

Long-term observation of the atmospheric exchange of CO₂ with a temperate deciduous forest in southern Ontario, Canada

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Abstract. This paper reports the results of the analysis of eddy covariance CO₂ data obtained at a successional forest of maple and aspen at Camp Borden in southern Ontario, Canada, between July 1995 and December 1997. Main findings are (1) The Michaelis-Menton model explains >50–65% of the observed variance of the daytime net ecosystem carbon exchange (NEE) during the growing season; leaf wetness appears to be an important variable contributing to the remaining variance. (2) The whole-ecosystem respiration rate as a function of the 5-cm soil temperature shows a seasonal “hysteresis” (higher rate in the later part of the year), suggesting a nonnegligible contribution by deep soil/roots and the influence of litter age. (3) There is evidence of photosynthetic activities immediately after the spring snowmelt/soil warming, but the daily NEE did not switch sign till about 40 days later; our best estimates of the annual net carbon uptake by the ecosystem (net ecosystem production (NEP)) are -1.0 , -1.2 , and -2.8 t C ha⁻¹ yr⁻¹ for the periods July 19, 1995, to July 18, 1996, January 1 to December 31, 1996, and January 1 to December 31, 1997, respectively, with an uncertainty of ± 0.4 t C ha⁻¹ yr⁻¹. (4) The higher NEP value in 1997 than in 1996 was caused by lower growing season soil temperature, cooler spring and fall transitional periods, and higher photon flux in 1997; possible enhancement in canopy photosynthetic capacity may also have played a role. In addition, three main sources of uncertainties, data gap, fetch, and mass flow, are discussed. It is suggested that collective use of the methods available for assessing the whole-ecosystem respiration (friction velocity threshold, mass flow theory, and dark respiration from the forest light response) may increase the confidence level of NEP estimates.

1. Introduction

There is considerable interest among the scientific community in observational studies of the atmospheric CO₂ flux using the tower-based eddy covariance (EC) technique to understand the role of forest ecosystems in the atmospheric carbon cycle [Tans and White, 1998]. A limited number of long-term (>1 year) studies have reported CO₂ flux data for tropical [Grace *et al.*, 1995a; Malhi *et al.*, 1998], temperate [Wofsy *et al.*, 1993; Greco and Baldocchi, 1996], and boreal forests [Goulden *et al.*, 1997; Black *et al.*, 1996; Lindroth *et al.*, 1998]. More studies are needed to expand the coverage by the tower flux network of forest types and climate gradients in order to allow cross-biome and within-biome syntheses.

The objective of this paper is to report the results of analysis of CO₂ flux data obtained at the Camp Borden forest over the period from July 1995 to December 1997. Since its establishment in 1985 as a pollution deposition research site by Environment Canada, the Camp Borden facility has supported sev-

eral major field campaigns, including canopy turbulence [Shaw *et al.*, 1988], ozone and volatile organic compound exchanges [Fuentes *et al.*, 1992; Fuentes and Wang, 1999], and nocturnal atmospheric processes [Lee *et al.*, 1996]. There are several important features about this forest that we wish to emphasize here. The site is located at a relatively northern latitude in comparison to temperate forests under investigation by other research groups and thus expands the climatic coverage of the tower flux monitoring network. The nocturnal drainage flow problem is probably not severe owing to the flat topography [Neumann *et al.*, 1989], but advection is a serious concern because a large wind direction sector does not have adequate fetch. The forest is a successional forest and has been undergoing a rapid shift in species composition [Neumann *et al.*, 1989], whereas forests at other sites with long flux records appear to have reached a climax.

2. Site and Instrumentation

2.1. Site

Measurements were conducted in a mixed deciduous forest on flat terrain in southern Ontario near Camp Borden (44°19'N, 79°56'W). The forest appears to be natural regrowth

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Table 1. Comparison of Forest Composition in 1985 and 1995

	1985	1995
Tree species*		
Large-tooth aspen <i>Populus grandidentata</i> Michx.	49	12
Red maple <i>Acer rubum</i> L.	31	36
Black cherry <i>Prunus serotina</i> Ehrh.	9	4
Trembling aspen <i>Populus tremuloides</i> Michx.	6	21
White ash <i>Fraxinus americana</i> L.	3	14
Eastern white pine <i>Pinus strobus</i> L.	3	5
Stem density, stems ha ⁻¹	3560	3400
Leaf area index	5.1	4.1
Clumping index	0.50	0.85

*Values are percentage of total stems.

on farmland abandoned at the turn of the century [Neumann *et al.*, 1989]. A major shift in the species composition was recorded from 1985 to 1995 (Table 1), indicating that the forest was in rapid succession. Large-tooth aspen, an early successional species very intolerant of shade, was dominant in 1985 and has since then been replaced by red maple and white ash, two subclimax and more shade tolerant species. The growing season leaf area index (LAI) and clumping index, obtained from leaf litter collection and optical methods [Neumann *et al.*, 1989; Staebler *et al.*, 1997], changed from 5.1 and 0.5 in 1985 to 4.1 and 0.85 in 1995, respectively, reflecting change of the forest from a two-layer structure (aspen over red maple) to a one-layer canopy (dominated by red maple and trembling aspen). In addition, drought during the spring leaf expansion may also have contributed to the reduced LAI in 1995. The seasonal course of LAI is given by Staebler *et al.* [1997]. The mean tree height was 21 m.

Figure 1 shows the surface cover map near the flux tower. The desirable wind directions lie in the sector 90°–255° (fetch 1.5–4 km). Unless stated otherwise, presentation of flux data and turbulence statistics will be limited to this sector. Of this subset of observations, <10% had wind from the military base. The influence of the base is not discernible on the flux observations because there is good fetch (>1.5 km) and the base is heavily wooded (80% forest cover, aerodynamically similar to the forest outside). A footprint analysis indicates that the typical daytime flux footprint reaches about 250 m from the tower. The variations in terrain height within the 4-km radius shown in Figure 1 are of the order of 1 or 2 m except a river valley of 20-m depth and 40-m width 1 km south of the tower. The forest is surrounded by agricultural land. Another major feature of the landscape is a 6-km-wide swamp located 5 km northwest of the tower.

Annual mean air temperature is 6.4°C (Table 2). Annual mean precipitation totals at 858 mm, with maximum in August (94 mm) and minimum in March (50 mm). Less than half of the precipitation is lost through evapotranspiration, and the remaining portion is lost as runoff (Table 2). The growing season, defined as the period when the mean daily temperature remains above 5°C, starts in early April and ends in late October. Leafing-out starts in mid-May, and leaf-fall is completed by the end of October.

2.2. Instrumentation

The configuration of the main EC system was similar to that deployed in previous field campaigns [Black *et al.*, 1996], with the following modifications. Air was drawn through a heated tubing of 50 m in length (Dekoron, ID 6.4 mm) at a flow rate of 20 L min⁻¹, which maintained turbulent state of flow [Leuning and Judd, 1996]. A fraction of this flow, 6 L min⁻¹, was passed via a 1-m-long tubing of the same type through a CO₂/H₂O analyzer (model 6262, LI-COR Inc., Lincoln, Nebraska) downstream of the pump. The air intake was located at 23 cm from the nearest transducer of the sonic anemometer. This EC unit was mounted at z (height above the ground) = 33.4 m, and operation has continued to date since mid-July, 1995.

During part of 1995 a second EC unit was operated at various heights within and above the forest. This unit was configured with a short sampling tubing (same type as above, 6 m in length, flow rate 6.5 L min⁻¹) and was used to check the overall system performance.

All EC signals were subject to low-pass filtering with a resistor-capacitor filter (cutoff frequency 50 Hz) and were sampled by an analog-to-digital system (AT-M10-16X with SCXI-1300 multiplexer, National Instruments, Texas) at 50 Hz. This was reduced to 10 Hz using a five-point block average to produce data files for archiving and analysis. The filter–block average arrangement prevents signal aliasing and effectively rejects the 60-Hz AC power line noise.

Air temperature was monitored at 12 levels ranging from 0.5 to 43.4 m with ventilated copper-constantan thermocouples. Soil temperature was monitored at depths of 0.05, 0.1, 0.2, 0.5, and 1.0 m with two profile systems consisting of precision thermistors and copper-constantan thermocouples, respectively. Two additional thermistors were buried at 5 cm near the soil heat flux plates for assessing heat storage in the top 7.5-cm soil layer. During the 1995 growing season a CO₂/H₂O profile system [Black *et al.*, 1996] was employed to measure CO₂ concentration and humidity at z = 1.0, 3.0, 10.0, 15.0, 20.0, 25.0, 34.0, and 45.0 m. Other continuous measurements included global radiation, photosynthetic photon flux density Q , wind speed, wind direction, air humidity, net radiation over the forest, soil heat flux, and bole temperature.

The CO₂ analyzers were run in differential mode with dry reference gases of near-ambient CO₂ concentration provided to the reference cell. CO₂ of the profile analyzer was calibrated at 10-min intervals against gases of known concentration. CO₂ of the EC analyzers was calibrated against standard gases at the time when the reference gas cylinder was replaced. All reference and calibration gases were traceable to the World Meteorological Organization scale maintained by the Scripps Institute of Oceanography. H₂O of both the profile and the EC systems was calibrated in situ against a dew point hydrometer (Model M1 with D2 sensor, General Eastern, Woburn, Massachusetts).

We compared the two EC systems at z = 33.4 m from July 19 to July 25, 1995. There was excellent agreement between the eddy CO₂ fluxes measured using long (y , mg m⁻² s⁻¹) and short (x , mg m⁻² s⁻¹) tubing, with $y = 1.003x - 0.023$ ($R^2 = 0.96$, $n = 282$). In our previous experiments we found that flux loss due to tube attenuation is negligible for the short tubing as long as the flow within the tubing is turbulent [Lee *et al.*, 1996]. This comparison shows that the attenuation is not detectable with the long tubing (the main EC unit), and hence no correction is made.

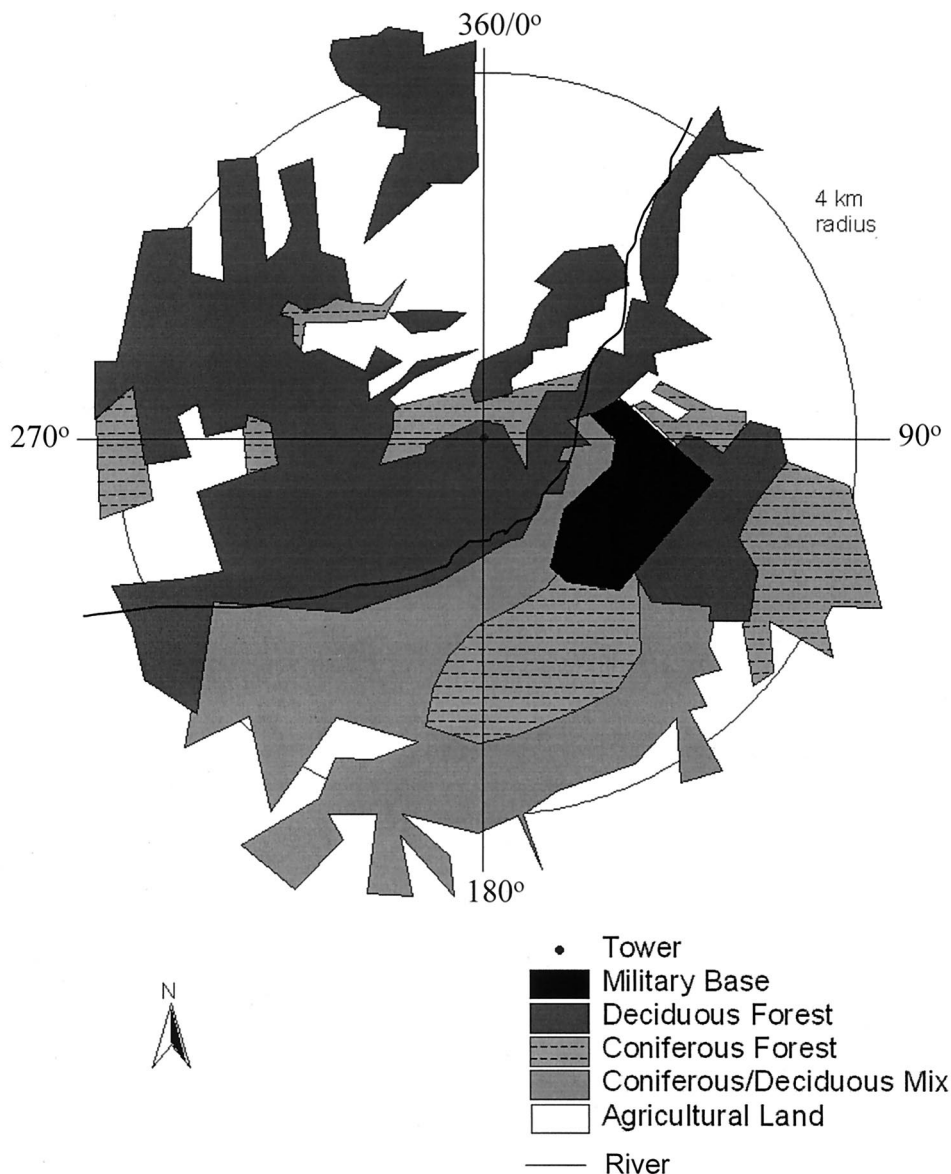


Figure 1. Map showing surface cover types in the vicinity of the flux tower. The desirable wind directions lie in the 90°–255° sector.

Over the period August 25 to October 5, 1995, the second unit was operated at $z = 25.0$ m, and the results were compared with the main unit as shown in Figure 2. The obvious outliers in this 1:1 plot are associated with very high standard deviations of CO_2 concentration, which are indicative of the influence of canopy gravity waves [Lee *et al.*, 1996]. The comparison suggests that a constant flux layer existed between $z = 25.0$ and 33.4 m both in the daytime and at night, but a large scatter is also evident.

3. Data Processing

Eddy flux of CO_2 , $\overline{w'c'}$, was computed over 30-min intervals using the Reynolds averaging procedure and was expressed in the natural coordinate system [Tanner and Thurtell, 1969]. Storage of CO_2 , S , in the 0 to 33.4-m air layer was computed on the basis of the profile data in the 1995 growing season and using the CO_2 concentration measured by the main EC unit

over other periods. Little systematic bias was found in S between the two methods in the 1995 growing season, consistent with Hollinger *et al.* [1994]. The half-hourly net ecosystem exchange (NEE) of CO_2 is $F_c = \overline{w'c'} + S$ and is expressed in units of $\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, noting that $1 \text{ mg m}^{-2} \text{ s}^{-1} = 22.7 \mu\text{mol m}^{-2} \text{ s}^{-1}$. NEE estimates of all integration intervals follow the usual sign convention in that a positive number indicates release of CO_2 from the forest and a negative number indicates uptake.

We use flux data with wind directions in the sector 90°–255° to examine the short-term response of NEE to environmental conditions and to compute NEE over longer intervals (daily, seasonal, and annual). The choice is a compromise that minimizes data gaps while still providing some forest buffers along the side edges (Figure 1). We also impose an outlier criterion, $|F_c| = 2.0 \text{ mg m}^{-2} \text{ s}^{-1}$. In addition, we compute the annual net ecosystem production (NEP) on the basis of flux data in

Table 2. Climatic Variables Recorded at Egbert Climate Station and at the Forest

Period	T_a , °C	P , mm	T_s , °C	Q , $\text{mol m}^{-2} \text{d}^{-1}$	E , mm
<i>Full Year</i>					
30-year norm	6.40	858
1995	7.32	844
1996	6.51	868	7.62	44.2	408
1997	6.81	682	7.37	44.2	315
<i>June–September</i>					
30-year norm	17.63	330
1995	19.34	281	...	77.3	...
1996	18.20	389	16.46	64.9	136
1997	18.19	249	15.47	70.1	106

Egbert climate station is located 20 km ESE of the forest. Mean air temperature T_a and total precipitation P were recorded at Egbert; 5-cm mean soil temperature T_s , mean above-canopy photosynthetic photon flux density Q , and total evapotranspiration E were recorded at the forest.

wind direction sectors 45° – 255° , 90° – 285° , and 0° – 360° to illustrate the importance of imposing a proper fetch criterion at sites like the Borden forest where the source/sink distributions are not aerodynamically homogeneous in the horizontal.

The data gaps caused by system maintenance and the above data screening are filled with a procedure described below. Each day is divided into light ($Q > 0 \mu\text{mol m}^{-2} \text{s}^{-1}$) and dark periods. For each day the Michaelis-Menten light response model,

$$F_c = a_1 - [a_2 Q / (a_3 + Q)], \quad (1)$$

is first fitted to the valid observations using a least squares method over a 15-day window centered at the current day, and data gaps of the light period are filled with the regression model. An advantage of this moving window technique is that it allows us to examine the seasonal course of the light response characteristics. Strictly, (1) is valid only when there is photosynthetic activity, a period coinciding in the present study with the 5-cm soil temperature $>5^\circ\text{C}$ (section 4.1.2). In the winter months the second term on the right-hand side of the equation becomes very small, and hence parameter a_1 from the regression represents essentially the daytime averaged NEE.

The Michaelis-Menten model is a base form of the leaf-level

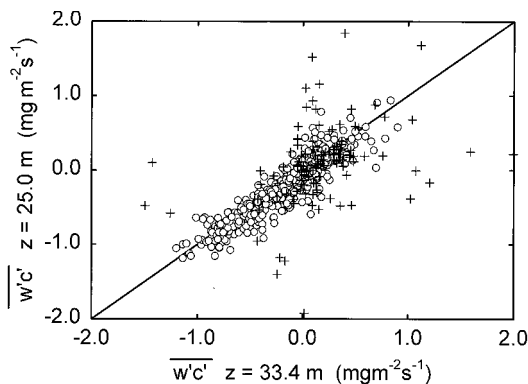


Figure 2. Comparison of CO_2 eddy fluxes observed at two heights over the forest showing the existence of a constant flux layer. Crosses indicate observations with the 30-min standard deviation of CO_2 of either system exceeding 4 ppm.

kinetics of photosynthetic light response, where a_1 is a dark respiration parameter, a_2 is the maximum rate of photosynthesis, and a_3 is the Michaelis-Menten constant. The model has been shown to be a useful framework for the whole ecosystem CO_2 exchange [Hollinger et al., 1994, 1998; Wofsy et al., 1993; Goulden et al., 1997; Chen et al., 1999; Lindroth et al., 1998], in a way analogous to the simple Penman-Monteith model for scaling up water vapor exchange from the leaf to the stand level.

To fill the gaps of the dark periods, we use the following exponential expression:

$$F_c = b_1 \exp(b_2 T_s), \quad (2)$$

where T_s is the 5-cm soil temperature. Coefficients b_1 and b_2 in (2) are evaluated with a least squares method on the basis of valid data of the midnight periods (2100–0300 LT) over the full year. To build robust regression, we have removed five top outliers in all the least squares analyses.

It is recognized by the flux monitoring community that the EC technique is likely to underestimate eddy fluxes under calm conditions at night, but there is no consensus as to how to best correct the problem. Several research groups have screened the nighttime data on the basis of a friction velocity u_* threshold [Goulden et al., 1996; Jarvis et al., 1997; Black et al., 1996; Lindroth et al., 1998]. We did see only a negligible trend of increasing NEE with u_* (Figure 3). However, in our later discussion of errors associated with carbon uptake estimates from the EC data we also calculate annual NEP using a u_* threshold of 0.15 m s^{-1} .

4. Results and Discussion

4.1. Environmental Controls on Short-Term NEE

4.1.1. Response to light. Figure 4 presents the response of the half-hourly NEE to the incident photosynthetic photon flux density Q during the light period in July and August of 1995–1997, with additional information given in Tables 3 and 4. Quantum yield when leaves were fully expanded was roughly $0.0025 \text{ mg CO}_2 \mu\text{mol}^{-1} \text{ photon}^{-1}$ ($0.057 \mu\text{mol CO}_2 \mu\text{mol}^{-1} \text{ photon}^{-1}$). This value is higher than observed for most forests

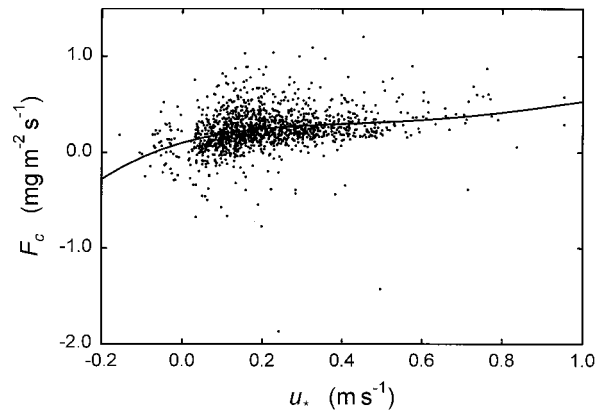


Figure 3. Half-hourly net ecosystem exchange (NEE) of CO_2 plotted as a function of friction velocity for midnight periods (2100–0300 LT) in July and August of 1995–1997. A negative u_* is defined as $u_* = -(u'w')^{0.5}$ if $u'w'$ (covariance between the horizontal and vertical velocity components) is positive. The solid line represents a fourth order polynomial fitted to the data.

(0.02–0.05 $\mu\text{mol CO}_2 \mu\text{mol}^{-1} \text{ photon}^{-1}$ [Wofsy et al., 1993; Hollinger et al., 1994, 1998; Goulden et al., 1997; Chen et al., 1998; Grace et al., 1995b]) and for agricultural fields (0.02–0.03 [Baldocchi, 1994; Rochette et al., 1995]). NEE became negative when Q was $>130\text{--}200 \mu\text{mol m}^{-2} \text{ s}^{-1}$. There was a gradual shift in the light response curve toward more negative values (higher carbon uptake by the forest) at given Q between 1995 and 1997. This trend could be evidence for increased canopy photosynthesis capacity and/or decreased respiration associated with lower soil temperatures.

The broad trend in the observations is captured by the Michaelis-Menten model (Equation (1)), which explains 51–65% of the observed variance. The remaining variance is a result of a host of biophysical variables other than solar radiation, such as vapor pressure deficit (VPD) and air temperature [Hollinger et al., 1994; Price and Black, 1990; Baldocchi, 1997; Goulden et al., 1997; Lindroth et al., 1998], to which stomata respond, and soil temperature, which affects the soil respiratory contribution. These factors tend to cause lower net carbon uptake at given Q in the afternoon than in the morning [e.g., Wofsy et al., 1993] because their magnitudes are higher in the afternoon. This systematic pattern is not evident in our data. Instead, we observed much larger scatter in the morning hours, particularly when relative humidity was high (Figure 4). We attribute this to leaf wetness. It was found in an earlier experiment that the forest canopy remained wet 50% of the time owing to dew formation and precipitation [Fuentes et al., 1992]. On many days, dew water remained till noon hours. Water films on the leaf surface, particularly those formed from condensation, block stomatal openings [Fuentes et al., 1994] and counteract the VPD effect. Depending on the extent of leaf wetness, we may observe either less negative NEE when most of the foliage is wet or more negative NEE when only the lowest portion is wet but carbon uptake by the upper canopy is enhanced owing to low VPD conditions. Leaf wetness poses a challenge to modelers who wish to simulate the whole-ecosystem photosynthesis in high-humidity environments because little quantitative information is available on forest dew microclimate.

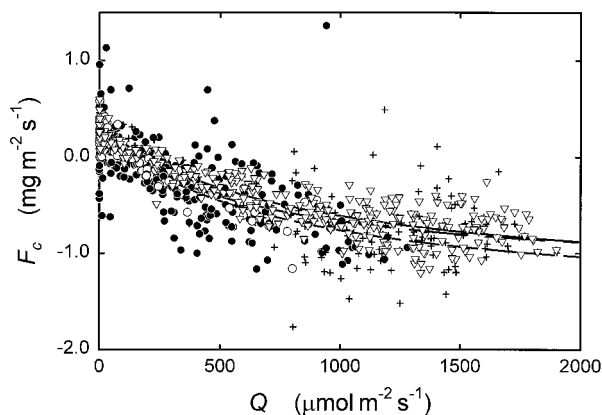


Figure 4. Response of mid-growing-season (July and August) half-hourly NEE of CO_2 to light. Lines represent equation (1) for 1995 (solid line), 1996 (long-dashed line), and 1997 (short-dashed line). For clarity of presentation, only data of 1996 are shown: solid circle, morning with relative humidity (RH) $> 90\%$; cross, morning with RH $< 90\%$; open circle, afternoon with RH $> 90\%$; triangle, afternoon with RH $< 90\%$.

Table 3. Light Response Characteristics of the Half-Hourly NEE in July and August

Year	a_1	a_2	a_3	Q_0	Quantum Yield	T_s	T_a
1995	0.33	1.70	793	195	-0.0021	19.20	21.65
1996	0.28	1.52	595	137	-0.0025	17.21	19.43
1997	0.27	1.79	721	131	-0.0025	16.25	18.82

NEE, net ecosystem exchange. Here a_1 ($\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), a_2 ($\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), and a_3 ($\mu\text{mol photon m}^{-2} \text{ s}^{-1}$) are coefficients in equation (1), Q_0 ($\mu\text{mol m}^{-2} \text{ s}^{-1}$) is the light compensation point, and quantum yield ($\text{mg CO}_2 \mu\text{mol}^{-1} \text{ photon}^{-1}$) is the slope of the light response curve at zero polysynthetic photon flux density. Also given are mean 5-cm soil temperature T_s ($^\circ\text{C}$) at the forest and air temperature T_a ($^\circ\text{C}$) at the Egbert climate station for July and August.

4.1.2. Effect of snowmelt. The snow cover period, which is determined on the basis of the diurnal amplitude of the 5-cm soil temperature T_s , ended abruptly on day 106 in both 1996 (April 15) and 1997 (April 16). Following the snowmelt, T_s increased rapidly from the near-freezing point (see Figure 8), and there was evidence of photosynthetic activities at high radiation levels (Figure 5), even though the daily integrated NEE did not change sign till about 40 days later. The correlation between NEE and Q was very poor before the snowmelt. Immediately after the snowmelt the Michaelis-Menten model captured a small but significant (confidence level < 0.001) variance in the observations. The model fit improved steadily till the full leaf expansion (mid-May). The reason for the midnoon carbon uptake this early in the spring is not completely understood but could be related to the bud break of deciduous trees after soil started to warm up or to the break of dormancy of a few pine trees (Table 1) and evergreen understory species scattered in the footprint.

4.1.3. Controls on ecosystem respiration. Figure 6 and Table 5 show the relations between nocturnal NEE or the whole-ecosystem respiration rate and soil temperature at 5 cm. While the correlation between observations and the regression fit with (2) is statistically significant (confidence level < 0.001), the scatter is considerable. Much of the scatter is attributed to atmospheric processes, including global intermittency (patchy turbulence occurring at temporal scales larger than the main eddy scale) and nonstationarity of the turbulence under stable stratifications [Mahrt, 1998; Gluhovsky and Agee, 1994; Nappo, 1981], canopy waves [Fitzjarrald and Moore, 1990; Lee et al., 1996; Lee, 1997] (see also Figure 2), and mass flow [Lee, 1998], and instrumental problems due to inadequate instrument response at high frequencies [Goulden et al., 1997; Leuning and Judd, 1996] and sensor separation [Lee and Black, 1994; Moore, 1986; Kristensen et al., 1997]. Ecological processes, such as moisture control on soil respiration [Pastor and Post, 1986; Hanson et al., 1993], leaf age [Ryan et al., 1997; Amthor, 1989],

Table 4. Half-Hourly NEE of CO_2 in July and August for Periods With $Q > 1000 \mu\text{mol m}^{-2} \text{ s}^{-1}$

	NEE, $\text{mg m}^{-2} \text{ s}^{-1}$		
	1995	1996	1997
Mean	-0.66	-0.70	-0.80
Standard deviation	0.26	0.27	0.30
Number of observations	236	214	134

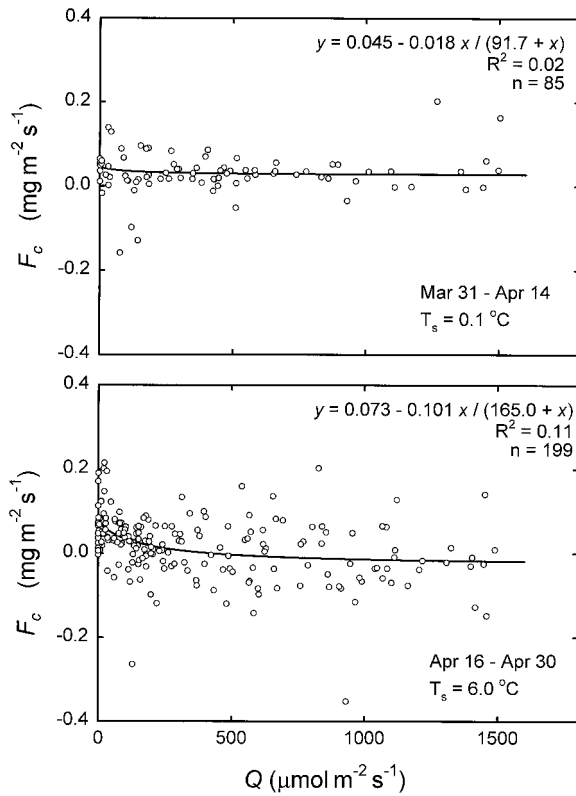


Figure 5. Response of half-hourly NEE of CO_2 to light immediately (top) before and (bottom) after snowmelt in 1996. A similar pattern of abrupt transition was also seen in 1997.

litter age [Aber and Mellilo, 1991], acclimation to temperature [Amthor, 1994], seasonal asymmetry in maintenance respiration [Ryan et al., 1997] and fine root production [Vogt et al., 1997], and contribution from deep soil/roots (see below), will also cause some deviation from the temperature dependence.

Of particular interest to us is how the “dark” respiration parameter a_1 (Equation (1)) compares with the whole-

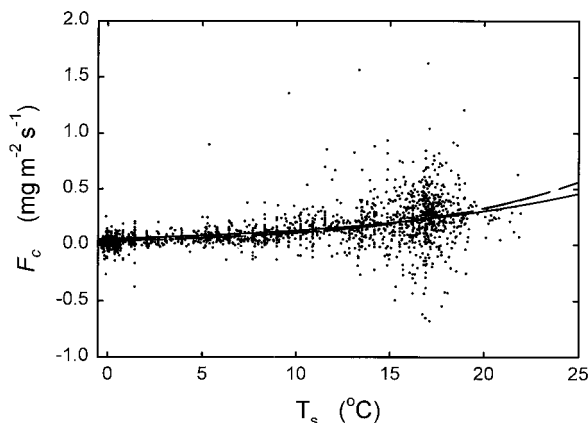


Figure 6. Nighttime (2100–0300 LT) half-hourly NEE as functions soil temperature at 5 cm (without u_* screening). Lines represent equation (2) for 1995 (solid line), 1996 (long-dashed line), and 1997 (short-dashed line, indistinguishable from the long-dashed line). For clarity of presentation, only data of 1996 are shown. Additional information is given in Table 5.

Table 5. Coefficients b_1 and b_2 in equation (2), Without and With u_* Threshold

Year	b_1 , $\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$	b_2 , $^{\circ}\text{C}^{-1}$	Q_{10}
<i>Without u_* Threshold</i>			
1995	0.0545	0.085	2.34
1996	0.0373	0.109	2.97
1997	0.0347	0.112	3.06
<i>With u_* Threshold</i>			
1995	0.0580	0.087	2.38
1996	0.0460	0.106	2.89
1997	0.0373	0.115	3.16

Also given is the value of Q_{10} (the rate of increase in NEE with a 10°C rise in temperature).

ecosystem respiration rate from the dark periods. While comparisons of this type are not new [Hollinger et al., 1994; Grace et al., 1995b; Hollinger et al., 1998], what is novel about our analysis below is that we use (1) over fairly fine time windows (15 days) to reveal the seasonal behavior of the whole-ecosystem respiration rate that cannot be obtained easily with the nighttime EC observations. Figure 7 shows the value of a_1 , determined from the 15-day moving window technique, as a function of the 5-cm soil temperature averaged over the same window for 1996. The tight correlation supports the argument that because the dark respiration rate is derived from daytime observations, it is perhaps less prone to problems seen at night under stable stratification. As shown in Figure 7, the respiration function established by regression with nighttime EC data was slightly lower than the respiration parameter a_1 . Screening the nighttime flux data on the basis of the threshold of $u_* = 0.15 \text{ m s}^{-1}$ brings the regression to a closer agreement with the a_1 estimate on the whole, as indicated by $y = 0.999a_1 + 0.008$ ($R^2 = 0.92$, $n = 366$; 1996 observations), where y ($\text{mg m}^{-2} \text{ s}^{-1}$) is NEE of the midnight periods (2100–0300 LT) averaged over 15-day moving windows and with the u_* threshold. This

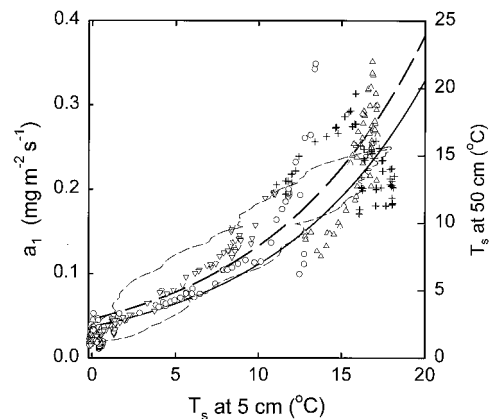


Figure 7. Dark respiration parameter a_1 from the 15-day moving window technique as a function of the 5-cm soil temperature averaged over the same window in 1996 (circles, January 1 to May 31; triangles, June 1 to July 31; crosses, August 1 to September 30; upside-down triangles, October 1 to December 31). The solid line and long-dashed line represent nocturnal respiration functions established with eddy covariance data of dark periods (2100–0300 LT) without and with a friction velocity threshold, respectively. The short-dashed line is soil temperature at 50 cm.

seems to be consistent with the contention that the EC technique tends to underestimate the whole-ecosystem respiration under poor ventilation conditions.

Another interesting feature in Figure 7 is a seasonal “hysteresis”: for a given T_s (soil temperature at 5 cm), the ecosystem respiration rate was systematically higher in the later part of the year. This pattern was, however, not clear in the nighttime EC data, even with the 15-day moving averaging (data not shown), owing to the large uncertainty inherent in the nighttime observations as discussed above. The hysteresis, which was also seen in 1995 and 1997, cannot be explained by leaf age, as young leaves respire at higher rates than old leaves [Ryan *et al.*, 1997] and are more likely to be produced by other factors. The first factor relates to the phase of the seasonal soil temperature wave which was progressively delayed with increasing depth so that temperature of the deep soil was higher in the later part of the year. For example, for the same T_s the temperature at 50 cm was about 7°C higher in the fall than in the spring (Figure 7). The hysteresis suggests that the deep soil, despite being mainly sandy, and roots [Boone *et al.*, 1998] may have contributed a nonnegligible amount to the whole-ecosystem respiration. Indeed, expressing the whole-ecosystem respiration as a function of temperature at a single height/depth within the system, as is done in this study and elsewhere, is a crude simplification because the ecosystem components (soil, roots, understory, stems, and foliage) are exposed to thermal conditions that are strongly stratified in the vertical. A second factor may be that the decomposition of litter accumulated in the later part of the growing season enhanced the whole-ecosystem respiration because fresh litter decays much faster than old litter [Aber and Mellilo, 1991; Bloomfield *et al.*, 1993]. In addition, seasonality of fine root biomass [Vogt *et al.*, 1997] and microbial activity stimulated by leaching of nutrients from fresh litter [Aber and Mellilo, 1991] may also have played a role.

4.2. Daily, Seasonal, and Annual NEE

4.2.1. General pattern. Figure 8 shows the seasonal patterns of the daily NEE from July 1995 and December 1997.

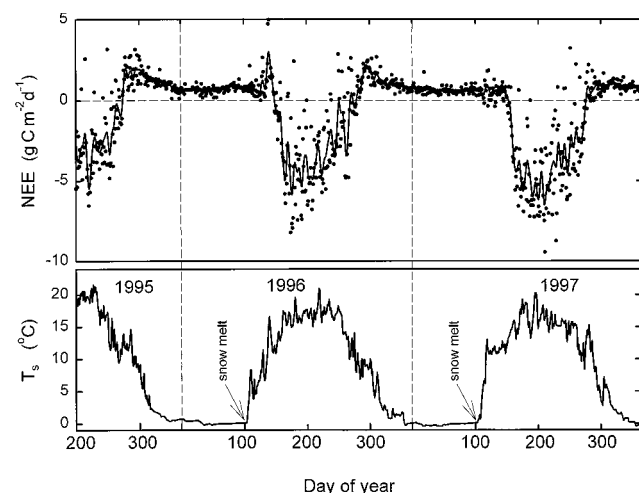


Figure 8. (top) Seasonal variations in daily NEE of carbon based on valid half-hourly observations with wind directions from the sector 90°–255° (dot, observation; solid line, low-pass signal equivalent to 10-day moving average). (bottom) Daily mean soil temperature at 5 cm.

Table 6. Annual Net Ecosystem Production Based on Half-Hourly NEE Data With Wind Directions From Various Sectors

Sector	Coverage, %	Annual Net Ecosystem Production, t C ha ⁻¹ yr ⁻¹		
		7/19/95–7/18/96	1/1/96–12/31/96	1/1/97–12/31/97
90°–255°	47	–1.3	–1.6	–3.1
90°–255°*	40	–0.6	–0.8	–2.7
45°–255°	50	–1.3	–1.6	–3.1
90°–285°	57	–0.7	–1.0	–2.9
0°–360°	94	1.8	1.9	–0.6

See Figure 1 for sectors. Read 7/19/95 as July 19, 1995. The desirable wind direction sector is 90°–255°. Data coverage is computed as percentage of valid half-hourly observations over the period July 19, 1995, to December 31, 1997.

Estimates with a friction velocity threshold of $u_ = 0.15$ m s⁻¹.

Here the desirable wind direction sector 90°–255° (fetch 1.5–4 km; Figure 1) is used to screen the data. Gaps in the data are filled with the appropriate regression equations as discussed above. The broad pattern resembles observations at other deciduous forests. The transition from source to sink occurred more rapidly during leaf-out than the sink-to-source transition during leaf-fall. During the growing season the carbon flux was negative, indicating a net carbon removal by the forest over the 24-hour interval, with a few exceptions (18 days in 1996 and 7 days in 1997) due to a combination of excessive cloudiness, leaf wetness, and high soil temperature.

The annual net ecosystem production (NEP), computed as the sum of the daily NEE values, is –1.3, –1.6, and –3.1 t C ha⁻¹ yr⁻¹ over the three annual intervals July 19, 1995, to July 18, 1996, January 1 to December 31, 1996, and January 1 to December 31, 1997, respectively (Table 6). Imposing the friction velocity threshold reduces the magnitude of the NEP estimates by 0.4–0.8 t C ha⁻¹ yr⁻¹. The interannual variabilities in NEP, on the other hand, appear less sensitive to the choice of the data processing procedure.

4.2.2. Interannual variability. There was a large difference (1.5–2 t C ha⁻¹ yr⁻¹) in NEP between 1996 and 1997. The growing season length, shown by previous studies [Goulden *et al.*, 1996; Chen *et al.*, 1998] to be a major factor controlling the interannual variations in NEP, does not appear to be the cause of the large change between 1996 and 1997. The onset and cessation of the actual growing season, defined by the first zero crossing of the low-pass-filtered daily NEE in the spring and last zero crossing in the fall, occurred on May 29 and October 5, respectively, in 1996 (growing season length 130 days) and on June 2 and October 4 (124 days) in 1997 (Figure 8). Furthermore, the midday Bowen ratio, another indicator of forest growth, also showed similar growing season lengths (data not shown).

Soil temperature was, however, 1°C and 0.25°C lower over the growing season and the full year, respectively, in 1997 than in 1996, even though air temperature was almost identical (Table 2). To assess this soil cooling effect, we apply (2) to both light and dark periods and estimate the total ecosystem respiration to be 11.8 and 10.3 t C ha⁻¹ for 1996 and 1997, respectively. The higher respiration in 1996 was contributed by a slightly higher basal rate or b_1 parameter in winter months (0.2 t C ha⁻¹; Table 5), warmer spring and fall transitional periods

(0.4; days 130–150 and 280–320; Figure 8), and warmer growing season (0.8). The exact cause of the cooling trend is not known, but we can rule out instrumental problems because identical trends were recorded by all four sensors at the 5-cm depth. The most likely scenario is the change in foliage density and/or structure of either understory or overstory vegetation between the two years, which was perhaps related to the successional change in species compositions (Table 1). Given other conditions being the same, soil temperature inside a canopy is controlled by the amount of solar radiation reaching the forest floor [Pastor and Post, 1986; Aber et al., 1982].

If for the sake of discussion we assume that soil was the dominant component contributing 70% to the whole ecosystem respiration [Black et al., 1996; Goulden et al., 1996; Amthor et al., 1994], we estimate the sensitivity of soil respiration to be $0.5 \text{ t C ha}^{-1} \text{ yr}^{-1}$ per degree Celsius change in the growing season soil temperature. (The sensitivity is much higher if the annual mean soil temperature is used.) This is larger than $0.2 \text{ t C ha}^{-1} \text{ yr}^{-1}$ per degree for temperate forest soil on the basis of the transitional response of soil carbon to temperature change [Trumbore et al., 1996] and $0.26 \text{ t C ha}^{-1} \text{ yr}^{-1}$ per degree on the basis of a review of soil respiration data from terrestrial and wetland ecosystems [Raich and Schlesinger, 1992] and is consistent with previous analyses about the sensitivity of NEE to temperature [Grace et al., 1995a; Lindroth et al., 1998]. The large sensitivity emphasizes that in addition to abiotic (e.g., climatic) variables, biotic factors such as forest succession, silvicultural treatments (pruning, thinning, fertilizing, selective timber harvesting), and insect activities will contribute to interannual variations in NEP through modifications of the overstory structure and therefore the soil thermal environment.

A second factor contributing to the interannual variability might be an enhanced net primary production due to enhanced photosynthetic capacity (Tables 3 and 4, Figure 4) and photon flux in 1997 (Table 2). It is difficult to quantify the effect of photosynthetic capacity for lack of leaf-level observations. To assess the impact of photon flux, we first use the observed photon flux data to compute, on the basis of (1), the daytime carbon uptake in the 1996 growing season. We then increase the photon flux density by 8% to simulate conditions in 1997 and compute the uptake again, keeping the same set of coefficients for (1). The resulting increase in the carbon uptake is about 0.3 t C ha^{-1} , smaller than the soil cooling effect but still significant.

4.3. Uncertainty in NEP Assessment

Main sources of uncertainty in the NEP assessment exist in how to handle missing data, poor fetch, and carbon exchange by mass flow. (The uncertainty due to a particular choice of the gap-filling procedure is not large.) To illustrate this, we have tested three alternative gap-filling procedures: (1) establishing the nighttime respiration function (equation (2)) using a 15-day moving window, (2) fitting the respiration function of exponential form to observations over 15-day moving windows but holding Q_{10} at a constant of 2 [Goulden et al., 1997], and (3) using a third-order polynomial instead of the Michaelis-Menten function for the light periods. The resulting change in the annual NEP is $<0.3 \text{ t C ha}^{-1} \text{ yr}^{-1}$.

To show the impact of poor fetch on the flux observation, we compare two subsets of nighttime observations from the midgrowing seasons, one with north wind (wind from agricultural land, poor fetch, Figure 1) and the other with south wind (good

fetch). The average temperature was similar for both sets, and yet an unusually high apparent flux of $0.59 \text{ mg m}^{-2} \text{ s}^{-1}$ was seen for the periods with north winds, compared to $0.28 \text{ mg m}^{-2} \text{ s}^{-1}$ with south winds. Clearly, the high efflux is not reasonable and should not be interpreted as to reflect the respiration rate of the agricultural land. One may view the high efflux as a result of horizontal advection expressed as $\bar{u} \partial \bar{c} / \partial x$, where \bar{u} is the mean horizontal wind speed and $\partial \bar{c} / \partial x$ is the horizontal CO_2 gradient. This is not likely because there is no reason why CO_2 concentration should be higher over the cropland than over the forest. (Indirect evidence suggests that CO_2 concentration is lower over the cropland than over the forest; see Lee et al. [1996, Figure 4]). Instead, we consider this as evidence for a mass flow component [Lee, 1998] arising from flow convergence or a positive mean vertical velocity in the transitional forest edge flow [Li et al., 1990; Wilson and Flesch, 1999].

The impact of fetch is even more striking if we use data of all wind directions to compute the annual NEP. Rather than seeing carbon removal from the atmosphere, we now have large positive NEP values for July 19, 1995, to July 18, 1996, and January 1 to December 31, 1996, and only slightly negative NEP for January 1 to December 31, 1997 (Table 6), leading to the wrong conclusion that the landscape (forest plus agricultural land) is mostly a carbon source. While it is apparent to all of us that use of flux data with poor fetch is not permitted, the result here does emphasize an important message: **Conventional footprint decomposition should be done with extreme caution at sites where the source/sink distributions are not aerodynamically homogeneous in the horizontal.**

Assuming negligible horizontal advection, Lee [1998] showed from mass conservation that NEE should consist of three components: air storage, eddy flux, and mass flow due to flow convergence/divergence or a nonzero mean vertical velocity \bar{w} at the height of EC observation. The last term is expressed as

$$\bar{w}_r \left(\bar{c}_r - \frac{1}{z_r} \int_0^{z_r} \bar{c} dz \right),$$

where \bar{c} is the mean CO_2 concentration and subscript r denotes values at the EC height z_r . The nonzero \bar{w} can result from daytime convections and thermal circulations driven by the thermal contrast between the forest and the surrounding landscape (agricultural fields and the swamp, section 2.1).

We have computed the 24-hour ensemble average of the mass flow over July 19 to October 11, 1995, a period when both valid \bar{w} and CO_2 profile data were available. The flux due to mass flow was mostly positive at night. If we extrapolate the slightly positive 24-hour average of the mass flow to the whole growing season (130 days), we obtain a bias of $0.4 \pm 0.3 \text{ t C ha}^{-1}$.

One major difficulty in applying the mass flow correction lies in the mean vertical velocity observations. Several methods for correcting the mean vertical velocity measurements are proposed [Lee, 1998; Finnigan, 1999; Paw U et al., 1998; Baldocchi et al., 1998]. Our analysis uses the procedure of Lee [1998]. We caution that a large inherent uncertainty exists in \bar{w} , as the experiment was designed without prior consideration to improve the quality of \bar{w} observations. As a result, large short-term (30-min) variations in the mass flow term are unavoidable. However, averaging over long time periods (weeks to months), the mass flow term should provide a useful way of estimating the error bound to the annual NEP values. In the present case, the three methods, u_* threshold, dark respiration

from the forest light response, and mass flow, all suggest an overestimate of the carbon removal by similar amounts if only nighttime EC flux and air storage data are used. Each of the three methods emphasizes a different aspect of the biophysical control on the surface-air exchange. Collective use of these methods (and other methods uncovered in the future) can provide clues to the workings of the ecosystem and the atmospheric boundary layer and therefore may increase our confidence level of the NEP estimates. In view of the discussion above, we consider -1.0 , -1.2 , and $-2.8 \text{ t C ha}^{-1} \text{ yr}^{-1}$ to be our best estimates of NEP for the three annual periods July 19, 1995, to July 18, 1996, January 1 to December 31, 1996, and January 1 to December 31, 1997, respectively, with an uncertainty of $\pm 0.4 \text{ t C ha}^{-1} \text{ yr}^{-1}$.

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References

- Aber, J. D., and J. M. Melillo, *Terrestrial Ecosystems*, 429 pp., Saunders College Publ., Philadelphia, Pa., 1991.
- Aber, J. D., J. M. Melillo, and C. A. Federer, Predicting the effects of rotation length, harvest intensity, and fertilization on fiber yield from northern hardwood forests in New England, *For. Sci.*, **28**, 31–45, 1982.
- Amthor, J. S., *Respiration and Crop Productivity*, 215 pp., Springer-Verlag, New York, 1989.
- Amthor, J. S., Plant respiration responses to the environment and their effects on the carbon balance, in *Plant-Environment Interactions*, edited by R. E. Wilkinson, pp. 501–554, Marcel Dekker, New York, 1994.
- Amthor, J. S., M. L. Goulden, J. W. Munger, and S. C. Wofsy, Testing a mechanistic model of forest canopy mass and energy exchange using eddy correlation: Carbon dioxide and ozone uptake by a mixed oak-maple stand, *Aust. J. Plant Physiol.*, **21**, 623–651, 1994.
- Baldocchi, D., A comparative study of mass and energy exchange rates over a closed C_3 (wheat) and an open C_4 (corn) crop, II, CO_2 exchange and water use efficiency, *Agric. For. Meteorol.*, **67**, 291–321, 1994.
- Baldocchi, D., Measuring and modelling carbon dioxide and water vapour exchange over a temperate broad-leaved forest during the 1995 summer drought, *Plant Cell Environ.*, **20**, 1108–1122, 1997.
- Baldocchi, D., K. Wilson, and K. T. Paw U, On measuring net ecosystem carbon exchange in complex terrain over tall vegetation, paper presented at 23rd American Meteorological Society Conference on Agricultural and Forest Meteorology, Albuquerque, N. M., 1998.
- Black, T. A., et al., Annual cycles of water vapour and carbon dioxide fluxes in and above a boreal aspen forest, *Global Change Biol.*, **102**, 219–229, 1996.
- Bloomfield, J., K. A. Vogt, and D. J. Vogt, Decay rate and substrate quality of fine roots and foliage of two tropical tree species in the Luquillo Experimental Forest, Puerto Rico, *Plant Soil*, **150**, 233–245, 1993.
- Boone, R. D., K. J. Nadelhoffer, J. D. Canary, and J. P. Kaye, Roots exert a strong influence on the temperature sensitivity of soil respiration, *Nature*, **396**, 570–572, 1998.
- Chen, W. J., et al., Effects of climatic variability on the annual carbon sequestration by a boreal aspen forest, *Global Change Biol.*, **5**, 41–53, 1999.
- Finnigan, J. J., A comment on the paper by Lee (1998): “On micrometeorological observations of surface-air exchange over tall vegetation,” *Agric. For. Meteorol.*, in press, 1999.
- Fitzjarrald, D. R., and K. E. Moore, Mechanisms of nocturnal exchange between the rain forest and the atmosphere, *J. Geophys. Res.*, **95**, 16,839–16,850, 1990.
- Fuentes, J. D., and D. Wang, On the seasonality of isoprene emissions from a mixed temperate forest, *Ecol. Appl.*, in press, 1999.
- Fuentes, J. D., T. J. Gillespie, D. den Hartog, and H. H. Neumann, Ozone deposition onto a deciduous forest during dry and wet conditions, *Agric. For. Meteorol.*, **75**, 1–19, 1992.
- Fuentes, J. D., Gillespie, T. J., and N. J. Bunce, Effects of foliage wetness on the dry deposition of ozone onto red maple and poplar leaves, *Water Air Soil Pollut.*, **74**, 189–210, 1994.
- Gluhovskiy, A., and E. Agee, A definite approach to turbulence statistical studies in planetary boundary layer, *J. Atmos. Sci.*, **51**, 1682–1690, 1994.
- Goulden, M. L., J. W. Munger, S. M. Fan, B. C. Daube, and S. C. Wofsy, Exchange of carbon dioxide by a deciduous forest: Response to interannual climate variability, *Science*, **271**, 1576–1578, 1996.
- Goulden, M. L., B. C. Daube, S.-M. Fan, D. J. Sutton, A. Bazzaz, J. W. Munger, and S. C. Wofsy, Physiological responses of a black spruce forest to weather, *J. Geophys. Res.*, **102**, 28,987–28,996, 1997.
- Grace, J., et al., Carbon dioxide uptake by an undisturbed tropical rain forest in southwest Amazonia, 1992–1993, *Science*, **270**, 778–780, 1995a.
- Grace, J., J. Lloyd, J. McIntyre, A. Miranda, P. Meir, H. Miranda, J. Moncrieff, J. Massheder, I. Wright, and J. Gash, Fluxes of carbon dioxide and water vapor over an undisturbed tropical forest in southwest Amazonia, *Global Change Biol.*, **1**, 1–12, 1995b.
- Greco, S., and D. D. Baldocchi, Seasonal variations of CO_2 and water vapor exchange rates over a temperate deciduous forest, *Global Change Biol.*, **2**, 183–197, 1996.
- Hanson, P. J., S. D. Wullschlegel, S. A. Bohlman, and D. E. Todd, Seasonal and topographic patterns of forest floor CO_2 efflux from an upland oak forest, *Tree Physiol.*, **13**, 1–15, 1993.
- Hollinger, D. Y., F. M. Kelliher, J. N. Byers, J. E. Hunt, T. M. McSeveny, and P. L. Weir, Carbon dioxide exchange between an undisturbed old-growth temperate forest and the atmosphere, *Ecology*, **75**, 134–150, 1994.
- Hollinger, D. Y., et al., Forest-atmosphere carbon dioxide exchange in eastern Siberia, *Agric. For. Meteorol.*, **90**, 276–290, 1998.
- Jarvis, P. G., J. M. Massheder, S. E. Hale, J. B. Moncrieff, M. Rayment, and S. L. Scott, Seasonal variation of carbon dioxide, water vapor, and energy exchanges of a boreal black spruce forest, *J. Geophys. Res.*, **102**, 28,953–28,966, 1997.
- Kristensen, L., J. Mann, S. P. Oncley, and J. C. Wyngaard, How close is close enough when measuring scalar fluxes with displaced sensors?, *J. Atmos. Oceanic Technol.*, **14**, 814–821, 1997.
- Lee, X., Gravity waves in a forest: A linear analysis, *J. Atmos. Sci.*, **54**, 2574–2585, 1997.
- Lee, X., On micrometeorological observations of surface-air exchange over tall vegetation, *Agric. For. Meteorol.*, **91**, 39–49, 1998.
- Lee, X., and T. A. Black, Relating eddy correlation sensible heat flux to horizontal sensor separation in the unstable atmospheric surface layer, *J. Geophys. Res.*, **99**, 18,545–18,553, 1994.
- Lee, X., T. A. Black, G. den Hartog, H. H. Neumann, Z. Nestic, and J. Olejnik, Carbon dioxide exchange and nocturnal processes over a mixed deciduous forest, *Agric. For. Meteorol.*, **81**, 13–29, 1996.
- Leuning, R., and M. J. Judd, The relative merits of open- and closed-path analysers for measurement of eddy fluxes, *Global Change Biol.*, **2**, 241–253, 1996.
- Li, Z., J. D. Lin, and D. R. Miller, Air flow over and through a forest edge: A steady-state numerical simulation, *Boundary Layer Meteorol.*, **51**, 179–197, 1990.
- Lindroth, A. A., A. Grelle, and A. S. Moren, Long-term measurements of boreal forest carbon balance reveal large temperature sensitivity, *Global Change Biol.*, **4**, 443–450, 1998.
- Mahrt, L., Flux sampling errors for aircraft and towers, *J. Atmos. Sci. Oceanic Technol.*, **15**, 416–429, 1998.
- Malhi, Y., A. D. Nobre, J. Grace, B. Kruijt, M. G. P. Pereira, A. Culf, and S. Scott, Carbon dioxide transfer over a central Amazonian rain forest, *J. Geophys. Res.*, **103**, 31,593–31,612, 1998.
- Moore, C. J., Frequency response corrections for eddy correlation systems, *Boundary Layer Meteorol.*, **37**, 17–35, 1986.
- Nappo, C. J., Sporadic turbulence and dispersion in the stable boundary layer, in *Air Pollution Modeling and Its Applications*, edited by H. Van Dop and D. G. Steyn, pp. 705–712, Plenum, New York, 1981.
- Neumann, H. H., G. den Hartog, and R. H. Shaw, Leaf area measure-

- ments based on hemispheric photographs and leaf-litter collection in a deciduous forest during autumn leaf-fall, *Agric. For. Meteorol.*, **45**, 325–345, 1989.
- Pastor, J., and W. M. Post, Influence of climate, soil moisture, and succession on forest carbon and nitrogen cycles, *Biogeochemistry*, **2**, 3–27, 1986.
- Paw U, K. T., D. Baldocchi, T. Meyers, and K. Wilson, The estimation of energy and mass fluxes from vegetated surfaces, paper presented at 23rd American Meteorological Society Conference on Agricultural and Forest Meteorology, Albuquerque, N. M., 1998.
- Price, D. T., and T. A. Black, Effects of short-term variation in weather on diurnal canopy CO₂ flux and evapotranspiration of a juvenile Douglas-fir stand, *Agric. For. Meteorol.*, **50**, 139–158, 1990.
- Raich, J. W., and W. H. Schlesinger, The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate, *Tellus, Ser. B*, **44**, 81–99, 1992.
- Rochette, P., R. D. Desjardins, E. Pattey, and R. Lessard, Crop net carbon dioxide exchange rate and radiation use efficiency in soybean, *Agron. J.*, **87**, 22–28, 1995.
- Ryan, M. G., M. B. Lavigne, and S. T. Gower, Annual carbon cost of autotrophic respiration in boreal forest ecosystems in relation to species and climate, *J. Geophys. Res.*, **102**, 28,871–28,883, 1997.
- Shaw, R. H., G. den Hartog, and H. H. Neumann, Influence of foliar density and thermal stability on profiles of Reynolds stress and turbulence intensity in a deciduous forest, *Boundary Layer Meteorol.*, **45**, 391–409, 1988.
- Staebler, R., J. D. Fuentes, H. H. Neumann, and J. Chen, Light interception of a temperate deciduous forest, paper presented at 9th AMS Conference on Atmospheric Radiation, Am. Meteorol. Soc., Long Beach, Calif., 1997.
- Tanner, C. B., and G. W. Thurtell, Anemoclinometer measurements of Reynolds stress and heat transport in the atmospheric surface layer, *Res. Dev. Tech. Rep. ECOM-66-G22F*, Univ. of Wis., Madison, 1969.
- Tans, P. P., and J. W. C. White, In balance, with a little help from the plants, *Science*, **281**, 183–184, 1998.
- Trumbore, S. E., O. A. Chadwick, and R. Amundson, Rapid exchange between soil carbon and atmospheric carbon dioxide driven by temperature change, *Science*, **272**, 393–396, 1996.
- Vogt, K., H. Asbjornsen, A. Ercelawn, F. Montagnini, and M. Valdes, Roots and mycorrhizas in plantation ecosystems, in *Management of Soil, Nutrients and Water in Tropical Plantation Forests*, edited by E. K. S. Nambiar and A. G. Brown, pp. 247–296, Aust. Cent. for Int. Agric. Res., Canberra, 1997.
- Wilson, J. D., and T. K. Flesch, Wind and remnant tree sway in forest openings, III, A windflow model to diagnose spatial variation, *Agric. For. Meteorol.*, **93**, 259–282, 1999.
- Wofsy, S. C., M. L. Goulden, J. W. Munger, S.-M. Fan, P. S. Bakwin, B. C. Daube, S. L. Bassow, and F. A. Bazzaz, Net exchange of CO₂ in a mid-latitude forest, *Science*, **260**, 1314–1317, 1993.

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