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Estimating potential forest NPP, biomass and their climatic sensitivity in New England using a dynamic ecosystem model

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Abstract.   Accurate estimation of forest net primary productivity (NPP), biomass, and their sensitivity to changes in temperature and precipitation is important for understanding the fluxes and pools of terrestrial carbon resulting from anthropogenically driven climate change. The objectives of this study were to (1) estimate potential forest NPP and biomass for New England using a regional ecosystem model, (2) compare modeled forest NPP and biomass with other reported data for New England, and (3) examine the sensitivity of modeled forest NPP to historical climatic variation. We addressed these objectives using the regional ecosystem model LPJ-GUESS implemented with eight plant functional types representing New England forests. We ran the model using 30-arc second spatial resolution climate data in monthly time-steps for the period 1901–2006. The modeled forest NPP and biomass were compared to empirically-based MODIS and FIA estimates of NPP and U.S. forest biomass. Our results indicate that forest NPP in New England averages 428 g $C \cdot m^{-2} \cdot yr^{-1}$ and ranges from 333 to 541 g $C \cdot m^{-2} \cdot yr^{-1}$ for the baseline period (1971–2000), while forest biomass averages 135 Mg/ha and ranges from 77 to 242 Mg/ha. Modeled forest biomass decreased at a rate of 0.11 Mg/ha ($R^2 = 0.74$) per year in the period 1901–1949 but increased at a rate of 0.25 Mg/ha ($R^2 = 0.95$) per year in the period 1950–2006. Estimates of NPP and biomass depend on forest type: spruce-fir had the lowest mean of 395 g $C \cdot m^{-2} \cdot yr^{-1}$ and oak forest had the highest mean of 468 g $C \cdot m^{-2} \cdot yr^{-1}$. Similarly, forest biomass was highest in oak (153 Mg/ha) and lowest in red-jack pine (118 Mg/ha) forests. The modeled NPP for New England agrees well with FIA-based estimates from similar forests in the mid-Atlantic region but was smaller than MODIS NPP estimates for New England. Nevertheless, the modeled inter-annual variability of NPP was strongly correlated with the MODIS NPP data. The modeled biomass agrees well with U.S. forest biomass data for New England but was less than FIA-based estimates in the mid-Atlantic region. For the region as a whole, the modeled NPP and biomass are within the ranges of MODIS- and FIA-based estimates. Forest NPP was sensitive to changes in temperature and precipitation: NPP was positively related to temperatures in April, May and October but negatively related to summer temperature. Increases in precipitation in the growing season enhanced forest NPP.

Key words: biomass; climatic sensitivity; forest inventory data; inter-comparison; LPJ-GUESS; MODIS NPP; net primary productivity; New England.

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INTRODUCTION

Forest net primary productivity (NPP) is a key component of the global carbon cycle and an important link between the biosphere and the atmosphere, influencing water fluxes, nutrient cycles, and climate variation (e.g., Prentice et al. 2000). Modeling both spatial and temporal

variations in forest NPP is important for improving estimates of the terrestrial carbon cycle (Cao et al. 2004) and for explaining variation in atmospheric carbon content (Potter et al. 1998). Modeling forest biomass is important not only for policy-makers to deal with greenhouse gas mitigation (Morales et al. 2007, Smith et al. 2008, Zhao and Running 2010) but also for forest managers to determine forest change and wild-fire regimes (Mickler et al. 2002). Accurate estimates of forest NPP and biomass therefore have implications for (1) analyzing long-term, large-scale changes in carbon stocks over space and time (Houghton 2005); (2) examining the dynamics of forest distribution and composition like the conversion of forested land to cultivated fields; and (3) providing data that are useful for model-based inter-comparison studies on forest carbon and biomass change (Brown et al. 1999, Jenkins et al. 2001).

Direct measurement of forest NPP and bio-mass on the ground is costly, time consuming and limited to short-term intervals (e.g., Houghton 2005). Forest inventories, satellite-based vegetation indices and vegetation models are typically used to estimate forest NPP and biomass. Forest inventories provide plot-level information about plant growth, diameter and litter fall, and the resultant estimates of NPP and biomass are often thought to be of high accuracy (Houghton 2005). However, they do not map the spatial patterns of forest NPP and biomass at broad scales without being scaled-up, which can introduce errors in the resultant estimates (Houghton 2005, Smith et al. 2008). In addition, forest inventory-based approaches rarely reveal the mechanisms that account for changes in forest NPP and biomass (Kauppi et al. 1992). Satellite-based vegetation indices can be incorporated into light-use efficiency models such as LULUE (Brogaard et al. 2005) to estimate forest NPP and biomass at large spatial scales (Markon and Peterson 2002, Dawson et al. 2003). However, these models often ignore site, biome or forest-type specific information about forest structure and composition and therefore risk producing biased NPP and biomass estimates at the regional scales (Jenkins et al. 2001). The use of satellite data to constrain relevant parameters in process-based vegetation models provides promise for improved estimation, but such techniques

are still under development (Smith et al. 2008).

Process-based vegetation models, including terrestrial biogeochemistry models (TBMs) like Biome-BGC (Running and Coughlan 1988) and dynamic global vegetation models (DGVMs) like LPJ-DGVM (Sitch et al. 2003), have been widely used in estimating forest NPP and biomass at broad spatial scales. These models include mechanistic representations of the ecosystem carbon cycle and its dynamic responses to external disturbances, including plant photosynthesis and the allocation of assimilated carbon to leaves, roots, sapwood and heartwood, and are therefore useful for quantifying forest NPP and biomass (Cramer et al. 2001, Morales et al. 2007). There remains a great need, however, to evaluate vegetation model-based NPP and biomass estimates (e.g., Gower et al. 2001). The utility of these models can be improved by (1) creating finer definition of forest types at regional scale (Jenkins et al. 2001), and (2) increasing the quality of model input data (e.g., the resolution of climate data).

A shortcoming in many current TBMs and DGVMs is that they are optimized to reproduce overall patterns and temporal variability in biomass production and stocks at global and continental scales, but tend to be too generalized to consistently provide reliable estimates at regional (e.g., New England) scales (Smith et al. 2001, Moorcroft 2003). Specifically, most large-scale models lack an explicit representation of tree population size structure, demography and life history differences, which are closely tied to the temporal and spatial variability of structure and function in forest landscapes (Purves and Pacala 2008). Dynamic vegetation models that are optimized for regional applications address these shortcomings through differentiation of tree life history groups, age or size classes, and their interactions in competition for light and soil resources (Smith et al. 2001).

Previous studies on forest NPP and biomass estimates in New England are mostly at plot and county-level scales (e.g., Brown et al. 1999) and few focus on regional scale mapping of forest NPP and biomass for New England (e.g., Zheng et al. 2008). The goals of this study were to (1) estimate forest NPP and biomass for New England using a regional dynamic vegetation-ecosystem model LPJ-GUESS (Smith et al. 2001),

(2) compare modeled NPP and biomass with other reported data for New England or for similar forests, and (3) examine the sensitivity of forest NPP to historical climatic variation. Toward these ends, we first parameterized LPJ-GUESS using eight plant functional types (PFTs) encompassing the major tree species of New England forests. We then ran the model driven by 30-arc second spatial resolution climate data in monthly-step for the period 1901–2006. The modeled NPP and biomass were compared with MODIS NPP data by Zhao et al. (2005), U.S. forest biomass data by Blackard et al. (2008) and forest inventory and analysis (FIA) based NPP and biomass estimates for the mid-Atlantic region of U.S. by Pan et al. (2006) and Jenkins et al. (2001). Sensitivity experiments were performed with the model to analyze the influence of historical climatic variation on forest NPP.

MATERIAL AND METHODS

The study region

New England is located in the northeastern United States and ranges from 73.72°W to 66.96°W and from 40.99°N to 47.45°N. New England forests consist of three widely-recognized forest types: boreal conifers (e.g., *Abies balsamea* and *Picea mariana*), northern deciduous hardwoods (e.g., *Acer saccharum* and *Fagus grandifolia*) and mixed oak–hickory forests (e.g., *Quercus alba* and *Quercus prinus*). The distribution of these forest types reflects regional climatic conditions: boreal conifers are currently widespread at higher elevations and in northern regions of New England, northern deciduous hardwoods are mainly distributed in the cooler central uplands, and mixed oak–hickory forests are found at lower elevations and more southerly regions. Although the current relationship between climate and New England forests is partly obscured by human activities and ecological succession following land abandonment (e.g., Parshall et al. 2003), historical evidence (e.g., Shuman et al. 2004) has demonstrated a strong relationship between climate and forest dynamic in New England. To evaluate the effects of historical climate variation on forest NPP and biomass in the study region, we excluded all land-cover types that are currently subject to substantial human use.

Estimates of forest NPP and biomass by LPJ-GUESS

We used LPJ-GUESS (Smith et al. 2001, Sitch et al. 2003; Hickler et al. *in press*) to estimate forest NPP and biomass in New England based on historical climate data. LPJ-GUESS is a general ecosystem simulator that combines mechanistic representations of plant physiological and biogeochemical processes and includes individual-based demographics such as sapling establishment and mortality, as well as the allocation of assimilated carbon through photosynthesis to leaf, root, sapwood and heartwood. LPJ-GUESS simulates the growth of individual trees on a number of replicate patches, where the height and diameter growth of individuals are regulated by carbon allocation, conversion of sapwood to heartwood and a set of prescribed allometric relationships (Smith et al. 2001, Sitch et al. 2003). Disturbance within each patch consists of both fire (Sitch et al. 2003) and random, patch-destroying disturbances (with a specified yearly probability of occurrence of 0.01) that correspond, for example, to storms and insect-attacks (Smith et al. 2008). No additional human-specific disturbances, such as forestry practices or clear-cutting, were implemented in this study. LPJ-GUESS has been applied in and validated by a number of studies in estimating forest NPP, biomass and carbon exchange at both regional and local scales (e.g., Badeck et al. 2001, Hickler et al. 2004, Morales et al. 2005, Smith et al. 2001, 2008).

A detailed description of LPJ-GUESS is available in Smith et al. (2001). The version used in this study includes a number of updates, and a brief description is given here. Further details are provided by Hickler et al. (*in press*). LPJ-GUESS has been updated to produce additional output for analysis, apply various minor corrections to detect numerical instabilities (in association with the implementation of allometric constraints, for example) and speed up the model runs. As an additional bioclimatic limit for establishment, Hickler et al. (*in press*) introduced a PFT-specific minimum (as averaged over the growing season) fraction of plant-available water holding capacity in the first soil layer as a measure of the ability of a sapling of a given PFT to tolerate drought (Table 1). Shade tolerance parameters were also calibrated to published forest succession patterns. Finally, the number of days with rainfall

Table 1. Definition and parameterization of the eight plant functional types under our simulations.

PFTs[1]	Phenology	Morphology	Shade tolerance	DrT[2]	FiR[3]	SLA[4] (mg²/kg C)	Lon[5] (years)	LeL[6] (years)	R$_{co}$[7]
1. Spruce-fir	Evergreen	Needle	Tolerant	0.23	0.08	13.1	300	5	2.0
2. White pine-cedar	Evergreen	Needle	Intermediate	0.10	0.05	12.0	250	3	1.5
3. Red-jack pine	Evergreen	Needle	Intolerant	0.20	0.09	11.0	180	2.5	2.0
4. Maple-beech-basswood	Deciduous	Broad	Tolerant	0.30	0.14	43.4	350	0.6	1.5
5. Oaks	Deciduous	Broad	Intermediate	0.28	0.14	33.0	400	0.6	1.5
6. Yellow birch-elm	Deciduous	Broad	Intermediate	0.30	0.05	41.3	250	0.6	1.5
7. Hickories	Deciduous	Broad	Intolerant	0.37	0.13	32.0	250	0.6	1.5
8. Aspen-birch	Deciduous	Broad	Intolerant	0.20	0.16	30.3	200	0.6	2.0

Notes: [1] Spruce-fir consists of balsam fir (*Abies balsamea*), black spruce (*Picea mariana*) and red spruce (*Picea rubens*); Pine-spruce-cedar consists of white pine (*Pinus strobus*), norway spruce (*Picea abies (L.)*.) and white cedar (*Thuja occidentalis*); Red-jack pine consists of jack pine (*Pinus banksiana*) and red pine (*Pinus resinosa*); Oaks consists of white oak (*Quercus alba*), chestnut oak (*Quercus prinus*) and black oak(*Quercus velutina*); birch-elm consists of yellow birch (*Betula alleghaniensis*) and American elm (*Ulmus americana L.*); Hickories consists of pignut hickory (*Carya glabra*), bitternut hickory (*Carya cordiformis*), mockernut hickory (*Carya tomentosa*) and shagbark hickory (*Carya ovata*); Aspen birch consists of quaking aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*). Shade tolerance (Smith et al. 2001; Hickler et al. *in press*); DrT[2]—drought tolerance (the value given is the minimum fraction of available soil water in the topmost (0.5 m) soil layer, averaged over the growing season (i.e., days with air temperature > 5°C), necessary for a PFT to establish. (See Hickler et al. *in press*); FiR[3]—Fire resistance; SLA[4]—specific leaf area; Lon[5]—Longevity; LeL[6]—Leaf longevity; R$_{co}$[7]—Respiration coefficient.

each month has been added as an input variable.

In LPJ-GUESS, carbon uptake through plant photosynthesis is estimated on a monthly-step using coupled photosynthesis and water balance models (Sitch et al. 2003, Gerten et al. 2004). The amount of gross primary productivity (GPP) fixed by each individual in each year is influenced by the quantity of photosynthetically active radiation captured, temperature, CO_2 concentration and stomatal conductance. LPJ-GUESS uses an empirical parameterization of the boundary layer conductivity from Huntingford and Monteith (1998) to relate stomatal conductance to transpiration and the amount of available water in the model's 1.5 meter soil column. Stomatal conductance is reduced when atmospheric evapotranspirational demand exceeds the maximum transpiration rate with fully open stomata.

The NPP of a PFT is calculated as the difference between its GPP and total respiration, which is the sum of maintenance respiration for its leaf (R_{leaf}), root (R_{root}) and sapwood (R_{sap}) compartments, and growth respiration.

More specifically, the leaf respiration in LPJ-GUESS is given by:

$$R_{leaf} = \begin{cases} 0.015 \times VM & \text{for } C_3 \text{ plants} \\ 0.02 \times VM & \text{for } C_4 \text{ plants} \end{cases} \quad (1)$$

where *VM* is non-water-stressed rubisco capacity (g C·m⁻²·d⁻¹) under the assumption that leaf nitrogen (N) is not limiting (Haxeltine and Prentice 1996). The sapwood respiration is

expressed as:

$$R_{sap} = R_{co} \times k \times CMS_{sap}/CtoN_{sap} \times gtemp_{air} \quad (2)$$

where R_{co} is PFT-specific respiration coefficient (Table 1) that is higher for boreal PFTs (Ryan 1991; Hickler et al. *in press*); *k* is a base respiration rate parameter with value of 0.095218 (Smith et al. 2001); CMS_{sap} is sapwood C biomass on grid cell area basis (kg C/m²); $CtoN_{sap}$ is PFT sapwood C:N ratio; $gtemp_{air}$ is the respiration temperature response (Sitch et al. 2003), and equals 1 at 10°C.

The root respiration is calculated in the following way under the assumption that root phenology follows leaf phenology:

$$R_{root} = R_{co} \times k \times CMS_{root}/CtoN_{root} \times gtemp_{root} \quad (3)$$

where CMS_{root} is fine root C biomass on a grid cell area basis (kg C/m²); $gtemp_{root}$ is the respiration temperature response to a given soil temperature.

Growth respiration is assumed to amount to one-third of NPP (Ryan 1991), given by:

$$R_g = 0.25 \times (GPP - R_m) \quad (4)$$

where R_m is total maintenance respiration, i.e., the sum of R_{leaf}, R_{root} and R_{sap}. The NPP (g C/m²) of a PFT is thus expressed as:

$$NPP = GPP - R_m - R_g. \quad (5)$$

The carbon assimilated through plant photosynthesis at the end of a simulation year is reduced further by a fixed fractional allocation to reproduction (e.g., flowers, cones, seeds and

vegetative propagules) for mature plants. The remaining carbon is then allocated to the living tissue compartments as new biomass, including leaf, root, sapwood and heartwood biomass. Allocation is performed on an annual-step in LPJ-GUESS, satisfying a set of allometric relationships specific to each PFT (see Smith et al. 2001 for details).

We ran LPJ-GUESS for New England following the general modeling protocol for LPJ-GUESS (e.g., Hickler et al. 2004). Simulations were started from "bare ground" with 10 replicate patches per cell for a total of 1106 simulation years, i.e., a 1000 year spin-up period followed by 106 simulation years. The 1000-year spin-up is viewed as the maximum years that are required for the vegetation and soil and litter pools to reach the equilibrium with the long-term climate (Koca et al. 2006), and for forest biomass to reach a steady state with generic patch-destroying disturbances and fire. The spin-up simulations used 30 years of monthly-step climate data for the period 1901–1930 that were detrended using a locally weighted scatter-plot smoothing algorithm (Cleveland 1979). Following the model spin-up, the model was run continuously using sequential historical climate data for the period 1901–2006.

PFT definitions and parameterization

We defined vegetation in New England using eight PFTs constructed on the basis of species morphological, phenological, shade-tolerance, and drought-tolerance traits (Tang et al. *submitted*) (Table 1). These PFTs consist of most dominant species currently distributed in New England. PFT-related parameters were assigned values with reference to published literature (e.g., Hickler et al. 2004, Withington et al. 2006) or the USDA (United States Department of Agriculture) Conservation Plant Characteristic (CPC) database ⟨http://plants.usda.gov.about_characteristics.html⟩. The sensitivity of the model to parameters related to tree species life history strategies (shade-tolerance, recruitment and mortality under varying resource availability) within LPJ-GUESS was investigated by Wramneby et al. (2008). They showed that variation within plausible ranges of the tree species parameters investigated could alter the competitive balance between species at a range of European forest

sites, but that the effect on ecosystem functioning, including ecosystem carbon fluxes and storage, was low. The CPC database classifies the relative tolerance of the trees to drought as none, low, medium or high as well as their relative ability to resprout, regrow or reestablish from residual seeds after a fire. Details of quantification of these classes are available in Tang et al. (*submitted*). Given the likelihood that multiple PFTs might coexist in a grid cell, we report the dominant forest type of a grid cell as the PFT that has the highest leaf area index.

Climate, soil and CO_2 data

We used monthly-step temperature (°C), precipitation (mm), percent sunshine (%) and wet day frequency (days) for the period 1901–2006 as input data to LPJ-GUESS. The temperature and precipitation data were derived from PRISM 2.5-arc second data sets (Daly et al. 2000) while monthly-step percent sunshine and wet day frequency were downscaled from the CRU TS 2.1 data sets at 0.5 degree resolution (Mitchell et al. 2004). We interpolated all monthly-step climate data into 30-arc second spatial resolution by targeting the SRTM 30-arc second elevation data (Farr and Kobrick 2000, Rosen et al. 2000). Details of our downscaling approach are available from Tang and Beckage (2010). Both annual mean temperature and total precipitation tended to increase over New England as a whole at a rate of 0.01°C ($R^2 = 0.24$) (relative to the annual mean of 4.7°C in 1901) and 0.11% ($R^2 = 0.10$) (relative to the annual total of 116 cm in 1901) over the years 1901–2006, respectively.

Our soil texture data for running LPJ-GUESS were derived from the USDA Soil Survey Geographic (SSURGO) Database ⟨http://soils.usda.gov.survey.geography.ssurgo⟩. The SSURGO data provide information about soil features on or near the surface of the Earth and are in vector digital and tabular format. The soil map units are linked to attributes in the National Soil Information System (NSIS) data base, which gives the proportionate extent of the component soils and their properties. We used ESRI ArcGIS to link model grid cells to the SSURGO digital soil map to query the representative percent content of sand, silt and clay in each grid cell from the NSIS tabular data base. We defined soil texture in New England into coarse (clay < 18%

and sand >65%), medium (clay <35% and sand <65% or sand ≤82% and clay >18%) and fine (clay >35%) classes following the FAO rules (FAO 1991) to match three of the nine soil texture classes defined in LPJ-GUESS (Sitch et al. 2003). Annual atmospheric CO_2 concentration data for the period 1901–2006 were increased smoothly from 291 ppm in 1901 to 377 ppm in 2006 (Schlesinger and Malyshev 2001).

The sensitivity experiment simulations

We performed two simulation experiments to examine the sensitivity of forest NPP in New England to variation of temperature and precipitation. In each simulation experiment, we allowed one input climate variable (e.g., temperature) to vary over the years 1901–2006 while others (e.g., precipitation and CO_2 concentration) were fixed at their 30-year mean levels for the period 1971–2000.

Data for model comparisons

We compared the modeled forest NPP for New England with MODIS NPP data by Zhao et al. (2005) and FIA-based NPP estimates for similar forests in the mid-Atlantic region of U.S. by Pan et al. (2006). The MODIS NPP data used in this study were gridded at 1-km resolution at the global scale, providing a useful comparison for the spatial distribution of our forest NPP estimates across New England. In addition, the MODIS NPP data cover the period of 2000–2006, allowing us to compare annual variation in our modeled and satellite-derived of NPP estimates. The FIA-based forest NPP data (Pan et al. 2006), on the other hand, are summarized by forest cover type, which enabled us to compare our modeled NPP in different forest types to these empirical estimates.

We also compared our modeled forest biomass for New England with U.S. forest biomass data by Blackard et al. (2008) and FIA-based data for similar forests in the mid-Atlantic region by Jenkins et al. (2001). The U.S. forest biomass data were gridded at a 250-meter resolution and originally derived from measured inventory plots using models that relate field-measured response variables to plot attributes (Blackard et al. 2008). Similar to the FIA-based NPP data, the FIA-based biomass data (Jenkins et al. 2001) are also tabular data summarized by forest cover type.

We reprojected both MODIS NPP and U.S. forest biomass data into geographic coordinates and then regridded them onto our model grid cells at 30-arc spatial resolution for comparison. The values of NPP and biomass in each regridded cell are assigned the values of its nearest neighbors in their original maps. The U.S. forest biomass values are aboveground forest biomass while our modeled forest biomass includes root biomass; we therefore added root biomass that approximates 20% of total biomass (e.g., Cairns et al. 1997, Blackard et al. 2008) to U.S. aboveground live forest biomass. To compare the modeled NPP and biomass with FIA-based estimates in the mid-Atlantic region, we grouped our eight PFTs into five categories that correspond to the forest types in Pan et al. (2006) and Jenkins et al. (2001): spruce-fir, white-red-jack pine, maple-beech-birch, oak-hickories and aspen-birch. When necessary, we converted all data to standard units of g C·m^{-2}·yr^{-1} (fluxes) for NPP and Mg/ha (pools) for biomass, using a factor of 0.45 to estimate gram carbon from plant dry weight (e.g., Olson et al. 1983).

Statistics for quantifying the agreement between compared data sets

We used both Pearson correlation coefficient and Tang's OI index (Tang 2008), as appropriate, to quantify the agreement between two sets of compared data. To calculate the OI index, assume that a and b refer to two sets of time-series simulations. Let vector $a_{i,j}$ and $b_{i,j} (i = 1, 2, \ldots, m, j = 1, 2, \ldots, n)$ be the simulated anomalies of an ecological variable in grid cell i at time step j, where m and n are the total number of grid cells and time steps, respectively. Let $c_{i,j}$ be the vector sum of $a_{i,j}$ and $b_{i,j}$, and α be the acute angle between the vector sum $c_{i,j}$ and the identity axis (see Tang 2008). Then, the OI index of two compared datasets is defined as:

$$OI = 1 - \theta/90.0^o \qquad (6)$$

where

$$\theta = \tan^{-1}\left(\sum_{i=1}^{m}\sum_{j=1}^{n}|c_{i,j}|\sin\alpha_{i,j}\Big/\sum_{i=1}^{m}\sum_{j=1}^{n}|c_{i,j}|\cos\alpha_{i,j}\right).$$

The value of the OI index varies from 0 to 1 with a value 0 (1) indicating that compared simulations are opposite (identical). An OI index with a

RESULTS

The modeled forest NPP and biomass for New England

Our modeled forest NPP and biomass in the baseline (1971–2000) condition varied spatially and temporally across New England. The modeled baseline forest NPP for New England averages 428 g $C \cdot m^{-2} \cdot yr^{-1}$ for grid cells and ranges from 333 to 541 g $C \cdot m^{-2} \cdot yr^{-1}$. Forest NPP decreases from south to north in New England (Fig. 1A). The highest annual NPP occurs in the states of Connecticut and Rhode Island and in eastern Massachusetts where annual mean temperature is relatively higher (>8.7°C) than other sub-regions in New England. The lowest annual NPP occurs in northern and northwestern Maine where annual mean temperature is relatively low (<1.4°C) (Fig. 1A, D). The modeled forest biomass for New England averages 135 Mg/ha for grid cells and ranges from 77 to 242 Mg/ha. Forest biomass also decreases from south to north (Fig. 1B). The highest biomass occurs in the corner of southeastern Massachusetts and the lowest biomass occurs in northwestern Maine. The modeled forest biomass is relatively low (<143 Mg/ha) at high elevations such as in the Green Mountains of Vermont and the White Mountains of New Hampshire (Fig. 1B, D).

The modeled forest NPP and biomass for New England depend heavily on the composition of the simulated vegetation in terms of PFTs (Fig. 1C) as also illustrated in other studies (e.g., Bondeau et al. 1999, Jenkins et al. 2001). For example, the modeled NPP for spruce-fir (i.e., areas dominated by spruce-fir) ranges from 339 to 473 g $C \cdot m^{-2} \cdot yr^{-1}$ and has the lowest mean of 395 g $C \cdot m^{-2} \cdot yr^{-1}$ among all eight PFTs simulated. In contrast, NPP in oak forests range from 391 to 574 g $C \cdot m^{-2} \cdot yr^{-1}$ and has the highest mean of 468 g $C \cdot m^{-2} \cdot yr^{-1}$ (Table 2). In addition, the modeled NPP is generally higher in deciduous forests (e.g., oak-hickory, maple-beech-basswood and aspen-birch forests) than in evergreen forests (e.g., spruce-fir and white-red-jack pine) (Table 3). Similar to our NPP estimates, oak forests have the highest mean biomass of 153 Mg/ha while red-jack pine forests have the lowest mean of 118 Mg/ha. The modeled biomass is also higher in deciduous forests than in evergreen forests except for in white pine-cedar (Table 2).

Our modeled average annual NPP for New England tended to decrease at a rate of 0.32 g $C \cdot m^{-2} \cdot yr^{-1}$ ($R^2 = 0.02$) in the period 1901–1949 but increase at a rate of 0.52 g $C \cdot m^{-2} \cdot yr^{-1}$ ($R^2 = 0.09$) in the period 1950–2006 (Fig. 2A). Forest biomass tended also to decrease at a rate of 0.11 Mg/ha ($R^2 = 0.74$) per year over the years 1901–1949 but increase at a rate of 0.25 Mg/ha ($R^2 = 0.95$) per year over the years 1950–2006 (Fig. 2B).

Comparison between modeled and reported forest NPP data

Three distinct discrepancies emerge when our model simulations were compared to MODIS NPP estimates for New England (Zhao et al. 2005). First, our modeled NPP estimates over the period 2000–2006 have a relatively narrow range from 262 to 627 g $C \cdot m^{-2} \cdot yr^{-1}$ while MODIS NPP estimates have a wider range from 39 to 1403 g $C \cdot m^{-2} \cdot yr^{-1}$ at a grid cell level (Fig. 3A, B). Second, our modeled NPP estimates decrease from south to north while MODIS NPP estimates do not show such a latitudinal trend. Third, MODIS NPP estimates in western New Hampshire and in mid- and southern Vermont are higher than in surrounding areas while such a pattern does not exist in the modeled NPP estimates (Fig. 3A, B). The modeled forest NPP for the whole of New England averages 437 g $C \cdot m^{-2} \cdot yr^{-1}$ over the years 2000–2006, which is about 137 g $C \cdot m^{-2} \cdot yr^{-1}$ lower than the MODIS NPP estimates, averaging 574 g $C \cdot m^{-2} \cdot yr^{-1}$ (Fig. 3C).

Our modeled inter-annual variation in NPP over the years 2000–2006 corresponds to the patterns in MODIS NPP data in most grid cells. For example, the calculated OI indices (Tang 2008) in 89.7% of the study region is greater than 0.6 (Fig. 3D), suggesting that (1) the sign of compared annual NPP anomalies in each year relative to its 7-year (2000–2006) mean is identical in those grid cells between modeled and MODIS NPP estimates, and (2) the amplitudes of changes in annual NPP in each year relative to its 7-year mean are similar in those grid cells when the two datasets were compared. Nevertheless, the modeled annual NPP varia-
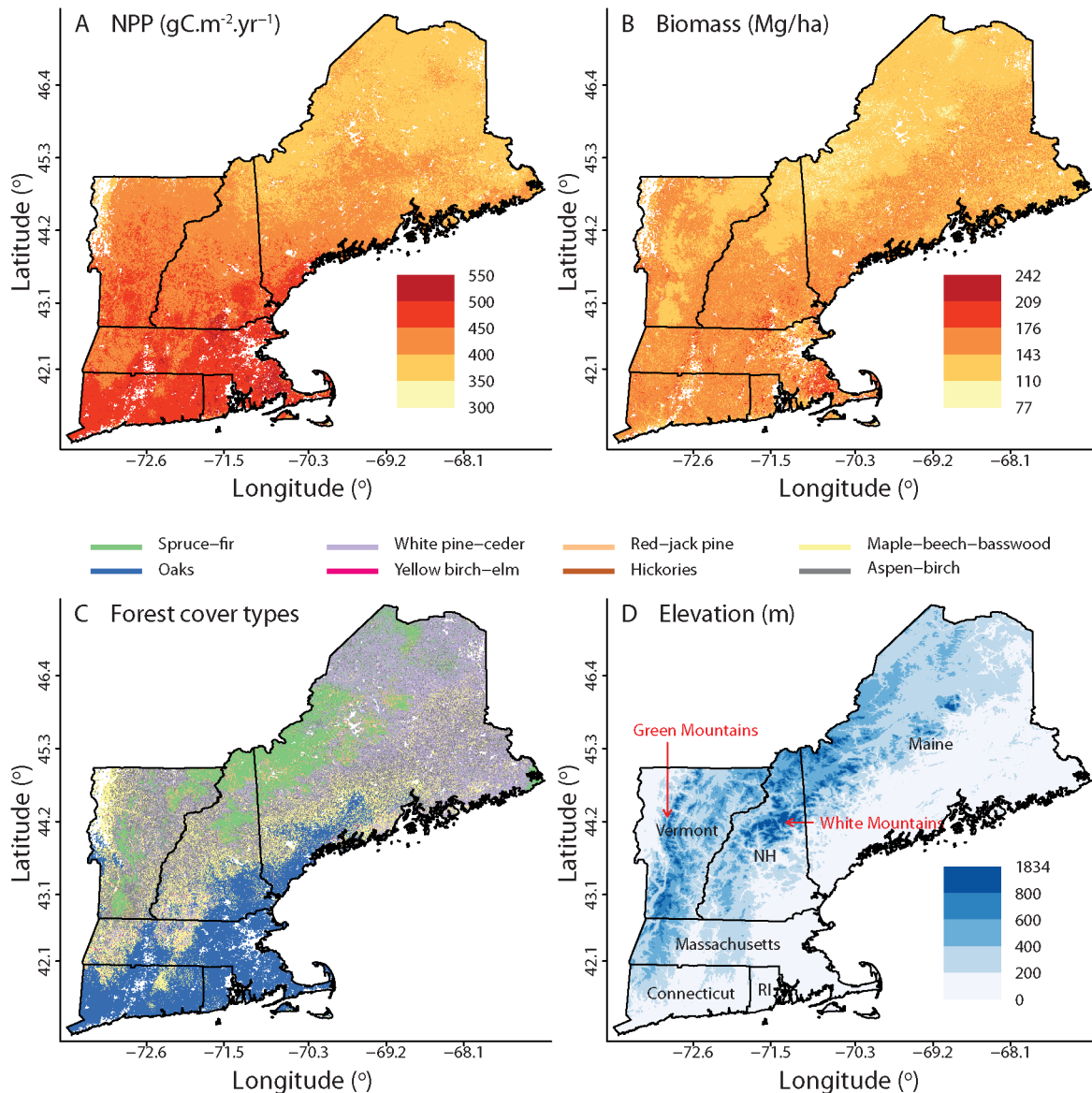
Fig. 1. The spatial patterns of modeled (A) forest NPP, (B) biomass and (C) dominant plant functional types (PFTs) for New England. The data are 30-year (1971–2000) mean annual NPP and biomass. The dominant PFT in a grid cell is defined as the PFT that has the highest leaf area index. (D) The topography and the states of New England. New Hampshire and Rhode Island are abbreviated to "NH" and "RI", respectively.

tions do not correspond well with those reflected in MODIS NPP data in some regions such as southern Connecticut, Rhode Island and the southeastern Massachusetts (Fig. 3D). In these regions (about 2.5% of the study region), the calculated OI indices are lower than 0.5, suggesting that the variations of our modeled annual NPP are opposite of those in MODIS NPP data

over the years 2000–2006. The overall good agreement between our modeled annual NPP variations and those from MODIS NPP data, however, is confirmed by the high correlation (R^2 = 0.86, p < 0.01) of mean annual NPP estimates (Fig. 3C).

Our modeled forest NPP for New England agrees well with FIA-based NPP estimates from

Table 2. The modeled forest NPP and biomass by dominant plant functional type.

	Forest NPP (g C·m^{-2}·yr^{-1})				Forest biomass (Mg/ha)			
Plant functional types	Min	Mean	Max	Std	Min	Mean	Max	Std
1. Spruce-fir	339	395	473	28	116	120	123	2
2. White pine-cedar	353	405	482	27	141	147	150	3
3. Red-jack pine	361	423	495	29	114	118	121	2
4. Maple-beech-basswood	354	408	492	32	142	149	154	4
5. Oaks	391	468	574	44	146	153	157	3
6. Yellow birch-elm	360	435	522	41	130	140	147	4
7. Hickories	399	463	562	5	121	127	134	3
8. Aspen-birch	388	430	510	27	124	129	133	3

Note: The forest NPP and biomass values are 30-year (1970–2000) mean values.

Table 3. Comparison between modeled and FIA-based NPP estimates by forest cover type.

	Modeled NPP (g C·m^{-2}·yr^{-1})[1]			FIA-based NPP (g C·m^{-2}·yr^{-1})[2]			NPP differences[3]	
Forest cover types	Min	Mean	Max	Min	Mean	Max	Magnitude	%
1. Spruce-fir	362	403	473	199	323	436	80	25
2. White-red-jack pine	373	413	494	232	399	483	14	4
3. Maple-beech-birch	354	426	517	266	446	489	−20	4
4. Oak-hickories	391	470	535	273	466	499	4	0.9
5. Aspen-birch	403	437	510	256	391	508	46	12

Notes: [1] The modeled NPP for each forest cover type is an average value for the period 1982–1997, which corresponds to the period of FIA-based inventory data measured for the six states in New England. [2] FIA-based annual mean NPP in the mid-Atlantic region of U.S. is from Pan et al. (2006) except for minimum and maximum annual NPP and annual mean NPP in aspen-birch, which are from Jenkins et al. (2001). [3] Mean NPP difference is measured in both magnitude and percent change relative to modeled mean NPP.
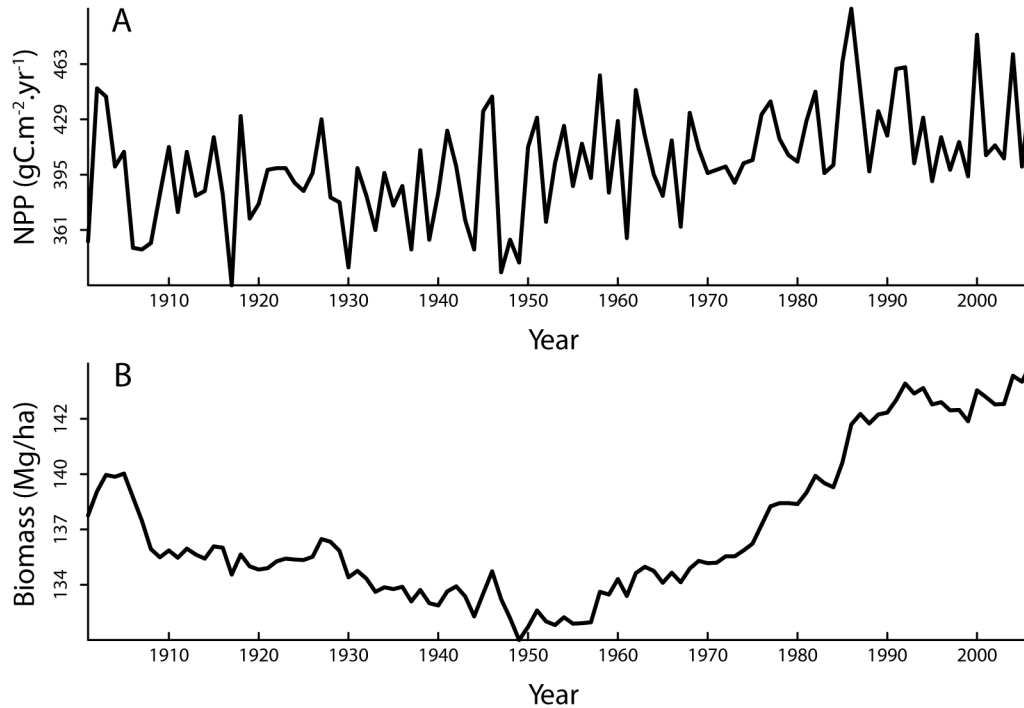

Fig. 2. The modeled trend of (A) forest NPP and (B) biomass for New England over the years 1901–2006.
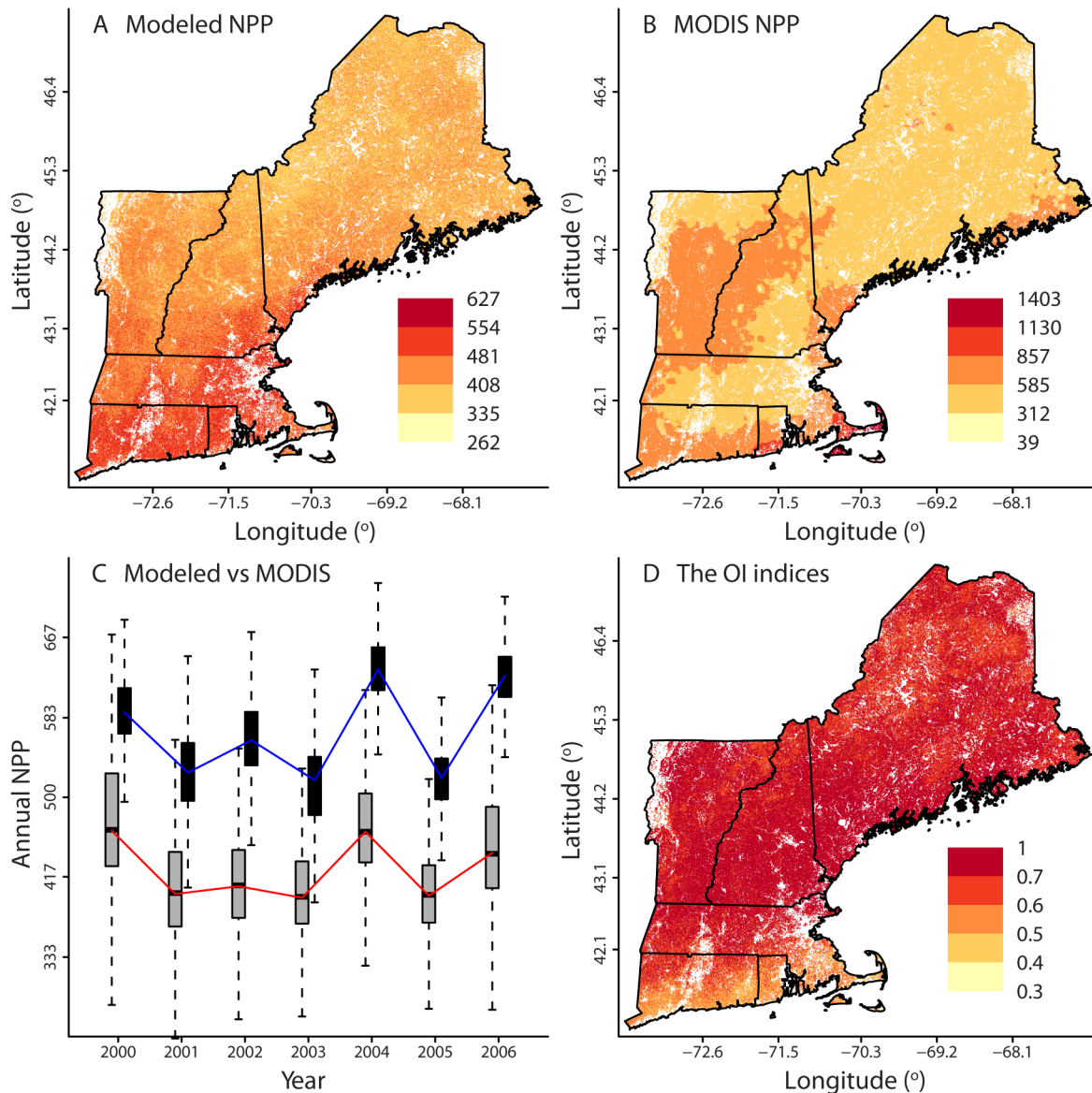
Fig. 3. Comparison between (A) modeled and (B) MODIS NPP (g C·m^{-2}·yr^{-1}) data (Zhao et al. 2005) for New England over the years 2000–2006. The data in (A) and (B) are averaged values for the period 2000-2006. (C) Comparison of modeled (gray boxes) and MODIS NPP (black boxes) estimates for the whole New England over the period 2000–2006. (D) The spatiotemporal agreement between modeled and MODIS NPP estimates across New England measured by the OI indices.

similar forests in the mid-Atlantic region of U.S. (Jenkins et al. 2001, Pan et al. 2006). For example, our modeled forest NPP averages 413 g C·m^{-2}·yr^{-1} in white-red-jack pine, 426 g C·m^{-2}·yr^{-1} in maple-beech-birch and 470 g C·m^{-2}·yr^{-1} in oak-hickory, approximating (difference < 4%) FIA-based NPP estimates of 399,

446 and 466 g C·m^{-2}·yr^{-1} from similar forests in the mid-Atlantic region, respectively (Table 3). However, our modeled NPP in spruce-fir (averages 403 g C·m^{-2}·yr^{-1}) and in aspen-birch (averages 437 g C·m^{-2}·yr^{-1}) forests are greater than FIA-based NPP estimates that average 323 g C·m^{-2}·yr^{-1} in spruce-fir and 391 g C·m^{-2}·yr^{-1} in

aspen-birch (Table 3). In addition, our modeled forest NPP values are less spatially variable than FIA-based NPP estimates as illustrated by the lower limits of modeled NPP values, which are greater than those of FIA-based NPP estimates while the upper limits are similar in all forests (Table 3).

Comparison between modeled and reported forest biomass data

Our modeled distribution of mean forest biomass for New England agrees well with U.S. forest biomass data for New England. For example, estimates of forest biomass from both approaches are between 124 and 171 Mg/ha in most areas (84.9% for model simulation and 63.4% for U.S. forest biomass data) of New England, especially at low elevations such as in southern New England and southern Maine (Fig. 4A, B). The good agreement between our modeled and U.S. forest biomass estimates for New England is indicated by the close correspondence of average forest biomass between the two approaches: 143.2 Mg/ha from the model simulation and 142.1 Mg/ha from U.S. forest biomass data. In addition, both modeled and U.S. forest biomass estimates in all grid cells for New England appear to be approximately normally distributed (Fig. 4C, D) with biomass values clustered symmetrically around their mean.

Localized differences in forest biomass estimates for New England still exist, however, between our modeled and U.S. forest biomass data. First, U.S. forest biomass estimates in the Green Mountains of Vermont and the White Mountains of New Hampshire are clearly higher (>170 Mg/ha) than our modeled forest biomass estimates (<170 Mg/ha) in these areas (Fig. 4A, B). Second, our modeled forest biomass estimates in eastern Maine are higher (>120 Mg/ha) than those in U.S. forest biomass data (<120 Mg/ha). This discrepancy was reversed in the corner of northwestern Maine and northern New Hampshire. Third, annual average biomass by grid cells has a lower variance in the modeled datasets compared with the observed data: the modeled biomass has a relatively narrow range from 79 to 241 Mg/ha while the U.S. forest biomass data have a wider range from 31 to 264 Mg/ha (Fig. 4C, D).

Our modeled forest biomass is less than FIA-based forest biomass estimates for similar forests in the mid-Atlantic region (Jenkins et al. 2001) (Fig. 5). For example, our modeled biomass ranges from 121.9 Mg/ha in spruce-fir to 146.7 Mg/ha in maple-beech-birch. In contrast, FIA-based biomass estimates are 63.4 Mg/ha higher in spruce-fir (average 185.3 Mg/ha) and 107.2 Mg/ha higher in maple-beech-birch (average 253.9 Mg/ha). In forests dominated by white-red-jack pine, oak-hickory and aspen-birch, our modeled forest biomass is about 73 to 103 Mg/ha lower than FIA-based biomass estimates in the mid-Atlantic region.

The sensitivity of NPP to the variation of temperature and precipitation

Simulations from our sensitivity experiment indicated that monthly NPP was positively correlated with monthly mean temperature in late spring (April-May) and fall (e.g., October) but negatively correlated with summer (June-July-August) and early fall (September) temperature in New England (Fig. 6A–G). For example, monthly NPP in the study period is modeled to increase at a rate of 15.6 g C/m^2 ($R^2 = 0.92$) in April and 5.0 g C/m^2 ($R^2 = 0.27$) in May if temperature increases by 1°C. In contrast, monthly NPP is modeled to decrease at a rate of 13.3 g C/m^2 ($R^2 = 0.92$) in June, 18.2 g C/m^2 ($R^2 = 0.92$) in July, 15.6 g C/m^2 ($R^2 = 0.94$) in August and 10.2 g C/m^2 ($R^2 = 0.88$) in September respectively if temperature increases by 1°C.

Monthly NPP in the growing season (May-September) was positively correlated with monthly precipitation (Fig. 6H–I). The strength of this positive relationship was stronger in summer (June-July-August) and September than in May. For example, monthly NPP is modeled to increase at rate of 0.50 g C/m^2 ($R^2 = 0.36$) in June, 1.28 g C/m^2 ($R^2 = 0.27$) in July, 1.14 g C/m^2 ($R^2 = 0.42$) in August, and 0.91 g C/m^2 ($R^2 = 0.26$) in September respectively when monthly precipitation increases by 1%. In contrast, the increasing rate is smaller in May (0.03 g C/m^2 ($R^2 = 0.01$)) if monthly precipitation increases by 1%. In other months (October to April), the effects of climatic variation in temperature or precipitation on monthly NPP are negligible.
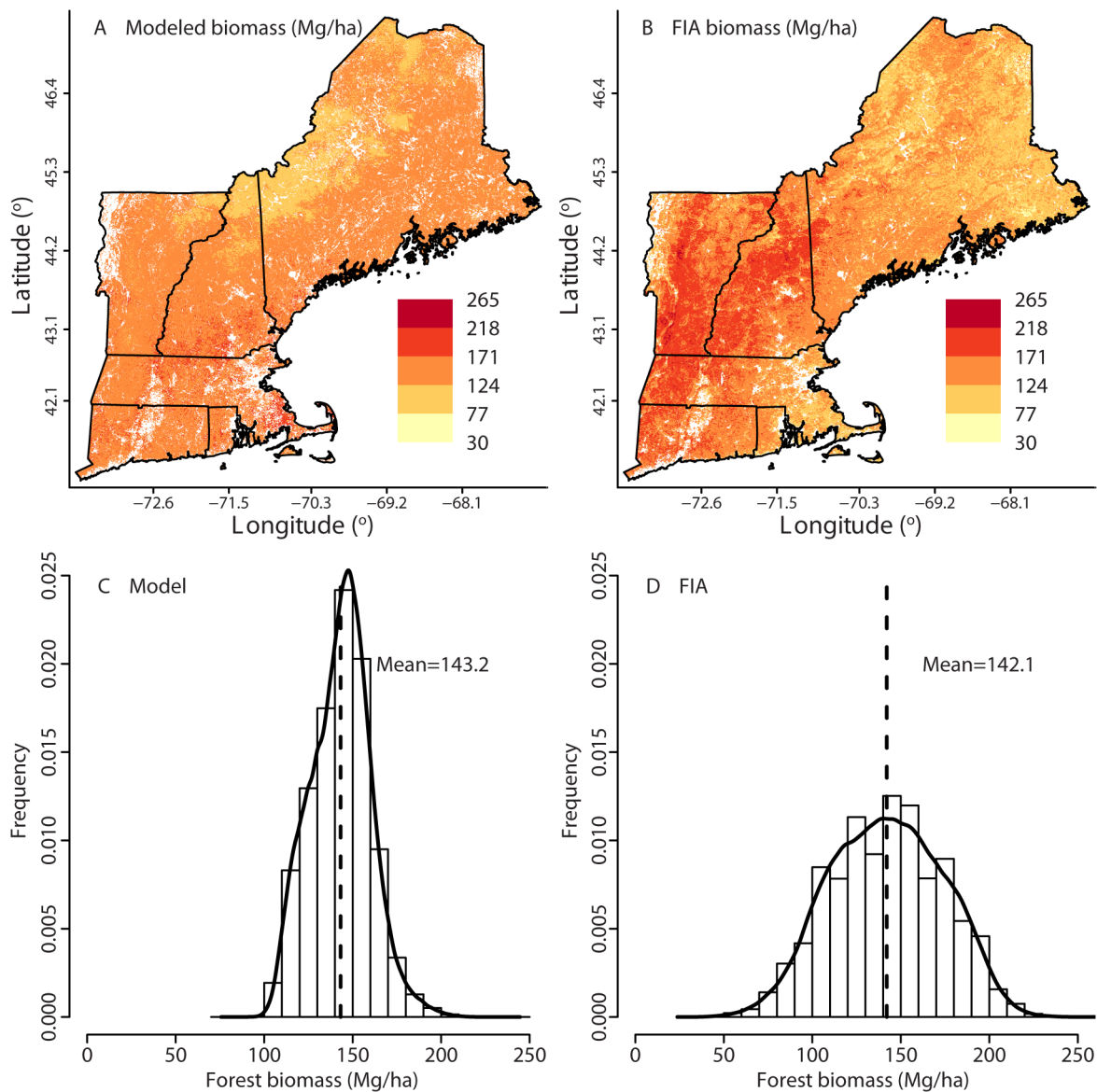
Fig. 4. Comparison of modeled biomass (A and C) with U.S. forest biomass (B and D) data (Blackard et al. 2008) for New England. The modeled forest biomass in each grid cell (A) is average annual mean biomass for the period 1990–2003, a period corresponding to the period of measured FIA data. The data in (B) and (D) are total biomass with the addition of root biomass, approximating 20% of total biomass (see Cairns et al. 1997, Blackard et al. 2008). (C) and (D) show the distribution of frequencies of modeled and FIA biomass values from all grid cells across New England.

DISCUSSION

The accuracy of forest NPP estimates

The agreement between our modeled NPP and FIA-based estimates justifies the model's utility for estimating forest NPP for New England. Our results are also in overall agreement with previous studies. For example, the measured NPP in pine dominated stands in Harvard forest (located in Petersham, Massachusetts) is 377 g $C \cdot m^{-2} \cdot yr^{-1}$ (Aber et al. 1995), close to (difference < 7%) the modeled NPP of 405 g $C \cdot m^{-2} \cdot yr^{-1}$ for
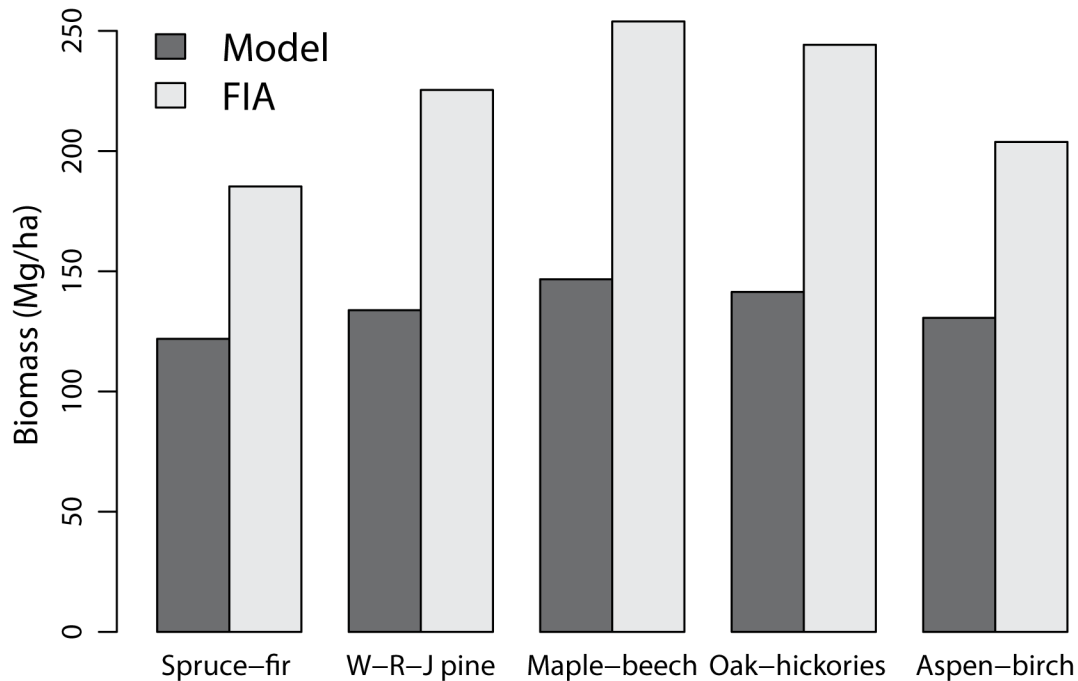
Fig. 5. Comparison between modeled and FIA-based forest biomass estimates in similar forests. The modeled data are for New England and the FIA-based data are for the mid-Atlantic region of U.S. (Jenkins et al. 2001). "W-R-J pine" ~ white-red-jack pine; "Maple-beech" ~ "Maple-beech-birch".

white pine in this study. Using a different model, Chertov et al. (2009) found that NPP for black spruce averages 371 g $C \cdot m^{-2} \cdot yr^{-1}$, approximating (difference < 6%) the modeled NPP of 395 g $C \cdot m^{-2} \cdot yr^{-1}$ for spruce-fir in this study. Our modeled NPP values are also within the range of FIA-based estimates for cool temperate and boreal forests. Gower et al. (2001) reported that the total NPP ranges from 52 to 868 g $C \cdot m^{-2} \cdot yr^{-1}$ (average 424 g $C \cdot m^{-2} \cdot yr^{-1}$) for the boreal forest biome, similar to our modeled values. Bond-Lamberty et al. (2004) reported that average NPP in black spruce-dominated boreal forests in areas west of Thompson (Canada), ranged from 106 to 406 g $C \cdot m^{-2} \cdot yr^{-1}$ for dry stands and from 72 to 534 g $C \cdot m^{-2} \cdot yr^{-1}$ for wet stands. NPP for hardwoods were reported to be 505 g $C \cdot m^{-2} \cdot yr^{-1}$ (Aber et al. 1995) and 565 g $C \cdot m^{-2} \cdot yr^{-1}$ in Harvard forest (Curtis et al. 2002), close to our modeled NPP in their areas, which ranged from 450 to 500 g $C \cdot m^{-2} \cdot yr^{-1}$ (Fig. 1A).

Our modeled forest NPP is generally lower for evergreen forests than deciduous forests, which is consistent with other studies. For example,

Gower et al. (2001) found that above ground NPP was consistently higher for deciduous than for evergreen boreal forests in boreal regions of Canada. Brown and Schroeder (1999) found that aboveground production of woody biomass for hardwood forests in Maine averaged 366 g $C \cdot m^{-2} \cdot yr^{-1}$, which is higher than for conifer forests, which average 222.7 g $C \cdot m^{-2} \cdot yr^{-1}$.

We suggest that LPJ-GUESS might better quantify forest NPP for New England than MODIS derived NPP estimates based on our comparison to FIA-based estimates of NPP (e.g., Jenkins et al. 2001). Other comparisons also indicate that MODIS NPP estimates tend to be larger than the modeled NPP estimates for New England forests (Table 4). Pan et al. (2006) argued that MODIS NPP might overestimate NPP for coniferous mixed forests in the mid-Atlantic region and inferred that the radiation conversion efficiency used in the MODIS NPP algorithm might be too large for vegetation in the mid-Atlantic region. We suspect that this might also be the case in New England. Nevertheless, our modeled inter-annual NPP variation in each
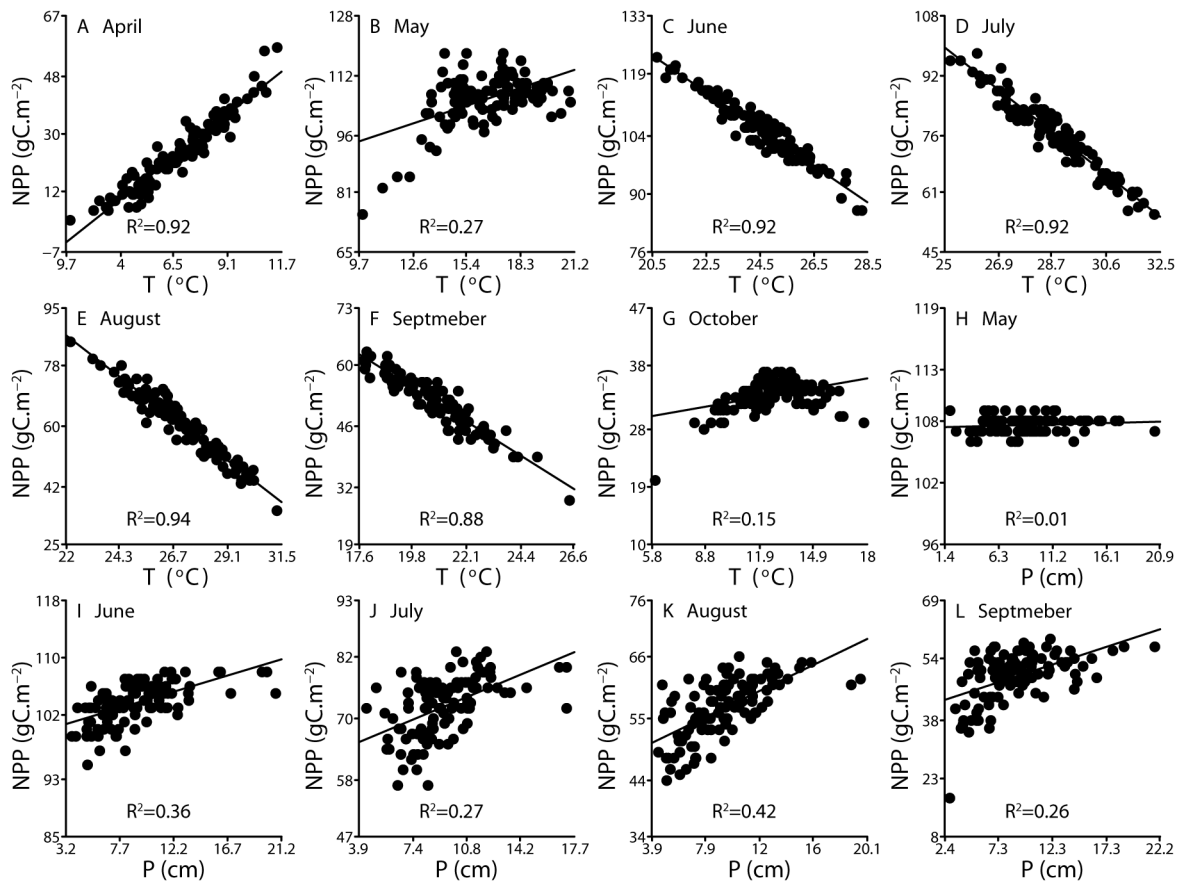
Fig. 6. The sensitivity of forest NPP to the variation of temperature alone in months from April to October (A–G), and to the variation of precipitation alone in months from May to September (H–L) over the years 1901–2006. We did not plot those months in which monthly NPP did not show any statistically significant effects such as in the late autumn (e.g., November), winter and early spring (e.g., March).

Table 4. Comparison between modeled and MODIS NPP estimates.

Plant functional types	Model NPP	MODIS NPP	OI index	Correlation coefficient	Mean Dev1	Mean Dev2	ΔDev (absolute)
1. Spruce-fir	387	563	0.71	0.62	28.5	40.6	12.1
2. White pine-cedar	409	555	0.71	0.65	28.6	44.3	15.3
3. Red-jack pine	415	567	0.70	0.62	26.7	42.0	15.3
4. Maple-beech-basswood	414	567	0.74	0.69	40.4	44.9	4.9
5. Oaks	497	609	0.68	0.53	45.6	36.6	8.9
6. Yellow birch-elm	451	568	0.73	0.66	50.8	41.6	9.2
7. Hickories	493	602	0.71	0.61	46.1	62.6	16.5
8. Aspen-birch	431	566	0.73	0.68	32.8	45.3	12.5

Notes: NPP is measured in $g\,C\cdot m^{-2}\cdot yr^{-1}$. "Mean Dev" represents the average NPP deviation from the 7-year mean calculated at a grid cell level. "Mean Dev1" and "Mean Dev2" are for modeled and MODIS NPP, respectively. ΔDev is the absolute difference between two average NPP deviations.

forest type is strongly correlated to the variation in the MODIS dataset as confirmed by the OI indices and correlation coefficients (Table 4). The

strong agreement between these two completely independent estimation methods suggests that both approaches likely capture the inter-annual

variation of NPP in New England in response to varying climatic conditions.

Although we suspect that MODIS NPP data might overestimate forest NPP for New England, the MODIS NPP algorithm is a powerful tool for monitoring terrestrial NPP because of its spatial coverage and temporal continuity (Pan et al. 2006, Zhao and Running 2010). While the application of the MODIS algorithm may be reasonable at global scales (e.g., Nemani et al. 2003), MODIS NPP estimates can be improved through (1) finer vegetation classifications and more precise parameterization of the radiation conversion efficiency, and (2) accurate quantification of the effects of soil water condition on forest NPP (Pan et al. 2006). In addition, improved climate data will contribute to a greater accuracy of MODIS NPP estimates.

The accuracy of forest biomass estimates

The agreement between our modeled and U.S. forest biomass data for New England indicates the utility of the model for estimating potential forest biomass across New England. In a review of biomass estimation studies for boreal forests, Pregitzer and Euskirchen (2004: Fig. 4) reported that the biomass ranged from approximately 44 to 176 Mg/ha across all boreal age classes. Chertov et al. (2009) similarly found that black spruce biomass in the central Canadian boreal forest could vary between 24.2 and 169.4 Mg/ha for well drained sites and between 48.4 and 204.6 Mg/ha for poorly drained sites. These represent wider ranges than were simulated by our model: 116 to 123 Mg/ha for spruce-fir and 114 to 121 Mg/ha for red-jack pine forests. Even in the mid-Atlantic region, Jenkins et al. (2001) reported that forest biomass ranged from 101 to 326 Mg/ha, a range wider than our modeled forest biomass ranges across all forests (Table 2). Thus, while our model reproduced mean biomass values, it did not simulate the full range of regional variability.

Part of the discrepancies between our modeled and FIA-based forest biomass estimates in the mid-Atlantic region can likely be explained by differences in the biomass components considered by the two approaches. LPJ-GUESS calculates forest biomass at a stand as the summation of leaf, fine root, sapwood and heartwood biomass compartments, which evolve dynami-

cally in the course of a simulation. The additional compartments like branches, twigs, stumps, coarse roots and standing dead trees included in the FIA-based approach (Jenkins et al. 2001) are implicit in the more generalized compartment set represented in the model. In addition, the difference in climatic condition between New England (comparatively shorter growing season and lower annual mean temperature) and the mid-Atlantic region (comparatively longer growing season and higher annual mean temperature) contributes to the lower modeled biomass for New England relative to FIA-based estimates for the mid-Atlantic region.

The modeled spatiotemporal pattern of forest NPP and biomass

Our modeled temporal dynamics of forest NPP and biomass in New England, i.e., decreases over the years 1901–1949 but increases over the years 1950–2006 (Fig. 2), are broadly consistent with findings in other studies. Bachelet et al. (2001) found that the total carbon storage (a summation of live vegetation and soil carbon) in U.S. forests remained stable in the early part of the 20th century until about 1940 and then began to increase until 1971. Such findings indicate some correspondence with our modeled temporal dynamics of forest biomass in New England. For example, our modeled forest biomass in New England increased at a rate of 0.17 Mg/ha per year ($R^2 = 0.81$) over the years 1950–1971 with annual mean temperature decreasing at a rate of 0.05°C ($R^2 = 0.33$) per year in this period (Fig. 7A). This cooling favored carbon sequestration (e.g., Bachelet et al. 2001). In addition, Liu et al. (2006) simulated that the biomass density in three eco-regions in the Appalachian region increased by a range from 63.4 to 102.8 Mg C/ha over the years 1972–2000. Our modeled increases in forest biomass over the years 1950–2006 also agree well with the reported increase in plant growth on timber land in the northern U.S. in the period 1953–1997 (USDA Forest Service 2000).

At decadal or shorter temporal scales, however, our modeled NPP dynamics differ from findings in others studies. For example, Nemani et al. (2003) reported that global NPP increased by 6.2% (3.42 Pg C) between 1982 and 1999. Regional studies in North America and in the
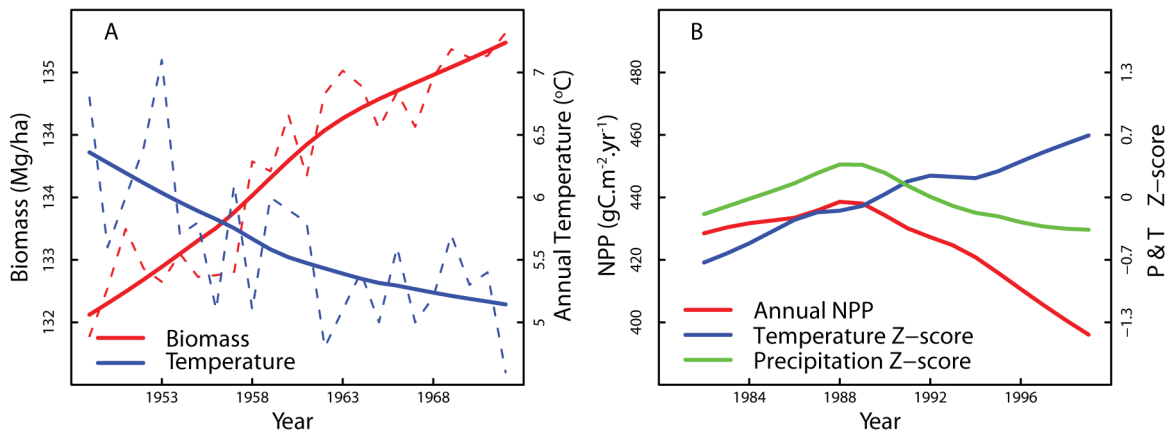
Fig. 7. (A) The modeled variability of forest biomass and annual mean temperature in New England over the years 1949–1972. (B) The modeled trend of annual NPP, summer temperature and precipitation in New England over the years 1982–1999. P ~ summer precipitation and T ~ summer temperature. For plotting, we converted summer temperature and precipitation into dimensionless Z-scores by subtracting the population mean from each individual observation and then dividing by their standard deviation.

U.S. reported an overall significant increase in NPP of 0.03 Pg C/yr over the years 1982–1998 (Hicke et al. 2002) but the largest increases occurred in the central and southeastern United States, and northwestern North America. However, our modeled forest NPP in New England did not show an increasing trend in this period (Fig. 7B). More specifically, our modeled forest NPP showed an increase in the 1980s but a decrease in the 1990s (Fig. 7B). In the 1980s, both summer temperature and precipitation tended to increase concurrently, resulting in an increase of forest NPP. In the 1990s, summer temperature in New England continued to increase while summer precipitation tended to decrease, leading to a decreasing forest NPP (Fig. 7B).

The sensitivity of forest NPP to the variation of temperature and precipitation

Previous studies have found that the carbon balance of a terrestrial ecosystem is particularly sensitive to warming in spring and autumn (e.g., Bergeron et al. 2007) as this increases plant photosynthesis (Piao et al. 2008). The positive relationship between forest NPP and variation of monthly temperature in April, May and October in our simulations are consistent with this general pattern, resulting primarily from a lengthening of the growing season, i.e., an earlier onset in the spring and longer duration in the fall

(e.g., Myneni et al. 1997, Linderholm 2006, Schwartz et al. 2006). However, summer temperature was negatively correlated with forest NPP in New England, largely because warming can increase soil moisture deficit and drought conditions (Fig. 8A–C). Forest NPP in the growing season was positively correlated with monthly precipitation. Increases in precipitation increases soil moisture, ameliorating potential drought conditions. For example, our modeled soil moisture content (as a fraction of soil water holding capacity) at the top 50 cm of soil layers was strongly and positively correlated with monthly precipitation in May, June, July, August and September (Fig. 8D–H).

The limitations of the model's application to New England

Our comparisons suggest that the regional ecosystem model LPJ-GUESS can provide useful estimates of forest NPP and biomass for New England. This model incorporates not only climatic and soil information, but in this study also was parameterized using fine-scale definitions of PFTs compared to global models. The model as it was used in this study does not, however, simulate the effects of human related activities and other factors on forest NPP and biomass. This may explain why the modeled forest NPP and biomass values have a more
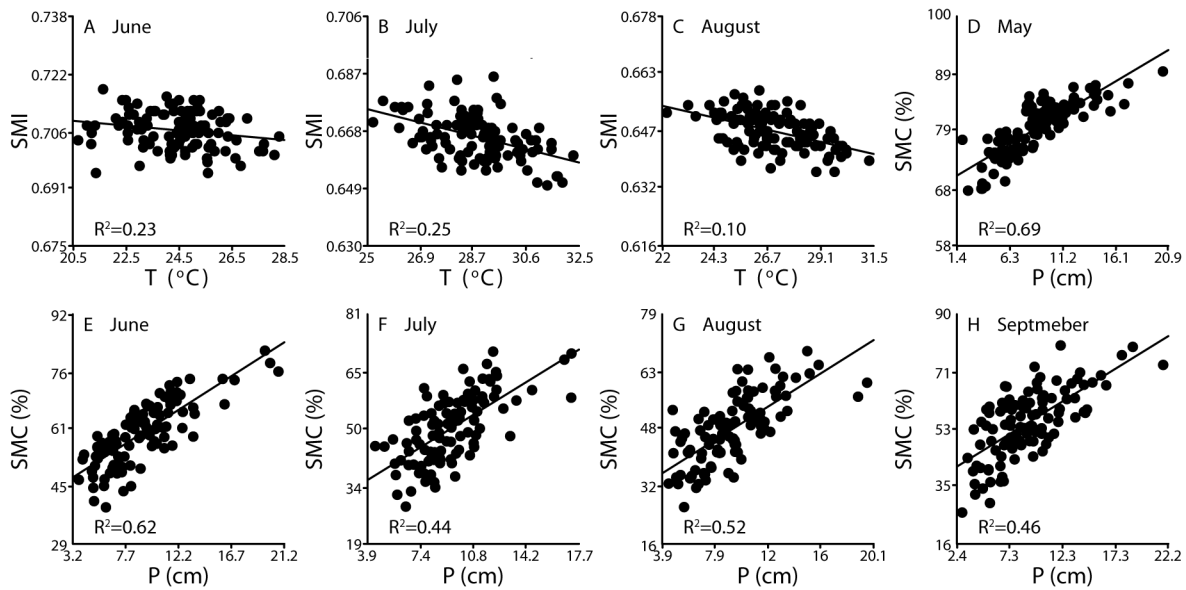
Fig. 8. (A–C) The negative relationship between soil moisture index (SMI, a ratio of actual evapotranspiration to potential evapotranspiration) and monthly mean temperature in June, July and August. (D–H) The positive relationship between soil moisture content (SMC, as a fraction of available water holding capacity) in the upper 50 cm of soil and monthly precipitation in the growing season.

narrow range compared to those estimates based on MODIS and FIA data. A wide range of MODIS NPP and FIA-based NPP and biomass estimates reflect both the spatial variability of climate and the effects of human land use on forests. As a result, these empirical estimates produce a wider range of values than found in our modeled data. Therefore, our modeled forest NPP and biomass are more representative of potential NPP and biomass as determined by climate and soil condition.

CONCLUSION

Our modeled forest NPP for New England agrees well with FIA-based estimates from similar forests in the mid-Atlantic region. The modeled annual variability of forest NPP is also significantly correlated with MODIS NPP estimates. The modeled forest biomass for New England is in agreement with the U.S. forest biomass data for New England but our model estimates are less than FIA-based estimates from the mid-Atlantic region. Both our modeled NPP and biomass, however, are within the ranges of reported NPP and biomass values, supporting

the use of the model for New England forests.

Vegetation models have inherent advantages in predicting the long-term pattern of forest NPP and biomass in response to climate change compared to empirical FIA-based approaches. The inclusion of the effects of human land use activities must be considered, however, in order to improve the accuracy of model-based estimates of forest NPP and biomass. Given the discrepancies in forest NPP and biomass estimates between these different approaches, continued efforts at inter-comparison and cross-validation are still needed for reducing the uncertainties in the quantification of the terrestrial carbon cycle.

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LITERATURE CITED

Aber, J. D., S. V. Ollinger, C. A. Federer, P. B. Reich, M. L. Goulden, D. W. Kicklighter, J. M. Melillo, and R. G. Lathrop. 1995. Predicting the effects of climate change on water yield and forest production in the northeastern United States. Climate Research 5:207–222.

Bachelet, D., R. P. Neilson, J. M. Lenihan, and R. J. Drapek. 2001. Climate change effects on vegetation distribution and carbon budget in the United States. Ecosystems 4:164–85.

Badeck, F.-W., H. K. Lischke, H. Bugmann, T. Hickler, K. Honninger, P. Lasch, M. J. Lexer, F. Mouillot, J. Schaber, and B. Smith. 2001. Tree species composition in European pristine forests: Comparison of stand data to model predictions. Climatic Change 51:307–347.

Bergeron, O., H. A. Margolis, T. A. Black, C. Coursolle, A. L. Dunn, A. G. Barr, and S. C. Wofsy. 2007. Comparison of carbon dioxide fluxes over three boreal black spruce forests in Canada. Global Change Biology 13:89–107.

Blackard, J. A., M. V. Finco, E. H. Helmer, G. R. Holden, M. L. Hoppus, D. M. Jacobs, A. J. Lister, G. G. Moisen, M. D. Nelson, R. Riemann, B. Ruefenacht, D. Salajanu, D. L. Weyermann, K. C. Winterberger, T. J. Brandeis, R. L. Czaplewski, R. E. McRoberts, P. L. Patterson, and R. P. Tymcio. 2008. Mapping U.S. forest biomass using nationwide forest inventory data and moderate resolution information. Remote Sensing of the Environment 112:1658–1677.

Bondeau, A., D. Kicklighter, and A. Kaduk. and Participants Potsdam NPP Model Intercomparison. 1999. Comparing global models of terrestrial net primary productivity (NPP): importance of vegetation structure on seasonal NPP estimates. Global Change Biology 5:35–45.

Bond-Lamberty, B., C. Wang, and S. T. Gower. 2004. Net primary production and net ecosystem production of a boreal black spruce wildfire chronosequence. Global Change Biology 10:473–487.

Brogaard, S., M. Runnstrom, and J. W. Seaquist. 2005. Primary production of Inner Mongolia, China, between 1982 and 1999 estimated by a satellite data-driven light use efficiency model. Global and Planetary Change 45:313–332.

Brown, S. L., and P. E. Schroeder. 1999. Spatial patterns of aboveground production and mortality of woody biomass for eastern U.S. forests. Ecological Applications 9:968–980.

Brown, S. L., P. Schroeder, and J. S. Kern. 1999. Spatial distribution of biomass in forests of the eastern USA. Forest Ecology and Management 123:81–90.

Cairns, M. A., S. Brown, E. H. Helmer, and G. A. Baumgardner. 1997. Root biomass allocation in the world's upland forests. Oecologia 111:1–11.

Cao, M. K., S. D. Prince, J. Small, and S. J. Goetz. 2004. Remotely sensed interannual variations and trends in terrestrial net primary productivity 1981-2000. Ecosystems 7:233–242.

Chertov, O., J. S. Bhatti, A. Komarov, A. Mikhailov, and S. Bykhovets. 2009. Influence of climate change, fire and harvest on the carbon dynamics of black spruce in Central Canada. Forest Ecology and Management 257:941–950.

Cleveland, W. S. 1979. Robust locally weighted regression and smoothing scatterplots. Journal of the American Statistical Association 74:829–836.

Cramer, W., A. Bondeau, I. C. Prentice, R. A. Betts, V. Brovkin, P. M. Cox, V. Fisher, J. Foley, A. D. Friend, C. Kucharik, M. R. Lomas, N. Ramankutty, S. Sitch, B. Smith, A. White, and C. Young-Molling. 2001. Global response of terrestrial ecosystem structure and function to CO_2 and climate change: results from six dynamic global vegetation models. Global Change Biology 7:357–373.

Curtis, P. S., P. J. Hanson, P. Bolstad, C. Barford, J. C. Randolph, H. P. Schmid, and K. B. Wilson. 2002. Biometric and eddy-covariance based estimates of annual carbon storage in five eastern North American deciduous forests. Agricultural and Forest Meteorology 113:3–19.

Daly, C., G. H. Taylor, W. P. Gibson, T. W. Parzybok, G. L. Johnson, and P. A. Pasteris. 2000. High-quality spatial climate data sets for the United States and beyond. Transactions of the American Society of Agricultural Engineers 43:1957–1962.

Dawson, T. P., P. R. J. North, S. E. Plummer, and P. J. Curran. 2003. Forest ecosystem chlorophyll content: implications for remotely sensed estimates of net primary productivity. International Journal of Remote Sensing 24:611–617.

FAO. 1991. The digitized soil map of the world (release 1.0). Vol. 67/1. Food and Agriculture Organization of the United Nations, Rome, Italy.

Farr, T. G., and M. Kobrick. 2000. Shuttle Radar Topography Mission produces a wealth of data. American Geophysical Union Eos 81:583–585.

Gerten, D., S. Schaphoff, U. Haberlandt, W. Lucht, and S. Sitch. 2004. Terrestrial vegetation and water balance—hydrological evaluation of a dynamic global vegetation model. Journal of Hydrology 286:249–270.

Gower, S. T., O. Krankina, R. J. Olson, M. Apps, S. Linder, and C. Wang. 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. Ecological Applications 11:1395–1411.

Haxeltine, A., and I. C. Prentice. 1996. A general model

for the light-use efficiency of primary production. Functional Ecology 10:551–561.

Hicke, J. A., G. P. Asner, J. T. Randerson, C. Tucker, S. Los, R. Birdsey, J. C. Jenkins, C. Field, and E. Holland. 2002. Satellite-derived increases in net primary productivity across North America, 1982–1998. Geophysical Research Letter 29:1427. [doi: doi: 10.1029.2001GL013578].

Hickler, T., B. Smith, M. T. Sykes, M. B. Davis, S. Sugita, and K. Walker. 2004. Using a generalized vegetation model to simulate vegetation dynamics in northeastern USA. Ecology 85:519–530.

Hickler, T., K. Vohland, J. Feehan, P. A. Miller, B. Smith, L. Costa, T. Giesecke, S. Fronzek, T. R. Carter, W. Cramer, I. Kühn, and M. T. Sykes. In press. Projecting tree species-based climate-driven changes in European potential natural vegetation with a generalized dynamic vegetation model. Global Ecology and Biogeography.

Houghton, R. A. 2005. Aboveground forest biomass and the global carbon balance. Global Change Biology 11:945–958.

Huntingford, C., and J. L. Monteith. 1998. The behaviour of a mixed-layer model of the convective boundary layer coupled to a big leaf model of surface energy partitioning. Boundary-Layer Meterorology 88:87–101.

Jenkins, J. C., R. A. Birdsey, and Y. Pan. 2001. Biomass and NPP estimation for the mid-Atlantic region (USA) using plot-level forest inventory data. Ecological Applications 11:1174–1193.

Kauppi, P. E., K. Mielikainen, and K. Kuusela. 1992. Biomass and carbon budget of European forests, 1971 to 1990. Science 256:70–74.

Koca, D., B. Smith, and M. T. Sykes. 2006. Modelling regional climate change effects on potential natural ecosystems in Sweden. Climatic Change 78:381–406.

Linderholm, H. W. 2006. Growing season changes in the last century. Agriculture Forest Meteorology 137:1–14.

Liu, J., S. Liu, and R. L. Thomas. 2006. Temporal evolution of carbon budgets of the Appalachian forests in the US from 1972 to 2000. Forest Ecology and Management 222:191–201.

Markon, C. J., and K. M. Peterson. 2002. The utility of estimating net primary productivity over Alaska using baseline AVHRR data. International Journal of Remote Sensing 23:4571–4596.

Mickler, R. A., T. S. Earnhardt, and J. A. Moore. 2002. Regional estimation of current and future forest biomass. Environmental Pollution 116:S7–S16.

Mitchell, T. D., T. R. Carter, P. D. Jones, and M. Hulme. 2004. A comprehensive set of high-resolution grids of monthly climate for Europe and the globe: the observed record (1901–2000) and 16 scenarios (2001–2100). Tyndall Working Paper 55. Tyndall Centre, UEA, Norwich, UK.

Moorcroft, P. R. 2003. Recent advances in ecosystem-atmosphere interactions: an ecological perspective. Proceedings of the Royal Society of London, Series B 270:1215–1227.

Morales, P., M. T. Sykes, I. C. Prentice, P. Smith, B. Smith, H. Bugmann, B. Zierl, P. Friedlingstein, N. Viovy, S. Sabaté, A. Sánchez, E. Pla, C. A. Gracia, S. Sitch, A. Arneth, and J. Ogee. 2005. Comparing and evaluating process-based ecosystem model predictions of carbon and water fluxes in major European forest biomes. Global Change Biology 11:2211–2233.

Morales, P., T. Hickler, D. P. Rowell, B. Smith, and M. T. Sykes. 2007. Changes in European ecosystem productivity and carbon balance driven by regional climate model output. Global Change Biology 13:108–122.

Myneni, R. B., C. D. Keeling, C. J. Tucker, G. Asrar, and R. R. Nemani. 1997. Increased plant growth in the northern high latitudes from 1981 to 1991. Nature 386:698–702.

Nemani, R. R., C. D. Keeling, H. Hashimoto, W. M. Jolly, S. C. Piper, C. J. Tucker, R. B. Myneni, and S. W. Running. 2003. Climate-driven increases in global terrestrial net primary production from 1982 to 1999. Science 300:1560–1563.

Olson, J. S., J. A. Watts, and L. J. Allison. 1983. Carbon in live vegetation of major world ecosystems. Report ORNL-258620. Oak Ridge National Laboratory, Oak Ridge, Tennessee, USA.

Pan, Y., R. Birdsey, J. Hom, K. McCullough, and K. Clark. 2006. Improved estimates of net primary productivity from MODIS satellite data at regional and local scales. Ecological Applications 16:125–132.

Parshall, T., D. R. Foster, E. Faison, D. Macdonald, and B. C. S. Hansen. 2003. Long-term history of vegetation and fire in pitch pine-oak forests on Cape Cod, Massachusetts. Ecology 84:736–748.

Piao, S., P. Ciais, P. Friedlingstein, P. Peylin, M. Reichstein, S. Luyssaert, H. Margolis, J. Fang, A. Barr, A. Chen, A. Grelle, D. Y. Hollinger, T. Laurila, A. Lindroth, A. D. Richardson, and T. Vesala. 2008. Net carbon dioxide losses of northern ecosystems in response to autumn warming. Nature 451:49–53.

Potter, C. S., E. A. Davidson, S. A. Klooster, D. C. Nepstad, G. H. De Negreiros, and V. Brooks. 1998. Regional application of an ecosystem production model for studies of biogeochemistry in Brazilian Amazonia. Global Change Biology 4:315–333.

Pregitzer, K. S., and E. S. Euskirchen. 2004. Carbon cycling and storage in world forests: biome patterns related to forest age. Global Change Biology 10:2052–2077.

Prentice, I. C., M. Heimann, and S. Sitch. 2000. The carbon balance of the terrestrial biosphere: Ecosys-

tem models and atmospheric observations. Ecological Applications 10:1553–1573.

Purves, D., and S. Pacala. 2008. Predictive models of forest dynamics. Science 320:1452–1453.

Rosen, P. A., S. Hensley, I. R. Joughin, F. K. Li, S. N. Madsen, E. Rodriguez, and R. M. Goldstein. 2000. Synthetic aperture radar interferometry. Proceedings of the IEEE 88:33–382.

Running, S. W., and J. C. Coughlan. 1988. A general model of forest ecosystem processes for regional applications, I. Hydrologic balance, canopy gas exchange and primary production processes. Ecological Modelling 42:125–154.

Ryan, M. G. 1991. Effects of climate change on plant respiration. Ecological Applications 1:157–167.

Schlesinger, M. E., and S. Malyshev. 2001. Changes in near-surface temperature and sea level for the Post-SRES CO_2-stabilization scenarios. Integrated Assessment 2:95–110.

Schwartz, M. D., R. Ahas, and R. A. Aasa. 2006. Onset of spring starting earlier across the Northern Hemisphere. Global Change Biology 12:343–351.

Shuman, B., P. Newby, and Y. Huang. and W. III Thompson. 2004. Evidence for the close climatic control of New England vegetation history. Ecology 85:1297–1310.

Sitch, S., B. Smith, I. C. Prentice, A. Arneth, A. Bondeau, W. Cramer, J. O. Kaplan, S. Levis, W. Lucht, M. T. Sykes, K. Thonicke, and S. Venevsky. 2003. Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ Dynamic Global Vegetation Model. Global Change Biology 9:161–185.

Smith, B., I. C. Prentice, and M. T. Sykes. 2001. Representation of vegetation dynamics in the modeling of terrestrial ecosystems: comparing two contrasting approaches within European climate space. Global Ecology and Biogeography 10:621–637.

Smith, B., W. Knorr, J.-L. Widlowski, B. Pinty, and N. Gobron. 2008. Combining remote sensing data with process modelling to monitor boreal conifer forest carbon balances. Forest Ecology and Management 255:3985–3994.

Tang, G. 2008. A new metric for evaluating the correspondence of spatial patterns in vegetation models. Global Ecology and Biogeography 17:465–478.

Tang, G., and B. Beckage. 2010. Projecting the distribution of forests in New England in response to climate change. Diversity and Distributions 16:144–158.

USDA Forest Service. 2000. U.S. Forest Facts and Historical Trends. ⟨http://fia.fs.fed.us/library/briefings-summaries-overviews/docs/ForestFactsMetric.pdf⟩.

Withington, J. M., P. B. Reich, J. Oleksyn, and D. M. Eissenstat. 2006. Comparisons of structure and life span in roots and leaves among temperate trees. Ecological Monographs 76:381–397.

Wramneby, A., B. Smith, S. Zaehle, and M. T. Sykes. 2008. Parameter uncertainties in the modelling of vegetation dynamics—effects on tree community structure and ecosystem functioning in European forest biomes. Ecological Modelling 216:277–290.

Zhao, M., and S. W. Running. 2010. Drought-induced reduction in global terrestrial net primary production from 2000 through 2009. Science 329:940–943.

Zhao, M., F. A. Heinscha, R. R. Nemani, and S. W. Running. 2005. Improvements of the MODIS terrestrial gross and net primary production global data set. Remote Sensing of Environment 95:164–176.

Zheng, D., L. S. Heath, and M. J. Ducey. 2008. Spatial distribution of forest aboveground biomass estimated from remote sensing and forest inventory data in New England, USA. Journal of Applied Remote Sensing 2:1–17.