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Comparing nocturnal eddy covariance measurements to estimates of ecosystem respiration made by scaling chamber measurements at six coniferous boreal sites

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Abstract. During the growing season, nighttime ecosystem respiration emits 30–100% of the daytime net photosynthetic uptake of carbon, and therefore measurements of rates and understanding of its control by the environment are important for understanding net ecosystem exchange. Ecosystem respiration can be measured at night by eddy covariance methods, but the data may not be reliable because of low turbulence or other methodological problems. We used relationships between woody tissue, foliage, and soil respiration rates and temperature, with temperature records collected on site to estimate ecosystem respiration rates at six coniferous BOREAS sites at half-hour or 1-hour intervals, and then compared these estimates to nocturnal measurements of CO_2 exchange by eddy covariance. Soil surface respiration was the largest source of CO_2 at all sites (48–71%), and foliar respiration made a large contribution to ecosystem respiration at all sites (25–43%). Woody tissue respiration contributed only 5–15% to ecosystem respiration. We estimated error for the scaled chamber predictions of ecosystem respiration by using the uncertainty associated with each respiration parameter and respiring biomass value. There was substantial uncertainty in estimates of foliar and soil respiration because of the spatial variability of specific respiration rates. In addition, more attention needs to be paid to estimating foliar respiration during the early part of the growing season, when new foliage is growing, and to determining seasonal trends of soil surface respiration. Nocturnal eddy covariance measurements were poorly correlated to scaled chamber estimates of ecosystem respiration ($r^2 = 0.06–0.27$) and were consistently lower than scaled chamber predictions (by 27% on average for the six sites). The bias in eddy covariance estimates of ecosystem respiration will alter estimates of gross assimilation in the light and of net ecosystem exchange rates over extended periods.

Introduction

Knowledge of respiration is essential for understanding and predicting forest ecosystem carbon dynamics because (1) respiration returns a large fraction of gross assimilation to the atmosphere [*Wofsy et al.*, 1993; *Ryan et al.*, 1994; *Sprugel et al.*, 1995; *Jarvis*, 1994; *Goulden et al.*, 1996a; *Baldocchi and Vogel*, 1996; *Baldocchi et al.*, 1997; *Black et al.*, 1996], and (2) respiratory fluxes are sensitive to climatic variability [*Ryan*, 1991; *Goulden et al.*, 1996a]. Ecosystem respiration is the sum of autotrophic respiration (roots, foliage, and woody tissues) and the respiration of soil heterotrophs. Eddy covariance can measure ecosystem respiration directly, by collecting measurements at night (F_n using the notation of *Jarvis* [1994] and *Ruimy et al.* [1995]). *Wofsy et al.* [1993], *Goulden et al.* [1996a], *Baldocchi et al.* [1997], and *Black et al.* [1996] used F_n to study ecosystem respiration and estimate net ecosystem exchange. *Hollinger et al.* [1994], *Amthor et al.* [1994], *Jarvis* [1994], *Ruimy et al.* [1995], *Grace et al.* [1995], and *Fan et al.* [1995] used functions derived from F_n with daytime measurements of net ecosystem flux (F_d) to calculate canopy gross assimilation rates and assess ecosystem-level photosynthetic responses to the environment.

While eddy covariance is a promising method, it is not certain that measurements made at night are reliable [*Goulden et al.*, 1996b]. Reliable measurement of flux between ecosystem and atmosphere requires adequate mixing of air in the ecosystem with air above the ecosystem, but low wind speed and deep boundary layer are common at night and inhibit the necessary mixing [*Wofsy et al.*, 1993; *Hollinger et al.*, 1994; *Grace et al.*, 1995; *Baldocchi et al.*, 1997; *Black et al.*, 1996]. Under such

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conditions, the CO_2 concentration of air within the ecosystem increases; measuring this change in storage and adding storage to the eddy flux improves estimation of ecosystem respiration [*Wofsy et al.*, 1993; *Jarvis*, 1994; *Ruimy et al.*, 1995; *Baldocchi et al.*, 1997; *Goulden et al.*, 1996a; *Black et al.*, 1996]. Even when storage and air turbulence are taken into account, however, uncertainty persists about the accuracy of measured ecosystem respiration. *Goulden et al.* [1996b] found that measurements of F_n that included storage and were made only while there was substantial turbulent air movement were still consistently lower than the scaled chamber measurements of component respiration rates and were variable. *Black et al.* [1996] found that observed F_n were approximately equal to observed soil respiration rates. However, respiration of foliage and wood were roughly equal to that of soil at this site [*Ryan and Lavigne*, this issue]. Therefore the eddy covariance values underestimated ecosystem respiration to the extent that foliage and woody tissues contributed to the nocturnal flux. More comparisons with scaled chamber measurements are needed to further assess the accuracy of eddy covariance measurements made at night.

Eddy covariance can distinguish soil plus understory derived respiratory fluxes of CO_2 from overstory derived fluxes when measurements are made above and below the canopy with paired instruments [*Baldocchi and Meyers*, 1991; *Baldocchi and Vogel*, 1996; *Baldocchi et al.*, 1997; *Black et al.*, 1996], but chamber measurements are still needed to provide finer resolution (e.g., microbial, root, foliage, and woody-tissue respiration). However, chamber measurements are only made on a small portion of the surface or biomass, and a large effort is required to collect sufficient data to scale to the ecosystem. It is important that adequately sized, representative samples of components are measured in chambers to obtain accurate estimates of average respiration rates in the portion of the ecosystem measured by eddy covariance. It is also important to gather accurate estimates of the amount of respiring biomass. Finally, measurements should be repeated frequently during the year to capture the seasonal variability of respiration.

The Boreal Ecosystem-Atmosphere Study (BOREAS) was an interdisciplinary project that put large efforts into making eddy covariance measurements and chamber measurements on selected sites near the northern and southern boundaries of the boreal forest [*Sellers et al.*, 1995]. This provided an opportunity to use several sites when comparing scaled chamber estimates to F_n. Such a comparison has been made at only one other site [*Goulden et al.*, 1996a, b], even though there is considerable uncertainty over the utility of F_n. We compared estimates of respiration obtained by the two methods for six coniferous stands to address the following questions. (1) Is there close agreement between estimates of ecosystem respiration made by the two methods, and can disagreements be explained? (2) How is ecosystem respiration partitioned between the ecosystem components? (3) What are the magnitudes and sources of uncertainty associated with scaling chamber measurements? (4) Do the difficulties in estimating respiration vary among sites? Attention to these issues will lead to better methods for estimating ecosystem respiration and interpreting net ecosystem flux data, and to increased understanding of the role of respiration in determining net ecosystem exchange.

Table 1. Respiring Autotrophic Biomass (Leaf Area Index and Sapwood Volume) in Coniferous BOREAS Sites at the Southern and Northern Study Areas Where Eddy Covariance Measurements Were Taken

	Leaf Area, m^2 m^{-2}		Sapwood Volume, m^3 m^{-2}
Site	Old	Current	
SOBS	5.67	0.55	0.0068
SOJP	1.80	0.70	0.0066
SYJP	2.26	0.68	0.0025
NOBS	4.54	0.63	0.0088
NOJP	2.02	0.32	0.0056
NYJP	1.39	0.38	0.0013

Site abbreviations are defined in the text.

Methods

Study Areas

Eddy covariance measurements were made at three sites near the northern boundary of the boreal forest (approximately 55°50′N latitude, 98°20′W longitude) and three sites near the southern boundary of the boreal forest (approximately 53°45′N latitude, 105°15′W longitude) in central Canada. There were mature black spruce stands in the north (northern old black spruce, NOBS) and south (southern old black spruce, SOBS), mature jack pine stands in the north (NOJP) and south (SOJP), and sapling-stage jack pine stands in the north (northern young jack pine, NYJP) and south (southern young jack pine, SYJP). The overstory was dominated by the species for which the stand was named. The SOBS was a forested peatland with thick organic soil, water table near the surface, and thick moss layer. Approximately half of the area of NOBS was forested peatland, and the remainder was an upland black spruce site. All jack pine sites were on deep, coarse-textured soils, with moderate amounts of shrubs and herbs in the understory. Additional stand information, provided by *Gower et al.* [this issue], is given in Table 1. BOREAS provided towers for eddy covariance measurements, other infrastructure, and logistical support.

All measurements were made during the 1994 field season. There were three intensive field campaigns (IFC) when an effort was made to have all respiratory fluxes measured. The first intensive field campaign, between May 23 and June 16, was timed to capture the start of the growing season, the second, between July 19 and August 8, was at the middle of the growing season, and the third campaign, from August 29 to September 20, included the end of the growing season. Many additional chamber and eddy covariance measurements were made between intensive campaigns and after the third campaign. *Sellers et al.* [1995] provide more complete information about the organization and accomplishments of BOREAS during the 1994 field season.

Chamber Respiration Measurements

The ecosystem respiration estimated from chambers (R_t) is the sum of predicted respiration by woody tissue (R_w), foliage (R_f), and soil (R_s; includes roots, soil heterotrophs, and lesser vegetation on the soil surface):

$$R_t = R_w + R_f + R_s \qquad (1)$$

where all terms are in units of μmoles of CO_2 per m^2 of land area per second. We denote CO_2 flux from the ecosystem to the atmosphere with positive numbers. We viewed the respiration rate of each ecosystem component as the product of the respiration per unit of respiring biomass and the amount of respiring biomass per unit of land area. Sapwood volume (V_s) was used to scale chamber measurements of woody tissue respiration [*Ryan*, 1990; *Sprugel*, 1990]:

$$R_w = \bar{r}_w V_s \tag{2}$$

where $\bar{r}_w$ is mean respiration rate per unit of sapwood volume (μmol m^{-3} s^{-1}), which is dependent on temperature and time of year. We scaled chamber measurements of foliar respiration rate with the following equation:

$$R_f = \sum_i \bar{r}_{f,i} L_i \tag{3}$$

where $\bar{r}_{f,i}$ is mean foliar respiration rate per unit of leaf area of the ith foliage age class (μmol m^{-2} s^{-1}), which is dependent on temperature and time of year, and L_i is leaf area index (m^2 m^{-2}) of the ith foliage age class. We estimated soil respiration directly from the time of year and temperature-dependent mean of sampled soil respiration rates ($\bar{r}_s$).

Respiration rates per unit of respiring biomass vary with temperature of the component. Moreover, temperature-specific respiration rates change during the year as growth rate changes [*Amthor*, 1989]. Methods used to measure tissue-specific respiration rates, establish relationships with tissue temperature, and incorporate seasonal changes in respiration are briefly described below.

Woody tissue respiration. Woody tissue respiration per unit of sapwood volume (r_w) was measured with automated manifold systems during IFCs and also during October [*Ryan et al.*, this issue; *Lavigne and Ryan*, 1997]. Additional measurements were made at the northern sites during and between IFCs with a portable system. An equation of the following form was used to model the temperature dependence of woody tissue respiration:

$$r_w = r_{w,15} Q_{10}^{(T-15)/10} \tag{4}$$

where $r_{w,15}$ is respiration rate at 15°C (μmol m^{-3} s^{-1}), Q_{10} is a parameter describing the rate of change of respiration for a 10°C change in temperature, and T is sapwood temperature (°C). There was substantial seasonal variation in $r_{w,15}$ due to stem growth that had to be accounted for when scaling woody tissue respiration. We used linear interpolation between means of measured $r_{w,15}$ to model this seasonal variation (Figure 1). Values of Q_{10} ranged from 1.7 to 2.2 between stands and remained constant during the entire study period.

Sapwood temperatures were measured each half hour at SOBS, SOJP, SYJP, and NYJP. These temperature records were used in (4) to estimate woody tissue respiration rates. Sapwood temperatures were not routinely measured at NOJP and NOBS. We established relationships between air temperature and sapwood temperature using data collected while woody tissue respiration was sampled, and used these relationships to estimate sapwood temperatures for the entire period.

Foliar respiration. Foliar respiration rates were measured on one night per stand during each IFC, using methods described in detail by *Ryan et al.* [this issue]; here they are briefly summarized. Current-year and older foliage were measured separately. Measurements were made on attached samples using portable photosynthesis systems (LI-6200, LI-COR, Inc., Lincoln, Nebraska, in the south; LCA-3, ADC, Hoddeston, England, in the north). Samples were equally distributed between base and top of the canopy, and they were accessed from scaffold towers provided by BOREAS. A temperature-controlled cuvette [*Hubbard et al.*, 1995] was used with two or three samples per stand to measure foliar respiration responses to temperature. Rates measured in the old jack pine stands were used to estimate foliar respiration in the young jack pine stands. For older foliage we did not observe a significant seasonal trend at three of four sites where measurements were made, and so we used single response curves throughout the study period for those stands (Table 2). We observed substantial seasonal variation at NOJP, which we incorporated into estimation procedures for old foliage respiration.

New foliage began growing during the first IFC and continued growing into the second IFC, but data on foliar development were not collected, and current-year foliar respiration rates were not measured until the second IFC. Therefore we made the following assumptions to account for current-year foliar respiration during the early growing season: current-year foliage did not respire before beginning growth, total respiration rates of growing foliage increased to the rates observed during the second IFC shortly after beginning growth, and the leaf area of fully grown new foliage was used to scale spatially for the entire period of foliage growth. Equations used to

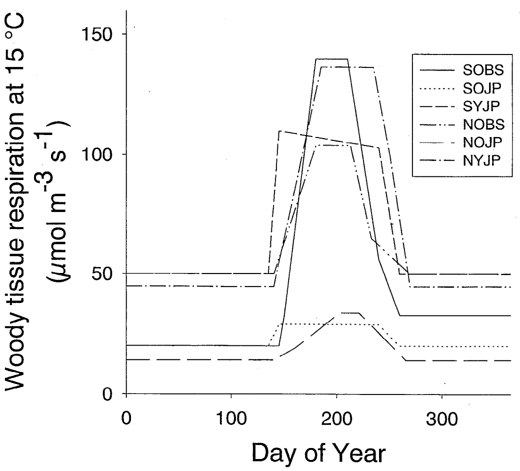

Figure 1. Seasonal course of mean woody tissue respiration rates per unit of sapwood volume at 15°C ($\bar{r}_{w,15}$) at six coniferous BOREAS eddy covariance sites.

Table 2. Equations Used to Estimate Foliar Respiration Rates of Older Foliage at Six Coniferous BOREAS Eddy Covariance Sites

Stand	R_{of}, μmol m^{-2} s^{-1}	DOY
SOBS	$0.37\ (2^{(T-15)/10})$	
SOJP	$0.60\ (2^{(T-15)/10})$	
SYJP		
NOBS	$0.26 \exp[0.07(T - 10)]$	
NOJP	$[0.53 + 0.000875(\text{DOY} - 160)]$	≤160
	$\cdot [\exp(0.07(T - 10))]$	
NYJP	$[0.37 - 0.002667(\text{DOY} - 220)]$	161–220
	$\cdot [\exp(0.07(T - 10))]$	
	$0.39 [\exp(0.07(T - 10))]$	>220

DOY, day of year; T, air temperature within the canopy or immediately above, depending on the stand. Stand abbreviations are defined in the text.

Table 3. Equations Used to Estimate Current-Year Foliage Respiration Rates at Six Coniferous BOREAS Eddy Covariance Sites

Stand	R_{cf}, μmol m^{-2} s^{-1}	DOY
SOBS	$[0 + 0.125(\mathrm{DOY} - 160)](2^{(T-15)/10})$	160–170
	$1.25(2^{(T-15)/10})$	171–210
	$[1.25 - 0.044(\mathrm{DOY} - 210)](2^{(T-15)/10})$	211–230
	$0.37(2^{(T-15)/10)})$	>230
SOJP	$[0 + 0.125(\mathrm{DOY} - 160)](2^{(T-15)/10})$	160–170
	$1.25(2^{(T-15)/10})$	171–210
	$[1.25 - 0.0325(\mathrm{DOY} - 210)](2^{(T-15)/10})$	211–230
	$0.60(2^{(T-15)/10})$	>230
SYJP	$[0 + 0.125(\mathrm{DOY} - 160)](2^{(T-15)/10})$	160–170
	$1.25(2^{(T-15)/10})$	171–210
	$[1.25 - 0.0325(\mathrm{DOY} - 210)](2^{(T-15)/10})$	211–230
	$0.60(2^{(T-15)/10})$	>230
NOBS	$0.26 \exp[0.07(T - 10)]$	
NOJP	$0.53 \exp[0.07(T - 10)]$	≤160
	$[0.53 + 0.005(\mathrm{DOY} - 220)] \cdot \exp[0.07(T - 10)]$	161–220
	$[0.59 - 0.008(\mathrm{DOY} - 220)] \cdot \exp[0.07(T - 10)]$	221–250
	$0.39 \exp[0.07(T - 10)]$	>250
NYJP	0	140–185
	$0.83 \exp[0.07(T - 10)]$	186–210
	$0.59 \exp[0.07(T - 10)]$	211–270

DOY, day of year; T, air temperature within the canopy or immediately above, depending on the stand. Stand abbreviations are defined in the text.

Table 4. Equations Used to Estimate Soil Respiration Rates at Six Coniferous BOREAS Eddy Covariance Sites

Stand	R_s, μmol m^{-2} s^{-1}	DOY
SOBS	$[0.8 + 0.0218(\mathrm{DOY} - 140)]\,(2.35^{(T-15)/10})$	140–195
	$[2.0 - 0.0143(\mathrm{DOY} - 195)]\,(2.35^{(T-15)/10})$	196–230
	$[1.5 - 0.0175(\mathrm{DOY} - 230)]\,(2.35^{(T-15)/10})$	231–270
	$0.8(2.35^{(T-15)/10})$	>270
SOJP	$0.776\,[\exp(0.0666T)]$	143–175
SYJP	$[0.776 + 0.0095(\mathrm{DOY} - 175)] \cdot \exp\{[0.0666 + 0.00155(\mathrm{DOY} - 175)]\,T\}$	176–187
	$0.8807[\exp(0.0867T)]$	188–203
	$[0.8807 - 0.0095(\mathrm{DOY} - 203)] \cdot \exp\{[0.0867 - 0.00183(\mathrm{DOY} - 203)]T\}$	204–213
	$0.776\,[\exp(0.0666T)]$	214–257
NOBS	$0.6\,[\exp(0.119T)]$	
NOJP	$1.158\,[\exp(0.0585T)]$	
NYJP	$0.644\,[\exp(0.0888T)]$	

DOY, day of year; T, soil temperature measured at 5 cm for southern sites and at 10 cm for northern sites. Stand abbreviations are defined in the text.

estimate current-year foliar respiration rates per unit of leaf area are given in Table 3. The respiration rates we used probably underestimated the actual respiration rate of current-year foliage during the early part of its growth, when relative growth rates are greatest, but this was offset by an overestimation of current-year leaf area respiring at that time. The respiration rates observed for current-year foliage during the second IFC were representative of the rates for late in the period of foliar growth. The foliage was nearly fully expanded when these measurements were made, and therefore our estimates for this period do not depend on assumptions. Air temperatures within, or immediately above, the canopy were recorded at flux towers and used with predictive equations to estimate foliar respiration rates.

Soil respiration. Soil respiration was measured at SOJP using a closed, dynamic system with chambers similar to that described by *Striegl et al.* [1992], at SOBS using an open system [*Rayment and Jarvis*, this issue], and at NOBS, NOJP, and NYJP using a closed, static chamber [*Crill*, 1991]. Methods used to measure soil respiration are briefly described by *Norman et al.* [this issue]. Frequency of measurements and sample size varied between sites. Predictive equations using soil temperature as the driving variable were produced from these data (Table 4). Soil temperature data were collected at all towers and used to drive predictive equations. Significant seasonal variation in the respiration-temperature relationship was found at SOBS and SOJP. We used equations derived from measurements made at SOJP to estimate respiration rates at SYJP. The Q_{10} of these soil-surface respiration-soil temperature relationships were between 2 and 3 for all sites except NOBS, for which the Q_{10} was 3.3. The Q_{10} at NOBS was similar to the value reported for temperate forest soils by *Kicklighter et al.* [1994]. Estimates of Q_{10} were lower at sites that divided the study period (May–September) into intervals to produce a series of predictive equations than at sites that combined data collected throughout the study period to produce a single predictive equation. We suspect that the growth of roots and the physiological state of soil microbes varied during the study period, influencing the estimation of Q_{10} at sites using a single equation for the entire study period. Changes in the physiological state of roots and soil microbes would cause the estimates of respiration rate at a reference temperature (15°C at SOBS, and 0°C at the other sites) to vary during the study period rather than influencing the estimate of Q_{10} when the study period was divided into shorter intervals to estimate a series of soil respiration prediction equations.

Nocturnal Ecosystem Flux Measurements

The net ecosystem flux of CO$_2$ at night (F_n) was measured by S. C. Wofsy and colleagues at NOBS (see *Goulden et al.* [this issue] for a description of methods). D. R. Fitzjarrald was responsible for measuring F_n at NOJP, and J. H. McCaughey made measurements at NYJP [*McCaughey et al.*, this issue]. P. G. Jarvis and colleagues [*Jarvis et al.*, this issue, *Moncrieff et al.*, 1997] measured F_n at SOBS, *Baldocchi et al.* [1997] made measurements at SOJP, and D. E. Anderson measured F_n at SYJP. Eddy covariance methods were used to measure CO$_2$ exchange rate between the ecosystem and the atmosphere at all sites. Instruments were affixed to towers for making eddy covariance measurements. Eddy fluxes (F_{eddy}) were calculated from the covariance of vertical wind velocity and CO$_2$ concentration measured above the ecosystem. Vertical wind velocities were measured with sonic anemometers, and CO$_2$ concentrations were measured with fast response infrared gas analyzers at all sites. Changes in the amount of CO$_2$ in the air space between the ground and the height of the eddy flux measurement (F_{stor}) were measured at SOBS, SOJP, SYJP, and NOBS for at least part of the 1994 measurement period. CO$_2$ concentrations were measured at several heights at regular intervals, and changes over time were calculated. Tower flux estimates of net ecosystem exchange of CO$_2$ (F_n) were the sum of eddy flux and changes in storage [*Wofsy et al.*, 1993]:

$$F_n = F_{\mathrm{eddy}} + F_{\mathrm{stor}} \tag{5}$$

These estimates were obtained over 1-hour periods at NOBS, and over half-hour periods at all other sites. At the NYJP and

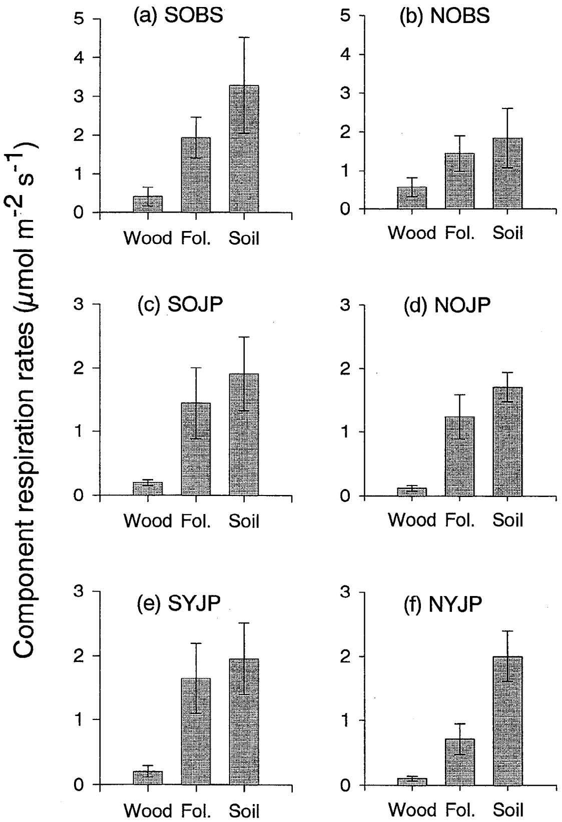

Figure 2. Component respiration rates calculated by scaling chamber estimates of respiration for every half-hour interval of the 1994 study period at six coniferous BOREAS eddy covariance sites. Error bars denote +1 standard deviation.

NOJP sites, we assumed that F_{stor} was negligible when there was substantial turbulent air movement, and hence that F_n was equivalent to F_{eddy}.

The F_n was expected to be dominated by F_{eddy} when wind speed was high, and by F_{stor} when winds were low. However, when wind speed was low, such as when horizontal wind speed was less than 2 m s^{-1} or friction velocity (u^*) was less than 0.25 m s^{-1}, the observed F_n might not represent the concurrent physiological activity of plants and soil heterotrophs within the ecosystem, particularly if the degree of turbulence was variable [*Goulden et al.*, 1996b]. It has been common practice to exclude these observations from further analysis and to substitute simulated F_n for observed F_n [*Black et al.*, 1996; *Goulden et al.*, 1996b] when estimating net ecosystem exchange at night. Therefore we excluded these observations from comparisons with scaled chamber estimates of ecosystem respiration.

Results and Discussion

Scaled Chamber Estimates of Ecosystem Respiration

Using the estimates of respiration rates (Tables 2–4) and of leaf areas and sapwood volumes (Table 1), we estimated the average nighttime respiration rates by each component for the entire study period (Figure 2). Soil surface respiration contributed 48–71%, R_f contributed 25–43%, and R_w contributed 4–15% to R_t. These partitions of total respiration among components were similar to that measured by *Goulden et al.* [1996b] in an aggrading, temperate deciduous forest. *Ryan et al.* [1994] found that autotrophic respiration was similarly partitioned among components for diverse pine stands.

Table 5. Error Estimates for Scaled Chamber Predictions of Mean Nocturnal Ecosystem Respiration for 1994 at Six Coniferous BOREAS Eddy Covariance Sites When Specific Respiration Rate at 15°C Parameters for Woody Tissues (r_w), Foliage (r_f), and Soil (r_s) and Respiring Biomass Values are Each Set at Their 95% Confidence Interval Values and When All Parameters Are Simultaneously Set at Their 95% Confidence Interval Values

		Change in R_t When Parameter Set at 95% Confidence Interval, μmol m^{-2} s^{-1}					
Stand	Mean R_t, μmol m^{-2} s^{-1}	r_w	r_f	r_s	V_s	L	Combined Error
SOBS	5.64	0.08	0.49	1.09	0.07	0.68	2.41
SOJP	3.52	0.04	0.49	0.63	0.07	0.37	1.60
SYJP	3.79	0.03	0.49	0.64	0.10	0.77	2.03
NOBS	3.87	0.14	0.55	0.61	0.12	0.19	1.61
NOJP	3.07	0.01	0.25	0.58	0.03	0.31	1.18
NYJP	2.82	0.03	0.14	0.73	0.08	0.36	1.34

Stand abbreviations are defined in the text.

Black spruce stands had higher R_t than jack pine stands at both northern and southern study areas (Figure 2). Lower $\bar{r}_{f.15}$ at the black spruce stands (Table 2), in comparison to the jack pine stands, did not completely offset their higher L (Table 1), and as a result, the black spruce stands had greater R_f. Because the R_s of black spruce stands were also higher than those of jack pine stands (Figure 2), there was a similar partitioning of respiration among components in all stands.

We did not make separate estimates of growth respiration and maintenance respiration [*Amthor*, 1989; *Sprugel et al.*, 1995] for this analysis because requisite data on growth of foliage, roots, and woody tissues for each half hour were not collected. Estimates of annual growth and maintenance respiration of stems are reported in a companion paper [*Lavigne and Ryan*, 1997].

Scaled chamber estimates of respiration could be in error if parameters in Figure 1 and Tables 2–4 did not accurately estimate the true $\bar{r}_{15}$ for vegetation and soils in the portion (footprint) of the ecosystem measured by eddy covariance, or the actual L or V_s in the footprint of flux towers differed from those used for scaling (Table 1). We calculated error estimates by recalculating R_t with all values for the $\bar{r}_{15}$, L, and V_s set at their 95% confidence interval values (Table 5). These error estimates were based on the spatial variability of process rates and respiring tissues; the calculations did not include errors that might be related to phenological changes (for example, if some of our predictive equations were more accurate at certain times during the growing season than at other times) or with errors in estimates of tissue temperatures. These bounds gave only a general indication of the variability inherent to scaling chamber estimates. R_t would change little if there were relatively large errors in R_w caused by both errors in $\bar{r}_w$ and V_s. Setting $\bar{r}_s$ at its 95% confidence value caused a large change in the estimate of R_t because the spatial variability of soil respiration was great and R_s was a large proportion of the total respiratory flux. These error calculations did not explicitly account for the possible differences between methods for measuring R_s found by *Norman et al.* [this issue]. Ramifications of the *Norman et al.* [this issue] study are discussed in more detail

Table 6. Comparisons of the Contributions of Eddy Covariance Flux (F_{eddy}) and storage (F_{stor}) to Estimates of Net Ecosystem Exchange of Carbon Dioxide (F_n) When the Air was Poorly Mixed ($u^* < 0.25$) and the Air Was Well Mixed ($u^* \geq 0.25$) for Observations Made During the Entire Study Period (May–September)

	$u^* < 0.25$ m s^{-1}				$u^* \geq 0.25$ m s^{-1}			
Stand	F_{eddy}, μmol m^{-2} s^{-1}	F_{stor}, μmol m^{-2} s^{-1}	F_n, μmol m^{-2} s^{-1}	T_{soil}	F_{eddy}, μmol m^{-2} s^{-1}	F_{stor}, μmol m^{-2} s^{-1}	F_n, μmol m^{-2} s^{-1}	T_{soil}
SOBS								
Mean	1.53 (0.05)	2.27 (0.15)	3.80 (0.15)	8.16 (0.08)	5.09 (0.18)	−0.06 (0.20)	5.03 (0.25)	9.33 (0.27)
Range	−1.5 to 13.48	−17.25 to 22.8	−9.75 to 24.29	1.58 to 15.94	2.01 to 15.69	−8.89 to 7.55	−2.42 to 23.24	3.31 to 14.42
SOJP								
Mean	1.34 (0.06)	1.29 (0.06)	2.65 (0.09)	11.44 (0.09)	2.22 (0.13)	0.44 (0.05)	2.66 (0.13)	11.96 (0.12)
Range	−11.5 to 12.14	−7.9 to 11.05	−10.82 to 17.16	4.1 to 19.04	−12.57 to 13.57	−6.77 to 4.59	−12.5 to 13.57	5.6 to 19.38
NOBS								
Mean	1.44 (0.12)	1.33 (0.13)	2.77 (0.13)	6.95 (0.17)	3.21 (0.20)	0.09 (0.13)	3.304 (0.19)	7.45 (0.21)
Range	−1.48 to 6.71	−4.40 to 6.40	−1.73 to 9.11	1.4 to 13.1	−9.38 to 15.64	−6.90 to 10.33	−10.0 to 11.46	2.3 to 13.9

Positive values indicate that the direction of flux was from ecosystem to atmosphere, and negative values indicate that the direction of flux was from atmosphere to ecosystem. Soil temperatures taken at 5 cm at southern sites and 10 cm at northern sites. Shown are means with standard errors in parentheses, followed by the range of observed values. Stand abbreviations are defined in the text.

below when we compare R_t and F_n. The potential error in R_f caused by errors in both $\bar{r}_f$ and L were comparable to the potential error in soil respiration. It was unlikely that all $\bar{r}_{15}$, L, and V_s would simultaneously be at the positive or negative limit of their 95% confidence interval, and therefore the calculated combined deviations from our original estimates of R_t probably represented much more than 95% confidence bounds.

Eddy Covariance Measurements of Nocturnal Ecosystem CO$_2$ Flux

Previous studies using eddy covariance data to examine physiological behavior of ecosystems discarded observations of F_n that were judged to have been unduly influenced by extraneous phenomena [*Wofsy et al.*, 1993; *Hollinger et al.*, 1994; *Grace et al.*, 1995; *Lloyd et al.*, 1995; *Goulden et al.*, 1996a, b; *Baldocchi and Harley*, 1995; *Baldocchi et al.*, 1997; *Baldocchi and Vogel*, 1996; *Black et al.*, 1996]. The editing has substantially reduced most data sets. For example, both *Wofsy et al.* [1993] and *Goulden et al.* [1996a] rejected approximately 40% of F_n measurements, *Lloyd et al.* [1995] created a so-called "elite" data set that contained less than 20% of observed F_n, *Baldocchi and Harley* [1995] used only 200 of 1300 flux measurements, and *Black et al.* [1996] used only 26% of observed F_n to establish a relationship with temperature. When F_{stor} was not measured, all observations of F_n made while the air was not mixing well must be excluded from the analyses. We observed that F_{stor} explained approximately 50% of F_n, on average, when air was not well mixed and that F_{stor} made negligible contributions, on average, to F_n when air was well mixed (Table 6). When air was mixing well, the F_{stor} was positive sometimes (storage was increasing) and negative sometimes (storage was decreasing), and its inclusion reduced the variability among measurements. F_{stor} was not measured at NOJP and NYJP; hence we did not compare measurements made during well-mixed and poorly mixed periods. Moreover, we believe that these data were noisier than they would have been had F_{stor} been measured. Too few measurements of F_{stor} were made at SYJP to permit comparing well-mixed and poorly mixed periods.

Even when F_{stor} was measured, F_n could be underestimated while the air was not well mixed, or if the turbulent air movement had occurred for less than a measurement interval, possibly because of cold air drainage moving air laterally from the footprint of the tower, sporadic mixing, a spectral shift toward high-frequency eddies, or fluctuations in vertical wind below the resolution of the sensor [*Goulden et al.*, 1996b]. We compared relationships between F_n and soil temperature for observations made while air was well mixed (friction velocity greater than 0.25 m s^{-1}) to observations made while the air was poorly mixed (friction velocity less than 0.25 m s^{-1}) for three sites measuring F_{stor} (Figure 3, Table 7). Coefficients of determination were higher for data sets containing measurements made during well-mixed periods, but estimates of ecosystem respiration at 15°C, and temperature response coefficients were not consistently different between data sets. Low coefficients of determination for relationships between F_n and soil temperature have been reported by *Baldocchi and Meyers* [1991], *Hollinger et al.* [1991], and *Goulden et al.* [1996b]; these reports together with our results indicated that F_n measurements were inherently noisy. *Black et al.* [1996] obtained better correlation between F_n and soil temperature than we did by using a higher standard for turbulent mixing of air than we used. Moreover, *Wofsy et al.* [1993] and *Black et al.* [1996] obtained better correlation between F_n and soil temperature by aggregating measurements over longer time intervals than the half-hour or 1-hour intervals used here. We chose to use observations with friction velocity greater than 0.25 m s^{-1} for subsequent analyses, even for sites where F_{stor} was measured, in order to reduce the amount of variation for F_n, but we did not aggregate measurements or use a higher standard for turbulent air movement because the sample size would have been severely reduced at some sites. Screened data sets contained 5–50% of the available measurements of net ecosystem flux of CO$_2$ at night, and these data sets were still noisy (Table 7). This level of screening reduced sample sizes to minimal levels at some sites (Table 9), but the range of soil temperatures for screened data sets was similar to the range encountered during the study period (Figure 3), and screening did not reduce the temporal distribution of observations at any site (Table 10).

The inherent variability of F_n is an issue that warrants more attention. One possible explanation for the high level of noise is that our screening did not eliminate measurements made when the requirement for steady state conditions was seriously violated. For example, mixing could have been sporadic during

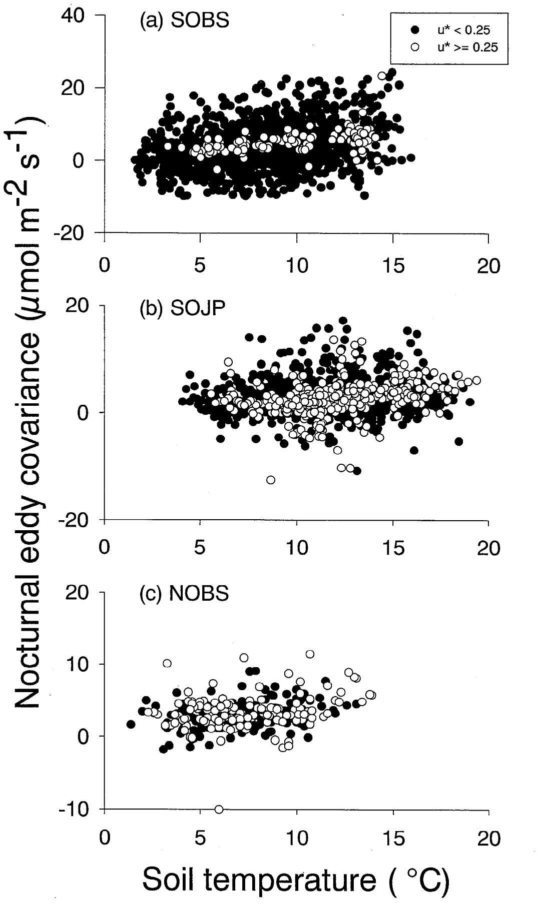

Figure 3. Relationship between soil temperature and nocturnal eddy covariance when air was well mixed ($u^* > 0.25$ m s^{-1}) and air was poorly mixed ($u^* < 0.25$ m s^{-1}) at (a) the old black spruce stand in the southern study area, (b) the old jack pine stand in the southern study area, and (c) the old black spruce stand in the northern study area.

many measurement intervals when the mean level of mixing for the period was above the threshold. Discarding these measurements, if they could be identified, would reduce the level of variation. We might also have discarded many measurements of F_n that accurately represented ecosystem physiological performance simply because the mean friction velocity for the interval was less than 0.25 m s^{-1}; identifying these measurements would increase sample sizes and make data sets more representative by including measurements from many more nights.

Table 7. Results of Regression Analyses of the Relationship Between Nocturnal Eddy Covariance Measurements and Soil Temperature ($R_t = R_{15}Q_{10}^{(T-15)/10}$) During Well-Mixed Measurement Intervals ($u^* > 0.25$) and Poorly Mixed Intervals ($u^* < 0.25$) for Three Coniferous BOREAS Sites

	$u^* < 0.25$ m s^{-1}				$u^* \geq 0.25$ m s^{-1}			
	R_{15}	Q_{10}	n	r^2	R_{15}	Q_{10}	n	r^2
SOBS	9.73 (0.62)	4.56 (0.58)	1358	0.10	8.21 (0.62)	2.53 (0.39)	129	0.24
SOJP	3.15 (0.14)	1.68 (0.19)	1106	0.02	3.71 (0.19)	3.53 (0.60)	439	0.10
NOBS	5.59 (0.76)	2.46 (0.45)	184	0.11	6.05 (0.84)	2.32 (0.46)	149	0.10

Stand abbreviations are defined in the text. Values in parentheses are standard errors.

Table 8. Regression Statistics of the Comparison Between Eddy Covariance Measurements of Nocturnal Ecosystem Respiration (F_n) and Scaled Chamber Estimates of Ecosystem Respiration (R_t)

Stand	b	r^2
SOBS	0.78 ± 0.032	0.27
SOJP	0.76 ± 0.042	0.12
SYJP	0.58 ± 0.034	0.13
NOBS	0.75 ± 0.039	0.14
NOJP	0.80 ± 0.037	0.06
NYJP	0.73 ± 0.049	0.27

Stand abbreviations are defined in the text. The model fit was $F_n = bR_t$. Coefficients of determination (r^2) were calculated according to *Kvalseth* [1985].

Comparing R_t and F_n

F_n was lower than R_t by 20–40% for all stands (Table 8). The value of the coefficient in the relationship $F_n = bR_t$ was significantly lower than 1.0 for all sites. Differences between R_t and F_n were also apparent when compared by paired t-tests (Table 9). In spite of these significant differences between R_t and F_n correlations were poor (Table 8) because of the variability inherent to F_n (Figure 4). We examined the possibility of reducing the variability of this relationship by aggregating measurements over longer time periods at NOBS, where both flux and storage were measured. There were 33 nights when the u^* was greater than 0.10 m s^{-1} for five consecutive hourly measurements. When regressing F_n against R_t for these hourly measurements ($n = 165$), the $r^2 = 0.11$, and when using nightly averages ($n = 33$), the $r^2 = 0.20$. There were 21 nights when u^* was greater than 0.20 m s^{-1} for five consecutive hourly measurements. The $r^2 = 0.21$ when using hourly measurements ($n = 105$) to regress F_n against R_t, and the $r^2 = 0.37$ ($n = 21$) when using nightly averages. Therefore aggregating measurements made only a moderate improvement in the degree of variability.

In the only other study that has compared R_t and F_n, *Goulden et al.* [1996b] observed that F_n was only about 65% of R_t in a temperate, deciduous forest. The consistent differences between estimates of ecosystem respiration raise the question of

Table 9. Average Nocturnal Eddy Covariance Measurement of Ecosystem Respiration (F_n), Average Scaled Chamber Estimate of Ecosystem Respiration (R_t) for the Same Intervals, and the Results of Pair t-Test Comparisons of F_n and R_t

Stand	F_n	R_t	Sample Size	P Value
SOBS	5.03	6.32	129	<0.001
SOJP	2.66	3.57	439	<0.001
SYJP	1.86	3.25	182	<0.001
NOBS	3.30	4.29	149	<0.001
NOJP	2.36	2.96	230	<0.001
NYJP	1.83	2.83	161	<0.001

Stand abbreviations are defined in the text.

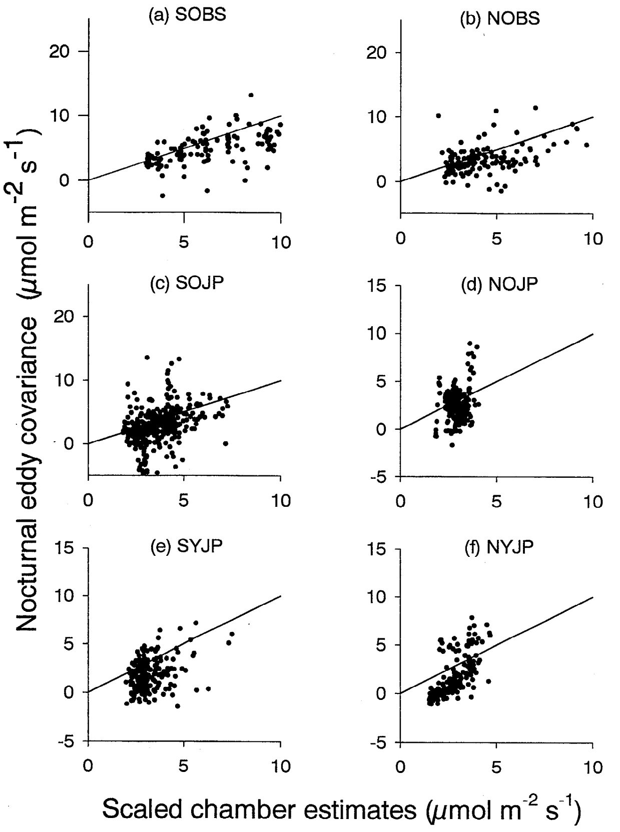

Figure 4. Comparison of scaled chamber estimates of ecosystem respiration to nocturnal eddy covariance measurements when air was well mixed ($u^* > 0.25$ m s^{-1}) at six BOREAS flux tower sites. Solid lines depict the 1:1 relationship between R_t and F_n.

whether scaled chamber or eddy covariance provide more accurate estimates of the actual ecosystem respiration rates. *Norman et al.* [this issue] suggested that soil respiration measurements we used at the northern sites and the southern jack pine sites might underestimate the true soil respiration rates by 10–20%, but making these adjustments would increase differences between R_t and F_n. *Norman et al.* [this issue] also suggested that soil respiration measurements we used at SOBS might overestimate the true soil respiration rates 20%, but making this adjustment would not eliminate the significant difference between R_t and F_n at that site. Scaled chamber values could consistently overestimate the actual ecosystem respiration in all of these stands, only if biomass and respiration rates were consistently overestimated. Our error analysis (Table 5) indicated that this possibility cannot be completely discounted. The environmental conditions that make eddy covariance measurements difficult at night or advective losses in cold air drainage might cause underestimates of ecosystem respiration rates [*Goulden et al.*, 1996b].

We examined the possibility that our estimates of R_t did not accurately capture seasonal changes in physiological activity of tissues and soil heterotrophs, and that this failure contributed to differences between R_t and F_n. For example, we might have inaccurately estimated foliar respiration during the period of foliar growth, or failed to incorporate seasonal variation in soil respiration because we did not make chamber measurements with the necessary frequency in some stands. Differences between R_t and F_n were consistent when comparing the early growing season, late growing season, and postgrowing season for SOBS and NOBS (Table 10), which implied that our estimates of R_t accurately captured seasonal trends and hence that discrepancies with F_n were primarily due to underestimates by eddy covariance measurements. In contrast, differences between F_n and R_t were not consistent during the study period at SOJP, NOJP, and NYJP (Table 10); we might have underestimated the R_t of jack pine stands early in the growing season because F_n was greater than R_t, if our estimates of foliage growth respiration were in error. The large discrepancies between F_n and R_t for NYJP, during late growing and postgrowing seasons, suggested that we overestimated the actual ecosystem respiration rates during those periods.

Table 10. Comparisons of the Relationships Between Eddy Covariance and Scaled Chamber Estimates of Ecosystem Respiration for the Early Growing Season (While Current-Year Foliage Was Growing), Late Growing Season (After Current-Year Foliage Had Grown), and Autumn (After the Growing Season Had Ended)

	Portion of Growing Season					
	Early		Late		Post	
Site	b	r^2	b	r^2	b	r^2
SOBS	0.72	0.36	0.84	0.11	0.75	0.05
SOJP	1.00	0.08	1.71	0.14	0.56	0.06
NOBS	0.76	0.11	0.85	0.32	0.65	0.06
NOJP	1.36	0.36	0.70	0.04	1.05	0.00
NYJP	1.38	0.60	0.48	0.60	0.35	0.27

Site abbreviations are defined in the text. Model fit was $F_n = bR_t$. Coefficients of determination were calculated according to *Kvalseth* [1985].

Conclusions

Eddy covariance measurements of ecosystem respiration at night were noisy, giving rise to low correlation with independent estimates of ecosystem respiration made by scaling chamber measurements. Eddy covariance measurements at night were consistently lower than ecosystem respiration rates based on scaling chamber measurements by 20–42%, and this systematic difference raises concerns about using nocturnal flux measurements to arrive at accurate estimates of gross assimilation during daylight, and of daily and annual net ecosystem exchange. We used eddy covariance measurements to identify some possible shortcomings in our estimates of R_t during the early portion of the growing season, and this suggested that F_n can be used to describe seasonal trends in ecosystem respiration.

Nocturnal ecosystem respiration uses a large fraction of the daily net carbon uptake in daylight; therefore accurate estimates are required to correctly estimate daily and annual net ecosystem exchange. Moreover, the seasonal course of ecosystem respiration differs from that of photosynthesis [*Baldocchi et al.*, 1997], and respiration responds to climatic variation differently than does photosynthesis [*Goulden et al.*, 1996a], and therefore a thorough understanding of respiration is required for predicting ecosystem responses to environmental change.

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