Ecological Applications, 16(1), 2006, pp. 125–132

IMPROVED ESTIMATES OF NET PRIMARY PRODUCTIVITY FROM MODIS SATELLITE DATA AT REGIONAL AND LOCAL SCALES

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Abstract. We compared estimates of net primary production (NPP) from the MODIS satellite with estimates from a forest ecosystem process model (PnET-CN) and forest inventory and analysis (FIA) data for forest types of the mid-Atlantic region of the United States. The regional means were similar for the three methods and for the dominant oak–hickory forests in the region. However, MODIS underestimated NPP for less-dominant northern hardwood forests and overestimated NPP for coniferous forests. Causes of inaccurate estimates of NPP by MODIS were (1) an aggregated classification and parameterization of diverse deciduous forests in different climatic environments into a single class that averages different radiation conversion efficiencies; and (2) lack of soil water constraints on NPP for forests or areas that occur on thin or sandy, coarse-grained soil. We developed the ''available soil water index'' for adjusting the MODIS NPP estimates, which significantly improved NPP estimates for coniferous forests. The MODIS NPP estimates have many advantages such as globally continuous monitoring and remarkable accuracy for large scales. However, at regional or local scales, our study indicates that it is necessary to adjust estimates to specific vegetation types and soil water conditions.

Key words: ecosystem modeling; forest inventory data; MODIS; net primary production (NPP); soil water index.

COMMUNICATIONS

INTRODUCTION

Estimates of net primary productivity (NPP) from the MODIS satellite integrate climate and broad vegetation classifications and have demonstrated utility at global to continental scales (Nemani et al. 2003, Running et al. 2004). Their utility at finer scales is less clear (Running et al. 2000, Turner et al. 2003, 2005). Here, we evaluated MODIS NPP estimates at regional to local scales, and developed a process to bring the estimates into closer alignment with those derived from a process-based ecosystem model (PnET-CN) and from forest inventory and analysis (FIA) data for the mid-Atlantic region of the United States. The results presented in this paper build on previous work to integrate field data with an ecosystem process model (Pan et al. 2004*a*, *b*) by comparing independent estimates of NPP from a satellite sensor, an ecosystem model, and field data, at a scale relevant to land managers.

The MODIS satellite estimates of NPP are based on an energy budget approach, taking advantage of remotely sensed information about the fraction of incident photosynthetically active solar radiation absorbed by the vegetation surface (Running et al. 2004). A key parameter in the MODIS productivity algorithm, the radiation conversion efficiency, ε, varies with different vegetation types and is also sensitive to climatic variables that constrain plant photosynthesis. The MODIS algorithm does not incorporate other factors that are strongly expressed at local to regional scales, such as nutrient availability, soil type, and soil water availability.

The process-based forest ecosystem model PnET-CN (Aber and Driscoll 1997) simulates carbon, nitrogen, and water cycles of forest ecosystems at a monthly time step. The model represents a mechanistic approach based on a large body of research results, and parameters are derived from field studies. For the mid-Atlantic region, PnET-CN has been validated against independent data (Pan et al. 2004*a*).

Estimates of NPP from Forest Inventory and Analysis (FIA) (Birdsey and Schreuder 1992) data are a useful benchmark for comparison since they reflect the net, aggregate effects of many kinds of disturbances on ecosystem parameters (Jenkins et al. 2001). For example, in the mid-Atlantic region, there is a long history of land-use change affecting nearly every forested area of land, as well as a continuing influence from increasing atmospheric CO_2, tropospheric ozone, and nitrogen deposition (Mickler et al. 2000).

Here, we describe the methods, data sources, and standard estimates of NPP from MODIS, PnET-CN, and FIA for Mid-Atlantic forests. Based on observed differences, we describe methods to adjust MODIS estimates, apply the adjustments, and compare the revised estimates with those from PnET-CN and FIA. Finally we discuss the utility of MODIS at different scales of analysis and the need to adjust MODIS-NPP estimates for some forest types.

Manuscript received 11 February 2005; revised 5 May 2005; accepted 31 May 2005; final version received 21 July 2005. Corresponding Editor: B. A. Hungate.

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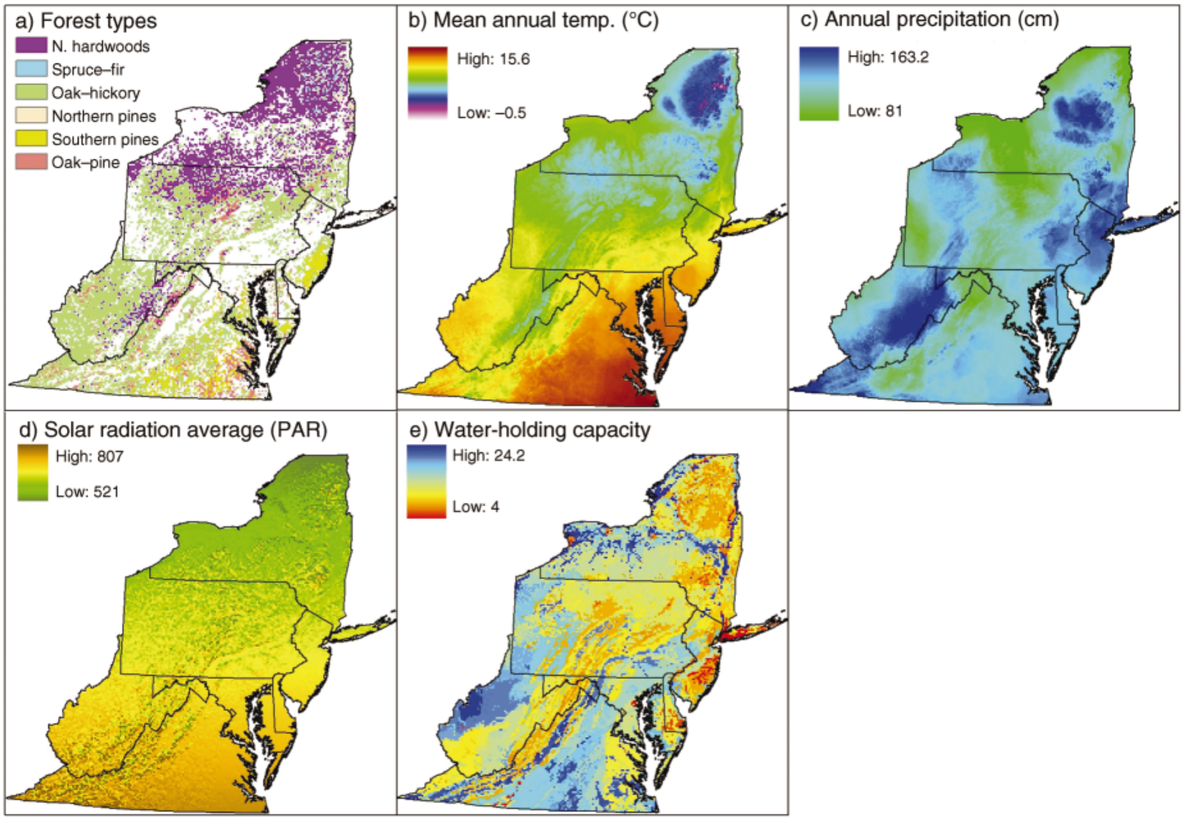

FIG. 1. Input data layers for PnET-CN: (a) forest types, (b) monthly minimum and maximum temperature (showing only an annual average), (c) monthly precipitation (showing only an annual total), (d) monthly photosynthetic active radiation, and (e) soil water-holding capacity.

DATA, METHODS, AND PRELIMINARY RESULTS

MODIS NPP

The MODIS NPP data we used are described as C5 MOD17 and were obtained from the Numerical Terra Dynamic Simulation Group (*available online*).[2] NPP data from 2001 to 2003 for the mid-Atlantic region were selected and averaged for the three-year period. The C5 MOD17 product has some newly improved features compared with C4 MOD17, mainly improved climatic data and FPAR/LAI values, and reconstruction of contaminated or missing data. The C5 MOD17 provides global NPP estimates at an 8-d interval with a nominal 1-km resolution. The annual NPP is the annual summations of 8-d calculations of net photosynthesis minus maintenance and growth respirations (Zhao et al. 2005, Running et al. 2004)

NPP estimates by the PnET-CN model

PnET-CN (Aber and Driscoll 1997) was modified to simulate regional NPP in the mid-Atlantic region (Pan et al. 2004*a*). Spatially referenced forest types, monthly minimum and maximum temperature, monthly precipitation, monthly solar radiation (PAR), and soil water holding capacity (WHC) are input data layers for the model (Fig. 1). For this study, a scenario including changes in atmospheric chemistry in the region was applied in the simulation (Y. Pan, R. Birdsey, J. Hom, and K. McCullough, *unpublished manuscript*), capturing atmospheric characteristics known to influence vegetation productivity: chronically elevated CO_2, N deposition and tropospheric ozone (Ollinger et al. 2002).

The forest types were based on Forest Service forest type groups (Zhu and Evans 1994) regrouped to five major forest types for modeling (Table 1). In the region, about 36% of the land is nonforested. Among the forests, about 53% are classified as oak–hickory, 29% as northern hardwood, 8% as pine, 9% as oak–pine, and 1% as spruce–fir (Table 1). As shown in Table 1, these five groups are further aggregated in the MODIS classification to either deciduous or coniferous. The regional and temporal spatial data layers of N deposition, ozone, climate, and soils are described elsewhere (Pan et al. 2004*a*; Y. Pan, R. Birdsey, J. Hom, and K. McCullough, *unpublished manuscript*). The model was run from year 1800 to 2000 to fully incorporate impacts of cultivating and harvesting on forest ecosystems in the past two centuries. PnET-CN estimates of NPP for year 2000 are used for comparison with MODIS and FIA estimates of NPP.

[2] ⟨http://www.ntsg.umt.edu⟩

TABLE 1. Forest cover types, regrouped forest types, and MODIS classifications.

		Regrouped types for PnET-CN		MODIS	
Forest cover types	Forest area (%)	Cover type	Forest area (%)	Class	Forest area (%)
Maple–beech–birch	29	northern hardwoods	29	deciduous	82
Elm–ash–cottonwood	†				
Oak–hickory	53	oak–hickory	53		
Spruce–fir	1	spruce–fir	1	coniferous	9
White–red-jack pine	3	pine forests	8		
Loblolly–shortleaf pine	5				
Long-leaf–slash pine	†				
Oak–pine	8	oak–pine	9	mixed	9
Oak–gum–cypress	1				

† Less than 1%.

NPP from forest inventory

The USDA Forest Service Forest Inventory Analysis (FIA) data are derived from inventory sample plots, which are randomly or systematically located to cover the inventory areas. Annual NPP estimates based on the FIA data have been published for forest types in the mid-Atlantic region (Jenkins et al. 2001). In the Jenkins et al. (2001) approach, the forest plots that match closely the mature, closed-canopy conditions were selected for analysis. However, only woody NPP (including stem and coarse root increment) was derived directly from FIA data and therefore reflects actual vegetation composition; the estimates of litterfall (leaf product) and fine roots were based upon field data from a small number of ecosystem studies, and applied uniformly to different forest types. Here, we used the woody NPP estimates from Jenkins et al. (2001), but applied the allocation ratios derived from a broader compilation of field data (White et al. 2000) to estimate leaf and fine root production, an approach which should improve the estimates by taking into account the variable productivity of different forest types. These same ratios were also used in the MODIS NPP algorithm, therefore minimizing differences between the MODIS and FIA approaches related to estimates of leaf and fine root production. We combined the FIA-based woody NPP estimates and the allocation ratios to calculate the total NPP (Table 2). We recalculated standard deviations for the total NPP based on the standard deviations and sample sizes inherited from FIA and the allocation data (Table 2). We used the inventory-based estimates of NPP as the reference for validating the NPP estimates by MODIS algorithm and the PnET-CN model.

Comparison among NPP estimates from MODIS, PnET-CN, and FIA

Map comparison.—Mean NPP estimates for the entire mid-Atlantic region from MODIS and the PnET-CN model are similar, with a slightly higher mean value from PnET-CN compared to MODIS (1065 vs. 1005 $g\cdot m^{-2}\cdot yr^{-1}$). However, the spatial patterns of NPP from these two methodologies differ (Fig. 2). The MODIS NPP estimates mainly reflect a pattern of climatic gradients: lower in the north because of lower temperature and precipitation compared to the south where temperature and precipitation are higher. The MODIS estimates of NPP are highest for forests in the New Jersey

TABLE 2. Estimates of NPP and its components for forests in the mid-Atlantic Region, based on forest inventory and analysis (FIA) and field data.

Forest cover types	Woody increment ($g\cdot m^{-2}\cdot yr^{-1}$)†	Stem increment ($g\cdot m^{-2}\cdot yr^{-1}$)‡	Leaf production ($g\cdot m^{-2}\cdot yr^{-1}$)‡	Fine root production ($g\cdot m^{-2}\cdot yr^{-1}$)‡	Total NPP ($g\cdot m^{-2}\cdot yr^{-1}$)§	Total SD¶	Samples (n, m, l)¶
Maple–beech–birch	544.3	446.2	202.8	243.4	990.5	135.4	964, 133, 9
Spruce–fir	389.0	301.6	137.1	191.9	717.9	227.8	43, 29, 29
White–red-jack pine	480.8	372.7	169.4	237.2	887.4	198.0	187, 29, 29
Loblolly–shortleaf pine	448.7	347.8	158.1	221.3	828.2	244.6	94, 29, 29
Oak–hickory	568.8	466.2	211.9	254.3	1035.0	141.6	1132, 133, 9
Oak–pine	488.5	389.2	176.9	230.0	895.4	180.3	106, 81, 19
Oak–gum–cypress	659.3	525.3	238.8	310.4	1208.5	289.0	16, 81, 19

† Woody increment includes NPP increments of stem and coarse roots (Jenkins et al. 2001).

‡ Stem increments, leaf productivity, and fine-root productivity are calculated based on the allocation ratios of coarse roots to new stem, new stem to new leaf, and new fine roots to new leaf (White et al. 2000).

§ Total NPP is calculated as woody increment (stem and coarse roots) plus leaf and fine-root NPP.

¶ Statistical analysis was applied to calculate total standard deviation; n is the number of sample plots of the forest inventory used for estimating woody increments (Jenkins et al. 2001); m and l are the number of samples used for calculating the allocation ratios (White et al. 2000).

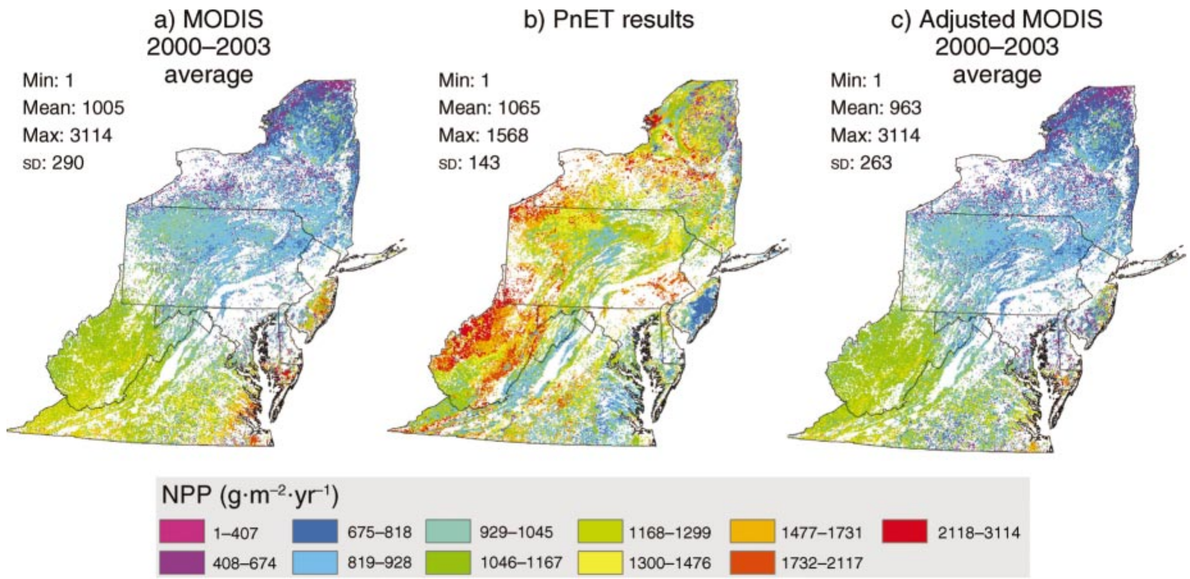

FIG. 2. Annual net primary production (NPP) in the mid-Atlantic region: (a) MODIS annual NPP averaged for the years 2000–2003; (b) annual NPP for the year 2000 modeled by PnET-CN; and (c) MODIS annual NPP after modified using the soil water indices. Visible changes in MODIS NPP are mainly evident in the southeastern coastal areas where pine or mixed oak–pine forests occur (see Fig. 5).

Pinelands (detailed results for this area are presented in *New Jersey Pinelands*). The PnET-CN NPP does not show a strong climate-controlled pattern, but rather a pattern reflecting the effects of forest types and soil moisture (Fig. 1). In addition, the standard deviations in the MODIS NPP have a much wider range than the PnET-CN NPP, with the highest estimates reaching 3114 $g \cdot m^{-2} \cdot yr^{-1}$ from MODIS and only 1568 $g \cdot m^{-2} \cdot yr^{-1}$ from PnET-CN (Fig. 2). The maximum NPP values estimated from MODIS are likely out of the reasonable range for this region (Whittaker 1975).

Point-to-point comparison.—Because the estimates of NPP from both MODIS and PnET-CN are at the same spatial resolution, a point-to-point comparison from spatial data sets can be performed. We randomly selected some pixels ($n = 4032$ of 283 546 total pixels) to illustrate the relationship between NPP estimates by MODIS and PnET-CN (Fig. 3a). This comparison highlights the differentiation in NPP for the forest type groups modeled by PnET-CN, in contrast to the continuously distributed NPP for deciduous and coniferous forests estimated by the MODIS algorithm. While the MODIS NPP has a much wider range than the PnET-CN NPP for oak-hickory forests, the averages are similar among the two approaches.

Comparison with forest inventory data.—The NPP estimates from the PnET-CN model are similar to the FIA estimates, but the model slightly overestimates NPP for deciduous forests and yields much narrower standard deviations for coniferous forests (Fig. 4a). MODIS estimates of NPP agree very well with the FIA estimates for the oak–hickory forests that dominate (53%) forest cover in the region. However, MODIS underestimates NPP for the northern hardwood forests and overestimates it for coniferous and mixed forests. In addition, the standard deviations of NPP from MODIS for different forests are much broader than those from the forest inventory data (Fig 4a).

New Jersey Pinelands.—The comparison among MODIS, PNET-CN, and FIA indicates that MODIS overestimates annual NPP for coniferous forests in the mid-Atlantic region. The contrasting estimates for the New Jersey Pinelands in particular are highly divergent—the highest average NPP values for the region were from MODIS (1319 $g \cdot m^{-2} \cdot yr^{-1}$; Fig. 5a), compared with the lowest values shown by the inventory data (485 $g \cdot m^{-2} \cdot yr^{-1}$; Pan et al. 2004*b* and this study). This likely occurs because the MODIS NPP approach reflects the temperature and precipitation pattern in the area, but apparently fails to incorporate the local constraint of soil water conditions. To explore this further, we conducted additional comparison and analysis for this area.

Although pitch pine (*P. rigida*) forests of the New Jersey Pinelands are grouped with the southern pine forest types in the Forest Service forest cover classification (Zhu and Evans 1994), species in these forests have specific features adapted to local edaphic conditions and disturbance regimes. The woody NPP estimates for the New Jersey Pinelands based on FIA data average 299 $g \cdot m^{-2} \cdot yr^{-1}$ (Pan et al. 2004*b*). Using the allocation indices we described in Table 2 to calculate NPP of foliage and fine roots, we estimate a mean annual NPP of 485 $g \cdot m^{-2} \cdot yr^{-1}$ with STD of 212 $g \cdot m^{-2} \cdot yr^{-1}$. Ground-based estimates of NPP at three CO_2 flux tower sites in the Pinelands indicate that NPP

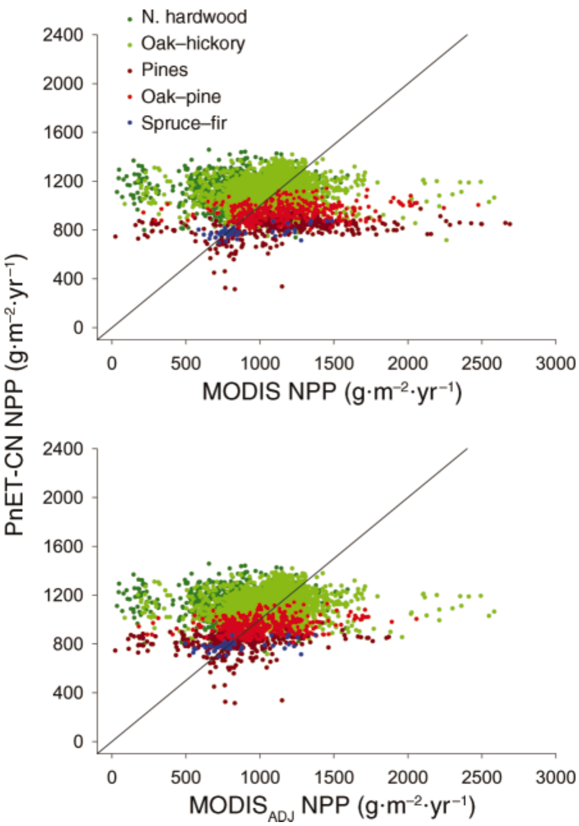

FIG. 3. The comparison between the MODIS NPP and modeled NPP from PnET-CN for randomly selected pixels at 1-km² resolution: (a) original MODIS NPP estimates and (b) MODIS NPP after adjusting to the soil water index.

estimates are not significantly different from the FIA data (K. Clark and J. Hom, *unpublished data*).

The PnET-CN model predicts a much lower NPP compared with MODIS, but much higher NPP compared with the FIA-based estimate (Fig. 5b). Even considering the large variability inherent in the field data-based estimates, the PnET-CN model prediction is still fully out of the range of the field data (835 ± 71 vs. 485 ± 212 g·m^{-2}·yr^{-1}).

REVISED METHODS AND RESULTS

Soil water corrections for MODIS NPP

To account for the impact of soil water availability on MODIS NPP estimates, we formulated a soil water correction index for the mid-Atlantic region. First, we define available soil water as

$$SW_{mon} = \mathrm{Min}(ppt_{mon}, whc). \quad (1)$$

Here, SW_{mon} is the monthly available soil water, ppt_{mon} is the monthly precipitation, and whc is water holding capacity. The simple soil water index is defined as follows:

$$SW_{index} = \mathrm{Min}(1, SW_{ann}/PET_{ann}) \quad (2)$$

$$SW_{index} = \mathrm{Min}[1, (RSW + SW_{gr\_mon})/PET_{gr\_mon}] \quad (3)$$

for evergreen coniferous and deciduous forests respectively. Here, SW_{index} is the soil water index; SW_{ann} is the annual soil water that is the aggregation of the monthly soil water based on Eq. 1; PET_{ann} is the annual potential evapotranspiration (PET) aggregated from monthly PET, calculated using the Penman-Monteith equations (Monteith 1973); SW_{gr_mon} is the total soil water for growing season that spans from April to August; PET_{gr_mon} is the PET for the growing season; and RSW is the residual soil water for nongrowing-season months (September–March), the sum of monthly differences between available soil water (SW_{mon}), and PET.

The soil water correction index captures the effect of available soil water on annual NPP, which is largely a function of water-holding capacity. For evergreen coniferous forests, water balance between available soil water and potential evapotranspiration is calculated on a yearly basis because photosynthesis occurs throughout the year. For deciduous forests, the water balance is calculated for the growing season, but available soil water has a surplus of soil water left over from non-

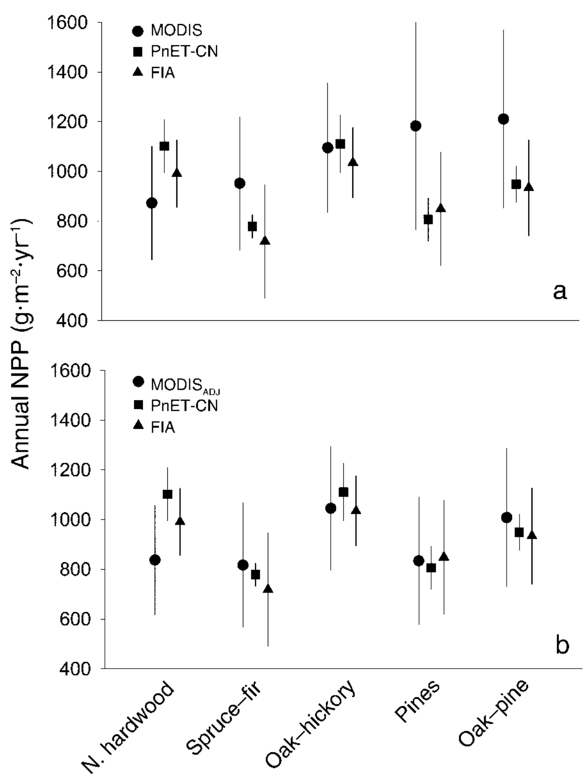

FIG. 4. Comparison of NPP estimates based on MODIS, the PnET-CN model, and FIA (forest inventory and analysis) data for major forest types in the mid-Atlantic region: (a) original MODIS NPP and (b) MODIS NPP after adjusting to the soil water index.

growing months when potential evapotranspiration is generally low because of low temperature and solar radiation. The soil water index is the minimal number between 1 and the ratio of available water to potential evapotranspiration. When available water cannot meet the need for evapotranspiration, the soil water index is smaller than 1 and annual NPP will be suppressed. We calculated the soil water indices spatially across the region and used them to modify the MODIS annual NPP estimates.

MODIS NPP after adjusting for soil water availability

After adjusting MODIS NPP estimates with the soil water indices, we compared them to the estimates based on PnET-CN and FIA at all scales (Figs. 2c, 3b, 4b, 5c). Changes in MODIS NPP are evident in the southeastern coastal areas where pine or mixed oak–pine forests occur (Fig. 1a). The soils in these areas are generally sandy with low water holding capacity, but PET is high because of the warm climate and high solar radiation. The comparison at the pixel level also shows an obvious shift of NPP values to the lower end of the range for coniferous/mixed forests that makes them more comparable to the PnET-CN results (Fig. 3b).

The comparison at the aggregated forest type level indicates that using the soil water indices significantly improves MODIS estimates of mean NPP (and its standard deviation) compared to NPP estimates from forest inventory for coniferous and mixed forests (Fig. 4b). Deciduous forests are likely to grow in the areas with intermediate conditions of temperature and precipitation, and under these climatic conditions, the soil water indices slightly reduce the MODIS NPP for deciduous forests and bring estimates for oak-hickory forests closer to the FIA data. Because the soil water index we formulated can only constrain the MODIS NPP rather than enhance it, the MODIS NPP estimates for the Northern hardwood forests remain underestimated.

The MODIS NPP estimates for the New Jersey Pinelands are reduced to values comparable to PnET-CN after adjusting for soil water conditions (Fig. 5b, c), but, as mentioned earlier, the MODIS NPP estimates are still much higher than NPP estimates derived from FIA data. The overestimates of NPP by MODIS and PnET-CN, even though the former is driven by remote sensing and the latter by a process-based model, are likely caused by coarse vegetation classification and inaccurate parameterization of the models. The MODIS NPP estimates are based on classes of biomes, and use the same parameters shown in the look-up table for evergreen needle-leaf forests (Heinsch et al. 2003). The PnET-CN NPP estimates are based on plant functional types and use the same parameters as those derived from regional pine forests to estimate NPP for pitch pines in the Pinelands. Although other climatic and soil variables may constrain NPP, the models are still unable to estimate NPP at an appropriate magnitude, likely because pitch pines that are specifically adapted to coastal, sandy, coarse-grained soils and extremely low nutrient status cannot be formulated in a general way in the models.

Discussion

The intercomparison and cross-validation among NPP results derived from different methodologies provides a powerful technique to validate and improve the NPP estimates from MODIS. For an area such as the mid-Atlantic region, our analysis indicates that MODIS NPP estimates are quite accurate for the dominant oak–hickory forests that constitute 53% of total forest cover in the region; but MODIS underestimates NPP for northern hardwood forests (29% of forest cover) and overestimates NPP for coniferous mixed forests (18% of forest cover).

In MODIS, the most sensitive parameter for estimating annual NPP is the radiation conversion efficiency, ε, which determines the maximum fraction of absorbed photosynthetically active solar radiation (PAR) that can be converted to carbon product (Running et al. 2004). This parameter is further constrained by temperature and vapor pressure deficit (VPD). For the mid-Atlantic region, since the MODIS NPP algorithm uses the same ε for cool temperate and temperate deciduous forests, it is not surprising to find lower NPP estimates for northern hardwood forests than for the oak–hickory forests because temperature is the main controlling factor that reduces ε. However, based on forest inventory data and field studies (Ollinger et al. 1998, Jenkins et al. 2001, Pan et al. 2004*b*), annual NPP in these two deciduous forests does not differ much (Fig. 4). Even though the growing season for the northern hardwood forests is shorter than for oak–hickory forests, northern trees may have adapted to the region's climate by having faster growth during the growing season and lower respiration rates (Chapin et al. 2002). Thus, the northern deciduous forests may have higher radiation conversion efficiency than the southern types.

The soil water index we developed in this study seems particularly useful for modifying MODIS NPP estimates in coniferous and mixed forest types in the mid-Atlantic region, which are often adapted to poor soil conditions (pine or oak–pine forests) or high runoff areas (spruce–fir forests) where water-holding capacity and available soil water are generally low. In the MODIS NPP algorithm, the only variable reflecting moisture conditions is the VPD scalar that modifies ε. VPD represents relative humidity, and the minimal and maximum VPD used in the MODIS algorithms defines ranges of general moisture conditions associated with vegetation types that geographically adapt to certain climatic environments. However, at regional and local scales, soil moisture can be diverse because different soil types occur within the same climatic zones. For this reason, the MODIS NPP estimates are biased for

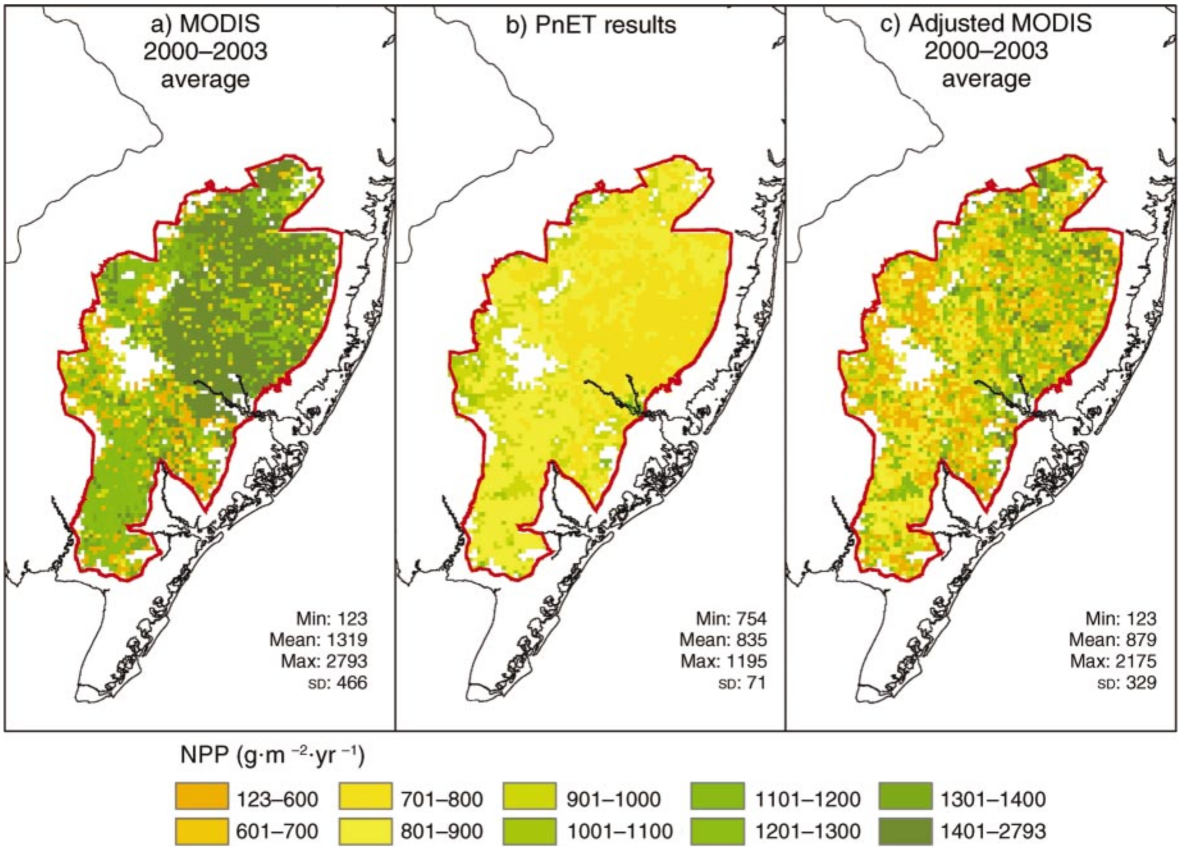

FIG. 5. Annual NPP of pine forests in the New Jersey Pine Barrens: (a) MODIS NPP; (b) PnET-CN estimated NPP; and (c) MODIS NPP after adjusting to the soil water index.

coniferous forests in the mid-Atlantic region. Likely, the soil water index may also be useful to improve other carbon models driven by satellite data, such as Glo-PEM (Prince and Goward 1995) and CASA (Field et al. 1995, Potter et al. 1999), that utilize a similar concept for converting remote-sensing information to vegetation productivity but often lack a function for soil water balance.

The process-based model, PnET-CN, seems to provide better NPP estimates because the model incorporates more climatic and soil information, and is parameterized more precisely using local experimental data and finer functional type classification. In addition, the PnET-CN model includes the effects of changing atmospheric conditions (CO_2, ozone, and N deposition), which has the additional benefit of quantifying how these factors affect NPP estimates (Y. Pan, R. Birdsey, J. Hom, and K. McCullough, *unpublished manuscript*). However, estimated NPP from PnET-CN has a very narrow range (Fig. 3) because the model is parameterized for undisturbed forests, i.e., pixels are either entirely forest or entirely nonforest. The variation in NPP estimates mainly reflects the spatial variability of interpolated climate and soils data, when in actuality this variation is much higher. In contrast, a wide range of variation in MODIS NPP estimates reflects the true variability of climate, and the inclusion of non-forest fractions in pixels classified as forest, which affects the MODIS reflection values and produces some low estimates of NPP not found in the modeled estimates.

We used the FIA-based NPP estimates in this study as the standard reference for the modeled NPP. The FIA data, in fact, provide accurate information primarily for woody increment. We used the allocation ratios in the MODIS NPP algorithm to calculate NPP in nonwoody tree components and performed the statistical analysis to recalculate the standard deviations. These NPP estimates based on the forest inventory and field data (Table 2) for major forest types in the Mid-Atlantic region should be more accurate than the previous work (Jenkins et al. 2001). In the future, improved NPP estimates based on field data will rely on better measurements of litterfall and woody debris in the region, and also on improved estimation of the carbon allocation to fine roots (Norby et al. 2004).

Nonetheless, the MODIS satellite remains a powerful tool for monitoring terrestrial productivity because of its timing, scale, and continuity, and the extent of spatial coverage and resolution. At the global scale, the MODIS NPP estimates are likely very reasonable (Nemani et al. 2003). At regional or local scales, two aspects should be considered when using the MODIS NPP product: (1) the accuracy of NPP estimates for less dominant forest types, which can be improved by finer vegetation classifications and more precise parameterization of the radiation conversion efficiency; and (2) the accuracy of NPP estimates for forests more affected by soil water conditions than geographical moisture conditions, which can be improved by using the soil water indices for corrections, as shown here. Continued effort at intercomparison and cross-validation of estimated carbon fluxes and stocks among various remote sensing systems, data, and models will improve our understanding and estimates of carbon dynamics, with the eventual goal of resolving uncertainties in quantifying the global carbon cycle.

Acknowledgments

We wish to acknowledge the support of the USDA Forest Service Global Change Research Program, the NASA grant NS-7641 and the grants of National Fire Plan (02.NES.A.1 and Eastern LANDFIRE Prototype). We are very grateful to Steve Running for his insightful comments and Bruce Hungate for his valuable suggestions to improve the manuscript.

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