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Component and whole-system respiration fluxes in northern deciduous forests

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Summary We measured component and whole-system respiration fluxes in northern hardwood (*Acer saccharum* Marsh., *Tilia americana* L., *Fraxinus pennsylvanica* Marsh.) and aspen (*Populus tremuloides* Michx.) forest stands in Price County, northern Wisconsin from 1999 through 2002. Measurements of soil, leaf and stem respiration, stem biomass, leaf area and biomass, and vertical profiles of leaf area were combined with biometric measurements to create site-specific respiration models and to estimate component and whole-system respiration fluxes. Hourly estimates of component respiration were based on site measurements of air, soil and stem temperature, leaf mass, sapwood volume and species composition. We also measured whole-system respiration from an above-canopy eddy flux tower.

Measured soil respiration rates varied significantly among sites, but not consistently among dominant species ($P < 0.05$ and $P > 0.1$). Annual soil respiration ranged from 8.09 to 11.94 Mg C ha^{-1} year^{-1}. Soil respiration varied linearly with temperature ($P < 0.05$), but not with soil water content ($P > 0.1$). Stem respiration rates per unit volume and per unit area differed significantly among species ($P < 0.05$). Stem respiration per unit volume of sapwood was highest in *F. pennsylvanica* (up to 300 µmol m^3 s^{-1}) and lowest in *T. americana* (22 µmol m^3 s^{-1}) when measured at peak summer temperatures (27 to 29 °C). In northern hardwood stands, south-side stem temperatures were higher and more variable than north-side temperatures during leaf-off periods, but were not different statistically during leaf-on periods. Cumulative annual stem respiration varied by year and species ($P < 0.05$) and averaged 1.59 Mg C ha^{-1} year^{-1}. Leaf respiration rates varied significantly among species ($P < 0.05$). Respiration rates per unit leaf mass measured at 30 °C were highest for *P. tremuloides* (38.8 nmol g^{-1} s^{-1}), lowest for *Ulmus rubra* Muhlenb. (13.1 nmol g^{-1} s^{-1}) and intermediate and similar (30.2 nmol g^{-1} s^{-1}) for *T. americana*, *F. pennsylvanica* and *Q. rubra*. During the growing season, component respiration estimates were dominated by soil respiration, followed by leaf and then stem respiration. Summed component respiration averaged 11.86 Mg C ha^{-1} year^{-1}. We found strong covariance between whole-ecosystem and summed component respiration measurements, but absolute rates and annual sums differed greatly.

Keywords: Acer saccharum, Fraxinus pennsylvanica, leaf respiration, Populus tremuloides, soil respiration, stem respiration.

Introduction

Forests are important in the global carbon (C) cycle (Post et al. 1990, Tans et al. 1990, Conway et al. 1994, Ciais et al. 1995, Keeling et al. 1996). However, there is considerable uncertainty regarding the net impact of forests on global C budgets (Houghton et al. 1999), because C balance and component C fluxes vary depending on vegetation age, soils, species composition and local climate (Cox et al. 1978, Brooks et al. 1991, Jarvis et al. 1993, Criddle et al. 1994, Ruimy et al. 1996, Gower et al. 1997, Valentini et al. 2000). To estimate changes in the global C cycle accurately, we need to improve our measurements of net changes in forest C storage and flux.

There are three dominant fluxes in forested sites: photosynthesis, autotrophic respiration and heterotrophic respiration. Measurements of these component fluxes as well as whole-system measurements are needed to gain a deeper understanding of ecosystem responses to environmental variation, and to aid in the development of models of ecosystem carbon cycling (Running and Coughlan 1988, Aber et al. 1996).

We describe measurements of respiration components in mixed hardwood stands and in aspen stands in northern Wisconsin. We also compared these fluxes with eddy covariance measurements. We measured leaf, stem and soil respiration at eight forest sites, and combined these with continuous measurements of temperature, soil water content and other environmental variables to model respiration component fluxes for the forest ecosystems. Our primary objectives were to quantify the respiratory fluxes in important northern forest ecosystems, to better describe the spatial and temporal variation in component ecosystem carbon flux, and to compare estimates of total ecosystem respiration flux based on chamber measurements with those observed by the eddy covariance method.

Methods

Site description

Measurement sites were centered on an above-canopy flux tower located near Willow Creek, in the Chequamegon National Forest of northern Wisconsin (90°07′ N, 45°48′ W). Eddy flux, micrometeorological, component flux and stand structural measurements were taken between April 1999 and December 2002. Mature (65 to 90 years old), second-growth northern hardwood forests occupy the area immediately surrounding the tower. *Acer saccharum* Marsh. (sugar maple), *Tilia americana* L. (basswood), *Fraxinus pennsylvanica* Marsh. (green ash) and *Quercus rubra* L. (red oak) are the most common species in northern hardwood forests. Nearby forest stands are also dominated by *Populus tremuloides* Michx. (aspen), *Fraxinus nigra* Marsh. (black ash) and *Ulmus* spp., (ash-elm), with small areas of mixed wetland vegetation. Slopes are less than 1%, and soil textures are predominantly sandy loams. Canopy height near the tower ranged between 18 and 26 m. Forest stand structure and other characteristics are summarized in Table 1.

Stand structure

Stand structure was measured on 20-m radius circular plots within each stand. There were four plots in northern hardwood stands, two in intermediate-aged aspen (24–27 years old) stands, and two in mature aspen stands (> 40 years old). Tree heights were measured with an optical hypsometer. Diameters at breast height (DBH, 1.3 m aboveground) were measured for all trees larger than 3 cm DBH on each plot. Because the intermediate aspen sites had a high stem density, DBHs on all trees smaller than 3 cm DBH were measured for a one-half to one-eighth section of each plot. Leaf biomass was measured with 12, 0.35-m^2 litter traps per plot. Litter was bagged, dried at 65 °C for 48 h, sorted by taxa and weighed.

Leaf respiration

Leaf respiration rates (R_l) were measured at each study site. A total of 241 leaves, approximately equally distributed across the six dominant broadleaf species, were collected at predawn, and respiration rates measured according to the protocols described in Bolstad et al. (1999). Measurements were made during periods of full leaf expansion, and on leaves from low, mid and high positions in the canopy. Branches were detached, immediately placed in a plastic bag with a moistened paper towel and transported in the dark to a laboratory. Branches were recut under water, placed in a darkened room and leaves detached just before measurement. All measurements were made within 6 h of branch harvest, and a subsample was measured in situ on a harvested branch to ensure no degradation in response. Respiration rates were measured at 15 and 30 °C with a controlled temperature LI-6400 gas exchange system (Li-Cor, Lincoln, NE). We adjusted R_l per unit area and mass for gasket bias as per Pons and Weschen (2002). Leaf area was measured with an optical scanner and digital summation (SigmaScan, SPSS, Chicago, IL). Leaves were dried at 65 °C for at least 2 days, weighed and ground for chemical analyses.

Leaf respiration rates at 30 °C were compared among species by analysis of variance (ANOVA) with species as the main factor. A two-point method was used to estimate leaf respiration parameters Q_{base} and R_{20} for a model proposed by (Tjoelker et al. 2001):

$$R_l = R_{20}(Q_{base} - 0.0455T)^{(T-20)/10} \quad (1)$$

where R_l is observed respiration rate at temperature T, and R_{20} and Q_{base} were estimated by simultaneous equations. This model form incorporates acclimation in leaf respiration, a common phenomenon in forest trees (Atkin et al. 2000, Tjoelker et al. 2001, Bolstad et al. 2003). Tests on leaves measured at five temperatures (10, 15, 20, 25 and 30 °C) indicated no difference in parameter estimates when compared with a two-point method. Equation 1 parameters were estimated across canopy position because fits showed no vertical trends in mass-based parameters ($P < 0.05$, t-test). Hourly canopy respiration rates were estimated from hourly canopy temperature measurements (shaded copper-constantan thermocouple, 13 m height). Canopy temperature was assumed to be similar at all sites. Respiration rates per unit leaf mass were scaled to whole-canopy rates by multiplication, adjusted by litterfall mass (Granier et al. 2001). Predicted whole-canopy respiration was scaled by above- versus below-canopy photosynthetically active radiation (PAR) measurements during leaf expansion, and mass-based empirical models were used to estimate construction respiration (Williams et al. 1987, Ryan 1991). Leaf respiration during senescence was also scaled by above- versus below-canopy PAR measurements.

Stem respiration

Stem respiration rates (R_w) were measured on 26 trees from May to the end of November 2002: eight *A. saccharum*, six *P. tremuloides*, six *F. pennsylvanica*, and six *T. americana*. Measurements of R_w followed the methods of Carey et al. (1996). Trees ranged from 19 to 58 cm DBH. Fixed plates were mounted with silicon sealant at < 2 m height at a random azimuth. A custom Plexiglas cuvette, 869 cm^3 with an opening area of 101 cm^2, was attached to the mounting plate just before each measurement. Respiration rates were measured with a Li-Cor LI-6400 gas exchange system when rates had stabi-

Table 1. Summary data for measurement plots used in this study. Abbreviation: LAI = leaf area index.

Site	Dominant species	Age (years)	Basal area (m^2 ha^{-1})	Dominant height (m)	LAI
NH1	*A. saccharum*	67	31.6	28.0	3.8
NH2	*A. saccharum*	72	30.7	27.5	4.7
NH3	*A. saccharum*	67	31.1	25.5	4.3
NH4	*A. saccharum*	67	30.9	28.5	4.1
MA1	*P. tremuloides*	48	26.1	23.0	5.0
MA2	*P. tremuloides*	42	29.2	21.5	4.5
IA1	*P. tremuloides*	27	27.1	17.5	2.9
IA2	*P. tremuloides*	24	27.5	15.0	4.0

lized, typically within 3 to 10 min. Stem temperature was measured with a copper-constantan thermocouple inserted about 0.8 cm into the stem above or below the cuvette. Trees were cored on one side of the cuvette to determine sapwood thickness and wood specific gravity. Respiration rates per unit area were converted to rates per unit sapwood volume assuming a wedge shape.

Among-species differences in stem respiration were tested by analyses of covariance (ANCOVA) with tree and species as categorical variables and temperature as a linear variable for each measurement date. Stem respiration models per unit live sapwood volume were fit by species using nonlinear regression, of the form:

$$R_w = R_{20} Q_{10}^{(T-20)/10} \quad (2)$$

where R_w is respiration rate per unit sapwood volume at temperature T, and R_{20} and Q_{10} are estimated parameters. Rates per unit volume were multiplied by branch and stem sapwood volume per hectare to estimate stem respiration per unit ground area. Tree stem and branch biomass volumes were calculated based on sapwood thickness and measured regional allometric equations (Crow 1978, Pastor and Bockheim 1981, Schmitt and Grigal 1981, Crow and Erdmann 1983, Hocker and Early 1983, Perala and Alban 1994, Ter-Mikaelian and Korzukhin 1997). Branch biomass, minus branch bark, was assumed to be all sapwood. Biomass was converted to volume based on measured specific gravities. Stem respiration per unit ground area was predicted for each hourly interval on each plot, scaled by volume per species from biometric measurements on each plot. Stem volume was assigned equally to south- and north-facing stem temperatures.

Soil surface CO_2 efflux measurements

Soil surface efflux (R_s) was measured approximately monthly at all plots when the ground was not snow-covered in 2001 and 2002. We measured R_s with a Li-Cor LI-6400 infrared gas analyzer (IRGA) equipped with a 1152 cm^3 chamber (Li-Cor 6000-09). Measurements at each plot were made on 10-cm diameter PVC collars inserted into the soil surface. Eight replicate collars were measured per plot. Previous measurements indicated that between eight and 30 samples were required to detect a difference of 1 μmol m^{-2} s^{-1} at the 95% confidence interval. We adopted a sampling design with collars nested within sites, nested within vegetation types. This yielded eight measurements per plot for comparisons among sites, and 32 measurements per type for comparisons among vegetation types. Measurements were made on fixed and on temporary collars on the northern hardwood and intermediate aspen sites, and on temporary collars on the mature aspen sites. Fixed collars were inserted about 2 cm into the soil or litter surface at random locations. Fixed collars were left in place for at least 1 day before the first measurement, and remained in place for the duration of each growing season. Temporary collars were typically measured between 6 and 15 h after collars were placed. We measured R_s on a set of temporary collars in a northern hardwood plot to estimate collar disturbance effects. Soil temperature was measured at a depth of 10 cm with a copper-constantan thermocouple inserted adjacent to each collar. Soil water content was measured to a depth of 30 cm by time-domain reflectometry (Campbell Scientific CS620, Logan, UT) and a locally derived calibration equation.

A general linear model (GLM) was used to estimate effects of vegetation type, site, collars, soil water content and soil temperature on soil respiration. Vegetation type was considered a fixed effect, with site nested within vegetation type and collars nested within site. Significance was determined with appropriate *F*-tests, based on the reduced sum of squares principle (Searle 1971).

Soil C fluxes were estimated for each plot, on an hourly time step for the 1999 to 2002 measurement period. Soil respiration was estimated based on observed respiration and measured soil temperature and soil water content at 10-cm depth. Forms of the models fit were:

$$R_s = \beta_0 + \beta_1 T \quad (3)$$

$$R_s = \beta_0 + \beta_1 T + \beta_2 T^2 \quad (4)$$

$$R_s = \beta_0 \exp^{\beta_1 T} \quad (5)$$

$$R_s = (k W_s R_{max}) / (k W_s + R_{max}) \exp^{\beta_1 T} \quad (6)$$

where T is soil temperature at 10 cm, W_s is soil water content (m^3 m^{-3}) at 10 cm, and β_0, β_1, β_2, k and R_{max} are estimated model parameters. Equation 6 is from Hanson et al. (1993). Parameters were estimated by linear regression for Models 3 and 4, and nonlinear regression for Models 5 and 6 (Gallant 1975, SAS, Cary, NC). Model parameters were estimated and parameter significance determined with appropriate *F*-tests in reduced sums of squares models (Searle 1971). The best model was chosen based on parameter significance and parsimony. We predicted R_s for each measurement plot at 1-h intervals, for the period 1999 through 2002. Hourly R_s predictions were summed by year to estimate total respiration. Regression models were used to predict plot-specific soil water content and temperature. Linear models adequately predicted plot soil water content and temperature from continuous measurements at the micrometeorological stations. Values of R^2 for plot-specific temperature models were above 0.98, and R^2 values for soil water content ranged from 0.5 to 0.87.

Micrometeorology and whole-system CO_2 flux measurements

Stand micrometeorology and whole-system CO_2 exchange with the atmosphere were measured at the Willow Creek flux tower (B.D. Cook et al., unpublished results). Turbulence and fluctuations of CO_2 were measured at 30 m with a tri-axial sonic anemometer. Micrometeorology and eddy covariance measurements and data reduction methods are described in detail by B.D. Cook et al. (unpublished results). Soil and air temperatures were measured at half-hour intervals with a

Campbell Scientific CS500 temperature probe or copper-constantan thermocouples. Stem temperatures were measured every hour with copper-constantan thermocouples inserted into the north and south sides of a 40-cm diameter *A. saccharum* at 1.3 m height. Soil water content was measured by time-domain reflectometry, and light was measured above and below the canopy with PAR sensors (Li-Cor 190SA).

Comparisons among chamber and whole-system measurements

Chamber-based component fluxes were calculated and compared for an area near the tower. A 1-km circle was used to identify a footprint in the prevailing upwind direction, the northwest. The tower was centered in the southeast quadrant of the circle. Ecosystem respiration was estimated from chamber-based equations and stand biometry for all stands included in the circle. Species, forest age, soil type, stem volumes, leaf area and sapwood volumes were obtained from field measurements and U.S. Forest Service compartment data. Environmental conditions were assumed to be similar to those observed at the tower or at the nearest micrometeorological station in the same vegetation type. Soil, stem and leaf respiration models were adapted to the specific mix of stands, and area-weighted estimates of respiration components were calculated. Nighttime stand respiration was averaged over these regions for the length of the data record available for each night from 1999 through 2002.

Net ecosystem exchange (NEE) and a subset of micrometeorological measurements were extracted and averaged by the nighttime period for each day. Night periods were calculated by Brock (1981). Flux measurements during stable atmospheric conditions or when winds were from the direction of nearby low-lying areas to the southeast were discarded (B.D. Cook et al., unpublished results). Mean NEE and micrometeorological conditions were calculated for nights when no more than four hourly measurements were missing. Component respiration fluxes and whole-system measured fluxes were compared for the nighttime periods.

Results

Leaf respiration

Leaf respiration rates per unit mass measured at 30 °C differed almost fourfold among species, ranging from a high of 55.2 nmol g^{-1} s^{-1} for *P. tremuloides* to a low of 13.1 nmol g^{-1} s^{-1} for *U. rubra*. Differences among species were statistically significant ($P < 0.01$, ANOVA, *F*-test), as were mean parameter values for Equation 1 models (Table 2). Effects of temperature on leaf respiration parameters fit with Equation 1 were similar for *A. saccharum*, *F. pennsylvanica*, *T. americana* and *Q. rubra* (Figure 1).

There was little interannual variation in the onset and completion of the growing season and hence the onset of leaf respiration during the study period, although there were differences among years in estimated seasonal peak and mean respiration rates. Leaf expansion began between Julian days 113 and 119 and ended between Julian days 148 and 155. Leaf senescence began between Julian days 267 and 270, and ended between Julian days 291 and 299. Predicted leaf respiration rates during 1999 were generally higher than during other years, and averaged about 1.5 µmol m^{-2} ground s^{-1} in midsummer. Midsummer respiration rates averaged about 1 µmol m^{-2} ground s^{-1} during 2000, and 1.2 µmol m^{-2} ground s^{-1} in 2001 and 2002.

Leaf respiration rates and response functions were similar to those previously reported for *A. saccharum*, *T. americana*, *P. tremuloides*, and *Q. rubra* (Ryan 1991, Ellsworth and Reich 1993, Mitchell et al. 1999). Values of Q_{10} between 2.2 and 3 are consistent with previous measurements. The relative ranking of *Q. rubra* > *A. saccharum* > *T. americana* based on R_l indicates that relative respiration rates may be consistent across wide areas. We found no previous reports on respiration in *U. rubra*.

Stem respiration

Stem respiration varied significantly both among species and among measurement periods ($P < 0.05$, *F*-test). Respiration rates for *F. pennsylvanica* were highest, reaching nearly 300 µmol m^{-3} s^{-1}, and those for *T. americana* were lowest, averaging about 20 µmol m^{-3} s^{-1} (Figure 2, Table 3). Rates for *A. saccharum* and *P. tremuloides* were intermediate. Stem respiration rates were highest in the spring and early summer. Compared with the other species, *F. pennsylvanica* had a lower ratio of sapwood volume to total stem volume. Because sapwood in this species was typically restricted to the outer 3 to 8 cm, respiration rates per unit stem surface area were similar to those of the other species.

Stem respiration response functions differed by species

Table 2. Mean (SE) measured leaf respiration rates and Equation 1 parameters (R_{20}, Q_{base}). Abbreviations: SLA = specific leaf area; and Q_{10} = respiratory quotient.

Species	SLA (cm^2 g^{-1})	Respiration at 15 °C (nmol g^{-1} s^{-1})	Respiration at 30 °C (nmol g^{-1} s^{-1})	R_{20}	Q_{base} 20 °C	Q_{10}	*n*
A. saccharum	229.1 (14.6)	7.84 (0.85)	30.87 (3.09)	11.6 (0. 50)	3.89 (0.156)	2.98	31
F. pennsylvanica	151.1 (3.2)	9.12 (1.14)	29.94 (1.96)	12.9 (0. 92)	3.81 (0.193)	2.90	14
P. tremuloides	175.7 (5.3)	18.82 (1.68)	55.22 (4.28)	25.8 (1.17)	3.29 (0.153)	2.38	21
T. americana	176.5 (11.1)	7.79 (0.72)	31.12 (3.34)	11.5 (0.52)	3.90 (0.283)	2.99	18
U. rubra	179.1 (7.7)	4.08 (0.74)	13.09 (2.48)	5.7 (0.32)	3.18 (0.214)	2.27	9
Q. rubra	114.5 (3.5)	10.06 (0.89)	31.90 (2.11)	13.9 (0. 94)	3.21 (0.140)	2.30	11

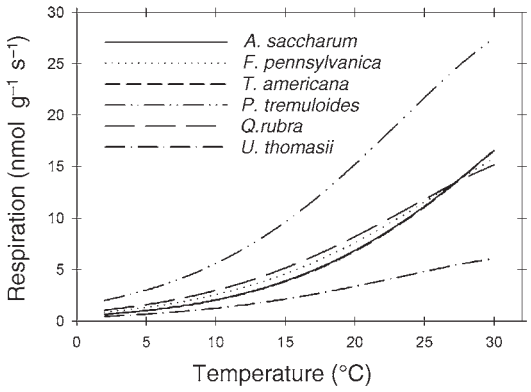

Figure 1. Leaf respiration–temperature response functions by species. Leaf respiration parameters were fit with Equation 1, based on measurements on 11–31 leaves per species.

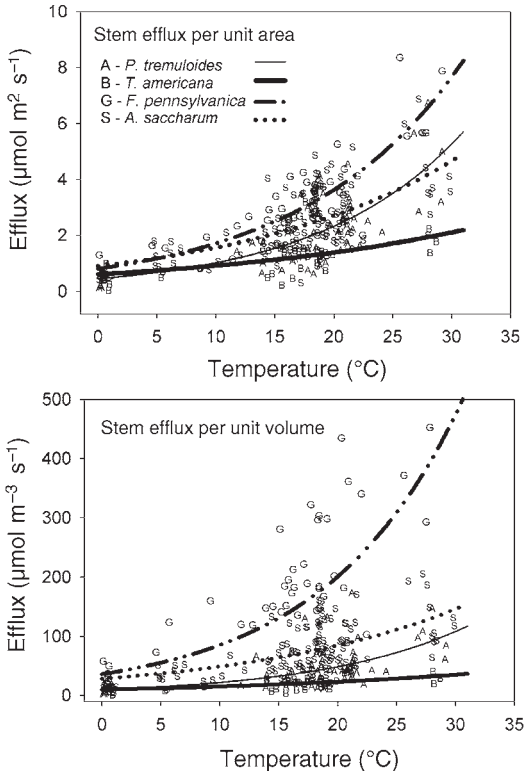

Figure 2. Stem respiration (efflux)–temperature response functions, per unit area (top) and per unit volume (bottom).

when expressed on a volume basis or an area basis (Figure 2). Respiration per unit area appeared to show less variation than respiration per unit volume. Model R^2 values were higher and mean errors were lower as a percent of predicted respiration for the area-based models than for the volume-based models. Per unit volume equations were used for estimating instantaneous and annual R_w to aid comparisons with previous studies.

Estimated R_w varied as a function of time of year ($P < 0.01$, *F*-test) and position on the stem ($P < 0.01$, *t*-test, e.g., Figure 3). Temperatures were higher on south-facing portions of tree stems than on north-facing portions during spring before leaf expansion and during fall after leaf fall (Figure 3). Stem temperatures on both the north and south sides of a tree may be higher, lower or equal to air temperatures because of thermal inertia in the stems and the passage of cooler or warmer air masses. Temperature differences among stem positions were not significantly different ($P > 0.1$, *t*-test) after canopy expansion. These characteristics led to differences in predicted stem respiration on north- versus south-facing sapwood depending on time of year. Stem respiration was higher in south facing sapwood than in north-facing sapwood during leaf-off periods; north- and south-facing R_w were similar during leaf-on periods (e.g., Figure 3, right panels).

Soil respiration

Soil respiration measurements varied between 0 and 8.1 µmol m^{-2} s^{-1} (Figures 4, 5), and increased with increasing temperature, but not with increasing soil water content ($P < 0.01$ and $P > 0.1$, respectively, *F*-test, GLM). Soil respiration did not differ significantly among vegetation types, but differed significantly among plots within vegetation types and because of temperature ($P < 0.05$, GLM). Temperatures were within normal ranges and rainfall was adequate to abundant during the 4-year study. Soil volumetric water contents were greater than one-half of capacity for 95% of the period, and no obvious symptoms of plant water stress were observed (Figure 4). There were no consistent significant differences in temperature among sites or vegetation types when compared at any fixed time period (Fisher's least significant difference test (LSD), $P > 0.1$), but there were significant differences among sites in soil water content (Fisher's LSD, $P < 0.05$), but not among vegetation types. One intermediate aspen site had a consistently higher soil water content than all other sites. This

Table 3. Stem respiration response function parameters (Equation 2) expressed on a unit area and a unit sapwood volume basis. Abbreviation: RMSE = root mean-square error.

Species	Area basis R_{20} (µmol m^{-2} s^{-1})	Area basis Q_{10}	RMSE, model significance ($P < 0.01$)	Volume basis R_{20} (µmol m^{-3} s^{-1})	Volume basis Q_{10}	RMSE, model significance ($P < 0.01$)
A. saccharum	2.7	1.72	1.07	84.7	1.72	32.1
F. pennsylvanica	3.63	2.11	0.74	201.1	2.36	16.3
T. americana	1.40	1.51	0.13	23.3	1.52	3.6
P. tremuloides	2.33	2.26	0.95	48.8	2.22	23.7

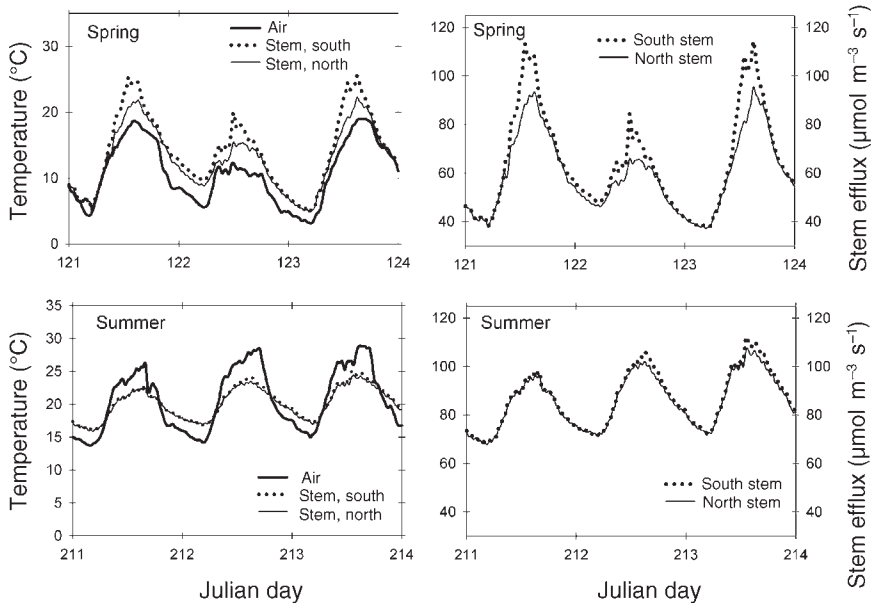

Figure 3. Predicted stem temperature and respiration (stem efflux) by position and day of year. Respiration rates were significantly higher ($P < 0.05$) on the south-side of stems than on the north-side of stems in spring, but the differences were not significant during summer.

higher soil water content did not appear to affect respiration, however, because soil water content was not a significant factor in the GLM ($P > 0.1$), nor was respiration at this site consistently higher or lower than at the other sites during the study.

Respiration was linearly related to temperature, but with substantial scatter about the fit line (Figure 5). Models were statistically significant for Equations 3 to 6. Model parameters related to soil water content in Equation 6 were not significant for any study plots ($P > 0.1$, asymptotic *t*-tests), nor were linear regressions of residuals from Equation 3 fits versus measured soil water content ($P > 0.1$, *t*-tests), indicating soil water contents measurements did not provide significant predictive value. The quadratic term in Equation 4 was not significant in seven of eight plots ($P > 0.1$), indicating that a linear model adequately described the effect of changing temperature on CO_2 flux at our plots, in contrast to general findings on soil respiration (Davidson et al. 1998, Fang and Moncrieff 2001). Davidson et al. (1998) noted that temperature and soil water may be confounded in north temperate forests, because high temperatures are often associated with low soil water contents during late summer. Under these conditions, low water availability may limit temperature responses and affect model fit. However, we observed high soil water contents coincident with high temperatures at the study sites, indicating that the conditions observed by Davidson et al. (1998) did not prevail during our study.

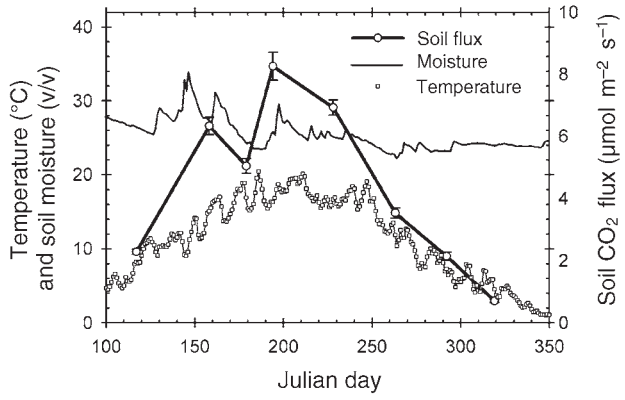

Figure 4. Soil respiration, temperature and soil water content time series for the 1999 growing season. Soil respiration and temperature showed strong seasonal trends, whereas soil water content peaked in late winter with snow-melt and was high throughout the growing season.

Equation 5 models, although significant ($P < 0.05$, asymptotic *t*-tests), consistently exhibited positive residuals at low temperatures, up to 200% above measured values. Intercepts in Equation 3 were significantly different from zero ($P < 0.05$, *F*-test) in three of eight plots, and negative *y*-intercepts were estimated for six of eight plots. Annual sums of soil respiration differed by less than 1% when predicted with Equation 3 with an intercept, when fitting a non-intercept model or when using the fit β_0 and setting negative soil respiration values to zero. We used Equation 3 models, and set predictions of negative respiration to zero.

The disturbance effect of collar placement appeared to last less than 5 h in our plots (Figure 6). Soil respiration was elevated after collar insertion, but declined to stable values after 6 h, and varied about these values for the following 3 days.

Cumulative ecosystem respiration

Total ecosystem respiration varied substantially on an annual cycle and was dominated by R_s, followed by R_w and R_l in contribution to the cumulative annual respiration (Figure 7). Modeled ecosystem respiration rates per unit ground area were typically less than 1 μmol m^{-2} s^{-1} during the winter, and ranged between 8 and 12 μmol m^{-2} ground s^{-1} during the sum-

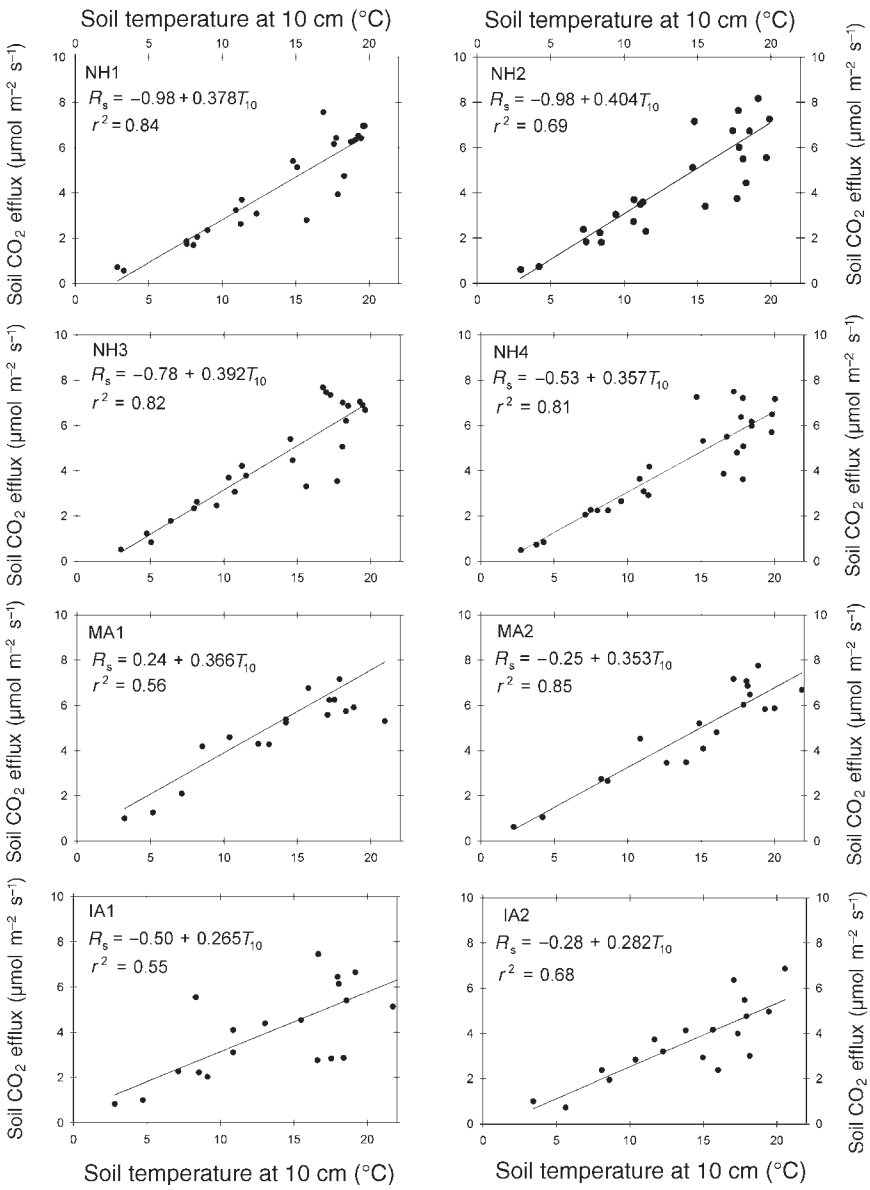

Figure 5. Soil respiration (CO_2 efflux) measurements and linear response functions, by site. Slopes were not significantly different among sites ($P > 0.1$), whereas intercepts were significantly different among sites ($P < 0.05$).

mer. Soil respiration was typically more than 60% of total ecosystem respiration during the growing season, and more than 90% of total ecosystem respiration during the non-growing season. Leaf respiration was typically much higher than stem respiration during the growing season. Because leaves were present for about 150 days of the year and stem respiration occurred year-round, cumulative annual stem respiration exceeded leaf respiration at the northern hardwood and mature aspen sites. Sapwood volumes were relatively smaller at the intermediate-aged aspen sites, resulting in cumulative annual leaf respiration exceeding stem respiration for all years.

Total ecosystem respiration estimated by summed chamber fluxes and models varied substantially among years and among forest types (Table 4). Estimated annual respiration was highest at the mature aspen plots, intermediate for the northern hardwood sites, and lowest for the intermediate-aged aspen plots. Differences among types were large; for example, total ecosystem respiration averaged more than 40% higher in mature aspen stands than in young aspen stands.

Modeled cumulative ecosystem respiration was highest in 2001 and lowest in 2002, and intermediate in 1999 and 2000 (Table 4). Differences appeared to be associated primarily with differences in mean temperature, particularly early and late in the growing season, and to a lesser extent with length of the growing season. Mean summer temperatures were highest in 1999 and 2001, winter temperatures were high in 2001, and spring and fall temperatures were higher in 2000 and 2001 than in other years. Year 2002 had a cool spring and fall. Taken together, respiration was sustained at relatively high rates for a longer period during 2001, and for the shortest period during 2002. Winter temperatures varied considerably among years; however, winter respiration rates were low, and it appears that higher mean winter temperatures did not have substantial impacts on cumulative annual respiration. Differences among

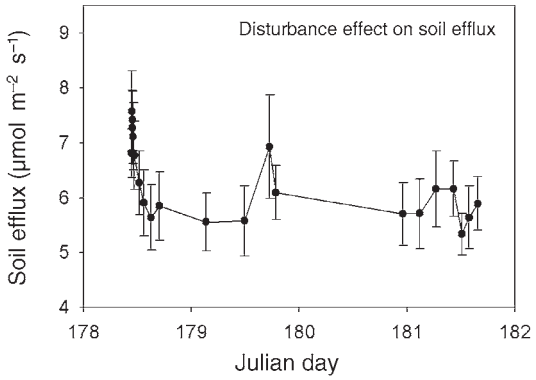

Figure 6. Collar disturbance and soil respiration. Means and standard deviations of eight collars are shown. Soil respiration rates were elevated for the first 6 h after collar placement. Thereafter, rates decreased and then fluctuated within a range of values for the next 3 days.

forest types were consistent among years, i.e., estimated cumulative respiration in mature aspen was always greater than that of northern hardwoods, and intermediate-aged aspen always had the lowest cumulative annual respiration (Table 4).

Eddy covariance flux–chamber comparisons

Peak summer respiration rates, summed across components, were within the range of rates reported for other deciduous forests: e.g., 8–12 µmol m^{-2} s^{-1} in a beech forest (Granier et al. 2000), 8–10 µmol m^{-2} s^{-1} in an oak–maple forest (Goulden et al. 1996), and 9–11 µmol m^{-2} s^{-1} in an aspen forest (Black et al. 1996), but above the peak rates observed by eddy flux measurements at other deciduous hardwood sites in temperate latitudes (Schmid et al. 2000). Peak rates are dominated by soil respiration, so differences in total respiration are likely caused by real differences in this component, or biases or errors associated with the eddy flux or component measurement systems and models used.

Table 4. Estimated annual respiration rates for whole ecosystems and their components for the period 1999–2002.

Forest type and respiration component	Respiration rate (Mg C ha^{-1} $year^{-1}$)			
	1999	2000	2001	2002
Northern hardwood				
Leaf	0.55	0.57	0.60	0.54
Stem	2.34	2.32	2.42	2.25
Soil	8.67	9.03	9.70	8.09
Total	11.55	11.92	12.71	10.89
Mature aspen				
Leaf	1.07	1.12	1.16	1.05
Stem	1.54	1.53	1.59	1.48
Soil	10.97	11.31	11.94	10.43
Total	13.57	13.96	14.69	12.95
Intermediate aspen				
Leaf	0.96	1.01	1.04	0.94
Stem	0.19	0.19	0.20	0.18
Soil	8.78	9.05	9.52	8.37
Total	9.93	10.24	10.76	9.49

Chamber-based estimates were generally higher than eddy covariance flux estimates of whole-ecosystem respiration (Figure 8). Eddy covariance estimates averaged about 4 µmol m^{-2} s^{-1} during peak summer fluxes, whereas chamber-based estimates of ecosystem respiration were usually above 8 µmol m^{-2} s^{-1}. Eddy covariance measurements generally followed the same pattern as chamber-based sums, with higher respiration rates in the summer and lower rates in the winter, but the increase in flux with season was much greater for the chamber-based estimates. A linear regression between the chamber-based and eddy covariance flux estimates was significant ($P < 0.05$, *t*-test), with a nonsignificant intercept and a slope that was significantly different from one ($P < 0.05$, *t*-test). Chamber-based estimates of respiration were about twice as high as eddy covariance estimates over the observed range.

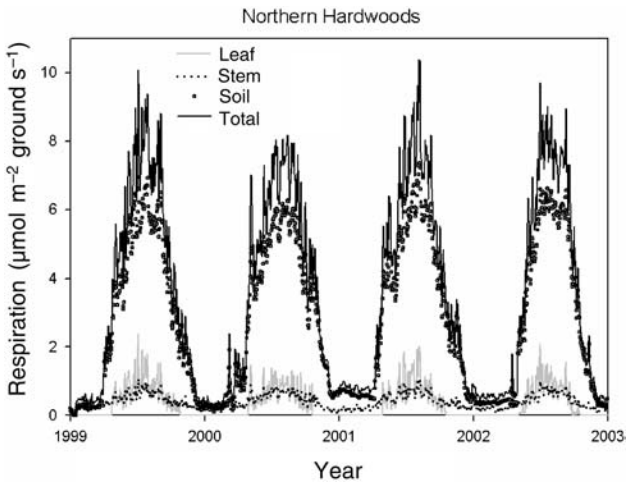

Figure 7. Soil, stem, leaf, and total respiration rates estimated from chamber-based measurements at site NH1.

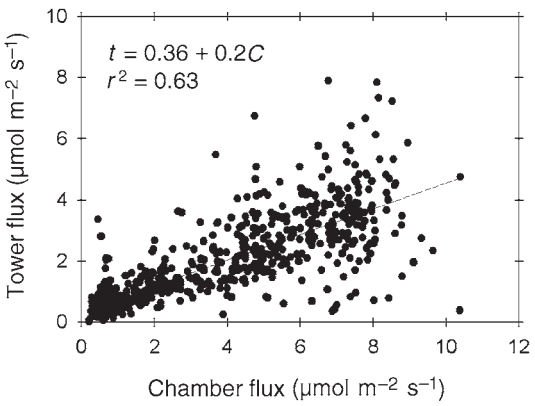

Figure 8. Eddy tower flux versus chamber-based estimates of ecosystem respiration for days on which soil, stem or leaf respiration rates were measured.

Discussion

Leaf, stem and soil respiration

Our study highlights the variation in component and ecosystem respiration that may occur in both space and time. We observed substantial differences in modeled whole-system respiration among different forest types and ages. We saw a nearly 40% difference in estimated annual respiration among different, fully stocked upland forest sites. We also observed interannual variation in respiration of up to 17% within upland sites. All of these sites were well-drained upland forests, on similar soils, with closed canopies and a relatively small complement of dominant species. Previous work has shown large differences in ecosystem respiration between wetland and upland sites, and between forests in significantly different topographic positions (Hanson et al. 1993, Law et al. 1999, Baldocchi et al. 2000, Schmid et al. 2000, Savage and Davidson 2001, Xu et al. 2001). Our results underscore the sensitivity of forest carbon balance to stand- and small-scale spatial variability within upland forest types.

Our component respiration measurements are consistent with those previously reported for eastern and northern deciduous forests, although when there were differences, our measured rates tended to be higher. Our soil and leaf respiration rates are near those reported for the deciduous forest sites in New England (Goulden et al. 1996, Savage and Davidson 2001, Davidson et al. 2002), the most similar forest ecosystem for which a long record of the component fluxes is available. Our observed mean summer soil respiration rates of 5.5, 5.9 and 4.6 μmol m^{-2} s^{-1} for northern hardwood, mature aspen, and intermediate aspen were near the 4.6 to 6.4 μmol m^{-2} s^{-1} for similar-aged deciduous forests in New England (Savage and Davidson 2001). Our respiration measurements were higher than the 3.6 to 4.5 μmol m^{-2} s^{-1} reported for an oak-hardwood eastern deciduous forest in Tennessee (Hanson et al. 1993), and substantially higher than the summertime rates reported for boreal or western forests (Norman et al. 1997, Law et al. 1999, Andrews and Schlesinger 2001, Xu et al. 2001).

Our annual cumulative soil respiration values were between 8.09 and 11.94 Mg C ha $year^{-1}$, and varied by site and year. The mean value across all plots was 9.65 Mg C ha $year^{-1}$, near the upper end of the annual soil respiration values reported for other deciduous forests: 6.20 to 9.40 in New England (Savage and Davidson 2001), 7.30 to 9.30 in Tennessee (Hanson et al. 1993), 7.07 and 7.94 in Minnesota (Reiners 1968), 3.34 in Quebec (Weber, 1990), and 10.13 in Missouri (Garrett and Cox 1973). As with most other forest sites, total ecosystem respiration in our study was dominated by soil respiration. Soil temperatures were high in the summer and remained above freezing through the winter, resulting in year-round respiration. Spatial and interannual variation in soil respiration is likely to drive total ecosystem respiration in our study area, and hence ecosystem carbon balance. Stem respiration rates on a unit sapwood area or volume basis were similar to those reported for other studies, although deciduous broad-leaved species have been measured in only a few studies (Edwards and Hanson 1996, Ryan et al. 1997, Xu et al. 2001, Maier 2001).

We observed an approximately linear relationship between soil temperature and soil respiration, in contrast to the curvilinear response observed in most studies (Fang and Moncrieff 2001). A linear response may reflect the best model under our conditions. Alternatively, a curvilinear response may be masked by sample variation, and may appear with a larger sample size or collar dimensions. Collar to collar variation in soil respiration was high (data not shown), particularly when using the small-area Li-Cor collar. Larger collars have been shown to reduce variation among samples and increase the ability to detect the shape of the response curve (Davidson et al. 2002), potentially at the expense of uneven mixing, greater susceptibility to gradient effects, and a slower response.

We found relatively little difference in cumulative soil respiration predictions when using Equations 3 versus Equation 4 or Equations 5 and 6, under most temperature conditions. Predicted respiration was consistently higher than observed rates when using Equation 4 or Equations 5 and 6 at low temperatures, and so these equations were not adopted. When using the linear response model, we set all negative predicted soil respiration values to zero. This had little impact on estimated cumulative respiration; annual sums differed by less than 1% when negative predictions were not set to zero.

Our results are consistent with other comparisons of chamber-based and eddy-covariance respiration data (Goulden et al. 1996, Lavigne et al. 1997, Schmid et al. 2000, Drewitt et al. 2002) in that the chamber-based flux estimates exceeded the eddy-covariance measurements. Although not universal, ecosystem respiration in forests is often less than the summed component respiration estimates. Eddy covariance systems may underestimate flux rates when there is incomplete mixing or advection of CO_2. We screened our eddy flux respiration measurements to remove periods of advection, but we still observed lower eddy flux estimates. Our results are similar to the observations of Goulden et al. (1996) and Lavigne et al. (1997) where eddy covariance flux estimates averaged 20 to 40% less than scaled chamber estimates.

We do not know why summed-component respiration estimates are routinely larger than whole-system estimates. The difference may be associated with errors in estimating soil respiration flux. Soil respiration typically constitutes 70% or more of total ecosystem respiration, and estimates of soil respiration often exceed whole-ecosystem respiration based on eddy flux towers. Several authors have identified sources of error in chamber-based estimates of soil respiration (Le Dantec et al. 1999, Buchmann et al. 2000, Hutchison and Livingston 2001, Davidson et al. 2002). These include sampling too soon after collar placement, under or over pressurization of the chamber, within-chamber turbulence, and induced lateral diffusion within the soil. We took precautions to avoid or minimize sources of measurement error, within the limitations of the equipment we used. We also verified equipment accuracy

against independent laboratory tests (Martin et al. 2004). The systematic difference between chamber and tower-based respiration estimates should be further investigated.

Litter fall data may be combined with root production and root respiration data to provide an independent estimate of mean annual soil respiration. If we assume no or slow net carbon accrual in the soil (Schlesinger 1990), litter fall plus belowground allocation should equal soil respiration. We measured litter fall at our sites, but did not measure belowground allocation. Belowground allocation may be estimated from fine and coarse root production, root respiration, and C allocated to root exudates. Fine and coarse root standing stock were measured, and were near values reported for studies in similar stands elsewhere in the region: standing stock of 2.47 Mg C ha^{-1} for roots < 2 mm at our sites, 2.7 Mg C ha^{-1} for roots < 3 mm (Burke and Raynal 1994), 2.14 Mg C ha^{-1} for roots < 3 mm (Nadelhoffer et al. 1985), 1.62 Mg C ha^{-1} for roots < 2 mm (Aber et al., 1985), and 3.70 Mg C ha^{-1} from Hendrick and Pregitzer (1993). Adopting the ratio of fine root standing stock to root production reported for similar sites (Hendrick and Pregitzer, 1993), we estimated belowground fine root production at 3.84 Mg C ha^{-1}. Aboveground litter inputs averaged 1.11 Mg C ha^{-1} over the study period, summing to 4.95 Mg C ha^{-1}. Root respiration, based on the models of Zogg et al. (1996) developed for similar stands, yielded another 5.02 Mg C ha^{-1}, for a sum of 9.97 Mg C ha^{-1}. This value assumes no C loss through leaching, which is low in the region, and does not include allocation to root exudates and mycorrhizae, for which few data are available for this region or for these species and forest types.

The budget estimates of soil respiration (9.97 Mg C ha^{-1} $year^{-1}$) were closer to chamber-based estimates (9.65 Mg C ha^{-1} $year^{-1}$) than to tower-based estimates (5.01 Mg C ha^{-1} $year^{-1}$) over the 4 years of our study. We acknowledge multiple sources of uncertainty in the budget estimates including: use of the ratio of fine root biomass to fine root production developed at other sites (Hendrick and Pregitzer 1993), and estimating root respiration from a published study (Zogg et al. 1996). Although these are the best data available and from sites with similar climates, soils, species and ages, the reported relationships may not apply across sites, and site-specific estimates would provide a stronger comparison. The lack of convergence in independent flux measurements deserves more study, given the importance of soil respiration in ecosystem carbon balance, and the widely observed disagreement between chamber-based and whole-ecosystem respiration measurements.

Scaling uncertainty may be particularly large for sapwood flux estimates. The distribution of sapwood within trees is poorly studied for most species, and changes with age, height, site conditions or region have not been investigated. We found no study detailing variation, nor any that provided guidance on the proportion of a stem likely to be in shaded versus sunny locations in a stand. Our assumptions of sapwood volume rest on a small empirical base. Effects of these errors on whole-ecosystem respiration estimates are probably small, because stem respiration was a small component of total ecosystem respiration. However, further study of the characteristics of sapwood variation and stem microclimate is required to improve our confidence in spatial predictions of sapwood flux.

Conclusions

We observed whole-ecosystem, mean nighttime respiration rates that ranged between zero and 14 μmol m^{-2} s^{-1} in forests in northern Wisconsin. Component measurements indicated between 74 and 88% of the observed respiration came from the soil. During the growing season, most of the remaining flux was from leaves, and stem flux was the second largest source of respiration flux on an annual basis. Mean eddy covariance measurements were substantially lower than chamber-based flux estimates across a range of respiration flux rates. Chamber-based respiration estimates appear to be systematically larger than eddy covariance measurements at high respiration rates. Based on our study and similar flux differences found at several other sites, we conclude that direct comparisons of chamber-based and eddy flux respiration measurements are not reconciled.

We observed notable differences in component and whole-system respiration fluxes across both space and time. Differences in respiration across space were particularly noteworthy, because our plots sampled deciduous forests that are relatively homogeneous, on similar soils, and in close proximity. Methods for scaling respiration estimates across space must integrate this variation when estimating aggregate flux.

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