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**Variation of root and
rhizosphere
respiration in a pine
forest**

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Contribution of root and rhizosphere respiration to the annual variation of carbon balance of a boreal Scots pine forest

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Abstract

A large part of gross primary production (GPP) is consumed in root and rhizosphere respiration (R_r). To measure R_r , a group of evergreen coniferous Scots pine (*Pinus sylvestris*) trees were girdled in a 45-year-old even aged forest in Hyytiälä, Southern Finland. In the girdling, phloem and bark were removed from breast height around the trees. We measured soil CO₂ effluxes with a dynamic chamber at the girdled plot and at a non-girdled control plot in close vicinity. Before the girdling, effluxes were 22% higher at the plot to be girdled compared to the control plot. We scaled the measurements so that before girdling the effluxes representing total soil respiration (R_s) were at the same level. We compared the R_r and R_d to GPP measured with eddy covariance system. Our results show that R_r has higher seasonal variation than R_d , and also spatial variability was higher for R_r . The annual R_r : R_s and R_r :GPP-ratios were 0.36 and 0.21, respectively. R_r : R_d varied seasonally and in late summer and in autumn R_r exceeded R_d . R_r followed GPP with a delay of several weeks. During winter and spring R_r was very low, even when GPP and soil temperature had significantly risen. We conclude that R_r and R_d have different response to the environment and that for R_r the substrate availability is a more important explaining variable than soil temperature.

1 Introduction

As gross primary production (GPP) determines the CO₂ flux to an ecosystem, total ecosystem respiration (TER) determines the CO₂ flux from the ecosystem to the atmosphere. In a forest ecosystem TER is the sum of aboveground respiration (R_a) and soil respiration (R_s). R_s consists of respiration originating from decomposition (R_d) and root and rhizosphere respiration (R_r). Plants act as sources of easily decomposable carbohydrates to soil by releasing root exudates, which sustain mycorrhizal fungal symbionts, but also other groups of specialized micro-organisms. Recent studies have shown that the consumption of carbohydrates by the mycorrhizae is important in the carbon bal-

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ance of forest ecosystems (Högberg and Read, 2006). It has also been shown that root exudates and other easily decomposable carbon can enhance the decomposition of old soil organic matter (Subke et al., 2006; Fontaine et al., 2007).

The environmental response of belowground respiration is complex. For example on a short time-scale, temperature explains soil respiration well, but on a longer time-scale substrate availability is much more important (Gu et al., 2004). Substrate availability has a confounding effect on the temperature response of soil respiration if it varies with measurement temperature (Kirschbaum, 2006). This is particularly important in boreal forests where the biological activity has a strong seasonal cycle.

R_r and R_d respond differently to the environment, and the responses may change during the year (Epron et al., 2001; Reichstein et al., 2005). Most of the substrate for R_r is fixed within preceding few days in photosynthesis and therefore the feedback between photosynthesis and R_r is relatively fast (Högberg et al., 2008; Knohl et al., 2005). In comparison, there is always substrate available for R_d , though substrate production of above and below ground litter also has a very strong seasonal cycle in boreal forest ecosystems. During the winter the vegetation is dormant and most of the respired CO_2 is originated from the decomposition of detrital matter, whereas in the summer the vegetation is active and introduces easily decomposable carbon into the soil. Moreover, respiratory processes are interconnected with each other and there are feedbacks to other processes, such as nutrient uptake of plants, as it is one of the main functions of the root system. Due to these reasons, the dynamics of R_r and R_d are different, and should be treated separately.

The partitioning of soil CO_2 effluxes within forest ecosystems have been studied with different approaches described in Hanson et al. (2000). In many studies R_r is determined as root and rhizosphere respiration to total soil respiration ratio ($R_r:R_s$), which further can be used to calculate R_r from R_s . As R_r and R_d respond differently on environment, $R_r:R_s$ -ratio changes on an annual scale. However, often only summertime and not annual $R_r:R_s$ -ratio has been defined (Subke et al., 2006). To our knowledge, so far, there is no ecosystem-level study of boreal Scots pine forests, in which annual

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R_r or $R_r:R_d$ -ratio is being determined, or compared to the GPP on an annual basis. For an overview of the studies separating R_s to R_r and R_r , see Bond-Lamberty et al. (2004) and Subke et al. (2006).

The aim of this study was to 1) quantify the proportions of root and rhizosphere respiration and respiration originating from decomposition from total soil respiration on both monthly and annual time scales, to 2) determine the environmental responses of R_d and R_r and 3) to estimate how much of the carbon assimilated in photosynthesis by trees is consumed in root and rhizosphere respiration on monthly and annual time scales. We determined the $R_r:R_s$ -ratio using a girdling experiment and compared the different components of soil respiration to GPP measured with eddy covariance system.

2 Materials and methods

2.1 Site description

The study site was in a 45-year-old coniferous evergreen Scots pine (*Pinus sylvestris*) dominated stand at SMEAR II measurement station in Hyytiälä, Southern Finland (61°51' N, 24°17' E, 180 m a.s.l.). The mean annual precipitation in Hyytiälä is 709 mm and mean annual temperature 3.8°C (1960–1990; Climatological statistics in Finland, 1991). The stand at the station has been regenerated by sowing after prescribed burning and plowing in 1962. Currently, the stand density (trees with diameter at 1.3 m height >5 cm) is 1370 ha⁻¹, basal area 24.0 m⁻² ha⁻¹ and summertime all-sided-LAI 6.7 m² m⁻² (Ilvesniemi et al., 2009). In FAO classification the soil is haplic podzol and soil depth is 0.05–1.6 m. For more details on the station, see Hari and Kulmala (2005).

2.2 The girdling experiment

We established a girdling experiment approximately 100 m NW of the eddy-covariance mast of the SMEAR II station in the beginning of June 2007 for studying the allocation

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of assimilated carbon to root and rhizosphere. The purpose of the girdling was to stop sugar flow in phloem into the soil and consequently stop root and rhizosphere respiration (R_r), leaving only respiration originating from decomposition (R_d) of soil organic matter. Girdling allows studying R_r over annual scale without stopping the transpiration stream of the trees and thus not significantly affecting the soil moisture. We girdled 19 dominant trees from an approximately rectangular area with a size of 13.5×18 m on 18 June 2007 (Fig. 1). Also understory trees, mainly aspen (*Populus tremula*), rowan (*Sorbus aucuparia*) and Norway spruce (*Picea abies*), were girdled. Forest floor vegetation was kept intact. In the girdling-procedure, vertically at least 3 cm of bark and phloem around the tree at breast height were removed. An aluminum scaffold was built to study changes in the physiology of the canopy and at different heights of the stem. Four trees close to the scaffold were girdled just below the canopy, making it possible to study changes in girdled stems at different distances from the rhizosphere. The continuous soil monitoring plot at SMEAR II station acted as an intact control area. Data was recorded from 30 May 2007 to 1 November 2008. We estimated the effect of girdling to transpiration by measuring sap flow of one girdled and two control trees using the Granier method (Granier, 1985) approximately at breast height. PAR, air temperature, soil temperature and soil water content were measured at the SMEAR II station (Fig. 2). Overall, the weather conditions during the measurement period were quite normal, for example no severe droughts occurred.

2.3 Soil CO₂ effluxes

CO₂ effluxes from the soil at the girdled and control plots were measured in the mornings of two consecutive days. Effluxes were measured on a weekly basis from May to October 2007, fortnightly from April to August 2008 and monthly during the winter time. The effluxes were measured using a non-transparent non-vented non-steady state flow-through chamber attached to permanent collars as described in Kolari et al. (2006). The CO₂ concentration and temperature within the chamber were recorded at 15-s intervals during a 3-min-long chamber deployment time with a portable EGM-4

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CO₂-analyzer (PP Systems, Hitchin, UK). Temperature in the chamber was measured with a K-type thermocouple connected to a portable temperature meter. The CO₂ effluxes were calculated from the CO₂ concentration change within the chamber by fitting a linear regression over 3 min period after the installation of the chamber. The first 30 s following the chamber installation were excluded from the calculation to avoid the disturbance in the CO₂ efflux resulted from the chamber installation. From 26 May 2008 onwards the CO₂ effluxes were measured with an identical chamber, but using a Vaisala GMP343 diffusion type CO₂-probe (Vaisala Oyj, Vantaa, Finland). The CO₂ effluxes measured with Vaisala GMP343 and EGM-4 were very close to each other according to the tests performed with calibration tank described in Pumpanen et al. (2004).

At the control plot, the collars (0.21 m in diameter and 0.05 m in height) were installed to approximately 0.05 m depth in the soil several years before the measurements, and thus the disturbance resulted from the installation of the collars was assumed to have disappeared. To avoid damaging the roots at the girdled area the collars (0.22 m in diameter and 0.05 m in height) were installed gently on the top of the soil and quartz sand was laid outside the collar at 2 cm radius for sealing. At the control plot totally 14 collars were installed randomly over an area of 1100 m² and at the girdled area totally 12 collars were installed systematically (Fig. 1). The smallest distance between the collars at the girdled site and the nearby non-girdled trees was 4.4 m.

2.4 Contribution of root and rhizosphere respiration (R_r) to total soil respiration (R_s)

We measured soil CO₂ effluxes at the plot to be girdled and at the control plot 4 times within 25 days before the girdling and noticed that the effluxes from the site to be girdled were 22% higher than those of the control plot. In order to determine the effect of the girdling on the effluxes we scaled the soil CO₂ effluxes measured at the girdled plot to represent the ecosystem respiration originating from decomposition (R_d). We took into account the 22% difference in the initial soil CO₂ effluxes at the plots and calculated

respiration originating from decomposition at given moment ($R_d(t_i)$) as follows

$$R_d(t_i) = 0.82F_g(t_i), \quad (1)$$

where 0.82 is the ratio of the average soil CO₂ efflux at the control and girdled plots before the girdling and $F_g(t_i)$ is the soil CO₂ efflux at the girdled plot at given moment ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). In the calculation we assumed that without girdling, the root and rhizosphere to total soil respiration ratio ($R_r:R_s$) between the plots would have been the same regardless of the time, and that without girdling, the relative systematic difference in R_s between the plots would not have changed over the time.

Respiration originating from roots and rhizosphere at given moment $R_r(t_i)$ was calculated as follows

$$R_r(t_i) = R_s(t_i) - R_d(t_i). \quad (2)$$

2.5 Temperature sensitivity of soil respiration

We determined temperature responses for R_r , R_d and R_s using a commonly used Arrhenius type exponential function (Lloyd and Taylor, 1994)

$$R = R_{10}e^{E(1-\frac{T_0}{T_s})}, \quad (3)$$

where R is R_r , R_d or R_s , T_s is soil temperature (°C), R_{10} average soil CO₂ efflux at 10°C and E temperature sensitivity. R_{10} and E are fitted parameters. Fittings were made to two approximately half year periods (11 July 2007–23 January 2008 and 18 February–29 July 2008) capturing maximal range of soil temperatures for both time periods. The used soil temperatures were averages of three replicates of temperatures measured in the humus layer and in the A-horizon at 2 cm depth in the mineral soil. Soil temperatures were measured at 15-min intervals using silicon based temperature sensors (Philips KTY81-110, Philips Semiconductors, Eindhoven, the Netherlands). Sensors were connected to AD-converters (Nokeval, Nokeval Oyj, Nokia, Finland) and the data was recorded to a computer. Respirations were modeled using half hour averages of soil temperatures, and integrated for the whole year.

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2.6 Net ecosystem exchange and gross primary production

Net ecosystem exchange (NEE) of the stand was measured using eddy covariance (EC) technique at the SMEAR II station (Vesala et al., 2005). TER and GPP were extracted from the measured NEE as described in Mäkelä et al. (2006). Half-hourly TER was modeled from night-time NEE measurements applying Eq. (3) to soil humus layer temperature, and the temperature sensitivity of TER was determined from night-time flux data measured in June–August 2007. The temperature dependence of night-time TER was applied to daytime, and the half-hourly GPP was computed by subtracting the estimated TER from the measured NEE. When measured NEE was not available for a half-hour period, GPP was estimated as a saturating function of light using GPP derived from the accepted NEE records. The base level of TER (respiration in standard temperature) and GPP (light-saturated photosynthesis) were estimated daily in a moving time window of 11 days.

3 Results

3.1 Soil CO₂ effluxes

After the girdling, the measured CO₂ effluxes ranged from 0.64 to 7.81 μmol CO₂ m⁻² s⁻¹ at the control plot and from 0.63 to 5.35 μmol CO₂ m⁻² s⁻¹ at the girdled plot (Fig. 3). Before the girdling, the control plot showed 22% lower values than the girdled plot. The difference was statistically significant ($p < 0.05$, $n = 46$). After the girdling the effluxes at the girdled plot decreased relative to the control plot; in August 2007 the effluxes at the girdled plot were 74% of those at the control plot. When the initially 22% higher effluxes at the girdled plot were scaled to the same level as the effluxes at the control plot, the efflux at the girdled plot showed a decrease of 40% relative to the control plot.

Before the girdling the standard error of the mean calculated from daily soil CO₂ ef-

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flux measurements at different collars was on average 0.12 and 0.13 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for control and girdled plots, respectively. From July to August after the girdling the corresponding values were 0.33 and 0.15, showing larger relative spatial variability in the soil CO_2 effluxes at the control plot.

The ratio of the CO_2 efflux between the control and girdled plots from July to September was 1.54 in 2007 and decreased to 1.32 in 2008, one year after the girdling. The annual non-scaled CO_2 effluxes from the control and girdled plots were 1029 and 769 g C m^{-2} .

3.2 Contribution of root and rhizosphere respiration (R_r) to total soil respiration (R_s)

We multiplied the measured CO_2 effluxes from the girdled plot with 1.22 to convert them to respiration originating from decomposition. We calculated the annual values using the modeled values from temperature response (Eq. 3) and monthly values from the measurements.

The annual root and rhizosphere respiration to total soil respiration ratio was ($R_r:R_s$) 0.36 and root and annual rhizosphere respiration to respiration originating from decomposition ratio ($R_r:R_d$) 0.56. We observed high seasonal variation in R_r and R_d and also $R_r:R_s$ -ratio varied markedly (Fig. 4). The seasonal pattern of R_r followed R_d with approximately one month delay. Between February and May when the respiration rates were low, the $R_r:R_d$ -ratio could not be determined (the calculated values were from -0.02 to -0.06). $R_r:R_d$ increased very rapidly in June and was 0.82 from June to July and reached its maximum (on average 1.39) between August and September. $R_r:R_d$ -ratio decreased during October to a rather constant value of 0.20 until February. 60% and 91% of the annual R_d and R_r , respectively, occurred during the four most active months from June to September ($R_r:R_s=0.44$).

Annual soil efflux from the control plot F_{ca} ($1029 \text{ g C m}^{-2} \text{ a}^{-1}$) was 64% higher than the mean annual total soil respiration of Hyytiälä forest ($R_{sa}=625 \text{ g C m}^{-2} \text{ a}^{-1}$) (Kolari

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et al., 2009). For comparing the absolute carbon budget, we scaled F_{Ca} to the same level as the ecosystem annual total soil respiration (R_{sa}). We multiplied the annual CO_2 effluxes by the ratio between R_{sa} and F_{Ca} (0.61).

The annual R_r and R_d were 225 and 400 g C m⁻², respectively. In wintertime monthly R_d was typically about 15 g C m⁻² and peaked 70 g C m⁻² during the summer. In late summer and autumn R_r exceeded R_d , the $R_r:R_d$ -ratio being 1.52 and 1.25 in August and September, respectively. To test the importance of all-year-round measurements, we estimated annual R_r using summertime $R_r:R_s$ -ratio (0.44) for the whole year, and we got 23% overestimation for the annual R_r .

3.3 Environmental response of soil respiration

We compared the sapflow measurements from the control and girdled plots from a 17 day period just before girdling to a 17 day period beginning on 10 August and the result was that transpiration was reduced 31% because of the girdling (data not shown).

Calculated temperature response values (Q_{10}) for spring and autumn ranged from 4.4 to 6.4 for total soil respiration (R_s), from 4.0 to 4.4 for respiration originating from decomposition (R_d) and from 5.3 to 31.5 for root and rhizosphere respiration (R_r), respectively (Table 1). The highest temperature sensitivity was observed for R_r and the lowest for R_d . R_s is a combination of R_r and R_d , and therefore Q_{10} of R_s should be between the Q_{10} of R_d and R_r , as we observed. The temperature responses were higher during the spring compared to the autumn, although the fitted time periods were selected so that both periods included both the highest and the lowest temperatures observed. Overall, the modeled respirations fit well to the measured CO_2 effluxes (Fig. 4). However, the fitting over the time period between June 2007 and February 2008 underestimated R_r in July and overestimated it in wintertime. Soil moisture did not have a notable effect on the soil respiration, as extreme wetness or drought were not observed during the period studied.

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3.4 Proportion of root and rhizosphere respiration (R_r) to gross primary production (GPP)

From 1 July 2007 to June 31 2008 the accumulated GPP calculated from eddy covariance was 1078 g C m^{-2} , which is in the range of a typical year in Hyytiälä (Kolari et al., 2009). 88% of the GPP was occurring between May and September. Wintertime photosynthesis was very low, the GPP between November and March contributing 2.3 % of the annual GPP. Annual total ecosystem respiration was 825 g C m^{-2} , leaving net ecosystem productivity 246 g C m^{-2} positive. The forest stand was a carbon sink from April to September.

Annual root and rhizosphere to gross primary production ratio (R_r :GPP) was 0.21%. Overall, R_r :GPP was rather constant during the year and the highest anomaly was observed in spring. R_r between April and May was so low that we could not determine it reliably, whereas during the same period respiration originating from decomposition was 15% and GPP 21% of the annual sum. In the autumn R_r was at its highest compared to R_d and GPP (Fig. 3). Annual R_s :GPP was 0.58.

4 Discussion

4.1 Contribution of root and rhizosphere respiration (R_r) to total soil respiration (R_s)

According to our measurements, it is important to take into account the seasonal variability in R_r : R_s -ratio and not only study the R_r : R_s -ratio of the growing season. To our knowledge, however, annual R_r : R_s -ratio of boreal Scots pine forests has not been studied before. Nevertheless, there is another girdling study of Scots pine forest (Högberg et al., 2001), where on average 54% percent decrease in CO_2 effluxes was observed due to girdling within the same growing season. Based on the same experiment, Bhupinderpal-Singh et al. (2003) reported that the decrease in the soil CO_2 effluxes was 65% one year after the girdling. They suggest that the data from one year after

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the girdling gives more reliable results of R_r , because during the first year, decaying of mycorrhizal fungi and consumption of starch storages in the roots may increase the CO_2 efflux at the girdled plot. On the contrary, we saw that after one year the effect of girdling decreased.

5 In overall, our result on the ratio of summertime and early autumn (between June and September) root and rhizosphere respiration to total soil respiration ratio ($R_r:R_s=0.52$) is consistent with previous studies of root and rhizosphere respiration (R_r) on various ecosystems (see review by Subke et al., 2006).

10 In the literature, annual $R_r:R_s$ -ratio for coniferous forests varies and our result (0.41) is a bit smaller than what has usually been reported. Our $R_r:R_s$ -ratio was lower than Vogel et al. (2005) reported for three Black spruce (*Picea mariana*) forests in Alaska (0.41–0.58), but higher than that of O’Connel et al. (2003), reported for a mature black spruce forest on feather-moss covered moderately drained soil (0.22). Lavigne et al. (2003) reported that $R_r:R_s$ -ratio was highly variable in three balsam fir (*Abies balsamea*) sites, but increased systematically as climate got warmer from 0.22 to 0.5. Saiz et al. (2006) observed that annual $R_r:R_s$ -ratio decreased as stand age increased from 0.59 to 0.5 in 10 to 47 year-old Sitka Spruce (*Picea sitchensis*) stands in temperate conditions in Ireland.

4.2 Environmental response of respiration

20 Traditionally the seasonal course of soil CO_2 efflux is most often been explained by soil temperature. Besides that, it is driven by changes in substrate availability (Gu et al., 2004; Kirschbaum, 2006) and Q_{10} values determined at different temperature ranges cannot be compared directly (Tjoelker et al., 2000). We defined Q_{10} values for temperature sensitivity of respirations for approximately half year periods, temperatures varying by approximately 15°C . Therefore, we realize that the absolute values of the determined Q_{10} values may be biased. However, their relative values can be compared to each other.

25 The Q_{10} values of R_r (5.2–31.5) and R_d (4.0–4.4) show higher temperature sensi-

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tivity for R_r than for R_d . Because R_r is probably not more sensitive to temperature (Bhupinderpal-Singh et al., 2003; Bååth and Wallander, 2003; Irvine et al., 2005), high values of Q_{10} reflect changes in other factors, such as high seasonal variation in labile carbon in soil. The variation in substrate availability for R_r (photosynthates), indeed, is much higher than in the case of R_d (litter). The main reason is that the lability of photosynthates is much higher than the lability of litter. Availability of photosynthates is dependent on GPP, which itself is seasonally dependent on temperature and in short term mainly on irradiation. As irradiation and soil temperature have a very strong causal relationship, statistical relationship between soil temperature and R_r can also be seen.

The modeled R_d from temperature response fits better to the measured R_d than the modeled R_r to the measured R_r , indicating further that other factors than soil temperature affect severely R_r (Fig. 5). Therefore, modeling the dynamics of R_r using only soil temperature (and moisture if it is limiting) is not sufficient. However, we believe that it is reasonable to assume that the annual R_r determined from the modeled R_r is close to correct.

4.3 Allocation of photosynthates

We estimated that annually 21% of the GPP is used in R_r , which is in agreement with Pumpanen et al. (2009), who reported that for Scots pine seedlings 26% of the GPP is used in R_r . In general, R_r followed GPP very well. However, our measurements show that before June, R_r stayed at a very low level, although both GPP and soil temperatures had significantly increased. It is known, that growing foliage and new shoots can be a very strong sink for carbon in the early part of growing season (Konôpka et al., 2005), leaving less carbon available for the root system to respire. Increase in plant sugar and starch pools may also partly explain the delayed increase of R_r . Therefore, plant allocation dynamics should not be forgotten when explaining the dynamics of R_r .

Widen and Majdi (2001) reported that the proportion of root respiration from R_s in a mixed Norway spruce and Scots pine forest in eastern central Sweden was at its highest in May. They measured fine root effluxes from excavated roots at temperature

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close to current soil temperature, but during May they measured the efflux at ambient air temperature. Though their result of actual R_r in May may be biased, we can conclude, that there was substrate available for root respiration. This indicates that the delay in respect to GPP we noticed in R_r in spring would be limited by plant allocation and growth strategies and not by low substrate availability. However, the changes in soil temperature and R_r are rapid during the spring and the spring was earlier in their study indicated by soil temperature, which varied in their study in May from 6 to 10°C, and in our study from 4.2 to 6.0°C.

Högberg et al. (2002) estimated that 75% of the carbon allocated belowground is respired and 25% used in growth. They assumed that $R_r:R_d$ -ratio is one, based on measurements during growing season (Högberg et al., 2001). Using formulas presented in their study and our result of annual $R_r:R_d$ -ratio of 0.79, we get that 55% and 45% of the belowground carbon allocation is used in R_r and growth, respectively. We used annual $R_r:R_d$ -ratio instead of summertime values, which probably mostly explains the difference. Also our summertime $R_r:R_d$ -ratio is lower than what Högberg et al. (2002) used, probably explaining the rest of the difference. Pumpanen et al. (2009) reported 56% and 44% of belowground carbon allocation for Scots pine seedlings, which agrees very well with the values calculated using the method of Högberg et al. (2002) and our annual $R_r:R_s$ -ratio.

4.4 Soil CO₂ effluxes

After the girdling, relative spatial variation of CO₂ efflux reduced in the girdled plot compared to the control plot. Our results indicate that R_r plays a significant role in the spatial variation of soil CO₂ effluxes.

Our purpose was to girdle a large enough area, so that roots from non-girdled trees would not reach the area where CO₂ efflux was measured. In our experiment, the minimum distance between the collars used in CO₂ efflux measurements at the girdled plot and the closest non-girdled trees was 4.4 m (Fig. 1). In a recent study, Göttlicher et al. (2008) found that in a 48–59-year-old Scots pine forest in Northern Sweden the

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lateral spread of Scots pine roots was typically 4 to 5 m. Also Kalliokoski et al. (2008) got similar results in a 51-year-old Scots pine stand near Hyytiälä in Finland. The mean proximal root length was 4.2 m and maximum radial root length was 9.5 m. This suggests that some roots from non-girdled trees may have been influencing the area where CO₂ effluxes were measured. Before the girdling, we noticed that CO₂ effluxes were the lowest in the middle of the girdled plot, but there was same trend also after the girdling, suggesting that only few roots of non-girdled trees were affecting the measured CO₂ effluxes. However, it may be that during the second year roots of non-girdled trees had already grown to the girdled area, and this would explain the difference in observations of us and Bhupinderpal-Singh (2003). It can also be, that R_d was enhanced after one year of the girdling as the death of the roots causes an increase in the substrate availability for R_d , but this was not observed in the study of Bhupinderpal-Singh et al. (2003). After the first year, based on visual observations, the needle litterfall was somewhat higher at the girdled plot compared to the control plot, also increasing the substrate availability for R_d .

Our results represent respiration of tree roots and associated rhizosphere not including the ground vegetation, because we kept it intact at the girdled plot. However, our measurements also include autotrophic respiration of ground vegetation increasing our values of R_d . On the other hand, girdling probably reduced also R_d , as root exudates released by trees are known to boost decomposition of soil organic matter (Subke et al., 2004; Fontaine et al., 2007), and these effects may counteract each other.

Our measured soil CO₂ effluxes were very high compared to previous ten years measurements at the SMEAR II site (Ilvesniemi et al., 2009). This may reflect temporal and spatial variation in the effluxes or systematic errors in the measurements. We changed the chamber and analyzer during the experiment, but we were not able to see any change in the soil CO₂ effluxes before and after the change. Also our tests performed in a calibration tank (see Pumpanen et al., 2004) showed very similar results for the two chambers and gas analyzers. We did not see an annual trend in total ecosystem respiration calculated from the eddy covariance measurements. However, the eddy co-

variance measurements represent much larger area than our chamber measurements, and can not detect changes that occur on small areas.

5 Conclusions

Large part of GPP is being consumed in root and rhizosphere respiration (R_r) in boreal Scots pine forests. Annually respiration originating from decomposition (R_d) is higher than R_r and also has a stronger seasonal cycle. $R_r:R_d$ -ratio is changing radically during the course of a year, hence using $R_r:R_s$ -ratio of growing season and a given annual total soil respiration to calculate annual R_r can result in a large overestimation of R_r . Our results suggest lower annual $R_r:R_s$ for boreal Scots pine forests that have been used previously, indicating that smaller part of the carbon allocated belowground is actually being respired and more is being used in growth.

R_d is mostly regulated by soil temperature, but also substrate availability is apparently affecting it. Soil temperature explains statistically R_r rather well, but substrate availability is a more important factor. Spatial variability seems to be higher for R_r than for R_d . There is also indication that plant allocation dynamics may play an important role in the seasonal variation of R_r .

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Table 1. Calculated Q_{10} values for respiration originating from decomposition (R_d), root and rhizosphere respiration (R_r) and total soil respiration (R_s). II/07 represents time period 3 July 2007–23 January 2008 and I/08 time period 18 February–29 July 2008. R_s is a combination of R_r and R_d , and the Q_{10} of R_s is therefore between the Q_{10} of R_r and R_d .

	Q_{10} (R_d)	Q_{10} (R_r)	Q_{10} (R_s)
II/07	3.99	5.20	4.44
I/08	4.43	31.52	6.41

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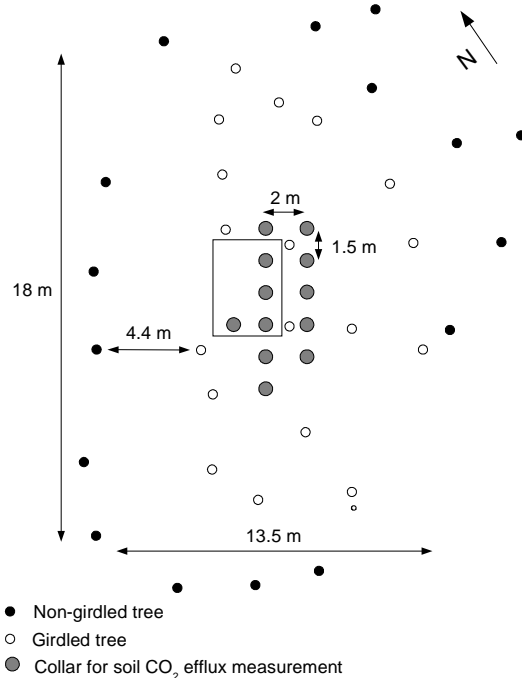


Fig. 1. Schematic map of the girdling plot. Location of trees, scaffold (rectangle) and CO₂ efflux measurement collars, distances between the collars, closest distance between a non-girdled tree and a collar, and closest distance between two non-girdled trees through the girdled area in two opposite directions are presented.

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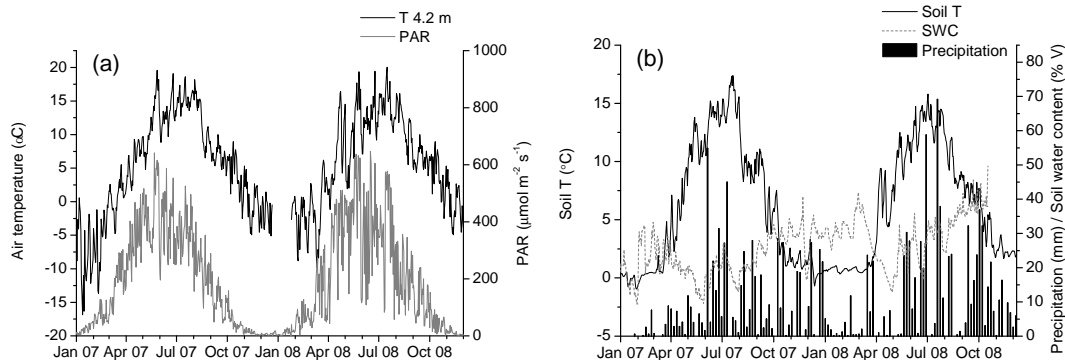


Fig. 2. (a) Daily mean values for air temperature (°C) at 4.2 m height and photosynthetically active radiation (PAR; $\mu\text{mol m}^{-2} \text{s}^{-1}$). (b) Daily mean values for soil temperature at humus layer (°C), soil water content at humus layer (%V) and 5-day cumulative precipitation (mm).

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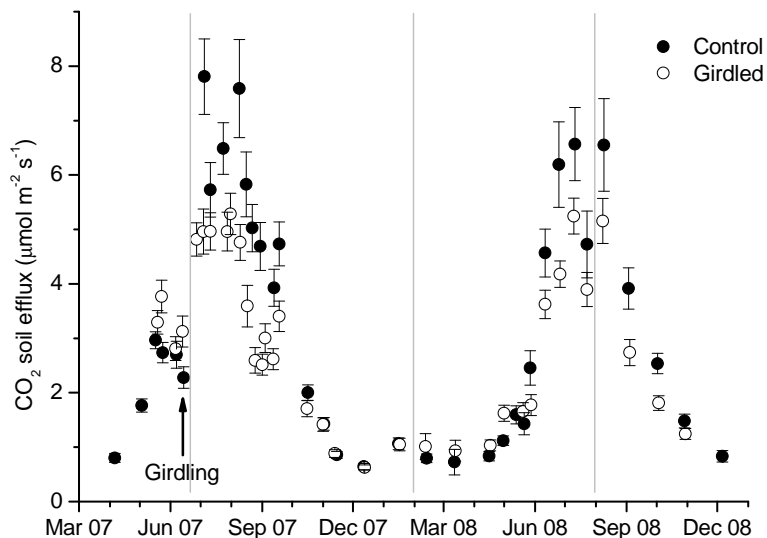


Fig. 3. Measured soil CO₂ effluxes from the girdled and control plots from 12 April 2007 to 12 December 2008. Error bars indicate standard errors of mean (*n*=12 for the girdled and 14 for the control plot). The vertical lines mark the two periods where the respiration temperature responses were fitted.

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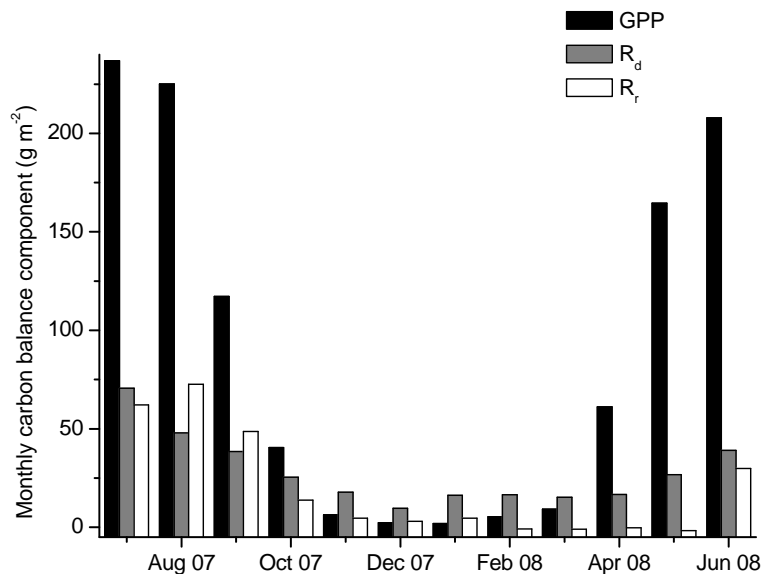


Fig. 4. Calculated monthly gross primary production (GPP), respiration originating from decomposition (R_d) and root and rhizosphere respiration (R_r) from July 2007 to June 2008. R_d and R_r are calculated from the monthly means of the measured effluxes. The negative values of R_r are related to inaccuracies in the measurements and the assumptions made. They occur when our estimation of respiration originating from decomposition is higher than total soil respiration. GPP is calculated from eddy covariance data using half-hourly values.

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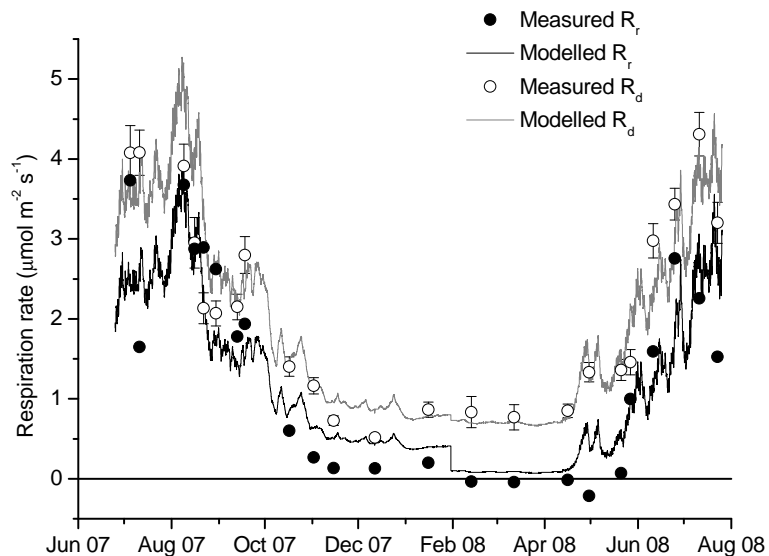


Fig. 5. Scaled measured respirations originating from decomposition (R_d) and from root and rhizosphere (R_r) between 10 July 2007 and 31 July 2008. Lines represent modeled half hour respirations using Arrhenius-type temperature regression. Error bars of R_r indicate standard errors of mean ($n=14$).

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