Respiratory carbon losses and the carbon-use efficiency of a northern hardwood forest, 1999–2003

P. S. Curtis[1], C. S. Vogel[2], C. M. Gough[1], H. P. Schmid[3], H.-B. Su[4] and B. D. Bovard[5]

[1]Department of Evolution, Ecology, and Organismal Biology, Ohio State University, Columbus, OH 43210, USA; [2]University of Michigan Biological Station, Pellston, MI 49769, USA; [3]Department of Geography, Indiana University, Bloomington, IN 47405, USA; [4]Department of Geography, East Carolina University, Greenville, NC 27858, USA; [5]Department of Environmental Studies, Florida International University, Miami, FL 33199, USA

Author for correspondence:
Peter S. Curtis
Tel: +1 614 292 0835
Fax: +1 614 292 2030
Email: curtis.7@osu.edu

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Summary

- Quantitative assessment of carbon (C) storage by forests requires an understanding of climatic controls over respiratory C loss. Ecosystem respiration can be estimated biometrically as the sum (R_Σ) of soil (R_s), leaf (R_l) and wood (R_w) respiration, and meteorologically by measuring above-canopy nocturnal CO_2 fluxes (F_{cn}).
- Here we estimated R_Σ over 5 yr in a forest in Michigan, USA, and compared R_Σ and F_{cn} on turbulent nights. We also evaluated forest carbon-use efficiency ($E_c = P_{NP}/P_{GP}$) using biometric estimates of net primary production (P_{NP}) and R_Σ and F_{cn}-derived estimates of gross primary production (P_{GP}).
- Interannual variation in R_Σ was modest (142 g C m^{-2} yr^{-1}). Mean annual R_Σ was 1425 g C m^{-2} yr^{-1}; 71% from R_s, 18% from R_l, and 11% from R_w. Hourly R_Σ was well correlated with F_{cn}, but 11 to 58% greater depending on the time of year. Greater R_Σ compared with F_{cn} resulted in higher estimated annual P_{GP} and lower annual E_c (0.42 vs 0.54) using biometric and meteorological data, respectively.
- Our results provide one of the first multiyear estimates of R_Σ in a forested ecosystem, and document the responses of component respiratory C losses to major climatic drivers. They also provide the first assessment of E_c in a deciduous forest using independent estimates of P_{GP}.

Key words: carbon cycle, ecosystem, eddy covariance, gross primary productivity (GPP), leaf, respiration, soil, wood.

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Introduction

Carbon cycling by terrestrial vegetation directly affects the chemical and biological properties of an ecosystem's solid, aqueous and gas-phase components, as well as sustaining human requirements for terrestrial sources of food, fuel and fiber. Elements of this cycle have been studied for many years, and for most widespread vegetation types the essential components of the C cycle are well understood and at least qualitatively well described (Geider *et al.*, 2001). However, a quantitative and temporally dynamic assessment of the terrestrial C cycle is of increasing interest because of concerns over anthropogenic alterations of atmospheric CO_2 concentration and the possibility of managing natural vegetation for enhanced C storage (Malhi *et al.*, 2002). Importantly, advancements in sensor technology over the past 20 yr have enabled measurements of CO_2 exchange at multiple scales and with a precision and speed that allow such an assessment (Baldocchi *et al.*, 1996).

A prominent part of current discussions of the terrestrial C cycle is how climate and ecosystem characteristics interact to affect the potential of vegetation and associated soils to store C and help mitigate anthropogenic emissions of CO_2 or, conversely, how these interactions might stimulate C loss and accelerate the rate of atmospheric CO_2 buildup (Melillo *et al.*, 2002; Pendall *et al.*, 2004; Xiao & Moody, 2004). An ecosystem's short-term C storage or loss rate in large part represents the difference between gross primary production (P_{GP}) and the combined release of CO_2 from the respiratory metabolism of autotrophs (R_a) and heterotrophs (R_h). Ecosystem respiration

(R_e) is the sum of R_a and R_h (see Table 1 for a list of variables used). While the accurate measurement of either P_{GP} or R_e presents formidable challenges, quantification of R_e has proven particularly difficult because of gaps in our understanding of the regulatory biochemistry of respiration, and the spatially complex and interdependent array of component sources of respiratory CO_2 release, including leaves, stems, roots, soil invertebrates, fungi and bacteria (Gifford, 2003).

Several different approaches have been used for estimating R_e: the biometric approach, in which measurements of respiratory fluxes from individual ecosystem components are scaled to a common land surface area basis and summed (R_Σ); the meteorological approach, which is based on eddy covariance measurements of nocturnal CO_2 fluxes (F_{cn}) including canopy air-layer storage fluxes; and diverse modeling approaches, which generally involve a combination of basic physiological principles and empirical relationships (Mäkelä *et al.*, 2000). While there is now a substantial database of short-term R_e estimates (e.g. Sanderman *et al.*, 2003), only rarely have annual measurements, or intercomparison of results from different measurement methods, been made. Ryan *et al.* (1997) used a biometric approach in several Canadian forests and estimated that annual R_a ranged from a low of 535 g C m^{-2} yr^{-1} in *Pinus banksiana* forests to a high of 908 g C m^{-2} yr^{-1} in *Populus tremuloides* stands. However, growing-season R_Σ was poorly correlated with F_{cn} and, on average, 36% higher (Lavigne *et al.*, 1997). Law *et al.* (1999b) reported the first full annual assessment of R_Σ. In the mixed-age *Pinus ponderosa* forest they studied, R_Σ was moderately correlated with F_{cn} and of similar magnitude during calm nights, but poorly correlated and up to 50% greater on turbulent nights. Bolstad *et al.* (2004) reported comparatively high annual R_Σ (up to 1469 g C m^{-2} yr^{-1}) in mature *P. tremuloides* stands and, although R_Σ also was moderately correlated with F_{cn}, it was up to 300% higher. Wang *et al.* (2004) estimated annual R_e in a Finnish *Pinus sylvestris* forest using both modeling and meteorological approaches. Their biophysical model, parameterized with respiratory data from the same site, showed an average R_e of 611 g C m^{-2} yr^{-1}, which did not differ significantly from F_{cn}-based estimates. These results indicate continued uncertainty regarding the accuracy of R_e estimates, and clearly support the suggestion of Canadell *et al.* (2000) that multiple approaches to estimating C-cycle components is a necessary element of climate-change research.

An ecosystem's C-storage potential is also reflected in the carbon-use efficiency (E_c) of its plant community, or the fraction of P_{GP} converted to net primary production (P_{NP}). That is, $E_c = P_{NP}/P_{GP}$. As $P_{GP} = P_{NP} + R_a$, E_c is inherently sensitive to factors affecting plant respiration. For forests, determination of E_c is made difficult primarily by uncertainties surrounding measurements of P_{GP} (Mäkelä *et al.*, 2000). Biometric, meteorological and modeling approaches have each been used, and P_{GP} estimates of similar forest types may vary considerably. For example, Janssens *et al.* (2001) summarized P_{GP} estimates from eddy covariance data above European forests and found an average uptake of 1340 g C m^{-2} yr^{-1} for less disturbed stands, including both evergreen and deciduous forests. However, the 'Pipestem' model of Mäkelä & Valentine (2001) predicted a minimum of ≈4000 g C m^{-2} yr^{-1} for mature Scots pine growing in northern Europe, well outside the range of values reported by Janssens *et al.* (2001). Modeled P_{GP} for eastern North American forests (2000–2900 g C m^{-2} yr^{-1}, White *et al.*, 1999) was also substantially higher than meteorological estimates from forests in this region (900–1500 g C m^{-2} yr^{-1}, Falge *et al.*, 2002). However, biometric estimates of P_{GP} from old growth *Pseudotsuga menziesii* (Harmon *et al.*, 2004) were within 25% of meteorological estimates from the same site (Paw *et al.*, 2004). Differences among P_{GP} estimates of the order 20–50%, not unreasonable given different estimation approaches, would translate into proportional differences in estimated E_c. Independent estimations and comparisons among sites and years will be necessary to resolve these differences and improve the utility of this measure in assessing forest C-storage potential.

Our objectives were to quantify R_e within an aspen-dominated mixed hardwood forest typical of the northern Great Lakes region of continental North America, and to partition this respiratory CO_2 flux into its primary source components of soil respiration (R_s), leaf respiration (R_l) and above-ground live wood respiration (R_w). The hardwood forests of this region cover ≈29×10^6 ha in the USA alone (USDA, 2001) and support a diverse forest products and recreational economy, as well as providing important ecological goods and services. Among the latter, C sequestration has received increased attention, and these ecosystems may play an important role in the suspected North American C sink (Fan *et al.*, 1998). We were interested in how different climatic factors affected these sources of respiratory CO_2 and how these fluxes varied interannually. We applied both biometric and meteorological approaches to estimate R_e and used these results to quantify forest E_c. Our results also contribute to the comparative database on ecosystem C-cycle dynamics that is a central objective of the multinational Fluxnet program (Baldocchi *et al.*, 2001).

Materials and Methods

Study site

Our study was conducted at the University of Michigan Biological Station (UMBS) in northern Michigan, USA (45°35′35.4″ N, 84°42′46.8″ W), in the transition zone between the mixed hardwood and boreal forests. The study site lies on a gently sloping high outwash plain with well drained spodosolic soils (92.9% sand, 6.5% silt, 0.6% clay, pH 4.8) derived from glacial drift and classified as entic haplorthods. Mean (1942–2003) annual temperature is

Table 1 Variables used and their description

Variable	Description
A_b	Bole basal area (m^2 ha^{-1})
A_l	Leaf area index (m^2 m^{-2})
A_{lmax}	Maximum annual A_l (m^2 m^{-2})
C_{af}	CO_2 concentration immediately above the forest floor (μl l^{-1})
D	Bole diameter at 1.3 m (cm)
E_c	Carbon-use efficiency (dimensionless)
E_{cb}	Biometric annual E_c (dimensionless)
E_{cm}	Meteorological annual E_c (dimensionless)
F_c	Above-canopy net CO_2 flux (μmol CO_2 m^{-2} s^{-1})
F_{cd}	Daytime F_c (μmol CO_2 m^{-2} s^{-1})
F_{cn}	Nocturnal F_c (μmol CO_2 m^{-2} s^{-1})
F'_{cn}	Estimated daytime R_e based on measured F_{cn} (μmol CO_2 m^{-2} s^{-1})
M_{aw}	Above-ground wood mass (g m^{-2})
M_{cl}	Fine litter C mass (g m^{-2})
p	Proportional contribution of a species to A_{lmax}
P_{fr}	Annual fine root mass production (g m^{-2} yr^{-1})
P_l	Annual leaf mass production (g m^{-2} yr^{-1})
P_w	Annual above- and below-ground wood mass production (g m^{-2} yr^{-1})
P_{NP}	Net annual primary production (g C m^{-2} yr^{-1})
P_{GP}	Gross annual primary production (g C m^{-2} yr^{-1})
Q_{10}	Temperature-response coefficient (dimensionless)
R_a	Autotrophic respiration rate (μmol CO_2 m^{-2} s^{-1}, g C m^{-2} yr^{-1})
R_e	Ecosystem respiration rate (μmol CO_2 m^{-2} s^{-1}, g C m^{-2} yr^{-1})
R_h	Heterotrophic respiration rate (μmol CO_2 m^{-2} s^{-1}, g C m^{-2} yr^{-1})
R_l	Leaf respiration rate, land surface area basis (μmol CO_2 m^{-2} s^{-1}, g C m^{-2} d^{-1}, g C m^{-2} yr^{-1})
R_{li}	Mean hourly R_l (μmol CO_2 m^{-2} s^{-1})
R_{la}	Leaf respiration rate, leaf area basis (μmol CO_2 m^{-2} s^{-1})
R_{lai}	Mean hourly R_{la} (μmol CO_2 m^{-2} s^{-1})
R_{l15}	R_{la} normalized to 15°C (μmol CO_2 m^{-2} s^{-1})
R_{lg}	Leaf growth respiration rate (g C m^{-2} h^{-1})
R_s	Soil respiration rate, land surface area basis (μmol CO_2 m^{-2} s^{-1}, g C m^{-2} d^{-1}, g C m^{-2} yr^{-1})
R_{s10}	R_s normalized to 10°C (μmol CO_2 m^{-2} s^{-1})
R_{si}	Mean hourly R_s (μmol CO_2 m^{-2} s^{-1})
R_w	Above-ground wood respiration rate, land surface area basis (μmol CO_2 m^{-2} s^{-1}, g C m^{-2} d^{-1}, g C m^{-2} yr^{-1})
R_{wi}	Mean hourly R_w (μmol CO_2 m^{-2} s^{-1})
R_{wv}	Wood respiration rate on a sapwood volume basis (μmol CO_2 m^{-3} s^{-1})
R_{wvi}	Mean hourly R_{wv} (μmol CO_2 m^{-3} s^{-1})
R_{w15}	R_{wv} normalized to 15°C (μmol m^{-3} s^{-1})
R_{Σ}	Sum of R_s, R_l, and R_w (μmol CO_2 m^{-2} s^{-1}, g C m^{-2} d^{-1}, g C m^{-2} yr^{-1})
T_a	Air temperature (°C)
T_{amin}	Minimum air temperature at which R_{la} measurements were made (°C)
T_{lref}	Leaf reference temperature (15°C)
T_s	Soil temperature (°C)
T_{si}	Mean hourly T_s (°C)
T_{sref}	Soil reference temperature (10°C)
T_w	Wood temperature (°C)
T_{wi}	Mean hourly T_w (°C)
T_{wmin}	Minimum wood temperature at which R_{wv} measurements were made (°C)
T_{wref}	Wood reference temperature (15°C)
$u*$	Friction velocity (m s^{-1})
V_{sw}	Sapwood volume (m^3 ha^{-1})
σ	Standard deviation of daily means
$\sigma_{\bar{R}}$	Standard error of $\bar{R}$
β_o, β_1	Regression coefficients (dimensionless)
θ_v	Volumetric soil water content (%)
θ_{vi}	Mean hourly θ_v (%)

Table 2 Stand characteristics of the 1.1 ha study plot detailing the abundance, mean height, mean diameter at breast height (D), bole basal area (A_b), above-ground mass (M_{aw}), sapwood volume (V_{sw}) and proportional contribution to maximum leaf area (p) of the dominant canopy tree species

Species	Stems (ha^{-1})	Height (m)	D (cm)	A_b (m^2 ha^{-1})	M_{aw} (Mg ha^{-1})	V_{sw} (m^3 ha^{-1})	p
Populus grandidentata	266	19.0 (0.2)	23.9 (0.3)	12.6	70	101	0.31
Pinus strobus	1373	5.7 (0.1)	6.7 (0.1)	7.1	17	26	0.09
Quercus rubra	124	12.1 (0.6)	15.7 (1.2)	4.3	33	11	0.24
Acer rubrum	300	11.2 (0.2)	10.7 (0.3)	3.4	11	19	0.22
Betula papyrifera	114	12.8 (0.4)	13.4 (0.6)	2.0	9	16	0.08
Fagus grandifolia	36	7.3 (0.5)	9.4 (0.7)	0.3	2	3	0.06
Total	2214			29.7	142	176	

All measures are from 2003 except height (1997) and p (mean across years). Standard errors for height and D are in parentheses.

5.5°C and annual rainfall 817 mm. The presettlement forest dominated by *Pinus strobus* L., *Pinus resinosa* Aiton. and *Tsuga canadensis* L. was cut starting in 1880 and disturbed repeatedly by subsequent cutting and fire until 1923 (Kilburn, 1960).

The forest within the 1.1 ha study plot surrounding our meteorological tower was dominated by *Populus grandidentata* Michx. (42% of total basal area, A_b), *P. strobus* (24% of total A_b), *Quercus rubra* L. (14% of total A_b), *Acer rubrum* L. (11% of total A_b), and *Betula papyrifera* Marsh. (7% of total A_b) (Table 2). Understory vegetation was primarily bracken fern (*Pteridium aquilinum* L.) and seedlings and saplings of *P. strobus* and *A. rubrum*. We used allometric equations to estimate above-ground (bole plus branch) wood mass (M_{aw}) from measurements of diameter at 1.3 m (D) of all individuals >3.0 cm D in the 1.1 ha plot (Curtis *et al.*, 2002). Annual above- and below-ground wood mass production (P_w) was estimated by measuring change in D using band dendrometers. Allometric equations were developed from on-site harvests (Cooper, 1981, A. W. Cooper, personal communication; Koerper, 1977) or from general allometries for north-eastern trees (Wiant *et al.*, 1977; Ker, 1980; Young *et al.*, 1980; Schmitt & Grigal, 1981; Crow & Erdmann, 1983; Hocker & Early, 1983; Perala & Alban, 1994; Ter-Michaelian & Korzukhin, 1997). Annual fine root mass production (P_{fr}) was calculated from estimates of fine root turnover from minirhizotron images and fine root standing stock from soil cores, and is described in more detail by Gough *et al.* (2005). Whole-tree sapwood volume (V_{sw}) was estimated on an annual basis from species-specific equations relating D to sapwood area described by Bovard *et al.* (2005), M_{aw}, and wood density measurements made on site or as reported by Perala & Alban (1994).

Changes in leaf area index (A_l) from leaf expansion through leaf abscision were monitored using an LAI-2000 Plant Canopy Analyzer (Li-Cor, Lincoln, NE, USA). Readings were taken every 3 m along seven transects in the 1.1 ha plot for an average of 120 samples on each of ≈12 sampling dates from May to November. Maximum A_l (A_{lmax}), the proportional contribution to A_{lmax} by each tree species (p), and annual leaf mass production (P_l) was measured each year using 20 litter traps (0.179 or 0.264 m^2) placed in a stratified random sample throughout the 1.1 ha plot. *Pinus strobus* retains its needles for 2 yr, dropping its oldest needles during the early summer of their third year (≈3 months after new needle expansion initiated), so its contribution to A_{lmax} and P_l was estimated as 2.25 times that recovered in litter traps. The contribution of *P. aquilinum* to A_{lmax} was estimated from a census of frond density and area in 60 1 m^2 subplots distributed randomly within the 1.1 ha plot.

In addition to the 1.1 ha plot, we established 60 0.1 ha plots located at 100 m intervals along radial transects extending up to 1000 m from the center of the 1.1 ha plot. Transects were located 20° apart from 255° to 15°, the primary wind direction in this area. Thus these plots allowed periodic sampling more extensively within the meteorological tower source footprint area (Schmid, 1997). Vegetation in the 0.1 ha plots was measured as described above, and was very similar in species composition to that in the 1.1 ha plot, again dominated by *P. grandidentata* (37% of A_b), *P. tremuloides* (17% of A_b), *B. papyrifera* (9% of A_b), *Q. rubra* (9% of A_b), and *A. rubrum* (18% of A_b), but with relatively less *P. strobus* (3% of A_b). Site index (base age 50 yr) of the 1.1 ha plot and eight of the 0.1 ha plots was calculated for *P. grandidentata* using equations from Lundgren & Dolid (1970) where the age of dominant overstory trees was estimated from growth rings.

Soil respiration

Point measurements Point measurements of soil respiration (R_s, µmol m^{-2} s^{-1}) were made using an LI-6400 portable photosynthesis system and LI-6400-09 soil CO_2 flux chamber (Li-Cor). In the absence of snow cover, the chamber was placed on 0.10 m diameter polyvinyl chloride (PVC) collars inserted ≈0.02 m into the forest floor. These collars were put in place in 1998. Within the 1.1 ha plot there were eight R_s measurement stations, and at each station there were three collars spaced 1 m apart. Stations were placed randomly within each of eight quadrats covering the entire plot (stratified random sampling). Leaf litter was left in the collars, although any woody debris was removed. During periods of snow cover the existing soil respiration collars were incrementally increased in length as snow depth increased, with interlocking PVC rings, such that soil respiration was measured through the existing snow pack. Measurement protocol followed standard operating procedure for this instrument: ambient CO_2 concentration just above the forest floor (C_{af}) was measured and, following manual placement of the chamber on the collar, the internal chamber CO_2 concentration was lowered 5–25 ppm below C_{af} and then allowed to rise the same amount above C_{af}. Recorded values of R_s represent the last of three cycles of CO_2 accumulation and lowering within the chamber. Measurements were made at varying times throughout the year: during the summer R_s typically was measured twice per week, but during the winter only twice per month. On a measurement day, one measurement was taken at each station, with the specific collar used alternating at random among measurement days. At each measurement station there were thermocouples inserted at 0.02 and 0.075 m into the soil, and one 0.30 m time domain reflectometry (TDR) probe (ESI model MP-917, ESI, Victoria, British Columbia, Canada). Point measurements of soil temperature (T_s) and volumetric soil water content (θ_v) were recorded immediately following R_s measurements. R_s was also measured four times during the 2000 growing season in 30 0.1 ha plots.

Exponential functions of the form:

$$\bar{R}_s = \beta_0 * e^{\beta_1 * \bar{T}_s} \qquad \text{Eqn 1}$$

were fitted to point measurements from the 1.1 ha plot using SIGMAPLOT (Systat Software, Inc., Richmond, CA USA), where $\bar{R}_s$ and $\bar{T}_s$ are the means ($n = 8$) of R_s and T_s, respectively, across measurement stations on a single day. Using this expression, the temperature coefficient, $Q_{10} = e^{\beta_1 * 10}$. Note that for soil, leaves and wood, equation 1 was developed from temperature measurements made over the course of weeks to months. Hence estimates derived from this equation necessarily reflect long-term rather than short-term temperature responses.

Curves were fitted separately for three phenological periods each year: winter, between day 280 (approximate beginning of leaf abscision) in 1 yr and day 129 (approximate beginning of leaf expansion) the following year; early season, between day 130 and day 200 (approximate mid-growing season); and late season, between days 201 and 279. Residuals from these regressions were analyzed further as either linear or logarithmic functions (based on r^2) of θ_v using SIGMAPLOT. Soil respiration at a soil reference temperature (T_{sref}) of 10°C (R_{s10}) was estimated from equation 1, and its standard error, $\sigma_{\bar{R}_{s10}} = \sigma/\sqrt{n}$, where n is the number of days R_s was measured during each phenological period and σ is the standard deviation among daily means. Statistical comparisons among temperature-normalized respiration rates were made using Tukey's test at $P < 0.05$.

To assess spatial variability in R_s within the eddy covariance tower footprint, we compared predicted values in the 1.1 ha plot with point measurements made in plots located up to 1000 m from the tower in the direction of the prevailing north-west winds. For this analysis, R_s, T_s and θ_v were measured in 30 0.1 ha plots on four dates in late summer 2000 (days 214–259). Predicted R_s values were generated using the late-season 2000 R_s model specific to the 1.1 ha plot, and T_s and θ_v input values from 0.1 ha plots. Predicted R_s values were compared directly with actual point measurements made in the 0.1 ha plots to evaluate the agreement between R_s in the 1.1 and 0.1 ha plots at common T_s and θ_v. Confidence intervals for predicted R_s values in the 1.1 ha plot were generated using the PROC NLIN procedure in SAS (SAS ver. 8.2; SAS Institute; Cary, NC, USA).

Scaling Point measurements of all respiratory components were scaled to a common soil surface area basis following the methods of Ryan *et al.* (1997). Mean hourly R_s (R_{si}, µmol m^{-2} s^{-1} for the *i*th hour) throughout the year was estimated from mean hourly T_s (T_{si}) and θ_v (θ_{vi}) by:

$$R_{si} = R_{s10} \times Q_{10}^{(T_{si} - T_{sref})/10} + f(\theta_{vi}) \qquad \text{Eqn 2}$$

where $f(\theta_{vi})$ was the linear or logarithmic function from the residual analysis described above. The standard error of R_{si}, $\sigma_{\bar{R}_{si}}$, was estimated as $\sigma_{\bar{R}_{s10}} \times Q_{10}^{(T_{si} - T_{sref})/10}$. This ignores any effects of $f(\theta_{vi})$ on $\sigma_{\bar{R}_{si}}$ and hence is a conservative error estimate as $f(\theta_{vi})$, where significant, increases the precision of R_{si} estimates. Soil temperature was measured continuously at 0.075 m depth in three locations spaced ≈10 m apart. Soil water content was continuously measured at one location in 1999 and at four locations in all other years using a CS616 soil moisture probe (Campbell Scientific, Logan, UT, USA). Output from the CS616 probes was calibrated against the TDR probes used for point measurements. Our T_s and θ_v point measurements encompassed the full range of continuous T_s and θ_v measurements. Daily and annual R_s are the sums of estimated hourly fluxes across 24 h and 1 yr, respectively. The standard error of annual R_s was estimated as the sum of hourly $\sigma_{\bar{R}_{si}}$.

Leaf respiration

Point measurements Point measurements of leaf dark respiration (R_{la}, µmol m^{-2} s^{-1} expressed on a leaf area basis) for all tree species were measured at night on fully expanded detached leaves using an LI-6400. For *P. aquilinum*, R_{la} was measured at night on attached fronds and during the day on attached, darkened fronds for ambient air temperature (T_a) > 20°C. Leaf temperature in the cuvette was maintained to within ≈0.5°C of T_a. Measurements on all species except *P. strobus* were corrected for overestimation of R_{la} caused by gas flow beneath the gaskets of the LI-6400 cuvette (Pons & Welschen, 2002; unpublished data).

Measurements were conducted in the 1.1 ha plot over multiple days in 1999 and 2001. For the four canopy-level hardwood species, R_{la} was typically measured in six upper-canopy and six lower-canopy leaves per night, although in some cases the sample size was less. These leaves came from the two or three trees of each species we could reach from our two canopy access towers. Understory *P. strobus* and *P. aquilinum* leaves were accessed from the ground. The number of nights that measurements were taken varied among species, ranging from one for *B. papyrifera* to nine for *P. aquilinum*. As measurements were made on fully expanded tissue, R_{la} was assumed to represent primarily local maintenance respiration plus some additional growth-dependent costs such as phloem loading (Amthor, 2000).

Measurements were averaged across leaves within a species and canopy position to yield mean daily point values ($\bar{R}_{la}$ and $\bar{T}_a$). These data were combined into three groups that showed similar absolute magnitude of $\bar{R}_{la}$ and responses to temperature: *P. grandidentata* and *Q. rubra*; *A. rubrum* and *B. papyrifera*; and *P. strobus* and *P. aquilinum*. Exponential functions as in equation 1 were fitted to these mean daily values to derive estimates for regression coefficients β_0 and β_1 for each group.

Scaling Leaf respiration at a leaf reference temperature (T_{lref}) of 15°C (R_{l15}) was estimated from equation 1. Mean hourly R_{la} (R_{lai}, μmol m^{-2} s^{-1}) throughout the year was estimated from R_{l15} and mean hourly T_a (T_{ai}) as in equation 2 but with no θ_v effects. Air temperature was measured continuously at one location 21 m above the forest floor. The minimum air temperature at which R_{la} measurements were made (T_{amin}) generally was consistent with minimum T_{ai} during the leaf expansion period for the deciduous species, and the fitted exponential function was used for all T_{ai} without modification. This was not true, however, for the evergreen *P. strobus*. For that species we assumed a linear decline in R_{lai} between $T_{ai} = T_{amin}$ (= 14.5°C) and T_{ai} = 0°C, and that R_{lai} = 0 when $T_{ai} \leq$ 0°C.

Mean hourly leaf respiration on a leaf area basis was scaled to a land surface area basis (R_{li}, μmol m^{-2} s^{-1}) by:

$$R_{li} = R_{lai} \times p \times A_l \qquad \text{Eqn 3}$$

For the deciduous species, A_l was assumed to increase linearly during leaf expansion and decline linearly during leaf abscision. Leaf growth respiration (R_{lg}) was estimated from P_l and a mass-based model that assumes 0.25 g respiratory CO_2 produced per g tissue constructed (Cannell & Thornley, 2000), and this respiratory cost was evenly distributed across days during leaf expansion. Daily and annual R_l are the sums of R_{li} across 24 h and 1 yr, respectively, except during leaf expansion when R_{lg} was added. Standard errors of R_{l15}, R_{li} and annual R_l were estimated as for R_s.

Above-ground wood respiration

Point measurements Point measurements of above-ground wood respiration expressed on a sapwood volume basis (R_{wv}, μmol m^{-3} s^{-1}) were measured in the 1.1 ha plot using a custom cuvette attached to an LI-6400. The cuvette was similar to that described by Xu *et al.* (2000), fashioned from opaque PVC, and its operation was analogous to that of the LI-6400-09 soil CO_2 flux chamber. Plastic collars, 0.10 m in diameter, were sealed to boles at ≈1.3 m above ground using silicone caulk, and left in place. For smaller diameter trees 0.052 m collars were used. The cuvette was attached to the collar with wire springs and respiratory CO_2 was allowed to accumulate within the cuvette. Cuvette air was stirred with a small fan and circulated in a closed loop to the infrared gas analyzer of the LI-6400. The volume of the cuvette, tree collar, and associated tubing averaged 0.40 l for the large tree cuvette and 0.15 l for the small tree cuvette. Bole respiration was calculated from the rate of increase in cuvette air CO_2 concentration as described above for R_s. Adjacent to each collar, a thermocouple was inserted to 0.01 m depth and wood temperature (T_w) was recorded during each R_{wv} measurement. Because D increases throughout the growing season, early and late-season R_{wv} included both growth and maintenance respiration, while winter R_{wv} was primarily maintenance respiration (Nelson, 1994). Respiratory CO_2 deriving from above-ground dead wood (coarse woody debris), either standing or down, was not considered in this analysis.

Wood respiration was measured on five tree species over multiple days in 1999–2001. Generally, only one or two species were measured on a given day. For the majority of days, at least three individuals per species were measured although this number ranged from one to nine. Measurements across individuals within a species were averaged to yield mean values for a given day ($\bar{R}_{wv}$ and $\bar{T}_w$). Exponential functions as in equation 1 were fitted to these mean daily values to derive estimates of regression coefficients β_0 and β_1 for each species. Curves were fitted separately for the three phenological periods in each year as described above.

Scaling Wood respiration at a reference temperature (T_{wref}) of 15°C (R_{w15}) was estimated from equation 1. Mean hourly R_{wv} (R_{wvi}, μmol m^{-3} s^{-1}) throughout the year was estimated from mean hourly T_w (T_{wi}) as in equation 2, but with no θ_v effects. Bole temperature was measured continuously on four trees throughout the year. The minimum bole temperature at which R_{wv} measurements were made (T_{wmin}) was not below ≈6°C for any species, although winter T_{wi} was often well below 0°C. Rather than extrapolating the fitted temperature relationship beyond T_{wmin}, we assumed a linear decline in R_{wvi} between $T_{wi} = T_{wmin}$ and T_{wi} = 0°C, and that R_{wvi} = 0 when $T_{wi} \leq$ 0°C.

Mean hourly bole respiration was scaled to a land surface area basis (R_{wi}, μmol m^{-2} s^{-1}) by:

$$R_{wi} = R_{wvi} \times \Sigma V_{sw} \qquad \text{Eqn 4}$$

where ΣV_{sw} is the summed individual tree V_{sw} within the 1.1 ha plot expressed per m^2 land area and incremented annually based on changes in *D*. Daily and annual R_w are the sums of R_{wi} across 24 h and 1 yr, respectively. Standard errors of R_{w15}, R_{wi}, and annual R_w were estimated as for R_s.

Above-canopy nocturnal CO_2 flux

We used eddy covariance methods to directly measure CO_2 exchanges between forest and atmosphere. Measurements were made at 46 m (approximately twice canopy height). Turbulent velocities were measured with a three-dimensional sonic anemometer (model CSAT-3, Campbell Scientific) and CO_2 concentrations were measured by a closed-path infrared gas analyzer (IRGA model Li-6262, LiCor). The anemometer and IRGA data were sampled at 10 Hz for calculation of above-canopy net CO_2 flux (F_c). As described by Schmid *et al.* (2003), hourly block averages of F_c were calculated from raw 10 Hz data from the anemometer and IRGA using Reynolds decomposition.

Nocturnal F_c (F_{cn}) was calculated for nights showing sustained periods of adequate turbulent mixing, defined as ≥4 h when the friction velocity (u^*) > 0.35 m s^{-1}. For nights meeting these criteria, we averaged F_c from all hours where u^* > 0.35 m s^{-1} to yield a mean F_{cn} (μmol m^{-2} s^{-1}). A total of 485 nights in years 1999–2001 met these criteria and were used in this analysis.

Ecosystem carbon-use efficiency

We calculated annual ecosystem E_c using biometrically and meteorologically derived estimates of P_{GP}. In both cases, P_{NP} was calculated as:

$$P_{NP} = P_w + P_l + P_{fr} \qquad \text{Eqn 5}$$

Biometric annual E_c (E_{cb}) was calculated as:

$$E_{cb} = P_{NP}/(P_{NP} + |R_a|) \qquad \text{Eqn 6}$$

where annual autotrophic respiration, $R_a = R_r + R_l + R_w$. Root respiration, R_r, was estimated as $0.5 \times R_s$ based on our analysis of root-free mineral soil and O-horizon respiration compared with total R_s (Gough *et al.*, 2005). This partitioning of soil autotrophic and heterotrophic components matches the average value reported by Hanson *et al.* (2000) but ignores likely seasonal variation in root compared with soil microbial respiration.

Meteorological E_c (E_{cm}) was calculated as:

$$E_{cm} = P_{NP}/\Sigma(F_{cd} + |F'_{cn}|) \qquad \text{Eqn 7}$$

where $\Sigma(F_{cd} + |F'_{cn}|)$ is the annual sum of hourly daytime ecosystem CO_2 flux (F_{cd}) plus the absolute value of estimated daytime ecosystem respiration for each hour based on measured nocturnal CO_2 fluxes (F'_{cn}). F'_{cn} was estimated from exponential functions as in equation 1 where hourly F_{cn} having u^* > 0.35 m s^{-1} was regressed against T_s measured at 0.02 m. Separate regressions were fitted for early season, late season and winter periods in each year. Gap-filling procedures for missing F_{cd} values were as described by Schmid *et al.* (2003).

Results

Climate and phenology

Patterns of T_a and T_s across the study period were typical for the upper Great Lakes region, with daily average T_a rarely exceeding 25°C during the summer, but remaining below 0°C for extended periods during the winter (Fig. 1a). Persistent snow cover during the winter effectively insulated the soil, with soil at 0.075 m rarely freezing (Fig. 1b). The winter of 2002/03 was exceptionally cold, however, resulting in T_s < 0°C for 90 d. Low T_a during this period resulted in 2003 having the lowest mean annual T_a and T_s of the 5 yr studied. Mean growing season (day 130–279) T_s was similar in 2000 and 2003, and highest in 1999. One late-winter thaw was recorded in 2000 before leaf expansion, when high T_a and a lack of snow cover resulted in increased T_s, followed thereafter by a return to colder temperatures before a sustained warming in the spring. Patterns of θ_v were also typical for this region and soil type, with rapid declines in θ_v in the absence of rainfall during the summer, but with few periods of θ_v < 10% lasting longer than ≈10 d (Fig. 1c).

The initiation of leaf expansion and leaf abscision was similar for years 1999–2001, which as a group were ≈15 d advanced in both measures relative to 2002–03 (Fig. 2). Maximum A_l measured from litter traps or assessed optically varied ≈20% during these years, being relatively higher in 2002 and 2003, and lower in 1999 and 2001. The majority of this leaf area was contributed by *P. grandidentata*, *Q. rubra* and *A. rubrum* (Table 2). The understory fern *P. aquilinum* contributed an additional 0.5 m^2 m^{-2} leaf area, and showed similar phenological timing to the canopy tree species.

Soil respiration

Soil respiration was well explained by seasonal variation in T_s and θ_v although the magnitude of R_s responses to these climate drivers varied across years (Table 3; Fig. 3). Winter R_s was never responsive to θ_v and showed little interannual variation in Q_{10} (data not shown), so a common temperature-response function was used during winter for all years. There was considerable interannual variation in the influence of θ_v on R_s during the growing season, however. During 1999, θ_v was a significant factor (P < 0.05) both early and late in the season, in 2003 θ_v was never significant, and in the remaining years

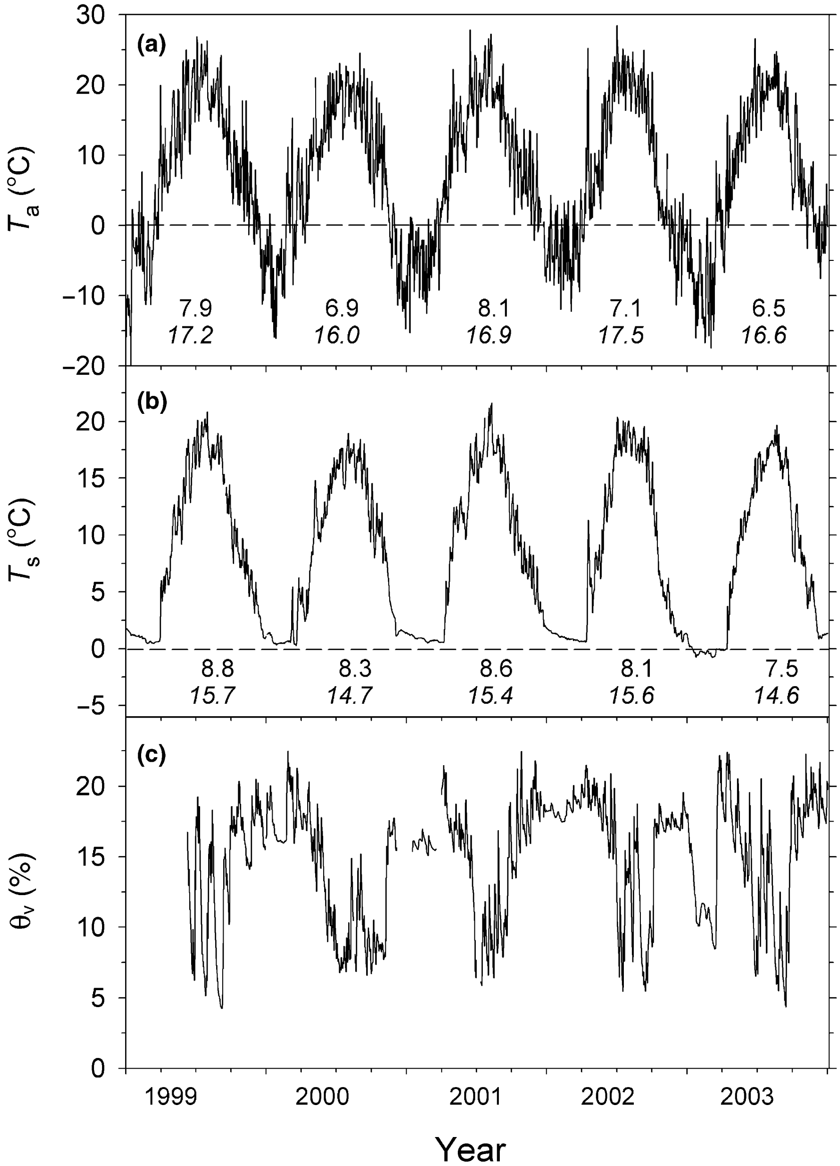

Fig. 1 Major environmental variables recorded in the 1.1 ha plot across the 5 yr study period: air temperature at 21 m (T_a, a), soil temperature at 0.075 m (T_s, b), and volumetric soil water content (θ_v, c). Mean annual and mean growing season (italic) T_a and T_s are shown for each year.

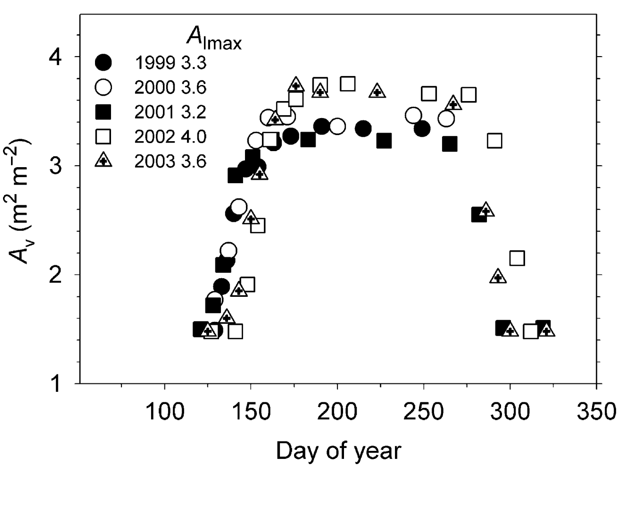

Fig. 2 Vegetation area index (A_v), measured optically and recorded between leaf expansion and leaf abscision of the deciduous canopy species in the 1.1 ha plot. Maximum leaf area index (A_{lmax}) for each year was measured from litter traps after leaf abscision.

its significance alternated among seasons (Table 3). Q_{10} varied between ≈2 and 3 across years, but there was no consistent rank order among seasons.

Soil respiration rates normalized to 10°C showed significant seasonal variation as well, but exhibited more consistent relationships across seasons (Table 3). Winter R_{s10} were consistently the lowest, averaging 2.3 μmol m^{-2} s^{-1} across years. Late-season R_{s10} was typically the highest, averaging 3.1 μmol m^{-2} s^{-1} across years compared with an average of 2.6 μmol m^{-2} s^{-1}

Table 3 Seasonal soil respiration rates (μmol m^{-2} s^{-1}) normalized to 10°C (R_{s10}), temperature response coefficients (Q_{10}) and the significance of soil water content [$f(\theta_v)$] in explaining residual variation in soil respiration across 5 yr in the 1.1 ha plot

Year	Season	R_{s10}	Q_{10}	$f(\theta_v)$	n
1999	Winter†	2.3 (0.08)[–]	2.87	ns‡	–
	Early	2.6 (0.10)[a]	3.14	**	28
	Late	3.5 (0.12)[b]§	2.12	**	18
2000	Winter	2.4 (0.10)[a]	2.87	ns	18
	Early	3.0 (0.10)[b]	1.96	ns	19
	Late	2.6 (0.10)[ab]	2.85	***	18
2001	Winter	2.4 (0.09)[a]	2.87	ns	19
	Early	2.7 (0.08)[b]	2.11	*	26
	Late	3.2 (0.09)[c]	2.06	ns	19
2002	Winter	2.2 (0.15)[a]	2.87	ns	8
	Early	2.4 (0.15)[a]	2.38	+	8
	Late	2.6 (0.16)[a]	2.66	***	7
2003	Winter	2.3 (0.21)[a]	2.87	ns	3
	Early	2.4 (0.11)[a]	3.16	ns	11
	Late	3.5 (0.12)[b]	2.02	ns	9
	Winter[1]	2.3 (0.08)[–]	2.87	ns	–

Early growing season was day 130–200; late growing season, day 201–279; winter, day 280 in year *x* – 1 through day 129 in year *x*, except in 1999 when winter began on day 1, and for the second winter period in 2003 which ended on day 365.
Standard error of R_{s10} shown in parentheses; *n* is the number of daily means included in the regressions.
†Generic models based on combined values across all winters.
‡+, $P < 0.1$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ns, $P > 0.1$.
§Similar superscripts within years indicate no significant difference, $P < 0.05$.

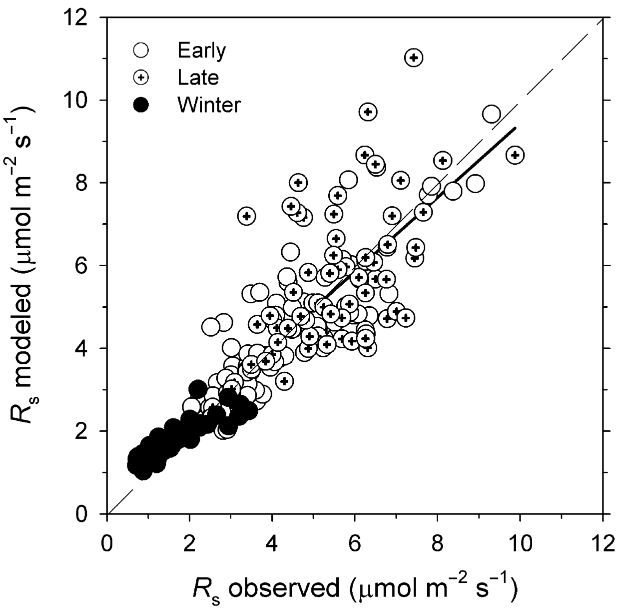

Fig. 3 Goodness of fit of modeled soil respiration (R_s) to observed R_s across seasons and years. Modeled values were derived from parameters shown in Table 2; observed values are daily means. Solid line, linear regression ($y = 0.48 + 0.90x$, $r^2 = 0.76$, $n = 211$); dashed line, 1 : 1 relationship.

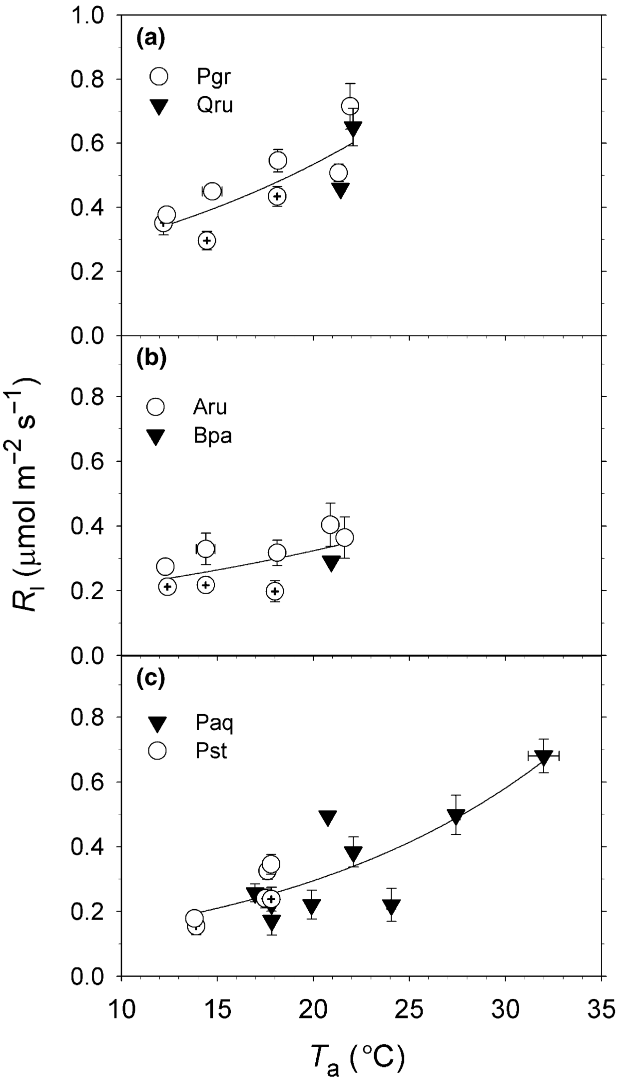

Fig. 4 Response of leaf respiration (R_l) to changes in ambient air temperature (T_a) in three groups of canopy species: (a) *Populus grandidentata* (Pgr) and *Quercus rubra* (Qru); (b) *Acer rubrum* (Aru) and *Betula papyrifera* (Bpa); (c) *Pteridium aquilinum* (Paq) and *Pinus strobus* (Pst). Symbols are nightly means and ±1 SE error in each variable. Open symbols, upper canopy leaves; crossed symbols, lower canopy leaves.

early in the season. Modeled R_s, based on these T_s and θ_v relationships, was well correlated with observed R_s (Fig. 3), with the slope of this relationship not differing significantly from 1 ($P = 0.76$; two-tailed *t*-test). There was a tendency for modeled R_s to overestimate observed R_s below 2 μmol m^{-2} s^{-1} and the model goodness-of-fit decreased with increasing R_s.

Leaf respiration

The temperature response of R_l was best characterized in three species: *P. grandidentata*, *A. rubrum* and *P. aquilinum* (Fig. 4),

Table 4 Species-specific leaf respiration (R_{l15}, μmol m^{-2} s^{-1}), above-ground wood respiration (R_{w15}, μmol m^{-3} s^{-1}), and their temperature response coefficients (Q_{10}) measured early (E) or late (L) in the growing season, or during winter (W)

		Species‡					
	Season	Pgr	Qru	Aru	Bpa	Pst	Paq
Leaf							
R_{l15}	E,L	0.6 (0.02)[a]†	0.6 (0.05)[a]	0.4 (0.02)[b]	0.3 (0.01)[bc]	0.2 (0.01)[c]	0.3 (0.04)[c]
Q_{10}	E,L	1.78	1.78	1.50	1.50	1.97	1.97
Bole							
R_{w15}	W	19.8 (2.10)[a]	101.8 (8.96)[a]	17.4 (1.85)[a]	29.5 (1.76)[a]	29.6 (2.47)[a]	
	E	41.4 (2.86)[b]	175.9 (10.05)[b]	37.4 (3.71)[b]	52.9 (4.05)[b]	48.4 (3.13)[ab]	
	L	42.1 (2.27)[b]	180.0 (8.94)[b]	26.0 (2.22)[b]	48.0 (3.28)[b]	42.4 (1.92)[b]	
Q_{10}	W	1.43	1.67	1.53	1.32	1.65	
	E	2.72	2.10	2.85	3.11	1.50	
	L	1.66	1.59	2.11	1.90	1.71	

Respiration rates are normalized to 15°C. Standard errors in parentheses.
†Similar superscripts indicate no significant difference, $P < 0.05$. Comparisons across species for R_{l15}, and across seasons within a species for R_{w15}.
‡Abbreviations as in Fig. 4.

which together accounted for >50% of A_{lmax}. More limited data were available for the remaining species, therefore each was combined with one of the first group based on similarity of response within the measured temperature range. *Populus grandidentata* and *Q. rubra* also had comparatively high leaf [N] (2.0 and 2.4%, respectively) relative to *A. rubrum* and *B. papyrifera* (1.5 and 1.8%, respectively). *Pinus strobus* and *P. aquilinum* were less similar in this regard (1.3 and 2.2% leaf [N], respectively) but both primarily grew in the understory and had similar R_l at T_a ≈18°C. For *P. grandidentata* and *A. rubrum*, upper canopy leaves had higher R_l compared with lower canopy leaves at similar T_a. Leaf respiration rates normalized to 15°C reflected these groupings (Table 4). *Populus grandidentata* and *Q. rubra* had significantly higher R_{l15} than all other species, *A. rubrum* was intermediate, followed by *B. papyrifera*, *P. strobus* and *P. aquilinum*. Temperature-response coefficients were fairly similar across species groups, averaging 1.75.

Wood respiration

There was considerable seasonal and interspecific variation in R_w (Fig. 5; Table 4). For all four deciduous species, Q_{10} and R_{w15} were highest early in the growing season and lowest during the winter. *Pinus strobus* showed little seasonal variation in Q_{10} but also lower R_{w15} during the winter. Note that R_{wv} was measured on only 2 d during the winter, but these days differed in T_w by >10°C. Among the diffuse porous deciduous species, *B. papyrifera* had the highest R_{w15} in each season and the highest mean annual R_{w15} ($P < 0.05$, Tukey's test), followed by *P. grandidentata* and *A. rubrum*. The high absolute R_{w15} in *Q. rubra* was caused by the comparatively small volume of sapwood in this ring-porous species.

Table 5 Yearly variation in total respiratory carbon loss (R_Σ) and its 5 yr mean in the 1.1 ha plot

Year	R_s	%	R_l	%	R_w	%	R_Σ
1999	1116 (43)	73	251 (11)	16	172 (23)	11	1538 (50)
2000	987 (37)	71	251 (11)	16	157 (21)	10	1396 (44)
2001	1005 (37)	71	237 (10)	17	171 (23)	12	1412 (45)
2002	946 (34)	67	292 (13)	21	165 (22)	12	1404 (43)
2003	960 (32)	70	250 (11)	18	165 (23)	12	1375 (41)
Mean	1003 (37)	71	256 (11)	18	166 (22)	11	1425 (45)

Absolute and percentage contribution of soil (R_s), leaf (R_l) and wood (R_w) respiration to R_Σ are shown together with the standard error in parentheses. The standard error of R_Σ was calculated as the quadratic sum of respiratory component standard errors. All units are g C m^{-2} yr^{-1}.

Daily and cumulative respiratory carbon losses

Continuous measurements of T_s, T_b, T_a and θ_v and the coefficients presented in Tables 3 and 4 were used to estimate daily respiratory C losses across years from soil, leaves and wood in the 1.1 ha plot (Table 5). In all years, R_s was the dominant component of R_Σ, contributing as much as 73% of the total flux (1999), with a 5 yr mean of 71%. Leaf respiration contributed on average 18%, and R_w 11% of R_Σ. There was relatively modest interannual variation in R_Σ, with 164 g C m^{-2}, or ≈10% of the 5 yr average, separating the lowest (2003) from the highest (1999) respiratory C-loss year. The largest difference in R_Σ between consecutive years was 142 g C m^{-2}, separating 1999 and 2000.

Within a year there was considerable variation in absolute rates of respiratory C loss, and the proportional contribution of soil, leaves and wood to that loss (Fig. 6). Considering

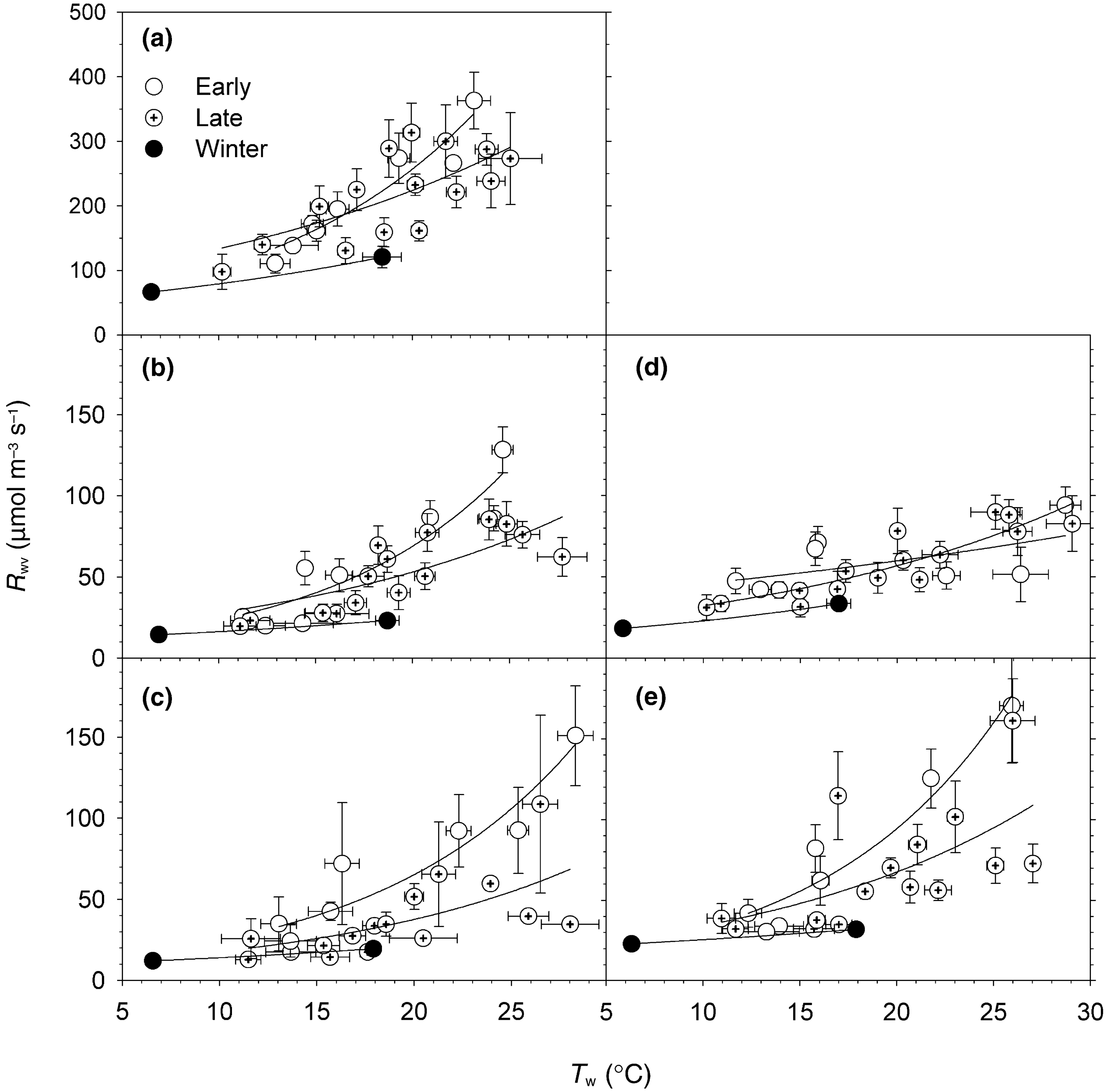

Fig. 5 Seasonal responses of above-ground wood respiration (R_{wv}) to changing wood temperature (T_w) in five tree species: *Quercus rubra* (a); *Populus grandidentata* (b); *Acer rubrum* (c); *Pinus strobus* (d); *Betula papyrifera* (e).

2001 as a typical year, R_s was >90% of R_Σ for most of the winter, with R_w contributing 10–20% in early spring or late autumn during periods of relatively warm T_a but outside the period of deciduous tree leaf development. Leaf respiration from the evergreen *P. strobus* was a negligible component of R_Σ during this period. Winter R_Σ averaged 1.5 g C m^{-2} d^{-1} (Fig. 7). In 2001, leaf expansion began on day 128 with 95% full leaf expansion observed on day 151. During this period, R_Σ rose dramatically and the relative contribution of R_s dropped to ≈60% (Fig. 6). The abruptness of the increase in R_l during leaf expansion reflects the combined inputs of annual growth and maintenance respiration. The relative contribution of R_s to R_Σ increased gradually during the growing season as soils warmed, reaching ≈75% at the time of leaf abscision in the autumn. Consequently, late-season R_Σ was typically higher than early season R_Σ (5 yr means, 8.5 and 6.9 g C m^{-2} d^{-1}, respectively, Fig. 7)

Comparison with eddy covariance measures

Measurement of F_{cn} using eddy covariance methods offers the opportunity for an independent assessment of R_Σ. However,

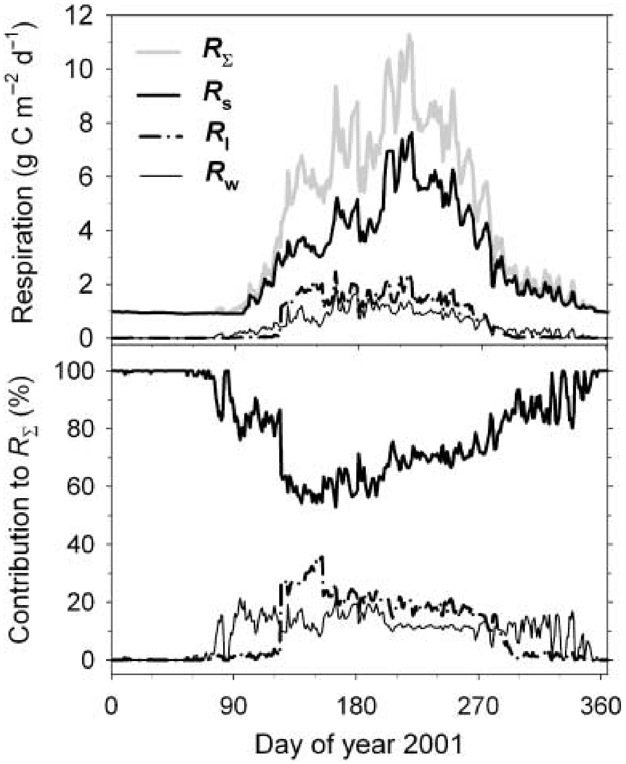

Fig. 6 Daily respiratory carbon loss in 2001 from soil (R_s), leaves (R_l), boles (R_w), and their sum (R_Σ) in the 1.1 ha plot (upper panel). Lower panel, percentage contribution of R_s, R_l and R_w to R_Σ.

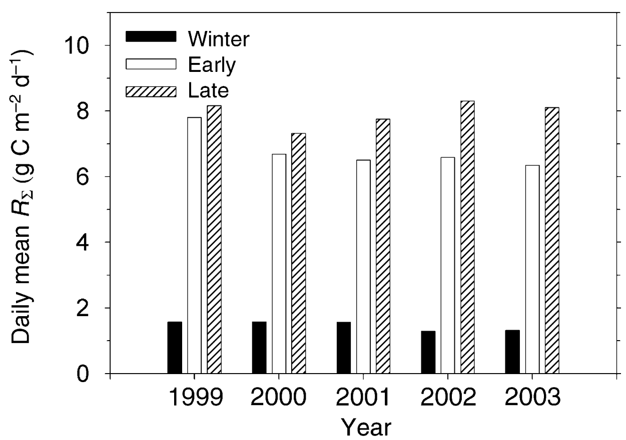

Fig. 7 Daily mean total respiratory carbon loss (R_Σ) across seasons and years in the 1.1 ha plot. Winter was day 1–129 and 280–365; early season, day 130–200; late season, day 201–279.

only a subset of our F_{cn} measurements was suitable for direct intercomparison. Of 1096 possible nights (1999–2001), 485 (44%) had ≥4 h of turbulent conditions ($u^* > 0.35$ m s^{-1}) from which a robust average F_{cn} could be calculated. Overall, F_{cn} and R_Σ were well correlated (Fig. 8, $r^2 = 0.77$). The relationship between the two variables departed significantly from 1 : 1, however, with R_Σ being greater than F_{cn} on

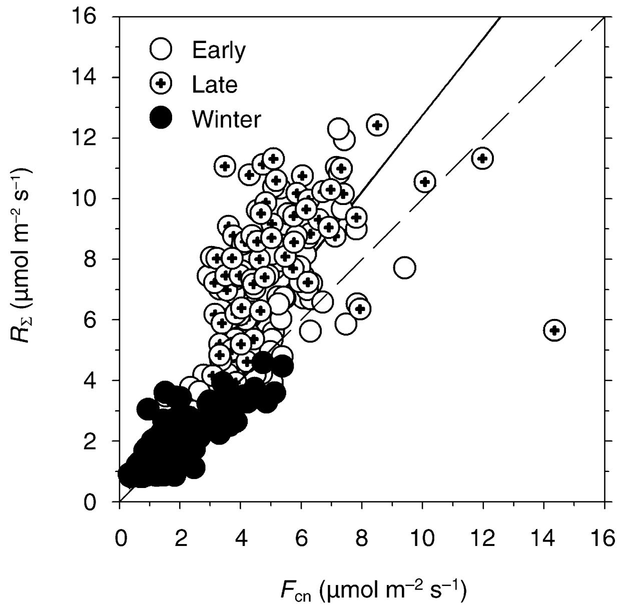

Fig. 8 Correlation between mean nighttime net ecosystem CO_2 flux (F_{cn}) measured using eddy covariance methods and total ecosystem respiration (R_Σ) estimated as the sum of soil, leaf and bole respiration. Only nights having ≥ 4 h F_{cn} with friction velocity (u^*) > 0.35 m s^{-1} were used. Solid line, linear relationship between variables ($y = 0.15 + 1.26x$, $r^2 = 0.77$); broken line, 1 : 1 relationship.

most nights. The relative magnitude of the difference was not uniform across seasons, being smallest during the winter (11% greater R_Σ), intermediate early in the season (28% greater R_Σ), and largest late in the season (58% greater R_Σ).

We examined whether a systematic difference between R_s in the 1.1 ha plot compared with that across the much larger eddy covariance footprint could help explain these differences. For this analysis, R_s, T_s and θ_v measurements were made on four dates in 30 0.1 ha plots located up to 1000 m from the eddy covariance tower. We then predicted R_s in the 1.1 ha plot based on the R_{s10}, $f(\theta_v)$ and Q_{10} values shown in Table 2. Most of the observed R_s measurements from the 0.1 ha plots (59) were within the 95% confidence interval of modeled R_s from the 1.1 ha plot; 55 were greater than the 95% CI of modeled values; and only six values were lower (Fig. 9). This suggests that R_s in the 1.1 ha plot was equivalent to, or less than, what would be expected across the flux tower footprint. We also found that R_s was well correlated with site index (Fig. 9, insert) and that the 1.1 ha plot site index (14.4 m) was significantly less than the mean 0.1 ha plot site index (17.6 m) ($P = 0.03$, one-tailed t-test).

Ecosystem carbon-use efficiency

Gross primary production estimated biometrically (P_{GPb}) as $P_{NP} + |R_a|$ showed similar interannual variation as seen in R_Σ, but with the highest year (1999) separated from the lowest year (2003) by only 92 g C m^{-2} (Table 6). Biometric E_c was

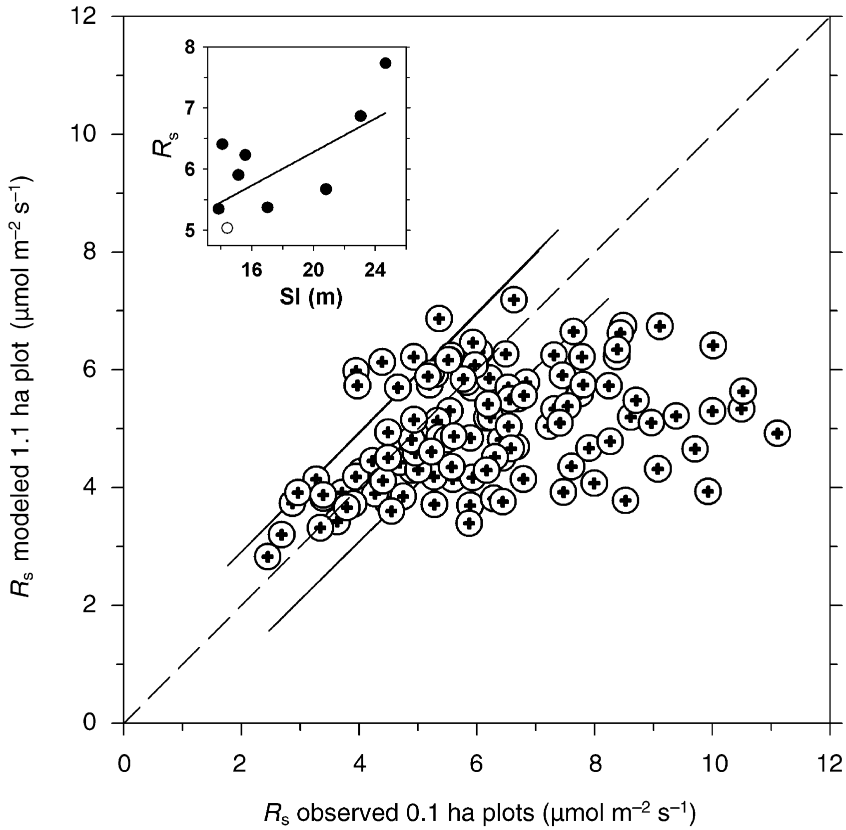

Fig. 9 Soil respiration (R_s) measured in the 0.1 ha permanent plots within the flux tower footprint and R_s modeled for the same conditions of soil temperature and soil water content in the 1.1 ha study plot. Solid lines are 95% confidence intervals around a modeled 1 : 1 relationship (dashed line). Insert, relationship between site index (SI) and R_s for eight 0.1 ha plots (closed symbols) and the 1.1 ha plot (open symbol).

Table 6 Ecosystem carbon-use efficiency estimated biometrically (E_{cb}) or meteorologically (E_{cm}) in the 1.1 ha plot across years

Year	P_{NP}†	R_a	P_{GPb}	E_{cb}	P_{GPm}	E_{cm}
1999	656	981	1637	0.40	1323	0.50
2000	678	902	1580	0.43	1235	0.55
2001	704	910	1614	0.44	1178	0.60
2002	618	931	1549	0.40	1240	0.50
2003	650	895	1545	0.42	1127	0.58
Mean	661	924	1585	0.42	1221	0.54

Annual gross primary production was estimated biometrically (P_{GPb}) as the sum of net primary production (P_{NP}) and autotrophic respiration (R_a) or meteorologically (P_{GPm}) from eddy covariance data. All production units are g C m^{-2} yr^{-1}.
†Data from Gough *et al*. (2005).

quite uniform across years (coefficient of variation of 2.5%), with a 5 yr mean of 0.42. Gross primary production estimated meteorologically (P_{GPm}) as $P_{NP}/\Sigma(F_{cd} + | F'_{cn} |)$ was weakly correlated with P_{GPb} ($r = 0.59$), and on average 23% lower. The spread between years also was somewhat greater (196 g C m^{-2} separating 1999 from 2003). The lower P_{GPm} compared with P_{GPb} estimates resulted in correspondingly higher meteorologically based E_c estimates, averaging 0.54 over 5 yr (coefficient of variation 6.0%.

Discussion

Soil respiration

The sensitivity of R_s to T_s and θ_v that we observed was typical for forest soils, with our overall mean Q_{10} across seasons and years of 2.7 comparing well with the global mean of 2.4 estimated by Raich & Schlesinger (1992). The coarse textured, well drained soils at UMBS are susceptible to episodic drought, and θ_v was often an important explanatory factor in modeling R_s, as has been observed in other eastern deciduous forests (Davidson *et al.*, 1998; Ehman *et al.*, 2002; Bolstad *et al.*, 2004). By incorporating both seasonal and interannual variation in sensitivity to T_s and θ_v, our model explained ≈75% of the variation in measured R_s across 5 yr, comparable in accuracy to other empirical models of R_s from diverse forest ecosystems (Hibbard *et al.*, 2005).

Although the observed pattern of R_s response to climate drivers was typical, hourly and cumulative annual R_s at UMBS was high compared with some other forests of similar P_{NP}. Raich & Nadelhoffer (1989) proposed an empirical relationship that suggested annual R_s C losses of approximately three times the mass of annual above-ground fine litterfall C (M_{cl}). Davidson *et al.* (2002a) confirmed this general relationship with an independent data set drawn only from studies using infrared CO_2 detection methods. Their analysis included 1 yr (1999) of data from UMBS, which was a notable outlier showing annual $R_s > 7 \times M_{cl}$. This suggested the possibility of nonsteady-state root or soil C stocks or above-average total below-ground C allocation at UMBS. Our present results, based on 5 yr of data and with an improved R_s model, show more congruence with other temperate deciduous forests, particularly those dominated by *Populus*. Our 5 yr mean annual R_s was 1044 g C m^{-2} yr^{-1}, or 5.6 times our mean M_{cl} of 185 g C m^{-2} yr^{-1} (Gough *et al.*, 2005). Mature deciduous forests in Tennessee, Wisconsin and New Zealand all showed single-year annual $R_s : M_{cl}$ ratios >5 (Davidson *et al.*, 2002a). In a further analysis of the Wisconsin site, Bolstad *et al.* (2004) reported a 4 yr mean annual R_s of 1116 g C m^{-2} yr^{-1} from a *P. tremuloides*-dominated stand ($A_{lmax} \approx 4.7$), while Russell & Voroney (1998) reported a 2 yr mean annual R_s of 887 g C m^{-2} yr^{-1} from a *P. tremuloides* forest in Saskatchewan, Canada ($A_{lmax} \approx 3.3$). We cannot rule out declining stocks of soil C below 10 cm, but neither soil C from 0 to 10 cm (Schaetzl, 1994) nor total root length density (Gough *et al.*, 2005) appears out of steady state on a 1–5 yr time frame at our site. Both *P. grandidentata* and *P. tremuloides* are early successional, rapidly growing species, and may have higher specific root respiration rates than later successional or slower growing species (Desrochers *et al.*, 2002; Burton & Pregitzer, 2003), perhaps contributing to relatively high R_s in *Populus* stands. Given the importance of R_s in determining R_e, resolving the underlying mechanisms responsible for variation in R_s across forest types remains an important challenge in climate change research.

Leaf respiration

There are both methodological and conceptual issues of importance in evaluating the accuracy of annual R_l estimates. We established R_l temperature response functions by measuring nocturnal R_l at different ambient temperatures over an entire growing season, rather than by exposing leaves to short-term temperature changes within the gas-exchange cuvette. There is considerable evidence that temperature acclimation of R_l occurs in temperate tree species (Atkin *et al.*, 2000; Bolstad *et al.*, 2003; Gifford, 2003), resulting in a relatively rapid lowering of respiratory capacity with increasing ambient temperature. As the majority of our gas-exchange measurements were made over the course of 100 d, it is very likely that temperature acclimation occurred in the individual trees we measured. One result of such an acclimatory response would be a flattening of the temperature response function and a reduction in Q_{10} relative to that obtained from short-term temperature manipulations (Gifford, 2003), and a consequent reduction in estimated annual R_l. Our Q_{10} values were at the low end of the 1.4–4.0 range for leaves reported by Amthor (1984), although comparable with those reported by Turnbull *et al.* (2001) for unacclimated *Q. rubra* (1.78–1.93) and *A. rubrum* (1.46–1.53). While accounting for temperature acclimation over time, our use of Q_{10} values derived from seasonal changes in T_a might fail to correctly describe short-term responses to diurnal temperature fluctuations. At UMBS these temperature fluctuations average ≈9°C during the growing season. On such a day, if we assume a uniform Q_{10} of 2.50 across species, more typical of values from unacclimated woody plants, R_l would be ≈10% higher than estimated using the 'acclimated' Q_{10}s in Table 3. Thus, to a first approximation, the short- vs long-term effects on estimated annual R_l of measuring acclimated vs unacclimated leaves will tend to offset each other.

We used three different Q_{10} functions to describe all R_l temperature responses, pooling sun and shade leaves and aggregating species based on similarity in R_{l15} and leaf [N]. While obscuring some variation present at the individual tree level, these simplifications probably had little impact on our ecosystem-level estimates. In a detailed study of 18 deciduous North American tree species, Bolstad *et al.* (1999) concluded that most interspecific and intracanopy variation in R_l was reflected in differences in R_{lref}, rather than Q_{10}. Furthermore, whole-canopy respiration predicted using the lumped parameter model PnET-II agreed well with results obtained by aggregating individual species-response curves (Vose & Bolstad, 1999). Our R_{l15} values are comparable with those for other deciduous and evergreen species (Bolstad *et al.*, 1999; Law *et al.*, 1999b), although we also would argue that between-study differences in estimated R_{l15} of <50% are effectively within current measurement error given the inaccuracy of standard leaf cuvettes (e.g. poorly quantified gasket effects) and most commercially available infrared gas analyzers working near their differential CO_2 concentration detection limits. Lastly, in calculating daily and annual R_l we assumed that dark respiration continued during the day at a rate unaffected by light. This is a common, though not universal (Bolstad *et al.*, 2004; Harmon *et al.*, 2004), assumption in C-cycle studies, and is supported by the results of Pinelli & Loreto (2003) who found, using isotope-sensitive infrared gas analysis, that mitochondrial respiration was unaffected by light in several herbaceous and woody species. Other evidence, however, has suggested substantial reductions in R_l during the day (Brooks & Farquhar, 1985) which, if correct, would substantially reduce estimated annual R_l.

There have been only two previous reports of annual R_l in temperate deciduous forests, both including mature, *Populus*-dominated ecosystems. Bolstad *et al.* (2004), working in a northern Wisconsin aspen forest with A_{lmax} of 4.7, mean annual T_a of 4.8°C and leaf-out period of ≈150 d, reported a 4 yr mean R_l of 110 g C m^{-2} yr^{-1}, summed over nocturnal periods only (P. Bolstad, personal communication). This estimate aligns very well with ours. We estimated a 5 yr average R_l of 256 g C m^{-2} yr^{-1} summed over 24 h, or 95 g C m^{-2} yr^{-1} summed over nocturnal periods only (mean A_{lmax} 4.0 including *P. aquilinum*, mean annual T_a 7.3°C, leaf-out period ≈160 d). Ryan *et al.* (1997) reported a considerably higher single-year

R_l of 464 g C m^{-2} yr^{-1}, assuming 24 h foliage respiration, in a southern Canadian aspen forest with A_{lmax} 3.3, mean annual T_a −0.4°C, and leaf-out period ≈120 d. However, they did not record making gasket corrections and therefore may have overestimated base R_l rates. Clearly, an analysis of biological processes that might lead to such differences must be combined with an improved understanding of the accuracy of these estimates. Independent estimates of R_l using meteorological methods (Law *et al.*, 1999a) or the ^{13}C signature of different sources of respiratory CO_2 (Dawson *et al.*, 2002) may provide important comparative data in this regard.

Above-ground wood respiration

Accurate assessment of annual R_w also can be a problematic element in the biometric analysis of forest R_e. There are two primary reasons for this. First, CO_2 fluxes measured at the stem surface may not accurately reflect the net exchange of respiratory CO_2 derived from cells lying beneath the gas-exchange cuvette itself. On the one hand, vertical transport of respiratory CO_2 in the xylem sap or storage in sapwood tissues will affect the magnitude of surface fluxes, generally leading to an underestimation of R_w (McGuire & Teskey, 2004). On the other hand, failure to account for refixation of respiratory CO_2 via corticular photosynthesis (Strain & Johnson, 1963) can lead to an overestimation of R_w. Second, scaling point measurements to the whole-tree or stand level introduces additional, often poorly defined errors. For example, measurements made at 1.3 m may not be representative of respiratory rates at other heights or in branches, due both to variation in the density and activity of living sapwood cells (Pruyn *et al.*, 2002) and to potentially large radial and vertical gradients in stem temperature (Stockfors, 2000). Additionally, stand-level estimates of total sapwood volume also carry with them large uncertainties (Oren *et al.*, 1998).

Our methods were similar to those of numerous other workers, and our calculated R_{w15} and Q_{10} values compare well with published reports (Edwards & Hanson, 1996; Ryan *et al.*, 1996; Ryan *et al.*, 1997; Bolstad *et al.*, 2004). Although we did not directly measure the effects of sap flow on R_w, an examination of meteorological data on days during the growing season when measurements were taken showed no clear relationship between R_w and vapor pressure deficit (unpublished data), the primary determinant of sap-flow velocity for the canopy species at UMBS (Bovard *et al.*, 2005). We also have not accounted for corticular photosynthesis, which certainly is present in several of our species. However, in *P. grandidentata* the thick bark characteristic of the mature trees at our site may act to reduce the magnitude of this effect (Cernusak & Marshall, 2000). Although we cannot rule out these potential artifacts as sources of error, the temporal variation we observed in R_{wv} was consistent with expectations based on the seasonality of growth and maintenance respiration in trees at our site. Winter R_{w15} and Q_{10} were lowest, reflecting the predominance of maintenance respiration at this time (Nelson, 1994). Bole radial growth (Gough *et al.*, 2005) and hence growth respiration generally was greatest early in the growing season, which showed the highest R_{w15} and Q_{10}, with both radial growth and R_{wv} then declining after day 200.

Recognizing these potential sources of error, estimated annual R_w was, perhaps surprisingly, quite similar in the three aspen forests studied to date. In the Canadian old aspen site, with a basal area of 27 m^{-2} ha^{-1} and height ≈20 m, single-year annual R_w was 123 g C m^{-2} yr^{-1} (Ryan *et al.*, 1997). In the Wisconsin mature aspen site of basal area 28 m^{-2} ha^{-1} and height ≈22 m, 4 yr mean R_w was 154 g C m^{-2} yr^{-1} (Bolstad *et al.*, 2004), while our 5 yr mean R_w was 166 g C m^{-2} yr^{-1} (basal area 30 m^{-2} ha^{-1}, height ≈19 m). This degree of congruence across forests of similar composition, structure and climate regime lends a measure of confidence to the accuracy of these estimates.

Summed respiratory components

At UMBS, R_Σ was dominated by R_s at all times of year, varying from a high of 100% during winter to a low of ≈60% during early summer. Leaf respiration was the second greatest contributor, representing ≈30% of R_Σ during leaf expansion and ≈18% on an annual basis. Above-ground wood contributed as much as 20% of R_Σ during early or late winter, and ≈11% overall. This pattern of partitioning of R_Σ among forest ecosystem components appears fairly typical (Lavigne *et al.*, 1997; Law *et al.*, 1999b; Wang *et al.*, 2004). Hence the relatively high R_Σ at UMBS compared with other deciduous forests was driven primarily by high annual R_s rather than large differences in component contributions.

The interannual variation we observed in R_Σ was modest, with the highest R_Σ year (1999) differing from the lowest (2003) by <15%. The largest difference between any two consecutive years was 142 g C m^{-2}, between 1999 and 2000, which differed in growing season air and soil temperatures by ≈1°C. This difference in R_Σ, while small relative to annual R_Σ (10% of the 5 yr mean) is nonetheless 50–100% of annual C storage in this, and other, northern hardwood forests (Lee *et al.*, 1999; Barford *et al.*, 2001; Curtis *et al.*, 2002; Schmid *et al.*, 2003; Gough *et al.*, 2005). This result supports the conclusions of Law *et al.* (1999b) that small changes in respiratory fluxes driven by small differences in temperature can have important effects on the overall magnitude of ecosystem C storage.

Biometric and meteorological comparison

Both biometric and meteorological approaches to the measurement of R_e carry with them significant sources of uncertainty. One benefit of colocating research using both strategies is the possibility of intercomparison of results from methods with independent errors, and thus the potential for assessment of accuracy and constraining flux estimates (Baldocchi, 2003). The direct intercomparison of R_Σ and F_{cn} has been reported only rarely (Lavigne *et al.*, 1997; Law *et al.*, 1999b; Bolstad *et al.*, 2004) and with varying results. However, with one exception (Law *et al.*, 1999b, when $u^* < 0.2$), R_Σ was greater than F_{cn}, often considerably. Our results fit this pattern as well. We found good correlation between average nightly R_Σ and F_{cn} on nights with sustained turbulence, but also a systematic offset of between +11% in the winter and +58% late in the growing season.

One possible reason for incongruence between R_Σ and F_{cn} is differences in the 'footprints' of the two methods. Perhaps the 1.1 ha plot, which surrounds our meteorological tower, had significantly higher R_Σ than those landscape elements contributing to the eddy covariance signal on turbulent nights. Two lines of evidence suggest this was not the case. First, R_s measured in 30 0.1 ha plots distributed throughout the likely tower footprint was almost always similar to, or higher rather than lower than, what would be expected under similar T_s and θ_v conditions in the 1.1 ha plot. Second, we found a strong correlation between site index and R_s, with the 1.1 ha plot having a relatively low site index compared with plots in the tower footprint. Although we cannot rule out abnormally high R_l or R_w in the 1.1 ha plot, the much smaller contribution of these components to R_Σ compared with R_s argues against footprint incongruity being the cause of the quantitative offset we observed in R_Σ and F_{cn}.

A second possibility is a systematic positive bias in chamber measurements relative to the true respiratory flux. Davidson *et al.* (2002b) considered this possibility at length for R_s measurements and concluded that most identifiable sources of error in both closed and open-chamber systems would tend to produce negative biases, not positive ones. Butnor & Johnsen (2004) evaluated the accuracy of the LI-6400-09 over inert media with a known CO_2 efflux, and also found small-to-moderate underestimations of the true flux. Failure to account for gasket effects in measuring R_l can lead to overestimation of R_l by as much as 50% (Pons & Welschen, 2002). While we corrected for this error, some degree of positive bias might have remained. In our system, reducing R_l by 50% results in a ≈12% reduction in R_Σ and therefore cannot fully account for the offset. Finally, biases in chamber measurements of R_w appear as likely to be negative (vertical CO_2 transport, sapwood temperature and specific activity variation) as positive (corticular photosynthesis). Hence we find no clear evidence of systematic, positive biases in the biometric estimate of R_Σ. Failure to include other possible sources of respiratory CO_2 in R_Σ, such as that from coarse woody debris, would also cause us to underestimate R_e.

Finally, eddy covariance measurements of F_{cn} may underestimate R_e by several mechanisms. Based on long-term flux measurements over Harvard Forest and UMBS, respectively, Goulden *et al.* (1996) and Schmid *et al.* (2003) showed that underestimation occurs during weak turbulent mixing periods (low u^*). The use of a u^* filter inevitably creates more data gaps, however, leading to questions regarding the validity of various gap-filling methods and their effects on annual F_c estimates (Falge *et al.*, 2001; Schmid *et al.*, 2003). Additionally, based on principles of mass balance, both vertical (Lee, 1998; Finnigan, 1999) and horizontal (Finnigan *et al.*, 2003) advection occurring under various atmospheric conditions and over nonflat terrain can lead to underestimation of R_e. Resolving these issues and understanding their relative importance remain important research questions within the Fluxnet community.

Ecosystem carbon-use efficiency

Our biometric estimates of P_{GP} are the first using modern gas-exchange and scaling methods published for a deciduous forest, and the second comparison of biometric and eddy covariance-based estimates of P_{GP} – the first, by Harmon *et al.* (2004), being from an old-growth *P. menziesii* stand. Earlier estimates of forest P_{GP} dating from the International Biological Program are summarized by Kira (1975) and Harris *et al.* (1975). As noted previously, P_{GP} estimates from similar forest types can vary considerably, depending on the methods used. There is thus little benefit in a comparative analysis for narrowly constraining P_{GP} estimates from our site. Both P_{GPb} and P_{GPm} estimates are easily accommodated within the range reported for temperate forests (Sanderman *et al.*, 2003). Carbon-use efficiency, however, may be a more sensitive comparative index. Amthor (2000) argued for a fundamental constraint on E_c between 0.20 and 0.65, but noted there was little empirical basis for constraints within the range 0.40–0.65. Crop plants growing under controlled conditions approach E_c values above 0.55, while forests are well represented by E_c values below 0.45 (Gifford, 2003). Waring *et al.* (1998) argued for the constancy of forest E_c at ≈0.47 across stand types and ages (but see Mäkelä & Valentine, 2001).

Our biometric and meteorological E_c estimates span the 0.47 value of Waring *et al.* (1998), suggesting either a forest of below-average E_c (≈0.40), perhaps connected with age-related declines, or one of above-average efficiency, in good years approaching that of crop plants (e.g. 0.60 in 2001). Studies of forest succession at UMBS indicate a maximum age of *P. grandidentata* stands of ≈90 yr, after which composition shifts to a dominance by *Q. rubra*, *Acer* spp. and *P. strobus* (Cooper, 1981). The forest within the tower footprint is a mosaic of even-aged *P. grandidentata* stands, with a mean age across 12 of the 0.1 ha plots of 70 yr, but with some plots as young as 30 yr, and the 1.1 ha plot being 81 yr old. This element of the canopy clearly is mature and would suggest a relatively low E_c. Other elements of the canopy, however, are of mixed age, and active recruitment of *Q. rubra*, *A. rubrum* and *P. strobus* is under way across the landscape. It therefore does not appear possible strictly to favor one estimate over the other based on purely biological criteria. Rather, present uncertainty in P_{GP} estimates from this and most other forests may make it impossible to resolve differences in E_c to better than ±0.1 units.

Conclusions

Respiratory C losses are important components of the forest C cycle and are sensitive to changing climatic conditions. In the aspen-dominated, mixed deciduous forest at UMBS, C losses from soils predominated, accounting for >70% of the estimated 1425 g C m^{-2} respired from the ecosystem each year. Maximum interannual variation in this loss (142 g C m^{-2} yr^{-1}), while modest compared with total R_e, was of a similar magnitude to overall annual ecosystem C storage. Our estimates of the carbon-use efficiency of this forest ranged from 0.40 based on biometric data and consistent with an aging aspen stand, to 0.60 based on meteorological data and consistent with a more productive, multi-aged forest.

Quantitative R_e assessments such as ours include many poorly constrained sources of error. Independent estimates of R_e from the same site and comparisons with other ecologically similar sites therefore are critical to assessing the accuracy of these R_e measurements. Our meteorologically based estimates of R_e provided important confirmation that our physiological measurements and scaling protocols could reproduce much of the short-term (hourly) and seasonal variation in R_e evidenced in above-canopy nocturnal CO_2 fluxes. They also showed a consistent positive offset between hourly biometric and meteorological estimates. The broad agreement of our multi-year R_e estimates with those from two other North American aspen-dominated forests supported the general robustness of our annual sums. Further improvements in our confidence in R_e estimates in this forest, as well as in others, is necessarily linked to continued research in these two areas: the inter-comparison of well matched biometric and meteorological data and the development of high-quality, long-term data sets in comparable ecosystems. These goals present a substantial and continuing challenge to the international C-cycle community.

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