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Abstract The quantification of carbon fluxes between the terrestrial biosphere and the atmosphere is of scientific importance and also relevant to climate-policy making. Eddy covariance flux towers provide continuous measurements of ecosystem-level exchange of carbon dioxide spanning diurnal, synoptic, seasonal, and interannual time scales. However, these measurements only represent the fluxes at the scale of the tower footprint. Here we used remotely-sensed data from the Moderate Resolution Imaging Spectroradiometer (MODIS) to upscale gross primary productivity (GPP) data from eddy covariance flux towers to the continental scale. We first combined GPP and MODIS data for 42 AmeriFlux towers encompassing a wide range of ecosystem and climate types to develop a predictive GPP model using a regression tree approach. The predictive model was trained using observed GPP over the period 2000-2004, and was validated using observed GPP over the period 2005-2006 and leave-one-out cross-validation. Our model predicted GPP fairly well at the site level. We then used the model to estimate GPP for each 1 km × 1 km cell across the U.S. for each 8-day interval over the period from February 2000 to December 2006 using MODIS data. Our GPP estimates provide a spatially and temporally continuous measure of gross primary production for the U.S. that is highly constrained by eddy covariance flux data. Our study demonstrated that our empirical approach is effective for upscaling eddy flux GPP data to the continental scale and producing continuous GPP estimates across multiple biomes. With these estimates, we then examined the patterns, magnitude, and interannual variability of GPP. We estimated a gross carbon uptake between 6.91 and 7.33 Pg C yr⁻¹ for the conterminous U.S. Drought, fires, and hurricanes reduced annual GPP at regional scales and could have a significant impact on the U.S. net ecosystem carbon exchange. The sources of the interannual variability of U.S. GPP were dominated by these extreme climate events and disturbances.

1. Introduction

The quantification of ecosystem carbon fluxes for regions, continents, or the globe can improve our understanding of the feedbacks between the terrestrial biosphere and the atmosphere in the context of global change and facilitate climate policy decisions (Law et al. 2006). Gross primary productivity (GPP) is the amount of carbon fixed by vegetation through photosynthesis and a key component of ecosystem carbon fluxes and the carbon balance between the biosphere and the atmosphere (Mäkelä et al. 2008). The accurate estimation of GPP is essential for the quantification of net ecosystem carbon exchange (NEE) as the latter is often a small difference of two large carbon fluxes – GPP and ecosystem respiration (R_e). The estimation of GPP for regions, continents, or the globe, however, can only be made by using ecosystem models (e.g., Prince and Goward 1995) and/or remotely sensed data (e.g., Running et al. 2004).

Eddy covariance flux towers have been providing continuous measurements of ecosystem-level exchange of carbon, water, and energy spanning diurnal, synoptic, seasonal, and interannual time scales since the early 1990s (Wofsy et al. 1993; Baldocchi et al. 2001). At present, over 500 eddy covariance flux towers are operating on a long-term and continuous basis around the world (FLUXNET, <http://daac.ornl.gov/FLUXNET>). This global network encompasses a large range of climate and biome types (Baldocchi et al. 2001), and provides probably the best estimates of ecosystem-level carbon fluxes. The flux towers directly measure NEE that can be separated into two major components: GPP and R_e (Reichstein et al. 2005; Desai et al. 2008). However, these estimates only represent fluxes at the scale of the tower footprint with longitudinal dimensions ranging between a hundred meters and several kilometers depending on homogeneous vegetation and fetch (Schmid, 1994; Göckede et al.,

2008). To quantify the exchange of CO₂ between the terrestrial biosphere and the atmosphere, significant efforts are needed to scale up flux tower measurements from the stand scale to landscape, regional, continental, or global scales.

Satellite remote sensing is a potentially valuable tool for scaling-up efforts (Running et al. 1999; Turner et al. 2003; Xiao et al. 2008). Several studies have integrated flux data with remote sensing data to quantify GPP over large areas. Zhang et al. (2007) estimated GPP for the Northern Great Plains grasslands using satellite and flux tower data. Yang et al. (2007) linked satellite observations to flux tower GPP data for the estimation of GPP for two broad vegetation types in the U.S. using a machine learning approach. Despite these efforts, to our knowledge, no study has upscaled AmeriFlux GPP data to the continental scale to produce spatially-explicit estimates of GPP across multiple biomes and to examine the patterns, magnitude, and interannual variability of GPP over the conterminous U.S.

Here we used a regression tree approach and remotely-sensed data from the Moderate Resolution Imaging Spectroradiometer (MODIS) to upscale flux tower GPP to the continental scale and produced wall-to-wall GPP estimates for multiple biomes across the conterminous U.S. First, we developed a predictive GPP model based on site-specific MODIS and flux tower GPP data, and validated the model using eddy flux data in both temporal and spatial domains. Second, we applied the model to estimate GPP for each 1 km × 1 km cell across the conterminous U.S. for each 8-day interval over the period 2000-2006 using wall-to-wall MODIS data. Third, we examined the patterns, magnitude, and interannual variability of GPP across the conterminous U.S.

2. Data and Methods

2.1. Regression tree approach

We used a modified regression tree approach implemented in the commercial software, Cubist, to upscale flux tower GPP to the continental scale. Regression tree algorithms typically predict class membership by recursively partitioning a dataset into more homogeneous subsets. The partitioning process splits each parent node into two child nodes, and each child node is treated as a potential parent node. Regression tree models can account for a nonlinear relationship between predictive and target variables and allow both continuous and discrete variables. Previous studies showed that regression tree methods are not only more effective than simple techniques including multivariate linear regression, but also easier to understand than neural networks (e.g., Huang and Townshend 2003).

Cubist constructs an unconventional type of regression tree, in which the terminal nodes or leaves are linear regression models instead of discrete values (Minasny and McBratney 2008). Cubist produces rule-based models containing one or more rules, each of which is a set of conditions associated with a multivariate linear submodel. Cubist is a powerful tool for generating rule-based predictive models. A Cubist model resembles a piecewise linear model, except that the rules can overlap with one another (RuleQuest 2008). Details on regression tree approaches and Cubist were described in Yang et al. (2003), Wylie et al. (2007), and Xiao et al. (2008). In our previous study, we used Cubist to develop a predictive NEE model and upscaled NEE estimates to the continental scale for the conterminous U.S. (Xiao et al. 2008). In this study, we used Cubist to construct a predictive GPP model based on MODIS and AmeriFlux GPP data. Cubist uses three statistical measures to evaluate the quality of the constructed predictive model, including mean absolute error (MAE), relative error (RE), and product-moment correlation coefficient (Yang et al. 2003; Xiao et al. 2008). MAE is calculated as:

$$MAE = \frac{1}{N} \sum_{i=1}^N |y_i - \hat{y}_i| \quad (1)$$

where N is the number of samples used to establish the predictive model, and y_i and $\hat{y}_i$ are the actual and predicted values of the response variable, respectively. RE is calculated as:

$$RE = \frac{MAE_T}{MAE_\mu} \quad (2)$$

where MAE_T is the MAE of the constructed model, and MAE_μ is the MAE that would result from always predicting the mean value. All three statistical measures were used to evaluate the performance of the constructed model.

2.2. Explanatory variables

GPP is influenced by a variety of physical, physiological, atmospheric, hydrological, and edaphic variables. At the leaf level, GPP is influenced by several factors, including incoming solar radiation, air temperature, vapor pressure deficit, soil moisture, and nitrogen availability (Ruimy et al. 1995; Clark et al. 1999, 2004). At the canopy or ecosystem level, GPP is also influenced by leaf area index (LAI) (Ruimy et al. 1995) and canopy phenology (Richardson et al. 2008a). At the stand or regional level, GPP is significantly affected by disturbances such as fire and harvest (Law et al. 2004). Many of these factors can be effectively assessed by satellite remote sensing. Surface reflectance depends on vegetation type, biophysical properties (e.g., biomass, leaf area, and stand age), soil background, soil moisture conditions, and sun-object-sensor geometry (Ranson et al. 1985; Penuelas et al. 1993; Schmidt and Skidmore 2003). Vegetation indices including normalized difference vegetating index (NDVI) and enhanced vegetation index (EVI) are closely correlated to the fraction of photosynthetically active radiation (fPAR; Asrar et al. 1984), and are also related to vegetation biomass and fractional vegetation cover (e.g., Tucker et al. 1985; Persson et al. 1993; Myneni

et al. 2001; Chen et al. 2004). Compared to NDVI, EVI is more responsive to canopy structural variations, such as LAI, canopy type, plant physiognomy, and canopy architecture (Gao et al. 2000). The normalized difference water index (NDWI; Gao 1996) was shown to be strongly correlated with leaf water content (Jackson et al. 2004) and soil moisture (Fensholt & Sandholt 2003) over time. LAI and fPAR characterize vegetation canopy functioning and energy absorption capacity (Myneni et al. 2002) and are key parameters in most ecosystem productivity and biogeochemical models (Sellers et al. 1997). We therefore selected surface reflectance, EVI, LST, LAI, fPAR, and NDWI as explanatory variables. All of these variables were derived from MODIS data, which also avoided the complications and difficulties to merge disparate data sources (Xiao et al. 2008).

2.3. AmeriFlux data

We obtained the following three types of data: GPP from eddy covariance flux towers, explanatory variables derived from MODIS, and a land cover map. The AmeriFlux network coordinates regional analysis of observations from eddy covariance flux towers across North America, Central America, and South America (Law 2006). We obtained the Level 4 data product for 42 AmeriFlux sites over the period 2000-2006 from the AmeriFlux website (<http://public.ornl.gov/ameriflux>) (Table 1). This product includes NEE data from most of the active flux sites in the network. These sites are distributed across the conterminous U.S. and cover a range of vegetation types: forests, shrublands, savannas, grasslands, and croplands. Moreover, the distribution of these sites in the mean annual climate space indicates that the sites we selected are fairly representative of typical U.S. climate types (Xiao et al. 2008). In addition, some of the forested sites (e.g., Austin Cary, FL; Metolius new young pine, OR; Metolius intermediate aged ponderosa pine, OR; Wisconsin intermediate hardwood, WI) are at

different stages since stand replacing disturbance, which are located in disturbance clusters of sites. In addition, some of the sites have received treatment, including the Howland Forest West Tower (ME; nitrogen fertilizer) and the Mead cropland sites (NE; irrigation versus rainfed, continuous maize versus maize/soybean rotation). We therefore believe that these sites are fairly representative of typical U.S. ecosystem and climate types.

The Level 4 product consists of two types of GPP data, including standardized (GPP_{st}) and original (GPP_{or}) GPP. GPP was calculated from NEE and ecosystem respiration (R_e):

$$\text{GPP}_{\text{st}} = R_e - \text{NEE}_{\text{st}} \quad (3)$$

and

$$\text{GPP}_{\text{or}} = R_e - \text{NEE}_{\text{or}} \quad (4)$$

where NEE_{st} and NEE_{or} are standardized and original NEE, respectively. NEE_{st} was calculated using the storage obtained from the discrete approach (single point on the top of the tower) with the same approach for all the sites, whereas NEE_{or} was calculated using the storage sent by the principal investigators that can be obtained with the discrete approach or using a vertical CO₂ profile system. Both NEE_{st} and NEE_{or} were gap-filled using the Marginal Distribution Sampling (MDS) method (Reichstein et al. 2005) and the Artificial Neural Network (ANN) method (Papale and Valentini 2003). The ANN method was generally, if only slightly, superior to the MDS method (Moffat et al. 2007). A number of methods are available for estimating GPP. Although Stoy et al. (2006) showed that the non-rectangular hyperbolic method (Gilmanov et al. 2003) produce estimates more consistent with independent data, we chose to use a method that relies on gap-filled nighttime data because it is more frequently used and less computationally demanding. We used GPP calculated from NEE data

that was gap-filled using the ANN method. For each site, if the percentage of the remaining missing values for GPP_{st} was lower than that for GPP_{or}, we selected GPP_{or}; otherwise, we used GPP_{st}. GPP_{st} was the first choice so that the processing procedure for GPP was the same for as many sites as possible. We used 8-day average GPP data ($\text{g C m}^{-2} \text{ day}^{-1}$) to match the compositing intervals of MODIS data.

2.4. MODIS data

We used the following four MODIS data products (Collection 4), including surface reflectance (MOD09A1; Vermote and Vermeulen 1999), daytime and nighttime LST (MOD11A2; Wan et al. 2002), EVI (MOD13A1; Huete et al. 2002), and LAI/fPAR (MOD15A2; Myneni et al., 2002). Surface reflectance and EVI are at a spatial resolution of 500m, while LST, LAI, and fPAR are at spatial resolution of 1 km. Surface reflectance, LST, LAI, and fPAR are at a temporal resolution of 8 days, while EVI is at a temporal resolution of 16 days. Sims et al. (2005) showed that the midday values of gross CO_2 exchange during satellite overpasses can be used to estimate 8-day mean gross CO_2 exchange, bridging the connection between continuous measurements of flux tower data and 8-day MODIS data. We used the 16-day EVI product instead of EVI calculated from 8-day surface reflectance despite the lower temporal resolution of the 16-day EVI product. Each 16-day EVI composite was composited from 16 daily observations (Huete et al. 2002). The VI algorithm applies a filter to the data based on quality, cloud, and viewing geometry, and only the higher quality, cloud-free, filtered data are retained for compositing; the maximum value composite (MVC) method employed selects the observation with the highest VI value to represent the compositing period (16 days) (Huete et al. 2002). MVC minimizes the contamination of clouds and aerosols and the effects of sensor view angles on VI (Hoblen 1986). For the 8-day surface reflectance

product, each pixel contains the best possible daily observation during an 8-day period as selected on the basis of high observation coverage, low view angle, the absence of clouds or cloud show, and aerosol loading (Vermote and Kotchenova, 2008), and the EVI calculated from the 8-day surface reflectance is less representative of the compositing period than the MODIS EVI product.

For each AmeriFlux site, we obtained MODIS ASCII (American Standard Code for Information Interchange) subsets (Collection 4) consisting of $7\text{ km} \times 7\text{ km}$ regions centered on the flux tower, including surface reflectance, daytime and nighttime LST, EVI, LAI, and fPAR over the period 2000-2006 from the Oak Ridge National Laboratory's Distributed Active Archive Center (ORNL DAAC 2006). We extracted average values for the central $3\text{ km} \times 3\text{ km}$ area within the $7\text{ km} \times 7\text{ km}$ cutouts to better represent the flux tower footprint (Schmid 2002; Rahman et al. 2005; Xiao et al. 2008). For each variable, we determined the quality of the value of each pixel within the area using the quality assurance (QA) flags included in the product. At each time step, we averaged the values of each variable using the pixels with good quality within the area to represent the values at the flux site. If none of the values within the $3\text{ km} \times 3\text{ km}$ area were of good quality, we treated the period as missing. Each 16-day EVI value was used for the two 8-day intervals corresponding with the compositing interval of other MODIS data products. NDWI was calculated from band 2 and band 6 of the surface reflectance product.

To estimate GPP at the continental scale, we obtained wall-to-wall MODIS data including surface reflectance, daytime and nighttime LST, LAI, and EVI over the period from February 2000 to December 2006 from the Earth Observing System (EOS) Data Gateway. For each variable, we determined the quality of the value of each pixel using the QA flags and

replaced the bad-quality value using a linear interpolation approach (Zhao et al. 2005). The NDWI was calculated from band 2 (near-infrared, 841-876 nm) and band 6 (shortwave infrared, 1628-1652 nm) of the surface reflectance product (MOD09A1). Similarly, each 16-day EVI composite was used for two 8-day intervals corresponding to the compositing interval of other MODIS products. NDWI was calculated from band 2 and band 6 of the surface reflectance product for each 8-day interval.

We also used the MODIS 8-day GPP product (MOD17A2; Running et al. 2004) to evaluate the performance of our model at both the site level. The MODIS GPP product is at a spatial resolution of 1 km, and a temporal resolution of 8 days. We obtained MODIS ASCII subsets (Collection 4) for the MODIS 8-day GPP product over the period 2005-2006 from the Oak Ridge National Laboratory's Distributed Active Archive Center (ORNL DAAC 2006). We also obtained the MODIS annual GPP product (MOD17A3; Running et al. 2004) for 2005 from the Numerical Terradynamic Simulation Group, University of Montana (<http://www.ntsg.umt.edu>) to evaluate the performance of our model at the continental scale.

2.5. Land cover

To construct a predictive GPP model, we obtained the land cover type for each AmeriFlux site based on the site descriptions (Table 1) and categorized each site into a class of the UMD (University of Maryland) land-cover classification system. Although the 42 AmeriFlux sites used in this study cover a variety of vegetation classes of this classification system, some classes (e.g., deciduous needleleaf forests, open shrublands) were not covered by any site. We therefore reclassified all vegetation classes of the UMD classification system to seven broader classes, following Xiao et al. (2008). Specifically, evergreen needleleaf forests and evergreen broadleaf forests were merged to evergreen forests, deciduous needleleaf forests

and deciduous broadleaf forests to deciduous forests, closed shrublands and open shrublands to shrublands, and woody savannas and savannas to savannas.

To estimate GPP for each $1 \text{ km} \times 1 \text{ km}$ pixel across the conterminous U.S., we obtained the land-cover type for each pixel from the MODIS land-over map with the UMD classification system (Friedl et al. 2002). Similarly, we reclassified the vegetation classes of the MODIS land-cover map to the seven broader classes. We then used the reclassified land cover map to specify the land cover of each $1 \text{ km} \times 1 \text{ km}$ cell across the conterminous U.S.

2.6. Model development

We developed a predictive GPP model using Cubist based on the site-specific MODIS and AmeriFlux GPP data. Our explanatory variables included land cover, surface reflectance (bands 1-7), daytime and nighttime LST, EVI, NDWI, fPAR, and LAI, and our response variable was GPP ($\text{g C m}^{-2} \text{ day}^{-1}$). Land cover was included as a categorical variable in the model. We split the site-level data set of AmeriFlux and MODIS data into a training set (2000-2004) and a test set (2005-2006). If a site only had GPP observations for the period 2000-2004, the site was only included in the training set; if a site only had GPP observations for the period 2005-2006, the site was only included in the test set; otherwise, the site was included in both training and test sets. The training and test sets included 40 and 34 AmeriFlux sites, respectively. We had a total of 4529 and 2240 data samples for the training and test sets, respectively. In addition to the full model that includes all of the 14 independent variables, we also developed a series of models by dropping one or more variables at a time using Cubist. To select the best model, we evaluated the performance of each model based on MAE, RE, and correlation coefficient. We chose the model with the minimal MAE and RE and maximum correlation coefficient as the best model. We also evaluated the model performance using the

Root Mean Squared Error (RMSE), scatterplots of predicted GPP versus observed GPP, and seasonal variations between the predicted and observed GPP.

We also evaluated the performance of our model in the spatial domain using leave-one-out cross-validation. In this approach, the data from a single site was used for validation, and the data from the remaining sites were used for training. The training and validation data were from different sites and were therefore independent from each other as these sites are generally hundreds of kilometers away from each other and the spatial autocorrelation between these sites was negligible. The leave-one-out cross-validation was conducted for each site, separately.

2.7. Continental-scale estimation of GPP

As mentioned earlier, the AmeriFlux sites used in this study are fairly representative of typical U.S. ecosystem and climate types. We believe that the predictive GPP model constructed from the 42 sites can be extrapolated to the conterminous U.S. We used the model to estimate GPP for each 1 km × 1 km cell across the conterminous U.S. for each 8-day interval over the period 2000-2006 using wall-to-wall MODIS data. GPP was not estimated for non-vegetated cells (e.g., urban, barren), and water bodies. We compared our estimate with the MODIS GPP product (MOD17A3; Running et al. 2004). With our 8-day GPP estimates, we examined the patterns, magnitude, and interannual variability of GPP.

3. Results and Discussion

3.1. Model development

3.1.1 Predictive GPP model

We chose the model containing five explanatory variables – land cover, EVI, daytime LST, LAI, and NDWI as the best model to predict GPP at the continental scale (RE = 0.38,

344 MAE = 1.22 g C m⁻² day⁻¹, R² = 0.74). The performance of the model was comparable to that
 345 of the full model (RE = 0.37, MAE = 1.19 g C m⁻² day⁻¹, R² = 0.74). Having only five
 346 explanatory variables could substantially reduce the computational complexity for continental-
 347 scale predictions compared to the full model. The model consisted of five committee models,
 348 each of which was made of a number of rule-based submodels. For instance, the first
 349 committee model was made of the following 23 rule-based submodels:

350 Rule 1: if land cover in {Deciduous forests, Mixed forests}, EVI ≤ 0.37, and LAI ≤
 351 2.64, then

$$352 \quad \text{GPP} = 0.28 + 0.012 \text{LST}_{\text{day}}$$

353 Rule 2: if LST_{day} ≤ 3.27, EVI > 0.22, then

$$354 \quad \text{GPP} = -0.64 + 4.8\text{EVI} + 0.6\text{NDWI} + 0.06\text{LAI}$$

355 Rule 3: if land cover in {Evergreen forests, Shrublands, Savannas, Grasslands,
 356 Croplands}, EVI ≤ 0.22, LAI ≤ 2.64, then

$$357 \quad \text{GPP} = 0.15 + 1.4\text{EVI} + 0.01 \text{LST}_{\text{day}}$$

358 Rule 4: if land cover in {Deciduous forests, Mixed forests, Savannas, Croplands},
 359 LST_{day} > 3.26, EVI ≤ 0.37, LAI ≤ 1.78, then

$$360 \quad \text{GPP} = -1.10 + 0.75\text{LAI} + 4.6\text{EVI}$$

361 ...

362 Rule 22: if NDWI ≤ -0.28, LST_{day} > 17.65, EVI > 0.58, then

$$363 \quad \text{GPP} = 10.49 + 1.9\text{EVI} + 0.02\text{LST}_{\text{day}} - 0.7\text{NDWI}$$

364 Rule 23: if land cover = Croplands, LST_{day} > 29.92, EVI > 0.37, then

$$365 \quad \text{GPP} = -24.85 + 5.47\text{LAI} + 58.9\text{EVI} + 0.124\text{LST}_{\text{day}} - 0.5\text{NDWI}$$

where LST_{day} is the daytime LST. As mentioned earlier, the rules of the model could overlap with one another. For instance, rule 1 overlapped with rule 4 as land cover could be deciduous forests in both cases; rules 22 and 23 overlapped with each other as EVI could be greater than 0.58 in both cases.

3.1.2. Model evaluation

The analysis of model residuals indicated that the residuals were not randomly distributed. Low GPP values were generally associated with low prediction errors, whereas high GPP values were associated with high prediction errors. The uncertainties of carbon flux measurements are directly proportional to the magnitudes of the fluxes (Richardson et al. 2008b). The residuals also exhibited a systematic component. For example, large GPP tended to have consistently negative residuals. The residuals also had a random component that arose partially from errors/uncertainties in the measured fluxes as well as MODIS data. Random errors in AmeriFlux GPP data are significant (Hagen et al. 2006) and these errors may ultimately limit the agreement between observed and predicted GPP values. In addition, the explanatory variables included in the model could not completely explain the variance of GPP. For example, the independent variables used in the model could not account for nitrogen availability, and may affect the accuracy of the model.

We compared our GPP estimates with observed GPP for each AmeriFlux site over the period 2005-2006 (Fig. 2). Our estimates captured most features of observed GPP including seasonality and year-to-year variations over the period 2005-2006. GPP was under- and over-predicted for some sites. The model could not capture exceptionally high GPP values for some sites, such as Audubon Research Ranch (AZ), Santa Rita Mesquite (AZ), and Fort Peck (MT). We averaged observed and predicted 8-day GPP for each site, and plotted mean predicted GPP

389 against observed GPP (Fig. 3). The model estimated GPP fairly well at the site level ($y = 0.95x$
390 $+ 0.21$, $R^2 = 0.84$, $p < 0.0001$; $RMSE = 0.77 \text{ g C m}^{-2} \text{ day}^{-1}$). Overall, the model slightly under-
391 and overestimated GPP for values greater or lower than $\sim 4 \text{ g C m}^{-2} \text{ day}^{-1}$, respectively. The
392 model performance also varied with site. Large underestimation occurred at some sites such as
393 the North Carolina Loblolly Pine (NCP, NC), Freeman Ranch Mesquite Juniper (FRM, TX),
394 and Walnut Gulch Kendall Grasslands (WGK, AZ), whereas large overestimation occurred at
395 some sites such as Lost Creek (LC, WI) and Mead Rainfed (MR, NE). The model predicted
396 GPP remarkably well at the biome level ($y = 0.99x - 0.13$, $R^2 = 0.91$, $p < 0.00001$; $RMSE =$
397 $0.42 \text{ g C m}^{-2} \text{ day}^{-1}$). The model slightly overestimated GPP for deciduous forests and croplands
398 and slightly underestimated GPP for all other biomes.

399 The disagreement between predicted and observed GPP values is likely due to the
400 following reasons. First, the MODIS and tower footprints do not match with each other and the
401 vegetation structure at the flux tower could be significantly different from that within the
402 MODIS footprint (Xiao et al. 2008). For example, the Tonzi Ranch site (CA) is dominated by
403 deciduous blue oaks (*Quercus douglasii*) and the understory and open grassland are mainly
404 cool-season C_3 annual species (Ma et al. 2007). The MODIS footprint consists of a larger
405 fraction of grassland than the tower footprint. Blue oaks and grasses have distinct phenologies
406 (Ma et al. 2007) and therefore had differential contributions to the carbon fluxes integrated
407 over the MODIS footprint over time (Xiao et al. 2008). Second, MODIS data is less sensitive
408 to changes in understory vegetation and damage to canopies that do not increase canopy gaps,
409 leading to overestimation of carbon assimilation rates. Third, the independent variables
410 included in the model could not account for other factors such as nitrogen availability (Clark et
411 al. 1999, 2004) and stand age (Ryan et al. 2004), all of which may influence GPP. Finally, we

estimated GPP for each 8-day interval, and therefore our estimates may not capture the variability of GPP within that period. The 8- or 16-day LST and EVI values do not always represent average environmental conditions and average fluxes over the 8- or 16-day period (Xiao et al. 2008), and the exclusion of days with high and low values could lead to underestimation and overestimation of GPP values, respectively. In addition, during drought or days with high vapor pressure deficits, the midday GPP may not be representative because of the skewed diurnal variation in GPP (Anthoni et al. 1999).

3.1.3. Model validation

We validated our model in both temporal and spatial domains. We first validated the model in the temporal domain using the test set over the period 2005-2006 (Fig. 1a). Our model estimated GPP fairly well ($R^2 = 0.74$, $p < 0.0001$; $RMSE = 1.99 \text{ g C m}^{-2} \text{ day}^{-1}$), although it slightly under- and overestimated GPP values greater and less than $3 \text{ g C m}^{-2} \text{ day}^{-1}$, respectively. By contrast, the MODIS GPP product estimated GPP for the AmeriFlux sites with a $RMSE$ of $2.43 \text{ g C m}^{-2} \text{ day}^{-1}$ ($y = 0.50x + 1.01$, $R^2 = 0.58$, $p < 0.0001$; Fig. 1b). The R^2 and $RMSE$ of our model were 28% higher and 18% lower than those of the MODIS GPP product, respectively.

We then validated the model in the spatial domain using leave-one-out cross validation. The cross-validation also showed that our model estimated GPP fairly well (Fig. 4). The model performance varied with site and biome type. Our model had a higher performance for forest ecosystems and croplands than shrublands, savannas, and grasslands. We averaged observed and predicted 8-day GPP for each site, and then plotted mean predicted GPP against observed GPP (Fig. 5). The cross-validation showed that our model estimated GPP fairly well at the site level ($y = 0.73x + 1.07$, $R^2 = 0.69$, $p < 0.0001$; $RMSE = 1.19 \text{ g C m}^{-2} \text{ day}^{-1}$) although the slope

and R^2 were lower and the RMSE was higher than those of the validation in the temporal domain, respectively. The cross-validation also showed that our model estimated GPP remarkably well at the biome level ($y = 0.86x + 0.48$, $R^2 = 0.91$, $p < 0.0001$; $RMSE = 0.33 \text{ g C m}^{-2} \text{ day}^{-1}$).

The validation of the model in both temporal and spatial domains showed that the performance of our model is encouraging, given the diversity in ecosystem types, age structures, fire and insect disturbances, and management practices. Our approach extensively used eddy covariance flux tower data involving typical U.S. ecosystem and climate types. Our study demonstrated that our empirical approach has great potential for upscaling flux tower GPP data to continental scales across a variety of biomes.

3.2. Gross Primary Production

3.2.1. Seasonal patterns

Our 8-day GPP estimates were highly constrained by eddy flux data, and provided a spatially and temporally continuous measure of GPP with high spatial and temporal resolution for the conterminous U.S., which made it possible to examine the patterns, magnitude, and interannual variability of GPP across the U.S. Our estimates showed that GPP exhibited large spatial variability and strong seasonal fluctuations (Fig. 6). The seasonal patterns of GPP and its spatial variability reflected the controlling effects of climate conditions. In the spring months, the Southeast and the Gulf Coast significantly assimilated carbon with GPP values reaching $\sim 100\text{-}250 \text{ g C m}^{-2} \text{ mo}^{-1}$ as the growing season started in early to mid-spring in these regions. The Pacific Coast is dominated by evergreen forests, and these ecosystems also assimilated carbon due to mild temperatures and moist conditions during the spring (Anthoni et al. 2002). The Mediterranean regions in California also assimilated carbon in the spring

because of a surplus of precipitation and relatively warm temperatures (Xu & Baldocchi 2004; Ma et al. 2007). By contrast, the Upper Great Lakes region and the northern Great Plains are dominated by croplands with most crops planted between April and June (Shroyer et al. 1996), whereas the New England region and the northern portion of the Upper Great Lakes region are dominated by temperate-boreal transitional forests. The relatively late greenup in these regions led to low GPP.

In the summer months, the eastern U.S., the Coastal Pacific Northwest, and some regions in California exhibited high GPP values ($\sim 250\text{--}450 \text{ g C m}^{-2} \text{ mo}^{-1}$) owing to favorable temperature and soil moisture conditions, while the vast majority of western landscapes, including the Great Basin, the Colorado Plateau, and the western Great Plains exhibited much lower GPP values due to sparse vegetation and precipitation deficits.

In the fall months (September–November), the GPP values of the Southeast and the Gulf Coast substantially decreased relative to those in the summer because vegetation began to senesce and days became shorter in these regions. The spatial patterns and magnitude of GPP were similar to those of the spring. The Upper Great Lakes region and the Great Plains had very low GPP values due to the harvesting of crops.

In the winter months (December–February), the majority of the U.S. had little or no photosynthesis as the canopies of most ecosystems were dormant. Some regions in the Pacific Coast, California, the Gulf Coast, and the Southeast slightly assimilated carbon because of the dominance of evergreen forests and mild temperatures (Waring & Franklin 1979; Clark et al. 1999; Anthoni et al. 2002; McGarvey et al. 2004). For example, Douglas-fir, a major species in the Pacific Northwest and California, is known to be highly plastic and able to photosynthesize in winter when temperatures are above the freezing point (Xiao et al. 2008).

Fig. 7 showed the trajectories of the spatially averaged and integrated 8-day GPP for each biome from February 2000 to December 2006. Deciduous forests and croplands had the largest intra-annual variability in spatial averaged GPP, followed by mixed forests; evergreen forests and savannas had intermediate intra-annual variability; grasslands and shrublands had the least variability (Fig. 7a). The temporal variability of spatially integrated GPP (or spatial total) also showed clear dependence on biome (Fig. 7). Collectively, the terrestrial ecosystems substantially assimilated carbon and had a peak spatial total of 50-55 Tg C day⁻¹. Taken separately, croplands had the highest intra-annual variability in spatially integrated GPP, with a peak spatial total of 25-30 Tg C day⁻¹, followed by deciduous forests; evergreen forests, mixed forests, savannas, and grasslands had intermediate intra-annual variability in spatially integrated GPP; shrublands had the least variability. Both spatially averaged and integrated GPP showed interannual variability for each biome.

3.2.2. Annual fluxes

We calculated annual GPP for each year over the period 2001-2006 from our 8-day GPP estimates, and then calculated the average annual GPP over the 6-year period (Fig. 8). Annual GPP varied considerably over space, and exhibited a large spatial gradient from the east to the west. The Gulf Coast, the Southeast, the coastal Pacific Northwest, and a part of the Pacific Southwest had high annual GPP (~1500-2000 g C m⁻² yr⁻¹); the Midwest and the Northeast had intermediate values (~1200-1500 g C m⁻² yr⁻¹), and the majority of the western half of the country including the Southwest, the western Great Plains, and the Rocky Mountain region had GPP values generally lower than 500 g C m⁻² yr⁻¹.

We estimated a total gross carbon uptake of 7.06 Pg C yr⁻¹ for the conterminous U.S. over the period 2001-2006. A quantitative breakdown of the 6-yr average annual GPP map by

regions (Table 2) showed that the North Central and South Central regions had the highest GPP, followed by the Southeast, the Rocky Mountain region, and the Northeast; the Pacific Northwest and the Pacific Southwest had the lowest GPP. The spatially averaged annual GPP of the U.S. was $\sim 1100 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Table 2). Regionally, the Southeast had the highest spatially averaged annual GPP, followed by the Northeast and the South Central regions; the North Central region, the Pacific Northwest, and the Pacific Southwest had intermediate values; the Rocky Mountain region had the lowest spatially averaged annual GPP.

A quantitative breakdown of the 6-yr average annual GPP by biomes (Table 3) showed spatially integrated annual GPP varied with biome. Croplands had the highest spatially integrated annual GPP; shrublands had lowest annual GPP; other biomes including evergreen forests, deciduous forests, mixed forests, savannas, and grasslands had intermediate annual GPP. Spatially averaged annual GPP also varied with biome (Table 3). Deciduous forests had the highest spatially averaged annual GPP, followed by evergreen forests, mixed forests, croplands, and savannas; grasslands had intermediate values; shrublands had the lowest values.

We compared our annual GPP estimate with annual GPP estimate from the MODIS GPP product (MOD17A3; Running et al. 2004) for 2005 (Fig. 9). Both estimates showed a large spatial gradient from the east to the west: the Southeast had the highest annual GPP; the Midwest had intermediate annual GPP, while the Rocky Mountain region had the lowest GPP. Both estimates showed that annual GPP is $\sim 300 \text{ g C m}^{-2} \text{ yr}^{-1}$ in the Rocky Mountain region. Annual GPP is also very similar in the New England region and the Upper Peninsula of Michigan. However, large discrepancies were observed between our estimate and the MODIS GPP product. Our estimate exhibited larger spatial variability than the estimate from the MODIS GPP product. Moreover, compared to our estimate, the MODIS GPP product

substantially underestimated GPP in some regions, particularly the Midwest and the coastal Pacific Northwest where ecosystems are highly productive. For example, our annual GPP for the croplands in the Midwest is $\sim 1200\text{--}1500 \text{ g C m}^{-2} \text{ yr}^{-1}$, while the MODIS annual GPP is only $\sim 700 \text{ g C m}^{-2} \text{ yr}^{-1}$. In many areas in the Southeast, our annual GPP estimate is $\sim 1500\text{--}2000 \text{ g C m}^{-2} \text{ yr}^{-1}$, while the MODIS annual GPP is only $\sim 1000\text{--}1500 \text{ g C m}^{-2} \text{ yr}^{-1}$.

The large discrepancies in annual GPP between our estimate and the MODIS GPP product can be attributed to the following reasons. First, the MODIS GPP product was developed using an algorithm optimized for global applications and meteorological fields with coarse resolution (1 by 1.25 degree) and large uncertainties (Zhao et al. 2006), and thereby likely contributed to the smaller spatial variability of MODIS GPP and affected the accuracy of the MODIS GPP estimates. Second, the maximum light use efficiency (ϵ_{max}) is an essential parameter of the LUE model used to develop the MODIS GPP product. The ϵ_{max} is only 0.68 g C MJ^{-1} for croplands in the MOD17 algorithm (Heinsch et al. 2003), which is likely too low for croplands and results in substantial underestimation of cropland GPP. Zhang et al. (2008) showed that MODIS annual GPP for an irrigated cropland in China was only about 20-30% of annual GPP derived from eddy covariance flux measurements, and attributed the substantial underestimation of cropland GPP to the underestimation of ϵ_{max} in the MOD17 algorithm. Third, our estimate was highly constrained eddy flux data, while some geographical regions and biomes are underrepresented by the AmeriFlux network, which could affect the accuracy of our estimates. For example, we merged savannas (tree cover 10-30%) and woody savannas (tree cover 30-60%) together in the development of the model because no sites representing typical savannas with tree cover below 30% were available in the model, which could lead to overestimation of GPP for areas that were classified as savannas (tree cover 10-30%).

Global annual GPP has been estimated to be 120 Pg C yr⁻¹ using ¹⁸O measurements of atmospheric CO₂ (Ciais et al. 1997) and 110 Pg C yr⁻¹ from 2001 to 2003 using the MODIS GPP product (Zhao et al. 2005). Our estimates suggested that the terrestrial ecosystems in the conterminous U.S. accounted for 5.9-6.5% of the global annual GPP, while its land area accounts for ~5.4% of the global land area. Our estimate of U.S. annual GPP was higher than other estimates. For example, the average annual GPP over the period 2001-2006 derived from MODIS GPP product (Running et al. 2004) was ~6.2 Pg C yr⁻¹. Our estimate was about 14% higher than the MODIS GPP estimate. Potter et al. (2007) estimated annual NPP between 2.67 and 2.79 Pg C yr⁻¹ over the period 2001-2004 using MODIS data and the NASA-CASA model. Our estimate was also higher than that estimated by Potter et al. (2007) assuming that NPP is about half of GPP (Lloyd & Farquhar 1996; Waring et al. 1998).

Our predictive model has advantages over empirical or process-based ecosystem models. Most ecosystem models are dependent on site-level parameterizations that are used as default parameters for a much broader spectrum of vegetation types and conditions, which may limit the accuracy of model simulations over large areas (e.g., Prince and Goward 1995; Running et al. 2004; Xiao et al. 2009). By contrast, our model was highly constrained by eddy flux data from a number of towers encompassing a range of ecosystem and climate types, and may lead to model parameters that are more representative of the full spectrum of vegetation and climate types and thereby more accurate estimates of carbon fluxes at regional scales. Moreover, our model consisted of rule-based, multivariate linear regression models, and is easier to understand and implement. Our model could substantially reduce computational complexity compared to many ecosystem models. On the other hand, however, our model also has disadvantages over empirical or process-based ecosystem models. Our model is an

empirical approach, and does not involve ecosystem processes such as photosynthesis and nitrogen cycling. Moreover, our model did not explicitly consider some factors influencing GPP such as nitrogen availability, stand age, and disturbance history that may be explicitly simulated in process-based ecosystem models (e.g., Aber et al. 1997). All these model differences contributed to the discrepancies in annual GPP estimates between our empirical approach and ecosystem models.

3.2.3. *Interannual variability*

The U.S. annual GPP varied between 6.91 and 7.33 Pg C yr⁻¹ over the period 2001-2006. The years 2002, 2004, and 2006 had lower GPP values relative to 2001, 2003, and 2005. Annual GPP exhibited positive and negative anomalies for each year, and the spatial patterns of these anomalies also varied from year to year (Fig. 10). The annual GPP anomalies were likely due to climate variability, disturbances, and management practices. Most notably, large negative GPP anomalies occurred in the Great Plains in 2002 and 2006. Moderate to severe drought affected over 50% of the country in both years, including the Southwest, the Great Plains, the Gulf Coast, and the coastal Southeast, particularly Texas and Oklahoma (U.S. Drought Monitor, <http://www.drought.unl.edu>). The annual precipitation of these two years was 467 and 458 mm for the U.S., respectively - lower than the 30-year mean annual precipitation (480 mm) taken over the PRISM climate database. Our GPP anomaly maps showed large negative GPP anomalies in many of the drought-affected regions. Notably, large negative GPP anomalies occurred in the Great Plains in 2002 and 2006. Our results further demonstrated severe drought could substantially affect ecosystem carbon fluxes (Xiao et al. 2009).

At landscape to regional scales, annual GPP also exhibited large anomalies. For example, our results showed large negative GPP anomalies in the region experienced the Biscuit fire in Oregon (Fig. 11). The 2002 Biscuit Fire was among the largest forest fires in modern U.S. history, encompassing $> 2000 \text{ km}^2$ primarily within the Rogue-Siskiyou National Forest (RSNF) in southwest Oregon (Campbell et al., 2007; Thompson et al. 2007). Large fires such as the Biscuit Fire damaged both overstory and/or understory vegetation, leading to a reduction in GPP and large negative GPP anomalies in the region in 2003, which may result in net carbon release into the atmosphere. Numerous wildfires occurred over the western half of the country due to dry weather and high winds, burning $1.5\text{-}4.0 \times 10^4 \text{ km}^2$ of forests from 2000 to 2006 (U.S. Fire Administration, <http://www.usfa.dhs.gov>). The drought along with wildfires likely led to the negative GPP anomalies in the western half of the U.S.

Our results also showed hurricanes could reduce GPP and lead to large negative GPP anomalies (Fig. 12). For example, Hurricane Katrina occurred in late August 2005 affected over $2 \times 10^4 \text{ km}^2$ of forest across Mississippi, Louisiana and Alabama, with damage ranging from downed trees, snapped trunks and broken limbs to stripped leaves (USDA Forest Service, <http://www.srs.fs.usda.gov>). Forest inventories indicated that the potential timber losses from Hurricane Katrina amounted to roughly $1.2 \times 10^8 \text{ m}^3$ (USDA Forest Service, <http://www.srs.fs.usda.gov>). Our results showed large negative GPP anomalies in 2006 in the Gulf Coast region severely affected by Hurricane Katrina (Fig. 12). The reduction in GPP and increased R_e resulting from increased litter could lead to substantial carbon release into the atmosphere (Chambers et al. 2007).

4. Conclusions

We used a regression tree approach and remotely-sensed data from MODIS to upscale AmeriFlux GPP data to the continental scale and to produce a GPP dataset with 8-day temporal resolution and 1 km spatial resolution for the conterminous U.S. over the period 2000-2006. Our results demonstrated that our empirical approach has great potential for upscale eddy flux GPP data to large areas across multiple biomes. Our GPP estimates provided a spatially and temporally continuous measure of gross primary production for the conterminous U.S. Our estimates also provided an alternative, independent dataset from the MODIS GPP product and simulations with biogeochemical models. Our GPP estimates were highly constrained by flux tower data from towers encompassing a large range of ecosystem and climate types as well as disturbance history. Our approach can be applied to the entire North America, other geographic regions including Europe, Southeast Asia, and South America, or to the global scale, and to produce continuous GPP estimates over continents or the globe. This approach can also be used to upscale other fluxes including evapotranspiration to large areas.

Our GPP estimates exhibited large spatial variability and strong seasonal variations, which reflected the controlling effects of climate conditions and vegetation distributions. We estimated a total gross carbon uptake of $7.06 \text{ Pg C yr}^{-1}$ for the conterminous U.S. over the period 2001-2006. Annual GPP varied substantially with geographical region and biome type. Our annual GPP estimate exhibited large spatial variability than the MODIS GPP product (MOD17A3; Running et al. 2004). Our results also showed that the U.S. annual GPP varied between 6.91 and $7.33 \text{ Pg C yr}^{-1}$ over the 6-year period. Extreme climate events (e.g., drought) and disturbances (e.g., fires and hurricanes) reduced annual GPP at regional scales and could have a significant impact on the U.S. net ecosystem carbon exchange. The interannual

variability of GPP was mainly caused by these extreme climate events (e.g., drought) and disturbances (e.g., fire, hurricane).

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973 Table 1. Site descriptions including name, latitude, longitude, vegetation type, years of data
 974 available, and references for each flux site.

Site	State	Lat	Lon	Vegetation type	Year	References
Audubon Research Ranch (ARR)	AZ	31.59	-110.51	Grasslands	2002-2006	
Santa Rita Mesquite (SRM)	AZ	31.82	-110.87	Savannas	2004-2006	Watts et al. 2007
Walnut Gulch (WKG)	AZ	31.74	-109.94	Grasslands	2004-2006	
Kendall Grasslands (KGO)	CA	33.37	-116.62	Shrublands	2004-2006	Lipson et al. 2005
Sky Oaks Old Stand (SOO)	CA	33.38	-116.62	Shrublands	2001-2006	Lipson et al. 2005
Sky Oaks Young stand (SOY)	CA	38.43	-120.97	Savannas	2001-2006	Ma et al. 2007
Tonzi Ranch (TR)	CA	38.41	-120.95	Grasslands	2001-2006	Xu and Baldocchi 2004
Vaira Ranch (VR)	CO	40.03	-105.55	Evergreen forests	2000-2003	Monson et al. 2002
Niwot Ridge Forest (NRF)	FL	28.61	-80.67	Shrublands	2000-2006	Dore et al. 2003
Kennedy Space Center -Scrub Oak (KSC)	FL	29.74	-82.22	Evergreen forests	2001-2005	Powell et al. 2008
Austin Cary - Slash Pine (AC)	IL	40.01	-88.29	Croplands	2001-2006	Hollinger et al. 2005
Bondville (Bon)	IL	41.86	-88.22	Croplands	2005-2006	
FNAL agricultural site (FAG)	IL	41.84	-88.24	Grasslands	2004-2006	
FNAL Prairie site (FPr)	IN	39.32	-86.41	Deciduous forests	2000-2005	Schmid et al. 2000
Morgan Monroe State Forest (MMS)	MA	42.54	-72.17	Deciduous forests	2000-2004	Urbanski et al. 2007
Harvard Forest EMS Tower (HFE)	MA	42.54	-72.18	Evergreen forests	2004	
Harvard Forest Hemlock Site (HFH)	MA	42.54	-72.18	Deciduous forests	2002-2005	
Little Prospect Hill (LPH)	ME	45.20	-68.74	Evergreen forests	2000-2004	Hollinger et al., 1999, 2004
Howland forest (HF)	ME	45.21	-68.75	Deciduous forests	2000-2004	Hollinger et al., 1999, 2004
Howland forest (west tower) (HFW)	MI	46.24	-89.35	Mixed forests	2002-2006	Desai et al., 2005
Sylvania Wilderness Area (SWA)	MI	45.56	-84.71	Mixed forests	2000-2003	Gough et al., 2008
Univ. of Mich. Biological Station (UMB)	MO	38.74	-92.20	Deciduous forests	2004-2006	Gu et al. 2006, 2007
Missouri Ozark (MO)	MS	34.25	-89.97	Grasslands	2002-2006	
Goodwin Creek (GC)	MT	48.31	-105.10	Grasslands	2000-2006	
Fort Peck (FPe)	NC	35.98	-79.09	Evergreen forests	2001-2005	Oren et al. 1998, 2006
Duke Forest loblolly pine (DFP)						

Duke	Forest	NC	35.97	-79.10	Deciduous forests	2003-2005	Pataki and Oren, 2003
hardwoods (DFH)							
North	Carolina	NC	35.80	-76.67	Evergreen forests	2005-2006	Noormets et al. submitted
loblolly pine (NCP)							
Mead	irrigated	NE	41.17	-96.48	Croplands	2001-2005	Verma et al. 2005
continuous maize site (MIC)							
Mead	irrigated	NE	41.16	-96.47	Croplands	2001-2005	Verma et al. 2005
rotation (MIR)							
Mead	rainfed (MR)	NE	41.18	-96.44	Croplands	2001-2005	Verma et al. 2005
Bartlett Experimental Forest (BEF)		NH	44.06	-71.29	Deciduous forests	2004-2005	Jenkins et al., 2007
Toledo	Oak	OH	41.55	-83.84	Savannas	2004-2005	Noormets et al. 2008b
Openings (TOO)							
ARM	Oklahoma	OK	36.61	-97.49	Croplands	2003-2006	
(ARM)							
Metolius intermediate aged ponderosa pine (MI)		OR	44.45	-121.56	Evergreen forests	2003-2005	Law et al. 2003; Irvine et al. 2007
Metolius new young pine (MN)		OR	44.32	-121.61	Evergreen forests	2004-2005	Law et al. 2003; Irvine et al. 2007
Brookings (Bro)		SD	44.35	-96.84	Grasslands	2004-2006	
Freeman Ranch		TX	29.95	-98.00	Savannas	2004-2006	
Mesquite Juniper (FRM)							
Wind River Crane Site (WRC)		WA	45.82	-121.95	Evergreen forests	2000-2004	Falk et al., 2008
Lost Creek (LC)		WI	46.08	-89.98	Deciduous forests	2000-2005	
Willow Creek (WC)		WI	45.81	-90.08	Deciduous forests	2000-2006	Cook et al., 2004
Wisconsin intermediate hardwood (WIH)		WI	46.73	-91.23	Deciduous forests	2003	Noormets et al. 2008a
Wisconsin mature red pine (MRP)		WI	46.74	-91.17	Evergreen forests	2002-2005	Noormets et al. 2007

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984 Table 2. Spatially averaged (spatial mean) and integrated (spatial total) annual GPP over the
 985 period 2001-2006 for each region: Northeast (NE), North Central (NC), Southeast (SE), South
 986 Central (SC), Rocky Mountain (RM), Pacific Northwest (PNW), and Pacific Southwest
 987 (PSW).

GPP	NE	NC	SE	SC	RM	PNW	PSW	US
Spatial Mean	1604.20	1212.55	2033.91	1457.97	438.20	1007.35	927.77	1103.92
(g C m ⁻² yr ⁻¹)								
Spatial Total	0.67	2.00	1.00	1.93	0.81	0.36	0.29	7.06
(Pg C yr ⁻¹)								

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1000 Table 3. Spatially averaged (spatial mean) and integrated (spatial total) annual GPP over the
 1001 period 2001-2006 for each vegetation type: evergreen forests (EF), deciduous forests (DF),
 1002 mixed forests (MF), shrublands (Sh), savannas (Sa), grasslands (Gr), and croplands (Cr).

GPP	EF	DF	MF	Sh	Sa	Gr	Cr	All
Spatial Mean	1431.26	1774.74	1447.31	303.78	1500.96	589.24	1500.38	1103.92
(g C m ⁻² yr ⁻¹)								
Spatial Total	0.85	0.83	0.67	0.33	0.63	0.83	2.92	7.06
(Pg C yr ⁻¹)								

Figure captions:

Fig. 1. Scatterplots of observed 8-day GPP versus predicted 8-day GPP. (a) Our estimate ($y = 0.85x + 0.37$, $R^2 = 0.74$, $p < 0.0001$). (b) MODIS GPP product (Running et al. 2004) ($y = 0.50x + 1.01$, $R^2 = 0.58$, $p < 0.0001$). For each plot, the solid line is the 1:1 line, and the dashed line is the regression line.

Fig. 2. Examples of time series plots of observed (open circles) and predicted (solid circles) 8-day GPP ($\text{g C m}^{-2} \text{ day}^{-1}$) for each AmeriFlux site over the period 2005-2006: (1) evergreen forests – AC (FL) and MRP (WI); (2) deciduous forests – DFH (NC); (3) mixed forests – SWA (MI); (4) shrublands – KSC (FL); (5) savannas – SRM (AZ), TR (CA), and VR (CA); (6) grasslands – ARR (AZ); (7) croplands – MIC (NE). For x-axis, the starting dates (month/day) of every two 8-day intervals are provided in parentheses under interval numbers. Dashed lines are used to separate 2005 from 2006. Site abbreviations are used here, and their full names are given in Table 1.

Fig. 3. Scatterplot of observed mean 8-day GPP versus predicted mean 8-day GPP across the AmeriFlux sites. Error bars are standard errors (defined as the standard deviation divided by the square root of the number of observations) of the observed and predicted 8-day mean GPP. The solid line indicates the 1:1 line, and the dashed line indicates the regression line ($y = 0.95 * x + 0.21$, $R^2 = 0.84$, $p < 0.0001$). Site abbreviations are used here, and their full names are given in Table 1.

Fig. 4. Examples of leave-one-out cross-validation scatterplots with observed 8-day GPP versus predicted 8-day GPP: (1) evergreen forests – HF ($y = 0.85x + 1.00$, $R^2 = 0.91$, $p < 0.0001$) and NRF ($y = 0.67x + 0.63$, $R^2 = 0.63$, $p < 0.0001$); (2) deciduous forests – HFE ($y = 0.97x + 0.24$, $R^2 = 0.87$, $p < 0.0001$) and WC ($y = 0.73x + 0.62$, $R^2 = 0.86$, $p < 0.0001$); (3)

mixed forests – SWA ($y = 0.89x + 0.03$, $R^2 = 0.89$, $p < 0.0001$) and UMB ($y = 0.92x + 0.66$, $R^2 = 0.93$, $p < 0.0001$); (4) shrublands – KSC ($y = 0.28x + 2.35$, $R^2 = 0.14$, $p < 0.0001$); (5) savannas – FRM ($y = 0.83x + 1.94$, $R^2 = 0.49$, $p < 0.001$); (6) grasslands – GC ($y = 0.76x + 2.03$, $R^2 = 0.55$, $p < 0.0001$); (7) croplands – MR ($y = 1.04x + 0.81$, $R^2 = 0.86$, $p < 0.0001$). The solid line indicates the 1:1 line, and the dashed line indicates the regression line. Site abbreviations are used here, and their full names are given in Table 1.

Fig. 5. Leave-one-out cross-validation scatterplot of observed mean 8-day GPP versus predicted mean 8-day GPP across the AmeriFlux sites. Error bars are standard errors of the observed and predicted 8-day GPP. The solid line indicates the 1:1 line, and the dashed line indicates the regression line ($y = 0.73 * x + 1.07$, $R^2 = 0.69$, $p < 0.0001$). Site abbreviations are used here, and their full names are given in Table 1.

Fig. 6. Monthly GPP ($\text{g C m}^{-2} \text{ mo}^{-1}$) for the conterminous U.S. from January through December in 2005.

Fig. 7. Spatially averaged and integrated 8-day GPP for each biome across the conterminous U.S. over the period 2001-2006. (a) Spatially averaged 8-day GPP ($\text{g C m}^{-2} \text{ day}^{-1}$). (b) Spatially integrated 8-day GPP (Tg C day^{-1}).

Fig. 8. Average annual GPP ($\text{g C m}^{-2} \text{ yr}^{-1}$) of the conterminous U.S. over the period 2001-2006. The gray lines indicate state boundaries. The black lines indicate boundaries of geographical regions: Northeast (NE), Southeast (SE), North Central (NC), South Central (SC), Rocky Mountain (RM), Pacific Northwest (PNW), and Pacific Southwest (PSW).

Fig. 9. Annual GPP ($\text{g C m}^{-2} \text{ yr}^{-1}$) for the conterminous U.S. for 2005. (a) Our estimate. (b) The MODIS GPP product (MOD17A3; Running et al. 2004).

Fig. 10. Annual GPP anomalies ($\text{g C m}^{-2} \text{ yr}^{-1}$) and annual precipitation anomalies (mm) for the conterminous U.S. for 2002 and 2006. The anomalies of annual GPP were relative to the 6-year period from 2001 to 2006, and the anomalies of annual precipitation were relative to the 30-year period from 1971 to 2000 taken from the PRISM climate database (PRISM Climate Group 2004).

Fig. 11. Impact of the Biscuit Fire ($> 2000 \text{ km}^2$) in Oregon on annual GPP in 2004. (a) Burned area. (b) The dots represent fire detections from Terra MODIS and Aqua MODIS MODIS (USDA Forest Service MODIS Active Fire Mapping Program, <http://activefiremaps.fs.fed.us>). (c) Burn severity based on the difference normalized burn ratio (dNBR; Lutes et al. 2004) from Landsat Thematic Mapper (TM) data acquired before and immediately after the fire. (d) Annual GPP in 2003 ($\text{g C m}^{-2} \text{ yr}^{-1}$).

Fig. 12. Impact of Hurricane Katrina on annual GPP in 2006. The units are $\text{g C m}^{-2} \text{ yr}^{-1}$. The white lines indicate the isotachs, including tropical storm, hurricane category 1, and hurricane category 2.

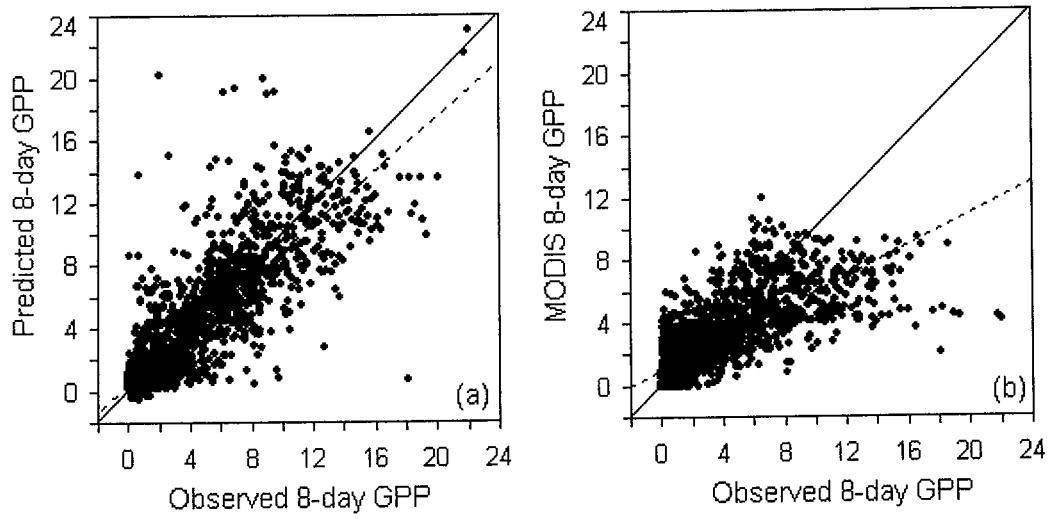


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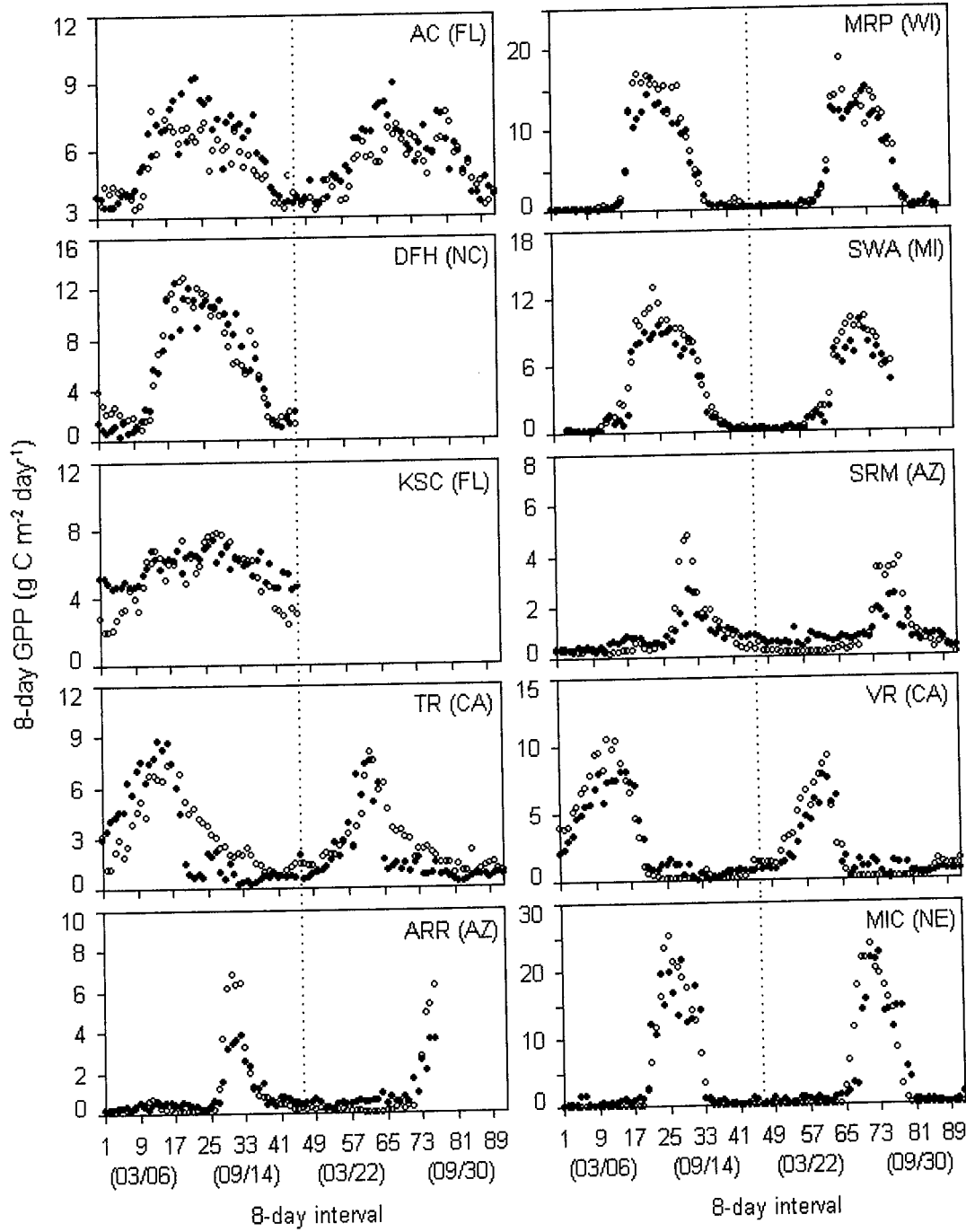


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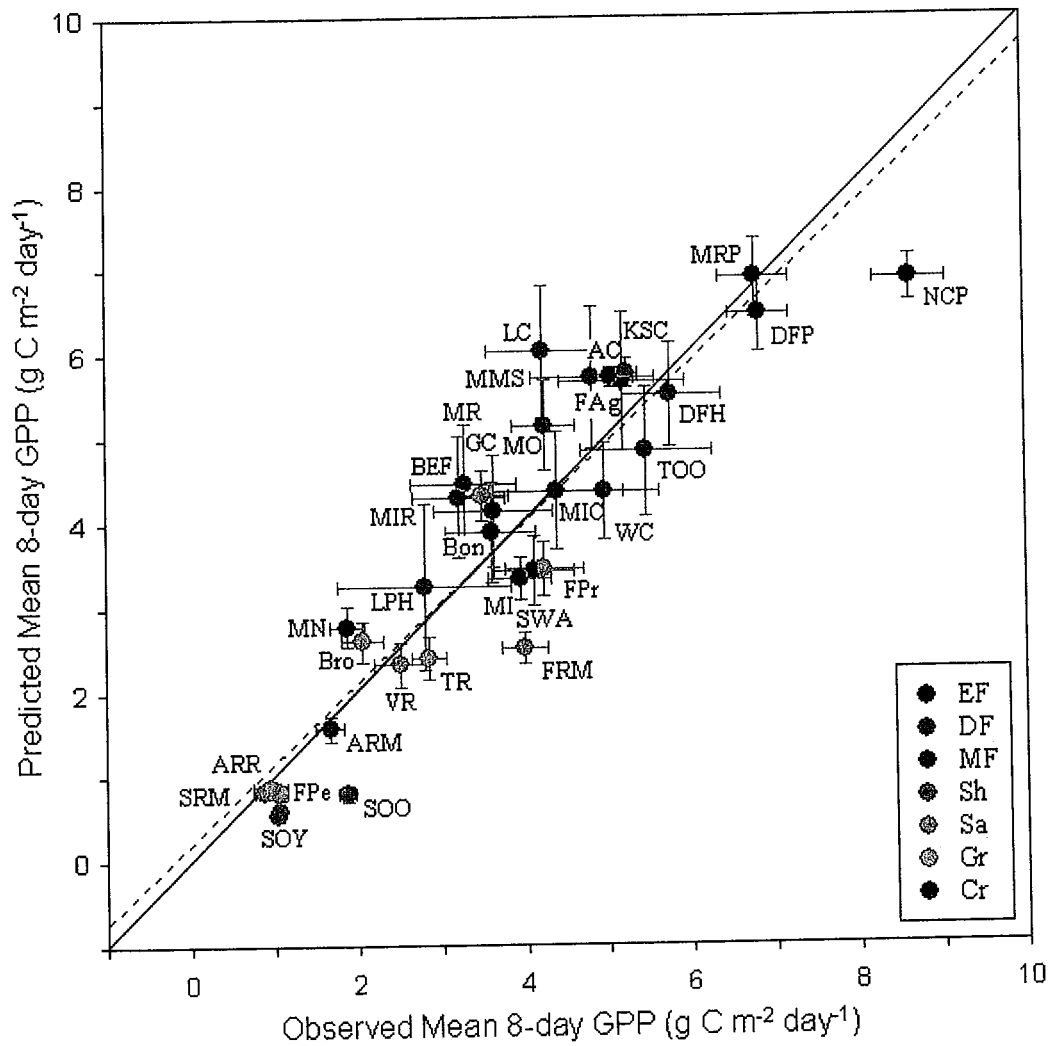


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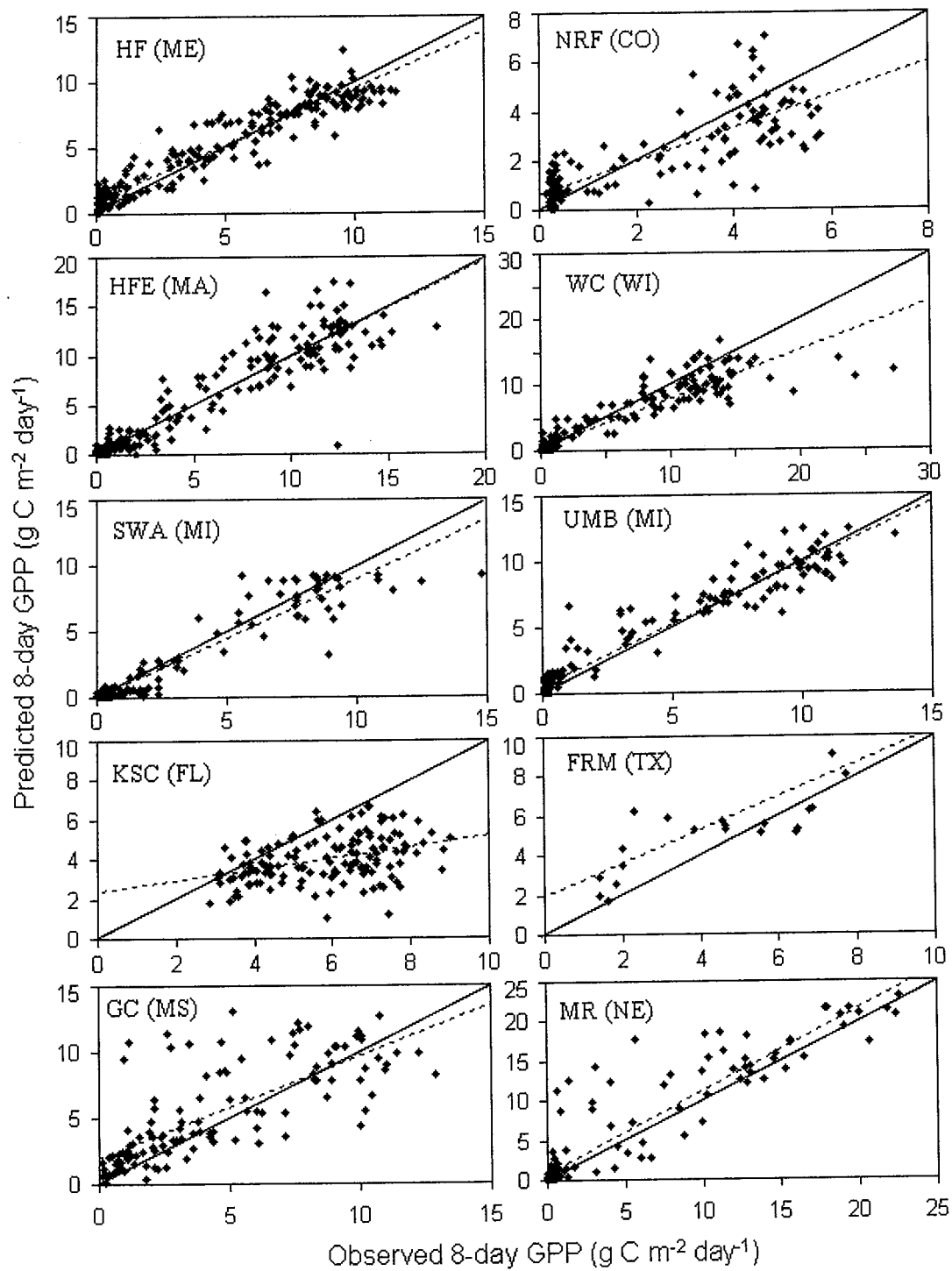


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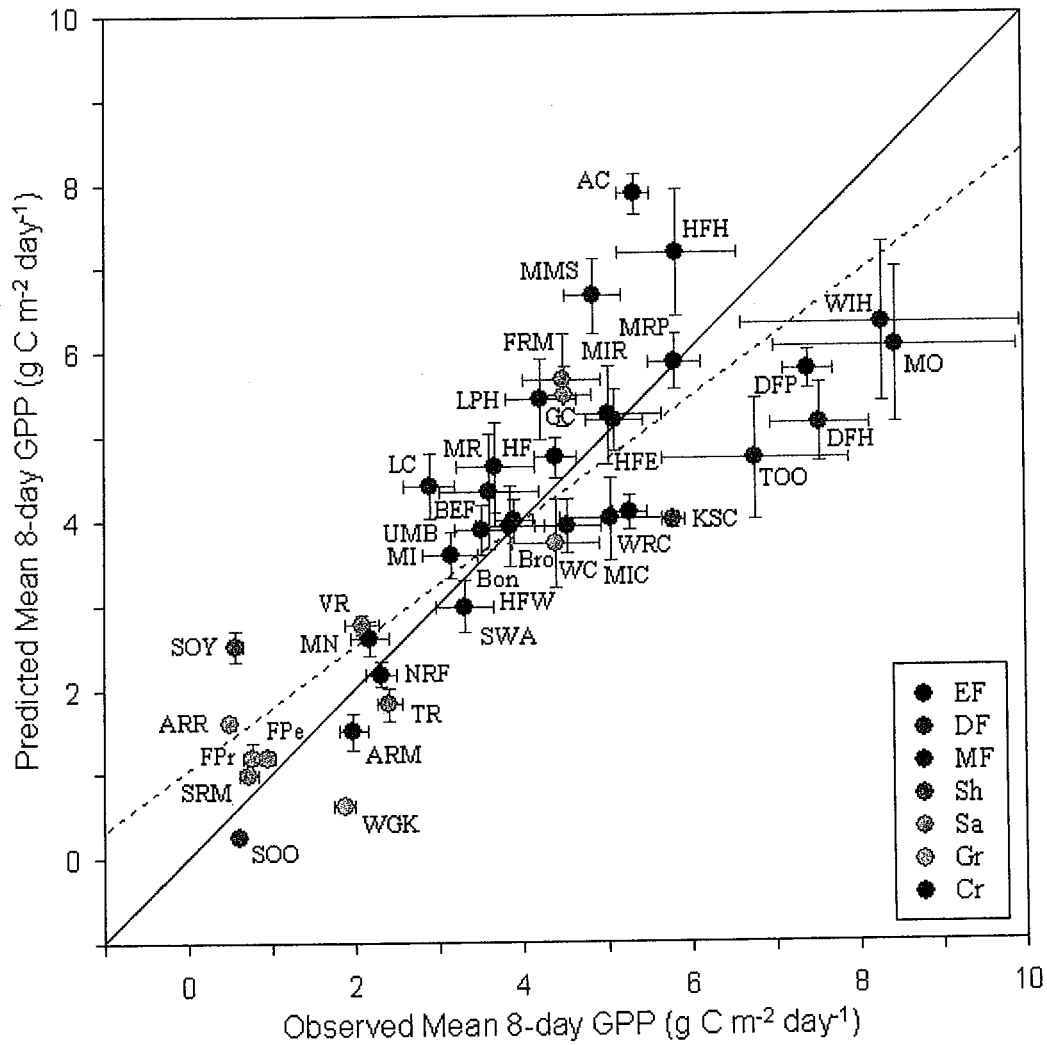


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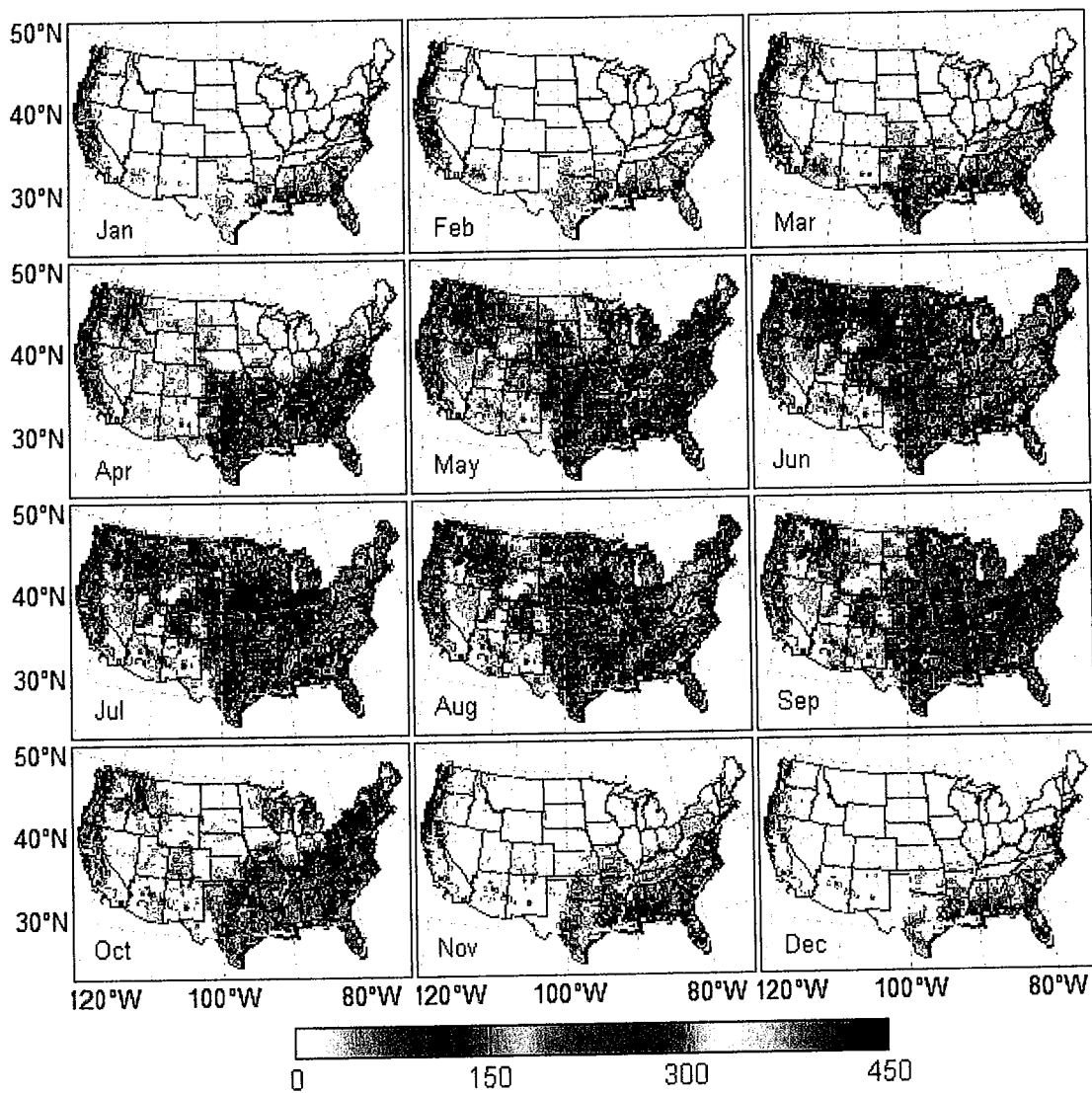


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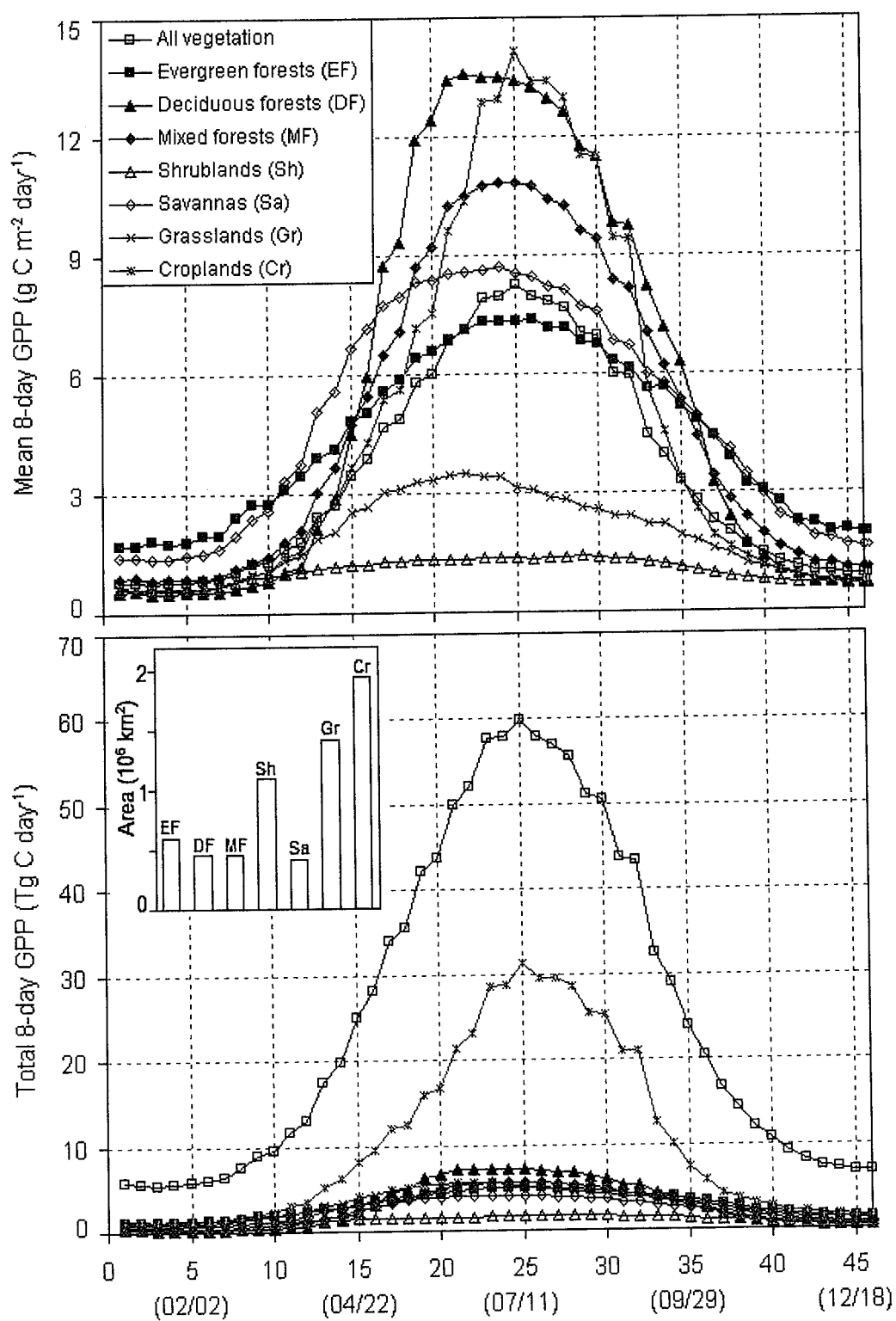


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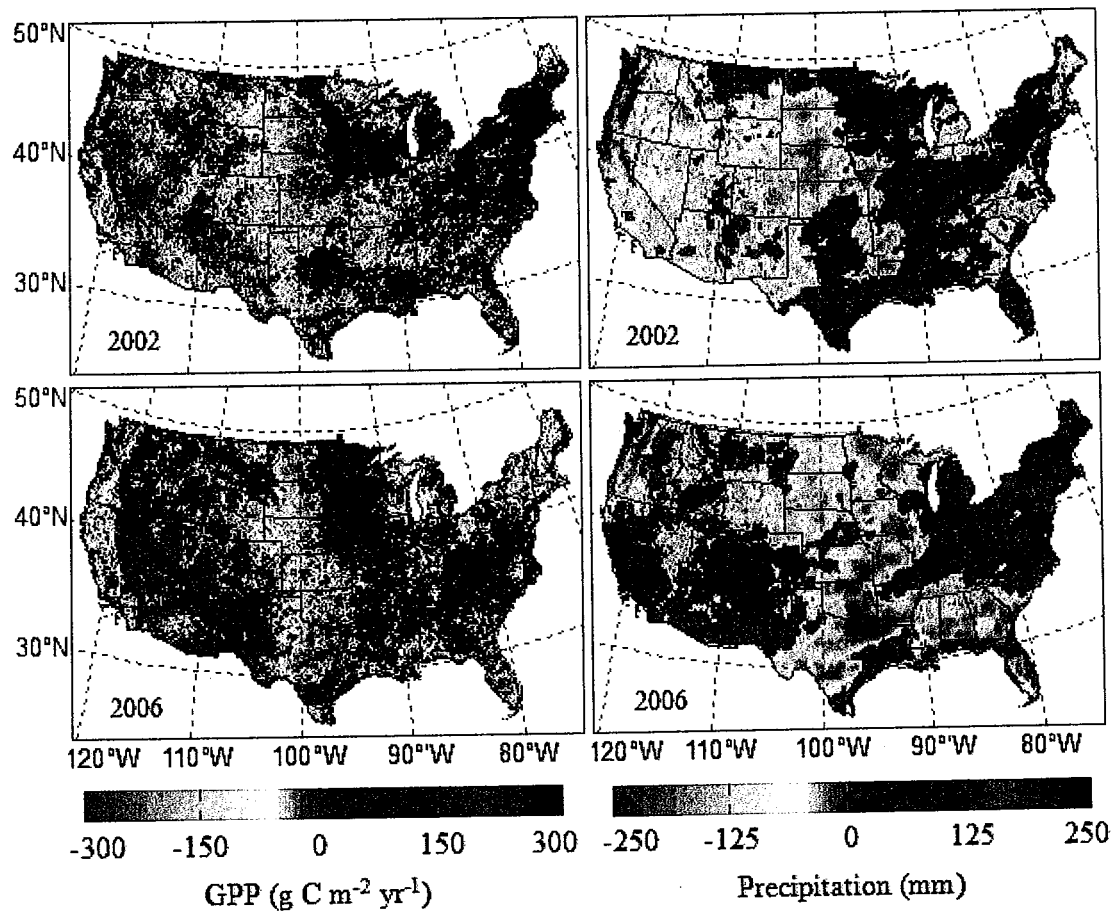


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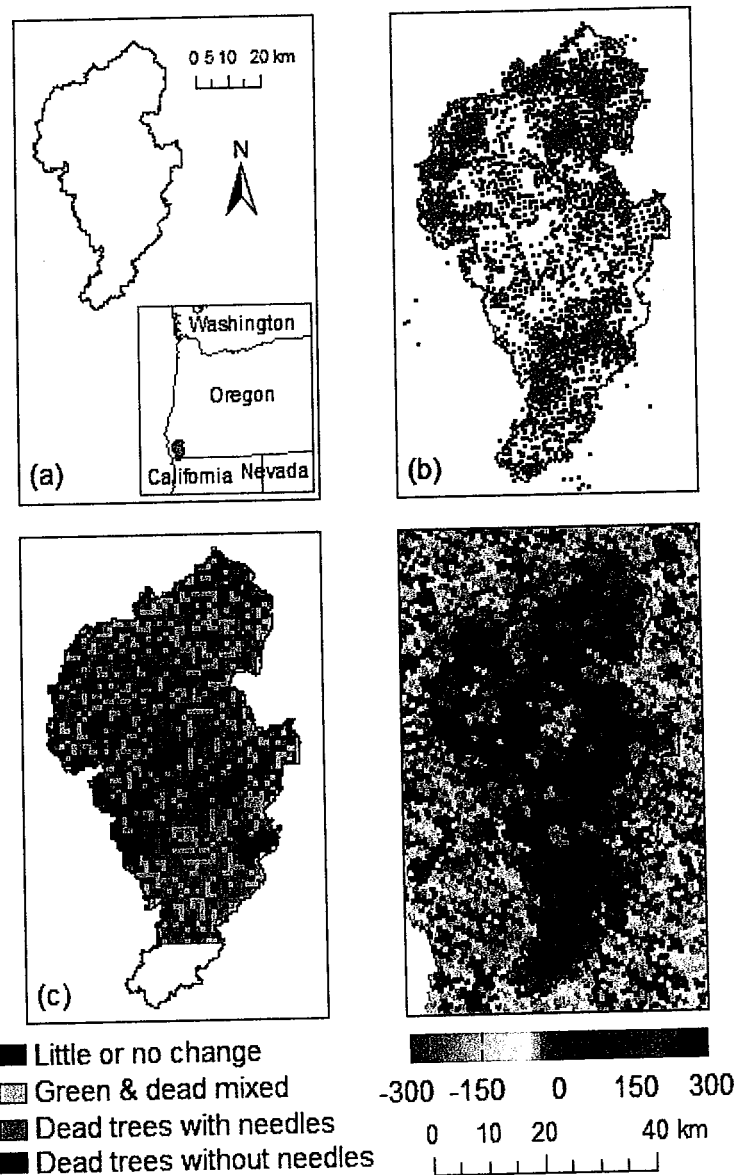


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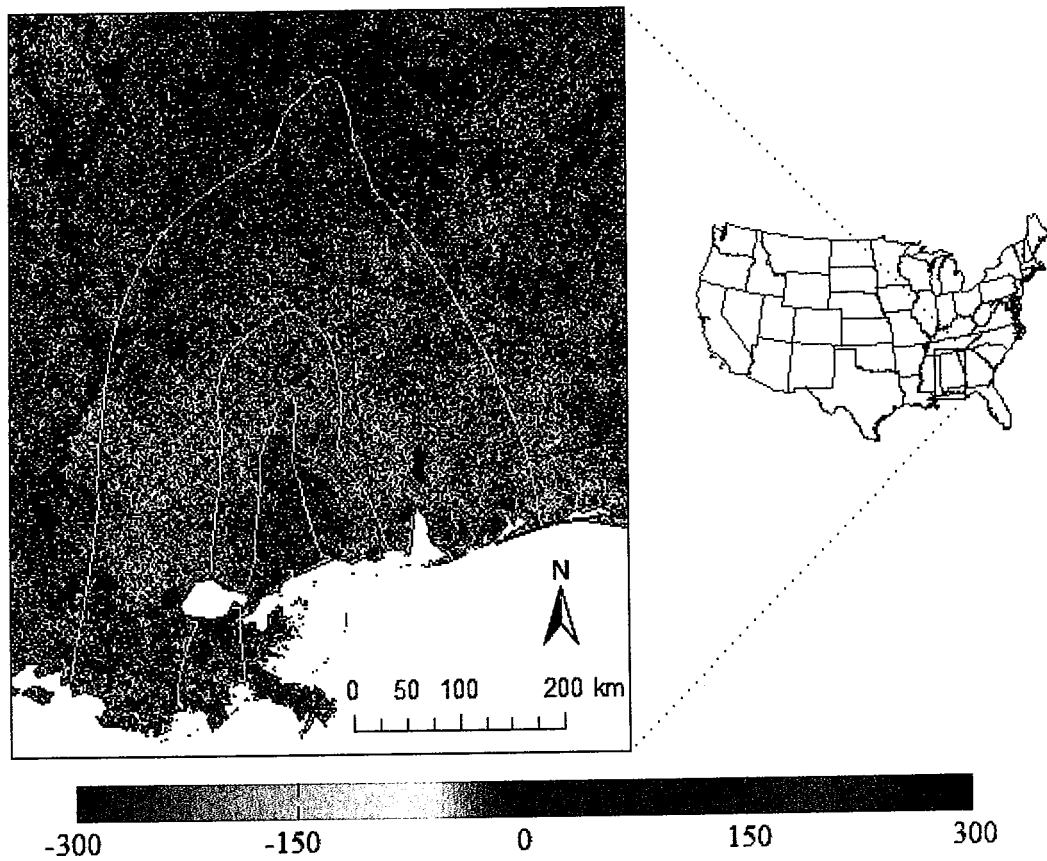


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