



Comparing net ecosystem exchange of carbon dioxide between an old-growth and mature forest in the upper Midwest, USA

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Abstract

Old-growth forests are often assumed to exhibit no net carbon assimilation over time periods of several years. This generalization has not been typically supported by the few whole-ecosystem, stand-scale eddy-covariance measurements of carbon dioxide exchange in old-growth forests. An eddy-flux tower installed in a >300-year-old hemlock–hardwood forest near the Sylvania Wilderness, Ottawa National Forest, MI, USA, observed a small annual carbon sink of CO₂ of $-72 \pm 36 \text{ g C m}^{-2} \text{ year}^{-1}$ in 2002 and $-147 \pm 42 \text{ g C m}^{-2} \text{ year}^{-1}$ in 2003. This carbon sink was much smaller than carbon sinks of $-438 \pm 49 \text{ g C m}^{-2} \text{ year}^{-1}$ in 2002 and $-490 \pm 48 \text{ g C m}^{-2} \text{ year}^{-1}$ in 2003 observed by a nearby flux tower in a 70-year-old mature hardwood forest (Willow Creek, WI). The mature forest had vegetation similar to the old-growth site prior to European settlement. Both sites had slightly larger carbon sinks in 2003, which was a drier and cooler year than 2002. However, the difference in sink strength between the two years was smaller than the uncertainty in the results arising from missing and screened data. Both sites also had significant systematic errors due to non-representative fluxes during certain micro-meteorological conditions, which required careful screening. The difference in sink strength between the two sites was driven mainly by greater ER at the old-growth site ($965 \pm 35 \text{ g C m}^{-2} \text{ year}^{-1}$ in 2002 and $883 \pm 69 \text{ g C m}^{-2} \text{ year}^{-1}$ in 2003) compared to the mature site ($668 \pm 21 \text{ g C m}^{-2} \text{ year}^{-1}$ in 2002 and $703 \pm 17 \text{ g C m}^{-2} \text{ year}^{-1}$ in 2003). GEP was lower at the old-growth site ($1037 \pm 47 \text{ g C m}^{-2} \text{ year}^{-1}$ in 2002 and $1030 \pm 41 \text{ g C m}^{-2} \text{ year}^{-1}$ in 2003) compared to the mature site ($1106 \pm 47 \text{ g C m}^{-2} \text{ year}^{-1}$ in 2002 and $1192 \pm 51 \text{ g C m}^{-2} \text{ year}^{-1}$ in 2003), especially in 2003. Observations also suggested that growing season ER had greater interannual variability at the old-growth site. These results imply that old-growth forests in the region may be carbon sinks, though these sinks are smaller than mature forests, mostly likely due to greater ER.

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1. Introduction

Old-growth forests are traditionally viewed to be in equilibrium with respect to net ecosystem exchange (NEE) of carbon (Caspersen and Pacala, 2001; Kira and Shidei, 1967). Forests typically start out as net carbon sources during stand initiation after disturbance and become large carbon sinks as they mature due to rapidly increasing production and slowly increasing respiration (Law et al., 2003). As forests move from stand reinitiation to old growth, carbon sink strength is expected to decline in magnitude and may reach neutrality as growth slows down and decomposition increases.

This decline is hypothesized to be attributable to increased respiration and decreased photosynthesis in an old-growth forest compared to a mature forest. Ecosystem respiration (ER) is expected to increase steadily with stand age due to increased decomposition (i.e., from greater amounts of coarse woody debris (CWD) arising from mortality) and sapwood maintenance respiration. Gross ecosystem production (GEP) typically peaks in mature forests and declines as stands age due to decreased stomatal conductance, decreased hydraulic conductivity from increased tree height, decreased nutrient availability, and increased tree and branch mortality (Gower et al., 1996; Murty et al., 1996).

Because many forest productivity models assume that net primary production (NPP) declines steadily after stem exclusion and approaches zero for old-growth stands, the ability of old-growth forests to act as carbon sinks may actually be underestimated (Carey et al., 2001). Continuous recruitment of various tree species of all ages in a natural old-growth forest could lead to positive net primary productivity (NPP), as opposed to carbon equilibrium expected in monospecific even-aged old stands or carbon uptake decline expected with individual old trees. In addition, the contribution of sapwood respiration to ER may not increase over the course of stand development (Carey et al., 1997; Ryan and Waring, 1992).

The objective of this study was to examine net ecosystem carbon exchange in an old-growth eastern hemlock (*Tsuga canadensis*)–northern hardwood forest located in the Ottawa National Forest, Michigan, USA, and compare it to a mature northern

hardwood forest located in the nearby Chequamegon-Nicolet National Forest, Wisconsin, USA. The old-growth stand is representative of the forest type found in the mature forest stand and much of northern Michigan and Wisconsin prior to European settlement in North America (Frelich, 1995; Manies and Mladenoff, 2000; Schulte et al., 2002). Prior to European settlement, hemlock–hardwood forests occupied almost half of the forested land area in Minnesota, Wisconsin, and Michigan (Frelich, 1995; Woods, 2000b). Harvesting from the late 1800s through mid 1900s resulted in the conversion of these forests to secondary forests of aspen (*Populus tremuloides*), yellow birch (*Betula alleghaniensis*), and sugar maple (*Acer saccharum*) that characterize the region today.

Carbon exchange seen at the old-growth site may be representative of carbon exchange at the mature site had it not been logged in the late 19th and early 20th centuries. Although only ~1% of primary forest and ~5% of old-growth forest that existed prior to European settlement remain in upper Great Lakes states (Minnesota, Wisconsin, Michigan), the decline of logging in the area during the 20th century has led to a resurgence of older forest that continues to expand in space and age (Caspersen et al., 2000; Frelich, 1995; Houghton et al., 1999). Thus, the undisturbed old-growth forest may also represent the potential for future carbon storage by late successional stands in the region (Woods, 2000b).

We measured the fluxes of carbon dioxide between the forest and atmosphere at the old-growth and mature forest stand over two years using the eddy covariance technique. Since the early 1990s, over 200 eddy covariance flux towers have been built in numerous ecosystems across the world. Few, however, are located in old-growth forests, and only one other is in an old-growth hemlock–northern hardwood forest (Hadley and Schedlbauer, 2002).

Most flux measurements from old-growth forests have shown small to moderate carbon sinks, contrary to the previously assumed carbon balance (e.g., Griffis et al., 2003; Hollinger et al., 1994; Knohl et al., 2003; Law et al., 2001). Based on these results and theories of forest succession, we tested the following hypotheses to better quantify stand age effects in models of forest carbon exchange and improve regional-scale estimates of NEE:

1. The old-growth site was a small carbon sink to the biosphere, corroborating what has been seen at other old-growth sites.
2. The old-growth site had significantly smaller annual NEE of carbon dioxide than the mature site, as would be expected according to traditional models.
3. Smaller NEE at the old-growth site was due primarily to larger ER at the old-growth site compared to the mature site.
4. GEP at the two sites was similar, though the old-growth site may be slightly smaller.
5. Interannual NEE, ER, and GEP will increase or decline at both sites by similar amounts in response to interannual climate variability.

2. Materials and methods

2.1. Site descriptions

2.1.1. Sylvania hemlock–hardwood old-growth forest

The old-growth site (hereafter referred to as Sylvania) was established in late 2001 and is located ~100 m north of the boundary to the Sylvania Wilderness and Recreation area, Ottawa National Forest, Michigan, USA ($46^{\circ}14'31''\text{N}$, $89^{\circ}20'52''\text{W}$) (Fig. 1). The 8500 ha Sylvania Wilderness in the Upper Peninsula of Michigan is one of few large tracts of old-growth forest in the Midwest (Frelich, 1995). Trees range from 0 to 350 years old, and dominant species are sugar maple and eastern hemlock. The forest occurs within a glacial outwash and moraine landscape (Ferrari, 1999), which creates an irregular and hummocky landscape with an average slope of 10% over short distances (Davis et al., 1996; Pastor

and Broschart, 1990). Average elevation is 517–567 m. The climate is northern continental, characterized by short growing seasons and cold winters. Dominant upland soils are moderately well-drained, coarse or sandy loam spodosols (Pastor and Broschart, 1990).

Sixty-six percent of the Sylvania tract is hemlock–northern hardwood forest comprised of 3–30 ha upland patches dominated by either eastern hemlock or sugar maple, with yellow birch, basswood (*Tilia americana*), and ironwood (*Ostrya virginiana*) also present in the overstory (Davis et al., 1994; Frelich et al., 1993; Pastor and Broschart, 1990). Old trees are a significant component of the canopy. Forested wetlands, marshes, and swales cover 13% of the Sylvania region. The remaining 21% of Sylvania is covered by lakes.

Widespread natural disturbances in Sylvania, primarily lightning-induced fire and windstorms, are infrequent. Disturbance histories, reconstructed from tree-ring studies, chronicle a tree turnover time at Sylvania over the past 150 years of 5.4% per decade, with an average canopy residence time of 186 years (Frelich and Graumlich, 1994). The Sylvania Wilderness tract is unique to the area in that it has never been logged, with the exception of large white pines high graded from lakeshores in the early 20th century (Davis et al., 1998). Fossil pollen studies from six small forest hollows suggest that the current mix and locations of hemlock and hardwood stands have not changed in the past 3000 years (Brugam et al., 1997; Davis et al., 1992). These results suggest that Sylvania is near long-term compositional equilibrium, but there is some evidence of compositional flux due to deer browsing and climate change (Davis et al., 1996; Woods, 2000a). These long-term changes, however, are unlikely to greatly impact short-term carbon exchange measurements over old-growth stands. Extensive studies exist of the Sylvania Wilderness and surrounding region that detail the understory (Miller et al., 2002; Scheller and Mladenoff, 2002), leaf litter (Ferrari and Sugita, 1996), nitrogen cycling (Ferrari, 1999; Fisk et al., 2002), and long-term disturbance histories (Frelich and Lorimer, 1991; Lorimer et al., 2001; Parshall, 1995).

The immediate 1 ha around the tower has relatively flat topography (<3% slope), except for a steeper decline (~12%) from the tower to the northeast. A



Fig. 1. Map with locations of Sylvania (▲), Willow Creek (●), and other ChEAS region eddy covariance flux towers (+).

closed canopy of sugar maple is dominant (71% of overstory stems) in the 1 ha surrounding the tower, which also contains hemlock (14%), yellow birch (7%), basswood, and ironwood (8%) in the overstory. However, hemlock is dominant in the 1 km² surrounding the tower. All upland forest in the entire 1 km² is old-growth forest except for about 600 m² to the northeast. Thus, the fluxes measured by the tower are considered representative of old-growth forest given typical flux footprints and wind patterns. There was no evidence of recent disturbance in the area.

Stand basal area measured in 2002 was 33.1 m² ha⁻¹ and typical canopy heights ranged from 20 to 27 m. Average leaf area index (LAI) measured on September 2002 with an LI-2000 (LI-COR Inc., Lincoln, NE) was 4.06. Significant coarse woody debris covers the understory. Sugar maple seedlings are abundant. There are four lakes in the vicinity of the tower: Helen Lake ~100 m to the northeast, Snap Jack Lake ~1 km to the northwest, Long Lake ~1 km to the west, and Clark Lake ~1 km to the east and southeast. The area southwest of the tower has the largest footprint of upland forest wilderness and no lakes. There are also three small (~10 ha) black spruce/sphagnum bogs, one to the southeast, and two ~800 m southwest of the tower.

2.1.2. Willow Creek mature forest regrowth

NEE of carbon and water in the mature upland hardwood forest have been observed since 1999 at the Willow Creek, Wisconsin, USA, AmeriFlux site (hereafter referred to as Willow Creek) (Cook et al., 2004). The site is located in the Chequamegon-Nicolett National Forest, WI, USA (45°48'21"N, 90°04'47"W) and is approximately 50 km from Sylvania (Fig. 1). Dominant species at this site are sugar maple, basswood, and green ash (*Fraxinus pennsylvanica*). The LAI is 5.3, and the stand is about 70 years old. Average canopy height is 24 m. The soil is sandy loam. Pre-settlement vegetation around Willow Creek consisted of hemlock, birch, sugar maple, and basswood trees of 25–35 cm in diameter (unpublished data, Pre-European Settlement Vegetation Database of Wisconsin, Department of Forest Ecology and Management, University of Wisconsin, Madison, 2000). Detailed site description for the Willow Creek site can be found in Cook et al. (2004).

2.1.3. ChEAS

The Sylvania and Willow Creek study sites complement a suite of nine other flux towers in the northern Wisconsin/upper Michigan region (Fig. 1), and are part of the Chequamegon Ecosystem Atmosphere Study (ChEAS; <http://cheas.psu.edu>). ChEAS is an affiliation of researchers conducting carbon and water cycle research in northern Wisconsin and upper Michigan. Sites in the ChEAS network allow for an examination of how age and succession affect forest carbon fluxes and storage. Additional site description and data access for the Sylvania and Willow Creek sites are available from the ChEAS website.

2.2. Measurements

Fluxes of CO₂, latent, and sensible heat were measured at the Sylvania and Willow Creek sites at 36 m (10 m above canopy) and 30 m (5 m above canopy) above the ground, respectively, from a narrow triangular tower (model 45G, Rohn, Peoria, IL). Instrumentation details for Sylvania are presented below. Willow Creek instrumentation was virtually identical to Sylvania and is described extensively in Cook et al. (2004). Flux measurements were made from the end of a 2 m boom oriented towards the SW, which is the predominant wind direction. A Campbell Scientific Inc. (Logan, UT) CSAT-3 sonic anemometer measured high-frequency (10 Hz) three-dimensional wind speed and sonic virtual temperature, while a LI-COR (Lincoln, NE) LI-6262 infrared gas analyzer measured CO₂ and H₂O mixing ratios in absolute mode at 10 Hz. Flow rates of approximately 9 L/min were drawn by a diaphragm pump (model UN89, KNF Neuberger Inc., Trenton, NJ). High-frequency mixing ratio measurements of water vapor and carbon dioxide were calibrated against low-frequency measurements made by a relative humidity probe (model HMP45C, Campbell Scientific Inc., Logan, UT) and a high-precision vertical CO₂ profiling system, respectively. These measurements follow the protocol as outlined by Berger et al. (2001).

Storage flux calculations and calibration of high frequency CO₂ were obtained by measuring low-frequency (3 min average, 21 min interval), high-precision (±0.2 ppm) CO₂ mixing ratios at seven levels between the ground and flux measurement

height. Air from each level was drawn ~60 m by a 6 L/min pump at 3.5 psi (model UN89, KNF Neuberger Inc., Trenton, NJ) and dried by a Nafion tube dryer (model MD-050-72P-2, Perma Pure LLC, Toms River, NJ) using a countercurrent of dry nitrogen. A subsample of air was passed through a LI-COR LI-6252 infrared gas analyzer at 100 mL min⁻¹. The analyzer was automatically calibrated at regular intervals throughout the day using three reference CO₂ gases. System design, measurement protocol, and calibration details of the high-precision CO₂ system are described by Bakwin et al. (1995), Cook et al. (2004), and Zhao et al. (1997).

In addition to flux and CO₂ mixing ratio measurements, a full suite of micrometeorological measurements were made at the site, including net radiation (model NR-LITE, Kipp and Zonen Inc., Saskatoon, SK, Canada), total photosynthetic active radiation (PAR) (model PAR-LITE, Kipp and Zonen Inc., Saskatoon, SK, Canada), air temperature and humidity (model HMP45C platinum resistance temperature and capacitive polymer humidity probe, Campbell Scientific Inc., Logan, UT), and total precipitation (model TE525WS tipping bucket rain gauge and CS705 snowfall adapter, Campbell Scientific Inc., Logan, UT). Precipitation data at the NCDC cooperative weather station in Vilas County, WI (Lac Vieux Desert), were used to account for an improperly placed precipitation gauge at Sylvania from January to May 2002. Soil temperature was measured using a copper–constantan thermocouple (type T, 24 gauge, Omega Engineering Inc., Stamford, CT) buried at 5 cm depth. Soil heat flux and storage were determined using a thermopile transducer (model HFT3, Campbell Scientific Inc., Logan, UT) at 0.075 m below ground and the soil temperature measurements. Other micrometeorological measurements including diffuse PAR, tree bole temperatures, below canopy precipitation, subcanopy wind velocity, along with air temperature, water vapor mixing ratio, PAR, soil temperature, and soil volumetric liquid water content vertical profiles, were also measured. A variety of additional biometric and chamber flux measurements, including soil, coarse woody debris and stem CO₂ efflux measurements, sapflux, stem growth measurements, leaf light response, and site characterizations, were made in the vicinity of the flux tower.

2.3. Flux calculation

Turbulent fluxes of momentum, heat, water vapor, and CO₂ were calculated at half-hourly intervals for both sites using linearly detrended 10 Hz measurements of these quantities. Berger et al. (2001) detail the calculation of fluxes. Wind velocity was rotated into the mean horizontal wind, and a long-term planar fit rotation correction in the vertical was applied to account for any possible non-level mounting of the sonic anemometer. Lagged covariances between vertical wind velocity and carbon dioxide or water vapor were computed and applied to account for lag times between the sonic anemometer and the closed-path infrared gas analyzer. A spectral correction was applied to account for loss of the high-frequency component of flux, following the method described in Berger et al. (2001). Spectral corrections for water vapor were computed by spectrally degrading the power spectrum of virtual sonic temperature to match water vapor. A correction factor for H₂O was computed from the ratio of temperature fluxes computed with and without power spectrum degradation. No degradation was found for CO₂ spectra, so the correction factor was computed from theoretical models of air flow through tubing. Fluxes were multiplied by these spectral correction factors, which typically ranged from 1.01 to 1.04 for CO₂ and 1.2 to 1.5 for H₂O.

Net ecosystem exchange at the surface is the sum of the turbulent flux at sensor height and the storage term below sensor height (Yi et al., 2000). This storage term accounts for the accumulation of the CO₂, water vapor, or temperature below the turbulence sensor height. Missing carbon dioxide storage data were filled using a one-month (expandable to four months until 10 non-missing days are found) moving window ensemble average so as to account for diurnal and seasonal variation in storage flux. Daily average CO₂ storage is typically an order of magnitude smaller than CO₂ flux, and averages to zero over longer time-scales. No attempt was made to calculate heat storage in aboveground biomass.

2.4. Quality control

Turbulent flux sampling quality and instrumentation calibration were assessed using the Ameriflux

relocatable reference system (http://public.ornl.gov/ameriflux/standards_roving.shtml). This system was located at Willow Creek for a week in summer of 2001 and at Sylvania for 10 days in the summer of 2003. Results showed that fluxes measured by the long-term system and the Ameriflux reference system were highly correlated with a slope near 1 at both sites (Loescher H., personal communication). Flux processing methods were validated by computing fluxes for the Ameriflux gold standard files (<http://public.ornl.gov/ameriflux/standards-gold.shtml>).

Additionally, surface energy balance measurements at both sites showed that the sum of sensible and latent heat flux was highly correlated ($r^2 > 0.8$) to the sum of net radiation and soil heat flux. A linear fit between the two quantities showed that long-term energy balance closure for 2002 and 2003 (ratio the sum of sensible and latent turbulent flux to the sum of net radiation and soil heat flux) was 68% for Willow Creek and 79% for Sylvania. These values are in the range reported by most flux sites (Wilson et al., 2002) and provide additional confirmation of turbulent flux quality (Moncrieff et al., 1997). We did not attempt to correct CO₂ fluxes for energy balance underestimation as some researchers have suggested (e.g., Twine et al., 2000).

2.5. Data screening

Two screening criteria were applied to exclude non-representative flux measurements. The first criteria were for weak turbulence friction velocity (u^*) at night. During times of weak or intermittent turbulence, often experienced at night, mixing is weak and the flux is underestimated presumably due to drainage of respired carbon dioxide to low-lying areas (Mahrt et al., 2001). As turbulence strengthens, these pools of carbon are hypothesized to vent into the atmosphere and consequently not be observed by the flux sensors located where the carbon was initially respired. Flux towers, typically built on uplands or hills, tend to find a decline in average nighttime NEE at low u^* (Baldocchi et al., 2001). A friction velocity cutoff was computed by comparing normalized nighttime NEE versus friction velocity. Deviations from mean normalized NEE were computed by subtracting the mean monthly nighttime NEE from the observed NEE and dividing the residual by the standard deviation of nighttime NEE for the month.

The friction velocity cutoff was found where the deviations from normalized NEE (averaged over 0.05 m s⁻¹ friction velocity bins) stayed consistently below zero.

The second screening criteria were for the sampling of non-representative conditions. Anomalous venting events occurred in the southeast quadrant (90–180°) for Willow Creek (Cook et al., 2004). Data from that direction were screened for Willow Creek. A detailed treatment and justification for screening these data can be found in Cook et al. (2004). For Sylvania, non-representative footprints include those contaminated by lakes, mostly found to the north of the tower, or wetlands, mostly found to the southeast of the tower. This screening was accomplished by site maps, directional dependencies evident in plots of friction velocity or NEE versus wind direction, measurements of CO₂ concentration across the landscape, and flux footprint analyses.

To assess our data-screening methods and flux measurement representativeness at Sylvania, we performed a flux footprint analysis that relied on an atmospheric surface layer model (Horst and Weil, 1992) and land cover maps. Sonic anemometer data were used to estimate roughness lengths and displacement heights that varied with wind direction based on a method of Martano (2000). Crosswind-integrated footprints were computed and converted to 2D footprints using simple Gaussian assumptions and sonic anemometer turbulent statistics of vertical and horizontal wind speed variability. A flux footprint contour extended to where it included 90% of the flux. A footprint climatology for all growing season (June–August) hours of 2002 and 2003 was computed from these footprints using a method similar to one presented by Amiro (1998). All footprints were overlaid to create a “footprint climatology”. This climatology was then compared to land cover statistics generated from a United State Geological Survey (USGS) topographical map for the region and results were segregated by wind direction and percentage of land cover sampled.

Table 1 shows the percentage of data screened in each month by the screening criteria. An average of 21% of all possible hours was screened by these criteria. The choice of screening criteria and the effects of data screening on NEE, ER, GEP are discussed in Section 3.2.

Table 1
Percentage of missing data and screened data per month

Month	Sylvania				Willow Creek			
	2002		2003		2002		2003	
	Missing (%)	Screened (%)	Missing (%)	Screened (%)	Missing (%)	Screened (%)	Missing (%)	Screened (%)
January	32	22	24	6	25	18	66	3
February	38	12	16	23	14	12	19	18
March	53	11	10	19	7	30	20	25
April	52	15	53	14	32	28	57	11
May	82	6	100	0	89	3	33	29
June	42	22	18	30	60	17	20	45
July	29	21	2	32	48	21	70	9
August	5	33	1	43	2	49	39	30
September	1	30	0	31	23	29	50	13
October	10	42	8	34	23	28	4	35
November	6	19	65	6	25	12	39	18
December	47	10	100	0	19	16	86	7
June–August	25	25	7	35	37	29	43	28
All year	33	20	33	20	31	22	42	20

Screening includes u^* and wind direction filters.

2.6. Missing data

Missing data occurred at both sites for various reasons including power outages, instrument failure, computer/data logging malfunction, on-site recalibrations, and sonic anemometer interference due to precipitation and condensation. Flux data were observed and collected in 67% of all possible half-hourly time periods (32,058) in 2002 and 2003 for Sylvania and 63% for Willow Creek. Table 1 shows the amount of missing data for each month. For Sylvania, most of these missing data occurred outside of the growing season, when fluxes were consistently small. The amount of missing and screened data at both sites is within range reported for other flux sites (Falge et al., 2001). Falge et al. (2001) show that gap-filling the kind and amount of missing data seen at our sites using non-linear regression (see Section 2.7) typically only introduces small, random errors and can reasonably approximate the original data.

We performed a simple Monte Carlo experiment to assess the first-order uncertainty in our annual estimates of NEE, ER, and GEP based on a method presented by Griffis et al. (2003). Between 10 and 50% of the existing observed data were removed using a uniform random number generator. Missing data gaps

were randomly selected to range from one missing half-hour to five days. Gap filling functions were recomputed and missing data were filled with modeled NEE (described in Section 2.7). This experiment was run 100 times for each year (2002 and 2003) at each site (Willow Creek and Sylvania).

2.7. Partitioning of carbon fluxes and filling data gaps

We followed the gap-filling methodology recommended by Falge et al. (2001) with some minor modifications. Missing and screened NEE data were filled by modeling ER and GEP using simple response functions driven by soil temperature and PAR. Parameters for each function were statistically computed from observed NEE and micrometeorology.

Respiration was computed using the Eyring function (Cook et al., 2004; Eyring, 1935; Glasstone et al., 1941), a theoretically derived chemical rate reaction kinetics model that is similar to the empirically derived Arrhenius model and based on transition state theory. This ER model produces theoretically meaningful parameters that can be used for site-to-site comparisons, and for modeling seasonal and longer term trends in ER. Cook et al. (2004) provide additional justification and derivation

of this equation. The Eyring function is:

$$ER = 10^{-6} \frac{k}{h} T_s e^{-(\Delta G^{++}/R^* T_s)} \quad (1)$$

where ER is ecosystem respiration rate in $\mu\text{mol m}^{-2} \text{s}^{-1}$, T_s the soil temperature in K, k the Boltzman's constant ($1.3806 \times 10^{-23} \text{ J K}^{-1}$), h the Planck's constant ($6.6262 \times 10^{-34} \text{ J s}^{-1}$), and R^* is the universal gas constant ($8.3143 \text{ J mol}^{-1} \text{ K}^{-1}$). ΔG^{++} is the Gibbs activation energy (J mol^{-1}) of the reaction, defined as:

$$\Delta G^{++} = \Delta H^{++} - T_s \Delta S^{++} \quad (2)$$

where ΔH^{++} is enthalpy (J mol^{-1}) and ΔS^{++} is entropy ($\text{J mol}^{-1} \text{ K}^{-1}$). Enthalpy and entropy are the variable parameters of this function. Standard Q_{10} values can also be derived from resulting fits.

We computed these parameters by fitting nighttime NEE against 5 cm soil temperature. There is negligible photosynthesis at night, so nighttime NEE is a measure of ER excluding any respiration components that only occur during the day. Near-surface soil temperature was used because it reflects temperatures near the largest source of heterotrophic respiration (and thus ER), and soil temperature and ER are typically correlated at short time-scales (hours to days). This function relies on soil temperature only. Sites in this region are rarely moisture limited and we were unable to find any strong relationship between ER and soil moisture on short time-scales at either site.

Daily values for ΔH^{++} and ΔS^{++} were found by fitting observed ER and soil temperature with a linearized form of Eq. (1) and a one-month moving window, expandable to four months until 200 good half-hourly points were found. We chose this window size so as to obtain a large enough temperature range to form a statistically meaningful fit and adequately cover large gaps. The moving window technique, as described by Falge et al. (2001), allows us to capture seasonal changes in phenology and litter quality. Poor statistical fits of ΔH^{++} and ΔS^{++} were evaluated for significance using a one-tailed t -test at the 90% confidence level. In cases of poor fits, we instead used mean hourly nighttime ER to represent hourly ER for the day. Otherwise, daytime ER was estimated by using daytime soil temperature and the time-varying fitted values of ΔH^{++} and ΔS^{++} .

GEP was computed from the difference between modeled half-hourly ER and observed NEE. To

produce ecosystem scale light response curves and to fill gaps, computed GEP was then fit to a Michaelis–Menton reaction rate equation (Falge et al., 2001; Ruimy et al., 1995):

$$GEP = \frac{b_1 \text{PAR}}{b_2 + \text{PAR}} \quad (3)$$

where PAR is photosynthetic active radiation in $\mu\text{mol m}^{-2} \text{s}^{-1}$, and b_1 and b_2 are the variable parameters of the function. We fitted daytime GEP (ER – NEE) against above canopy PAR to find b_1 and b_2 (one set per day). The same moving window technique and statistical t -test as described for fitting the ER parameters were applied. The moving window technique accounts for seasonal changes in phenology and ecosystem light use efficiency. For poor fits, b_2 was set to zero and b_1 was set to the mean GEP.

3. Results

3.1. Climate

The climate of the region is northern continental, with short, moist growing seasons (June–August) and cold, relatively drier winters. Leaf emergence typically occurs in mid-late May, and leaf fall typically completes by late September/early October. Table 2 shows monthly average air temperature and precipitation for both sites in 2002 and 2003, along with National Climate Data Center (NCDC) cooperative weather observatory 30-year averages from stations near to each site. These data suggest that Sylvania and Willow Creek are in mostly identical climate zones, despite an expectation in increased influence of Lake Superior at Sylvania.

The average annual temperature averaged for both sites was 4.0°C , with January the coldest month (-12.8°C) and July the warmest (18.6°C). On an annual basis, Sylvania was slightly cooler than Willow Creek in both years, primarily due to a colder winter and spring. Temperatures in 2003 were cooler than 2002, especially in the first half of the year, with the exception of May, which was significantly warmer. Growing season and late fall/winter temperatures were similar between the two years. The primary exception was October 2003, which was notably warmer than October 2002.

Table 2
Monthly and annual average air temperature and total precipitation

Month	Sylvania			Willow Creek		
	2002	2003	71-00 average	2002	2003	71-00 average
Average air temperature (°C)						
January	-7.1	-12.9	-12.7	-5.8	-12.5	-12.8
February	-5.9	-13.2	-10.2	-4.3	-11.7	-9.8
March	-7.8	-5.1	-4.1	-6.3	-3.2	-3.9
April	2.4	2.1	3.2	3.8	4.3	3.9
May	7.2	10.6	10.9	8.6	11.6	11.7
June	16.7	14.8	15.8	17.4	16.4	16.3
July	20.5	18.0	18.5	20.9	18.5	18.7
August	17.2	18.7	17.3	18.2	19.7	17.6
September	13.9	12.7	12.6	14.5	13.4	12.7
October	3.1	5.2	6.4	2.9	6.8	6.2
November	-2.9	-2.8	-1.8	-2.4	-1.8	-1.9
December	-6.8	-6.2	-9.1	-5.8	-5.7	-9.7
Annual	4.2	3.5	3.9	5.1	4.7	4.1
Total precipitation (mm)						
January	12	1	36	14	1	31
February	60	15	27	52	15	23
March	82	42	52	87	42	46
April	127	101	53	200	101	60
May	88	100	81	98	107	84
June	104	77	90	79	86	97
July	154	92	81	155	67	101
August	70	38	91	89	42	115
September	128	70	94	134	55	99
October	97	45	73	83	35	68
November	6	68	56	4	41	58
December	1	21	38	0	31	33
Annual	928	670	771	995	625	815

Also shown are 30-year averages of these quantities from the National Climate Data Center (NCDC) cooperative weather observatories in Watersmeet, MI, for Sylvania and Minocqua, WI, for Willow Creek.

Precipitation at both sites was similar in both years, even though on average, Sylvania is slightly drier than Willow Creek, primarily due to lower growing season precipitation. Average annual precipitation averaged across both sites was 793 mm, with 68% falling from May–October. Precipitation from mid November to early April is primarily snow. Annual precipitation in 2002 was significantly above average, with April–July and September–October being significantly wet months. August was drier than average, while November and December were very dry. The dry anomaly at the end of 2002 continued through March 2003. Other than April and May, most months in 2003 were at or below average precipitation. There was a persistent drought from August to October.

Monthly average 5 cm soil temperature showed a similar trend to air temperature (Fig. 2), with 2003 being slightly cooler than 2002. Soil temperatures at Willow Creek were generally higher than Sylvania. Monthly average incoming PAR (Fig. 2) was almost identical at both sites, suggesting that the sites experience similar levels of daytime cloudiness. Both years had similar PAR, with June and October 2003 PAR slightly higher than 2002, and July 2003 slightly lower than 2002.

3.2. Impact of data screening of carbon fluxes

Friction velocity thresholds of 0.325 and 0.3 m s⁻¹ were observed for Sylvania and Willow Creek,

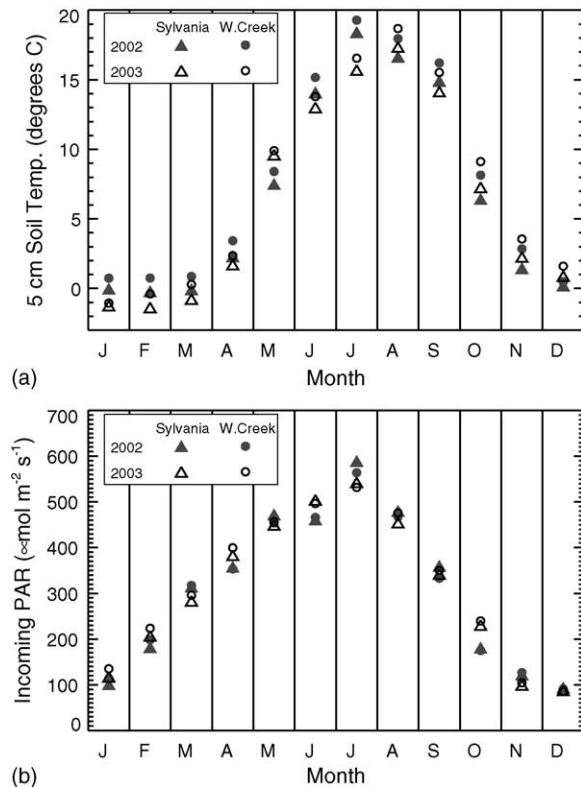


Fig. 2. Monthly average (a) 5 cm soil temperature and (b) total above-canopy incoming photosynthetic active radiation (PAR).

respectively. Nighttime NEE decreased significantly when u^* was below these values, implying weak turbulence and non-1D flow at these sites (i.e., respired carbon flowed to lower lying areas). These thresholds are within range of values seen at other forested eddy flux sites (Falge et al., 2001). Nighttime observations were discarded when u^* fell below these thresholds. The impact of u^* screening was felt mostly in ER, which increased on average by 11% over no screening for Willow Creek and 16% over no screening for Sylvania (Table 3). GEP increased over no screening on average by 4% at Willow Creek and 8% at Sylvania. These results imply more vigorous “drainage” flow at Sylvania and is consistent with an observed steeper and more well-defined slope from the tower to lower lying areas at Sylvania compared to Willow Creek. Daytime low- u^* observations were not discarded, since no NEE difference with u^* was detected and convection can continue to occur during daytime at low u^* .

Data screening arising from filtering of flux measurements with wind direction had a large effect on NEE, ER, and GEP (Table 3). Carbon fluxes from the SE quadrant ($90\text{--}180^\circ$) were screened at Willow Creek due to anomalous venting events not associated with fluxes from the forest ecosystem (Cook et al., 2004). Discarding these abnormally large fluxes (often larger

Table 3
Annual NEE, ER, and GEP as a function of screening criteria

Site	Year	Screening	NEE	ER	GEP	Screen (%)
Sylvania	2002	No screen	-164	693	857	0
		u^* Screen only	-122	823	945	19
		Wind screen only	-119	847	967	16
		All screen	-72	965	1037	30
	2003	No screen	-239	624	863	0
		u^* Screen only	-208	708	916	17
		Wind screen only	-186	780	966	20
		All screen	-147	883	1030	30
Willow Creek	2002	No screen	-228	908	1136	0
		u^* Screen only	-159	1002	1161	16
		Wind screen only	-440	659	1099	13
		All screen	-438	668	1106	29
	2003	No screen	-383	821	1204	0
		u^* Screen only	-347	915	1262	17
		Wind screen only	-477	712	1189	11
		All screen	-490	703	1192	29

Also shown is percentage of data screened for these various criteria.

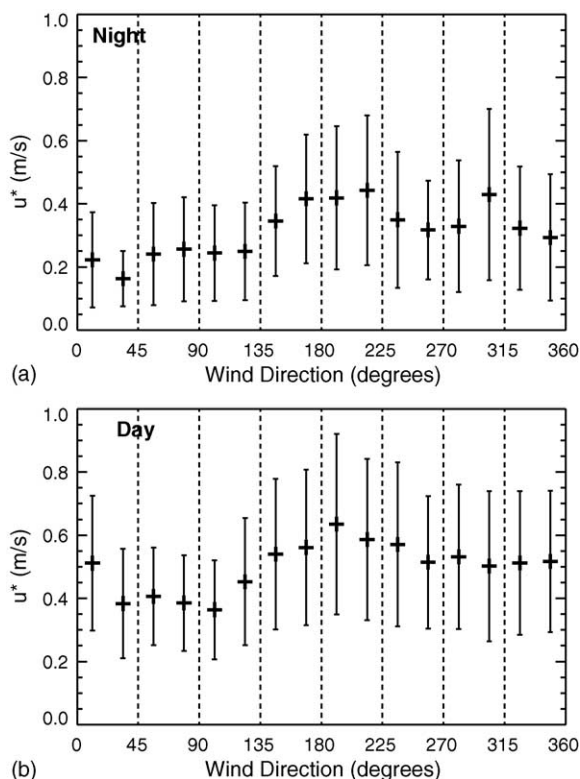


Fig. 3. Variation of u^* with wind direction from June–August at Sylvania for (a) night and (b) day. Data points are mean and standard deviation for 22.5° bins.

than biologically possible) had a large impact on carbon fluxes at Willow Creek (Table 3), primarily on ER. Wind screening reduced ER by 20% and GEP by 2% on average over both years compared to no screening. The impact was larger for 2002 compared to 2003, partly because SE winds were less common in 2003.

Lakes to the north and east of Sylvania appeared to have had an impact on fluxes measured when the wind was from these directions. Fig. 3 shows u^* as a function of wind direction for June–August averaged across 2002 and 2003. Significantly lower than average friction velocity was observed with wind direction from about 30° to 90° of north in daytime. The radial extent of this u^* decline was coincident with the direction of Helen Lake, the closest lake to the Sylvania tower. We assumed that fluxes from this direction were non-representative of the old-growth forest ecosystem we were trying to sample, and screened all flux data when the wind was from 30° to

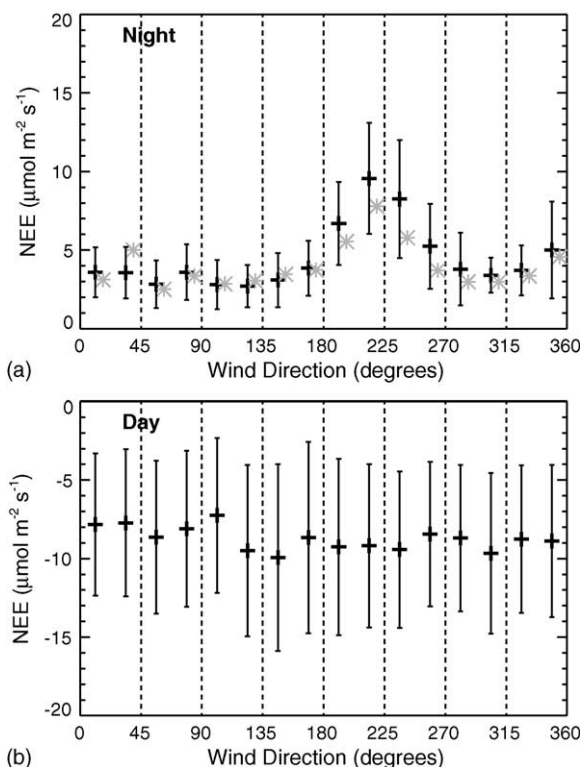


Fig. 4. Variation of NEE with wind direction from June–August at Sylvania for (a) night and (b) day. Data points are mean and standard deviation for 22.5° bins. Gray stars represent same data with temperature correction applied as described in Section 3.2.

90°. This screening did not remove much additional data, since less than 9% of wind directions were between 30° and 90°, and a majority of these data had u^* below 0.325 m s^{-1} .

A plot of Sylvania NEE versus wind direction (Fig. 4) suggests that at night, lakes had a large impact in all directions outside of the SW quadrant (180–270°). Nighttime NEE from the SW was almost twice other directions. This may have been due to warmer synoptic flow from that direction. To assess this claim, the effect of temperature on nighttime NEE was removed by using a simple exponential model:

$$\text{ER}_{15} = \text{ER}_T e^{\beta[15-T]} \quad (4)$$

where ER_T is ecosystem respiration (nighttime NEE), ER_{15} the ecosystem respiration at 15 °C, T the nighttime 5 cm soil temperature, and β is the respiration–temperature sensitivity parameter. β was computed by fitting observed nighttime NEE to T and was found to

be 0.8. Fig. 4 shows that nighttime NEE remained variable with wind direction after this temperature correction. Thus, neither u^* nor temperature variability with wind direction can completely explain the observed variability in NEE with wind direction.

Footprint climatology and land cover analysis showed that nighttime bin-averaged temperature-corrected ER_{15} was correlated ($r^2 = 0.8$) with the percent of forest within the flux footprint. Lakes within the flux footprint tended to reduce ER_{15} by a magnitude similar to the amount of lake in the footprint. Footprint analyses also showed that typical footprints had a 90% inclusion contour of around 1 km. At that range, the southwest direction was the least contaminated by lakes and had the footprint with the largest amount of wilderness.

However, the small wetlands ~ 800 m to the southwest of the flux tower (described in Section 2.1.1) could have been acting as an anomalous respiration source. CO_2 measurements made on several nights in the wetlands suggest that the wetlands did not have anomalously high nighttime CO_2 concentrations (which would imply high ER) compared to measurements near the tower. Additionally, lake temperature measurements made on several nights in the summer at Helen Lake showed that the lake was typically much warmer than the air at night, suggesting that the lake could have been producing buoyant thermals that were venting respired forest CO_2 prior to reaching the flux tower. This type of effect (horizontally advected CO_2 converging at a warm lake and then venting vertically) was evidenced during the BOREAS experiment by Sun et al. (1998). The authors speculated that this effect caused lower than expected flux measurements at a nearby tower. This effect is also consistent at Sylvania with the appearance of the low NEE anomaly only at night and only in the summer. Finally, initial results from scaled soil and stem efflux measurements suggest that larger fluxes to the SW are more representative of ecosystem ER (Tang et al., in preparation).

Thus, we speculate that air mass modification by the presence of lakes occurred, especially at night when footprints can be large in lateral extent. We assumed that the nighttime CO_2 fluxes measured in the southwest direction were representative of the stand-scale integrated ER, whereas nighttime CO_2 fluxes from other directions were diluted by the presence of

lakes. We decided to screen June–October nighttime NEE data when the wind was not between 180° and 270° , removing around half of the nighttime growing season data. No strong variation in observed NEE was seen in the daytime or outside the June–October timeframe. The effect of wind screening on carbon fluxes was large (Table 3). Compared to no screening, wind directional screening increased ER by 24% when averaged over both years. GEP also increased by 12%.

The net effect of u^* and wind screening was to make Willow Creek a larger net carbon sink by 60% and make Sylvania a smaller net carbon sink by 47% on average over both years. Screening had a greater impact at both sites in 2002 compared to 2003. The results did not significantly alter NEE or GEP comparisons between the two sites, but it did complicate the comparison of ER. However, we believe that the choices made for screening of systematic errors were based on rigorous analysis and observation.

Uncertainty in NEE, ER, and GEP caused by both missing data and removing screened data was computed with a Monte Carlo simulation as described in Section 2.6. The results showed that modeled annual NEE was able to reproduce total annual NEE to within 4%, giving confidence in our gap-filled methodology. Table 4 documents the annual total and standard deviation of annual totals from the Monte Carlo experiment for NEE, ER, GEP at each site for each year. The average uncertainty in annual NEE computed with this method was $\pm 44 \text{ g C m}^{-2} \text{ year}^{-1}$. We used the uncertainties shown in Table 4 for assessing the significance of differences in NEE, ER, and GEP between the two sites and between the two years.

3.3. Net ecosystem exchange of CO_2

Negative total monthly NEE (net biospheric uptake) occurred from June to August at both sites

Table 4
Annual NEE, ER, GEP, and estimate of uncertainty caused by gap-filling for each using the Monte Carlo analysis

Site	Year	NEE	ER	GEP
Sylvania	2002	-72 ± 36	965 ± 35	1037 ± 47
	2003	-147 ± 42	883 ± 69	1030 ± 41
Willow Creek	2002	-438 ± 49	668 ± 21	1106 ± 51
	2003	-490 ± 48	703 ± 17	1192 ± 51

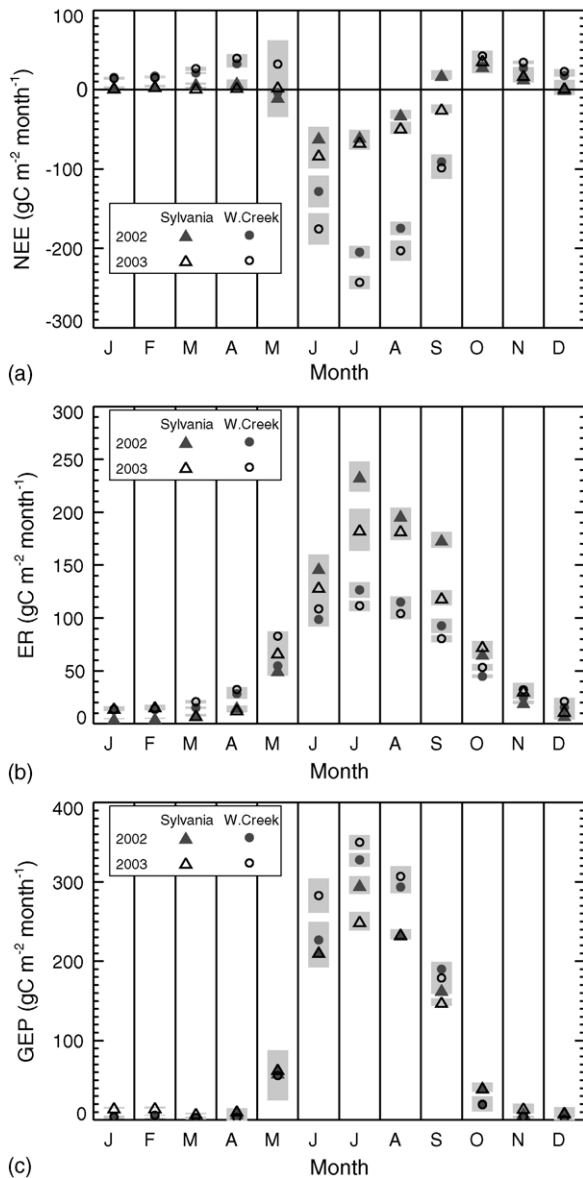


Fig. 5. Total monthly (a) NEE, (b) ER, and (c) GEP. Gray boxes represent uncertainty in these values.

in both years (Fig. 5a). Small negative NEE also occurred in September except for Sylvania in 2002. Willow Creek was a significantly larger sink of carbon dioxide during the growing season than Sylvania in both years. For both sites, uptake was slightly larger in 2003 than 2002, but the difference at Sylvania was smaller than the uncertainty for June and July. Maximum total monthly negative NEE

occurred in June for Sylvania and July for Willow Creek. Sink strength steadily declined from late July to September. Late fall NEE at both sites was similar, but winter NEE was slightly larger (bigger source) at Willow Creek than Sylvania, especially in March and April. At both sites, there was no significant difference in late fall or winter NEE between 2002 and 2003.

Weekly cumulative NEE plotted in Fig. 6a shows steadily increasing cumulative NEE from January to mid-May, and a steady decline until September. In both sites in both years, the switch from increasing cumulative NEE to decreasing cumulative NEE occurred in mid-May. However, since Willow Creek was a larger winter source of NEE, the peak maximum cumulative NEE was larger than Sylvania. January to April cumulative NEE release rates were $5.9 \text{ g C m}^{-2} \text{ month}^{-1}$ in 2002 and $2.5 \text{ g C m}^{-2} \text{ month}^{-1}$ in 2003 for Sylvania and $19.5 \text{ g C m}^{-2} \text{ month}^{-1}$ in 2002 and $21.4 \text{ g C m}^{-2} \text{ month}^{-1}$ in 2003 for Willow Creek. Growing season (June–August) NEE uptake rates were $-46.3 \text{ g C m}^{-2} \text{ month}^{-1}$ in 2002 and $-59.4 \text{ g C m}^{-2} \text{ month}^{-1}$ in 2003 for Sylvania, which were significantly smaller than rates of $-186.5 \text{ g C m}^{-2} \text{ month}^{-1}$ in 2002 and $-223.1 \text{ g C m}^{-2} \text{ month}^{-1}$ in 2003 observed at Willow Creek. Maximum negative cumulative NEE occurred in late September for Willow Creek, whereas for Sylvania, the maximum occurred in early to mid-September and remained at a minimum through the rest of the month before increasing again in October. At both sites, the summer uptake rate was slightly larger in 2003 than 2002. The data also show that the length of the growing season was similar in both years and at both sites. Fall (October–November) NEE release rates were slightly higher at Willow Creek than Sylvania, and 2003 NEE was slightly larger than 2002, as expected given the summer uptake rates. Annual NEE at Sylvania was $-72 \pm 36 \text{ g C m}^{-2} \text{ year}^{-1}$ in 2002 and $-147 \pm 42 \text{ g C m}^{-2} \text{ year}^{-1}$ in 2003, while for Willow Creek, it was $-438 \pm 49 \text{ g C m}^{-2} \text{ year}^{-1}$ in 2002 and $-490 \pm 48 \text{ g C m}^{-2} \text{ year}^{-1}$ in 2003. Uncertainty analysis results make it difficult to differentiate annual NEE in 2002 from 2003 (Table 4).

3.4. Ecosystem respiration

Nighttime NEE to soil temperature response curves are plotted in Fig. 7a. These curves are for all data

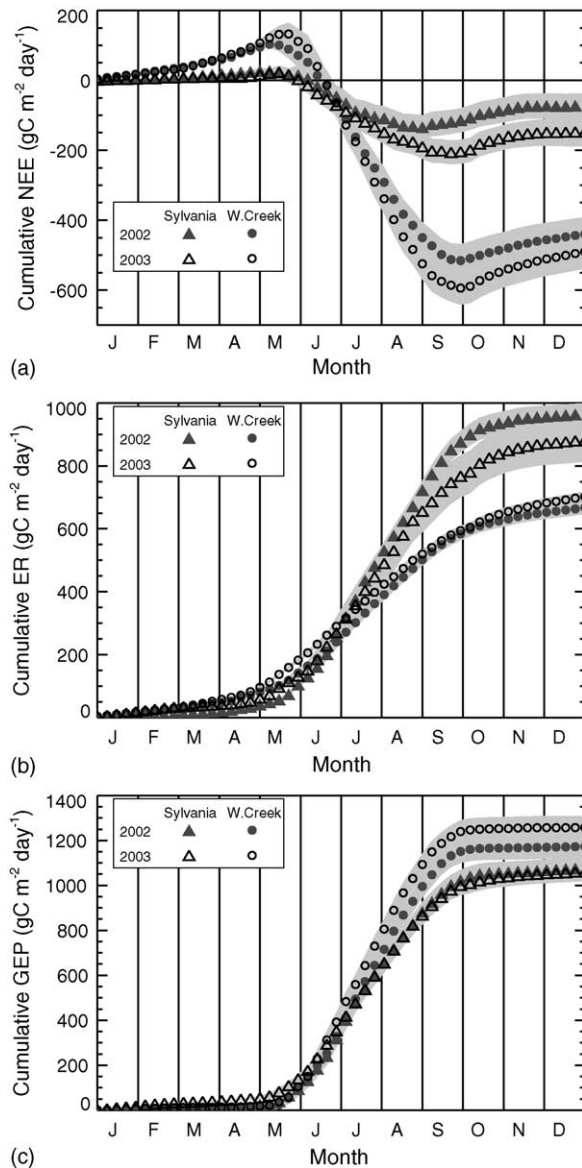


Fig. 6. Weekly cumulative (a) NEE, (b) ER, and (c) GEP. Gray background represents uncertainty in the cumulative values.

from May to October. While the gap-filling algorithm used a one-month moving window for computing ER, the curves shown in Fig. 5a represent the average response curve for the entire growing season. At Willow Creek, the soil temperature to ER relationship did not significantly change from 2002 to 2003. However, at Sylvania, there was significantly smaller ER in 2003 compared to 2002 for soil temperatures

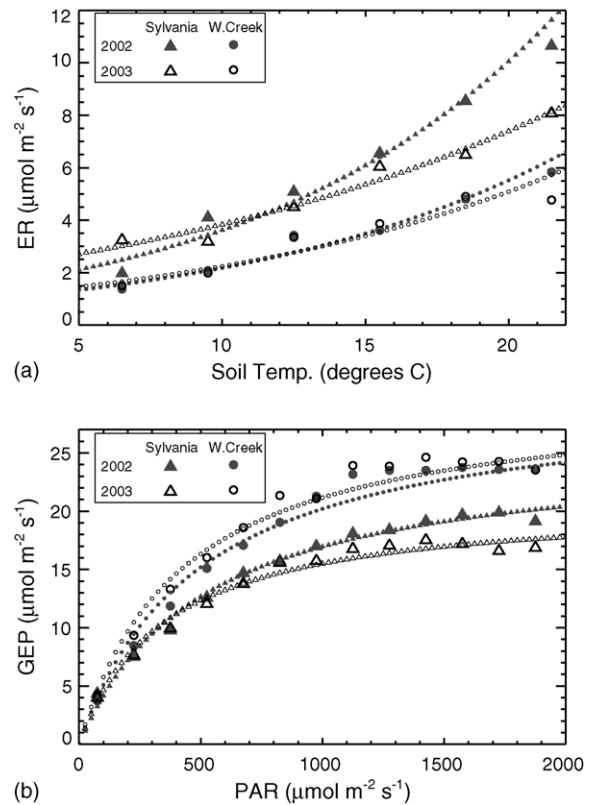


Fig. 7. Response of (a) nighttime NEE to 5 cm soil temperature for May–October and (b) GEP to PAR from June to August. Observations were binned using 3 °C intervals for soil temperature and 150 μmol m⁻² s⁻¹ intervals for PAR. Fits were computed using the equations described in Section 2.7.

above 15 °C. Sylvania ER is greater than Willow Creek for all temperatures above 5.0 °C in both years. The data suggest that while the respiration base rate at Sylvania is greater than Willow Creek, the slope of the response curves are roughly similar. The ratio of ER from 20 to 10 °C (Q_{10}) was found to be 2.8 in 2002 and 1.9 in 2003 at Sylvania and 2.5 in 2002 and 2.3 in 2003 at Willow Creek, similar to typical Q_{10} value of 2.0 observed for forests (Ryan, 1991). Q_{10} at both sites decreased from 2002 to 2003, suggesting a coherent response to change in growing season climate; however, the change at Willow Creek was small.

ER at Sylvania was much larger than Willow Creek from June to October in both years (Fig. 5b); however, the uncertainty is larger than the difference for June. ER peaks at both sites in June and steadily declines afterwards. ER from June to September was smaller in

2003 compared to 2002 at both sites. This difference between years was much larger at Sylvania than Willow Creek, suggesting that Sylvania ER was more sensitive to climate than Willow Creek ER. ER was greater in October 2003 than 2002, reflective of the warm conditions during that month. Winter ER was slightly larger at Willow Creek, especially in March and April, and winter 2003 had slightly higher ER than 2002 at both sites. Cumulative ER plots (Fig. 6b) show that Willow Creek had a slightly larger ER release rate in early winter, but was greatly eclipsed by Sylvania after May. Sylvania cumulative ER surpassed Willow Creek by mid-August. June–August release rates of ER were $219.7 \text{ g C m}^{-2} \text{ month}^{-1}$ in 2002 and $185.1 \text{ g C m}^{-2} \text{ month}^{-1}$ in 2003 for Sylvania, which were much larger than rates of $123.3 \text{ g C m}^{-2} \text{ month}^{-1}$ in 2002 and $111.4 \text{ g C m}^{-2} \text{ month}^{-1}$ in 2003 for Willow Creek. Both sites had similar ER release rates in the fall (October–November), and both had larger fall ER release rates in 2003 than 2002. Annual ER at Sylvania was larger than Willow Creek in both years, but uncertainty analysis precludes differentiation of annual ER in 2002 from 2003 (Table 4). Annual ER at Sylvania was $965 \pm 35 \text{ g C m}^{-2} \text{ year}^{-1}$ in 2002 and $883 \pm 69 \text{ g C m}^{-2} \text{ year}^{-1}$ in 2003, while it was $668 \pm 71 \text{ g C m}^{-2} \text{ year}^{-1}$ and $703 \pm 17 \text{ g C m}^{-2} \text{ year}^{-1}$ at Willow Creek.

3.5. Gross ecosystem production

GEP, computed by subtracting NEE from modeled ER, was found to be strongly correlated with above-canopy incoming PAR (Fig. 7b). Response curves shown in Fig. 7b are for June to August. GEP at Sylvania was smaller than Willow Creek for all PAR above $300 \mu\text{mol m}^{-2} \text{ s}^{-1}$, with a maximum GEP at saturating irradiance (A_{max} , averaged over 1500–2000 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ PAR) of $19.4 \mu\text{mol m}^{-2} \text{ s}^{-1}$ in 2002 and $17.2 \mu\text{mol m}^{-2} \text{ s}^{-1}$ in 2003 at Sylvania, which were smaller than A_{max} values of $23.6 \mu\text{mol m}^{-2} \text{ s}^{-1}$ in 2002 and $24.2 \mu\text{mol m}^{-2} \text{ s}^{-1}$ in 2003 at Willow Creek. A_{max} values did not significantly change at Willow Creek from 2002 to 2003, whereas Sylvania A_{max} had a substantial decrease. Ecosystem quantum yield, defined here as the slope of GEP to PAR from 0 to $500 \mu\text{mol m}^{-2} \text{ s}^{-1}$, was smaller for Sylvania (2002/2003 average of $25.1 \text{ mmol CO}_2 \text{ mol}^{-1} \text{ PAR}$) than Willow Creek

($31.5 \text{ mmol CO}_2 \text{ mol}^{-1} \text{ PAR}$). There were no significant differences in quantum yield between 2002 and 2003 at either site.

Sylvania monthly average GEP was slightly higher than Willow Creek in the winter (Fig. 5c), especially in 2003, possibly due to photosynthesis occurring by the coniferous hemlock. Willow Creek had higher GEP than Sylvania from June to September. October–November GEP was somewhat higher at Sylvania, once again most likely due to the presence of hemlock. Peak GEP occurred in July for both sites. Summer GEP was higher in 2003 compared to 2002 for Willow Creek; however, the difference is only greater than uncertainty for July. Sylvania, on the other hand, had similar or lower GEP in summer 2003 compared to 2002. Cumulative GEP (Fig. 6c) showed that within the range of uncertainty, it was difficult to differentiate annual GEP at Willow Creek from Sylvania in 2002, although Willow Creek appears to be slightly larger. In 2003, Willow Creek cumulative GEP is higher than Sylvania, with divergence starting in July. In both years, increased October and November GEP at Sylvania allowed Sylvania to get closer to Willow Creek total GEP by late fall. Annual GEP for Sylvania was $1037 \pm 47 \text{ g C m}^{-2} \text{ year}^{-1}$ in 2002 and $1030 \pm 41 \text{ g C m}^{-2} \text{ year}^{-1}$ in 2003 and for Willow Creek was $1106 \pm 47 \text{ g C m}^{-2} \text{ year}^{-1}$ in 2002 and $1192 \pm 51 \text{ g C m}^{-2} \text{ year}^{-1}$ in 2003.

3.6. Partitioning between GEP and ER

Even though there were larger differences in ER and GEP at Sylvania between the growing seasons 2002 and 2003 compared to Willow Creek (Fig. 5), the monthly GEP:ER ratio was more variable between years at Willow Creek (Fig. 8). Since GEP and ER are small in winter, we believe the GEP:ER ratio outside of the growing season is subject to larger uncertainty. The reason for the larger change in GEP:ER ratio at Willow Creek compared to Sylvania was because Willow Creek summer ER had a small decrease, whereas summer GEP at Willow Creek increased. Sylvania summer ER and GEP both decreased slightly from 2002 to 2003. June–August GEP:ER increased at both sites from 2003 compared to 2002. At Willow Creek, it was 2.5 in June–August 2002 and 2.9 in 2003, whereas for Sylvania it was 1.3 in 2002 and 1.4 in 2003. On an annual basis, GEP:ER ratio in both years was very similar. At Willow Creek, it

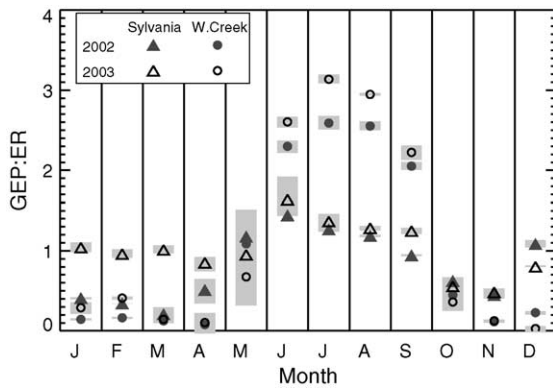


Fig. 8. Monthly average GEP:ER ratio.

was 1.7 in both years, and at Sylvania, it was 1.1 in 2002 and 1.2 in 2003.

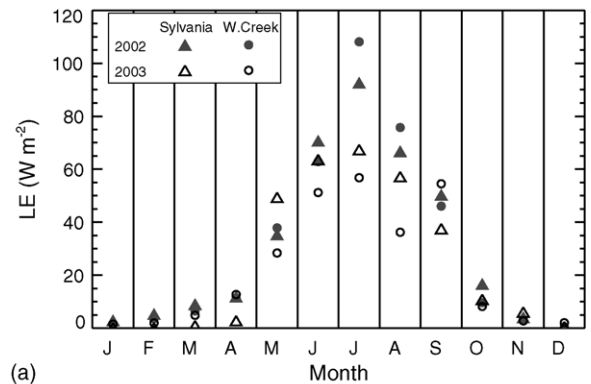
3.7. Evapotranspiration

Mean monthly latent heat fluxes are shown in Fig. 9a. Evapotranspiration peaked in July and in general was much larger in 2002 compared to 2003 at both sites. The decline of latent heat flux from 2002 to 2003 was more pronounced at Willow Creek than Sylvania. Similarly, monthly water use efficiency (WUE) (ratio of GPP:transpiration) has a larger increase from 2002 to 2003 at Willow Creek compared to Sylvania (Fig. 9b). Growing season WUE averaged to around $0.1 \mu\text{mol J}^{-1}$, except for June and August 2003 at Willow Creek, where it was closer to $0.14 \mu\text{mol J}^{-1}$.

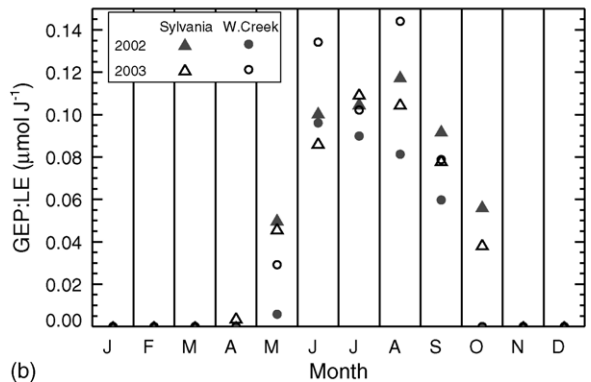
4. Discussion

4.1. Old-growth carbon sink

Sylvania was a small carbon sink, significantly different than zero, regardless of screening criteria in both years. This result is consistent with the finding from most older forest sites in the Fluxnet network, which have shown small to moderate carbon sinks (e.g., Griffis et al., 2003; Hollinger et al., 1994; Knohl et al., 2003; Malhi et al., 1999). Increases in growing season length due to climate warming, carbon dioxide fertilization due to fossil fuel emissions, nutrient fertilization due to nitrogen deposition, or small-scale disturbance are all possible explanations for carbon



(a)



(b)

Fig. 9. Mean monthly (a) average latent heat flux and (b) GEP:LE ratio.

sinks in old-growth forests. The reason for a carbon sink at Sylvania is not known. It is also unknown to what extent the tower measurements were representative of carbon fluxes for all old-growth forest in the Sylvania Wilderness. Footprint analyses suggest that the tower sampled a representative mix of old-growth hemlock and maple forest that is characteristic of the region.

Law et al. (2003) argue that the existence of a small carbon sink in an old-growth ponderosa pine forest may be caused by small-scale disturbances creating dense tree growth in canopy gaps that are smaller than the spatial scale of flux measurements. Additionally, Saleska et al. (2003) argue from observations at old-growth forests in the Amazon that small-scale disturbances may create small “hotspots” that are large sources of carbon, while most of the region outside these disturbances remains a small sink. This would imply that, given the low disturbance frequency rates observed around Sylvania: (1) measurements

made at an individual tower may not necessarily be representative of regional scale fluxes, and (2) regional scaling of carbon fluxes would require fine spatial detail resolution of disturbance history and stand age.

The WLEF television station tall (436 m) eddy flux tower in Park Falls, WI, samples a large footprint of mixed forest (of a range of stand ages, mostly 60–80 years old) and wetlands across northern Wisconsin. This site has shown a consistent small source of CO₂ to the atmosphere since 1997 (Davis et al., 2003), possibly due to the effect of disturbance and forest management in the region. These results suggest that quantifying regional scale carbon fluxes and the influence of disturbance on it from eddy flux towers in the ChEAS region requires a denser network of sites and/or a combination of novel techniques, measurements, modelling, and remote sensing.

4.2. Comparison of old growth to mature carbon fluxes

Over two years, total NEE of CO₂ at Sylvania was $24 \pm 11\%$ of the total NEE observed at Willow Creek. This result provides strong evidence that the old-growth site was a significantly smaller carbon sink than the mature site. This difference in NEE existed despite the similarity of the two sites in location, temperature, precipitation, cloudiness, growing season length, soil type, and pre-European settlement composition. The primary differences between the two sites were time since last disturbance and consequently, successional stage and species composition. Although other unaccounted factors (e.g., soil carbon stock) may be also different between the two sites, we believe that stand age and succession stage are the fundamental differences. The difference in species composition led to lower LAI (~30% smaller) at Sylvania compared to Willow Creek.

The primary cause of the smaller carbon sink strength at Sylvania compared to Willow Creek over the two years was larger ER at Sylvania, which in sum over two years was $134 \pm 12\%$ of ER at Willow Creek. This is in contrast to GEP at Sylvania, which was $90 \pm 8\%$ of GEP at Willow Creek. The hypothesis that ER explains the primary differences in NEE between the two sites was confirmed for 2002, but inconclusive for 2003, where the difference in sink strength was caused almost equally by larger ER and

smaller GEP at Sylvania compared to Willow Creek. We found that the larger ER at Sylvania than Willow Creek was not necessarily due to a larger ER-temperature sensitivity (Q_{10}), but because of a larger base respiration rate. This finding is consistent with the idea that larger ER at old-growth forests occurs due to greater amounts of coarse woody debris and larger tree biomass. Sylvania had considerably more CWD than Willow Creek. Initial scaled component and chamber respiration measurements suggest that Willow Creek combined soil and stem efflux is roughly similar or even slightly larger than Sylvania (Bolstad et al., 2004; Tang et al., in preparation). Thus, we speculate that CWD respiration at Sylvania was the primary cause of increased ER. Comparison of scaled chamber flux ER between the two sites is difficult, since Willow Creek chamber ER was much greater than eddy covariance measured ER (Bolstad et al., 2004), whereas initial Sylvania chamber flux scaled ER results appear to be roughly similar to eddy covariance ER. Thus, more work is needed to verify our conclusion that ER explains the primary difference in NEE.

Systematic errors arising from screening of non-representative fluxes also complicate these results. If we chose not to screen non-representative fluxes at either site, then ER would have been larger at Willow Creek compared to Sylvania (Table 3). Thus, quantifying fluxes at these sites require a better understanding of the spatial pattern of nighttime ER in the vicinity of the tower.

GEP between the two sites was almost undistinguishable, given the range of uncertainty, in 2002. Willow Creek GEP increased in 2003 compared to 2002, leading to a more pronounced difference in GEP between the two sites. Although annual GEP was only slightly lower at Sylvania than Willow Creek, average June–August A_{\max} values at Sylvania were significantly lower than Willow Creek. The smaller than expected difference in GEP exists due to higher GEP at Sylvania in the spring and especially in the fall, presumably from the presence of coniferous species at Sylvania. Nevertheless, lower total GEP, lower quantum yield/light use efficiency, and lower A_{\max} at Sylvania were all indicative of overall lower productivity of old-growth stands. We believe that the lower productivity in the growing season is primarily due to lower LAI and different species composition.

Another hypothesis for a mechanism of lower GEP at old-growth sites is that hydraulic limitation reduces photosynthetic potential of larger and older trees (Ryan et al., 2004). If this were the case, we might expect transpiration fluxes or WUE would be lower in old-growth forests compared to younger forests. Results from a comparison of evapotranspiration at Willow Creek and Sylvania were inconclusive on this point. Fig. 9a shows that mean monthly latent heat fluxes in the growing season were lower at Sylvania than Willow Creek in July–September of 2002 and September of 2003, but the opposite was observed in June 2002 and May–August of 2003. Ecosystem WUE (ratio of GEP:LE) also had similar patterns (Fig. 9b). Thus, we believe that the primary reason for lower GEP at Sylvania was lower photosynthetic capacity of old-growth species and not hydraulic limitation. Initial leaf-level photosynthesis measurements appear to support this conclusion (Kreller, L., personal communication).

On an annual basis, GEP:ER ratio at each site was the same for both years, suggesting that this may continue to remain similar with time in the near future. The GEP:ER ratio at Sylvania (1.2) was 29% smaller than Willow Creek (1.7). Both sites had GEP:ER ratios typical of those found in other forests evergreen and deciduous sites in North America, which ranged from 0.87 to 2.1 (Falge et al., 2002). We speculate, based on the evidence presented here, that the GEP:ER ratio at Willow Creek, and consequently NEE, will eventually decline as the forest ages, unless affected by disturbance or management.

4.3. Comparison of 2002 to 2003

Annual totals of NEE, ER, and GEP could not be differentiated between 2002 and 2003 within the range of uncertainty at either site even though 2003 was slightly colder and significantly drier than 2002. However, there were some significant increases in monthly NEE at both sites during the growing season. Both sites had a small increase in NEE in 2003 compared to 2002. At Sylvania, this was because growing season ER declined in 2003 compared to 2002 more than GEP did. At Willow Creek, growing season GEP slightly increased, while ER slightly declined. Thus, in response to climate variability,

carbon sink strength at the old and mature sites both increased; however, they did so for different reasons.

The cause of significantly reduced ER at Sylvania over the growing season of 2003 compared to 2002 appears to be a combination of cooler growing season temperatures and a smaller ER to temperature sensitivity (Q_{10}). While late growing season ER at Willow Creek was smaller in 2003 compared to 2002, annual ER at Willow Creek increased in 2003 even though ER to temperature sensitivity did not significantly change and temperatures were overall cooler. Annual ER increased because of increased ER in May, June, and October. May and October 2003 were warmer than 2002. Although Sylvania ER was also larger in May and October, this larger ER was masked by the significantly decreased ER to temperature sensitivity during the growing season.

Saleska et al. (2003) argued that old-growth Amazonian forests had larger carbon uptake during the dry season due to inhibited respiration and increased incoming radiation. We suspect that the larger change in ER and ER sensitivity at Sylvania was possibly due to the effect of dry conditions inhibiting respiration from CWD and stems. Aboveground respiration, in general, is less insulated from the effects of dry conditions than the soil efflux. Since there was very little CWD at Willow Creek, we might expect not to observe as large an effect at Willow Creek. It may also be the case that hemlock autotrophic respiration was more significantly affected by drought. Component flux measurements will help refine our analyses (Tang et al., in preparation).

We found that growing season GEP at Sylvania declined in 2003 compared to 2002. We suspect dry conditions inhibited carbon uptake by overstory trees. Fig. 9 shows that both latent heat fluxes and WUE were lower in 2003 after July as the drought progressed. However, GEP in fall 2003 was larger than fall 2002, presumably due to warmer temperatures allowing hemlock photosynthesis to continue. The net effect was that annual GEP in 2003 at Sylvania was nearly identical to GEP in 2002.

GEP increased at Willow Creek, even though growing season latent heat fluxes were significantly reduced from 2003 to 2002, by an even larger magnitude that Sylvania (Fig. 9a). Consequently, WUE increased at Willow Creek in 2003 compared to

2002 over the growing season (Fig. 9b). We are unsure of the reason for increased GEP during dry conditions at Willow Creek.

Because GEP increased while ER decreased at Willow Creek during the growing season, the summer GEP:ER ratio significantly changed from 2002 to 2003 (Fig. 8). Thus, while Sylvania had larger variability in ER from one year to the next, Willow Creek had larger variability in growing season GEP:ER. Overall, the results are inconclusive on whether Sylvania's annual carbon sink strength is more sensitive to annual climate variability than Willow Creek. Results were also inconclusive as to whether NEE, GEP, and ER interannual trends were coherent between the two sites. While growing season interannual trends at the two sites were similar, these trends were smaller than the range of uncertainty. More years of measurements will help improve our conclusions.

4.4. Comparison to other studies

The number of eddy covariance measurements in old-growth forests is increasing. However, there are few published multiple site, multiple stand age whole ecosystem carbon flux studies. Several studies from North America are reviewed below and compared to results found at our study site.

Biometric and chamber flux-based NEE measurements made at a chronosequence of ponderosa pine (*Pinus ponderosa*) forest ranging from 9 to >300 years old in Metolius, Oregon, USA, showed the highest carbon uptake in mature (95–106 years old) stands ($-170 \text{ g C m}^{-2} \text{ year}^{-1}$), lowest carbon uptake in old-growth (190–216 years old) stands ($-35 \text{ g C m}^{-2} \text{ year}^{-1}$), moderate uptake in young (56–89 years old) stands ($-118 \text{ g C m}^{-2} \text{ year}^{-1}$), and large carbon release in recently initiated (9–23 years old) stands ($124 \text{ g C m}^{-2} \text{ year}^{-1}$) (Law et al., 2003). The old stands had an average NEE that was 30% of the mature stands, similar to what was observed between Sylvania and Willow Creek (24%). The researchers found that there was rapid increase in total ecosystem carbon storage until forests were about 200 years old, with little or no decline in carbon storage at older sites. Little or no stand age variation was found for heterotrophic respiration. Instead, declines in above and below ground NPP explained the weaker carbon

sink in old forests compared to mature forests (Law et al., 2003).

Portable eddy flux systems were deployed for short time periods in four young and mature boreal forests (11, 19, 36, and 70 years old) sites in Northern Manitoba, Canada, and were compared to continuous carbon flux measurements at an old-growth site (130 years old) (Litvak et al., 2003). The researchers found that ER increased with stand age. Extrapolated annual NEE showed that carbon uptake increased with age up to 36 years and then declined to zero uptake in the old-growth site. The authors argue that increased respiration in older stands was due to greater autotrophic respiration and decomposition of CWD. Decreased carbon uptake in older stands also occurred due to lower canopy photosynthesis rates, as leaf area declined and species composition changed. These results corroborate the results from Sylvania and Willow Creek.

Growing season (July–September) eddy covariance measurements at Douglas-fir (*Pseudotsuga menziesii*) forests in Oregon, USA, of 20-, 40-, and 450-year-old stands showed that all three sites were net carbon sinks (Chen et al., 2004). The 40-year-old site was the largest sink, followed by the 450-year-old site, and then the 20-year-old site. The old-growth site exhibited large interannual variability, being a moderate carbon source during a dry summer and a significant carbon sink in the following, significantly moister year. The authors suggest that the old-growth site may continue to exhibit large interannual variability in NEE.

Contrary to the studies mentioned above, a study in eastern North America showed a carbon sink that was larger in old-growth than nearby mature forests. This old-growth (200-year-old) eastern hemlock forest in central Massachusetts, USA, reported NEE from October 2000 to October 2001 of $-295 \text{ g C m}^{-2} \text{ year}^{-1}$, significantly larger than Sylvania (Hadley and Schedlbauer, 2002), even though the overstory vegetation is similar. This contrasts to the Harvard Forest mature (60-year-old) deciduous mixed broad-leaf forest in central Massachusetts, which had an NEE in between -120 and $-280 \text{ g C m}^{-2} \text{ year}^{-1}$ between 1991 and 2000 (Barford et al., 2001; Goulden et al., 1996; Wofsy et al., 1993). Also, a 90-year-old red spruce/eastern hemlock/Douglas fir boreal forest in Howland, ME, had an NEE in 1996 of $-210 \text{ g C m}^{-2} \text{ year}^{-1}$ (Hollinger et al., 1999).

In general, these and other studies corroborate the results found at Sylvania and Willow Creek. Except for the hemlock site in Massachusetts, older growth stands had smaller carbon sinks than mature and young stands. Both increased ER and decreased GEP explained this difference at the various sites. Increased ER was most likely due to increased autotrophic respiration and/or increased CWD decomposition. Decreased GEP occurred due to lower LAI, changes in species composition, and/or hydraulic limitations. Results were generally inconclusive on which stand age sites had the greatest sensitivity of NEE to climate variability.

5. Conclusion

Our study encompassed observations of eddy covariance fluxes of whole ecosystem carbon dioxide and water vapor exchange over two years at an old-growth (>300 year) eastern hemlock/northern hardwood old-growth and 70-year-old northern hardwood mature site in the upper Midwest, USA. We found that:

1. Non-representative carbon fluxes due to landscape heterogeneity or anomalous micrometeorological conditions required careful consideration. In this case, a simple wind direction screening was found to be sufficient for both sites.
2. The old-growth site was a small sink of carbon, similar to what has been seen at other old-growth sites, but contrary to theoretical assumptions of carbon balance.
3. Carbon sink strength at the mature site was three to four times larger than the old-growth sites over two years of measurements. GEP:ER ratios were 30% larger at the mature site. Both sites had similar composition prior to European settlement and near identical climate over the two years.
4. The primary cause of decreased NEE in 2002 was higher ER at the old-growth site, whereas both higher GEP at the mature site and higher ER at the old-growth site explained the NEE difference in 2003. ER to soil temperature sensitivity was generally similar at both sites, but ER base rates were larger at the old-growth site. These results were sensitive to choices of screening non-representative carbon fluxes. We believe that increased CWD respiration and/or autotrophic respiration may be the primary mechanisms. However, scaled chamber flux measurements suggest that ER at the old site was similar or lower than the mature site. Thus, this finding is inconclusive, and more work is needed to constrain ER at both sites.
5. Summer GEP was slightly higher at the mature site than the old-growth site, especially in 2003. Annual GEP between sites could not be differentiated within the range of uncertainty in 2002. We believe that the lower growing season GEP at the old-growth site was caused mainly by lower photosynthetic capacity (A_{\max}) due to lower LAI and different species composition, which countered the effect of the longer growing season for hemlock.
6. The climate of 2003 was cooler and drier than 2002, but the changes in annual NEE, ER, and GEP between the two years at either site were smaller than the uncertainty in these values. However, it appeared that growing season NEE, ER, and GEP were affected by dry conditions in late summer 2003. At both sites, growing season carbon uptake was larger in 2003. This larger uptake occurred at the old-growth site due to smaller ER in 2003 over 2002, arising from decreased ER to soil temperature sensitivity. At the mature site, greater carbon uptake was due mainly to larger GEP. We were unable to conclude which site had overall greater sensitivity in NEE, ER, and GEP to climate variability.
7. Other multi-site studies have typically shown a similar trend of declining carbon uptake with stand age. Together, these results are part of a growing consensus that forest stand age and site disturbance history are important determinants of whole ecosystem carbon uptake over time-scales of decades to centuries.

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