caveats notwithstanding, the record to date from La Selva provides a first opportunity to quantify possible CO₂ fertilization effects on NPP based on a long series of field observations (>10 annual censuses) in a tropical forest. The [CO₂]-associated production responses indicated by the significant models are 2.41 g m⁻² yr⁻¹ yr⁻¹ for reproductive litterfall (annualizing the modeled change over the 12 years); 2.83 g m⁻² yr⁻¹ yr⁻¹ for wood production (annualizing the increasing difference over the 12 years between production predictions from the two- and three-factor models); and 0 g m⁻² yr⁻¹ yr⁻¹ for leaf litterfall and twig litterfall. Thus, the total contemporary effect of increasing [CO₂] on ANPP* discernible from the long-term La Selva field records is 5.24 g m⁻² yr⁻¹ yr⁻¹. This quantity is of similar magnitude to the annual [CO₂] enhancements of total NPP (which also includes belowground NPP and unmeasured aboveground components; see Figure S2) estimated for Amazonian forests over a recent 18 year period from modeling experiments with two vegetation-process models [*Hashimoto et al.*, 2010]: 5.34 g m⁻² yr⁻¹ yr⁻¹ (LPJ); and 9.32 g m⁻² yr⁻¹ yr⁻¹ (Biome-BGC) (values converted to biomass assuming a 50% C fraction).

[41] This comparison suggests that current process models may be overestimating the [CO₂]-productivity response for the tropical forest biome. As a first approximation, the La Selva field-derived estimate could be viewed as a reasonable upper bound for the current [CO₂] response of tropical forest ANPP. La Selva's volcanically derived soils are at the high-fertility end of the tropical forest fertility spectrum [*Powers et al.*, 2005]. Given the lower fertility of most tropical forests (e.g., much of Amazonia), greater nutrient-limitation constraints on CO₂ fertilization would be expected to produce smaller productivity increases across most of the biome [*Townsend et al.*, 2011; *Fisher et al.*, 2012; *Goll et al.*, 2012].

[42] It is also instructive to relate our estimate of the [CO₂] response of wood production at La Selva to recent findings of increasing aboveground biomass in small plots distributed across Amazonia [*Phillips et al.*, 2008] and Africa [*Lewis et al.*, 2009b]. From their composite analyses based on the active plots in each interval, the authors estimated yearly increases in aboveground biomass of 0.62 and 0.63 Mg C ha⁻¹ yr⁻¹, respectively, for those two tropical forest regions. As recognized by these authors, changes over time in stand-level biomass are the net result of temporal changes in tree floristics, mortality rates, and growth. A further issue is the likelihood of an upward bias in estimates of biomass trends when the data are based on one or a few small plots in each landscape, due to the localized nature of disturbances (cf. [*Körner*, 2009]). The very small [CO₂]-associated rate of change we have estimated for wood production by La Selva's comparatively fertile forest, 0.01 Mg C ha⁻¹ yr⁻¹ yr⁻¹ (assuming a 50% C fraction) suggests that rising [CO₂] could account for very little of the remarkably large yearly biomass increases estimated for Amazonia and Africa in those studies [also see *Wright*, 2012].

4.4. Directional Change in Forest Productivity?

[43] The long-term field measurements of aboveground production at La Selva make it possible to directly test the hypothesis that CO₂ fertilization has increased tropical forest productivity over recent decades [Lloyd and Farquhar, 2008; Lewis et al., 2009a]. In addition to affecting the rate of atmospheric CO₂ accumulation [Clark et al. 2003; Adams and Piovesan, 2005; Denman et al., 2007; Booth et al., 2012], a directional change in primary production in this biome would produce many impacts on ecological processes and on the hyperdiverse biota in these ecosystems. A progressive increase in leaf litterfall, for example, would alter many aspects of forest biogeochemical cycles by changing the annual inputs of C and nutrients to the forest floor [Wood et al., 2012]. In the present study, however, we found no directional change in total ANPP* or in wood production, leaf litterfall, or twig litterfall. These findings from a tropical forest at the high-fertility end of the biome's fertility spectrum [Powers et al., 2005], where CO₂ fertilization would be expected to be at its strongest, do not support this hypothesis.

[44] For only one minor ANPP* component, reproductive litterfall (Figure 1), was the long-term La Selva data series consistent with an increase over time (Figure 5b). In another Central American lowland forest (Barro Colorado Island, Panama), a 17 year litterfall data series (for 1987–2003) [Wright and Calderon, 2006] indicated a progressive increase in the number of tree species flowering at any given time, but no long-term change in estimated annual seed production. Monitoring of reproductive production should be given high priority, in spite of this component's small contribution to total NPP. Directional change in the production of seeds and fruits in tropical forests would produce large impacts on the biodiverse consumer community and on forest nutrient cycling.

4.5. Take-Home Lessons

[45] The long-term measurements and analyses to date from this on-going study at La Selva provide several guides for investigating the trends and environmental responses of NPP in other tropical forests. For two distinct reasons, data uncertainty is greatly reduced when the measurements come from replicate plots distributed over the same forest landscape. When observations are based on a single plot, considerable noise can be introduced into the NPP record by episodic disturbance or other stochastic processes; in contrast, in field studies based on replicate plots, the important effects of localized forest disturbance are always included, but without masking the landscape-scale NPP signal. A second strength is statistical. As found in the current study (section 3.1), the much reduced uncertainty associated with the landscape-scale metrics, a benefit of the Central Limit Theorem, makes smaller effects detectable. As data series lengthen (the number of censuses at ≥ 1 year intervals, as opposed to years spanned), our ability increases to detect climatic and [CO₂] responses of ecosystem production [see also Clark and Clark, 2010]. When the two significant [CO₂] models were based on shorter segments of the La Selva data series, the significance of the involved drivers diminished or disappeared (Table 3). Quantifying ecosystem responses to climatic factors and to increasing [CO₂] based on field observations will require many successive re-censuses at annual or longer time steps. For the short-lived components

of ANPP*, unmeasured biological processes may contribute to interannual variation. For detection of a climatic/CO₂ response by these production components, the environmental driver(s) would need to dominate the noise introduced by those unmeasured processes. Annual data through one or more decades may be required to span a sufficient range in the environmental drivers for detecting their impacts, if such exist [see Clark and Clark, 2010, Figure 1]. There is a stark contrast between the many published model-driven analyses of climate-change impacts on tropical forests and the few analyses based on actual field measurements of production and climate. For this data-poor biome [Clark et al., 2001b; Townsend et al., 2011; Booth et al., 2012; Wood et al., 2012], we are in the exploratory phase for identifying the key climatic sensitivities of forest productivity based on field observations. At this stage, it is necessary to probe long-term field data series with diverse climatic metrics singly and in combination. An open mind and extensive climatic testing are likely to yield important surprises. Examples from this study include the lack of effect from changes in annual radiation, the strong negative effect of dry-season high VPD, and the recent decline in actual vapor pressure at La Selva. Mean temperature, commonly used in current global process models, was much less informative than more specific metrics (temperature sums $>28^{\circ}\text{C}$, daily minimum temperatures) that are more mechanistically revealing. Without the use of multiple-factor models, the most compelling climatic/CO₂ responses indicated by the long-term La Selva ANPP* data (e.g., Figures 3, 5a, and S5) would have been missed altogether due to the noise introduced by the uncorrelated interyear variation in the other important drivers. Finally, local meteorological data taken at hourly time-steps can be critical for identifying climatic drivers (e.g., the proportion of dry-season daytime hours with high VPD; Figure 3b). Without quality-control to ensure the long-term consistency of local climatic records, however, such data could actually be counter-productive for investigating the climatic responses of tropical-forest productivity [cf. Clark and Clark, 2010].

[46] How process-level understanding can deepen over the course of a long-term study is illustrated by comparing the climatic/[CO₂] responses we have now identified for annual wood production at La Selva, with those based on the first 10 annual measurements [Clark et al., 2010]. In both studies, annual wood production was found to be significantly associated with both minimum temperatures and dry-season rainfall. In the current study, however, the evidence of a strong negative effect of higher minimum temperatures was sharpened considerably (Table 2) when two-factor models controlled for the uncorrelated interyear variation in either of two ecophysiological interpretable metrics of water limitation. In contrast, dry-season rainfall, a strictly meteorological parameter, was unassociated with annual wood production in a two-factor model controlling for the interannual temperature changes during the 12 year period (Tables 2 and S3). Most notably, while no [CO₂] association was detectable for annual wood production in the one- or two-factor analyses in both studies, a three-factor model controlling for both minimum temperatures and dry-season high VPD (Figure 5a) revealed a highly significant [CO₂] association. Retrospective analysis (Table 3) shows that this association would have been undetectable with the same model based on only 8 years of the La Selva record.

5. Conclusions and Implications

[47] An imminent “new normal” of unprecedented temperature means and extremes has been projected for all tropical regions [Diffenbaugh and Scherer, 2011]. Given our findings based on a 12 year record of annual production by the lowland tropical forest at La Selva, Costa Rica, such climatic change would be expected to lead to declining forest productivity at this site through coming decades. In recent years with very small increases in minimum temperatures, the production of new aboveground forest biomass at La Selva declined sharply. In addition, the small countervailing effects consistent with $[CO_2]$ fertilization that were indicated by the long-term records from La Selva, where the relatively fertile soils should maximize such benefits, raise the possibility that productivity enhancement from increasing $[CO_2]$ [c.f. Lloyd and Farquhar, 2008] will be too limited to counter the impacts on tropical forests from increasing temperatures. If vapor pressure deficits (the relative dryness of the air) also increase across the biome as the temperatures climb, additional negative effects such as those seen from this stressor at La Selva may further impact many tropical forests. Multidecadal annual-scale field data series from across the biome are needed to quantify the degree of sensitivity of these biodiverse ecosystems both to these climatic stressors and to increasing $[CO_2]$. If the responses of other tropical forests are similar to those we have found for La Selva, two large consequences would be pervasive negative effects on tropical species and increasing tropical $[CO_2]$ emissions, a positive feedback to global warming.

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