

## Calibration and validation of an empirical approach to model soil CO<sub>2</sub> efflux in a deciduous forest

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**Abstract.** Soil respiration ( $R_s$ ) was monitored periodically throughout 2001 and 2003 in a pedunculate oak (*Quercus robur* L.) stand located in the Belgian Campine region. An empirical model originally developed for a neighboring pine stand, that accounts for variation in temperature, soil moisture, rewetting of the surface layers by rain during dry periods and seasonal fresh litter inputs, was fitted to the data. The model explained 92% and 94% of the temporal variability in  $R_s$  during 2001 and 2003 respectively. Monthly measurements of  $R_s$  can suffice to build a robust empirical model if temperature is the main controlling factor. However, during the driest period of the year a weekly sampling schedule was needed to capture the combined effect of temperature, soil water content (SWC) and the short-term effect of rewetting played. Although the model was developed for gap-filling purposes it also showed a remarkable predictive ability for this site and these conditions. Annual emissions of carbon (C) estimated with the model were significantly higher in 2001 than in 2003 (7.8 and 5.9 ton C ha<sup>-1</sup> year<sup>-1</sup>, respectively). The severe drought during most of the growing season in 2003 caused a high fine root mortality and a decrease in microbial activity, and was likely the main responsible factor of the almost 2 ton C ha<sup>-1</sup> year<sup>-1</sup> differences in  $R_s$  between both years. Pulses of  $R_s$  during drying/rewetting cycles accounted for a substantial fraction of the total flux, especially during the driest year. Finally, our results show that quality of the substrate may play an important role in both the intensity of the rewetting pulses of CO<sub>2</sub> and the seasonality of  $R_s$ .

### Introduction

A large number of studies have shown that the organic matter in terrestrial soils is very sensitive to climate (e.g. Raich and Schlesinger 1992). The projected increases in temperature and precipitation patterns (IPCC 2001) are therefore expected to affect the current carbon (C) content of terrestrial soils. Especially soils from mid- and boreal latitudes of the Northern Hemisphere, where most of the terrestrial soil organic matter is concentrated (Dixon et al. 1994) and where temperature increases are expected to be highest (IPCC 2001), may act as a key factor in the global C cycle. However, there are still very different opinions about how future climate changes will affect the different C pools (e.g. Giardina and Ryan 2000 vs. Davidson et al. 2000b) and about

uncertainties surrounding the effect of the future temperature-induced changes on soil water content (SWC), net primary production (NPP) or vegetation composition.

On a global scale, soil respiration (Rs) is the second largest carbon flux between the atmosphere and the terrestrial biosphere (Schlesinger and Andrews 2000). In recent years there have been numerous attempts to develop empirical models for quantifying and predicting soil CO<sub>2</sub> efflux (Rs) (Janssens et al. 2003). These models typically predict Rs from variables such as temperature and SWC (e.g. Epron et al. 1999). Although empirical models usually quantify the annual total Rs accurately, their predictive ability is reduced because the simplicity of their algorithms contrasts strongly with the complexity of soil processes. Thus, there is a clear need for process-based models. However, to date process-based models often perform worse than empirical models, highlighting the multitude of remaining uncertainties in our understanding of Rs. Among others, partitioning between autotrophic and heterotrophic respiration and the climate sensitivity of different components of Rs remain unresolved (Giardina and Ryan 2000; Davidson et al. 2000b). Hence, empirical models remain more frequently used than process-based models (Lankreijer et al. in press).

The overall aim of this study was to test the performance and the predictive ability of an empirical model in a pedunculate oak stand. This empirical approach was developed in a Scots pine stand (Curiel Yuste et al. 2003) and differs from others empirical models because it not only accounts for the effects on RS of seasonal changes in soil temperature and SWC but also for the effect of rewetting during dry periods. Under drought conditions, rain strongly stimulates soil CO<sub>2</sub> emissions (Birch 1958, 1960; Andersson 1973; Borken et al. 1999; Davidson et al. 2000a; Rey et al. 2002). These rewetting pulses of Rs have been attributed to the cycles of microbial mortality and rapid re-growth after rewetting due to the availability for the surviving microbes of sugars and nutrients of dead cells (Orchard and Cook 1983; Borken et al. 1999). Some other explanations suggest that rapid changes in soil water potential associated with rewetting may cause microbes to undergo osmotic shock, inducing microbial cell lysis which may produce a pool of labile C and N rapidly mineralize by the remaining microbes (Birch 1958; Kieft et al. 1994). Alternatively, drying-rewetting may cause soil aggregates to break apart, exposing physically protected organic matter (Adu and Oanes 1978; Lundquist et al. 1999) that may be rapidly mineralized by microbes (Apple 1998). Although the exact causes of this phenomenon are still not clear, drying and rewetting cycles may significantly increase mineralization rates (Mamilov and Oliver 2002) and are important to accurately predict future C emissions from soils.

During the years 2001 and 2003, Rs was monitored regularly in a pedunculate oak (*Quercus robur* L.) stand. Pedunculate oak, one of the most widely distributed species of the European temperate forest, occupies the whole of the Atlantic region (high rainfall) and the western transition zone of the central

continental regions (cold winters, moderately warm summers) (Stanners and Bourdeau 1995). In the Belgian Campine region, pedunculate oak is by far the most important deciduous tree species. Particularly, the aims of this study were (1) to test the performance of the empirical model for  $R_s$  in a pedunculate oak stand; (2) to test the predictive ability of the model; (3) to study temporal variability of  $R_s$  and to understand which environmental factors control it; (4) to quantify the annual C emissions in a wet year (2001) and an extremely dry year (2003).

## Materials and methods

### *Site description*

The experimental forest site 'De Inslag' is located in Brasschaat, 20 km NE of Antwerp in the Belgian Campine region (51°18' N and 4°31' E). Pedunculate oaks were planted in 1936, with current tree density of 310 trees ha<sup>-1</sup>, mean tree height of 17.9 m, mean DBH of 25.9 cm and median DBH of 24.0 cm. The site has a temperate maritime climate, with mean annual temperature of 9.8, 3 and 18 °C as mean temperatures of the coldest and warmest month, respectively (Janssens et al. 1999). Mean annual precipitation is 750 mm. Topography is almost flat (slope: 0.3%), and the elevation is 16 m. The forest has a moderately wet, sandy soil with a distinct humus and/or iron B-horizon (Baeyens et al. 1993). The soil type is a psammentic haplumbrept (U.S.D.A. classification) or a umbric regosol (F.A.O. classification). The site has poor drainage due to a clay layer at a depth of 1.5–2 m. The soil is thus moist, but rarely saturated, due to a high hydraulic conductivity in the upper layers (sand). Moisture typically fluctuates around field capacity (0.123 m<sup>3</sup> m<sup>-3</sup>). More detailed information on the soil and local climatic conditions can be found in Baeyens et al. (1993), Janssens et al. (1999) and Kowalski et al. (2000).

### *Soil CO<sub>2</sub> efflux measurements*

A closed dynamic system (IRGA: CIRAS-1, soil chamber: SRC-1, both PP-Systems, Hitching, UK) was used to measure  $R_s$ . To mitigate spatial variability, we enlarged the surface area sampled by the chamber by attaching a PVC-rim to the base of the chamber. The bottom side of the PVC rim had a slot in which a rubber joint provided an airtight seal for the soil collars (Janssens et al. 2000a, b). Modification of the chamber did not alter the measured fluxes (Janssens et al. 2000a, b; Pumpanen et al. 2004). Ten PVC-collars (20-cm diameter, 16-cm height) were installed randomly within an area of approximately 1000 m<sup>2</sup> in November 2000. For more

information about collar design and installation we refer to Curiel Yuste et al. (2003). Soil temperature and SWC were logged continuously in the vicinity of a meteorological tower, 200 m away from the oak plot. Soil temperature was measured at 30-min intervals with two thermocouples located at 2 and 9 cm in the mineral soil. SWC was measured at 25 and 30 cm in the mineral soil respectively using two 50 cm-long, horizontally installed TDR probes, cable tester Tectronix 1502B, USA (Meiresonne et al. 2002). SWC measurements were conducted at two different locations near the tower; one with a shallow clay layer (1 m) and one with a deeper clay layer (2 m). We averaged moisture data from both plots to account for the spatial variability in the depth of the clay layer (Meiresonne and Overloop 1999). Measurements were taken about twice a week and were linearly interpolated. Precipitation (tipping-bucket rain gauge, Didcot DRG-51, UK), relative humidity and temperature (psychrometer, Didcot DTS-5A, UK) measurements were collected at the meteorological tower, and were continuously stored as half-hourly means or totals on a data logger (Campbell CR10, CSI, Logan, UT, USA). In addition to the measurements in the vicinity of the meteorological tower, atmospheric and soil temperature, as well as SWC, were also measured in between the soil collars during the Rs measurements. Atmospheric temperature and temperature at 2, 9 and 15 cm in the mineral soil were measured with a mobile thermocouple that was installed close to the collar while Rs was being measured. SWC was measured with a Profile Probe type PR1 (Delta-T Devices Ltd, UK) at 25 and 35 cm in the mineral soil at three different locations in between the collars. Only very small differences in soil moisture and negligible differences in soil temperature occurred between the plot and the meteorological tower (Curiel Yuste et al. 2004). Although many site-specific data were missing due to technical problems, sufficient data were available to establish a linear regression between soil moisture measured in the plot and that measured continuously near the meteorological tower. This relationship was used to reconstruct the seasonal soil moisture cycle.

Measurements of Rs were performed during two entire years: 2001 (measurements started 2 months after collars were inserted) and 2003 (measurements started 11 months after collars were re-installed). During 2001, 66 Rs measurements were collected during 26 different weeks randomly chosen during the year on 37 different days, indicating that in some weeks there were more than one sampling day. During 2003, 20 Rs measurements were collected during 17 different weeks randomly chosen during the year. In a previous study carried out at the same site, no significant differences in Rs were found between day and night (Janssens et al. 2001a). Therefore, Rs was never measured at night in this experiment and measurements were taken between 6:00 am and 8:00 pm. To get a more accurate estimate of Rs, each measurement was duplicated and the mean was used in the calculations. Rs was pooled over all 10 collars. No significant differences were found between consecutive measurements (data not shown).

*Testing of the rewetting model in oaks*

To simulate the  $R_s$  during both years, the model developed in Curiel Yuste et al. (2003) was used. This model not only takes into account the influence of seasonal variation in soil temperature and soil moisture but also the role of precipitation in rewetting the soil after drought periods. To assess the predictive ability of this method the model was parameterized with the 2001 data set, and the simulated fluxes compared to the 2003 measurements.

The temperature sensitivity of  $R_s$  was estimated by means of a  $Q_{10}$  function:

$$R_s = R_{s_{10}} * Q_{10}^{((T-10)/10)} \quad (1)$$

in which  $R_s$  is the predicted soil  $CO_2$  efflux,  $R_{s_{10}}$  is the simulated  $R_s$  at 10 °C,  $Q_{10}$  is the temperature sensitivity of  $R_s$  (the respiratory flux at one temperature over the flux at a temperature 10 °C lower), and  $T$  is the measured soil temperature at 2 cm in the mineral soil. The function was fitted first to the entire annual data set to get a single  $R_{s_{10}}$  and  $Q_{10}$  for each year. Additionally, the annual data set was divided into three different subsets: winter (winter and early spring), growing season (spring and summer) and fall (fall and early winter). Each of the three datasets was then fitted to the  $Q_{10}$  function to test for seasonal changes in temperature sensitivity. To avoid confounding effects of drought on the temperature response, the following data were removed from the datasets: (I) Measurements taken under drought conditions, defined as SWC below the water holding capacity (WHC) ( $0.123 \text{ m m}^{-3}$ ). (II) Measurements taken more than 30 h after the last significant rain event ( $> 1 \text{ mm h}^{-1}$ ). These data were excluded, because the upper layers, where most of the organic matter and fine roots are located (Janssens et al. 1999), dry out rapidly. Therefore, drought could occur in these upper layers, even if SWC at 25 cm is above WHC. (III) Measurements taken just after a rain event. These data were excluded to avoid possible stimulative effects due to rewetting of the upper soil layers (Birch 1958, 1960; Anderson 1973; Kelliher et al. 1999; Lee et al. 2002; Rey et al. 2002). Thus,  $R_{s_{10}}$  and  $Q_{10}$  were estimated under unlimited moisture conditions and avoiding confounding effects by rain.

When SWC was below WHC, the following model was fitted to the data:

$$R_s = f(T) * f(SWC), \quad (2)$$

where  $R_s$  is the soil  $CO_2$  efflux,  $f(T)$  is Eq. (1) and  $f(SWC)$  a linear function of SWC:

$$f(SWC) = a * SWC + b, \quad (3)$$

where SWC is soil water content in  $\text{m}^3 \text{ m}^{-3}$ , and  $a$  and  $b$  are parameters that were fitted for 2001 and 2003 separately. This linear function was fitted to the residuals of the temperature-normalized fluxes that were not subject to any rewetting effect (solid squares in Figure 1).

Under limited SWC conditions, Rs was enhanced by significant rain events. To define where rewetting was significant and where not, we needed to quantify the rewetting potential of rain events. We assumed that rewetting capacity would be positively related to the water inputs (amount of precipitation) and negatively to the water losses (evaporation, uptake by roots and percolation). Because percolation and uptake by roots were impossible to estimate, we used time since the last rain event as a proxy for these water losses. Also evaporation was not measured. Because vapor flux density is positively related with the atmospheric vapor pressure deficit ( $VPD_a$ ; Penman–Monteith equation), we used  $VPD_a$  as a proxy for the evaporative water losses from the soil surface.

Thus, quantification of the rewetting capacity by rain events was simulated with a rewetting index ( $I_w$ ) that included the absolute amount of precipitation during the rain event,  $VPD_a$ , and time since the last rain. We obtained the best fit to the temperature-normalized fluxes residuals with a logarithmic function of the form:

$$I_w = c + \text{Log}[\text{sqrt}(P)/(\text{VPD}_a * (t)^2)], \quad (4)$$

where  $c$  is a constant (2.5),  $P$  represents the amount of precipitation during the last rainfall event (mm),  $t$  is the time in hours since the last rain event (h) and  $VPD_a$  the mean vapor pressure deficit of the atmosphere at 1.5 m above the forest floor (kPa), averaged over the last 24 h. Thus,  $I_w$  was intended to be a rough representation of the rewetting intensity in the upper soil layers where no moisture sensors were installed.

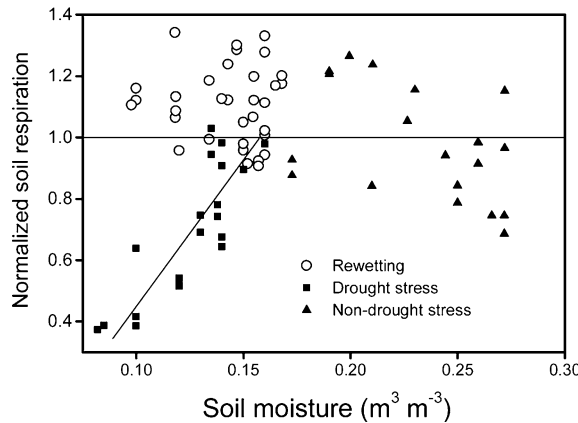


Figure 1. Soil respiration data normalized for temperature (measured Rs was divided by Rs predicted from the temperature response under non-water stress conditions) and plotted vs. soil water content (SWC). Solid triangles represent data with  $SWC > 0.16$  mm and rewetting index ( $I_w$ )  $> -0.7$ ; full squares represent data with  $SWC < 0.16$  mm and  $I_w < -0.7$ ; open circles represent data with  $SWC < 0.16$  and  $I_w > -0.7$ . The solid line represents the linear correction for drought stress.

When the rewetting index was below a certain threshold (e.g. 0.3 in the pine stand), we assumed that fluxes were not affected by rewetting and Eq. (2) was applied. When the rewetting index equaled or exceeded the given threshold we assumed that fluxes were affected by rewetting. For more information about the index and the empirical model design see Curiel Yuste et al. (2003).

Compared to the pine stand, some additional adjustments were necessary to improve the fitting of this rewetting effect. Firstly, it was found that the threshold for rewetting fixed at 0.3 in Curiel Yuste et al. (2003) was too high and needed to be adjusted for this stand. It was observed that rewetting affected the measurements as soon as  $I_w$  exceeded  $-0.7$ . Moreover the stimulation caused by the rewetting during drought increased fluxes on average 10% above those predicted by the  $Q_{10}$  function (Figure 1). To increase the stimulation effect during these rewetting events, the original output of the model during these rewetting events was increased by 10% to avoid underestimation of fluxes during these periods.

Furthermore, it was observed that fluxes were not sensitive to very small rain events ( $< 0.5 \text{ mm day}^{-1}$ ). Hence, rain events smaller than  $0.5 \text{ mm day}^{-1}$  were neglected. In addition, we observed that Rs started to decline as soon as SWC was below  $0.16 \text{ m}^3 \text{ m}^{-3}$ . Therefore, the drought correction was applied whenever soil moisture was below  $0.16 \text{ m}^3 \text{ m}^{-3}$ .

In contrast to the pine site for which the model was developed, we observed large differences in Rs at similar temperatures in spring and fall (Figure 2a). Using a single  $Q_{10}$  function, as is the case in this model, therefore leads to serious under- and overestimation of fluxes during different parts of the year. One of the possible causes of this hysteresis is the different amount of fresh, readily decomposable litter in spring as compared to the fall. Therefore, residuals of the measured data normalized for soil temperature, soil moisture and rewetting effect were plotted against the cumulative aboveground fine litter in  $\text{ton C ha}^{-1}$  at the time the soil respiration was measured. The best fit to these residuals was found with a logarithmic function. The model was then corrected with a seasonality index of the following shape

$$I_s = d * \ln(L + e), \quad (5)$$

where  $I_s$  is the index of seasonality,  $d$  and  $e$  are parameters (Table 1) and  $L$  is the cumulative aboveground fine litter during the year in  $\text{ton C ha}^{-1}$ . This logarithmic correction therefore decreases the modeled fluxes in spring and increases them in fall (Figure 2b), improving substantially the fit with the measured fluxes.

The final shape of the model consists of three different equations that will be applied to three different Rs data pools:

$$\text{Rs(non-stressed)} = f(T) * f(I_s), \quad (6)$$

$$\text{Rs(drought)} = f(T) * f(\text{SWC}) * f(I_s), \quad (7)$$

$$\text{Rs(rewetting)} = 1.1 * (f(T) * f(I_s)), \quad (8)$$

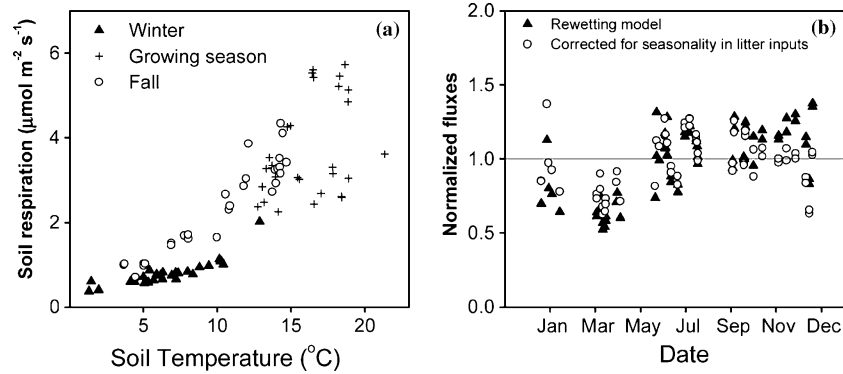


Figure 2. (a) Soil respiration as a function of soil temperature at a depth of 2 cm in mineral soil for 2001. Triangles represent winter/early spring measurements, crosses spring summer measurements and open circles fall measurements. Arrows represent the seasonal direction of the soil respiration evolution. (b) Soil respiration data normalized for temperature (measured Rs was divided by Rs predicted from the temperature response under non-water stress conditions) and plotted vs. day of the year. Full triangles represent fluxes normalized with the rewetting model developed in Curiel Yuste et al. (2003) and open circles fluxes normalized with the model corrected for seasonality ( $I_s$ ). Arrows represent the direction of the change of normalized fluxes.

Table 1. Values of the parameters  $a$ ,  $b$ ,  $c$  and  $d$  of Eqs. (2) and (3) (values of soil sensitivity to temperature ( $Q_{10}$ ), and basal soil respiration at 10 °C ( $Rs_{10}$ ) calculated on an annual basis and excluding the water affected data. Correlation coefficient ( $R^2$ ), and  $p$ -value of the model fit).

Year	Drought		$I_s$		T. sensitivity		Statistics	
	$a$	$b$	$d$	$e$	$Q_{10}$	$Rs_{10}$	$R^2$	$p$ -Value
2001	6.9701	-0.2423	0.60071	3.789	5.65 (0.6)	1.67 (0.08)	0.92	< 0.0001
2003	6.3533	-0.1922	0.60071	3.789	5.9 (2.3)	1.66 (0.16)	0.94	< 0.0001

where  $Rs$  (non-stressed) is soil  $CO_2$  efflux during periods of SWC above  $0.16 \text{ m}^3 \text{ m}^{-3}$ ;  $Rs$  (drought) the  $Rs$  during dry periods, when SWC was below  $0.16 \text{ m}^3 \text{ m}^{-3}$  and  $I_w$  below  $-0.7$ ; and  $Rs$  (rewetting) the  $Rs$  during rewetting events with SWC below  $0.16$  and  $I_w$  above  $-0.7$ . The model was applied on a half-hour basis and results were then integrated to estimate emissions of C on a yearly basis. To evaluate the sensitivity of the model to the temporal scale at which variables such as SWC or litter are defined, the model was also applied using monthly average soil temperature, SWC and fine litter production. Also, in order to assess the relevance of the drought effect and the drying/rewetting cycles to the seasonal and annual soil C emissions the model was run for both years with and without correcting for drought and for the rewetting effect, respectively.



*Seasonal fine root biomass and litter production*

Aboveground litterfall was measured from 2001 to 2003 under the oak canopy using 19 randomly placed collectors (surface area of 0.3 m<sup>2</sup>) with nylon-mesh netting. Litter was collected nearly every month and during periods of higher litter production, such as beginning of the growing season or fall, every 20 days. All litter was oven-dried (2 days, 75 °C) and sorted into branches, foliage and reproductive organs.

Both biomass and necromass of fine (<2 mm) and small roots (2–5 mm) were estimated by repeated core sampling. Samples were collected in the first weeks of February, April, June, August and October 2003. This sampling scheme was selected according to the expected annual minimum (after winter: February) and maximum (after the summer growth peak: August) root masses.

At each sampling date, 25 soil columns of almost 40 cm long were sampled in each forest stand by a metal auger with an inner diameter of 7.0 cm. Then, the soil columns were separated into the organic horizon (O) including the dark uppermost layer of the mineral soil (*A*<sub>1</sub>, 1–2.5 cm thick), and subsequent 10-cm thick soil layers, i.e. pure mineral soil with depths 0–10, 10–20, 20–30 cm. The soil samples were transferred in plastic bags and stored inside a deep-freezer until processed. Roots were manually picked out of the samples, washed and sorted into three diameter classes: 0–1, 1–2, and 2–5 mm. Live and dead roots were separated by visual inspection. Roots considered as live had lighter color than dead ones, typical with high resilience, firm and good cohesion between the cortex and periderm. Dry mass (24 h at 75 °C) of each sample was determined and expressed in mg cm<sup>-3</sup> of soil. Production, mortality and disappearance of roots in between samplings were estimated using the decision matrix of Fairley and Alexander (1985). For more information about the methodology used to calculate fine root production, mortality and disappearance as well as seasonal changes in fine root biomass and necromass see Konôpka et al. (in press). In 2001, fine root productivity was not assessed and therefore fine and small root productivity in 2001 was calculated as the proportion of fine root productivity to total productivity (above and belowground fine litter productivity) as observed in 2003.

*Statistical analysis*

A non-linear least squares fitter (ORIGIN version 5.0; Northampton, MA, USA) was used to determine the exponential fittings of *R*s against temperature.

In order to evaluate the uncertainties associated to the sampling regularity, six different dataset sizes were defined: 6, 10, 12, 23, 40 or 60 samples. This statistical analyze was performed with the larger 2001 dataset. From each of the six defined dataset sizes, eight different replicates were taken. Each of the replicates for each of the defined sample sizes were taken trying to cover the seasonal variation of *R*s. The 48 resulting replicates were then fitted to Eq. (1)

after excluding water-affected data, as explained above. The resulting  $R_{s10}$  and  $Q_{10}$  were applied to the model to obtain an annual estimate of  $R_s$ . The relative error made when calculating annual  $R_s$  within each dataset size was calculated as follows:

$$R_{\text{error}} = \text{SD}/R_s * 100, \quad (9)$$

where  $R_{\text{error}}$  is the percentage error made within each dataset sizes (6, 10, 12, 23, 40 and 60),  $R_s$  and  $\text{SD}$  the mean and the standard deviation of the eight replicated values of annual  $R_s$ .

## Results

### *Measured fluxes*

Climatic conditions were very different in both years (Figure 3a–d). Year 2003 showed clearly more seasonality of soil temperature than 2001, with lower temperatures in winter (some occasions below 0 °C) and higher in summer (up to 24 °C at 2-cm depth in the mineral soil). In 2003 SWC was below the water holding capacity (WHC; 12.3 vol%; Janssens et al. 2000b) during more than three months (from mid-June to beginning of October) and on some occasions close to the wilting point (4% volumetric water content; Janssens et al. 2000b) (Figure 3b). During this year there were also extended periods without precipitation (Figure 3d). In contrast, in 2001, SWC decreased below the WHC only during short periods was never close to the wilting point (Figure 3a), and with more frequent precipitation events (Figure 3c).

Soil respiration ranged from 0.4 to 5.6  $\mu\text{mol m}^{-2} \text{s}^{-1}$  in 2001 and from 0.4 to 3.9  $\mu\text{mol m}^{-2} \text{s}^{-1}$  in 2003 (Figure 3e and f). There were therefore large inter-annual differences in the seasonality of  $R_s$ , especially due to the differences in late spring and summer rates. In both years, fluxes were similar during winter and early spring, fluctuating around 0.4  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , and began to rise in the third week of April. Despite the higher soil temperatures during the summer of 2003, fluxes were substantially lower than in 2001 during the same period.

### *Modeled fluxes*

The uncertainties associated to sample size followed an exponential shape (Figure 4). As expected, the largest uncertainties were found with number of samples per year ( $n$ ) = 6 while the lowest when  $n$  = 60. According to Figure 4 to reduce the uncertainty related to sample size below 5% on annual  $R_s$ , at least 10 measurements were needed. To reduce the uncertainty below 2% 20 measurements were needed. With 60 samples the error reached the 1% uncertainty.

When parameterized with the whole data set, the model explained most of the temporal variability in soil respiration (Table 1). Annual emissions of C

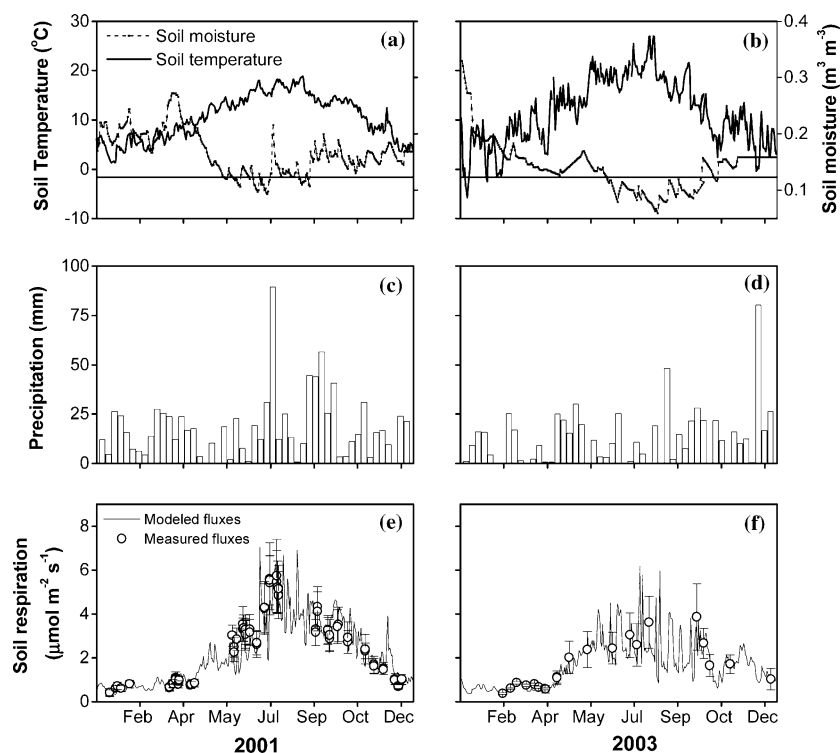


Figure 3. Modeled and measured soil respiration under pedunculate oak stand during 2001 (a) and 2003 (b). Vertical bars represent standard deviation. Weekly total precipitation (open columns) during 2001 (c) and 2003 (d). Daily mean soil temperature (ST) at 2-cm depth in the mineral soil (solid line), soil water content (SWC) at 25-cm depth in mineral soil (line + square symbol) during 2001 (e) and 2003 (f). The horizontal bar represents the water holding capacity ( $0.123 \text{ m}^3 \text{ m}^{-3}$ ).

estimated with the model were significantly higher in 2001 than in 2003 (Table 2). Even with the parameters derived from 2001 data, the model performed well in 2003 (Figure 5), with a fit slightly lower than that obtained when the model was parameterized with 2003 data ( $R^2$  0.88 compared to 0.94). When the model was applied using monthly averaged soil temperature, SWC and litter inputs, results were similar to the half-hourly averaged at both years (Figure 6a and b). Total annual C emissions estimated with both approaches (half-hourly and daily time step) were also very similar (Table 2).

#### *Environmental factors controlling $R_s$*

Despite the differences in climatic conditions and in seasonal evolution of  $R_s$ , the temperature sensitivity represented as annual  $Q_{10}$  (excluding the drought-affected and rewetting data) and annual basal respiration rates represented as

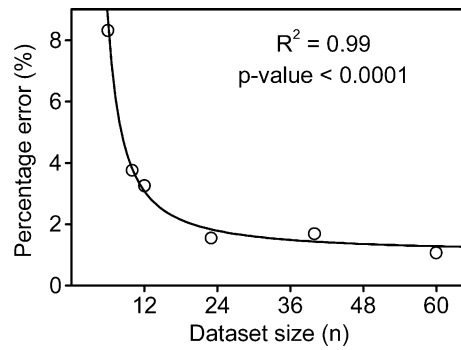


Figure 4. Percentage of error (%) as a function of the number of sampling dates in the dataset ( $n$ ) (open circles) and the exponential fit (solid line).

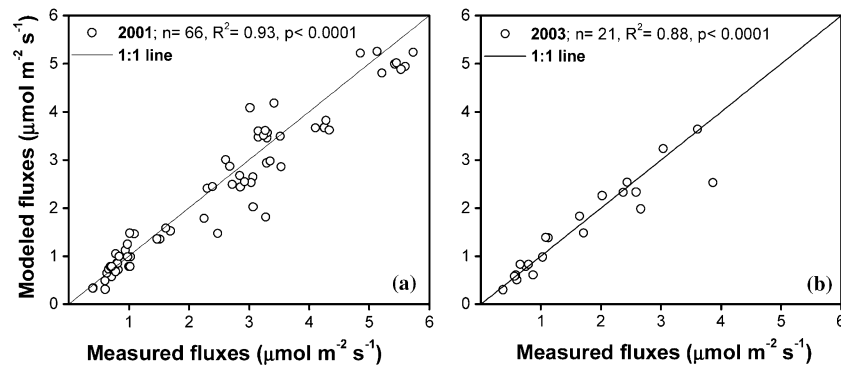


Figure 5. Measured vs. modeled fluxes for 2001 (open circles) and 2003 (full triangles). Number of measurements ( $n$ ), correlation coefficients ( $R^2$ ) and  $p$ -values for each year are also shown. The solid line represents the 1:1 line.

Table 2. (Total  $R_s$ ) above- and belowground litter inputs (above litter and below litter respectively) and sum of the litter inputs (total litter) are also shown.

Year	Ton C ha <sup>-1</sup> year <sup>-1</sup>						
	Annual soil C emissions				Annual C inputs via litter		
	Half-hourly	Monthly average	Half-hourly no SWC	Half-hourly no rewetting	Above litter	Below litter	Total litter
2001	7.8	8.1	9.2	7.1	2.9	1.2	4
2003	5.9	6.0	8.6	5.1	3.2	1.3	4.5

$R_{s10}$ , were very similar in both years (Table 1). Similar to the pine stand in the same forest (Curiel Yuste et al. 2003) temperature control over  $R_s$  was only limited during the growing season, whereas the rest of the year temperature explained most of the variability in  $R_s$  (Figure 7).

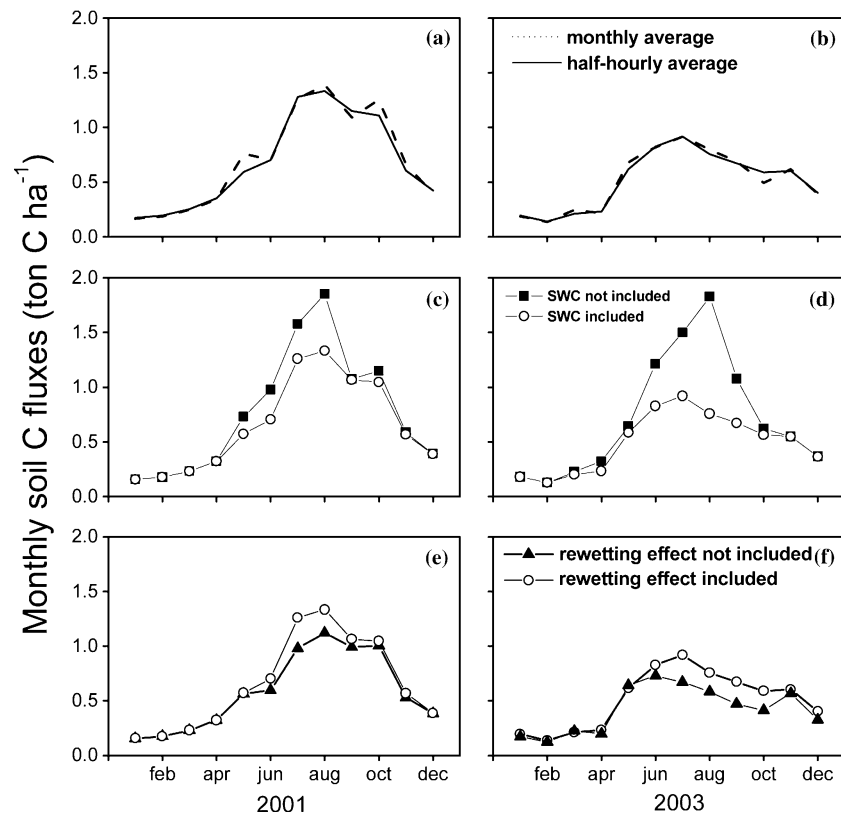


Figure 6. Total monthly soil respiration modeled using monthly average (solid line) and half-hourly average soil temperature, SWC and litter production in 2001 (a) and 2003 (b). Total monthly soil respiration modeled with (open circles) and without (solid triangles) applying the correction for SWC in 2001 (c) and 2003 (d). Total monthly soil respiration modeled with (open circles) and without (solid triangles) applying the rewetting index in 2001 (e) and 2003 (f).

When the correction for SWC was not applied in the model, annual soil C emissions increased substantially in both years (Table 2). Drought thus exerted a strong effect on Rs especially during summer, but also in spring and fall (Figure 6c and d). Assuming that in the absence of water limitation, Rs would be controlled by temperature and the seasonality of litter production, drought accounted for a reduction of the annual fluxes of approximately  $1.4 \text{ ton C ha}^{-1}$  during 2001 (15% of the annual total) and  $2.7 \text{ ton C ha}^{-1}$  during 2003 (32% of the annual total) (Table 2). Differences between both modeling approaches were especially pronounced June and September 2003 (Figure 6d), which coincides with the driest period of this data set.

Drying and rewetting cycles also played an important role in Rs during the summer (Figure 6e and f). In 2001 the rewetting effect was important only during the months of July and August, the driest and warmest months of the

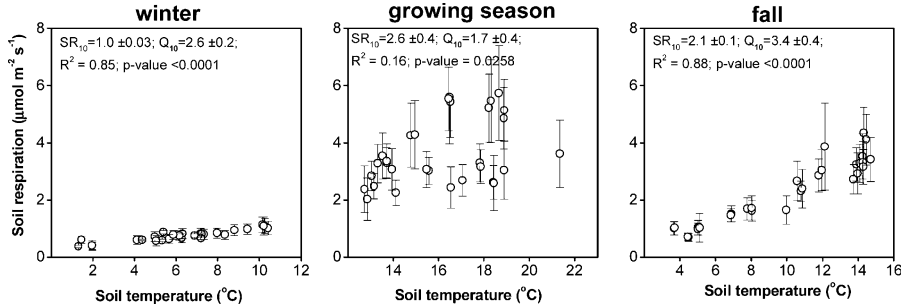


Figure 7. Soil respiration as a function of soil temperature at a depth of 2 cm in mineral soil for winter, growing season and fall periods and its corresponding  $Q_{10}$ ,  $RS_{10}$  and statistics ( $R^2$  and  $p$ -value). Vertical bars represent standard deviation.

year, and accounted for an increase of  $0.7 \text{ ton C ha}^{-1} \text{ year}^{-1}$ , almost 9% of the total annual soil C emissions (Table 2). In 2003 the model without the rewetting algorithm systematically underestimated  $R_s$  during four months (July–October; Figure 6f) and the rewetting effect accounted for an increase of  $0.9 \text{ ton C ha}^{-1} \text{ year}^{-1}$ , 13.5% of the total annual soil C emissions (Table 2). Moreover, unlike in the neighboring pine stand, these rain-induced  $\text{CO}_2$  pulses exceeded the fluxes predicted by simple temperature function (Figure 8).

Fine root biomass in the pine stand underwent larger seasonal changes than in the oak stand, although biomass of fine roots was typically higher in the oak than in the pine stand (Figure 9). Hence, fine root productivity during early

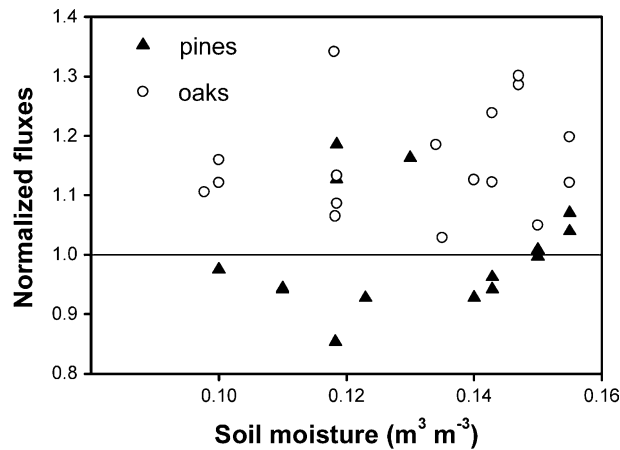


Figure 8. Soil respiration data from rewetting fluxes ( $\text{SWC} < 0.16 \text{ mm}$  and  $I_w > 0.3$ ) normalized for temperature (measured  $R_s$  was divided by  $R_s$  predicted from the temperature response under non-water stress conditions) and plotted vs. soil water content (SWC). Solid triangles represent data from a neighboring Scots pine stand and open circles data from the oak stand.

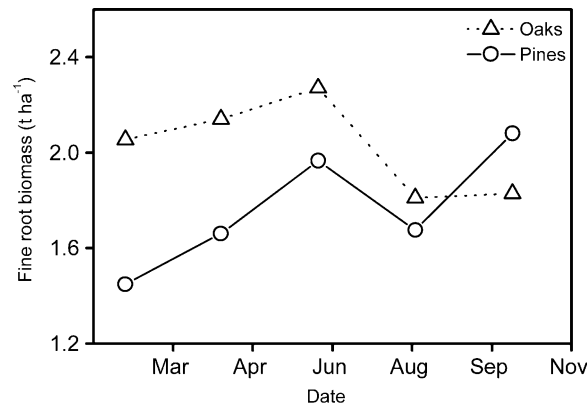


Figure 9. Seasonal evolution of fine root biomass (< 2 mm) in pines and oaks.

spring and summer was higher under pines than under oaks (Konôpka et al. in press), which explains the observed larger increase in fine root biomass under pines from winter to summer. Also, pine roots recovered better from the severe summer drought, responsible for the massive fine root mortality during July and August 2003 (Konôpka et al. in press), resulting in higher biomass under pine than under oak during the last part of the year. However, no relationship was found between seasonal changes in root biomass and the residuals of the fluxes normalized for temperature and drought (data not shown). Although some of the highest values of  $R_s$  coincided with a period of high root biomass and maximal fine root productivity (June–August, see Konôpka et al. in press), the peak in  $R_s$  occurred during the period of minimal fine root biomass and fine root productivity (early September).

## Discussion

### *Model performance*

Despite the complexity of the processes that control soil biological activity, this empirical approach that includes climate and seasonality of fresh litter inputs explained a large portion of the interannual and seasonal variation of  $R_s$ . Our results indicate that approximately one sample per month (10–12 samples spread along the year), may produce relatively good annual estimates of  $R_s$ . This uncertainty was, however, calculated under unlimited moisture and thus strong temperature control ( $Q_{10}$ 's were calculated only with the data not affected by water limitation). Therefore, during periods of unlimited moisture not many samples are needed to capture the seasonal variation in  $R_s$ . However, as shown in this study, drought and rewetting effect played a very important role during the growing season (Figure 7). Both, drought and rewetting are

opposite effects and hence do not occur at the same time. Therefore, to capture the water effect, the sample strategy should at least be multiplied by 3, which imply to measure at least three times per month during the growing season. The good characterization of the drought and rewetting effects in this model was possible because  $R_s$  was measured on approximately weekly basis during the driest period of the year.

The good fit obtained when the model with 2001 parameters was compared to 2003 flux data suggests that although the model was initially developed for gap-filling purposes, it also holds a certain predictive ability. This empirical approach however does not take into account management practices such as thinning or important biological processes such as changes in live microbial biomass and exudates produced by roots and mycorrhizae or current photosynthate allocation to roots. Therefore, the observed predictive ability is probably limited to site-specific relatively short-term predictions of  $R_s$ .

Values of annual  $R_s$  for 2001 and 2003 were in the range reported by Janssens et al. (2001b) for European forest (3.8–8.5 ton C ha<sup>-1</sup> year<sup>-1</sup>). The agreement in annual C emissions between the model applied to variables (soil temperature, SWC and litter input) averaged on a half-hourly and a monthly basis (Table 2) indicates that part of the model did not need such a short-term resolution as that used in the original model. However, the rewetting effect of rain events cannot be modeled on monthly basis because this phenomenon is only detectable on a daily time scale (Borken et al. 1999; Davidson et al. 2000a; Rey et al. 2002). Although daily means would have suffice to characterize annual  $R_s$ , we used a finer temporal scale simply because the original model was developed at a half-hourly resolution (Curiel Yuste et al. 2003).

#### *Environmental factors controlling $R_s$*

The values of annual  $Q_{10}$  (Table 1) were clearly higher than those reported in other studies (e.g., Raich and Schlesinger 1992) and probably reflect not only temperature but also other seasonal factors that covary with temperature, such as root or mycorrhizal biomass (Davidson et al. 1998; Curiel Yuste et al. 2004, in press). The lack of relationship between seasonal changes in root biomass and  $R_s$  suggest that root biomass and root activity are not the same and hence that root biomass cannot be used as a proxy for root activity. Temperature, soil moisture, nitrogen availability and especially substrate supply to the roots may influence the seasonality of growth and maintenance respiration of fine roots (Pregitzer et al. 2000; Högberg et al. 2001). However, root activity as well as seasonality of substrate supply to belowground components was not studied in this experiment. Moreover, we also observed large development of extramatrical ectomycorrhizal (ECM) during the onset of the growing season (De Clerck 2004), which also was not accounted for in this study. Thus, part of the large seasonal changes in  $R_s$  in the oaks may originate from ECM activity.



Due to the apparent complexity of this relationship this model therefore did not include the influence of fine root dynamics on  $R_s$ , but we encourage future studies to explore the connection between  $R_s$  and plant C allocation to root and mycorrhizal activity.

Despite the higher temperatures reached during the growing season of 2003,  $R_s$  calculated with the model was larger in 2001 (Table 2) indicating that other factors besides temperature exerted an important influence in  $R_s$ . A finer analysis of the temperature sensitivity of  $R_s$  suggests that temperature was the main controlling factor during a large part of the year, but it cannot explain the variability of  $R_s$  during the growing season (Figure 7). Figure 6c and d show the very important role that SWC played during the warmest and most active period of the year. According to our model, drought reduced  $R_s$  by 15% during 2001 and by 32% during 2003, indicating the important role that drought played during 2003. During 2003, the period of maximal differences between both models (also the period with lowest SWC; Figure 3b) coincided with strong fine root mortality and low decomposition rates (Konôpka et al. in press). Although no record of fine root biomass was available for summer 2001, it is therefore likely that a large portion of the 24% difference in annual  $R_s$  between years were caused by the drought-induced fine root mortality and low microbial activity observed during summer 2003. This observation emphasizes the role that C allocation to fine root production and maintenance may have in annual values of  $R_s$ , as already observed in other studies (Högberg et al. 2001; Campbell et al. 2004).

The reduction of the threshold of the rewetting index ( $-0.7$  compared to the  $0.3$  of the pine stand), indicated that the oak stand was more sensitive to rain pulses than the pine stand. No relation between the intensity of the rewetting and temperature or SOM quantity (data not shown) was found in our study, indicating that other variables might be responsible for the observed dissimilarity in the intensity of the  $CO_2$  pulses. We hypothesize that the quality of the substrate may have played a very important role in the observed interspecific differences in magnitude and duration of this effect. It is well recognized that litter from evergreen species tends to have both higher lignin and lower nutrient concentrations than deciduous litter (Coley et al. 1985), which generally results in slower decomposition of the substrate (Van Cleve 1974; Heal et al. 1981; Hobbie 1996). The less nutrient-poor soil and the more decomposable litter of the oak plot may therefore have facilitated the microbial proliferation in the rewetted soil and litter layer explaining the stronger rewetting effect. Although this empirical approach does not explain the processes that drive this fast response of  $R_s$  to sudden changes in water availability, it highlights the importance of rewetting for  $R_s$  even in the relative humid conditions of the study area (Figure 5e and f and Table 2). When drought periods were more extended in time with longer rain-free gaps between precipitation events, as in 2003 (Figure 3a–d), the rewetting effect became more important. The meteorological conditions during 2003 may therefore have caused a stronger dependence on these cycles of microbial

mortality and subsequent microbial growth stimulation during the long drought.

The addition of the seasonality correction  $f(I_s)$  to the model was necessary and increased the fitting with the measured  $R_s$ . Several causes may explain this seasonal hysteresis of the flux. Firstly, because fluxes were plotted against soil temperature measured at just one depth (2 cm in the mineral soil), the hysteresis might be an artifact caused by the seasonal differences in soil thermal properties below the temperature sensor. In winter and early spring only the uppermost parts of the soil profile are warm enough for microbial activity, while after summer, deeper layers of the soil profile are warmer than in winter and likely more metabolically active. However this seasonal hysteresis did not occur in the neighboring pine stand where much more carbon resided in the mineral soil than under oak (Curiel Yuste et al. in press), suggesting that this temperature effect did not play such an important role. Seasonality of fine root biomass could not explain this observation either. Fine root biomass under pines experimented larger seasonal changes than under oaks with less fine root biomass during winter but substantially higher fine root biomass than oaks during fall (Figure 9), which clearly contrasted with the differences in seasonal evolution of  $R_s$  between plots. Another, more plausible explanation might be that in fall, much more fresh material becomes available for decomposition in the oaks, enhancing the heterotrophic respiration and, hence,  $R_s$  rates are higher than in spring at a similar temperature. Under the deciduous canopy of this study site, the input of fresh litter peaked in the second part of the year when temperature as well as SWC was still high enough for microbial growth. Such an effect of seasonality of fresh plant material inputs to soil has previously been reported by Schlesinger (1977) and Rey et al. (2002) and was attributed to the incorporation of soluble carbon and readily decomposable material in the soil. Because microbes preferably use the short-lived fractions of SOM as an energy source (Parton et al. 1987; Trumbore et al. 1990; Schimel et al. 1994) and, as explained above, deciduous litter is typically easier to decompose than evergreen litter, it is likely that microbial activity in the last part of the year was more enhanced in oaks than in pines.

## Conclusions

Our results show that monthly measurements of  $R_s$  can suffice to build a robust model if temperature is the main controlling factor, in this study  $R_s$  was measured on a weekly basis during the critical summer periods to capture the important influence of drought and rewetting during summer. Temperature exerted dominant control during most of the year. However, during the most active period of the year, SWC and drying/rewetting cycles exerted a stronger control over  $R_s$ , especially during the warmer and drier year. Seasonality of fresh litter inputs played an important role during the last part of the year,

probably by enhancing microbial activity. Although no correlation between seasonal changes in fine root biomass and  $R_s$  was found in this study, this does not imply that there was no dependence of  $R_s$  on fine root activity. Moreover, an important portion of the large differences in  $R_s$  between years was probably caused by the large summer fine root mortality in 2003. Future studies should take into account the influence of seasonality of plant C allocation to fine root and mycorrhizal activity in  $R_s$ .

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