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Modeling the spatial and temporal variability in climate and primary productivity across the Luquillo Mountains, Puerto Rico

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Abstract

There are few studies that have examined the spatial variability of forest productivity over an entire tropical forested landscape. In this study, we used a spatially-explicit forest productivity model, TOPOPROD, which is based on the FOREST-BGC model, to simulate spatial patterns of gross primary productivity (GPP), net primary productivity (NPP), and respiration over the entire Luquillo Experimental Forest (LEF) in the mountains of northeastern Puerto Rico. We modeled climate variables (e.g. solar insolation, temperature, rainfall and transpiration) using a topography-based climate model, TOPOCLIM. The simulated GPP ranged from 8 to 92 t C/ha per year with a mean of 51 t C/ha per year. The simulated NPP ranged from 0.5 to 24 t C/ha per year with a mean of 9.4 t C/ha per year. The simulated plant respiration ranged from 31 to 68 with a mean of 42 t C/ha per year. Simulated GPP and respiration declined with increased elevation whereas simulated NPP increased from low to middle elevation but decreased from middle to high elevations. Statistical analyses indicate that variation in solar insolation, which decreases with increase in elevation, is the most important factor controlling the spatial variation of forest productivity in the LEF. Validation with the limited spatial empirical data indicated that our simulations overestimated GPP by 2% for a middle elevation test site, and by 43% for a mountain peak site. Our simulations also overestimated NPP in the middle elevation Colorado forest and higher elevation Dwarf forest by 32 and 36%, respectively, but underestimated NPP in the Tabonuco and Palm forests at low to middle elevations by 9–15% and 18%, respectively. Simulated GPP and NPP would decrease under CO_2 doubling as projected temperatures increase and precipitation decreases. Different forest types respond differently to potential climate change and CO_2 doubling. Comparison with other tropical forests suggests that the LEF as a whole has higher GPP (51 t C/ha per year versus 40 t C/ha per year) but lower NPP (9.4 t C/ha per year versus 11 t C/ha per year) than other tropical rain forests.
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Keywords: Modeling; Climate; Primary productivity; Spatial variability; Luquillo Mountains

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1. Introduction

Gross primary productivity (GPP) supports both net primary productivity (NPP) and plant respiration. NPP is the carbon fixed by photosynthesis and represents the carbon available for plant allocation to leaves, stems, roots, defensive compounds, and reproduction. Currently, there are few data on GPP and NPP in tropical forests due to the difficulty in making direct measurements of both aboveground and belowground biomass increment (Jordan and Escalante, 1980; Vogt et al., 1993, 1996; Silver, 1998; Tanner et al., 1998; Clark et al., 2001). Moreover, even where accurate measurements of above- and belowground production and respiration are possible, it is still hard to sample and measure NPP over a large area. Ecosystem process-based modeling coupled with remote sensing can be used to estimate carbon and nitrogen fluxes and storage over large areas (landscape to regional and global scales) and to predict the changes of carbon and nitrogen fluxes and storage with possible climate change (Raich et al., 1991; Rastetter et al., 1991; Running and Gower, 1991; Churkina and Running, 1998; Waring and Running, 1998). FOREST-BGC is an ecosystem process model that calculates carbon, nitrogen and water fluxes through a forest ecosystem (Running and Coughlan, 1988; Running and Gower, 1991; Running and Hunt, 1993). The model has been validated for temperate forests (Running and Coughlan, 1988; Running and Gower, 1991; Churkina and Running, 1998; Waring and Running, 1998) and tropical forests (e.g. Marley, 1998).

At a global scale, temperature and rainfall are the main factors that control variability in GPP and NPP (Rosenzweig, 1968; Lieth, 1975; Churkina and Running, 1998; Silver, 1998). But at landscape or regional scales, other environmental factors may play an important role in controlling the variability in NPP. The Luquillo Experimental Forest (LEF) in northeastern Puerto Rico (Fig. 1) is ideal for examining the spatial and temporal variation in GPP and NPP, due to the large changes in geography, climate, soil and vegetation over a relatively small area (Odum and Pigeon, 1970; Brown et al., 1983; Hall et al., 1992; Marley, 1998; Waide et al., 1998). Field studies have found a decline in forest growth as elevation increases in the LEF (Weaver et al., 1973; Brown et al., 1983; Weaver and Murphy, 1990; Lugo et al., 1995; Weaver, 1995; Waide et al., 1998). The causal factors proposed include reduced solar insolation (Weaver et al., 1973), lower temperature, higher cloudiness (Grubb, 1977), reduced transpiration rates (Odum, 1970), high winds and exposure, saturated soils (Weaver and Murphy, 1990; Weaver, 1995); reduced soil oxygen (Silver et al., 1999) and the interplay between nutrient availability and disturbance (Weaver, 1995; Waide et al., 1998). There are, however, no empirical or modeling studies of the spatial pattern of forest productivity over the elevational gradient of the Luquillo Mountains that might help us to resolve which factors influence productivity at the regional scale.

In this research, we attempt to (1) simulate the spatial and temporal variability in GPP, NPP and the physical factors associated (light, temperature, water, CO_2 concentration, vapor pressure deficit (VPD)) in the LEF using mechanistic equations of plant/vegetation physiological response to the changing environmental gradient of the FOREST-BGC model; (2) evaluate the controls over GPP and NPP as a function of landscape properties; and (3) analyze the response of primary production to different scenarios of climate change and elevated CO_2.

2. Study area

The LEF is located between 18°14′45.78″ and 18°20′58.23″N latitude and between 65°42′26.56″ and 65°53′53.33″W longitude (Fig. 1). The total area of the LEF is approximately 11,000 ha and elevations range from about 100 to 1075 m above sea level over a distance of only 10 km (Weaver and Murphy, 1990). Mean annual rainfall increases with elevation from approximately 2450 mm per year at lower elevations to over 4000 mm per year at higher elevations, while mean annual temperature declines from 23 to 19 °C along the same gradient (Brown et al., 1983; Weaver and Murphy, 1990; Scatena and Lugo, 1995; Silver et al., 1999). The upper ridges and summits are frequently enveloped in clouds, reducing solar insolation and increasing soil moisture (Briscoe, 1966; Baynton, 1968; Weaver, 1972). Evapotranspiration decreases along the elevational gradient, while relative humidity and wind velocity increase (Briscoe, 1966; Weaver, 1990; Weaver and Murphy, 1990).

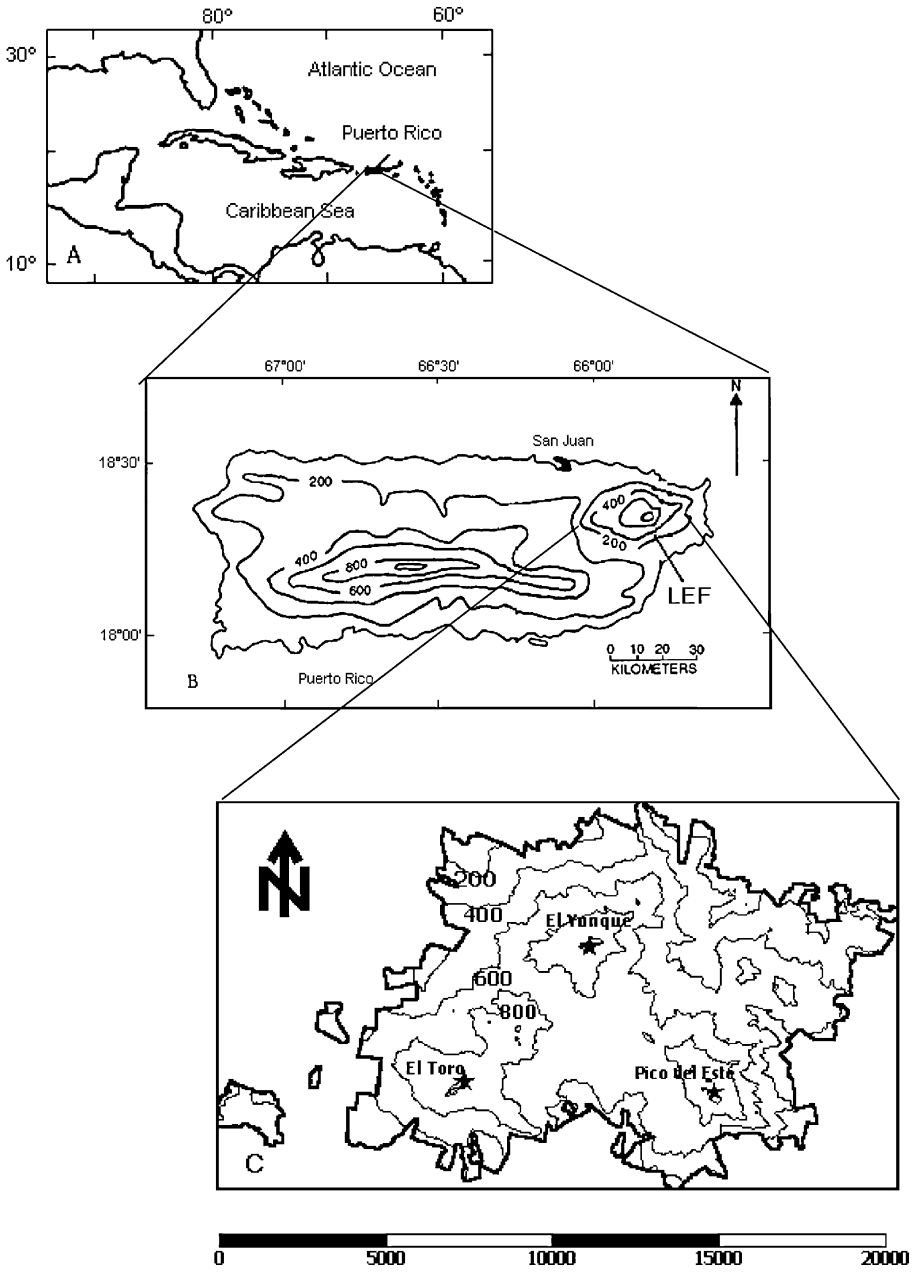

Fig. 1. Maps showing: (A) Puerto Rico relative to the Atlantic Ocean and Caribbean Sea; (B) Puerto Rico with elevation contours at 200-m intervals and (C) the Luquillo Experimental Forest (LEF) with elevation contours at 200-m intervals and three peaks (El Yunque, El Toro and Pico del Este) in the LEF.

Within the Luquillo Mountains, there are four distinct types of forest along the elevation gradient (Fig. 2): lower montane rain forest (locally known as Tabonuco forest) on better-drained ridges below 600 m, montane rain forest (locally known as Colorado forest) between 600 and 900 m, and Dwarf (also called Cloud forest, Elfin forest and Mossy forest) on the exposed slopes or ridges above 900 m, and Palm

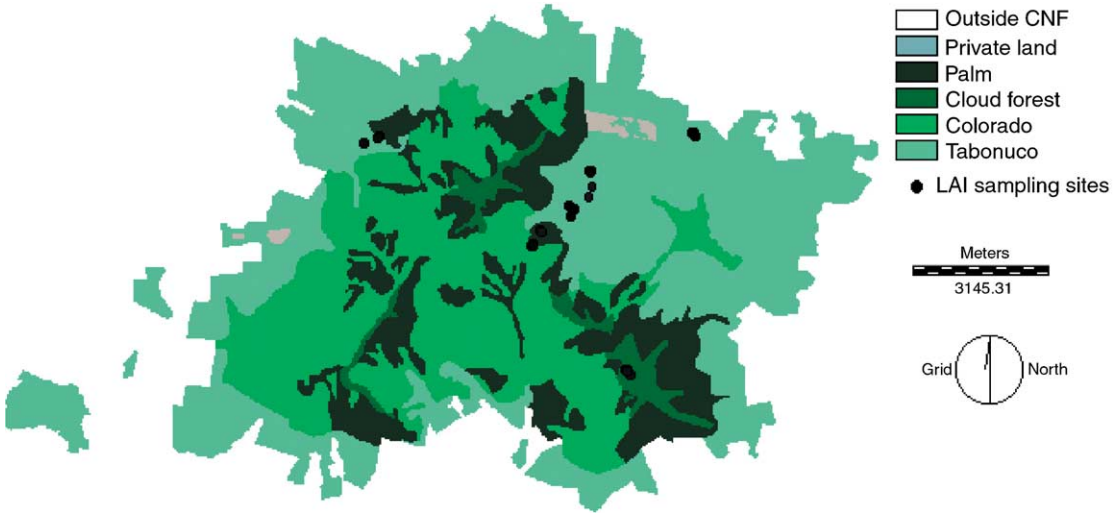

Fig. 2. Map of vegetation distribution of Tabonuco, Colorado, Palm and Cloud forests and 14 sites (at a 30 m × 30 m resolution) for leaf area index sampling over the Luquillo Experimental Forest, Puerto Rico (source: digitized from the USGS 1:24,000 Forest Service Vegetation map of 1989 by the International Institute of Tropical Forestry at Puerto Rico).

forest scattered on steep slopes and drainage above 500 m (Weaver, 1983; Weaver and Murphy, 1990). Each forest type differs greatly from the other types in species composition, richness, structure, productivity, litterfall and environmental factors (Weaver and Murphy, 1990; Weaver, 1991; Silver et al., 1999). The Tabonuco, Colorado, Palm and Dwarf forests cover 70, 17, 11 and 2%, respectively, of the LEF (Brown et al., 1983).

The geology of the Luquillo Mountains is described as a completely faulted and folded terrain, which is underlain by Cretaceous volcanic rocks and subordinate Cretaceous and/or Tertiary intrusive bodies and minor lower Tertiary volcanic and sedimentary rocks (Seiders, 1971). Soils within the LEF are derived from the volcanoclastic sediments and are quite diverse taxonomically (Brown et al., 1983; Silver et al., 1999). There are four soil associations, representing 19 soil series. The principal soil orders are ultisols and inceptisols, occupying approximately 50 and 20%, respectively, of the LEF (Brown et al., 1983). The ultisols are generally deep, highly weathered (high clay, Al and Fe contents), leached, low in pH, with base saturation less than 35% at 1.25 m, whereas less weathering and no significant illuviation characterizes the inceptisols. Geomorphically and topographically, the Luquillo Mountains are characterized by a steep, highly dissected topography with slopes varying between ca. 2 and 75° (22° on average) and complicated geomorphologic combinations of ridge, slope, upland valley and riparian valley (Garcia-Montiel and Scatena, 1994; Scatena and Lugo, 1995).

3. Model and data

We used an ecosystem modeling approach to simulate the spatial and temporal variability in GPP and NPP as well as the responses of forest to possible climate change and elevated CO_2. We simulated the climate in the Luquillo Mountains using a spatially-explicit climate model and then used the outputs of climate as forcing inputs into the forest productivity model, TOPOPROD.

3.1. Mountain climate model—the TOPOCLIM model

We used the TOPOCLIM model (TOPO graphically driven CLIMate model) to simulate climatic variables in the LEF using both empirical and mechanistic approaches. The model produces estimates of solar

insolation, temperature, relative humidity, and rainfall above the canopy for the Luquillo Mountains (Wooster, 1989; Everham et al., 1991; Marley, 1998; also available at http://www.esf.edu/course/sysecol/topoclim/TOPOCLIM.HTM). Slope, aspect, and the elevation data sets were used as input data for the model. The 30 m × 30 m Digital Elevation Model (DEM) for the LEF was obtained from the US Geological Survey and was projected onto State Plane Coordinates. Historical climate data compiled by Briscoe (1966), Odum (1970), and Garcia-Martino et al. (1996) were used to parameterize the model. We generated hourly estimates of solar insolation, temperature and transpiration, as well as daily and monthly totals and averages. Rainfall is estimated monthly. Solar irradiance was modeled as incident radiation including direct, reflected, and diffuse radiation on an inclined surface to account for the topographic effects. The model also accounts for terrain shading (blocking of the sun) by the adjacent landscape. Cloud cover is simulated with a simple stochastic cloud simulator in which the probability of cloudiness is based upon elevation, season, and time of day. Diurnal variation in temperature is modeled with a method developed by Parton and Logan (1981). This method uses a modified sine function for daytime temperatures and an exponential decay function for night-time temperature. Minimum and maximum daily temperatures are derived from a linear regression of data from several meteorological stations within or around the LEF. The elevations of these stations range from near sea level to 1059 m. The details of the equations used in the TOPOCLIM model are given in Appendix A.

3.2. Primary productivity model—the TOPOPROD model

The TOPOPROD model (Marley, 1998) is a model of tropical ecosystem productivity in mountainous areas, which is based on the FOREST-BGC model (Running and Coughlan, 1988; Running and Gower, 1991). The FOREST-BGC is a canopy process model, which simulates the flux of CO_2, water and associated primary production over a day in a forest. It is at this time perhaps the most widely used canopy photosynthesis model, but it is not the only possible formulation (see Section 5). Full details of the TOPOPROD model are given in Appendix B.

3.3. Derivation of leaf area index (LAI) image from remote sensing data

We derived the image of leaf area index (LAI) for the LEF from remotely sensed data. Quinones-Orfila (1997) sampled LAI with the LiCor LAI-2000 Plant Canopy Analyzer across the entire elevation gradient in the LEF in 1995–1996 based on 29 10 m × 10 m plots (Quinones-Orfila, 1997). We extrapolated these LAI values to a 30 m × 30 m resolution by grouping 26 plots of original LAI data (excluding three pasture plots) based on their geographical coordinates into 16 new data points and then averaged the original LAI data in each group (some new groups have only one original plot and then we assumed that they are also representative at a 30 m × 30 m resolution). Fourteen new groups of LAI data (with their elevation, slope and aspect data) were used in regression analysis (Fig. 2). We used the other two (one is in the Tabonuco forest, the other is in the Colorado forest) as well as the average LAI value (2.68 m^2/m^2) for Pico del Este from Quinones-Orfila's six measurements for validation.

The University of Puerto Rico provided the LANDSAT TM data acquired on 21 January 1985 with a resolution of 30 m × 30 m. The original file format is in the ENVI format and these data are orthorectified and georeferenced. We used ENVI software to convert it to ERDAS IMAGINE-recognized format (LAN). We calculated the Normalized Difference Vegetation Index (NDVI) as follows:

$$\mathrm{NDVI} = \frac{\mathrm{NIR} - \mathrm{RED}}{\mathrm{NIR} + \mathrm{RED}} \quad (1)$$

where NIR is band 4 (0.76–0.9 μm) and RED is band 3 (0.63–0.69 μm) reflectance from LANDSAT TM. Because topographic effects on spectral signatures hamper the interpretation of remote sensing in rugged terrain we corrected the derived NDVI for topographic effects using the Lambertian Topographic Normalization model in the ERDAS IMAGINE routine. We made two assumptions before conducting regressions between NDVI and LAI: (1) there was no significant difference in LAI in different months; and (2) the vegetative canopy had recovered completely to pre-Hugo levels in 6 or 7 years before the image was acquired. There was a significant linear relation between NDVI and LAI at the LEF. When we corrected the image further for elevation, slope and

aspect, the equation below has a better fit:

$$\begin{aligned}\text{Predicted LAI} &= 8.2961 \times \text{NDVI} - 0.0003 \times \text{elevation (m)} \\ &\quad + 0.0492 \times \text{slope}(^\circ) + 0.0023 \\ &\quad \times \text{aspect}\,(^\circ) - 1.7832\,(R^2 = 0.676)\end{aligned} \quad (2)$$

We used this multiple linear equation to derive a LAI image using IDRISI 32 GIS (Clark University). Locations with LAI ≤ 0 were assigned the minimum observed value of LAI (1.99, Quinones-Orfila, 1997). After calculating LAI, we check various landscape positions to evaluate if our results are reasonable with respect to topographic positions.

3.4. Simulation of climate change and elevated CO_2

The general circulation models (GCMs) project that concentrations of atmospheric CO_2 will double above the pre-industrial value near the middle of this century, with significant concomitant changes in climatic variables (Houghton et al., 1990; Melillo et al., 1993). Based on the existing climate-elevation relation of the LEF, changes in air temperature of 1.5–2.5 °C and changes in precipitation of −11 to 33% would alter the distribution of forest types in the LEF dramatically (Scatena, 1998). We designed a series of scenarios to examine the effects of climate change and CO_2 change on forest productivity in the LEF. We used three temperatures (+0, +1.5, and +2.5 °C), three precipitation regimes (0, −11, and +33%) with and without elevated CO_2. Air temperature is expected to increase as CO_2 doubles (e.g. Hansen et al., 1998; Schlesinger and Andrews, 2000). Precipitation may also change with a doubling of CO_2 but the magnitude and direction of change are uncertain. Therefore, two scenarios for elevated CO_2 with temperature increase (+2.5 °C) and possible precipitation change (−11 and +33%) were also included in the analyses. In the simulation, we assumed a 20% reduction of canopy conductance and a 30% reduction in leaf nitrogen for a doubling of atmospheric CO_2 (Pan et al., 1998). It takes about 10 min to complete simulation of one scenario on an IBM PC with a Pentium III processor (450 MHz).

3.5. Statistical analyses

We analyzed simulation results for a total of 300 points randomly selected by GIS-IDRISI over the entire DEM image where 154 points fall within the LEF boundary. We then conducted simple and multiple linear regressions of simulated GPP, NPP versus various climatic variables for the selected locations using STATISCA (Statsoft, 1997). We then used these points for statistical analyses.

4. Results

Our simulation showed that simulated GPP, NPP and plant respiration rates in the LEF were in approximate agreement with the (relatively few) measured values. Variation in insolation, which decreases with increases in elevation, is the most important factor controlling the spatial variation of simulated forest productivity in the LEF.

4.1. Modeling validation

Our simulated climatic variables were generally in good agreement with observations. For example, our comparison of simulated air temperature with an independent set of observed air temperature in 1997–1998 along the elevation gradient in the LEF indicated that the TOPOCLIM model is accurate in estimating mean monthly temperature in the Luquillo Mountains to within 0.7 °C in March and within 1.5 °C in October (Fig. 3). Simulated transpiration rates at lower elevations (e.g. El Verde and Bisley watershed) compare well with observations, but this is less true at higher elevations. For example, although simulated transpiration rates at sites in the Palm and Dwarf forests fall within the observed range, our model tends to overestimate transpiration by 15% (Table 1). The aerodynamic resistance, r_a, is an important parameter in estimating transpiration in the Penman–Monteith equation. Schellekens (2000) found that typical values of r_a at the Bisley watershed in the Tabonuco forest are between 2.1 and 20 s/m. We used a r_a of 2.1 s/m versus larger values in our simulation because this value of r_a gives the best estimation of transpiration compared to the data (Schellekens, 2000). Generally speaking, the Penman–Monteith equation estimates transpiration in the LEF reasonably well, although the equation tends to overestimate transpiration by 5–29% compared to the corresponding catchment water-budget-based estimates (Schellekens, 2000).

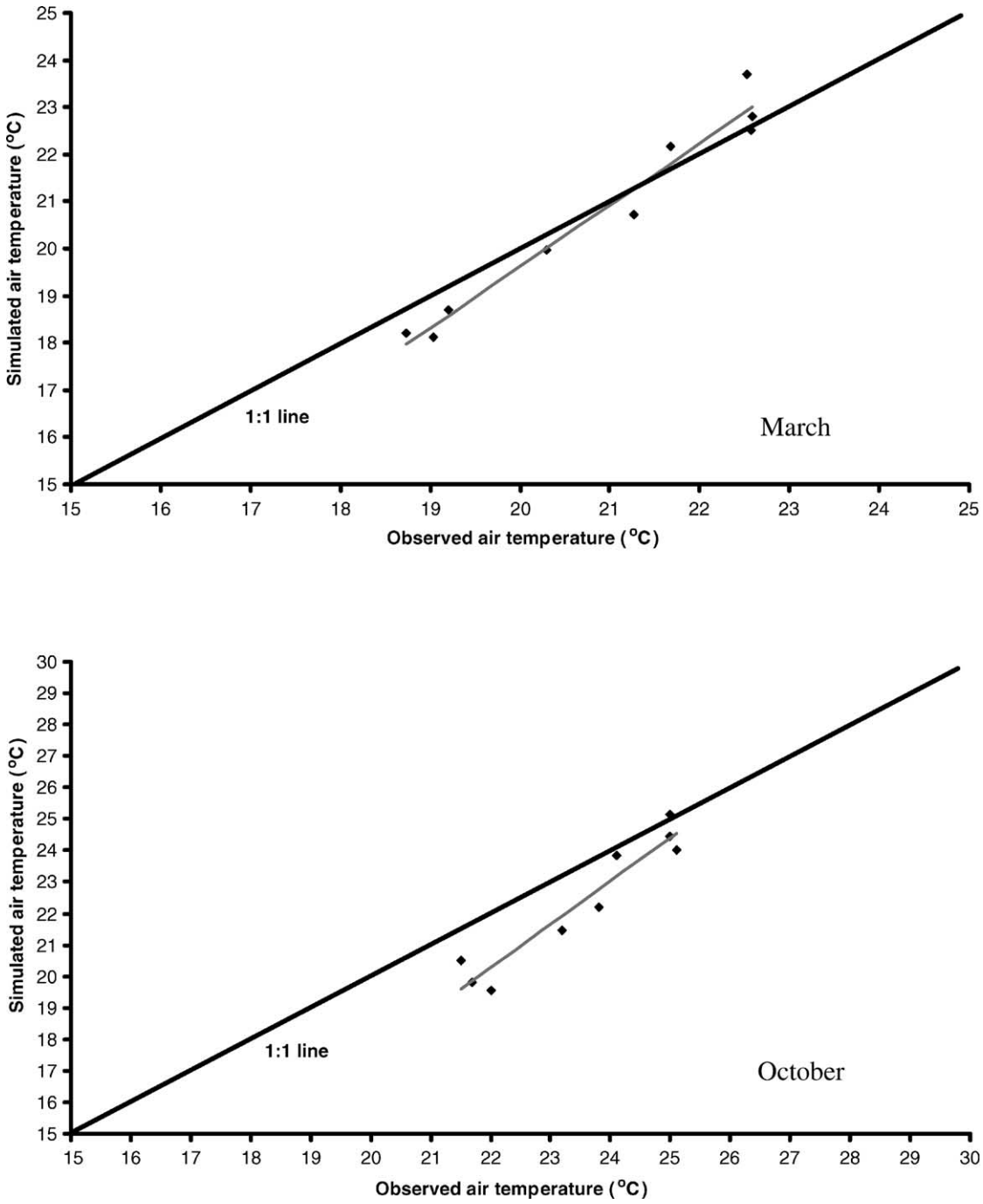

Fig. 3. Validation of simulated mean monthly air temperature using the TOPOCLIM model with an independent data set collected by Scatena et al. (see data source below) along the elevation gradient in 1997 in March and October in the Luquillo Experimental Forest, Puerto Rico. The nine sites are Sabana forest, Bisley watershed, Gate of roads 966 and 191, Yokahu, Parrot trail, Colorado site, Palm forest near road 930, Tall cloud and Short cloud sites with elevation ranging from 153 to 1011 m. Data source: http://www.fs.fed.us/global/iitf/research/ecosyste/leftemp/main.html.

Table 1
Comparison of simulated GPP, NPP, transpiration with observed GPP, NPP and transpiration at selected locations of the major forest types in the Luquillo Experimental Forest (LEF), Puerto Rico

Vegetation type	Tabonuco		Colorado	Palm	Dwarf
Location	El Verde	Bisley		Near Santo River	Pico del Este
Elevation (m)	450	400	700	750	1050
Rainfall (mm per year)	3530	3480		3725	4200
GPP (t C/ha per year)					
Simulated	60.32	70.38	43.21	41.28	24.08
Observed	59.04[a]				16.75[b]
NPP (t C/ha per year)					
Simulated	11.63	12.69	7.86	10.32	7.35
Observed (ANPP)[c]	10.5	10.8[c,d]	4.05	9.75	3.7
Total NPP[e]	12.3[a]	14.04	5.27	12.68	5.4[a]
Respiration (t C/ha per year)					
Simulated	48.69	57.69	35.35	30.96	16.73
Observed	46.74[a]				
Transpiration (mm per day)					
Simulated	2.27	2.46	1.76	1.66	1.10
Observed	2.136[a]	2.2–2.4[f]		0.5–2.27[g]	0.44[h]
	0.288–4.608[h]			1.43 (mean)[g]	0.56–0.87[b]
					0.086–1.09[h]

[a] Odum and Pigeon, 1970; Murphy, 1975.
[b] Brown et al., 1983, based on LAI = 2.68.
[c] Weaver and Murphy, 1990.
[d] After recovery from Hugo, Scatena et al., 1996.
[e] Assumed belowground NPP/aboveground NPP ratio = 0.3.
[f] Schellekens, 2000.
[g] Frangi and Lugo, 1985.
[h] Weaver, 1973, 1975.

Relatively few measurements of the spatial distribution of annual GPP and, especially, NPP are available for model validation in the LEF. In general, the model simulates GPP at low elevations more accurately than at high elevations. For example, the simulated GPP at El Verde is 60.32 t C/ha per year, which is within 2% of observed GPP (59.04 t C/ha per year). However, at the Pico del Este site (1050 m), the simulated GPP is 24.08 t C/ha per year, 43% higher than the observed GPP of 16.75 t C/ha per year (Fig. 4 and Table 1).

There are no direct measurements of belowground NPP in the LEF. We used a ratio of below-ground NPP to aboveground NPP (BNPP/ANPP) of 0.3 based on the estimation of below- and aboveground biomass for the entire LEF. This BNPP/ANPP ratio is close to the lower bound for estimates of BNPP (=0.2–1.2 × ANPP and is often treated as 0.5 × ANPP, e.g. Waring and Running, 1998) for tropical forests (Clark et al., 2001). A comparison of simulated NPP in the LEF with the limited observations of NPP at different measuring periods indicates that simulations of annual NPP are more accurate at low elevations than at high elevations (Table 1). Our simulated NPP for El Verde is 11.63 t C/ha per year, approximately 5% lower than observed (12.3 t C/ha per year). Raich et al. (1991) used the TEM model and predicted that the NPP value at El Verde was 9.0 t C/ha per year with a range of 3.5–10.4 t C/ha per year. Thus our estimates of annual NPP using the TOPOPROD model are comparable to estimates from the few existing observations, and with estimates by other ecosystem models such as the TEM model. Our simulated NPP for a site in the Bisley watershed, also a Tabonuco forest site, is 12.69 t C/ha per year, approximately 9% lower than the observed value of 14.04 t C/ha per year (Table 1). At a test site in

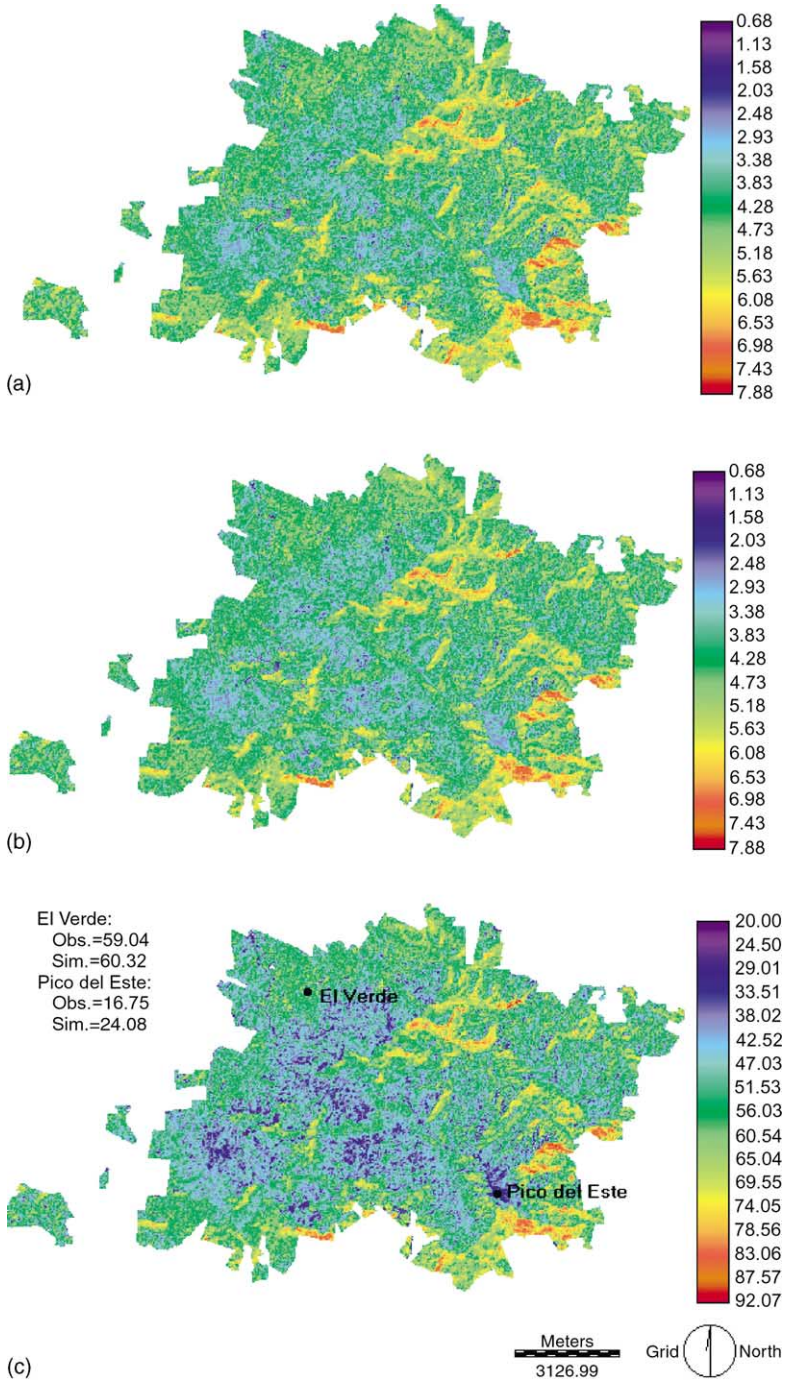

Fig. 4. Simulated GPP (t C/ha per month) distribution in March (a), October (b) and simulated annual GPP (t C/ha per year) (c) with comparison of simulation with data at two test sites in the Luquillo Experimental Forest (LEF), Puerto Rico.

the Colorado forest our simulated NPP is 7.86 t C/ha per year, 32% higher than the one observed value, 5.27 t C/ha per year (Table 1). The simulated NPP is 10.32 t C/ha per year at a Palm forest site, also in the middle elevation in the LEF as is the Colorado test site, approximately 18% lower than the observed value, 12.68 t C/ha per year. Our estimate for NPP at the highest elevation at Pico del Este, a cloud forest site, was 7.35 t C/ha per year, about 36% higher than observed value of 5.4 t C/ha per year (Table 1). One reason for our overestimates of GPP and NPP may be that we tend to overestimate LAI at higher elevations from remotely sensed data. The reason for the overestimation of LAI at high elevations is probably the high reflectance at NIR band by wet canopy and low reflectance at RED band by high soil moisture. We need more high quality field measurements, especially belowground measurements to parameterize and to evaluate TOPOPROD performance in tropical forests accurately.

4.2. Spatial and seasonal patterns of climatic variables in the Luquillo Mountains

The simulated monthly temperature, transpiration rates and daily solar insolation under current climate conditions decrease as elevation increases, with minor topographic variation. For example, in a relatively rainy season month (e.g. October), air temperature decreases from 26 °C at low elevation to 20 °C at mountain peaks; transpiration rate decreases from 110 to 25 mm per month and solar insolation decreases from approximately 20 MJ/m^2 per day to approximately 8 MJ/m^2 per day along the same gradient (Fig. 5). Simulated annual transpiration rates across the Luquillo Mountain decline from about 1269 mm at lower elevations to 372 mm at highest elevations, with a mean of 753 mm for the entire forest. Rainfall, however, increases as elevation increases. Rainfall in October increases from 200 mm in the lowlands to 370 mm at the peaks. Climatic variables also vary with season. During the dry season (e.g. March), monthly rainfall in the LEF is between 125 and 250 mm, while in the rainy season (e.g. October) the range of rainfall for the entire LEF is 200–370 mm (Fig. 5).

4.3. Spatial patterns of leaf area index in the Luquillo landscape

The derived values for LAI ranged from 2.0 to 7.05 with a mean of 4.45 (Fig. 6 and Table 2). The derived LAI values tended to decrease from the Tabonuco forest at low elevations to the Dwarf forest at high elevations. Mean LAI decreased from 4.52 in the Tabonuco forest to 4.03 in the Colorado forest, 4.49 in the Palm forest and 3.9 in the Dwarf forest. The distribution of simulated LAI also showed spatial heterogeneity within each forest type (Table 2). Using random checking we found that the variation in the LAI distribution was associated with locations of streams, roads, trails, landslides, treefalls and, most importantly, earlier human disturbances such as land use change. For example, we found that the derived LAI values were low (less than 3 m^2/m^2) near the El Verde Work Center where Route 186 and Rio Espiritu River intersect and where there are Mahogany plantations. The derived LAI values were also low in areas close to streams and along the ''Trade Wind'' trail near the southwest boundary of the LEF. In the northeast corner of the LEF, the low derived LAI values may be related to the lower forest cover as the nearby areas are covered with pasture or human dwellings. Our LAI estimates are in good agreement

Table 2
Summary of our LAI values derived from NDVI compared to ground measurements for the Luquillo Experimental Forest (LEF), Puerto Rico

Vegetation type	Derived	Quinones-Orfila	Weaver and Murphy
Tabonuco	2.14–7.05 (4.52)	2.36–6.28 (4.33)	6.00–7.00
Colorado	2.50–6.50 (4.03)	4.90–5.56 (5.23)	3.00–5.00
Palm	2.60–6.30 (4.49)	3.51–4.89 (4.62)	3.30
Dwarf	2.00–5.50 (3.90)	1.99–3.35 (2.40)	3.00–3.50
All	2.00–7.05 (4.45)	1.99–6.28 (4.01)	3.00–7.00

Values of NDVI were calculated from LANDSAT TM data acquired on 21 January 1985; mean values are given in parentheses.

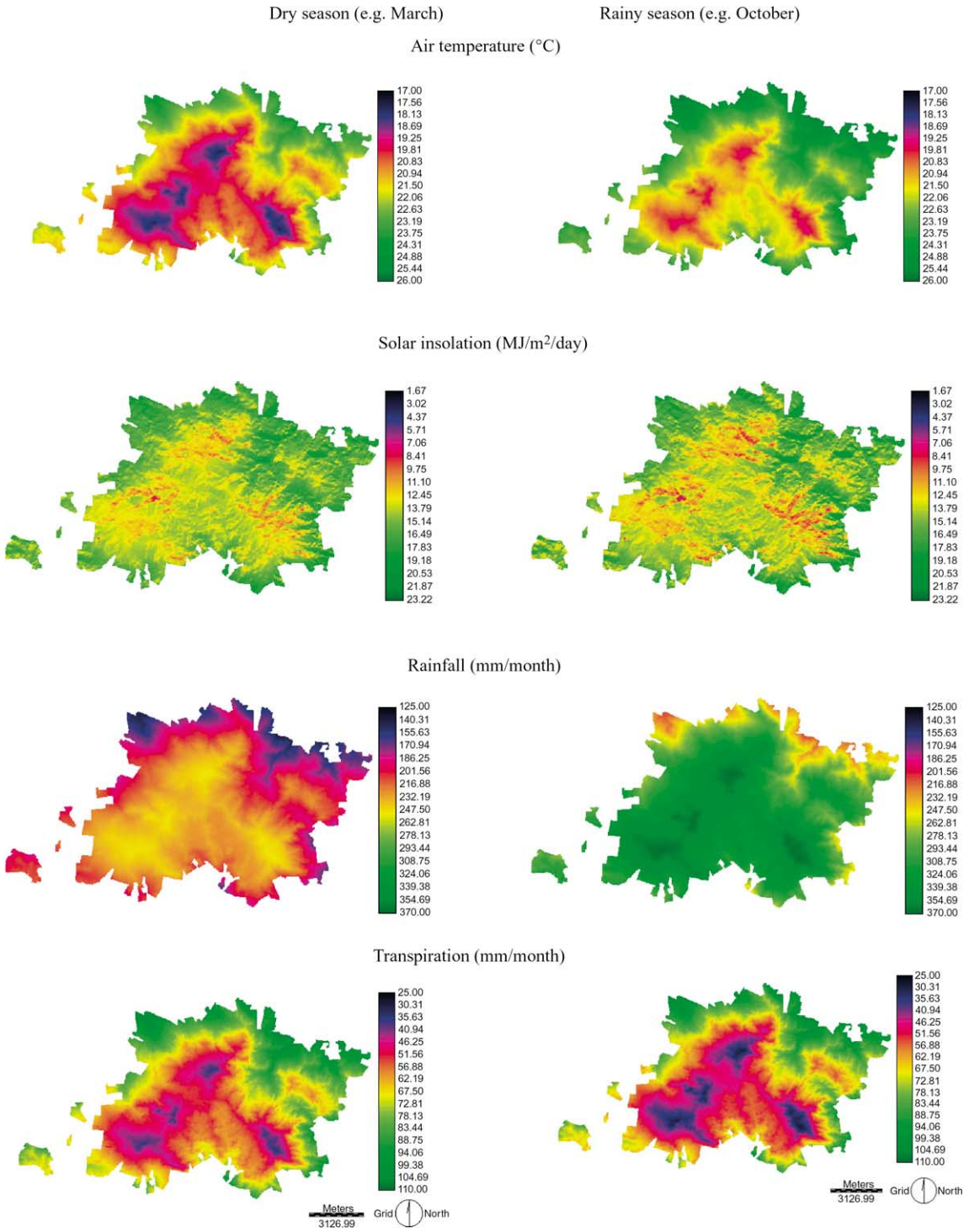

Fig. 5. Simulated air temperature (°C), solar insolation (MJ/m^2 per day), rainfall (mm per month) and transpiration (mm per month) in dry and rainy seasons in the Luquillo Experimental Forest, Puerto Rico.

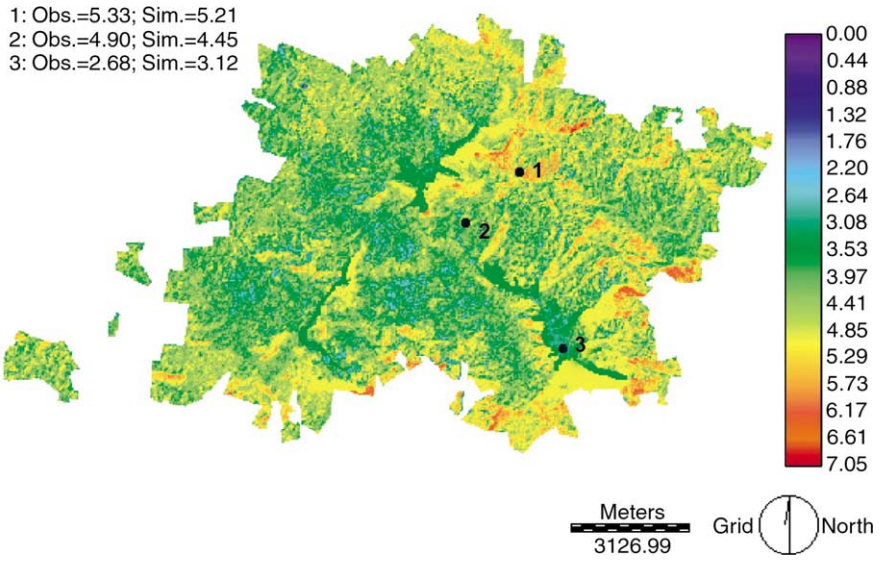

Fig. 6. Simulated leaf area index image derived from NDVI–topography–LAI relationship and observed LAI at three test sites in the Luquillo Experimental Forest, Puerto Rico. The equation is: predicted LAI = 8.2961 × NDVI − 0.0003 × elevation (m) + 0.0492 × slope (°) + 0.0023 × aspect (°) − 1.7832 (R^2 = 0.676).

with field measurements (Quinones-Orfila, 1997) in the Tabonuco at low elevations and Palm forest at middle elevations. Our derived LAI values appear to be overestimates for the Colorado and Dwarf forests (Table 2). Weaver and Murphy (1990) reported that in mature, undisturbed closed forest stands the LAI values range from 6 to 7 in the Tabonuco forest, 3 to 5 in the Colorado forest, 3.3 in the Palm forest and 3 to 3.5 in the Dwarf forest. The LAI values derived through simulation in this study were somewhat lower than Weaver and Murphy's estimates for the Tabonuco forest but higher than their estimates for the other three forest types at higher elevations.

4.4. Spatial and seasonal patterns of forest productivity in the LEF

The annual GPP simulated over the entire LEF using the TOPOPROD model ranged from 8.45 to 92.07 t C/ha per year with a mean of 51.2 t C/ha per year (Fig. 4). Terrain features affect the spatial pattern of GPP in the Luquillo Mountains strongly. GPP is related significantly to elevation, slope and vegetation type (Table 3). Simulated GPP decreases as elevation increases but increases as slope increases. No significant difference in GPP was found for different aspects although GPP tends to decrease from south- to north-facing slopes.

The simulated annual NPP in the LEF ranged from 0.5 t C/ha per year near the northern boundary to a maximum of 23.91 t C/ha per year in the middle elevation in the Tabonuco forest (Fig. 7). There is a general trend of NPP increasing from the lowland

Table 3
Comparison of statistical analysis of the importance of topographic positions and forest types in explaining spatial distribution of simulated annual GPP, NPP and transpiration derived from the TOPOPROD model

S.no.	Variable	Coefficient	*P*-level	R^2
1	Annual GPP (t C/ha per year)			0.38
	Elevation	−0.019	0.0000	
	Slope	0.578	0.0000	
	Vegetation type	1.715	0.0189	
2	Annual NPP (t C/ha per year)			0.48
	Elevation	0.009	0.0000	
	Slope	0.154	0.0000	
	Vegetation type	−0.54	0.0275	
3	Annual transpiration (mm per year)			0.90
	Elevation	−0.916	0.0000	
	Slope	0.458	0.0005	
	Vegetation type	2.392	0.0420	

Significance level was set at $\alpha = 0.05$, $N = 154$.

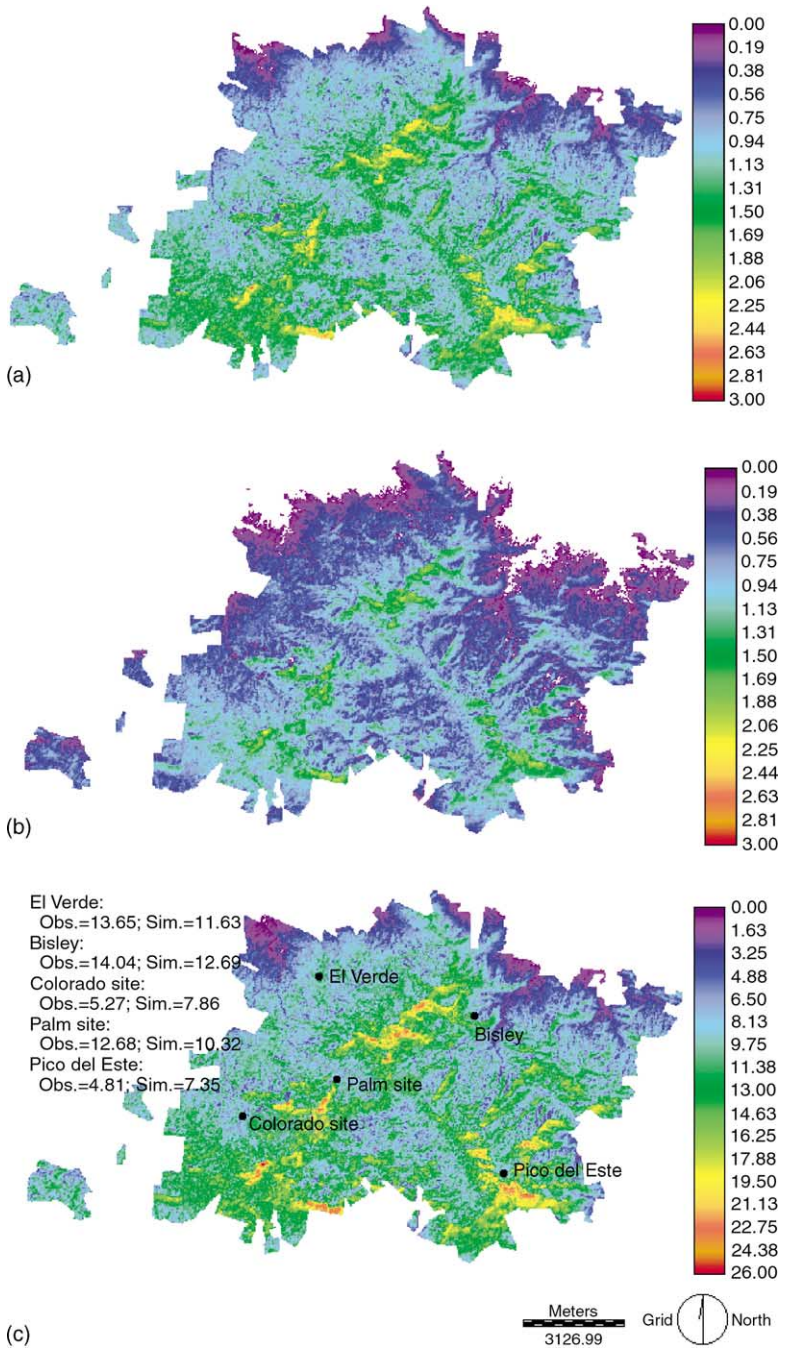

Fig. 7. Simulated NPP (t C/ha per month) distribution in March (a), October (b) and simulated annual NPP (t C/ha per month) (c) with comparison of simulated and measured values at five test sites in the Luquillo Experimental Forest (LEF), Puerto Rico.

Tabonuco forest (mean NPP = 8.04 t C/ha per year) to the middle elevation (Palm forest: mean NPP = 11.73 t C/ha per year and Colorado forest: mean NPP = 10.44 t C/ha per year in 500–800 m) and then decreasing to the cloud forest (9.7 t C/ha per year). But, within each vegetation type, there are substantial variations in predicted GPP and NPP across the Luquillo landscape. These variations are due to the heterogeneity of climatic variables (e.g. temperature), soil physical and chemical features, species composition and distribution, as well as natural and anthropogenic disturbances across the Luquillo Mountains (Waide et al., 1998).

Respiration, including both growth and maintenance respiration, also tends to decrease with elevation (from 68 to 31 t C/ha per year with a mean of 42 t C/ha per year), and at a given location, total respiration increases from the cooler dry months to warmer and rainy summer months. For example, the mean simulated monthly respiration in the Luquillo landscape increases from 4.7 t C/ha in January to 5.7 t C/ha in July, an increase of more than 20%.

The simulated GPP in each month for all four forest types from sampled locations shows weak seasonality, whereas the simulated NPP in each month shows a strong seasonality due to the strong seasonal pattern in respiration (Fig. 8). Both the simulated GPP and NPP peak in April when insolation, temperature and rainfall favor plant growth in all four forest types. However, the simulated NPP for the four forest types in the relatively rainy season is generally lower than that in the relatively dry season due in large part to the increased cloudiness, reduced insolation and increased soil saturation. The simulated GPP decreased in the order: Tabonuco > Palm > Colorado > Dwarf (Fig. 8). The simulated NPP decreased in the order: Palm > Colorado > Dwarf > Tabonuco (Fig. 8).

4.5. Climatic factors affecting primary productivity in the Luquillo Mountains

Multiple linear regression analyses of simulated annual GPP and NPP against climatic variables indicated that simulated GPP is related significantly (in this order of importance) to incoming canopy radiation (RAD), net longwave radiation (Rnl), air temperature, and vapor pressure deficit (VPD), while simulated NPP is related closely to incoming canopy radiation, net longwave radiation, vapor pressure deficit and transpiration (except in October) (Table 4). In March, the spatial pattern of simulated NPP also is related closely to rainfall (Table 4). We used March (end of dry season) and October (wet season) as the 2 months in our analyses of monthly distribution of forest productivity and respiration.

When we conducted Pearson correlation analyses between simulated GPP, NPP and simulated individual driving variables, we found that canopy radiation is the most important factor that drives GPP in the LEF (Table 5). While canopy radiation is also the most important factor for NPP in March, vapor pressure deficit determines the NPP variation in October. This suggests that variability in canopy radiation dominates the spatial variability of primary production in the Luquillo Mountains. The decrease in GPP with elevation is associated primarily with the decrease in solar insolation caused by the increase in cloudiness in the Luquillo Mountains. Plant transpiration is also an important factor in controlling the spatial variability in GPP. Plant transpiration is positively correlated with GPP but negatively correlated with NPP (Table 5). Increases in temperature increase GPP due to the increased net longwave radiation, but decrease GPP due to reduced mesophyll CO_2 conductance and canopy stomatal conductance of water. Increase in temperature may reduce NPP due to the increase in plant maintenance respiration more than the increase in GPP. Temperature is correlated positively with GPP but negatively with NPP in our simulation (Table 5).

4.6. Effects of climate change and elevated CO_2 on forest productivity

When air temperature and species composition are held constant, increasing rainfall by 33% increases annual GPP by 0–0.3% and annual NPP by 0–1.5%, whereas decreasing rainfall by 11% would reduce both GPP by 0–0.7% and NPP by 0–2.7% (Table 6). There is only a little change in GPP and NPP in the Colorado, Palm and Dwarf forests at high elevations from the simulated change in rainfall in the LEF.

When rainfall is held constant, increases in temperature of either 1.5 or 2.5 °C reduce annual GPP and NPP for the forest by 2.8–16.6 and 54–93%, respectively. A 1.5 °C increase would reduce GPP by 1.2–7.1%, and NPP by 30.9–69%. Simulated annual GPP

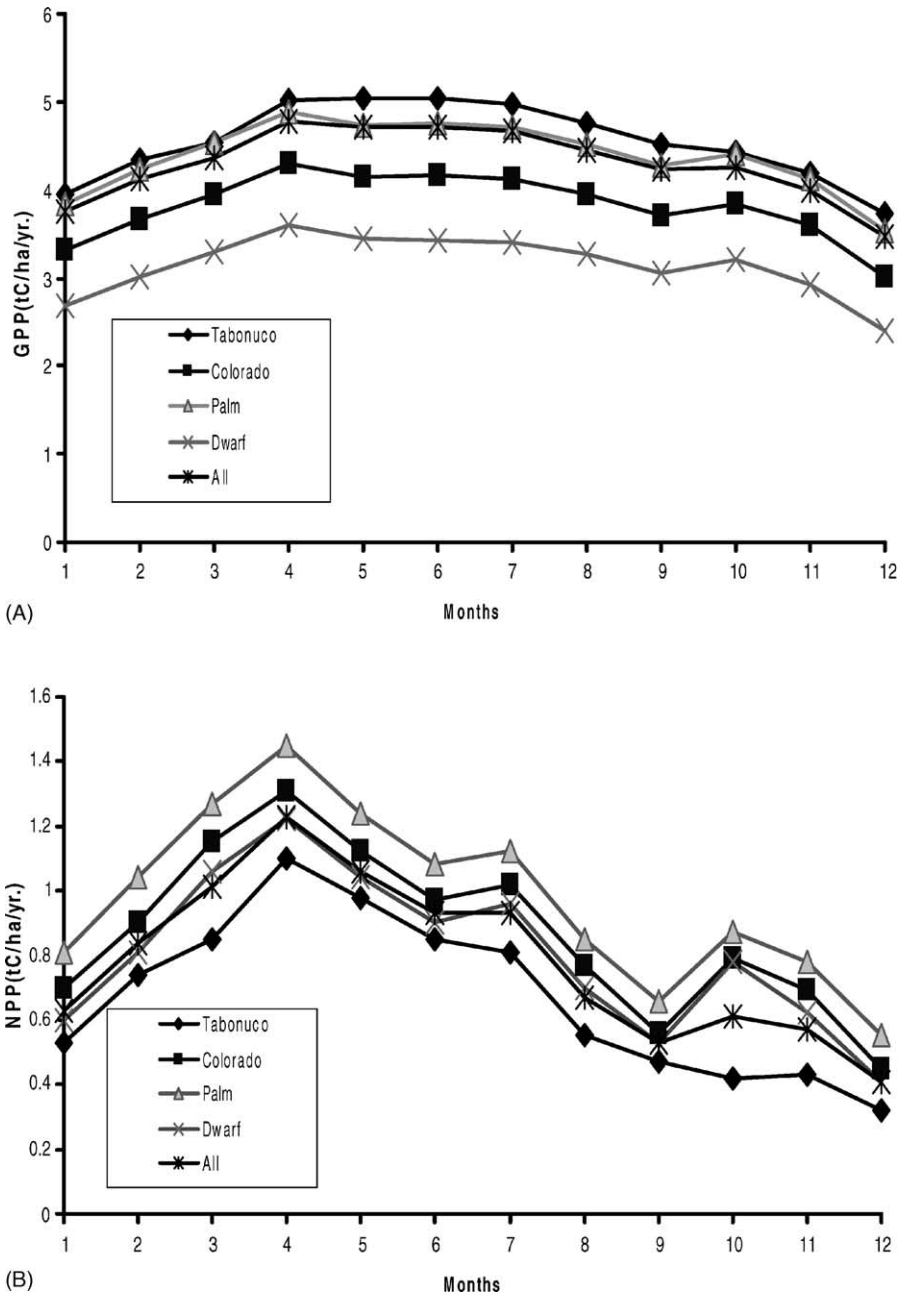

Fig. 8. Seasonal patterns of simulated GPP (A) and NPP (B) for Tabonuco, Colorado, Palm and Dwarf forests in the Luquillo Experimental Forest, Puerto Rico.

and NPP are especially sensitive to temperature increases in the Tabonuco forest at low elevations compared to the Colorado, Palm and Dwarf forests at high elevations. An increase in temperature of 2.5 °C decreases annual GPP by 17% and annual NPP by 94% in the Tabonuco forest, much more than the corresponding values for the average of all the forest types.

Table 4
Multiple regressions of simulated monthly GPP and NPP at selected locations from the TOPOPROD model against climatic factors (including simulated transpiration) in the Luquillo Experimental Forest (LEF), Puerto Rico

S.no.	Variables	RAD (MJ/m^2 per day)	Rnl (MJ/m^2 per day)	Temperature (°C)	VPD (mbar)	Rainfall (mm per month)	R^2
1	January-GPP						0.95
	Coefficient	0.363	−0.815	0.631	−0.92		
	P-level	0.0000	0.0000	0.0000	0.0000	NS	
2	January-NPP						0.93
	Coefficient	0.057	−0.052		−1.467		
	P-level	0.0000	0.0000	NS	0.0000	NS	
3	March-GPP						0.97
	Coefficient	0.33	−0.972	0.778	−1.23		
	P-level	0.0000	0.0000	0.0000	0.0000	NS	
4	March-NPP						0.92
	Coefficient	0.046	0.14		−2.13	0.003	
	P-level	0.0000	0.0000	NS	0.0000	0.0000	
5	July-GPP						0.98
	Coefficient	0.372	−1.327	0.806	−1.101		
	P-level	0.0000	0.0000	0.0000	0.0000	NS	
6	July-NPP						0.92
	Coefficient	0.044	−0.175		−2.051		
	P-level	0.0000	0.0000	NS	0.0000	NS	
7	October-GPP						0.97
	Coefficient	0.327	−0.949	0.551	−0.8		
	P-level	0.0000	0.0000	0.0000	0.0000	NS	
8	October-NPP						0.91
	Coefficient	0.065	−0.09	0.218	−0.592		
	P-level	0.0000	0.0000	0.0021	0.0000	NS	

RAD: incoming canopy radiation; Rnl: net longwave radiation; VPD: vapor pressure deficit; NS: not significant. Significance level was set at $\alpha = 0.05$, $N = 154$.

Table 5
Pearson correlation between simulated GPP, NPP and climate variables at selected locations ($N = 154$) in the Luquillo Experimental Forest (LEF), Puerto Rico

	RAD	Rnl	Temperature	VPD	Transpiration	Rainfall
March						
GPP	0.85	0.67	0.37	0.35	0.42	0.01
NPP	0.59	0.52	−0.37	−0.39	−0.31	0.38
October						
GPP	0.64	0.29	0.45	0.42	0.46	−0.09
NPP	−0.34	−0.58	−0.61	−0.65	−0.61	0.37

All correlations are significant at $P < 0.05$ except rainfall vs. GPP. RAD: incoming canopy radiation; Rnl: net longwave radiation; VPD: vapor pressure deficit.

Table 6
Responses of simulated gross primary productivity (GPP) and net primary productivity (NPP) to scenarios of potential climate change and doubling of CO_2 in the Luquillo Experimental Forest (LEF), Puerto Rico

Scenario	GPP					NPP				
	Tabonuco	Colorado	Palm	Dwarf	All	Tabonuco	Colorado	Palm	Dwarf	All
Base (+0 °C, +0% ppt)										
Value	54.53	45.78	52.53	37.71	51.21	8.04	10.44	11.73	9.72	9.37
+0 °C, −11% ppt										
Value	54.16	45.75	52.47	37.7	51.07	7.82	10.41	11.69	9.72	9.28
Change	−0.68	−0.07	−0.11	−0.03	−0.27	−2.74	−0.29	−0.34	0	−0.96
+0 °C, +33% ppt										
Value	54.7	45.78	52.54	37.71	51.66	8.16	10.44	11.75	9.73	9.49
Change	0.32	0	0.02	0	0.88	1.49	0	0.17	0.1	1.28
+1.5 °C, +0% ppt										
Value	50.67	44.76	51.12	37.27	48.98	2.5	6.12	6.56	6.72	4.3
Change	−7.08	−2.23	−2.68	−1.17	−4.35	−68.91	−41.38	−44.08	−30.86	−54.11
+1.5 °C, −11% ppt										
Value	47.82	44.51	50.62	37.21	47.29	2.16	5.95	6.3	6.67	4.02
Change	−12.31	−2.77	−3.64	−1.33	−7.65	−73.13	−43.01	−46.29	−31.38	−57.09
+1.5 °C, +33% ppt										
Value	52.53	44.86	51.32	37.29	50.03	2.85	6.19	6.71	6.73	4.54
Change	−3.67	−2.01	−2.3	−1.11	−2.3	−64.55	−40.71	−42.8	−30.76	−51.55
+2.5 °C, +0% ppt										
Value	45.44	43.45	49.09	36.65	45.43	0.52	2.97	3	4.39	1.72
Change	−16.67	−5.09	−6.55	−2.81	−11.29	−93.53	−71.55	−74.42	−54.84	−81.64
+2.5 °C, −11% ppt										
Value	42.38	42.31	46.93	36.38	43.06	0.37	2.58	2.6	4.23	1.46
Change	−22.28	−7.58	−10.66	−3.53	−15.91	−95.4	−75.29	−77.83	−56.48	−84.42
+2.5 °C, +33% ppt										
Value	50.44	43.93	50.14	36.77	48.44	0.77	3.23	3.37	4.47	1.98
Change	−7.5	−4.04	−4.55	−2.49	−5.41	−90.42	−69.06	−71.27	−54.01	−78.87
2x CO_2, +2.5 °C, −11% ppt										
Value	83.22	78.64	94.76	85.6	84.37	24.8	30.54	36.56	37.0	28.87
Change	52.61	71.77	80.39	126.9	64.75	208.4	192.14	211.67	280.64	208.1
2x CO_2, +2.5 °C, +33% ppt										
Value	91.7	79.5	96.36	86.0	89.43	29.26	31.19	37.8	37.2	31.63
Change	68.16	73.65	83.43	128.05	74.63	263.9	198.7	222.2	282.7	237.5

Value: t C/ha per year, change (%) = [(future GPP or NPP − base GPP or NPP)/base GPP or NPP]× 100, ppt: precipitation.

The greatest reductions in GPP and NPP for all forest types occur for the scenario of the combined 2.5 °C increase in temperature and 11% decrease in rainfall. The average decreases in annual GPP and NPP in the LEF are 16 and 84%. The greater reduction in NPP compared to GPP is due to the increased plant respiration at higher temperatures. For example, plant maintenance respiration would increase by 24% when temperature was increased by only 2.5 °C.

When both elevated CO_2 concentration and an associated 2.5 °C increase in temperature are simulated, both simulated annual GPP and NPP increase due to promotion of plant growth by elevated CO_2. Since Eq. (B.1) has photosynthesis as a linear response

to CO_2 then this model simply responds linearly to the CO_2. Whether this would actually occur is quite unlikely, and the degree of response is the subject of intense scientific debate that is outside the scope of this paper. Nevertheless, this model indicates that the reduction of productivity due to increased temperature and reduced rainfall does not cancel the growth increase attributable to elevated CO_2. Moreover, the simulated forest productivity in the LEF is likely to increase even more if rainfall increases. Of course, the responses of simulated annual GPP and NPP vary with forest types. Under the two CO_2 doubling scenarios, simulated GPP in the Tabonuco forest increases less than GPP in the other three forest types at higher elevations, whereas simulated NPP in the Tabonuco forest increases more than simulated NPP in the other three forest types (Table 6). For example, simulated GPP in the Tabonuco forest under the expected climate of $2\times$ CO_2 and $+2.5\ ^{\circ}C$ and $+33\%$ in precipitation increases by an average of 68%, lower than the 73, 83 and 128% in the Colorado, Palm and Dwarf forests, respectively. These responses indicate a much greater decrease in respiration in the Tabonuco forest than in other forest types in the LEF under an environment of increased CO_2, temperature and precipitation.

5. Discussion

5.1. Explanations for the patterns in primary production

Both simulation and field studies are in agreement that GPP declines with elevation in the LEF, but our simulated NPP increases slightly from low to middle elevation and decreases from middle to high elevations (e.g. Brown et al., 1983; Weaver and Murphy, 1990; Waide et al., 1998 and Table 6). In general, the spatial pattern of primary production of ecosystems depends on the variation of plant responses and adaptations to environmental driving variables such as light energy, temperature, CO_2 concentration, and water and nutrient availability (Medina, 1995). The LEF cannot be an exception. Sensitivity analysis of the TOPOPROD model in the Rio Mameyes watershed of the LEF indicated that solar insolation is the primary factor controlling GPP (Marley, 1998). Our multiple regression analysis also showed that incoming radiation of the canopy and net longwave radiation are the primary driving variables of primary production in the LEF (Tables 4 and 5). Bruijnzeel and Veneklaas (1998) also found that the decrease of canopy photosynthesis in tropical montane cloud forests is due mainly to the low radiation (persistent cloudiness) and low leaf area index. Radiation can be reduced by 15–50% in montane forests compared to lowland forests (Bruijnzeel and Veneklaas (1998). It should be noted that forest productivity is controlled by more than one environmental factor. At a global scale, temperature and water availability appear to be the dominant controlling factors, other than solar radiation, on forest production (Lieth, 1975; Churkina and Running, 1998).

There are other indications that montane forests such as the dwarf forest in the LEF are less productive than lowland forests such as the Tabonuco forest, as evidenced, for example, by the small amount of litterfall and diameter increment (e.g. Weaver and Murphy, 1990). But, our simulations indicated a slight increase in simulated NPP in the LEF, or simulated average NPP 9.72 t C/ha per year for Dwarf forest versus 8.04 t C/ha per year for Tabonuco forest (Table 6). Possible reasons for this discrepancy include: (1) there are no direct measurements of belowground NPP, and tropical montane forests appear to have a relatively larger root production as an adaptation to adverse environments such as increased wind, heavy rainfall, cloudiness, soil saturation and low temperature (Weaver and Murphy, 1990; Bruijnzeel and Veneklaas, 1998); (2) net photosynthetic capacity of montane forests is not necessarily lower than that of lowland forests; (3) previous field data are from limited samples and our point-sampled simulated data could also show NPP in the order: Tabonuco forest > Colorado forest > Dwarf forest (see Table 1). Long-term monitoring of permanent plots in the Tabonuco forest prior to Hurricane Hugo and Georges also showed that net growth has slowed since the 1940s (Weaver, 1983; Waide et al., 1998).

The complexity of the spatial patterns of GPP and NPP in the LEF cannot be described by a generalization of the few sampling points or even our complex simulations. Besides the spatial variation of mountainous climatic variables, possible P or K limitation, other factors such as treefalls, landslides, hurricanes,

and human disturbances also contribute to the complex spatial variation of forest productivity in the LEF (Zimmerman et al., 1995a; Waide et al., 1998). For example, young stands in valleys tend to have higher productivity than old stands due to the more-frequent landslides and treefalls, and more intense hurricane effects there. Forest productivity tends to increase following the removal of hurricane-generated debris due to the reduced nutrient immobilization in the decomposing coarse woody debris (Zimmerman et al., 1995b).

5.2. Comparison with other tropical forests

Comparison of GPP, NPP and respiration in the LEF with limited data in other tropical forests is summarized in Table 7. Leigh (1999) proposed two constants for tropical lowland rain forest: constant gross primary production (40 t C/ha per year) and constant evapotranspiration (about 1400 mm per year) due to the similarity in LAI in all such forests (around 7). Our simulated mean annual GPP is 51.2 t C/ha per year, higher than the 40 t C/ha per year (Table 7). The LEF in general has much higher gross primary production than most other tropical rain forests (Table 7). But, the mean value of NPP in the LEF (9.4 t C/ha per year) is lower than the 11 t C/ha per year of tropical rain forest in general (Murphy, 1975; Whittaker and Likens, 1975; Melillo et al., 1993) (Table 7). Frequent disturbances such as hurricanes and others are thought to be partially responsible for the lower NPP in the LEF compared with other tropical forests (Marley, 1998). Various disturbances, especially hurricanes, could result in the higher respiration in the LEF. The simulated mean respiration, 42 t C/ha per year, is similar to the respiration rate in tropical forest in Thailand (Larcher, 1983).

The ratio of simulated NPP to simulated GPP ranged from 0.16 to 0.36, with a mean value of 0.29, for the entire LEF. Unlike temperate forests which have a NPP/GPP ratio of 0.45 ± 0.05 (Waring and Running, 1998; Waring et al., 1998), the LEF has a variable and lower NPP/GPP ratio, indicating a larger respiration to gross production ratio, especially in the lower elevation Tabonuco forest. Previous ecosystem studies in the Tabonuco forest in the LEF (Odum and Pigeon, 1970; Brown et al., 1983) have also shown that plant respiration at lower elevations is high so that the NPP/GPP ratio is 0.13, in approximate agreement with our model.

5.3. Responses of primary productivity to changes in climate and CO_2

It is not possible to compare the response of simulated GPP and NPP to elevated CO_2 and climate

Table 7
Comparison of simulated GPP and NPP in the Luquillo Experimental Forest (LEF), Puerto Rico with other tropical forests

Forests	GPP	NPP	Respiration	Reference
LEF, PR				
Simulated	8.45–92.07 (51.2)	0.5–23.9 (9.4)	31–68 (42)	This study
Observed	12–60 (?)[a]	4.8–14 (?)[a]	?–53 (?)[a]	LTER-LUQ
Dry forest, south coast, PR		5.5		Murphy et al., 1995
Rondonia, Brazil	27			Leigh, 1999
Barro Colorado			24	Leigh, 1999
Ducke Reserve, Manaus			35.8	Leigh, 1999
Tropical rain forest, Thailand	65	14.3	49.5	Larcher, 1983
Tropical rain forest in general	40 (constant of the forest)			Leigh, 1999
Tropical rain forest		5–18 (11)		Whittaker and Likens, 1975
Tropical seasonal forest		5–12 (8)		Whittaker and Likens, 1975
Tropical evergreen forest		4.07–14.22 (10.98)		Melillo et al., 1993
Tropical rain forest		2.7–16.1 (10.8)		Murphy, 1975
Tropical rain forest		12.7–18.4 (15.6)		Grace et al., 2001

Unit: t C/ha per year; values in parenthesis are means.
[a] ? indicates no data available.

change to measured values because there are no appropriate field experiments in any of the four forest types. Increased rainfall could reduce NPP due to the lowered nutrient supply caused by the increase in anaerobic conditions in wetter soils, or increase NPP due to increased nutrient availability in drier soils (Ryan, 1991b; Pan et al., 1998; Silver, 1998). Our simulations indicate that increases in rainfall alone would increase NPP slightly in the LEF (Table 6). This is probably due to the aerobic conditions of soils in a large area in the LEF, especially at the low elevations. Melillo et al. (1993) have found that when simulated temperature and precipitation were increased in the TEM model, simulated NPP for a tropical evergreen forest decreased from 8.9 to 20.6% due to the increased temperature and cloudiness. Our simulations also showed this trend but with a higher reduction (30–90% due to the larger changes in temperature and rainfall. Increased temperature would enhance plant respiration enough to decrease NPP in tropical forests where nitrogen is not limiting to NPP. In addition, increased temperatures would increase the evaporation rate that would lead to non-linear effects such as increased stomatal closure (Cropper et al., 1997). Increased cloudiness in tropical forests may decrease PAR enough to reduce NPP.

Melillo et al. (1993) also found in their simulation that for tropical forests the direct effects of elevating CO_2 are the most important contribution to increases in NPP. One reason for increased NPP with elevated CO_2 is that elevated CO_2 may decrease the respiration rates of trees, although the underlying mechanism of this response is not well understood (Ryan, 1991a, 1991b). Other studies in temperate forests indicated that a doubling of the CO_2 concentration might result in increased NPP for trees even with the increased respiration caused by a 4 °C temperature increase (e.g. Cropper et al., 1997). Sampson et al. (1997) and Teskey et al. (1997) also found that elevated CO_2 has a much greater effect on simulated NPP response than temperature and precipitation changes. The greater increase in NPP than GPP in our simulations (Table 6) is probably due to the inhibition of plant respiration under CO_2 doubling. But, we did not incorporate any of the possible negative feedbacks of CO_2 doubling that might compensate for some of the direct effects of CO_2 increase on plant growth at this time because their applicability to the LEF was not clear. From the perspective of forest management, the Tabonuco forest plays a greater role in carbon storage under future elevated CO_2 conditions than the other forest types.

It should be noted that our predictions of the LEF responses to potential climate change and elevated CO_2 concentration represent our current understanding of the potential effects of climate change and elevated CO_2 on forest productivity. There are many uncertainties associated with these predictions. For example (1) there is an uncertainty in predictions of future climate change in Puerto Rico; (2) we did not include soil nutrient status, plant-nutrient uptake and the effects of nutrient limitation on tree physiology and growth or the response of photosynthesis to changing CO_2 concentration; and (3) we assume that the basic canopy photosynthesis equations from FOREST-BGC model are appropriate for the Luquillo forest where in fact its components have not been measured explicitly nor have other possible basic formulations been studied. These and other potential limitations could significantly alter the responses of photosynthesis, maintenance respiration, transpiration, carbon allocation, storage, and growth patterns. On the other hand, our new field measurements of gross photosynthesis and ecosystem respiration over the entire elevational gradient will help answer many questions.

Acknowledgements

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Appendix A. The TOPOCLIM model

The TOPOCLIM model was used to generate simulated values of climatic variables in the LEF. The simulated climatic variables then were used as input into the TOPOPROD model to simulate the GPP and NPP across the entire Luquillo Mountain. The derivation of the TOPOCLIM model is as follows.

Relative humidity is calculated as the ratio of water vapor content to the saturation vapor pressure. The actual water vapor pressure (WVP) is computed as a function of temperature using the following equation (Wooster, 1989):

$$\text{water vapor pressure (mbar)} = -0.474 + 1.161 \times T_{\min}, \quad R^2 = 0.97 \tag{A.1}$$

where $T_{\min}$ is the minimum night-time temperature (°C).

Saturation vapor pressure (SVP) is calculated using the method of Murray (1967):

$$\text{SVP} = 6.1078 \ \exp\left(\frac{17.27 \times T_{\text{air}}}{T_{\text{air}} + 237.3}\right) \tag{A.2}$$

where T_{air} is air temperature (°C). SVP is important in calculating vapor pressure deficit, which is the difference between the SVP and WVP for a given period.

We simulated average annual rainfall using a rainfall-elevation equation that is developed for the LEF from Garcia-Martino et al. (1996) as follows:

$$\text{mean annual rainfall (mm year)} = 2300 + 3.8 \times \text{Elev} - 0.0016 \times \text{Elev}^2 \tag{A.3}$$

Monthly rainfall at any site is derived using the pattern of monthly rainfall at the El Verde Field Station (400 m). This monthly pattern is used to derive monthly values of rainfall over the entire LEF because annual and seasonal variations in rainfall are similar along the elevational gradient in the LEF (Brown et al., 1983).

Canopy transpiration is calculated with the Penman–Monteith equation for the relation among latent heat efflux, net radiation influx, air saturation vapor pressure deficit and the aerodynamic and stomatal conductance:

$$\text{Trans} = \frac{(\text{slope} \times \text{RAD}) + (\text{CP} \times \text{PA} \times \text{VPD})/r_{\text{a}}}{(\text{slope} + \text{gamma}(1 + r_{\text{c}}/r_{\text{a}}))/\text{LE}} \times \text{DAYL} \tag{A.4}$$

where Trans is transpiration rate (mm per day), slope the slope of the saturation vapor pressure curve at air temperature (kPa/°C), RAD average net radiation received by the canopy (MJ/m^2 per day), CP specific heat of air (MJ/kg/°C), PA density of air (kg/m^3), VPD vapor pressure deficit, r_{c} canopy surface resistance to water vapor (s/m), r_{a} canopy aerodynamic resistance (s/m), gamma psychrometric constant (kPa/°C), and LE is latent heat of vaporization (MJ/kg). The slope and RAD were calculated as follows:

$$\text{slope} = \frac{2504 \times \exp(17.27 \times T_{\text{air}}/(T_{\text{air}} + 237.3))}{(T_{\text{air}} + 237.3)^2} \tag{A.5}$$

and

$$\text{RAD} = (1 - \alpha) \times Q - \text{Rnl} \tag{A.6}$$

where α is canopy albedo, Q canopy daily average radiation (KJ/m^2 per day, see Appendix B), Rnl is net longwave radiation (MJ/m^2 per day) (Allen et al., 1998) and

$$\text{Rnl} = \sigma \times \left\{\frac{(T_{\max}^4 + T_{\min}^4)}{2}\right\} \times (0.34 - 0.14 \times \text{WVP}^{0.5}) \times (1.35 \times \text{Rsso} - 0.35) \tag{A.7}$$

where σ is Stefan-Boltzmann constant (MJ/K^{-4}/m^2 per day), $T_{\max}$ and $T_{\min}$ maximum and minimum absolute temperature in Kelvin during the 24-hour period (K = °C + 273.16), Rsso is relative short-wave radiation, and

$$\text{Rsso} = \frac{\text{Rs}}{0.75 \times \text{Ra}} \tag{A.8}$$

where Rs is solar radiation at the location studied (MJ/m^2 per day), Ra is daily extraterrestrial radiation entering the top of the atmosphere at a given latitude (MJ/m^2 per day) (Allen et al., 1998), and

$$\text{gamma} = 0.665 \times 101.3 \times \left\{\frac{(293 - 0.0065 \times \text{Elev})}{293}\right\}^{5.26} \tag{A.9}$$

where Elev is elevation in meters above sea level.

Appendix B. The TOPOPROD model

The TOPOPROD model is based on the FOREST-BGC model (Running and Coughlan, 1988; Running and Gower, 1991). In FOREST-BGC, canopy photosynthesis is computed as a function of the CO_2 diffusion gradient between the inside of a leaf and the atmosphere, canopy stomatal conductance, radiation- and temperature-controlled mesophyll CO_2 conductance, leaf area index and day length. Daily photosynthesis is simulated as follows (Running and Coughlan, 1988):

$$\mathrm{PSY} = \left(\frac{0.2727 \times \Delta CO_2 \times \mathrm{CC} \times \mathrm{CM}}{\mathrm{CC} + \mathrm{CM}}\right) \times \mathrm{LAI} \times \mathrm{DAYL} \quad \text{(B.1)}$$

where PSY is daily canopy photosynthesis (kg C/m^2 per day), 0.2727 a coefficient to convert CO_2 to carbon, ΔCO_2 the CO_2 diffusion gradient from leaf surface to air (kg/m^3), CC canopy stomatal conductance (multiply by 1.6 for CO_2/H_2O diffusion correction, m/s), CM canopy CO_2 mesophyll conductance (m/s), leaf area index (LAI, m^2/m^2), and DAYL is day length (hour). The resulting value is converted to t C/ha and summed to derive monthly and annual gross primary productivity.

Canopy stomatal conductance of water (CC) is computed as a function of the leaf water potential (CCw) and the absolute humidity deficit of the air:

$$\mathrm{CC} = \mathrm{CCw} - (\mathrm{CCw} \times \mathrm{DCCh} \times \mathrm{ABSHD}) \quad \text{(B.2)}$$

$$\mathrm{CCw} = \mathrm{CC}_{\max} - \mathrm{DCCw} \times (\mathrm{LWP} - \mathrm{LWP}_{\min}) \quad \text{(B.3)}$$

where CC is the canopy stomatal conductance to water vapor, CCw the canopy stomatal conductance to water vapor, DCCh the slope of CC versus ABSHD (m/(s μg m^3)), ABSHD the absolute humidity deficit (μg/m^3), $\mathrm{CC}_{\max}$ the maximum canopy conductance (m/s), DCCw the slope of CC versus LWP, LWP the daily maximum leaf water potential (MPa), and $\mathrm{LWP}_{\min}$ is minimum leaf water potential inducing stomatal closure (MPa). Leaf water potential is calculated as follows (Running and Coughlan, 1988):

$$\mathrm{LWP} = \frac{0.2}{\mathrm{SWF}_{\mathrm{rac}}} \quad \text{(B.4)}$$

where $\mathrm{SWF}_{\mathrm{rac}}$ is monthly soil water fraction and can be calculated as:

$$\mathrm{SWF}_{\mathrm{rac}} = \frac{\mathrm{RAN} - \mathrm{Trans}}{\mathrm{SWC}} \quad \text{(B.5)}$$

where RAN is monthly rainfall from the TOPOCLIM model, Trans monthly transpiration, SWC maximum soil water holding capacity, derived as 30 cm in the Luquillo Mountain, from soil survey data (USDA, 1991).

The mesophyll CO_2 conductance, CM, is computed from leaf nitrogen, light and temperature:

$$\mathrm{CM} = \mathrm{CM}_{\max} \times \mathrm{CMn} \times \mathrm{CMq} \times \mathrm{CMt} \quad \text{(B.6)}$$

where $\mathrm{CM}_{\max}$ is maximum mesophyll conductance (m/s), CMn a leaf nitrogen scalar (0−1), and

$$\mathrm{CMn} = 18.2 \times \mathrm{LeafN} + 0.5 (\textit{Marley}, 1998) \quad \text{(B.7)}$$

where LeafN is leaf nitrogen content (ca. 1.2% for the LEF), and CMq is a radiation scalar (0−1), and

$$\mathrm{CMq} = \frac{Q - Q_0}{Q + Q_{0.5}} \quad \text{(B.8)}$$

where Q is canopy daily average radiation above the canopy (KJ/m^2 per day), Q_0 photosynthesis light compensation point (KJ/m^2 per day), $Q_{0.5}$ radiation level where CMq is half of maximum, and CMt is a temperature scalar (KJ/m^2 per day) and

$$\mathrm{CMt} = \frac{(T_{\max} - T_{\mathrm{air}}) \times (T_{\mathrm{air}} - T_{\min})}{T_{\max}^2} \quad \text{(B.9)}$$

where $T_{\max}$ is the maximum temperature photosynthesis compensation point (°C), T_{air} daily average air temperature (°C), and $T_{\min}$ is minimum temperature photosynthesis compensation point (°C).

LAI for each grid cell is derived from NDVI–LAI equation for the LEF as detailed in the text. Day length (DAYL), temperature ($T_{\max}$, $T_{\min}$, T_{air}) and solar insolation are calculated from the TOPOCLIM model (Wooster, 1989).

Absolute humidity deficit is calculated as a function of vapor pressure deficit and air temperature:

$$\mathrm{ABSHD} = \frac{217 \times \mathrm{VPD}}{T_{\mathrm{air}} + 273.16} \quad \text{(B.10)}$$

Average daily radiation of the canopy, Q, is calculated from Beer's law:

$$Q = \frac{\mathrm{Rs} \times (1 - \exp((\mathrm{LAI}/2.2) \times \mathrm{EXT}))}{-\mathrm{EXT} \times (\mathrm{LAI}/2.2)} \quad \text{(B.11)}$$

where Rs is incoming solar radiation (MJ/m^2 per day) from TOPOCLIM (Wooster, 1989), and EXT is the radiation extinction coefficient through the canopy.

NPP is the net annual carbon gain by the vegetation. NPP is calculated as:

$$\mathrm{NPP} = \mathrm{GPP} - R_{\mathrm{growth}} - R_{\mathrm{maintenance}} \quad \text{(B.12)}$$

Plant growth respiration is assumed to be a constant proportion of tissue accumulation, about 25% (Ryan, 1991a; Waring et al., 1998). Plant maintenance respiration is modeled as three components, respiration from leaf, stem and root:

$$R_{\mathrm{maintenance}} = R_{\mathrm{leaf}} + R_{\mathrm{stem}} + R_{\mathrm{root}} \quad \text{(B.13)}$$

$$R_{\mathrm{leaf}} = \left[0.00084 \times \exp\left(\mathrm{LN}\left(\frac{Q_{10}}{10}\right) \times T_{\mathrm{air}}\right) \times \mathrm{C}_{\mathrm{leaf}}\right] \times \frac{\mathrm{LAI}}{7.05} \quad \text{(B.14)}$$

$$R_{\mathrm{stem}} = \left[0.00048 \times \exp\left(\mathrm{LN}\left(\frac{Q_{10}}{10}\right) \times T_{\mathrm{air}}\right) \times \exp(0.67 \times \mathrm{LN}(\mathrm{C}_{\mathrm{stem}}))\right] \times \frac{\mathrm{LAI}}{7.05} \quad \text{(B.15)}$$

$$R_{\mathrm{root}} = \left[0.000334 \times \exp\left(\mathrm{LN}\left(\frac{Q_{10}}{10}\right) \times T_{\mathrm{soil}}\right) \times C_{\mathrm{root}}\right] \times \frac{\mathrm{LAI}}{7.05} \quad \text{(B.16)}$$

Table 8
Parameters used in simulation of mountainous climate variables and primary productivity in the Luquillo Experimental Forest (LEF), Puerto Rico, using the TOPOPROD model[a]

Variable	Value	Description	Unit
$\mathrm{LWP_{min}}$	0.5	Minimum leaf water potential	MPa
LWPsc	1.65	Leaf water potential at stomatal closure	MPa
$\mathrm{CC_{max}}$[b]	0.0025	Maximum stomatal conductance	m/s
$\mathrm{CM_{max}}$[b]	0.00125	Maximum mesophyll conductance	m/s
Ext	0.5	Canopy light extinction coefficient	
DCCh	0.05	Slope of stomatal conductance vs. Humidity curve	m/(s μg m^3)
CutCnd	0.00005	Cuticular conductance	m/s
RadSct	3000	Radiation stomatal conductance threshold	kJ/m^2 per day
LeafNC[c]	0.012	Leaf nitrogen content	kg N/kg
Q_0	432	Photosynthesis light compensation point	kJ/m^2 per day
$Q_{0.5}$	9730	Photosynthesis half maximum light	kJ/m^2 per day
TemScl	4	Temperature scalar	
PsnMxT	40	High temperature compensation point	°C
PsnMnT	0	Low temperature compensation point	°C
$\mathrm{AirCO_2}$	0.0006	Atmospheric $\mathrm{CO_2}$ concentration	kg/m^3
$\mathrm{CO_2Com}$	0.00007	$\mathrm{CO_2}$ compensation point	kg/m^3
CP	1.013×10^{-3}	Specific heat of air	MJ/kg/°C
r_a[d]	2.1	Canopy aerodynamic resistance	s/m
r_c[d]	58	Canopy surface resistance to water vapor	s/m
LE	2.45	Latent heat of vaporization	MJ/kg
α	0.23	Canopy albedo	
σ	4.903×10^{-9}	Stefan-Boltzmann constant	MJ/K^{-4}/m^2 per day
$\mathrm{C_{leaf}}$[e]	7.9	Carbon storage in leaf	t/ha
$\mathrm{C_{stem}}$[e]	72.7	Carbon storage in stem	t/ha
$\mathrm{C_{root}}$[e]	36.3	Carbon storage in root	t/ha

[a] All parameters from Running and Coughlan (1988), except.
[b] Running and Hunt (1993).
[c] Odum (1970).
[d] Schellekens (2000).
[e] Frangi and Lugo (1985, 1992), Weaver and Murphy (1990), Lugo et al. (1995), Scatena and Lugo (1995).

where Q_{10} (=2.3) is the change in respiration rate with a 10 °C change in temperature (Ryan, 1991a); C_{leaf}, C_{stem}, and C_{root} carbon storages in leaf, stem and root at maximum LAI (=7.05), 7.9, 72.7 and 36.3 t/ha, respectively, for the LEF (Odum, 1970; Frangi and Lugo, 1985, 1992; Weaver and Murphy, 1990; Lugo et al., 1995; Scatena and Lugo, 1995). Parameters used in the TOPOPROD model are summarized in Table 8.

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