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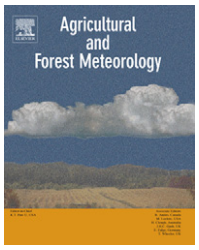


# Ecosystem respiration and its components in an old-growth forest in the Great Lakes region of the United States

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ABSTRACT

Ecosystem respiration and its components are sensitive to age, species, stand structure, and environmental conditions, and substantially influence net ecosystem productivity. We measured ecosystem respiration and component respiration including soil, woody debris, stem and leaf respiration in old-growth hardwood-dominated and hemlock-dominated stands in northern Michigan, USA in 2002 and 2003. Respiration was mainly controlled by temperature, peaked in July–August and reached minimums in January–March. Total ecosystem respiration averaged 1013 g C $m^{-2}$ $y^{-1}$ in the hardwood stand and 922 g C $m^{-2}$ $y^{-1}$ in the hemlock stand. Cumulative annual soil respiration, coarse woody debris respiration, stem respiration, and leaf respiration were 724, 43, 131, 115 g C $m^{-2}$ $y^{-1}$, respectively, accounting for 72%, 4%, 13%, and 11% of total ecosystem respiration in the hardwood stand, and 614, 29, 207, 72 g C $m^{-2}$ $y^{-1}$, respectively, accounting for 67%, 3%, 22%, and 8% in the hemlock stand. Ecosystem respiration and its components except for leaf respiration in 2002 were larger than year 2003 due primarily to lower temperature in 2003. Component respiration except for stem respiration was higher in the hardwood stand than the hemlock stand. Daily mean ecosystem respiration upscaled from chamber measurements agreed well with eddy covariance measurements, with $r^2$ of 0.96. By comparing respiration from the old-growth with a nearby young and a mature second-growth forest based on chamber measurements, we found that both age class and species are important in determining the magnitude and proportion of component respiration. Total ecosystem respiration generally increased from the young forest to the mature forest, and then decreased from the mature to the old-growth forest.



## 1. Introduction

Net ecosystem exchange (NEE) between the atmosphere and forests has become a focus of climate change research due to the potential of forests to reduce enhanced atmospheric $CO_2$ concentration (IPCC, 2001; Tans et al., 1990; Fan et al., 1998). Because NEE is the small difference between two large fluxes of photosynthesis and respiration and is typically an order of magnitude smaller than respiration or photosynthesis (Goulden et al., 1996a; Law et al., 1999), NEE is sensitive to both respiration and photosynthesis and often changes sign within and among sites (e.g., Euskirchen et al., 2006). Despite the possibly higher importance of respiration than photosynthesis in determining the variability of NEE across latitudinal

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gradients (Valentini et al., 2000), respiration and its components have been the focus of fewer studies (Law et al., 1999).

Ecosystem respiration is composed of autotrophic and heterotrophic components whose contributions to total respiration vary in space and time. There is no consensus on methods for measuring each component of respiration and estimating the annual sum. Components of respiration include soil respiration, stem respiration, leaf respiration, and woody and surface litter respiration. Soil respiration may be further partitioned into root respiration with associated rhizosphere respiration, and microbial respiration. These components all respond primarily to temperature, but many components are affected by additional factors. For example, soil respiration may be controlled by photosynthesis in additional to environmental variables (Hogberg et al., 2001; Tang et al., 2005a). Soil moisture is an important control on soil respiration in arid and semi-arid ecosystems (Xu and Qi, 2001; Tang and Baldocchi, 2005). Precipitation frequency and duration may affect soil respiration during and after the drought (Xu et al., 2004). Leaf respiration may be driven by temperature and related to species and leaf nitrogen content (Bolstad et al., 1999). It is therefore difficult to measure and model respiration components.

The eddy covariance technique has provided a useful tool to continuously measure NEE from hourly to daily, annual and interannual periods (Aubinet et al., 2000; Baldocchi, 2003). However, eddy covariance measurements do not provide direct information on component fluxes and are difficult in assessing over spatially heterogeneous areas due to inherent variation in the measurement footprint with time. Eddy covariance methods need to be complemented and compared to component fluxes in order to interpret and understand the variability of fluxes. As a complementary method, chamber measurements have been used to sample component fluxes and upscale to the annual carbon budget (Law et al., 1999; Xu et al., 2001; Bolstad et al., 2004).

Studying carbon fluxes from old-growth forests helps us to understand the successional change of carbon fluxes and the future trend of current second-growth forests. While there are a large and growing number of eddy flux sites (Baldocchi, 2003), there are relatively few in old-growth forests (Paw et al., 2004; Chen et al., 2004; Desai et al., 2005), which have received negligible human disturbance and are dominated by trees greater than two centuries old. Whole system and component measurements in older forests allow us to test the conceptual model that forest net primary production (NPP) and NEE declines with forest age (Kira and Shidei, 1967; Odum, 1969; Ryan et al., 1997; Gower et al., 1996), and to test the assumption that old-growth forests reach NEE equilibrium compared with young and recovering forests (Carey et al., 2001). NEE is typically positive (i.e., a carbon source) during stand establishment periods due to large heterotrophic losses to the atmosphere from the soil and surface litter. NEE becomes negative (i.e., a carbon sink) as standing biomass increases and net photosynthesis balances and then surpasses ecosystem respiration. Respiration is expected to continuously increase as stems and detritus accumulate in older forests, and eventually balances deceasing photosynthesis when forests age (Odum, 1969; Kira and Shidei, 1967). However, there are no empirical data to support this conceptual model that old forests reduce photosynthesis but enhance respiration (Ryan et al., 2004). A few empirical studies directly measuring NEE using the eddy covariance method have revealed that old-growth forests are carbon sinks (Grace et al., 1995; Carswell et al., 2002; Roser et al., 2002; Paw et al., 2004; Desai et al., 2005), possibly due to the fertilization effect from increasing atmospheric $CO_2$ concentration and nitrogen deposition rates (Grace et al., 1995). Despite the importance of old-growth forests in studying respiration over the course of succession, we have seen few publications separately measuring component respiration in old-growth forests except for Law et al. (2001) and Harmon et al. (2004).

Our objectives were to (1) measure respiration components from two stands with different dominant species in an old-growth northern forests, (2) estimate the annual sum of respiration and percentage of each component, and (3) compare respiration from the old-growth forest with a young and a mature second-growth forest under similar climate, and derive the successional pattern of respiration.

## 2. Materials and methods

### 2.1. Site description

The study area is located on the boundary of the Sylvania Wilderness and Recreation Area of the Ottawa National Forest in the upper peninsula of Michigan, USA (46°14′31″N, 89°20′52″W). Average elevation is 542 m. The climate is northern continental, characterized by short growing seasons and long, cold winters. Annual average precipitation and air temperature measured in a nearby weather station over 1961–1990 is 896 mm and 3.9 °C, respectively. Precipitation is evenly distributed in all seasons. Dominant upland soils are moderately well-drained, coarse or sandy loam spodosols (Pastor and Broschart, 1990).

The 8500 ha Sylvania Wildness is one of only two large tracts of old-growth forest remaining in the Great Lakes region. The Sylvania Wilderness is a hemlock – northern hardwood forest comprised of 3–30 ha patches dominated by either eastern hemlock (*Tsuga canadensis*) or sugar maple (*Acer saccharum*), with yellow birch (*Betula alleghaniesis*), basswood (*Tilia americana*), and ironwood (*Ostrya virginiana*) also present in the overstory (Frelich et al., 1993; Pastor and Broschart, 1990).

We studied two adjacent forest stands. The first stand (hardwood stand) comprised 1 ha centered on a tower equipped for eddy covariance measurements of carbon exchange (Desai et al., 2005). This stand was dominated by sugar maple (71% of trees) in addition to hemlock (14%), yellow birch (7%), and basswood and ironwood (8%). Trees ranged from 0 to 350 years old, but old trees dominated the canopy. Average canopy height was approximately 22 m. Stand density was 439 trees per hectare for all trees greater than 7 cm in diameter at breast height (DBH), with an average DBH of 25.9 cm and basal area of 33.1 $m^2\ ha^{-1}$ measured in 2002. Leaf area index (LAI) averaged 4.1 in September 2002 measured with an LAI-2000 (LI-COR, Inc., Lincoln, NE). Leaf debris and coarse woody debris covered the ground. Tree seedlings and saplings, maiden-hair fern (*Adiantum* spp.), jack in the pulpit

(*Arisaema triphyllum*), and *Lycopodiaceae* spp. were scattered under the closed canopy.

The second stand (hemlock stand), located about 150 m away from the eddy covariance measurement tower, was dominated by hemlock with less than 5% of trees comprised of yellow birch and sugar maple. Average stand density was 566 trees per hectare with an average DBH of 38.8 cm and basal area of 83.8 $m^2$ $ha^{-1}$. LAI averaged 3.8 when measured with the LAI-2000. The canopy was closed with very few tree seedlings and understory plants.

The study site is unique in that it is in a rare old natural forest. Fossil pollen studies indicated that the current mix of hemlock and hardwood coverage in Sylvania has not changed during the past 3000 years (Brugam et al., 1997). Tree ring studies suggested an average canopy residence time of 186 years and natural disturbances such as lightning-induced fire and windstorm will not change the patch dynamics in the old-growth hemlock-hardwood forest (Frelich and Graumlich, 1994). Harvest in this area was restricted to large white pines along nearby lakeshores around 1900, with little influence on most upland forests (Pastor and Broschart, 1990; Davis et al., 1998). The site is a representative late-successional forest with long-term compositional stability, though small and slow successional processes may still occur (Woods, 2000a,b).

### 2.2. Soil respiration

Soil respiration was measured using an LI6400-09 soil chamber connected to an LI-6400 portable photosynthesis system (LI-COR, Inc., Lincoln, NE). Twenty soil collars, each with a height of 4.4 cm and a diameter of 11 cm, were inserted into the soil in each stand at random locations. Surface efflux was measured three times in succession for each collar during each measurement period. Soil temperature at 10 cm was measured adjacent to each respiration collar with a portable temperature probe provided with the LI-6400. Soil volumetric water content at 0–20 cm was measured by a portable time domain reflectometer (Hydrosense, Campbell Scientific, Inc., Logan, UT) installed vertically. The measurements were made every 3–4 weeks in the 2002 and 2003 growing seasons.

In addition to periodic measurements of soil temperature and moisture coincident with respiration measurements, continuous soil temperatures were measured at 0, 5, 10, 25, 50, and 100 cm using copper-constantan thermocouples (Omega Engineering, Inc., Stamford, CT), and soil water contents were measured at 5, 10, 20, 50, and 100 cm using time domain reflectometers (CS615, Campbell Scientific, Inc., Logan, UT) installed horizontally at the center of the hardwood stand. Thirty-minute average of data were computed and stored in dataloggers (CR10X and 23X, Campbell Scientific, Inc., Logan, UT).

We used an exponential equation to analyze the relationship between respiration and temperature:

$$R = R_0 e^{\beta T} \quad (1)$$

where $R$ is the component respiration (soil, coarse woody debris, stem or leaf), $T$ is the temperature of each component, and $R_0$ and $\beta$ are fitted parameters. The respiration parameter $Q_{10}$ can be derived from $Q_{10} = \exp(10\beta)$. Estimated parameters were used to predict component respiration for every 0.5 h over 2 years based on continuous temperature measurements.

### 2.3. Coarse woody debris respiration

We established four transects in the hardwood stand, each 50 m long and 15 m wide, to estimate the volume and surface area of coarse woody debris (CWD) that was scattered on the ground. CWD was classified into three categories, <2.5 cm, 2.5–7.5 cm, and >7.5 cm in diameter. We counted the number and measured length of CWD less than 2.5 cm and between 2.5 and 7.5 cm in diameter within the transects. For CWD greater than 7.5 cm in diameter, we measured the individual diameter as well as length and total number. The volume and surface area of CWD in the hemlock stand was considered the same as in the hardwood stand.

Twenty soil collars, each with a height of 4.4 cm and a diameter of 11 cm, were inserted into randomly selected, large-diameter CWD in each stand. Similar to the protocol of soil respiration measurement, CWD respiration was measured by the LI-6400 portable photosynthesis system (LI-COR, Inc., Lincoln, NE). CWD temperature at 5 cm depth was also measured with the portable temperature probe provided with the LI-6400. The measurements were made every 3–4 weeks during the growing season.

We used the exponential equation (Eq. (1)) to analyze the relationship between CWD respiration and CWD temperature. The surface area based measurement of CWD respiration was upscaled to the stand level based on the estimation of total surface area of CWD, which is greater than ground-projected area of CWD. Continuous measurements of soil temperature at 5 cm were used to approximate CWD temperature and to upscale CWD respiration. We did not use the volume based upscaling method because we did not find any significant difference in CWD respiration between different sizes of debris for sizes greater than 7.5 cm in diameter. Therefore, we used surface area of CWD for upscaling. We only counted CWD greater than 7.5 cm in diameter when upscaling CWD respiration because it comprised majority of total volume of CWD. The small-sized woody debris was often buried in leaf debris with no difference between projected area and surface area, and we observed small differences between soil respiration and small-sized woody debris respiration.

### 2.4. Stem respiration

Stem respiration was measured on 19 sugar maple, 15 hemlock and 12 yellow birch trees in the hardwood stand, using the methods described in Bolstad et al. (2004). Tree samples ranged from 8 to 86 cm in DBH. Fixed plates were mounted on each tree with silicon sealant at an approximately 137 cm height and a random azimuth. A custom Plexiglas cuvette, 869 $cm^3$ in volume with 101 $cm^2$ in an opening, was closely attached to the mounting plate just before each measurement. Stem respiration rates from the area covered by the cuvette were measured monthly with an LI-6400 portable photosynthesis system (LI-COR, Inc., Lincoln, NE) in the growing season. Measurements were recorded when flux readings had stabilized, typically within 3–10 min. Continuous stem temperature was measured with a thermocouple

inserted into the sapwood near the cuvette of each tree. Sapwood thickness and wood mass density of each tree were measured with tree cores.

Measured stem respiration rates per unit area were converted to rates per unit of sapwood volume based on sapwood depth and tree DBH, assuming a wedge-shape volume that contributed to the respiration rates. We used the exponential function ($Q_{10}$ function) to analyze the response of stem respiration per unit of sap wood volume by each species to stem temperature (Eq. (1)).

To upscale chamber measurements of stem respiration to the stand level, we estimated the total sapwood volume per unit of ground area in each stand. We assumed that branch respiration per volume had the same rate as stem (bole) respiration, similar to the assumptions made by Law et al. (1999), Xu et al. (2001), and Bolstad et al. (2004). Based on regional allometric biomass equations (Eq. (2)) for each species (Perala and Alban, 1993; Ter-Mikaelian and Korzukhin, 1997) and measured DBH and sapwood thickness, we estimated bole biomass (excluding bark), heartwood biomass, branch biomass (excluding bark) and thus derived total sapwood biomass.

$$M = aD^b \quad (2)$$

where $M$ is the oven-dry weight of the biomass component of a tree (kg), $D$ is the DBH (cm) of the tree (for bole biomass and branch biomass) or of the heartwood (for heartwood biomass), and $a$ and $b$ are parameters. Table 1 reports the parameters for the three primary species found at our sites (Perala and Alban, 1993; Ter-Mikaelian and Korzukhin, 1997).

Total sapwood biomass was derived from Eq. (3) assuming that branch biomass without bark consisted all of sapwood.

$$M_s = M_b - M_h + M_{br}, \quad (3)$$

where $M_s$ is the sapwood biomass, $M_b$ is the bole biomass, $M_h$ is the heartwood biomass, and $M_{br}$ is the branch biomass. Sapwood biomass was converted to sapwood volume based on wood mass density with 0.63 g cm$^{-3}$ for sugar maple, 0.40 g cm$^{-3}$ for hemlock, and 0.62 g cm$^{-3}$ for yellow birch.

After estimating sapwood volume of 46 sample trees, we found a good relationship between sapwood volume and DBH fitted by a power function:

$$V_s = \alpha D^\beta \quad (4)$$

**Table 1 – Parameters for calculating biomass in the equation $M = aD^b$**

| Species | Bole and heartwood | | Branch | |
|---|---|---|---|---|
| | $a$ | $b$ | $a$ | $b$ |
| Sugar maple | 0.1179 | 2.3467 | 0.0208 | 2.5311 |
| Hemlock | 0.0545 | 2.3570 | 0.0586 | 1.9157 |
| Yellow birch | 0.0548 | 2.6190 | 0.0175 | 2.5500 |

$M$ is the oven-dry weight of the biomass component of a tree (kg), and $D$ is the DBH (cm) of the tree (for bole biomass and branch biomass) or of the heartwood (for heartwood biomass).

**Table 2 – Parameters for calculating sapwood volume in the equation $V_s = \alpha D^\beta$**

| Species | $\alpha$ | $\beta$ | $r^2$ | $p$ | Sample ($n$) |
|---|---|---|---|---|---|
| Sugar maple | 8.7881 | 2.2167 | 0.9944 | <0.0001 | 19 |
| Hemlock | 4.0689 | 1.9504 | 0.9415 | <0.0001 | 15 |
| Yellow birch | 8.8767 | 2.2360 | 0.9827 | <0.0001 | 12 |

$V_s$ is the sapwood volume including that from stems and branches (m$^3$), and $D$ is DBH (m).

where $V_s$ is the sapwood volume including that from stems and branches (m$^3$), $D$ is DBH (m), and $\alpha$ and $\beta$ is estimated parameters (Table 2). Eq. (4) was used to estimate the sapwood volume of the whole stand and the average sapwood volume per ground area.

### 2.5. *Leaf respiration*

Leaf respiration was measured from 20 leaves collected from 7 sugar maple trees, 30 leaves from 10 hemlock trees and 22 leaves from 7 yellow birch trees in June, July and August. Following the method of Bolstad et al. (2004), branches from three species with random height and direction in the canopy were detached at night and immediately placed in a plastic bag with a moistened paper towel and transported in the dark to a nearby laboratory. Fully expanded leaves were detached just before measurement. All measurements were made within 3 h of branch harvest. Leaf respiration rates were measured with an LI-6400 portable photosynthesis system (LI-COR, Inc., Lincoln, NE) fitted with a broadleaf chamber (2 cm by 3 cm). Respiration rates were recorded when flux readings had stabilized, typically within 3–10 min.

Each leaf sample was measured at three temperature levels: low, ambient and high temperature. Temperature was adjusted by placing the measurement chamber in Peltier thermoelectric coolers, which can increase or decrease ambient temperature for measurements. The real leaf temperature, ranging from 19 to 33 °C, was recorded with a thermocouple inside the chamber.

Leaf area was measured with an optical scanner and digital summation (SigmaScan, SPSS, Chicago, IL). The effective respiration measurement area of broadleaves such as those from sugar maple and yellow birch was the chamber area (6 cm$^2$), while the effective area of hemlock was the sum of total needle areas, usually less than the chamber area. Leaves were oven-dried at 65 °C and weighed. Effective leaf biomass covered by the chamber was directly measured for hemlock leaves (less than chamber area), or calculated based on proportional mass for deciduous leaves covered by the chamber. Leaf respiration measurements based on chamber area were then converted to leaf respiration per dry biomass. Converting to mass-based respiration helped remove the factor of leaf sampling position in the canopy (Bolstad et al., 2004).

We used the exponential equation (Eq. (1)) to fit leaf respiration per dry biomass as a function of leaf temperature for each species. Continuous leaf respiration over the season was estimated from Eq. (1), canopy temperature and leaf biomass per ground area. Canopy temperature per half-hour was approximated by air temperature in the canopy at 10 m.

Ground-based leaf biomass of each species was estimated from litterfall while also taking into account seasonal variation. We placed 10 baskets, each with an area of 1969 $cm^2$ in both stands to collect litterfall. The time for leaf expansion and leaf senescence for deciduous trees was determined from above- and below canopy photosynthetically active radiation (PAR) measurements. The minimum and maximum of fractional absorbed PAR (fPAR = 1 – below PAR/above PAR) indicated leaf off and full leaf, respectively, for deciduous trees. Leaf biomass during the full leaf period was measured by litterfall data. The leaf expansion and senescence periods were determined by the increase and decrease of fPAR from its minimum and maximum. We assume a constant leaf area during all seasons for hemlock, guided by the lack of seasonality in litterfall. Hemlock leaf biomass was calculated from litterfall data multiplied by 3 years of leaf longevity (Barnes and Wagner, 1981). We computed dark leaf respiration for the nighttime period determined by periods when above canopy PAR $<10\ \mu mol\ m^{-2}\ s^{-1}$.

### 2.6. Net ecosystem exchange

Fluxes of $CO_2$ were measured from a tower at 36 m above-ground at the center of the hardwood stand, described in detail in Desai et al. (2005). High-frequency (10 Hz) three-dimensional wind speed was measured by a sonic anemometer (CSAT-3, Campbell Scientific, Inc., Logan, UT). $CO_2$ and $H_2O$ mixing ratios at 10 Hz were measured by an infrared gas analyzer (LI-6262, LI-COR, Lincoln, NE). Flow rates were drawn by a diaphragm pump (model UN89, KNF Neuberger, Inc., Trenton, NJ). Storage flux calculations and calibration of high frequency $CO_2$ were obtained by measuring low-frequency (3 min average, 21 min interval), high-precision ($\pm$ 0.2 ppm) $CO_2$ mixing ratios at seven levels (0.6, 1.8, 3, 7.6, 14, 21, 36 m) between the ground and flux measurement height.

Turbulent fluxes of $CO_2$ were calculated at half-hourly intervals as the covariance of vertical wind velocity and the scalar factors, while considering the lag and spectral corrections (Berger et al., 2001). Net ecosystem exchange (NEE) for the forest was calculated as the sum of the turbulent flux at sensor height and the storage term below sensor height. NEE data were screened for weak turbulence friction velocity at night and non-representative footprints contaminated by lakes and wetlands (Desai et al., 2005). Nighttime NEE was assumed to be a measurement of ecosystem respiration, and was extrapolated to all times by using a temperature response function as described by Cook et al. (2004) and Desai et al. (2005).

In addition to flux measurements, a full suite of micrometeorological measurements was made at this site, including net radiation, total photosynthetic active radiation above and below canopy, air temperature, humidity, and precipitation.

## 3. Results

### 3.1. Soil respiration

Measurements of soil respiration indicated that the seasonal pattern of soil respiration ranged from 1.3 to 4.5 $\mu mol\ m^{-2}\ s^{-1}$ in the hardwood stand and from 1.1 to 4.0 $\mu mol\ m^{-2}\ s^{-1}$ in the hemlock stand (Fig. 1). Soil respiration in the hardwood stand was systematically higher than that in the hemlock stand, except on days 270 and 283 in 2003. Soil respiration peaked in July (day 199) in 2002 but peaked in late August (day 238) in 2003 in the hardwood stand, and peaked at the end of June (day 179) in 2002 but in late August (day 238) in 2003 in the hemlock stand. The later peak in soil respiration in 2003 was consistent with measured soil temperature. Daily mean soil temperature at 10 cm peaked in July (day 183) 2002 at 20.2 °C while it peaked in August (day 233) in 2003 at 19.6 °C. Soil moisture did not appear to be a constraint to soils and plants since precipitation was evenly distributed throughout the growing season in both years. Daily mean soil volumetric moisture at 10 cm varied between 0.18 and 0.31 $m^3\ m^{-3}$ in 2002, and between 0.10 and 0.31 $m^3\ m^{-3}$ in 2003. It peaked in the middle of April when snow melted. Soil moisture reached minima in July for 2002 and in September for 2003. Year 2003 was cooler and drier compared with 2002. The mean air temperature was 4.3 °C in 2002 and 3.6 °C in 2003. The total precipitation was 928 mm in

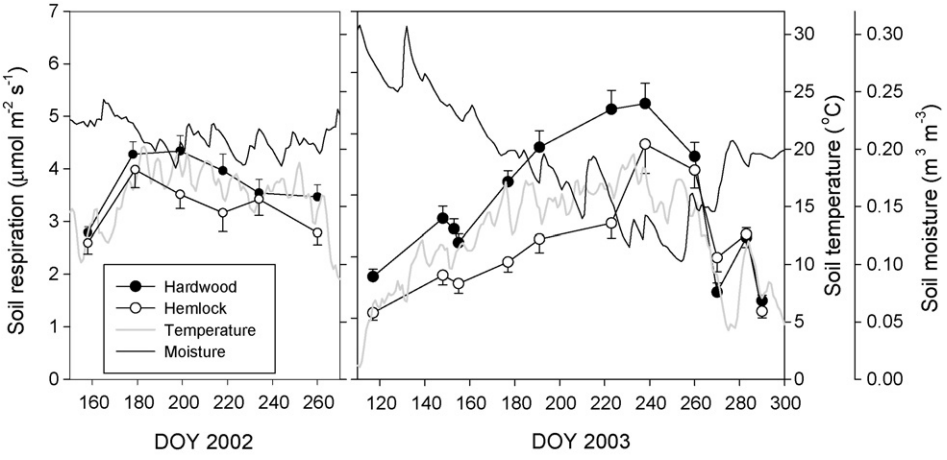


**Fig. 1 – Measurements of soil respiration in the hardwood and hemlock stands with daily mean soil temperature and moisture in 2002 and 2003. Each datapoint of soil respiration is a spatial average with error bars indicating standard errors (upward ones for the hardwood stand, and downward ones for the hemlock stand).**

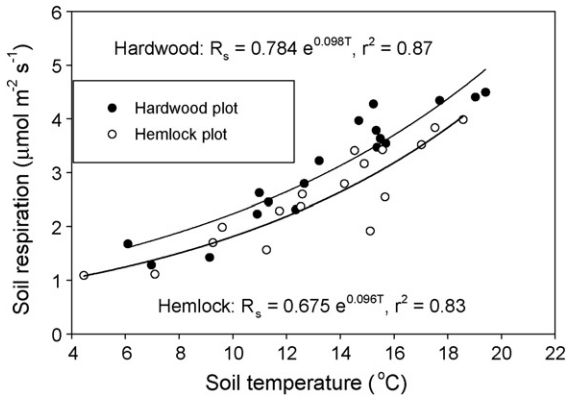


**Fig. 2 – Soil respiration as a function of soil temperature at 10 cm in the hardwood and hemlock stands.**

2002 and 537 mm in 2003. Despite the lower precipitation, there does not appear to be a decrease in soil respiration due to lower soil moisture in 2003. Respiration rates during the period of the lowest soil moisture in 2003 were comparable to rates at similar temperatures in 2002 (Fig. 1).

Soil respiration strongly correlated with soil temperature. Plots of spatially averaged soil respiration against average soil temperature show a strong exponential relationship between soil respiration and soil temperature (Fig. 2). The parameters in Eq. (1) for soil respiration are summarized in Table 3. $Q_{10}$ was derived as 2.66 for the hardwood stand and 2.62 for the hemlock stand. The two fitted lines indicated that the temperature sensitivity in the two stands were similar while the reference respiration ($R_0$) in the hardwood plot was larger than that in the hemlock stand.

Eq. (1) allows us to estimate year-round soil respiration with input from soil temperature. Cumulative soil respiration summed to be 741.6 g C $m^{-2}$ $y^{-1}$ in 2002 and 707.0 g C $m^{-2}$ $y^{-1}$ in 2003 in the hardwood stand, and 628.5 g C $m^{-2}$ $y^{-1}$ in 2002, and 599.7 g C $m^{-2}$ $y^{-1}$ in 2003 in the hemlock stand. The lower soil respiration in 2003 was consistent with the lower air temperature in 2003 compared with 2002. The average of annual soil respiration over the two stands was 669 g C $m^{-2}$ $y^{-1}$.

**Table 3 – Parameters in the temperature response function (Eq. (1)) for soil respiration ($R_s$, μmol $m^{-2}$ $s^{-1}$) in two stands, woody debris respiration ($R_w$, μmol $m^{-2}$ $s^{-1}$) in two stands, stem respiration ($R_{sb}$, μmol $m^{-3}$ $s^{-1}$) from three species, and leaf respiration ($R_l$, μmol $kg^{-1}$ $s^{-1}$) from three species**

| | | $R_0$ | $\beta$ | $Q_{10}$ | $r^2$ |
|---|---|---|---|---|---|
| $R_s$ | Hardwood | 0.784 | 0.098 | 2.66 | 0.87 |
| | Hemlock | 0.675 | 0.096 | 2.62 | 0.83 |
| $R_w$ | Hardwood | 0.453 | 0.116 | 3.19 | 0.96 |
| | Hemlock | 0.398 | 0.094 | 2.55 | 0.90 |
| $R_{sb}$ | Sugar maple | 5.044 | 0.083 | 2.30 | 0.84 |
| | Hemlock | 4.830 | 0.092 | 2.50 | 0.90 |
| | Yellow birch | 5.909 | 0.080 | 2.23 | 0.70 |
| $R_l$ | Sugar maple | 3.957 | 0.066 | 1.94 | 0.51 |
| | Hemlock | 0.882 | 0.082 | 2.28 | 0.46 |
| | Yellow birch | 4.601 | 0.064 | 1.89 | 0.49 |

The unit of temperature is °C.

### 3.2. *Coarse woody debris respiration*

CWD volume was estimated as 12 $m^3$ $ha^{-1}$ for diameter <2.5 cm, 8 $m^3$ $ha^{-1}$ for diameter between 2.5 and 7.5 cm, and 59 $m^3$ $ha^{-1}$ for diameter >7.5 cm. The total surface area of CWD greater than 7.5 cm in diameter per unit of ground area was 0.083 $m^2$ $m^{-2}$.

Spatially averaged CWD respiration and CWD temperature at 5 cm in both stands were used to estimate parameters in Eq. (1). The parameters are shown in Table 3. $Q_{10}$ was derived to be 3.19 for the hardwood stand, and 2.55 for the hemlock stand.

Daily mean CWD respiration in the hardwood stand was consistently higher than that in the hemlock stand. Cumulative CWD respiration per unit of ground area was estimated as 44.7 g C $m^{-2}$ $y^{-1}$ in 2002 and 41.8 g C $m^{-2}$ $y^{-1}$ in 2003 in the hardwood stand, and 29.8 g C $m^{-2}$ $y^{-1}$ in 2002, and 28.4 g C $m^{-2}$ $y^{-1}$ in 2003 in the hemlock stand. The average of annual CWD respiration was 36 g C $m^{-2}$ $y^{-1}$.

### 3.3. *Stem respiration*

Measurements of the seasonal variation of stem respiration per sapwood volume indicated that stem respiration peaked in late June and early July and then followed a decreasing trend with time (Fig. 3). The change of stem respiration correlated with the change of sapwood temperature. We did not find significant difference of stem respiration between sugar maple, hemlock, and yellow birch in 2003, but we found that stem respiration from hemlock was greater than sugar maple and yellow birch in 2002.

After plotting stem respiration against sapwood temperature, we found an exponential correlation between stem respiration and sapwood temperature (Fig. 4). The parameters are shown in Table 3. $Q_{10}$ was derived to be 2.30 for sugar maple, 2.50 for hemlock, and 2.23 for yellow birch.

Using sapwood volume for three species (Table 4) and hourly measurements of sapwood temperature, we estimated continuous stem respiration of the three species and calculated the annual sums (Table 5). Because of differences in stand density of each species, stem respiration from sugar maple was much greater than from hemlock, yellow birch and other species in the hardwood stand. Stem respiration in the hemlock stand was primarily from hemlock trees. The order of magnitude of stem respiration in the hardwood stand was

**Table 4 – Sapwood volume ($m^3$ $ha^{-1}$) for three species in two stands**

| Species | Hardwood stand | Hemlock stand |
|---|---|---|
| Sugar maple | 201.4 | 20.8 |
| Hemlock | 27.5 | 367.6 |
| Yellow birch | 67.4 | 60.1 |
| Sum | 296.3 | 448.5 |

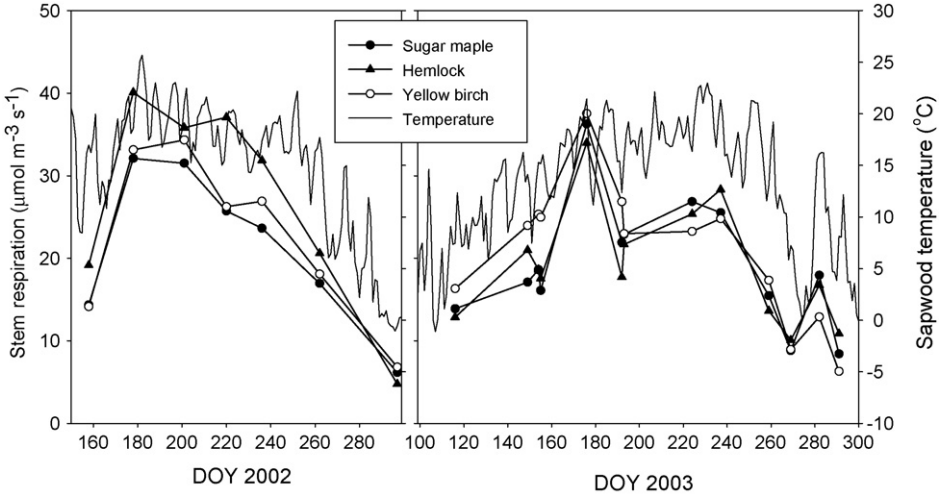


**Fig. 3 – Measurements of stem respiration based on sapwood volume for three species with daily mean sapwood temperature in 2002 and 2003.**

sugar maple, yellow birch and hemlock. This pattern was reversed in the hemlock stand. Stem respiration in both stands was slightly smaller in 2003 than in 2002, primarily due to lower summer temperatures in 2003. The average of annual stem respiration over the two stands was 169 g C $m^{-2}$ $y^{-1}$.

### 3.4. *Leaf respiration*

Leaf respiration per leaf biomass responded exponentially to leaf temperature (Fig. 5). The parameters in temperature response functions are summarized in Table 3. $Q_{10}$ was derived to be 1.94 for sugar maple, 2.28 for hemlock, and 1.89 yellow birch.

Yellow birch leaves had slightly higher respiration than sugar maple leaves. Hemlock had substantially less leaf respiration per unit of biomass but higher temperature sensitivity than the two deciduous trees. Fractional absorbed PAR (fPAR) data indicated that deciduous leaf expansion occurred from day 125 to 162. LAI remained high from day 162 and 281, and then senesced from day 281 to 311. Table 6 indicates the maximum leaf biomass for deciduous trees and the constant leaf biomass for hemlock. Leaf biomass in 2002 was less than in 2003. Leaf biomass in the hardwood stand was less than in the hemlock stand, though the LAI measured by LAI-2000 in the hardwood stand was greater than in the hemlock stand. This is because hemlock had lower specific leaf area ($cm^2$ $g^{-1}$) than the broadleaf species observed in the stands.

Cumulative leaf respiration per ground area for three species indicated that the hardwood stand had much higher total leaf respiration than the hemlock stand, and leaf respiration in both stands in 2002 was lower than in 2003 (Table 7), corresponding mainly with lower leaf biomass in 2002. In the hardwood stand, the proportion of leaf respiration decreased in the order from sugar maple, yellow birch, and hemlock with a dominant proportion from sugar maple. Hemlock-dominated leaf respiration in the hemlock stand. The average of annual leaf respiration over the two stands was 93 g C $m^{-2}$ $y^{-1}$.

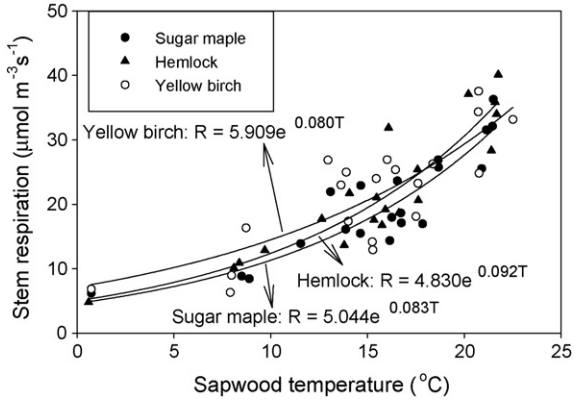


**Fig. 4 – Stem respiration per sapwood volume from sugar maple, hemlock, yellow birch as functions of sapwood temperature.**

### 3.5. *Ecosystem respiration*

Seasonally, daily mean ecosystem respiration varied between 0.9–8.5 μmol $m^{-2}$ $s^{-1}$ in 2002 and 0.7–7.9 μmol $m^{-2}$ $s^{-1}$ in 2003 in the hardwood stand, and varied between 0.8–7.8 μmol $m^{-2}$ $s^{-1}$ in 2002 and 0.6–6.9 μmol $m^{-2}$ $s^{-1}$ in 2003 in the

**Table 5 – Cumulative stem respiration per ground area (g C $m^{-2}$ $y^{-1}$) for three species and their sums in two stands in 2002 and 2003**

| | Hardwood stand | | Hemlock stand | |
|---|---|---|---|---|
| | 2002 | 2003 | 2002 | 2003 |
| Sugar maple | 86.2 | 85.3 | 8.9 | 8.8 |
| Hemlock | 12.7 | 12.6 | 170.6 | 167.1 |
| Yellow birch | 32.4 | 32. 0 | 29.0 | 28.5 |
| Sum | 131 | 130 | 209 | 204 |

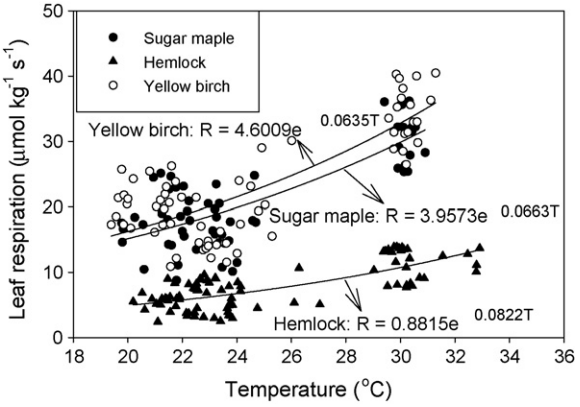


**Fig. 5 – Leaf respiration per leaf biomass from sugar maple, hemlock, yellow birch as functions of leaf temperature.**

**Table 6 – Total leaf dry biomass (g $m^{-2}$) for three species in two stands in 2002 and 2003**

| | Hardwood stand | | Hemlock stand | |
|---|---|---|---|---|
| | 2002 | 2003 | 2002 | 2003 |
| Sugar maple | 172.8 | 199.6 | 5.2 | 6.9 |
| Hemlock | 64.2 | 69.1 | 258.7 | 298.4 |
| Yellow birch | 46.0 | 50.3 | 39.7 | 41.1 |
| Sum | 283 | 319 | 304 | 346 |

**Table 7 – Cumulative leaf respiration per ground area (g C $m^{-2}$ $y^{-1}$) for three species and their sums in two stands in 2002 and 2003**

| | Hardwood stand | | Hemlock stand | |
|---|---|---|---|---|
| | 2002 | 2003 | 2002 | 2003 |
| Sugar maple | 74.9 | 84.7 | 2.3 | 3.0 |
| Hemlock | 11.7 | 12.4 | 47.1 | 53.6 |
| Yellow birch | 22.2 | 23.8 | 19.1 | 19.4 |
| Sum | 109 | 121 | 69 | 76 |

hemlock stand (Fig. 6). Ecosystem respiration averaged 0.9 μmol $m^{-2}$ $s^{-1}$ in the winter. Ecosystem respiration minimized in January–March, and rapidly increased after mid-April. It peaked in early July in 2002 and in mid-August in 2003. The change of peak time between 2 years was corresponding with interannual variability in local climate. Ecosystem respiration dropped to the winter value in mid-November. The component respiration demonstrated the similar seasonal variations to ecosystem respiration.

Cumulative ecosystem respiration and its components in 2002 and 2003 are summarized in Table 8. Total ecosystem respiration averaged 1013 g C $m^{-2}$ $y^{-1}$ in the hardwood stand and 922 g C $m^{-2}$ $y^{-1}$ in the hemlock stand. Average of ecosystem respiration was estimated as 967 g C $m^{-2}$ $y^{-1}$ from two stands. Cumulative annual soil respiration, CWD respiration, stem respiration, and leaf respiration were 724, 43, 131, 115 g C $m^{-2}$ $y^{-1}$, respectively, accounting for 72%, 4%, 13%, and 11% of total ecosystem respiration in the hardwood stand, and 614, 29, 207, 72 g C $m^{-2}$ $y^{-1}$, respectively, accounting for 67%, 3%, 22%, and 8% in the hemlock stand. Respiration from most components was higher in the hardwood stand than those in the hemlock stand, with the exception of stem respiration. In both stands, ecosystem respiration from year 2002 was larger than year 2003 due primarily to lower temperature in 2003. Aboveground autotrophic respiration (stem + leaf respiration) comprised 24% of total respiration, with stem respiration slightly higher than leaf respiration in the hardwood stand. Woody debris respiration only accounted for 4% of total ecosystem respiration, or 6% of soil respiration in the hardwood stand. Compared with the hardwood stand, the proportion of soil respiration in the hemlock stand was smaller but aboveground respiration was larger, accounting for 30% of total respiration. Unlike the hardwood stand, stem respiration in the hemlock stand was more than twice leaf respiration. Similar to the hardwood stand, woody debris respiration in the hemlock stand accounted for only 3% of total ecosystem respiration, or 5% of soil respiration.

## 4. Discussion

### 4.1. *Controls on respiration*

Temperature was the primary control on respiration in this northern forest site, and an exponential response function appears to explain most of the observed temporal variation. While temperature sensitivity ($Q_{10}$) may be temperature-dependent (Lloyd and Taylor, 1994; Kirschbaum, 1995), and $Q_{10}$ may change with soil moisture (Xu and Qi, 2001; Tang et al., 2005b), fixed $Q_{10}$ values over the season provide useful estimates for component and summed total ecosystem respiration at our site.

In contrast to some recent findings at arid sites, soil water had little impact on respiration relative to temperature at this site. In arid or semi-arid ecosystems as reported in Xu and Qi (2001) and Tang et al. (2005b), soil water is the major factor limiting ecosystem activities and hence respiration and its

**Table 8 – Ecosystem respiration, component respiration (g C $m^{-2}$ $y^{-1}$) and percentage (%) in two stands in 2002 and 2003 and the average over two years from two stands**

| | Hardwood stand | | Hemlock stand | | Average |
|---|---|---|---|---|---|
| | 2002 | 2003 | 2002 | 2003 | |
| Soil respiration | 741.6 (72%) | 707.0 (71%) | 628.4 (67%) | 599.7 (66%) | 669 (69%) |
| Woody debris respiration | 44.7 (4%) | 41.8 (4%) | 29.8 (3%) | 28.4 (3%) | 36 (4%) |
| Stem respiration | 131.8 (13%) | 129.6 (13%) | 208.5 (22%) | 204.4 (23%) | 169 (17%) |
| Leaf respiration | 108.8 (11%) | 120.9 (12%) | 68.5 (8%) | 75.9 (8%) | 93 (10%) |
| Ecosystem respiration | 1027 (100%) | 999 (100%) | 935 (100%) | 908 (100%) | 967 (100%) |

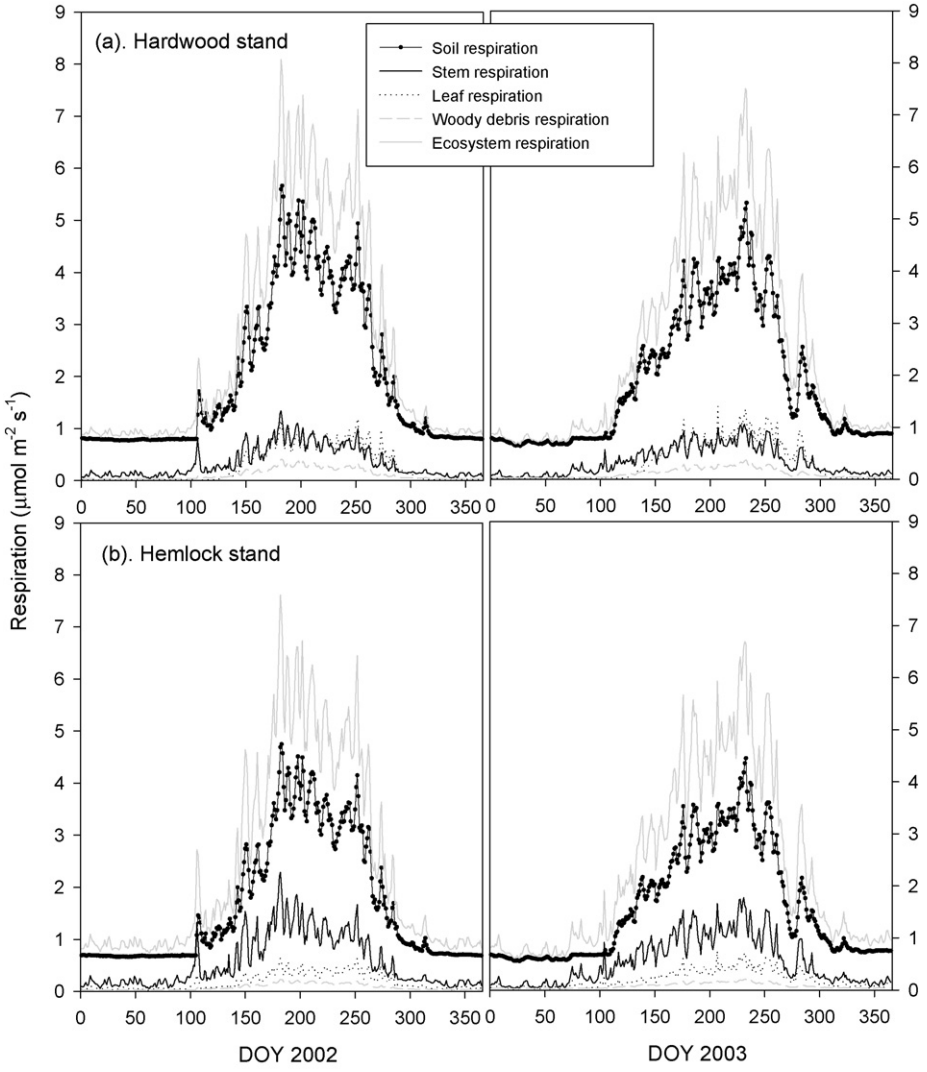


**Fig. 6 – Estimated daily mean soil, stem, leaf, woody debris, and total ecosystem respiration during years 2002 and 2003 in the hardwood and hemlock stands.**

sensitivity to temperature, particularly in the summer. Water appears to be sufficient at our site to maintain microbial activity and plant physiology with an annual average of 0.21 $m^3\ m^{-3}$ at 10 cm, although a summer drought in a dry year may reduce the annual soil respiration in nearby mature forests in Northern Wisconsin (Martin and Bolstad, 2005). The sufficiency in soil moisture may explain the insignificant control of soil moisture on respiration at our site. Noormets et al. (in press) showed that moisture typically only had a small impact (8% on average) in improving regressions between eddy-flux measured ecosystem respiration and soil temperature for 14 sites in Northern Wisconsin and Michigan. Therefore, soil temperature may be a primary determinant for soil respiration in wet areas.

Similar to the controls on soil, stem and leaf respiration, temperature appeared to be a dominant and sufficient control to upscale CWD respiration. The potential controlling factors for CWD respiration include temperature, moisture, and decay status (Wang et al., 2002; Chambers et al., 2001; Mackensen et al., 2003). At our site, the moisture in CWD was not an important control, but the decay status may be important in explaining the spatial variation of measurements. We found the variation in CWD respiration was greater than soil respiration, which could possibly be explained by the variation in debris decay class or age. However, we did not quantify the decay class in this study. Consequently, our results averaged spatial samples with different decay status to study the correlation with temperature over the season. This may introduce some errors into our total respiration estimates. However, detrital contributions were small relative to total respiration. Thus, the error in pooling CWD was small.

This site is typically snow-covered for approximately 4–5 months each year. However, during this period, there was still small $CO_2$ efflux from the soil, stems, conifer leaves, and woody debris. Soil temperature measurements indicate that soil temperatures deeper than 25 cm never fall below 0 °C, and soil temperatures at 5 cm are typically above freezing, even in winter because of insulation of snowpack. Thus, the small amount of soil respiration under snow cover could be from microbial decomposition from unfrozen soils and from root

maintenance respiration occurring at deep soils. $CO_2$ efflux under snow could diffuse to the snow surface (McDowell et al., 2000; Panikov and Dedysh, 2000). Stems and conifer leaves also release $CO_2$ in the winter non-growing season as maintenance respiration (Ryan, 1990; Ryan et al., 1995). The temperature in large woody debris that was in close contact with the ground could also be above 0 °C and thus resulted in a small woody debris respiration in the winter.

### 4.2. *Uncertainty analysis*

The uncertainties of our estimated annual sums of respiration were mainly induced from instruments, sampling, and upscaling processes. First, measurements based on closed dynamic chambers may create sampling biases by disturbing air pressure and $CO_2$ concentration gradients in the soil (Livingston and Hutchinson, 1995; Healy et al., 1996; Davidson et al., 2002; Conen and Smith, 1998). This chamber-induced error has been widely discussed in the literature. A well-designed venting system may reduce the error. The second error source may be induced from sampling. The standard errors for spatially sampling (sample size = 20) soil respiration and woody debris respiration averaged 8% of the mean over the sampling period (monthly). The standard errors for sampling stem respiration (sample size = 19, 15, 12 for sugar maple, hemlock, and yellow birch, respectively) and leaf respiration (sample size = 20, 30, 22 for sugar maple, hemlock, and yellow birch, respectively) based on species were 12% and 6%, respectively, of the sample means. The third error source may be induced from upscaling of measurements, both spatially and temporally. The uncertainty for spatial upscaling, which was difficult to quantify, involved in the estimations of total woody debris surface area, total sapwood volume, and total leaf biomass. The temporal upscaling was associated with using regression-based equations to predict respiration. Under a 95% confidence interval, the uncertainties in predicting daily mean soil respiration, woody debris respiration, stem respiration, and leaf respiration averaged 9%, 10%, 11%, and 9%, respectively, of predicted values.

### 4.3. *Comparison with other old-growth forests*

We did not find other studies in similar ecological zones using chamber methods to estimate total ecosystem respiration from old-growth forests. However, the magnitude of our cumulative respiration is comparable to other studies from similar ecosystems using eddy covariance measurements. For example, our result from the old-growth hemlock stand is very close to a preliminary estimation of ecosystem respiration (920 g C $m^{-2}$ $y^{-1}$) based on eddy covariance measurements from a 200-year-old hemlock forest in central New England, USA (Hadley and Schedlbauer, 2002). Our total ecosystem respiration is slightly larger than that from a 120-year-old black spruce boreal forest in Canada at a range of 790–890 g C $m^{-2}$ $y^{-1}$ (Goulden et al., 1998).

Our results are also comparable to a study using the similar chamber and biometric measurement method for an old-growth ponderosa pine forest in the Pacific Northwest of USA characterized by a Mediterranean-type climate, which reported total ecosystem respiration to be 1014 g C $m^{-2}$ $y^{-1}$ (Law et al., 2001). For component fluxes, Law et al. (2001) reported more soil respiration (780 g C $m^{-2}$ $y^{-1}$) than our study, similar woody debris respiration (36 g C $m^{-2}$ $y^{-1}$), much less stem respiration (63 g C $m^{-2}$ $y^{-1}$), and more leaf respiration (131 g C $m^{-2}$ $y^{-1}$).

Another study using biometric measurements and modeling in an old-growth Douglas-fir-western hemlock forest in the Pacific Northwest of USA reported much larger ecosystem respiration averaged as 1886 g C $m^{-2}$ $y^{-1}$ (Harmon et al., 2004). Harmon et al. (2004) reported a similar stem and branch respiration (160 g C $m^{-2}$ $y^{-1}$) to our study, but much higher leaf respiration (577 g C $m^{-2}$ $y^{-1}$), and higher soil respiration (441 g C $m^{-2}$ $y^{-1}$ from roots and 577 g C $m^{-2}$ $y^{-1}$ from heterotrophic respiration). The higher respiration reported by Harmon et al. (2004) is probably due to the biometric measurement method used to derive respiration, which is of much difference from direct flux measurements in our study.

Ecosystem respiration from our site is also much smaller than that from old-growth Amazon tropic forests based on eddy covariance measurements such as an estimation of 2337.6 g C $m^{-2}$ $y^{-1}$ (Grace et al., 1996), and of 3070 g C $m^{-2}$ $y^{-1}$ (Carswell et al., 2002). Higher temperature, longer growing seasons, and higher photosynthesis and growth rates in tropic forests may explain higher respiration than that from northern forests.

### 4.4. *Comparison between chamber and eddy covariance measurements*

Eddy covariance measurements of NEE at this site indicated a small sink (−72 g C $m^{-2}$ $y^{-1}$ in 2002 and −147 g C $m^{-2}$ $y^{-1}$ in 2003) (Desai et al., 2005). Based on eddy covariance measurements, annual ecosystem respiration was estimated as 965 g C $m^{-2}$ $y^{-1}$ in 2002, and 883 g C $m^{-2}$ $y^{-1}$ in 2003 (Desai et al., 2005). Since the hardwood stand and hemlock stand represented most of the footprint area of the eddy covariance measurement, we averaged chamber measurements from two stands to compare with the eddy covariance measurements. The chamber-based measurement of ecosystem respiration was upscaled as 981 g C $m^{-2}$ $y^{-1}$ in 2002 and 954 g C $m^{-2}$ $y^{-1}$ in 2003. These numbers are close to the results from the eddy covariance measurement with 2% larger in 2002 and 8% larger in 2003 than eddy covariance measurements.

Daily mean ecosystem respiration based on chamber measurements and eddy covariance measurements are plotted in Fig. 7. The well-fitted linear curve indicates a good correlation between these two independent measurements methods with $r^2 = 0.96$. By comparing with the line $y = x$ we found that eddy covariance measurements are typically less than chamber measurements when the values are low (less than 3 μmol $m^{-2}$ $s^{-1}$) in winter, while eddy covariance measurements are larger than chamber measurements when the values are high in summer (larger than 4 μmol $m^{-2}$ $s^{-1}$). The error sources for explaining this discrepancy are complicated, including those from the disturbance of chamber measurements (Livingston and Hutchinson, 1995; Davidson et al., 2002), chamber upscaling processes, nocturnal eddy covariance measurements with low friction velocity, extrapolation of nighttime respiration from the eddy covariance measurement to daytime respiration, and footprint analysis.

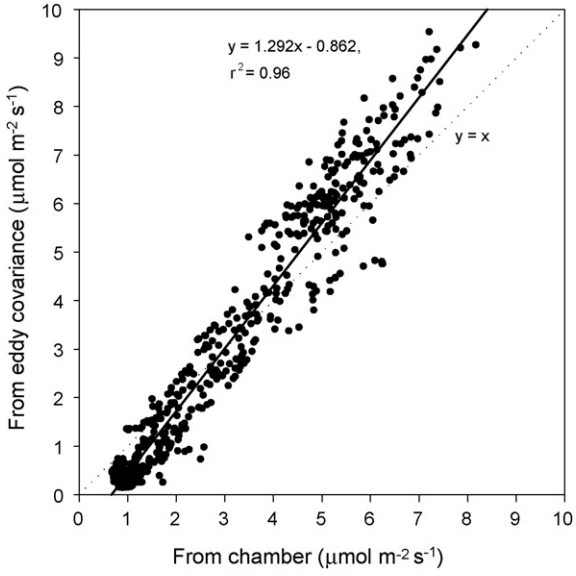


**Fig. 7 – Comparison between chamber-based and eddy covariance measurements of ecosystem respiration. Data are daily mean respiration in 2002 and 2003. The solid line indicates a linear fit. The dot line is y = x.**

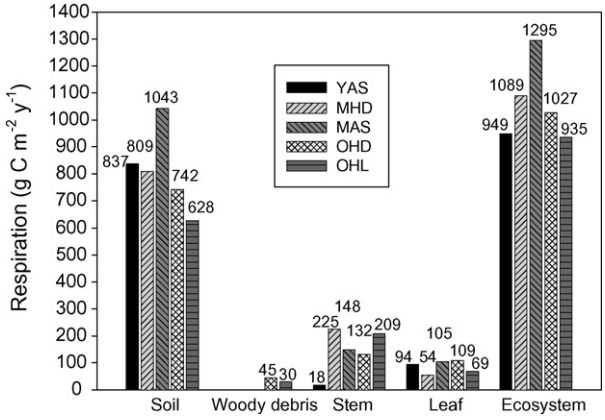


**Fig. 8 – Soil, woody debris, stem, leaf and total ecosystem respiration from the young aspen (YAS), mature northern hardwood (MHD), mature aspen (MAS), old-growth hardwood (OHD), and old-growth hemlock (OHL) stands in 2002. The numbers indicate cumulative respiration over a year.**

Our comparison between chamber and eddy covariance measurements of respiration has a better agreement than several other studies (Law et al., 1999; Goulden et al., 1996b; Lavigne et al., 1997), although all these studies suggested larger chamber measurements than eddy covariance measurements. The lower magnitude of respiration from eddy covariance measurements is probably mainly due to underestimation of nocturnal respiration when turbulence is weak and drainage is significant.

### 4.5. *Comparison in respiration between the old-growth, a young and a mature second-growth forest*

Ecosystem respiration and its components from a young (24–27 years old) and a mature (65–90 years old) second-growth hardwood forest, about 50 km from our site with similar climate, have been estimated using the chamber method (Bolstad et al., 2004) and the eddy covariance method (Cook et al., 2004; Desai et al., 2005). The chamber method reported total ecosystem respiration of 949 g C $m^{-2}$ $y^{-1}$ in the young northern hardwood stand dominated by aspen (LAI = 3.5, basal area = 27.3 $m^2$ $ha^{-1}$), 1089 g C $m^{-2}$ $y^{-1}$ in the mature northern hardwood stand (LAI = 4.2, basal area = 27.4 $m^2$ $ha^{-1}$) facilitated with an eddy covariance measurement tower, and 1295 g C $m^{-2}$ $y^{-1}$ in a nearby mature aspen stand (LAI = 4.8, basal area = 22.3 $m^2$ $ha^{-1}$) dominated by aspen in 2002 (Bolstad et al., 2004).

We plotted soil, woody debris (only from old-growth), stem, leaf, and total ecosystem respiration from the young aspen (YAS), mature second-growth northern hardwood (MHD), mature aspen (MAS), old-growth hardwood (OHD, or hardwood stand), and old-growth hemlock (OHL, or hemlock stand) stands in 2002 in Fig. 8. We found that both age class and species are important in determining the magnitude and proportion of component respiration, but total ecosystem respiration generally increased from the young stand to the mature stands, and then decreased from the mature stands to old-growth stands. Within age classes, the mixed mature hardwood stand (MHD) had less total respiration and soil respiration than the aspen-dominated mature hardwood stand (MAS), while the mixed old-growth hardwood (OHD) had more total respiration and soil respiration than the hemlock-dominated old-growth (OHL). Across different age classes, soil respiration increased from the young aspen stands to the mature aspen stands, but soil respiration from the mature northern hardwood stands was slightly less than the young aspen stands. Soil respiration from the old-growth stands was generally less than the second-growth stands. Stem respiration substantially increased from the young stand to the mature second-growth stands. By comparing stem and leaf respiration between old-growth hardwood and mature hardwood stands, we found that the old-growth hardwood had less stem respiration but more leaf respiration than the mature second-growth hardwood. In contrast, the hemlock-dominated old-growth had more stem respiration but less leaf respiration than the aspen-dominated mature hardwood. No woody debris respiration was reported in the young and mature sites, indicating an insignificant proportion of woody debris respiration in the young and mature sites.

A most recent report about component respiration in a mature northern hardwood forest at the University of Michigan Biological Station in northern Michigan confirms our result that mature forests have the highest respiration (Curtis et al., 2005). Using chamber and biometric measurement methods, Curtis et al. (2005) reported 1425, 1003, 166, and 256 g C $m^{-2}$ $y^{-1}$ of ecosystem respiration, soil respiration, stem respiration, and leaf respiration, respectively, higher than those in our old-growth hardwood stand.

The successional pattern of respiration from the northern forests, peaking in the mature and declining in the old-growth,

is in disagreement with the traditional hypothetical pattern of respiration (Odum, 1969; Kira and Shidei, 1967; Gower, 2003), but consistent with more recent findings (Ryan et al., 2004; Ryan and Waring, 1992). The forest succession model suggests that forest aboveground NPP (ANPP) increases with age from the young to the mature, and then declines from the mature to old (Kira and Shidei, 1967; Odum, 1969; Ryan et al., 1997; Gower et al., 1996). Although this is a common pattern observed from forest inventory studies, the reasons for the decline in ANPP, or the successional pattern of photosynthesis and respiration that contribute to NPP is still not well understood. ANPP may decline due to increased respiration (Odum, 1969; Kira and Shidei, 1967), decreased gross primary production (GPP), shifted carbon allocation (Ryan et al., 2004), or decreased soil nutrient availability and increased stomatal/hydraulic limitation leading to decreased photosynthetic rates (Gower et al., 1996).

Our measurements in northern mixed forests suggest that aboveground autotrophic respiration (stem + leaf respiration), the cost for tree growth and maintenance in stems and leaves, increased from 112 g C $m^{-2}$ $y^{-1}$ for the young aspen stand to 266 g C $m^{-2}$ $y^{-1}$ for the average of mature hardwood stands, and then slightly decreased to 241 g C $m^{-2}$ $y^{-1}$ for the old-growth hardwood (excluding conifer-dominated). If the decline in ANPP with stand age is universal and applicable to our site, this decline can only occur when GPP decreases more rapidly than respiration given the observed decrease in respiration. Therefore, we speculate that initially, the increase in GPP should be more rapid than the increase in respiration so that NPP would increase when forests grow; as forests age, the decrease in GPP should be more rapid than the decrease in respiration so that NPP would correspondingly decrease. The decrease in GPP has been observed from eddy covariance measurements that reported GPP of 1034 g C $m^{-2}$ $y^{-1}$ in our old-growth forest and 1149 g C $m^{-2}$ $y^{-1}$ in the nearby mature forest (Desai et al., 2005). We noticed that the above results were drawn only from three chronosequential stages of forest succession. More chronosequences and replications may be needed to support the above speculation that both GPP and respiration decline in old forests with more rapid decline in GPP.

The component fluxes may have different successional patterns from the total ecosystem respiration described above. Compared with the mature hardwood stand, the old-growth hardwood decreases in stem respiration but increases in leaf respiration. The decrease in stem respiration in the old-growth stand, though with a higher total sapwood volume, could be explained by the decrease in growth respiration rates (respiration per unit of sapwood) and probably in maintenance respiration rates as well in the old-growth stand (Ryan et al., 1997). The increase in leaf respiration in the old-growth forest, despite a similar LAI to the mature, probably suggests higher leaf respiration costs for photosynthesis in the old-growth forest.

The old-growth hardwood-dominated stand has different component fluxes relative to the conifer-dominated stand. Higher basal area and sapwood volume in the hemlock stand caused higher stem respiration than that in the hardwood stand. Despite the longer leaf presence over the season for hemlock and higher total leaf biomass for the hemlock stand, leaf respiration in the hemlock stand was lower than in the hardwood stand, mainly due to the lower leaf respiration rate per biomass for the hemlock. These results suggest that the hemlock old-growth stand respires more carbon from stems but less from leaves than the mixed hardwood-hemlock stand. This difference in component respiration indicates that even though these two stands share the similar climate and ecological zone, the different development due to soil type, topography, and disturbances has resulted in different spatial pattern and species composition (Pastor and Broschart, 1990; Frelich and Graumlich, 1994), and further resulted in different carbon budgets.

Our result based on chamber measurements that the old-growth forest has less ecosystem respiration than the mature forest is discrepant with the result from eddy covariance measurements. Even though the chamber method and eddy covariance method agreed well in the old-growth forest reported in this paper, these two methods did not agree well in the mature forest. Chamber measurements of ecosystem respiration from the mature northern forest (Bolstad et al., 2004) were 63% larger than eddy covariance measurements (Desai et al., 2005). Correspondingly, eddy covariance measurements reported an increase in ecosystem respiration in the old-growth forest compared with the mature forest (Desai et al., 2005). Due to complex error sources, the reason for this discrepancy is not well understood and subject to further investigation. The complex footprint covered by the eddy covariance measurements from the mature forest and the spatial heterogeneity for upscaling chamber measurements may be the major reasons.

## 5. Conclusions

Chamber-based flux measurements combined with spatial and temporal upscaling allow us to estimate component respiration and total ecosystem respiration. Temperature was the primary control on respiration in the old-growth forest in the Great Lake region. Exponential functions explained most of the observed temporal variations in respiration in response to temperature.

Cumulative ecosystem respiration was estimated to be 1013 and 922 g C $m^{-2}$ $y^{-1}$ in the hardwood and hemlock stands, respectively. Respiration from most components was higher in the hardwood stand than the hemlock stand, with the exception of stem respiration. Soil respiration, woody debris respiration, stem respiration, and leaf respiration accounted for 72%, 4%, 13%, and 11%, respectively, of ecosystem respiration in the hardwood stand, and 67%, 3%, 22%, and 8%, respectively, in the hemlock stand. The proportion of stem respiration in the hemlock stand was much larger than that in the hardwood stand.

By comparing with respiration in young and mature forests, we found that total ecosystem respiration generally increased from the young forest to the mature forest, and then decreased from the mature to the old-growth forest. Both age class and species are important in determining the magnitude and proportion of component respiration. The decline in ecosystem respiration with forest age was accompanied by more rapid decline in GPP. However, more

chronosequence studies in respiration and GPP are suggested to support this pattern.

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