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PRODUCTIVITY AND GLOBAL CLIMATE REVISITED: THE SENSITIVITY OF TROPICAL FOREST GROWTH TO PRECIPITATION

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Abstract. The response of tropical forest carbon balance to global change is highly dependent on the factors limiting net primary productivity (NPP) in this biome. Current empirical global NPP–climate relationships predict that the response of NPP to climate diminishes at higher levels of mean annual precipitation (MAP) and mean annual temperature (MAT), but data have been relatively scarce in warm and wet tropical ecosystems. By integrating data from a new comprehensive global survey of NPP from tropical forests and a climate gradient from Maui, Hawaii, along with data previously used to develop NPP–climate relationships, I show that there is a strong negative relationship between MAP and NPP in humid ecosystems. The relationships derived here clearly demonstrate that NPP in wet tropical forests is sensitive to climate, and that future forest growth may be limited by increased precipitation forecast by global climate models for the wet tropics.

Key words: carbon; global climate; mean annual precipitation; mean annual temperature; net primary productivity; tropical forest; tropics.

INTRODUCTION

At the global scale, climate is the primary driver of net primary productivity (NPP) in terrestrial biomes. Previously published global NPP–climate relationships predict that NPP becomes less sensitive to climate at high mean annual precipitation (MAP) and mean annual temperature (MAT). The empirical relationships between NPP and climate, originally developed from the International Biological Program (IBP) data set (Lieth 1972, 1975*a*, *b*), have been strengthened by additional studies including recent data syntheses (Gower 2002), and continue to be used as drivers for global ecosystem models (e.g., Dai and Fung 1993). In general, these empirical relationships show that, in drier and colder ecosystems, NPP increases linearly with increases in MAP and MAT. This increase in NPP diminishes in mesic and warm ecosystems, beyond which there is no change in NPP in wetter and hotter ecosystems with additional increases in MAT and MAP. However, NPP data for tropical forests, where warm and wet climate regimes are common, have been relatively scarce. The lack of data, especially at the climatic extremes, has meant that the global relationship between NPP and climate is less certain for the wet tropics, and may be obscured by the use of biome averages across humid tropical areas that may actually vary widely in climate.

The validity of these NPP–climate relationships informs the current debate about carbon sequestration in tropical forests. Tropical forest is the largest terrestrial biome (Dixon et al. 1994), and accounts for one-third of potential terrestrial NPP (Mellilo et al. 1993, Field et al. 1998). Because of the large annual fluxes of carbon between terrestrial ecosystems and the atmosphere, this biome is likely to influence global carbon balance in response to projected changes in climate. However, whether or not tropical forests are carbon sources or sinks is unclear. It is hotly debated whether tropical forests are currently sequestering carbon (Fan et al. 1990, Grace et al. 1995, Keller et al. 1996, Mahli et al. 1998, Phillips et al. 1998, Clark 2002), and how this biome will respond in the future to global climate change (Kindermann et al. 1996, Braswell et al. 1997, Tian et al. 1998, Cox et al. 2000). Determining the sensitivity of tropical forest to climate is critical for understanding the potential for carbon cycling in this biome to respond to changes in temperature, precipitation, and other factors such as CO_2 fertilization.

This synthesis addresses the relationship between global climate and NPP by combining data from the original IBP data set (Lieth 1975*a*) with newly accumulated data from tropical forests worldwide (Clark et al. 2001*b*, Schuur and Matson 2001). Using this wider range of MAP and MAT, I developed new relationships between climate and NPP, and demonstrate the significance of these new relationships for tropical forest NPP globally. These empirical climate–NPP relationships are critical for the development and testing of mechanistic NPP models used in projections of global C cycling.

METHODS

To examine the relationship between global climate and NPP, I compiled results from three different sources that represented two approaches. The first two sources used an extensive approach; data from the original International Biological Program (IBP) data set included sites from four latitudinal transects that crossed five

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continents but contained relatively few sites from the warm, wet, climatic extreme (Lieth 1972, 1975*a*, *b*). These data were combined with a recent global survey of tropical forest NPP that comprehensively reviewed all published data from tropical ecosystems in Australia, Asia, Africa, and the Americas (Clark et al. 2001*b*). The other approach used six intensively studied sites distributed across a mesic-to-wet precipitation gradient on Maui, Hawaii (Schuur and Matson 2001, Schuur et al. 2001). Although the total number of sites on the Maui moisture gradient was low, careful site selection allowed precipitation to vary among sites while temperature and other state factors (parent material, substrate age, organisms, and topography [Jenny 1941]) that control NPP remained relatively constant. Altogether, this global analysis includes NPP from almost 100 sites distributed across six continents.

Net primary productivity presented here includes above ground and below ground plant production in units of Mg C·ha^{-1}·yr^{-1}. Studies that presented only mass of dry matter (Lieth 1975*a*) were converted to mass C by assuming that vegetation was, on average, 50% C (Clark et al. 2001*b*). Because actual NPP includes components that are difficult to measure (Clark et al. 2001*a*; i.e., root exudates, volatile C emissions, etc.), some components at some sites were estimated by the authors of the original data syntheses (Lieth 1975*a*, Clark et al. 2001*b*). Additionally, tropical NPP data in Clark et al. 2001*b* was presented as a high and low NPP estimate for each site, with the range depending on assumptions for estimating missing components. The mean NPP derived from the high and low estimate at each site was used in this analysis. Lastly, total NPP data from the Maui sites was estimated as the sum of above- and belowground NPP (Schuur and Matson 2001) following the standard methods of Clark et al. 2001*a*. Aboveground NPP was quantified with measurements of annual litterfall and annual increment of increase in total biomass. Belowground NPP was estimated by measuring soil CO_2 fluxes and applying the method of Raich and Nadelhoffer (1989). A least-squares curve-fitting procedure was used to define the best-fit curve separately across the global range of precipitation and temperature for the entire data set. Additional data from dry-to-mesic ecosystems (Gower 2002,) were not included in this analysis because they covered the same climate range and described the same relationships as the IBP data. Including those data did not significantly alter the climate relationships presented here.

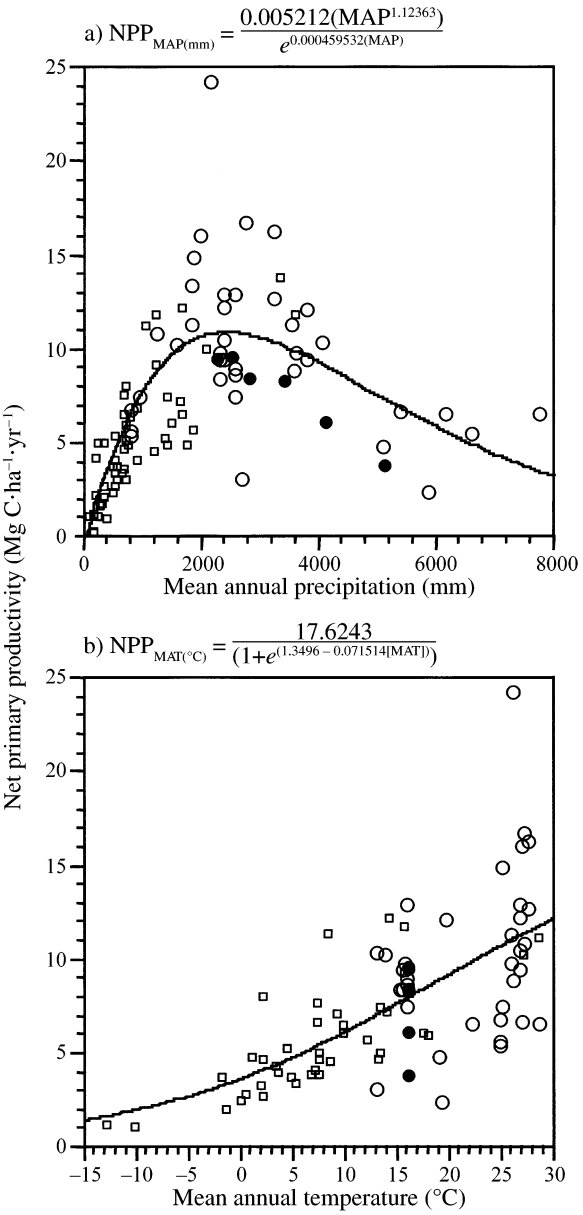

FIG. 1. The relationships between net primary productivity and (a) mean annual precipitation and (b) mean annual temperature. Open squares are International Biological Program sites, open circles represent the tropical forests survey, and dark circles are sites on the Maui moisture gradient that varied in precipitation (MAP = 2200–5050 mm), but not in temperature (MAT = 16).

RESULTS AND DISCUSSION

This new synthesis showed a strikingly different relationship between climate and NPP for precipitation (Fig. 1a; $R^2 = 0.56$) and for temperature (Fig. 1b; $R^2 = 0.47$) from the widely accepted IBP-type relationships in warmer and wetter ecosystems. While the IBP-type relationship predicted little or no effect of increased temperature or moisture on plant growth in warm and wet tropical ecosystems, this more comprehensive data set showed that NPP continues to increase linearly with increased temperature, but declines at high precipitation in tropical ecosystems. This precipitation relationship predicted that NPP reaches a maximum value at 2445 mm MAP. High-precipitation sites in this analysis included both lowland and upland tropical forests, indicating that this pattern was not a result of temper-

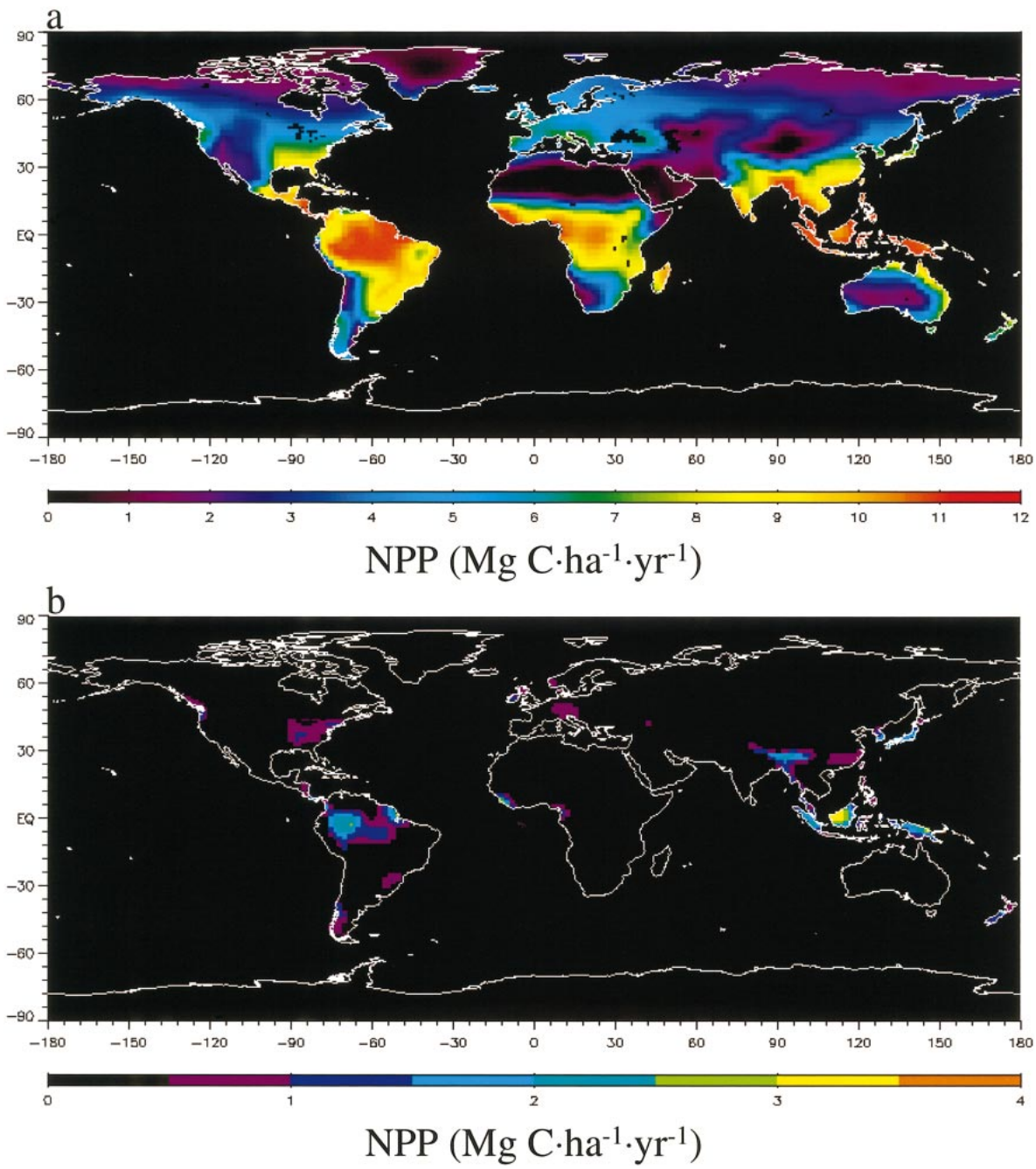

FIG. 2. (a) Potential global net primary productivity predicted by these new climate relationships and (b) the difference in NPP predicted using the climate relationships from the International Biological Program data set and these revised climate relationships. NPP calculated with the revised relationships is lower than that calculated with the IBP data set.

ature biases. Importantly, the relationships derived here are a result of the exceptionally wide range of climate covered by all the sites together, and could not be determined from any of the individual data sets alone. While seasonal fluctuations in temperature and distribution of precipitation may explain some of the remaining variance, across this wide range of global precipitation and temperature it is clear that warm and wet tropical forests do respond strongly to changes in mean annual climate regime.

These climate relationships were used to predict potential global NPP (Fig. 2a). Net primary productivity was calculated using global precipitation and temperature data sets separately at a 1° longitude × 1° latitude grid-cell resolution (Leemans and Cramer 1990). The NPP of each grid cell was defined as the minimum NPP

calculated using either MAP or MAT, assuming that plant productivity is limited by a single climate variable (Lieth 1975*b*). Redefining the relationship between global climate and potential NPP had the strongest effect in the tropics, shown as the difference between the IBP climate relationships and the lower NPP calculated here (Fig. 2b). The largest and most widespread differences occur in tropical forest across Southeast Asia, in the western Amazon, and, to a lesser degree, in coastal Africa and coastal South America. Differences in NPP in these areas using the revised climate relationships are large, ranging up to 3.5 Mg C ha^{-1} yr^{-1} less than previously estimated in some tropical wet forests. Scaling grid cells to account for relative land area, the total potential tropical NPP (30° S to 30° N) declined by 25% using these revised climate relationships.

Much of the decline in the predicted NPP of the tropics was a result of the negative effect of high rainfall in humid tropical forests, most likely an indirect effect on plant growth mediated by the availability of other resources. While water acts predominantly as a resource in dry-to-mesic ecosystems, increased precipitation may reduce NPP by decreasing radiation inputs, increasing nutrient leaching, or reducing soil oxygen availability in humid ecosystems. The precipitation gradient on Maui provides further insight into mechanisms because the other state factors that can control NPP were similar among sites while precipitation alone ranged from 2200 to over 5000 mm MAP (Schuur et al. 2001). Across this highly constrained moisture gradient, the negative effect of precipitation alone is very clear. Net primary productivity drops by a factor of two across the sites, and is strongly negatively correlated with precipitation (Fig. 1a, $R^2 = 0.96$, $P < 0.01$, $n = 6$), but not correlated with temperature, which did not vary across the gradient (Fig. 1b). At these sites, decreased nutrient cycling and availability for plant uptake was associated with the decrease in NPP (Schuur and Matson 2001). Higher rainfall decreased decomposition rates because the slow diffusion of oxygen through water-filled soil pores could not match aerobic demand by roots and microbes (Schuur 2001). While oxygen limitation did not appear to affect plant growth directly, slower decomposition rates decreased nutrient availability and limited the supply of nutrients for plant growth (Schuur and Matson 2001). No other factor was clearly associated with the decline in NPP in the wetter forests on this gradient.

Increased nutrient limitation via decreased decomposition and leaching may play the same role in the nutrient-poor soils that dominate many other tropical forests regions. On Maui, larger pools of soil organic matter accumulate in wetter forests as a consequence of decreased decomposition rates (Schuur 2001, Schuur et al. 2001). Because carbon and nutrient mineralization are coupled processes, a greater proportion of the ecosystem nutrient capital is locked up in these soil organic-matter pools, thus increasing nutrient limitation to plants, all else being equal. While specific information on nutrient cycling is not available to test this as a global trend, it has been shown that soil organic matter pools continue to increase with increased MAP in humid forests worldwide (Post et al. 1982, Zinke et al. 1984). This suggests that decreases in decomposition and rates of nutrient cycling could be global phenomenon that occurs with increased rainfall in wet tropical forests.

On the other hand, other factors that did not appear to play a role in limiting NPP on Maui may turn out to be important in other humid ecosystems. Light is an important driver of many global-scale NPP models (Potter et al. 1993, Field et al. 1995, Sellers et al. 1997), which often use absorbed photosynthetically active radiation (APAR) estimated by remote sensing to model photosynthesis. Increased precipitation may be coupled to increased cloudiness, which in turn may decrease solar radiation at the forest canopy below photosynthetic light saturation. While APAR is an effective driver for modeling photosynthesis, it combines both light availability and the potential for the canopy to absorb incoming radiation, determined in part by leaf nitrogen content. Direct evidence of light limitation to NPP by itself in tropical wet forest is scarce. A light augmentation experiment performed on individual tropical trees during the rainy season in Panama (MAP = 2000) found that higher light availability increased instantaneous CO_2 uptake at the leaf level, and the length and reproductive output of illuminated branches (Graham et al. 2003). However, another study found that there was no correlation between light availability, interannual rainfall, and tree growth in a Costa Rican tropical wet forest (MAP = 4000 mm) over the time scales where NPP is measured (Clark and Clark 1994). In any case, both nutrient availability and light availability may contribute to the global pattern of decreased NPP with increased rainfall in humid forests.

These new climate relationships add to our conceptual understanding of the effect of precipitation in humid tropical forests. This has broad implications for the response of carbon sequestration in tropical wet forest to global change. The negative relationship between precipitation and forest growth reported here predicts that forest growth may not respond to factors such as CO_2 fertilization (e.g., Chambers et al. 2001) because of other limiting factors. In addition, global climate models consistently predict increases in future precipitation for most wet tropical areas, although the magnitude of this increase is not well known (Cubash et al. 2001, Intergovernmental Panel on Climate Change [IPCC] 2001). Based on these new climate relationships, increases in precipitation will limit or decrease future forest growth in tropical wet forest. Because the climate relationships were derived here from relatively mature ecosystems, the response of NPP to the transient state of climate change will depend strong-

ly on the mechanisms driving these climate relationships. In tropical wet forests where indirect factors are likely to limit NPP, factors such as light availability should respond in parallel with changes in precipitation, thus NPP would be expected to respond relatively rapidly to changes in climate. In contrast, the response of NPP to changes in factors such as nutrient availability would lag behind changes in climate as soil organic matter pools accumulated or decayed as they re-equilibrated with changing environmental conditions. This synthesis shows that water in excess of biological demand has a fundamental impact on ecosystem carbon balance in humid tropical forests. The specific mechanisms driving the relationships between NPP and climate in wet tropical forests need to be explored further on a more widespread scale to determine the rate at which tropical NPP will respond to climate change.

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