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Influence of vegetation and seasonal forcing on carbon dioxide fluxes across the Upper Midwest, USA: Implications for regional scaling

Ankur R. Desai[a,*], *Asko Noormets*[b], *Paul V. Bolstad*[c], *Jiquan Chen*[d], *Bruce D. Cook*[c], *Kenneth J. Davis*[e], *Eugenie S. Euskirchen*[f], *Christopher Gough*[g], *Jonathan G. Martin*[h], *Daniel M. Ricciuto*[i], *Hans Peter Schmid*[j], *Jianwu Tang*[k], *Weiguo Wang*[l]

[a] *University of Wisconsin, Department of Atmospheric & Oceanic Sciences, Madison, WI, USA*
[b] *North Carolina State University, Department of Forestry and Environmental Resources, Raleigh, NC, USA*
[c] *University of Minnesota, Twin Cities, Department of Forest Resources, St. Paul, MN, USA*
[d] *University of Toledo, Department of Environmental Sciences, Toledo, OH, USA*
[e] *The Pennsylvania State University, Department of Meteorology, University Park, PA, USA*
[f] *University of Alaska, Fairbanks-Institute of Arctic Biology, Fairbanks, AK, USA*
[g] *Ohio State University, Department of Evolution, Ecology and Organismal Biology, Columbus, OH, USA*
[h] *Oregon State University, Department of Forest Science, Corvallis, OR, USA*
[i] *Oak Ridge National Laboratory, Oak Ridge, TN, USA*
[j] *Indiana University, Department of Geography, Bloomington, IN, USA*
[k] *Chicago Botanic Garden, Glencoe, IL, USA*
[l] *Pacific Northwest National Laboratory, Richland, WA, USA*

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ABSTRACT

Carbon dioxide fluxes were examined over the growing seasons of 2002 and 2003 from 14 different sites in Upper Midwest (USA) to assess spatial variability of ecosystem–atmosphere CO_2 exchange. These sites were exposed to similar temperature/precipitation regimes and spanned a range of vegetation types typical of the region (northern hardwood, mixed forest, red pine, jack pine, pine barrens and shrub wetland). The hardwood and red pine sites also spanned a range of stand ages (young, intermediate, mature). While seasonal changes in net ecosystem exchange (NEE) and photosynthetic parameters were coherent across the 2 years at most sites, changes in ecosystem respiration (ER) and gross ecosystem production (GEP) were not. Canopy height and vegetation type were important variables for explaining spatial variability of CO_2 fluxes across the region. Light-use efficiency (LUE) was not as strongly correlated to GEP as maximum assimilation capacity (Amax). A bottom-up multi-tower land cover aggregated scaling of CO_2 flux to a 2000 km^2 regional flux estimate found June to August 2003 NEE, ER and GEP to be -290 ± 89, 408 ± 48, and 698 ± 73 gC m^{-2}, respectively. Aggregated NEE, ER and GEP were 280% larger, 32% smaller and 3% larger, respectively, than that observed from a regionally integrating 447 m tall flux tower. However, when the tall tower fluxes were decomposed using a footprint-weighted influence function and then re-aggregated to a regional estimate, the resulting NEE, ER and GEP were within 11% of the multi-tower aggregation. Excluding wetland and young stand age sites from the aggregation

* *Corresponding author*. Present address: University of Wisconsin-Madison, Atmospheric & Oceanic Sciences Dept., AOSS 1549, 1225 W Dayton St, Madison, WI 53706, USA. Tel.: +1 608 265 9292; fax: +1 608 262 0166.
E-mail address: desai@aos.wisc.edu (A.R. Desai).
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worsened the comparison to observed fluxes. These results provide insight on the range of spatial sampling, replication, measurement error and land cover accuracy needed for multi-tiered bottom-up scaling of CO_2 fluxes in heterogeneous regions such as the Upper Midwest, USA.

1. Introduction

Quantifying the exchange of carbon dioxide between the terrestrial ecosystems and the atmosphere at regional scales (10–1000 km) is needed to understand the CO_2 dynamics of entire biomes. The variability in the magnitude of this CO_2 exchange is controlled by many factors. Vegetation type, canopy successional stage, temperature and precipitation are all seen to be major factors in explaining this variability over space and time (Baldocchi et al., 2001; Law et al., 2002, 2004; Valentini et al., 2000). Assessment of regional CO_2 flux in heterogeneous regions such as the forests of the Upper Midwest (USA) requires adequate representation of these governing factors.

Net CO_2 exchange at the length scale of tens to thousands of meters can be ascertained with biometric and eddy covariance methods (Baldocchi, 2003), while CO_2 fluxes at the continental to global scale can be estimated with tracer-transport inversion models, biogeochemical process models and/or remote sensing-based ecosystem models (Running et al., 1999; Tans et al., 1990). However, methods to assess and verify regional (10–1000 km) ecosystem CO_2 flux in heterogeneous regions over time scales of months to years are not as well constrained (Chen et al., 2004). Both top-down and bottom-up methods for measuring regional CO_2 flux can be used (Desjardins et al., 1997; Gerbig et al., 2003; Song and Woodcock, 2003).

Canopy towers (10–20 m short towers above vegetation canopy) for eddy-covariance flux measurements are used to measure ecosystem CO_2 exchange at the scales of 1–2 km, as is currently being done at over 200 sites across the world (Olson et al., 2004). The eddy covariance method allows for mostly continuous measurement of net ecosystem CO_2 flux. Cost, site access and labor/data processing requirements, however, prevent ubiquitous deployment of these systems to assess regional CO_2 exchange. While remote sensing, ecosystem models and inverse methods can be used at the regional scale, these methods alone do not elucidate mechanisms for CO_2 exchange and their application at these scales is experimental.

The North American Carbon Plan (NACP, U.S. Carbon Cycle Science Steering Group, http://www.esig.ucar.edu/nacp/) calls for using a multi-tiered approach for scaling of CO_2 flux, which includes (1) comprehensive measurements by remote sensing, (2) low-intensity, high spatial density inventory measurements (e.g., Forest Inventory Analysis), (3) moderate-intensity, moderate density carbon process measurements (e.g., biometric carbon stock and flux measurements) and (4) high-intensity, low density intensive measurements (e.g., eddy covariance flux towers). Questions remain, however, regarding the required density and kinds of measurements needed at each scale.

Our study examined the role of eddy covariance flux measurements within this framework for assessing regional CO_2 exchange in one specific region. The Upper Midwest region of northern Wisconsin and Michigan is a highly productive region of dense forest with low human population density (<10 people km^{-1}) and relatively flat terrain. The land cover in this region is a highly heterogeneous mixture of upland forests and lowland wetlands. The region also has the highest density of eddy covariance flux towers of any region in the world to date, due to the presence of the Chequamegon Ecosystem–Atmosphere Study and related projects (http://

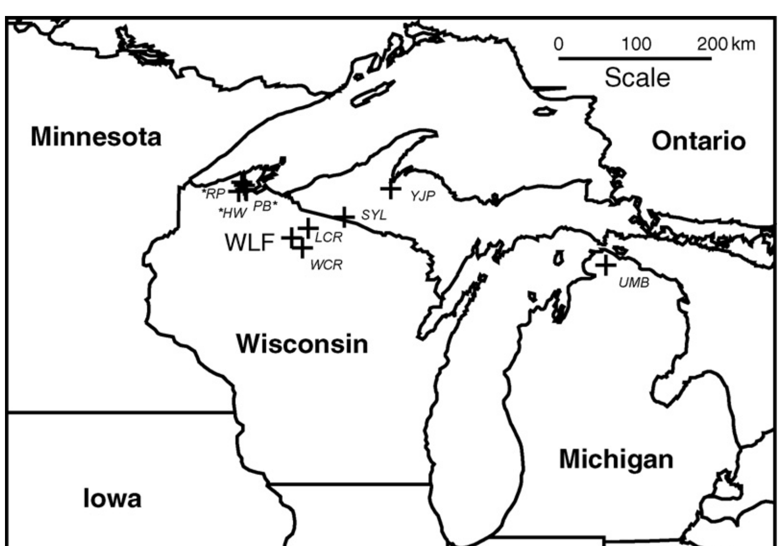

Fig. 1 – Map of Upper Midwest (USA) and flux towers (+) analyzed in this study.

www.cheas.psu.edu). Over the summers of 2002 and 2003, 11 eddy flux tower systems were deployed in 14 different sites spanning a range of ecosystem types and stand ages, including a regionally representative 447-m tall tower (Fig. 1). Thus, the region is an ideal place to address flux station density requirements for scaling regional carbon fluxes in a heterogeneous landscape.

The objective of this study was to examine the variability of net ecosystem exchange of carbon dioxide (NEE), ecosystem respiration (ER), gross ecosystem production (GEP) and the attendant parameters across the 14 sites over the 2 years, examine which site parameters were most important to explain this variability and understand how these results inform bottom-up scaling of regional CO_2 flux. We asked (1) which vegetation type, stand age and meteorological forcing explained most of the variability of CO_2 exchange across these sites, (2) what mechanisms explained variability of CO_2 exchange, (3) if these flux towers sufficiently sampled the landscape to compute regional CO_2 flux, and if not how these data can be used to inform multi-tiered scaling.

Valentini et al. (2000) showed that variation in NEE across Europe was mostly a function of latitude and due primarily to variation in ER, with little variation in GEP. However, few studies have quantified the variation in carbon flux over small areas with heterogeneous cover. We hypothesized that ecosystem type would be the most important variable in explaining CO_2 flux variability across space, followed by stand age, and these factors would explain the majority of flux variability across space, whereas variability due to climate forcing or latitude would be insignificant across space, and coherent across time but smaller than cross-site variability.

2. Materials and methods

2.1. Site descriptions

Northern Wisconsin and Michigan, USA is an area of relatively flat, forested boreal transition forest with many small glacial lakes and wetlands. The majority of upland forest consists of mature northern hardwood forests of maple (*Acer* spp.), basswood (*Tilia americana*), birch (*Betula allghaniesis*) and ash (*Fraxinus* spp.) along with younger fast-growing aspen (*Populus termulouides*) forests. Coniferous species, primarily red pine (*Pinus resinosa*), jack pine (*Pinus banksiana*), eastern hemlock (*Tsuga canadensis*) and white pine (*Pinus strobus*) forests cover smaller areas. Fire-dependent pine barren shrublands are found scattered in the region, primarily in northwest Wisconsin. Around 1/3 of the region is lowland wetlands, including forested wetlands that contain primarily black spruce (*Picea mariana*), white cedar (*Thuja occidentalis*) or tamarack (*Larix laricina*), shrub wetlands typically containing alder (*Alnus* spp.) or willow (*Salix* spp.) species and open meadows. Presettlement upland vegetation consisted primarily of eastern hemlock, white pine, birch and maple species (Schulte et al., 2002). The region was heavily clear-cut beginning in the late 19th century and logging continues today, though its magnitude and intensity are in decline (Caspersen and Pacala, 2001; Frelich and Reich, 1995). Many forests in the area remain intensively managed.

Eddy-covariance CO_2 flux measurements were initiated in the region in late 1995 from a 447-m tall television tower with station call letters WLEF, hereafter referred to as WLF (Davis et al., 2003; Ricciuto et al., submitted for publication). Tower footprint includes aspen, northern hardwood and coniferous stands along with forested and shrub wetlands (Davis et al., 2003). The mean L_{ai} computed as a spatially weighted sum across the major ecosystems is 3.7 (Burrows et al., 2002) and typical stand age is around 51 years for upland and 69 years for wetlands (R. Anderson, 2007, personal communication). Flux measurements were made at heights of 30, 120 and 396 m above ground in an attempt to measure the CO_2 flux integrated over this heterogeneous region. A "preferred" NEE algorithm was employed to assimilate data from all three levels to create a record of hourly regional-scale NEE (Berger et al., 2001; Davis et al., 2003). Typical flux footprints from this tower are on the order of 5–50 km, depending on the conditions and measurement level used (Horst and Weil, 1992; Wang et al., 2006). Tall tower fluxes from summer 2002 unfortunately had to be discarded due to instrument failures.

Since the establishment of CO_2 flux measurements on the tall tower, various investigators have initiated flux measurements in specific ecosystems using short towers, typically about 10 m above the local canopy. By the summer of 2002, 11 flux towers existed in a range of ecosystem types and forest stand ages (Table 1) that spanned the range of dominant land cover types in the region. Three of these towers were on mobile type platforms and moved to other sites in the summer of 2003. The locations of the sites are mapped on Fig. 1. Site vegetation, stand age, name abbreviations and other information are detailed in Table 1.

This study focused on eddy-flux data collected over the core growing season months of June, July and August, when all sites were operational. Only five sites operated across all seasons. However, it is in the growing season when the largest spatial variability in absolute magnitude of fluxes is typically seen, whereas winter fluxes, during the time deciduous leaves are off and temperatures are below freezing, are generally an order of magnitude smaller (Fig. 2).

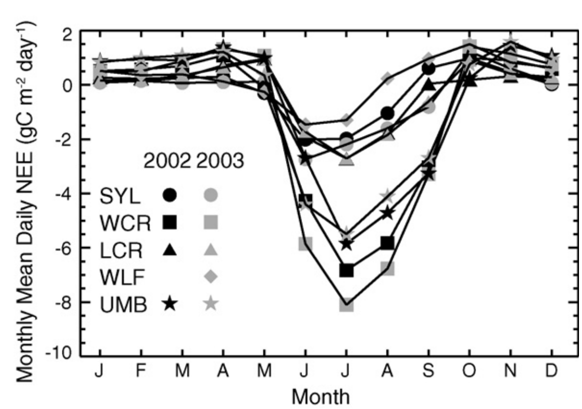

Fig. 2 – Monthly average NEE for the 5 flux towers with measurements in all seasons of 2002 and/or 2003.

Table 1 – Location and site characteristics for all CO_2 eddy flux measurements made in the region

Site	Code	Date range	Citation	Location	Latitude	Longitude	Dominant cover	L_{ai}	Age class	Stand age (years)	Canopy height (m)	Tower height (m)
Deciduous broadleaf												
Young hardwood	YHW	Summer 2002	A. Noormets et al. (submitted for publication)	Chequamegon-Nicolet National Forest, Washburn Ranger District, WI	46 43′ 18″	91 15′ 04″	Aspen, red maple	1.2	Young	3	1.5	3
Intermediate hardwood	IHW	Summer 2003	This paper	Chequamegon-Nicolet National Forest, Washburn Ranger District, WI	46 00′ 34″	91 13′ 21″	Aspen	3.0	Intermed	17	6	9
Mature hardwood	MHW	May 2002–	A. Noormets et al. (submitted for publication)	Chequamegon-Nicolet National Forest, Washburn Ranger District, WI	46 38′ 04″	91 05′ 57″	Red maple, sugar maple, aspen, birch	3.9	Mature	65	21	26
Willow Creek	WCR	1999–	Bolstad et al. (2004), Cook et al. (2004)	Chequamegon-Nicolet National Forest, Park Falls Ranger District, WI	45 48′ 21″	90 04′ 47″	Sugar maple, basswood, green ash	5.3	Mature	70	24	30
UMBS	UMB	1999–	Curtis et al. (2005), Schmid et al. (2003)	Pellston, MI	45 33′ 35″	84 42′ 51″	Aspen, white pine, red oak, sugar maple	3.7	Mature	90	20	50
Evergreen needleleaf												
Young jack pine	YJP	2002–2003	Euskirchen et al. (2006)	Alberta, MI	46 38′ 47″	88 31′ 10″	Jack pine	0.9	Young	14	2.3	9
Young red pine	YRP	Summer 2002	A. Noormets et al. (submitted for publication)	Chequamegon-Nicolet National Forest, Washburn Ranger District, WI	46 37′ 10″	91 04′ 56″	Red pine, jack pine	0.5	Young	8	4	6
Intermediate red pine	IRP	Summer 2003	This paper	Chequamegon-Nicolet National Forest, Washburn Ranger District, WI	46 41′ 51″	91 07′ 19″	Red pine	–	Intermed	21	6	9
Mature red pine	MRP	May 2002–	A. Noormets et al. (submitted for publication)	Chequamegon-Nicolet National Forest, Washburn Ranger District, WI	46 44′ 21″	91 09′ 60″	Red pine, aspen	2.5	Mature	63	18	23
Mixed forest												
WLEF	WLF	1997–	Davis et al. (2003)	Park Falls, WI	45 56′ 45″	90 16′ 20″	Northern hardwoods, aspen, forested wetlands	3.7	Mature	Mean: 50–70	20	30/122/396
Sylvania	SYL	September 2001–	Desai et al. (2005)	Ottawa National Forest, Watersmeet Ranger District, MI	46 14′ 31″	89 20′ 22″	Eastern hemlock, sugar maple, birch	4.1	Old	200	26	35
Shrub												
Pine barren A	PBA	Summer 2002	A. Noormets et al. (submitted for publication)	Chequamegon-Nicolet National Forest, Washburn Ranger District, WI	46 37′ 09″	91 16′ 44″	Sweet fern, black cherry, willow, red Pine	0.2	Young	12	0.5	3
Pine barren B	PBB	Summer 2003	This paper	Chequamegon-Nicolet National Forest, Washburn Ranger District, WI	46 37′ 16″	91 17′ 35″	Sweet fern, black cherry, willow, red pine	–	Young	2	0.5	3
Wetland												
Lost Creek	LCR	2000–	Cook et al. (in preparation)	Lac Du Flambeau, WI	46 04′ 59′	89 58′ 45″	Alder, willow shrubs	4.9	Intermed	20	2	10.2

Table 2 – Analyzer type, flux screening parameters and amount of missing or screened data for each site

Site	Year	IRGA type	u^* Cutoff	Wind direction screen	%Missing data	%Screened data	%Missing day	%Screened day	%Missing night	%Screened night
Deciduous broadleaf										
YHW	2002	Open	0.2	120–170	16	25	17	19	15	37
IHW	2003	Open	0.11	120–170	29	26	29	25	30	38
MHW	2002	Open	0.4	120–170	18	22	18	17	19	29
MHW	2003	Open	0.34	120–170	22	25	21	17	24	35
WCR	2002	Closed	0.3	90–180	37	31	37	17	37	18
WCR	2003	Closed	0.3	90–180	38	32	41	25	32	40
UMB	2002	Closed	0.35	–	23	29	19	21	29	42
UMB	2003	Closed	0.35	–	21	32	17	23	28	48
Evergreen needleleaf										
YJP	2002	Open	0.3	–	16	40	16	40	16	40
YJP	2003	Open	0.3	–	37	33	37	33	37	33
YRP	2002	Open	0.18	120–170	17	25	17	13	18	43
IRP	2003	Open	0.11	120–170	17	45	18	34	16	52
MRP	2002	Open	0.32	120–170	11	31	12	23	9	42
MRP	2003	Open	0.2	120–170	9	36	9	25	8	48
Mixed forest										
WLF	2003	Closed	0.3	–	5	44	5	24	6	77
SYL	2002	Closed	0.325	270–180, night	23	27	25	13	21	49
SYL	2003	Closed	0.325	270–180, night	1	38	1	16	1	64
Shrub										
PBA	2002	Open	0.21	120–170	22	26	24	13	20	47
PBB	2003	Open	0.12	120–170	23	36	26	22	17	54
Wetland										
LCR	2002	Closed	0.05	–	7	11	7	3	8	25
LCR	2003	Closed	0.05	–	12	16	12	5	10	36

2.2. *Instrumentation and calculations*

Site publications (Table 1) detail specific instrumentation and calculation details. All sites used 3-D sonic anemometers and open or closed path infrared gas analyzers (Licor, Inc. LI-6262 for closed path or LI-7500 for open path) mounted on triangular or scaffold towers (Table 2). Data are recorded from these sensors at high-frequency (either 5 or 10 Hz) to datalogger and computer. Standard micrometeorological measurements of air temperature, relative humidity, soil temperature, precipitation, soil moisture and photosynthetic active radiation (PAR) were made at most sites. Missing micrometeorology data at sites were filled with data from nearby sites or other cooperative observer sites. Linear calibration of PAR sensors across sites was accomplished by comparing clear-sky measurements at all sites.

Similar methods were used to compute carbon dioxide fluxes among the sites as outlined in individual site publications. Details for closed-path systems can be found in Berger et al. (2001). Fluxes were computed at half-hourly intervals at all sites except at WLF, where it was computed hourly. Coordinates of sonic anemometer data were rotated horizontally into the mean wind and vertically using the planar fit method (Berger et al., 2001; Finnigan et al., 2003; Paw et al., 2000). Calibration of temperature- and pressure-corrected CO_2 sensor signals were accomplished with either manufacturer factory calibrations or against local independent high-precision CO_2 measurements. For closed-path systems, lagged autocorrelations were computed to account for lag times between the anemometer and gas analyzer. High-frequency spectral corrections were also applied in closed-path systems to account for attenuation of high-frequency components of signals in tubing. Webb–Pearman–Leuning scalar flux density corrections (Webb et al., 1980) were applied where appropriate. No low-frequency flux corrections were attempted. Independent comparison of flux instrumentation and calculation was performed using the Ameriflux relocatable reference system at WCR, UMB and SYL.

NEE of CO_2 was computed from the sum of turbulent flux and below canopy storage flux. Below canopy storage flux was computed from the time derivative of measured column CO_2 below the height of the high frequency sensors. Column CO_2 was estimated by vertically integrating CO_2 measurements made at several levels (Bakwin et al., 1995; Cook et al., 2004) or with a multi-level mixing volume sampling scheme (A. Noormets et al., submitted for publication).

Resulting NEE data was screened for data spikes, low friction velocity (u^*), and non-representative or obstructed wind directions. CO_2 fluxes during conditions of low u^* at night are typically found to underestimate ecosystem flux (Gu et al., 2005). Friction velocity cutoffs were found for each site-year by comparing normalized nighttime NEE to u^* and visually determining u^* below which NEE significantly declined. Non-representative wind directions were found by examining site land cover maps, running footprint models and considering tower geometry. We relied on individual site investigator choices for these data screens, which are summarized in Table 2 and detailed in individual site publications. Final output NEE and related micrometeorological data were put in a common format with common units and timezone at all sites.

2.3. Calculation of filled NEE, ER and GEP

Empirical functions were used to fill missing or screened NEE data and to decompose observed NEE into modeled ER and GEP. On average, 18% of data was missing (range 1–37%) from June to August, while 29% of data was screened for low u^* or non-representative wind directions (range 11–44%) (Table 2). Thus, the total amount of data that require gap-filling was on average 48% (range 18–70%). The amount of missing data is in the range seen at most eddy flux towers (Moffat et al., 2007). Empirical functions have been shown to accurately fill simulated gaps of this size in flux data at many sites (Falge et al., 2001). Significant missing data are screened at many sites at night (Table 2).

We used the same model on all sites for filling of NEE and computing of ER and GEP (Moffat et al., 2007). The model relies on a non-linear regression of nighttime NEE to near-surface (typically 5 cm) soil temperature to compute ER, and a non-linear regression of daytime ER–NEE to above canopy PAR to compute GEP (Cook et al., 2004; Desai et al., 2005; Eyring, 1935). Since nighttime NEE is equivalent to nighttime ER (no photosynthesis at night) and the source of most ER is typically from near-surface soil (Bolstad et al., 2004; Tang et al., 2008), we used near surface soil temperature and nighttime NEE to compute the daily fit parameters. The difference between modeled ER and NEE is GEP. This GEP was modeled to fill gaps and produce ecosystem light-response parameters. The Michaelis–Menten reaction rate equation was applied to GEP and above canopy PAR (Falge et al., 2001; Ruimy et al., 1995). This GEP/ER technique was shown to produce similar ER and GEP estimates to within 10% compared to more than 20 other methods in a multiple site intercomparison (Desai et al., submitted for publication).

A 1-month daily moving window was used for these fits to account for change in parameters with time (due to any changes in leaf phenology, litter quality and/or light use efficiency). Smaller windows were not used since they did not often allow for a large enough sample in the fit. In regions with significant missing data, the moving window size was allowed to expand up to 4 months until 200 good half-hourly measurements were found. Data outside the June to August analysis time frame were included when necessary.

A first-order, conservative estimate of error due to filling missing data was computed using a simple Monte Carlo experiment (Desai et al., 2005; Griffis et al., 2003). Between 5% and 45% of existing NEE data from June to August was removed using a uniform random number generator. Gaps could range from one hour to two days. Gap filling functions were recomputed with the remaining data and gaps were filled. This was done 100 times for each site. The resulting statistics from the experiment were used to put error bounds on season total ER and GEP for each site-year. NEE error bounds were computed as the sum of ER and GEP error bounds.

2.4. Parameter analysis and statistics

In addition to NEE, GEP and ER, we compared several growing season averaged fit parameters using the filled datasets across the sites in order to deduce mechanisms for differences in NEE, GEP and ER. A GEP:ER ratio (unitless) was computed from season total GEP (a value derived from ER-NEE) divided by season total ER. ER parameters computed include Q_{10} and R_{10}. We compared Q_{10} and R_{10} across sites due to their common usage among many ecosystem models and simpler intuitive mechanistic understanding. Q_{10} (unitless) was found using monthly June to August nighttime filled ER at each site, by using the fit parameters to compute modeled ER at 20° and dividing it by modeled ER at 10°. Similarly, modeled ER at 10° was interpreted as R_{10} (μmol CO_2 $m^{-2}\,s^{-1}$).

GEP parameters computed include light use efficiency (LUE), maximum assimilation capacity (A_{max}) and quantum yield (QY). LUE (μmol CO_2 μmol^{-1} aPAR) was computed as the ratio of total GEP to total absorbed PAR (aPAR). Total absorbed PAR was modeled from total incoming PAR (iPAR) using the Beer–Lambert Law:

$$a_{PAR} = I_o(1 - e^{(-k \cdot L_{ai})}) \quad (1)$$

where I_o is incoming PAR in $\mu mol\, m^{-2}\, s^{-1}$, k the canopy extinction coefficient (assumed to be 0.5) and L_{ai} is leaf area index. Though canopy extinction values vary by site cover type, we found the value of 0.5 to generally explain the PAR profile at most sites. Modeled absorbed PAR compared favorably to observations at sites with observed canopy incoming PAR profiles. A_{max} and QY were found by taking monthly June to August GEP data at each site and applying the following relationship:

$$GEP = \frac{Q \cdot A_{max} \cdot P}{A_{max} + Q \cdot P} \quad (2)$$

where P is PAR and Q is QY. Here we are assuming the canopy acts as a single layer ‘‘big leaf’’. Standard statistical tests (t-test, one-way ANOVA) on CO_2 fluxes and its parameters were then performed to test our hypotheses and compare the significance of differences in means and variances among various vegetation and stand age sub-groupings.

2.5. Multi-tower aggregated scaling

We used a simple linear model to aggregate flux measurements from the canopy-scale towers to the region and compared them to the flux observed from June to August 2003 at the WLF tall tower. Land cover statistics for a 40 km radius around WLF were derived from the State of Wisconsin Department of Natural Resources WISCLAND database (http://www.dnr.state.wi.us/maps/gis/datalandcover.html). Land cover classification in this database was computed from a supervised clustering of remotely sensed 30 m resolution U.S. National Aeronautics and Space Administration (NASA) Landsat Thematic Mapper (TM) data acquired primarily in 1992. Land cover classes were generalized to represent major vegetation types in the region. Stand-age distribution of forest stands sorted by major vegetation type around the tall tower was derived from aggregated statistics of U.S. Forest Service Forest Inventory Analysis (FIA) plot data. Due to database searching restrictions, a minimum radius of 65 km was chosen for analysis, representing 1309 individual plots.

No significant difference in cover type percentages was seen in the WISCLAND database between the 40 and 65 km radius (chi-square test, 95% confidence). While 40 km is larger than the tall tower footprint, a large radius for the land cover data was required to improve land cover accuracy and minimize mismatch with stand age data. Overall, changes in individual land cover percentages with radius were small (<5%) between 1 and 65 km, with the exception of jack pine, which increased from 1.5% to 9.6% cover with decreasing radius. Below 1 km radius, the proportion of grassland increases greatly due to the presence of a 200 m grassy clearing around the tall tower (Davis et al., 2003).

We linked each major existing cover type (hardwood, conifer, jack pine, shrub, wetland/forested lowland)/stand age class (young, intermediate, mature, old) pair with the most representative flux tower among the 13 measured ecosystems (excluding WLF), using 2003 data when available, otherwise using 2002. Where multiple flux towers were appropriate for the same cover and age class, each tower was assumed to represent equal portions of that class. This first order partitioning of land cover to flux tower can be conceptualized as:

$$C_{v,a} = \frac{W_v \cdot (F_{v,a}/\sum_a F_{v,a})}{N_{v,a}} \quad (3)$$

where C is percent cover, v the vegetation type, a the age class, W the WISCLAND percent land cover as a function of v, F the FIA based percent cover as a function of v and a, and N is number of representative towers. This is the basis for a very simple upscaling model.

Two methods were used to up-scale the fluxes. In method 1, month and season total NEE, ER and GEP from each flux tower were multiplied by the appropriate percent cover. CO_2 fluxes from non-vegetated areas (water, barren and urban) were assumed to be zero. CO_2 fluxes for agricultural/grassland areas were estimated from the average of growing season normalized daily average fluxes found in the published literature for other agricultural and rangeland eddy flux sites as reported in Falge et al. (2002).

Uncertainty in land cover statistics was propagated with a simple Monte Carlo method. Percent cover types were allowed to deviate randomly by 50% of the computed cover percentage and rescaled such that total cover did not exceed 100%. Regional NEE, ER and GEP were then recomputed 1000 times, and maximum and minimum results were used to assess the range of uncertainty due to land cover. This uncertainty was added directly to the uncertainty due to flux tower gap-filling as described in Section 2.3. Sensitivity of the scaling to stand age and vegetation class was studied by limiting choice of flux towers to only (a) mature forested sites (most common age class) and wetlands (second most dominant cover), (b) hardwood sites (most common vegetation class) or (c) mature hardwood forested sites.

For method 2, we modeled regional hourly NEE from the computed site values of Q_{10}, R_{10}, QY and A_{max} as described in Section 2.4 along with percent cover types:

$$N_{\text{predicted}}(t) = \sum_i c_i(w_{\text{dir}}(t)) \cdot \left(R_{10_i} \cdot Q_{10_i}^{((T_{s,i}(t)-10)/10)} - \frac{Q_i \cdot A_{\max_i} \cdot P(t)}{A_{\max_i} + Q_i \cdot P(t)} \right) \quad (4)$$

where $N_{\text{predicted}}(t)$ is NEE at time t, $c_i(w_{\text{dir}}(t))$ the percent cover for site i as a function of wind direction, $T_{s,i}(t)$ the soil temperature for site i and time t, Q_i the QY for site i and $P(t)$ is incoming PAR at WLF. Cover percentages were allowed to vary with wind direction as a first-order way to account for variability in land cover sampling due to variability in surface flux footprints. WISCLAND 40 km radius land cover data were divided into eight wedges with a width of 45° centered on 0°, 45°, 90°, 135°, 180°, 225°, 270° and 315° of true north. Division in this way was not possible with FIA data, so stand age distribution was assumed not to vary with wind direction. Hourly wind direction from the tall tower (gap-filled with data from all levels and nearby flux towers) was then used to assign the appropriate cover percentages for each model time-step.

In addition to comparing aggregation results directly to the tall tower, we also compared the aggregation results against a flux footprint and land cover weighted decomposition and re-aggregation of tall tower observed NEE (Wang et al., 2006). Multiple-level tall tower NEE was decomposed using a combination of hourly-computed flux footprint influence functions (Horst and Weil, 1992) and the WISCLAND land cover database. Each hourly footprint NEE was convolved with the landcover types found within the flux footprint influence function. ER and GEP parameters were then derived for each major land cover type over the entire growing season by solving for the overconstrained matrix of flux observations over the different land covers. The technique is described in detail in Wang et al. (2006). ER and GEP parameters derived from this method were then applied to the land covers found within a 40-km radius of the flux tower and assuming the WLEF tower meteorology measurements were representative of the region. This method allows us to remove the influence of flux footprint bias on tall-tower observed NEE due to sampling in a land-cover heterogeneous environment.

3. Results and discussion

3.1. *Meteorological forcing*

All sites observed roughly similar mean monthly and seasonal air temperatures, soil temperatures, total incoming PAR and monthly total precipitation within either year (Fig. 3). A drier year was observed in 2003 compared to 2002 with cooler temperatures in June and July 2003 compared to 2002, warmer in August, and a similar level of incoming radiation. Compared to measurements from National Climate Data Center cooperative observer site in Park Falls, WI from 1971 to 2000, both years were warmer than average, though 2003 was closer to average and significantly cooler (t-means test, 95% confidence) than 2002, except in August. Near surface soil temperature had

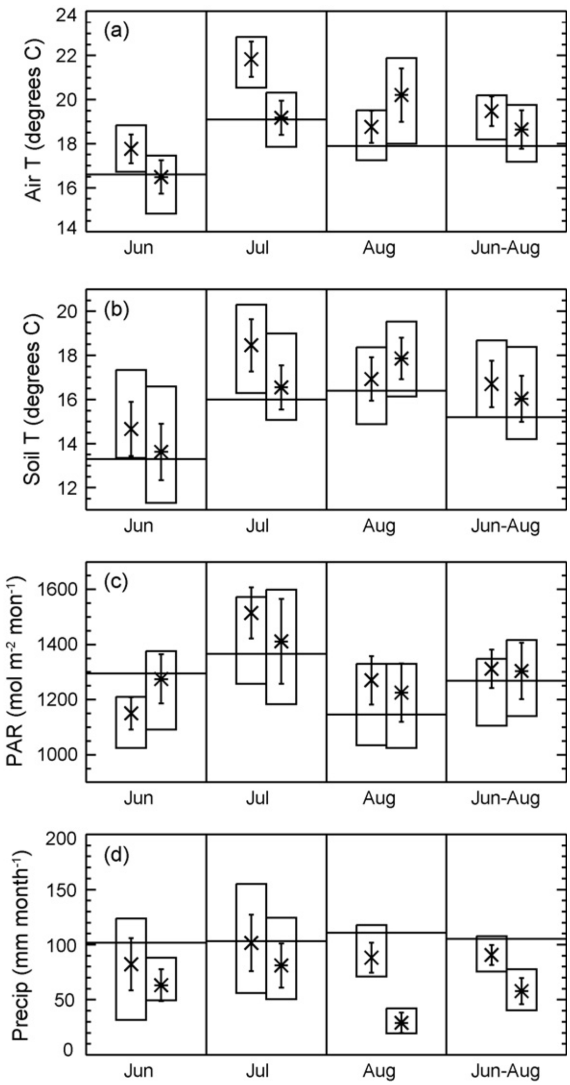

Fig. 3 – Monthly and seasonal (a) average air temperature, (b) average soil temperature, (c) total PAR and (d) total precipitation for 2002 (left bar) and 2003 (right bar). Also shown are cross-site mean (*), one standard deviation (vertical line), minimum and maximum (box), and long term average (horizontal line—temperature and precipitation are 1971–2000 averages from Park Falls, WI cooperative observer, PAR and soil temperature are 1996–2003 averages from micrometeorology sites near WLF tall tower).

similar trends to air temperature though cross site variability was higher than air temperature, reflecting differences in soil thermal conditions and canopy cover. Total monthly PAR was essentially similar in 2002 and 2003 and slightly above average PAR observed at WLF from 1996 to 2003. Across site variability in incoming PAR was moderate, possibly due to increased cloudiness for sites near Lake Superior, but sensor intercalibration issues may be imperfect. Total precipitation was below average in both years across most sites. Variability in precipitation across sites was insignificant (t-test, 95% confidence) except for June 2002 and July 2002, possibly due to the impact of localized convective storms.

3.2. *Spatial and temporal variability of CO_2 flux and relationship to seasonal forcing*

Spatial variations of temperature, precipitation and incoming radiation across the region were minimal, as expected, and unable to explain the variations in NEE, ER and GEP seen across the region. Within site variability in NEE, ER and GEP between summer 2003 and summer 2002 was smaller at all sites compared to across site variability in either year for the seven sites with data in both years (MHW, WCR, SYL, MRP, YJP, UMB, LCR), except for NEE at MHW (Table 3). Smaller variability across years was seen in the GEP:ER ratio (average 10%, range 4–17%), suggesting that GEP:ER was a more conservative value at the sites, though it should be noted that GEP:ER is not independent, given the derivation of GEP from ER and NEE. ER parameters of Q_{10} and R_{10} were more variable across years than GEP parameters of LUE, A_{max}.

Temporal variability across years at any one site was not negligible. Within site variability over 2 years was about half the spatial variability due to age and vegetation, except for GEP, which was closer to 70%. This is also reflected in the average coefficient of variation (standard deviation divided by mean) across years for NEE, ER and GEP, which were -0.10 ± 0.10, 0.10 ± 0.04 and 0.08 ± 0.07, respectively, while for across those same sites were −0.43, 0.23 and 0.13. All sites except LCR had larger (more negative, greater uptake by biosphere) NEE in 2003 compared to 2002. The change in NEE at all sites was smaller than the variability in NEE across sites except at MHW and smaller than the uncertainty in NEE due to gap-filling except at WCR and MHW. While the changes in NEE were generally coherent across the 2 years (a warmer, wetter year vs. a cooler, drier year), changes in ER and GEP were not. Three sites (MHW, MRP, LCR) had greater ER in 2003 than 2002, two sites (SYL, UMB) had less ER and two sites (WCR, YJP) had less ER but smaller than uncertainty. Four sites (MHW, WCR, MRP, LCR) had higher GEP in 2003 than 2002, two sites (SYL, UMB) had lower GEP and one site (YJP) had lower GEP but smaller than uncertainty. No strong correlations were seen between monthly CO_2 fluxes and air temperature, soil temperature, precipitation, incoming PAR, evaporative fraction (EF—ratio of latent heat flux to sum of sensible and latent heat flux) or radiative dryness index (RDI—ratio of net radiation to precipitation) (Budyko, 1971).

Despite the lack of coherence in GEP or ER across all site over the 2 years, GEP parameters (QY, LUE, A_{max}) had strong coherence over the 2 years at most sites. Coherent changes in at least six out of seven sites were seen in LUE (all but SYL), A_{max} (all but MHW) and QY (all but UMB). Evapotranspiration flux per unit GEP increased at all sites. These changes in photosynthetic parameters (increased efficiency at low PAR, lower uptake at high PAR, larger water use efficiency (WUE)) suggest that flux parameters are sensitive to moisture (e.g., vapor pressure deficit), as might be expected to occur due to plant stomatal closure in dry conditions, leading to a shift in carbon assimilation to earlier in the day.

Although it is difficult to diagnose temporal seasonal variability of growing season fluxes from only 2 years of data, results from 6 years of data at WLF and 4 years of data of WCR suggest that the variability seen over the 2 years at the six sites was similar in magnitude to the variability seen across the

Table 3 – Growing season total and mean CO_2 fluxes and parameters for all sites and years used in this study

Site	Year	CO_2 fluxes				ER parameters		GEP parameters			
		NEE (gC m^{-2})	ER (gC m^{-2})	GEP (gC m^{-2})	GEP:ER (unitless)	Q_{10} (unitless)	R_{10} (μmol m^{-2} s^{-1})	LUE (μmol CO_2 $μmol^{-1}$ aPAR)	QY (μmol CO_2 $μmol^{-1}$ iPAR)	A_{max} (μmol m^{-2} s^{-1})	LUE per L_{ai} (μmol CO_2 $μmol^{-1}$ aPAR)
Deciduous broadleaf											
YHW	2002	53 ± 25	572 ± 14	519 ± 9	0.9	3.5	2.1	0.011	0.105	12.9	0.0092
IHW	2003	−179 ± 65	591 ± 36	771 ± 28	1.3	5.2	2.2	0.013	0.071	22.8	0.0043
MHW	2002	−489 ± 22	242 ± 8	731 ± 13	3.0	1.4	2.0	0.015	0.060	23.2	0.0038
MHW	2003	−716 ± 33	283 ± 17	1000 ± 16	3.5	2.4	1.7	0.020	0.111	27.3	0.0051
WCR	2002	−521 ± 37	360 ± 15	882 ± 21	2.4	1.8	2.1	0.019	0.054	32.3	0.0036
WCR	2003	−635 ± 21	340 ± 10	976 ± 11	2.9	1.1	2.9	0.021	0.068	31.5	0.0040
UMB	2002	−417 ± 45	494 ± 18	911 ± 26	1.8	3.7	2.2	0.023	0.051	28.0	0.0062
UMB	2003	−433 ± 33	404 ± 17	837 ± 16	2.1	3.2	1.9	0.024	0.045	24.9	0.0065
Evergreen needleleaf											
YJP	2002	−317 ± 43	474 ± 24	792 ± 17	1.7	1.4	3.8	0.017	0.045	29.9	0.0189
YJP	2003	−344 ± 28	440 ± 14	785 ± 12	1.8	2.1	3.5	0.018	0.069	24.6	0.02
YRP	2002	−248 ± 26	406 ± 12	654 ± 13	1.6	2.3	2.5	0.014	0.047	21.7	0.028
IRP	2003	−379 ± 67	499 ± 27	878 ± 39	1.8	1.1	3.4	0.017	0.178	21.1	0.011*
MRP	2002	−415 ± 26	342 ± 11	757 ± 14	2.2	2.3	2.0	0.016	0.065	23.7	0.0064
MRP	2003	−435 ± 33	413 ± 17	848 ± 15	2.1	1.9	2.7	0.020	0.152	20.9	0.008
Mixed forest											
WLF	2003	−76 ± 26	601 ± 13	677 ± 12	1.1	1.9	4.1	0.014	0.040	26.2	0.0038
SYL	2002	−153 ± 48	614 ± 28	767 ± 19	1.3	2.0	4.5	0.016	0.051	25.6	0.0039
SYL	2003	−199 ± 44	522 ± 26	721 ± 16	1.4	2.2	3.6	0.015	0.059	21.6	0.0037
Shrub											
PBA	2002	−169 ± 41	368 ± 24	538 ± 15	1.5	6.3	0.7	0.011	0.037	17.8	0.055
PBB	2003	−63 ± 26	297 ± 11	361 ± 13	1.2	1.3	2.5	0.007	0.176	8.0	0.035*
Wetland											
LCR	2002	−199 ± 12	382 ± 5	581 ± 5	1.5	2.8	2.3	0.012	0.036	41.0	0.0024
LCR	2003	−196 ± 26	434 ± 11	631 ± 13	1.5	1.8	3.4	0.013	0.046	36.6	0.0027

Table 4 – CO_2 fluxes and parameters aggregated first by vegetation category and stand age class

Age class	Vegetation category	CO_2 fluxes			ER parameters			GEP parameters		
		NEE ($gC\ m^{-2}$)	ER ($gC\ m^{-2}$)	GEP ($gC\ m^{-2}$)	GEP:ER (unitless)	Q_{10} (unitless)	R_{10} ($\mu mol\ m^{-2}\ s^{-1}$)	LUE ($\mu mol\ CO_2\ \mu mol^{-1}$ aPAR)	QY ($\mu mol\ CO_2\ \mu mol^{-1}$ iPAR)	A_{max} ($\mu mol\ m^{-2}\ s^{-1}$)
Young/Intermediate	Deciduous broadleaf	−63	582	645	1.1	4.3	2.2	0.020	0.088	17.9
	Evergreen needleleaf	−322	455	777	1.7	1.8	3.7	0.052	0.085	24.3
	Shrub	−116	333	450	1.3	3.8	1.6	0.096	0.106	13.0
	Wetland	−198	408	606	1.5	2.3	2.9	0.014	0.041	19.8
Mature	Deciduous broadleaf	−535	354	890	2.6	2.3	2.1	0.022	0.065	32.0
	Evergreen needleleaf	−425	377	803	2.1	2.1	2.3	0.025	0.108	22.3

longer time records. WLF had NEE, ER and GEP variability (one standard deviation of growing season total flux) of 43, 50 and 45 $gC\ m^{-2}$, respectively (for more detail see Ricciuto et al., submitted for publication). At WCR, the standard deviations in annual NEE, ER and GEP were 155, 32 and 131 $gC\ m^{-2}$. The standard deviations of the 2002–2003 differences in NEE, ER and GEP, computed across all seven sites, were 45, 40 and 63 $gC\ m^{-2}$, respectively, and thus is in a similar range as the longer records. These data suggest that GEP variability was slightly greater than ER variability, as might be expected since GEP is sensitive to incoming radiation which was more variable than temperature at most sites.

3.3. *Impact of disturbance and canopy structure on CO_2 fluxes*

Differences were seen in NEE, ER and GEP across successional stages (Table 4). Canopy height showed stronger correlation with CO_2 fluxes than did stand age (Fig. 4). Young and intermediate short canopy height forests typically had smaller NEE than mature, taller ecosystems, due both to larger ER and smaller GEP. ER at the old-growth site was larger than at the mature sites and comparable to the young sites. The lack of replicated chronosequence sites limits our ability to draw strong conclusions; however, the existence of this unparalleled flux tower dataset of multiple ages over a single region does provide some preliminary insights on the importance of stand age on regional CO_2 fluxes.

Stand development trajectories of NEE, ER and GEP follow expected trends (Pregitzer and Euskirchen, 2004) for red pine and hardwood successional sequences, similar to multiple stand-age eddy flux measurements made in a Canadian boreal forest (Litvak et al., 2003). NEE increased (greater uptake) with age until reaching the mature stage, while the old-growth forest had much smaller net CO_2 uptake. For hardwood sites, the largest increase in CO_2 uptake occurred between intermediate and mature species, whereas for the red pine sites, this occurred from young to intermediate. In both cases, there was a small increase in ER from young to intermediate, followed by a larger decline in ER from intermediate to mature. The hardwood successional sequence had larger changes in NEE, ER and GEP both in terms of absolute fluxes and percentages than did the red pine successional sequence.

Stand age and canopy height were not as strongly correlated with derived parameters as they were with CO_2 fluxes. Young and intermediate ecosystems had similar QY and a larger LUE than mature ecosystems and smaller A_{max} values, as would be expected given the lower L_{ai} (Table 4). Canopy height was positively correlated with A_{max} ($r^2 = 0.34$) and negatively correlated with LUE ($r^2 = 0.28$), and these correlations were both stronger than the correlations between these parameters and stand age (0.18 and 0.14, respectively). Large changes in A_{max} were seen in the hardwood successional sequence (increasing with age until old growth), compared to smaller changes in QY, while red pine sites had small changes in A_{max} with age, but larger and opposite sign changes in QY.

The mechanism for the change in GEP with stand age appeared to be captured by considering the ratio of LUE to leaf area (Table 3), which generally declined with increasing age

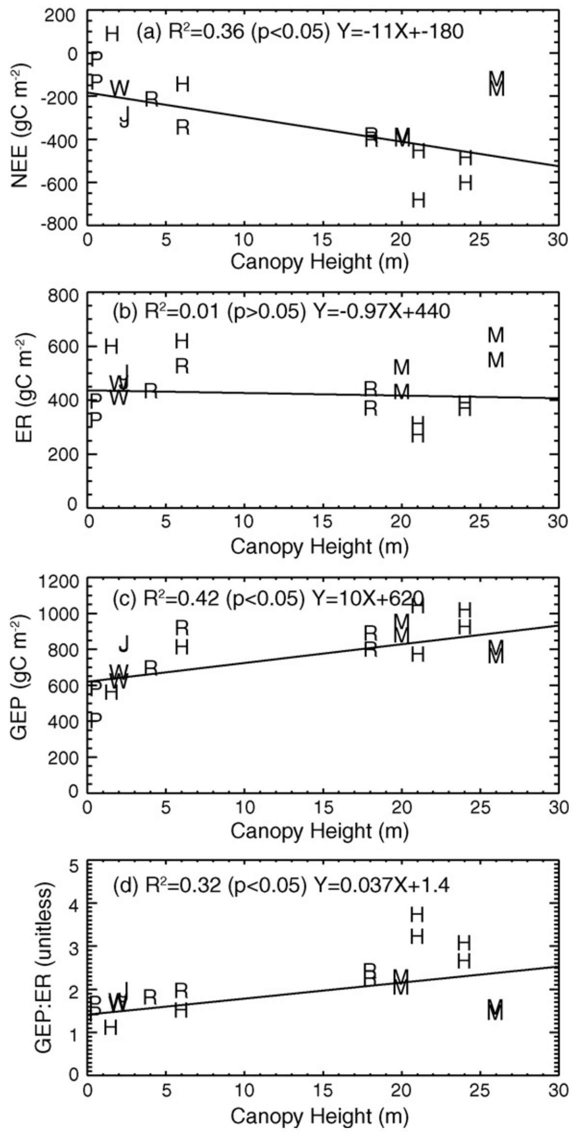

Fig. 4 – Effect of canopy height on growing season total (a) NEE, (b) ER, (c) GEP and (d) GEP:ER at all sites, excluding WLF. Letters denote primary vegetation type (H: hardwood, J: jack pine, P: pine barren, R: red pine, M: mixed, W: wetland).

and canopy height in the hardwood and red pine chronosequences, even though total LUE and GEP (Table 3) tended to increase with age until canopy closure. The trade-off between increased leaf area and fPAR on one hand and the decline in LUE per unit leaf area on the other was strongest between young and intermediate age stands, i.e. the transition from open to closed canopy systems. The decline in LUE per leaf area with age is likely the result of percentage of leaves directly exposed to sunlight. After canopy closure, increases in L_{ai} and therefore absorbed PAI are limited, yet total GEP and therefore LUE continued to decline at the Sylvania old-growth site, when compared to the Willow Creek mature site (Table 3). Declines in LUE and GEP for older forests may be related to either decreased L_{ai} and/or decreased capacity for photosynthesis as has been hypothesized by several studies (Gower et al., 1996; Murty et al., 1996). Light use efficiency is also sensitive to cloudiness and VPD (Cook et al., 2004; Heinsch et al., 2006), though variation in cloudiness across sites was minimal.

ER in young and intermediate aged stands were similar (unlike GEP), with largest declines occurring in mature stands. ER parameters as a whole did not have any significant correlations with stand age ($r^2 = 0.07$) or canopy height ($r^2 = 0.01$). Both R_{10} (base respiration) and Q_{10} (temperature sensitivity) changed with stand age and in different ways for the hardwood and red pine successional sequences. Changes in these factors across all sites with age were not significant (F-test, 95% confidence). It has been suggested that these empirically derived parameters cannot be compared individually across sites due to their interdependence (A.N. Noormets et al., submitted for publication).

The lack of replicates among old-growth species limits our ability to conclude that ER increases with age for late successional ecosystems. Component flux studies in the region have shown that ER may instead decrease with age (A. Noormets et al., submitted for publication; Tang et al., 2008). This conflicts with eddy-covariance flux measurements which show an increase in ER as a function of stand age comparing the same two sites (Desai et al., 2005). A review of CO_2 flux and stand age studies across the planet suggests that while old-growth forests are smaller CO_2 sinks than mature forests, heterotrophic respiration does not necessarily increase in old-growth forests (Pregitzer and Euskirchen, 2004). Thus, further investigation in old-growth forests is warranted, especially given the decline in logging in the area and the expansion of old forest.

3.4. *Variability of CO_2 flux by vegetation type*

The variability of GEP and ER across vegetation type depended on age class (Table 4). In the young and intermediate aged ecosystems, smallest net growing season NEE was seen on average in deciduous broadleaf forests (−63 gC m^{-2}), followed by shrublands (−116 gC m^{-2}), wetlands (−198 gC m^{-2}) and evergreen needleleaf forests (−322 gC m^{-2}). The smaller NEE in deciduous forests was the consequence of its larger ER compared to the other vegetation types, whereas the larger uptake in evergreen forests was more reflected in its large GEP. Coniferous forests also had the highest GEP:ER ratio. In contrast to the younger ecosystems, the largest NEE among mature species was in deciduous forests (−535 gC m^{-2}), while coniferous forests had smaller NEE (−425 gC m^{-2}) and GEP:ER ratios (Table 4). Also unlike the younger sites, deciduous forests had GEP (890 gC m^{-2}) larger than coniferous forests (803 gC m^{-2}), while conifers (377 gC m^{-2}) had slightly larger ER then deciduous forests (354 gC m^{-2}). The relatively similar GEP by vegetation type suggests that canopy closure leads to confluence in GEP.

Overall, variations in NEE by vegetation type and successional stage across a small region were larger than those observed by 15 sites over 3 years across a 24° latitudinal gradient in Europe (Valentini et al., 2000). In that study, the region with the largest variation in NEE (50–52° north latitude) had a maximum difference of 462 gC m^{-2} year^{-1}, which was smaller than the maximum difference of 769 gC m^{-2} observed in this study over only 1° of latitude over 3 months.

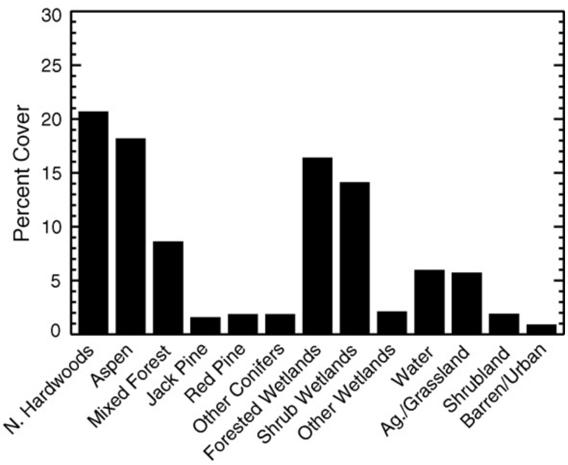

Fig. 5 – Fractional cover amounts for generalized land cover types in a 40 km radius around the WLF tall tower derived from the WISCLAND database.

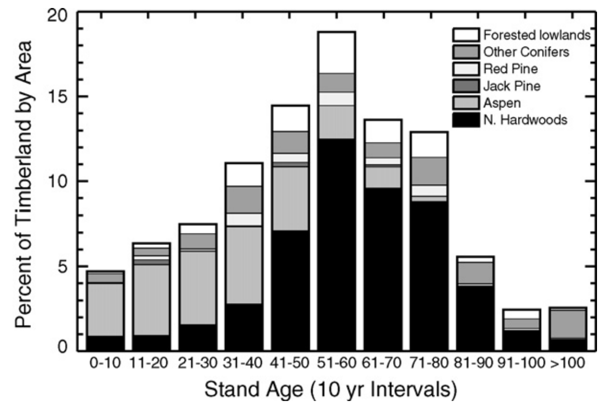

Fig. 6 – Distribution of forest stand age by major vegetation type in a 65 km radius around the WLF tall tower based on Forest Inventory Analysis.

Valentini et al. (2000) also argue that difference across site NEE were mainly explained by ER, whereas GEP was conservative across sites. Our study suggests that both GEP and ER were equally important for explaining variations in NEE across sites. It should be noted that this analysis focused on growing season only. Annual sums across the sites could have smaller variability and be more in line with the estimates of Valentini et al. (2000). However, analysis at sites that ran all year showed relatively small variation in winter time NEE, suggesting that the results would not be significant different (Fig. 2).

3.5. *Multi-tower scaling of CO_2 fluxes*

3.5.1. *Regional land cover*

WISCLAND land cover data (Fig. 5) reveals the dominance of two major classes of cover types in the WLF tall tower region: forested mixed hardwoods (48%, primarily northern hardwoods and aspen) and wetlands (33%, roughly equal parts shrub and forested). Coniferous species accounted for 5% of the land area around WLF, with the remaining land was classified as shrubland, grassland, barren, water or urban. Forest Inventory Analysis (FIA) data showed similar distributions of forested land around the WLF tower (Fig. 6). Dominant stand age for FIA plots around the WLF tower was between 50 and 60 years old. Mature stands were dominated by northern hardwoods (63%), while young and intermediate aged stands were dominated by aspen (55%).

Table 5 lists percent cover by vegetation type and stand age as determined from WISCLAND and FIA for the WLF region and the best flux towers that fit within each category. Total wetland coverage was generally constant with wind direction (range 23–27%), with the largest area to the southeast and the smallest to the NE. Among hardwood stand types, maximum aspen coverage occurred to the south, while maximum northern hardwood coverage occurred to the north and west.

Table 5 – Relative cover of major vegetation classes in a 40 km radius around tall tower derived from WISCLAND database and Forest Inventory Analysis along with most representative eddy flux tower

Cover type	Subclass	%Cover	Represented by
Hardwood and mixed	Young	5.7 (4.2–7.0)	YHW
	Intermediate	8.3 (6.1–10.1)	IHW
	Mature	30.7 (22.7–37.6)	WCR, UMB, MHW
	Old-growth	2.7 (2.0–3.3)	SYL
Red pine and other conifers	Young	0.3 (0.1–0.6)	YRP
	Intermediate	0.9 (1.0–4.1)	IRP
	Mature	2.5 (1.0–4.1)	MRP
Jack pine		1.6 (0–4.0)	YJP
Wetlands	Shrub and open	16.2 (10.2–24.0)	LCR
	Forested	16.4 (11.0–25.7)	LCR
Shrubland		1.9 (0.4–5.4)	PBA/PBB
Agricultural/rangeland		5.7 (1.5–10.2)	Synthetic
Water		6.0 (1.3–16.0)	–
Other		1.1 (0.4–1.8)	–

Range of cover type percentages across the eight 45° wedges is also shown.

Table 6 – Monthly and summer total NEE, ER and GEP from the tall tower, a footprint decomposed and landcover aggregated flux based on tall tower observations, and the multi-tower aggregation methods

Quantity	Month	Tall tower observation	Footprint weighted decomposition	Multi-tower synthesis aggregation	
				Method 1	Method 2
NEE (gC m^{-2})	June	−43 ± 16	−95 ± 20	−89 ± 30	−122 ± 20
	July	−40 ± 9	−83 ± 20	−112 ± 35	−103 ± 26
	August	7 ± 10	−80 ± 18	−89 ± 35	−72 ± 27
	June–August	−76 ± 26	−258 ± 56	−290 ± 89	−298 ± 72
ER (gC m^{-2})	June	175 ± 8	130 ± 11	108 ± 14	112 ± 13
	July	219 ± 5	115 ± 16	156 ± 19	153 ± 20
	August	207 ± 6	130 ± 12	144 ± 20	162 ± 21
	June–August	601 ± 13	375 ± 36	408 ± 48	426 ± 53
GEP (gC m^{-2})	Jun	218 ± 8	225 ± 20	198 ± 26	234 ± 6
	July	259 ± 4	198 ± 21	268 ± 28	256 ± 7
	August	200 ± 4	210 ± 18	233 ± 26	235 ± 6
	June–August	677 ± 12	633 ± 55	698 ± 73	724 ± 18

Also shown is total uncertainty in observations due to uncertainty gap-filling, parameter estimation and land cover percentages.

3.5.2. *Estimates of monthly regional CO_2 flux*

Multi-tower aggregated NEE for June to August 2003 using method 1 showed NEE, ER and GEP of −290 ± 89, 408 ± 48 and 698 ± 73 gC m^{-2}, respectively (Table 6). Results from method 2 were essentially equivalent to method 1, given the range of error for both methods. Compared to observations at the WLF tall tower, which showed NEE, ER and GEP of −76 ± 26, 601 ± 13, and 677 ± 12 gC m^{-2}, multi-tower aggregated NEE, ER and GEP were 280% larger, 32% smaller and 3% larger, respectively. Observed NEE at WLF had a small growing season CO_2 sink to the biosphere, although monthly total NEE was a net source in August 2003, during significantly dry conditions. Over the annual cycle, WLF is typically a source of CO_2 to the atmosphere (Davis et al., 2003; Ricciuto et al., submitted for publication), in contrast to most of the stand-level flux towers in the region.

The large mismatch in NEE was due primarily to significantly lower ER from the multi-tower aggregation compared to the tall tower. The cause for this lack of agreement between WLF ER and these aggregate estimates is not clear, and is discussed in more detail by Wang et al. (2006) and Davis et al. (submitted for publication). Ricciuto et al. (submitted for publication) provides detailed discussion of the multi-year WLF database.

When the tall tower NEE was decomposed using footprint-weight influence functions and re-aggregated using the 40 km radius land cover data, the resulting NEE, ER and GEP of −258 ± 56, 375 ± 36 and 633 ± 55 gC m^{-2}, respectively, were much closer in agreement to the multi-tower aggregation. The multi-tower aggregation NEE, ER and GEP were on average only 10% larger than the footprint decomposition method, and the differences were not significant, given the range of error. These results suggest that the tall tower ER measurements are biased high or alternatively that the scaling methods fail to identify large ER sources. More discussion on this point is provided in Section 3.6.

The multi-tower aggregation scaling is sensitive to exclusion of certain land cover types according to the sensitivity tests performed (Table 7). Using only mature and wetland flux towers in the aggregation led to larger NEE, smaller ER, larger GEP and increased the difference between aggregation and tall tower. Limiting scaling to only hardwood sites led to even larger NEE and revealed that excluding other vegetation types had a small impact on scaled ER, but a larger impact on GEP.

Table 7 – Sensitivity of multi-tower carbon flux aggregation method to limitation of data set to only including dominant land cover and/or stand age subcategories

Quantity	Month	All sites	Mature only	Hardwood only	Mature HW only
NEE (gC m^{-2})	June	−89 ± 30	−112 (−79 to −148)	−135 (−84 to −163)	−134 (−179 to −196)
	July	−112 ± 35	−143 (−110 to −181)	−159 (−99 to −195)	−221 (−239 to −170)
	August	−89 ± 35	−118 (−84 to −158)	−132 (−73 to −169)	−194 (−142 to −213)
	June–August	−290 ± 89	−373 (−282 to −476)	−427 (−268 to −515)	−595 (−457 to −637)
ER (gC m^{-2})	June	108 ± 14	101 (90–118)	108 (83–115)	96 (75–102)
	July	156 ± 19	134 (122–156)	165 (126–176)	125 (102–130)
	August	144 ± 20	128 (112–151)	151 (113–163)	123 (94–130)
	June–August	408 ± 48	362 (330–419)	423 (329–446)	343 (274–359)
GEP (gC m^{-2})	June	198 ± 26	212 (187–247)	243 (189–254)	275 (227–284)
	July	268 ± 28	277 (255–315)	324 (258–334)	347 (290–354)
	August	233 ± 26	246 (224–282)	283 (225–290)	315 (266–321)
	June–August	698 ± 73	735 (675–839)	850 (679–870)	937 (790–952)

3.5.3. Hourly correlation of regional flux estimates
Hourly aggregated NEE, ER and GEP from method 2 was well correlated with NEE ($r^2 = 0.55$), ER ($r^2 = 0.65$) and GEP ($r^2 = 0.59$) observed at WLF (Fig. 7). Aggregated ER was consistently smaller than tall tower ER across the entire range of observed ER, with both a negative offset and a slope less than one. Mean relative error increased at high ER. Aggregated GEP was generally larger except for high magnitude GEP. Fit slope was close to 1. Variability in observed GEP (ER-NEE) increased with modeled GEP magnitude, likely reflecting the effects of random error on observed fluxes (Mann and Lenschow, 1994; Hollinger et al., 2004). This variability was positively skewed at high GEP and aggregated GEP leveled off at 20 μmol m^{-2} s^{-1}, suggesting the tower-optimized A_{max} values were too low. Higher correlation ($r^2 = 0.94$) and low root mean square error (R.M.S.E. = 1.8) was observed in comparison of hourly NEE from the multi-tower aggregation to the tall tower flux footprint decomposition method (Fig. 8), however this is mostly a result of both methods relying on similar ecosystem models of ER and GEP.

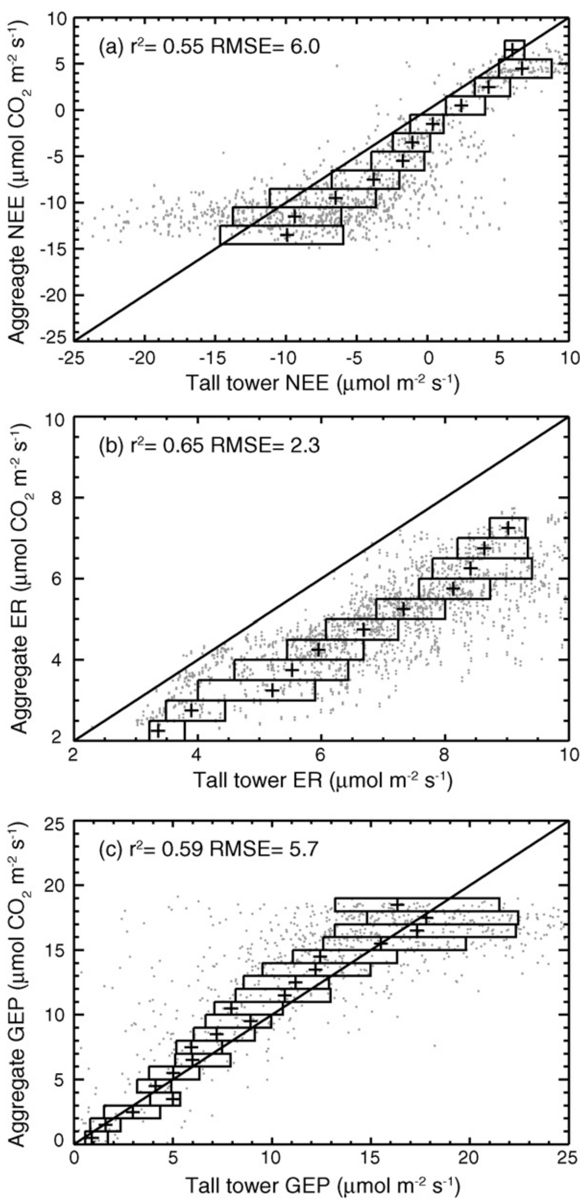

Fig. 7 – Comparison of hourly (a) NEE, (b) ER and (c) GEP observed from the WLF tall tower to the multi-tower aggregate flux derived from flux tower parameters. Also shown are median observed values (+) for (a) 1.5, (b) 0.5, (c) 1.0 μmol m^{-2} s^{-1} modeled bins and 25% and 75% quartile range (box).

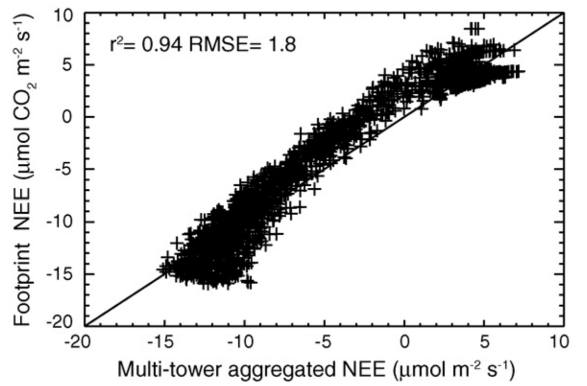

Fig. 8 – Comparison of hourly NEE inferred from parameters derived from tall tower flux footprint decomposition to multi-tower aggregate flux.

3.6. Implications for regional CO_2 flux scaling

3.6.1. Flux tower representativeness
Our simple upscaling exercise and the sensitivity results showed that despite the dominance of mature hardwood forest in the region, other vegetation types (e.g., wetlands) and stand age classes (e.g., young aspen forests) have an impact on regional CO_2 flux. The sensitivity study showed that excluding non-hardwood forests in the aggregation had a larger impact on GEP than ER, while excluding non-mature sites impacted both ER and GEP. While mature hardwood sites accounted for 42% of the aggregated GEP, due to their dominance in spatial area, they only accounted for 25% of ER due to their relatively low ER rates. Wetlands as a whole accounted for 30% of GEP and 34% of ER, while young and intermediate hardwood forests accounted for 13% of GEP and 20% of ER. In contrast, coniferous, shrubland and old-growth sites in total only accounted for 10% of ER and GEP. However, while these sites were not prevalent in the 40-km radius region around the tower, certain parts of the region have larger spatial extents of these covertypes.

While the high-density of eddy covariance CO_2 flux towers in the region sampled a representative variety of vegetation types and stand ages in the region, the multi-tower upscaling of fluxes from these towers was larger than the observed NEE at the WLF tall tower for June to August 2003, primarily due to differences in ER. These results suggest that there are additional sources of ER around the WLF tall tower that were not being sampled by the other flux towers. The model GEP lid effect suggests that occasional large GEP sources existed, occurring primarily in midday, that also were not sampled by the stand-level towers. Conversely, the footprint influenced decomposition and aggregation method suggests that the WLF tall tower estimates of ER were biased high. Additionally, flux error or quality control issues are inherent at all flux tower sites. We consider several model, observational and sampling errors here.

3.6.2. *Error analysis*

Even with 11 flux towers sampling 14 ecosystems, several ecosystems were undersampled. Non-vegetated cover classes were not sampled at all. While agricultural and urban land uses could be large CO_2 sinks or sources, they cover only 6% and 0.2% of the 40-km radius region around the tall tower, and thus are not likely to be important on a regional basis. CO_2 fluxes from open water, which cover 6% of the region, are most likely near zero, though they may increase in certain convective conditions (Eugster et al., 2003). Another study over several lakes in northern Wisconsin suggested lake CO_2 efflux on the order annual of 10–100 gC m^{-2} $year^{-1}$, with the bulk occurring at ice out and fall mix up (Riera et al., 1999). Over the growing season, these lakes were small sinks of CO_2. If all three undersampled ecosystems cover 12.2% of the region had CO_2 effluxes or uptakes over the growing season of 100 gC m^{-2}, the net error on regional flux would be $\sim$12 gC m^{-2}, less than 4% of the estimated growing season regional NEE.

The region does have many recently cut or disturbed young aspen stands (Bresee et al., 2004). The scaling sensitivity results showed that including young and intermediate aged ecosystems increased ER. It is possible that existing flux measurements in these stands do not capture the range of ER in these stands, and that a large ER signal is missed in this upscaling. Additional flux tower measurements are underway in these stands. The flux footprint and land cover based decomposition of the tall tower CO_2 flux (Wang et al., 2006) suggests that aspen regions had larger ER and GEP than those observed from the young and intermediate hardwood flux tower data used in this study.

Additionally, since wetlands cover almost 33% of the region, fluxes from one shrub wetland tower cannot be considered representative of all wetlands in the region, especially for forested wetlands and open meadows. Wang et al. (2006) suggest that forested wetlands have large ER and GEP, larger than the fluxes observed at our one wetland tower. Old-growth forests, although not large in aerial extent, could also be another large source of ER based on comparison of the Sylvania flux tower to Willow Creek (Desai et al., 2005), which recent continued observations at both sites corroborates (unpublished data). Results from the mature forest class showed moderate variation in ER across similar ecosystems, suggesting that replicated respiration measurements in wetlands, young forests and mature to old hardwood/mixed forests may uncover large ER sources. However, given the spatial extent of these three cover classes, they would need to have more than twice the currently observed ER for the multi-tower upscaling results to match WLF-observed ER. Such large respiration rates seem unlikely.

Land cover uncertainty analysis suggested that uncertainty in land cover and forest age alone cannot account for the differences in regional carbon flux. Almost all flux towers measured ER that was smaller than the WLF tall tower; therefore most combinations of land cover and forest age would produce ER lower than the tall tower in this simple scaling exercise. Nevertheless, the interaction of resolution, accuracy and flux footprints (He et al., 2002) should be considered in selecting spatial information on land cover.

Species-specific land cover classes are subject to lower accuracy than aggregated forest type classes, but may be required for adequate scaling. For example, a regional scaling of tree transpiration measurements compared well to WLF evapotranspiration fluxes, but required separation of aspen from maple land cover types (MacKay et al., 2002). Additionally, assignment of land cover types to ground based measurements can be complicated by the presence of mixed land cover types and stand age classes within the flux footprint. Plot-level observations reveal the existence of considerable quantities of white cedar and balsam fir (*Abies balsamea*) in the WLF landscape that occur in mixed forest stands, which are not separately categorized by WISCLAND.

Classification accuracy of wetlands can be particularly complicated. About 81% of all pixels classified as a wetland cover class in WISCLAND were actually wetland as observed in wetland inventory maps, an accuracy level slightly lower than level II forested classes, which had on average 92% accuracy (http://www.dnr.state.wi.us/maps/gis/datalandcover.html). Separation of shrub from forest wetland is subject to even lower accuracy. Land use change and forest succession since collection of WISCLAND data may be significant in this region (D. Ahl, 2005, personal communication).

Stand age analysis from FIA data is another source of error. We have not quantified these uncertainties. Our results also suggest that canopy height measurements, which serve both as a proxy for stand age and aboveground biomass, may be a better measure than stand age for variation in CO_2 flux with successional stage. Spatial measurements of canopy height or above-ground biomass could be derived from FIA, canopy lidar (Lim et al., 2003) or other remote sensing methods (Zheng et al., 2004).

Finally, we need to consider whether the WLF tall tower is an accurate measure of regional flux. Flux footprints are typically 10–100 times the measurement height and narrow, especially in the daytime convective conditions (Schmid, 2002; Wang et al., 2006). WLF fluxes are an agglomeration of multiple levels (30, 122 and 436 m), and at night, due to boundary layer decoupling of higher level flows, only 30 m data were used (Davis et al., 2003). Overrepresentation of a $\sim$200 m grass clearing surrounding the tower may have occurred when using nighttime estimates of NEE to compute ER. Multi-level error analyses (Ricciuto et al., submitted for publication) suggest that nighttime footprints were large enough to generally avoid undue influence from the grassy clearing. The footprint decomposition results (Wang et al., 2006) suggest that aspen and forested wetland sites have a disproportionate impact on the WLF tall tower compared to their prevalence in the region. Thus, additional footprint and cover analysis around the WLF tall tower is needed.

Quality control, missing data and land surface heterogeneity issues affect all the flux towers. The Ameriflux relocatable portable reference eddy flux system (http://public.ornl.gov/ameriflux/standards_roving.shtml) has been tested at three sites (WCR, UMB and SYL) with moderate to good results. Additional intersite instrument comparison is warranted, especially between open and closed-path infrared gas analyzer systems and other methodological differences (Baldocchi, 2003; Chen et al., 2004). Flux calculation methods for several systems have been verified with the Ameriflux gold standard files (http://public.ornl.gov/ameriflux/standards-gold.shtml). Significant non-representative flux anomalies have been observed and screened at some sites (Cook et al., 2004; Desai et al., 2005), but others may remain. Scaled component chamber flux measurements of ER at some sites were larger than (Bolstad et al., 2004) or smaller than (Tang et al., 2008) eddy covariance based estimates of ER, suggesting errors in either or both methods which require quantification (Chen et al., 2004). Horizontal and vertical advection have been shown to be significant at certain times of the day at the tall tower, though its influence on 30 m NEE was inferred to be less than 10% (Yi et al., 2000; Davis et al., 2003). Canopy-level towers may also be subject to advection related errors, especially at night.

3.6.3. *Other regional fluxes*

Recent studies using carbon dioxide mixing ratios and atmospheric budget based methods, regional inversions and/or ecosystem models to estimate regional fluxes in the region (Bakwin et al., 2004; Helliker et al., 2004; Nicholls et al., 2004) find good agreement between modeled regional flux estimates and monthly average fluxes observed at the tall tower, especially over the growing season. Since these methods in general agree with the observations at the tall tower, our regional upscaling has larger (more negative) regional NEE compared to these methods. Mixing ratio based methods are subject to other issues that might cause divergence from the WLF measurements including large concentration footprints (on the order of 10^6 m) (Gloor et al., 2001), the influence of fossil fuel emissions (Bakwin et al., 2004) and inaccurate descriptions of boundary layer transport. SiB ecosystem model based regional fluxes had slightly larger than observed tall tower midday NEE (Baker et al., 2003) and larger uptake in late afternoon (Denning et al., 2003). These results are consistent with our upscaling model observations and suggest that tall tower afternoon uptake was limited by factors not included in ecosystem models or observed by the canopy level flux towers, or alternatively, the tall tower suffered from non-uniform time-varying footprint-biased sampling. The Ecosystem Demography model, tuned to regional FIA data, showed monthly NEE more inline with the simple upscaling than the tall tower (Desai et al., 2007), leading some credence to the latter theory.

Remote sensing is another approach to quantifying regional fluxes. However, our results indicate remote sensing GEP algorithms that rely on look-up table biome-scale LUE may fail to accurately represent variability in GEP due to changes with successional stage. GEP for similar ecosystems can change by as much as 50% due to the changes in LUE and L_{ai} with stand age (Table 4). Comparisons of remotely sensed NASA EOS MODIS GPP to flux tower GEP suggest that while the remote sensing method was able to discern differences in GEP across latitudinal gradients, it had more trouble differentiating GEP within smaller regions with heterogeneous vegetation types (Heinsch et al., 2006). Growing season GEP variability by vegetation type was explained better by A_{max}, which could possibly be used as an alternative parameter for estimating GEP by remote sensing. It has also been suggested that species-specific LUE is more appropriate that biome-specific LUE in this region, due to the large within-biome spatial and temporal variability in this factor (Ahl et al., 2004).

This study focused on growing season (June–August) CO_2 fluxes, when flux differences across stands are largest. However, small differences in winter season fluxes across sites can lead to large variation in annual cumulative NEE. Winter respiration fluxes can respire as much as 50% of growing season GEP and its spatial variation is related to soil carbon availability and length of snow covered season (Brooks et al., 2005). CO_2 exchange in spring and fall is strongly controlled by vegetation phenology. Remote sensing based GEP methods often have difficulty in modeling CO_2 exchange in these times with rapidly changing leaf area (Heinsch et al., 2006). Therefore, future work should also focus on examining non-growing season fluxes from year-round measurements.

3.7. *Alternative factors impacting regional CO_2 flux*

In addition to sampling an adequate range of vegetation types and stand ages and accurately including cover amounts, a number of other factors, such as moisture/nutrient limitation, forest management and disturbance could also be important in the region for influencing regional CO_2 flux. Incorporating soil moisture into models of ER improved half-hourly correlations only by an average of 8%, though this improvement varied by stand type, L_{ai} and age (A.N. Noormets et al., submitted for publication). Soil moisture appears to be an important factor at the WLF tall tower (Ricciuto et al., submitted for publication), suggesting that it may have a larger impact on other unsampled ecosystems in the region. Variations in regional moisture, water table depth (Cook et al., in preparation) and radiative forcing (Noormets et al., 2004) have been shown to lead to variation in wetland carbon dioxide flux (Updegraff et al., 2001), methane flux (Shurpali and Verma, 1998; Werner et al., 2003) and wetland composition (Updegraff et al., 2001; Weltzin et al., 2003).

Various forest management plans are applied to both public and private forested lands, which have been shown to have an impact on CO_2 sink strength (Euskirchen et al., 2002; A. Noormets et al., submitted for publication; Reich et al., 2001), forest landscape structure (Crow et al., 1999), species or size-class composition (Gustafson et al., 2000) and stand age distribution (Frelich, 1995; Hurtt et al., 2002). Harvest leads to a net export of carbon into wood products, whose decomposition may occur outside the region and over long timescles. Accounting for these effects are necessary for measuring net biome productivity (NBP) (Law et al., 2004). Rates of large-scale natural disturbance in the region are relatively low (Frelich and Lorimer, 1991), but rates vary by region (Bresee et al., 2004; Woods, 2000), species type/successional stage (Bresee et al., 2004; Dahir and Lorimer, 1996; Radeloff et al., 1999) and amount of forest fragmentation (Frelich and Reich, 1995). Different scale disturbances, from small-area disturbance "hot spots" (Saleska et al., 2003), to regional-scale forest fragmentation and edge effects (Brosofske et al., 1999; Euskirchen et al., 2001), to large-area recurring pest outbreaks (Cook et al., submitted for publication) have differential effects on landscape dynamics (Romme et al., 1998). Ecosystem models that can parameterize the effects of both prescribed large-scale disturbance and stochastic small scale disturbances, such as the Ecosystem Demography (ED) model (Desai et al., 2007; Moorcroft et al., 2001), LANDIS (He and Mladenoff, 1999; Scheller and Mladenoff, 2005), LandNEP (Euskirchen et al., 2002) or RegCarb (Song and Woodcock, 2003), may be better suited for modeling regional CO_2 flux and explaining observed CO_2 flux variability than simpler process models.

4. Conclusions

The results from this study showed that:

(1) Significant variations were found in growing season NEE, ER, GEP and associated parameters among forest stands within a regional-scale heterogeneous landscape that had contiguous external meteorological forcing. Variations in NEE were occasionally larger than the magnitude of NEE at the sites. Both ER and GEP were important for explaining differences in growing season NEE across sites in our study.

(2) Spatial variations in NEE, ER and GEP were correlated with differences in ecosystem type, canopy height and stand age. Many of these variations followed expected patterns as a function of vegetation type and stand age, but these factors alone cannot explain all observed variability, suggesting that other factors, such as moisture/nutrient limitation may also need to be considered for this region.

(3) While vegetation type had a strong effect on spatial variation of NEE, ER and GEP, its effect on CO_2 fluxes must first be segregated by stand age since disturbance. The effect of stand age on fluxes was stronger on the hardwood successional sequence than the red pine successional sequence. Canopy height had stronger correlation to CO_2 fluxes than stand age, suggesting that maps of canopy height may improve regional CO_2 flux estimates. However, given the lack of replicates in the chronosequence sites, these conclusions should only be considered preliminary.

(4) Traditional biome-based scaling parameters such as LUE and Q_{10} were not sufficient for explaining variability across all sites. Other parameters such as A_{max} and R_{10} were more important for determining variation across vegetation type and stand age. Thus, flux towers can play an important role in determining both optimal choice and number of parameters needed for regional scaling (Aalto et al., 2004; Braswell et al., 2005; Wang et al., 2001) and reducing uncertainty in model parameters (White et al., 2000).

(5) Seasonal temporal variability of CO_2 fluxes and parameters at any one site was significant, but about half the magnitude of variations across space. The sign of change in NEE across years was consistent at most sites with more than 1 year of data, but changes in ER and GEP were not, reflecting differential ecosystem effects in response to seasonal forcing, though these results are limited by the short time span of available data at most sites.

(6) Bottom-up multi-tower aggregation of flux data to a regional 2000 km^2 aggregate showed GEP that was similar to growing season GEP measured from a very tall eddy flux tower, but ER that was smaller by 30%. However, tall tower and multi-tower aggregated fluxes were in closer agreement when using a land-cover and flux footprint influence model to decompose and re-aggregate tall tower observations. Despite the dominance of mature hardwood forest in the region, both younger sites and wetland sites had large impacts on regional aggregated flux estimates.

Well-placed eddy flux towers in ecosystems representing the dominant sources and sinks along with less intensive measurements across gradients and processes important to the region can enable regional upscaling of CO_2 fluxes. An effective sampling strategy, however, is essential to success. Our study suggests that both vegetation type (especially forested vs. non-forested) and stand age must be sampled in Upper Midwestern forests to represent regional CO_2 flux variability accurately. Exploring variability of ER in under-sampled regions and replicating measurements in dominant cover types to assess intrinsic variability within any one cover type/age class would improve our ability to upscale fluxes across the region. Temporary roving flux towers have proven to be a useful tool in this endeavor. Independent regional flux estimates such as tall-tower flux measurements or boundary layer budgets are necessary for evaluating these upscaling approaches.

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