Fine root longevity and carbon input into soil from below- and aboveground litter in climatically contrasting forests

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ABSTRACT

The major part of carbon (C) flow into forest soil consists of continually renewed fine roots and aboveground litterfall. We studied the belowground C input from the fine root litter of trees and understorey vegetation in relation to their aboveground litterfall in two Norway spruce (*Picea abies* L.) stands located in northern and southern Finland. The production of fine roots was estimated by using turnover and biomass data from minirhizotrons and soil cores. The foliage litter production of trees was estimated from litter traps, and that of the understorey vegetation from its annual growth and coverage. Finally, we augmented the data with four spruce plots in Sweden in order to study the above- and belowground litter ratios along latitudinal and soil fertility gradients.

The fine root biomass of spruce trees per stand basal area was almost double in the northern site compared to the southern site. Furthermore, spruce fine roots in the north persisted significantly longer (97 ± 2 weeks) than spruce roots in the south (89 ± 2 weeks) or understorey fine roots at both sites. The annual production of tree foliage litter was higher in the southern stand, but the total amount of litter (including trees and understorey, above- and belowground) was similar at both sites, as was the ratio between the above- and belowground litter production.

The role of understorey vegetation was greater in the northern site where it was responsible for 23% and 33% of below- and aboveground litter production, respectively, compared to 11% and 15% in the south. Thus, both below- and aboveground understorey C input is substantial and should be taken into account in ecosystem C cycle models.

The regression between the aboveground:belowground litter production-ratio and the C:N-ratio of the organic layer (combined data from Finland and Sweden), showed that the share of belowground litter production increased when site fertility decreased. This shift in the litter production pattern from above- to belowground in the least fertile sites may have an impact on litter C quality and soil C storage.

1. Introduction

The largest pools of terrestrial organic carbon (C) are found in soils, especially boreal forest soils and wetlands (IPCC, 2007). In the boreal region, *Picea* forests have the highest forest floor C stocks, followed by *Pinus* and broadleaf forests (Gärdenäs, 1998; Ågren et al., 2007; Stendahl et al., 2010; Vesterdal et al., 2013). Soil C stocks are controlled by the input of C by litter production and the output of C by decomposition (heterotrophic respiration), autotrophic respiration and leaching. Forest floor C turnover is most influenced by foliar litter quantity and quality, whereas mineral soil C turnover is affected by root litter and dissolved organic C (Vesterdal et al., 2013). Many studies have quantified C pools and fluxes (Gaudinski et al., 2000; Lehtonen, 2005; Jansson et al., 2008; Kleja et al., 2008; Hansson et al., 2013b), but as there are a large number of influencing factors in each ecosystem the estimates vary considerably.

Abundant data is available for C input through aboveground litter (Starr et al., 2005; Saarsalmi et al., 2007; Ukonmaanaho et al., 2008), whereas belowground litter C input is more laborious to

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quantify. Therefore, it is often predicted using biomass allocation functions (e.g. Marklund, 1987; Repola, 2009) and a constant turnover ratio. Several empirical methods exist for quantifying root biomass and turnover rate and litter production, such as sequential cores, ingrowth cores and nets, rhizotrons and minirhizotrons, all with their pros and cons. Some of the methods give more comparable results than others (Neill, 1992; Samson and Sinclair, 1994; Makkonen and Helmisaari, 1999; Jose et al., 2001; Tierney and Fahey, 2002; Ostonen et al., 2005; Guo et al., 2008b and references therein, Gaul et al., 2009; Brunner et al., 2013). As a result, one of the major uncertainties in C flow studies is estimating the fine root litter production. According to Peltoniemi et al. (2004) fine root turnover affected the average C stock and C accumulation rate most when the turnover rate of other tree compartments were kept constant. Fine root litter production ranged from 0.65 (with low turnover) to three times (with high turnover) the needle litter production.

For estimating fine root turnover, we used the minirhizotron (MR) method, acknowledged by Hendricks et al. (2006) as the most reliable method for root production estimates. In addition to choice of the method, the extremely heterogenic soil environment and continuously renewed roots also challenge root research. Changes in environmental conditions, the length of the study period, vertical distribution of roots in the soil, and root order and diameter have all been shown to affect root survival (Godbold et al., 2003; Baddeley and Watson, 2005; Guo et al., 2008a,b; Valenzuela-Estrada et al., 2008; Kitajima et al., 2010). According to the cost-benefit hypothesis (Eissenstat et al., 2000) fine roots should live longer in harsh environmental conditions, where the construction costs in means of expended C are higher, compared to the sites with more favorable temperature, water and nutrient availability conditions.

During the past few decades the main interest in forest research has been in net primary production, whereas currently the whole C cycle, especially the annual C input into the forest soil and the soil C storage, has also become an important topic (Lehtonen, 2005; Lal, 2005; Meier and Leuschner, 2010; Hansson et al., 2013b). However, litter or net primary production studies often focus either on the aboveground or the belowground part, which results in a poor understanding of the whole tree and stand level interactions. Complete C cycle studies include soil C inputs by trees, understorey and mycorrhizal fungi and C outflows by auto- and heterotrophic respiration as well as by leaching. In Scandinavian conifer forests C cycle studies have been performed e.g. by Lehtonen (2005), Kleja et al. (2008), Ilvesniemi et al. (2009) and Hansson et al. (2013b). However, the conclusions regarding the major litter sources, or even the C balance, have not been consistent.

Norway spruce (*Picea abies* (L.) Karst) is one of the two most common coniferous tree species of the European boreal region. It has a large canopy with 6–10 needle cohorts (Sander and Eckstein 2001). Norway spruce does not shed needles of one needle cohort at a time, but the long-term mean can be considered as being equivalent to such a behavior. Norway spruce aboveground litterfall has been quantified at many different sites in Scandinavia (Bille-Hansen and Hansen, 2001; Saarsalmi et al., 2007; Ukonmaanaho et al., 2008; Nilsen and Strand, 2013), but fine root litter production only at a few sites (Majdi and Andersson, 2005; Hansson et al., 2013a; Leppälammi-Kujansuu et al., 2014). The annual aboveground understorey litter production is generally estimated as being equal to annual growth (Helmisaari, 1995; Schulze et al., 2009) or as biomass multiplied by turnover rate (Lehtonen, 2005; Kleja et al., 2008; Hansson et al., 2013b). The contribution of understorey to the total aboveground litter production in spruce forests varies widely, between 14 and 35% (Kleja et al., 2008; Hansson et al., 2013b). At northern latitudes, especially belowground understorey vegetation is known to play an

important role in annual biomass production and carbon and nutrient cycling (Helmisaari et al., 2007; Olsrud and Christensen, 2004; Kleja et al., 2008; Helmisaari, 1995). Nevertheless, it is still neglected in most litter production studies. This may lead to substantial underestimations of C flux into the soil, as fine roots can produce more biomass annually than the other parts of the tree combined (Helmisaari et al., 2002), and half of the fine root biomass in the soil can be understorey fine roots and rhizomes (Helmisaari et al., 2007). According to Peltoniemi et al. (2006), turnover rates of fine roots and understorey vegetation comprise one of the most significant parameters for soil C stock. Overall, in order to obtain a better understanding of the function of the whole ecosystem, it is important to include both above- and belowground parts of both trees and understorey in the analyses.

In this study two, and eventually six, climatically different Norway spruce stands were investigated regarding their C input into the soil via below- and aboveground litter production. The amount of root-origin litter was determined from tree and understorey fine roots and rhizomes and the quantity of aboveground litter from foliage litterfall and from the litter produced by understorey vegetation. As the growing season is shorter and soil organic layer C:N-ratios are higher in the north, we hypothesized that more of the litter production would be directed belowground than aboveground in the northern site compared to the southern site, in order to guarantee sufficient acquisition of nutrients. Based on the cost-benefit hypothesis, we expected that plants growing in the northern site would have a longer root lifespan than plants growing in the south. We also hypothesized that the share of belowground litter production would increase along the latitudinal gradient.

2. Material and methods

2.1. Site descriptions

The northern (N) site, Kivalo, was located in the northern boreal region in Finnish Lapland (66°20′N/26°40′E) and the southern (S) site, Olkiluoto, in the southern boreal region in Eurajoki, southwestern Finland (61°13′N/21°28′E) (Fig. 1). Understorey vegetation at Kivalo represented mesic site type (Hylocomium–Myrtillus type, HMT) and the most abundant species were *Vaccinium myrtillus* and forest mosses (*Pleurozium schreberi*, *Hylocomium splendens* and *Dicranum* spp.). Olkiluoto represented a more fertile site type (Oxalis–Myrtillus type, OMT) and was characterized by an abundant forest moss layer with many herb and fern species. The cover of dwarf shrubs was only 2–4% (Aro et al., 2012). Soil type in Kivalo was podsolic loamy sand (Smolander and Kitunen, 2011) and in Olkiluoto fine-textured till (Rautio et al., 2004). At Olkiluoto, there were birch trees (17% of overall tree number) growing among the spruces. Root biomass and foliage litterfall of these birch trees were excluded from the data. Stand, climate and soil characteristics of the sites are described in Helmisaari et al. (2009), Aro et al. (2012) and in Tables 1 and 2.

For widening the variation in above- and belowground litter C input and discussing it in relation to site nutrient availability, we included four additional Norway spruce sites from a north–south transect in Sweden (Fig. 1): Flakaliden (64°07′N/19°27′E), and Knottåsen (61°00′N/16°13′E) in the boreal zone, Asa (57°08′N/14°45′E) in the boreo-nemoral zone (Kleja et al., 2008) and Tönnersjöheden (56°40′N/13°03′E) in the cold temperate vegetation zone (Hansson et al., 2011). Climatic conditions (Table 1) as well as nutrient availability change along the latitude gradient: Tönnersjöheden, the southernmost site, is a site with high N deposition (18 kg ha^{-1} yr^{-1}, Bergholm et al., 2003), leading to high N mineralization and availability (Olsson et al., 2012) whereas at

Fig. 1. Location of the study sites in Finland and four extra sites in Sweden.

Table 2

Soil characteristics. Stoniness is an average between the plots unless only one plot is included. The pH and C:N-ratio of the organic layer at the sites were provided by Smolander and Kitunen (2002), Potila et al. (2007), Hansson et al. (2011) and Berggren et al. (2004).

		Organic layer			Mineral soil
		Thickness (cm)	pH	C:N-ratio	Stoniness (%)
Finland	Kivalo	4.4	4.0	32	25
	Olkiluoto	–	3.9	24	34
Sweden	Flakaliden	2.3	4.2	40	26
	Knottåsen	3.4	4.2	35	44
	Asa	4.8	3.6	32	33
	Tönnersjöheden	6.7	4.1	24	39

taken continuously on two sides of each tube, and the total length of the image column was 10–19 cm in the vertical tubes and 57 cm in the horizontal tubes. A total of 8452 images were taken during the study period, of which 2849 at Kivalo and 5603 at Olkiluoto.

The survival of fine roots was analyzed by RooTracker (Duke University, Durham, N.C.) (Kivalo) and WinRHIZOTron MF 2005 (Regent, Quebec, Canada) (Olkiluoto) softwares. As root orders (Pregitzer et al., 2002) are difficult to trace with the MR method (Withington et al., 2006), we considered every segment (mostly root tips) as an individual root; remembering that distal roots could not survive if the connected higher order root had died. All traced roots from the first session (404 of the 3563 roots) were excluded from the analysis because the birth time of the fine roots was unknown. Appeared roots were followed until estimated to be dead on the basis of visual criteria: unsuberized, turgid roots turned to dark brown/black (grass roots light brown), wrinkled and produced no new roots in subsequent viewings. The time of death and birth were fixed in the midpoint between the sessions. The disappeared roots were treated as "censored" because in our earlier paper (Leppälammi-Kujansuu et al., 2014) we showed that only a small fraction of the disappeared roots were actually grazed. Most roots disappeared for other reasons (e.g. became covered by fungal mycelia, other roots or soil), and were thus presumably still alive at the time of disappearance. Likewise, roots living at the end of the monitoring period were treated as censored. For the survival analysis, the data from all MR tubes per site were combined.

The mean diameter (D), length and location of each root and ectomycorrhizal (EcM) root tip were recorded, and the roots were classified as tree, dwarf shrub or grass/herb roots. The fine roots were divided in five D classes: 1: <0.2 mm, 2: 0.2–0.3 mm, 3: 0.3–0.4 mm, 4: 0.4–0.5 and 5: >0.5 mm. The longevity of fine roots was analyzed separately for two depths: (1) topsoil: all the fine roots growing in the horizontal tubes plus those growing in the upper five centimeters of the vertical tubes and (2) mineral soil: the rest of the fine roots in the vertical tubes. As MR tubes at the sites were of different length (i.e. different total image area per tube), the number of MR tubes could not be used for comparing the total elongation or the number of fine roots. Therefore, when

Flakaliden, the northernmost site, the annual N deposition load is on the same level as at Kivalo (less than 3 kg ha^{-1} yr^{-1}, Lindroos et al., 2007; Kleja et al., 2008) and N mineralization and availability were low (Smolander and Kitunen, 2002; Andersson et al., 2002).

2.2. Minirhizotrons

Fine root elongation and longevity were monitored using the MR method (Majdi et al., 2005). At Kivalo, nine MR tubes, three in each of the three plots (25 m × 25 m), were installed vertically in the soil in 2003. At Olkiluoto, five MR tubes were installed in June 2007. Due to high stone content of the soil at Olkiluoto (Table 2) horizontal tubes were also used: two vertical and three horizontal tubes were inserted in the soil of one (30 m × 30 m) plot. At both sites, image collection with the MR camera (BTC-2; Bartz Technology, Santa Barbara, USA) started one year after the installation, continuing through three growing seasons. Roots were photographed 11 times at Kivalo in 2004–2006 and 15 times at Olkiluoto in 2008–2010 (Table 3). Images of 1.1 × 2.0 cm were

Table 1

General stand and climate characteristics of the study sites. The stand characteristics were measured at Kivalo in 2000 (Smolander and Kitunen, 2002), at Olkiluoto and Tönnersjöheden in 2009 (Aro et al., 2010; Hansson et al., 2011) and at the other Swedish sites in 2001 (Kleja et al., 2008; Berggren et al., 2004). In both countries the mean annual precipitation (MAP), mean annual temperature (MAT) and mean length of the growing season (>5 °C, MLGS) were calculated for a 30-yr period (in Finland 1981–2011, based on the dataset of the Finnish Meteorological Institute, and in Sweden 1961–1990, Alexandersson et al., 1991; Kleja et al., 2008), except the MLGS at Tönnersjöheden (Olsson and Staaf, 1995). Ba = stand basal area.

		Stem density (ha^{-1})	Ba (m^2 ha^{-1})	Mean stem D (cm)	Age of dominant trees (yr)	MAP (mm yr^{-1})	MAT (°C)	MLGS (d yr^{-1})
Finland	Kivalo	939	20	18	74	517	0.7	112
	Olkiluoto	667	31	31	96	545	5.3	162
Sweden	Flakaliden		20		42	523	1.2	120
	Knottåsen		18	11	37	613	3.4	160
	Asa	1528	26		38	688	5.5	190
	Tönnersjöheden	614	29	25	54	1053	6.4	204

comparing the number or the elongation of fine roots between the sites, the variable was divided by the number of images filmed per session at each site. For comparing the mean D of a fine root of the sites the independent samples t-tests (IBM SPSS Statistics 20) were used with the level of statistical significance of $\alpha = 0.05$, and each side of the MR tube was considered as an independent replicate (10 in Olkiluoto, 17 in Kivalo).

We estimated the median and mean longevity of the fine roots as well as differences between the survival probabilities of different groups by a parametric regression model with Weibull error distribution (Weibull, 1951) using the SurvReg function in the R program (R 2.13.0). In order to provide comparability with many earlier fine root publications, we also estimated the median longevity of fine roots using the non-parametric Kaplan–Meier survival function (Surv function in the R program) (Kaplan and Meier, 1958). The regression model uses the survival data more effectively than the Kaplan–Meier function through the assumption of equal variances of longevity in different treatment classes.

2.3. Root sampling

For the fine root measurements, sixty soil cores at Kivalo (40 mm in D, in August 1999, twenty cores per plot) and six soil cores at Olkiluoto (60 mm in D, in August 2008) were randomly sampled. Autumn sampling was chosen on the basis of the results of previous boreal conifer studies, according to which the seasonal maximum fine root biomass occurs at the end of the growing season (Makkonen and Helmisaari, 1998; Ostonen et al., 2005). At Kivalo the organic layer was separated and thereafter the mineral soil was divided into 10 cm layers. At Olkiluoto, we did not separate the organic layer but instead divided the cores into 5 cm layers, because the organic layer was not clearly distinguishable and the upper mineral soil layer consisted of a mixture of organic and mineral soil. Owing to the high stoniness of the site, the maximum sampling depth at Olkiluoto was only 15 cm whereas at Kivalo it was 34 cm. The stoniness of each plot (Table 2) was taken into consideration when calculating the dry mass of the weighed fine roots in the mineral soil by using the stoniness index (Viro, 1952; Tamminen, 1991).

Roots were wet-sieved and sorted under a dissecting microscope into different tree species, understorey, biomass and necromass categories according to their color, elasticity and toughness (Persson, 1983). Understorey roots were further separated into dwarf shrub roots and grass & herb roots. Roots smaller than 2 mm were regarded as fine roots (Persson, 1983; Vogt et al., 1983), and living tree fine roots (plus understorey fine roots at Olkiluoto) were further sorted into two D classes: 1–2 mm or <1 mm, the latter including EcM short root tips. As practically all spruce root tips are colonized by EcM in boreal spruce forests (Taylor et al., 2000), no separation between EcM and non-EcM root tips was made. At both sites 10% of the roots in each sorted sample of living roots <1 mm in D were used for counting the number of EcM tips on short roots with the aid of a microscope, and weighed separately. The root samples were dried at 70 °C for 48 h, and weighed.

2.4. Below- and aboveground litter production

For estimating the belowground litter production the median fine root age of trees and understorey in the stands perceived from the survival analyses and the fine root biomass data from the soil cores of the same stands were used. As the majority (99.8%) of the fine roots traced for the survival analysis was <1 mm in D, only the biomass of the tree roots <1 mm in D was used in the production calculations. For understorey the fine root biomass <2 mm in D was used because at Olkiluoto all shrub fine roots and 34% of grass fine roots were <1 mm in D. Thus, the error resulting from using a

different upper D was considered to be minor. For estimating the annual fine root production (kg ha^{-1}), fine root biomass (kg ha^{-1}) in different soil layers was divided by the fine root turnover time (yr) in the topsoil and the mineral soil.

At Kivalo, the aboveground litterfall of the understorey vegetation was assessed in 2000 by Nieminen and Smolander (2006). Their estimate, 100 g m^{-2} yr^{-1}, was used as a proxy of the annual aboveground understorey litterfall at Kivalo.

At Olkiluoto, the aboveground litterfall of the understorey vegetation was estimated according to the annual biomass in August 2008. Six vegetation-humus squares sized 30 cm × 30 cm were chosen in the buffer zone of the vegetation monitoring plot (30 m × 30 m). The monitoring design of vegetation is described in Aro et al. (2012). The squares were located systematically along one side of the plot and the total studied area was 0.54 m^2. The organic layer (including the ground litter) and all the ground vegetation growing on each square was removed in one piece. The understorey vegetation was divided according to plant species and the current-year growth; older living parts and dead biomass were separated, oven-dried (60 °C) and weighed.

The aboveground tree foliage litterfall was collected by 12 conical traps located systematically on the stands. The traps had a collection area of 0.5 m^2 and were placed 1.5 m above ground level. The collection took place about once a month during the growing season during the period of October 1999 – October 2002 at Kivalo, and from November 2007 to the end of October 2011 at Olkiluoto. The samples were oven-dried, sorted to needles and other components (leaves, twigs, cones and all other material) and weighed. We excluded birch leaf litter from the aboveground litter production of Olkiluoto, and pooled other components than needle litter. The average annual litter production of the collection period is reported. For further information about the foliage litterfall at the sites, see Aro et al. (2012) and Ukonmaanaho et al. (2008). The total annual litter production was calculated by combining the above- and belowground litter production. The flux of C was estimated as 50% of the litter production.

We augmented the data with four spruce plots in Sweden in order to study the above- and belowground litter ratios along latitudinal and soil fertility gradients. The original data from Flakaliden, Knottåsen and Asa was published in Kleja et al. (2008) and from Tönnersjöheden by Hansson et al. (2013a,b). We used the data published in these papers to calculate aboveground:belowground litter production-ratio against the organic layer C:N-ratio. However, our fine root production data from Tönnersjöheden differs from the papers by Hansson et al. (2013a,b) as we calculated belowground spruce root litter production for roots <1 mm in D instead of <2 mm in D published in Hansson et al. (2013a,b).

3. Results

3.1. Fine roots and mycorrhiza

We observed and followed the lifecycle of a total of 2323 new fine roots at the Kivalo site and 834 roots at the Olkiluoto site, of which 40% and 58%, respectively, were spruce roots and the rest understorey roots and rhizomes. Practically all traced roots (99.8%) were <1 mm in D. The mean D of spruce fine root differed significantly ($P < 0.01$) between the sites (0.27 ± 0.08 mm at Kivalo and 0.32 ± 0.10 mm at Olkiluoto, measured with the MR method) (Fig. 2a). For the understorey the corresponding numbers for the mean root D were 0.20 ± 0.09 mm at Kivalo and 0.27 ± 0.12 mm at Olkiluoto (Fig. 2b), with only a tendency of thinner understorey roots at Kivalo ($P = 0.082$).

We compared the number and the elongation of roots per MR image between the sites. For this, at both sites, the total number
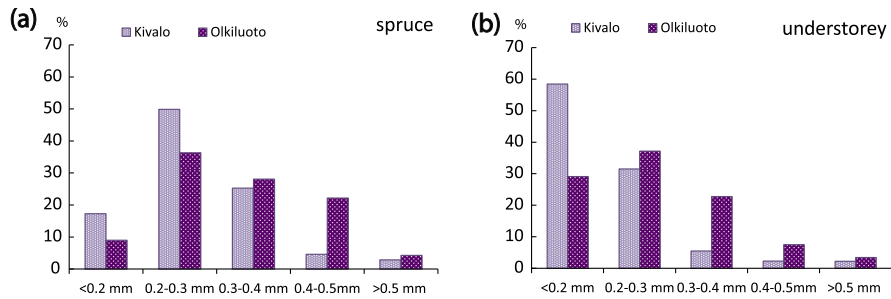
Fig. 2. Diameter class distribution of (a) spruce fine roots and (b) understorey roots and rhizomes at the Kivalo (N) and Olkiluoto (S) study sites.

and total elongation of spruce fine roots were divided by the number of MR images per session. There were more than twice as many spruce fine roots and twofold root elongation per image at Kivalo than at Olkiluoto (3.6 roots and 12.4 mm elongation vs. 1.3 roots and 4.9 mm elongation at Kivalo and Olkiluoto, respectively) (Fig. 3).

Spruce fine root biomass (<1 mm in D) was similar at the two sites (336 g m^{-2} and 285 g m^{-2} at Kivalo and Olkiluoto, respectively, Fig. 4a) although the sampling depth was lower at Olkiluoto due to high stoniness of the soil. However, taking into account the stand size, i.e. calculating fine root biomass on the basis of stand basal area, the tree fine root biomass at Kivalo was almost double compared to that at Olkiluoto (Fig. 4b). The percentage of spruce roots <1 mm in D of spruce roots <2 mm in D was 66% and 67% at Kivalo and at Olkiluoto, respectively.

Understorey fine root biomass (<2 mm in D) was three times higher at Kivalo than at Olkiluoto (Fig. 4c). In the north, shrubs formed the greatest part of this biomass (82%) whereas in the south, practically all understorey fine roots were grass/herb roots. The share of understorey of total fine root biomass (<2 mm in D) was 17% at Kivalo and 7% at Olkiluoto.

Both the frequency and the number of EcM root tips per square meter were substantially higher at Kivalo than at Olkiluoto (Fig. 5a); at Kivalo the average number of EcM root tips mg^{-1} of fine root was 6.9 whereas at Olkiluoto the frequency was 4.5 EcM root tips mg^{-1} of fine root (<1 mm in D). The number of EcMs per stand basal area was fourfold at Kivalo compared to Olkiluoto (Fig. 5b).

3.2. Fine root survival

At the end of the 3 yr study period, 54% and 20% of all tree fine roots had died at Olkiluoto and Kivalo, respectively. The share of disappeared roots was the same at both sites (26%).

The survival of spruce fine roots in the northern site was significantly higher than in the southern site ($P < 0.05$), and higher than
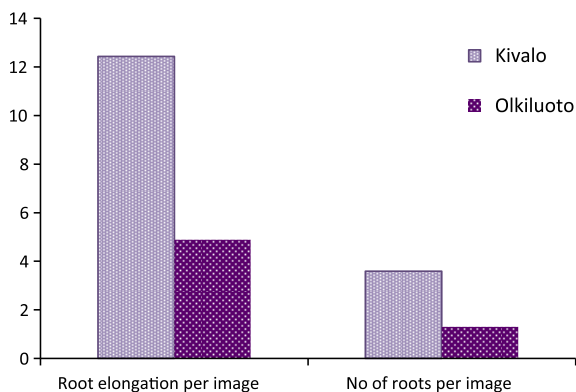
the survival of understorey fine roots at both sites (Table 3). There was no substantial difference in the median longevities between the regression model with the Weibull error distribution and the Kaplan–Meier survival function (Table 3). By treating the disappeared roots as dead instead of censored the median root longevities were 16–26% shorter in the regression model with Weibull error distribution, and 15–41% shorter estimated by Kaplan–Meier survival function (data not shown).

At Olkiluoto, soil depth did not affect either spruce or understorey root survival. At Kivalo, roots growing in the topsoil had shorter longevity than roots growing in the mineral soil ($P < 0.01$, Table 3). The percentage of traced spruce fine roots in the topsoil and mineral soil were 79% and 21% at Olkiluoto, whereas at Kivalo the corresponding distribution was even.

The comparison of the root cohorts born in the first filming year strongly indicated a shorter lifespan of the roots born during the winter months (Fig. 6a–d), but at Olkiluoto the number of roots in some cohorts was low. During the whole study period, most of the fine roots (both spruce and understorey) were born in July and August. According to the total number of deaths, one third of deaths occurred outside the growing season. However, as the period lengths were not even, we standardized them by dividing the number of deaths by the number of weeks in each period. After this correction, the majority of spruce and understorey roots died in August and in July, respectively.

3.3. Below- and aboveground litter C

The total below- and aboveground litter C flux (including trees and understorey) was 272 and 235 g C m^{-2} yr^{-1} at Kivalo and Olkiluoto, respectively (Table 4). The aboveground:belowground litter production ratio was 1.3 for Kivalo and 1.5 for Olkiluoto. At the northern site, the understorey litter comprised 28% of the total, whereas the corresponding figure at the southern site was 13%.

The annual belowground C input from fine root litter, both tree and understorey, was higher at Kivalo than at Olkiluoto (Table 4). The share of understorey fine root litter of the belowground litter production was 23% and 11% at the northern and southern site, respectively.

The annual aboveground litter C input from foliage and understorey was almost equal at Kivalo (153 g C m^{-2}) and Olkiluoto (142 g C m^{-2}) even though aboveground understorey litter production was 2.4 times higher at Kivalo than at Olkiluoto (Table 4). At both sites tree foliage litter production varied between the years (data not shown), but the average foliage litterfall was 1.2 times higher at Olkiluoto than at Kivalo (2419 and 2067 kg ha^{-1} yr^{-1} at Olkiluoto and Kivalo, respectively, Table 4). Needle litter consisted of 50% and 46% of total foliar litterfall at Olkiluoto and Kivalo, respectively (average between the years). At Kivalo, the aboveground understorey litter consisted mainly of mosses (coverage 37%) and bilberry (coverage 22%) (Nieminen and Smolander, 2006), whereas at Olkiluoto 58% of annual biomass production (dry weight g m^{-2}) was produced by mosses (Haapanen, 2010).

Fig. 3. Spruce root elongation (mm) and the number of spruce roots per MR image at Kivalo (N) and Olkiluoto (S).
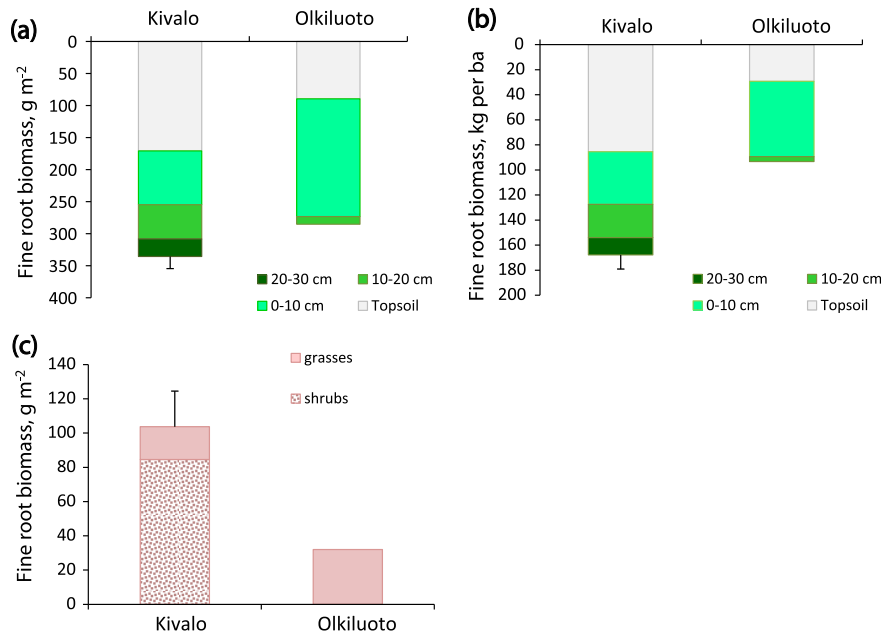
Fig. 4. Spruce fine root biomass (<1 mm in D) per (a) square meter (m^2), (b) stand basal area (ba), and (c) understorey fine root biomass (<2 mm in D) g m^{-2} at Kivalo (N) and Olkiluoto (S). Bar indicate standard deviation; Kivalo n = 3, Olkiluoto n = 1.
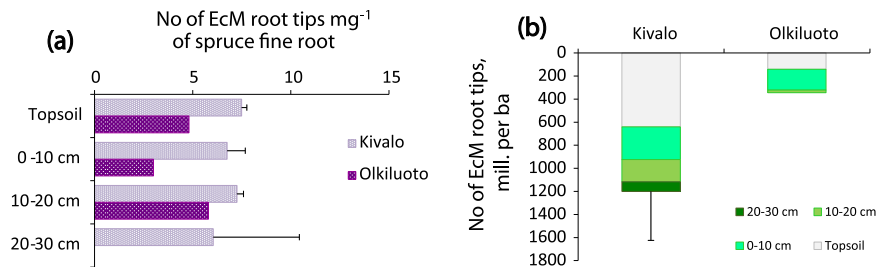

Fig. 5. Number of ectomycorrhizal (EcM) root tips per (a) mg of fine root (<1 mm in D) and (b) stand basal area (ba) at Kivalo (N) and Olkiluoto (S). Bar indicate standard deviation; Kivalo n = 3, Olkiluoto n = 1.

Table 3
Median (weeks ± se) longevity of Norway spruce and understorey fine roots at the Kivalo and Olkiluoto study sites estimated by the regression model with Weibull error distribution, at two soil depths. Median longevity (with 95% confidence limits) estimated by the Kaplan–Meier survival function resulted in nearly similar values as the regression model, with significant ($P < 0.01$) differences in spruce fine root survival between the sites. N = number of roots.

	Spruce		Understorey	
	Kivalo	Olkiluoto	Kivalo	Olkiluoto
N	930	487	1393	347
Weibull	97 ± 2[b]	89 ± 2[a]	86 ± 1[a]	86 ± 2[a]
Kaplan–Meier	102 (102–107)	93 (84–98)	98 (83–98)	98 (79–98)
Topsoil	103 ± 3[β]	89 ± 2	104 ± 3[δ]	87 ± 2
Mineral soil	89 ± 3[α]	89 ± 7	77 ± 1[γ]	92 ± 11

The letters (a–b, α–β and γ–δ) indicate significant ($P < 0.01$) differences between the groups.
Image collections at Kivalo 23.6.2004; 27.7.2004; 25.8.2004; 5.7.2005; 4.8.2005; 1.9.2005; 27.9.2005; 31.5.2006; 11.7.2006; 9.8.2006; 12.9.2006.
Image collections at Olkiluoto 26.6.2008; 15.8.2008; 11.9.2008; 15.10.2008; 26.5.2009; 1.7.2009; 4.8.2009; 3.9.2009; 6.10.2009; 18.5.2010; 22.6.2010; 27.7.2010; 1.9.2010; 5.10.2010; 18.5.2011.

The inclusion of data from four more Norway spruce stands, Tönnersjöheden, Asa, Knottåsen and Flakaliden (Fig. 1) along a north–south gradient, allowed us to examine relations of below-ground and aboveground litter production with more data. The aboveground tree litterfall decreased significantly towards the higher organic layer C:N-ratio ($P < 0.01$), and to a lesser extent towards the lower stand basal area ($P < 0.05$). For trees, the total litter C input (including below- and aboveground) tended to decrease towards higher C:N-ratios (R^2 = 0.59, P = 0.08) (Fig. 7a), whereas for the understorey the trend was the opposite (R^2 = 0.64, P = 0.06) (Fig. 7b). The southernmost site, Tönnersjöheden, was the most fertile site (lowest C:N-ratio), with highest forest productivity highest site index and here the tree foliage litterfall was 2.2 times higher than the belowground litter C input (Fig. 7c). At the least productive sites the share of belowground litter C input was almost equal to the aboveground input. Thus, the shift in allocation from aboveground to belowground did not follow tree age, latitude or the length of growing season gradient ($P > 0.05$) but rather the organic layer C:N-ratio gradient (R^2 = 0.70, $P < 0.05$) (Fig. 7c).

4. Discussion

4.1. Fine root biomass and morphology

The sites clearly differed in climate, with lower mean annual temperature and a shorter growing season at Kivalo than at Olkiluoto. Both sites were rather fertile, but fertility is always connected to site location through climate, especially the length of the growing season. A fertile site in Lapland is not comparable to a fertile
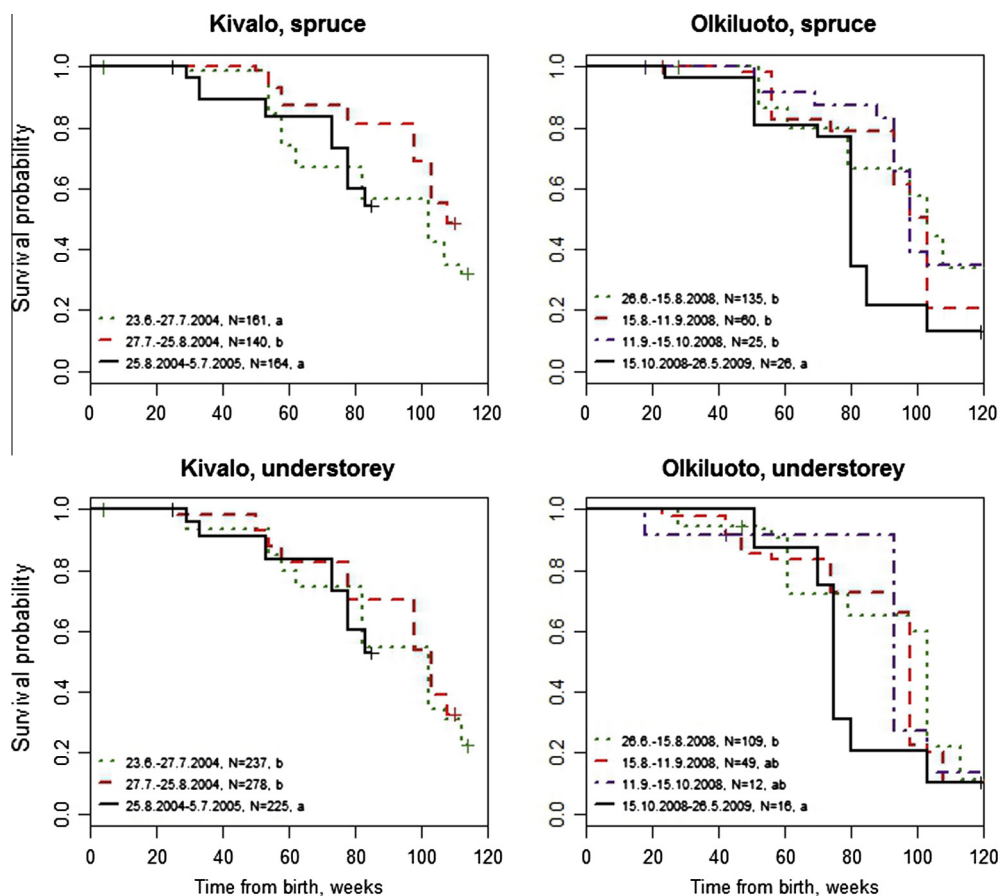
Fig. 6. Survival curves of spruce and understorey fine root cohorts born during the first year of image acquisition (2004–2005 at Kivalo, 2008–2009 at Olkiluoto).

Table 4
The annual belowground (BG) C input (C g m^{-2}) into the different soil depths via fine roots and aboveground (AG) litter C in six Norway spruce stands along a latitudinal gradient. The original data from Flakaliden, Knottåsen and Asa was published in Kleja et al. (2008) and from Tönnersjöheden partly by Hansson et al. (2013a,b).

	Belowground					Aboveground						BG % of total
	Topsoil	Mineral soil	Sum spruce	US	BG total	Needles	Branches	Other	Sum spruce	US	AG total	
Kivalo	43	48	91	27	118[a]	48	4	51	103[c]	50[e]	153	43
Olkiluoto	26	57	83	10	93[b]	59	18	43	121[d]	21[f]	142	40
Flakaliden	9	48	57	41	98				60	32	92	62
Knottåsen	38	44	82	50	132				68	33	101	66
Asa	22	62	84	17	101				101	17	118	50
Tönnersjöheden	38	19	57	1	58				128	24	152	31

[a] Soil coring in 1999, MR image collection 2004–2006.
[b] Soil coring in 2008, MR image collection 2008–2010.
[c] Foliage litter trapping 2000–2002.
[d] Foliage litter trapping 2008–2011.
[e] Vegetation analysis & ground vegetation sampling 2000.
[f] Vegetation analysis & ground vegetation sampling 2008.

site in southern Finland, which can also be seen from the higher C:N-ratio in the organic layer (Table 2) and lower net N minerali-zation rate (Potila et al., 2007; Olsson et al., 2012) at Kivalo com-pared with Olkiluoto. Due to differences in site conditions, root characteristics and litter production at the sites were not expected to be identical.

At higher northern latitudes with a lower temperature sum, spruce short roots have been shown to grow thinner and longer (Ostonen et al., 2007, 2011), to have more EcM root tips (Helmisaari et al., 2009) and fine root biomass (Helmisaari et al., 2007) in relation to foliage mass and basal area than trees growing at lower latitudes. In this study there were similar trends: Firstly, the fine root biomass per square meter at the sites was almost equal,

but calculating per stand basal area there was a clear difference: spruces in the north had twofold higher fine root biomass than spruces at Olkiluoto. Secondly, the morphology of fine roots at the sites differed: fine roots tended to be thinner and grow more length in the north than in the south. This is supported by the earlier cli-mate gradient studies where the Norway spruce EcM root tips were observed to be 2.1 times longer and significantly thinner in the northern Finland than in Germany (Ostonen et al., 2011, 2013). Thirdly, the frequency of EcM root tips and the number of EcM roots per stand basal area at Kivalo were multiple compared to Olkiluoto. This is in accordance with the result of Helmisaari et al. (2009) and Ostonen et al. (2007, 2011), who reported increases in root tip num-bers along the latitudinal gradient (up to tenfold).
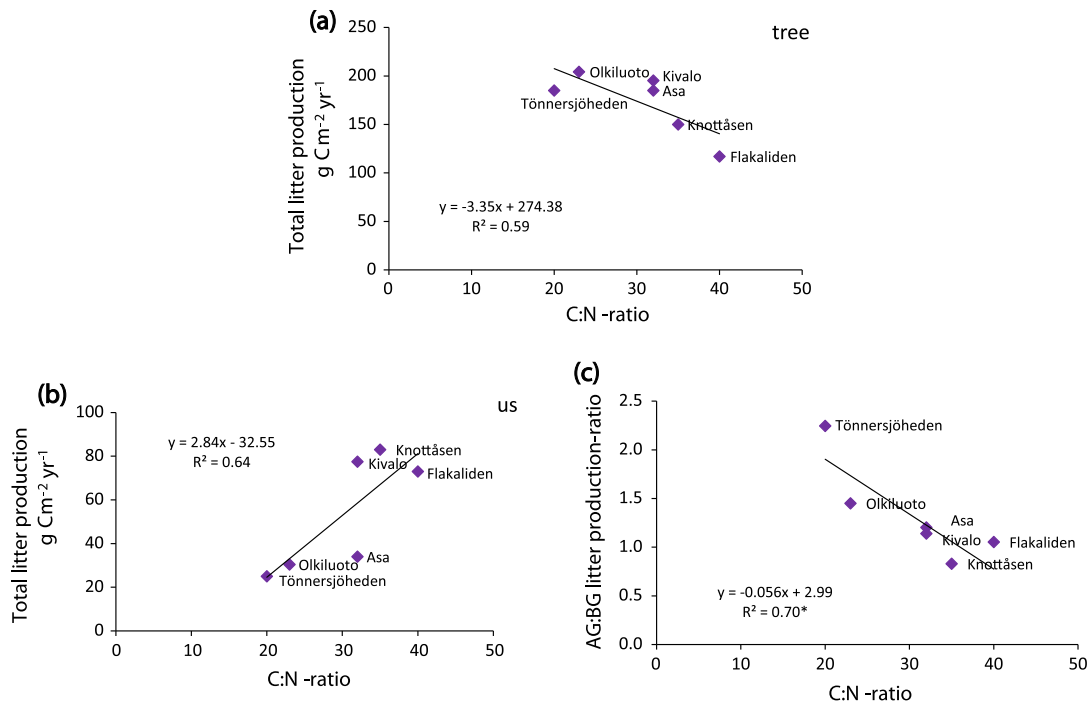
Fig. 7. The total litter production of (a) Norway spruce and (b) understorey, as well as c) tree aboveground (AG):belowground (BG)-ratio in relation to organic layer C:N-ratio. The original data from Flakaliden, Knottåsen and Asa was published in Kleja et al. (2008) and from Tönnersjöheden partly by Hansson et al. (2013a,b).

Trees growing at higher latitudes turn to the extensive foraging strategy, increasing fine root biomass and length to enlarge root absorbing area and to provide sufficient water and nutrient uptake (Ostonen et al., 2011). Our results showed clearly higher fine root elongation rate, biomass and EcM tip number per stand basal area in the north, supporting that concept. Lower fine root elongation, biomass and root tip number per stand basal area in the southern site might indicate higher nutrient uptake efficiency of fine root area unit (intensive foraging), which has been achieved by morphological adaptations or changes in associated microbial and mycorrhizal symbionts (Lõhmus et al., 2006; Ostonen et al., 2011). An increase in the number of mycorrhizal root tips in the north is also in accordance with the increased share of organic N uptake in the low-productivity forests (Nordin et al., 2001; Kielland et al., 2007), where mycorrhizal communities are known to be able to degrade polymeric N compounds and to absorb amino acids for growth (Näsholm et al., 2009).

The share of understorey of all fine root biomass (<2 mm in D) was 17% at Kivalo and 7% at Olkiluoto. These figures are within the range of reported values from northern (16–43%) and southern (1–14%) Norway spruce stands (Helmisaari et al., 2007), and reflect the thinner crown of the northern Norway spruce, which allows more light to penetrate to the forest floor. The share of spruce fine roots <1 mm in D of roots <2 mm in D (66% and 67% at Kivalo and Olkiluoto, respectively) was also comparable to the reported percentages in Sweden (62%, Leppälammi-Kujansuu et al., 2013), Estonia (66%, Ostonen et al., 2005), Finland (55%, Helmisaari et al., 2007) and Norway (41–55%, Børja et al., 2008). Ectomycorrhizal short root tips have been reported to account for 50% of the biomass of spruce roots less than 1 mm in D (Helmisaari et al., 2009), which are generally of first and second order (Ostonen et al., 2011).

4.2. Root survival

Spruce fine roots lived longer at the northern site (Kivalo) than at the southern site (Olkiluoto). This is in line with the results of

several publications on temperature and fertility gradients (Hendrick and Pregitzer, 1993; Eissenstat and Yanai, 1997; Gill and Jackson, 2000; Nadelhoffer, 2000; Yuan and Chen, 2010), and also with the observation that roots tend to exhibit low mortality rates over winter (Hendrick and Pregitzer, 1993; Andersson and Majdi, 2005). At Kivalo, the winter is longer and the snow cover thicker than at Olkiluoto. Thick snow cover provides protection against deep soil frost (Solantie, 2000) but also delays soil thawing. Delayed soil thawing experiments have shown cold soil temperatures to be associated with lower water and nutrient uptake, especially nitrogen (Repo et al., 2007; Dong et al., 2001), which also relates to lower availability. Fine root nitrogen concentration has been shown to be lower at Kivalo than at Olkiluoto (Helmisaari et al., 2007; Haapanen, 2009), which is in accordance with the decreasing trend of nitrogen concentration of Norway spruce fine roots along a latitudinal gradient (Högberg et al., 1998). On the other hand, fine root nitrogen concentrations have been shown to correlate positively with fine root mortality (Pregitzer et al., 1995; Majdi and Andersson, 2005; Withington et al., 2006; McCormack et al., 2012). Mild winters in the south may also have caused cryoturbation (frost churning), and stress to the plant roots (Tierney et al., 2001; Kreyling et al., 2012), and thus may have decreased the spruce fine root lifespan in the south.

At the northern site, fine roots lived longer in the mineral soil, whereas at the southern site fine root longevity was not related to the soil layer. At Olkiluoto soils are pedologically young (500–2000 years) and weakly developed (Tamminen et al., 2007) due to their location on a land-up lift area, whereas Kivalo soils are fully developed podzols, with a thick moss layer limiting the surface soil temperature (Sirén, 1955). The birches growing among the spruces at Olkiluoto may also have altered the soil properties (Smolander and Kitunen, 2002; Smolander et al., 2005; Smolander and Kitunen, 2011). Bioturbation and root grazing (Stevens and Jones, 2006) were probably higher at the southern site, which was the case in Southern Sweden compared to Kivalo (Olsson et al., 2012). Furthermore, moss and shrub-dominated understorey vegetation contributed to the development of the

thick organic humus layer at Kivalo, whereas moss and herb-dominated understorey at Olkiluoto produced a more favorable organic layer. Also, due to the high stoniness in Olkiluoto soils, horizontal MR tubes were also used, which led to a considerably higher proportion of fine roots in the organic layer than in the mineral soil.

Seasonality affects fine root longevity, as has been widely observed (Johnson et al., 2000; Kern et al., 2004; Andersson and Majdi, 2005; Finér et al., 2011; Gu et al., 2011; Wu et al., 2013). By using the MR method we confirmed that fine roots mostly grew in the late summer and early autumn (July–August), corresponding to the root growth maximum reported by Hansson et al. (2013a) and Noguchi et al. (2005). In boreal conditions, Norway spruce root growth in early summer is likely to be hindered by low soil temperatures. We also recorded that fine roots born in the end of the growing season (after shoot growth), when the soil was still warm and sufficient C was available, had better survival compared to roots born outside the growing season. The result is comparable to the seasonality of Norway spruce fine root survival in the Flakaliden soil warming experiment (Leppälammi-Kujansuu et al., 2014). The effects of seasonal changes in carbohydrate availability on root lifespan were also discussed by Anderson et al. (2003) and Eissenstat and Yanai (1997).

The survival of understorey fine roots at both sites was comparable to spruce survival at Olkiluoto, which is in line with the results of Hansson et al. (2013a) who found no significant difference between the longevity of understorey fine roots and birch/pine fine roots of similar D class. In some studies, understorey fine roots have been recorded to have shorter lifespans than those of trees (Finér and Laine, 2000; Majdi and Andersson, 2005) or to live longer at high altitudes compared to low altitudes (Fitter et al., 1998). However, it must be kept in mind that combining all understorey vegetation is somewhat arbitrary because this flora includes a variety of species from annual to perennial plants with different lifespans.

4.3. Litter production and C flux

The total litter C input (235 and 272 g C m^{-2} yr^{-1}) at the sites was comparable to the reported litter C fluxes in other Nordic Norway spruce forests, 190–233 g C m^{-2} yr^{-1} (<1 mm in D, Kleja et al., 2008) and 282 g C m^{-2} yr^{-1} (<2 mm in D, Hansson et al., 2013b). The aboveground-belowground litter production (both trees and understorey)-ratio was 1.3 in Kivalo and 1.5 in Olkiluoto.

The contribution of understorey vegetation to stand litter production differed between the sites. In the north 23% of belowground and 33% of aboveground litter was produced by understorey vegetation whereas the corresponding percentages at Olkiluoto were 11% and 15%. Kleja et al. (2008) reported contributions of 40% and 15% for below- and aboveground field vegetation in northern, and 17% and 1% in southern spruce forest in Sweden. Majdi and Andersson (2005) reported corresponding percentages (35–40%) when studying the belowground production in a northern spruce forest. A litter component study in Finnish boreal forests supports our results as in the southern forests litter produced by the trees constituted the most important litter C stock whereas dwarf shrubs dominated litter C stock in the north (Hilli et al., 2010). Understorey vegetation may also affect the size of soil C storage: in pine forest in southeastern USA the soil C storage was lower in plots where the understorey vegetation had been eliminated, with or without fertilization (Shan et al., 2001). After combining the production of tree and understorey roots, there was no difference in fine root production between the sites, but the absorbing root area was higher in the northern site compared to the south, as pointed out in the previous section. Our C flux from spruce root litter (83–91 g C m^{-2} yr^{-1}) falls within the relatively wide range of other reported C fluxes from Norway spruce forests: 25–57 g C m^{-2} yr^{-1} (<1 mm in D, Majdi and Andersson, 2005; Lukac and Godbold, 2010), 130–143 g C m^{-2} yr^{-1} (<2 mm in D, Hansson et al., 2013b; Majdi and Nylund, 2001) and 276 g C m^{-2} yr^{-1} (<5 mm in D, van Praag et al., 1988).

The calculation of understorey root litter production was based on roots less than 2 mm in D, whereas roots less 1 mm in D were used for spruce root litter. Furthermore, the fine root turnover time was estimated only for roots less than 1 mm in D. This led to a slight overestimation of the amount of understorey litter production. The understorey root separation data from Olkiluoto (to <1 and 1–2 mm in D, not shown) showed that all shrub roots and 34% of grass/herb roots were less than 1 mm in D. By calculating the understorey litter production at both sites based on D distribution data at Olkiluoto, the litter C flux into the soil would have been 4 g C m^{-2} yr^{-1} and 6 g C m^{-2} yr^{-1} lower at Kivalo and Olkiluoto, respectively. However, our understorey fine root litter production of 10 and 27 g C m^{-2} yr^{-1} is on the same level as 17–50 g C m^{-2} yr^{-1} reported by Kleja et al. (2008) and 37 g C m^{-2} yr^{-1} by Majdi and Andersson (2005).

Tree foliar litterfall was 1.2 times higher in the south than in the north, but due to the abundant aboveground understorey litter production the total aboveground litter C flux was slightly higher in the north. As the majority of litter production at both sites originated from trees (72% and 87% at Kivalo and Olkiluoto, respectively), the larger trees (higher basal area) with greater foliage at Olkiluoto provide one explanation for this, which is supported by expansion of the regression analysis to include the Swedish sites as well. Furthermore, the needle retention time in the northern parts of Finland is longer and thus the needle production is correspondingly lower (Ukonmaanaho et al., 2008). In addition, the northern spruce trees (*Picea abies* ssp. odovata) have a genetic tendency to grow narrower crowns with less foliage mass than southern spruce trees (*Picea abies*) (although they are genetically similar and belong to the same species (Krutovskii and Bergmann, 1995)).

Mean aboveground spruce litter productions (2067 kg ha^{-1} yr^{-1} in the north and 2418 kg ha^{-1} yr^{-1} in the south) were on the same level as the means of 18 spruce stands throughout Finland, 1200 and 2800 kg ha^{-1} yr^{-1} in the north and south, respectively (Saarsalmi et al., 2007). Ukonmaanaho et al. (2008) reported higher spruce litterfall values in southern Finland and lower values in northern Finland, but their dataset was smaller (two sites in northern and five sites in southern Finland). According to Saarsalmi et al. (2007), the most reliable predictors of annual canopy litterfall were latitude, mean temperature sum and of the stand characteristics mean tree height. Starr et al. (2005) reached the same conclusions based on 34 Scots pine stands throughout Finland.

Nitrogen deposition in Central Europe is higher than in Scandinavia (Högberg et al., 1998; Lindroos et al., 2007; Dise et al., 2011), and nitrogen cannot be considered to be a growth-limiting factor in central European forests. By contrast, in northern Europe the C:N-ratio well describes the nutrient availability and forest productivity of a site. Regressing the ratio of above- and belowground spruce litter production against the C:N-ratio of the organic layer of the sites revealed the significant relationship of site productivity with above- and belowground litter C input: the lower the C:N-ratio, the relatively more litter was produced aboveground than belowground.

The significance of nutrient availability, especially nitrogen, for the C allocation patterns of Norway spruce has been demonstrated in several modeling studies (Mäkelä et al., 2008; Dewar et al., 2009; Valentine and Mäkelä, 2012). The result also supports the functional equilibrium hypothesis (Brouwer 1963), which predicts that plants increase the relative production of a responsible absorbing organ in order to improve the uptake of a limiting resource and reduce stress. Thus, according to the regression, the

lower the forest productivity, the higher the share of root-origin litter C, which may have an impact on C sequestration into the forest soil. Some studies have found differences in root litter quality (Uselman et al., 2012) or decomposability (Vivanco and Austin, 2006; Hansson et al., 2010; Freschet et al., 2013) compared with leaf litter which suggest that the mean residence time of the root litter in the soil could be longer than that of leaf litter. This point needs further research, and if validated, should be taken into account in C cycle models.

The ratio of aboveground:belowground litter production at the sites was close to one (0.8–1.4), except at Tönnersjöheden. As in our study only the belowground litter C input from fine roots less than 1 mm in D was estimated; the actual belowground litter production was greater than reported here. Fine roots 1–2 mm in D as well as coarse roots also produce litter, even if with a slower turnover (Nygren et al., 2009). In addition, the survival of fine roots less than 0.5 mm in D could be shorter than the estimated 86–97 weeks for roots <1 m in D in this study, as observed in several studies (Wells and Eissenstat, 2001; Wells et al., 2002; Anderson et al., 2003) with broadleaf species. For Norway spruce, Hansson et al. (2013) however reported similar fine root lifespans for fine roots <0.5 and 0.5–1 mm in D in Sweden. Even if the fine roots with EcM short roots with a D < 1 mm produce most of the belowground litter adding also the thicker root compartments in belowground litter C input estimates would mean that the total belowground litter C input probably exceeds the aboveground litter C input in the majority of boreal forests.

5. Conclusions

Two Finnish Norway spruce stands growing in climatically contrasting conditions showed no difference in absolute amounts of fine root biomass per square meter, but after taking into account the lower basal area, the fine root biomass was higher in the northern stand. The survival of spruce fine roots was higher in the north than in the south, whereas there was no difference in the longevity of understorey fine roots between the sites. The spruce trees growing in the south produced more foliar litter than trees growing in the north, but the substantial contribution of understorey vegetation in the north led to higher total aboveground litter C input in the north than in the south. The belowground litter C input (from trees and understory) at the sites was almost equal, but analogous to aboveground, in the belowground the litter C input originating from the understory vegetation was substantially higher in the north than in the south. Longer lifespan of fine roots, thinner roots, more fine root biomass per basal area, and number of roots and EcM root tips in the north compared to the south, all point to adaptation of spruce to Nordic conditions in order to sustain sufficient acquisition of nutrients in climatically harsh conditions.

Expanding the data with four Swedish Norway spruce stands revealed that the aboveground:belowground litter production-ratio was more related to the organic layer C:N-ratio than to latitude. The less productive sites produced relatively more litter belowground than aboveground and a substantial part of the litter originated from the understory. These differences in the origin of litter C may have an effect on C residence time in the soil, and should thus be examined more and possibly taken into account in future C cycle models. As demonstrated, the below- and aboveground components of litter are strongly intertwined and should always be studied in conjunction with each other.

Acknowledgements

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