

Comparison of soil respiration methods in a mid-latitude deciduous forest

C.A. WAYSON^{1,*}, J.C. RANDOLPH¹, P.J. HANSON²,
C.S.B. GRIMMOND³ and H.P. SCHMID³

¹*School of Public and Environmental Affairs, Indiana University, Bloomington, IN 47405, USA;* ²*Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, TN 37831, USA;* ³*Department of Geography, Indiana University, Bloomington, IN 47405, USA;*
**Author for correspondence (e-mail: cwayson@indiana.edu; phone: +1-812-855-4953; fax: +1-812-855-7547)*

Received 31 March 2005; accepted in revised form 31 January 2006

Key words: Carbon cycling, CO₂ efflux, Deciduous forests, Net ecosystem productivity, Soil respiration

Abstract. In forest ecosystems the single largest respiratory flux influencing net ecosystem productivity (NEP) is the total soil CO₂ efflux; however, it is difficult to make measurements of this flux that are accurate at the ecosystem scale. We examined patterns of soil CO₂ efflux using five different methods: auto-chambers, portable gas analyzers, eddy covariance along and two models parameterized with the observed data. The relation between soil temperature and soil moisture with soil CO₂ effluxes are also investigated, both inter-annually and seasonally, using these observations/results. Soil respiration rates (R_{soil}) are greatest during the growing season when soil temperatures are between 15 and 25 °C, but some soil CO₂ efflux occurs throughout the year. Measured soil respiration was sensitive to soil temperature, particularly during the spring and fall. All measurement methods produced similar annual estimates. Depending on the time of the year, the eddy covariance (flux tower) estimate for ecosystem respiration is similar to or slightly lower than estimates of annual soil CO₂ efflux from the other methods. As the eddy covariance estimate includes foliar and stem respiration which the other methods do not; it was expected to be larger (perhaps 15–30%). The auto-chamber system continuously measuring soil CO₂ efflux rates provides a level of temporal resolution that permits investigation of short- to longer term influences of factors on these efflux rates. The expense of building and maintaining an auto chamber system may not be necessary for those researchers interested in estimating R_{soil} annually, but auto-chambers do allow the capture of data from all seasons needed for model parameterization.

Introduction

In forest ecosystems the single largest respiratory flux influencing net ecosystem productivity is the total soil CO₂ efflux (e.g., Longdoz et al. 2000; Savage and Davidson 2001; Borken et al. 2002; Curtis et al. 2002; Davidson et al. 2002a; Ehman et al. 2002; Irvine and Law 2002; Rey et al. 2002; Hanson et al. 2003; Pumpanen et al. 2003). However, it is difficult to make measurements of this flux that are appropriate to the ecosystem scale (Davidson et al. 1998, 2002b; Hanson et al. 2000, Hooper et al. 2002).

Net ecosystem production (NEP), the annual net exchange of carbon in any ecosystem, is a result of the balance between gross primary productivity through photosynthesis and carbon losses by ecosystem respiration. Ecosystem respiration is the total respiration from plants (autotrophic), and animals and microbes (heterotrophic). Soil CO₂ efflux, often simply referred to as soil respiration, results from autotrophic respiration of plant roots and associated mycorrhizae and the organisms that decompose above-ground woody debris and litter, below-ground litter, and soil organic matter. Understanding the relative contributions of autotrophic and heterotrophic respiration to the total soil CO₂ efflux has proven difficult, as discussed by Hanson et al. (2000). Many methods have been used to provide this estimate ranging from relatively inexpensive to costly both in terms of material and time.

This paper examines patterns of soil CO₂ efflux made using five different methods based on auto-chambers, portable gas analyzers, and eddy covariance in which the observations vary both temporally and spatially. The relation between both soil temperature and soil moisture with soil CO₂ effluxes, both intra- and inter-annually are also investigated using two models and the observed data from each method. Since May, 1998 we have made periodic manual measurements of soil respiration using portable instruments in forest plots with differing topography and species composition at the Morgan-Monroe State Forest (MMSF) AmeriFlux site located in south-central Indiana, USA (Schmid et al. 2000; Ehman et al. 2002).

These data allow spatial comparisons, but their temporal resolution is limited. Since September 2001, soil respiration has also been measured continuously using an automated chamber system. These continuous observations are limited to a small area near the flux tower, but represent a nearly complete record of the CO₂ flux, soil moisture, soil temperature, air temperature, and precipitation.

Materials and methods

Study site

The managed Morgan-Monroe State Forest (MMSF) with a total area of 9733 ha is located in south-central Indiana (39°19' N, 86°25' W, 275 m a.s.l.). The 30-year mean annual air temperature is 10.8 °C and precipitation is 1094 mm for the nearest National Weather Service cooperative station located 11.8 km north in Martinsville, Indiana (National Climatic Data Center 1971–2000). For the years 1999–2002, the mean annual temperature measured at the tower at 46 m was 12.6 °C and the mean annual precipitation was 1105 mm. The region (Figure 1) is covered predominantly with secondary successional broadleaf forests located within the maple-beech to oak-hickory transition zone of the Eastern Deciduous Forest (Braun 1950; Barrett 1995) resulting in a diverse tree community (Van Kley et al. 1995). Soils in the area are mesic typic Dystrochrepts dominated by the Berks-Weikert complex, defined as moderately deep and shallow, steep and very steep, well drained soils formed in residuum from sandstone, siltstone, and shale (USDA 1980). This soil association is characteristic of upland areas in this region.

An inventory of tree species larger than 70 mm dbh in 360 plots within 500 m of the MMSF tower site identified 29 tree species. Dominant species (nearly 75% of the total basal area = 23.2 m² ha⁻¹) are tulip poplar (*Liriodendron tulipifera* L.; 5.8 m² ha⁻¹), sugar maple (*Acer saccharum* L.; 4.9 m² ha⁻¹), white ash (*Fraxinus americana* L.; 1.9 m² ha⁻¹), sassafras (*Sassafras albidum* (Nutt.) Nees; 1.6 m² ha⁻¹), white oak (*Quercus alba* L.; 1.6 m² ha⁻¹), and red oak (*Quercus rubra* L. 1.2 m² ha⁻¹). The mean canopy height of the forest is 27 m. Common understory species include pawpaw (*Asimina triloba* L.), spicebush (*Lindera benzoin* L.), and sweet cicely (*Osmorhiza claytonii* Michx.) as well as seedlings and saplings of the dominant tree species. Herbaceous vegetation ground cover is dominated by spring ephemerals, but is present throughout the growing season. Most of Indiana was deforested by the early 1900s but afforestation has occurred in much of central and southern Indiana after abandonment of marginally productive agricultural land. Some timber has been harvested selectively from forests in the vicinity of the flux tower but there is little evidence of recent disturbance (no harvesting within the last 20 years).

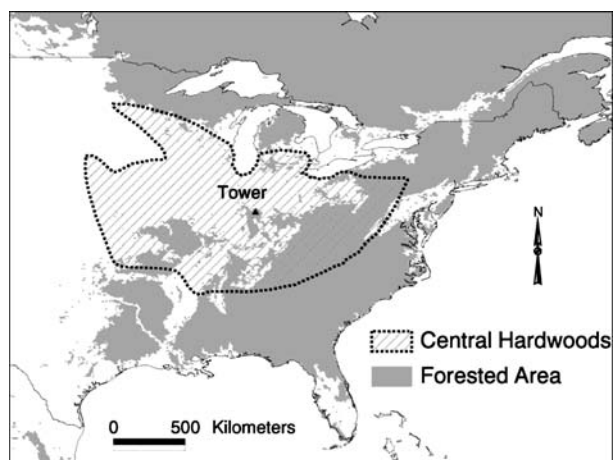


Figure 1. Forested land within eastern North America (WCMC 1999) and the MMSF site location, marked 'Tower'. The site is on the periphery of current Central Hardwoods coverage, but in the center of their historical domain.

Measurements

In this paper five methods (Table 1) are used to estimate soil CO₂ efflux.

Sparse point-in-time observations (SPT)

Periodic measurements (bi-weekly during the growing season; monthly dormant season) of soil respiration were made using either a Li-Cor 6200 or 6400 infrared gas analyzer system in five plots with a range of topographic settings (north- and east-facing, south- and west-facing, and ridge tops). In each plot, 10 PVC collars (0.104 m diameter, 45 mm height) were set 25 mm into the soil and left in place for subsequent measurements. Annual soil CO₂ efflux estimates were generated by using linear interpolation between measurement points.

Simple model (SM)

The sparse point-in-time data were used to parameterize a curvilinear model based on Hanson et al. (1993, 2003) and published in Ehman et al. (2002) relating soil temperature at 0.10 m depth (T_s , °C) and observed soil water potential (Ψ_{10} , MPa) at 0.1 m (i.e., the zone of maximum rooting density) with soil respiration (R_s , $\mu\text{mol m}^{-2} \text{s}^{-1}$):

$$R_{s,SM} = -6.07 \times Q^{((T_s-20)/10)} \times (\Psi_{\max} - \Psi_{10})/\Psi_{\max} \quad (1)$$

where Q (value of 2.23 ± 0.124) is the rate of change in R_s for a 10 °C increase in soil temperature (i.e., the Q_{10} value). Ψ_{\max} (-2.0 MPa) is the estimated soil matric potential in MPa corresponding to the complete inhibition of R_s ($n=2673$, $P<0.001$, $R^2=0.31$). The individual collar observations ($n=2673$) are used in the parameterization which reduces the standard error for the parameter Q , but maintains the overall variance of soil CO₂ efflux rates as seen in the low R^2 value for the model fit. The model was driven with data for soil temperature and volumetric soil moisture at 0.10 m depth collected with thermocouples and CS615 TDR soil moisture rods logged by Campbell Scientific CR10X data-loggers since May, 1998 at five locations in MMSF. Soil water potential, a measure of biologically available water, was converted from volumetric water content using the following equation based on site data:

$$\Psi = -1 \times [2.61E8 \times 189^{(-2.51 \times \text{TDR}^{0.1386})}] \quad (2)$$

Complex model (CM)

Total soil CO₂ efflux (R_{soil}) from all contributing components was modeled following a subset of the equations of Hanson et al. (2003) for those variables available at Morgan Monroe State Forest:

$$R_{s,CM} = M_{\text{resp}} + G_{\text{resp}} + L_{\text{resp}} \quad (3)$$

Table 1. Summary of soil CO₂ efflux methods.

Name	Method	Inputs	Time interval	Comments
SPT	Sparse, point-in-time measures of soil CO ₂ efflux	None. Direct measure of soil CO ₂ efflux	Bi-weekly during growing season, monthly during winter	Measures in 10 rings in each of five plots on different slope aspects near tower
SM	Simple model with only one layer	Soil temperature and soil moisture	Run hourly and integrated for annual sum	Model parameterized with R_{soil} data from measures distributed spatially and collected generally bi-weekly for 1999 and 2002
CM	Complex model with surface layer wetness incorporated	Soil temperature, and soil moisture	Run hourly and integrated for annual sum	Model parameterized with R_{soil} data from AC data and other parameters estimated based on data from Tennessee
AC	Auto-chamber method	None. Direct measure of soil CO ₂ efflux	Each of eight chambers measured once hourly for 2002	Measures limited 8 subsamples within one location near the tower. Data gap-filled using imputation
EC	Eddy covariance	Soil temperature	Run hourly and integrated for annual sum	Estimate of total ecosystem respiration not just R_{soil} . Model parameterized with only nighttime CO ₂ flux data

$$M_{\text{resp}} = R_{20} \times Q^{((T_{\text{soil}} - 20)/10)} \times [(\Psi_{\text{max}} - \Psi_{10})/\Psi_{\text{max}}], \quad (4)$$

$$L_{\text{resp}} = (L_{20} \times b^{\text{O}_{i\text{wp}}}) \times [Q_1^{(\text{O}_{i\text{temp}} - 20)/10}] \times (\text{O}_i \text{ litter mass per m}^2 \text{ of ground}), \quad (5)$$

where M_{resp} is the combined maintenance respiration rate of roots plus soil microbes and has the same form and inputs as (1). Within (4) R_{20} is the combined maintenance respiration of roots and soil microbes when temperatures approach 20 °C, and the other variables are as defined for (1). (5) describes the contribution of litter layer decomposition to total forest floor CO₂ losses controlled by temperature and predicted dynamics of litter water content. $\text{O}_{i\text{wp}}$, in MPa is the O_i litter water potential, $\text{O}_{i\text{temp}}$ is the O_i layer temperature in °C, L_{20} (7.1 nmol C g⁻¹ s⁻¹) is the litter-specific respiration at 20 °C and maximum litter water potential, b (3.48 dimensionless) defines the shape of the relation between litter water potential and litter temperature, and Q_1 (4.05 dimensionless) is the temperature response coefficient for a 10 °C change in litter temperature. Model parameters for (4) were derived from nonlinear regression using the continuous chamber data ($n = 4423$). Measured litterfall quantities and litter standing pools measured at Morgan Monroe were used to initiate the O_i mass term of (5), but it was parameterized for hardwood litter based on data for a similar upland-oak forest in east Tennessee (Hanson et al. 2003). Litter water content data were modeled from observed rainfall data estimated to reach the forest floor, forest floor temperature observations, atmospheric relative humidity data, and surface energy balance calculations for the forest litter layer.

The CM was run using environmental data for 2002 from the auto-chamber system or with independent below-canopy micrometeorological (precipitation) and soil (soil temperature and moisture) data from the micro-met station near the chamber system.

Auto-chambers (AC)

Soil respiration has been measured nearly continuously using an automated chamber based on the open-flow design (Field et al. 1989) since September, 2001. The auto-chamber system was designed and implemented to address the potential problem of calculating annual soil CO₂ efflux rates using temporally limited data. The automated system consists of eight chambers arranged radially at approximately 45° intervals from a central measurement and control enclosure. The site was selected to be within the most probable flux footprint of the eddy covariance measurements from the MMSF AmeriFlux tower (Schmid et al. 2003). This location is also near a below-canopy micrometeorological station for which over 5 years of continuous data are available. Within the spatial domain of the auto-chambers, the dominant tree species of MMSF are well represented.

Each chamber consists of clear polycarbonate cylinder and a pneumatically operated lid modified from a design by Crill et al. (2000). The lids were fabricated from machined aluminum and Lexan (GE Plastics). They are counterweighted in a normally open position and are closed with a pneumatic piston. The polycarbonate cylinder (chamber) is 0.3048 m both in diameter and height. The chambers are set 25 mm into the soil. A steel cylinder of the same diameter was used as a template to cut the soil before the chambers were installed. The internal diameter of each chamber is 0.292 m and the height above the surface varies slightly with respect to topography but is between 0.22 and 0.25 m. The surface area for which the flux is measured deviates less than 1% from 0.067 m². Thus, the average internal volume is 15 l. The chamber inlet and outlet connect to the central measurement and control system via 6.25 mm o.d. UV-resistant Dekabon (LDPE wrapped aluminum) tubing (Du Pont). Tube lengths are kept consistent at 15 m to ensure constant pressure drops between each cylinder and the gas analyzer. Figure 2 shows a top view of the chamber inlet and outlet arrangement. Each cylinder is first flushed with the lid open for 30 s to mix the air in the chamber and to bring the concentration in the tubes down to ambient levels. After the chamber closes, the air is scrubbed with soda lime to reduce the chamber CO₂ concentration slightly below ambient levels before measurement of the flux begins. During times of high respiration (high soil temperatures > 25 °C, not moisture limited) the scrub is less effective at reducing chamber concentrations at the set flow

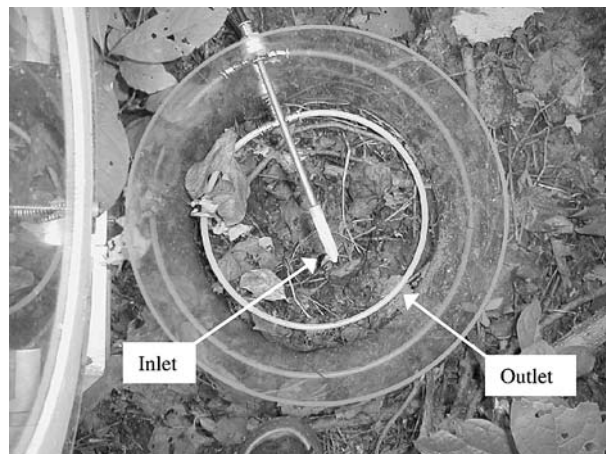


Figure 2. Top view of one auto-chamber showing the inlet and outlet configurations.

rate. The flow rate allows for 4 complete air exchanges per sample and is maintained at an IRGA sample pressure of 70 kPa. (Please contact the corresponding author for additional details and schematic drawings of the system.).

A CR23X datalogger with a SDM-16 relay control board (Campbell Scientific) is used to control the system and for data storage. The system cycles through all eight chambers every hour, calculating individual chamber fluxes based on a best-fit linear regression of the increasing $[\text{CO}_2]$ with time using 45 data points taken at 5 s intervals. CO_2 concentrations are measured with a Li-6262 Infrared Gas Analyzer (Licor) and output to the datalogger as 1 s averages. The data are spatially limited (eight locations in fairly close proximity to each other and near the flux tower) but CO_2 flux, soil moisture, soil temperature, air temperature, and precipitation data are essentially temporally continuous. Gaps in the dataset were filled by imputation using a most similar neighbor technique (Crookston et al. 2002). This technique requires few *a priori* assumptions of the relation of the variables used for the process and soil surface CO_2 efflux rates, and it does not simply interpolate the data points.

Eddy covariance (EC)

Total ecosystem respiration also has been estimated at hourly intervals based on eddy-covariance CO_2 flux data as described in Schmid et al. (2000). In brief, seasonally variable Q_{10} relations similar to the first part of (Equation (1)) were developed based on soil temperature (50 mm depth) and measured above-canopy (46 m) CO_2 fluxes during well ventilated conditions (friction velocity $u^* > 0.35 \text{ m s}^{-1}$) from nighttime and leaf-off periods. These Q_{10} relations were used to gap-fill the eddy-covariance flux data series, and to separate the net ecosystem exchange flux into its ecosystem respiration and gross ecosystem production components. Total annual ecosystem respiration is the sum of all hourly values. Although the Q_{10} relations used in this method are based on soil temperature, the measured fluxes that form their basis include respiration contributions from all parts of the ecosystem, including stems and leaves that are not accounted for by the chamber method.

Results and discussion

Environmental conditions 1999–2002

The greatest inter-annual variability in soil temperature at 0.1 m occurs in early spring, just before leaf-out (approximately DOY 60–120) and the least in the summer (approximately DOY 180–240) (Figure 3a). At this site, soil water potential at 0.1 m has reached -2 MPa only once, briefly in late September, 1999, since

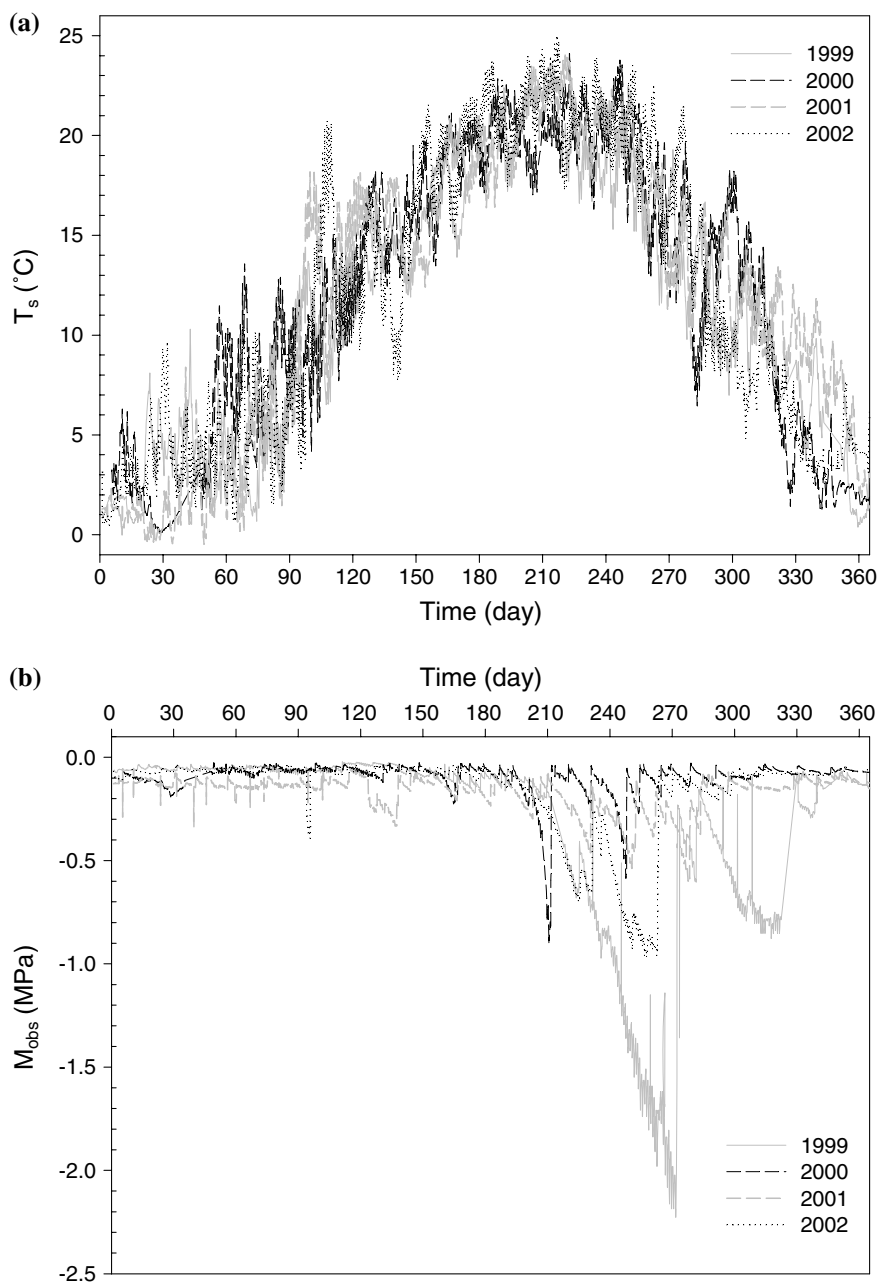


Figure 3. Soil characteristics at 0.1 m depth for 1999–2002 for (a) temperature and (b) soil water potentials.

measurements began in 1998 (Figure 3b) suggesting that water is seldom a limiting factor at this site at the level of the ecosystem, but it can limit component processes in surface litter or soil layers that wet and dry at rates different from the bulk soils.

SPT estimates for 1999–2002

The values of soil CO_2 efflux as estimated from the sparse point in time measures ranged from of 878 to 1090 $\text{g C m}^{-2} \text{y}^{-1}$ with a mean value of 1012 $\text{g C m}^{-2} \text{y}^{-1}$. As will be shown, these values are 150–200 g less

than most other methods predict. Leaf-on measures showed the greatest spatial variability with fluxes ranging from ~ 2 to $8 \mu\text{mol m}^{-2} \text{s}^{-1}$ on any given sampling day. During leaf off periods the range was only ~ 0.6 to $1.5 \mu\text{mol m}^{-2} \text{s}^{-1}$. These results indicate that soil CO_2 efflux rates are primarily influenced by temperature, though, during leaf-on periods, temperature is not the only controlling factor as evidenced by the very large range of efflux rates measured on a single day.

SM and EC estimates for 1999 and 2000

Figure 4a shows results using the parameterized soil respiration model (SM) for 1999 and 2000. As data for 2001 and 2002 are virtually identical to those for 2000 they are not shown. SM respiration (Figure 4a) and EC ecosystem respiration (Figure 4b) show similar seasonal patterns. However, two key differences are apparent: (1) the influence of the late summer drought in 1999 is more pronounced in the forest floor

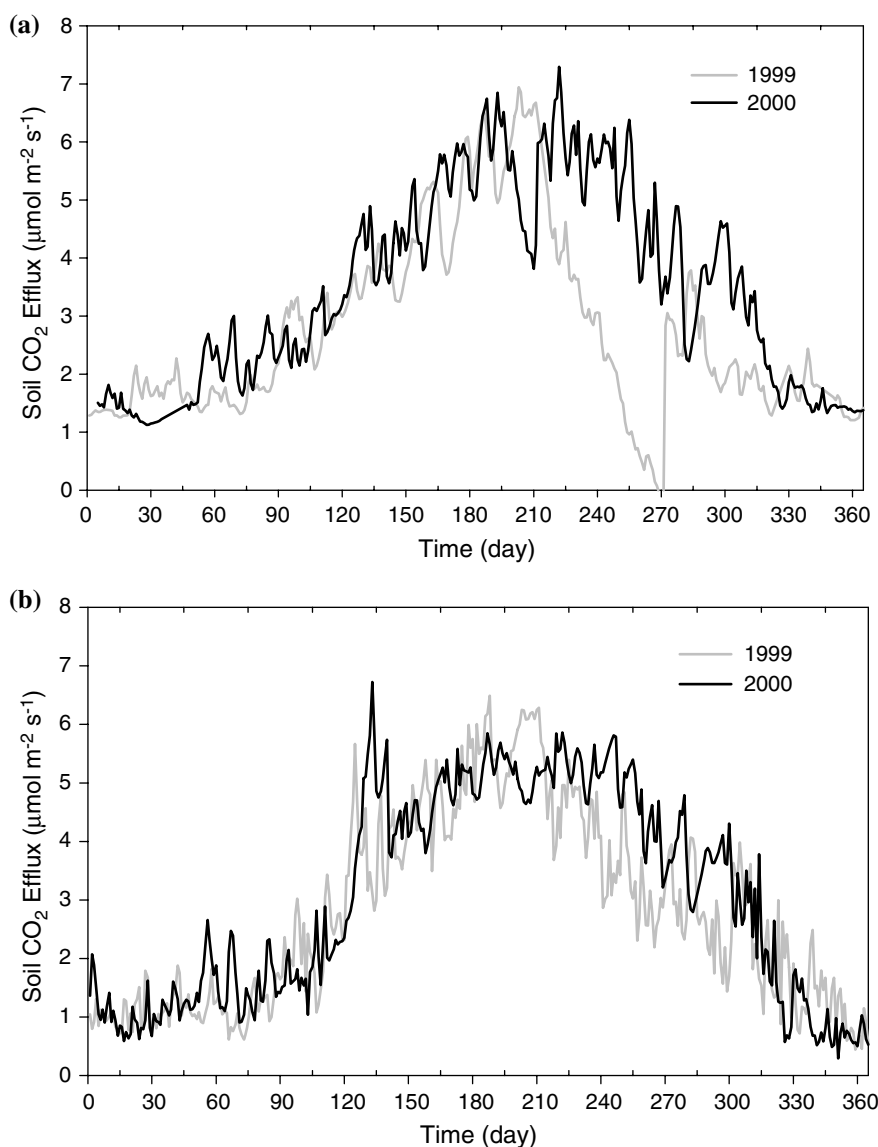


Figure 4. Soil CO_2 efflux determined for 1999–2000 using (a) SM and (b) by eddy covariance (EC) estimates at 46 m.

respiration and (2) increased rates of respiration in May (approximately DOY 120–150) in both 1999 and 2000 are more pronounced in the eddy covariance results. The late season drought in 1999 reduced soil respiration and resulted in an increased net ecosystem productivity, compared to 1998 (Ehman et al. 2002) as well as 2000–2003 (Randolph et al., unpublished). Measurements of photosynthetic rates in individual tree leaves made in July and August 1999 did not show reduced photosynthesis. Although not measured at that time, presumably foliar and stem respiration rates were not reduced either and would be included in the eddy covariance results but not the forest floor measurements. The warm temperatures in May would increase foliar and stem respiration rates that would be included in the eddy covariance results and not the forest floor measurements which is likely contributing less to overall ecosystem respiration since the lowest levels of fine root biomass occur in May at our site (unpublished data).

Annual soil CO₂ effluxes, as estimated by the SM model and ecosystem respiration from the EC model, were very similar for 1999: 1041 and 1040 g C m⁻² y⁻¹, respectively. However, for 2000, the SM and EC estimates differed by more than 189 g C m⁻² y⁻¹ (1332 and 1143 g C m⁻² y⁻¹, respectively). The flux tower estimates of total ecosystem respiration are expected to be 10–15% greater than soil surface CO₂ estimates due to autotrophic bole, branch and leaf respiration (Chapin et al. 2002, P. Curtis, pers. comm. from the University of Michigan Biological Station (UMBS) AmeriFlux site). However, recent research from sites similar to ours has shown that bole, branch and leaf respiration may be as high as 30% of overall ecosystem respiration (Hanson et al. 2003, 2004; Curtis et al. 2005). For our site, foliar respiration for 2002 was estimated using a simple model from Vose and Bolstad (1999) with their parameters for all species and yielded an annual estimate of ~310 g C m⁻² y⁻¹. This value is close to that of ~300 g C m⁻² y⁻¹ reported by Hanson et al. (2003, 2004) for Walker Branch (WB) and of 292 g C m⁻² y⁻¹ Curtis et al. (2005) at UMBS. Bole and stem respiration for both sites (WB and UMBS) were 175 g C m⁻² y⁻¹ and 165 g C m⁻² y⁻¹ respectively. Data from MMSF are not available, but are likely to be very similar to these values based on similar species composition, mean temperatures and precipitation. Overall, then, EC estimates should be ~450–500 g C m⁻² y⁻¹ higher than soil CO₂ efflux estimates at MMSF.

To date, annual soil CO₂ efflux rates estimated with soil surface measures or estimates as shown here are consistently at, or greater than, estimates of annual total ecosystem respiration by the tower. Although unlikely, this could be because of a mismatch between the soil CO₂ efflux plot locations and the flux tower measurement source areas. Current crosswind-integrated footprint models show the source area to overlap our plot locations under most meteorological conditions. Nighttime advection loss of CO₂ due to cold-air drainage from the forest during stable atmospheric conditions (Froelich and Schmid 2002) may cause a systematic underestimation of eddy covariance derived ecosystem respiration and could potentially account for this difference. However, quantitative estimates of this effect are difficult to obtain and are not currently available. Moreover, Froelich and Schmid (2002) show that vertical mass flow divergence (the vertical trace of drainage flow advection) is negligible in well-ventilated conditions when $u^* > 0.35 \text{ m s}^{-1}$, so that advective losses are not likely to account for the lack of difference between the forest floor respiration estimates and the eddy flux based total ecosystem respiration totals.

Auto-chamber (AC) system for 2002

For 2002, soil respiration rates measured using the auto-chamber system can be compared with the estimates from SPT (Figure 5) and SM (Figure 6). The annual estimate of 878 g C m⁻² y⁻¹ using sparse measures is much lower than that of the 1160 g C m⁻² y⁻¹ value for the auto-chambers. Due to the periodic nature of the measures for the SPT estimate, the day on which the measures are taken, especially in the summer months, can greatly influence the annual estimate. If the days leading up to the measurement day differ much from average moisture and temperature conditions the fluxes measured may be unusually high (DOY 207, Figure 5) or low (DOY 217, Figure 5). Gaps in the dataset due to equipment failure, etc. (DOY 148–207, Figure 5) influence greatly the annual estimate as seen in 2002. The average fluxes climbed shortly after day 148, and continued so until day 207. However, the SPT method used linear interpolation between the two points and underestimates the overall flux for that period.

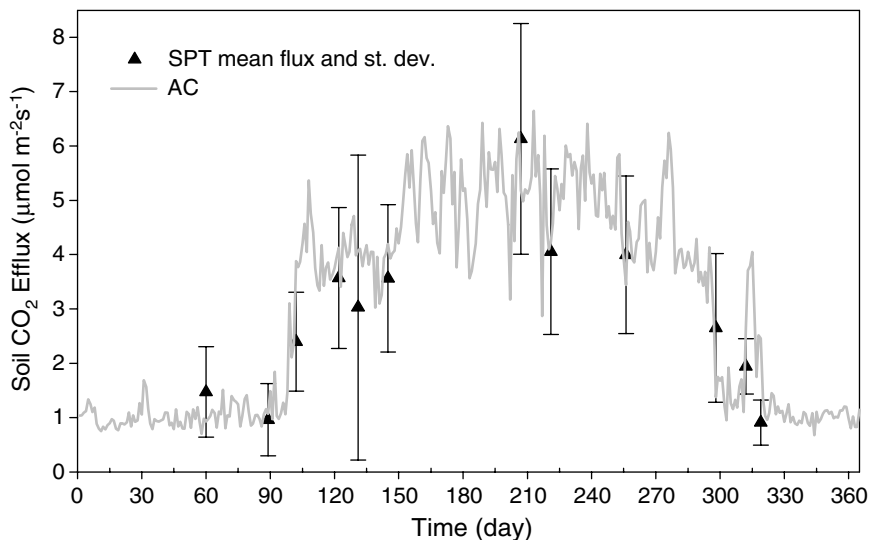


Figure 5. Soil CO₂ effluxes for 2002 based on auto-chamber (AC) respiration estimates and SPT.

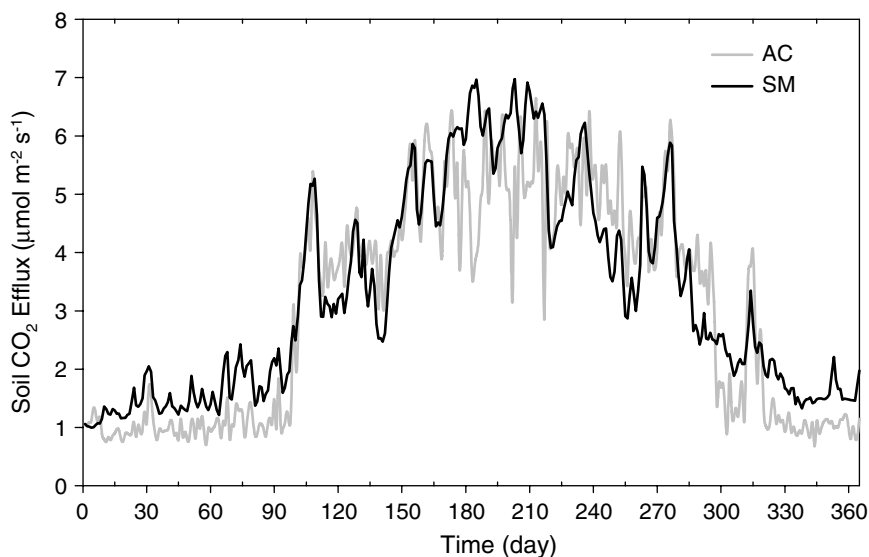


Figure 6. Soil CO₂ effluxes for 2002 based on auto-chamber (AC) respiration estimates and SM.

For SM, the annual values are similar: $1240 \text{ g C m}^{-2} \text{ y}^{-1}$ from the model and $1160 \text{ g C m}^{-2} \text{ y}^{-1}$ from the auto-chambers. Soil respiration rates are highest during the growing season (May to Sep.) when soil temperatures are between 15 and 25 °C, but some R_{soil} occurs throughout the year. As expected the SM results of soil respiration are highly related to soil temperature, particularly during the spring and fall (Figure 7a). Both the modeled results and the auto-chamber data (Figure 7b) show a distinct increase in soil respiration around DOY 100 and a smaller but noticeable increase again about DOY 315. From our phenological observations, DOY 100 precedes the date of maximum bud burst (defined as 50% of the trees observed having predominantly open buds; DOY 108 in 2002). Kramer and Kozlowski (1979) note that, in the temperate zone, root elongation begins earlier in the spring and continues later in the autumn than shoot elongation in the same tree. Thus, these elevated fluxes in the early spring likely result from increased autotrophic root respiration as well as from increased soil temperature. DOY 315 is 10 days later than the

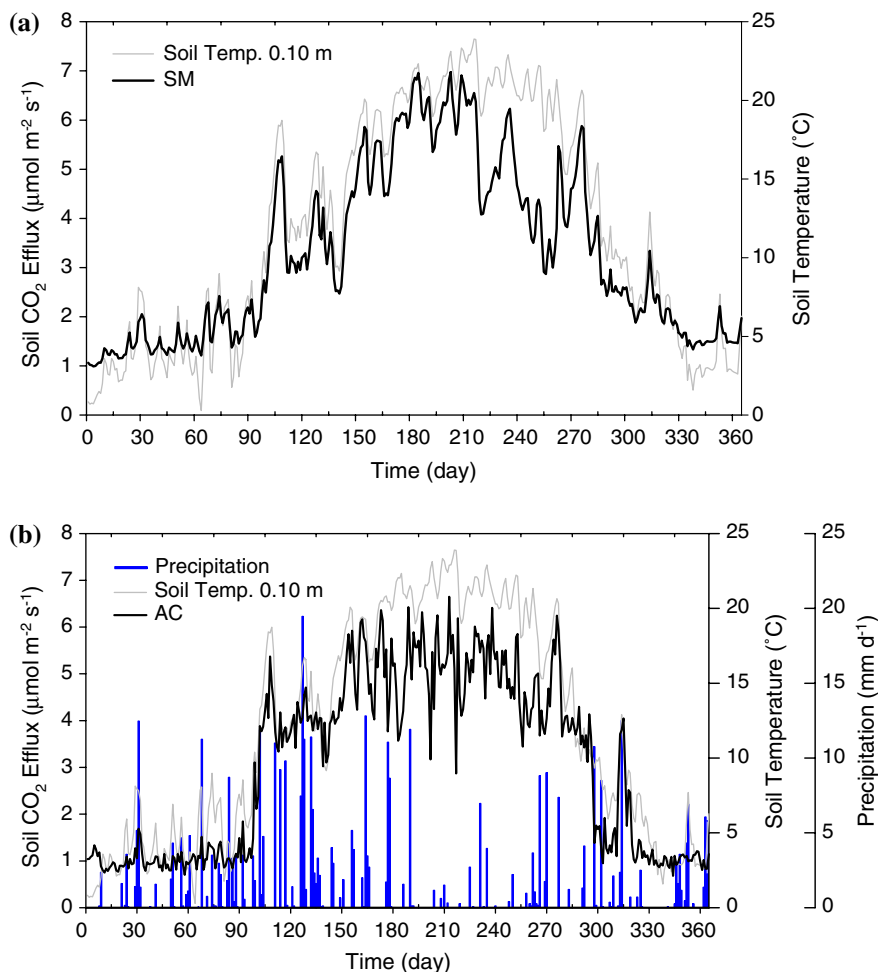


Figure 7. SM with soil temperatures at 0.1 m depth for 2002 (a). Auto-chamber (AC) respiration estimates with soil temperatures at 10 cm depth and precipitation events for 2002 (b).

date of maximum leaf fall (defined as 50% of the trees observed having lost 50% of their leaves; DOY 305 in 2000) and appears primarily linked to temperature. The auto-chamber data show the rapid increase in soil CO₂ effluxes around DOY 100 to be more distinct and with a slightly higher peak value than seen in the model results. Also, as seen in both data sets, but particularly in the auto-chamber data, short-duration temperature increases before DOY 100 did not result in any appreciable increases CO₂ efflux. Not surprisingly, the continuous dataset from the auto-chambers is quite useful in detecting these shorter-term responses.

During the winter, the model consistently estimates higher rates of soil CO₂ efflux than were measured with the auto-chambers (Figure 6). This difference could be related to the range of temperatures from which the data were collected for use in the model parameterization (Figure 7; Ehman et al. 2002). Unintentionally, field measurements using a portable system were biased toward ‘good weather’ days to protect the instrument and for the convenience of the investigator. By under-sampling during the winter months, SM is extrapolated for conditions beyond the development data domain.

From DOY 200 to 270 in the SM results and DOY 180 to 270 in the AC data (Figure 7a and b), neither graph show any strong relations between soil respiration rate and soil temperatures. However, the measured data show increased soil CO₂ efflux in response to precipitation events during the latter part of the growing season: rainfall events and the corresponding increased soil CO₂ efflux rates are easily seen in

Figure 7b. Such data indicate that during the latter part of the growing season, soil moisture, especially in the litter and upper soil layer, has a large controlling effect on efflux rates.

Surface layer wetness model (CM) for 2002

As the above results indicate, the wetting and drying of the litter layer influence soil CO₂ efflux rates. Thus, it is important to adjust the simple soil temperature/soil water potential model (SM) to account for surface wetting and drying using information from the auto-chamber data. Root growth is included in the R_{20} term of (4) along with baseline root respiration and heterotrophic respiration. Although not necessarily correct, the form of the model used here (4 plus 5) assumes the apparent temperature sensitivity of root respiration and heterotrophic metabolism of soil carbon to be the same. Values of R_{20} , Q , and Ψ_{\max} were estimated using all available data or data for time periods when the surface litter layers were dry (Table 2). Modeled values for Oi-layer litter respiration were taken from Hanson et al. (2003) and applied to the MMSF data as a first approximation of the short-term dynamics of soil CO₂ efflux during wetting and drying of the Oi layer. Site-specific data for litter mass were used, but similar data for litter-specific CO₂ flux from the litter materials derived from the species present at MMSF would be an improvement.

Non-linear regression of the data (SPSS 11.0 for the Macintosh, SPSS Inc.) with respect to (4) provided a statistically significant fit to the complete set of measured data, and a subset of the data associated with dry surface conditions. A plot of measured and modeled soil CO₂ efflux throughout 2002 (Figure 8) demonstrates the agreement between measured data and model outputs and underscores the importance of seasonal patterns of temperature and soil water potential as drivers of the combined processes that contribute to soil CO₂ effluxes. Some lack of agreement between measured data and the nonlinear regression-based model projections late in the growing season (DOY 230–300) may be the result of inappropriate parameterizations of Oi-litter decomposition and/or seasonal changes in the pool sizes for labile soil carbon and root stocks. The later two pools of carbon responsible for CO₂ losses from the mineral soil horizons are often assumed to be constant for intra-annual interpolation of soil CO₂ efflux, but that has not been determined for this site. Gu et al. (2004) have shown the importance of variable carbon pools for the interpretation of soil heterotrophic respiration.

The agreement between CM and the AC is less (Figure 8) than expected. During the winter months, CM shows patterns similar to the simpler temperature and moisture model (SM), a time when modeled CO₂ efflux rates are higher than the auto-chamber data. During periods of warmer temperatures, CM produces much higher estimates of CO₂ efflux than the auto-chamber data. This could be due to the litter respiration coefficient in (5) being determined from a site that has high litter decomposition rates different than those seen at the MMSF site.

On an annual basis, the surface layer wetness model (CM) produces an estimate of 1266 g C m² y⁻¹ compared to the 1160 g C m⁻² y⁻¹ estimate from the auto-chamber data.

EC estimate for 2002

A comparison of the flux tower estimate of total ecosystem respiration (EC) and the auto-chamber (AC) estimate (Figure 9) shows excellent agreement during the nongrowing season months, with no overesti-

Table 2. Model parameter estimates ($\pm 95\%$ C.I.) for (3) for soil temperature and water potential measurements at 0.1 m.

Data source	Model variable estimates			
	R_{20}	Q	Ψ_{\max}	R^2
All R_{soil} data	5.61 \pm 0.09	2.61 \pm 0.07	-10.7 \pm 0.9	0.69
R_{soil} for dry litter	5.40 \pm 0.13	2.26 \pm 0.09	-9.0 \pm 0.8	0.61

Similar estimates based on reference environmental conditions at 0.2 m showed no improvement in overall fit.

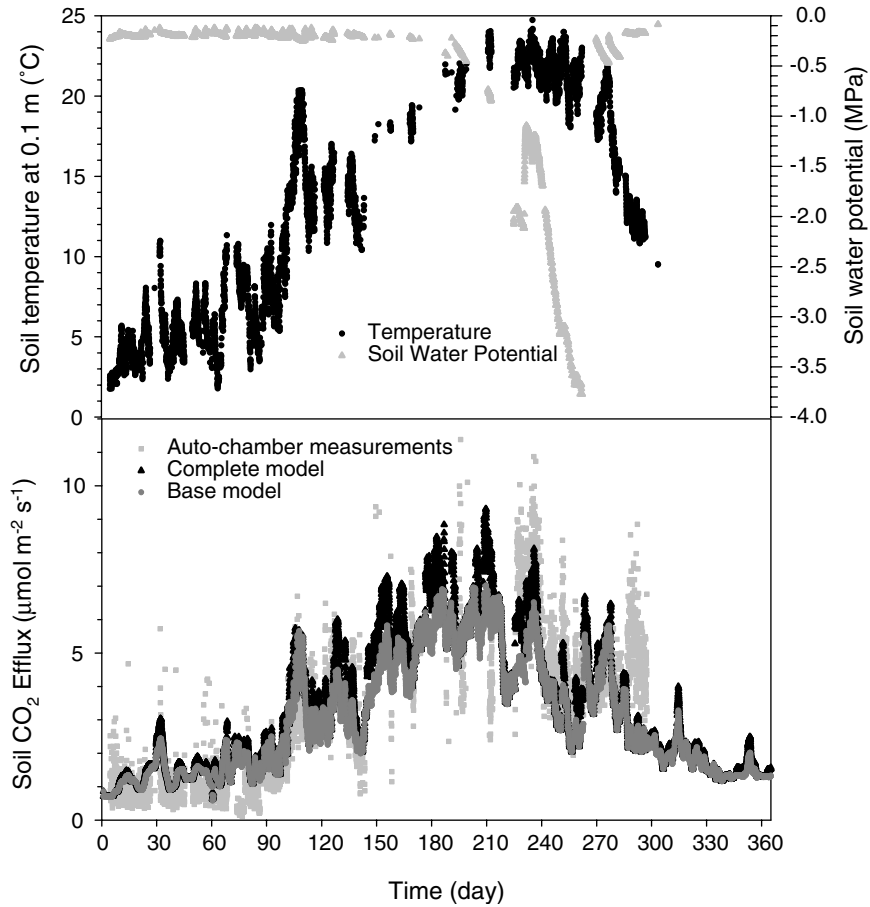


Figure 8. Observed soil temperature and water potential at 0.1 m (a) and the observed (AC) and CM soil CO₂ efflux (b). The base model represents the best fit of the measured data under dry surface conditions to (4), and the complete model includes simulations of the possible influence of surface wetting and drying on Oi-layer decomposition processes.

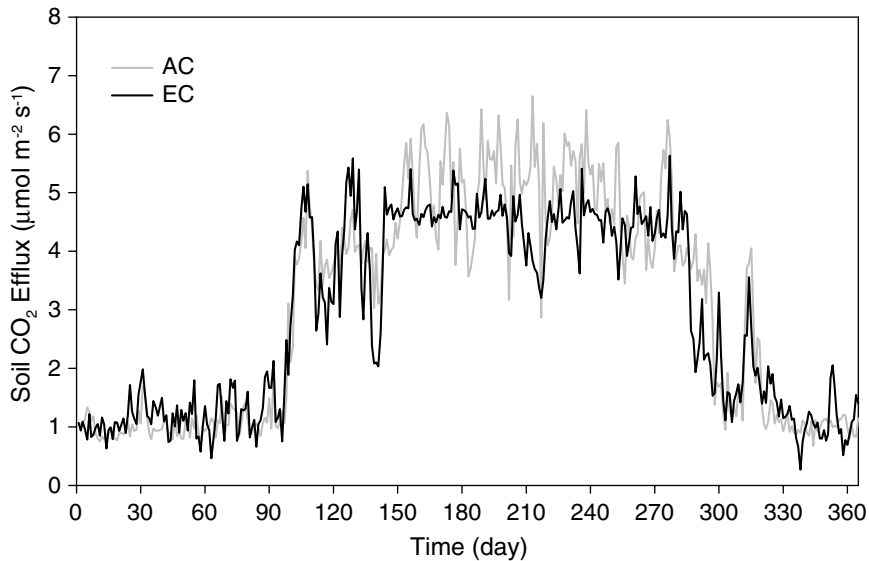


Figure 9. Ecosystem respiration (EC) compared with the auto-chamber (AC) soil CO₂ efflux for 2002.

Table 3. Summary of soil respiration estimates ($\text{g C m}^{-2} \text{y}^{-1}$) for the five methods (see Table 1) for 1999–2002.

Year	Method					Bud burst (DOY)	Leaf off (DOY)
	SPT	SM	CM	AC	EC		
1999	1000	1041	n/a	n/a	1040	99	308
2000	1090	1332	n/a	n/a	1143	117	305
2001	1080	1263	n/a	n/a	1353	100	314
2002	878	1240	1266	1160	1095	108	315
Mean	1012	1219			1158		
St. Dev.	98	125			137		

Note that the flux tower estimate (EC) is total ecosystem respiration. (n/a – not available).

mation of flux rates. The tower estimate also shows the sharp increase in respiration rates near DOY 100. During the growing season, however, the eddy-covariance method does not capture the short-duration respiration increases during, and shortly after, precipitation events. One possible explanation is that during rain events the sonic anemometers needed for flux measurements often produce invalid data; thus, the fluxes during these periods must be gap filled using a model parameterized under dry conditions (see above). This potential bias of eddy covariance based respiration estimates needs to be explored further.

Overall, all methods produced similar annual estimates. Table 3 provides a summary of each estimate and differences with the auto-chamber estimate serving as the reference value. Most striking in this comparison is that the flux tower estimate is consistent with or lower than annual soil CO_2 efflux estimates from any other method. The reasons for this difference are not clear, though Figure 10 clearly shows that for the range of temperature and moisture conditions seen in 2002 SM and CM tend to overestimate fluxes at cooler temperatures and higher soil moistures than does the EC method. This is most likely due to the EC method parameterizing its model for leaf-on and leaf-off periods separately to adjust for shifts in base respiration rates related to photosynthetic activity. This, however, raises the question yet again of why the EC estimate of total ecosystem respiration is not higher than AC measures of soil CO_2 efflux.

Conclusions

For annual time intervals, where the shorter term dynamics are not as important, simple models parameterized with periodic measures of soil CO_2 efflux from the range of conditions generally observed at a site are sufficient for use in estimating NEP. However, wintertime soil CO_2 efflux rates estimates from temperature and moisture dependent models are consistently higher than the auto-chamber estimates. This result implies that models should be parameterized and run for winter and nonwinter conditions separately and their results then aggregated for annual soil CO_2 efflux estimates. This result is important. The expense of building and maintaining an auto chamber system may not be necessary for those researchers interested in estimating R_{soil} annually, though the auto-chambers would still be an advantage capturing data from all seasons for better model parameterization. Also, an auto-chamber system continuously measuring soil CO_2 efflux rates can provide a level of temporal resolution that enables researchers to investigate short- to longer term influences of factors on these rates and a complete record of the annual cycle. The chamber system is an important tool in the effort to better understand factors influencing soil CO_2 efflux and can provide a comprehensive dataset to parameterize and validate models of soil respiration of varying degrees of complexity.

Annual estimates of total ecosystem respiration by the flux tower have consistently been at, or somewhat lower, than estimates of total soil CO_2 efflux. This could be attributed to the limitations of the eddy-covariance technique or over-estimations from model and auto-chamber analysis. If the latter were true, estimates of net ecosystem productivity for the MMSF AmeriFlux site through biometry would be consistently lower than net ecosystem exchange estimates with data from the flux tower. However, to date, this

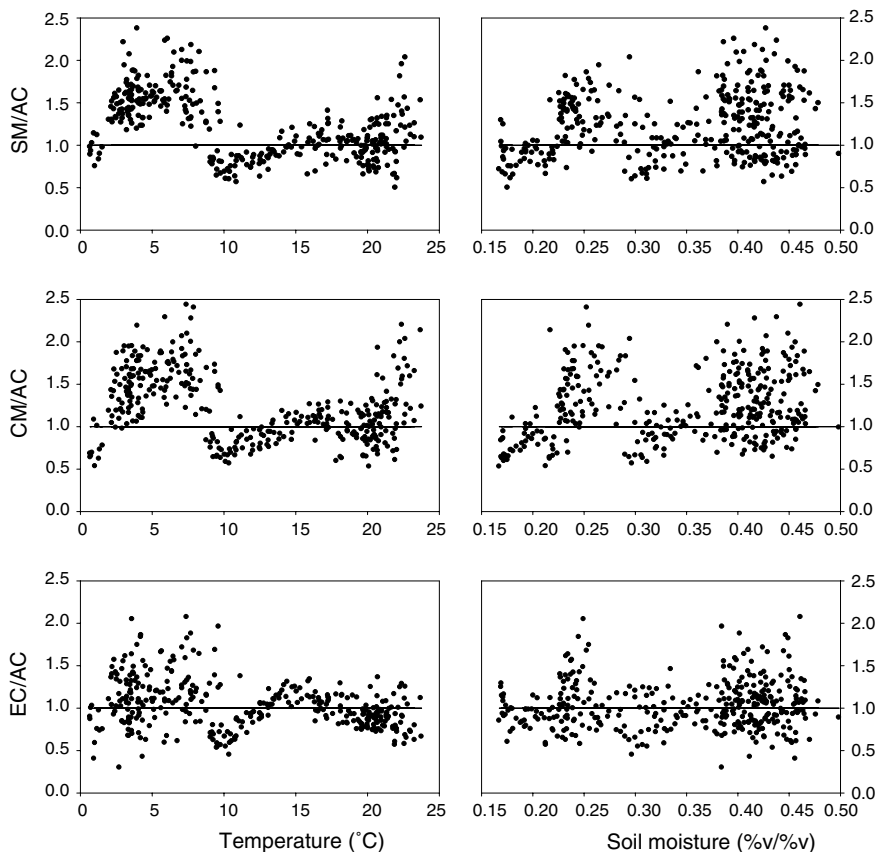


Figure 10. Model performance of SM, CM and EC relative to AC with temperature (left column) and soil moisture (right column). A perfect model would have a ratio of 1.

is not the case. For the past 6 years NEP estimates using biometric methods have been at or somewhat higher than the NEE estimates from the eddy-covariance method (Wayson et al., unpublished).

In recent years, there has been increased interest in measuring and modeling soil respiration as various ecosystem-level carbon dynamics studies (e.g., Wofsy et al. 1993; Barford et al. 2001; Curtis et al. 2002; Ehman et al. 2002; Law et al. 2003; Baldocchi 2003) have continued to identify the importance of this flux. A second automated chamber system has been constructed for the MMSF and was installed in the spring of 2005. We will examine the partitioning of soil respiration into its autotrophic and heterotrophic components, as discussed by Hanson et al. (2000), as well as conduct a careful examination of the relative influences of soil water content and soil temperature (e.g., Davidson et al. 1998, 2002a, b). Other recent observations of soil respiration provide excellent opportunities for comparative analysis both within the eastern deciduous forest (Hanson et al. 2003; Bolstad et al. 2004; Curtis et al. 2005) and across biomes (Borken et al. 2002; Irvine and Law 2002; Raich et al. 2002; Rey et al. 2002).

Acknowledgements

This research was supported by the Biological and Environmental Research Program (BER), U.S. Department of Energy, through the Midwestern Regional Center of the National Institute for Global Environmental Change (NIGEC) under Cooperative Agreement No. DE-FC03-90ER61010. The authors would also like to acknowledge the invaluable aid of B. Offerle with the auto-chamber system design and implementation.

References

- Baldocchi D.D. 2003. Assessing the eddy covariance technique for evaluating carbon dioxide exchange rates of ecosystem: past, present and future. *Global Change Biol.* 9: 479–492.
- Barford C.C., Wofsy S.C., Goulden M.L., Munger J.W., Pyle E.H., Urbanski S.P., Hutryra L., Saleska S.R., Fitzjarrald D. and Moore K. 2001. Factors controlling long- and short-term sequestration of atmospheric CO₂ in a mid-latitude forest. *Science* 294: 1688–1691.
- Barrett J.W. 1995. *Regional Silviculture of the United States*. John Wiley and Sons Inc., New York, 656 pp.
- Bolstad P.V., Davis K.J., Martin J., Cook B.D. and Wang W. 2004. Component and whole-system respiration fluxes in northern deciduous forests. *Tree Physiol.* 24: 493–504.
- Borken W., Xu Y.-J., Davidson E.A. and Beese F. 2002. Site and temporal variation of soil respiration in European beech, Norway spruce, and Scots pine forests. *Global Change Biol.* 8: 1205–1216.
- Braun E.L. 1950. *Deciduous Forests of Eastern North America*. The Blakiston Co., Philadelphia, 596 pp.
- Chapin F.S., Matson P.A. and Mooney H.A. 2002. *Principles of Terrestrial Ecosystem Ecology*. Springer-Verlag, New York.
- Crill P.M., Keller M., Weitz A., Grauel B. and Veldkamp E. 2000. Intensive field measurements of nitrous oxide emissions from a tropical agricultural soil. *Global Biogeochem. Cycles* 14: 85–95.
- Crookston N.L., Moer M., Renner D.L. 2002. User's guide to the Most Similar Neighbor Imputation. Program Version 2. *General Technical Report*, RMRS-GTR-96. Ogden, UT: USDA Rocky Mountain Research Station, 35 pp.
- Curtis P.S., Hanson P.J., Bolstad P., Barford C., Randolph J.C., Schmid H.P. and Wilson K.B. 2002. Biometric and eddy-covariance based estimates of ecosystem carbon storage in five eastern North American deciduous forests. *Agric. Forest Meteorol.* 113: 3–19.
- Curtis P.S., Vogel C.S., Gough C.M., Schmid H.P., Su H.-B. and Bovard B.D. 2005. Respiratory losses and the carbon-use efficiency of a northern hardwood forest, 1999–2003. *New Phytol.* 167: 437–456.
- Davidson E.A., Belk E. and Boone R.D. 1998. Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. *Global Change Biol.* 4: 217–227.
- Davidson E.A., Savage K., Bolstad P., Clark D.A., Curtis P.S., Ellsworth D.S., Hanson P.J., Law B.E., Luo Y., Pregitzer K.S., Randolph J.C. and Zak D. 2002a. Below-ground carbon allocation in forests estimated from litterfall and IRGA-based soil respiration measurements. *Agric. Forest Meteorol.* 113: 39–51.
- Davidson E.A., Savage K., Verchot L.V. and Navarro R.I. 2002b. Minimizing artifacts and biases in chamber-based measurements of soil respiration. *Agric. Forest Meteorol.* 113: 21–37.
- Ehman J.L., Schmid H.P., Grimmer C.S.B., Randolph J.C., Hanson P.J., Wayson C.A. and Cropley F. 2002. An initial inter-comparison of micrometeorological and ecological estimates of carbon exchange in a mid-latitude deciduous forest. *Global Change Biol.* 8: 575–589.
- Field C.B., Ball T.J. and Berry J.A. 1989. Photosynthesis: principles and field techniques. In: Pearcy R.W., Ehleringer J.R., Mooney H.A. and Rundel P.W. (eds), *Plant Physiological Ecology Field Methods and Instrumentation*, Chapman & Hall, London, pp. 209–253.
- Froelich N., Schmid H.P. 2002. An investigation of advection and gully flows in complex forested terrain. Preprints, 25th Conference on Agricultural and Forest Meteorology, Amer. Meteorol. Soc., Boston, 10.8.
- Gu L., Post W.M. and King A.W. 2004. Fast labile carbon turnover obscures sensitivity of heterotrophic respiration from soil to temperature: a model synthesis. *Global Biogeochem. Cycles* 18: GB1022.
- Hanson P.J., Wullschlegel S.D., Bohlman S.A. and Todd D.E. 1993. Seasonal and topographic patterns of forest floor CO₂ efflux from an upland oak forest. *Tree Physiol.* 13: 1–15.
- Hanson P.J., Edwards N.T., Garten C.T. and Andrews J.A. 2000. Separating root and soil microbial contributions to soil respiration: a review of methods and observations. *Biogeochemistry* 48: 115–146.
- Hanson P.J., O'Neill E.G., Chambers M.L.S., Riggs J.S., Joslin J.D. and Wolfe M.H. 2003. Soil respiration and litter decomposition. In: Hanson P.J. and Wullschlegel S.D. (eds), *North American Temperate Deciduous Forest Responses to Changing Precipitation Regimes*, Springer-Verlag, New York, pp. 163–189.
- Hanson P.J., Amthor J.S., Wullschlegel S.D., Wilson K.B., Grant R.F., Hartley A., Hui D., Hunt E.R. Jr., Johnson D.W., Kimball J.S., King A.W., Luo Y., McNulty S.G., Sun G., Thornton P.E., Wang S., Williams M., Baldocchi D.D. and Cushman R.M. 2004. Oak forest carbon and water simulations: model intercomparisons and evaluations against independent data. *Ecol. Monogr.* 74: 443–489.
- Hooper D.U., Cardon Z.G., Chapin F.S. III and Durant M. 2002. Corrected calculations for soil and ecosystem measurements of CO₂ flux using the Li-Cor 6200 portable photosynthesis system. *Oecologia* 132: 1–11.
- Irvine J. and Law B.E. 2002. Contrasting soil respiration in young and old-growth ponderosa pine forests. *Global Change Biol.* 8: 1183–1194.
- Kramer P.J. and Kozlowski T.T. 1979. *Physiology of Woody Plants*. Academic Press, New York.
- Law B.E., Sun O.J., Campbell J., Van Tuyl S. and Thornton P.E. 2003. Changes in carbon storage and fluxes in a chronosequence of ponderosa pine. *Global Change Biol.* 9: 510–524.
- Longdoz B., Yernaux M. and Aubinet M. 2000. Soil CO₂ efflux measurements in a mixed forest: impact of chamber disturbances, spatial variability and seasonal evolution. *Global Change Biol.* 6: 907–917.
- National Climatic Data Center. Normals for 1971–2000 – Indiana. <http://www.ncdc.noaa.gov/oa/ncdc.html>, accessed 16 March 2004.

- Pumpanen J., Ilvesniemi H., Perämäki M. and Hari P. 2003. Seasonal patterns of soil CO₂ efflux and soil air CO₂ concentration in a Scots pine forest: comparison of two chamber techniques. *Global Change Biol.* 9: 371–382.
- Raich J.W., Potter C.S. and Bhagawati D. 2002. Interannual variability in global soil respiration, 1980–94. *Global Change Biol.* 8: 800–812.
- Rey A., Pegoraro E., Tedeschi V., De Parri I., Jarvis P. and Valentini R. 2002. Annual variation in soil respiration and its components in a coppice oak forest in Central Italy. *Global Change Biol.* 8: 851–866.
- Savage K.E. and Davidson E.A. 2001. Interannual variation of soil respiration in two New England forests. *Global Biogeochem. Cycles* 15: 337–350.
- Schmid H.P., Grimmond C.S.B., Copley F.D., Offerle B. and Su H.-B. 2000. Measurements of CO₂ and energy fluxes over a mixed hardwood forest in the midwestern United States. *Agric. Forest Meteorol.* 103: 355–373.
- Schmid H.P., Su H.-B., Vogel C.S., Curtis P.S. 2003. Ecosystem–atmosphere exchange of carbon dioxide over a mixed deciduous forest in northern lower Michigan. *J. Geophys. Res.*, 108 (D14), Art. No. 4417.
- USDA 1980. Soil Survey of Monroe County, Indiana. US Soil Conservation Service, Washington, DC, 184 pp.
- Van Kley J.E., Parker G.R., Franzmeier D.P., Randolph J.C. 1995. Field Guide: Ecological Classification of the Hoosier National Forest and Surrounding Areas of Indiana. USDA Forest Service, 75 pp.
- Vose J.M. and Bolstad P.V. 1999. Challenges to modelling NPP in diverse eastern deciduous forests: species-level comparisons of foliar respiration responses to temperature and nitrogen. *Ecol. Model.* 122: 165–174.
- Wofsy S.C., Goulden M.L., Munger J.W., Fan S., Bakwin P., Daube B., Bassow S. and Bazzaz F. 1993. Net exchange of CO₂ in a mid-latitude forest. *Science* 260: 1314–1317.
- World Conservation Monitoring Centre 1999. Generalised world forest map. United Nations Environment Programme, <http://www.wcmc.org.uk/services/forest/wfm.e00.Z>, accessed 15 November 1999.