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# A distinct seasonal pattern of the ratio of soil respiration to total ecosystem respiration in a spruce-dominated forest

E. A. DAVIDSON*, A. D. RICHARDSON†, K. E. SAVAGE* and D. Y. HOLLINGER‡

*Woods Hole Research Center, PO Box 296, Woods Hole, MA 02543, USA, †Complex Systems Research Center, University of New Hampshire, Durham, NH 03824, USA, ‡USDA Forest Service NE Research Station, 271 Mast Rd., Durham, NH 03824, USA*

## Abstract

**Annual budgets and fitted temperature response curves for soil respiration and ecosystem respiration provide useful information for partitioning annual carbon budgets of ecosystems, but they may not adequately reveal seasonal variation in the ratios of these two fluxes. Soil respiration ($R_s$) typically contributes 30–80% of annual total ecosystem respiration ($R_{eco}$) in forests, but the temporal variation of these ratios across seasons has not been investigated. The objective of this study was to investigate seasonal variation in the $R_s/R_{eco}$ ratio in a mature forest dominated by conifers at Howland, ME, USA. We used chamber measurements of $R_s$ and tower-based eddy covariance measurements of $R_{eco}$. The $R_s/R_{eco}$ ratio reached a minimum of about 0.45 in the early spring, gradually increased through the late spring and early summer, leveled off at about 0.65 for the summer, and then increased again to about 0.8 in the autumn. A spring pulse of aboveground respiration presumably causes the springtime minimum in this ratio. Soil respiration 'catches up' as the soils warm and as root growth presumably accelerates in the late spring, causing the $R_s/R_{eco}$ ratios to increase. The summertime plateau of $R_s/R_{eco}$ ratios is consistent with summer drought suppressing $R_s$ that would otherwise be increasing, based on increasing soil temperature alone, thus causing the $R_s/R_{eco}$ ratios to not increase as soils continue to warm. Declining air temperatures and litter fall apparently contribute to increased $R_s/R_{eco}$ ratios in the autumn. Differences in phenology of growth of aboveground and belowground plant tissues, mobilization and use of stored substrates within woody plants, seasonal variation in photosynthate and litter substrates, and lags between temperature changes of air and soil contribute to a distinct seasonal pattern of $R_s/R_{eco}$ ratios.**

*Keywords:* ameriflux, carbon cycle, $CO_2$, eddy covarience, Howland, phenology, temperature response

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## Introduction

Differences in rates of net ecosystem carbon sequestration (NEE) between sites and years have been attributed in large part to variation in rates of ecosystem respiration (Cox *et al*., 2000; Valentini *et al*., 2000; Barford *et al*., 2001; Janssens *et al*., 2001; Saleska *et al*., 2003). However, the aboveground and belowground components of ecosystem respiration may respond differentially to variation in temperature, precipitation, and availability of substrate. Insight into these responses can be obtained only by partitioning the total ecosystem respiration flux.

Efflux of $CO_2$ from the surface of the forest floor, often called 'soil respiration' ($R_s$), typically contributes 30–80% of annual total ecosystem respiration ($R_{eco}$) in forests. The annual $R_s/R_{eco}$ ratio was 0.68 in a temperate hardwood forest in Massachusetts, USA (Goulden *et al*., 1996a); 0.76 in a mixed-age ponderosa pine forest in Oregon, USA (Law *et al*., 1999); 0.48–0.71 among coniferous boreal forests of central Canada (Lavinge *et al*., 1997); 0.73 in a boreal aspen forest in Saskatchewan, Canada (Griffis *et al*., 2004); 0.38–0.99 among Euroflux forested study sites (Janssens *et al*., 2001); 0.38 in a mature evergreen forest in the central Amazon Basin

Correspondence: Eric A. Davidson, tel. +1 508 540 9900, fax +1 508 540 9700, e-mail: edavidson@whrc.org

(Chambers *et al*., 2004); and 0.31 in a mature evergreen forest of the eastern Amazon Basin (Saleska *et al*., 2003). While these ratios of annual estimates of $R_s$ and $R_{eco}$ provide useful information for partitioning annual carbon budgets of ecosystems, they do not consider seasonal variation of this ratio or seasonal variation of the processes that contribute to these fluxes.

Soil respiration is a combination of soil microbial respiration and root respiration, whereas total ecosystem respiration also includes respiration of aboveground foliage, boles, branches, twigs, and dead wood. In temperate and boreal climates, seasonal changes in soil temperature usually lag behind changes in air temperature, which could cause differences in seasonal patterns of aboveground and belowground processes. In some ecosystems, plants may have access to deep soil water, which may buffer potential drought stress experienced by autotrophs compared with the heterotrophs concentrated near the soil surface. Hence, there is good reason to expect that the $R_s/R_{eco}$ ratio might vary seasonally, and that this variation could provide insight into ecosystem responses to varying weather and climate.

The objective of this study was to investigate seasonal variation in the $R_s/R_{eco}$ ratio in a mature forest dominated by evergreen conifers near Howland, ME, USA. We use chamber measurements of $R_s$ and tower-based eddy covariance measurements of $R_{eco}$. Comparisons with estimates of $R_{eco}$ derived by scaling and summing chamber measurement of soil, foliar, and bole respiration or derived from eddy covariance measurements have indicated that the sum of chamber measurements is often higher than the eddy covariance estimates (Goulden *et al*., 1996a; Lavinge *et al*., 1997; Chambers *et al*., 2004; Griffis *et al*., 2004). These authors have discussed the numerous uncertainties in both methodological approaches, which we do not pursue further here. However, we do address several possible sources of error and bias that are specific to calculating $R_s/R_{eco}$ ratios, and we assume that any additional unknown biases in our estimates of either $R_s$ or $R_{eco}$ are consistent across seasons.

## Methods

### Site description

The Howland Forest research site is located about 35 miles north of Bangor, Maine (45.20407°N, 68.74020°W; 80 masl). The forest is owned and actively managed by International Paper, Ltd. Stands in this forest consist primarily of red spruce (*Picea rubens* Sarg.) and eastern hemlock (*Tsuga canadensis* (L.) Carr.), with lesser quantities of other conifers (primarily balsam fir, *Abies balsamea* (L.) Mill., white pine, *Pinus strobus* L., and northern white cedar, *Thuja occidentalis* L.) and hardwoods (red maple, *Acer rubrum* L. and paper birch, *Betula papyrifera* Marsh.). The forest stand around the eddy covariance tower has a live basal area of about 43 $m^2\,ha^{-1}$, leaf area index (LAI) of $\sim 6\,m^2\,m^{-2}$ and is about 20 m in height. This stand was selectively logged (not clear-cut) early in the 1900's, but has been minimally disturbed since that time. Topographically, the region varies from flat to gently rolling, with a maximum elevation change of less than 68 m within 10 km. Soils range from well drained to very poorly drained over relatively small areas (Levine *et al*., 1994). Upland soils are fine sandy loams, classified as Aquic Haplorthods. Physical and chemical data on the soil were provided by Fernandez *et al*. (1993). Mean annual temperature is $+5.5\,°C$, and mean annual precipitation is about 1000 mm. The 7-year average NEE for the forest is a net uptake of $1.7\,Mg\,C\,ha^{-1}\,y^{-1}$ (Hollinger *et al*., 2004).

### Eddy covariance measurements of $R_{eco}$

The eddy covariance flux measurement system was established on the Howland main tower in 1995 and on a second tower in 1998. Fluxes have been measured at a height of 29 m with a system consisting of a model SAT-211/3 K three-axis sonic anemometer (Applied Technologies, Inc., Longmont, CO, USA) and a model LI-6262 fast response $CO_2/H_2O$ infrared gas analyzer (LiCor, Inc., Lincoln, NE, USA), with data recorded at 5 Hz. The flux measurement system and calculations are described in more detail in Hollinger *et al*. (1999, 2004). Half-hourly flux values were excluded from further analysis if the wind speed was below $0.5\,m\,s^{-1}$, sensor variance was excessively high or extremely low, rain or snow was falling, for incomplete half-hour sample periods, or instrument malfunction. Over the 1996–2003 period, 70% of all possible nocturnal data from the main tower with no seasonal bias were available following these exclusions. A similar percentage of data were available from the second flux tower. Data from stable nocturnal periods were also excluded, specifically when the friction velocity ($u^*$; Goulden *et al*., 1996b) was $<0.25\,m\,s^{-1}$ (Hollinger *et al*., 2004). Using this $u^*$ threshold removed about one-half of the available nocturnal data (Hollinger *et al*., 2004) so that data from a low of 30% (summer) to a high of 38% (spring) of all nocturnal half-hourly periods were available for analysis.

### Chamber measurements of $R_s$

Our chamber measurements of soil respiration have been described in detail by Savage & Davidson (2001, 2003). Briefly, manual measurements of soil respiration, using a vented, recirculating, nonsteady-state system (Hutchinson & Livingston, 2002), have been made once per week during the growing season and one to two times per month during the late autumn, winter, and early spring since 1996. A portable infrared gas analyzer (IRGA, model 6252, Licor Inc., Lincoln, NE, USA), mounted on a backpack frame, was calibrated each measurement day using a zero $CO_2$ standard and a $523\,\mu L\,L^{-1}$ $CO_2$ certified standard. The IRGA was connected to a vented white acrylonitrile–butadiene–styrene (ABS) chambertop (10 cm in height) that was placed over each collar already in the ground. When a snowpack was present, the chamber top was gently inserted directly into the snow. A pump circulated air at a rate of $0.5\,L\,min^{-1}$ from the chambertop to the IRGA and back to the chambertop. The collars, 25 cm in diameter, were made from thin wall PVC tubing cut to 10 cm lengths, and were inserted into the ground to a depth of approximately 5 cm. Pressure differences between the chamber headspace and ambient air outside the chamber were below detection limits (0.1 Pa measured by a micromanometer, Infiltec, Waynesboro, VA, USA). The chambertop was left on the collar for about 5 min, and the change in $CO_2$ concentration within the chamber was recorded at 12 s intervals. A linear regression was preformed on the increasing concentration to determine a flux rate, which was corrected for atmospheric pressure and chamber air temperature. Potential errors and biases of this method are discussed in detail by Davidson *et al*. (2002). Annual estimates were derived by interpolating between measurement dates and then summing for the year.

To address the question of whether manual chamber measurements adequately represent soil respiration for comparisons with eddy covariance measurements of total ecosystem respiration at higher temporal frequencies, we installed six automated soil respiration chambers at the main tower study site in the spring of 2004. A respiration measurement was made on each of the chambers every half hour throughout the summer. The automated flux measurements are based on the same principals as the manual measurements, and the details of the system design are given by Savage & Davidson (2003).

### *Calculating the* $R_s/R_{eco}$ *ratio*

For each soil respiration sampling date, a mean was calculated for 16 manual flux measurements in the area of a moderately well-drained upland soil within about 100 m of the tower. Half-hourly night-time (photosynthetically active photon flux density $<5\,\mu mol\,m^{-2}\,s^{-1}$) eddy covariance estimates of NEE of $CO_2$, recorded when $u^*$ exceeded a threshold of 0.25, were binned by week and averaged. These estimates of mean weekly night-time $R_{eco}$ were paired with corresponding soil respiration measurements to calculate a ratio. We chose to aggregate eddy covariance data for estimating $R_{eco}$ because the nights directly before and after the soil respiration chamber measurements sometimes did not include sufficient numbers of half-hourly NEE estimates when winds exceeded the $u^*$ threshold. By aggregating the eddy covariance data over a week, we were able to obtain a $R_{eco}$ estimate to match each $R_s$ measurement. We assume that a week is sufficiently short to preclude confusion with seasonal variation in temperature. Synoptic weather patterns that occurred midway through a week could have added variation that we do not consider here.

### *Temperature and water content*

Air temperature was measured at 26.5 m above the soil surface with a 100 Ω platinum resistance thermometer (model RTD-810, Omega Inc., Stamford, CT, USA) used in a four-wire configuration with a 0–5 V linearizing module (model OM5-IP4-100C, Omega Inc.). The sensor was mounted in a model 076B-1 (Met One, Grants Pass, OR, USA) aspirated radiation shield. Soil temperature was measured by manually inserting a probe to 10 cm depth adjacent to each soil respiration chamber at the time of flux measurements. A mean of 16 soil temperature measurements was recorded for each sampling date. Soil moisture was monitored at 5, 10, 20, 50, and 100 cm depths using soil moisture probes (Hydra-Vitel, Stevens Water Monitoring Systems Inc., Beaverton, OR, USA) that make a high-frequency (50 MHz) complex dielectric constant measurement to determine soil moisture and salinity.

### *Statistical analyses*

Temperature sensitivities of $R_s$ and $R_{eco}$ over the entire year were characterized by fitting the data to a Lloyd & Taylor (1994) function using nonlinear least squares fitting:

$$R = \alpha e^{-E_0/(T-T_0)},$$

where $R$ is respiration, $\alpha$ was set proportional to the mean flux over the observation period, and $E_0$ and $T_0$ are fitted parameters (Savage & Davidson, 2001).

The distribution of $R_s/R_{eco}$ ratios was not significantly different from a normal distribution. The seasonal pattern of the $R_s/R_{eco}$ ratios combined for all years was characterized using a second-order Fourier regression with day of year (expressed as radians):

$$\mathrm{DOY}^* = \mathrm{DOY}(2\pi/365)$$

as the independent variable using SAS 9.1 (SAS Institute, Cary, NC, USA):

$$R_s/R_{eco}\ \text{ratio} = k + s_1 \sin(\mathrm{DOY}^* + \phi_1) + s_2 \sin(2 \times \mathrm{DOY}^* + \phi_2) + \varepsilon,$$

where $k$ is a regression constant that equals the mean ratio across the entire year, the $s_1$ and $s_2$ parameters control the amplitude, and the $\phi_1$ and $\phi_2$ parameters control the phase shift of the first- and second-order sine waves, respectively, and $\varepsilon$ is the regression residual.

## Results

Annual estimates of soil and ecosystem respiration measured at the main tower indicate that the annual $R_s/R_{eco}$ ratio ranges from 0.55 to 0.76, with a mean of 0.62 (Table 1). Combining data across all seasons of all years, the fitted $E_0$ and $T_0$ values of the Lloyd & Taylor (1994) temperature functions were nearly identical for $R_s$ and $R_{eco}$ (Fig. 1a, c). The ratio of the two fitted temperature functions ($R_s/R_{eco}$) was nearly constant at 0.60 across the temperature range, which is consistent with a mean annual estimate of 0.62. However, considerable variation was found in observed respiration rates both above and below the regression lines of the temperature functions (Fig. 1a, c). Inspection of the residuals of these functions reveals negative residuals for $R_{eco}$ whenever autumn soil temperatures were <6 °C (Fig. 1b). Hence the nearly constant ratio ($R_s/R_{eco}$) of 0.60 of the fitted temperature functions across the temperature range may belie significant seasonal variation of the observed $R_s/R_{eco}$ ratios.

Plotting the 7-year time line for $R_s$, $R_{eco}$, and $R_s/R_{eco}$ ratios reveals a repeated annual pattern (Fig. 2a, b). Each spring, the $R_s/R_{eco}$ ratios typically fell to about 0.4. The ratios then increased during the spring, summer, and autumn, peaking near 1.0 by the late autumn and winter (Fig. 2b). The ratios occasionally exceeded 1.0 in the late autumn and winter, when the fluxes are small and the measurement error is probably large relative to the mean flux. We attempted to correlate the slopes of the linear regression lines in Fig. 2b with interannual variation in annual precipitation, summertime precipitation, and soil water content, but found no significant correlations to help explain the apparent interannual variation in the fitted slopes.

**Table 1** Annual estimates of soil respiration ($R_s$; Savage & Davidson, 2001 and more recent unpublished data), total ecosystem respiration ($R_{eco}$; Hollinger *et al.*, 1999, 2004), and their ratio

| Year | $R_s$ (Mg C ha$^{-1}$) | $R_{eco}$ (Mg C ha$^{-1}$) | $R_s/R_{eco}$ |
|---|---|---|---|
| 1997 | 6.1 | 11.0 | 0.55 |
| 1998 | 7.6 | 12.5 | 0.61 |
| 1999 | 7.5 | 12.0 | 0.63 |
| 2000 | 7.3 | 11.8 | 0.62 |
| 2001 | 7.3 | 12.7 | 0.57 |
| 2002 | 7.5 | 11.3 | 0.66 |
| 2003 | 8.1 | 10.6 | 0.76 |
| Mean | 7.3 | 11.7 | 0.62 |

Not surprisingly, springtime increases in soil temperature lagged increases in air temperature, and autumn decreases in air temperature preceded autumn decreases in soil temperature (Fig. 3). The difference between air and soil temperature was negatively correlated with the $R_s/R_{eco}$ during the autumn (Fig. 4c). In other words, as the air cooled more rapidly than the soil, the contribution of soil respiration to total ecosystem respiration increased.

The seasonal variation in $R_s/R_{eco}$ ratios may not follow the linear pattern that is suggested in Fig. 2b. Combining the $R_s/R_{eco}$ ratios for all years, a second-order Fourier function describes a general seasonal trend (Fig. 5a). The $R_s/R_{eco}$ ratios tend to reach a minimum of about 0.45 in the late winter or early spring (March). The $R_s/R_{eco}$ ratios increase during April, May, and early June, and then tend to level out at an average of about 0.65 during the summer. By late September, however, the upward trend of $R_s/R_{eco}$ ratios resumes, and the average ratio for the autumn is about 0.8. Winter values for the ratio are poorly constrained by the available data, and probably remain high before dropping rapidly again in the spring. The second-order sine term of the Fourier function is statistically significant, indicating that the springtime increase, mid-summer plateau, and subsequent autumn increase require a curve that is more complex than a simple sine wave.

The same seasonal pattern is observed when $R_{eco}$ data from the tower 775 m to the west of the main tower are used to calculate the $R_s/R_{eco}$ ratios (Fig. 5b). The summertime ratios tend to be a bit higher, reflecting that the night-time $R_{eco}$ at the west tower was slightly (<5%, on average) lower than $R_{eco}$ at the main tower during the 1999–2001 period (Hollinger *et al.*, 2004). A $t$-test indicates that the regression constants ($k$), which account for the slight offset between the two lines, differ between the two models ($P = 0.05$). More importantly, a joint $F$-test indicates that the hypothesis that the remaining four model parameters ($s_1$, $s_2$, $\phi_1$, and $\phi_2$) in the west tower model are equal those of the main tower model could not be rejected ($F_{4,74} = 0.99$, $P = 0.42$). The latter test confirms that the overall shape, and hence seasonal pattern, is the same for the west tower and main tower models.

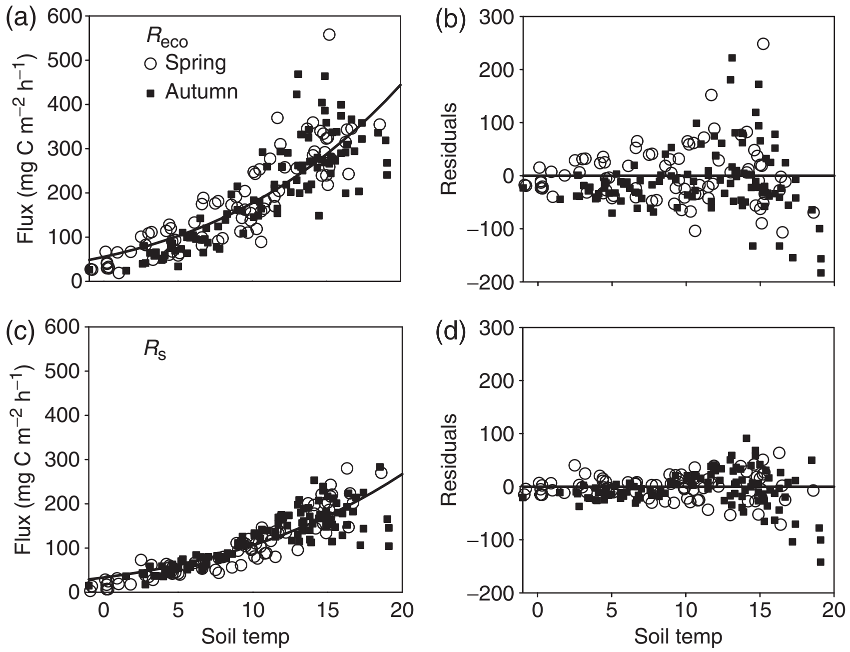

**Fig. 1** Temperature response curves (a, c) and analysis of residuals (b, d) for total ecosystem respiration ($R_{eco}$; a, b) and for soil respiration ($R_s$; c, d) for all data combined from 1996 to 2003 at the Howland Forest, using the Lloyd & Taylor (1994) function. Open circles represent data for the period of increasing fluxes (spring), and filled squares represent data for the period of decreasing fluxes (autumn). The parameters for the fitted temperature functions are: $R_{eco}$ flux = 1 330 000 × $e^{-776/(T-196)}$; where $T$ is soil temperature in Kelvin; $R^2 = 0.75$. $R_s$ flux = 832 000 × $e^{-782/(T-196)}$; where $T$ is soil temperature in Kelvin; $R^2 = 0.79$.

Manual and automated measurements of soil respiration were in good agreement (Fig. 6). Summing the mean half-hourly automated chamber measurements during the 75-day measurement period in 2004 yielded a flux estimate of 350 g C m$^{-2}$ 75 days$^{-1}$, whereas interpolating the mean manual flux measurements over the same period yielded 330 g C m$^{-2}$ 75 days$^{-1}$.

## Discussion

The aggregated annual estimate of 0.62 for $R_s/R_{eco}$ ratio reported here is similar to those reported for other temperate and boreal forests (Goulden *et al.*, 1996a; Lavinge *et al.*, 1997; Law *et al.*, 1999; Janssens *et al.*, 2001; Griffis *et al.*, 2004). In previous work, we reported that below-canopy respiration measured by an eddy covariance system accounted for between about 40% and 100% of total respiration (Hollinger *et al.*, 1999), broadly in agreement with the present more detailed soil chamber analysis.

Here, we show a seasonal pattern of $R_s/R_{eco}$ ratios that is not apparent in aggregated annual ratios or in ratios of temperature functions. The ratios vary widely and only part of this variation can be attributed to the seasonal patterns that we have identified. Remaining variation may include responses to synoptic weather patterns, spatial and temporal mismatches between $R_s$ and $R_{eco}$ measurements, and measurement errors.

The seasonal patterns of varying $R_s/R_{eco}$ ratios that are apparent in these data are not simply a function of temperature, because the ratios increase with both increasing spring temperatures and decreasing autumn temperatures. When data from the entire year are combined, as in the temperature response functions shown in Fig. 1a and 1c, possible hysteresis in responses to spring warming and autumn cooling is ignored. Because soil warming and cooling lags changes in air temperature, it is not surprising that aboveground and belowground processes might follow somewhat different seasonal patterns of respiration. In addition to responses to temperature, the phenology of foliar and root growth and senescence may also affect seasonal patterns of respiration (Curiel Yuste *et al.*, 2004), which likely affect $R_s/R_{eco}$ ratios. Although we did not conduct chamber measurements of foliar and root respiration, our partitioning of $R_{eco}$ into aboveground and belowground sources provides a basis for the following plausible explanations of seasonal patterns.

### *Spring*

An increase in respiration of aboveground plant tissues in March and early April may precede obvious bud

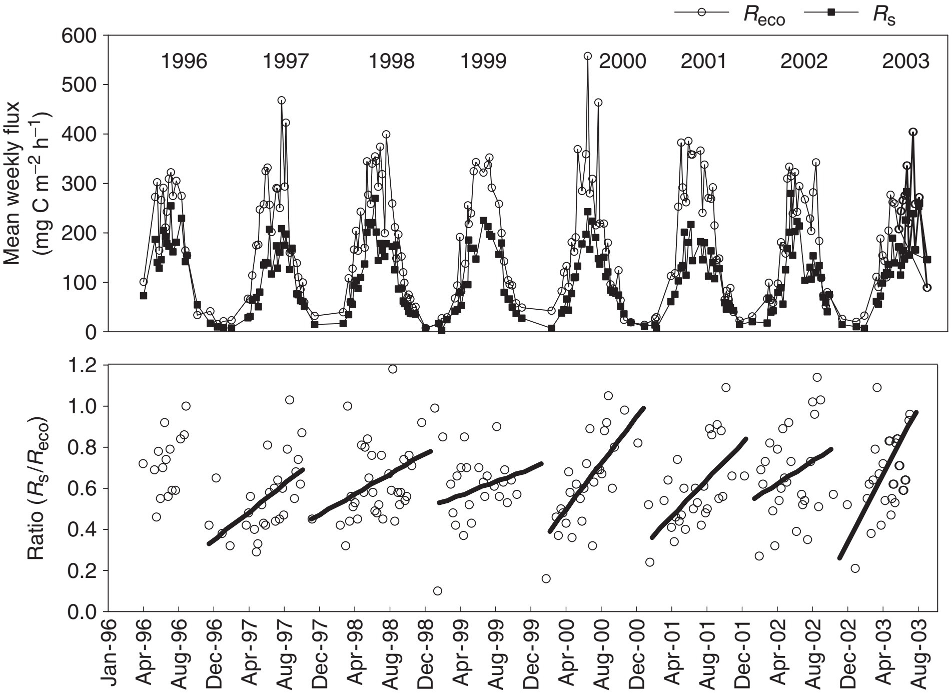

**Fig. 2** Seven-year record of soil respiration ($R_s$) and total ecosystem respiration ($R_{eco}$) at the Howland Forest. Weekly mean fluxes are shown in the upper panel (a). The ratios of $R_s/R_{eco}$ are plotted in the lower panel (b), with least-squares linear fits for each entire calendar year (excluding 1996 because measurements did not begin until June 1996). The linear regressions for day of year and $R_s/R_{eco}$ ratios are statistically significant at $P<0.01$ for 1997, 2000, 2001, and 2003, with $R^2$ values ranging from 0.23 to 0.45. The regressions are not significant ($P>0.05$) for the other years.

break and foliar expansion. An increase in aboveground respiration in advance of soil respiration may rely on mobilization of stored carbohydrates, as is the case for springtime upward sapflow. Activation of aboveground respiration, as buds first begin to swell, could be a phenological response to increased day length. Intermittent warm days in the spring may also enhance aboveground respiration quickly, while the soil takes much longer to warm. Indeed, the winter snowpack at Howland typically does not melt until mid-April (DOY 109 ± 7, mean and standard deviation). Hence, aboveground respiration appears to increase sooner than belowground respiration, causing the $R_s/R_{eco}$ ratios to reach a minimum when aboveground respiration is first stimulated by responses to either phenology or warming or both. Our data suggest that this period of a $R_s/R_{eco}$ minimum is fairly abrupt and brief in the late winter and early spring, and that the timing may vary by a few weeks from year to year.

As spring proceeds, the soils begin to warm and root growth presumably accelerates. For many temperate tree species, root elongation tends to peak several weeks after springtime foliar expansion is complete (Joslin *et al*., 2001). Lee *et al*. (2003) presented evidence that root respiration is affected more by phenology of carbon allocation than soil temperature. Hence, the heterotrophic and autotrophic components of soil respiration only gradually 'catch up' to aboveground respiration during the late spring, causing the $R_s/R_{eco}$ ratios to increase during this period.

### *Summer*

As soils continue to warm during the summer, soil respiration might be expected to increase further relative to aboveground respiration. However, summer droughts are common in many temperate forests and are associated with decreases in soil respiration (Davidson *et al*., 1998; Epron *et al*., 1999; Savage & Davidson, 2001; Xu & Qi, 2001; Borken *et al*., 2002, 2005; Hanson *et al*., 2003; Curiel Yuste *et al*., 2004). Soils tend to dry from the surface downward, causing the largest variations in water content to occur in the litter layer (Borken *et al*., 2003). Therefore, respiration in the litter layer, which is dominated by heterotrophs, may be most susceptible to drought. In contrast, plants that have access to deeper soil horizons may not experience such severe drought stress, resulting in less reduction of aboveground respiration.

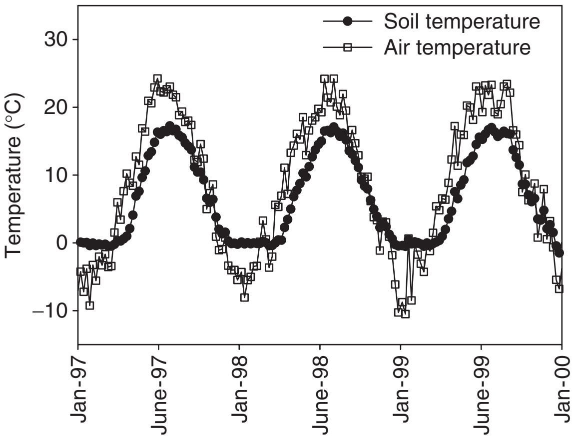

**Fig. 3** Examples of seasonal variation in soil temperature (10 cm depth) and air temperature (26.5 m above the soil surface) at the Howland Forest.

We did not find a statistically significant correlation between mineral soil water content and $R_s/R_{eco}$ ratios. Measurements of water contents of the organic horizon (Borken *et al*., 2003, this issue) may provide better indications of the effects of summer drought than the mineral soil measurements that were available to us for this study. It is difficult to demonstrate statistically an explanation for lack of variation of a variable (summertime $R_s/R_{eco}$ ratios), but the opposing effects of increasing temperature and summertime drought offer an ecologically plausible explanation (Davidson *et al*., 1998). The summertime leveling-off of the $R_s/R_{eco}$ is consistent with a drought-induced suppression of the increases in $R_s$ that would be expected based on increasing soil temperatures alone, thus delaying any further increase in $R_s/R_{eco}$ ratios.

### *Autumn*

Several factors may contribute to further increases in $R_s/R_{eco}$ ratios during the autumn. First, rainfall events can cause a recovery of soil respiration rates after summer drought, although simultaneously decreasing soil temperatures dampen the response to wetting (Davidson *et al*., 1998; Savage & Davidson, 2001). Second, the autumn air temperature declines more rapidly than the soil temperature (Fig. 3), so that aboveground respiration would be expected to decline more rapidly than belowground respiration. Finally, senescence of foliage and leaf fall (in the case of deciduous species) causes a reduction in substrate for aboveground respiration and an increase in substrate for heterotrophic respiration in the litter layer. Hence, the highest $R_s/R_{eco}$ ratios might be expected under these conditions in the autumn.

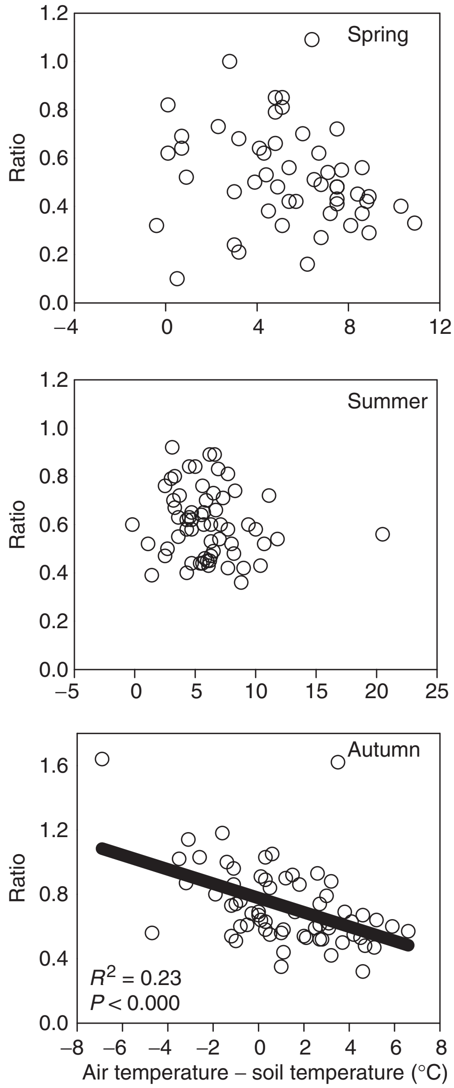

**Fig. 4** Correlation of the difference between air and soil temperatures (Fig. 3) and $R_s/R_{eco}$ ratios for three seasons (day of year 60–161, 162–243, 244–334) using data from all years. The significant linear regression for the autumn is: $R_s/R_{eco}$ ratio = 0.78–0.045 (air temperature–soil temperature).

### *Winter*

Soil respiration declines substantially during the winter, but respiration does not cease (Winston *et al*., 1997). Very little aboveground respiration likely occurs in deciduous species during the winter, and it may vary considerably among evergreen coniferous species and climates. At Howland, which is dominated by spruce and hemlock, with a minor (~10%) hardwood component, and where wintertime air temperatures are generally < 0 °C, the majority of wintertime respiration appears to be from the soil.

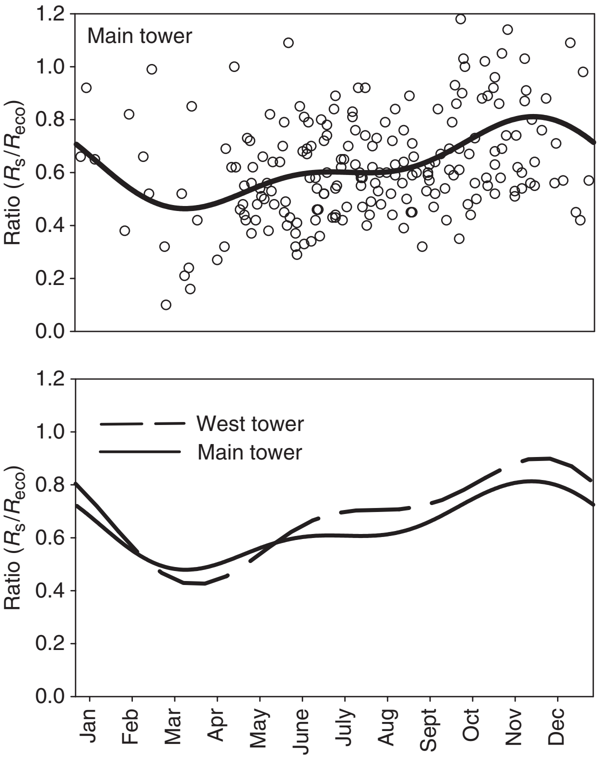

**Fig. 5** (a) Second-order Fourier function fitted to $R_s/R_{eco}$ ratio data (each point is an estimate of the $R_s/R_{eco}$ ratio for a week) from all years, where

$$R_s/R_{eco} = 0.625 - 0.132\sin(\mathrm{DOY}^* - 0.405) - 0.070\sin(2 \times \mathrm{DOY}^* - 0.438),$$

$$\mathrm{DOY}^*(\text{in radians}) = \text{Day of Year}\,\frac{2\pi}{365}.$$

This model has $n = 208$, $R^2 = 0.17$. The regression constant and the coefficients on the two sin terms are significant at $P \leq 0.01$; (b) second-order Fourier functions as in (a), but with $R_s/R_{eco}$ ratios calculated using $R_{eco}$ estimates from the eddy covariance tower 775 m to the west of the main tower. The fitted function for the west tower calculation is $R_s/R_{eco} = 0.677 - 0.187\ \sin(\mathrm{DOY}^* - 0.303) - 0.091\ \sin(2 \times \mathrm{DOY}^* - 0.912)$. The west tower model has $n = 79$, $R^2 = 0.33$; as with the main tower model, the regression constant and the coefficients on the two sin terms are significant at $P \leq 0.01$.

### *Spatial and temporal uncertainties associated with comparing* R$_s$ *and* R$_{eco}$

Previous work at the Howland study area has shown lower soil respiration fluxes from very poorly drained wetlands and somewhat higher fluxes from the less common well-drained upland sites (Savage & Davidson, 2001). Using a digital soil map of the tower footprint area, Davidson *et al.* (2002) demonstrated that the mean flux from the moderately well-drained site provided a good estimate (within 15%) of the spatially averaged mean flux across all purported probable tower footprints. Hence, we have use the mean $R_s$ flux from the moderately well-drained site at the base of the main tower area for comparison with tower-based estimates of $R_{eco}$.

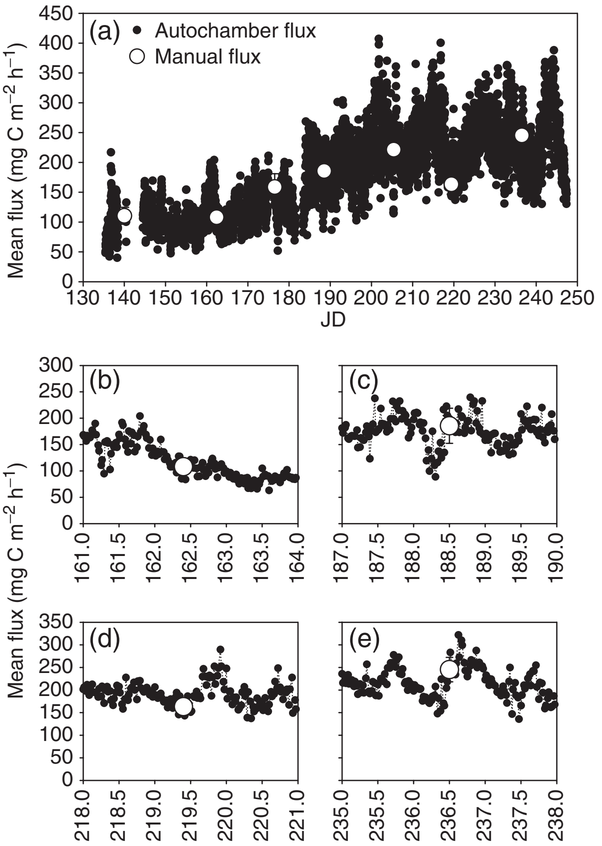

**Fig. 6** Comparison of infrequent mean ($n = 8$) manual soil respiration measurements and mean ($n = 6$) half-hourly automated soil respiration measurements for the entire 75-day measurement period in 2004 (a) and for selected diel cycles (b–e).

Comparing $R_s$ to $R_{eco}$ at a second tower site provided further assurance that biases in wind direction and spatial heterogeneity around the main tower were not the cause of the observed seasonal patterns in $R_s/R_{eco}$ ratios. Because the wind is predominantly from the north-west in the winter and the south-west in the summer, a weaker soil $CO_2$ source area north-west of the tower could have been the cause of lower late winter $R_s/R_{eco}$ ratios. However, it would be an unusual coincidence if the same directional spatial patterns of local source strengths of $CO_2$ would occur around each of the two independent towers located 775 m apart within the forest stand. Hence, the observation of the same seasonal patterns in $R_s/R_{eco}$ ratios regardless of which tower is used to estimate $R_{eco}$ (Fig. 5b) provides confidence that the seasonal pattern is because of seasonal variations in aboveground and belowground processes rather than because of a seasonal bias in wind direction and local $CO_2$ sources.

In addition to the question of spatial footprints of these measurements, potential temporal mismatches must also be considered. The manual $R_s$ fluxes were made during the day on only 1 day in the week, whereas the $R_{eco}$ estimates were derived from night-time data and averaged over a week. Using night-time eddy covariance to estimate daily $R_{eco}$ is a controversial topic that has no easy answer and that is beyond the scope of this paper. This approach is widely used in the eddy covariance literature, although the assumption that daytime and nighttime $R_{eco}$ varies primarily as a function of temperature has not been well tested. Falge *et al*. (2002) showed that $R_{eco}$ calculated from light response curves (during the day) compared reasonably well to $R_{eco}$ derived from nighttime data. If the assumption that nighttime $R_{eco}$ can be used to estimate daytime $R_{eco}$ is correct for some seasons and false for others, then our analysis of seasonal variation in $R_s/R_{eco}$ ratios could be affected.

The representativeness of manual $R_s$ measurements in this study was confirmed by good agreement with half-hourly automated chamber measurements at the same site (Fig. 6). Interpolated manual measurements underestimating fluxes by only about 6% during the 75-day comparison period. In a similar comparison of weekly manual measurements and hourly, automated measurement of $R_s$ at the Harvard forest in Massachusetts, the manual measurements underestimated the daily mean flux by 13% (Savage & Davidson, 2003). Irvine & Law (2002) found that twice-daily manual measurements overestimated the daily mean flux by 7% compared with more frequent automated measurements. Hence, although manual and automated measurements do not always yield identical estimates, the differences do not appear to be a consistent bias in one direction, and the error appears to be $<15\%$ for these temperate forests.

## Conclusions

While many Fluxnet sites produce measurement of both soil respiration and ecosystem respiration, most comparisons are made only as part of annual carbon budgets. Potential mismatches of spatial footprints, time of day of measurement, and sampling frequencies of chamber-based soil respiration measurements and eddy covariance-based ecosystem fluxes have made comparisons difficult. We have analyzed these sources of potential errors and biases at the Howland Forest in central Maine in order to provide confidence in seasonal estimates of $R_s/R_{eco}$ ratios. While the mean $R_s/R_{eco}$ ratio across the entire year at the conifer forest of Howland is about 0.6, a consistent seasonal pattern in this ratio observed across 7 years demonstrates seasonal differences in aboveground and belowground C cycling processes. A spring pulse of aboveground respiration appears to cause a minimum in this ratio in March and early April. Soil respiration ‘catches up’ as the soils warm and as root growth presumably accelerates in the late spring, causing the $R_s/R_{eco}$ ratios to increase. The ratio becomes relatively constant during July and August, perhaps because summer drought tends to suppress $R_s$ more than $R_{eco}$, causing the $R_s/R_{eco}$ ratios to stop increasing as soils continue to warm. Declining air temperatures and litter fall contribute to resumption of an increased in $R_s/R_{eco}$ ratios in the autumn. These explanations are largely speculative, but the observed patterns demonstrate that partitioning $R_{eco}$ into its components reveals differential responses to seasonal climatic patterns. The observed distinct seasonal pattern of $R_s/R_{eco}$ ratios points to a need for improved understanding of differences in the phenology of growth of aboveground and belowground plant tissues, mobilization and use of stored substrates within woody plants, seasonal variation in photosynthate and litter substrates, and lags between temperature changes of air and soil.

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## References

Barford CC, Wofsy SC, Goulden ML *et al*. (2001) Factors controlling long- and short-term sequestration of atmospheric $CO_2$ in a mid-latitude forest. *Science*, **294**, 1688–1691.

Borken W, Davidson EA, Savage K *et al*. (2003) Dryng and wetting effects on carbon dioxide release from organic horizons. *Soil Science Society of America Journal*, **67**, 1888–1896.

Borken W, Xu YJ, Davidson EA *et al*. (2002) Site and temporal variation of soil respiration in Eurpoean beech, Norway spruce, and Scots pine forests. *Global Change Biology*, **8**, 1205–1216.

Borken W, Savage K, Davidson EA, Trumbore SE (2005) Effects of experimental drought on soil respiration and radiocarbon efflux from a temperature forest soil. *Global Change Biology*, doi: 10.1111/j.1365-2486.2005.01058.x

Chambers JQ, Tribuzy ES, Toledo L *et al*. (2004) Respiration from a tropical forest ecosystem: an exception to the constant respiration/photosynthesis ratio? *Ecological Applications*, **14**, S72–S88.

Cox PM, Betts RA, Jones CD *et al*. (2000) Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature*, **408**, 184–187.

Curiel Yuste J, Janssens IA, Carrara A *et al*. (2004) Annual Q10 of soil respiration reflects plant phenological patterns as well as temperature sensitivity. *Global Change Biology*, **10**, 161–169.

Davidson EA, Belk E, Boone RD (1998) Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. *Global Change Biology*, **4**, 217–227.

Davidson EA, Savage KE, Verchot LV *et al*. (2002) Minimizing artifacts and biases in chamber-based measurements of soil respiration. *Agricultural and Forest Meteorology*, **113**, 21–37.

Epron D, Farque L, Lucot E *et al*. (1999) Soil $CO_2$ efflux in a beech forest: dependence on soil temperature and soil water content. *Annals of Forest Science*, **56**, 221–226.

Falge E, Baldocchi D, Tenhunen J *et al*. (2002) Seasonality of ecosystem respiration and gross primary production as derived from FLUXNET measurements. *Agricultural and Forest Meteorology*, **113**, 53–74.

Fernandez IJ, Rustad LE, Lawerence GB (1993) Estimating total soil mass, nutrient content, and trace metals in soils under a low elevation spruce-fir forest. *Canadian Journal of Soil Science*, **73**, 317–328.

Goulden ML, Munger JW, Fan S-M *et al*. (1996a) Measurements of carbon sequestration by long-term eddy covariance: methods and a critical evaluation of accuracy. *Global Change Biology*, **2**, 169–182.

Goulden ML, Munger JW, Fan S-M *et al*. (1996b) $CO_2$ exchange by a deciduous forest: response to interannual climate variability. *Science*, **271**, 1576–1578.

Griffis TJ, Black TA, Baumont-Guay D *et al*. (2004) Seasonal variation and partitioning of ecosystem respiration in a southern boreal aspen forest. *Agricultural and Forest Meteorology*, **125**, 207–223.

Hanson PJ, O'Neill EG, Chambers MLS *et al*. (2003) Soil respiration and litter decomposition. In: *North American Temperate Deciduous Forest Responses to Changing Precipitation Regimes* (eds Hanson PJ, Wullschleger SD), pp. 163–189. Springer-Verlag, New York.

Hollinger DY, Aber J, Dail B *et al*. (2004) Spatial and temporal variability in forest-atmosphere $CO_2$ exchange. *Global Change Biology*, **10**, 1689–1706.

Hollinger DY, Goltz SM, Davidson EA *et al*. (1999) Seasonal patterns and environmental control of carbon dioxide and water vapor exchange in an ecotonal boreal forest. *Global Change Biology*, **5**, 891–902.

Hutchinson GL, Livingston GP (2002) Soil–atmosphere gas exchange. In: *Methods of Soil Analysis: Part 4, Physical Methods* (eds Dane JH, Topp GC), pp. 1159–1182. Soil Science Society of America, Madison, WI.

Irvine J, Law BE (2002) Contrasting soil respiration in young and old-growth ponderosa pine forests. *Global Change Biology*, **8**, 1183–1194.

Janssens IA, Lankreijer H, Matteucci G *et al*. (2001) Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. *Global Change Biology*, **7**, 269–278.

Joslin JD, Wolfe MH, Hanson PJ (2001) Factors controlling the timing of root elongation intensity in a mature upland oak forest. *Plant and Soil*, **228**, 201–212.

Lavinge MB, Ryan MG, Anderson DE *et al*. (1997) Comparing nocturnal eddy covariance measurements to estimates of ecosystem respiration made by scaling chamber measurements at six coniferous boreal sites. *Journal of Geophysical Research*, **102**, 28977–28986.

Law BE, Ryan MG, Anthoni PM (1999) Seasonal and annual respiration of a ponderosa pine ecosystem. *Global Change Biology*, **5**, 169–182.

Lee M, Kakine K, Nakatsubo T *et al*. (2003) Seasonal changes in the contribution of root respiration to total soil respiration in a cool-temperate deciduous forest. *Plant and Soil*, **255**, 311–318.

Levine ER, Knox RG, Lawrence WT (1994) Relationships between soil properties and vegetation at the Northern Experimental Forest, Howland, Maine. *Remote Sensing of Environment*, **47**, 231–241.

Lloyd J, Taylor JA (1994) On the temperature dependence of soil respiration. *Functional Ecology*, **8**, 315–323.

Saleska SR, Miller SD, Matross DM *et al*. (2003) Carbon in Amazon forests: unexpected seasonal fluxes and disturbance-induced losses. *Science*, **302**, 1554–1557.

Savage KE, Davidson EA (2001) Interannual variation in soil respiration in two New England forests. *Global Biogeochemical Cycles*, **15**, 337–350.

Savage KE, Davidson EA (2003) A comparison of manual and automated systems for soil $CO_2$ flux measurements: tradeoffs between spatial and temporal resolution. *Journal of Experimental Botany*, **54**, 891–899.

Valentini R, Matteucci G, Dolman AJ *et al*. (2000) Respiration as the main determinant of carbon balance in European forests. *Nature*, **404**, 861–865.

Winston GC, Sundquist ET, Stephens BB *et al*. (1997) Winter $CO_2$ fluxes in a boreal forest. *Journal of Geophysical Research*, **102**, 28795–28804.

Xu M, Qi Y (2001) Soil-surface $CO_2$ efflux and its spatial and temporal variations in a young ponderosa pine plantation in northern California. *Global Change Biology*, **7**, 667–677.