An initial intercomparison of micrometeorological and ecological inventory estimates of carbon exchange in a mid-latitude deciduous forest

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Abstract

The role of mid-latitude forests in the sequestration of carbon (C) is of interest to an increasing number of scientists and policy-makers alike. Net CO_2 exchange can be estimated on an annual basis, using eddy-covariance techniques or from ecological inventories of C fluxes to and from a forest. Here we present an intercomparison of annual estimates of C exchange in a mixed hardwood forest in the Morgan-Monroe State Forest, Indiana, USA for two years, 1998 and 1999. Based on eddy-covariance measurements made at 1.8 times canopy height from a tower, C uptake by the forest was 237 and 287 $g\,C\,m^{-2}\,y^{-1}$ for 1998 and 1999, respectively. For the same time period, biometric and ecophysiological measures and modelled estimates of all significant carbon fluxes within deciduous forests were made, including: change in living biomass, aboveground and belowground detritus production, foliage consumption, and forest floor and soil respiration. Using this ecological inventory method for these same two time periods, C uptake was estimated to be 271 and 377 $g\,C\,m^{-2}\,y^{-1}$, which are 14.3% and 31.4% larger, respectively, than the tower-based values. The relative change between this method's annual estimates is consistent with that of the eddy-covariance based values. Our results indicate that the difference in annual C exchange rates was due to reduced heterotrophic soil respiration in 1999.

Keywords: biometry, carbon fluxes, deciduous forest, ecophysiology, eddy covariance, micrometeorology, net ecosystem production, net primary production, soil respiration

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Introduction

Current estimates of CO_2 exchange between the oceanic, terrestrial and atmospheric carbon reservoirs, and sources from anthropogenic combustion, leave a considerable amount of carbon ($\sim 1.4\,Pg\,C\,y^{-1}$) unaccounted for (Houghton *et al.*, 1996). Widespread regrowth occurring in mid-latitude forests of the northern hemisphere makes this region a prime candidate for this missing carbon sink (Tans *et al.*, 1990; Ciais *et al.*, 1995; Fan *et al.*, 1998a). To assess the role of various ecosystems in sequestering carbon, long-term flux networks (e.g. AmeriFlux,

Euroflux, LBA) measuring surface-atmosphere carbon dioxide exchanges have been established (Baldocchi *et al.*, 2000, 2001). However, these methods are plagued by the extreme variability of terrestrial ecosystems at a multitude of scales, distinct interannual variability, and uncertainty in some aspects of long-term flux measurements (Lee, 1998; Paw *et al.*, 1998; Finnigan, 1999; Schmid *et al.*, 2000a,b). Thus current estimates of carbon exchange rates are virtually unconstrained by reliable benchmark values. Running *et al.* (1999) proposed an integrative framework for addressing some of these issues. However, before tower-based C flux data can be confidently scaled to regions, a direct and independent evaluation of tower-based flux measurements is necessary. At present, literature on such validations or comparisons is limited.

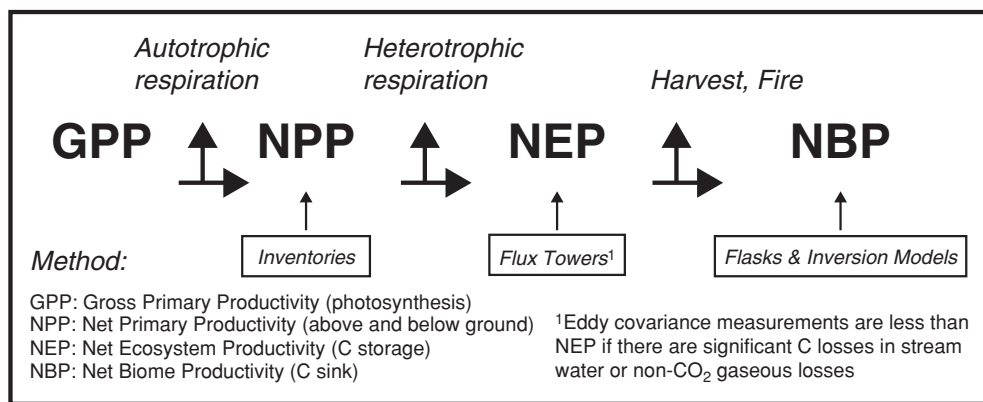Correspondence: Jeffrey L. Ehman, tel. 812-855-8963, fax 812-855-7547, e-mail: jlehman@indiana.edu

Fig. 1 Relationship between different concepts of ecosystem carbon exchange and associated observation methods. After Schulze & Heimann (1998).

Our objective is to compare tower-based, micrometeorological estimates of net carbon exchange for an AmeriFlux site, Morgan-Monroe State Forest (MMSF, Indiana, USA), with those determined from independent ecological inventory techniques. Our specific goals are three-fold: (1) to use ecological inventory methods to provide estimates of the major CO_2 fluxes in this forest ecosystem; (2) to demonstrate that these complementary measurements can help to explain interannual differences by examining the component processes responsible for net CO_2 flux; and (3) to compare two spatially and temporally integrated independent estimates of net C exchange for two years (1998–99).

As will be seen, the lack of reliable measures of the uncertainties of either method emerges as the most important problem barring the way to measures of annual carbon sequestration that are quantitatively sound.

Background

The exchange of carbon between a mid-latitude forest and the atmosphere is overwhelmingly dominated by CO_2 (e.g. Fan *et al.*, 1998). Net CO_2 flux (F_{CO2}) is commonly measured using eddy covariance techniques, in hourly or half hourly increments, to derive estimates of net ecosystem exchange (NEE) (e.g. Baldocchi *et al.*, 1996). Positive (or negative) values of NEE correspond to upward (or downward) transport, or a net loss (or net gain) of carbon by the forest. Net exchange of carbon by the forest over a given period of time (i.e. a growing season or year) is also termed net ecosystem production (NEP). NEP captures a host of vegetation and soil processes and feedbacks associated with C metabolism, including photosynthesis and respiration, and responses of ecosystems to climate variation and other perturbations. The primary differences between the usage of the terms NEP and NEE is based on the time scale under

consideration. NEE values from hourly increments integrated over a year, yield an annual estimate of NEP. The sign conventions are: NEE is positive for fluxes to the atmosphere, and NEP values are positive for net carbon uptake (i.e. sequestration) by vegetation and soils. As presented in Fig. 1:

$$NEP = NPP - R_h \tag{1}$$

where, NPP is net primary production and R_h is heterotrophic respiration (primarily from microbes and soil fauna). The latter is related total soil respiration (R_s) as follows:

$$R_s = R_h + R_r \tag{2}$$

We use Wiant (1967) definition of root respiration (R_r): 'all respiration derived from organic compounds originating in plants including the respiration of living root tissue, the respiration of symbiotic mycorrhizal fungi and associated microorganisms, and the decomposing organisms operating on root exudates and recent dead root tissues in the rhizosphere'.

An alternative approach to measuring NEP by the eddy-covariance method is the calculation of NEP from inventories of various C compartments and process-level flux measurements. The following relation (Waring & Schlesinger, 1985) can be used for NEP estimation, in conjunction with Equation (1):

$$NPP = \Delta B_{living} + D_{total} + H \tag{3}$$

where, for some unit of time (usually one year), ΔB_{living} is change in living biomass, D_{total} is the sum of aboveground and belowground detritus production (D_a and D_b), and consumption (H) is equated to aboveground leaf herbivory. Belowground detritus production is defined as all C transferred from roots and their associated mycorrhizae to the soil from exudation, sloughing of surface tissues, herbivory, or mortality (Raich & Nadelhoffer, 1989).

Substituting Equation (3) into Equation (1):

$$NEP = \Delta B_{living} + D_{total} + H - R_h \qquad (4)$$

Estimation of ΔB_{living}, in practice, relies heavily upon allometric relationships relating tree biomass with easily measured parameters, such as diameter at breast height (d.b.h.). Litterfall and fine root turnover data are necessary to estimate detritus production. Leaf herbivory data are required to estimate consumption. Modelled, annual R_s rates as well as estimates of the $R_h:R_r$ ratio are necessary to estimate soil heterotrophic respiration. Finally, both heterotrophic respiration from decomposers of coarse woody debris (CWD) and from foliar consumers (Consumers) must be accounted for in the R_h term (i.e. $R_{h(Total)} = R_{h(Soil)} + R_{h(CWD)} + R_{h(Consumers)}$).

Due to differences in measurement approach, sensor position, and sensor technology, the micrometeorological and ecological inventory measurements refer to different fields-of-view or 'footprints'. To compare the different methods, the footprint of the atmospheric measurements needs to be spatially consistent with the locations sampled in the ecological inventory. A comparison of the two methods assumes implicitly that both estimates have appropriately sampled the spatial variability of the ecological processes, such that they are representative samples of the exchange processes on the ecosystem scale (Schmid, 1997; Schmid & Lloyd, 1999).

The temporal resolution of the two methods is different. The eddy-covariance method can yield annual NEP estimates, but also provides estimates of NEE for short time periods (e.g. hourly fluxes). While tree bole diameter growth measured with dendrometers can be used to predict C uptake on a weekly basis, other components needed for the calculation of NEP using the ecological inventory method do not allow a similar temporal resolution. This is especially true for root growth data, commonly derived from multi-year observations (Joslin et al., 2000, 2001). Thus, our intercomparison is limited to annual estimates of C sequestration.

Materials and methods

Study site

Morgan-Monroe State Forest (MMSF) is located in south-central Indiana (39°19'N, 86°25'W, 275 m above sea level), approximately 25 km north of Bloomington (Fig. 2). Mean annual temperature is 11.1 °C and mean annual precipitation is 1012 mm. This managed forest has a total area of 67 000 ha. This region is just south of the limit of the late Wisconsinian glaciation and is dominated by ridge/ravine topography with a relative relief of less than 60 m and an overall drop of 90 m in 4 km. The region is covered primarily by 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). As with other uplands in this region, soils at the study site 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).

Timber harvests in the vicinity of the flux tower used selection and seed-tree methods and have occurred on a 20–25 years rotation for several decades. One seed-tree management area, harvested in 1991, is located to the north of the eddy covariance tower out of the main fetch. In addition to past harvests, some stands in the tower area were impacted by a wind storm in 1990. Overall, the forest is closed canopy, dominated by 60–80-year-old-trees. The study site is located so that the minimum fetch of the tower is mostly uninterrupted forest at least 4 km in any direction and up to 8 km in the principal wind direction (westerly to south-westerly).

Atmospheric flux measurements

Details of instrumentation, data processing, and results of diurnal and seasonal variations of energy and CO_2 fluxes are provided in Schmid et al. (2000a). The tower-based micrometeorological flux measurements reported here are conducted at the 46-m level. Turbulence measurements are obtained from a three-dimensional sonic anemometer (C-SAT, Campbell Scientific Inc. (CSI), Logan (UT) mounted with an azimuth orientation of 230°. The CO_2 concentrations are measured by pumping sample air from the 46-m height to a closed-path IRGAs (LI-6262, Li-Cor, Lincoln, NE) inside the shelter at the base of the tower. These variables are sampled at 10 Hz and preprocessed by a data acquisition unit and the LabView software from National Instruments Inc., Austin, TX. Eddy covariance fluxes are then obtained during post-processing by shifting the scalar and vertical velocity time series to maximize the cross-correlation. These turbulent flux measurements yield the net fluxes of carbon dioxide (F_{CO2}).

In addition to the turbulent fluxes, a suite of other variables is measured continuously at multiple heights and locations. These include the four-component radiation balance, photosynthetically active radiation (PAR), profiles of temperature, humidity and CO_2 concentration, soil temperature (T_s), soil moisture and soil heat flux. PAR from above canopy and T_s are used in a parametric model of NEE to fill gaps in the F_{CO2} measurements.

The scalar flux footprint model of Schmid (1994, 1997) was used to examine the assumption that the eddy-covariance measurements sample a representative
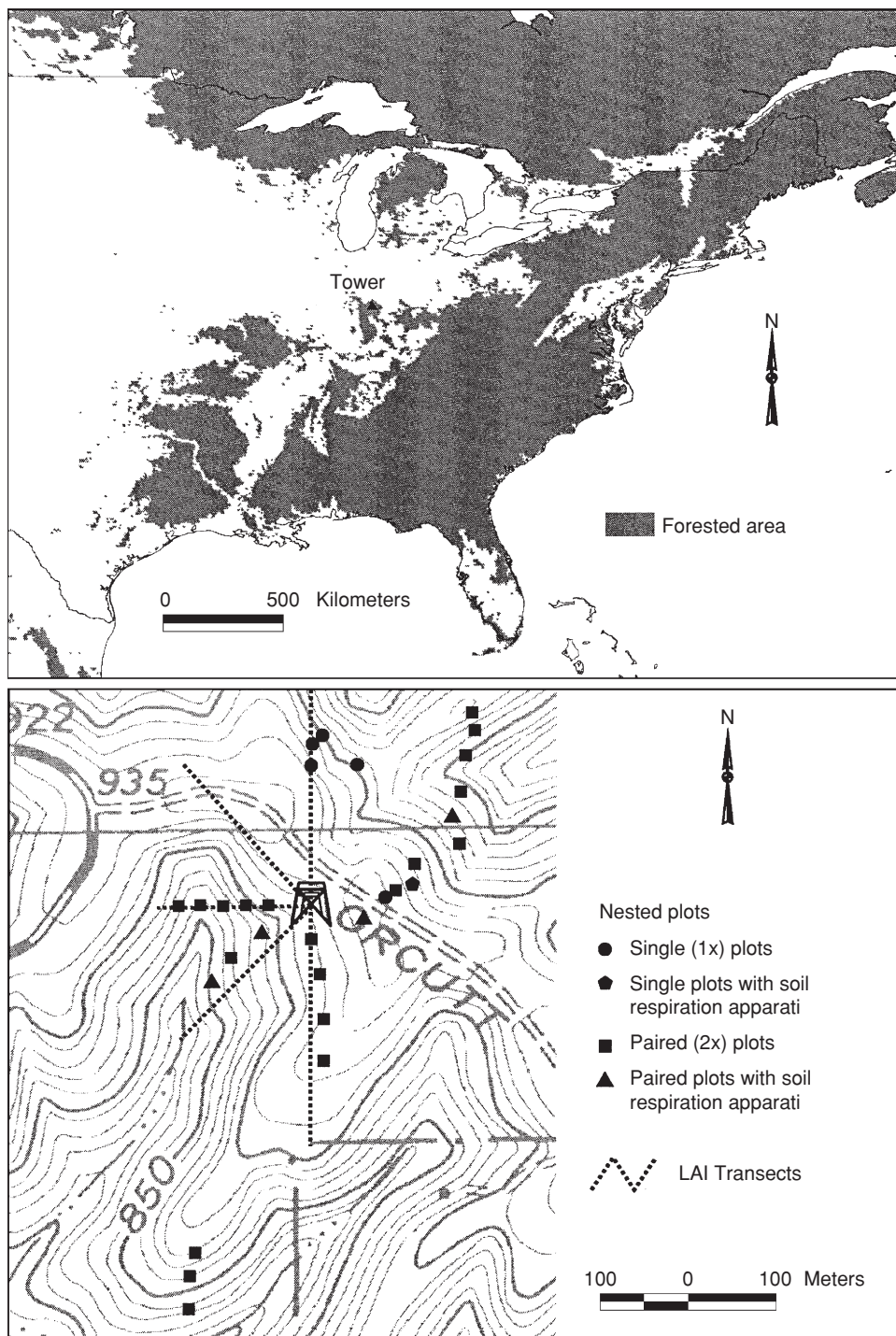
Fig. 2 The regional map depicts forested land within eastern North America (World Conservation Monitoring Service, 1999) and the MMSF site location. The local site map shows hypsography, roads, tower location, and the locations of plots and transects.

portion of the ecosystem. This model uses an analytical approach to the advection–diffusion equation (Horst & Weil, 1992, 1994) to identify the area of forest canopy with the greatest influence on a flux measurement. The model is restricted to surface layer scaling conditions and does not account for along-wind diffusion, transport below canopy, or topography. See the results of source area modelling below.

Ecological inventory method

All ground-based measurements, unless indicated otherwise, were conducted in 54 rectangular 150-m^2 plots in the vicinity of the tower (Fig. 2). The plots were established in two phases, both along systematically located transects. In the first set, plots were located along leaf area index (LAI) transects. A second set of plots was necessary to provide a representative sample of the different tree communities around the tower site, each associated with a particular topographically induced microclimate (Braun, 1950) and edaphic condition. These plots were randomly located adjacent to transects which were stratified according to topographic position. Species, height, and d.b.h. were recorded for all trees ≥ 7 cm d.b.h. Nested subplots (10 m^2, 1 m^2, and 0.0625 m^2) were sampled to quantify C stocks of smaller trees, seedlings, herbaceous vegetation, and forest floor and soil compartment constituents. Tree d.b.h. was measured each winter at the same position on all trees ≥ 7 cm d.b.h. Band dendrometers (designed after McLaughlin & Downing, 1996) were used to monitor biweekly changes in circumference for 165 trees ≥ 10 cm d.b.h. in 24 of these plots during days 151–318 of the 1998 (1998/151–318) growing season and every two weeks throughout 1999.

Changes in bole, branch, and large root biomass were calculated using pre- and post-growing season d.b.h. values in conjunction with published allometric equations. Species-specific regressions relating d.b.h. to dry biomass were employed as available from the literature (Smith & Brand, 1983; Ter-Mikaelian & Korzukhin, 1997). For species with several equations available (e.g. *Acer saccharum*), preference was given to equations developed in ecologically similar sites (Crow & Schlaegel, 1988), rather than to those from geographically proximate sites. Allometric equations for 'general hardwoods' ≥ 10 cm d.b.h. developed for an eastern Tennessee site (Harris *et al*., 1973) were used for species with no published specific relationships.

Vegetation area index (VAI, consisting of foliage, branches, and boles) was measured periodically at 30 locations on three transects from the tower in southwestern, north-western, and western directions using a Li-Cor LAI-2000 sensor (see Schmid *et al*., 2000a for further details). Full sky reference was measured at the top of the tower. The phenological development of leaves on a sample of 62 trees (within the 150-m^2 plots) is observed weekly during the growing season margins.

Growth increment data from dendrometers was considered unreliable until late spring in 1998 (1998/86–151). The missing information was estimated by applying a relationship established between 1999 leaf phenology and 1999 bole growth increment data to the 1998

phenology data. To develop this relationship, 1999 average weekly leaf (or leaflet for compound leaves) length estimates (1999/83–162) were first converted to percentages of the final leaf length (1999/162). Second, 1999 spring biweekly bole growth increments (1999/90–98, 99–112, 113–126, 127–140) were halved to generate weekly increments centred on the day of the leaf length information (% of maximum). Third, basal area increments were calculated from the bole growth (circumference) increments. Fourth, an exponential model, which predicts bole growth (BG) in cm^2 as a function of percentage leaf-out (LO), was developed:

$$BG = 0.3258\,e^{0.0209\,LO} \quad (n = 62, R^2 = 0.92) \qquad (5)$$

Last, the model was used to estimate bole growth increments for each individual tree for spring 1998, by applying the corresponding 1998 LO value.

In addition to the 165 'larger' trees equipped with dendrometers (d.b.h. ≥ 10 cm), many 'smaller' trees (d.b.h. < 10 cm) are present in the sample plots, although these constitute only a minor fraction (4%) of the total basal area of all trees. C uptake by smaller trees was accounted for by scaling the increments from larger trees (I_{lt}) to the plot level (I_{plot}) on the basis of the fraction of plot relative dominance (RD_{plot}) comprised of large trees (RD_{lt}): $I_{plot} = I_{lt} * (RD_{plot}/RD_{lt})$. Because our annual remeasures of all plot trees with d.b.h. ≥ 7 cm indicated that the biomass increment of smaller trees was only 44% that of larger trees, the scaling was adjusted accordingly. Dry biomass was converted to C mass for this and all other components using compartment-specific C content (g C g^{-1} biomass) as determined for samples by a Perkin-Elmer CHN analyser (Castellanos & Randolph, 2001).

The allometric equation for roots of general hardwoods is applicable to the 'stump central root and the large support lateral roots within a radius of 60 cm from the base of the stump' (Harris *et al*., 1973). Hence, an accounting of the annual biomass increment for lateral and fine roots located > 60 cm from the stump was needed to complement the allometric-based 'large root' estimate. Here, a space-for-time substitution methodology (Pickett, 1989) was employed to derive a long-term mean annual increment from empirical data. Fine and coarse roots were sieved from soil collected from 79 soil pits stratified across a chronosequence of nearby forest stands. Each pit was 0.0625 m^2 in area and was excavated to a depth of one meter (or less if bedrock was encountered). Mean coarse and fine root standing crop (B_{rcf}) was found to increase as a function of stand age (A_{stand}) at a rate of approximately 4.6 g C m^{-2} y^{-1}.

$$B_{rcf} = 336.9 + 4.6\,A_{stand} \quad (R^2 = 0.93) \qquad (6)$$

Litterfall (D_a) was collected at the site in circular mesh baskets, each 0.5 m^2 in area, at 20 locations at seven

different times each during 1998 and 1999. Six of these collections were performed at two-week intervals during the primary autumn defoliation period. Litterfall was separated into leaf, seed, and woody components, oven-dried to constant mass, and weighed. The mean leaf and seed yield from the 20 locations were used. The height of the baskets' rim (~0.5 m above the forest floor) necessitated separate measurements of detritus production from the herbaceous layer. Herbaceous dry biomass was determined by harvesting 1 m^2 plots in mid-summer ($n = 23$ in 1998, and $n = 46$ in 1999). Woody litterfall was assumed to be associated with growth during a previous year, and tree death is not necessarily congruous with an immediate change in bole, branch, or root C. The decomposition of large woody debris is accounted for as heterotrophic respiration (see below).

Belowground detritus production (D_b) was estimated as the product of fine root standing crop and the annual fine root turnover ratio (TR_{rf} = production/standing crop, % y^{-1}). The latter was modelled using the regression equation presented for nitrate-dominated hardwood forests in Aber *et al.* (1985) in which nitrogen availability (N_{avail}, kg $ha^{-1} y^{-1}$) is the independent variable:

$$TR_{rf} = 0.377 - 0.0064 \, N_{avail} + 0.000141 (N_{avail}^2)$$
$$(P < 0.01, R^2 = 0.99) \quad (7)$$

Annual N_{avail} for MMSF was estimated at 120 kg $ha^{-1} y^{-1}$. This value is based on the sum of N mineralization (N_{min}) and N deposition (N_{dep}, wet + dry). A preliminary estimate of annual N_{min} was 110.4 kg $ha^{-1} y^{-1}$ from an incubated and *in situ* bag experiment conducted at the study site from May 1999 to November 2000. Annual N_{dep} is typically considered to be ~9 kg ha^{-1} in Indiana (Kuperman, 1999), although the rate may be as high as 13.5 kg $ha^{-1} y^{-1}$ (Pryor *et al.*, 1999).

The standing crop of fine roots (< 2 mm diameter) was measured to 0.2 m depth at 16 locations at the study site. Equation (7) was developed using a fine root size class of < 3 mm. Therefore, a correction factor was needed to account for fine roots at MMSF between 2 and 3 mm. Fine root data for white oak forests (Joslin & Henderson, 1987) indicates that about 18% of root biomass in the 0–2 mm size class is present in the biomass of the 2–3 mm root size class.

An alternative belowground root production estimate can be derived using a soil C budget method based on the conservation of mass (Raich & Nadelhoffer, 1989) used to estimate belowground C allocation in forests. Assuming forest soil C stocks are in equilibrium over the short-term (i.e. the amount of C entering the soil yearly equals the annual soil loss), then:

$$R_h \cong D_a + D_b \quad (8)$$

Substitution with Equation (2) gives:

$$R_s - D_a \cong D_b + R_r \quad (9)$$

Assuming that R_r is one-half of R_s, i.e. $R_h : R_r = 1$ (Hanson *et al.*, 2000), and that the herbivory component does not leave the system, this equation becomes:

$$D_b \cong R_{h(Soil)} - D_a - H \quad (10)$$

As with the previous method, this budget method assumes that C exchanges other than litterfall, R_s, and belowground (root) detritus production are negligible. Other possible contributions include C in precipitation, dry deposition, leaching, runoff, and erosion. This method considers soils to include soil organic matter and fine litter on the soil surface; coarse woody debris (CWD) on or above the soil is excluded. Hence, CWD inputs to the soil as detritus are excluded, as is the CWD component of heterotrophic respiration.

Leaf herbivory was estimated at full leaf-out (1998/191 and 1999/190) and just prior to leaf fall in the autumn (1998/282 and 1999/268) for both years. Herbivore foliage consumption estimates (recorded as percentage of total leaf area) were based on visual observation (with binoculars, when necessary) of leaves in three separate canopy layers on 62 trees within the 150-m^2 plots. The autumn herbivory estimates were scaled to the entire plot level following the method described above for changes in bole and branch carbon. In this case, relative leaf mass for the sets of trees within each plot was calculated, employing the Harris *et al.* (1973) equation relating leaf biomass to d.b.h. Herbivory (H) estimates are then multiplied by the leaf litter yield to estimate consumption. We estimated herbivore respiration as 8.5%, the product of assimilation efficiency and metabolic rate (Phillipson, 1966; Price, 1975). This small upward flux was subtracted to yield the final consumption value.

Total respiration from the soil and forest floor was measured using a Li-Cor LI-6200 analyser and portable soil respiration chamber. In early spring 1998, 10 PVC rings (10 cm diameter and 5 cm height) were placed in the soil in a 1 by 5 m rectangular pattern in five of the 150-m^2 plots (2 north-facing, 2 south-facing, 1 broad ridge-top). Four measurements of CO_2 flux from the soil were made from each ring between 1000 and 14.00 h at approximately three-week intervals during the 1998 growing season and at 2-week intervals in the 1999 growing season. In conjunction, soil temperature (thermocouple) and moisture (gravimetric) measurements were made at 10-cm depth. While temporally restricted, these measurements were spatially distributed to account for the variable topo-edaphic conditions in the area, and to examine the spatial variability of R_h. The autotrophic root component (R_a) of the total soil C efflux rate (R_s) was assumed to be 50% (Hanson *et al.*, 2000).

Respiration from the decomposition of large woody debris was not included in the soil respiration measurements and required an inventory-based estimate. Dimensions of all coarse woody debris (diameter $> 7 \, cm$) in the $150 \text{-} m^2$ plots were determined. A decomposition class, ranging from 'freshly fallen' to 'very decomposed', was assigned to every individual dead branch, stem, or stump present at the forest floor. Wood density and C content was measured for each of the four different decomposition classes. The product of these terms and the individual calculated volumes yield mean C content for coarse woody debris. A 10% annual decomposition rate for coarse woody debris (Todd *et al.*, 1976) was then applied to estimate the annual C exchange from this pool.

Respiration measurement and modelling

Two independent estimates of ecosystem and soil respiration were developed. The first is based on measured values of night-time F_{CO2} from the 46-m eddy-covariance system during the period when the canopy was not present or beginning to develop (November–April). This method yields total ecosystem respiration (R_E, including forest floor, bole and a minor amount of canopy respiration, see Schmid *et al.*, 2000a). This approach is similar to that suggested by Wofsy *et al.* (1993), except that they used eddy-covariance fluxes corrected for storage change. Recent work by Schmid *et al.* (2000b) shows that the storage correction is not sufficient to account for the difference between measured and expected respiratory fluxes. Thus, this respiration model was developed using only eddy covariance fluxes under well-ventilated conditions (friction velocity, $u^* > 0.5$), to ensure well-developed turbulence and mixing between the sensor level and the forest floor. The 1998 data were averaged in bins of $1\,°C$ width and an exponential function fitted to the bin-averages:

$$R_E = 1.08 ex^{(0.064\,Ts)} \quad (n = 1111, \ R^2 = 0.66) \qquad (11)$$

where R_E is in $\mu mol\,m^{-2}\,s^{-1}$ and Ts is soil temperature (°C). The equivalent Q_{10} value of this relationship is 1.89. For 1999, the data were divided into periods of 10 days, and a model similar to Equation 11 was fit to each period independently. This method implicitly accounts for factors other than temperature that may vary during the seasons.

The second estimate, modified from Hanson *et al.* (1993), is based on direct measurements of mean soil respiration during the growing season. Using a nonlinear curve fitting method in SPSS, the relation between soil temperature at $10\,cm$ depth (T_s, °C) and soil water potential (M_{obs}, MPa) with soil respiration (R_s, $\mu mol\,m^{-2}\,s^{-1}$) was defined as:

$$R_s = -6.07^* Q_{10}^{((Ts-20)/(10)^*} ((M_{max} - M_{obs})/M_{max})$$
$$(n = 2673, \ P < 0.001, \ R^2 = 0.31) \qquad (12)$$

where the Q_{10} value is 2.23 and M_{max} is the maximum soil water potential ($-2.0\,MPa$).

Data were collected under a variety of soil moisture and soil temperature conditions, although soil respiration during winter is under represented. Figure 3 shows the range of conditions (black dots) in which data were collected using the Li-Cor LI-6200 soil respiration unit. This figure also shows that measurements were made during critical periods, where the soil respiration model (grey line) was most sensitive to soil moisture and soil temperature conditions. Because the scatter in Fig. 3 is large, we evaluated intra vs. interplot variability of soil moisture conditions. Intra-plot variability was on the order of 5%, while interplot variability was observed to be between 5 and 6%. Thus, the amount of scatter cannot be explained by spatial variability alone. Although the inclusion of soil moisture effects into the model increases its predictive capacity, it appears that either measurement uncertainties, or other (unknown) influences on soil respiration remain significant. However, Fig. 3 indicates that the scatter is distributed randomly around the model curve, so that some cancellation of random errors can be expected in the time integration.

Results and discussion

Phenology

The winter of 1997/98 was unusually mild in this region (mostly attributed to a strong El Niño event during that period) with bud break ($> 50\%$ of observed trees having open buds) being about two weeks earlier than usual. Bud break began around 13 April (1998/103) and was complete ($\geq 75\%$ of observed trees having $> 75\%$ of full leaf extension) by 18 May (1998/138), after which VAI remained fairly constant at $4.7 \pm 0.5(SE)$ until the beginning of August. From 1998/217 through the first half of September (1998/258), herbivory decreased the VAI to $4.48 \pm 0.4(SE)$. Senescence (defined as $> 50\%$ of observed trees having more than 50% change in colour or having lost $> 50\%$ of their leaves) was recorded on 16 October (1998/289), and leaf fall continued until 1 November (1998/305).

After another mild winter, bud break for 1999 was observed $4\,d$ earlier than 1998, on 9 April (1999/99) and leaf-out continued until 11 May (1999/118). Senescence was recorded on 5 October (1999/278) and leaf fall continued until 6 November (1999/308), closely matching the 1998 observations. VAI values in 1999 were very similar to those recorded for 1998, with differences well within the error margin.
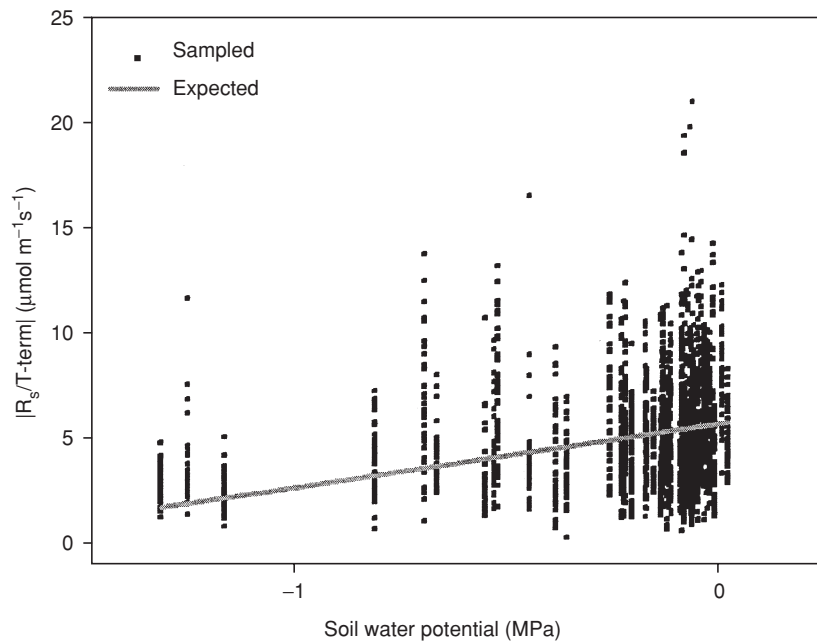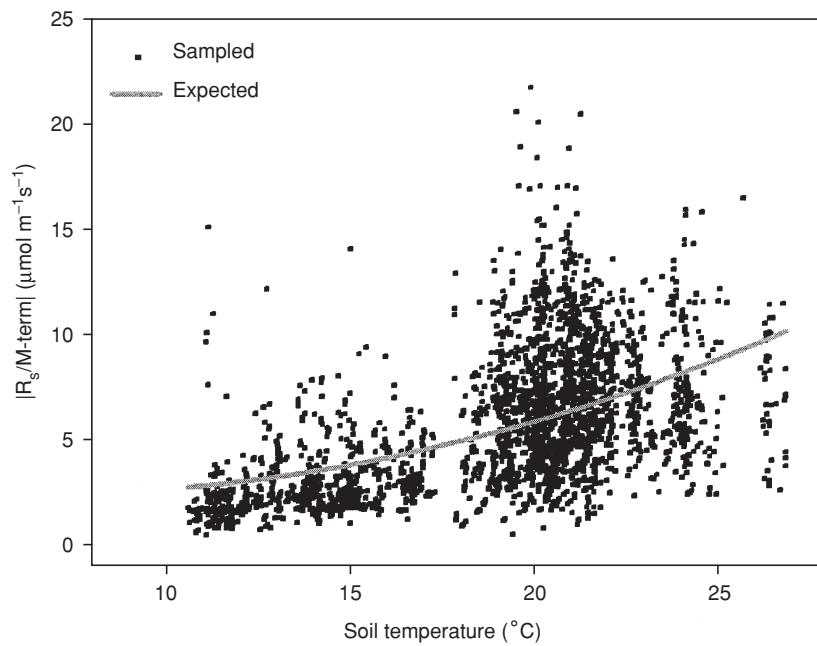
Fig. 3 Observations and model values of the parametric soil respiration model of Equation 12. To separate the model performance with respect to soil temperature from that with respect to soil moisture, the values are scaled by the soil moisture component (M-term $= (M_{max} - M_{obs})/M_{max}$) in the top panel, and by the soil temperature component (T-term $= Q_{10}^{((Ts-20)/(10))}$ in the bottom panel.

Micrometeorological method

Schmid *et al.* (2000a) present hourly F_{CO2} values obtained at the MMSF site for the study period. Their results show that while respiration was still dominant throughout April 1998, the forest clearly had become a net C sink in early May, both in 1998 and 1999 (Fig. 4). Measured daily average respiration rates are 1–3 $\mu mol\, m^{-2}\, s^{-1}$ during most of winter. With warmer temperatures in April, respiration rates increase to result in a daily mean net exchange of about −5 $\mu mol\, m^{-2}\, s^{-1}$. At the peak of the growing season (June and July) the
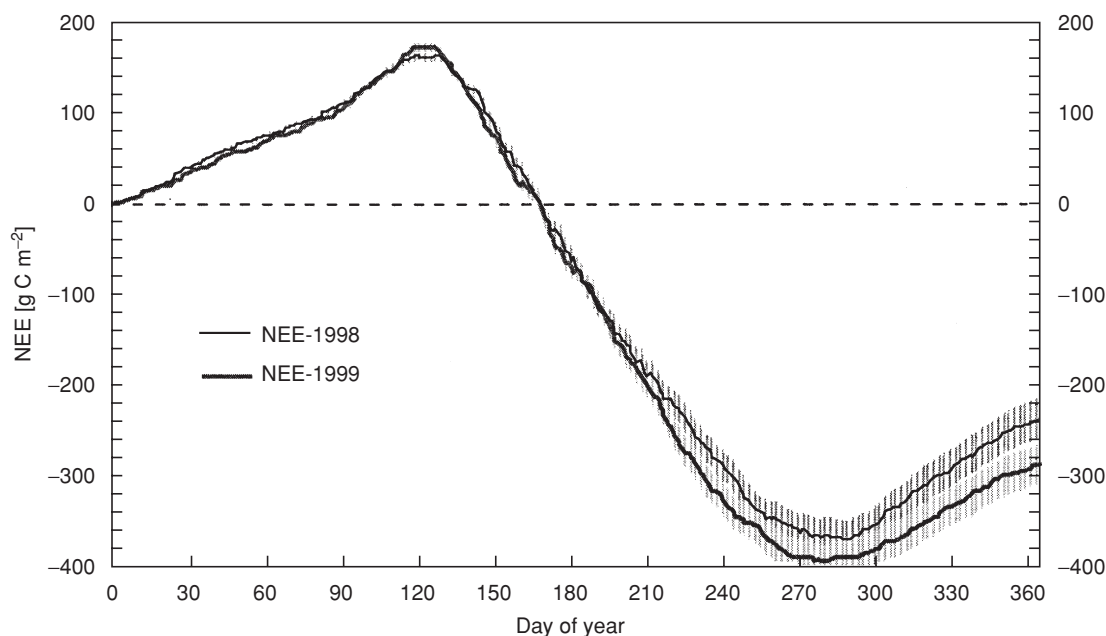
Fig. 4 Seasonal trend of cumulative NEE ($g\,C\,m^{-2}$) for the years 1998 and 1999. The period before day 60/1998 is an estimate based on the respiration model for 1998 and flux data of 1999. The hatched strips around the two curves indicate an estimate of the cumulative measurement uncertainty. The difference between the two annual NEP values lies just beyond the uncertainty estimates.

maximum daytime net F_{CO2} into the forest ranged up to $30\,\mu mol\,m^{-2}\,s^{-1}$.

To obtain annual totals, hourly eddy-covariance data must be integrated. However, eddy-covariance measurements become unreliable or unavailable in periods of precipitation, icing in winter, or very weak turbulence, in particular at night. To account for these times, Schmid *et al.* (2000a) applied simple parametric models for gross ecosystem photosynthesis (based on measured PAR) and for ecosystem respiration (based on T_s) (see above section). With these corrections applied (29% of total time), Schmid *et al.* (2000a) estimated annual NEP as $237\,g\,C\,m^{-2}$ for 1998. Using a similar methodology, the corresponding NEP estimate for 1999 is $287\,g\,C\,m^{-2}\,y^{-1}$. The 1998 net value is the result of $530\,g$ of atmospheric $C\,m^{-2}$ uptake by the forest between May and October, and total net respiration during the off-leaf period of $290\,g\,C\,m^{-2}$ (Fig. 4). The total annual ecosystem respiration was estimated to be 1110 and $1040\,g\,C\,m^{-2}\,y^{-1}$ for 1998 and 1999, respectively. The higher NEP value in 1999 seems to be mainly accounted for by the decreased soil respiration in 1999.

Estimates of uncertainty in F_{CO2} are problematic, since random instrument errors are likely to combine with systematic errors from a variety of sources. Here we follow Goulden *et al.* (1996), who estimate the measurement uncertainty of hourly eddy-covariance fluxes as 5%. Since annual values of NEE derive from the sum of hourly F_{CO2} measurements, the combined effect of random

errors is expected to decay with the square root of the number of summands, by mutual cancellation. However, systematic errors do not necessarily mutually cancel one another. As both the magnitudes and signs of such systematic errors are unknown (despite considerable research on this topic; e.g. Lee, 1998), we attempt to account for these errors tentatively by the following assumptions. We allow only 50% of the standard random cancellation of hourly errors on daily totals of NEE, and no cancellation in the accumulation of daily totals to the annual value. This results in the cumulative uncertainty estimate shown as the hatched strips surrounding the NEE curves in Fig. 4. For the annual accumulations, this cumulative uncertainty estimate is just below 10% of the annual NEP.

Ecological inventory method

Estimates for each component of the ecological inventory method are presented in Table 1, along with ranges of potential estimates (discussed below).

Twenty-nine tree species were identified at the study site. Nearly 75% of the total basal area is composed of sugar maple (*Acer saccharum*), tulip poplar (*Liriodendron tulipifera*), sassafras (*Sassafras albidum*), white oak (*Quercus alba*), and black oak (*Quercus nigra*). The mean canopy height of the forest is 26 m. Smaller trees ($7\,cm \leq d.b.h. < 10\,cm$) present in the 24 sampled plots comprise $\sim$4% of total plot basal area. The estimated

Table 1 Results from ecological inventory method [$g\,C\,m^{-2}\,y^{-1}$]. Parentheses indicate values estimated using the soil C budget method. Negative budget values indicate carbon released to the atmosphere

Year	1988		1999	
	Estimate	Range	Estimate	Range
Change in biomass	311.3		308.0	
Boles and branches	285.8	203.7–367.9	285.6	222.1–349.1
Central stump and main lateral roots	20.9	13.3–28.4	17.8	14.1–21.5
Secondary lateral roots	4.6	2.9–6.9	4.6	2.9–6.9
Detritus production	642.3		658.3	
Herbaceous plants	16.4	9.7–23.1	19.9	14.8–25.0
Tree leaves	198.4	182.0–214.7	210.6	195.7–225.5
Tree seeds	14.3	5.3–23.3	14.6	6.5–22.7
Fine roots	413.2 (368.6)	347.6–448.7	413.2 (270.7)	347.6–448.7
Consumption (Leaf herbivory)	13.5	12.3–14.5	14.3	13.2–15.2
Heterotrophic respiration	− 696.4		− 604.0	
Forest floor and soil	− 603.8	− 857.4− −277.7	− 520.5	− 739.1–239.4
Coarse woody debris	− 91.5	− 137.3− −45.8	− 82.4	− 123.6–41.2
Aboveground herbivores	− 1.1	− 1.2− −1.0	− 1.1	− 1.2–1.0
Net exchange	270.7 (222.6)		376.6 (228.4)	

The numerical precision with which these values are reported is intentionally kept higher than warranted by their significant figures to avoid accumulation of round-off errors in the summation.

uptake by the bole and branch compartment during the 1998 leaf-out period (1998/86–151), in which growth increment data was unreliable, was $77.1\,g\,C\,m^{-2}$, or 27% of the total.

The site-level estimates of herbivory of total leaf area were 7.0% and 6.7% for 1998 and 1999, respectively. These values are similar to those reported by Shure *et al.* (1998) in oak-dominated forests at Oak Ridge National Laboratory. Each value was multiplied by the leaf litter yield for their respective years, yielding consumption values of 13.5 and $14.3\,g\,C\,m^{-2}\,y^{-1}$ for 1998 and 1999, respectively.

A TR_{rf} value of 1.64 was calculated using the estimated N_{avail} sum. This ratio is higher than that (1.32) calculated by Edwards & Harris (1977) for a tulip poplar and oak-hickory forest in eastern Tennessee which is subject to greater seasonal variability of soil moisture availability. Fine root density was determined to be $213.6\,g\,C\,m^{-2}$ from consumptive sampling. Applying the adjustment (*1.18) to the MMSF fine root ($\leq 2\,mm$) density value, gives $252.1\,C\,m^{-2}$. This stock was then multiplied by the TR_{rf} value of 1.64 to obtain the $D_b = 413.2\,g\,m^{-2}\,y^{-1}$.

The observed rates of soil respiration for 2-min sampling periods at individual soil rings ranged from 1.1 to $14.0\,\mu mol\,CO_2\,m^{-2}\,s^{-1}$. Using Equation (12), the annual soil respiration was estimated to be 1207.2 and $1038.8\,g\,C\,m^{-2}\,y^{-1}$ for 1998 and 1999, respectively. If both independent estimates of annual respiration were correct for 1998, the small difference would imply a smaller than expected bole- and canopy-respiration (estimated at about 15% of the forest floor respiration by Wofsy *et al.*, 1993). However, the estimate based on eddy-covariance is preliminary. The temporal dynamics of model output for this time period in relation to T_s are presented in Fig. 5. Assuming R_h is one half of R_s (Hanson *et al.*, 2000), $R_h \sim 603.8$ and $520.5\,g\,m^{-2}\,y^{-1}$ for 1998 and 1999, respectively.

Mean C content for coarse woody debris was $915\,g\,m^{-2}$ from the inventory. Hence, the 10% decay rate (Todd *et al.*, 1976) yields fluxes to the atmosphere of 91.5 and $82.4\,g\,C\,m^{-2}\,y^{-1}$ for 1998 and 1999, respectively. MacMillan (1988) found a maximum decay rate for CWD in old growth forests in Indiana to be less than 5%. However, the debris items in those forests were larger and had a much lower surface to volume ratio than those present at our study site and hence were more persistent.

Figure 5(a,b) illustrates that while the 1998 and 1999 growing seasons were similar in temperature, the latter part of 1999 was noticeably drier. Figure 5(c) shows the
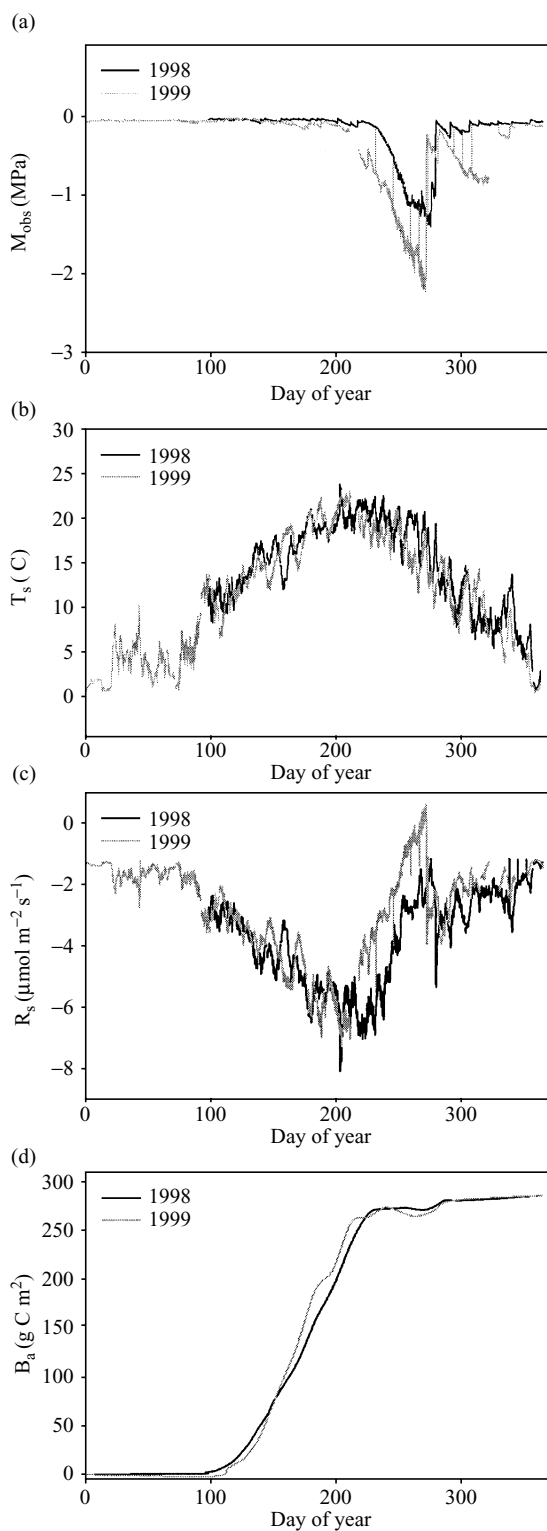
(a)

(b)

(c)

(d)

Fig. 5 Soil water potential (M_{obs}) and soil temperature (T_s) at -10 cm, total soil respiration (R_s), and bole and branch carbon accrual (B_a) are depicted (a, b, c, and d, respectively). These graphs show that moisture conditions inhibited soil respiration in 1999, while only minor interannual variation was evident for carbon storage in the bole and branch compartment.

primary impact of the 1999 late summer drought conditions on C dynamics: a substantial reduction in soil respiration after DOY 200. The combination of these two factors in 1999 led to a 38.8% increase over the 1998 NEP value (Table 1).

Neither early season phenology nor late season differences in bole and branch growth caused the variation in net exchanges between the two years. The variability results from differing edaphic conditions affecting soil respiration during late summer and early fall. The micrometeorological estimate supports this: the cumulative NEE curves do not diverge until around DOY 200 (evident in Fig. 4). However, without examining the functional components of the net exchange, one might assume that the increase in C uptake was due to differences in phenological development or length of growing season.

The soil carbon budget method (Eqn. 8) yields fine root production values (D_b) of 368.6 and 270.7 g C m^{-2} y^{-1} for 1998 and 1999, respectively. Because heterotrophic and root respiration were assumed to contribute equally to total soil respiration (i.e. $R_h = R_r$, and $R_h + R_r = R_s$), and because CWD was not considered a part of the balanced budget, substituting Equation 10 into Equation 4 allows simplification to the following relationship: $NEP = \Delta B_{living} - R_{h(CWD)}$. Thus, the soil carbon budget method yields a net uptake of 222.6 g C m^{-2} y^{-1} for 1998 and 228.4 g C m^{-2} y^{-1} for 1999. The discrepancy between the nearly identical values estimated in this manner, and the interannual variability present in those estimated through the full inventory method and in the eddy-covariance method (Table 1), is due to the soil C budget method of estimating D_b. The fundamental assumption that the annual amount of C entering the soil is equal to the annual soil loss does not account for climatic conditions affecting the decomposition environment that would alter this balance (i.e. the late-summer drought in 1999). Hence, although the soil C budget method may provide reasonable estimates for 'climatically normal' years or longer-term averages, this method is less useful for deriving component exchanges for specific years or interannual comparisons.

Uncertainty and error analysis

We consider the evaluation of error in the results from both methods as the single most important issue deserving of future work. Problems arise due to lack of suitable benchmark values to constrain individual carbon budget values. Our hope is that intercomparisons between independent methodologies, such as ours, will in time enhance estimates of uncertainty. The potential role of systematic errors in the micrometeorological method was discussed briefly above. Here, we address the nature of errors in the inventory method and attempt

to provide quantitative estimates for the individual components.

At least four types of errors potentially exist in our exchange estimates: those associated with sampling strategy, measurement (i.e., instruments), models, and model inputs. While more than one type of error could have contributed to the overall error for a given exchange, here we used the one thought to be the largest source of error to quantify a range for Table 1. For the majority of the components, the largest source of error was likely attributable to sampling (i.e., inter-plot variability). For these components, the "range of potential estimates" presented in Table 1 were simply the 95% confidence intervals for the sampled data. There were four components for which the ranges were developed differently: change in biomass of secondary lateral roots (B_{rcf}), production of fine roots (D_b), and heterotrophic respiration of the forest floor and soil ($R_{h(Soil)}$), and $R_{h(CWD)}$. The estimate range for B_{rcf} increment was a 95% CI for the slope of the linear model respecting stand age (eqn 6). The $R_{h(CWD)}$ estimate range was developed by varying the 10% decomposition rate applied to the CWD standing crop by $+/-$ 5%. Note that the consumption and above-ground heterotroph estimate ranges were set proportionately to the tree leaves range estimate from which they were derived.

For $R_{h(Soil)}$, the estimate range was developed by applying a range of root:heterotroph partition coefficients, for ecologically similar sites, to the output from the (total) soil respiration model (eqn. 12). These values, expressed in terms of heterotrophic component of total soil efflux, ranged from 23–71% (Hanson *et al.*, 2000). Although the sample size in generating the soil respiration model was relatively large and the model output agreed well with that of the micro-meteorological method, increased confidence in this exchange component is desirable; our measurements of soil respiration incorporated the spatial variability at the study site, but were temporally limited. Accordingly, an automated, continuous sampling system using eight chambers and a Li-Cor LI-6262 analyzer has been installed near the tower.

Estimating an annual fine root turnover ratio solely on the basis of nitrogen availability was more tenuous. The D_b estimate, and thus the overall net exchange estimate, was sensitive to small changes in the independent variable of eqn. 7, (i.e., N_{avail}). Although the soils and species composition of the MMSF site were typical of those found on a fertile site, published ranges of N_{min} (80–120 kg N ha y^{-1}, Vitousek *et al.*, 1982, Vitousek pers comm.) and N_{avail} (Fan *et al.*, 1998b) rates for the study region indicated that our estimates may have been high, thus overestimating fine root production. In comparison to our estimate of -413.2 g C m^{-2} y^{-1}, Vogt (1991), in a review that included nine broadleaf sites, found annual fine root NPP to range from 135 to 335 g C m^{-2}. Thus, for the D_b

estimate range, a downward-skewed range of N_{avail} inputs was used: 110–125 kg ha^{-1} y^{-1}.

The two exchange components with the largest contributions to the C budget derived from the ecological inventory method (Table 1) were of opposite sign: D_b was negative, and $R_{h(Soil)}$ was positive. Both were derived from statistical models relating flux estimates to proxy data, and thus they had relatively large uncertainties. Because of their magnitude, even small changes in these two variables would have dramatically changed the net result. More generally, it is must be noted that no less than four individual components exceeded or were nearly as large as the net exchange value. Hence, errors in measuring or estimating any one of these terms could have led to relatively large errors in the net exchange.

These potential errors would have included a combination of systematic and random components. In time integration of the modeled values, some of the random errors would be expected to cancel, but systematic bias could have accumulated. However, because we lacked reliable reference values, the systematic errors were not easily separated from the random components. The determination of systematic bias in the measurements leading to annual budgets of carbon is an ongoing research question.

Monte Carlo simulation was used to investigate the aggregation of error from the components to the net exchange estimates. A large number of trials (3000) generated very tight 95% CIs (270.8–287.7 and 361.6–375.1 g C m^{-2}y^{-1} for 1998 and 1999, respectively). However, we believe that the standard deviations of the sample populations of net exchange estimates (234.9 and 187.4 g C m^{-2}y^{-1} for 1998 and 1999, respectively) are more useful metrics for this analysis.

Comparison of annual total carbon sequestration estimates

All natural ecosystems are heterogeneous at some scale, and so the question arises whether measurements of F_{CO2} on a single tower or inventory estimates based on a limited number of plots represent the same average composition of ecosystem components. The spatial representativeness of F_{CO2} measurements is estimated by the sensor location bias, following Schmid (1997), whereas the degree of representativeness of the inventory plots is dependent on the plot distribution strategy.

Using measured hourly values of stability and wind direction, a footprint climatology was established for 1999 with the scalar flux footprint model of Schmid (1994, 1997). Individual footprints were overlain with a high-resolution distribution of normalized difference vegetation index (NDVI, pixels 4×4 m) generated from an IKONOS satellite scene centred on the tower (6×6 km). The use of NDVI here assumes that this index is a suitable surrogate for both the assimilative

and the respiratory distribution within this ecosystem. The average NDVI contained in the footprints were then compared with the average NDVI of the entire scene, and quantified as the sensor location bias, following Schmid (1997). The hourly location bias values were multiplied with the associated measurements of F_{CO2}, and summed over the year. The result was scaled by the total measured NEE and is termed the annual weighted flux bias. It is interpreted as an estimate of the relative error of the eddy-covariance derived NEE value that is attributable to location bias of the flux sensor. For the year 1999, the annual weighted flux bias for NEE amounted to only 1.8%. Despite the crudeness of the footprint model used, this result is an encouraging confirmation that the power of turbulent mixing up to our measurement height of 46 m is sufficient to blend the natural inhomogeneities surrounding the MMSF tower. Details of this work will be described elsewhere. Upon completion of a multihectare tree survey around the tower, evaluation of the spatial representativeness of the ecological estimates and their spatial consistency with the footprint of the NEE measurements will be accessible.

The estimated uptake rates of 271 and 377 g C m^{-2} y^{-1} are 14.3% and 31.4% larger than those estimated using the micrometeorological approach (237 and 287 g C m^{-2} y^{-1}) for 1998 and 1999, respectively. This general consistency suggests that some confidence be placed in both approaches, despite inherent, but not easily quantifiable uncertainties. Some eddy-covariance data had to be simulated for periods of missing data and conditions of poorly developed turbulence at night. Also, possible complications due to drainage flow and mesoscale circulations may affect these estimates.

One possible explanation for the difference between NEE and NEP estimates is an overestimation of fine root production. If the MMSF forest behaves like some other Central Region sites (Edwards & Harris, 1977), then a second peak in fine root production may have been reduced by late season drought, particularly in 1999. This reduced fine root production would not have been accounted for in the N_{avail}-based model.

Conclusions

This research compares an ecological inventory approach for quantifying carbon exchanges in a deciduous forest with independent micrometeorological estimates based on eddy-covariance measurements from a tall flux tower. In addition to the methodological differences between the two approaches, they also refer to different spatial (forest plot scale vs. flux footprint scale) and temporal scales (seasonal to annual for the ecological approach vs. hourly to annual for the micrometeorological approach). Both methodologies face significant difficulties, resulting in potential systematic biases of unknown magnitude or sign that currently are the subject of significant research efforts in the ecological and the micrometeorological communities. The present comparison is not an absolute validation of one methodology against the other, but may begin to serve as a cross-validation that gives insight into the strengths and uncertainties of both approaches. We conclude:

Based on the results of the ecological inventory method, the interannual difference in the net CO_2 exchange for 1998 and 1999 is driven primarily by differences in soil respiration. The independent evaluation of ecosystem respiration by the micrometeorological method confirms this finding.

Several exchange components exceed or are nearly as large in magnitude as the net exchange value. Errors in measuring or estimating any one of these terms can lead to relatively large errors in the net exchange.

Because belowground processes appear to account for a significant part of the interannual variability and are the least well-known, efforts to develop better (more direct and continuous) measurements are essential.

We consider the lack of validation standards, constraints, and benchmarks for the individual components of the carbon balance to be issues requiring considerable attention before more conclusive estimates of annual carbon sequestration can be established by either of the methodologies compared here.

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