GLOBAL POTENTIAL NET PRIMARY PRODUCTION PREDICTED FROM VEGETATION CLASS, PRECIPITATION, AND TEMPERATURE

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Abstract. Net primary production (NPP), the difference between CO_2 fixed by photosynthesis and CO_2 lost to autotrophic respiration, is one of the most important components of the carbon cycle. Our goal was to develop a simple regression model to estimate global NPP using climate and land cover data. Approximately 5600 global data points with observed mean annual NPP, land cover class, precipitation, and temperature were compiled. Precipitation was better correlated with NPP than temperature, and it explained much more of the variability in mean annual NPP for grass- or shrub-dominated systems ($r^2 = 0.68$) than for tree-dominated systems ($r^2 = 0.39$). For a given precipitation level, tree-dominated systems had significantly higher NPP ($\sim$100–150 g C·m^{-2}·yr^{-1}) than non-tree-dominated systems. Consequently, previous empirical models developed to predict NPP based on precipitation and temperature (e.g., the Miami model) tended to overestimate NPP for non-tree-dominated systems. Our new model developed at the National Center for Ecological Analysis and Synthesis (the NCEAS model) predicts NPP for tree-dominated systems based on precipitation and temperature; but for non-tree-dominated systems NPP is solely a function of precipitation because including a temperature function increased model error for these systems. Lower NPP in non-tree-dominated systems is likely related to decreased water and nutrient use efficiency and higher nutrient loss rates from more frequent fire disturbances. Late 20th century aboveground and total NPP for global potential native vegetation using the NCEAS model are estimated to be $\sim$28 Pg and $\sim$46 Pg C/yr, respectively. The NCEAS model estimated an $\sim$13% increase in global total NPP for potential vegetation from 1901 to 2000 based on changing precipitation and temperature patterns.

Key words: ecosystem modeling; global NPP; Miami model; National Center for Ecological Analysis and Synthesis (NCEAS) model; nitrogen losses; water stress.

INTRODUCTION

Terrestrial net primary production (NPP) is among the most important ecosystem variables that have been studied extensively during the last 40 years (Lieth 1975, Roy et al. 2001). NPP is one of the main causes for the observed seasonal changes in atmospheric CO_2 levels (Keeling et al. 1996) and is one of the main sources for human food resources, wood products, and fuel. NPP has been measured for all of the major managed and natural ecosystems in the world (Scurlock et al. 1999, Cramer et al. 2001) and is one of the most important output variables from ecosystem models that are compared to observed data sets (Jager et al. 2000). The two most common methods for estimating NPP

include measuring the biomass produced during the growing season (Landsberg and Gower 1997) and measuring net gas exchange (gross plant production minus autotrophic respiration). In this paper, we focus on evaluating how NPP estimated using biomass produced during the growing season is correlated with precipitation and temperature.

One of the first and most well-known models that relates NPP to precipitation and temperature is the Miami model (Lieth 1975). This model is based on the law of the minimum; mean annual NPP is a function of the minimum of empirical mean annual precipitation (MAP) and mean annual temperature (MAT) functions. The precipitation equation in the Miami model is curvilinear and predicts that NPP increases with precipitation at a gradually decreasing rate as precipitation rises up to $\sim$4000 mm/yr. The temperature equation is S-shaped but close to linear. Schuur (2003) also estimated NPP as a function of precipitation and

temperature but used a more extensive data set of observed NPP values that included data from tropical forests with high (>4000 mm/yr) precipitation. The main difference between the Miami and Schuur models is that the Schuur precipitation equation shows NPP peaking at ~2200 mm and then gradually declining as precipitation increases up to ~8000 mm. Our goals were to investigate the relationships between MAP, MAT, and NPP using a large global data set, to develop a new NPP model based on these relationships, to evaluate the Miami and Schuur models, and to use our new model to better estimate global NPP for potential native vegetation under current climate and to estimate global trends in NPP in response to 20th century climate change.

METHODS

Data sets used

We primarily used NPP, climate, and vegetation class data from the Ecosystem Model–Data Intercomparison (EMDI) project (Olson et al. 2001). The goals of the project were to establish a consistent global NPP data set with which to compare and improve models and data collection methods. About a dozen different biogeochemical, satellite-driven, and dynamic vegetation global models were used in EMDI workshops held at the National Center for Ecological Analysis and Synthesis (NCEAS) in Santa Barbara, California, USA. NPP data were compiled from a variety of literature sources for ~1000 global points and ~4500 regional 0.5° latitude/longitude cells in the central and eastern United States and Australia, based on field observations and allometric relationships. This represents the largest global NPP data set collected to date and is available at the Distributed Active Archive Center, Oak Ridge National Laboratory web site.[10]

NPP for the 0.5° latitude/longitude cells for the eastern United States was based on county-level FIA (forest inventory and analysis) wood increment measurements and regression equations (Gillespie 1999). NPP for the 0.5° cells in the U.S. Great Plains was based on thousands of observations and a region-specific precipitation regression (Sala et al. 1988). NPP for the 0.5° cells in Australia was based on hundreds of data points and regressions that accounted for precipitation, soil fertility, and other ecosystem parameters (Barrett 2001). Climate data for each grid cell from 1961 to 1990 were obtained from the Potsdam Institute for Climate Change Research. We obtained land cover data from original publications or the University of Maryland land cover project (Hansen et al. 2000). EMDI includes both aboveground (ANPP) and total (TNPP) NPP data. Analyses were performed on both ANPP and TNPP because ANPP was more reliably estimated, but some data sets reported only TNPP and previous models (e.g., Lieth 1975, Schuur 2003) only estimated TNPP.

Although the EMDI represents the largest global NPP data set collected to date, it contained few points with precipitation above ~3000 mm. Consequently, we supplemented the EMDI data with NPP data from other sources. TNPP data (~40 points) from tropical forests compiled by Schuur (2003) and Clark et al. (2001) and ANPP data (~45 points) from tropical forests compiled by Keeling and Phillips (2007) were included in our analyses.

Mean annual precipitation (MAP) and mean annual temperature (MAT) were annual 30-yr means from the period 1961–1990 except for the non-EMDI data mentioned previously, in which case the mean values represented varying time periods, depending on the data source. ANPP and TNPP values were annual means for the years in which measurements were available for the different points or cells.

To quantify moisture stress, we also calculated actual evapotranspiration (AET) and potential evapotranspiration (PET) for the EMDI data points. AET and PET are the means for all the EMDI models that calculated these variables. For the types of models used in this analysis AET and PET are calculated as a function of temperature, solar radiation, and leaf area index. Leaf area index is simulated as a function of vegetation type, phenology, and plant growth rates. AET is also controlled by soil water content, which is influenced by texture, soil depth, and rooting distribution. As with MAP and MAT, AET and PET were annual 30-yr means from the period 1961–1990. We used the ratio of water supply (AET) to water demand (PET) as an index for moisture stress.

Data analysis

Correlation coefficients were calculated for linear regressions of ANPP and TNPP vs. MAT and MAP, and the ability of previous models to predict TNPP was evaluated. Initial analysis showed that tree-dominated systems (boreal, temperate, and tropical forests) and non-tree-dominated systems (grasslands, shrublands, deserts, and savannas) had strongly different ANPP and TNPP responses to MAT and MAP, so these two plant functional groups were analyzed separately. The analyses reported here are based on biome means for NPP; means and medians were similar for tree-dominated systems, but medians were lower for non-tree-dominated systems, indicating a skewed distribution. We developed a new model, NCEAS, named for the National Center for Ecological Analysis and Synthesis in Santa Barbara, California, USA, because much of the data analysis was performed there as part of the EMDI project. The NCEAS model is based on the equations presented by Schuur (2003). Schuur (2003) used exponential functions for MAT and MAP to estimate TNPP, which is defined as the minimum value predicted by the two equations. Parameters in the equations from Schuur (2003) were optimized by
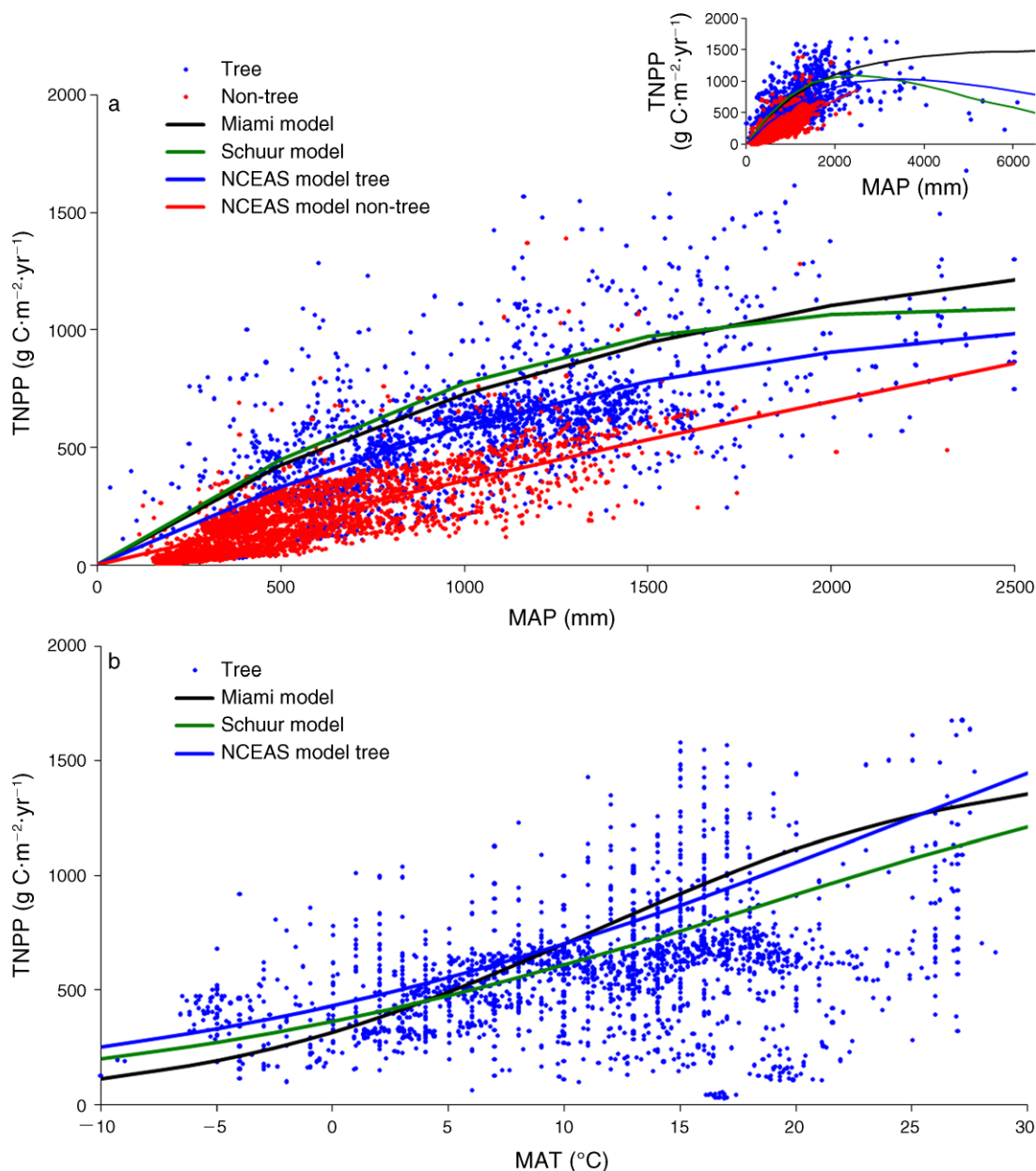
Fig. 1. (a) Total net primary production (TNPP) for tree-dominated (blue dots) and non-tree-dominated (red dots) systems compared with mean annual precipitation (MAP), TNPP as a function of MAP in the Miami (Lieth 1975) and Schuur (2003) models, and TNPP as a function of MAP for tree- and non-tree-dominated systems in the National Center for Ecological Analysis and Synthesis (NCEAS) model described in this paper. (b) TNPP for tree-dominated systems as a function of mean annual temperature (MAT) in the Miami (Lieth 1975), Schuur (2003), and NCEAS models.

minimizing the root mean square error (RMSE) for modeled and observed ANPP and TNPP. We used the RMSE criterion instead of optimizing by maximizing the correlation coefficient (r^2) because a model can have a high r^2 but still be very biased. That is, r^2 could equal one, but the model predictions could be, for example, five or 10 times higher on average than the observations. Optimizing by minimizing RMSE ensures that the mean

predicted value will be identical (or very close) to the mean observed value.

We developed global maps for ANPP and TNPP based on the NCEAS model, 0.5° latitude/longitude potential biome classification maps, and 0.5° latitude/longitude MAT and MAP data. Biome data were from the Potsdam NPP Model Intercomparison (Cramer and Field 1999, Cramer et al. 1999) and climate data (1901–

Table 1. Mean error, root mean square error (RMSE), and coefficients of determination (r^2) for modeled and observed net primary production.

Model	Mean error	RMSE	r^2
Non-tree-dominated systems			
Miami	137.3	260	0.67
Schuur	144.2	275	0.63
NCEAS	7.2	93	0.68
Tree-dominated systems			
Miami	13.0	240	0.35
Schuur	6.3	229	0.30
NCEAS	−0.4	204	0.40
Overall			
Miami	55.9	253	0.61
Schuur	53.9	260	0.53
NCEAS	2.2	142	0.75

Note: The three models are the Miami model (Lieth 1975), the Schuur model (Schuur 2003), and the National Center for Ecological Analysis and Synthesis (NCEAS) model described in this paper.

2000) were from the Climate Research Unit (CRU; *available online*).[11] The NCEAS model was run from 1901 to 2000 and mean TNPP and ANPP from 1981 to 2000 were calculated and mapped. We also made a difference map by subtracting TNPP predicted by the NCEAS model from TNPP derived from the Miami model over the same time period. To estimate the impacts of 20th century climate change on TNPP of potential vegetation we calculated the slope of the linear regression of TNPP vs. time from 1901 to 2000 for each grid cell, and multiplied the slope by 100 to estimate the change in TNPP for this time period. Because this analysis was based entirely on model results, we used all slopes, regardless of significance.

Results

As expected, we found a strong relationship between TNPP and MAP (Fig. 1a). More interestingly, tree-dominated systems showed a significantly different TNPP response compared to non-tree-dominated systems. On average, for a given amount of MAP, tree-dominated systems fixed ~100–150 g C·m^{-2}·yr^{-1} more than non-tree-dominated systems. Consequently, the Miami and Schuur models overestimated TNPP for non-tree-dominated systems (Fig. 1a, Table 1). In response, we parameterized separate equations for tree-dominated and non-tree-dominated systems for our NCEAS model. After optimizing parameters, our NCEAS model for NPP is:

$$TNPP = 6116 \times [1 - \exp(-6.05 \times 10^{-5} \times MAP)]$$

if non-tree

$$Min[F(MAP), F(MAT)]$$

if tree

[11] ⟨www.cru.uea.ac.uk/⟩

where $F(MAP) = 0.551 \times MAP^{1.055}/\exp(0.000306 \times MAP)$ and $F(MAT) = 2540/[1 + \exp(1.584 - 0.0622 \times MAT)]$; and

$$ANPP = 4000 \times [1 - \exp(-4.77 \times 10^{-5} \times MAP)]$$

if non-tree

$$Min[F(MAP), F(MAT)]$$

if tree

where $F(MAP) = 0.1665 \times MAP^{1.185}/\exp(0.000414 \times MAP)$ and $F(MAT) = 3139/[1 + \exp(2.2 - 0.0307 \times MAT)]$.

Compared to the Miami model, our model predicts lower TNPP, particularly at high MAP values. Compared to the Schuur model, lower TNPP at low MAP values, and higher TNPP at high MAP values are predicted (Fig. 1a). The temperature equations are similar except that our temperature equation predicts higher TNPP at low MAT ranges, and the Miami model predicts lower TNPP at high temperature ranges (Fig. 1b).

Surprisingly, we found MAT to be a minor controller of TNPP. Tree-dominated systems showed a relatively weak ($r^2 = 0.17$) positive temperature effect, and including temperature in the overall TNPP equation resulted in a marginally better ($r^2 = 0.40$ vs. 0.39) model fit with the data than MAP alone. The effect of temperature in non-tree-dominated systems was negative and was thus not included in our NCEAS model.

To investigate whether the differential TNPP response for tree-dominated and non-tree-dominated systems could be explained by trees occupying less water-stressed zones, we selected a subset of data points for both systems that had moderate to high water availability (MAP > 1000 mm and AET/PET > 0.5). When TNPP was regressed with MAP, there remained a high degree of separation (Fig. 2), suggesting that factors other than residing in climate zones with minimal water stress contribute to tree-dominated systems having higher TNPP for a given range of MAP. The patterns described previously held for ANPP also, so figures and statistics are not presented for ANPP. Separate analyses for the global data points and the regional cells also led to identical conclusions, so the results are not reported.

Comparing the NCEAS TNPP map with the map of potential vegetation shows highest NPP in the tropics followed by temperate forests (Fig. 3a, b). Tundra and deserts have the lowest TNPP, and boreal forest, savannas, and grasslands have moderate NPP. Comparing the NCEAS and Miami models shows that the Miami model estimated substantially higher TNPP in grasslands and savannas (Fig. 3c). The Miami model yielded somewhat higher TNPP in temperate and tropical forests but lower TNPP in boreal forests (Fig. 3c). The NCEAS map of ANPP (Fig. 3d) shows patterns similar to those for TNPP.
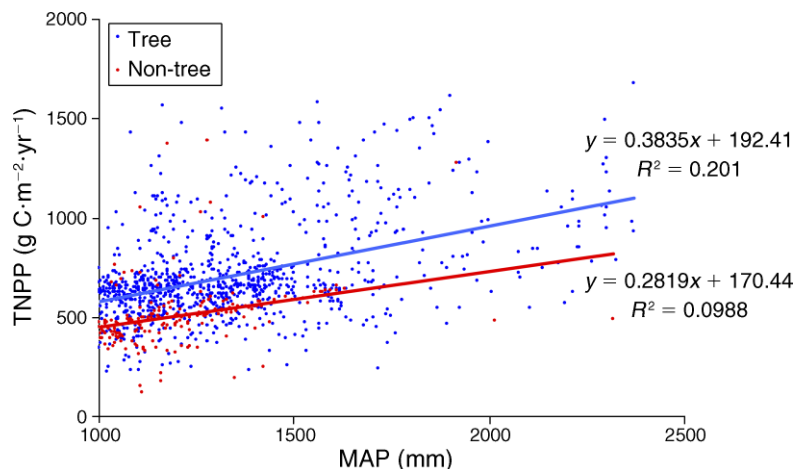
FIG. 2.   Total net primary production (TNPP) as a function of mean annual precipitation (MAP) for a subset of data points with MAP >1000 mm and actual evapotranspiration divided by potential evapotranspiration >0.5, for tree-dominated (blue dots and blue line) and non-tree-dominated systems (red dots and red line).

Both the NCEAS and Miami models predict highest biome TNPP in tropical forests, and the models differed in TNPP in forests by at most 22% (Table 2). However, the models differed substantially (32–75%) in non-tree-dominated systems, with deserts and grasslands showing the greatest discrepancies. Although boreal forests have lower TNPP than temperate forests on a unit area basis, biome TNPP for boreal forests estimated by NCEAS is close to that of temperate deciduous forests because boreal forests cover greater area (Table 2).

The NCEAS model shows TNPP increasing or neutral for most global grid cells during the period from 1901 to 2000 (Fig. 3e). The largest increases were in grasslands and savannas in South America, mainly the result of increased precipitation in these regions. Tropical forests in Brazil and Indonesia showed increases and decreases, depending on grid cell, while forests and savannas in West Africa showed a marked decrease in TNPP (Fig. 3e). Warmer temperatures were primarily responsible for NPP increases in boreal forests that were fairly consistent in magnitude, although some cells in Siberia showed a decrease. At the biome level, boreal and temperate coniferous forests showed the largest increase, followed by temperate deciduous forests, grasslands, and savannas (Table 2). Overall, the NCEAS model estimated an ~13% increase in global TNPP from 1901 to 2000 for potential vegetation.

DISCUSSION

Our most important finding is that the response of aboveground net primary production (ANPP) and total net primary production (TNPP) for tree-dominated and non-tree-dominated systems is significantly different, with tree-dominated systems having higher NPP per unit of water input in the range of mean annual precipitation (MAP) less than ~3000 mm. Tree-dominated and non-

tree-dominated systems also showed contrasting NPP trends in response to temperature, which is correlated with energy inputs (positive for tree-dominated and negative for non-tree-dominated systems). This separation persisted for other correlates of NPP, including actual evapotranspiration (AET), which is correlated with water and energy inputs, and Normalized Difference Vegetation Index (NDVI), which is influenced by water, temperature, and nutrient availability (data not shown). One reason for the separation may be that the field methods used could overestimate NPP for tree-dominated systems. However, we think the methods used in this analysis are more likely to underestimate leaf NPP for trees because NPP lost to herbivory/defoliation is not counted. Our results are consistent with previous work showing higher ANPP for forests than grassland (Webb et al. 1978), although the geographical extent and number of data points were much smaller in this earlier study.

Because trees generally allocate a larger proportion of TNPP to aboveground biomass than grasses, one would expect that ANPP would be higher in tree-dominated compared to non-tree-dominated systems. But our analysis suggests that, on average, TNPP is also larger in tree-dominated systems for a given range of water or energy inputs. We propose four hypotheses/mechanisms that may contribute to this separation: climate zones, water use efficiency, nutrient use efficiency, and disturbance frequency. Trees tend to reside in climate zones where water stress is minimal so NPP should be higher. However, after removing data points from grasslands that occupied moisture-limited sites, there was still a clear separation between non-tree-dominated and tree-dominated TNPP (Fig. 2). Afforestation tends to increase water use efficiency (Farley et al. 2005, Jackson et al. 2005), and forests have higher water use efficiency than deserts and grasslands (Webb
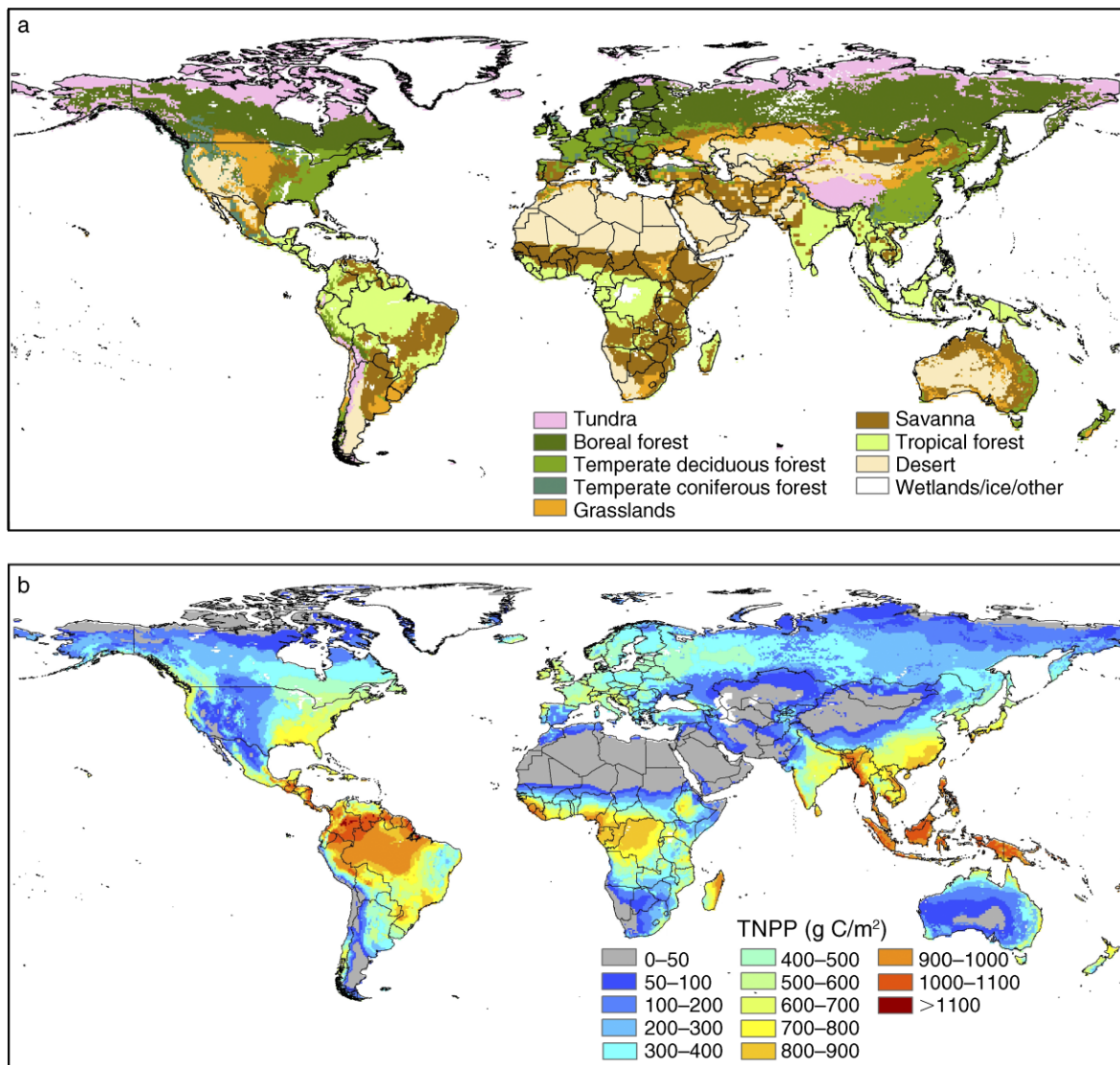
FIG. 3. (a) Potential biome classification; (b) total net primary production (TNPP) for potential native vegetation predicted by the NCEAS model described in this paper; (c) TNPP predicted using the NCEAS model subtracted from TNPP predicted by the Miami model (Lieth 1975); (d) aboveground net primary production (ANPP) for potential native vegetation predicted by the NCEAS model; and (e) the trend in TNPP from 1901 to 2000 estimated using the NCEAS model.

et al. 1978). Trees are more efficient water harvesters than grasses and shrubs because greater interception reduces surface runoff and deeper roots decrease leaching below the rooting zone. Woody biomass has higher carbon : nutrient ratios than leaf biomass, so higher nutrient use efficiency may contribute to higher TNPP for trees. Lastly, differences in external nitrogen inputs from symbiotic fixation and nitrogen losses from the system related to disturbance patterns may be responsible for the separation. Non-tree-dominated systems generally have higher frequencies of burns than forests (Jeltsch et al. 2000, Heisler et al. 2003) so nutrient losses are higher, which may limit NPP for grasslands. This hypothesis is consistent with measure-

ments showing that nitrogen additions increased ANPP to a greater extent than irrigation for a tallgrass prairie (Owensby et al. 1970), implying that at least some non-tree systems may be limited more by nutrients than by water.

TNPP simulations using CENTURY (*available online*),[12] a model that includes nitrogen losses from disturbances, showed biome separation similar to the observed data reported here when typical fire cycles were simulated, but the separation decreased when fire was not simulated. Furthermore, CENTURY simulations showed higher TNPP and nitrogen mineralization for

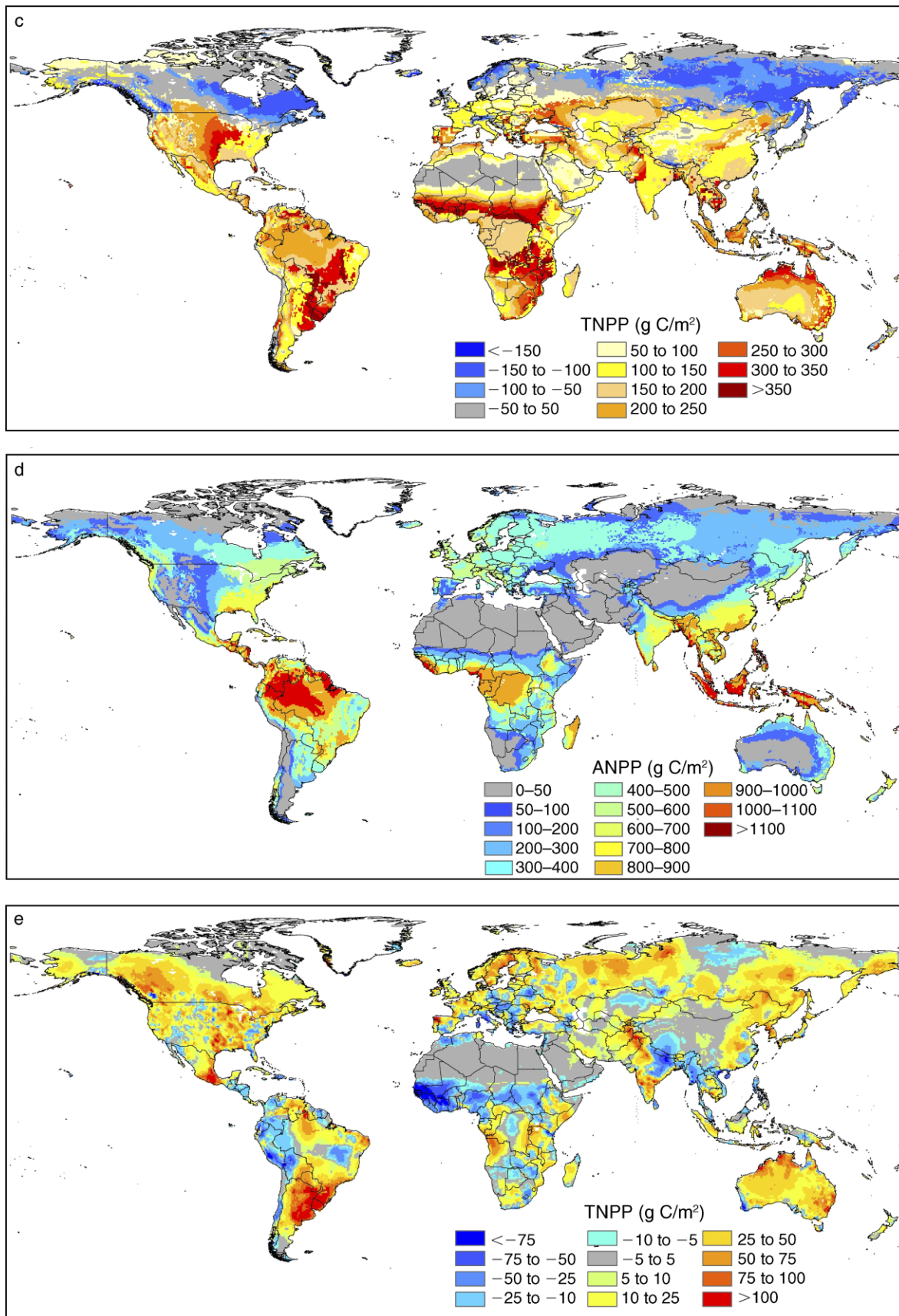[12] ⟨http://www.nrel.colostate.edu/projects/century/⟩

FIG. 3. Continued.

TABLE 2. Biomes, total net primary productivity (TNPP) estimated by the NCEAS and the Miami models, aboveground net primary productivity (ANPP), and mean change in TNPP from 1901 to 2000 estimated using the NCEAS model for major terrestrial biomes.

| Biome | Area (ha × 10^6) | TNPP (Pg) | | ANPP (Pg) | TNPP (% Δ) (Miami − NCEAS)/ Miami | Mean change in TNPP 1901–2000 (g C/m^2); NCEAS |
		NCEAS	Miami	NCEAS		
Tundra	1030	1.2	1.8	0.6	32	9.6
Boreal forest	1900	6.0	4.9	4.0	−22	22.6
Temperate deciduous forest	1206	6.6	7.7	4.2	14	18.2
Temperate coniferous forest	246	1.2	1.4	0.8	11	23.1
Grasslands	968	1.6	3.8	0.8	57	16.7
Savanna	3197	12.1	19.0	7.2	37	14.3
Tropical forest	1747	15.2	18.6	9.6	18	3.4
Desert	2607	1.0	3.8	0.4	75	6.3
Wetlands	227	1.1	1.4	0.7	24	17.3
Total	13 128	46	62.4	28.3	26	12.8

Note: All columns, with the exception of the column on the far right, show annual means for 1981–2000.

forests than for savannas or grasslands over a broad range of AET values, but the differences between biome types disappeared when TNPP was regressed with nitrogen mineralization (Schimel et al. 1996). Future model runs that varied water inputs, rooting depth, and burning frequency for tree-dominated and non-tree-dominated systems could help identify which of the mechanisms proposed here are the most important.

MAP showed a stronger relationship with TNPP in non-tree-dominated systems when compared to tree-dominated systems (Table 1). This is likely related to non-tree-dominated systems existing where water tends to be limiting, while tree-dominated systems tend to exist in less moisture-stressed environments. The law of the minimum also helps explain why tree-dominated systems showed a positive response to temperature but non-tree-dominated systems a negative response. Non-tree-dominated systems reside in environmental space where moisture stress is likely to be limiting, and increasing temperature tends to increase moisture stress and hence decrease TNPP. In contrast, forests reside in zones of sufficient moisture so that increasing temperature is associated with higher TNPP.

The relationship between TNPP and MAP was fairly strong, especially for non-tree-dominated systems. However, there was a minority of data points that showed TNPP values much different than expected (Fig. 1a). Some points classified as non-tree-dominated had NPP values greater than most trees for a given MAP range, while some points classified as tree-dominated had TNPP values that fall below the grass line. Assuming these points were not the result of faulty reporting or methodology, we argue that MAP and MAT do not entirely determine water stress and energy inputs and, thus, TNPP. The timing and duration of precipitation events and growing season length may greatly influence moisture and temperature stress. Some additional factors that influence TNPP include nutrient availability, residence in an erosional or depositional zone, pathogen outbreaks, and herbivory.

We found it surprising that even though trees tend to reside where moisture stress is not great, the TNPP regressions with MAP were stronger than TNPP regressions with temperature, which is correlated with energy inputs. This can be at least partially explained by considering cross-correlations among the weather variables. In the environmental space where trees tend to reside, MAP and MAT were highly correlated ($r = 0.69$), but they were not well-correlated at all where non-tree-dominated systems reside ($r < 0.0001$). In other words, MAP includes a large amount of information regarding energy inputs to the environments in which trees reside. MAP is also correlated with long-term limiting factors such as nitrogen inputs to the system. This is supported by the observation that MAP was found to be better at predicting mean NPP across sites than actual precipitation was at predicting interannual variability in NPP within sites for grasslands in North America (Lauenroth 1979).

The Schuur and Miami models estimated much higher TNPP for grasslands and savannas than our NCEAS model (Tables 1 and 2, Fig. 3c) because unlike the NCEAS model, they do not distinguish biome types. However, our extensive data set shows a clear distinction between tree-dominated and non-tree-dominated systems (Fig. 1a). The NCEAS model estimated higher NPP in boreal forests compared to the Miami model (Fig. 3c). This is due to the NCEAS model predicting higher NPP than the Miami model at low temperature ranges. The NCEAS model estimates global annual TNPP for potential vegetation at 46 Pg C compared to 61 Pg C using the Miami model (Table 2). The NCEAS estimate is closer to the estimates of 50 Pg and 48 Pg C by the process-based models FBM (Frankfurt biosphere model) and CASA (Carnegie Ames Stanford Approach), respectively (Kohlmaier et al. 1997).

The NCEAS model estimated a 13% increase in TNPP for potential native vegetation at the global scale from 1901 to 2000. The increase in TNPP at northern latitudes was driven primarily by increased temperature,

and NPP changes in lower latitudes were driven mainly by changes in precipitation. The trends generated by the NCEAS model are consistent with TNPP trends estimated using a process-based model driven by satellite and weather data that showed a 6% increase in global TNPP from 1982 to 1999 (Nemani et al. 2003). NCEAS showed large increases in TNPP during the 20th century in northern forests, also consistent with the observations of Nemani et al. (2003) and with climate change scenarios conducted by Cao and Woodward (1998). Cao and Woodward (1998) estimated NPP trends from 1861 to 2070 using climate generated by the Hadley Centre (Johns et al. 1997) and the CEVSA (carbon exchange between vegetation, soil, and atmosphere) process-based model, and found that TNPP increased by ~13% in northern systems. However, they point out that this increase in TNPP in northern systems was compensated for by a similar decrease in TNPP for tropical systems during the time period analyzed (Johns et al. 1997).

CONCLUSIONS

These results support the general ideas behind previous models (i.e., precipitation and temperature influence NPP). However, our analyses revealed two interesting trends not accounted for in previous empirical NPP models: tree-dominated and non-tree-dominated systems have different NPP responses to precipitation, and temperature is positively correlated with NPP only for tree-dominated systems. The conclusion that tree-dominated systems have higher NPP does not appear to be entirely due to tree-dominated systems residing in areas with less moisture stress. We suggest that lower water and nutrient use efficiency and higher nutrient losses in non-tree-dominated systems related to higher fire frequency are responsible for the observed NPP differences. Lastly, precipitation alone explained $>50\%$ of variability in non-tree-dominated systems ($r^2 = 0.68$) but precipitation and temperature together explained $<50\%$ of variability in tree-dominated systems ($r^2 = 0.40$).

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