

Components of ecosystem respiration and an estimate of net primary productivity of an intermediate-aged Douglas-fir stand

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Abstract

Continuous half-hourly chamber-measured belowground (R_s) and eddy covariance (EC)-measured total ecosystem (R_e) respiration in a 56-year-old Pacific west coast Douglas-fir stand from 2003 to 2005 were analyzed to study their seasonal and interannual variability. Seasonal variation in both R_s and R_e was better predicted by soil temperature at the 5 cm depth than at any other depth and air temperature. R_e was more responsive than R_s to changes in temperature and soil water content. While nighttime (R_{sn}) and daytime (R_{sd}) soil respiration showed no difference in their response to soil temperature, daytime ecosystem respiration (R_{ed}) was less responsive than its nighttime counterpart (R_{en}) to changes in soil temperature. Half-hourly R_{ed} was almost always smaller than R_{en} possibly due to photoinhibition while daily total R_{ed} was higher than daily total R_{en} during summer and spring months but smaller in winter and autumn months with the latter due to fewer daylight hours. A distinct seasonal pattern in the R_s to R_e ratio was observed. The 3-year mean seasonal R_s/R_e was at its minimum of 0.52 in spring followed by 0.63 in summer, 0.81 in autumn and a maximum of 0.86 in winter. Both daily total and half-hourly R_{sd}/R_{ed} were larger than R_{sn}/R_{en} . It appears that the different responses of R_s and R_e to environmental variables arise as a result of seasonal variations in photosynthesis, mobilization and use of stored carbohydrates, and differences in the phenology of aboveground and belowground plant tissues. On an annual basis, R_s accounted for 62% of R_e with the latter accounting for 86% of the carbon (C) assimilated in annual photosynthesis or gross primary productivity (GPP), leaving the net C sequestration efficiency ($1 - R_e/GPP$) at 14%. In the relatively dry year of 2003, both R_s and R_e as well as GPP were the lowest but with the highest net ecosystem productivity (NEP) of the 3 years. The relatively wetter growing season soil moisture regime in 2005 resulted in the highest R_e and GPP. Partitioning of R_s into its autotrophic and heterotrophic components indicated that 54% of GPP was respired back to the atmosphere as autotrophic respiration and an additional 32% was lost in the decomposition of litterfall and soil organic matter. The mean annual estimate of net primary productivity (NPP) at 843 g C m⁻² accounted for 47% of the mean annual GPP of 1815 g C m⁻².

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1. Introduction

Ecosystem respiration (R_e) is the dominant process determining whether a given ecosystem is a carbon (C) source or a sink (Cox et al., 2000; Valentini et al., 2000; Giardina and Ryan, 2000; Janssens et al., 2001).

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R_e integrates several different soil and plant processes. As respiratory fluxes in conifer ecosystems are generally more sensitive than gross primary productivity (GPP) to seasonal and interannual climate variability (e.g., Goulden et al., 1996; Hui et al., 2003; Morgenstern et al., 2004) and R_e returns a large fraction of C assimilated in photosynthesis or GPP back to the atmosphere as autotrophic respiration (Wofsy et al., 1993; Black et al., 1996; Baldocchi et al., 1997), it is important to quantify components of R_e in order to better understand forest ecosystem C dynamics. Also, partitioning of R_e to its belowground (soil respiration, R_s) and aboveground (canopy respiration) components is needed to better understand the cause of seasonal and interannual variability in R_e . Above all, the aboveground and belowground components of R_e may respond differently to variation in temperature, precipitation, and availability of substrate (Ekblad et al., 2005; Davidson et al., 2006a,b).

Since, soil CO_2 source strength is concentrated near the soil surface (e.g., Jassal et al., 2005), biophysical controls of R_s generally involve soil temperature (T_s) and soil water content at shallow soil depths. Trees, on the other hand, are exposed to air temperature (T_a) and have the capacity to draw water from deeper soil layers, so biophysical controls of R_e may be different than for R_s . It has been assumed that decomposition of soil organic matter (SOM) and therefore R_s will accelerate faster than net primary productivity (NPP) in response to global warming (Kirschbaum, 1995). On the other hand, Liski and Westman (1997) and Liski et al. (1999) have shown that the positive effect of higher temperatures on soil C inputs was far more pronounced than the effect on C losses through SOM decomposition in boreal coniferous forests. Thus, it is likely that the ratio of R_s to R_e (R_s/R_e) will vary seasonally, and that this variation could provide insights into ecosystem responses to varying weather and climate. Davidson et al. (2006b) have reported that R_s/R_e in a spruce-dominated stand in Maine, USA varies seasonally, from 0.45 in early spring to 0.65 in summer and 0.80 in autumn, and that these fall within a wide range of 0.3–0.8 reported for annual R_s/R_e for forest ecosystems globally with the differences arising from vegetation type and stand age. For a mixed coniferous—deciduous forest in the Belgian Campine region, however, seasonal R_s/R_e was found to be at a minimum of 0.50 in summer and maximum of 0.94 in winter (Yuste et al., 2005). However, mean monthly R_s/R_e in plots dominated by deciduous overstory reached a maximum of 0.50 during summer and minimum of 0.30 during winter, which they (Yuste et al., 2005) attributed to more pronounced

seasonality of belowground metabolic activity in deciduous trees. R_s in both of the above-mentioned studies were obtained from manual chamber measurements every 2–3 weeks and monthly or seasonal totals were obtained from fitted R_s versus T_s relationships.

Below- and above-canopy eddy covariance (EC) measurements have been used to determine the role of soil plus understory respiratory fluxes in R_e (e.g., Falk et al., 2006). However, continuous automated chamber measurements of R_s , concomitant with EC-measured R_e , are needed to distinguish the responses of belowground and aboveground components of R_e to seasonal variations in their environmental controls. Though R_s is generally the major contributing source to R_e , few studies have simultaneously and continuously measured R_s and R_e using independent methods in forest ecosystems. Recently, Gaumont-Guay et al. (2006) reported continuous measurements of R_s , R_b (bole respiration) and R_e in a boreal aspen stand to study the influence of long-term variations of environmental and biological variables on component-specific and whole-ecosystem respiration processes. We have made continuous multi-year simultaneous measurements of R_s and R_e in a Pacific west coast intermediate-aged Douglas-fir stand, which provide independent means to identify and understand their biophysical controls and to constrain the ecosystem C budget. Relatively mild, wet winters and moderately warm, dry summers characterize the climate of this region. The low summer precipitation can cause summer droughts, which contrasts this region with most other temperate regions in Europe and Asia where precipitation is relatively constant throughout the year (Waring and Franklin, 1979). The objectives of this study were: (1) to investigate seasonal and interannual variations in components of R_e and R_s/R_e in a 56-year-old Douglas-fir stand, (2) to determine what proportions of GPP are lost in heterotrophic and autotrophic respiration, and (3) to obtain an estimate of NPP.

2. Materials and methods

2.1. Site description and climate measurements

Measurements were made during 3 years (2003 through 2005) in an intermediate-aged Douglas-fir stand (~130 ha) located about 10 km southwest of Campbell River (49°52'N, 125°20'W), on the east coast of Vancouver Island, Canada. The site slash-burned in 1943 followed by planting with Douglas-fir seedlings in 1949 resulting in an almost homogeneous stand. The site is on a 5–10° sloping terrain (300 m above sea level)

and extends at least 400 m in all directions (700 m in the prevailing daytime and nighttime wind directions) from the meteorological tower. The stand has been classified as seasonal dry temperate rainforest in the coastal western hemlock biogeoclimatic zone CWHxm2/05 (Meidinger and Pojar, 1991). Tree density was about 1100 stems ha⁻¹, tree height was about 33 m, and mean tree diameter at the 1.3 m height was 29 cm. The stand consists primarily of Douglas-fir (*Pseudotsuga meneziesii* (Mirbel) Franco) (77%), with lesser quantities of western redcedar (*Thuja plicata* Donn) (18%) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) (4.6%). Understory at the site is sparse, consisting mostly of various species of shrubs, ferns, herbs and mosses. The soil is a deep Humo-Ferric Podzol with a variable surface LFH organic layer of 0–6 cm thick. Below the organic layer, soil texture gradually changes from gravelly loamy sand in the upper 40 cm to sand with increasing depth. The mean annual temperature and precipitation at the site is 8.6 °C and 1450 mm, respectively.

Half-hourly measurements of soil water content and soil temperature profiles were made continuously. Soil volumetric water content was measured at two locations using water content reflectometers (model CS-615, Campbell Scientific Inc. (CSI), Logan, UT, USA). At each location four of these sensors were installed at the 1–2, 10–12, 35–48 and 70–100 cm depths. Soil temperature measurements were made at the 5, 10, 20, and 50 cm depths with copper-constantan thermocouples at the location of CO₂ efflux measurements, which were located about 5 m from one of the CS-615 profiles. Air temperature and relative humidity were measured at the height of the EC instrumentation using a temperature and humidity probe (model HMP-35C, Vaisala Oyj, Helsinki, Finland). Rainfall was measured using two tipping-bucket rain gauges (model 2501, Sierra Misco, Berkeley, CA, USA). Downwelling photosynthetically active radiation (model LI-190SB quantum sensor, LI-COR Inc., Lincoln, NE, USA) and solar irradiance (model CNR1, Kipp & Zonen B.V., Delft, The Netherlands) were measured above the canopy.

2.2. Measurement of soil respiration

Soil respiration measurements were made with a manual portable chamber prior to 15 June 2003 and with both manual and automated non-steady-state chambers since then. Manual measurements were taken every 2 weeks between 4 June and 25 November in 2003 at 10 locations (5 each in the daytime and nighttime flux

footprint areas) within 140 m of the EC tower. At each location, two PVC collars (i.d. 10 cm, length 6 cm) were pre-set (2.5 cm into forest floor) and on each site visit, two replicates of R_s were obtained on each collar. Manual measurements of R_s were taken using a portable chamber system made in our laboratory. The system consisted of an IRGA (mode LI-800, LI-COR), a datalogger (model CR21X, CSI), a diaphragm pump (model TD-4X2N, Brailsford Co., Rye, NY, USA), a storage module (model SM192, CSI) and an opaque PVC chamber (i.d. 10.8 cm, volume 1426 cm³). The chamber was equipped with a temperature and relative humidity sensor (model HMP35CF, CSI). A 20 cm long tube, internal diameter 4 mm, was set into the chamber through the cap to maintain pressure equilibrium between inside and outside the chamber. During measurement (2 min in this study), the pump drew air from the chamber at 2.5 dm³ min⁻¹ through the sampling tube diverting 0.8 dm³ min⁻¹ to the IRGA. A separate line returned air to the chamber mixing the chamber air. All measurements (i.e., CO₂ concentration, temperature and relative humidity) were recorded and stored at 1 s intervals. The rate of change in CO₂ mixing ratio in the chamber headspace (ds_c/dt , mol CO₂ mol⁻¹ dry air s⁻¹) when the chamber was closed was used to calculate the CO₂ efflux, F_e (mol m⁻² s⁻¹) using:

$$F_e = \frac{\rho_a a V}{A} \frac{ds_c}{dt} \quad (1)$$

where ρ_a is the density of dry air in the chamber headspace (mol m⁻³), A the area of ground covered by the chamber (m²), and a is the ratio of the effective volume to the geometric volume (V) of the chamber. CO₂ mixing ratio is used instead of mole fraction ($\mu\text{mol CO}_2 \text{ mol}^{-1}$ moist air) to account for the dilution effect of water vapour in the chamber headspace during measurements (Welles et al., 2001).

From 15 June 2003 to 31 December 2005, R_s was continuously measured every half-hour using a dynamic closed (i.e., non-steady-state) automated chamber at a location about 4 m away from the soil moisture profile. The automated chamber consisted of a PVC cylinder and a transparent Plexiglas dome that was fitted to the cylinder with a hinged aluminium frame. The PVC cylinder dimensions were 52.5 cm internal diameter, 13 cm height, and 1 cm thickness while the nearly hemi-spherical dome had a height of 20.5 cm. The cylinder was inserted to about 2 cm below the soil surface. Main components of the system included an IRGA (model LI-820, LI-COR), a data logger (model CR21X, CSI), an AC linear pump (model

SPP-40GBLS-101, GAST Manufacturing Corp., Benton Harbor, MI, USA) and a solenoid valve. When the chamber was closed (3 min every half-hour), CO₂ concentration in the chamber headspace was measured by circulating air at 15 dm³ min⁻¹ between the chamber headspace and the IRGA. Detailed information about this chamber system and its operation can be found in Jassal et al. (2005). The IRGA was calibrated at the site every 3–4 weeks. With very low evaporation rates from the forest-floor (a maximum of 0.4 mm/day), calculations showed that water vapour dilution effects on CO₂ efflux (Welles et al., 2001) were less than 1%, and were, therefore, not considered in the case of the automated chamber measurements.

Measured respiration data were analyzed using an exponential relationship between respiration and temperature as:

$$R_x = R_{10} Q_{10}^{(T-10)/10} \quad (2)$$

where R_x refers to either ecosystem or soil respiration, and T is either T_a or shallow-depth (e.g., 5 cm depth) T_s . As the variation in R_x with respect to temperature shows heteroscedasticity, i.e., the variance of R_x varies with temperature (Morgenstern et al., 2004), a non-linear OLS fit should not be used to fit the regression line (Tabachnick and Fidell, 2001). Thus, a linear OLS fit to log-linearized data was used. The random error in the independent variable (i.e., T_s) is usually very small. Eq. (2) was written as:

$$\ln R_x = A + BT \quad (3)$$

The slope (B) of Eq. (3) was converted to the Q_{10} value in Eq. (2) using $Q_{10} = \exp(10B)$, which is the relative increase in respiration for a 10 °C increase in temperature. The intercept of Eq. (3) (i.e., A) was converted to a reference respiration rate, here taken to be at 10 °C, as $R_{10} = Q_{10} \exp(A)$.

The proportion of R_s due to microbial decomposition, i.e., the heterotrophic respiration (R_h) was measured during July–November 2005 using a modified small-area trenched plot technique described in Jassal and Black (2006).

2.3. Measurement of nighttime ecosystem respiration

Nighttime EC-measured net ecosystem exchange (NEE), after applying a friction velocity (u_*) threshold filter has been considered to provide reliable estimates of nighttime ecosystem respiration (R_{en}) (Black et al., 1996; Goulden et al., 1996). NEE was calculated as the

sum of the half-hourly EC-measured flux of CO₂ (F_C) and the rate of change in CO₂ storage (F_S) in the air column between the ground and the EC measurement level (43 m above the ground surface):

$$NEE = F_C + F_S \quad (4)$$

F_C was calculated using $F_C = \bar{\rho}_a \overline{w's'_c}$, where $\bar{\rho}_a$ is the mean molar density of dry air and $\overline{w's'_c}$ is the covariance between the vertical velocity (w) and the mole-mixing ratio of CO₂ (s_c). The overbar and prime denote time average (half-hour) and fluctuation from the average, respectively. Calculated NEE under well-mixed conditions at night ($u_* > 0.3 \text{ m s}^{-1}$, see Morgenstern et al., 2004), provided R_{en} . In these well-mixed conditions, advection was assumed to be negligible. About 30% of the R_{en} data satisfied this u_* threshold condition. Mean annual energy balance closure for half-hourly measurements for this site is 0.88 (Morgenstern et al., 2004). As this lack of energy balance closure may be attributed to errors in the measurement of net radiation, energy storage in the air column and biomass, and soil heat flux, no correction for energy balance closure is applied in the present analysis. F_S was calculated using $F_S = h_m \bar{\rho}_a \overline{\Delta s_c} / \Delta t$ (Hollinger et al., 1994), where h_m is the EC measurement height (i.e., 43 m), $\overline{\Delta s_c}$ is the difference between the average (half-hourly mean) CO₂ mixing ratio, \bar{s}_c , of the following and previous half-hours, and $\Delta t = 3600 \text{ s}$. Detailed description of the EC system and its operation can be found in Morgenstern et al. (2004).

Net ecosystem productivity (NEP), which is equal to $-NEE$, is approximately equal to C sequestration, because in upland forest ecosystems C losses from deep percolation of dissolved inorganic or organic carbon are generally negligible compared to other fluxes. The sign convention followed in this paper is that both GPP and R are positive so that $GPP = NEP + R$.

2.4. Estimating daytime ecosystem respiration

Concerns have been raised (e.g., Janssens et al., 2001; Reichstein et al., 2005; Wohlfahrt et al., 2005) about the overestimation of annual R_e due to the use of nighttime NEE versus temperature relationships to calculate daytime ecosystem respiration (R_{ed}) as a result of ignoring the reduction in leaf respiration in light relative to darkness (i.e., photoinhibition). To avoid this problem, many workers (e.g., Lee et al., 1999; Suyker and Verma, 2001; Reichstein et al., 2002; Griffis et al., 2003; Xu and Baldocchi, 2004) have obtained estimates of R_{ed} from daytime NEP (NEP_d) measurements using a

form of the Michaelis–Menten relationship as:

$$\text{NEP}_d = \frac{\alpha Q_t A_{\max}}{\alpha Q_t + A_{\max}} - R_{\text{ed}} + \varepsilon \quad (5)$$

where α is the apparent quantum yield, Q_t the total incident PAR above the canopy, A_{\max} the canopy-scale photosynthetic capacity, and ε is the random error (residual). However, it has been shown that R_{ed} obtained by using Eq. (5) are doubtful, because the variation in R_{ed} values with respect to temperature shows heteroscedasticity, i.e., ε is not normally distributed (Morgenstern et al., 2004; Richardson and Hollinger, 2005; Cai, 2007). To avoid this, we modified Eq. (5) by restricting it to low Q_t conditions so that a linear relationship could be used as follows:

$$\text{NEP}_d = \alpha Q_t - R_{\text{ed}} + \varepsilon \quad (6)$$

A 15-day moving window, advanced 1 day at a time, was used to obtain R_{ed} values from the regression of NEP_d against Q_t for a Q_t range of 0–300 $\mu\text{mol m}^{-2} \text{s}^{-1}$. These daily estimates of R_{ed} were used to develop an annual exponential relationship between R_{ed} and T_s . The value of T_s associated with each R_{ed} estimate was the average of half-hourly values corresponding to the Q_t values used in the regression. We found that ε in Eq. (6) showed a normal distribution with no dependence on T_s . A Q_t range of 0–300 $\mu\text{mol m}^{-2} \text{s}^{-1}$ was used because (a) a survey of a large number of leaf gas exchange experiments showed that the inhibition effect does not increase above a PAR level of approximately 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Wohlfahrt et al., 2005), (b) inclusion of higher values of Q_t risks using data beyond the linear response region (Shapiro et al., 2004) and violating the statistical assumption of normal distribution of ε , and (c) using an upper limit <300 $\mu\text{mol m}^{-2} \text{s}^{-1}$ may not have sufficient daytime influence since many of the shaded leaves deep in the canopy would be still in darkness.

2.5. Calculation of annual totals

We used continuously measured half-hourly R_{en} , R_{sn} and R_{sd} to compute daily and annual totals after gap filling. Gaps in data of less than 2 h were filled by linear interpolation. Larger gaps were filled using a stepwise fit of the respiration versus temperature relationship. For this purpose, a 15-day moving window was used to account for seasonal variations arising due to variations in soil water content and photosynthesis, etc. following Barr et al. (2004) procedure. Half-hourly values of R_{ed} were obtained by using the previously mentioned R_{ed} versus T_s relationship in the above 15-day moving

window procedure, and summed to obtain daily and annual totals. The varying number of daylight hours in different seasons of the year was taken into account when computing daily totals and means of R_{en} , R_{ed} , R_{sn} and R_{sd} . Half-hourly GPP values were obtained as $\text{NEP}_d + R_{\text{ed}}$. Gaps in GPP were filled using a Michaelis–Menten GPP versus Q_t relationship fitted to daytime data when $T_a > -1^\circ\text{C}$ (see Morgenstern et al., 2004) using the 15-day moving window procedure. Gaps in NEP were then filled using the above R_e and GPP values.

Uncertainty associated with annual estimates of R_e and its components was estimated by assigning a random error of 20% (after Davidson et al., 2002; Pumpanen et al., 2004; Gaumont-Guay et al., 2006) to each half-hourly measurement. The half-hourly fluxes within the $\pm 20\%$ variation were re-sampled using a bootstrap Monte Carlo method and annual sums calculated. This procedure was repeated 500 times and the 95% confidence intervals were calculated.

3. Results

3.1. Spatial representativeness of soil respiration measurements

Fig. 1 compares R_s measured at the same location using the portable manual and the automated chamber systems at different times between June and November 2003. R_s measured with the two chamber systems agreed well ($R_{s,\text{manual}} = -0.35 + 1.07R_{s,\text{auto}}$, $r^2 = 0.985$). During the same time we also made 274 manual measurements of R_s at 10 locations in the EC tower flux footprint and compared these with daytime measurements made with the automated chamber installed at a representative location. The large scatter of manual measurements on small collars (78 cm^2 compared to 2165 cm^2 surface area in case of automated measurements) (Fig. 2) indicates large spatial variability. However, the efflux versus temperature relationships for the two data sets were very similar with Q_{10} of 2.59 ± 0.11 and 2.63 ± 0.16 , and R_{10} of 3.23 ± 0.04 and $3.00 \pm 0.09 \mu\text{mol m}^{-2} \text{s}^{-1}$ in case of automated and manual chambers, respectively. Using these to calculate cumulative daytime R_s for the period between 25 June and 25 November gave values of 293 ± 7 and $300 \pm 14 \text{ g C m}^{-2}$ for the auto and the manual chamber systems, respectively, which are within the 95% confidence interval. In 2005, efflux measurements made using the automated chamber were compared with manual measurements from another experiment made using four collars located about 50 m away from the automated chamber (Table 1) and the

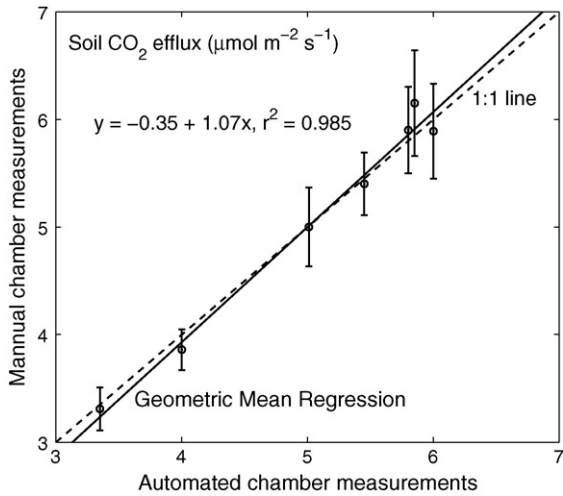


Fig. 1. Comparison of soil CO₂ effluxes measured using manual and automated chambers. Two collars each of 78 cm² surface area for manual measurements were installed within the larger collar of 2160 cm² of the automated chamber. Measurements were made from June to November 2003. Each manual data point is mean of eight measurements, two on each small collar taken before and two after the corresponding half-hour measurement with the auto-chamber. Vertical bars denote ± 1 standard deviation. Since, x -axis variable would also contain stochastic and measurement error, a geometric mean regression is preferred over standard linear regression.

two agreed very well ($R_{s_manual} = 0.14 + 0.95R_{s_auto}$, $r^2 = 0.99$). These results showed that continuous R_s measurements with the automated chamber approximated quite well the R_s in the EC tower flux footprint.

3.2. Seasonal and interannual variability of soil and ecosystem respiration and environmental variables

Fig. 3, showing time series of R_{en} , R_{ed} , R_{sn} , R_{sd} , R_{sn}/R_{en} , soil and air temperatures, soil water content and precipitation over the 3 years, reveals a similar annual pattern in the variations of soil and ecosystem respiration as well as soil and air temperatures. Soil water content clearly showed the regular summer minimum for the west coast with a prolonged summer

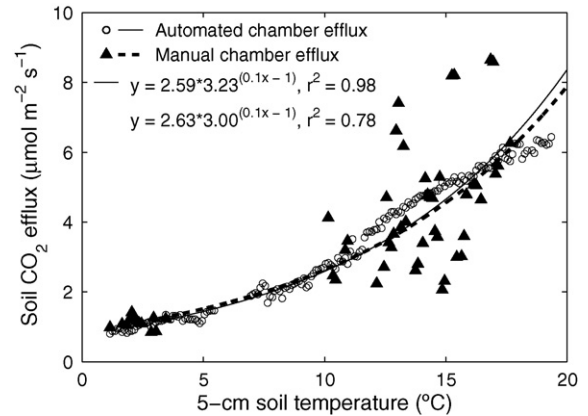


Fig. 2. Temperature response functions of daytime soil CO₂ effluxes measured with manual and automated chambers. Manual measurements were made between May and November of 2003 using 10 collars spread over the flux footprint. The data from both sets were binned using bin widths of 0.1 °C soil temperatures at the 5 cm depth.

drought in 2003 and a wetter 2005 especially during the growing season. Both R_{ed} and R_{en} as well as R_{sd} and R_{sn} followed soil and air temperatures while R_{sn}/R_{en} seasonally decreased with increasing temperature. Though R_{sd} , in general, was slightly higher than R_{sn} , the time series of R_{sd} and R_{sn} are indistinguishable at the time scale shown in Fig. 3a. The drier soil moisture regime during 2003 reduced R_{en} , R_{ed} and R_s .

We found that using the initial linear part of the Michaelis–Menten NEP_d versus Q_t relationship (i.e., Eq. (6)), the calculated R_{ed} during winter months was lower than R_s (Fig. 3a), which is physically unrealistic. This indicates the limitation of this method of estimating R_{ed} from the intercept of photosynthesis versus light curve for winter conditions. Even using Eq. (5), Lee et al. (1999) observed that the correlation between NEP_d and Q_t in a temperate deciduous forest was very poor in winter months, but a high correlation existed between R_{ed} calculated using the NEP_d versus Q_t relationship and T_s , thereby suggesting that the former estimates are less prone to problems seen at night under stable stratification. Moreover, the NEP_d

Table 1

A comparison of soil CO₂ efflux ($\mu\text{mol m}^{-2} \text{s}^{-1}$) measurements made with automated and manual chambers in 2005

Date and approx local time (hh:mm)	Manual chamber mean ^a (and range)	Automated chamber
08 July, 10:00	4.24 (4.05–4.42)	4.46
21 July, 13:30	4.88 (3.63–5.58)	4.96
17 August, 19:00	5.03 (4.03–6.12)	4.93
30 August, 11:00	5.94 (4.52–6.59)	5.56
21 September, 13:00	3.71 (3.19–4.17)	3.62
17 November, 15:00	1.62 (1.13–2.08)	1.58

^a Mean of six observations made on three collars with two replications $R_{s_auto} = 0.14 + 0.95R_{s_manual}$, $r^2 = 0.99$.

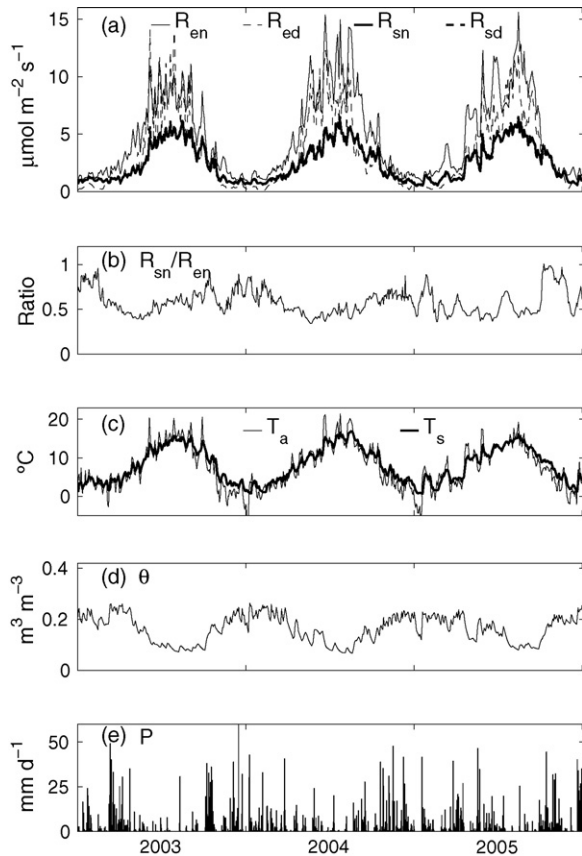


Fig. 3. Time series (1-day running mean) of measured nighttime (R_{en}) and daytime (R_{ed}) ecosystem respiration and soil respiration (R_{sn}) (a), and R_{sn}/R_{en} (b) in relation to 5 cm soil (T_s) and air (T_a) temperatures (c), 0–30 cm soil water content (θ) (d), and daily rainfall (P) (e). R_{sd} was somewhat higher than R_{sn} , though the two variables are indistinguishable at the scale shown.

versus Q_t relationship may be altered with the seasonal changes in soil water availability (Suyker and Verma, 2001). Low R_{ed} during winter months (Fig. 3a) did not affect estimates of annual R_e significantly because fluxes were very low during winter months, though it would tend to overestimate the photoinhibition effect. Constraining R_{ed} as $R_{ed} \geq R_{sd}$ had negligible impact on estimates of annual R_e . For these reasons, we have used only nighttime values, i.e., R_{sn} and R_{en} for describing variation in the ratio of soil to ecosystem respiration on a half-hourly or daily basis.

Table 2 shows seasonal means of environmental variables along with totals of R_s , R_e and their ratio, and R_{en} and R_{ed} . Both R_s and R_e were at their minimum in winter, followed by autumn, spring and summer in ascending order of magnitude, and the trends were similar to those in air and soil temperatures while the difference between these two temperatures had no influence on R_s and R_e . The seasonal R_s/R_e ratio varied between 0.48 during spring of 2004 and 0.97 in winter of the same year. The mean seasonal R_s/R_e ratio over the 3 years was maximum at 0.86 in winter, followed by 0.81 in autumn, 0.63 in summer and a minimum of 0.52 in spring.

Annually, both R_s and R_e were best described by an exponential function (Eq. (2)) of soil temperature at the 5 cm depth (Table 3). Table 3 shows that annually both R_s and R_e were better correlated to shallow depth soil temperature than to air temperature during all the 3 years, and that annual R_e was more sensitive (i.e., higher Q_{10}) than R_s to temperature. While responses of R_{sn} and R_{sd} to soil temperature were similar (Fig. 4b), R_{ed} was

Table 2

Seasonal totals (g C m^{-2}) of soil (R_s) and ecosystem (R_e) respiration and their ratio in relation to seasonal rainfall and means of other environmental variables ($\theta_{\text{top } 30}$: volumetric soil water content in the 0–30 cm layer; ΔT_{d-n} : difference between maximum daytime and minimum nighttime soil temperatures)

Season ^a	T_{air} (°C)	T_{soil} (°C)	$\theta_{\text{top } 30}$ ($\text{m}^3 \text{m}^{-3}$)	Rain (mm)	R_s (g C m^{-2})	$R_e (=R_{en} + R_{ed})$ (g C m^{-2})	R_s/R_e	ΔT_{d-n} (°C)
Wnt03	3.88	3.63	0.25	414	100	109 (83 + 26)	0.92	0.8
Spr03	10.16	8.66	0.21	212	235	438 (189 + 249)	0.54	1.4
Sum03	15.87	13.68	0.10 (0.09) ^b	91	443	712 (303 + 409)	0.62	1.5
Aut03	3.96	5.94	0.23	539	142	180 (132 + 48)	0.79	0.6
Wnt04	2.57	3.07	0.26	377	111	113 (85 + 28)	0.97	0.7
Spr04	11.83	9.94	0.22	169	289	597 (256 + 341)	0.48	1.3
Sum04	15.58	14.14	0.16 (0.10)	198	461	670 (354 + 316)	0.69	1.2
Aut04	5.10	6.41	0.24	498	156	197 (144 + 53)	0.79	0.7
Wnt05	3.47	3.56	0.25	240	90	130 (102 + 28)	0.69	0.6
Spr05	11.02	9.38	0.24	397	263	475 (221 + 254)	0.55	1.0
Sum05	14.46	13.35	0.16 (0.10)	129	460	801 (370 + 431)	0.58	1.1
Aut05	4.22	5.68	0.25	556	170	197 (129 + 68)	0.86	0.5

^a The winter (Win), spring (Spr), summer (Sum) and autumn (Aut) seasons have been classified as January–March, April–June, July–September, and October–December, respectively.

^b Values in parenthesis are for soil water content at the 2 cm depth.

Table 3
Annual temperature sensitivity of soil and ecosystem respiration in a 56-year-old Pacific west coast Douglas-fir stand

Parameter	2003		2004		2005	
	R_s	R_e	R_s	R_e	R_s	R_e
Using T_{soil}						
Q_{10}	4.46	7.60	4.27	6.93	5.42	7.15
R_{10} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	2.61	3.58	2.55	3.63	2.85	4.29
R^2	0.96	0.72	0.95	0.70	0.95	0.78
Using T_{air}						
Q_{10}	2.90	3.81	2.85	3.80	2.94	3.65
R_{10} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	2.47	2.94	2.49	3.23	2.51	3.62
R^2	0.83	0.69	0.81	0.69	0.73	0.69

less responsive than R_{en} to changes in soil temperature (Fig. 4a). Also at a given temperature, daily mean R_{ed} was less than daily mean R_{en} , most likely due to photoinhibition. Fig. 4c shows a slight decreasing trend in R_{sn}/R_{en} with increasing temperature. On average, R_{sn}/R_{en} varied between 0.70 in winter and 0.50 in summer, suggesting R_{en} responded more than R_{sn} to variation in temperature and photosynthesis.

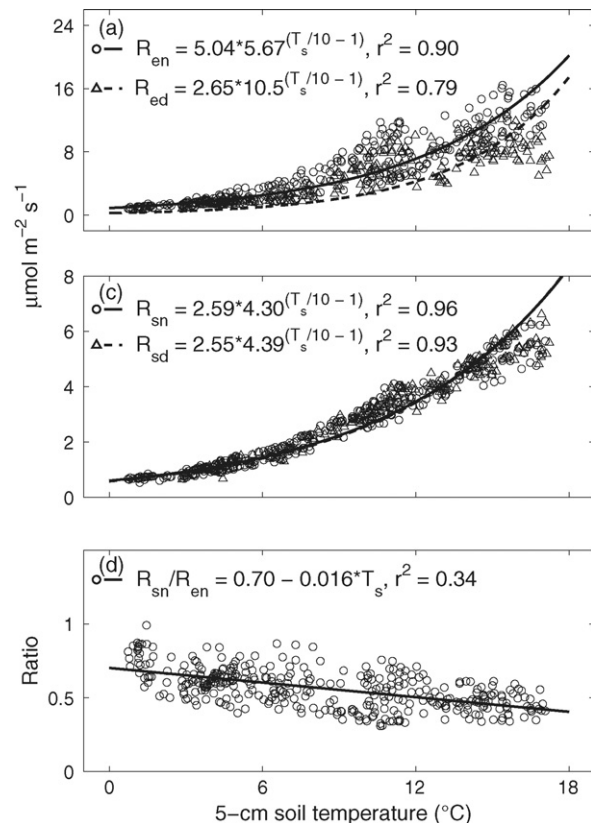


Fig. 4. Response of daily mean nighttime and daytime ecosystem (R_{en} and R_{cd} , respectively) and corresponding soil (R_{sn} and R_{sd} , respectively) respiration and their ratios to variation in 5 cm soil temperature.

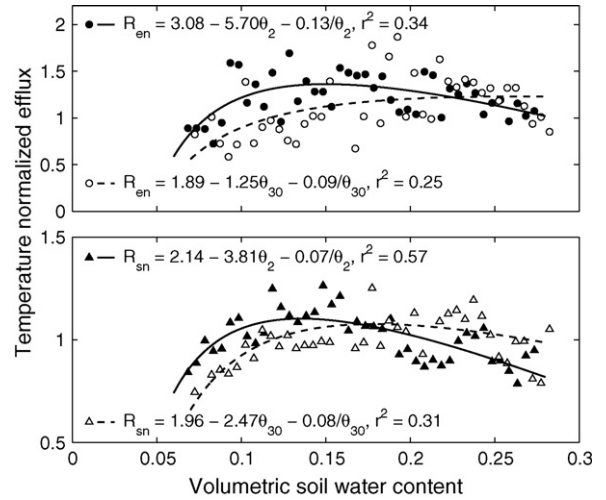


Fig. 5. Effect of soil water content ($\theta_2 = 2$ cm depth (solid line, filled symbols); $\theta_{30} = 0\text{--}30$ cm (broken line, open symbols) on temperature normalized nighttime ecosystem ($R_{en}/R_{en}(T_s)$, top panel) and soil ($R_{sn}/R_{sn}(T_s)$, lower panel) respiration. The data are binned using bin widths of $0.005 \text{ m}^3 \text{ m}^{-3}$ soil water content.

Quantifying soil water content control of R_s and R_e is complicated by the confounding effect of a negative correlation between soil water content and soil temperature (Davidson et al., 1998). Nevertheless, using continuous half-hourly data for the whole year, covering a wide range of soil water contents, it is still possible to see and compare the responses of temperature-normalized R_{sn} and R_{en} to variations in shallow and deep soil water contents. Normalized R_{sn} and R_{en} , obtained by dividing the measured fluxes by those predicted with their best-fit values from Eq. (2), showed a slightly increasing trend at low soil water contents, reaching a maximum at a 2 cm soil water content of about $0.13 \text{ m}^3 \text{ m}^{-3}$ and decreasing thereafter (Fig. 5). We fitted to these data the parabolic relationship:

$$R_{norm} = a + b\theta + \frac{c}{\theta} \quad (7)$$

where R_{norm} is the temperature-normalized component respiration (i.e., $R/R(T_s)$), θ the volumetric soil water content, and a , b and c are regression coefficients. Based on coefficients b and c , it appears (Fig. 5) that temperature-normalized R_{en} was slightly more responsive than temperature-normalized R_{sn} to changes in soil water content at both high and low soil water contents. Also, effects of changes in 0–30 cm soil water content on both temperature-normalized R_{sn} and R_{en} were less pronounced than those of 2 cm soil water content. Rain events following dry spells did not influence R_e and the R_s/R_e ratio much, though R_s was somewhat increased.

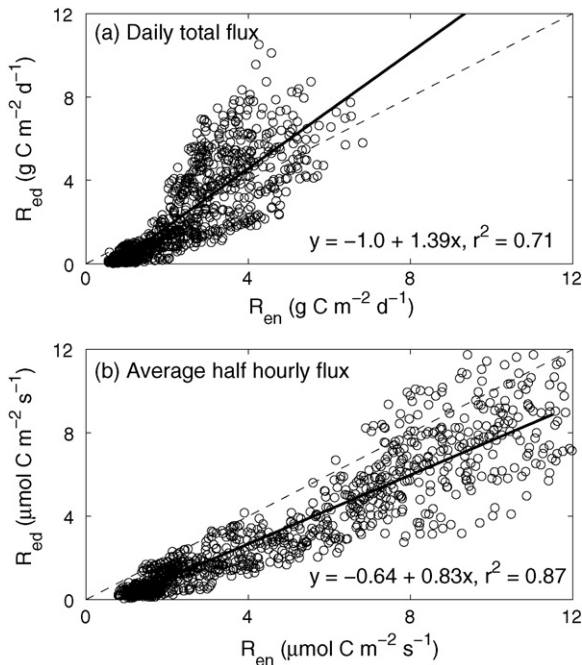


Fig. 6. Relationship between same-day daytime (half-hourly solar irradiance $>1 \text{ W m}^{-2}$) ecosystem respiration (R_{ed}) and nighttime (half-hourly solar irradiance = 0) ecosystem respiration (R_{en}) for 2003–2005: (a) daytime and nighttime totals (the average annual R_{ed} and R_{en} values for the 3 years were 759 and 797 $\text{g C m}^{-2} \text{ y}^{-1}$, respectively), and (b) half-hourly averaged over the daytime and nighttime periods.

Daytime ecosystem respiration was closely related to nighttime ecosystem respiration. On a daily basis, R_{ed} was higher than R_{en} during spring and summer months, when the fluxes were high, due to longer daytime periods and higher daytime temperatures, but the opposite was true in winter and autumn months (Fig. 6a). However, in terms of half-hourly values averaged over daytime and nighttime periods, R_{ed} was 17% lower than R_{en} for the same day (Fig. 6b), most likely due to photoinhibition. This was despite the fact that daytime temperatures were somewhat higher than nighttime temperatures. When R_{ed} was corrected for differences between mean daytime and nighttime soil temperatures at the 5 cm depth, using the estimated Q_{10} (Fig. 4a), daily mean half-hourly R_{ed} was 20% lower than daily mean half-hourly R_{en} .

3.3. Annual totals and interannual variability

Table 4 shows that mean annual R_{s} and R_{e} in this intermediate-aged Douglas-fir forest during 2003–2005 were 981 and 1557 $\text{g C m}^{-2} \text{ y}^{-1}$, respectively. The mean annual $R_{\text{s}}/R_{\text{e}}$ was 0.62. The results further indicate that higher air temperatures during summer 2004 and higher soil water content during summer 2005 resulted in increased R_{e} and R_{s} with a slightly lower $R_{\text{s}}/R_{\text{e}}$ compared to 2003. Prolonged summer drought during 2003 resulted in the minimum annual values of R_{s} and R_{e} of the 3 years.

Mean annual R_{en} at 797 $\text{g C m}^{-2} \text{ y}^{-1}$ was slightly higher than mean annual R_{ed} at 759 $\text{g C m}^{-2} \text{ y}^{-1}$ with

Table 4

Annual totals ($\text{g C m}^{-2} \text{ y}^{-1}$) of different respiration components and other C fluxes in a Pacific west coast Douglas-fir forest in relation to mean annual temperatures ($^{\circ}\text{C}$) and volumetric soil water contents ($\text{m}^3 \text{ m}^{-3}$)

Variable	2003	2004	2005	Mean \pm S.D. ^a
R_{s}	932	1016	994	981 \pm 43
R_{e}	1454	1593	1621	1557 \pm 89
$R_{\text{s}}/R_{\text{e}}$	0.64	0.60	0.61	0.62 \pm 0.02
$R_{\text{h}} = 0.6R_{\text{s}}$	549	610	596	585 \pm 32
$R_{\text{a}} = R_{\text{e}} - R_{\text{h}}$	906	985	1026	972 \pm 61
R_{en}	713	846	831	797 \pm 72
R_{ed}	741	747	790	759 \pm 27
NEP	306	194	273	258 \pm 56
GPP	1761	1789	1895	1815 \pm 70
$\text{NPP} = \text{GPP} - R_{\text{a}}$	855	804	869	843 \pm 34
R_{s}/GPP	0.51	0.55	0.56	0.54 \pm 0.03
R_{e}/GPP	0.83	0.89	0.86	0.86 \pm 0.03
NPP/GPP	0.48	0.45	0.46	0.47 \pm 0.02
T_{air}	8.51 (11.25) ^b	8.80 (13.74)	8.32 (12.76)	8.54 \pm 0.24
$T_{\text{soil}} (5 \text{ cm})$	8.05 (13.03)	8.41 (12.06)	8.03 (11.39)	8.16 \pm 0.21
$\theta_{2 \text{ cm}}$	0.16	0.16	0.16	0.16 \pm 0.00
$\theta_{0-30 \text{ cm}}$	0.20 (0.16)	0.22 (0.19)	0.22 (0.20)	0.21 \pm 0.01

^a S.D. is the standard deviation.

^b Values in parenthesis are the growing season (1 April to 30 September) means.

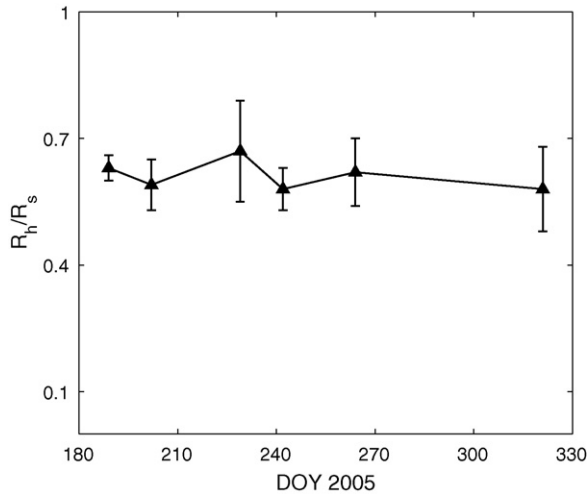


Fig. 7. Seasonal variation in heterotrophic respiration (R_h) as a proportion of soil respiration (R_s) in a 56-year-old Douglas-fir stand measured using the modified small-area trenched plot technique described by Jassal and Black (2006). Vertical bars denote ± 1 standard deviation.

R_{ed} exceeding R_{en} during 2003. Random variability was estimated to be ± 47 and ± 39 $\text{g C m}^{-2} \text{y}^{-1}$ for R_{en} and R_{ed} , respectively. Thus annually, R_{en} and R_{ed} were the same within the uncertainty at the 95% confidence. It may be remembered that apart from the process of photoinhibition, the ratio of daily R_{en} to R_{ed} also depends on: (1) length of daytime, which depends on time of year and thus on the season, and (2) daily temperature amplitude (ΔT_{d-n}), i.e., difference between maximum daytime and minimum nighttime temperatures, which depends on season as well as on cloud cover. Higher R_{ed} than R_{en} during 2003 was most likely due to the relatively higher daytime than nighttime soil temperatures during spring and summer, the seasons of highest respiratory fluxes (Table 2).

Based on our measurements of R_s and R_h during July–November 2005 (Fig. 7) suggesting negligible seasonal variation in R_h/R_s , we assumed that annual R_h accounted for 60% of annual R_s . So we were able to obtain estimates of total autotrophic (aboveground + belowground) respiration (R_a) as well as net primary productivity ($\text{NPP} = \text{GPP} - R_a$). GPP increased with decreasing growing season soil temperature and increasing 0–30 cm soil water content (Table 4). NPP was minimum during 2004 when the mean annual and the growing season air temperatures were the highest of the 3 years.

4. Discussion

Fitting annual data to Eq. (3) showed that soil temperature at the 5 cm depth was a better predictor of

both R_e and R_s than air temperature. Annual Q_{10} values (Table 3) indicated that R_e was more sensitive to temperature than R_s . Reference respiration for R_e was about 1.5 times greater than that for R_s . Q_{10} values far exceeding the widely-accepted Q_{10} of 2 suggest that the temperature response function (Eq. (2)) may integrate, in addition to metabolic activity of the heterotrophs and autotrophs, a number of other different simultaneous processes such as rates of photosynthesis, root growth and senescence. Davidson et al. (2006a) argued that Q_{10} values for respiration that are significantly above 2.5 probably indicate that some unidentified processes of substrate supply are confounded with observed temperature variation. Moreover, a single depth soil temperature is not likely to provide the true Q_{10} for either R_s or R_e because of variation in source strength distribution with depth.

Seasonally, both R_s and R_e were highest in summer and lowest in winter in all the 3 years, but R_s/R_e was maximum in winter and minimum in spring (Table 2). Seasonal changes in R_e were larger than in R_s . In winter, very low aboveground respiration occurs due to low air temperature, but some heterotrophic soil respiration continues in the warmer deeper soil layers. In summer, both R_s and R_e increased in response to increasing temperature with the increase in R_e being greater because of its higher Q_{10} and because autotrophic respiration is implicitly or explicitly linked to photosynthesis rates (Gifford, 2003; Gaumont-Guay et al., 2006), which were highest in summer. The summertime mean soil water content in the top 30 cm layer was the lowest in 2003 among all the 3 years, which reduced R_e significantly but did not affect R_s as much (Table 2). This was because most of the source strength for R_s resides near the soil surface (Jassal et al., 2005) and the summertime near-surface (2 cm depth) soil water content was the same, closer to the wilting point (-1500 kPa) soil water content, during the 3 years. This was possible in this rapidly draining soil despite the seasonal rainfall being much higher during the summer of 2004 and 2005 compared to that during 2003 (Fig. 3e).

Combining data across all the 3 years, R_s/R_e varied between 0.52 in spring and 0.86 in winter. This variation in R_s/R_e is similar to that observed by Davidson et al. (2006b) for a spruce dominated mixed forest stand on the north-east coast of USA and by Yuste et al. (2005) for a mixed coniferous—deciduous forest in the Belgian Campine region. Davidson et al. (2006b) found that springtime increases in soil temperature (at the 10 cm depth) lagged behind increases in air temperature and attributed the lowest springtime R_s/R_e value to the faster

increase in R_e compared to R_s . In the present study, however, no lag was observed between 5 cm soil and air temperatures. Thus, the seasonal variation in R_s/R_e appears to be due to differences in the response of R_s and R_e to changes in temperature and soil water content. Also, an increase in aboveground respiration in spring, in advance of belowground respiration, could be due to springtime mobilization of stored carbohydrates (Davidson et al., 2006b).

The mean annual R_s/R_e ratio of 0.62 found in this study was the same as that for spruce dominated forest stands in Maine, USA (Davidson et al., 2006b) and compares to 0.67 for mixed temperate forest in the Belgian Campine region (Yuste et al., 2005), 0.69 for European forests (Janssens et al., 2001), and 0.48–0.71 for boreal forests (Lavigne et al., 1997; Griffis et al., 2004) (R_e in the Lavigne et al. (1997) study was determined by component fluxes rather than by EC measurements). Higher annual R_e and R_s during 2004 and 2005, and correspondingly higher GPP, were likely due to higher mean growing season air temperature and soil water content, respectively (Table 4).

Mean annual NPP estimate of this intermediate-aged Douglas-fir stand was 843 g C m^{-2} . On average 54% of the C assimilated in photosynthesis (i.e., GPP) was lost to the atmosphere as autotrophic respiration, and an additional 32% was lost as R_h . Thus, the net C sequestration (i.e., NEP) of this Douglas-fir stand was only 14% of GPP. The mean annual ratio of NPP to GPP of 0.47 is consistent with those for many temperate ecosystems, which indicate that about 50% of the C fixed in GPP is used in autotrophic respiration and the other 50% is used to build plant tissues, i.e., NPP (Ryan

and Waring, 1992; Waring et al., 1998; Nabuurs et al., 2003), and compare to NPP estimates of only 25–30% of GPP in boreal conifer (Ryan et al., 1997) and tropical (Chambers et al., 2004) forests, and 54% for a boreal trembling aspen (Griffis et al., 2004).

Using the R_{en} versus T_s relationships to calculate R_{ed} would have resulted in annual total R_e estimates of 1695, 2078 and $1972 \text{ g C m}^{-2} \text{ y}^{-1}$ for the years 2003, 2004 and 2005, respectively, which are on average 23% higher than the estimates obtained in this study. This is also apparent in Fig. 8, which compares daily R_{ed} values for 2003–2005 calculated in this study using the photosynthesis versus light relationship (Eq. (6)) with those using the traditional method of R_{en} versus T_s relationship (Eq. (2)). This compares to a 22% reduction due to photoinhibition in daytime ecosystem respiration in a tallgrass prairie (Suyker and Verma, 2001) and a maximum of 15% in European forests estimated by Janssens et al. (2001). Griffis et al. (2004), using Eq. (5), found that in boreal mature aspen, black spruce and jack pine stands, the reduction in R_{ed} due to photoinhibition was about 10%, and stated that this was within the uncertainty of the R_{en} estimates. Falge et al. (2002) compared annual totals of R_e with R_{ed} calculated using Eq. (5) and those estimated from the R_{en} versus temperature relationship for temperate and boreal forest stands, grasslands and crops, and found that the two agreed well for many of the ecosystems; however, there were also many exceptions, e.g., in boreal black spruce, annual R_e calculated using light response function was about 28% lower than that calculated using the R_{en} versus temperature relationship. Furthermore, calculating R_{ed} using the R_{en} versus T_s relationship in the present study would have decreased the mean annual value of R_s/R_e to 0.52 and resulted in about a 20% increase in annual GPP thereby decreasing the mean annual NPP/GPP estimate to 0.39, which appears to be somewhat low for this productive temperate Douglas-fir stand. Coops et al. (2007) found that the MODIS (Moderate Resolution Imaging Spectroradiometer) product and the 3PGS model under-predicted annual GPP compared to EC measurements (with the R_{en} versus temperature relationship), e.g., MODIS algorithm using local meteorology and $fPAR$ (fraction of total PAR absorbed) predicted 26% lower GPP compared to EC estimates. Our results show that when R_{ed} was obtained from the NEP_d versus Q_t relationship rather than using the R_{en} versus temperature relationship as in the above case, the mean annual GPP estimate of 1815 g C m^{-2} was closer to that predicted with MODIS and 3PGS.

Reichstein et al. (2005) reported that using short-term temperature sensitivity, compared to annual

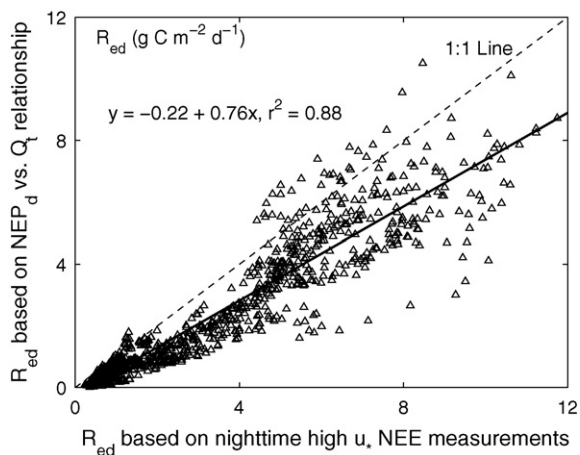


Fig. 8. Relationship between daily R_{ed} for 2003–2005 calculated using the R_{en} (nighttime high u^* NEE) vs. T_s relationship and those calculated using the R_{ed} vs. T_s relationship with R_{ed} obtained from the NEP_d vs. Q_t ($0\text{--}300 \mu\text{mol m}^{-2} \text{ s}^{-1}$) relationship.

temperature sensitivity, in the R_{en} versus T_s relationships resulted in lower annual estimates of respiration. Richardson et al. (2006) and Stoy et al. (2006) also report similar results. Our 15-day moving window procedure ensures that short-term sensitivity is taken into account using either of the R_{en} versus T_s and NEP_d versus Q_t relationships. We feel using the daytime light response curve to infer daytime R_e is more appropriate, especially in ecosystems such as this stand with large foliar biomass ($\text{LAI} \approx 8$). Further support is provided by leaf-level gas exchange measurements at this site, which show mitochondrial respiration to be approximately 50% of that in darkness (Ethier, 2006). However, using Eq. (6) to calculate R_{ed} failed to provide good estimates of R_{ed} during winter months, as was also found by Lee et al. (1999) using Eq. (5). More research is needed to resolve this issue of correctly estimating R_{ed} and GPP, and hence NPP, using EC. Comparing R_{ed} calculated using Eqs. (2), (5) and (6) to that obtained from scaled-up soil, bole and branch chamber measurements, which are becoming technologically feasible, should help in this pursuit.

5. Conclusions

This 3-year (2003–2005) study in an intermediate-aged west coast Douglas-fir stand showed that:

- (1) R_s and R_e responded differently to seasonal variations in soil temperature and soil water content as well as photosynthesis so that the seasonal mean value of R_s/R_e was minimum (0.52) in spring and maximum (0.86) in winter. Despite strong seasonal variation, annual R_s/R_e was fairly constant at 0.62 for the 3 years.
- (2) Seasonal variations in both R_s and R_e were better explained by soil temperature at the 5 cm depth than air temperature. R_e was more responsive than R_s to changes in temperature and soil water content. While R_{sn} and R_{sd} showed no distinction in their response to soil temperature, R_{ed} was less responsive than R_{en} to changes in temperature. Half-hourly R_{ed} was almost always smaller than R_{en} due to photoinhibition while daily total R_{ed} were higher than daily total R_{en} during summer and spring months but smaller in winter and autumn months with the latter due to fewer daylight hours.
- (3) In the relatively dry year of 2003, both R_s and R_e as well as GPP were the lowest but with the highest NEP among the 3 years. The relatively wetter growing season soil moisture regime in 2005 resulted in the highest R_e , GPP as well as NPP.
- (4) Mean annual R_e and GPP were 1557 and 1815 g C m^{-2} , respectively, with annual R_e accounting for 86% of GPP, of which 54% was lost as autotrophic respiration and 32% lost in the decomposition of soil organic matter and litter, leaving the ecosystem C fixation efficiency (NEP/GPP) at just 14%. Mean annual NPP was estimated at 843 g C m^{-2} , which accounted for 47% of mean annual GPP. However, there is a need to confirm these NPP estimates with independent methods like destructive sampling of belowground and aboveground biomass.

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