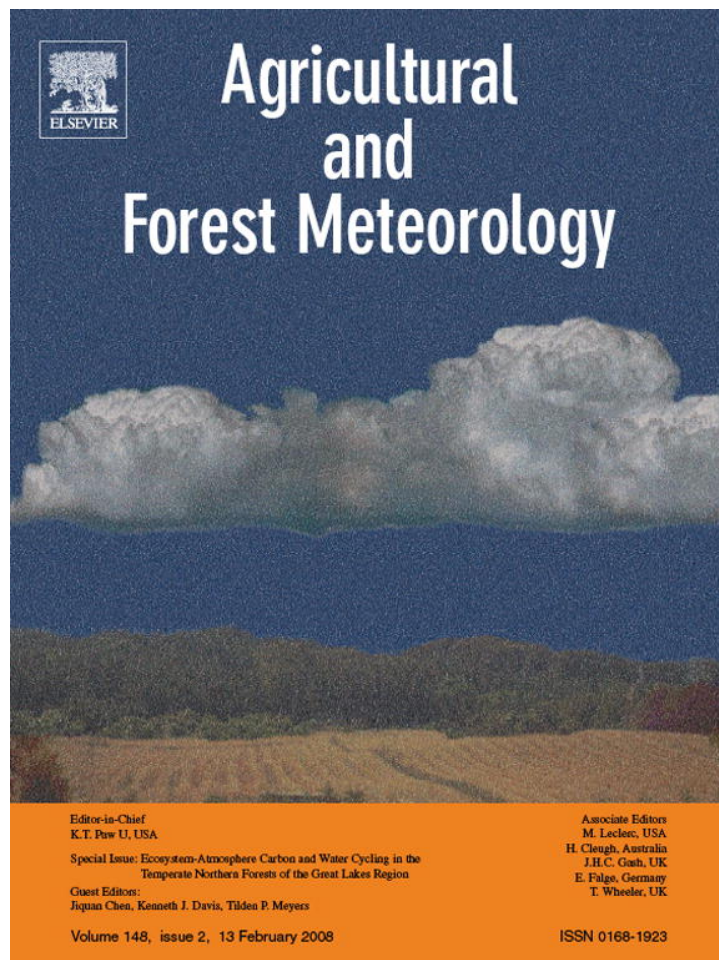


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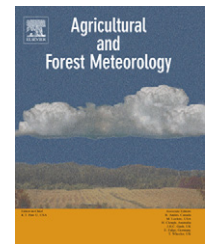


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Comparisons between PnET-Day and eddy covariance based gross ecosystem production in two Northern Wisconsin forests

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ABSTRACT

The PnET-Day model was independently parameterized to compare with estimated eddy covariance gross ecosystem production (GEP; $\text{gC m}^{-2} \text{day}^{-1}$) in a mature mixed hardwood and a mature red pine (*Pinus resinosa*) forest in Northern Wisconsin during the growing season of 2002 and 2003. The mature hardwood forest was dominated by *Populus tremuloides*, *Populus grandidentata*, *Betula papyrifera*, *Quercus rubra*, *Acer rubrum*, and *Acer saccharum*. We evaluated the model's capability to predict the seasonal and interannual dynamics of GEP and explored the sources of discrepancy between PnET-Day and eddy covariance GEP estimates. GEP was directly estimated from the two eddy-flux towers, one for each forest type, during 2002 and 2003. PnET-Day growing season GEP for the mature hardwood forest was 12% higher in 2002 and 12% lower in 2003 than eddy covariance GEP estimates, while the modeled growing season GEP of the mature red pine forest was overestimated by 43 and 32% compared to eddy covariance GEP in 2002 and 2003, respectively. The disagreement between the two methods was attributed to year-to-year variability in foliage biomass and foliar nitrogen (N) in the mature hardwood forest and to high foliage biomass and specific leaf weight in the mature red pine forest (>50% larger than red pine in Harvard Forest where the model was developed and validated). The difference between PnET-Day and eddy covariance GEP estimates was greatest in May in the hardwood forest, primarily due to the discrepancy between the true and parameterized foliage onset day. Our results suggest that improved prediction of foliage onset is necessary to improve PnET-Day estimation of GEP in a hardwood forest.

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1. Introduction

Carbon exchange between the forest canopy and atmosphere is a fundamental terrestrial ecosystem function (Amthor et al., 1994; Thornton et al., 2002; Wofsy et al., 1993). Substantial effort has been made to measure exchanges of carbon, water,

energy, and other ecologically important gases between the forest canopy and the atmosphere. Since we cannot conduct direct measurements continuously in every ecosystem, biophysical models estimating these exchanges have been widely applied to quantify forest-atmosphere interactions at broader temporal and spatial scales (Law et al., 2000). We can

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make predictions with improved confidence after evaluating models across a range of forest types, climate zones, and disturbance regimes (Amthor et al., 1994; Hanson et al., 2004; Law et al., 2000). Ideally, robust mechanistic models can extrapolate measurements across spatial and temporal scales to estimate carbon fluxes (Rastetter et al., 2003; Thornton et al., 2002). This study focused on comparing model predictions (PnET) and in situ long-term eddy-flux tower measurements of gross carbon production (GEP) in the two dominant forest types in the northern hardwood region of the Upper Great Lakes (Desai et al., 2008; Noormets et al., 2008).

We chose to evaluate the accuracy of PnET-Day in this study because the model requires few parameters and has the potential to be applicable from watershed to regional levels. PnET-Day is the core mechanism of the PnET model family. The PnET model family has been used in various forest types to predict regional-scale changes in net primary production (Aber et al., 1995; Jenkins et al., 1999; Ollinger et al., 1998), net ecosystem production (Aber et al., 1995; Law et al., 2000), water yield (McNulty et al., 1996; Ollinger et al., 1998; Sun et al., 2000), and nitrate leaching (Aber et al., 1997). These models have also been used to evaluate the response of ecosystems to a number of different scenarios, such as climate change, N deposition, tropospheric ozone, CO₂ concentration, and land-use history (Aber et al., 1997; Bauer et al., 2004; Ollinger et al., 2002; Rastetter et al., 2003). PnET-Day was originally developed to validate the photosynthetic algorithms in the broader series of PnET models (Aber et al., 1996). The evaluation of model predictions can lend more confidence to the PnET model family and illustrate improvements to the model that enable it to be applied to a broader range of environmental conditions (Medlyn et al., 2003). PnET-Day has thus far been validated for a limited number of forest ecosystems (Aber et al., 1996), none in the Great Lakes region. Clearly, examining ecosystem models in different regions and forest types is necessary in order to apply them for scaling-up ecosystem processes from individual sites to regions. This is the primary contribution of this study to this Chequamegon Ecosystem-Atmosphere Study (ChEAS) special issue of Agricultural and Forest Meteorology.

The objective of this study was to compare the PnET-Day GEP predictions with eddy-flux tower-based GEP estimates in Northern Wisconsin and to identify possible causes of any disagreement. We compared the GEP estimates within a mature northern mixed hardwood and a mature red pine (*Pinus resinosa* Aiton) forest, which are major forest types in the region with differing physiological dynamics (e.g., deciduous and evergreen). We focused primarily on evaluating the accuracy of PnET-Day in predicting interannual and seasonal variation of GEP and identifying the sources of disagreement between the model and eddy-flux tower GEP estimates.

2. Methods

2.1. Study area

The study landscape was located in the Washburn Ranger District of Chequamegon National Forest (CNF) in Northern Wisconsin, USA (46°30'–46°45'N, 91°02'–91°22'W). The major

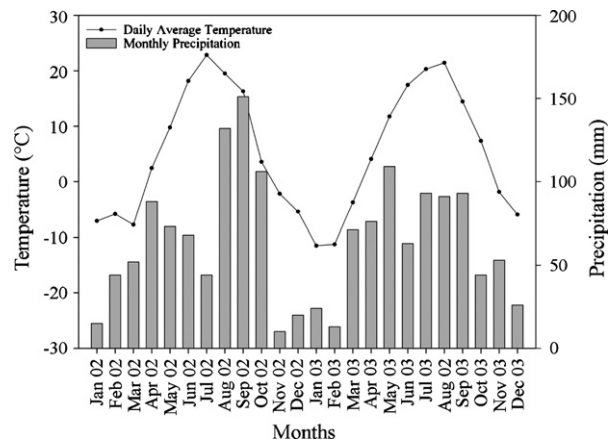


Fig. 1 – Monthly average temperature and monthly precipitation during 2002 and 2003 in Chequamegon National Forest, Wisconsin.

forest types are northern mixed hardwood, red pine, and jack pine (*P. banksiana* Lambert) (Bresee et al., 2004; Brosofske et al., 2001). Mature hardwood forest was dominated by trembling aspen (*Populus tremuloides* Michx.), bigtooth aspen (*Populus gradidentata*, Michx.), paper birch (*Betula papyrifera* Marsh.), red oak (*Quercus rubra* L.), red maple (*Acer rubrum* L.), and sugar maple (*A. saccharum* Marsh.). The landscape geology consists of Precambrian shield bedrock and was glaciated during the Wisconsin glaciation. The topography is flat to rolling and the elevation ranges from 232 to 459 m above sea level. Landforms are terraces and pitted outwash, composed of deep, coarse-textured soils. The climate is characterized by a short, hot summer with between 120 and 140 growing days and a long cold winter (Fig. 1).

2.2. Eddy-flux tower measurement

Net ecosystem production (NEP; equivalent to net ecosystem exchange or NEE) was measured continuously May through October (2002 and 2003) in a mature hardwood and a mature red pine (MRP) forest using the eddy covariance (EC) method (Noormets et al., 2008). The towers were located in the middle of each stand, allowing for uniform fetch in all directions (>30 sensor heights in MHW and about 50 sensor heights in MRP). Each EC system included a LI-7500 open-path infrared gas analyzer (IRGA, Li-Cor, Lincoln, NE, USA), a CSAT3 3-dimensional sonic anemometer (Campbell Scientific (CSI), Logan, UT, USA), and a CR5000 data logger (CSI). The 30 min mean fluxes of CO₂ were computed as the covariance of vertical wind speed and the concentration of CO₂ after removing spikes (>6 standard deviations), correcting sonic temperatures for humidity and pressure, and rotating wind coordinates around two axes so that mean vertical and mean cross-wind vectors equaled zero for the 30 min period (Lee et al., 2004). The fluxes were corrected for fluctuations in air density using the Webb–Pearman–Leuning expression (Leuning, 2004).

The flux data were almost continuous during the study period, with less than 10% missing due to instrument or power

failure. Upon screening the data and flagging periods of precipitation and dew, inadequate turbulent mixing, out of range fluxes (e.g., $|\text{NEP}| > 50$ ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and low battery voltage (< 10.5 V), the amount of usable data was 60–70% of the total data, which is typical for eddy covariance measurement during the growing season (Falge et al., 2002). In addition to the above criteria, the flux data were also flagged for out-of-range CO_2 or H_2O density, wind speed, air pressure and air temperature. Often, unusable data was identified by more than one flag. Gaps in data were filled using the rectangular hyperbola light response model with embedded dynamic temperature response function for ecosystem respiration (Noormets et al., 2008):

$$\text{NEP} = R_{10} e^{\frac{E_a}{R} \left(\frac{1}{T_{\text{ref}} - T_0} - \frac{1}{T_a - T_0} \right)} + \left(\frac{\alpha \times \phi \times P_{\text{max}}}{\alpha \times \phi + P_{\text{max}}} \right) \quad (1)$$

where R_{10} is reference respiration, normalized to a common temperature ($T_{\text{ref}} = 283.15 \text{ K} = 10^\circ\text{C}$), E_a is activation energy ($\text{kJ mol}^{-1} \text{ K}^{-1}$), R is the universal gas constant ($8.3134 \text{ J mol}^{-1} \text{ K}^{-1}$), T_0 is the temperature below which respiration is assumed to be zero ($T_0 = 227.15 \text{ K}$), T_a is the air temperature above the canopy, α is the apparent quantum yield ($\mu\text{mol CO}_2 \mu\text{mol}^{-1} \text{ PAR}$), ϕ is PAR ($\mu\text{mol quanta m}^{-2} \text{ s}^{-1}$) and P_{max} is the maximum apparent photosynthetic capacity of the canopy ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). The respiration component of the model was re-fitted at monthly intervals with seasonally fixed E_a , whereas a common seasonal parameterization was used for the assimilatory component. The model explained 71 and 84% of the variation in measured NEP in mature hardwood and mature red pine forests, respectively. Tower GEP estimates had uncertainties which could not be quantified, because ecosystem respiration cannot be directly measured. Since respiration was always positive, we estimated GEP ($\text{gC m}^{-2} \text{ day}^{-1}$) as:

$$\text{GEP} = \text{NEP} + R \quad (2)$$

2.3. PnET-Day parameterization

PnET-Day (version 5.1; Aber et al., 1996) model was derived from the PnET model, which models the whole forest carbon and water balance, to predict the seasonal change of whole forest canopy photosynthesis using daily climate data. The core mechanism of the model is the relationship between the foliar nitrogen (N) concentration and maximum photosynthetic rate with response functions of radiation intensity, temperature, vapor pressure deficit and changes in radiation intensity and specific leaf weight (SLW) within a canopy. The model estimates maximum gross photosynthesis and it is adjusted with daily foliage mass, radiation and temperature. The model does not consider water stress and the GEP estimation of the model is independent of respiration routine in the model.

PnET-Day (Aber et al., 1996) requires photosynthesis, canopy, and site related parameters. Among the photosynthesis related parameters, we used model default values for interception (AmaxA) and slope (AmaxB) of the foliar nitrogen concentration (FolNCon; %, w/w). Default values were used for instantaneous maximum photosynthesis (Amax; μmol

Table 1 – Input parameters used for the study (please refer to Aber et al. (1996) for further details on each parameter)

	Mature hardwood	Mature red pine
Photosynthesis parameters		
AmaxA	−46	5.3
AmaxB	71.9	21.5
AmaxFrac	0.76	0.76
BaseFolRespFrac	0.1	0.1
RespQ ₁₀	2	2
HalfSat (μE)	150	150
PsnTMin ($^\circ\text{C}$)	4	2
PsnTOpt ($^\circ\text{C}$)	24	22
Canopy parameters		
FolNCon (w/w, %)	1.83	1.1
SLWmax (g m^{-2})	81	321
SLWdel ($\text{g m}^{-2} \text{ g}^{-1}$ foliage)	0.001	0
k	0.61	0.48
GDDFolStart	332	332
GDDFolEnd	764	1031
SenescStart (day)	272	272
FolMassMin (g m^{-2})	0	600
FolMassMax (g m^{-2})	400	1200
Lat ($^\circ$)	46.6	46.6

$\text{CO}_2 \text{ m}^{-2} \text{ leaf s}^{-1}$) relationships, daily average maximum photosynthesis (AmaxFrac), dark respiration (BaseFolRespFrac), foliage respiration Q_{10} , and minimum temperature for photosynthesis (PsnTMin; $^\circ\text{C}$) (Table 1; Aber et al., 1996; Goodale et al., 1998).

We estimated or modified the default values of optimum photosynthesis temperature (PsnTOpt; $^\circ\text{C}$) and half saturation of photosynthesis for light (HalfSat; μE), which is a measure of the light level at which the photosynthesis becomes half of Amax. Optimum temperature for photosynthesis was estimated from the mean July temperature of the central region within tree species' distribution. Among dominant tree species, sugar maple and bigtooth aspen were chosen to estimate optimum temperature for photosynthesis for mature hardwoods due to the comparatively narrow native habitat in which they are found (<http://climchange.cr.usgs.gov/data/atlas/little/>). The estimated optimum temperature for photosynthesis was 24 and 22 $^\circ\text{C}$ for hardwood and red pine, respectively.

We measured the light response curve and half saturation point of a total of 19 mature (> 60 years old) trees, including five paper birch, red oak, red maple, and sugar maple trees and four bigtooth aspen trees, using a LiCor 6400 portable photosynthesis system (LiCor Lincoln, NE) (Table 2). All photosynthesis measurements were performed under ambient CO_2 concentrations ($350\text{--}370 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) in mid- to late summer (June 24 to September 8) between 8 a.m. and 5 p.m. Measurements were replicated at least three times per tree species, and light response curves were measured at the upper, middle, and lower levels of the crown following the vertical light zone of each tree. The half saturation of photosynthesis for light of each tree was estimated by averaging the half saturation of photosynthesis for light at the three-crown positions. The half saturation of photosynth-

Table 2 – Half saturation of photosynthesis for light (μE) of five major species in Chequamegon National Forest, Wisconsin

Species	Canopy position		
	U	M	L
<i>Acer saccharum</i>	140 (23)	99 (13)	62 (7)
<i>Populus gradidentata</i>	259 (29)	248 (21)	208 (42)
<i>Populus tremuloides</i>	187 (53)	118 (19)	103 (10)
<i>Acer rubrum</i>	176 (4)	175 (33)	100 (5)
<i>Quercus rubra</i>	258 (54)	206 (44)	91 (8)

The data was collected at three positions in the canopy: the top 1/3 of crown (U), middle of crown (M), and bottom 1/3 of crown lower (L). The mean values are reported with one standard error in parentheses.

esis for light of the hardwood forest was calculated by multiplying the estimated tree half saturation of photosynthesis for light with the ratio of foliage biomass between species in the mature hardwood forest, which was estimated by field survey and allometric equations (TerMikaelian and Korzukhin, 1997; Zheng et al., 2004).

For the field survey, five 490 m² plots were randomly established for each mature hardwood and mature red pine, and the diameters at breast height in the plot were recorded (Zheng et al., 2004). Foliage biomass was estimated using published biometric equations (TerMikaelian and Korzukhin,

1997). The estimated half saturation of photosynthesis for light in the mature hardwood forest was 150 μE . Aber et al. (1996) reported that the half saturation of photosynthesis for light values were the same for the northern hardwood and red pine forests, thus we assumed the same half saturation of photosynthesis, 150 μE , applied both to hardwood and red pine forests (Table 1).

All canopy-related parameters were independently measured or estimated (Table 1). Foliar N concentration and SLW (g m^{-2}) were measured in August of 2003 for seven dominant species in the CNF: red maple, sugar maple, paper birch, big tooth aspen, trembling aspen, red oak, and red pine (Table 3). Foliage samples were collected from five dominant trees per species, which were marked for timber harvesting by the USDA Forest Service. Each crown was evenly divided into six sections (by north and south halves and three vertical heights), and one sample was taken per section. Foliar N concentration and SLW of each foliage sample were measured using a 2400 Series II CHNS/O Analyzer (Perkin-Elmer, Inc., Boston, MA, USA) and WinFolia 2002a or WinNeedle 2002a (Regent Instruments Inc., Quebec, Canada), respectively. Foliar N concentration was averaged by crown position (Table 3), and then by species (i.e., mean foliar N concentration by crown position was averaged). All species showed a positive correlation and an overall significantly ($p = 0.01$) positive relationship ($\text{SLW} = 0.11 \times \text{light half saturation} + 48.67$, $r^2 = 0.41$) between SLW and light half saturation.

Table 3 – Mean (AVE) foliar nitrogen concentration and specific leaf weight of seven major species in the Chequamegon National Forest, Wisconsin

Species	Character Direction Position	Foliar nitrogen (%)		Specific leaf weight (g m^{-2})	
		North	South	North	South
		AVE (S.E.)	AVE (S.E.)	AVE (S.E.)	AVE (S.E.)
<i>Acer rubrum</i>	U	1.6 (0.09)	1.5 (0.05)	71 (1.7)	68 (5.9)
	M	1.7 (0.05)	1.5 (0.10)	63 (3.5)	61 (4.9)
	L	2.0 (0.28)	1.5 (0.07)	64 (4.4)	51 (6.2)
<i>Acer saccharum</i>	U	1.4 (0.03)	1.6 (0.00)	74 (4.8)	79 (3.0)
	M	1.5 (0.01)	1.6 (0.00)	57 (4.0)	57 (0.9)
	L	1.6 (0.10)	1.5 (0.04)	48 (3.0)	46 (2.3)
<i>Betula papyrifera</i>	U	1.8 (0.15)	1.7 (0.13)	87 (5.1)	88 (6.1)
	M	1.9 (0.16)	1.8 (0.13)	79 (9.4)	80 (8.0)
	L	1.9 (0.07)	1.7 (0.14)	68 (3.4)	72 (6.1)
<i>Populus gradidentata</i>	U	2.1 (0.08)	2.2 (0.07)	73 (4.5)	75 (3.5)
	M	2.3 (0.06)	2.2 (0.10)	64 (6.7)	64 (3.1)
	L	2.1 (0.08)	2.2 (0.05)	73 (2.4)	59 (2.6)
<i>Populus tremuloides</i>	U	1.9 (0.13)	2.0 (0.20)	81 (3.4)	84 (6.2)
	M	2.0 (0.16)	1.9 (0.09)	75 (4.9)	76 (5.3)
	L	2.1 (0.18)	2.0 (0.22)	61 (4.0)	61 (3.0)
<i>Quercus rubra</i>	U	1.9 (0.07)	2.1 (0.05)	100 (1.7)	78 (4.1)
	M	2.1 (0.13)	2.0 (0.04)	68 (8.2)	61 (4.5)
	L	2.2 (0.07)	2.2 (0.25)	53 (3.9)	52 (3.5)
<i>Pinus resinosa</i>	U	1.1 (0.08)	1.0 (0.10)	258 (3.6)	258 (4.2)
	M	1.0 (0.06)	1.1 (0.09)	250 (7.9)	255 (11.3)
	L	1.1 (0.06)	1.0 (0.03)	256 (9.3)	233 (7.2)

Samples were collected from two directional (north and south) and three vertical positions (top 1/3 of crown (U), middle of crown (M), and bottom 1/3 of crown lower (L)). One standard error (S.E.) is included in parentheses after each value.

The maximum SLW (SLW_{Max}) of a species was estimated by averaging SLW measurements from the top of the crown, which was the position on the tree where the highest SLW was found. The hardwood maximum SLW was calculated from a weighted averaged maximum SLW of the dominant species using the estimated foliage biomass ratio. To calculate the change in SLW with canopy depth (SLW_{Del}; $\text{g m}^{-2} \text{g}^{-1}$ foliage biomass), we first calculated SLW change over varying vertical heights in the crown. The differences in the SLW between the top and bottom of the crown were calculated for each tree and then divided by the foliage biomass, which was estimated from allometric equations (TerMikaelian and Korzukhin, 1997). The hardwood SLW_{Del} was calculated by averaging species SLW_{Del} with foliage biomass ratio. SLW_{Del} of each species was the mean value of each tree's change in SLW over its crown depth.

Light attenuation (k) in the forest canopy was derived by the Beer-Lambert exponential decay function (Aber et al., 1996). We measured leaf area index (LAI) and light intensity to estimate the k values of the hardwood and pine forests. LAI was estimated by the biometric method. Photosynthetically active radiation (PAR; $\mu\text{moles m}^{-2} \text{s}^{-1}$) inside and outside of the canopy was assessed between noon and 3 p.m. The outside PAR was measured in the center of an open space with a diameter of at least three tree heights. Another set of LAI was also estimated independently in this study using hemispherical photo and WinScanopy Trade Mark 2003d software (Regent Instruments Inc., Quebec, Canada) in the mature hardwood forest in 2002 and 2003.

We estimated the foliage onset growing degree days (GDD_{FolStart}), growing degree days (GDD) without foliage growth (GDD_{FolEnd}), and senescence date (SenescStart) using normalized vegetation index (NDVI). We collected 8-day composite 250 m-resolution MODIS images from April to November and masked them with previous classification (Bresee et al., 2004) to estimate the NDVI dynamics of mature hardwood and mature red pine forests. We estimated the parameters by averaging the 2002 and 2003 values (Table 1). GDD_{FolStart} was estimated to be 332 for both mature hardwood and mature red pine forests (Fig. 2). GDD_{FolEnd} was estimated as 764 and 1031 for mature hardwood and mature red pine forests, respectively (Fig. 2). SenescStart was estimated as Julian day 272 for both mature hardwood and mature red pine. As previously indicated, foliage biomass was estimated from field surveys and biometric equations (TerMikaelian and Korzukhin, 1997) developed in the Great Lakes region. The maximum foliage biomass (FolMass_{Max}) was set equal to the estimated foliage biomass. The minimum foliage biomass (FolMass_{Min}) was set to zero for hardwood forests and half of maximum foliage biomass for red pine (Aber et al., 1996).

Daily minimum and maximum air temperature and daily mean PAR were measured above the canopy. Daily mean PAR values were only used when greater than 20 ($\mu\text{mol quanta m}^{-2} \text{s}^{-1}$). To assess possible causes of disagreement between PnET-Day GEP (Model GEP) and eddy-flux tower GEP (tower GEP) estimates, we calculated ΔGEP ($\text{gC m}^{-2} \text{day}^{-1}$; $\Delta\text{GEP} = \text{Tower GEP} - \text{Model GEP}$). Monthly root mean square (RMS) of ΔGEP was the square root value of monthly averaged ΔGEP^2 . All statistical analyses were performed using S-plus 6.1 (Insightful Corp., Seattle, WA, USA).

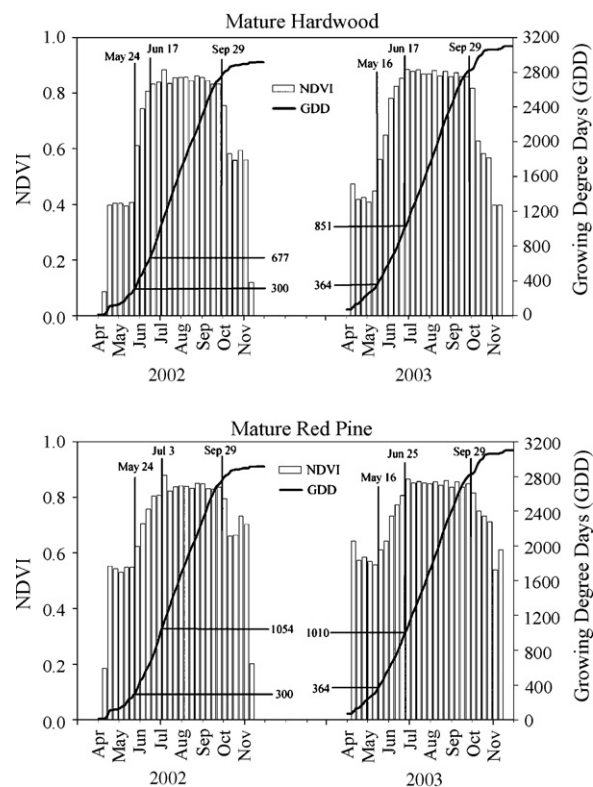


Fig. 2 – NDVI dynamics and growing degree days (GDD) in 2002 and 2003. NDVI was estimated from 8-day composite 250 m-resolution MODIS images. The foliage onset, foliage growing period, and their GDD values are included.

3. Results

3.1. Mature hardwood

Overall, modeled GEP agreed well with tower GEP, though differences existed by year and season (Figs. 3–5). A linear regression between the two values yielded slopes of 1.12 and 0.88 for 2002 and 2003, respectively (Fig. 4a–c), indicating that the model estimated GEP to be 12% higher than tower GEP in 2002 and 12% lower in 2003. Moreover, the modeled and tower GEP values followed similar patterns (Fig. 3a–c) and exhibited a good linear relationship with $r^2 = 0.89$ and 0.83 in 2002 and 2003, respectively (Fig. 4a–c). We observed seasonality in the discrepancies between modeled and tower GEP. Monthly RMS of ΔGEP was largest in September of 2002 and May of 2003 (Fig. 5a). Modeled GEP was 31.6 % (mean value; $2.0 \text{gC m}^{-2} \text{day}^{-1}$) larger than tower GEP between August 23 and September 18, 2002 (Fig. 3a). Tower-based estimates of GEP were positive before foliage onset, but model-based estimates were zero during the same time (Fig. 3a–c).

The RMS of ΔGEP was also large in May of 2002 and September of 2003 (in both cases, the second largest by year; Fig. 5a). The RMS was smallest in June and July of 2002 and 2003, respectively (Fig. 5a). Although the RMS values were generally lower in 2003 than 2002, there was an exception in May (when it was 2.4 in 2003 and 1.5 in 2002; Fig. 5a). The ΔGEP

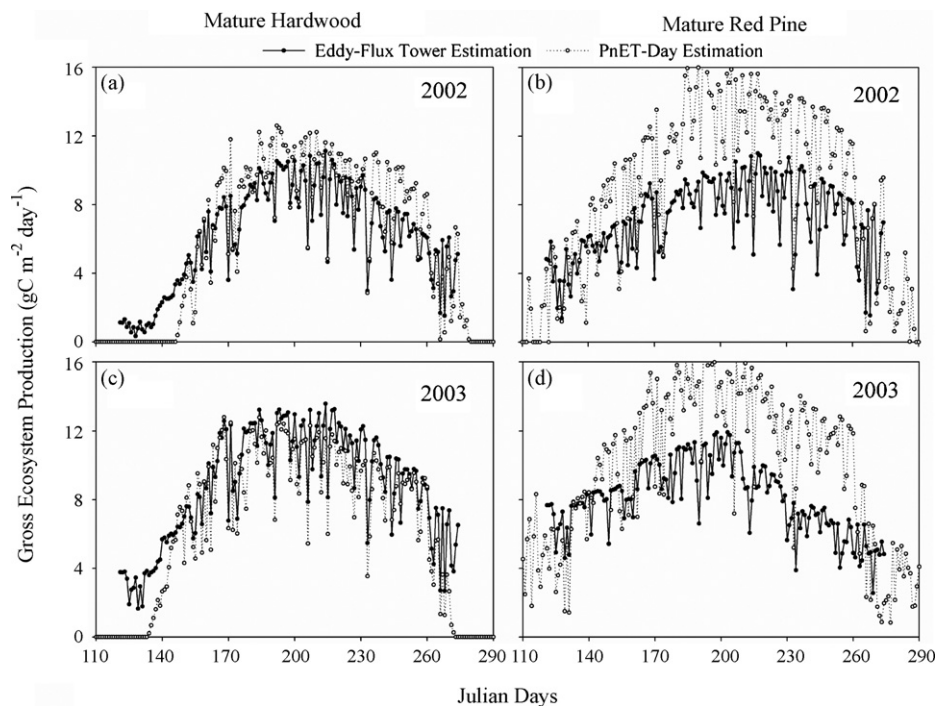


Fig. 3 – Comparisons of the PnET-Day gross ecosystem production (GEP; $\text{gC m}^{-2} \text{day}^{-1}$) estimate with eddy-flux tower GEP estimate in mature hardwood and mature red pine forests over time for the growing seasons of 2002 and 2003. (a) 2002 mature hardwood forest, (b) 2002 mature red pine forest, (c) 2003 mature hardwood forest, and (d) 2003 mature red pine forest.

($\text{gC m}^{-2} \text{day}^{-1}$) was less scattered in July and August than in May, June, and September (Fig. 5a). ΔGEP ranged from -3.8 to 5.4 , while monthly RMS ($\text{gC m}^{-2} \text{day}^{-1}$) varied from 1.0 to 2.4 (Fig. 5a).

3.2. Mature red pine

Modeled GEP did not agree well with tower GEP (Figs. 3–5) in the mature red pine forest. The model estimated GEP to be 43 and 32% higher than tower GEP in 2002 and 2003, respectively (Fig. 4b and d). Their seasonal patterns were similar (Fig. 3b–d), but the two estimates showed a poor linear relationship in 2003 ($r^2 = 0.81$ and 0.32 for 2002 and 2003, respectively) (Fig. 4). We observed that tower GEP started to decrease in late July (Fig. 3b–d). Monthly mean ΔGEP ($\text{gC m}^{-2} \text{day}^{-1}$) ranged from -8.8 to 4.8 , while the monthly RMS ($\text{gC m}^{-2} \text{day}^{-1}$) of ΔGEP varied from 1.7 to 5.0 (Fig. 5b).

The seasonal patterns of RMS (tower-model GEP differences) in mature red pines were opposite those of mature hardwood (Fig. 5a and b). Furthermore, monthly RMS values of ΔGEP were larger in the mature red pine than in the mature hardwood forest (Fig. 5b). Monthly RMS of ΔGEP followed a U-shaped pattern in the mature hardwood forest and a bell-shaped pattern in the mature red pine forest. The monthly RMS ($\text{gC m}^{-2} \text{day}^{-1}$) of ΔGEP for the mature red pine stand was smallest in May of both years (1.9 and 1.7 in 2002 and 2003, respectively) (Fig. 5b), and largest in July in 2002 (5.0) and August in 2003 (4.8). The second largest value occurred in August in 2002 (4.0) and July in 2003 (4.3) (Fig. 5b). Considering that maximum tower GEP was 11.0 and 11.9 in 2002 and 2003,

respectively, the fact that means RMS of ΔGEP ranged from 4.0 to 5.0 was an indication of large amounts of error. Modeled GEP matched tower GEP better earlier in the growing season (May–June) than later (July–August) (Fig. 3b–d). Observed (tower) GEP sharply decreased at the beginning of August 2003 in the red pine forest (Fig. 3d).

4. Discussion

4.1. Mature hardwood

We suspect that an improper parameter value related to canopy characteristics (Table 1) caused the interannual change in slope of fit between modeled and tower GEP since canopy characteristics change annually in nature but were fixed in the simulations. PnET-Day estimated gross photosynthesis from the foliage biomass, SLW, and foliar N, which was expected to vary from year to year, thus generating interannual variation. Foliage biomass can vary between years because it is determined by complex interactions between physiological and meteorological factors (e.g., nutrient availability, water availability, and wind). Mean NDVI during July and August was higher in 2003 (0.88) than in 2002 (0.86) ($p < 0.05$), implying higher foliage biomass in 2003 (Fassnacht et al., 1997). Estimated LAI using hemispheric photos was 3.30 ± 0.13 (mean \pm one standard error) and 3.56 ± 0.61 in 2002 and 2003, respectively. It was not possible to estimate the actual foliage biomass in the two study years from the LAI estimates due to lack of field data, but the results implied that

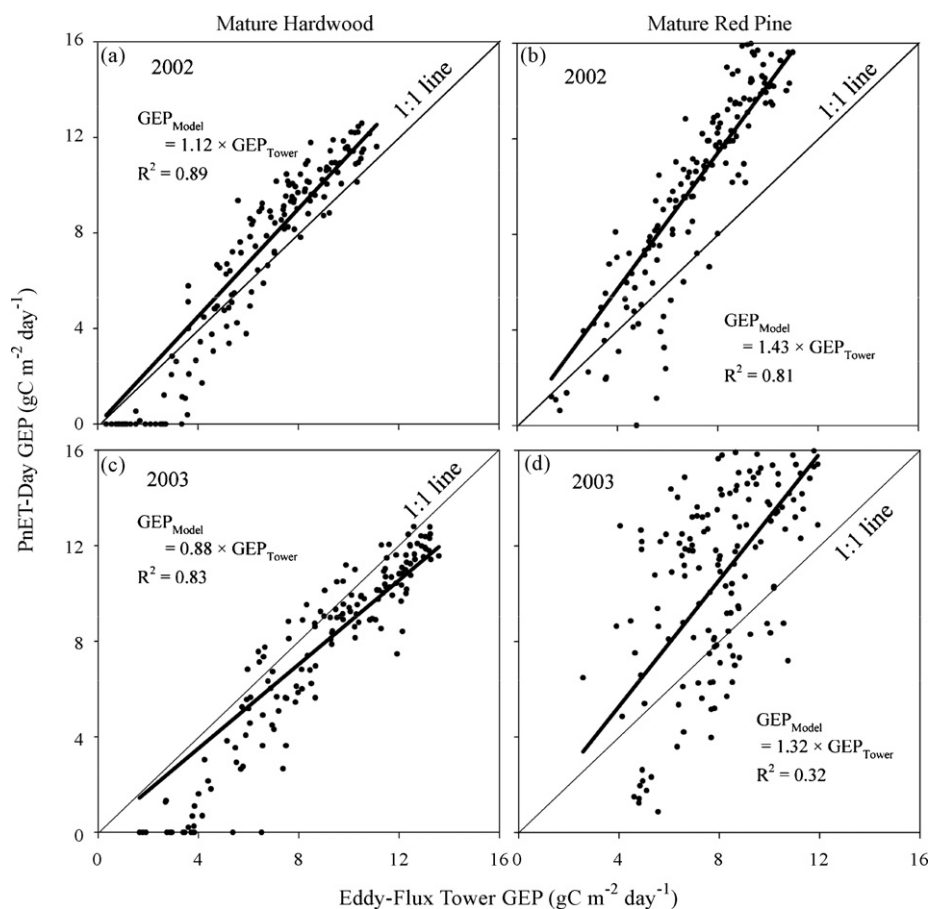


Fig. 4 – Linear regression analysis comparing the PnET-Day gross ecosystem production (GEP; $\text{gC m}^{-2} \text{day}^{-1}$) estimates with eddy-flux tower GEP estimates in mature hardwood and mature red pine forests during the growing seasons of 2002 and 2003. Regression coefficients (slope) and r^2 values are included for: (a) 2002 mature hardwood forest, (b) 2002 mature red pine forest, (c) 2003 mature hardwood forest, and (d) 2003 mature red pine forest.

foliage biomass was approximately 8% higher in 2003 than in 2002. We used the (low) 2002 foliage biomass estimate in the model simulation, which may explain a large portion of the disagreement between modeled and tower GEP in 2003.

A possible explanation for the tower-model GEP difference in 2002 was foliar N concentration. Foliar N concentration is a fundamental variable in predicting the maximum photosynthesis rate (Aber and Federer, 1992; Aber et al., 1995) and can vary annually. Foliar N concentration for 2002 was not available and might have been lower than our estimate based on 2003 field data. The difference between model and tower GEP increased later in the growing season (Fig. 3a); it was unclear what caused this trend.

RMS of tower-model GEP differences was high in May for both years due to the predicted foliage onset day. PnET-Day predicts foliage onset day using the foliage onset GDD data, which we estimated using NDVI. However, only 8-day composite images were available to track NDVI seasonal dynamics, which limited our ability to estimate foliage onset GDD. RMS of tower-model GEP differences decreased with decreasing foliage onset GDD value. Our results suggested that a more accurate foliage onset parameter would be critical in reducing model error.

4.2. Mature red pine

Modeled GEP was higher than tower GEP throughout the year. We suspect foliar N and foliage biomass were the principle causes of this discrepancy. Foliage biomass in the CNF (1200 g m^{-2}) was 50% higher than reported foliage biomass (800 g m^{-2}) in the Harvard Experimental Forest (HEF), Massachusetts (Aber et al., 1996). The foliage biomass estimates seem reasonable given that the red pine forests in CNF and HEF showed similar biometric LAI values (3.74 and 4.00, respectively), but the SLW was substantially higher in the CNF (321 and 200 g m^{-2} for CNF and HEF, respectively) (Aber et al., 1996). Foliar N concentration was the same ($1.1\% \text{ mgN g}^{-1}$) in these two forests. Because the PnET-Day model calculated GEP using a linear relationship between foliar N per foliage mass and maximum photosynthesis rate (Aber et al., 1996; Reich et al., 1995, 1991), 50% more foliage biomass with the same foliar N concentration would result in 50% more GEP. We question model assumptions about the relationship between foliar N per foliage mass and photosynthesis because forests can have higher foliage biomass due to higher SLW, as we found in CNF. However, we could not rule out the possibility that the differences between modeled and tower GEP was

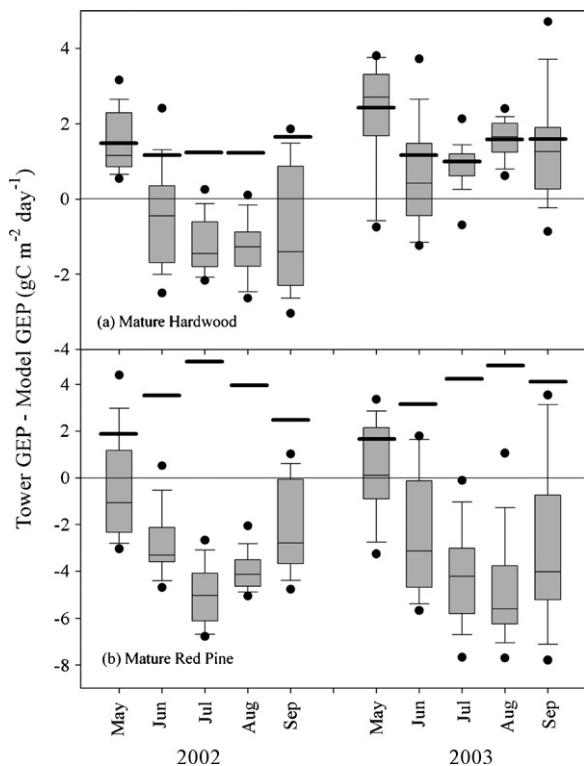


Fig. 5 – Monthly distribution of the difference between the daily-sum eddy-flux tower gross ecosystem production (GEP; $\text{gC m}^{-2} \text{day}^{-1}$) estimate and PnET-Day's daily GEP estimate in (a) mature hardwood and (b) mature red pine. The thick bar indicates the root mean square value (RMS). Bars of box-whisker plots represent 5, 25, 50, 75, and 95% values of the absolute difference of the month and dots are the maximum and minimum value of the month.

caused by the error in foliage biomass estimation using biometric equations, DBH sampling error compared to the footprint of the tower flux measurement, and the uncertainties in ecosystem respiration estimation.

We propose two possible ways to improve modeled GEP in mature red pine forests. The first is to apply a relationship between foliar N per foliage area and photosynthesis in PnET-Day in order to calculate gross photosynthesis. This will reduce the problem of GEP overestimation caused by high foliage biomass and SLW. Employing this relationship could improve the applicability of PnET-Day over large areas, where SLW varies due to varying light intensity. Ellsworth and Reich (1992) reported a significant relationship between foliar N per foliage area and photosynthesis. The second possible improvement is to develop a localized linear relationship between foliar N and photosynthesis. However, applying PnET-Day to larger areas would then require more labor-intensive and time-consuming studies.

We observed high RMS of tower-model GEP differences in July and August, and suspect that these values could result from changing physiological dynamics of foliar N and foliage biomass. Pine trees tend to relocate N, commonly a limiting factor in this forest type, from needles to twigs to increase their N use efficiency (Son et al., 2000). Red pines in Wisconsin

were reported to start retranslocating N in August (Son and Gower, 1991). Leaf nitrogen (N) concentration is closely related to photosynthesis (Aber et al., 1996; Reich et al., 1995, 1991); decreased N concentration results in a decreased photosynthetic rate. Because PnET-Day assumes that foliar N is constant throughout the growing season, it would not capture a late summer decrease in foliar N concentration. The effect of foliar N decrease on GEP could be simulated by early leaf shedding in the current model structure. Chlorophyll concentration has a close relationship with foliar N and Zhang et al. (2005) showed that PAR absorption by chlorophyll started to decrease earlier than PAR absorption by the canopy. Kinerson et al. (1974) and Sampson et al. (2003) revealed that foliage biomass peaked in August and started to drop in September, which is 1 month prior to major senescence in North Carolina loblolly pine (*Pinus taeda* L.). It would not be possible to identify small amounts of needle loss (<10%) with NDVI, because NDVI commonly saturates at a LAI of 3.0–3.5 (Fassnacht et al., 1997). Our results suggest that an improved representation of the physiological dynamics of foliar N and foliage biomass is likely to improve PnET-Day's GEP prediction.

4.3. General observation in parameter preparation

Previous studies have shown contradictory results with respect to changes in foliar N concentration as a function of vertical canopy position (Brooks et al., 1994; Ellsworth and Reich, 1993; Hirose et al., 1988). Foliar N concentrations of seven species in our study did not show any clear relationship to height within the crown (Table 3). The observed decrease of SLW with height in the canopy is likely due to the changing light conditions throughout the canopy (Hirose et al., 1988). N mass per unit foliage area changed with altitude within the canopy, but N mass per unit foliage mass did not (Tables 2 and 3)

5. Conclusions

In a mature hardwood forest, modeled GEP (PnET-Day) was 12% higher than tower-based measurements in 2002 and 12% lower in 2003. We believe that this difference was caused by interannual variation in foliage biomass and foliar N concentration. In a mature red pine forest, model GEP was 43 and 32% higher than tower GEP in 2002 and 2003, respectively. We suspect the difference resulted from high foliage biomass combined with high SLW in the red pine forest, where gross photosynthesis was estimated by an assumed linear relationship between foliar N per foliage mass and photosynthesis. Our results showed that employing this linear relationship in the PnET-Day model could cause major disagreement when the foliage biomass and SLW are considerably different from those in the Harvard Experimental Forest, where the model was developed. Additionally, differences could be caused by any errors in foliage biomass estimation using biometric equations, DBH sampling error compared to the footprint of the tower flux measurement, and uncertainties in estimating ecosystem respiration.

Our results suggest that investigating the relationship between foliar N per foliage area and photosynthesis and

incorporating results into the model may enhance the application of the model to a wide range of ecosystems, where SLW varies greatly due to different light intensities. The RMS of Δ GEP in May was highest during the growing season in the mature hardwood forest mainly due to errors in the prediction of foliage onset. Our results suggest that improving the prediction of foliage onset would improve PnET-Day's GEP prediction in this mature hardwood forest. Model GEP would also be effected by N retranslocation and needle shedding prior to fall senescence in the mature red pine forest. Our results suggest that adding a N retranslocation term for the red pine forest might improve model accuracy. In conclusion, this study has identified several ways to improve PnET-Day's ability to predict GEP accurately in this region. Our suggestions should further aid in the effort to scale-up carbon flux estimates from individual sites to the region through modeling.

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