The differences in carbon dynamics between boreal dwarf shrubs and Scots pine seedlings in a microcosm study

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Abstract

Aims
The ground level of boreal pine forests consists of a dense layer of ericaceous shrubs, herbs, grasses, mosses and lichens. The primary productivity of this forest floor vegetation is notable but the role the most common ericoid dwarf shrub plant species, Calluna vulgaris, Vaccinium myrtillus and Vaccinium vitis-idaea, play in carbon (C) cycling in these ecosystems is poorly understood. Here, we studied their C dynamics in detail using plants of similar size (age 14–19 months) in a microcosm study.

Methods
We determined the full C balances of these dwarf shrubs for the first time and compared them to those of Pinus sylvestris by using long-term biomass accumulation, ¹³C pulse labelling and CO₂ exchange measurements in a controlled laboratory experiment.

Important Findings
Pinus sylvestris had significantly higher biomass-based C fluxes than dwarf shrubs, both aboveground and belowground, but the dwarf shrubs did not differ in the biomass-based fluxes. We showed that root respiration of the evergreen ericoid dwarf shrubs was sensitive to the aboveground light conditions as belowground respiration was 50–70% higher under light compared with dark conditions. Such light-related differences were not observed for Scots pine. The observed differences in C dynamics are important in estimating the origin of belowground CO₂ fluxes and in evaluating their biological relevance. Our results improve current understanding of CO₂ sources and sinks in boreal ecosystems.

Keywords: photosynthesis, autotrophic respiration, NPP, ¹³C labelling

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INTRODUCTION
The ground layer of boreal pine forests is vegetated and therefore photosynthetically active, unlike in many other forest ecosystems. A dense community of plant species consisting of ericaceous shrubs, herbs, grasses, mosses and lichens colonizes the ground of boreal pine forest ecosystems. They affect the ecosystem and soil functioning in several ways, for example physically by providing a buffer between air and soil affecting soil temperature and moisture which are crucial factors in many belowground processes (Adamczyk et al. 2016; Nilsson and Wardle 2005; Wardle et al. 2003; Wardle and Zackrisson 2005). In addition, the ground vegetation of boreal forests also makes important contributions to the cycling of essential nutrients like nitrogen (DeLuca et al. 2002; Näsholm et al. 1998).

The primary productivity of this ground vegetation is notable (Goulden and Crill 1997; Kolari et al. 2006; Kulmala 2011; Moren and Lindroth 2000). The share of ground vegetation contributing to CO₂ uptake of a forest ecosystem naturally depends on site and vegetation characteristics but it has been reported varying momentarily between 3% and 50% (Goulden and Crill 1997; Subke and Tenhunen 2004). Most common annual estimates lay between 10% and 20% (Bergeron et al. 2009; Ilvesniemi et al. 2009; Kolari et al. 2006; Kulmala et al. 2011; Swanson and Flanagan 2001).

A large proportion of the soil CO₂ emissions originates from root exudates containing carbohydrates that are
rapidly metabolized by microorganisms (Högberg et al. 2001; Pumpanen et al. 2009). These microorganisms are involved in the decomposition of organic substances in soil due to the so called priming effect (Kuzyakov et al. 2000). Belowground carbon (C) allocation is mainly studied using canopy layer plant species. However, it is evident that also dwarf shrubs in the ground layer allocate C belowground to microorganisms associated to their roots including symbiotic mycorrhiza and bacteria (Smith and Read 2008).

As listed above, there is a variety of estimates for the primary production of ground vegetation in boreal forests. However, it is still unclear how much of this primary productivity is truly allocated to long-lived structural compounds or if it is briefly stored and released via root exudates and autotrophic respiration. The carbon balance of ground vegetation plant species is poorly identified and it is not known which part of the observed CO2 emissions by soil chambers or the eddy covariance (EC) technique actually originates from the ground vegetation and which fraction originates from trees and the decomposition of soil organic matter. The partitioning of EC-derived net ecosystem exchange into respiration and gross primary production was recently shown to be uncertain (Wehr et al. 2016). Therefore, additional information on the species-specific carbon balance, i.e. biomass accumulation and rates of belowground and aboveground respiration, is needed to improve our understanding of the carbon fluxes inside a boreal forest ecosystem.

The aim of this study was to improve the reliability of Scots pine boreal forest carbon balance estimates by quantifying the primary production of the most common species on the forest floor and reveal their C allocation patterns using biomass analysis (long-term allocation), 13C-labelling (short-term allocation) and CO2 exchange measurements (photosynthesis and respiration). As a tool, we used microcosms as Pumpanen et al. (2009) who studied the carbon dynamics of common tree seedlings but did not consider the dwarf shrubs.

MATERIALS AND METHODS

The plant material

The seedlings of Vaccinium vitis-idaea L. (Vacvit), Vaccinium myrtillus L. (Vacmyr) and Calluna vulgaris (L.) Hull (Calvul) were propagated from seeds originating from southern Finland. The berries of Vacvit and Vacmyr were picked in late summer 2011 and stored in freezer (−18°C) for 9 months. The berries were melted in room temperature for 3 h before washing. The samples were then separated into organs (stem, leaves, rhizome, roots), weighted and ground into a fine powder for stable isotope sampling (see later) with a mechanical grinder (2000–230 Geno/Grinder, Spex SamplePred, USA). Total biomass was treated as daily growth (mg d−1) to allow the comparison of seedlings with the slightly different growth periods. Differences in growth rates and in the biomass of different organs of the species were compared using an one-way analysis of variance (ANOVA) and Tukey honest significant difference (HSD) test in R (version 3.0.2, R Core Team, 2014) after an arcsine square root transformation. The shares of aboveground parts were measured by enclosing them in airtight compartment chambers (see for details Pumpanen et al. 2009). First, we enclosed the seedling in darkness and measured the CO2 emissions of the belowground parts. To keep the air pressure unaltered, synthetic compensation air with controlled CO2 and H2O concentrations was introduced in the chamber at 0.5 l min−1 flow while the concentrations of the outflow was analysed using a Licor LI-840 a Licor LI-7000 (Li-Cor Inc., Lincoln, Nebraska). We continued to measure the flux for ~1.5 h controlling the temperature to 25°C with a cooling system circulating cold water around chambers. Then, we measured CO2 and H2O concentration of the aboveground compartment chamber outflow similarly. After measuring the belowground and aboveground fluxes of four darkened plants, we repeated the same measurements but this time placed a light source (PAR = 120 µmol m−2 s−1) in front of the plant. The experimental setup used to measure gas exchange rates in these microcosms is described in detail by Pumpanen et al. (2009) that used the same setup when
comparing the carbon allocation between common boreal tree species.

Gas exchange rates of the different species in the aboveground and belowground compartments in light and dark conditions were separately calculated from the difference in gas concentration between the outflow and the reference channel with known air flow (Pumpanen et al. 2009). The fluxes were relatively stable after 1.5 h but to be exact, we fitted a saturating Michaelis–Menten type equation over the CO2 fluxes during the 1.5 h to determine the steady state, \( F \) (µmol s\(^{-1}\)), as follows:

\[
f(t) = \frac{F_t}{\alpha + t}
\]

In the equation, \( f(t) \) is the measured CO2 flux (µmol s\(^{-1}\)) at moment \( t \) whereas \( F \) (µmol s\(^{-1}\)) and \( \alpha \) (s) are fitted parameters. The parameters were estimated using ‘nlm’ function in R. Obtained \( F \) values were used as the CO2 fluxes in the further analyses. Insufficient stabilizing of the flux was detected from two samples i.e. \( f(1.5 \text{ h}) \) differed greatly from \( F \). These were a belowground measurement of a Pinus sylvestris in light and dark and a belowground measurement of a Vaccinium myrtillus in the dark. This indicated potential gaseous leakage in the experimental chamber and these fluxes were eliminated from further analysis.

All measured CO2 fluxes are summarized in the Fig. 1. The respiration aboveground (\( R_{\text{above}} \)) and net exchange (\( NE_{\text{above}} \)) were determined as the \( F \) values derived from the aboveground compartment in darkness and in light, respectively. \( R_{\text{above}} \) was always positive indicating respiratory emissions, whereas \( NE_{\text{above}} \) was negative since the rate of photosynthetic uptake of CO2 exceeded the rate of respiratory emissions. Assuming that \( R_{\text{above}} \) is same in light and darkness, rate of photosynthesis (\( P \)) can be calculated as the difference between \( R_{\text{above}} \) and \( NE_{\text{above}} \):

\[
P = R_{\text{above}} - NE_{\text{above}}
\]

The CO2 emissions from the humus (\( R_{\text{humus}} \)) were determined as the mean \( F \) in the control microcosms that did not contain a seedling. Root respiration (\( R_{\text{root}}^{\text{light}} \) and \( R_{\text{root}}^{\text{dark}} \)) was calculated as the difference between the \( F \) value in the belowground compartment (\( R_{\text{below}}^{\text{light}} \) and \( R_{\text{below}}^{\text{dark}} \)) and \( R_{\text{humus}} \) both in light and in dark conditions:

\[
R_{\text{root}}^{\text{light}} = R_{\text{below}}^{\text{light}} - R_{\text{humus}}
\]

\[
R_{\text{root}}^{\text{dark}} = R_{\text{below}}^{\text{dark}} - R_{\text{humus}}
\]

Total respiration (\( R_{\text{tot}} \)) was calculated as the sum of \( R_{\text{above}} \) and \( R_{\text{root}} \) where \( R_{\text{root}} \) was determined as an average of \( R_{\text{root}}^{\text{light}} \) and \( R_{\text{root}}^{\text{dark}} \) where possible negative values were replaced by the species-specific mean of available measurements:

\[
R_{\text{tot}} = \frac{1}{2}(R_{\text{root}}^{\text{light}} + R_{\text{root}}^{\text{dark}}) + R_{\text{above}}
\]

All fluxes were normalized by dividing them by either total mass or leaf mass. Net primary production (NPP) was calculated as the difference between \( P \) and \( R_{\text{tot}} \).

Rate of transpiration (\( T \), mmol s\(^{-1}\)) was calculated as the H2O emission from the aboveground compartment in light. Water use efficiency (WUE) was calculated from the rates of photosynthesis and transpiration, as follows,

\[
WUE = \frac{P}{T}
\]

The differences between the species in the normalized fluxes were tested using an one-way ANOVA and the Tukey HSD test.

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**Figure 1**: summary of the measured CO2 fluxes.
in R after verifying the normality of the data sets by Shapiro–Wilk test (R). The differences between root respiration in light
and dark conditions were tested with paired t-test in R.

Stable isotope labelling
Stable isotope labelling took place after the gas exchange measurements. The seedlings were grown in a constant light
environment and exposed to 13C for 2 h per day over a 5-day period. 1.5 ml of 100% 13CO2 was injected into a 1000 ml
shoot cuvette made of Perspex ® glass and the cuvette was made airtight for the incubation. Eight individuals per species
were labelled whereas six per species acted as unlabelled controls. We used a standard harvesting protocol where all plants
were harvested 3 to 4 days after the last labelling event. We chose the timing according to Pumpanen et al. (2009) who
found in a similar microcosms experiment that the label in Scots pines seedlings started to show up in the root and rhizo-
sphere respiration after 12 h remaining high until 1 week fol-
lowing the labelling.

A subsample of each organ was sent to UC Davis Stable
Isotope Facility (Davis, CA, USA) for 13C analysis. 13C levels
were measured by an Elementar Vario EL Cube or Micro Cube
elemental analyzer (Elementar Analysensysteme GmbH,
Hanau, Germany) interfaced to a PDZ Europa 20-20 isotope
to mass spectrometer (Sercon Ltd., Cheshire, UK). This
analysis also provided C and N quantities. In order to study short-term allocation of the assimilated carbon, we derived
the relative distribution of the 13C label by first deriving the
mean of the signatures (δs) in each unlabeled organ (x) of the
species s and then deriving the individual differences between
labelled signatures and the unlabeled mean (δs = δ̄s – δs). We
used the absolute δs values in this estimate. Then, we calcu-
lated the mean share of the label in different organs of a plant
by deriving each difference by the sum of differences of that
individual (δs/δ̄s) (see online supplementary Table S1) except for Vacmyr that has annual leaves unlike the other
species. Vacmyr allocated 21% of the biomass to the leaves
and 31% to the stems, whereas those of the other species
were 42–52% and 13%, respectively. Calvul had the highest
aboveground share (66%) but that of Pinsyl (60%) did not differ significantly. Vaccinium are the only species with
rhizomes included in this study. Vaccit and Vacmyr allocated
15% and 6% of their biomass to the rhizome, respectively.
The share of roots did not differ between the species, although
the rhizome increased the belowground share of Vacmyr and
Vaccit.

The carbon content of the organs was ~49% (see online
supplementary Table S1) without any significant differences
between the species. The C/N ratios of the organs differed
significantly between the measured species being overall the
highest in Calvul and lowest in Pinsyl (see online supplemen-
tary Table S2).

CO2 exchange and transpiration
Pinsyl had the highest rate of photosynthesis (nmol g−1 s−1).
Aboveground and belowground respiration and transpiration
differed significantly from those of dwarf shrubs when nor-
malized by total biomass (Table 2). Vacmyr, which has annual
leaves, had similar NEabove, P, Rtot and T compared to Pinsyl
but differed significantly from those of Vaccit and Calvul
when normalized by leaf mass only (see online supplement-
ary Table S3). The NPP values were similar between the species
(Table 2). The mean Rhumus per dry mass was 0.317 µmol
kg−1 s−1.

Table 1: the number of samples (N) and the growth rates (mg d−1) of total biomass and specific fractions ± standard error of the measured species

<table>
<thead>
<tr>
<th>Species</th>
<th>Calvul</th>
<th>Pinsyl</th>
<th>Vacmyr</th>
<th>Vacvit</th>
</tr>
</thead>
<tbody>
<tr>
<td>N</td>
<td>14</td>
<td>14</td>
<td>14</td>
<td>12</td>
</tr>
<tr>
<td>Total</td>
<td>8.08 ± 3.03</td>
<td>6.02 ± 2.29</td>
<td>5.44 ± 2.04</td>
<td>6.57 ± 1.92</td>
</tr>
<tr>
<td>Above ground</td>
<td>5.31 ± 2.10 (66)a</td>
<td>3.60 ± 1.48 (60)ab</td>
<td>2.85 ± 1.28 (52)c</td>
<td>3.62 ± 1.20 (55)bc</td>
</tr>
<tr>
<td>Below ground</td>
<td>2.77 ± 1.25 (34)a</td>
<td>2.42 ± 0.91 (40)ab</td>
<td>2.60 ± 0.91 (48)c</td>
<td>2.95 ± 1.21 (45)bc</td>
</tr>
<tr>
<td>Stem</td>
<td>1.08 ± 0.54 (13)a</td>
<td>0.76 ± 0.28 (13)ab</td>
<td>1.69 ± 0.69 (31)c</td>
<td>0.86 ± 0.28 (13)a</td>
</tr>
<tr>
<td>Leaves</td>
<td>4.23 ± 1.70 (52)a</td>
<td>2.84 ± 1.23 (47)ab</td>
<td>1.16 ± 0.63 (21)c</td>
<td>2.76 ± 0.98 (42)bc</td>
</tr>
<tr>
<td>Roots</td>
<td>2.77 ± 1.25 (34)ab</td>
<td>2.42 ± 0.91 (40)a</td>
<td>2.24 ± 0.89 (41)a</td>
<td>2.00 ± 1.09 (30)b</td>
</tr>
<tr>
<td>Rhizome</td>
<td>0.00 ± 0.00 (0)a</td>
<td>0.00 ± 0.00 (0)a</td>
<td>0.35 ± 0.23 (6)bc</td>
<td>0.95 ± 0.45 (15)c</td>
</tr>
</tbody>
</table>

The percentage of the organ in the total biomass (%) is given in parentheses. Different letters indicate significant difference in the proportions
between the measured species (P < 0.05).

RESULTS

Plant growth rates and biomass allocation

The biomass growth rates of Calvul and Vacmyr were sig-
nificantly different from each other with Calvul exhibiting
the highest growth rate while Vacmyr exhibited the lowest
growth rates (Table 1). The biomass allocation was similar
between the species (Table 1, see online supplementary Fig.
S1) except for Vacmyr that has annual leaves unlike the other
species. Vacmyr allocated 21% of the biomass to the leaves
and 31% to the stems, whereas those of the other species
were 42–52% and 13%, respectively. Calvul had the highest
aboveground share (66%) but that of Pinsyl (60%) did not differ significantly. Vaccinium are the only species with
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The carbon content of the organs was ~49% (see online
supplementary Table S1) without any significant differences
between the species. The C/N ratios of the organs differed
significantly between the measured species being overall the
highest in Calvul and lowest in Pinsyl (see online supplemen-
tary Table S2).
The belowground CO₂ emissions (R\text{light}_\text{root} and R\text{dark}_\text{root}) of the dwarf shrubs were very low especially in dark conditions. The R\text{dark}_\text{root} of the dwarf shrubs was ~10% to 20% of P whereas for Pinsyl, R\text{dark}_\text{root} was ~46% of P (Table 2). The R\text{light}_\text{root} of Pinsyl was of a similar magnitude than R\text{dark}_\text{root} but for dwarf shrubs, R\text{light}_\text{root} was ~50% to 70% higher than that of R\text{dark}_\text{root}. The difference between R\text{light}_\text{root} and R\text{light}_\text{root} was significant with Vacvit (P = 0.016) and Calvul (P = 0.004), whereas it was not significant with Pinsyl (P = 0.201). Even if R\text{light}_\text{root} of Vacmyr were in general higher than R\text{dark}_\text{root}, the difference was not clearly significant (P = 0.066).

Pinsyl had the highest transpiration when normalized by total biomass (Table 2) but when normalized by leaf mass, Vacmyr had similar transpiration rates significantly differing from those of Vacvit and Calvul (see online supplementary Table S3). Vacmyr and Pinsyl had the highest WUE i.e. they lost the lowest amount of water per assimilated carbon but WUE values did not significantly differ between the species.

**Stable isotopes**

Stable isotope signatures were the most negative in leaves of the unlabeled dwarf shrubs and increased slightly in the stems, rhizomes and roots (see online supplementary Table S4). The differences were significant only with Vacmyr whose leaves had a lower signature than that of the other organs (app. −31.1 vs. −28.1‰, respectively). The unlabeled control soil without a plant had a δ\text{13}C signature of −28.4‰ with a standard error of 0.06 ‰.

The relative distribution of the 13C-label was the highest in leaves decreasing towards roots for all the dwarf shrubs whereas for Pinsyl, the highest share of 13C was in the stem (Fig. 2). The distribution of δ\text{13}C widely differed from the biomass fractions (Fig. 2, see online supplementary Fig. S1). The biggest differences were found in roots whose relative share of δ\text{13}C was much lower than their relative biomass. Instead,

### Table 2: the mean aboveground net CO₂ exchange (NE\text{above}), respiration (R\text{above}), photosynthesis (P), root respiration in light (R\text{light}_\text{root}) and darkness (R\text{dark}_\text{root}), total respiration (R\text{total}), net primary production (NPP), transpiration (T) and water use efficiency (WUE) with standard error of the measured species

<table>
<thead>
<tr>
<th>Species</th>
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<th>Vacmyr</th>
<th>Vacvit</th>
</tr>
</thead>
<tbody>
<tr>
<td>N</td>
<td>8</td>
<td>7</td>
<td>7</td>
<td>8</td>
</tr>
<tr>
<td>NE\text{above} (nmol g⁻¹ s⁻¹)</td>
<td>−2.41 ± 0.46 a</td>
<td>−6.27 ± 0.64 b</td>
<td>−2.72 ± 0.22 a</td>
<td>−2.88 ± 0.25 a</td>
</tr>
<tr>
<td>R\text{above} (nmol g⁻¹ s⁻¹)</td>
<td>1.69 ± 0.12 a</td>
<td>3.34 ± 0.69 b</td>
<td>1.24 ± 0.24 a</td>
<td>1.65 ± 0.26 a</td>
</tr>
<tr>
<td>P (nmol g⁻¹ s⁻¹)</td>
<td>4.10 ± 0.55 a</td>
<td>9.61 ± 1.14 b</td>
<td>3.96 ± 0.24 a</td>
<td>4.53 ± 0.46 a</td>
</tr>
<tr>
<td>R\text{light}_\text{root} (nmol g⁻¹ s⁻¹)</td>
<td>0.73 ± 0.34 a</td>
<td>4.53 ± 0.96 b</td>
<td>0.41 ± 0.24 a</td>
<td>0.78 ± 0.24 a</td>
</tr>
<tr>
<td>R\text{dark}_\text{root} (nmol g⁻¹ s⁻¹)</td>
<td>1.27 ± 0.41 a</td>
<td>4.30 ± 0.92 b</td>
<td>0.69 ± 0.31 a</td>
<td>1.16 ± 0.26 a</td>
</tr>
<tr>
<td>R\text{total} (nmol g⁻¹ s⁻¹)</td>
<td>2.95 ± 0.31 a</td>
<td>7.75 ± 1.41 b</td>
<td>2.21 ± 0.24 a</td>
<td>2.81 ± 0.38 a</td>
</tr>
<tr>
<td>NPP (nmol g⁻¹ s⁻¹)</td>
<td>1.15 ± 0.47 a</td>
<td>1.86 ± 0.59 a</td>
<td>1.76 ± 0.20 a</td>
<td>1.73 ± 0.24 a</td>
</tr>
<tr>
<td>T (µmol g⁻¹ s⁻¹)</td>
<td>1.34 ± 0.21 a</td>
<td>2.56 ± 0.47 b</td>
<td>0.89 ± 0.10 a</td>
<td>1.44 ± 0.18 a</td>
</tr>
<tr>
<td>WUE (mmol mol⁻1)</td>
<td>3.28 ± 0.33 a</td>
<td>4.16 ± 0.42 a</td>
<td>4.67 ± 0.40 a</td>
<td>3.39 ± 0.40 a</td>
</tr>
</tbody>
</table>

All fluxes are normalized by total biomass. Different letters indicate significant difference in the fluxes between the measured species (P < 0.05).

**Figure 2:** the relative distribution of assimilated 13C in different seedling organs. Error bars represent standard error. Different letters indicate significant difference in the proportions between the measured species (P < 0.05).

more δ\text{13}C was found aboveground compared with the biomass shares, especially in the stems of Pinsyl. In leaves, the biomass shares and δ\text{13}C values were similar to one another except for Pinsyl whose share of δ\text{13}C in leaves was decreased notably and for Vacmyr, whose share of δ\text{13}C in leaves was more than double that of biomass. The share of δ\text{13}C in the rhizome of Vacmyr was much higher than the share of biomass in contrast to Vacvit where the distribution of δ\text{13}C in the rhizome and biomass were similar.

**DISCUSSION**

We determined the full carbon balance of the three most common ericoid dwarf shrub species from boreal Scots pine forests for the first time and compared them to Pinus sylvestris. We were able to detect significant differences in the C dynamics of these forest plant species using three different approaches. This knowledge will significantly improve
current understanding of CO₂ sources and sinks in boreal ecosystems.

Our results indicated that the growth rates of the studied dwarf shrub species are similar in the environmental conditions tested. Differences in seedling age and environmental conditions such as light availability, competition and soil nutrition were naturally reflected in the growth rate. For example, the growth rate of Scots pine would be greater in high light conditions as a pioneer species. However, the conditions we selected represent the common environmental conditions found on the forest floor in the southern boreal zone.

The long-term allocation rate was also surprisingly similar within the species tested. The mean shoot:root ratio of *C. vulgaris* (1.92) is very similar to that previously reported 1.97 for 1-year-old seedlings in Norway (Verburg et al. 1998). However, a value of 1.2 was reported for ~2-year-old seedlings (Meyer-Gruenefeldt et al. 2015). Nevertheless, our seedlings germinated from seeds and it is therefore difficult to compare biomass allocation in our study with that reported in earlier studies. Earlier field studies for Vaccinium species mostly fail to identify roots individually or species-specifically (Chapin and Shaver 1996; Gerdol et al. 2004; Grogan and Jonasson 2003).

Carbon allocation patterns of the different plant organs are known to vary throughout the life cycle of plants (Kozlowski 1992). The biomass of plants reflects long-term allocation of C. ¹³C pulse labelling can be used to detect short-term C allocation. It was shown that at the age of the labelling (1.3–1.6 years), all species accumulate more carbon above ground than the distribution biomass amongst organs would suggest. The share of the label in roots was ~50% lower short-term assays than the overall share in biomass which indicates that in these conditions, all species measured first grow sufficient root biomass before greater allocation to aboveground parts. However, the share of rhizome in Vaccinium species increases as the plants age (Kaur et al. 2012) which is consistent with our study as an increased allocation of recently assimilated C to rhizome in V. myrtillus.

Compared with the dwarf shrubs, *P. sylvestris* seems to allocate most of recently assimilated C to the stem, which at this age is probably due to the plant’s capacity to grow tall trunks. On the other hand, the lower relative share of the label in the leaves of Scots pine may indicate higher transport rate of assimilates compared to those of dwarf shrubs. Our sampling time was selected according to Pumppanen et al. (2009) to study and follow the relative share of the label within the plants. Nevertheless, it would have required a different experimental setup to see how much of the label was actually bind to biomass and how much the observed differences reflect the variation in transport rate and storage potential.

*Pinus sylvestris* clearly has the highest flux rates of all showing increased metabolism compared with ericoid plants. Remarkably, the increased metabolism did not result in significantly faster accumulated biomass or a higher NPP compared to ericoid plants as their carbon losses in autotrophic respiration were the highest. Scots pine appears to have a particularly rapid belowground activity caused by either roots or root-associated microflora. The reason for this might relate to its ectomycorrhizal fungi that can be more predominant and large in biomass than the ericoid mycorrhizal fungal association in dwarf shrubs. In this study, we did not follow the differences in these associations between the species studied but ericoid mycorrhiza do not typically form extensive hyphal networks in soil in contrast to many ectomycorrhizal species (Smith and Read, 2008). Vigorous fungi associated with pine would explain the generally higher rate of metabolism that limited biomass accumulation. Ectomycorrhizal fungi are a great sink of carbon and for ericoid species; the lack of such strong sink might have down-regulated also photosynthetic activity (Paul and Foyer 2001). The higher CO₂ emissions resulting from higher C input belowground might also indicate that Scots pine has a higher priming effect on the decomposition of soil organic matter than the ericoid dwarf shrubs. Further studies are needed to determine whether the decomposition of organic matter in the microcosms containing Scots pine seedlings was higher than in those containing dwarf shrub seedlings.

Remarkably, the evergreen dwarf shrubs have lower root respiration in darkness than in light, i.e. when the shoot is photosynthesizing. Meanwhile, root respiration by Scots pine was independent of light conditions. The reason for this remains unclear but it might be that Scots pine has a better capacity to regulate internal carbon storages than dwarf shrubs allowing rather continuous C flow belowground despite the variation in photosynthesis. Another explanation, also related to the continuous belowground C flow, is that the constant activity of root-associated fungi may balance out differences in CO₂ output from the ectomycorrhizal roots in light and dark conditions. However, further studies including detailed microbial data are required to support these assumptions.

Many studies on grasslands or on similar short vegetation show minor time lags (0–4 h) between changes in GPP and soil respiration (e.g. Bahn et al. 2009; Han et al. 2014; Yan et al. 2011). Our results support these findings and suggest that in the short term, photosynthesis and maintenance respiration in Scots pine seem to be more independent of each other than in especially the evergreen dwarf shrubs. Nevertheless, some studies indicate that autotrophic respiration of trees also has a diurnal cycle (Kodama et al. 2008; Marron et al. 2009; Savage et al. 2013). A compilation of 47 studies concluded that the transfer of labelled C belowground takes a few days and that the rate of transfer differs between broadleafed and coniferous species decreasing with temperature and soil water content (Epron et al. 2012). Our results suggest that the relatively higher proportion of forest floor CO₂ emissions during the daytime originate from ground vegetation rather than trees compared with the night time fluxes due to the light-dependent nature of root respiration in evergreen dwarf shrubs.

Another possibility is the lack of light-related differences in the root respiration of Scots pine might lie in the high-transpiration rate. There is evidence that some of the expired
CO₂ is transported upwards to the stem during high transpiration (Bloemen et al. 2014; Grossiord et al. 2012). However, the difference in the biomass-based root respiration between Scots pine and dwarf shrubs was many folds higher than the difference in the transpiration rates indicating that the internal transport of CO₂ is not the most plausible cause of the observed differences in this study. The transpiring plants may have decreased the soil moisture faster than the control soil and consequently caused differences in the heterotrophic respiration (Davidson et al. 1998; Skopp et al. 1990). The presence or absence of a plant also has a big impact on the microbial community composition in the soil as the root-associated microflora generally differs in composition from heterotrophic microbial communities (Buee et al. 2009). To estimate the proportion of heterotrophic (basal) respiration from autotrophic respiration in non-disturbed soils with plant roots is a challenge that needs further investigations with sophisticated methods (e.g. ¹³CO₂ or ¹⁴CO₂ labelling). Nevertheless, in our study, the species-specific differences are detectable despite a possible offset of heterotrophic respiration. Environmental conditions in the field fluctuate but our experimental design enabled a reliable partitioning of the fluxes by stabilizing the environment, most importantly the temperature.

CONCLUSIONS

Our results indicate that despite obvious differences for example in leaf morphology and in biomass allocation, young dwarf shrubs have similar rates of aboveground and belowground CO₂ exchange that differ significantly from those of Scots pine. The root-originated respiration rates of the dwarf shrubs differ greatly in light and dark conditions, whereas those of Scots pines appear to be independent of the aboveground photosynthesis. Although larger plants may have different carbon dynamics than the seedlings studied in this microcosms experiment, our results suggest that especially evergreen ericoid plants rapidly allocate assimilated C to belowground compartments and outside roots. Therefore, much of the soil CO₂ production detected in soil respiration measurements during light hours is likely to be derived from the activities of these plant species. In contrast, our data suggest that the nighttime soil respiration measurements may better reflect contributions of the tree root-associated autotrophic respiration. The soil chambers commonly used in the field also include dwarf shrubs. Therefore, our data can be used to estimate the contribution of dwarf shrubs to soil CO₂ fluxes allowing a better prediction of the effects of environmental changes on the source and sink capabilities of boreal forest ecosystems.

SUPPLEMENTARY MATERIAL

Supplementary material is available at Journal of Plant Ecology online.

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