Annual Pattern of Carbon Exchange and Evapotranspiration
in an Upland Deciduous Forest in Northern Wisconsin, USA

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Running title (45 characters): Forest Carbon Exchange and Evaporation
Fluxes of CO2 and evapotranspiration were measured above an upland forest in north central Wisconsin during 1999 and 2000. Maple (Acer saccharum), basswood (Tilia americana), and green ash (Fraxinus pennsylvanica) species found in this forest also comprise a substantial portion of the landscape in the northern Great Lakes region and area, and it has been hypothesized that forests of this age (60 to 80 years) are responsible for enhanced uptake of atmospheric CO2 over North America. Carbon, water vapor, temperature, and turbulent fluxes were continuously measured using the eddy covariance method. Mean CO2, water vapor, and temperature profile measurements were used to improve flux estimates during periods of low turbulence, and were effective for friction velocities ($u^*$) >0.175 m s$^{-1}$. Forest transpiration was responsible for most of the water released to the atmosphere, and closure of stomata under intense sunlight was responsible for decreases in whole-ecosystem evapotranspiration and photosynthetic uptake of CO2. Local surface geography and unique meteorological conditions at this location allowed us to occasionally observe turbulent venting of CO2 pools from low-lying areas. These relatively infrequent events increased annual NEE estimates by about 300 g C m$^{-2}$ yr$^{-1}$, and required us to develop screening methods that would preserve homogeneity and spatial representativeness of annual NEE estimates for this forest. We estimated that the forest was a large sink for atmospheric carbon, and cumulative NEE of CO2 was estimated to be -425 g C m$^{-2}$ yr$^{-1}$ during 2000. If corrections for energy budget errors were applied, uptake would increase by an additional 70 g C m$^{-2}$ yr$^{-1}$. Apparent photosynthesis was high (1120 g C m$^{-2}$ yr$^{-1}$) and ecosystem respiration was low (695 g C m$^{-2}$ yr$^{-1}$) in comparison to spatially integrated, landscape-scale observations from WLEF, a 477 m tower located 22 km to the northeast (Davis
et al., this issue). Scaling of stand-scale fluxes from this site and others in the region will be discussed in a future publication.
Introduction

Rising concentrations of carbon dioxide (CO$_2$) in the atmosphere have received considerable attention from scientists and policy makers, because CO$_2$ is emitted to the atmosphere by anthropogenic activities and may contribute to climate change (Schlesinger, 1997). The terrestrial biosphere is a large and dynamic reservoir of carbon that can exchange with the atmosphere on short time scales (hours to decades); however, sources and sinks are not well defined (Ciais et al., 1995; Tans et al., 1990), and causes of spatial and temporal variability of the carbon balance of the terrestrial biosphere are not well understood (Conway et al., 1994; Keeling et al., 1996). To enhance our understanding of the terrestrial carbon cycle, a global network of sites has been established to conduct continuous, long-term observations of carbon and water vapor exchange between terrestrial ecosystems and the atmosphere (Baldocchi et al., 2001).

Numerous studies have quantified carbon pools and flows in northern temperate and boreal forests stands, but few have encompassed regional scales (100s of km$^2$) on a continuous basis for multiple years. This is an objective of the Chequamegon Ecosystem-Atmosphere Study (ChEAS), currently being carried out in the Chequamegon-Nicolett National Forest of north central Wisconsin, using a network of eddy-covariance measurements and biophysical observations (Davis et al., this issue). A centerpiece of ChEAS is eddy flux measurements of CO$_2$ and H$_2$O exchange from a 447-m-tall TV transmitter tower (Davis et al., this issue; Berger et al., 2001), which is unique among the global network, because observations from its multiple levels integrate many different land cover and soil types. Our goal is to measure stand-scale and component carbon fluxes within nearby representative forest stands, to analyze the relationships between these component and whole-stand fluxes, and to develop and test methods to upscale CO$_2$ fluxes to landscape-scale observations from the tall tower. To this end we have established
stand-scale observations at three sites near the tall tower: an upland deciduous forest (Willow Creek), an alder-willow-sedge wetland (Lost Creek), and an old growth maple-hemlock forest (Sylvania Wilderness Area).

In this paper, we present observations of net ecosystem exchange of CO$_2$ (NEE) and evapotranspiration from the upland deciduous forest located at the Willow Creek study site, 22 km from the tall tower. This forest is composed of broadleaf tree species that comprise a substantial portion of the landscape in the northern Great Lakes region and the area surrounding the tall tower. The stand is approximately 60 to 80 years old, and is typical of re-growth that may be responsible for some of the enhanced uptake of CO$_2$ in North America (Caspersen et al., 2000; Pacala et al., 2001). A 30 m tower was installed at this site and instrumented to measure mean CO$_2$ and H$_2$O mixing ratio profiles, and fluxes of CO$_2$, latent heat, and sensible heat using the eddy-covariance method. This paper outlines methods that will be used at each of the three stand-scale eddy-covariance towers, and presents initial observations from the first two years of operation (1999 and 2000) at the Willow Creek hardwood site.
Materials and Methods

Site description

Measurements were collected in an upland hardwood forest of the Chequamegon-Nicolett National Forest in northern Wisconsin (45.806° N, 90.080° W, elevation approx. 515 m). This 60 to 80 year-old stand has a closed canopy approximately 24 m in height with a leaf area index (LAI) of about 4.2, and consists primarily of sugar maple (*Acer saccharum*), basswood (*Tilia americana*), and green ash (*Fraxinus pennsylvanica*). The understory is composed of sugar maple and ironwood (*Ostrya virginiana*) saplings, leatherwood (*Dirca palustris*), maidenhair (*Adiantum pedatum*) and bracken ferns (*Pteridium aquilinum*), and blue cohosh (*Caulophyllum thalictroides*). The stand occupies about 260 ha, and is relatively homogeneous except for a narrow drainageway (about 80 m wide and 500 m long) located about 0.3 km west of the observation tower, which is characterized by red maple (*Acer rubrum*), black ash (*Fraxinus nigra*), and slippery elm (*Ulmus rubra*).

Glacial features such as drumlins, moraines, poorly drained depressions, and outwash plains are typical features of the regional landscape (Hole, 1976), and upland areas are generally characterized by slightly elevated ground moraines and southwest-trending drumlins. The terrain of the upland forest at Willow Creek is rolling to undulating, and elevation ranges from 490 to 530 m across low profile, oval-shaped ridges (Fig. 1). Slope at the tower base is about 1%, sloping downward towards the southwest.

Sandy loam soils at this site (about 54% sand, 33% silt, and 13% clay in the upper 30 cm) have developed from acidic, reddish, unsorted, coarse glacial till with 10 to 40% rock fragments. Soils have been subjected to mixing by windthrows, burrowing animals and earthworm activity, and frost action. Mottling and saturated soils were observed between 50 and 100 cm below the
surface at different times during the year in these somewhat poorly drained soils. Total carbon and nitrogen in the litter layer and underlying mineral soil (0 to 30 cm) was about 10.7 and 0.74 kg m$^{-2}$, respectively.

Land surveys conducted between 1857 and 1886 (Schulte and Mladenoff, 2001) indicate that pre-European settlement vegetation consisted primarily of hemlock (*Tsuga canadensis*), birch (*Betula spp.*), sugar maple (*Acer saccharum*), and basswood (*Tilia americana*; unpublished data, Pre-European Settlement Vegetation Database of Wisconsin, Dept. of Forest Ecology and Management, University of Wisconsin-Madison). Diameters of these “witness” trees (trees sampled in early land surveys) ranged from about 25 to 35 cm. The forests in this region were harvested extensively by the early 1900s, and it is likely that trees growing on this site were harvested at least twice since these early land surveys.

**Eddy-covariance measurements**

A 30 m tower (Rohn, Peoria, IL, model 45G) was instrumented at 29.6 m above the soil surface, about 5 meters above the forest canopy, for carbon and energy flux measurements using the eddy-covariance method. A three-dimensional sonic anemometer (Campbell Scientific Instruments, Logan, UT, model CSAT-3) was used to measure wind speeds and virtual temperature, and an infrared gas analyzer (Li-Cor, Lincoln, NE, model LI-6262) was used to measure fluctuations of CO$_2$ and H$_2$O vapor mixing ratios. Measurements were collected at a frequency of 10 Hz, and the gas analyzer was calibrated with low frequency, high precision CO$_2$ and humidity measurements of the ambient air, as described by Berger *et al.* (2001). Low frequency CO$_2$ profile measurements were measured with a similar gas analyzer (see CO$_2$ profile measurements below), and humidity was measured using a chilled mirror hygrometer.
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(EdgeTech, Milford, MA, model 200 DewTrak) and a relative humidity probe (Campbell Scientific Instruments, model CS500). The anemometer and air sample inlet were attached to the end of a 2 m boom pointed in the predominant wind direction (west). Air was drawn through a teflon filter (1 µm pore size) and about 3 m of teflon PFA tubing (3.18 mm id) before passing through the gas analyzer and diaphragm pump (Brailsford & Co., Rye, NY, model TD-4X2). Measurements were made in absolute mode by maintaining a constant flow of CO2/H2O-free N2 gas through the reference cell. Sample flow rates were about 3 L min⁻¹, and an analysis of CO2 and H2O signal spectra (see Berger et al., 2001) showed no relative degradation at frequencies less than 1 and 0.8 Hz, respectively (data not shown). ‘White’ noise was observed in both the spectra at frequencies greater than 1 Hz.

CO2 vertical profile measurements

Mixing ratios of CO2 were measured at 0.6, 1.5, 3.0, 7.6, 13.7, 21.3, and 29.6 m above the soil surface using an infrared gas analyzer (Li-Cor, Lincoln, NE, model LI-6251). Zhao et al. (1997) and Bakwin et al. (1995) describe a similar system for obtaining high precision CO2 measurements at unattended sites. Solenoid valves (Neumatics, Inc., Highland, MI, model L01) were used to control flow from each of the levels and each of three working gas standards (approx. 340, 440, and 550 ppm CO2 in dry air) through analyzer sample cell. Mixing ratios of CO2 in working gas standards were determined with an infrared gas analyzer that was calibrated with CO2 standards (approx. 340 and 550 ppm) prepared by the Climate Monitoring and Diagnostics Laboratory of the National Oceanic and Atmospheric Administration (Kitzis and Zhao, 1999).
Measurements were made in differential mode by maintaining a constant flow of compressed dry air containing approx. 440 ppm CO₂ through the reference cell of the analyzer. A backpressure regulator (Porter Instrument, Hatfield, IA, model 9000) was used to equalize pressure in the sample and reference cells. Samples of air from the tower profile were drawn through a teflon filter (1 μm pore size) and variable lengths of Dekabon tubing (Saint-Gobain Performance Plastic, Wayne, NJ, model 1300, 5.5 mm id) to the analyzer at the tower base. Air entering the sample cell was dried in a Nafion drier (Permapure, Toms River, NJ, model MD-050-72P using a countercurrent of N₂ gas) followed by a chemical desiccant (Mg(ClO₄)₂). Air was drawn continuously through each tube, and each height was sampled for 3 minutes every 21 minutes. Two minutes were required to flush the system, and measurements were collected and averaged during the following minute. Reference cell gas was passed through the sample cell every 42 minutes to obtain a “zero” value, and a sequence of all three standards was measured every 3 to 4 hours. Calibration data were fit to a second order polynomial function, and coefficients were interpolated using a cubic spline function (Research Systems Inc., 1998) to obtain calibration equations for each 3-minute measurement.

Micrometeorological observations

Radiation and atmospheric pressure were measured at a frequency of 1 Hz with sensors mounted on the tower at 29.6 m. Four individual sensors were used for measuring incoming and reflected solar radiation, and incoming and emitted infrared radiation (Kipp & Zonan, Bohemia, NY, model CNR1); net radiation (Rn) was calculated by summing values from all four sensors. A quantum sensor (Li-Cor, Lincoln, NE, model LI190SZ) was used to measure incoming photosynthetically active radiation (Q). Ambient atmospheric pressure was measured with a
barometer equipped with a silicon capacitive sensor (Vaisala, Helsinki, Finland, model PTB101B).

Air and soil temperature profiles, soil moisture and soil heat flux ($G_s$) were measured every 10 minutes. Platinum resistance temperature probes (R. M. Young, Traverse City, MI, model 41342; Campbell Scientific, Inc., Logan, UT, model CS500) and Cu-Cs thermocouples (type T) were positioned at 29.6, 24.4, 18.3, 12.2, 7.6, 1.0, 0.5, 0.2, 0.1, and 0.05 m above the soil surface to measure the air temperature, and atmospheric humidity was measured at 29.6, 18.3, 12.2, 7.6, and 2 m. Air temperature and humidity profile measurements were used to calculated changes in energy stored in air above the soil surface ($S$). Thermocouples also were positioned at 0.01, 0.05, 0.1, 0.2, 0.5, and 1.0 m below the soil surface to measure soil temperature. Heat transfer in the soil was measured with a thermopile transducer (Radiation and Energy Balance Systems, Seattle, WA, model HFT-3.1) installed 7.5 cm below the surface. Volumetric water content was measured at the same depths at the soil thermocouples using water content reflectometers (Campbell Scientific, Logan, UT, model CS615) that were calibrated in the laboratory using soils from this location.

Analog-to-digital signal conversion and data acquisition was accomplished with two data loggers (Campbell Scientific, Inc., Logan, UT, models CR10X and CR23X) connected to a notebook computer.

Turbulent and storage flux calculations

Fluxes of CO$_2$, latent heat (LE), and sensible heat (H) were calculated using methods described by Berger et al. (2001). Half-hour fluxes were calculated after computing sonic-analyzer lag times, sonic rotation angles, and calibration coefficients for the CO$_2$/H$_2$O analyzer.
Throughout this paper, positive values indicate fluxes from the surface to the atmosphere. Latent heat fluxes were spectrally corrected by mathematically degrading the temperature signal to match the observed H$_2$O spectra, and multiplying the fluxes by the ratio of the non-degraded to degraded temperature flux (Goulden et al., 1996b). Degradation of the CO$_2$ spectra was not observed. It may exist, but if so it is masked by instrumental noise that dominates at high frequencies (Berger et al., 2001). Thus a CO$_2$ spectral correction factor was computed based on the literature of flow through tubes and the characteristics of this apparatus. The correction factors that multiplied the uncorrected fluxes were about 1.003 and 1.2 for CO$_2$ and H$_2$O, respectively. Berger et al. (2001) discussed this spectral correction methodology using eddy-covariance data from the WLEF tall tower.

Storage fluxes were calculated from temporal changes in storage of CO$_2$, H$_2$O, and temperature between the soil surface and the height of the eddy flux measurement (29.2 m). Carbon dioxide mixing ratios from each sampling height were interpolated to produce three minute time series that were vertically integrated to calculate storage within the air column. Aboveground heat storage was computed in the same manner using air temperature and water vapor measurements. There was insufficient data to accurately assess storage of heat in the standing biomass, so this component was not included in energy budget estimates using micrometeorological observations. Storage of heat in the soil ($G_s$) above the soil heat flux plate (0 to 7.5 cm) was calculated using the soil heat capacity ($C_s$) and the time rate of change in soil temperature:

$$C_s = \rho_b C_d + \theta_v \rho_w C_w$$  \hspace{1cm} (1)

where $\rho_b$ is the soil bulk density ($1.3 \times 10^{-3}$ kg m$^{-3}$), $C_d$ is the heat capacity of dry soil (approx. $0.84 \times 10^3$ J kg$^{-1}$ K$^{-1}$), $\theta_v$ is the volumetric soil water content (m$^3$ H$_2$O m$^{-3}$ dry soil) at 5 cm below
the soil surface, $\theta_v$ is the density of water (approx. 1000 kg m$^{-3}$) and $C_w$ is the heat capacity of water (approx. $4.19 \times 10^3$ J kg$^{-1}$ K$^{-1}$); and

$$G_s = \frac{(\Delta T_s C_s d)}{\Delta t} \tag{2}$$

where $\Delta T_s$ is the change in soil temperature (K) at 5 cm below the soil surface, $d$ is the depth of upper soil layer (0.075 m), and $\Delta t$ is the interval between soil temperature measurements (600 s). This storage term ($G_s$) was added to the soil heat flux density measurement to obtain total heat flux at the soil surface ($G$).

**Data screening**

Data were screened to eliminate instrumental error due to sensor limitations or interference by precipitation, and methodological errors associated with geography and micrometeorological conditions. For humidity measurements greater than 100%, atmospheric humidity was calculated from saturated vapor pressure as a function of temperature. A leaf wetness sensor (Campbell Scientific, Inc., Logan, UT, model 237) was used to discard solar radiation measurements when moisture was present.

Micrometeorological conditions are not always suitable for measuring fluxes using the eddy-covariance technique, especially during night when light wind conditions and near-surface temperature inversions restrict vertical mixing and may cause decoupling of the subcanopy and overlying air (Mahrt *et al.*, 2000). A storage term was used to account for the accumulation of CO$_2$ beneath the turbulence sensors (see above), but this was not always sufficient due to spatial heterogeneity within the forest, and weak horizontal winds beneath the canopy (Pattey *et al.*, 1997). At this site, it was necessary to discarded fluxes on the basis of low friction velocity ($u^* < 0.175$ m s$^{-1}$), and a unique combination of micrometeorological conditions (i.e., temperature...
inversion at the canopy; winds upslope of the tower and from the direction of a distant wetland) that created non-representative sampling conditions. Identification and selection of these screening criteria are discussed in the results section.

Gap filling and annual Net Ecosystem Exchange (NEE) calculations

Net ecosystem exchange (NEE) is defined as the sum of carbon fixed by photosynthesis and carbon released as CO2 by heterotrophic and autotrophic respiration, and was computed by summing the spectrally corrected CO2 flux, obtained by the eddy-covariance method, and the CO2 storage flux. Partitioning of NEE between apparent photosynthesis and ecosystem respiration was estimated using nighttime NEE rates—which integrate leaf dark respiration, plant construction and maintenance respiration, and heterotrophic respiration—as a measure of total ecosystem respiration (RT).

Nighttime NEE rates were fit to an empirical equation that describes an exponential response of RT to temperature,

\[ RT = a_0 e^{a_1(T_s-a_2)} \]  \hspace{1cm} (3)

where T_s is soil temperature (°C) at 5 cm below the surface.

Apparent photosynthesis (PA) was computed subtracting RT (3) from daytime NEE rates, and fitting data to a “big leaf” model that describes a response to quantum flux density (Ruimy et al., 1995):

\[ PA = b_2 - \frac{(b_0Q)}{(b_1+Q)}. \]  \hspace{1cm} (4)

The variables in this equation provide estimates of photorespiration (b_2), maximum assimilation rate (b_0) and photon flux density required for half saturation (b_1).
Annual sums of NEE require gaps in the data to be filled. We modeled $P_A$ and $R_T$ on a monthly time scale using micrometeorological variables to fill missing half-hour measurements (Falge et al., 2001). Monthly averaged response functions cannot distinguish short-term acclimation of photosynthesis and respiration to temperature (e.g., Tjoelker et al., 2001; Gunderson et al., 2000; Larigauderie and Korner, 1995), but provide better spatial sampling across a range of temperatures. Also, short-term acclimation of water and carbon fluxes in forest vegetation has been shown to affect annual ecosystem sums by less than 10% (Kutsch et al., 2001a). Missing storage fluxes were filled using diurnal averages from the 14 days proceeding and 14 days following the missing period. Data from 1999 included gaps of up to a month, so gap filling and annual NEE calculations were only performed for the 2000 calendar year.
Results and Discussion

Environmental constraints

Climatic conditions during this two-year study are presented in Fig. 2. Air temperatures during 1999 and 2000 were similar to long-term observations from Minocqua, WI, located about 50 km east of the site. With few exceptions, mean monthly air temperatures were within the range of data containing 80% of all monthly averages from 1905 to 2001 (National Climatic Data Center, Asheville, NC). Departures in air temperature included warm anomalies during November 1999 (+4°C) and March 2000 (+3°C), and a cool period during December 2000 (-6°C). Annual cumulative precipitation at Minocqua, WI, during 1999 and 2000 was 86 and 83 cm, which was only slightly higher than the long-term average of 79 cm. Cumulative precipitation during May 1999 was the greatest on record for that month, and cumulative precipitation during July of both years was almost two times greater than the long-term average. Abundant rainfall during the first half of the 1999 and 2000 growing seasons was offset by less than average precipitation during the fall (September through November) of both years. Annual precipitation at this site was similar to other deciduous and mixed deciduous forests where carbon and water fluxes are being measured (Harvard Forest, MA; University of Michigan Biological Station, MI; Camp Borden, Ontario), but annual and mid-summer air temperatures were about 1 to 3°C lower.

Systematic errors associated with low turbulence

Micrometeorological conditions were not always suitable for measuring fluxes using the eddy-covariance technique, especially during night when light wind conditions and near-surface temperature inversions restricted vertical mixing. Storage fluxes were included in the NEE
calculation to reduce errors associated with turbulent fluxes, but significant bias can still occur due to drainage of cold surface air (e.g., Anthoni et al., 1999). Observations from the Willow Creek flux tower were segregated by friction velocity ($u^*$) and used to identify a threshold value below which NEE measurements were significantly less than monthly averages (Fig. 3). A $u^*$ threshold of 0.175 m s$^{-1}$ was observed at this site, which was similar to values used at other forested locations (Goulden et al., 1996b; Aubinet et al., 2000; Falge et al., 2001). About 6% of the observations from 1999 and 2000 were discarded on this basis, which was somewhat less than most sites (Falge et al., 2001). Removal of low turbulence data had a relatively small effect on annual NEE, which is discussed below.

Systematic errors associated with surface geography and microclimate

There is a natural tendency to install towers on upland sites, where construction and maintenance is simplified by drier soils. Nearly all sites also observe systematically low CO$_2$ fluxes under very stable conditions. These phenomena may be linked with drainage flows causing carbon losses due to advection away from the tower, as discussed above. At this location, however, we were also confronted with uncertainty associated with the venting of large amounts of CO$_2$ that we hypothesize has pooled in nearby lowlands.

The venting is suggested by unusually high NEE measurements (Fig. 4a). The magnitude of the extreme positive NEE measurements increased with soil temperature and decreased when soil moisture exceeded about 0.35 m$^3$ m$^{-3}$ (data not shown), suggesting a biological source such as microbial respiration from soils. However, direct soil surface flux measurements from numerous locations within the tower footprint were consistently less than 8 µmol CO$_2$ m$^{-2}$ s$^{-1}$ (Martin and Bolstad, this issue), and the belowground component represented about 70% of $R_T$. 

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at this site (Bolstad et al., this issue). Only about 3% of all NEE observations exceeded 10 µmol CO$_2$ m$^{-2}$ s$^{-1}$, but these measurements made a substantial contribution to the total respiratory flux, discussed below, and were not representative of spatially integrated respiration from the forest stand.

Anomalous NEE measurements were characterized by a large respiratory signal in the turbulent flux measurements, and were not associated with weak turbulence (represented by friction velocity, Fig. 4b) or “pooling” of cold air and CO$_2$ near the tower at night. Furthermore, these measurements were observed for periods lasting several hours, and did not appear to be associated with occasional downward bursts of turbulence (e.g., Mahrt, 1985; Baldocchi and Meyers, 1991). Rather, these events were observed during steady and moderately high wind speeds above the forest canopy (2.5 ± 0.98 m s$^{-1}$, mean ± std. dev.). Most of the NEE values greater than 20 µmol m$^{-2}$ s$^{-1}$ were associated with winds between 90 and 180º of true north (Fig. 4a), from the direction of low elevation wetlands located about 0.6 to 1.3 km from the tower (Fig 1). Lowlands have the potential to be a greater source of CO$_2$ than forested uplands, because 1) soil organic matter content is often higher, and respiration rates can be greater if aeration is not limited by excess soil moisture; and 2) CO$_2$ from the surrounding landscape may be concentrated in lower elevations by cold air drainage.

Wind speeds and friction velocities ($u^*$) were reduced when winds were from an easterly direction (Fig. 4b,c), indicating that a geographic obstacle was blocking air upwind of the tower. In a geographic setting such as this, relatively fast winds and weak stability might lead to laminar flow over an obstacle and create a turbulent wake on the leeward side (Stull, 1988). Also, the roughness transition from wetland to forest can generate turbulence, and this turbulence can be sensed as far away as 25 times the displacement height (Irvine et al., 1997). The distance to the
nearest wetland is 100 times the displacement height (Fig. 1), and any turbulence generated at
the forest-wetland boundary is unlikely to be detected at the Willow Creek tower. We also
observed that anomalous NEE measurements were characterized by moderately high wind
speeds (see above), and a relationship with atmospheric stability was confirmed by evaluating
the difference between forest canopy surface temperature and above-canopy air temperature (Fig.
5). Most of the anomalous observations occurred when there was a slight temperature inversion
above the forest canopy (0.1 to 1°C), a condition that also signifies the decoupling of air in the
forest subcanopy from air measured by eddy-covariance sensors at the top of the tower.
To summarize, we hypothesize that: 1) During the growing season when soil respiration rates
are high, CO₂-rich air accumulates in low-lying wetlands due to a combination of local
respiration and cold air drainage under stable conditions; 2) on occasion, moderately fast winds
and weak stability allows CO₂-rich air from the wetlands east of the tower to flow up and over
elevated terrain on the wetland-upland boundary; 3) a temperature inversion across the forest
canopy top prevents the advected wetland air from mixing with air within the forest canopy,
minimizing the dilution of this CO₂-rich air; 4) at a point fairly close to the tower, the laminar
flow becomes turbulent, resulting in upwards mixing of the CO₂-rich air and the extremely large
NEE values observed. This hypothesis will require further investigation. These extreme NEE
measurements are not representative of local fluxes and were screened by removing data during
the growing season (Julian day 100 to 300) when winds were between 50 and 225° and there was
a temperature inversion of >0.1°C above the forest canopy
Screening data for low turbulence (u* < 0.175 m s⁻¹) and for these anomalous respiratory
fluxes removed about 23% of the observations, but provided confidence that systematic errors
were minimized in the annual carbon budget. The consequence of excluding these data is discussed below.

Surface energy balance

Achieving closure of the energy budget \((H + LE)/(Rn – G – S) = 1\) is important for calculating and interpreting surface energy partitioning, and validating the CO₂ and H₂O flux calculations (Verma et al., 1995; Moncrief et al., 1997). The overall energy balance for this site was 71% (Fig. 6), which was calculated using ‘fitexy’, an algorithm that fits a straight-line model to data with errors in both coordinates (Press et al., 1992). Screening data for low turbulence conditions did not balance the surface energy budget, and lack of closure occurred during both daytime and nighttime periods.

Closure was improved when incoming radiation and turbulence were high, i.e., during midday and mid-growing season. A synthesis of eddy-covariance data from 22 FluxNet towers demonstrated similar energy imbalances and relationships with turbulence and daily radiation (Wilson et al., in press). Wilson et al. (2001) observed that the magnitude of NEE was reduced when the energy closure was poor. These results suggested that systematic errors are at least partially due to advection losses during periods of low turbulence, and NEE cannot be corrected by adjusting based on the energy budget imbalance without accounting for atmospheric stability.

A linear fit of all the data from 2000 is strongly influenced by daytime values (Fig. 6), when closure is improved by greater incoming radiation and turbulence. During nighttime, when net radiation is low and fluxes are primarily characterized by longwave exchange, the linear fit appears to overestimate closure of the energy budget. For the purpose of correcting NEE measurements on the basis of energy budget errors, it was necessary to provide estimates of
closure throughout the day. For this explicit purpose, we used a simple polynomial equation to
describe the energy balance of the system:

\[ H + LE = 0.0002(Rn-G_s-S)^2 + 0.589(Rn-G-S) + 0.786 \]  

(5)

This function is largely dependent on solar energy inputs, and does not take into account
measurement errors associated with Rn, G, or S. The difference between the linear and non-
linear model estimates is subtle, but the non-linear function appears to provide a better estimate
of closure for both daytime and nighttime observations (Fig. 6).

Ecophysiological relationships and partitioning of carbon

Parameters used to model missing NEE observations in 2000 are presented in Table 1. These
parameters were determined via empirical fits to existing NEE data. Daily averaged nighttime
NEE throughout 2000 exhibited a linear response to surface soil temperatures (Fig. 7), appearing
as though reaction rates were constant throughout the year (i.e., \( Q_{10} \approx 1 \)). This simplification of
the actual processes involved does not take into account such factors as soil moisture, seasonal
changes in root respiration and turnover, short-term acclimation of respiration to temperature in
plants, changes in microbial populations, and nutrient and substrate availability (i.e., litterfall);
however, it allows us to utilize simple micrometeorological models to scale component fluxes at
this site (Bolstad et al., this issue; Martin and Bolstad, this issue). Soil moisture contents
remained high throughout 1999 and 2000, ranging from 0.26 to 0.40 m\(^3\) m\(^{-3}\), and seemed to be
less important than temperature for predicting belowground respiration (Martin and Bolstad, this
issue). However, elevated soil moisture and soil physical properties may limit aeration and
suppress respiration rates at higher temperatures (Fig. 7; Bouma and Bryla, 2000). Bolstad et al.
(this issue) compared tower-based and chamber-based respiration measurements from this site, and found there is general good agreement between both methods.

Photosynthesis parameters are only meaningful during the leaf-on period, which was between early-May and late-September in 2000. Apparent photosynthesis was modeled on a monthly time scale (Table 1), revealing peak assimilation (maximum values of the light response, $b_0$, and light saturation, $b_1$) during July and August. Estimated leaf photorespiration ($b_2$) was greatest during June, which is expected during rapid leaf expansion (e.g., Wilson et al., 2001; Law et al., 1999; Ryan et al., 1997). Light response and respiration coefficients were somewhat less than those reported by Lee et al. (1999) for Camp Borden, a deciduous forest located at a similar latitude in southern Ontario, Canada. In contrast to Willow Creek, the rapidly growing forest at Camp Borden is largely composed of mid-succession species, *Acer rubrum*, *Populus tremuloides* and *Fraxinus americana*. The comparison between sites highlights the importance of species composition and stand age on photosynthetic uptake and variability within broad latitudinal bands.

Partitioning of carbon between $P_A$ and $R_T$ during 2000 is shown in Figure 8. In springtime, both $P_A$ and $R_T$ increased rapidly after disappearance of the snow cover, and when mean air temperatures and surface soils warmed to $>10^\circ C$ (Fig. 1). This is consistent with post-winter recovery of other tree species growing at high latitudes (Bergh and Linder, 1999; Lee et al., 1999), and evidence that belowground respiration is largely driven by warmer bulk soils (Fig. 7; Russell and Veroney, 1998) and increased availability of photoassimilates in rhizosphere soil (Högberg et al., 2001). This suggests that onset of spring and length of the growing season will be a critical determinant in interannual variability at this site (Goulden et al., 1996a).
Photosynthetic uptake ended abruptly with senescence of leaves in late-September, while ecosystem respiration continued at relatively high rates for an additional month. After leaf fall, the proportion of radiation reaching the forest floor increases, and fresh litterfall provides a readily available resource for heterotrophic microorganisms. These results indicate that the occurrence and timing of freezing soil temperatures and snowpack development have a large impact on annual respiration and net exchange of carbon (Brooks et al., 1997; Savage and Davidson, 2001; Goulden et al., 1996a).

Stand-scale measurements from the upland hardwood forest at Willow Creek were substantially different from landscape-scale fluxes measured from a 447 m WLEF tower located about 22 km NW of Willow Creek (Davis et al., this issue; Cook et al., 2001). Photosynthesis rates during the 2000 growing season were consistently higher at Willow Creek, resulting in annual photosynthetic uptake that was 38% greater than at WLEF (Cook et al., 2001). The flux footprint at WLEF includes less productive wetlands and recently logged or thinned forest, and may explain lower photosynthetic fluxes. In contrast to photosynthetic uptake, respiration rates during 2000 were higher at WLEF, resulting in annual respiration fluxes that were 27% greater than at Willow Creek. Differences in respiration appear to be related to seasonal fluctuations in surface water depth and temperatures of wetland soils; $R_T$ rates at WLEF were highest in July and August, when $T_s$ was highest and surface water depth was lowest in nearby wetlands (Cook et al., 2001). Belowground respiration can be enhanced by as much as two orders of magnitude when the water table is lowered, as has been observed in wetland drainage experiments (Silvola et al., 1996), root growth studies (Kutsch et al., 2001b), soil incubations (Updegraff et al., 1995), ecosystem models (Savage and Davidson, 2001), and eddy-covariance measurements (Lafleur et al., 1997).
Annual net ecosystem exchange (NEE) of carbon

Annual NEE was estimated for 2000 only, because gaps during January and June/July of 1999 were too large to fill with confidence. Three different treatments of the dataset were gap-filled and used to compare the relative effect of data screening methods on annual carbon exchange estimates: (1) no screening; (2) data was screened to remove periods of weak turbulence ($u^* < 0.175 \text{ m s}^{-1}$); and (3) data was screened for weak turbulence and turbulent venting from lowlands to the southeast (discussed above). In all instances, Willow Creek was found to be a carbon sink during the 2000 calendar year (Fig. 9). Screening for weak turbulence had the least effect on annual NEE, increasing the cumulative total without screening from $-132$ to $-94 \text{ g C m}^{-2}$. This correction is much lower than estimates for a broadleaf deciduous forest in hillier terrain, which showed a difference in annual NEE of $240 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Schmid et al., 2000), suggesting that advection away from the flux tower is not as problematic at this site.

Screening observations for turbulent venting had a substantial effect, increasing ecosystem uptake by almost $300 \text{ g C m}^{-2}$ (Fig. 9). These suspect data inflated nighttime respiration measurements and reduced daytime estimates of photosynthetic uptake, creating a large net effect when these observations were removed. Our best estimate of annual NEE for 2000 is $-425 \text{ g C m}^{-2}$. Though this number relies heavily on gap filling (Fig. 9) using micrometeorological data and physiological relationships (Table 1), it should best represent fluxes from within the upland forest stand at the Willow Creek site. Average data coverage during 2000 was 70.8% without any screening, which was reduced to 66.9 and 52.6% with screen for low $u^*$ and turbulent venting, respectively. This compares annual data coverage of 65% from other flux sites (Falge et al., 2001).
A persistent problem with the tower-based eddy-covariance measurements in forests is failure to balance energy going into and out of the system (Twine et al., 2000; Wilson et al., in press), and observations at this location were no exception (Fig. 6). Correcting carbon fluxes for energy balance errors has rarely been attempted (Twine et al., 2000), because the sources of error are often unknown and may vary from site to site (Mahrt, 1998). We found no evidence that imbalances in the energy budget at Willow Creek were associated with either filtering of low frequency flux data, spatial sampling differences, or sensor calibration. In the absence of such information, Twine et al. (2000) suggest that the energy balance should be closed using a method that maintains the Bowen ratio. Sensible and latent heat fluxes in Equation 5 were adjusted in the same proportion to force closure of the energy balance, and carbon fluxes were adjusted by the same amount to produce a dataset that was subsequently gap-filled and used to estimate annual NEE (Fig. 9). Correcting eddy-covariance measurements for energy imbalances results in a cumulative NEE of -495 g C m\(^{-2}\) during 2000, a 20% increase in uptake relative to our best estimate.

Even without correcting for energy balance errors, annual net uptake of carbon at Willow Creek was greater than has been observed at Harvard Forest, University of Michigan Biological Station, and Camp Borden, where annual NEE typically ranges from 140 to 310 g C m\(^{-2}\) yr\(^{-1}\) (Goulden et al., 1996a; Baldocchi et al., 2001; Schmid et al., 2000; Lee et al., 1999). These sites are all deciduous forests within the same latitudinal band, but they show distinct differences in species composition, soil characteristics, land use history and local climatic conditions. In each case, recovery from past disturbance is the likely cause of net uptake of carbon from the atmosphere by these forests (Caspersen et al., 2000; Post and Kwon, 2000). The importance of species composition and soil characteristics is further emphasized by large-scale measurements.
Forest Carbon Exchange and Evaporation

from WLEF, the 447-m-tall tower located about 22 km NW of the Willow Creek flux tower (Davis et al., this issue). Observations at WLEF integrate fluxes from many land cover types, including upland deciduous forest similar to that surrounding the Willow Creek tower. Both sites are located in the same geographical region and exposed to the same climatic conditions, and estimates of cumulative NEE at WLEF in 1997 (+16 g C m\(^{-2}\) yr\(^{-1}\); Davis et al., this issue) indicate that the local landscape is close to carbon balance with the atmosphere. The forest surrounding these towers is heavily managed, and land cover and land use history within the tower footprints may also explain these differences. Land use history is typically correlated with species composition and soil type in northern Wisconsin (Cole et al., 1999; Curtis, 1959).

Forest evapotranspiration and relationship to CO\(_2\) exchange

Forest evapotranspiration is regulated by solar radiation, vegetation, atmospheric humidity, wind, and plant water availability. Prior to leaf emergence in spring, H increased dramatically (Fig 10a) due to increased incoming radiation and disappearance of snow cover (Fig. 1). Latent heat fluxes increased rapidly during May and June (Fig. 10b), coinciding with leaf emergence and continued increase of incoming radiation. This transition in energy partitioning was also observed after leaf fall, but the rate of change was greatly reduced (Fig. 10c). Wilson et al. (2000) observed this same trend for a broadleaf deciduous forest in Oak Ridge, TN, and attributed the more gradual fall transition to non-uniform timing of senescence, a warmer atmosphere, and negative soil heat fluxes.

Whole ecosystem LE was low during leaf-free periods, <0.2 MJ m\(^{-2}\) d\(^{-1}\), and was highly variable during the growing season (Fig. 10b). Day-to-day fluctuations were associated with daily energy inputs, and Bowen ratios were maintained at about 0.3 during the growing season.
(Fig. 10c). During the growing season ET approached that of a saturated surface, 

\[ \frac{\text{ET}_{\text{actual}}}{\text{ET}_{\text{potential}}} \approx 1 \] (Fig. 10d). The Priestly-Taylor coefficient \((\alpha = \frac{\text{ET}_{\text{actual}}}{\text{ET}_{\text{potential}}})\) was not sensitive to the amount of water in the upper 1 m of soil (Fig. 1), indicating that ET was controlled at the leaf level, and not by limitations imposed by soil water availability. Daily averaged LE was more variable than have been observed at other locations (Anthoni et al., 1999; Wilson et al., 2000), suggesting that conductance was not limited by high moisture tensions imposed by low soil hydraulic conductivity.

Soil water holding capacity was high at this site, and soil water content was consistently high throughout 2000. One upland sites in northern Wisconsin that are characterized by high soil nutrient and water availabilities, such as Willow Creek, sugar maple has the highest probability of becoming the dominant, late-successional tree species during forest regeneration (Walter and Reich, 1997; Curtis, 1959). Fertile soils and highly productive tree species (i.e., sugar maple, basswood, and ash) at Willow Creek may explain higher carbon assimilation than similar aged forests at this latitude (discussed above). Soils characterized by low porosity and high moisture contents also may limit soil aeration and exchange of soil CO₂ by mass flow and diffusion, and can limit soil microbial growth and activity. Reduced belowground respiration in these soils may also explain lower respiration rates than were observed at the WLEF tall tower during 2000 (Cook et al., 2001).

Fluxes of CO₂ and water vapor from forests are closely linked (Baldocchi and Meyers, 1998), and show varying degrees of coupling with net radiation, vapor pressure deficit (VPD), and aerodynamic and canopy resistances (Verma et al., 1986). Using individual leaves, Lange et al. (1971) demonstrated that stomata respond directly to atmospheric humidity, and Wong et al. (1979) demonstrated that stomatal aperture could control carbon assimilation. Following the
example of Anthoni et al. (1999), we compared the effect of VPD on the exchange of water vapor and CO₂ for specific levels of incoming radiation (Fig. 11). Incoming radiation influences surface leaf temperatures and VPD, and each has a distinctive affect on stomata opening and leaf conductance (Kutsch et al., 2001a; Lange et al., 1971). Normalized evapotranspiration (α) responded positively to increasing VPD (Fig. 11a), and the response diminished rapidly with increased sunlight. Figure 11a shows that transpiration is reduced by stomatal closure when Q >1500 µmol m⁻² s⁻¹, since α does not appear to respond to increased VPD. The effect of stomatal closure on apparent photosynthesis was not noticeable unless leaves were exposed to intense sunlight (Q >1500 µmol m⁻² s⁻¹), at which point VPD >2 kPa could reduce NEE by 50% (Fig. 10b). These data suggest that a model based on both Q and VPD observations might be better suited than Eq. 4 for filling data gaps in CO₂ and H₂O exchange.
Conclusions

We observed seasonal patterns of carbon exchange and evaporation from an upland deciduous forest in north central Wisconsin during 1999 and 2000. The site is one of several observation points in the Great Lakes region that will be used to scale-up component and eddy-covariance measurements from discrete ecosystems to regional observations from the WLEF tower near Park Falls, WI, and for regional model validation (Baker et al., 2002; Denning et al., 2002). We estimated that cumulative NEE of CO₂ at the Willow Creek site was -425 g C m⁻² yr⁻¹ during the 2000 calendar year. Applying a Bowen ratio correction for energy budget errors increased ecosystem uptake by an additional 70 g C m⁻² yr⁻¹. Snow cover, soil temperatures, and length of the growing season were important environmental constraints on annual carbon and water vapor exchange. Photosynthetic uptake in 2000 was 1120 g C m⁻² yr⁻¹, which is quite large when compared with data from WLEF (Davis et al., this issue) and similar forests at this latitude (Goulden et al., 1996a; Baldocchi et al., 2001; Schmid et al., 2000; Lee et al., 1999). Total ecosystem respiration was 695 g C m⁻² yr⁻¹, and rates exhibited an atypical, linear response to surface soil temperatures (Q₁₀ ≈ 1).

It was hypothesized that Rₜ was limited by the same soil physical properties (e.g., soil moisture retention, porosity) that make this a highly productive forest site for maple, basswood, and ash species. Surface soil moisture ranged from 0.26 and 0.40 m³ m⁻³ throughout 1999 and 2000, and variation in the water content of the upper 1 m of soil had no discernable influence on normalized rates of evapotranspiration (ET) during the growing season. Latent heat fluxes were depressed (<0.2 MJ m⁻² d⁻¹) during the leaf-off period, and increased dramatically from June through September due to forest transpiration. Forest transpiration allowed ET to approach levels approximating a saturated surface, and partial closure of stomata influenced normalized
rates at all light intensities. In contrast, total exchange of CO$_2$ was only affected under intense sunlight (Q >1500 µmol m$^{-2}$ s$^{-1}$) and high vapor pressure deficits (VPD >2 kPa). These relationships will help us develop more realistic empirical models for predicting carbon and water vapor fluxes from observations of incoming radiation, leaf temperature, and humidity.

Under certain conditions we detected evidence of advection of CO$_2$ from lowlands located 0.6 to 1.3 km from the tower. We hypothesize that turbulence was generated by the undulating surface topography and change in roughness at the wetland-forest interface, and that this turbulence was responsible for mixing and transporting CO$_2$ in stable layers near the wetland surface to the tower. These observations highlight the site-specific problems that can arise with flux measurements by eddy-covariance when the assumption of horizontal homogeneity is invalid. A rigorous data screening procedure was implemented to discard unreliable eddy-covariance data when turbulence was low ($u^* <$0.175 m s$^{-1}$), and for specific wind directions and micrometeorological conditions (i.e., a temperature inversion above the forest canopy).
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References


Table 1. Parameter estimates for filling gaps in observed net ecosystem exchange of carbon (NEE) during 2000.

<table>
<thead>
<tr>
<th>Month</th>
<th>Ecosystem respiration ($R_T$)</th>
<th>Apparent photosynthesis ($P_A$)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$a_0$</td>
<td>$a_1$</td>
</tr>
<tr>
<td>January</td>
<td>0.985</td>
<td>0.0288</td>
</tr>
<tr>
<td>February</td>
<td>18.8</td>
<td>0.318</td>
</tr>
<tr>
<td>March</td>
<td>8.96</td>
<td>0.205</td>
</tr>
<tr>
<td>April</td>
<td>4.95</td>
<td>0.110</td>
</tr>
<tr>
<td>May</td>
<td>5.76</td>
<td>0.139</td>
</tr>
<tr>
<td>June</td>
<td>4.78</td>
<td>0.0595</td>
</tr>
<tr>
<td>July</td>
<td>4.64</td>
<td>0.0748</td>
</tr>
<tr>
<td>August</td>
<td>5.16</td>
<td>0.215</td>
</tr>
<tr>
<td>September</td>
<td>4.19</td>
<td>0.0639</td>
</tr>
<tr>
<td>October</td>
<td>4.15</td>
<td>0.0613</td>
</tr>
<tr>
<td>November</td>
<td>8.06</td>
<td>0.199</td>
</tr>
<tr>
<td>December</td>
<td>3.28</td>
<td>0.0869</td>
</tr>
</tbody>
</table>

$^\S R_T = a_0 e^{a_1(T_s-a_2)}$, where $T_s$ is soil temperature (°C) at 5 cm below the surface.

$^\P P_A = b_2 - (b_0Q)/(b_1+Q)$, where $Q$ is incoming photosynthetically active radiation ($\mu$mol m$^{-2}$ s$^{-1}$).
Figure Legends

Figure 1. Local topography at the Willow Creek Flux tower site (US Geological Survey, Pike Lake SE, Wisconsin, scale 1:24 000, series V861, sheet 1, US Government Printing Office, 1997).

Figure 2. Meteorological observations at or near the Willow Creek flux tower: (a) Maximum daily photosynthetically active radiation \( Q \); (b) mean daily air temperature at 29.6 m above the soil surface (solid line), and mean daily soil temperature at 5 cm below the soil surface (dashed line); (c) mean daytime vapor pressure deficit at the canopy top (20.3 m); (d) mean water equivalent precipitation rates; (e) mean daily soil moisture content at 20 cm below the soil surface (solid line), and mean daily soil water integrated to 1 m below the soil surface; and (f) mean daily snow depth.

Figure 3. Normalized nighttime NEE as a function of \( u^* \). Data were binned by \( u^* \) in increments of 0.05 m s\(^{-1}\), and included all nighttime data for 1999-2000 except when winds were from 50\(^\circ\) to 225\(^\circ\).

Figure 4. Non-Screened net ecosystem exchange (NEE) from 1999-2000, showing (a) exceptionally large respiration fluxes, (b) reduced wind speeds, and (c) lowered friction velocities (\( u^* \)), when winds originated from about 50\(^\circ\) to 225\(^\circ\).
Figure 5. Relationship between large respiration fluxes and temperature inversion above the canopy (difference in air temperature at 29.6 and 18.3 m), when winds originated from 50° to 225° and $u^*$ was greater than 0.1 m s$^{-1}$.

Figure 6. Surface energy balance based on 30-minute averages from the Willow Creek tower (1999-2000) characterized by a linear ‘fitexy’ algorithm (dashed line) and a second-order polynomial function (solid line).

Figure 7. A linear function describing the relationship between daily averaged nighttime NEE and soil temperature (5 cm depth) at the Willow Creek site during 2000.

Figure 8. Partitioning of NEE between apparent photosynthesis (circle) and ecosystem respiration (triangle) using daily, gap-filled data from the Willow Creek flux tower (2000).

Figure 9. Daily accumulation of carbon at the Willow Creek site during 2000; a ‘plus’ signifies that at least 50% of the daily value is derived from direct observations; a ‘triangle’ signifies that more than 50% of the daily value is derived from gap-filled data; and negative values indicate ecosystem uptake.

Figure 10. Seasonal changes in daily integrated (a) sensible and (b) latent heat fluxes; (c) integrated midday (1000 to 1400 CST) Bowen ratio; and (d) the Priestley-Taylor constant, $\alpha=\frac{ET_{\text{Actual}}}{ET_{\text{Potential}}}$, from the Willow Creek flux tower (1999-2000).
Figure 11. Influence of vapor pressure deficit (VPD) and incoming radiation on (a) relative evapotranspiration and (b) apparent photosynthesis observed from the Willow Creek flux tower during 2000. Symbol color indicates level of photosynthetically active radiation (Q): medium gray, 500 to 1000; light gray, 1000 to 1500; black, >1500 µmol m$^{-2}$ s$^{-1}$).
Figure 1.
Figure 2.
Figure 3.
Figure 4.
Figure 5.
Figure 6.
Respiration = 0.1899(Soil T_{5 \text{ cm}}) + 0.326
R^2 = 0.87

Figure 7.
Figure 8.
Figure 9.
Figure 10.
Figure 11.