

---

# Photosynthetic and Water Use Efficiency Responses to Diffuse Radiation by an Aspen-Dominated Northern Hardwood Forest

Adrian V. Rocha, Hong-Bing Su, Christoph S. Vogel, Hans Peter Schmid, and Peter S. Curtis

---

**ABSTRACT.** Clouds can exert strong effects on ecosystem CO<sub>2</sub> and water vapor fluxes and may be important determinants of terrestrial primary production. We used three years of eddy-covariance and meteorological data from an aspen-dominated northern hardwood forest in Michigan to investigate how canopy photosynthesis ( $P$ ), evapotranspiration ( $E$ ), and water use efficiency (WUE) responded to changes in cloud cover, or the proportion of diffuse ( $I_f$ ) to total ( $I_t$ ) photosynthetically active radiation (PAR). Canopy quantum efficiency (the initial slope of the  $P$  versus PAR response curve) increased with increasing cloud cover, but both midday canopy  $P$  and canopy photosynthetic potential (the asymptote of the  $P$  versus PAR response curve) were greatest under partly cloudy skies ( $I_f/I_t = \sim 0.57$ ). Midday canopy  $E$  decreased and midday canopy WUE increased with increasing  $I_f/I_t$ . The relationship between canopy  $P$  and cloud cover varied with soil moisture. Canopy  $P$  was insensitive to changes in soil moisture under overcast skies ( $I_f/I_t > 0.70$ ), whereas under clearer skies, canopy  $P$  was lower during periods of low compared to high soil moisture. These results further our understanding of cloud cover effects on canopy physiological processes and will aid in more accurate assessments of forest responses to climatic change. FOR. SCI. 50(6): 793–801.

**Key Words:** Canopy photosynthesis, clouds, net ecosystem CO<sub>2</sub> exchange, evapotranspiration, eddy covariance.

---

**F**OREST CARBON AND WATER EXCHANGES are dependent on radiation regimes, with the result that changes in cloud cover may substantially alter ecosystem productivity. Cloud monitoring stations, long-term radiation measurements, and satellite data have recorded

increased cloud cover over the North American mid-latitudes (McGuffie and Henderson-Sellers 1988, Henderson-Sellers 1989, Karl and Steurer 1990), but decreased cloud cover over tropical regions (Chen et al. 2002, Wielicki et al. 2002) during the past 50 years. For the same time period,

---

Adrian V. Rocha, The Ohio State University, Columbus, OH 43210. Present address: Department of Earth Science, University of California, Irvine, CA 92697—[arocha@uci.edu](mailto:arocha@uci.edu). Hong-Bing Su, East Carolina University, Greenville, NC 27858—[suh@mail.ecu.edu](mailto:suh@mail.ecu.edu). Christoph S. Vogel, University of Michigan Biological Station, Pellston, MI 49769—[csvogel@umich.edu](mailto:csvogel@umich.edu). Hans Peter Schmid, Indiana University, Bloomington, IN 47405—[hschmid@indiana.edu](mailto:hschmid@indiana.edu). Peter S. Curtis, corresponding author, Department of Evolution, Ecology, and Organismal Biology, The Ohio State University, 318 W. 12th Avenue, Columbus, OH 43210-1293—Phone: (614) 292-0835; Fax: (614) 292-2030; [curtis.7@osu.edu](mailto:curtis.7@osu.edu).

**Acknowledgments:** We thank M. Goulden, J. Arnfield, M. Miriti, and A. Shenoy for helpful comments on earlier drafts of this article. This research was supported in part by the Office of Science, US Department of Energy, through the Midwestern Regional Center of the National Institute for Global Environmental Change under Cooperative Agreement No. DE-FC03-90ER610100.

increased terrestrial primary productivity has been proposed in both the North American mid-latitudes (Keeling et al. 1996, Myneni et al. 1997) and the Amazonian rainforest (Nemani et al. 2003). A better understanding of how sky conditions affect forest carbon and water exchanges is needed to more accurately determine how these ecosystems will respond to changing climatic conditions.

Previous work has shown that clouds exert strong effects on ecosystem  $\text{CO}_2$  and water vapor exchanges. Measurements from a variety of ecosystems using micrometeorological methods have reported higher net  $\text{CO}_2$  fluxes ( $F_c$ ) and lower evapotranspiration ( $E$ ) on cloudy compared to clear days (Price and Black 1990, Law et al. 2002, Monson et al. 2002). Consequently, canopy water use efficiency (WUE) (defined as  $F_c/E$ ) is higher during cloudy periods (Fan et al. 1995, Lamaud et al. 1997, Freedman et al. 2001). Determining the biophysical or physiological mechanisms responsible for increases in  $F_c$  and WUE at the ecosystem scale during cloudy periods has been difficult because clouds simultaneously affect a number of environmental variables. Increased cloud cover results in decreases in solar radiation at the earth's surface ( $S$ ),  $E$ , photosynthetically active radiation (PAR), leaf temperature, and vapor pressure deficit (VPD) (Gu et al. 1999, Freedman 2001). Although leaf-level photosynthesis and transpiration may be reduced by decreases in total incident PAR ( $I_t$ ), they may also be enhanced by reduced VPD and leaf temperature (Knapp et al. 1989). As a result, increased ecosystem  $F_c$  under cloudy conditions has been attributed to lower VPD (Freedman et al. 2001), lower leaf respiration attributed to decreased leaf temperature (Baldocchi 1997), altered stomatal dynamics associated with fluctuating light (Fitzjarrald et al. 1995), and increases in incident diffuse beam PAR ( $I_f$ ) (Hollinger et al. 1994, Fan et al. 1995, Goulden et al. 1997).

Although clouds reduce the absolute magnitude of  $I_t$ , they also alter the amount of  $I_f$  relative to incident direct beam PAR ( $I_d$ ) (Gu et al. 1999). This is important because  $I_f$  attenuates much faster than  $I_d$  with increasing depth into forest canopies (Baldocchi et al. 1985). Forest canopies also exhibit vertical gradients in nitrogen (Hirose and Werger 1987) and leaf-level photosynthetic capacity (Wilson et al. 2000). During periods of high  $I_t$ , overstory leaves in dense canopies are at photosynthetic light saturation, whereas understory leaves are light-limited. Because  $I_f$  is distributed more evenly throughout forest canopies than is  $I_d$  (Weiss 2000), increases in  $I_f$  may increase overall light use efficiency and canopy  $P$  (Sinclair et al. 1992, Sinclair and Shiraiwa 1993, Healy et al. 1998). That is, although increased cloud cover always decreases  $I_t$ , increases in the diffuse fraction ( $I_f/I_t$ ) can cause  $I_t$  to be vertically distributed more evenly such that canopy  $P$  may be greater under partly cloudy compared to clear conditions. Increases in  $I_f$  can increase light use efficiency and yield by as much as 50% in agricultural crops (Healy et al. 1998).

The development of networked long-term tower-based carbon cycle research sites in recent years (Baldocchi et al. 2001) provides direct measurements of ecosystem-atmosphere exchange of water and carbon and associated climate

and environment variables over a variety of terrestrial ecosystems. These measurements provide an opportunity to examine the effects of clouds on ecosystem-atmosphere exchange of carbon and water and determine how these effects may differ over ecosystems with differing canopy morphologies and in different climates. Improved understanding of the effects of clouds on canopy physiological processes also may help explain global-scale patterns of  $\text{CO}_2$  exchange between biosphere and atmosphere. For example, Roderick et al. (2001) and Gu et al. (2003) proposed that the unexpected decline in the rate of atmospheric  $\text{CO}_2$  buildup after the Mt. Pinatubo eruption in 1991 was caused by increased terrestrial primary production after an enhancement of  $I_f/I_t$  by volcanic aerosols. Based on satellite reflectance data, however, Slayback et al. (2003) and Lucht et al. (2002) contended that primary productivity did not increase after the eruption and attributed the trends in atmospheric  $\text{CO}_2$  increase to decreased surface temperatures and lower ecosystem respiration. One factor complicating this debate is the different data sources being used. Gu et al. (2003) based their conclusions on direct flux measurement made at one site in north-central Massachusetts, whereas those of Slayback et al. (2002) were based on indirectly derived productivity trends but with broader spatial coverage of ecosystems.

Our study focuses on one of these long-term carbon cycle research sites. Our objective was to examine how changes in cloud cover affect carbon and water vapor exchange in a temperate deciduous forest. We hypothesized that canopy light-use efficiency would increase with increasing clouds (higher  $I_f/I_t$ ), that midday canopy  $P$  would peak at intermediate cloudiness, and that cloud cover and soil moisture would interact such that high  $I_f/I_t$  ameliorates water stress and increases WUE. To test these hypotheses, we examined the relationships between cloud cover, canopy  $P$ ,  $E$ , and WUE, and determined the effect of contrasting soil moisture conditions on these relationships.

## Methods

### Site Description

Our study was conducted at the University of Michigan Biological Station (UMBS) in northern lower Michigan, USA (45°35'35.4" N, 84°42' 46.8" W). The forest surrounding our eddy-covariance tower (described below) lies on a gently sloping high outwash plain with well-drained spodosolic soils (92.9% sand, 6.5% silt, 0.6% clay) derived from glacial drift (Pearsall 1995). The 30-year average annual temperature at UMBS is 6.2°C and precipitation is 750 mm. The forest within a permanent 1.1-ha plot around the tower is dominated by *Populus grandidentata* Michx. (39% of total basal area), *Acer rubrum* L. (14% of total basal area), *Quercus rubra* L. (12% of total basal area), and *Betula papyrifera* Marsh. (10% of total basal area) (Curtis et al. 2002). Understory vegetation is primarily bracken fern (*Pteridium aquilinum* L.) and seedlings of the overstory species. Leaf area index (LAI) within the 1.1-ha plot was measured periodically from leaf bud-break to leaf fall using an LAI meter (LAI-2000, LiCor, Inc., Lincoln, NE) and also

by leaf litter baskets. Mean canopy height was  $\sim 20$  m and maximum LAI was  $\sim 3.7 \text{ m}^2 \text{ m}^{-2}$ . The vertical distribution of leaf density was bimodal with high LAI occurring at  $\sim 2$  and  $\sim 17$  m above the forest floor (Schmid et al. 2003). Soil moisture (SM, % vol.) was measured periodically at eight locations using time domain reflectometry (Environmental Sensors, Inc., Victoria, BC, Canada), and continuously at a single location using a water content reflectometer (model CS615-L, Campbell Scientific, Inc., Logan, UT).

### Meteorological and Eddy-Covariance Measurements

We used a 46-m meteorological tower to measure energy and mass exchanges between forest and atmosphere. Measurements were made at 46 m (approximately twice canopy height). Net radiation was measured with a thermopile net radiometer (model Q\*7, REBS, Seattle, WA), PAR was measured with a silicon diode quantum sensor (model Li-190SZ-50, LiCor, Inc.), and incoming solar radiation above the canopy ( $S$ ) was measured with a silicon pyranometer (model Li-200SZ-50, LiCor, Inc.). Turbulent velocities were measured with a three-dimensional sonic anemometer (model CSAT-3, Campbell Scientific Inc.) and water vapor and  $\text{CO}_2$  concentrations were measured by a closed-path infra-red gas analyzer (IRGA model Li-6262, LiCor, Inc.). The sonic and IRGA data were sampled at 10 Hz for calculation of  $F_c$  and water vapor fluxes ( $F_w$ ). Above-canopy  $F_w$  was considered equivalent to forest  $E$ . Relative humidity ( $\phi$ ) and air temperature ( $T_a$ ) were measured on the top of the tower by a temperature and relative humidity probe (model HPO-43, Rotronic Instrument Corp., Huntington, NY). Precipitation was measured at the top of the tower with a tipping-bucket rain gauge (model TE-525, Texas Electronics, Dallas, TX). Soil temperature was measured at several locations surrounding the micrometeorological tower at a depth of 2 cm using a type E thermocouple.

Data used in this study include three growing-seasons (day of year 160–240; 1999, 2000, 2001) (Table 1). 2000 was somewhat cooler than 1999 and 2001, although all three years were above the 30-year growing-season average ( $17.3^\circ \text{C}$ ). Total growing-season rainfall in 1999 was nearly identical to the 30-year average (216 mm). Precipitation was above average in 2000, although over half the growing-season precipitation (285 mm) fell over the course of three days

**Table 1. Environmental conditions during growing seasons (days 160–240) in 1999, 2000, and 2001.**

	1999	2000	2001
Precipitation (mm)	216.1	417.2	174.7
Soil moisture (%)	11.5	9.2	9.9
$T_a^a$ ( $^\circ \text{C}$ )	22.0	19.7	21.8
VPD <sup>b</sup> (kPa)	1.11	0.92	1.10
$I_t^c$ ( $\mu\text{mol m}^{-2} \text{ s}^{-1}$ )	744.9	698.2	662.7
$I_f^c$ ( $\mu\text{mol m}^{-2} \text{ s}^{-1}$ )	340.3	349.8	322.5

Precipitation and soil moisture are the cumulative and average of hourly values, respectively, over 24-hour periods.

<sup>a</sup>  $T_a$  = air temperature at 46 m.

<sup>b</sup> VPD = vapor pressure deficit

<sup>c</sup>  $I_t$  (total incident PAR) and  $I_f$  (diffuse incident PAR) are hourly averages for daytime periods ( $I_t > 0$ ).

late in the season (day of year 229–231). Hence, 2000 and 2001 were drier than 1999, which is reflected in their lower average soil moisture contents. Average  $I_t$  and  $I_f$  were similar for the three years.

Eddy-covariance fluxes  $F_c$  and  $F_w$  were calculated from block averages of raw 10-Hz data from the sonic anemometer and IRGA using Reynolds decomposition, as described in Schmid et al. (2003). Inadequate turbulent mixing may lead to underestimates of  $F_c$  and  $F_w$  using the eddy-covariance method (Baldocchi et al. 2001). Only measurements during periods of adequate turbulent mixing (defined as the friction velocity  $u^* > 0.35 \text{ m s}^{-1}$ ) were used in this study. Hourly averages of  $T_a$ ,  $\phi$ ,  $S$ , and  $I_t$  were used to compute  $I_f$  (see below). Soil moisture data also were aggregated into hourly averages to determine the effects of varying cloud cover on canopy  $P$  during low versus high soil moisture conditions.

### Canopy Photosynthesis Light Response Curves

Canopy  $P$  was estimated from measurements of daytime  $F_c$  and estimated daytime ecosystem respiration ( $R_d$ ), where

$$P = R_d - F_c \quad (1)$$

Daytime ecosystem respiration was estimated from soil temperature at 2 cm ( $T_s$ ) based on the exponential relationships in Schmid et al. (2003) relating nighttime  $F_c$  under turbulent conditions to  $T_s$ . That is,

$$R_d = ae^{bT_s} \quad (2)$$

where  $a$  and  $b$  are coefficients estimated separately for each growing season. We assumed that nighttime  $F_c$  was equivalent to nighttime ecosystem respiration and that the  $R:T_s$  relationships were the same during the day and night (Goulden et al. 1997). Midday WUE was calculated as the ratio of midday canopy  $P$  to midday  $E$ .

We used a rectangular hyperbola to describe the relationship between  $I_t$  and  $P$ ,

$$P = \frac{\alpha\beta I_t}{\beta + \alpha I_t} \quad (3)$$

where  $\alpha$  is the canopy quantum efficiency and  $\beta$  is the canopy photosynthetic potential (i.e.,  $\beta = P$  as  $I_t$  approaches infinity). We used Sigma Plot 2000 (SPSS, Chicago, IL) to fit the light response curves by nonlinear least squares regression.  $F$ -statistics were constructed from the residual sum of squares for each regression line to test for significant differences among curves following Potvin et al. (1990).

### Estimation of Diffuse Beam Radiation

We used the radiation-partitioning (RP) model of Gu et al. (2002) to partition the diffuse and direct components of  $I_t$ . The RP model uses empirical relationships from Reindl et al. (1990) and Alados and Alados-Arboldedás (1999) to calculate  $I_f$  based on direct measurements of  $S$ ,  $T_a$ ,  $\phi$ , and  $I_t$ , and calculations of the solar zenith angle ( $\theta$ ), extraterrestrial solar radiation ( $S_o$ ) (Spitters et al. 1986), and the clearness index  $k_t$ , where  $k_t = S/S_o$ . In the RP model,  $k_t$ ,  $\theta$ ,  $T_a$ , and  $\phi$  are used as input variables to estimate hourly values of the

diffuse fraction of extraterrestrial global solar radiation ( $S_f/S_o$ ) in a piecewise fashion according to  $k_t$ , because the dependence of  $S_f/S_o$  on  $k_t$  decreases as  $k_t$  increases (Equation 4, a–c, below). Because multiple predictors are used in the piecewise model, constraints are used on calculated values of  $S_f/S_o$  for each interval of  $k_t$ , so that certain combinations of the dependent variables do not cause the model to output anomalous values, e.g.,  $S_f/S_o > 1$ .

For the interval  $0 \leq k_t \leq 0.3$  with the constraint that  $S_f/S_o \leq k_t$ ,

$$S_f/S_o = k_t[1 - 0.232k_t + 0.023 \cos \theta - 6.82 * 10^{-4}T_a + 0.0195\phi]. \quad (4a)$$

For the interval  $0.3 < k_t < 0.78$  with the constraint that  $0.1 k_t \leq S_f/S_o \leq 0.97k_t$ ,

$$S_f/S_o = k_t[1.329 - 1.716k_t + 0.267 \cos \theta - 3.57 * 10^{-3}T_a + 0.0106\phi]. \quad (4b)$$

For the interval  $k_t \geq 0.78$  with the constraint that  $S_f/S_o \geq 0.1 k_t$ ,

$$S_f/S_o = k_t[0.426k_t + 0.0256 \cos \theta - 3.49 * 10^{-3}T_a + 0.007\phi]. \quad (4c)$$

The ratio of diffuse PAR to diffuse global radiation ( $I_f/S_f$ ) was then calculated as

$$I_f/S_f = 2.282 - 0.78S_f/S_o + 0.067 \ln \varepsilon + 0.007T_d \quad (5)$$

and

$$\varepsilon = \frac{1 + (S - S_f)/(S_f \cos \theta) + 1.041\theta^3}{1 + 1.041\theta^3}, \quad (6)$$

where  $\varepsilon$  is a clearness parameter and  $T_d$  is dew point temperature.

The RP model was developed and tested for temperate regions and has been used to estimate  $I_f$  in mixed deciduous, tallgrass prairie, and Scots pine ecosystems (Gu et al. 2002). We verified our RP model results against measured  $I_f$  and  $I_r$  data from another temperate deciduous forest, Walker Branch, Tennessee, USA (Ameriflux, public.ornl.gov/ameriflux/Site\_Info/siteInfo.cfm?KEYID=us.walker\_branch.01, Feb. 15, 2001) and found very good agreement between measured and calculated  $I_f$  ( $R^2 = 0.75$ ) and  $I_r$  ( $R^2 = 0.93$ , data not shown).

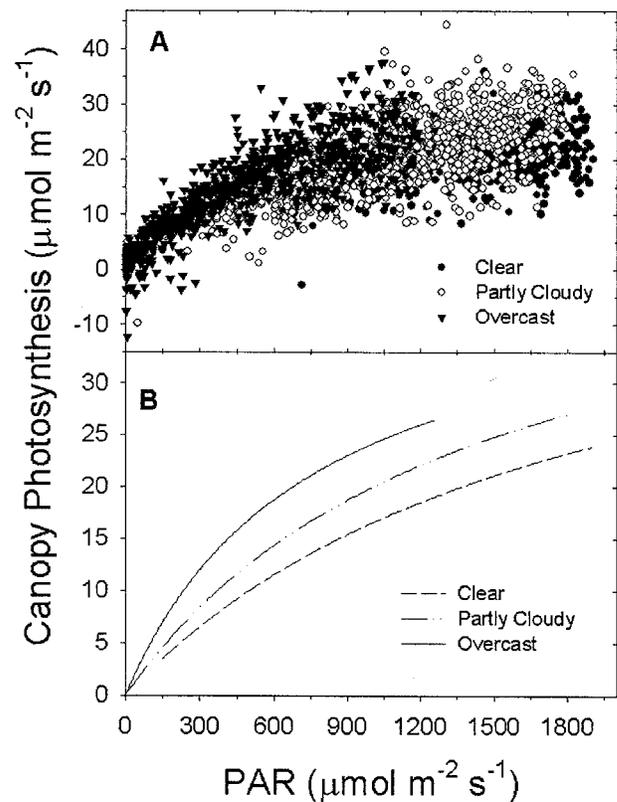
### Sky Condition and Soil Moisture Classes

Carbon and water fluxes, VPD, and  $I_t$  from the three growing seasons were pooled and aggregated into classes based on hourly average SM and  $I_f/I_t$ . Sky condition classes were clear ( $I_f/I_t < 0.30$ ), partly cloudy ( $0.30 \leq I_f/I_t \leq 0.70$ ), and overcast ( $I_f/I_t > 0.70$ ) and SM classes were dry ( $SM < 7.5\%$ ) and wet ( $SM > 12\%$ ). Limits for each SM class were chosen to maximize the contrast between dry and wet SM conditions while maintaining similar sample sizes between classes. Sky condition classes represented cloud cover of <23%, 23–65% and >65% of total sky, respectively

(Freedman et al. 2001). Statistical analyses of midday canopy  $P$  during different soil moisture and sky conditions were made using analysis of variance (ANOVA), and familywise comparisons (Fisher's LSD) determined significant differences among groups. Statistical tests were conducted using Minitab (Minitab, Inc., State College, PA).

## Results

At low light levels, canopy  $P$  increased rapidly with increasing PAR, reaching a maximum rate of 20–30  $\mu\text{mol m}^{-2} \text{s}^{-1}$  above  $\sim 1,000 \mu\text{mol m}^{-2} \text{s}^{-1}$  PAR (Fig. 1A). The shape of the photosynthetic light response curve differed significantly with sky condition class, however (Fig. 1B). Under clear skies (diffuse fraction  $< 0.3$ ), the initial slope of the canopy light response curve, or quantum efficiency ( $\alpha$ ), was less than half that under overcast skies (diffuse fraction  $> 0.7$ ), and 26% lower than under partly cloudy skies (diffuse fraction between 0.3 and 0.7) (Table 2). Canopy photosynthetic potential ( $\beta$ ) was lowest under overcast skies and greatest under partly cloudy skies. Although the complete light response curves were significantly different from one another based on an analysis of the residuals ( $F_{2,2704} = 127.54$ ,  $P < 0.001$ ), the relatively better fit of the model to data at low compared to high PAR resulted in different levels of statistical confidence in the derived coefficients,  $\alpha$  and  $\beta$ . The differences among  $\alpha$



**Figure 1.** The response of canopy photosynthesis to varying levels of PAR under different sky conditions (clear, partly cloudy, and overcast). Hourly canopy photosynthesis derived from eddy covariance measurements is shown in panel A, and the best fit curves are shown in panel B. Regression coefficients and goodness-of-fit statistics for these curves are shown in Table 2.

**Table 2. Canopy quantum efficiency ( $\alpha$ ; unitless), and canopy photosynthetic potential ( $\beta$ ;  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) under different sky condition and soil moisture (SM) classes.**

Sky Condition	$\alpha$	$\beta$	$R^2$	$n$
Clear	0.025 (0.004)	47.3 (5.26)	0.32	460
Partly cloudy	0.034 (0.002)	48.4 (2.53)	0.54	963
Overcast	0.056 (0.002)	42.5 (1.91)	0.78	746
Clear + partly cloudy				
SM wet	0.034 (0.003)	49.8 (8.47)	0.52	355
SM dry	0.039 (0.004)	36.8 (3.50)	0.41	1,068

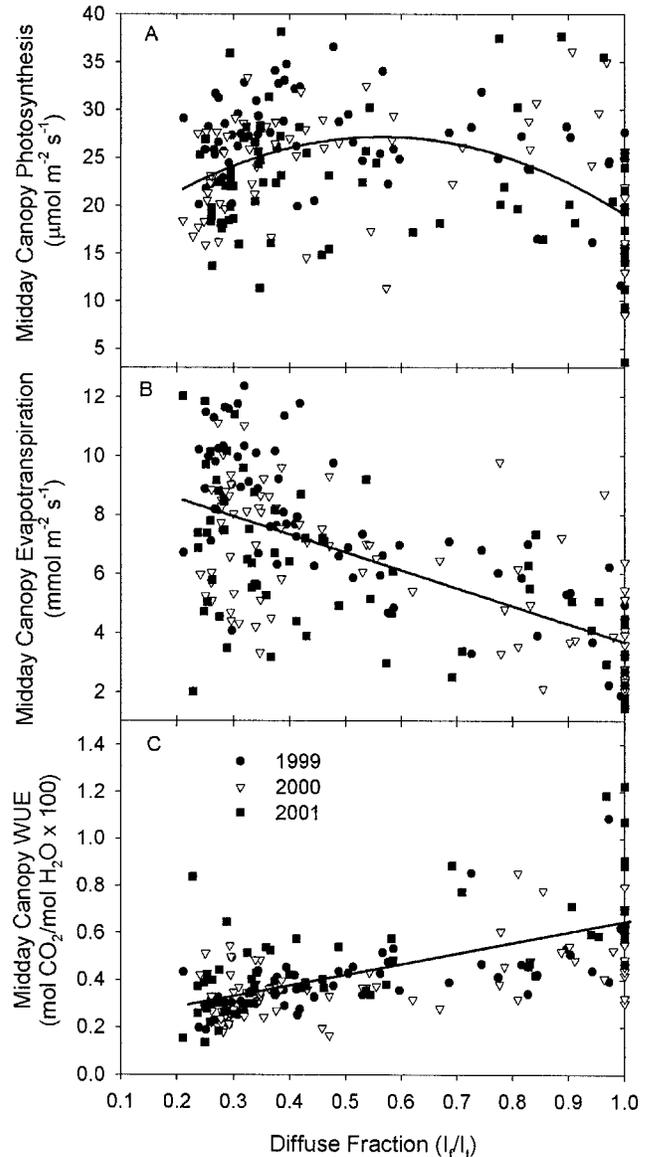
Numbers in parentheses are the 95% confidence intervals of the coefficients derived from fitting Equation 3 to the data presented in Figures 1 and 3. All regressions were significant at  $P < 0.001$ .

values were large with nonoverlapping 95% confidence intervals (CIs) suggesting significant sky condition effects. The differences among  $\beta$  values were considerably smaller and there were several overlapping CIs, suggesting less of an effect of sky condition on canopy photosynthetic potential as PAR increased.

These contrasting photosynthetic light responses were reflected in midday (solar noon) canopy  $P$ , which showed a nonlinear response to increasing diffuse fraction of PAR (Fig. 2A). Midday  $P$  increased with increasing  $I_f/I_t$ , reaching maximum uptake rates in each measurement year between 0.5 and 0.6  $I_f/I_t$ . Across all three years, midday canopy  $P$  was highest at a diffuse fraction of 0.57. There appeared to be a trend toward greater reduction in midday canopy  $P$  at high compared to low  $I_f/I_t$ , although this was most pronounced in 1999. Note that absolute levels of  $I_t$  may vary substantially at equivalent values of  $I_f/I_t$ , accounting for some of the scatter around the regression line. The decline in midday  $P$  at high  $I_f/I_t$  was largely a result of low  $I_t$  levels, because normalizing  $P$  on  $I_t$  resulted in a linear positive relationship with  $I_f/I_t$  (data not shown).

There was a significant, negative linear relationship between midday  $E$  and  $I_f/I_t$ , with approximately 50% less water vapor loss from vegetation and soils under overcast than under clear skies (Fig. 2B). This steep drop in  $E$  with increasing cloud cover, but only modest reductions in  $P$  even under overcast skies, resulted in a doubling in canopy WUE with increasing diffuse fraction, from  $\sim 0.003$  mol  $\text{CO}_2/\text{mol H}_2\text{O}$  under clear skies to  $\sim 0.006$  mol  $\text{CO}_2/\text{mol H}_2\text{O}$  under overcast skies (Fig. 2C). This effect was consistent across years, and accounted for 40% of the observed variation in midday hourly WUE.

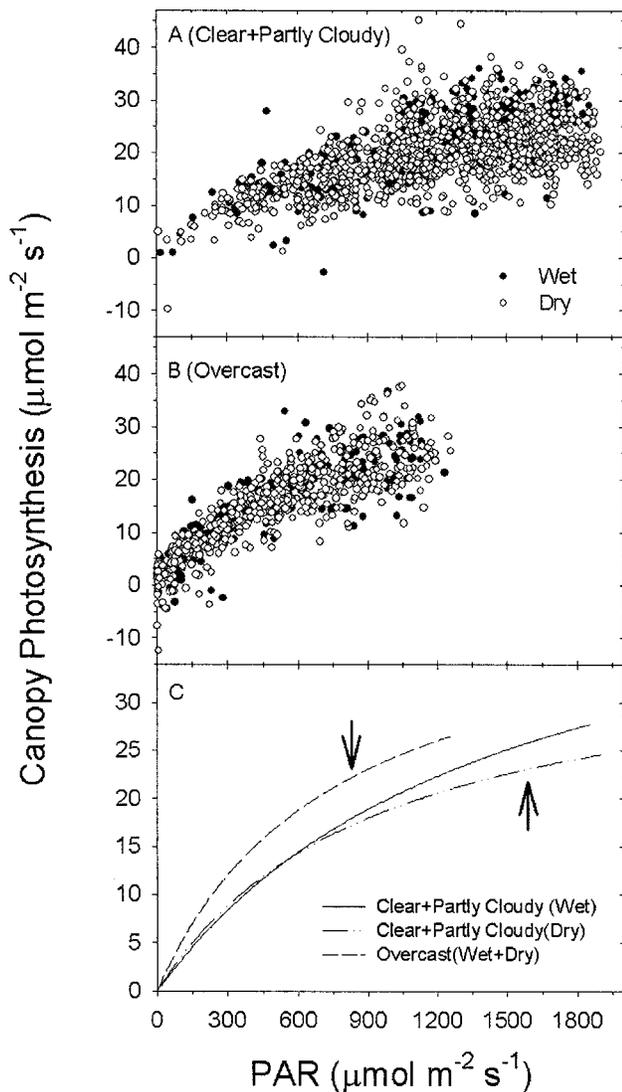
Soil moisture availability had a significant effect on canopy photosynthetic light responses but only under clear or partly cloudy sky conditions (Fig. 3). In this analysis, data from the clear sky class were pooled with those from the partly cloudy sky class because of the small sample size of clear sky combined with wet soil conditions. In the clear + partly cloudy class, fitted light response curves for dry and wet soils were significantly different from each other ( $F_{2, 1811} = 113.97$ ,  $P < 0.001$ ) primarily at higher PAR values (Fig. 3C) and in  $\beta$  (Table 2). Low soil moisture reduced  $\beta$  26% compared to wet soil conditions, with no overlap in coefficient CIs. There were no apparent effects of soil moisture on  $\alpha$  in the clear + partly cloudy class. Under overcast skies, there was no significant difference between



**Figure 2.** The relationships between  $I_f/I_t$  and (A) midday canopy photosynthesis ( $P_m$ ), (B) evapotranspiration ( $E$ ) and (C) water use efficiency (WUE) across three years. Regression equations were: (A)  $P_m = 13.39 + 48.8 * I_f/I_t - 43.09 * (I_f/I_t)^2$ ,  $R^2 = 0.17$ ,  $P < 0.001$ ; (B)  $E = 9.78 - 6.08 * I_f/I_t$ ,  $R^2 = 0.41$ ,  $P < 0.001$ ; (C)  $WUE = 0.19 + 0.46 * I_f/I_t$ ,  $R^2 = 0.40$ ,  $P < 0.001$ .

light response curves fitted to data from either soil moisture class ( $F_{2, 741} = 1.19$ ,  $P > 0.10$ ).

Midday canopy  $P$  reflected the results from the fitted



**Figure 3.** The relationships between canopy photosynthesis and PAR under different sky conditions: (A) clear + partly cloudy, and (B) overcast, under wet (closed symbols) or dry (open symbols) soil moisture conditions. Hourly canopy photosynthesis derived from eddy covariance measurements is shown in panels A and B, and the results of fitting the light response model, Equation 3, to these data is shown in panel C. Regression coefficients and goodness-of-fit statistics for these curves are presented in Table 2. Arrows indicate average midday (solar noon) PAR levels in the different sky condition classes.

**Table 3.** Midday canopy photosynthesis ( $P$ ,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), vapor pressure deficit (VPD, kPa), and total ( $I_t$ ) and diffuse ( $I_f$ ) incident PAR ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) under different sky condition (clear + partly cloudy or overcast) and soil moisture (dry or wet) classes.

Midday $P$	Clear + Partly Cloudy		Overcast	
	Dry	Wet	Dry	Wet
1999	26.0 (1.19, 11) <sup>a</sup>	28.0 (0.73, 24) <sup>a</sup>	25.8 (1.19, 3) <sup>a</sup>	25.7 (1.82, 7) <sup>a</sup>
2000	20.8 (1.34, 16) <sup>a</sup>	23.8 (2.41, 5) <sup>a</sup>	25.0 (5.64, 3) <sup>a</sup>	20.7 (1.81, 4) <sup>a</sup>
2001	23.2 (0.94, 16) <sup>a</sup>	21.1 (1.58, 13) <sup>a</sup>	24.0 (3.92, 7) <sup>a</sup>	18.8 (1.12, 11) <sup>a</sup>
All years	23.0 (0.73, 43) <sup>a</sup>	25.4 (0.84, 42) <sup>b</sup>	24.7 (2.34, 13) <sup>ab</sup>	21.3 (1.06, 22) <sup>a</sup>
Midday VPD	1.39 (0.06, 43) <sup>a</sup>	1.25 (0.06, 42) <sup>a</sup>	0.82 (0.13, 13) <sup>b</sup>	0.76 (0.08, 22) <sup>b</sup>
Midday $I_t$	1633 (30.0, 43) <sup>a</sup>	1610 (26.9, 42) <sup>a</sup>	805 (91.1, 13) <sup>b</sup>	856 (53.4, 22) <sup>b</sup>
Midday $I_f$	591 (17.7, 43) <sup>a</sup>	592 (19.3, 42) <sup>a</sup>	768 (68.06, 13) <sup>b</sup>	789 (58.5, 22) <sup>b</sup>

Different superscripts within a row indicate significant difference at  $P < 0.05$  or  $P < 0.08$  where underlined.

Midday  $P$  is shown for each growing season separately and for all 3 years combined. VPD and  $I_t$  are shown for the 3 years combined only. Mean (SE,  $n$ ).

light response curves (Table 3). Although there was substantial interannual variation in midday  $P$ , across all years we observed a modest (10%) but significant reduction in midday  $P$  under dry soils and clear or partly cloudy skies. There was no significant effect of soil drought on midday  $P$  under overcast skies, and indeed the trend across years was for higher midday  $P$  under dry compared to wet soils. Neither midday VPD nor midday  $I_t$  varied with soil moisture, although both were significantly lower under overcast compared to clear + partly cloudy skies (Table 3).

## Discussion

We examined the effects of cloud cover on canopy  $P$ ,  $E$ , and WUE in an aspen-dominated northern hardwood forest in the upper Great Lakes region. Ours is the first study to demonstrate that changes in environmental conditions associated with increasing cloud cover can lead to either positive or negative effects on canopy net carbon uptake and that these effects are sensitive to soil moisture. Our study also is the first to incorporate information on  $I_f/I_t$  into the analysis of eddy covariance data from a northern hardwood forest.

We found that, across all sky classes, canopy quantum efficiency ( $\alpha$ ) and photosynthetic potential ( $\beta$ ) of the UMBS forest fell within the range previously reported for broadleaf forests ( $\alpha$ : 0.009–0.102;  $\beta$ : 7.64–81.70) (Ruimy et al. 1995). Likewise, canopy  $P$ , WUE, and  $E$  also were similar to rates reported for other mixed deciduous forests (Law et al. 2002). Our results highlighted three important physiological responses of the UMBS forest to sky conditions. First, canopy  $P$  light response curves under clear, partly cloudy, and overcast skies were significantly different from one another, with  $\alpha$  increasing with increasing cloud cover but  $\beta$  being greatest under intermediate cloud cover. Second, midday canopy  $P$  was highest under partly cloudy skies and declined with either increasing or decreasing cloud cover. Third, increases in  $I_f/I_t$  during the middle of the day led to decreased  $E$  and increased WUE.

We found that, under partly cloudy or overcast skies,  $\alpha$  increased 26% and 40%, respectively, over clear sky conditions. These results agree with those from temperate deciduous (Baldocchi et al. 1997), boreal (Goulden et al. 1997, Fan et al. 1995), subalpine (Monson et al. 2002), and temperate evergreen forests (Price and Black 1991) which all showed higher light use efficiency under cloudy skies.

Higher  $\alpha$  under cloudy skies has been attributed to increases in understory PAR and a slight decrease in overstory PAR, resulting in an overall increase in canopy light use efficiency. At UMBS, increased cloud cover decreased overstory PAR and increased the percentage of diffuse PAR. Increased diffuse PAR results in a more even distribution of light throughout the canopy (Weiss 2000), enhancing photosynthesis by understory leaves. We expect this phenomenon to be especially significant at UMBS because of the bimodal distribution of leaves over the vertical extent of the canopy.

Although  $\alpha$  was greatest under overcast skies, we found that this level of cloud cover resulted in lower  $\beta$ . This may be because, although overcast skies increase  $I_f/I_t$ , they also substantially reduce  $I_t$ , such that canopy  $P$  becomes light-limited and  $\beta$  decreases. However, Goulden et al. (1997) and Monson et al. (2002) reported higher  $\beta$  under cloudy compared to clear skies. A number of factors may account for these differing results, including different methods for defining cloud cover and numbers of cloud cover classes considered in the analyses. If we considered only two cloud cover classes, clear versus cloudy, as was done in the previously cited work, we would also have found an increase in  $\beta$  with increasing clouds. Distinguishing heavy cloud cover (overcast skies) from intermediate levels (partly cloudy skies), as was done in our study, revealed a nonlinear response of  $\beta$  to increasing clouds, a result supported by our measurements of midday canopy  $P$ . Gu et al. (2002) assumed that both  $\alpha$  and  $\beta$  were linear functions of the fractions of diffuse and direct beam PAR, an assumption that our results suggest may not be met for all forest types. In the UMBS forest, midday canopy  $P$  was greatest with a diffuse fraction of 0.57, very similar to the value of 0.56 predicted by Gu et al. (2003) from a simulation model of deciduous forest canopy  $P$ . Our results agree with those of Fan et al. (1995) who showed that boreal forest gross  $\text{CO}_2$  assimilation was greater under partly cloudy compared to clear skies but was reduced under heavy cloud cover. In a mixed deciduous forest, prolonged periods of cloud cover reduced net carbon uptake (Goulden et al. 1996). Using actual cloud observations, Freedman et al. (2001) found that overcast skies substantially decreased  $I_t$  and resulted in decreased carbon uptake. All of these studies reported maximum canopy  $P$  at intermediate cloud cover and decreased canopy  $P$  under dense cloud cover. Our results confirmed that this also was the case at the UMBS forest site, and that it is important to distinguish photosynthetic responses between intermediate and heavy cloud cover conditions.

Although midday  $P$  responded nonlinearly to increasing  $I_f/I_t$ , we found a strong linear decrease in  $E$  and a linear increase in WUE with increasing cloudiness. This suggests that, under high  $I_f/I_t$ , the decrease in  $E$  is disproportionately greater than the decrease in canopy  $P$ . Increased WUE under cloudy skies has been attributed to increases in canopy  $P$  because of increased diffuse radiation, and decreases in  $E$  because of decreased VPD (Price and Black 1990). However, Freedman et al. (2001) found that  $E$  was reduced under cloudy conditions largely because of decreases in

available energy to evaporate water, whereas Law et al. (2002) reported a weak relationship between WUE and VPD across a number of deciduous forests. In both a coniferous forest and sclerophyll shrub ecosystem, increases in cloud cover contributed to a  $\sim 50\%$  increase in WUE (Tenhunen et al. 1990, Price and Black 1991), similar to the increase in WUE we observed between clear and overcast skies. This is the first study to demonstrate the linear relationships between the diffuse fraction and  $E$  and WUE.

Gu et al. (2003) suggested that environmental controls on canopy carbon exchange may behave differently under cloudy compared to clear skies and that factors other than an increase in diffuse light affect canopy  $P$  during changes in cloud cover. We found that canopy  $P$  was insensitive to changes in soil moisture under overcast conditions but that it was reduced by low soil moisture under clearer skies. One mechanism to explain this observation is that, under overcast skies, canopy  $P$  is most strongly limited by low  $I_t$ , whereas low  $E$  and high WUE under these conditions reduces the likelihood of water stress as soils dry. By contrast, under clear skies with high  $E$  and low WUE, canopy  $P$  will be much more sensitive to the physiological effects of drought, such as midday stomatal closure. Further canopy-level physiological studies will be necessary to test this hypothesis.

## Summary

We used eddy-covariance and meteorological observations to show that clouds play an important role in forest gas exchange. Our results corroborated those from previous studies demonstrating the importance of diffuse radiation in forest physiological processes, and provide insight into cloud-vegetation feedbacks in the aspen-dominated hardwood forests of the upper Great Lakes region. Our study is unique in that canopy  $P$ ,  $E$ , and WUE were simultaneously analyzed to determine how these processes react to changes in cloud cover and interact with each other. Although increased  $I_f/I_t$  with increasing cloud cover played an important role in increasing canopy  $P$ , heavy cloud cover ultimately reduced net  $\text{CO}_2$  uptake resulting from decreased  $I_t$ . We also found that changes in environmental conditions associated with increasing cloud cover could lead to either positive or negative effects on canopy carbon uptake, and that these effects were sensitive to soil moisture. These findings contribute significantly to our knowledge of cloud cover effects on forest canopy physiological processes and provide information of importance to our understanding of the consequences of climate change on forest ecosystem function.

## Literature Cited

- ALADOS, I., AND L. ALADOS-ARBOLEDAS. 1999. Direct and diffuse photosynthetically active radiation: Measurements and modeling. *Agric. For. Meteorol.* 93:27–38.
- BALDOCCHI, D.D. 1997. Measuring and modeling carbon dioxide and water vapor exchange over a temperate broad-leaved forest during the 1995 summer drought. *Plant Cell Environ.* 20:1108–1122.

- BALDOCCHI, D.D., B.A. HUTCHISON, D.R. MATT, AND R.T. MC-MILLEN. 1985. Canopy radiative transfer models for spherical and known leaf inclination distribution angles: A test in an oak-hickory forest. *J. Appl. Ecology* 22:539–555.
- BALDOCCHI, D.D., E. FALGE, L.H. GU, R. OLSON, D. HOLLINGER, S. RUNNING, P. ANTHONI, C. BERNHOFER, K. DAVIS, R. EVANS, J. FUENTES, A. GOLDSTEIN, G. KATUL, B. LAW, X.H. LEE, Y. MALHI, T. MEYERS, W. MUNGER, W. OECHEL, K.T. PAW U, K. PILEGAARD, H.P. SCHMID, R. VALENTINI, S. VERMA, T. VESALA, K. WILSON, AND S. WOFSY. 2001. FLUXNET: A new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapor and energy flux densities. *Bull. Am. Meteorol. Soc.* 82:2415–2435.
- CHEN, J., E. CARLSON, AND A.D. DEL GENIO. 2002. Evidence for strengthening of the Tropical General Circulation in the 1990s. *Science* 295:838–841.
- CURTIS, P.S., P.J. HANSON, P. BOLSTAD, C. BARFORD, J.C. RANDOLPH, H.P. SCHMID, AND K.B. WILSON. 2002. Biometric and eddy-covariance based estimates of annual carbon storage in five eastern North American deciduous forests. *Agric. For. Meteorol.* 113:3–19.
- FAN, S.M., M.L. GOULDEN, J.W. MUNGER, B.C. DAUBE, P.S. BAKWIN, S.C. WOFSY, J.S. AMTHOR, D.R. FITZJARRALD, K.E. MOORE, AND T.R. MOORE. 1995. Environmental controls on the photosynthesis and respiration of a boreal lichen woodland: A growing season of whole-ecosystem exchange measurements by eddy correlation. *Oecologia* 102:443–452.
- FITZJARRALD, D.R., K.E. MOORE, R.K. SAKAI, AND J.M. FREEDMAN. 1995. Assessing the impact of cloud cover on carbon uptake in the northern boreal forest (abstract). *American Geophysical Union, EOS Trans. Spring Meeting Suppl.* 76(17), S125.
- FREEDMAN, J.M., D.R. FIRZJARRALD, K.E. MOORE, AND R.K. SAKAI. 2001. Boundary layer clouds and vegetation-atmosphere feedbacks. *J. Climatol.* 14:180–197.
- GOULDEN, M.L., J.W. MUNGER, S.M. FAN, B.C. DAUBE, S.C. WOFSY. 1996. Exchange of carbon dioxide by a deciduous forest: Response to interannual climate variability. *Science* 271:1576–1578.
- GOULDEN, M.L., B.C. DAUBE, S.M. FAN, D.J. SUTTON, A. BAZAZ, J.W. MUNGER, AND S.C. WOFSY. 1997. Physiological responses of a black spruce forest to weather. *J. Geophys. Res.* 102:28987–28996.
- GU, L., J.D. FUENTES, H.H. SHUGART, R.M. STAEBLER, AND T.A. BLACK. 1999. Responses of net ecosystem exchanges of carbon dioxide to changes in cloudiness: Results from two North American deciduous forests. *J. Geophys. Res.* 104:31421–31434.
- GU, L., D.D. BALDOCCHI, S.B. VERMA, T.A. BLACK, T. VESALA, E.M. FALGE, AND P.R. DOWTY. 2002. Advantages of diffuse radiation for terrestrial ecosystem productivity. *J. Geophys. Res.* 107:31421–31434.
- GU, L., D.D. BALDOCCHI, S.C. WOFSY, J.W. MUNGER, B. URBAN, J.J. MICHALSKY, AND T.A. BODEN. 2003. Response of a deciduous forest to the Mt Pinatubo eruption: Enhanced photosynthesis. *Science* 299:2035–2038.
- HEALY, K.D., K.G. RICKER, G.L. HAMMER, AND M.P. BANGE. 1998. Radiation use efficiency increases when the diffuse component of incident radiation is enhanced. *Aust. J. Agric. Res.* 49:665–672.
- HENDERSON-SELLERS, A. 1989. North American total cloud amount variations this century. *Palaeogeograph. Palaeoclimatol. Palaeoecol.* 75:175–194.
- HIROSE, T., AND M.J.A. WERGER. 1987. Maximizing daily canopy photosynthesis with respect to the leaf nitrogen allocation pattern in the canopy. *Oecologia* 72:520–526.
- HOLLINGER, D.Y., F.M. KELLIHER, J.N. BYERS, J.E. HUNT, T.M. MCSEVENY, AND P.L. WEIR. 1994. Carbon dioxide exchange between an undisturbed old-growth temperate forest and the atmosphere. *Ecology* 75:134–150.
- KARL, T.R., AND P.M. STEURER. 1990. Increased cloudiness in the United States during the first half of the twentieth century: Fact or fiction? *Geophys. Res. Lett.* 17:1925–1928.
- KEELING, C.D., J.F.S. CHIN, AND T.P. WHORF. 1996. Increased activities of northern vegetation inferred from atmospheric CO<sub>2</sub> measurements. *Nature* 382:146–149.
- KNAPP, A.K., W.K. SMITH, AND D.R. YOUNG. 1989. Importance of intermittent shade to the ecophysiology of subalpine herbs. *Funct. Ecol.* 3:753–758.
- LAMAUD, E., Y. BRUNET, AND P. BERBIGIER. 1997. Radiation and water use efficiencies of two coniferous forest canopies. *Phys. Chem. Earth* 21:361–365.
- LAW, B.E., E. FALGE, L. GU, D.D. BALDOCCHI, P. BAKWIN, P. BERBIGIER, K.J. DAVIS, H. DOLMAN, M. FALK, J. FUENTES, A.H. GOLDSTEIN, A. GRANIER, A. GRELLE, D. HOLLINGER, I. JANSSENS, P. JARVIS, N.O. JENSEN, G. KATUL, Y. MALHI, G. MATTEUCCI, R. MONSON, J.W. MUNGER, W. OECHEL, R. OLSON, K. PILEGAARD, K.T. PAW U, H. THORGEIRSSON, R. VALENTINI, S. VERMA, T. VESALA, K. WILSON, AND S. WOFSY. 2002. Carbon dioxide and water vapor exchange of terrestrial vegetation in response to environment. *Agric. For. Meteorol.* 113:97–120.
- LUCHT, W., I.C. PRENTICE, R.B. MYNENI, S. SITCH, P. FRIEDLINGSTEIN, W. CRAMER, P. BOUSQUET, W. BUERMANN, AND B. SMITH. 2002. Climatic control of the high-latitude vegetation greening trend and Pinatubo effect. *Science* 296:1687–1689.
- MCGUFFIE, K., AND A. HENDERSON-SELLERS. 1988. Is Canadian cloudiness increasing? *Atmosphere-Ocean* 26:608–623.
- MONSON, R.K., A.A. TURNIPSEED, J.P. SPARKS, P.C. HARLEY, L.E. SCOTT-DENTON, K. SPARKS, AND T.E. HUXMAN. 2002. Carbon sequestration in a high-elevation, subalpine forest. *Global Change Biol.* 8:459–478.
- MYNENI, R.B., C.D. KEELING, C.J. TUCKER, G. ASRAR, AND R.R. NEMANI. 1997. Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature* 386:698–702.
- NEMANI, R.R., C.D. KEELING, H. HASHIMOTO, W.M. JOLLY, S.C. PIPER, C.J. TUCKER, R.B. MYENI, AND S.W. RUNNING. 2003. Climate-driven increases in global terrestrial net primary production from 1982 to 1999. *Science* 300:1560–1563.
- PEARSALL, D.R. 1995. *Landscape ecosystems of the University of*

- Michigan Biological Station, northern Lower Michigan: Ecosystem diversity and biological diversity. Ph.D. thesis, University of Michigan, Ann Arbor. 392 p.
- POTVIN, C., M.J. LECHOWICZ, AND S. TARDIF. 1990. The statistical analysis of ecophysiological response curves obtained from experiments involving repeated measures. *Ecology* 71:1389–1400.
- PRICE, D.T., AND T.A. BLACK. 1990. Effects of short-term variation in weather on diurnal canopy CO<sub>2</sub> flux and evapotranspiration of juvenile Douglas-fir stand. *Agric. For. Meteorol.* 50:139–158.
- PRICE, D.T., AND T.A. BLACK. 1991. Effects of summertime changes in weather and root-zone soil water storage on canopy CO<sub>2</sub> flux and evapotranspiration of two juvenile Douglas-fir stands. *Agric. For. Meteorol.* 53:303–323.
- REINDL, D.T., W.A. BECKMAN, AND J.A. DUFFIE. 1990. Diffuse fraction correlations. *Solar Energy* 45:1–7.
- RODERICK, M.L., G.D. FARQUHAR, S.L. BERRY, AND I.R. NOBLE. 2001. On the direct effect of clouds and atmospheric particles on the productivity and structure of vegetation. *Oecologia* 12:121–130.
- RUIMY, A., P.G. JARVIS, D.D. BALDOCCHI, AND B. SAUGIER. 1995. CO<sub>2</sub> fluxes over plant canopies and solar radiation: A review. *Adv. Ecol. Res.* 26:1–63.
- SCHMID, H.P., H-B SU, C.S. VOGEL, AND P.S. CURTIS. 2003. Ecosystem-atmosphere exchange of carbon dioxide over a mixed hardwood forest in northern lower Michigan. *J. Geophys. Res.* 108: 4417–4436.
- SINCLAIR, T.R., AND T. SHIRAIWA. 1993. Soybean radiation-use efficiency as influenced by nonuniform specific leaf nitrogen distribution and diffuse radiation. *Crop Sci.* 22:808–812.
- SINCLAIR, T.R., T. SHIRAIWA, AND G.L. HAMMER. 1992. Variation in crop radiation-use efficiency with increased diffuse radiation. *Crop Sci.* 33:1281–1284.
- SLAYBACK, D.A., J.E. PINZON, S.O. LOS, AND C.J. TUCKER. 2003. Northern hemisphere photosynthetic trends 1982–1999. *Global Change Biol.* 9:1–15.
- SPITTERS, C.J.T., H.A.J.M. TOUSSAINT, AND J. GOUDRIAAN. 1986. Separating the diffuse and direct component of global radiation and its implications for modeling canopy photosynthesis. 1: Components of incoming radiation. *Agric. For. Meteorol.* 38:217–229.
- TENHUNEN, J.D., A. SALA SERRA, P.C. HARLEY, R.L. DOUGHERTY, AND J.F. REYNOLDS. 1990. Factors influencing carbon fixation and water use by Mediterranean sclerophyll shrubs during summer drought. *Oecologia* 82:381–393.
- WEISS, S.B. 2000. Vertical and temporal distribution of insolation in gaps in an old-growth coniferous forest. *Can. J. For. Res.* 30:1953–1964.
- WIELICKI, B.A., T. WONG, R.P. ALLAN, A. SLINGO, J.T. KIEHL, B.J. SODEN, C.T. GORDON, A.J. MILLER, S.K. YANG, D.A. RANDALL, F. ROBERTSON, J. SUSSKIND, AND H. JACOBOWITZ. 2002. Evidence for large decadal variability in the tropical mean radiative energy budget. *Science* 295:841–844.
- WILSON, K.B., D.D. BALDOCCHI, AND P.J. HANSON. 2000. Spatial and seasonal variability of photosynthesis parameters and their relationship to leaf nitrogen in a deciduous forest. *Tree Physiol.* 20:565–587.