

Heterogeneity of light use efficiency in a northern Wisconsin forest: implications for modeling net primary production with remote sensing

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Abstract

Light use efficiency (LUE) models are often used with remotely sensed data products to estimate net primary production (NPP) from local to global scales. However, data on the variability of the LUE coefficient, ϵ , on the landscape are minimal and sometimes conflicting. The objectives of this study were to (1) quantify and compare the variability of LUE among five forest cover types: aspen, northern hardwoods, red pine, forested wetland, and upland conifer; and (2) quantify the variability of ϵ between two years, 1999 and 2000, and relate differences to environmental conditions. The study site was in a northern temperate forest in Wisconsin, USA. Northern hardwood forests, primarily consisting of sugar maple, had the highest ϵ each year followed by aspen, red pine, forested wetlands, and upland conifer. NPP was estimated using radial growth measurements and published allometric equations. Absorbed photosynthetically active radiation (APAR) was estimated optically using a Li-Cor Plant Canopy Analyzer. Growing season ϵ of all forest cover types increased significantly from 0.42 in 1999 to 0.47 (gC MJ^{-1}) in 2000. Annual ϵ of all forest cover types increased significantly from 0.33 in 1999 to 0.36 (gC MJ^{-1}) in 2000. Growing season and annual ϵ differed significantly ($p \leq 0.001$) among forest cover types for each year. Future research should consider variations in LUE among mixtures of many land cover types, especially forested wetlands. Results from this study show that LUE models should consider species-specific efficiency factors rather than biome-specific factors. Remote sensing-based land cover classifications should also reflect species differences for this area if the classification map is used in estimating NPP with an LUE model.

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1. Introduction

Net primary production (NPP), the difference between gross primary production (GPP) and autotrophic respiration, is an important ecosystem process because it removes carbon dioxide (CO_2) from the atmosphere and stores it in short-lived (foliage and fine roots) and long-lived (wood) tissues. The gross uptake of CO_2 (GPP) and the allocation of carbon to autotrophic respiration and biomass components

are sensitive to climate change, yet a clear understanding of this process is lacking (Canadell et al., 2000). Ecosystem process models that simulate NPP require inputs on the ecophysiological and biophysical characteristics of the ecosystem of interest. Remotely sensed data indirectly provide some of the spatial information (e.g., land cover, leaf area index) needed to simulate carbon dynamics from landscape to global scales (Asrar et al., 1985; Field et al., 1995; Tucker & Sellers, 1986; Waring & Running, 1998). Land cover and leaf area index (LAI) data can be used for species- or life form-specific model parameterization. Ecosystem models driven with remotely sensed data will

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be an integral part of developing a global carbon monitoring system (Running et al., 1999). Several different approaches have been used to estimate carbon exchange from regional to global scales (Goetz & Prince, 1999). However, model estimates of global NPP vary by twofold (40–80 PgC year⁻¹), reflecting the need to better understand the underlying processes influencing NPP and the appropriate means to monitor those processes (Cramer et al., 1999).

The positive relationship between NPP and absorbed photosynthetically active radiation (APAR) is the basis for the light use efficiency (LUE) model (Gower et al., 1999; Monteith, 1972). In this paper, we focus on the variability of ϵ because it has been used in estimating NPP and is often coupled with remote sensing data products (Bartelink et al., 1997; Coops et al., 1998; Choudhury, 2001; Franklin et al., 1997; Goetz & Prince, 1998; Gower et al., 1999; Landsberg & Gower, 1997; Medlyn, 1998; Running et al., 1994; Turner et al., 2002). The LUE concept was proposed by Monteith (1972, 1977). NPP and APAR are related by light use term such that

$$\text{NPP} = \epsilon \text{APAR} \quad (1)$$

where ϵ is the LUE coefficient and is expressed as the amount of carbon produced per unit of absorbed PAR (gC MJ⁻¹). Two advantages of modeling NPP using Eq. (1) are: (1) it is theoretically simple to use, and 2) it can be driven with remotely sensed data (Anderson et al., 2000; Field et al., 1995; Gower et al., 1999; Kumar & Monteith, 1982; Prince & Goward, 1995). The simplicity of LUE models is partly due to the functional convergence hypothesis, which predicts that ϵ should be similar among functional plant groups subject to biophysical constraints, such as light availability, aerodynamic resistance, and time lags associated with light absorption and net photosynthesis (Field, 1991). Estimating global NPP is simplified greatly if ϵ varies little among species or plant functional groups. However, Goetz and Prince (1998) suggest that ϵ converges better for gross production than net production. Several authors have suggested that more work is needed to examine the variation of ϵ over time and among different species (Goetz & Prince, 1998; Gower et al., 1999; Landsberg & Waring, 1997; Running et al., 1994).

Remote sensing continues to play an essential role in providing products used in estimating global NPP (Running et al., 1999). In particular, the correlation between a remote sensing-based vegetation index and APAR makes remote sensing attractive to use in models that rely on APAR (Goetz & Prince, 1999; Kumar & Monteith, 1982). One potential limitation of modeling based on a vegetation index is that it is based on one point in time. For example, if simulated climate change alters plant growth, then this is likely to alter the vegetation index (Field et al., 1995). In addition to APAR, remote sensing can provide land cover information. Land cover is important, because the physiological differences among vegetation types affect carbon and water exchange (Landsberg & Gower, 1997). Image

processing is used to group remote sensing data into specific land cover classes (e.g., aspen, red pine, urban, water, etc.). However, the land cover detail needed to drive various ecosystem models is often limited by the remotely sensed data. Currently, the algorithm for deriving global estimates of NPP from MODIS data, for example, includes the use of a generalized land cover classification scheme (Thomlinson et al., 1999).

While there is some evidence of a functional convergence in ϵ , estimates of NPP from LUE models may be improved if vegetation specific ϵ values are used (Goetz & Prince, 1999). Running et al. (1999) identify three factors that may contribute to differences between satellite-based NPP estimates and direct field measurements including (1) spatial resolution, (2) land cover classification scheme, and (3) ϵ estimates. Little attention has been given to the variability of ϵ among forest cover types across a heterogeneous landscape (e.g., Goetz & Prince, 1996). If ϵ differs significantly among species, stands, or functional plant groups, then these differences should be accounted for when estimating NPP with remotely sensed data products. In this study, we examine how ϵ varies among five forest cover types within a 10 km² area for two years, 1999 and 2000. We measure NPP and APAR using field techniques and then calculate ϵ from Eq. (1). We hypothesized that ϵ would be different among forest cover types. The specific objectives of this study are to (1) quantify and compare the variability of ϵ among forest cover types and (2) quantify the variability of ϵ between 1999 and 2000. We then discuss the implications for using remotely sensed data to estimate NPP with LUE models.

2. Methods

2.1. Study site

The study area is an EOS Validation site (<http://modis-land.gsfc.nasa.gov>) centered on a 447-m-tall communications tower (WLEF tower; 45.9450°N, 90.2733°W) in northern Wisconsin, USA. An extensive field survey grid of 312 plots was established to capture the spatial variability of leaf area index (LAI), land cover, and NPP for the area (Burrows et al., 2002). LAI ranges approximately from 1.0 to 8.0 m² m⁻² and averages 3.6 (Burrows et al., 2002). The topography is slightly rolling with an elevation difference of 45 m between highest and lowest elevations. The climate is cool, temperate continental, with mean air temperatures ranging from -12 to 19 °C for January and July, respectively. Average precipitation is 811 mm/year for this region (Barish & Meloy, 2000).

Much of northern Wisconsin, including the study area, was logged in the late 1800s–early 1900s, and a heterogeneous mixture of forest cover types has regrown, reflecting a combination of complex glacial history and forest management (Fassnacht & Gower, 1997). Outwash, pitted outwash,

and moraines comprise almost 63% of the geomorphic landform for this study site. Red pine plantations (*Pinus resinosa* Ait.) dominate on well-drained glacial outwash. Northern hardwood species occur on fine textured moraines and include sugar maple (*Acer saccharum* Marsh.) and basswood (*Tilia americana* L.) primarily. Trembling aspen (*Populus tremuloides* Michx.), and balsam fir (*Abies balsamea* (L.) Mill.) dominate intermediate sites in this area. Poorly drained lowland organic soils (peat) comprise approximately 30% of the area and are dominated by

speckled alder (*Alnus rugosa* DuRoi), white cedar (*Thuja occidentalis* L.), and tamarack (*Larix laricina* DuRoi), with some balsam fir and black spruce (*Picea mariana* Mill.) throughout. Wetland grass, shrub, and open water communities comprise about 7% of the area.

2.2. Research design

In this research, 59 plots (Fig. 1) were used to quantify ϵ for the primary forest cover types in the area. NPP was

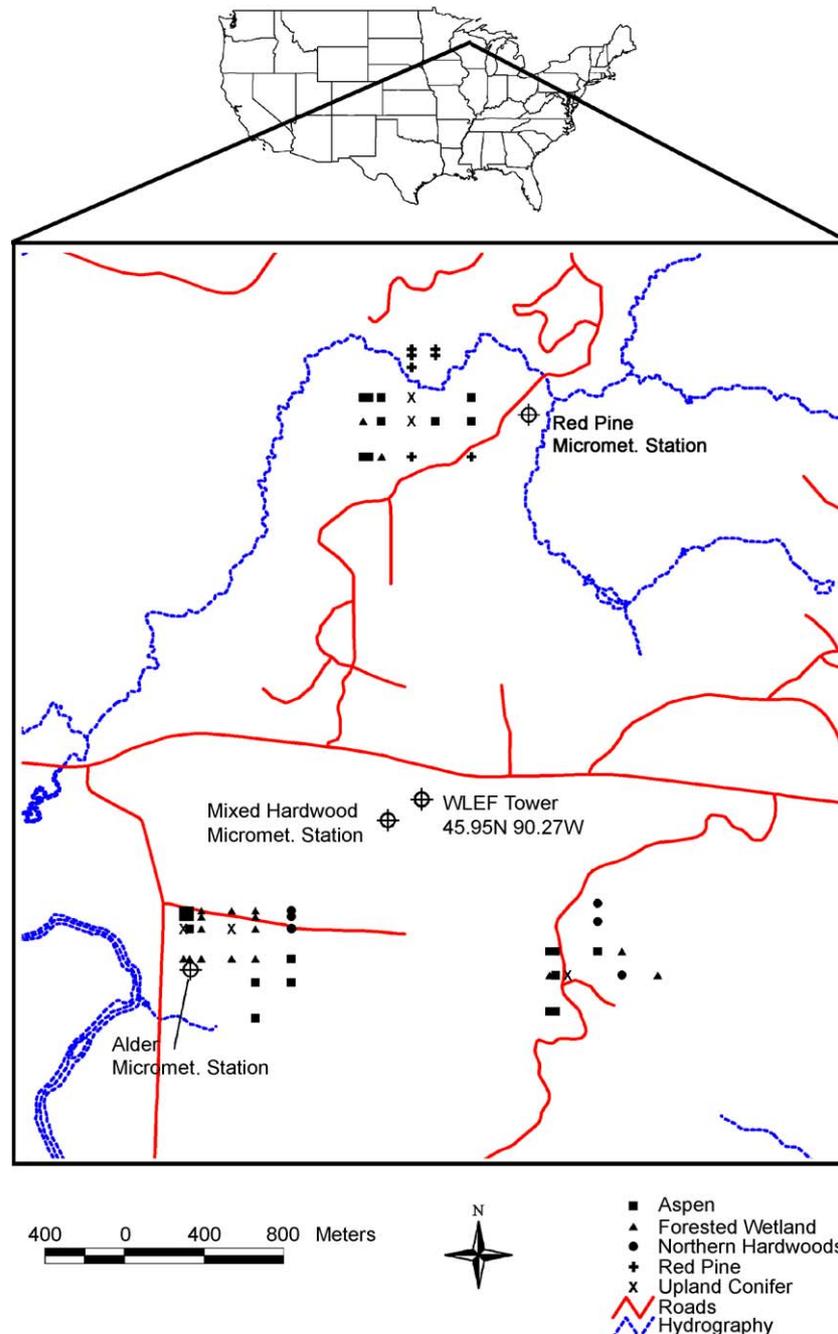


Fig. 1. Study area with plot and micrometeorological station locations. Overstorey net primary production (NPP_o) and light transmittance data were measured at each plot in 1999 and 2000. The WLEF Tower is located approximately 15 km east of Park Falls, WI.

estimated for two consecutive years, 1999 and 2000, for trembling aspen, northern hardwoods, red pine, forested wetlands, and upland conifer. The 59 plots were part of a cyclical sampling design used to quantify the spatial variability of LAI and NPP for this area (Burrows et al., 2002). A cyclic design uses a repeating pattern of samples such that information may be obtained about all lags (time or space between measurements). Plot size was defined at 30×30 m to correspond with Landsat pixel size. Basal area and species composition were measured at all plots in 1998 using variable radius plots. These 59 plots were chosen, of the original 312, because light transmittance and NPP data were available for each plot each year. The light transmittance data were used to calculate the fraction of photosynthetically active radiation absorbed by the vegetation in each plot. We calculated both a growing season ϵ , ϵ_{gs} and an annual ϵ , ϵ_a . We tested differences in ϵ_a and ϵ_{gs} between 1999 and 2000 for all 59 plots, and within forest cover types each year.

2.3. Plot classification

Each plot was classified into one of five forest cover types using the site-specific classification scheme adapted from Thomlinson et al. (1999). This scheme was selected because it is used to validate MODIS products (Cohen & Justice, 1999). Each forest cover type can be aggregated into the International Geosphere-Biosphere Programme (IGBP) classification scheme using the tables provided by Thomlinson et al. (1999). Each plot was categorized based on the

dominant tree species in the plot, determined from basal area measurements and visual inspection of each plot (Table 1). We used a combination of resources to distinguish forested wetlands from other forest classes. First, we used the Wisconsin Wetland Inventory to help distinguish wetlands from uplands. Second, we used soils data from the U.S. Forest Service to help identify areas with poorly drained soils. Finally, we used field observations at each plot to identify common wetland species (e.g., black spruce, white cedar, black ash, speckled alder) and drainage characteristics (e.g., lowland, poorly drained). The tree structural criteria for a forested wetland remained the same as upland forests as provided by Thomlinson et al. (1999).

2.4. Micrometeorological measurements

Micrometeorological data were available at hourly increments for the site each year (<http://cheas.psu.edu>) and included above canopy photosynthetically active radiation (PAR), wind speed, air temperature, precipitation, and relative humidity. Diurnal PAR data at the WLEF tower were summed to provide daily estimates. Gaps in the PAR data were filled with PAR data collected at a micrometeorological station approximately 10 km away. Air temperature, soil temperature, and below canopy PAR were available at three additional micrometeorological stations within 2.5 km of the WLEF tower located in stands dominated by mixed hardwoods (upland deciduous site), red pine (upland coniferous site), and alder (lowland deciduous site), respectively (Fig. 2).

Table 1
Plot classification and structural characteristics used to categorize each plot

Forest cover type	IGBP class	Aboveground biomass	Leaf longevity (year)	Leaf type	Percent woody ^a (%)	Woody Height (m)	LAI	General description
Aspen	Deciduous broadleaf	Woody	<1	Broadleaf	>50	>2	3.29 (0.48)	Upland sites typically comprised of trembling aspen with balsam fir in the understory
Forested Wetland	Mixed forest	Woody	< or >1	Broadleaf or needleleaf	>50	>2	3.69 (0.53)	Lowlands with overstory dominated by woody vegetation, can consist of alder, fir, cedar, spruce, some aspen, and mosses as groundcover
Northern Hardwood	Deciduous broadleaf	Woody	<1	Broadleaf	>50	>2	3.45 (0.51)	Upland site mostly comprised of sugar maple with some basswood
Red Pine	Evergreen needleleaf	Woody	>1	Needleleaf	>50	>2	4.22 (0.60)	Sandy upland sites, all red pine plantations
Upland Conifer	Evergreen Needleleaf	Woody	>1	Needleleaf	>50	>2	3.07 (0.47)	Upland sites with mostly balsam fir, can also have white spruce, aspen, yellow birch, and sugar maple

Criteria adapted from Thomlinson et al. (1999). This study categorized each plot into one of the five site-specific classes (forest cover type), which represents nearly 80% of the basal area and land cover in the study area. LAI with standard error in parentheses are from Burrows et al. (2002).

^a Percent woody was determined from basal area measurements and verified with visual inspection of each plot.

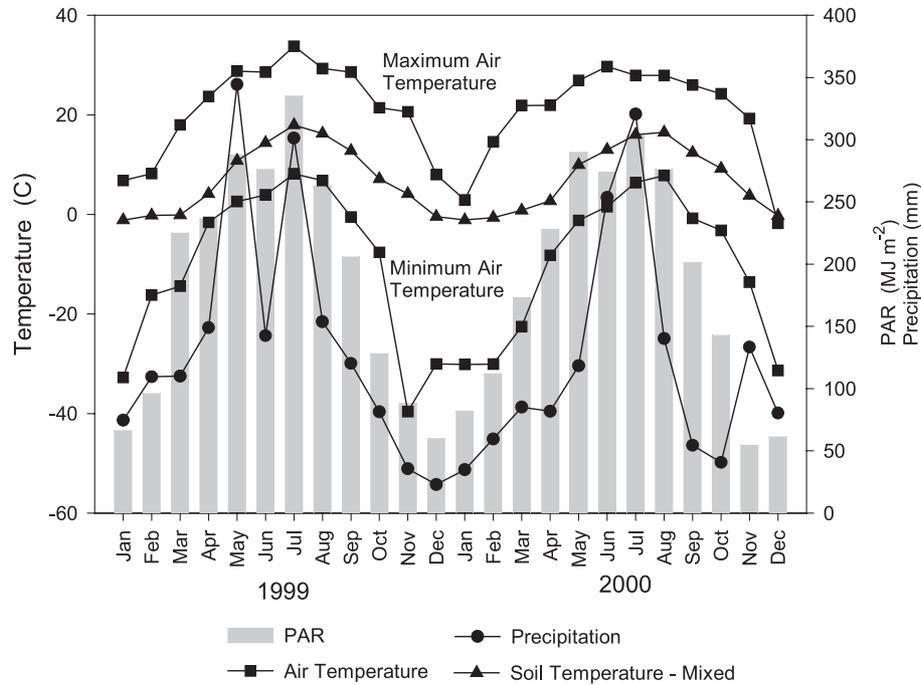


Fig. 2. Monthly environmental conditions for 1999 and 2000. Minimum and maximum air temperature for each month includes all three micrometeorological stations. Soil temperature represents the monthly average at 10 cm depth at the mixed hardwoods micrometeorological station.

2.5. Net primary production

Total annual NPP_T ($gC\ m^{-2}$) for each plot was calculated as the sum of overstory and belowground NPP:

$$NPP_T = NPP_o + NPP_b \quad (2)$$

where NPP_o is overstory NPP (stem, branches, and foliage), and NPP_b is belowground NPP (coarse and fine roots). Understory vegetation (primarily grasses and mosses) were not included in the calculation of NPP_T because the light transmittance data did not include understory vegetation. NPP_o was measured at all 59 plots (Fig. 1). In the fall of 2000, tree diameter was measured at breast height (1.37 m) on all trees, typically 10–15 trees, in a variable radius plot located at plot center. The basal area factor of the wedge prism varied from 1 to 4 depending on the size and density of the trees. Each tree in the variable radius plot was cored at breast height. Radial growth for the last 5 years was measured using WinDENDRO® software (Regent Instruments, 2001). Aboveground annual biomass increment (woody plus foliage) was estimated as the difference in biomass between 2000 and 1998. A complete description of the field methods including allometric equations used to calculate biomass is provided in Burrows et al. (2003) and Ter-Mikaelian and Korzukhin (1997). NPP_b for deciduous and coniferous dominated plots was estimated using belowground/aboveground NPP coefficients of 0.2 and 0.4, respectively (Gower et al., 1999). Carbon content was estimated by assuming biomass for all species as 50% C (Gower et al., 1997; Landsberg et al., 1997).

2.6. APAR

APAR was calculated from f_{IPAR} at each plot for each year, 1999 and 2000, as

$$APAR_A = f_{IPAR} \sum_{day=1}^{365} PAR_{day} \quad (3)$$

where $APAR_A$ is the annual absorbed photosynthetically active radiation ($MJ\ m^{-2}$), PAR_{day} is the daily incident PAR ($MJ\ m^{-2}$), f_{IPAR} is the fraction of intercepted PAR. Absorbed PAR was expressed both on an annual ($APAR_A$) and growing season basis ($APAR_{GS}$) because previous studies have used both approaches (see Gower et al., 1999). It was assumed that f_{IPAR} approximated the fraction of light absorbed and does not incur large errors (<5%; Gower et al., 1999). Campbell and Norman (1998) state that canopy foliage masks twigs and branches so that f_{IPAR} is a reasonable approximation of absorbed radiation. For deciduous forest species plots, PAR_{day} was set to zero when the foliage was absent. The presence of foliage was determined from below the overstory canopy PAR measurements recorded at the mixed hardwoods and alder micrometeorological stations.

Growing season APAR ($APAR_{GS}$) was calculated from incident PAR by using air and soil temperature constraints on photosynthesis and reducing the amount of usable PAR (O'Connell et al., 2003; Runyon et al., 1994) as

$$APAR_{GS} = f_{IPAR} \sum_{day=1}^{365} PAR_{day} f(T_{soil}, T_{air}) \quad (4)$$

where T_{soil} is the average daily soil temperature ($^{\circ}\text{C}$) at 10 cm depth, and T_{air} is the daily minimum air temperature ($^{\circ}\text{C}$). The binary constraint, $f(T_{\text{soil}}, T_{\text{air}})$, is defined by

$$f = 1 \quad T_{\text{soil}} \text{ and } T_{\text{air}} > 0 \quad (5a)$$

$$f = 0 \quad T_{\text{soil}} \text{ or } T_{\text{air}} \leq 0 \quad (5b)$$

Growing season days were calculated from soil and air temperature obtained from each of the three micrometeorological stations (upland deciduous, upland coniferous, lowland deciduous) and applied to each plot according to the dominant leaf habit (deciduous or evergreen) and topographic position (upland or lowland) of the plot (Table 1). We chose a soil and air temperature threshold of 0°C based on previous studies that suggest the amount of carbon assimilated at extreme air temperatures (e.g., $<0^{\circ}\text{C}$) is negligible (see Bergh & Linder, 1999; Öquist, 1983).

Light transmittance was measured in each plot each year using a Li-Cor LAI-2000 Plant Canopy Analyzer (Li-Cor, Lincoln, NE). Standard field measurement methods were used (Gower & Norman, 1991; Gower et al., 1999). Measurements were taken midsummer to correspond with maximum LAI for that site. Fifteen measurements were taken per plot. Three measurements approximately 30 cm apart were taken and averaged at each of five locations. The five locations included the plot center and four locations 7.5 m north, south, east, and west of plot center. The data from the five locations were averaged to provide an estimate for the entire plot. The fraction of radiation intercepted by the canopy (both foliage and branches), f_{IPAR} , for each plot was calculated as

$$f_{\text{IPAR}} = 1.0 - \tau \quad (6)$$

where τ is the fraction of light transmitted by the canopy as determined from optical measurements with the LAI-2000. A more detailed description of the measurements and methods used with the LAI-2000 are described in Burrows et al. (2002).

2.7. Statistical analyses

Statistical analyses (F and t tests) were performed using the SAS/MIXED[®] software (SAS Institute, 2000). A mixed linear model was used with fixed effects parameters and covariance parameters as determined from a variogram (nugget, sill, range). NPP was specified as the dependant variable with APAR, year, and plot classification as effects. LUE was calculated as the slope of the model with intercept set to zero. APAR_A and APAR_{GS} were used separately to calculate ϵ_a and ϵ_{gs} , respectively, for each forest cover type.

3. Results

3.1. Variability among forest cover types

The mean air temperature was 5.1, 5.5, and 4.7°C in 1999, and 4.2, 4.7, and 3.9°C in 2000 at the red pine, mixed hardwood, and alder micrometeorological stations, respectively. The mean soil temperature at 10 cm in 1999 was 7.2, 7.3, and 7.6°C at the red pine, mixed hardwood, and alder micrometeorological stations, respectively, and 6.9°C in 2000 at all three stations. Monthly data are given for these sites in Fig. 2.

There was some evidence that ϵ_{gs} differed significantly ($p=0.05$) among all forest cover types tested in 1999. In 1999, ϵ_{gs} ranged from 0.52 gC MJ^{-1} (northern hardwoods) to 0.31 gC MJ^{-1} (upland conifer; Table 2). Aspen ϵ_{gs} was significantly greater than forested wetland and upland conifer, while northern hardwood was significantly greater than upland conifer (Table 3).

Among all forest cover types tested in 2000, ϵ_{gs} was not significantly different ($p=0.12$). In 2000, ϵ_{gs} ranged from 0.56 gC MJ^{-1} (northern hardwoods) to 0.35 gC MJ^{-1} (upland conifer; Table 2). Only the paired aspen and upland conifer were significantly different (Table 3).

In 1999, ϵ_a differed significantly ($p \leq 0.001$) among all forest cover types tested and ranged from 0.49 gC MJ^{-1}

Table 2
Annual (ϵ_a) and growing season (ϵ_{gs}) light use efficiency (gC MJ^{-1}) for the five major forest cover types described in Table 1

Forest cover type	1999				2000				<i>n</i>
	Annual		Growing season		Annual		Growing season		
	ϵ_a	S.E.	ϵ_{gs}	S.E.	ϵ_a	S.E.	ϵ_{gs}	S.E.	
Aspen	0.42	(0.04)	0.47	(0.04)	0.45	(0.05)	0.51	(0.05)	24
Forested wetland	0.28	(0.03)	0.37	(0.04)	0.31	(0.04)	0.41	(0.05)	17
Northern hardwood	0.49	(0.07)	0.52	(0.08)	0.53	(0.09)	0.56	(0.10)	6
Red pine	0.27	(0.05)	0.46	(0.08)	0.30	(0.05)	0.50	(0.09)	7
Upland conifer	0.18	(0.04)	0.31	(0.06)	0.21	(0.04)	0.35	(0.08)	5
Deciduous broadleaf ^a	0.45	(0.15)	0.49	(0.17)	0.50	(0.15)	0.54	(0.17)	30
Evergreen needleleaf ^b	0.23	(0.14)	0.39	(0.17)	0.25	(0.14)	0.42	(0.12)	12

One standard error in parentheses (S.E.). Results are from a mixed linear model, $\text{NPP}=\text{APAR}$, using net primary production (NPP) as the dependant variable with absorbed photosynthetically active radiation (APAR), year, and plot classification as effects. The slope of the model (intercept set to zero) was used to determine light use efficiency.

^a Deciduous broadleaf calculated using data from aspen and northern hardwoods.

^b Evergreen needleleaf calculated using data from red pine and upland conifer.

Table 3

P-value comparisons of light use efficiency (ϵ) among the five major forest cover types described in Table 1

Pair comparison		1999		2000	
		Annual	Growing season	Annual	Growing season
Aspen	Forested wetland	<0.001	0.043	<0.001	0.066
	Northern hardwood	0.330	0.441	0.670	0.833
	Red pine	0.026	0.951	0.004	0.841
	Upland conifer	<0.001	0.023	<0.001	0.029
Forested wetland	Northern hardwood	0.005	0.062	0.017	0.214
	Red pine	0.857	0.237	0.725	0.375
	Upland conifer	0.034	0.454	0.019	0.421
Hardwood	Red pine	0.017	0.573	0.019	0.743
	Upland conifer	<0.001	0.038	0.001	0.114
Red pine	Upland conifer	0.092	0.120	0.140	0.180

Results are from statistical analyses used to derive ϵ reported in Table 2.

(northern hardwood) to 0.18 gC MJ⁻¹ (upland conifer; Table 2). Aspen ϵ_a in 1999 was significantly greater than forested wetland and upland conifer, while hardwoods were significantly greater than upland conifer (Table 3).

In 2000, ϵ_a differed significantly ($p \leq 0.001$) among all forest cover types tested and ranged from 0.53 gC MJ⁻¹ (northern hardwoods) to 0.21 gC MJ⁻¹ (upland conifer, Table 2). All paired comparisons differed significantly with the exception of aspen and hardwood, forested wetland and red pine, and red pine and upland conifer (Table 3).

3.2. Variability between 1999 and 2000

Mean annual air temperature across all three micro-meteorological stations decreased from 5.1 °C in 1999 to 4.3 °C in 2000. Mean annual soil temperature at 10 cm across all three stations decreased slightly from 7.2 °C in 1999 to

6.9 °C in 2000. Annual precipitation was 970 mm in 1999 and 730 mm in 2000. Total annual PAR was 1983 MJ m⁻² in 1999, and 1922 MJ m⁻² in 2000.

Mean ϵ_{gs} across all plots was significantly less ($p \leq 0.001$) in 1999 (0.41 gC MJ⁻¹) than in 2000 (0.46 gC MJ⁻¹; Fig. 3). Mean ϵ_a across all plots was significantly less ($p \leq 0.001$) in 1999 (0.32 gC MJ⁻¹) than in 2000 (0.36 gC MJ⁻¹; Fig. 4).

Both Figs. 3 and 4 show two points with a low APAR (300–400 MJ m⁻²) in 1999 and appear to increase >600 MJ m⁻² in 2000. Our field data indicate that light transmittance decreased by almost half in these plots from 1999 to 2000, therefore nearly doubling APAR. Measurement error, slight differences in total available PAR, changes in the presence of understory vegetation, and length of estimated growing season likely contribute to some of this change. These two points represent plots in the same stand dominated by

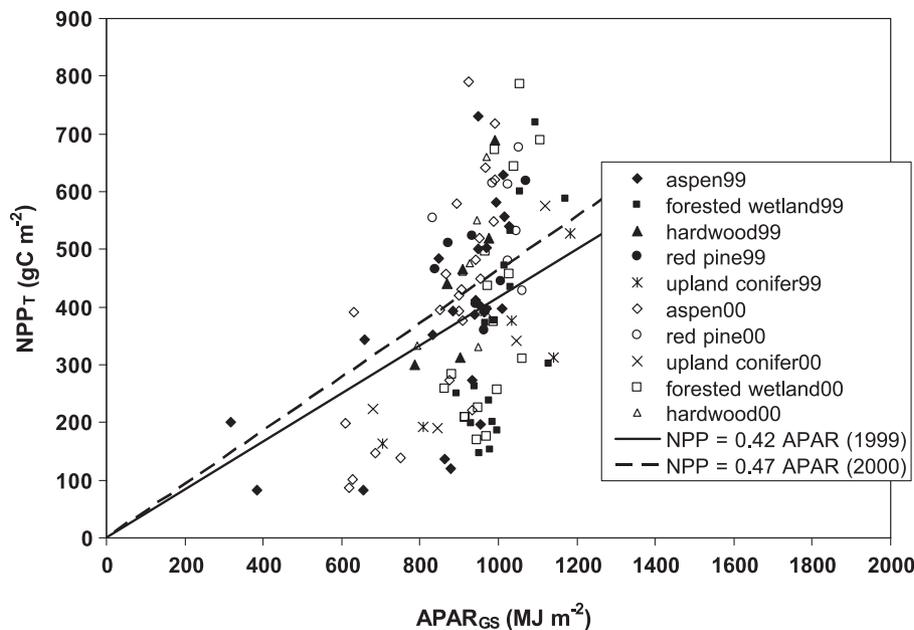


Fig. 3. The relationship between total net primary production (NPP_T) and growing season absorbed photosynthetically active radiation ($APAR_{GS}$) for all plots in 1999 and 2000. Data corresponding to forest cover types in 1999 and 2000 are represented by closed and open symbols, respectively. The coefficient of variation was 0.38 and 0.37 for 1999 and 2000, respectively. Lines are least squares fit to all plots each year.

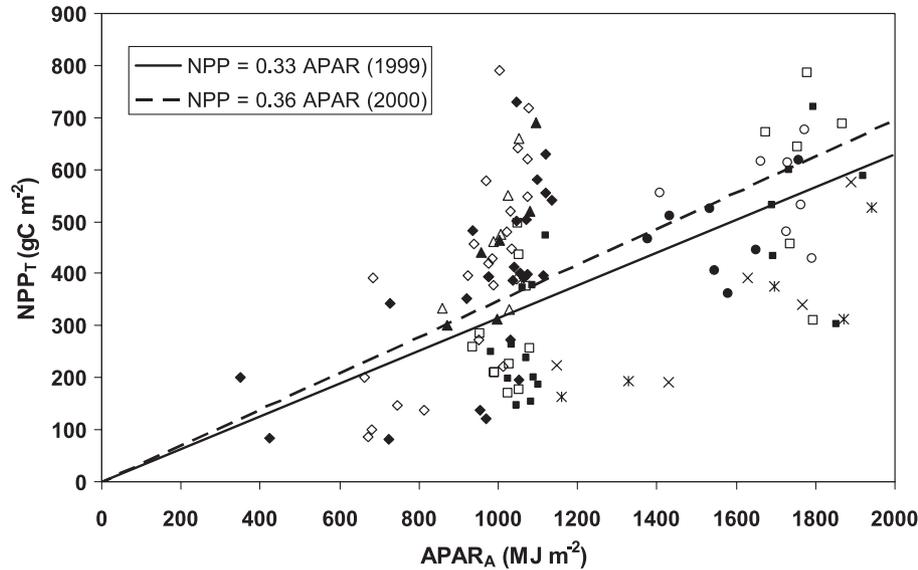


Fig. 4. The relationship between total net primary production (NPP_T) and annual absorbed photosynthetically active radiation ($APAR_A$) for all plots in 1999 and 2000. The coefficient of variation was 0.40 and 0.39 for 1999 and 2000, respectively. Marker symbols are as in Fig. 3. Lines are least squares fit to all plots each year.

trembling aspen with a low LAI (around 1.0). Observations from frequent field visits and our data suggest it is not unusual for a stand of this type (low LAI, fast-growing aspen) to significantly increase total leaf area between years.

4. Discussion

4.1. LUE variability

Light use efficiency differed significantly among forest cover types and between 1999 and 2000. The LUE coefficients calculated in this study compared well with others. Gower et al. (1999) report growing season ϵ values of 0.74 (g NPP MJ^{-1}) and 0.60 (g NPP MJ^{-1}) for northern Wisconsin hardwoods and red pine, respectively. Goetz and Prince (1998) report mean annual ϵ values of 0.16 (gC MJ^{-1}) and 0.47 (gC MJ^{-1}) for black spruce and mature aspen, respectively, in northern Minnesota. Potential confusion may arise when comparing or using ϵ if it is based on an annual or growing season duration. Annual ϵ is less than ϵ_{gs} for conifers because of the increased APAR in Eq. (1).

However, ϵ changes little between annual and growing season for deciduous stands, because leaf phenology is considered in Eq. (4). In this study area, ϵ is more similar among forest cover types when it is based on a growing season duration rather than an annual one. Remote sensing data products will need to account for leaf phenology depending on how the LUE model is defined.

There was considerable variation in NPP_T among forest cover types (Figs. 3 and 4, Table 4) despite a similar LAI (~ 3.6) and APAR ($\sim 950 \text{ MJ m}^{-2}$) in many plots. An analysis of the factors causing variation in NPP is beyond the scope of this paper and sampling design (see Burrows et al., 2003) but should be considered by when estimating NPP for this area. However, two other studies may provide some insight and direction for future work. Burrows et al. (2002) used 312 plots in the same area to examine the spatial patterns of LAI as they relate to anthropogenic and abiotic site conditions. Because LAI is positively correlated to NPP, they suggest that factors including elevation, timber management, soil properties, topography, and the interactions among these effects may influence the variability in NPP at this site. In another study near this site, Ewers et al.

Table 4

Mean total net primary production (NPP_T ; $\text{gC m}^{-2} \text{ year}^{-1}$) and fraction of intercepted photosynthetically active radiation (f_{IPAR}) for the five major forest cover types described in Table 1

Forest cover type	1999				2000			
	NPP_T		f_{IPAR}		NPP_T		f_{IPAR}	
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
Aspen	401	(175)	0.85	(0.18)	428	(193)	0.86	(0.13)
Forested wetland	358	(176)	0.93	(0.04)	399	(200)	0.92	(0.04)
Northern hardwood	465	(144)	0.84	(0.10)	482	(127)	0.91	(0.06)
Red pine	462	(85)	0.78	(0.06)	529	(85)	0.88	(0.07)
Upland conifer	285	(147)	0.81	(0.81)	311	(153)	0.82	(0.15)

NPP_T includes overstory plus belowground biomass. Standard error in parentheses (S.E.).

(2002) showed that canopy transpiration among forest cover types varied by a factor of two due to species effects on sap flux, sapwood area, leaf water potential, and hydraulic conductance.

4.2. Site and environmental effects

Growing season and annual ϵ increased significantly by 10% from 1999 to 2000. Varying the PAR availability, temperature, or respiration may explain the change in ϵ (Field, 1991; Goetz & Prince, 1999; Waring et al., 1995). Air temperature decreased slightly, but mean growing season temperature did not differ significantly between 1999 and 2000 ($p=0.06$). The number of growing season days used to calculate APAR_{GS} was very similar (<7 days difference) for both coniferous and deciduous stands including deciduous lowlands because of the air and soil temperature constraints. Precipitation decreased from 1999 to 2000, but the effect of this decrease on NPP is unclear because Ewers et al. (2002) concluded that soil moisture did not affect transpiration. PAR decreased by 4% from 1999 to 2000, which was not significantly different ($p=0.5$).

Burrows et al. (2002) reported that mean LAI increased by 17% from 1999 to 2000. The increase in LAI corresponded well with the average 4% increase in f_{IPAR} due to the nonlinear relationship between LAI and light attenuation given by the Beer–Lambert Law. However, the impact of varying LAI should be small with ϵ remaining stable over a range of LAI (Duncan et al., 1967; Sinclair & Horie, 1989; Bartelink et al., 1997). Short-term variability in ϵ may be due in part to time lags associated with short-term variations in climate (Field, 1991). This study site experienced a severe drought in 1998, with the trees likely recovering through 1999 and 2000 (Burrows et al., 2002). An analysis of varying respiration costs is beyond the scope of this paper but should be considered in future studies as they are correlated to climate variables, such as temperature and moisture (Goetz & Prince, 1999).

4.3. Remote sensing and modeling

Remote sensing will be used extensively to drive LUE process models using biome-specific efficiency factors that simulate NPP (Running et al., 1999). An increasing number of studies suggest that ϵ varies among plant functional groups and among species within a plant functional group (Goetz & Prince, 1999; Gower et al., 1999; O'Connell et al., 2003; Turner et al., 2002). Modeling NPP may be complicated further by the spatial and temporal scale of remote sensing data used and the detail of land cover information that can be obtained from different sensors. For example, the land cover classification scheme (similar to the IGBP scheme in Table 1) used to derive MODIS NPP products is a coarser or more generalized scheme compared to the site-specific classification used in this study. Using coarse-grained sensor data (e.g., 1 km) with an IGBP-type

classification assumes that NPP can be estimated accurately within a cell, and that mixed pixels have little effect or variation in estimating NPP (Reich et al., 1999).

This study examined ϵ from a site-specific land cover classification perspective commonly derived from high spatial resolution remote sensing data (e.g., ETM+). Many studies have calculated ϵ for upland homogeneous stands (see Gower et al., 1999). It is important to note that the forested wetland class used in this study (35% of the landscape) can consist of a mixture of trembling aspen, alder, balsam fir, white cedar, black spruce, or tamarack, including mosses as groundcover. Therefore, it is unclear how mixtures of this type will affect ϵ estimates and how these scale to the landscape (e.g., Whitehead & Gower, 2001). Bartelink et al. (1997) used simulated data and concluded that mixed stands can yield different ϵ values but may stabilize or converge over long time frames. Integrated seasonal estimates of the normalized difference vegetation index (NDVI) used to derive APAR may in turn be used to calculate an integrated estimate of maximum ϵ for mixed stands, but it may be important to know the species composition of the stand (Coops et al., 1998; Waring et al., 1995).

In this study, ϵ_{gs} was similar for forested wetlands and other classes (Table 2). However, the ϵ_{a} estimate for forested wetlands differed significantly from all other classes except red pine for both years. This is an important result for two reasons. First, past studies have not reported ϵ for forested wetlands, yet this is a common land cover type. The forested wetlands in this area comprise nearly 35% of the surface area (Mackay et al., 2002). Additionally, forested wetlands are common throughout the Great Lake States. If NPP is to be estimated using LUE models then more information is needed on wetland types and how they affect ϵ and NPP estimates.

Second, forested wetlands are very difficult to identify with satellite imagery alone (Sader et al., 1995). Often, other ancillary data are needed to delineate forested wetlands (e.g., soils maps). The IGBP classification, for example, does not have a category for forested wetlands. The translation from a site-specific classification to the IGBP classification used in global model NPP validation would aggregate forested wetlands into a mixed category (Thomlinson et al., 1999). This study suggests that in terms of estimating NPP with LUE models, aggregating forested wetlands with upland species may cause large errors in NPP estimates. More work is needed on these type of aggregating effects (e.g., Turner et al., 2002) and the ϵ of forested wetlands with different species mixtures.

The design and use of a LUE algorithm to estimate NPP may be complicated further if there is interannual variation in ϵ . Some models may account for this variation by adding environmental scalars to adjust for temperature or vapor pressure deficit, for example. The results from this study and others at this site (e.g., Burrows et al., 2003) suggest that the underlying factors causing variability in ϵ should be determined and then incorporated into the LUE algorithm.

Estimates of terrestrial NPP range from 40 to 80 PgC year⁻¹ (Cramer et al., 1999). Ruimy et al. (1999) compared results of 12 global models and showed a range of 0.3 to 0.67 gC MJ⁻¹ for globally averaged ϵ . They suggested that differences found in modeled NPP are due to differences in ϵ that result from inconsistent definition of (1) biomes, (2) ϵ , and (3) sampling biases (e.g., using biome means). Long-term field studies with continuous NPP, APAR, and environmental measurements are needed to validate models that will be used to monitor the effects of climate change on the terrestrial carbon budget (e.g., Nemani et al., 2003).

5. Conclusions

Light use efficiency differed significantly among forest cover types and between years in this study. This is likely to affect how efficiency factors are used in modeling NPP with remotely sensed data products. More work is needed to understand the factors that affect ϵ , notably interannual variation in climate and respiration, and to determine if ϵ varies over longer time scales.

When land cover will be used in conjunction with LUE models for estimating NPP, care must be taken in when representing the land cover of a region derived from remotely sensed data. For example, there are few data on the ϵ of forested wetlands, a lack of information that may present significant problems in some regions (e.g., Lake States, boreal forests). Forested wetlands may consist of mixtures of many species, and they are extremely difficult to map with satellite imagery alone. Given the results of this study, there is a need to review the process of defining and aggregating land cover types in the context of using remotely sensed data for modeling NPP.

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References

- Anderson, M. A., Norman, J. M., Meyers, T. P., & Diak, G. R. (2000). An analytical model for estimating canopy transpiration and carbon assimilation fluxes based on canopy light-use efficiency. *Agricultural and Forest Meteorology*, *100*, 265–289.
- Asrar, G., Kanemasu, E. T., Jackson, R. D., & Pinter, P. J. (1985). Above-ground phytomass production using remotely sensed data. *Remote Sensing of Environment*, *17*, 211–220.
- Barish, L. S., & Meloy, P. E. (2000). Wisconsin blue book 1999–2000. Madison: Wisconsin Legislative Reference Bureau.
- Bartelink, H. H., Kramer, K., & Mohren, G. M. J. (1997). Applicability of the radiation-use efficiency concept for simulating growth of forest stands. *Agricultural and Forest Meteorology*, *88*, 169–179.
- Bergh, J., & Linder, S. (1999). Effects of soil warming during spring on photosynthetic recovery in boreal Norway spruce stands. *Global Change Biology*, *5*, 245–253.
- Burrows, S. N., Gower, S. T., Clayton, M. K., Mackay, D. S., Ahl, D. E., Norman, J. M., et al. (2002). Application of geostatistics to characterize LAI for flux towers to landscapes. *Ecosystems*, *5*, 667–679.
- Burrows, S. N., Gower, S. T., Norman, J. M., Diak, G., Mackay, D. S., Ahl, D. E., et al. (2003). Spatial variability of aboveground net primary production for a forested landscape in northern Wisconsin. *Canadian Journal of Forest Research*, *33*, 2007–2018.
- Campbell, G. S., & Norman, J. M. (1998). An introduction to environmental biophysics. New York: Springer-Verlag.
- Canadell, J. G., Mooney, H. A., Baldocchi, D. D., Berry, J. A., Ehleringer, J. R., Field, C. B., et al. (2000). Carbon metabolism of the terrestrial biosphere: A multi-technique approach for improved understanding. *Ecosystems*, *3*, 115–130.
- Choudhury, B. J. (2001). Estimating gross photosynthesis using satellite and ancillary data: Approach and preliminary results. *Remote Sensing of Environment*, *75*, 1–21.
- Cohen, W. B., & Justice, C. O. (1999). Validating MODIS terrestrial ecology products: Linking in situ and satellite measurements. *Remote Sensing of Environment*, *70*, 1–3.
- Coops, N. C., Waring, R. H., & Landsberg, J. J. (1998). Assessing forest productivity in Australia and New England using a physiologically-based model driven with averaged monthly weather data and satellite-derived estimates of canopy photosynthesis capacity. *Forest Ecology and Management*, *104*, 113–127.
- Cramer, W., Kicklighter, D. W., Bondeau, A., et al. (1999). Comparing global models of terrestrial net primary productivity (NPP): Overview and key results. *Global Change Biology*, *5*(Suppl. 1), 1–15.
- Duncan, W. G., Loomis, R. S., Williams, W. A., & Hanau, R. (1967). A model for simulating photosynthesis in plant communities. *Hilgardia*, *38*, 181–205.
- Ewers, B. E., Mackay, D. S., Gower, S. T., Ahl, D. E., Burrows, S. N., & Samanta, S. S. (2002). Influence of forest cover type on diurnal and daily patterns of canopy transpiration. *Water Resources Research*, *38*.
- Fassnacht, K. S., & Gower, S. T. (1997). Interrelationships among the edaphic and stand characteristics, leaf area index, and aboveground net primary production of upland forest ecosystems in north central Wisconsin. *Canadian Journal of Forest Research*, *27*, 1058–1067.
- Field, C. B. (1991). Ecological scaling of carbon gain to stress and resource availability. In H. Mooney (Ed.), *Response of plants to multiple stresses* (pp. 35–65). San Diego, CA: Academic Press.
- Field, C. B., Randerson, J. T., & Malmström, C. M. (1995). Global net primary production: Combining ecology and remote sensing. *Remote Sensing of Environment*, *51*, 74–88.
- Franklin, S. E., Lavigne, M. B., Deuling, M. J., Wulder, M. A., & Hunt, E. (1997). Landsat TM derived forest cover types for modelling net primary production. *Canadian Journal of Remote Sensing*, *23*, 243–251.
- Goetz, S. J., & Prince, S. D. (1996). Remote sensing of net primary production in boreal forest stands. *Agricultural and Forest Meteorology*, *78*, 149–179.
- Goetz, S. J., & Prince, S. D. (1998). Variability in carbon exchange and light utilization among boreal forest stands: Implications for remote sensing of net primary production. *Canadian Journal of Forest Research*, *28*, 375–389.
- Goetz, S. J., & Prince, S. N. (1999). Modelling terrestrial carbon exchange and storage: Evidence and implications of functional convergence in light-use efficiency. *Advances in Ecological Research*, *28*, 57–92.
- Gower, S. T., & Norman, J. M. (1991). Rapid estimation of leaf area index in conifer and broad-leaf plantations. *Ecology*, *72*, 1896–1900.

- Gower, S. T., Kucharik, C. J., & Norman, J. M. (1999). Direct and indirect estimation of leaf area index, fapar, and net primary production of terrestrial ecosystems. *Remote Sensing of Environment*, 70, 29–51.
- Gower, S. T., Vogel, J., Norman, J. M., Kucharik, C. J., Steele, S. J., & Stow, T. K. (1997). Carbon distribution and aboveground net primary production in aspen, jack pine and black spruce stands in Saskatchewan and Manitoba, Canada. *Journal of Geophysical Research-Atmospheres*, 102(D24), 29029–29041.
- Kumar, M., & Monteith, J. L. (1982). Remote sensing of crop growth. In H. Smith (Ed.), *Plants and the daylight spectrum* (pp. 133–144). London: Academic.
- Landsberg, J. J., & Gower, S. T. (1997). Application of physiological ecology to forest management. San Diego: Academic Press.
- Landsberg, J. J., Prince, S. D., Jarvis, P. G., McMurtrie, R. E., Luxmoore, R., & Medlyn, B. E. (1997). Energy conversion and use in forests: An analysis of forest production in terms of radiation utilization efficiency. In H.L. Gholz, K. Nakane, & H. Shimoda (Eds.), *The use of remote sensing in the modeling of forest productivity at scales from the stand to the globe* (pp. 273–298). Dordrecht: Kluwer Academic.
- Landsberg, J. J., & Waring, R. H. (1997). A generalized model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. *Forest Ecology and Management*, 95, 209–228.
- Mackay, D. S., Ahl, D. E., Ewers, B. E., Gower, S. T., Burrows, S. N., Samanta, S., et al. (2002). Aggregation effects of remotely sensed vegetation cover on estimates of evapotranspiration in a northern Wisconsin forest. *Global Change Biology*, (in press).
- Medlyn, B. E. (1998). Physiological basis of the light use efficiency model. *Tree Physiology*, 18, 167–176.
- Monteith, J. L. (1972). Solar radiation and productivity in tropical ecosystems. *Journal of Applied Ecology*, 9, 747–766.
- Monteith, J. L. (1977). Climate and the efficiency of crop production in Britain. *Philosophical transactions of the Royal Society of London. Series B*, 281, 277–294.
- Nemani, R. R., Keeling, C. D., Hashimoto, H., Jolly, W. M., Piper, S. C., Tucker, C. J., Myneni, R. B., & Running, S. W. (2003). Climate-driven increases in global terrestrial net primary production from 1982 to 1999. *Science*, 300, 1560–1563.
- O'Connell, K. E. B., Gower, S. T., & Norman, J. M. (2003). Comparison of net primary production and light-use dynamics of two boreal black spruce forest communities. *Ecosystems*, 6, 236–247.
- Öquist, G. (1983). Effects of low temperature on photosynthesis. *Plant, Cell and Environment*, 6, 281–300.
- Prince, S. D., & Goward, S. N. (1995). Global primary production: A remote sensing approach. *Journal of Biogeography*, 22, 815–835.
- Regent Instruments. (2001). Homepage. <http://www.regentinstruments.com>. Accessed 2002 Jan 23.
- Reich, P. B., Turner, D. P., & Bolstad, P. (1999). An approach to spatially distributed modeling of net primary production (NPP) at the landscape scale and its application in validation of EOS NPP products. *Remote Sensing of Environment*, 70, 69–81.
- Ruimy, A., Kergoat, L., Bondeau, A., et al. (1999). Comparing global models of terrestrial net primary productivity (NPP): Analysis of differences in light absorption and light-use efficiency. *Global Change Biology*, 5(Suppl. 1), 56–64.
- Running, S. W., Baldocchi, D. D., Turner, D. P., Gower, S. T., Bakwin, P. S., & Hibbard, K. A. (1999). A global terrestrial monitoring network integrating tower fluxes, flask sampling, ecosystem modeling and EOS satellite data. *Remote Sensing of Environment*, 70, 108–127.
- Running, S. W., Justice, C. O., Solomonson, V., Hall, D., Barker, J., Kaufmann, Y. J., et al. (1994). Terrestrial remote sensing science and algorithms planned for EOS/MODIS. *International Journal of Remote Sensing*, 15, 3587–3620.
- Runyon, J., Waring, R. H., Goward, S. N., & Welles, J. M. (1994). Environmental limits on net primary production and light-use efficiency across the Oregon transect. *Ecological Applications*, 4, 226–237.
- Sader, S. A., Ahl, D. E., & Liou, W. S. (1995). Accuracy of Landsat-TM and GIS rule-based methods for forest wetland classification in Maine. *Remote Sensing of Environment*, 53, 133–144.
- SAS Institute. (2000). *SAS/STAT User's Guide, vol. 1., 4th ed.* Cary, SC, USA: SAS Institute.
- Sinclair, T. R., & Horie, T. (1989). Leaf nitrogen, photosynthesis, and crop radiation use efficiency: A review. *Crop Science*, 29, 90–98.
- Ter-Mikaelian, M. T., & Korzukhin, M. D. (1997). Biomass equations for sixty-five North American tree species. *Forest Ecology and Management*, 97, 1–24.
- Thomlinson, J. R., Bolstad, P. V., & Cohen, W. B. (1999). Coordinating methodologies for scaling land cover classifications from site-specific to global: Steps toward validating global map products. *Remote Sensing of Environment*, 70, 16–28.
- Tucker, C. J., & Sellers, P. J. (1986). Satellite remote sensing of primary production. *International Journal of Remote Sensing*, 7, 1395–1416.
- Turner, D. P., Gower, S. T., Cohen, W. B., Gregory, M., & Maiersperger, T. K. (2002). Effects of spatial variability in light use efficiency on satellite-based NPP monitoring. *Remote Sensing of Environment*, 80, 397–405.
- Waring, R. H., Law, B. E., Goulden, M. L., Bassow, S. L., McCreight, R. W., Wofsy, S. C., & Bazzaz, F. A. (1995). Scaling gross ecosystem production at Harvard Forest with remote sensing: A comparison of estimates from a constrained quantum-use efficiency model and eddy correlation. *Plant, Cell and Environment*, 18, 1201–1213.
- Waring, R. H., & Running, S. W. (1998). *Forest ecosystems: Analysis at multiple scales.* San Diego: Academic Press.
- Whitehead, D., & Gower, S. T. (2001). Photosynthesis and light-use efficiency by plants in a Canadian boreal forest ecosystem. *Tree Physiology*, 21, 925–929.