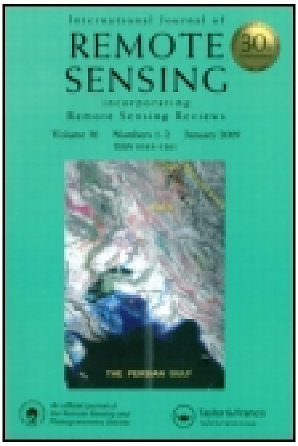

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Effects of forest type and environmental factors on forest carbon use efficiency assessed using MODIS and FIA data across the eastern USA

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The carbon use efficiency (CUE) of a forest, calculated as the ratio of net primary productivity (NPP) to gross primary productivity (GPP), measures how efficiently a forest sequesters atmospheric carbon. Some prior research has suggested that CUE varies with environmental conditions, while other suggests that CUE is constant. Research using Moderate Resolution Imaging Spectroradiometer (MODIS) data has indicated a variable CUE, but those results are suspected because MODIS NPP data have not been well validated.

We tested two questions. First, whether MODIS CUE is constant or whether it varies by forest type, climate, and geographic factors across the eastern USA. Second, whether those results occur when field-based NPP data are employed. We used MODIS model-based estimates of GPP and NPP, and forest inventory and anlaysis (FIA) field-based estimates of NPP data. We calculated two estimates of CUE for forest in 390 km^2 hexagons: (1) MODIS CUE as MODIS NPP divided by MODIS GPP and (2) F/M Z_{CUE} as the standardized difference between FIA NPP and MODIS GPP.

MODIS CUE and F/M Z_{CUE} both varied similarly and significantly in relation to forest type, and climatic and geographic factors, strongly supporting a variable rather than a constant CUE. The CUE was significantly higher in deciduous than in mixed and evergreen forests. Regression models indicated that CUE decreased with increases in temperature and precipitation and increased with latitude and altitude. The similar trends in MODIS CUE and F/M Z_{CUE} support the use of the more easily obtained MODIS CUE.

1. Introduction

Forest ecosystems play a major role in the global carbon (C) cycle (Lorenz, Lal, and Jimenez 2010). The carbon use efficiency (CUE) of different forest types has drawn increasing interest as it indicates their efficiency to sequester atmospheric carbon (Gifford 2003; DeLucia et al. 2007). The CUE of a forest is calculated as the ratio of net primary productivity (NPP) to gross primary productivity (GPP). GPP is the total mass of C assimilated by photosynthesis, and NPP is the amount of C stored following the loss of C from GPP through autotrophic respiration (hereafter respiration). A better understanding of how forest CUE varies in relation to biotic and abiotic factors can provide valuable information for forest management about which forest conditions most efficiently sequester atmospheric carbon (Pyorala, Kellomaki, and Peltola 2012).

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Many studies of terrestrial C cycle modelling have assumed a constant CUE in which NPP comprised a constant proportion of GPP (Waring, Landsberg, and Williams 1998). Their reasoning was that since respiration ultimately depends on sugars from photosynthesis, respiration would scale linearly with GPP and result in a constant value of CUE (McCree and Troughto 1966; Dewar, Medlyn, and McMurtrie 1998; Waring, Landsberg, and Williams 1998). Following this reasoning, while GPP would vary with environmental factors such as climate (Kanniah, Beringer, and Hutley 2011; Kanniah, Beringer, and Hutley 2013; Purves and Pacala 2008) and species composition or age (Van Iersel 2003), the CUE in those different environments would remain constant (Dewar, Medlyn, and McMurtrie 1998). A comparative analysis made by Waring, Landsberg, and Williams (1998) of 12 managed evergreen and deciduous plantation sites in the USA, New Zealand, and Australia suggested a constant CUE of 0.47. This constant CUE value has been widely implemented in ecosystem process models such as CASA (Potter et al. 1993) and FOREST-BGC (Running and Coughlan 1988) as a means to circumvent the complex assumptions of how respiration interacts with environmental factors.

Other research has suggested a variable CUE in which NPP comprised a variable proportion of GPP (Reich et al. 2006; DeLucia et al. 2007). Their reasoning is that since respiration is proportional to the live biomass (Reich et al. 2006), and since the annual increment of live biomass varies with resource availability (DeLucia et al. 2007; Zhang et al. 2009), then respiration and thus also NPP should be a variable proportion of GPP. Reich et al. (2006) demonstrated that plant respiration is linearly related with plant size and nitrogen content, using a large data set of tree saplings and herbaceous plants. A meta-analysis by DeLucia et al. (2007) of data collected over various forest types concluded that CUE varied spatially in response to resource availability.

These two different views on how respiration is regulated have been successfully combined in a number of studies by separating respiration into the two components of maintenance respiration and growth respiration. They then employed a variable CUE perspective to model maintenance respiration as proportional to biomass and employed a constant CUE perspective to model growth respiration as proportional to GPP (Goetz et al. 1999; Ito and Oikawa 2002). Moderate Resolution Imaging Spectroradiometer (MODIS) products of primary productivity have been estimated using this combined approach by implementing separate models to estimate maintenance and growth respiration. However, since the MODIS algorithm separated the process to calculate GPP and respiration, the modelling of respiration does not affect the quality of GPP.

The MODIS algorithm employs the radiation use efficiency (RUE) concept to estimate GPP, using satellite-derived MODIS input of leaf area index (LAI) and fraction of photosynthetic active radiation (*f*PAR), and independent estimates of surface meteorological data. These MODIS GPP estimates have been well validated through various approaches including eddy covariance methods (Turner et al. 2006; Heinsch et al. 2006), process-based ecosystem models (Nightingale et al. 2007), and field-based forest inventory sites (Weiskittel, Crookston, and Radtke 2011; Kwon and Larsen 2012). On the other hand, MODIS NPP estimates are derived as the difference between the annual sum of daily estimates of MODIS GPP and the annual estimates of maintenance and growth respiration. Since the calibration of model parameters for complex tree components of respiration is difficult, the quality of MODIS NPP is still in question and, indeed, estimates of MODIS NPP have not been well validated at local scales (Turner et al. 2005, 2006).

Zhang et al. (2009) calculated CUE using global MODIS products of GPP and NPP data and found that CUE varied spatially with ecosystem type, geographic location, and climate, supporting the variable CUE. The results of this global-scale MODIS analysis are uncertain for two reasons. First, MODIS NPP estimates had not been field validated. Second, since MODIS NPP is derived from GPP, it is possible that the support they found for a variable CUE was a result of that perspective having been built into the model parameters that estimate respiration.

To test whether the variable CUE perspective is true, we suggest the use of independent, local, field-based estimates of NPP, combining them with the reliable MODIS estimates of GPP, to create an alternative estimate of CUE. National forest inventories, such as the US Forest Services Forest Inventory and Analysis (FIA) programme, provide tens of thousands of plot scale measures of tree growth (McRoberts et al. 2005) from which estimates of NPP can be accurately constructed (Clark et al. 2001). The use of FIA NPP in place of MODIS NPP has two major advantages. First, since FIA NPP and MODIS GPP are independent of each other, their use should give a better indication of whether CUE is variable or constant. Second, since FIA plots are distributed across broad environmental gradients, they should prove useful in assessing CUE across diverse environmental conditions.

The objectives of this study are to calculate and compare the CUEs for forests across the eastern USA using two approaches. First, we calculate CUEs using both model-based MODIS estimates of NPP and GPP. Second, we calculate CUEs using field-based estimates of FIA NPP and model-based estimates of MODIS GPP. Since that calculation requires standardization of both data sets to make them compatible, this measure is referred to hereafter as the F/M Z_{CUE}. Trends in both estimates of CUE will be assessed relative to forest types, climatic gradients of temperature and precipitation, and geographic factors of latitude and altitude. Although FIA NPP and MODIS NPP have been directly compared (Jenkins, Birdsey, and Pan 2001; Pan et al. 2006), the spatial relations were not strong and they did not assess variations with environmental conditions. Thus, the replacement of MODIS NPP with FIA NPP in the calculation of CUE does not automatically mean that MODIS CUE and F/M Z_{CUE} will exhibit the same trends with forest types, climatic gradients, and geographic factors. If the results using F/M Z_{CUE} provide support for a variable CUE, and if its relations with environmental trends are similar to those obtained using MODIS CUE, then it will support the use of the more easily obtained MODIS CUE.

2. Materials

2.1. Study area

The study area is the 31 easternmost states, including parts of five of the 11 ecosystem divisions that Bailey (1995) identified in the conterminous USA: Continental Hot, Continental Warm, Prairie, Savannah, and Subtropical. The eastern US forests had a net carbon storage of 350 Tg CO_2 eq. reported in the year 2005 (Smith, Heath, and Nichols 2010) and were a net carbon sink that offset 6% of the total US greenhouse gas emissions (CO_2 eq.) (EPA 2010).

2.2. FIA data set

FIA NPP data were calculated using the publicly available Forest Inventory and Analysis Database (FIADB ver. 5.0, hereafter FIADB), collected by the FIA programme of the Forest Service, US Department of Agriculture. The FIA programme has adopted an annual inventory system since 1998 (VanDeusen 1997), in which approximately 20% of the plots in eastern US states and 10% in western US states are inventoried every year, using a nationally common, fixed-area plot configuration (McRoberts et al. 2005). Locational accuracy issues related to ‘perturbed’ and ‘swapped’ plot data (McRoberts et al. 2005) are negligible

Table 1. FIA inventory years vary by state based on different start year of annual inventory and data availability. Calculation of growth rate requires two consecutive complete 5 year cycles of annual inventories.

States	Measurement cycles
Alabama, Arkansas, Georgia, Illinois, Indiana, Iowa, Kentucky, Louisiana, Maine, Michigan, Minnesota, Mississippi, Missouri, New York, New Hampshire, Ohio, Pennsylvania, South Carolina, Tennessee, Wisconsin	1998–2002 and 2003–2007
Connecticut, Delaware, Florida, Maryland, Massachusetts, New Jersey, North Carolina, Rhode Island, Vermont, West Virginia	2001–2005 and 2006–2010

in this study since plots are aggregated into large areal units. Also, it has been suggested that the effect of perturbation on spatial patterns of FIA forest volume is negligible when non-perturbed volumes are compared with perturbed volumes smoothed over an area within a 5 km radius of the FIA plot (McRoberts et al. 2005). We used two complete 5 year cycles of annual inventory (Table 1, measurement years ranged from 1998 to 2010 depending on the data availability) to temporally cover the 4 year average of MODIS products from 2001 to 2004.

2.2.1. Calculation of plot-level FIA NPP

Plot-level net annual growth was calculated for the interval between two consecutive inventories (Table 1) to account for the major component of above-ground NPP.

The above-ground gross woody production was first calculated as a sum of net annual growth of growing-stock volume (GSV) (FIADB variable: GROWCFGS) and annual mortality of growing-stock volume (FIADB variable: MORTCFGS) in timberland. Timberland in the FIA programme is defined as an area that is producing or capable of producing in excess of 1.4 m^3 ha^{-1} $year^{-1}$ of wood at the end of the mean annual increment (MAI).

The components of above-ground woody production included in this study are survivor growth (the growth on trees tallied at time t that survive until re-measurement), growth on ingrowth (volume of trees reaching 12.5 cm dbh during the period), and mortality growth (the growth of trees that died from natural causes between measurement periods) (Birdsey and Schreuder 1992). These individual tree-level estimates of gross annual volume increments were then expanded to a per-acre value by multiplying them by tree-per-acre values (TPA) in FIADB.

The gross annual volume increments of GSV in the unit of volume per acre (G_i) was, following Bechtold and Patterson (2005), calculated as

$$G_i = \sum_j^4 \sum_t y_{ijt} / \sum_j^4 a_{ij}, \tag{1}$$

where, y_{ijt} is annual gross change in volume (ft^3, 1 cubic foot = 0.0283 m^3)) for tree t on macroplot, subplot, or microplot j of plot i; and a_{ij} is the total area (acre, 1 acre = 4047 m^2)) used to observe the volume increment on plot i. The value of y_{ijt} is computed as $[(V_2 - V_1)/(T_2 - T_1)]$, where V is volume, T is year of measurement, and subscripts 1 and 2 denote the past and current measurements, respectively.

Table 2. Basic conversion factors of weight per volume and percentage carbon for major forest types.

US region	Forest type	Kg m^{-3}	Percentage carbon
South	Loblolly pine	469.57	0.531
	Longleaf pine	539.54	0.531
	Oaks and Hickories	609.34	0.479
Northeast and mid-Atlantic	Pines	409.54	0.521
	Spruces and Firs	369.67	0.521
	Oaks and Hickories	609.34	0.498
	Maples, Beeches, Birches	609.34	0.498
North Central	Pines	409.54	0.521
	Spruces and Firs	369.67	0.521
	Oaks and Hickories	609.34	0.498
	Maples and Beeches	579.40	0.498
	Aspens and Birches	459.49	0.498

Adopted from Birdsey (1996).

The G_i values in ft^3 $acre^{-1}$ were then converted to biomass units (g C m^{-2}) using species- and region-specific allometric models developed by Jenkins et al. (2004) and standard conversion rates for weight per volume and carbon percentage (Table 2, Birdsey (1996)). These allometric models provide the best estimates for above-ground live tree volume which include tree components of foliage, stem bark, stem wood, and coarse roots (Jenkins, Birdsey, and Pan 2001; Jenkins et al. 2004). The models were developed by compiling a vast literature into tree species groups within similar geographic origins. Forest types varied from those with a low density such as the spruce and fir in the north-central region to those with a high density such as oak and hickory in the southern region (Table 2). Forest types not listed in Table 2 were converted using the average of the conversion factors from the appropriate region.

The biomass measures from all 80,125 FIA plots were then subjected to three quality control checks. First, we excluded FIA NPP values of greater than 1500 g C m^{-2} $year^{-1}$ that visual examination of a frequency histogram indicated to be outliers. Second, we removed plots with an artificial regeneration stand. Third, we removed newly established plots because they did not have the two sequential measurements required to calculate NPP. Following the application of these quality checks, a total of 59,984 FIA plots remained.

2.3. MODIS data set

We employed three MODIS data sets: (1) 8 day composite GPP pixel values from the Land Processes Distributed Active Archive Center (LP DAAC) (http://lpdaac.usgs.gov); (2) annual NPP pixel values from the Numerical Terradynamic Simulation Group (NTSG) (http://www.ntsg.umt.edu/modis); and (3) the MODIS land-cover data set (collection 5, MOD 13) used to limit both MODIS GPP and NPP pixels to forest-related land covers. A total of 34.7% of the eastern US study area had pixels with one of the five forest-related land-cover classes: evergreen needle-leaved (1.7%), evergreen broad-leaved (2.7%), deciduous needle-leaved (0.1%), deciduous broad-leaved (15.6%), and mixed (14.7%) forests. MODIS data sets were processed into an Albers equal area conic projection. Non-forest pixels, those that MOD 13 indicated to have one of the nine non-forest cover types, were set to null.

2.3.1. *Annual MODIS GPP values*

The annual GPP pixel values were calculated as the sum of 8 day composites for the period from 1 January 2001 to 31 December 2004. We employed a pixel-level quality assurance (QA) check to filter out low-quality MODIS estimates (QA number > 48) and non-terrestrial and non-modelled estimates (QA number 32,761–32,767), following the procedures of Kwon and Larsen (2012). A total of 16% of the forested MODIS pixels were filtered out due to low QA values. In addition, two 8 day composites were not available due to a reset of the MODIS instrument (day of year, 209–224 in 2001) and a third composite was not available due to LP DACC download errors (day of year, 96–104 in 2002). The three missing composite values were replaced by linear interpolations between the values of the previous good 8 day period and those of the next good 8 day period. The 4 year sums of GPP values were then temporally averaged to get a mean annual GPP.

2.3.2. *Annual MODIS NPP values*

MODIS NPP data were obtained from the NTSG, which developed photosynthesis (PSN) and NPP algorithms (www.ntsg.umt.edu/modis). The MODIS NPP data are only produced for individual calendar years. Although the MODIS NPP product has been considered not to have been strongly validated (Turner et al. 2005), it has been steadily improved (Zhao et al. 2005; Heinsch et al. 2006). The improvements included modification of the Biome Parameter Look-Up Table (BPLUT) based on the 12 flux tower measurements (Zhao et al. 2005) and enhanced interpolation of coarse-resolution meteorological input data with temporal filling of cloud-free upstream LAI and *f*PAR data (MOD 15) (Zhao, Running, and Nemani 2006). The most recent collection (C5, MOD 17) was assumed to be the best quality and was obtained for this study. The 4 year sums of NPP values were then temporally averaged to get a mean annual NPP.

2.3.3. *Annual MODIS respiration values*

Respiration was calculated for each MODIS pixel as MODIS GPP minus MODIS NPP for each of the four years of 2001 to 2004. The sum of the four annual respiration values was averaged to obtain the mean annual respiration.

2.4. *Environmental variables*

To examine trends in CUE by forest type, the 1,802,773 forested MODIS GPP and NPP pixels were classified using the pixel-level land-cover classification (MOD13) as evergreen (a combination of the two MODIS evergreen classes), deciduous (a combination of the two MODIS deciduous classes), and mixed forest. The 59,984 FIA plots were classified as the equivalent softwood (hereafter FIA evergreen), hardwood (hereafter FIA deciduous), or mixed forest using the 28 FIA species group codes (Figure 1).

Climatic and geographic information was obtained at an approximately 4 km × 4 km (16 km^2) spatial resolution for the conterminous USA from the Parameter-elevation Regressions on Independent Slopes Model (PRISM) data sets developed by the PRISM Climate Group (Daly et al. 2008) (Figure 2). Climatic variables of temperature and precipitation data were downloaded as monthly values for the four years of 2001 to 2004, from which we calculated annual mean temperature and monthly mean precipitation. The geographic variable of latitude ranged from 25° N to 50° N, and altitude from 0 to 1500 m.

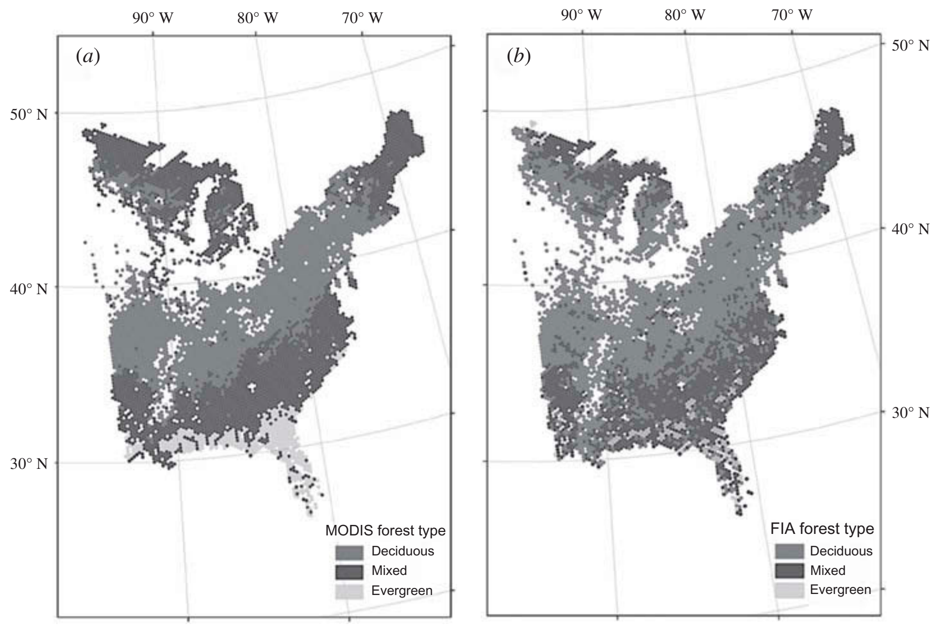

Figure 1. Forest types mapped in 390 km^2 hexagons ($n = 6741$ hexagons). (*a*) MODIS land-cover classification. (*b*) FIA land-cover classification.

3. Methods

3.1. MODIS CUE

Three components of MODIS primary productivity – GPP, NPP, and respiration as GPP minus NPP – were calculated for each of the 1,802,773 forest pixels, and resulting MODIS CUE values were calculated as the mean annual MODIS NPP divided by the mean annual MODIS GPP calculated as

$$\text{MODIS CUE} = \text{MODIS NPP}/\text{MODIS GPP}, \tag{2}$$

where MODIS NPP and MODIS GPP values are pixel-level estimates (g C m^{-2}) and MODIS CUE is a pixel-level unitless mean value.

The means were of the four years 2001 to 2004 for the forest-related land covers after the application of pixel-level quality controls for MODIS GPP values, and of the same land covers for MODIS NPP. For visual interpretation, the MODIS CUE values were scaled up to 390 km^2 hexagons by aggregating pixel values, though for statistical analyses all 1,802,773 pixels were employed.

3.2. F/M Z_{CUE}

The F/M Z_{CUE} was calculated as part of a five-step procedure that increased the compatibility of the area-based estimates of MODIS GPP and the plot-based estimates of FIA NPP. The five steps are organized into a flowchart (Figure 3), and their details are as follows. In the first step, FIA NPP plots and MODIS GPP pixels were processed using the quality controls described in Sections 2.2.1 and 2.3.1.

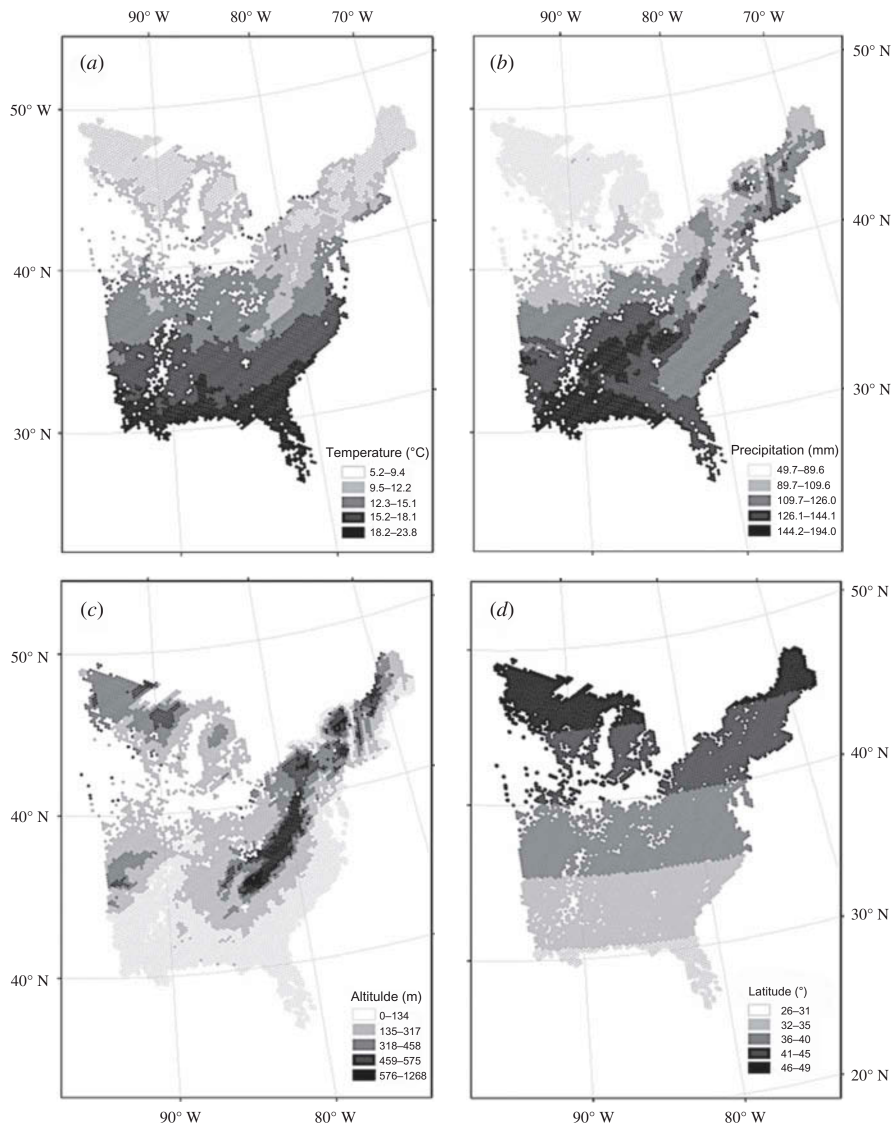

Figure 2. Climatic and geographic variables mapped in 390 km^2 hexagons ($n = 6741$).

In the second step, FIA NPP plots and MODIS GPP pixels were scaled up into co-located 390 km^2 hexagons. The 390 km^2 hexagonal size was chosen to minimize scaling mismatches between the coarse resolution of MODIS model inputs and fine resolution of individual FIA plots (Kwon and Larsen 2013). In the case of FIA data, it has systematic spatial sampling intensity of one plot for every 24.3 km^2, while 1 km × 1 km pixel resolution of MODIS GPP products are modelled estimates that heavily rely on meteorological input variables – which is approximately 14,000 km^2 (Zhao, Running, and Nemani 2006). Thus, at the size of 390 km^2, each hexagon is larger than the systematic FIA mean plot coverage and smaller than the resolution of the MODIS meteorological input variables. Of the 7253 MODIS and 7050 FIA hexagons of this size, 6741 were co-located. The FIA NPP

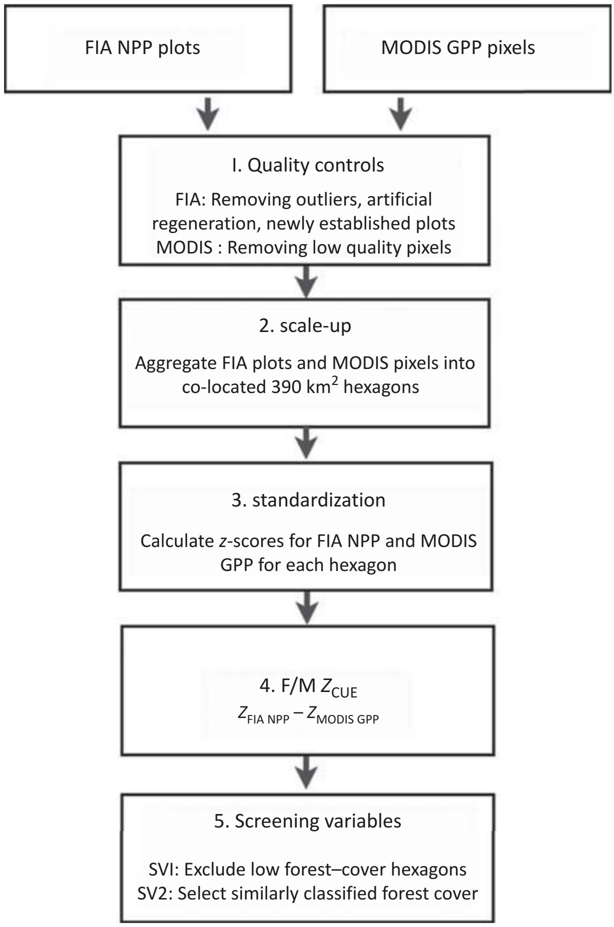

Figure 3. Flow chart for the calculation of standardized CUE (F/M Z_{CUE}).

plot-level values in each hexagon were scaled up using a weighted mean (WM), and pixel-level MODIS GPP values were scaled up using a conventional non-weighted mean (NM). The WM was developed because Kwon and Larsen (2012) found that FIA plots with more tally trees had the most improved plot-level relations between MODIS GPP and FIA NPP. The mean number of trees in each of the 59,984 FIA plots was calculated as a weighted mean as follows:

$$W_{ij} = \text{number of tally trees in plot } i/(\text{number of plots in unit } j \times 33.3 \text{ trees}), \quad (3)$$

where W_{ij} is a dimensionless ratio calculated using all plots i in each hexagon j, and 33.3 is the mean number of tally trees in the 59,984 FIA plots.

The WM FIA NPP value in each hexagon was then calculated as

$$\text{FIA NPP}_j = \sum_{t}^{n} \text{NPP}_{ij} \times W_{ij}, \quad (4)$$

where FIA NPP_j was measured in g C m^{-2} of forest in hexagon j, NPP_{ij} was the NPP from each plot i in each hexagon j, and W_{ij} was the unitless weight factor for plot i in hexagon j.

The MODIS GPP value in each hexagon was scaled up from individual MODIS pixels as a conventional average of all pixels that had their centre located in the hexagon:

$$\text{MODIS GPP}_j = \sum_{t}^{n} \text{GPP}_{ij}/n, \tag{5}$$

where MODIS GPP_j was the average GPP in hexagon j (g C m^{-2}), GPP_{ij} was the annual GPP (g C m^{-2}) in each pixel i, and n was total number of forested pixels within each hexagon.

In the third step, standardization was applied to the MODIS GPP and FIA NPP data. This was done because the mean and standard deviation of their values in the 390 km^2 hexagons were quite different: MODIS GPP had a mean of 1354 g C m^{-2} and a standard deviation of 41 g C m^{-2}, while FIA NPP had a mean of 217 g C m^{-2} and a standard deviation of 234 g C m^{-2}. Using these values, a CUE of 0.15 was obtained as FIA NPP divided by MODIS GPP. This value is much lower than the CUE of 0.49 that was obtained for the same hexagons as MODIS NPP divided by MODIS GPP (see Section 4.1). The differences in these two CUEs occur because the mean FIA NPP value of 217 g C m^{-2} is much lower than the mean MODIS NPP value of 664 g C m^{-2}. The two measures of NPP likely differ so greatly for two reasons. First, the MODIS NPP algorithm includes understorey and fine root growth while FIA NPP does not. Second, there are differences between the allometric models used in FIA NPP and the parameters of RUE used in the MODIS algorithm.

Since an absolute measure of CUE calculated in the standard manner using MODIS GPP and FIA NPP would be biased by their frequency histograms differing in their mean and standard deviation, a standardized z-score of MODIS GPP and of FIA NPP for each hexagon was calculated as

$$Z = (x - \mu)/\sigma, \tag{6}$$

where x is the mean hexagon-level value of either GPP or NPP to be standardized, μ is the mean of either all hexagon-level GPP or NPP values, and σ is the standard deviation of either all hexagon-level GPP or NPP values.

In the fourth step, F/M Z_{CUE} values were calculated for the 390 km^2 hexagons as the differences between the standardized hexagon-level z-values of FIA NPP and MODIS GPP as follows:

$$\text{F/M } Z_{\text{CUE}} = Z_{\text{FIA NPP}} - Z_{\text{MODIS GPP}}, \tag{7}$$

where $Z_{\text{FIA NPP}}$ and $Z_{\text{MODIS GPP}}$ are the values calculated in Equation (6).

The FIA NPP and MODIS GPP values were converted into standardized z-scores with a mean of zero and a standard deviation of one, based on the normal distribution. Highly positive F/M Z_{CUE} values indicate greater efficiency in sequestering atmospheric carbon, while highly negative F/M Z_{CUE} values indicate lower CUE. F/M Z_{CUE} could not be calculated as a ratio of NPP and GPP, as division with negative numbers could produce the same CUE for the ecologically very different situations of a negative numerator with a positive denominator and of a positive numerator with a positive denominator. One solution to that problem would be to add a sufficiently large constant value to all standardized NPP and GPP values such that they would all become positive, and then divide NPP by GPP. A simpler solution, which gives the same result as that first, is the subtraction approach of Equation (7).

In the fifth step, two screening variables (SVs) were used to increase the similarity of the forest conditions in the MODIS and FIA data (cf. Kwon and Larsen 2012). SV1 involved removing hexagons with low forest cover, by selecting only hexagons which contained more than the mean number of forested MODIS pixels and more than the mean number of FIA plots. SV2 employed a two-part process to remove the 390 km^2 hexagons with misclassified forest covers. In the first part, FIA plots and MODIS pixels were classified as evergreen, deciduous, or mixed forest. A FIA plot was classified using the 28 FIA species group codes as FIA evergreen or FIA deciduous if more than 60% of both its basal area and number of stems was hardwood or softwood, and mixed forest if neither made up more than 60%. A MODIS pixel was classified as evergreen (a combination of the two MODIS evergreen classes), deciduous (a combination of the two MODIS deciduous classes), and mixed forest. In the second part, the 390 km^2 FIA hexagons and MODIS hexagons were classified as evergreen or deciduous if, respectively, 60% or more of their plots or pixels were classified as evergreen or deciduous; the remaining forested hexagons were classified as mixed forest as less than 60% of their plots or pixels were classified as either evergreen or deciduous.

3.3. Relations between MODIS CUE and F/M Z_{CUE}

MODIS CUE and F/M Z_{CUE} were compared using regression analysis of co-located 390 km^2 hexagons. Various regression models were tested including polynomial (first, second, and third order), logarithmic, exponential, and power; the best-fit model was chosen as the one with the highest $R^2{}_{\mathrm{adj}}$. Higher order polynomial regressions were not employed because, although they had slightly higher $R^2{}_{\mathrm{adj}}$ values than did lower-order polynomial regressions, they appeared to be over-fitting the data. Regressions were made using all 6741 co-located hexagons, and using the 1965 hexagons that remained after applying the filters of SV1 and SV2. We tested to see whether the improved correlation that occurred following the application of SVs came at too high a cost in the number of hexagons. To do this, the correlation coefficients between the two data sets were transformed into the normally distributed r' using procedures developed by Fisher (1921) (Equation 8), and the z-statistic was then calculated to compare standardized correlation coefficients as (Equation 9):

$$r' = 0.5 \ln |(1 + r)/(1 - r)| , \tag{8}$$

$$z = \left(r'_1 - r'_2\right) / \sqrt{\frac{1}{n_1 - 3} - \frac{1}{n_2 - 3}}, \tag{9}$$

where correlation coefficients (r) were transformed to r' (Equation 8), n was the number of plots, and subscripts 1 and 2 represent, respectively, the criterion for that hexagon size with the highest and lowest correlation coefficients, and the transformed r' has the approximate variance of $\mathrm{V}(r') = 1/(n - 3)$.

3.4. CUE trends with environmental factors

Variations in CUE were assessed relative to vegetation type and then to abiotic factors. First, the values of MODIS GPP, NPP, and respiration were compared for the three MODIS forest types at pixel-level ($n = 1{,}802{,}773$), and then values of MODIS CUE and F/M Z_{CUE} were compared across vegetation types. An ANOVA was used to test whether the mean values of CUE differed between the three forest types. The statistical significance of the tests was determined with the Tukey *post hoc* test using a 95% confidence level. Second, regression analysis was conducted to determine whether MODIS CUE and F/M Z_{CUE} varied similarly across a range of conditions for mean annual temperature, total annual precipitation, altitude, and latitude. MODIS CUE and the environmental variables were regressed at the scale of pixels ($n = 1{,}802{,}773$). Relations between F/M Z_{CUE} and the environmental variables were made at the scale of 390 km^2 hexagons ($n = 6741$ for all hexagons, and $n = 1965$ for hexagons following the application of SVs), requiring that the environmental data also be aggregated to the hexagon size. The scaling-up process employed taking the average of the PRISM environmental conditions that occurred in the centre of each forested pixel in a hexagon. Regression analyses were conducted over the full range of conditions for temperature and latitude, and over a reduced range for precipitation and altitude as they contained outlying observations at high values that might exert undue influence on the regression relation. The regression models that were tested included polynomial (first, second, and third order), logarithmic, exponential, and power, with the best-fit model identified as the one with the highest R^2_{adj}.

4. Results

4.1. MODIS CUE

The mean MODIS GPP, NPP, and respiration values for the eastern US forest were 1354, 655, and 699 g C m^{-2}, respectively, resulting in a mean MODIS CUE value of 0.49. The highest MODIS CUE values (>0.58) were clustered in the northwest of the study area, and scattered in the Appalachians and Florida (Figure 4). Intermediate MODIS CUE values

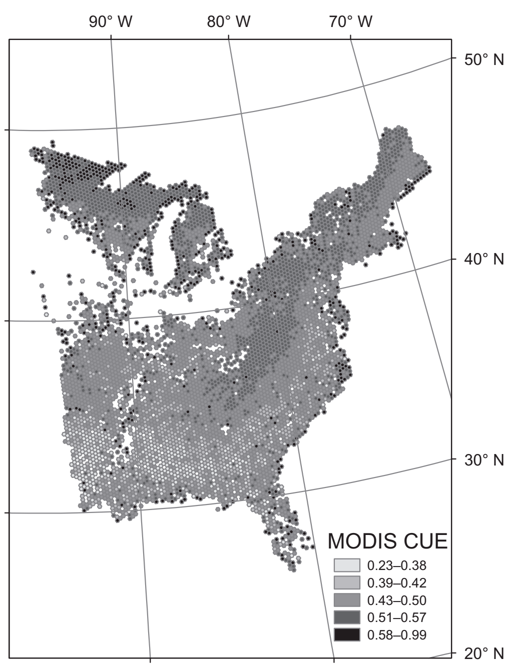

Figure 4. Choropleth map of MODIS CUE using 390 km^2 hexagons ($n = 6741$ hexagons).

(0.43–0.50) predominated in the Appalachian Mountains. The lowest MODIS CUE values ($<$0.30) were in Louisiana and Mississippi, and additional low MODIS CUE values ($<$0.38) extended northeastward from there in a band between the Atlantic coast and the Appalachians.

4.2. F/M Z_{CUE}

The five steps in the calculation of F/M Z_{CUE} resulted in reductions in the number of FIA plots and hexagons. The first step that applied quality controls in F/M Z_{CUE} reduced the original number of plots to 59,584 FIA NPP, with the excluded plots consisting of 8547 with an artificial plot condition, 2402 with extremely high values of volume increments, and 9592 newly established plots. No reductions were made in the number of MODIS GPP pixels since the low-quality MODIS GPP pixels were replaced with the neighbouring good 8 day period. The second step that employed scaling-up of plots and pixels into the 390 km^2 hexagons resulted in a total of 7253 MODIS and 7301 FIA hexagons, with 6741 of these being co-located. The third and fourth steps did not result in further reductions in the number of hexagons. The fifth step that applied screening variables resulted in the number of co-located hexagons decreasing to 2449 following the application of SV1, and to 1965 following the application of both SV1 and SV2.

The means of the FIA NPP and MODIS GPP for the study areas were, respectively, 214 and 1350 g C m^{-2} in the 6741 co-located hexagons, 225 and 1327 g C m^{-2} in the 2449 hexagons, and 231 and 1317 g C m^{-2} in the 1965 hexagons. The resulting F/M Z_{CUE} calculated as the differences between the standardized *z*-values of FIA NPP and MODIS GPP was –0.13, –0.05, and 0.07, respectively, for the 6741, 2449, and 1965 hexagons. The use of the SVs resulted in higher correlations between F/M Z_{CUE} and each of the four climatic and geographic variables; *z*-value analyses indicate that these correlations were sufficiently high to make up for the reduced number of hexagons (*z*-values for the full and reduced data set ranged from 3.31 to 4.42, all were significant at $p < 0.001$).

The spatial pattern of F/M Z_{CUE} for all 6741 hexagons was a cluster of low values in mid-latitude states such as Arkansas and Tennessee, with high values scattered throughout the study area but most common in the north (Figure 5(*a*)). The spatial pattern of F/M Z_{CUE} for the screened subset of 1965 hexagons exhibited a clearer pattern of low CUE values (F/M $Z_{\mathrm{CUE}} < -0.83$) in the south and high values (F/M $Z_{\mathrm{CUE}} > 1.57$) in the north (Figure 5(*b*)).

4.3. Relations between MODIS CUE and F/M Z_{CUE}

The linear regression between MODIS CUE and F/M Z_{CUE} produced a higher R^2 than did any of the other regression models, when considered either with the complete data set of 6741 hexagons or the reduced data set of 1965 following the applications of SVs 1 and 2 (Figure 6). The linear relation between MODIS CUE and F/M Z_{CUE} ($R^2 = 0.26$, $p < 0.001$) for the reduced data set ($n = 1965$) was significantly higher ($Z = 4.27$, $p < 0.001$) than that for the full data set ($R^2 = 0.18$, $n = 6741$, $p < 0.001$).

4.4. CUE trend with environmental factors

4.4.1. ANOVA result by forest types

4.4.1.1. MODIS CUE. The GPP, NPP, and respiration values were all highest for evergreen, intermediate for mixed, and lowest for deciduous forests (Figure 7(*a*)). Respiration

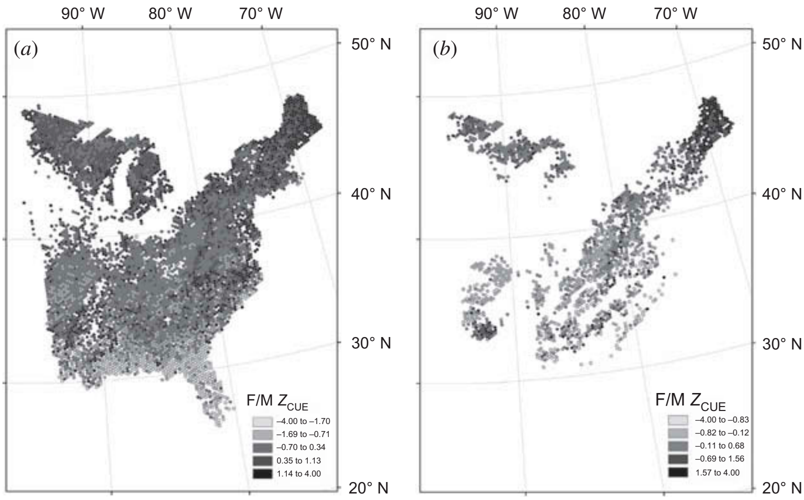

Figure 5. Choropleth maps of F/M Z_{CUE} using 390 km^2 hexagons for (*a*) all 6741 co-located FIA and MODIS hexagons and (*b*) the 1965 hexagons remaining after the application of the screening variables in Step 5 of the flow chart in Figure 3.

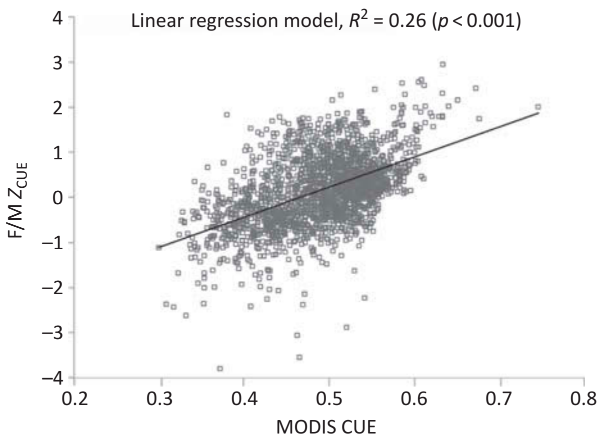

Figure 6. Relations between MODIS CUE and F/M Z_{CUE} for the 1965 hexagons that remained following the application of the screening variables in Figure 3.

was higher than NPP in all three forest types. MODIS CUE values were highest for deciduous (0.51), intermediate for mixed (0.49), and lowest for evergreen forest (0.47) (Figure 7(*b*)). The standard deviation for MODIS CUE was, however, smallest for deciduous (0.06), intermediate for mixed (0.07), and largest for evergreen forest (0.10). A null hypothesis of constant CUE was rejected by the ANOVA, as the CUE value for deciduous (n = 576,887) was significantly higher than those for mixed (n = 1,063,637) and for evergreen forest (n = 162,249) (Tukey test, $p < 0.0001$).

4.4.1.2. F/M Z_{CUE}. F/M Z_{CUE} values were highest for FIA deciduous (0.18), intermediate for mixed forest (–0.15), and lowest for FIA evergreen forest (–fo49) (Figure 7(*c*)). More highly positive z-values indicate higher CUEs because F/M Z_{CUE} was calculated as

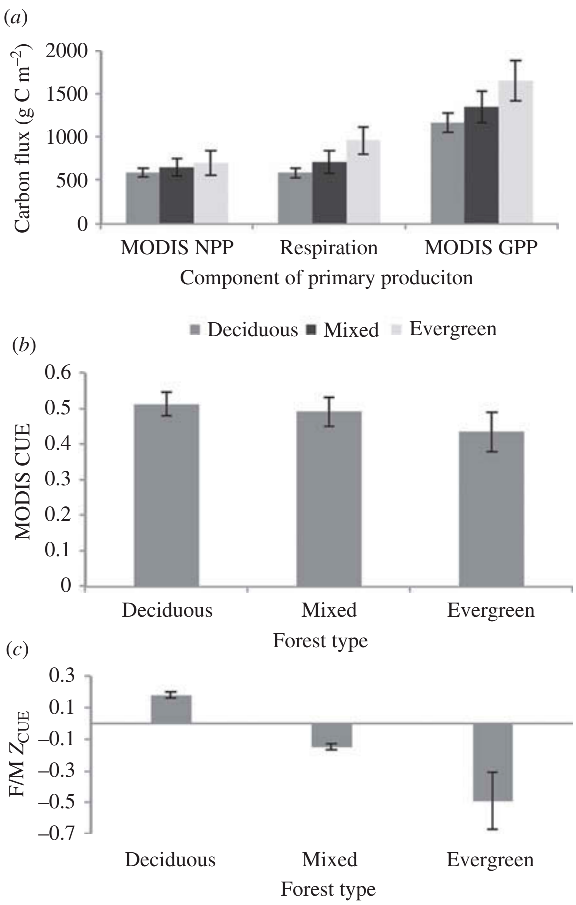

Figure 7. CUE and its components for different forest types. (*a*) MODIS NPP, respiration, and GPP for the three MODIS forest types. (*b*) MODIS CUE for the three MODIS forest types. (*c*) F/M Z_{CUE} for the three FIA forest types. MODIS values are calculated using 1,802,773 pixels, and F/M Z_{CUE} values are calculated using the 1965 hexagons that remained after the applications of screening variables in Figure 3. Error bars indicate one standard deviation.

standardized NPP minus GPP. The standard deviation for F/M Z_{CUE} was smallest for both mixed and deciduous (0.02) and largest for evergreen forest (0.18). The null hypothesis of a constant CUE was rejected by the ANOVA, as the F/M Z_{CUE} for deciduous ($n = 906$) was significantly higher than those for mixed ($n = 1010$) and for evergreen forest ($n = 49$) (Tukey test, $p < 0.0001$).

4.4.2. Regression analyses

MODIS GPP, NPP, and respiration values in forested pixels ($n =$ 1,802,773) all increased steadily with higher temperature and precipitation and decreased with higher altitude and latitude (Figure 8). At low values of temperature (<11.5°C) and precipitation (<127 mm), the carbon flux of respiration was lower than that of NPP, and at higher temperatures (>11.6°C) and precipitation (>128 mm) the carbon flux of respiration was higher than that of NPP (Figures 8(*a*) and (*b*)). In contrast, at lower values of altitude (<700 m) and

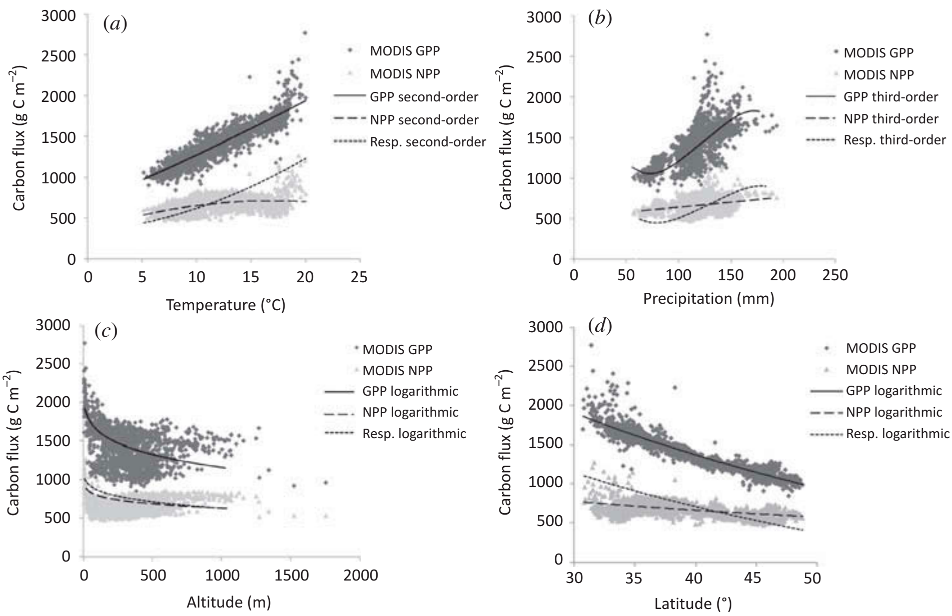

Figure 8. Trends in GPP, NPP, and respiration at the plot scale (n = 1,802,773 pixels) with (a) temperature, (b) precipitation, (c) altitude, and (d) latitude. R^2 values for trend line are ranged between 0.47 and 0.82; all are significant at $p < 0.001$. Values for respiration are not plotted due to overlap with NPP, but its trend line is shown.

latitude (<41.5° N), the carbon flux of respiration was higher than that of NPP, and at higher altitudes (>701 m) and latitudes (>41.6° N) the carbon flux of respiration was lower than that of NPP (Figures 8(c) and (d)).

The regression line for FIA NPP increased with higher temperature and precipitation and decreased with higher altitude and latitude (Figure 9). The patterns were similar to those for MODIS NPP, although the pattern was not as strong. Unlike for MODIS, the FIA data do not provide information on GPP and respiration.

MODIS CUE and F/M Z_{CUE} both decreased with increased temperature and precipitation (Figure 10). MODIS CUE decreased non-linearly with temperature, exhibiting a convex inflection point at 7°C and a shallowing of the trendline slope above 17°C (Figure 10(a)). MODIS CUE decreased linearly with increased precipitation (Figure 10(c)). F/M Z_{CUE} decreased non-linearly with increased temperature and decreased linearly with increased precipitation (Figures 10(b) and (d)). MODIS CUE and F/M Z_{CUE} both increased non-linearly with altitude, exhibiting a convex inflection point at 600 m in the MODIS and 800 m in the F/M Z_{CUE} data, beyond which CUE declined (Figures 10(e) and (f)). MODIS CUE and F/M Z_{CUE} both gradually increased with higher latitude, and for both best-fit models, there was a logarithmic regression (Figures 10(g) and (h)).

For all four independent variables, the variance explained was higher for MODIS CUE than it was for F/M Z_{CUE}, with the difference in the two R^2_{adj} ranging from a high of 0.28 for altitude to a low of 0.12 for latitude (Figure 10). The highest R^2_{adj} (0.58) was between MODIS CUE and temperature, and the lowest R^2_{adj} (0.13) was between F/M Z_{CUE} and altitude. In addition, the R^2_{adj} for the best-fit model between each of the four environmental variables and F/M Z_{CUE} was significantly lower for the full data set of

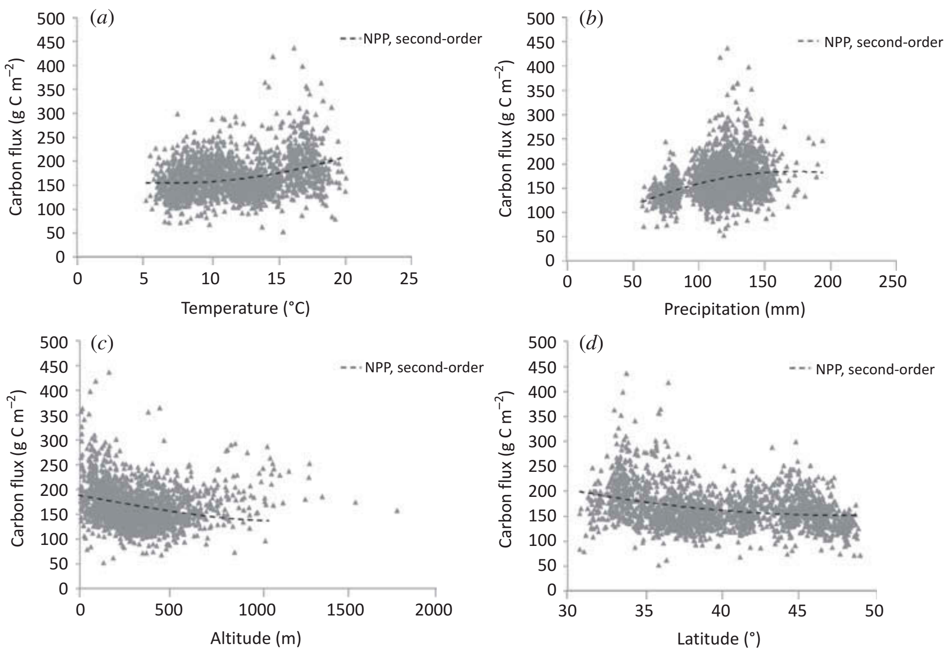

Figure 9. Trends in FIA NPP at the hexagon scale following the application of screening variables in Figure 3 ($n = 1965$ hexagons) for (*a*) temperature, (*b*) precipitation, (*c*) altitude, and (*d*) latitude. R^2 values for trend line are ranged between 0.27 and 0.58; all are significant at $p < 0.001$.

6741 hexagons than it was for the reduced data set of 1965 hexagons created by the application of SVs 1 and 2 (z-values for the full and reduced data set ranged from 3.89 to 4.88, all being significant at $p < 0.001$).

5. Discussion

5.1. MODIS and F/M Z_{CUE} for the eastern USA

The results show that both MODIS CUE and F/M Z_{CUE} vary significantly and consistently in relation to forest type and climatic and geographic factors, thus providing strong support for a variable CUE. The similarity of the results indicates that although MODIS NPP has not been well validated, it does not create biased values of MODIS CUE. The average MODIS CUE of 0.49 for the eastern US forest is similar to the suggested universal global-scale CUE value of 0.47 from the study by Waring, Landsberg, and Williams (1998). It was also similar to a mean CUE of 0.53 obtained in a meta-analysis of 23 papers that employed a range of methods to estimate CUE including field, flux, and modelling (DeLucia et al. 2007), and to a CUE of 0.46 for the 18 of those 23 papers that studied deciduous, coniferous, and mixed forests in the eastern USA.

5.2. CUE trends by environmental factors

5.2.1. Forest type

MODIS CUE and F/M Z_{CUE} both showed that deciduous forests have significantly higher CUEs than do mixed and evergreen forests. This is opposite to what was found in a global

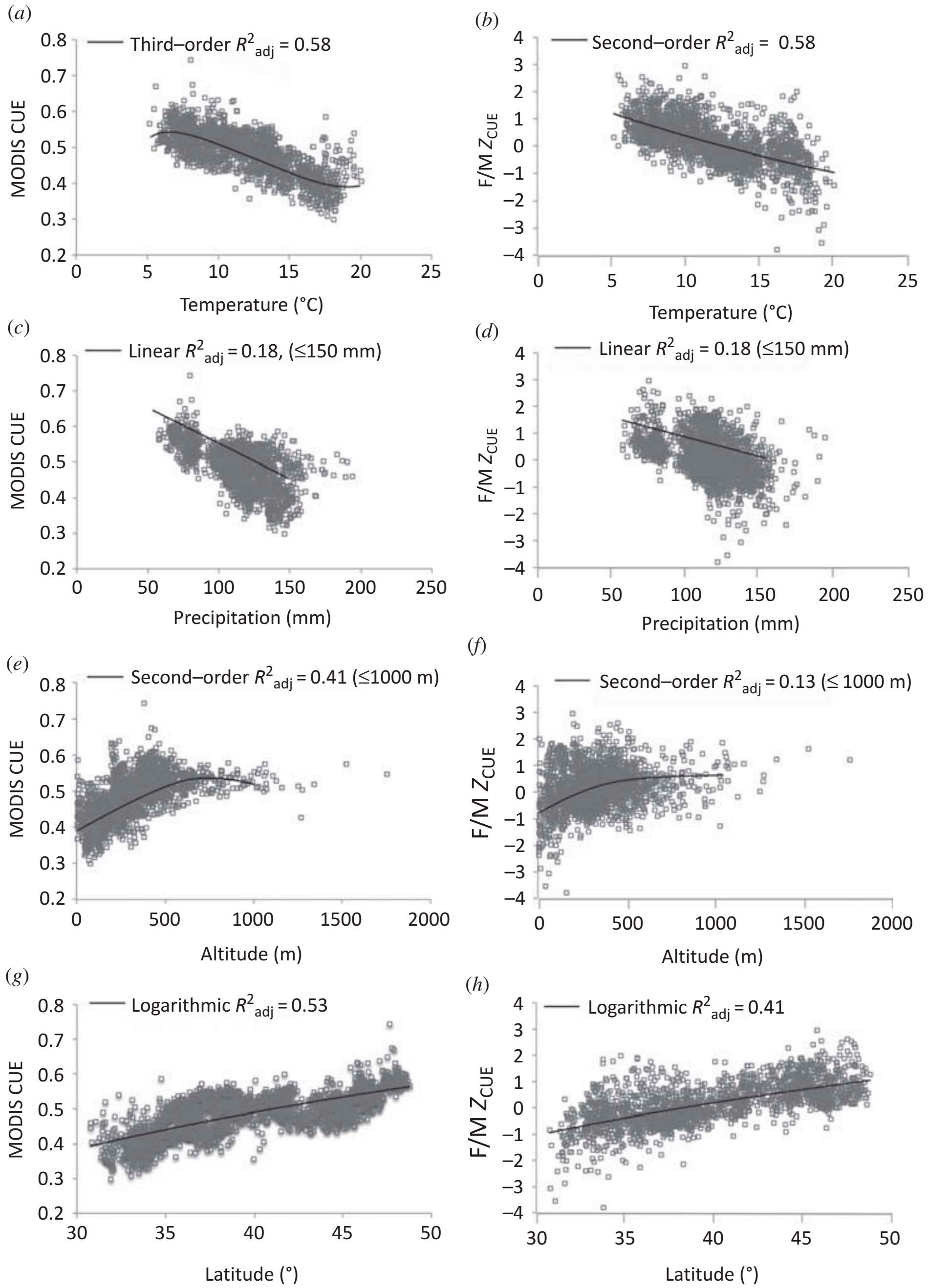

Figure 10. Trends in MODIS CUE (left column) and F/M Z_{CUE} (right column) for the 1965 hexagons that remained following the application of the screening variables, for (*a*, *b*) temperature, (*c*, *d*) precipitation, (*e*, *f*) altitude, and (*g*, *h*) latitude. The trend model chosen for each plot is that which had the highest R^2_{adj}; all are significant at $p < 0.001$. The precipitation and altitude plots have data points for the full range of both variables (up to 200 mm precipitation and 1700 m altitude), but the trend models created and plotted exclude high values of greater than 150 mm precipitation and 1000 m altitude.

analysis of MODIS CUE by Zhang et al. (2009), who found lower CUEs in deciduous broad-leaved than in evergreen needle-leaved forests. This difference is likely due to most of their evergreen forests being high-latitude boreal forests, while most of the evergreen forests in the eastern USA are in the southeast (Figure 1). Empirical research has shown that absolute respiration costs are higher, and thus CUE should be lower, in deciduous than in evergreen trees (Cannell 1982). However, the high respiration costs for our southeastern evergreen forests, due to high temperature and precipitation there, would result in the low CUEs that they exhibit. To explore the relative importance of forest type and environment on CUE, future research could compare MODIS CUE and F/M Z_{CUE} values for similar forest types found in different environments, and for different forest types found within the same environment.

5.2.2. Climatic factors

The trend lines for the relations between CUEs and temperature and precipitation found in this study are similar to those found in other studies (Chambers et al. 2000; Gower 2002; Zhang et al. 2009). The decrease in CUEs with increased temperature is due to higher energy requirements to maintain living tissue, which results in the rate of respiration increasing exponentially with temperature (Ryan et al. 1994). Further, the relation between MODIS CUE and temperature was a convex one that peaked at 7°C, similar to global scale analyses that found a convex relation that peaked at 11°C (Piao et al. 2010) and an asymptotic relationship that plateaued at 10°C (Zhang et al. 2009). The fact that no other study found the shallowing of the slope in MODIS CUE at 18°C that was found in this study suggests that it may be due to the unique combination of temperature and precipitation conditions in the eastern USA. The decrease in CUE with increased precipitation could be due to a variety of factors: increased cloudiness, shortage of soil oxygen, and slowing of organic matter decomposition resulting in a decreased nutrient supply (Schuur and Matson 2001).

5.2.3. Geographic factors

The regression models between CUEs and altitude had the lowest R^2_{adj} of the four environmental factors, while the models for latitude exhibited the highest and second highest R^2_{adj} values for F/M Z_{CUE} and MODIS CUE, respectively. These mixed results are not surprising as these geographical variables are not phenomenological driving variables, but contain a mix of driving variables such as temperature, precipitation, and length of growing season (Valentini, Matteucci, and Dolman 2000). For example, for the eastern USA, PRISM data indicated that latitude was strongly correlated with two important phenomenological variables, temperature (Pearson $r = 0.95$) and precipitation ($r = 0.74$), while altitude was less strongly correlated with temperature ($r = -0.54$) and precipitation ($r = -0.41$). Due to this multi-collinearity, the relations with these geographic variables are only useful descriptively.

5.3. Sources of uncertainty

Both measures of CUE contain sources of uncertainty that reduce their explanatory power. Two major sources of uncertainty in the calculation of MODIS CUE are related to LAI inputs and to GPP predictions. First, the LAI inputs to the calculation of MODIS NPP are for only five types of forests, and thus have very limited ability to account for different stages of stand development within any forest type. This is the case because the assumption made in the MODIS algorithm that live woody mass is related to annual maximum LAI would somewhat artificially reduce the biomass variance, especially when compared with field-measured biomass data (results not shown). This limitation in LAI seems to result in a MODIS CUE sensitive to large-scale meteorological variables rather than local site conditions. Second, MODIS band saturation could result in underestimation of GPP in warm and humid regions (Kwon and Larsen 2012), which would lead to the overestimation of CUE in low latitudes. Similarly, a tower-based validation reported a tendency of MODIS to underestimate GPP in cold and dry regions (Turner et al. 2006), which would also lead to CUE being overestimated in high latitudes.

A potential source of uncertainty in the calculation of F/M Z_{CUE} is related to differences in the NPP components accounted for by allometric models in FIA and by the biophysical parameters in the MODIS GPP components. While MODIS GPP accounts for both above- and below-ground NPP, though not organic carbon stored in soil, FIA NPP's allometric models do not include all of those components. The missing components for FIA are: litterfall, fine roots, forest floor seedlings and saplings (i.e. stems <12.5 cm dbh), and understorey herbaceous plants. The exclusion of litterfall and fine roots should result in FIA NPP being underestimated by 60% (Jenkins, Birdsey, and Pan 2001), while the exclusion of forest floor and understorey should underestimate ecosystem carbon pools by 7% and 2%, respectively (Shifley et al. 2012). These values together suggest that FIA NPP should be 69% lower than MODIS NPP and, indeed, our FIA NPP was 67% lower than MODIS NPP. However, these average values cannot be used to simply rescale FIA NPP to MODIS NPP values, as above- and below-ground biomass appears to exhibit complex log–log linear relations (Enquist and Niklas (2002). It is also possible that the screening process, which excluded hexagons with low data quality and misclassified forest covers, might have resulted in an environmentally biased subset of pixels and plots being employed and thus a biased CUE being obtained. However, the environmental variables for the hexagons that were employed and those that were screened out exhibited similar median values and variances.

5.4. *Relations between MODIS CUE and F/M Z_{CUE}*

5.4.1. *Similarity*

The statistically significant regression between MODIS CUE and F/M Z_{CUE}, and the fact that the strongest model was a linear one, confirms that both CUEs share a common signal. The marked similarity of MODIS CUE to F/M Z_{CUE} supports the usage of MODIS CUE for monitoring carbon balance in the eastern USA. It is unlikely that the similar results stem from them both employing GPP as the denominator in the calculation of CUE, as the numerators of MODIS NPP and FIA NPP are not closely correlated (Pearson $r = 0.11$ at the plot- and pixel-scale, $p < 0.001$).

5.4.2. *Dissimilarity*

The higher regression relations for MODIS CUE suggest that there is more error in F/M Z_{CUE} than in MODIS CUE, which is surprising as it was expected that predictions of MODIS respiration, and thus CUE, would contain large errors (Turner et al. 2005). Although MODIS CUE has stronger regression relations with environmental data than does

F/M Z_{CUE}, there are at least three key differences between the MODIS and FIA data that suggest caution in concluding that MODIS CUE is a superior measure. The first difference is that while FIA NPP, the denominator in F/M Z_{CUE}, is completely independent of the environmental data, MODIS respiration and GPP are both predicted using climatic data, and thus MODIS CUE is not independent of the environmental data. This issue should be explored further in future research.

The second difference is that while MODIS CUE was calculated using absolute values, F/M Z_{CUE} was calculated using standardized FIA NPP and MODIS GPP data. This use of standardized data might result in a mismatch of them that does not occur for absolute data. A solution to this problem could be addressed through the development of a method to predict plot-scale GPP that employs the plot-scale estimates of FIA NPP.

The third difference is that while individual MODIS pixels are 1 km^2 and can only have one of five forest classes, individual FIA plots are 0.0041 km^2 and have 28 forest classes. The smaller size of the FIA plots should allow better matching of CUE with local environmental factors, and the greater number of forest classes should allow the better consideration of the influence of species physiological properties on CUE. To take advantage of this information in FIA plots, research should explore the ability to apply it to co-located MODIS pixels, and thus provide more accurate estimates of CUE.

6. Conclusions

This research examined forest CUEs using both field-based FIA data sets and remotely sensed MODIS data and concluded that CUE varies over environmental and geographic variables across the eastern USA. Although MODIS NPP and its use to calculate CUE have not been strongly validated, the linear relations found between MODIS CUE and F/M Z_{CUE} support the research use of the more easily obtained MODIS CUE. Differences between the two CUEs in their relations with environmental variables point to improvements that need to be made in both the MODIS and FIA data sets. These improvements will increase our understanding of how CUE varies with climate, and thus how the global CUE may respond to future climate change.

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