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Norway spruce fine root dynamics and carbon input into soil in relation to environmental factors

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Academic dissertation

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ABSTRACT

Knowledge of the quantity of belowground litter carbon (C) input is scarce but highly valued in C budget calculations. Specifically, the turnover rate of fine roots is considered as one of the most important parameters in the estimation of changes in soil C stock. In this thesis Norway spruce (*Picea abies* L. (Karst.)) fine root lifespan and litter production were studied and their responses to nutrient availability and temperature were examined. Aboveground foliage and understory litter C inputs were also quantified. Furthermore, fine root isotopic C ages were compared to fine root lifespans.

Increased nutrient availability and higher temperature shortened spruce fine root lifespan both in the manipulation treatments and along a latitude gradient. Fertilization improved tree growth and the absolute amount of litter production, both below- and aboveground. Soil warming, by contrast, increased the belowground litter production in relation to aboveground foliage litterfall but did not lead to long-term increases in aboveground tree growth. In warmed soil, the changes in spruce short root morphology indicated nutrient deficiency. Fine root litter C input into the soil in relation to the aboveground litter C input was higher towards lower fertility, due particularly to the greater contribution of understory vegetation. The structural ^{14}C age of fine roots was consistently 3 - 6 years older than fine root lifespan determined with the minirhizotron method indicating that root growth may use also use stored or recycled C.

In almost all stands, fine root litter C input into the soil at least equalled the aboveground input, which confirms the significance of belowground litter production in the boreal forest C cycle. The importance of understory vegetation was also significant. In addition on understory vegetation, different stand age and tree species, more studies should also focus on the shift in the litter production pattern from above- to belowground along environmental change as this may have an impact on litter C quality and soil C storage in boreal forest soils.

Keywords: fine root biomass and turnover, litter C input, belowground:aboveground -ratio, C age

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LIST OF ORIGINAL ARTICLES

This thesis consists of an introductory review followed by four research articles and one manuscript, which are referred to in the review by their Roman numerals. The articles are reprinted with kind permission of the publishers.

I **Leppälammi-Kujansuu, J.**, Ostonen, I., Strömgren, M., Nilsson, LO., Kleja, DB., Sah, S. & Helmisaari, H-S. 2013. Effects of long-term temperature and nutrient manipulation on Norway spruce fine roots and mycelia production. Plant and Soil 366: 287-303.
http://dx.doi.org/10.1007/s11104-012-1431-0

II **Leppälammi-Kujansuu, J.**, Salemaa, M., Kleja, DB., Linder, S. & Helmisaari, H-S. 2014. Fine root turnover and litter production of Norway spruce in a long-term temperature and nutrient manipulation experiment. Plant and Soil 374:73-88.
http://link.springer.com/article/10.1007%2Fs11104-013-1853-3

III **Leppälammi-Kujansuu, J.**, Aro, L., Salemaa, M., Hansson, K., Kleja, DB. & Helmisaari, H-S. 2014. Fine root longevity and carbon input into soil from below- and aboveground litter in climatically contrasting forests. Forest Ecology and Management 326: 79-90
http://www.sciencedirect.com/science/article/pii/S0378112714001935

IV Sah, S., Bryant, C., **Leppälammi-Kujansuu, J.**, Lõhmus, K., Ostonen, I. & Helmisaari, H-S. 2013. Variation of carbon age of fine roots in boreal forests determined from ^{14}C measurements. Plant and Soil 363: 77-86.
http://link.springer.com/article/10.1007%2Fs11104-012-1294-4

V Helmisaari, H-S., **Leppälammi-Kujansuu, J.**, Bryant, C., Sah, S., & Kleja, DB. Old carbon in young fine roots in boreal forests. Under revision for Biogeochemistry.

AUTHOR'S CONTRIBUTION

Jaana Leppälammi-Kujansuu was responsible for the summary part of this thesis. In papers I and II the field trial was originally planned and started by S. Linder in the 1990s and the experimentation had been continuing since then. In these papers, where the planning of the studies had been carried out by others, this author analyzed the data concerning fine roots, interpreted the results and in paper II also performed the field measurements of belowground compartments followed by the minirhizotron image and survival analyses. In paper III this author participated in the planning of the study, performed the fine root survival analysis and interpreted the results. Jaana Leppälammi-Kujansuu was the main author in papers I, II, and III. In paper IV she participated in the writing process and in paper V in planning, field measurements and the figures and in writing of the manuscript.

LIST OF TERMS AND ABBREVIATIONS

C	carbon
N	nitrogen
DOC	dissolved organic carbon
SOM	soil organic matter
EcM	ectomycorrhiza
EcMB	ectomycorrhizal short root dry weight
MAT	mean annual temperature
D	diameter
L	length
SRL m g^{-1}	specific root length (root length /short root dry weight)
RTD kg m^{-3}	root tissue density (dry weight of the root sample/ volume of short roots in the sample)
MR	minirhizotron
K-M	Kaplan-Meier survival analysis
WFI	warmed-fertilized-irrigated treatment
WI	warmed-irrigated treatment
FI	fertilized-irrigated treatment
I	irrigated/reference treatment
C	non-manipulated control

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1 INTRODUCTION

Of all the terrestrial carbon (C) stores, forest ecosystems are the most important because they store vast amounts of C in living biomass, but particularly in the soil. Globally, soils contain three times more C than terrestrial vegetation (Schlesinger 1977, Lal 2005), high-latitude forest soils reserving even greater amounts (Dixon et al. 1994, White et al. 2000). In relation to the atmospheric C pool, boreal vegetation and soil together contain ~300 Pg of C, which amounts to approximately half of the C in the atmosphere (Gower et al. 2001).

In terrestrial ecosystems, C circulates among atmosphere, biomass and soil (Figure 1). C is assimilated into ecosystems via photosynthesis and then allocated to the different plant components. Traditionally, research has focused on the aboveground biomass, i.e. forest growth, but during recent decades the importance of the belowground part has also been acknowledged. In recent years, fine roots and root-associated fungi have been shown to play the most significant role in long-term C sequestration in boreal forests (Godbold et al. 2006, Högberg et al. 2008, Clemmensen et al. 2013).

Living plant components release part of the C back to the atmosphere via respiration (Figure 1), and from belowground parts also as rhizodeposition. After senescence, the biomass turns into litter. Soil animals, saprotrophs and bacteria decompose organic matter and release C into the atmosphere via heterotrophic respiration. A part of the organic C is lost from the system via leaching of DOC or via biomass harvesting (Figure 1). Thus, soil C stocks are controlled by the input of C by both below- and aboveground litter production and exudation and the output of C by decomposition, autotrophic respiration and leaching.

According to current knowledge, the inputs of C exceed the outputs in boreal forests, meaning that boreal forests constitute an important sink for atmospheric carbon dioxide (CO_2) (Liski et al. 2003). Climate change has been predicted to be the most pronounced in northern regions (IPCC 2007), leading to boreal and artic areas experience more warming than any other biome. In the boreal zone warmer climate would enhance N mineralization and lengthen the growing season, thus clearly increasing vegetation productivity (Chapin & Shaver 1996, King et al. 1997, Norby & Luo 2004, Jansson et al. 2008,). As a result, the amount of aboveground tree and understory litterfall would increase, thus increasing the flux of C into the forest floor. However, the belowground responses are far less well known and predictions of the effects of global warming-related changes such as elevated CO_2, nutrient availability, moisture and temperature on the belowground processes are much more uncertain (Hyvönen et al. 2007, Allison & Treseder 2011, Nannipieri 2011, Pickles et al. 2012). In addition to the methodological challenges of studying belowground phenomena, the conclusions are often based on short-term studies, which may show only a temporary response or no response at all because it would have required a longer period of time for the effects to become detectable. Furthermore, many studies have investigated only the above- or belowground part without taking into consideration the whole ecosystem, even though the two components are inseparably interconnected.

In one Finnish C budget study, fine roots and foliage together comprised 80 - 90% of litterfall, of which fine roots alone accounted for more than 50% (Lehtonen 2005). As the belowground net primary production such as root production has been far less studied than the aboveground C input, there is considerable uncertainty in the quantification of Finnish forest C stocks and fluxes (Lehtonen 2005, Peltoniemi et al. 2006). Fine root turnover has been shown to affect the average C stock and C accumulation rate most when the turnover

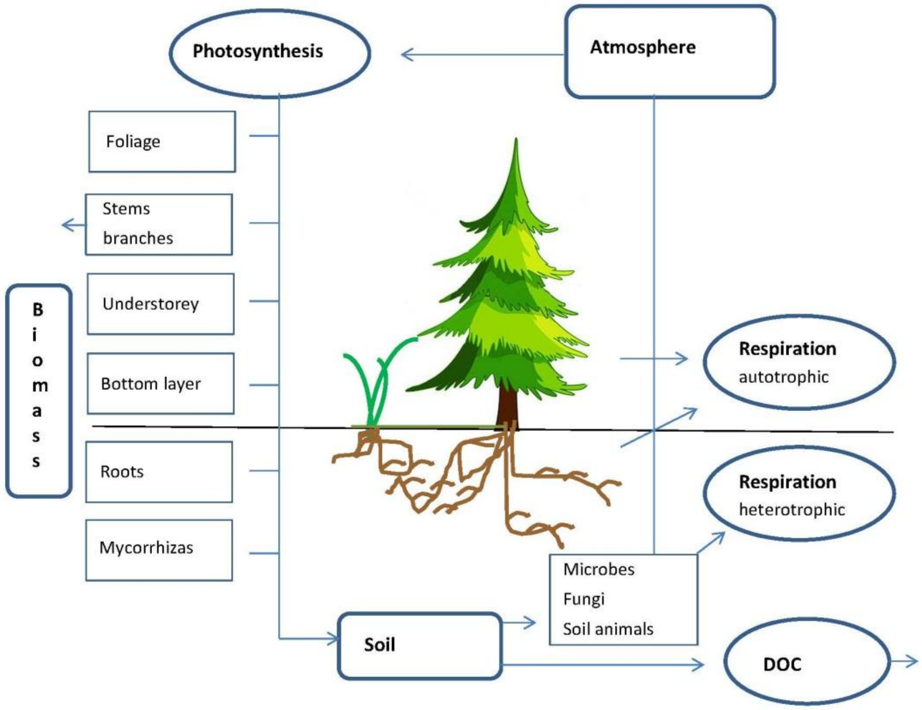

Figure 1 Simplified carbon cycle in a forest, in which the pools are displayed in rectangles and fluxes in ellipses.

rates of other tree compartments are kept constant: by setting the fine root turnover rate to its lower or upper limit (from the literature), fine root litter production ranges from 0.65 (with low turnover) to threefold (with high turnover) the needle litter production (Peltoniemi et al. 2004). In order to improve the robustness of soil carbon models, and of C budget estimations, it is important to collect empirical data of the belowground processes, especially on fine roots and their responses to environmental changes. The ultimate goal is to increase our understanding of overall ecosystem processes and thus contribute to our ability to predict what will happen to the soil C storage in the future.

1.1 Definition of fine root

Generally, fine roots are defined as roots less than 2 mm in diameter (D) and very fine roots less than 0.5 mm in D (Gill & Jackson 2000). Thicker roots are called coarse roots. Fine roots are considered as non-woody, absorbing organs which together with their mycorrhizal associates account for the bulk of nutrient and water uptake and are the most dynamic component of the forest ecosystem (Ruess et al. 2006). The primary infection point for ectomycorrhizas is the distal root tip. The lateral fine root branches are both morphologically and physiologically responsive to changes in water and nutrient availability (Pregitzer et al. 1993, 2002).

Previously, fine roots have been considered as a homogeneous root pool but currently we know that this ‘pool’ is a mixture of highly heterogeneous ‘populations’ (Fahey & Hughes 1994, Wells & Eissenstat 2001, Pregitzer et al. 2002, Gu et al. 2011). Rather than a D-based definition, a more functional definition of the fine root (Wells & Eissenstat 2001, Wang et al. 2006), such as dividing fine roots according to their branching orders (similar to a stream order classification in which the most distal, unbranched roots are classified as first order and the point where two first order roots join represents a second order root and so on (Pregitzer et al. 2002)) has been suggested.

Root orders have been shown to differ anatomically (Withington et al. 2006, Valenzuela-Estrada et al. 2008), morphologically (Wells et al. 2002, Guo et al. 2004, Valenzuela-Estrada et al. 2008), functionally (Rewald et al. 2011) and dynamically (Valenzuela-Estrada et al. 2008, Wells et al. 2002). Basically, the hydraulic transport capacity increases and the absorbance of water and nutrients decreases along root orders (Valenzuela-Estrada et al. 2008, Rewald et al. 2011, Hishi 2007). For example Valenzuela-Estrada et al. (2008) examined the root system of *Vaccinium corymbosum* and reported that fine roots less than 1 mm in D had up to 7 root orders: First and 2nd order roots were almost identical anatomically and according to mycorrhizal colonization, and differed only regarding their C:N -ratio and SRL. Hydraulic transport capacity increased along root orders; 5th and higher order roots were primarily used only for conduction, 1st and 2nd order roots in contrast were for absorbing of water and nutrients, and 3rd and 4th order roots were transitional. With some species, some of these functional differences can be captured by dividing fine roots into more frequent D classes, such as <0.5 mm, 0.5 - 1 mm and 1 - 2 mm, but as Valenzuela-Estrada et al. (2008) showed with *Vaccinium corymbosum* this is not applicable to all species. In recent studies, Norway spruce roots have also been divided into tighter diameter classes, the smallest diameter cut-off being at 1 or even at 0.5 mm (Hansson et al. 2013). The proportion of fine roots with a diameter <1 mm of those with a diameter <2 mm was 55% (Helmisaari et al. 2009a), showing the quantitative importance of the classification.

It appears that first order roots are relatively inexpensive to build because of their high SLR and low structural content, but costly to maintain due to their high N content and respiration rate (Eissenstat & Yanai 1997, Pregitzer et al. 1997, 2002) – which leads to their high turnover rate, particularly in fertile sites. By contrast, in less fertile sites the mycorrhizal partnerships become more abundant and mycorrhizal short roots can have a longer lifespan than non-mycorrhizal roots (King et al. 2002).

Currently, the fine root – coarse root classification system is under evaluation as division can also be done into fibrous (feeder, short or absorbtive roots) and pioneer roots (long, framework or skeletal roots) (Zadworny & Eissenstat 2011) – or in case of boreal conifers, into EcM short roots and other roots (Helmisaari et al. 2009a, Keel et al. 2012). This functional division should improve the accuracy of estimations of fine root dynamics, as the borderline of 2 mm includes a great share of woody roots. For example, in case of Norway spruce, all roots with D >1 mm are woody (Helmisaari et al. 2009a).

However, as long as the functional separation lacks accepted guidelines, fine root separation on the bases of D is a common practice in fine root research. In addition, some fine root methods are poorly applicable to root order-based separation (e.g. rhizotrons and minirhizotrons, (Withington et al. 2006, Baddeley & Watson 2005), and root sorting in its current form is already extremely labour-intensive.

1.2 Assessing fine root turnover, production and C input into soil

Litter production, both above- and belowground, is a vital flux component in the biogeochemistry of forest ecosystems. As fine roots and associated mycelium are reported to contribute significantly to soil C (Clemmensen et al. 2013), accurate quantification of their annual biomass production and the share of soil litter input is crucial for C balances. Above ground, it is generally assumed that in a stabilized plant community, the litter crop equals the annual production of leaves and shoots (Mork 1946, Mälkönen 1974). This can be applied belowground by determining the annual fine root and mycelia production. Generally, C content is estimated to be 50% of root biomass (dry mass basis), which is used when estimating the annual fine root litter C input into soil. C sequestration by fungal mycelia production has been estimated via correspondence factor to ergosterol content (Wallander er al. 2011). Conceptually, belowground net primary production during the two time intervals is calculated as:

$$Belowground\ NPP = \Delta B + \Delta H + \Delta E + \Delta D \tag{1}$$

where ΔB is the change in belowground biomass, ΔH the amount of biomass consumed by herbivores, ΔE the amount of biomass lost to rhizodeposition, and ΔD is the amount of biomass lost due to death and detachment (Lauenroth 2000). Generally both roots and ectomycorrhizal mycelia growing around the root tip (mantle) and between the cortical cells are incorporated in the (fine) root biomass whereas the biomass of external mycelia is estimated with different methods (Wallander et al. 2013). Biomass loss to rhizodeposition is complicated to determine as the term rhizodeposition includes a wide range of processes by which C enters the soil, such as 1) death and lysis of root cells (cortex, root hairs etc.), 2) leakage of solutes from living cells (root exudates), 3) root cap and border cell loss, 4) gaseous losses, and 5) insoluble polymer secretion from living cells (mucilage) (Jones et al. 2009). However, currently there is no proper method to quantify the amount of biomass loss either to herbivory or to rhizodeposition.

Traditionally, the change in root biomass has been calculated directly from sequentially collected soil samples (Böhm 1979). There are several different approaches to processing the data obtained from soil cores, such as comparing mass on two sampling dates (Persson 1980, McClaugherty et al. 1982), if the mass change is significant (Gower et al. 1992, Publicover & Vogt 1993), or recording the difference between the annual maximum and minimum values (Brunner et al. 2013). Some approaches, such as the Compartment flow (Santantonio & Grace 1987), also include the decomposition rate of fine roots. However, regardless of the chosen approach, the sequential coring method is strongly criticized for being based on tenuous assumptions (Hendricks et al. 2006, Majdi et al. 2005) as it assumes that no production, mortality, additional peaks or lows of standing root mass occur between the sampling dates, and therefore often leads to erroneous estimates (Kurz & Kimmins 1987, Milchunas 2009). Furthermore, distinguishing dead roots from SOM also is subject to considerable error.

Another common method to measure fine root production is the ingrowth core method (Lund et al. 1970, Persson 1983), which is based on removing all roots from a known volume of soil and monitoring the regrowth. Sorting roots from the ingrowth cores is easier and faster than from soil cores, but due to the altered conditions of root-free soil, severing of roots at the edge of the core, ignoring simultaneous root mortality and too short incubation time, this method often leads to underestimates of root production (Fahey &

Hughes 1994, Finér & Laine 2000, Lauenroth & Gill 2003, Ostonen et al. 2005, Milchunas 2009). The method is thus more suitable for comparing different treatments, rather than for assessing the actual root production (Makkonen & Helmisaari 1999). The modification of ingrowth cores, the ingrowth meshes (Fahey & Hughes 1994, Jentschke et al. 2001, Godbold et al. 2003, Hirano et al. 2009), provide some solutions to the above-mentioned shortcomings, as their installation causes less disturbance, and the physical properties of the soil remain unchanged.

The N and C budget methods (Nadelhoffer et al. 1985, Raich & Nadelhoffer 1989) are based on quantifying the element fluxes in the ecosystem. The N budget method gives an estimation of root turnover when the total annual mass of N allocated to fine roots is divided by the mean fine root N content. Further, fine root production can be estimated by using equation 3. The C budget method does not provide an estimate of root production, but it sets an upper limit (derived using other methods) of what it can be (Nadelhoffer & Raich 1992) by providing the total BG C allocation. However, several studies have shown that the flux measurements do not have sufficient accuracy (Ruess et al. 1996 Hendricks et al. 2006) and the budget methods suffer from serious uncertainties as errors associated with the measurement of each process may cumulatively render the root production estimates unreliable.

The alternative way to approach the annual fine root production is to determine fine root longevity (yr) and root biomass.

$$\textit{Root production} = \textit{root longevity} * \textit{root biomass} \qquad (2)$$

Root turnover rate (yr^{-1}) is calculated by using the equation of Gill & Jackson (2000)

$$\textit{Root turnover rate} = \frac{\textit{annual BG production}}{\textit{maximum BG root biomass}} \qquad (3)$$

but root turnover can also be calculated from root length or root area data (Lauenroth & Gill 2003). The MRs (and rhizotrons) differ from the other methods as they can separate growth and mortality. The MR is a less destructive *in situ* method in which a transparent tube is inserted into an auger hole in the ground for estimating fine root longevity. Differing from other methods, MR method (Bates 1937, Böhm 1979) allows the observation of individual fine roots from their first appearance until their death or disappearance, including the timing of the different phases, as well as the monitoring of rooting density, root length, colour and diameter. Although the MR method has been claimed to provide the most reliable method (Aerts et al. 1989, Majdi et al. 2005, Hendricks et al. 2006), it also has its limitations, of which the most important is the difficulty of distinguishing between live and dead roots in MR images (Wang et al. 1995, Comas et al. 2000, Withington et al. 2003). The material of the MR tube, the stabilization time after tube installation, the length of the study and the sampling frequency may also cause variation in the turnover estimates (Joslin & Wolfe 1999, Withington et al. 2003, Satomura et al. 2007). Furthermore, even with the MR method there is several different ways how to define fine root turnover (yr^{-1}), varying 5.6-fold across the methods of calculation (Satomura et al. 2007).

Currently, the tracer techniques, such as artificial labeling with ^{14}C or ^{13}C either in pulses or continuously, and the ^{13}C natural abundance method, are commonly used for the estimation of C input into the soil by plants. In artificial labeling methods, the label is introduced via photosynthesis and followed until it is no longer detectable in the root-soil system, whereas the ^{13}C natural abundance method is based on the discrimination of ^{13}C and ^{12}C isotopes during CO_2 assimilation by plants with different photosynthesis type. The pulse-labeling method is the most commonly used: it is cheap, easy to handle and provides information on the recent photosynthate distribution. The major weakness of pulse labeling is that it is not steady-state, so appearance in different pools vary, but also the results show only the relative distribution of assimilated C for a specific growth period and cannot be applied to the whole growth period – which is the advantage of the continuous labeling method. However, the continuous labeling method is very expensive and limited to only a few places in the world, and the same disadvantage applies to the ^{13}C natural abundance method as it demands unnatural conditions where soils developed under C3 vegetation allow the growth of C4 plants and vice versa (Kuzyakov & Domanski 2000).

1.3 Carbon age of fine roots

A more recently introduced approach in root research is the radiocarbon (^{14}C), ‘bomb C’ -method (Gaudinski et al. 2000, 2001), which is based on the comparison of $\Delta^{14}C$ concentrations in root mass and the historic record of ^{14}C in atmospheric CO_2 - a legacy of thermonuclear weapons testing in the atmosphere in the early 1960s. ^{14}C isotopes allow an estimation of the age of C in structural plant C components such as cellulose and lignin and ideally it would correspond to the root age, as several studies have shown that recently assimilated C is used to produce fine root cellulose (Gaudinski et al. 2001, Matamala et al. 2003, Trumbore et al. 2006).

When Gaudinski et al. (2000) first published the ^{14}C values of SOM and CO_2 samples for quantifying the residence time of C in different fractions in the plant-soil system, the observation of 5 to 10 years residence time of C in root litter led to a series of ^{14}C studies (Gaudinski et al. 2001, Tierney & Fahey 2002, Vargas & Allen 2008, Sah et al. 2011, Solly et al. 2013) with a common aim to clarify the mystery of why fine root C age was greater than the turnover time or lifespan obtained by other methods. As a result, several researchers have confirmed that living fine roots can include C which is several years (Gaudinski et al. 2000, Sah et al. 2011), or even more than a decade old (Vargas et al. 2009, Gaudinski et al. 2001). As the majority of fine root turnover studies carried out with several other different methods have reported much shorter, close to annual, turnover times (Hendrick & Pregitzer 1992, 1993, Burke & Raynal 1994, Fahey & Hughes 1994, Coleman et al. 2000, Brunner et al. 2013, Repo et al. 2014), there is a great uncertainty concerning whether C age can be used for the fine root turnover estimate; not least among the modellers (Peltoniemi et al. 2006).

According to Gaul et al. (2009) minirhizotron observations and sequential coring reflect the turnover rates of fast-cycling roots, whereas those from radiocarbon analyses mirror the rates of long-lived roots: the finest roots are under-represented and new roots may be constructed with storage C (Vargas et al. 2009). The alternative hypotheses are that fine roots are built by the C storage reservoirs (Vargas et al. 2009) or that roots take up C from SOM either directly or via mycorrhizal associations (Simard et al. 1997, Deslippe & Simard 2011), and incorporate it into their tissues. Some evidence has been presented that after disturbances plants use reservoir C to grow new fine roots (Vargas et al. 2009, Gaudinski et al. 2009), but at the same time in some studies the C age matched rather well (max 2 years lag) with the contemporary CO_2 in the atmosphere (Gaudinski et al. 2001, Tierney & Fahey 2002, Matamala et al. 2003). Gaudinski et al. (2001) disputed the hypothesis of fine roots taking up C from SOM, as fine root $\Delta^{14}C$ content was greater than that of SOM at many depths in the soil profile. However, in northern vegetation zones mycorrhizas have been demonstrated to take up organic nitrogen (e.g. amino acids) (Bending & Read 1995a, 1995b, Näsholm et al. 1998, 2009, Kielland et al. 2007), although the quantification still needs to be assessed.

1.4 Effects of environmental factors on fine roots

Temperature

One might erroneously consider soil as a stable and constant environment for organisms to live in. Although soil temperature varies less and with lower oscillation than the air temperature, soils experience a wide range of different thermal conditions. In the summer, the temperature gradient from the soil surface to the deep mineral soil can be a decrease of several degrees Celsius, whereas in the winter the temperature gradient is the opposite. In Scandinavia, average soil temperature during the summer varies between 7 and 11 °C (Strömgren & Linder 2002), rarely reaching 15 °C. Interestingly, many plant species have their optimal root growth temperature much higher than they ever experience in their natural habitat (Barney 1951, Lyr & Hoffman 1967, Tryon & Chapin III 1983, Kaspar & Bland 1992). In the summer, the soil surface is the warmest and most nutrient-rich place for roots to grow and live in but at the same time this layer experiences the most severe conditions (temperature, moisture, and disturbance). The higher temperature enhances metabolic activity and respiration of the fine roots (Marshall & Waring 1985, Ruess et al. 2003, Schindlbacher et al. 2009), which is associated with the regularly observed earlier senescence and increased mortality of fine roots in surface soil than in mineral soil (Baddeley & Watson 2005, Chen & Brassard 2013).

When growing as a monoculture, Norway spruce has a shallow rooting pattern compared to Scots pine and silver birch (Hansson et al. 2013a) and is even more superficial in northern Finland than in southern Finland (Helmisaari et al. 2007). In a mixed stand, the vertical distribution of fine root biomass was similar in all three species, i.e. a shift in the rooting pattern of spruce had occurred from the humus layer to the mineral soil, probably due to increased belowground competition (Kalliokoski et al. 2010). Roots have adapted successfully to different local soil conditions and to both diurnal and seasonal temperature variation.

Moisture

In boreal forests soil moisture, or drought, are generally not the limiting factors for tree growth, except in peatlands. Spruce roots tolerate poorly waterlogged soils (Russel 1977, Xu et al. 1997), as stagnant water soil restricts soil aeration. Therefore, the water table practically determines the maximum rooting depth. Soil moisture and irrigation/drought experiments accomplished with other species than Norway spruce, such as Scots pine, are largely not comparable as their physiological resilience against high/low soil moisture content among species is so different. A few months of experimental drought in a Norway spruce stand in SW Sweden led to no statistical differences in fine root biomass between the drought and control treatments, even though in the drought treatment the fine root biomass in the surface litter was lower than in the control treatment (Persson et al. 1995). This rather superficial effect was caused by the fine root response to extend deeper in the soil where more water was available. The substantial amount of necromass in the drought treatment was suggested to result from high mortality of fine roots or slow decomposition of dead fine roots. In a spruce stand in central Germany an induced drought resulted in strong aboveground effects such as reduced growth and photosynthetic capacity, whereas the fine root biomass did not respond very distinctly (Bredemeier et al. 1998). Their data provided no evidence that roots were either dying due to the drought or that root growth was increased to maintain the water supply.

Nutrients

Limited nitrogen availability strongly restricts tree growth (Tamm 1991, Linder & Flower-Ellis 1992, Reich et al. 2006, Lukac et al. 2010) in boreal forests because of limited cycling from soil, in contrasts to temperate and tropical forests where N typically cycles rapidly and most of the ecosystem N is found in live biomass (Lukac et al. 2010). The greatest pool of N (1000 - 2500 kg N ha^{-1}) in the northern forests is in soil (Mälkönen 1974, Helmisaari 1995, Finér et al. 2005, Lukac & Godbold 2011), but due to the cold climate, it is locked up in undecomposed organic matter with a low turnover rate. Therefore, the soil quality is commonly described by the C:N -ratio of the organic layer which determines how much N is mineralized per unit of C respired and influences the amount of this N that is immobilized by decomposers (Accoe et al. 2004)

Microbes are the key actors in soil N cycling as they account for releasing the organic N to mineral form. When they decompose SOM with a high C:N -ratio, they also immobilize N (Nilsson et al. 2012) and, especially in the case of fungal mycelia, translocate N into the decaying biomass. Tree stumps, for example, offer a long term N source for vegetation for years, even for decades (Palviainen et al. 2010). In this kind of highly patchy and heterogeneous environment fine roots and mycorrhizal hyphal networks proliferate intensively in the microsite nutrient patches (Lyr & Hoffman 1967, Pregitzer et al. 1993, Robinson et al. 1999) but overall, the poorer the site fertility, the wider root system incl. mycorrhizas, trees need in order to acquire a sufficient amount of N and other nutrients.

According to the functional equilibrium hypothesis (Brouwer 1963, 1983), plants increase the relative production of a responsible absorbing organ in order to improve the uptake of a limiting resource and reduce stress. Thus, in conditions of nutrient or water deficiency plants allocate relatively more C to belowground than aboveground biomass, which has been observed (Keyes and Grier 1981, Gower et al. 1994, Ruess et al. 2006, Helmisaari et al. 2007), and also modeled on the bases of empirical data sets (Mäkelä et al. 2008, Dewar et al. 2009, Valentine and Mäkelä 2012). According to the C optimization theory (Eissenstat 1992), trees growing in nutrient-poor habitats invest large amounts of C in the construction of new fine roots for improved nutrient acquisition. As the cost of construction is high in relation to the cost of maintenance and nutrient uptake in nutrient poor sites, root lifespan is expected to increase (Schoettle & Fahey 1994, Eissenstat et al. 2000).

CO_2

Although the current atmospheric C supply is not a growth-limiting factor for vegetation growth (Körner 2003), the increasing CO_2 concentration in the atmosphere is seen as a potential for increasing forest growth, C storage in the vegetation and belowground C input in the future. Plants exposed to CO_2 enrichment realize a significant increase in photosynthesis and growth, and C allocation to belowground processes is often stimulated even to a greater extent than to aboveground processes (Pritchard 2011). However, even though the fine root production and biomass generally respond positively to elevated CO_2

levels (Phillips et al. 2012, Smith et al. 2013), the amount of C input into the soil also depends on turnover rate. The elevated CO_2 has been shown to increase fine root diameter (Rogers et al,. 1992a, Milchunas et al. 2005), stimulate fine root proliferation in deeper soil (Norby et al. 2004) and increase root tissue density (Ryser 1996, Eissenstat et al. 2000), which all correlate positively with fine root longevity, thus decreasing the root litter C input into the soil. Overall, the responses of fine root longevity to elevated CO_2 have been highly controversial (Thomas et al. 1999, Johnson et al. 2000, Milchunas et al. 2005, Johnson et al. 2006, Pritchard et al. 2008, Pritchard 2011), probably due to the multiple interacting factors. For example, Sigurdsson et al. (2013) and Reich et al. (2006) observed that low N availability progressively suppressed the positive response of plant biomass to elevated CO_2 and in a Norway spruce forest in Sweden elevated CO_2 concentration caused no effect on tree height and stem increment unless extra nutrients were supplied (Sigurdsson et al. 2013). This may be an important finding with regard to the effects of global warming on boreal forest growth.

pH

Finnish forest soils are acid, due to the principal soil forming process in coniferous forests: podzolisation. Spruce and pine form slowly decomposable needle litter, which accumulate on the forest floor and acidic solutes from this litter cause leaching of the upper layers with accumulation of material in lower layers. Podzolisation is a natural process, and it includes the acidification caused by naturally acidic rainwater. Boreal tree roots are mostly adapted to these conditions.

Anthropogenic acidification is a process caused by atmospheric deposition (low in northern Europe) or long-term N fertilization. Basically it is the same process as natural acidification but being too potent it exceeds the buffering capacity of the soil: the base saturation of the cation exchange sites of the mineral soil is reduced, which leads to a decrease in the storage of base cations such as Mg and Ca and increases the availability of potentially toxic ions such as Al (Ulrich et al. 1994). The concentration of available Al is highest in the subsoil, which is probably the reason for the shallow rooting pattern (Jentschke et al. 2001, Godbold et al. 2003) and higher fine root mortality (Godbold et al. 2003) observed in acidified soil. Also, the lower the pH of the soil gets, the more difficult it becomes for the plants to acquire nutrients from the soil. However, unless too severe, tree roots and associated mycorrhizas have several means to reduce the negative impacts of acidifying soil such as changing the composition of EcM communities, enhancing the formation of adventitious roots and adjusting the fine root growth in the most appropriate soil depth (Cudlin et al. 2007).

1.5 Other belowground C inputs

The most visible part of the belowground C input is fine roots and their mycorrhizal fungal associates. Part of the ectomycorrhizal mycelia growing around the root tip (mantle) and between the cortical cells is incorporated in the fine root biomass (about 3% of the Norway spruce fine root biomass, Kårén & Nylund 1997), but the majority is spread throughout the soil as external mycelia including sporocarps (Colpaert et al. 1992, Kårén & Nylund 1997, Wallander et al. 2001). External mycorrhizal mycelia is known to form a strong sink of C (Godbold et al. 2006, Cairney 2012), but accurate estimation of extramatrical mycelia production is difficult (Ekblad et al. 2013, Wallander et al. 2013). According to Hobbie &

Wallander (2006) 5 - 28% of NPP of forest trees is directed to EcMs. Further, merely in Swedish Norway spruce forests, estimations of the amount of annual production of EcM external mycelia have varied from 110 kg ha^{-1} (Hagerberg et al. 2003) to 125 - 200 kg ha^{-1} (Wallander et al. 2001) and 590 kg ha^{-1}(Wallander et al. 2004). Thus, the contribution of EcM to total C input into the soil may be considerable. In addition to fine roots, mycorrhizal mycelia and other forms of rhizodeposition, coarse roots, stumps, decomposing saprotrophic mycelia and soil animals all form a heterogeneous flux of C into the soil which is currently impossible to determine per fraction. According to approximate estimations, rhizodeposition could amount to one quarter of C allocated to roots (Jones et al. 2009), but the estimations vary considerably between cereals, grasses and trees (Kuzyakov & Domanski 2000).

1.6 Aboveground litter C inputs

Due to the long traditions of forest management in Europe, the aboveground wood production has for long been subjected to intensive research. However, as the timber is normally harvested, the aboveground litter C input into the soil consists only of tree foliage and understory vegetation litter, and after the tree harvest, of harvest residues. Foliage litterfall is rather simple to collect, although for example in the case of Norway spruce the collection must be organized around the year in order to catch all the shed needles (the foliage of Norway spruce consists of 6 - 10 needle cohorts and it does not shed all the needles of one needle cohort at the same time (Sander & Eckstein 2001)). Collection should also be continued for long periods in order to register the inter-annual variation – which can be considerable, even between consecutive years (Saarsalmi et al. 2007). In Finland the amount of annual aboveground litterfall has been reported to range from 651 to 4912 kg ha^{-1} (average for seven spruce stands 2986 kg ha^{-1} (Ukonmaanaho et al. 2008)) and from 614 to 5046 kg ha^{-1} (average for 18 stands 2539 kg ha^{-1} (Saarsalmi et al. 2007)), i.e. the variation between stands can be 8-fold. However, if only the needle litter was considered, the variation between the southern and northern stands was an order of magnitude. The total litterfall of spruce correlates with the total aboveground biomass (Ukonmaanaho et al. 2008) and with the annual volume increment (Hansen et al. 2009) which can be seen as higher amounts of litterfall e.g. in southern Sweden and Denmark (Nilsson & Wiklund 1992, Bille-Hansen & Hansen 2001, Hansen et al. 2009) where the fertility (and N deposition) is generally higher than in Finland.

The contribution of understory vegetation (shrubs, herbs, mosses, lichens, and understory trees) to the total biomass is significant in the early stages of succession but later in succession, especially after canopy closure when the light conditions change, the share of understory of the total stand biomass decreases, eventually comprising only a minor part e.g. in mature spruce or mixed hardwood forests (Seedre & Chen 2010, Hansson et al. 2013a). However, although representing only a small fraction of total biomass, bryophyte and understory vegetation production can equal or exceed the foliage litter production (Gower et al. 1997, Kleja et al. 2008, Seedre et al. 2011).

Compared to the foliage litterfall collection, the annual biomass production of understory vegetation is much more challenging to measure and is often omitted from the NPP studies. However, depending on the ecosystem, the share of understory vegetation can be considerable (Mälkönen 1974, Kleja et al. 2008, Hansson et al. 2013b). The most straightforward way is to estimate the understory annual growth (Helmisaari 1995, Schulze et al. 2009), but correlations between the tree stand mean diameter, height or leaf biomass (Hansson et al. 2013b), percentages of the total biomass (Hansson et al. 2013b) or turnover rates (Lehtonen 2005, Kleja et al. 2008) have also been used.

2 OBJECTIVES

The overall objective of this thesis was to study how environmental conditions affect fine root production and fine root litter C input into the soil. To achieve this aim, fine root biomass and turnover were determined for Norway spruce stands under different environmental conditions, both manipulated and natural. In order to obtain a more holistic view of the whole ecosystem, the aboveground stand foliage and understory litter C input were also determined.

As a part of the on-going discussion concerning the observed surprisingly long residence times of C in fine roots, we analyzed the age of root ^{14}C of the fine roots and compared it to the root longevities obtained by the minirhizotron (MR) method. In addition, we studied the changes in root ^{14}C age with varying conditions and traced the origin of ‘old’ C by analyzing the root ^{14}C age in conifer seedlings of known age.

The specific objectives in the sub-studies were:

- to investigate Norway spruce belowground responses to varying soil temperature, length of the growing season and nutrient availability by determining the biomass, morphology (**I**, **III**) and turnover rate (**II**, **III**) of fine roots;

- to quantify the annual input of C into the soil from Norway spruce fine root litter in varying environmental conditions and to relate this to the aboveground foliage litter C input (**II**, **III**), including the understory vegetation (**III**);

- to define the age of C in fine roots from soil core roots for investigating how root C age changes along with root diameter, soil depth, soil fertility, tree species (**IV**) and soil temperature (**V**), and to compare the known age of fine roots from the ingrowth cores and minirhizotrons with the estimated age of root C based on radiocarbon (**V**). Furthermore, we tested the hypothesis that the old C in fine roots could originate from soil by analyzing the fine root C age of spruce and pine seedlings of known age (**V**).

3 MATERIALS AND METHODS

3.1 Study sites

Flakaliden

A unique long-term nutrient optimization, and later soil-warming (studies **I** and **II**) experiment is being conducted in a boreal Norway spruce (*Picea abies* (L.) Karst.) forest in Flakaliden (64°07′N, 19°27′E, 310 m a.s.l.) in northern Sweden (Figure 2). At this site, the forest is even-aged; the stand was planted in 1963 with four-year old Norway spruce seedlings of local origin after clear-felling. At the time of establishment, stand density was ca. 2400 trees ha^{-1} and no thinnings have subsequently been carried out. Understory vegetation mainly consists of *Vaccinium vitis-idaea*, *Vaccinium myrtillus*, *Deschampsia flexuosa* and *Empetrum* spp., and the ground is covered by forest mosses.

Soil at the site is a thin podzolic, sandy, post-glacial till with mean depth of about 120 cm, classified as Spodosol according to USDA Soil Survey Staff (1999), with soil water content normally not limiting tree growth (Bergh et al. 1999). The site fertility is low (tree growth <4 m^3 ha^{-1} yr^{-1}, Berggren et al. 2004) and the annual deposition of total nitrogen in the region is also low (≤3 kg ha^{-1}) (Berggren et al. 2004). Climate is boreal; long cool days in the summer and short cold days in the winter; the mean monthly temperature varies from −7.5 °C in February to 14.6 °C in July (mean for 1990 - 2009). Mean annual precipitation is ~600 mm with approximately one-third falling as snow, which usually covers the frozen ground from mid-October to early May. For more information concerning the experimental site, see Berggren et al. (2004) and Table 1.

Figure 2 Location of the study sites in Finland, Sweden and Estonia. Studies **I**, **II** and **V** were located in Flakaliden, study **III** in Olkiluoto and Kivalo and study **IV** in Mekrijärvi, Punkaharju and Voore. The additional sites in the study **III** were Flakaliden, Knottåsen and Asa (Kleja et al. 2008) and Tönnersjöheden (Hansson et al. 2013a,b).

Olkiluoto

In the latitudinal gradient study in Finland (study **III**), Olkiluoto represents the southern site. In association with the decision for choosing Olkiluoto (in Eurajoki, south-western Finland (61°13'N, 21°28'E, 10 m a.s.l., Figure 2) as a final disposal site for spent nuclear fuel, a massive current biosphere programme has been conducted. Our study site, a 93-year-old Norway spruce stand (FIP10) is one of the intensive monitoring sites. The spruce plot represents rather high fertility herb-rich heath forests (i.e. Oxalis-Myrtillus type, OMT (Cajander 1949)), but due to the relatively high age of the trees, the period of maximum stand volume increment has been passed (Aro et al. 2012). Soil is fine-textured till (Rautio et al. 2004) and pedologically rather young after the previous glaciation (Tamminen et al. 2007). The understory vegetation is characterized by an abundant forest moss layer with many herb and fern species, whereas the cover of dwarf shrubs is only 2 - 4% (Aro et al. 2012). There are 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. The mean monthly temperature varies from −4.2 °C in February to 17.1 °C in July (mean for 1993 - 2009) (Haapanen 2010). For a more detailed site description, see Aro et al. (2012), Helmisaari et al. (2009c), Haapanen (2010) and Table 1.

Kivalo

In the latitude gradient study in Finland (study **III**), Kivalo (66°20'N, 26°40'E, 486 m a.s.l.Figure 2) represents the northern site. The stand (including three 25 m x 25 m plots) was clear-cut and prescribed to be burned in 1926, and planted in 1930. Understory vegetation at Kivalo represents a mesic site type (Hylocomium-Myrtillus type, HMT (Cajander 1949)) and the most abundant species are *Vaccinium myrtillus* and forest mosses (*Pleurozium schreberi*, *Hylocomium splendens* and *Dicranum* spp.). On average, 20% and 12% of the total stem volume of the stand are birch and pine trees, respectively (Smolander & Kitunen 2002). Soil type in Kivalo is podsolic loamy sand (Smolander & Kitunen 2011) and the annual total N deposition and N mineralization at the site are low (~2 kg ha^{-1} yr^{-1} and <4 kg ha^{-1} yr^{-1}, respectively, Lindroos et al. 2007, Olsson et al. 2012). The mean monthly temperature varies from –12.3 °C in January to 15.1 °C in July (mean for 1981 - 2011). For more information concerning the site, see Smolander & Kitunen (2002, 2011) and Table 1.

Additional sites in Sweden

For widening the variation in above- and belowground litter C input in study **III** and discussing it in relation to site nutrient availability, data from four earlier published Norway spruce sites from a north-south transect in Sweden were included: Flakaliden (64°07'N, 19°27'E, 310 - 320 m a.s.l.), and Knottåsen (61°00'N, 16°13'E, 315 - 320 m a.s.l.) in the boreal zone, Asa (57°08'N, 14°45'E, 190 - 200 m a.s.l.) in the boreo-nemoral zone (Kleja et al. 2008) and Tönnersjöheden (56°40'N, 13°03'E, 70 - 90 m a.s.l.) in the cold temperate vegetation zone (Hansson et al. 2011) (Figure 2). 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 Flakaliden, the northernmost site, the annual N deposition load and N mineralization (~4 kg ha^{-1} yr^{-1}, Andersson 2002, Olsson et al. 2012) is on the same level as in Kivalo (2 - 3 kg ha^{-1} yr^{-1}, Kleja et al. 2008, Lindroos et al. 2007).

Table 1 Stand characteristics. The C:N -ratio of the organic layer at the sites was provided by Smolander & Kitunen (2002), Helmisaari et al. (2007), Potila et al. (2007), Berggren et al. (2004), Hansson et al. (2011) and (Ostonen et al. 2007a). The stand characteristics were measured at Kivalo and Voore in 2000 (Smolander & Kitunen 2002, Ostonen et al. 2011), at Mekrijärvi in 1983 (Helmisaari et al. 2002), at Olkiluoto and Tönnersjöheden in 2009 (Aro et al. 2010, Hansson et al. 2011) and at the other Swedish sites in 2001 (Berggren et al. 2004, Kleja et al. 2008). In all 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-year period: in Finland 1981 - 2011, based on the dataset of the Finnish Meteorological Institute, in Sweden and in Estonia 1961 - 1990 (Alexandersson et al. 1991, Kleja et al. 2008, Ostonen et al. 2011), except the MLGS at Tönnersjöheden (Olsson & Staaf 1995). p = pine, s = spruce, Ba = stand basal area, D = diameter, dom. = dominant, d = day.

	C:N	Stem density (trees ha^{-1})	Ba (m^2 ha^{-1})	Mean stem D (cm)	Age of dom. trees (yr)	MAP (mm yr^{-1})	MAT (C °)	(MLGS) (d yr^{-1})
Finland								
Kivalo	32	939	20	18	74	517	0.7	112
Mekrijärvi		432	26	27	100	589	2.4	140
Punkaharju (p)	42	956	17	21	36	532	3.9	163
Punkaharju (s)	21	378	28	32	45			
Olkiluoto	24	667	31	31	96	545	5.3	162
Sweden								
Flakaliden	40		20		42	523	1.2	120
Knottåsen	35		18	11	37	613	3.4	160
Asa	32	1528	26		38	688	5.5	190
Tönnersjöheden	24	614	29	25	54	1053	6.4	204
Voore	29	1050	50	26	65	647	5.4	177

Mekrijärvi, Punkaharju, Voore

The research sites in the ^{14}C study (study **IV**) were located in boreal forest zone, at Punkaharju (61°48′N, 29°19’E) and Mekrijärvi (62°47′, 30°58′E) in Finland, and in the hemiboreal zone, Voore (58°42′N, 21°59′E, 90 m a.s.l.) in Estonia (Figure 2). The Punkaharju site had stands of both tree species (Norway spruce and Scots pine (*Pinus sylvestris* L.)). At the time of soil core sampling, the age of the stands varied between 35 and 100 years, and in all stands the canopy was closed. The two lowest fertility sites were on podzol soils: Punkaharju pine stand (between *Vaccinium vitis-ideae* type (VT) and *Calluna* type (CT) (Cajander 1949)) and Mekrijärvi pine stand *(*VT type), of which understory vegetation consisted of *Vaccinium vitis-idaea* L., *Vaccinium myrtillus* L., *Calluna vulgaris* (L.) Hull and *Pleurozium schreberi* (Brid.) Mitt. The Punkaharju spruce stand (OMT) is on more fertile cambic arenosol and Voore stand (Oxalis type, OT) on still more fertile umbric luvisol. At the latter site the dominating tree species was Norway spruce, with a 10% mixture of pine and birch trees. More information on the Mekrijärvi and Punkaharju sites can be found from Helmisaari et al. (2002) and Sah et al. (2011), and on the Voore site from Ostonen et al. (2007).

3.2 Nutrient availability and soil warming manipulations

The Flakaliden fertilization experiment (Figure 3) was established in 1987, with the aim of optimizing the nutritional status of the stand without leaching of nutrients to groundwater. All essential macro- and micro-nutrients were supplied every second day during the period of active growth (early June–mid-August). The amount and composition of the nutrient mix (Table 2) was determined annually on the basis of foliar analysis, nutrient concentrations in the soil water, and from the predicted growth response. The amount of irrigation was set to maintain soil water potential above –100 kPa. After ten years of optimized fertilization (at the time of installing the heating cables) in the fertilized plots the annual stem volume production had more than quadrupled (from 3 to 14 m^3 ha^{-1} $year^{-1}$) and the trees were higher compared to those in the non-fertilized treatment. At the time of our study, the basal area (ba) of the WFI plots was 43 and 50, FI plots 41, WI 22, I 22 and C 19 m^2 ha^{-1} (study **I**). For further details on this, see Bergh et al. (1999) and Linder (1995).

In the summer of 1994, six 85 m long heating cables (DEVI, Elektrovärme AB, Vällingby, Sweden) were buried in the soil of the buffer zone of the fertilization and/or irrigation plots. The cables were installed between the organic and mineral soil layer (spacing ~20 cm). Soil warming started in April 1995, five weeks before the snowmelt, with an increase of 1 °C per week, until a 5 °C difference between warmed and non-warmed plots was attained. In the autumns, the soil temperature was correspondingly allowed to decrease by one degree per week to the ambient level after the soil temperature in the control plots approached 0 °C. Soil temperature was recorded in the organic layer and at 5, 10, 20, 30 and 40 cm depths of mineral soil. In addition to increased soil temperature, the aim was to lengthen the growing season by two months. Irrigation was included in the soil warming treatment in order to avoid unwanted drying effects. For further information about the warming treatment, see Bergh & Linder (1999) and Strömgren & Linder (2002).

For the studies **I** and **II**, only 10 m x 10 m sub-plots of the 50 m x 50 m treatment plots were used with following treatments: soil warming-fertilization-irrigation (WFI), soil warming-irrigation (WI), fertilization-irrigation (FI), irrigation (I) and control plot (C). In these two studies, the experimental plots were exactly the same in WI and WFI treatments.

Table 2 The amounts of macro- and micro-nutrients (kg ha^{-1}) supplied with irrigation water during the period 1987 - 2010 in (a) WFI, FI (studies **I** and **II**) and (b) I reference treatment (study **II**). For further details see Linder (1995) and Strömgren & Linder (2002).

		N	P	K	Ca	Mg	S	Mn	Fe	Zn	B	Cu	Mo
1987-2006		1350	211	591	79.3	121	53.1	4.0	7.0	0.3	3.95	0.3	0.1
a	2007	50	15	15	22.5	4	3.3	0	0	0	0.37	0	0
	2008	50	15	15	22.5	4	3.3	0	0	0	0.37	0	0
	2009	50	10	42	2.9	4	3.9	0.2	0.2	0.03	0.10	0	0
	2010	50	10	42	2.9	4	3.9	0.2	0.2	0.03	0.10	0	0
	Tot.	**1550**	**261**	**705**	**130.1**	**137**	**67.5**	**4.4**	**7.4**	**0.36**	**4.89**	**0.3**	**0.1**
b	2007	100	30	30	46	8	6.0	0	0	0	0.37	0	0
	2008	100	30	30	46	8	6.0	0	0	0	0.37	0	0
	2009	50	10	42	3	4	3.9	0.2	0.2	0.03	0.10	0.02	0.004
	2010	50	10	42	3	4	3.9	0.2	0.2	0.03	0.10	0.02	0.004
	Tot.	**300**	**80**	**144**	**98**	**24**	**19.8**	**0.4**	**0.4**	**0.1**	**0.94**	**0.04**	**0.008**

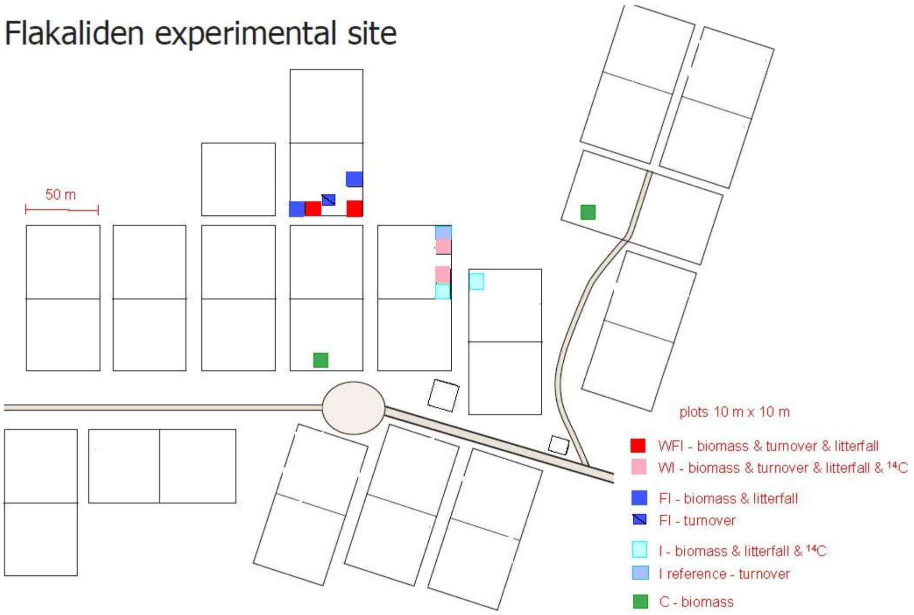

Figure 3 Design of the long-term soil warming and fertilization experiment at the Flakaliden research site, in northern Sweden. In the figure the study plots used for the fine root biomass and necromass sampling (study **I**), fine root turnover estimation (study **II**), foliage litterfall (study **II**) and fine root C age determination (study **V**) of Norway spruce are described.

In the FI treatment the experimental plots were the neighbour ones, but in the I, the treatments were slightly different. Therefore when referring to the treatment I in a study **II**, it is called reference treatment instead of irrigation (Figure 3). When calculating the EcM short root characteristics (study **I**) and fine root longevity (study **II**), the data from the two plots in the WFI and WI were pooled together.

3.3 Belowground measurements

Fine root biomass and short root morphology

For determining fine root biomass (studies **I** and **III**) soil samples were taken with a cylindrical soil corer from Flakaliden, Kivalo and Olkiluoto, at 2 - 5 m distance from the MR tube. When possible, the autumn sampling was favoured 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 (Ostonen et al. 2005, Makkonen and Helmisaari 1998). At Flakaliden and Kivalo the organic layer was separated and thereafter the mineral soil was divided into 10 cm layers. At Olkiluoto, the whole core was divided 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. At Olkiluoto, due to the high stoniness the maximum sampling depth was only 15 cm (study **III**) whereas at Kivalo it extended to 34 cm (study **III**) and at Flakaliden to 37 cm (study **I**). The stoniness of the site was taken into consideration when weighing the dry mass of the fine roots in the mineral soil by using the stoniness index (Viro 1952, Tamminen 1991) (studies **I** and **II**). For studies of EcM short root morphology, an additional sampling of organic layer was conducted at the end of the growing season in Flakaliden (study **I**) and in Kivalo (study **III**, published in Ostonen et al. (2007a).

Roots for the biomass measurements were wet-sieved and sorted under a dissecting microscope into different tree species, understory, biomass and necromass categories according to their colour, elasticity and toughness (Persson 1983). Understory roots were further separated into dwarf shrub roots and grass & herb roots (study **III**). Roots smaller than 2 mm were regarded as fine roots by Persson (1983) and Vogt et al. (1993), but tree fine roots (plus understory fine roots at Olkiluoto) at our sites were further sorted into two D classes: 1 - 2 mm or <1 mm, the latter including EcM short roots. As practically all spruce short roots are colonized by EcM in boreal spruce forests (Taylor et al. 2000, Ostonen et al. 2011), no separation between EcM and non-EcM short roots was made. A subsample of roots in each sorted sample of living roots <1 mm in D was used for counting the number of EcM root 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. The biomass of Kivalo fine roots <2 mm in D has been published by Ostonen et al. (2007a), but in this study (study **III**) only <1 mm in D were used.

EcM short root (Figure 4) for the morphology analysis were cleaned with a small soft brush to remove all soil particles, and counted under a microscope (180 - 360 first and second order roots per treatment (study **I**)) after separation from the long roots. The length, D and projection area of short roots were defined using WinRHIZO™ Pro 2003b (resolution 800 dpi, Regent Instruments Inc. 2003). The air-dry short root were dried at 70 °C for 2 - 3 h to constant weight and weighed. RTD (kg m^{-3}) and specific root length (SRL) (m g^{-1}) were determined as described by Ostonen et al. (2007a). In Olkiluoto the SRL was determined for the fine roots <1 mm in D (study **III**) by using the same software. EcM short root tip mass (tip W, mg) was calculated as the dry mass of all the EcM short root tips in a sample divided by the number of root tips in the sample (study **I**). To quantify the EcM short root tip biomass (EcMB) m^{-2} for the studied soil profile the mean tip W and

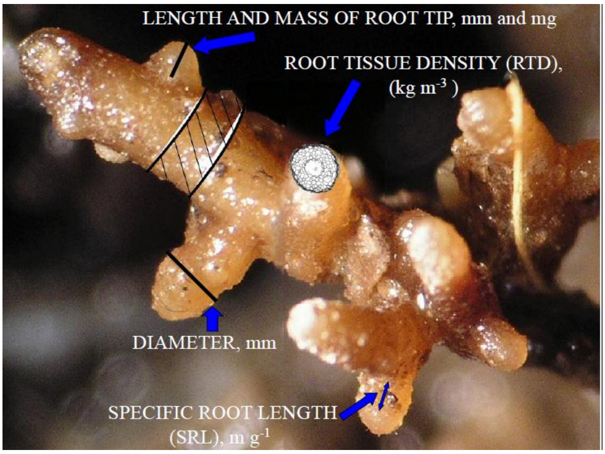

Figure 4 Ectomycorrizal (EcM) short root, consisting of 1st and 2nd order roots, and measured EcM short root morphology parameters.
(Picture: Ivika Ostonen)

their number m^{-2} were used, and this fraction was compared to the total fine root biomass in order to determine the proportion of nutrient- and water -absorbing organs. The relation of EcMB to BA was used as an indication of the functional relationship between above- and belowground parts and has proven useful in the comparison between sites with varying tree sizes and/or numbers.

Due to the low number of replicate plots (n = 1, 2 and 3 in Olkiluoto, Flakaliden and Kivalo, respectively), the emphasis on statistical analyses is limited and no difference in fine root biomass between the sites was statistically tested. At Flakaliden (study **I**), the differences between four irrigated treatments were tested using the Univariate, General Linear model (GLM) SPSS (PASW Statistics 18.0). The significance among means was tested by using the Least significant difference (LSD) test. STATISTICA 7.0 software was used for testing the differences in short root morphology between the treatments. When testing the effect of fertilization or warming only, or their interactions, two treatments were pooled together (for warming: WFI + WI vs. FI + I (n = 4) and for fertilization: WFI + FI vs. WI + I (n = 4)) and full factorial design was applied. In both cases the control (C) is included only in the figures. Linear regression models were used to test the relationship between fine root and needle biomass as well as BA. Linear regression model was also used when relating the above- and belowground litter production to the C:N -ratio of organic layer. The significance level $\alpha = 0.05$ was accepted in all cases.

Fine root turnover

For estimating the fine root turnover rate (studies **II** and **III**), the MR method (Hendrick & Pregitzer 1992) was utilized. Digital images of fine roots were repeatedly collected via transparent, acrylic tubes during three consecutive growing seasons. At Flakaliden, the tubes were installed almost 15 years earlier, at the time when Majdi & Öhrvik (2004) studied the short-term response of root growth to soil warming, but at Kivalo and Olkiluoto they were installed a year before the image collection started. The images were collected 8 - 15 times using a MR camera (BTC-2; Bartz Technology, Santa Barbara, USA) between 11.6.2008 - 8.10.2010 at Flakaliden (study **II**), 23.6.2004 - 12.9.2006 at Kivalo and 26.6.2008 - 18.5.2011 at Olkiluoto (study **III**). A total of 13458 images were taken during the study period, of which 5006 at Flakaliden, 2849 at Kivalo and 5603 at Olkiluoto.

At Flakaliden, the number of tubes (installed at an angle of 45°) in the treatments were: 10 at WFI, 8 at WI, 4 at FI and 5 at I, and about 23 digital photos (size 1.1 x 2.0 cm) were taken at each point, thus one stripe per tube. Due to technical problems the autumn image collection session in 2009 was missed, which led to uncertainty in recording which roots were born or died before or after the winter in the images of 2.6.2010. Therefore, the birth and death times of new and dead roots observed on this date were randomized and divided according to the distribution of root life status in 2008 autumn and 2009 spring. These values were then used for estimating the percentage of the new and dead roots observed 2.6.2010 to have been born or died already in the previous autumn.

At Kivalo, all nine MR tubes (three in each plot) were vertically installed, whereas in Olkiluoto due to the high stone content of the soil horizontal tubes were also used: two vertical and three horizontal ones, with different lengths. Therefore, when comparing the number or the elongation of fine roots between the sites, the variables were calculated for an image rather than for a tube by dividing the variable by the number of images filmed per session at each site. Two stripes of images were taken of each tube, from different sides of the tubes (study **III**).

The images were analyzed at Flakaliden and Olkiluoto with WinRHIZOTron MF 2005 and 2008c (Regent, Quebec, Canada) and at Kivalo with RooTracker (Duke University, Durham, N.C.) softwares. As root orders (Pregitzer et al. 2002) are difficult to trace with the MR method (Withington et al. 2006) every segment was considered as an individual root, remembering that the distal roots could not stay alive if the connected higher order root was defined as dead. 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. At Flakaliden, understory roots were excluded from the analysis, but at Kivalo and Olkiluoto they were classified into two groups: dwarf shrub and grasses/herbs. At Flakaliden the disappeared roots were separated into two groups: visually disappeared roots (GV), which became covered by mycelia/soil or had grown out of the image and apparently grazed roots (GG). In the analysis, the GG roots were treated as ‘dead’ and GV roots were as ‘censored’ as generally they were probably alive at the time of disappearance (became covered by mycelia, other roots or soil). Likewise, roots living at the end of the monitoring period were treated as ‘censored’.

The mean diameter (D), length and location of each root and short root tip were recorded and they were divided into 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 and two depth classes: topsoil (0 - 5 cm, from vertical tubes the five uppermost images, from horizontal tubes all images) and mineral soil (the rest of the images after the top five). The term ‘topsoil’ was chosen instead of ‘organic layer’ because the thickness of the organic layer varied between the tubes, or because the organic layer was not in all cases easily distinguishable.

All traced roots from the first session were excluded from the survival analysis because the birth time of the fine roots was unknown (in Kivalo and Olkiluoto 404 and 258, respectively, of the total of 3819 roots (incl. understory) and in Flakaliden 373 of the total of 2213 spruce roots). In the Olkiluoto and Kivalo data, the times of death and birth were fixed to the midpoint between the sessions. For the survival analysis, the data from all MR tubes per site or per treatment were combined.

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, version R 2.13.0 (R Development Core Team). 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 & 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. When comparing the mean D of a fine root (from the MR images) of the Kivalo and Olkiluoto sites the independent sample t-tests (IBM SPSS Statistics 20) were used with the level of statistical significance of $\alpha = 0.05$, and each strip of the MR tube was considered as an independent replicate (10 in Olkiluoto, 17 in Kivalo). In Flakaliden the D comparisons were included in the morphological investigation and the D was measured from the EcM short roots of first and second orders (Figure 4) instead of MR images.

EcM mycelia production

The production of EcM mycelia was estimated using ingrowth mesh bags (Wallander et al., 2001), filled with quartz sand and buried in the organic horizon of each treatment plot (study **I**) in Flakaliden. The bags were collected two years afterwards and the extent of fungal colonization was estimated by two different methods: the phospholipid fatty acid (PLFA) method (Frostegård et al. 1991, 1993) using the fungal biomarker 18:2ω6,9; and ergosterol concentration analysis (Wallander & Nylund 1992) using conversion factors (Salmanowicz & Nylund 1988, Olsson et al. 2003).

Belowground litter production

For estimating the belowground root litter production the median fine root age of trees and understory in the stands (studies **II** and **III**), perceived from the survival analyses, and the fine root biomass data (studies **I** and **III**), from the soil cores, were used (equation 2). The treatments were the same in the WFI, WI and FI regarding the fine root biomass and longevity data, but in the case of the reference treatment I, the treatments were slightly different: the treatment I in the fine root longevity study (study **II**) received a solution of nutrients (Table 2) during four growing seasons before the MR data collection. However, it is still considered as a reference treatment.

As more than 99.5% (studies **II** and **III**) of the fine roots traced in the MR images were <1 mm in D, only the biomass of the spruce roots <1 mm in D was used in the production calculations. For understory the fine root biomass <2 mm in D was used, as in Kivalo no separation to the smaller D group was made. However, the D separation at Olkiluoto showed that all shrubs and 34% of grass fine roots were <1 mm in D, and at Kivalo the field layer consisted of dwarf shrubs only. Thus, the error resulting from this was considered to be acceptable. For estimating the annual fine root production (kg ha^{-1}), fine root biomass (kg ha^{-1}) in different soil layers was multiplied by the fine root turnover rate (yr^{-1}) in the topsoil and the mineral soil. The flux of C is reported as 50% of the litter production.

3.4 Aboveground litter production

The spruce foliage litterfall (studies **II** and **III**) was collected using 8 - 12 conical traps (a collection area of 0.5 - 0.8 m^2) located in the stands, at a height of 0.9 - 1.5 m above ground level. The foliage litterfall in the treatment I (study **II**) was collected from the same plots as the fine root biomass (study **I**) (Figure 3). Litterfall collection was implemented during three to four years: 2008 - 2010 at Flakaliden (study **II**), 2008 - 2011 at Olkiluoto (study **III**) and 2000 - 2002 at Kivalo (study **III**). The samples were oven-dried at 65 °C for 24 h, sorted to needles and other components (leaves, twigs, cones and all other material) and weighed. The deciduous leaf litter from the aboveground litter production of Olkiluoto was excluded (study **III**), and other components than needle litter were pooled. The average annual foliage litter production during the whole collection period was used (studies **II** and **III**).

The estimate of aboveground biomass production of understory vegetation was made at Kivalo in 2000 by Nieminen & Smolander (2006), and the assessed value of 100 g m^{-2} yr^{-1} was used as a proxy of the annual aboveground understory litterfall (study **III**). At Olkiluoto, the aboveground understory litterfall was estimated by sampling six 30 cm x 30 cm (in total 0.54 m^2) plant-humus-litter samples in August 2008 (study **III**). The organic layer (L, F, H horizons) and all the understory vegetation growing on each square was removed in one piece, placed on plastic boards in large plastic bags, and separated into individual plant species. The annual aboveground biomass production of dwarf shrubs was calculated as the sum of leaves and stems grown in 2008. The whole shoot of lower herbs and ferns represented the growth in 2008. In perennial species the annual growth was estimated by dividing the shoot biomass by three (estimated age) and in diannual species by two. The annual growth of mosses was estimated by dividing the biomass of the upper part by 2.5, representing the average number of the annual growth segments according to field observations. For further information on the litter collection of foliage and understory in Olkiluoto, see Aro et al. (2012). The total annual litter production was calculated by combining the above- and belowground litter production either with or without the understory litter production (studies **II** and **III**). The flux of C was estimated as 50% of the litter production (studies **II** and **III**).

3.5 Radiocarbon dating

The radiocarbon dating takes advantage of the elevated levels of ^{14}C in atmospheric CO_2 that resulted from thermonuclear weapons testing in the early 1960s. This global ^{14}C isotope can be used to determine the time since ^{14}C in plant tissues was fixed in photosynthesis. After the nuclear test ban treaty in 1963, the amount of ^{14}C in atmospheric CO_2 has decreased due to exchange with the ocean and terrestrial biosphere, and dilution by burning of ^{14}C-free fossil fuels (Gaudinski et al. 2001). As the atmospheric ^{14}C value is nowadays close to the detection limit, it is reasonable to use archive root samples in which the ^{14}C signature is higher. The soil cores (36 mm in D, 12 in each site) were lifted up at the Mekrijärvi site in September 1986, at Punkaharju in September 1989 (both pine and spruce stands), and at Voore (spruce) in October 1996. The cores were divided into sections comprising the organic layer and the 10 cm thick mineral soil layers, of which only the roots from the 0 to 10 cm upper mineral layer were utilized (study **IV**). At Punkaharju we additionally used roots from the organic layer. After collection, the roots had been washed free of soil and the tree roots separated from understory roots and divided into living or dead roots and into two D classes: <2 mm (fine roots) and >2 mm (coarse roots), dried at 70 °C for 48 h and weighed (Helmisaari et al. 2002). For ^{14}C analyses, the fine roots were further separated (under a microscope) into D classes <0.5 mm and 1.5 - 2 mm. There were a total of 31compiled samples, the replicate number of samples being mostly 3 but in a few cases 2 (study **IV**). Cellulose was isolated from root samples as described in Sah et al. (2011) and the ^{14}C analysis was carried out at the SUERC AMS Laboratory, East Kilbride, UK (Freeman et al. 2008). The ^{14}C enrichment of a sample was measured as a percentage (or fraction) of the ^{14}C activity relative to a modern standard (oxalic acid provided by the US National Bureau of Standards), where 100% modern is defined as the value in AD 1950, in the absence of any anthropogenic influences. Overall analytical precision is quoted at 1σ.

As our archived fine root sample size was inadequate (only two samples) for statistical analyses for some of the dates and sites, we combined the root C age values from different stands by D and soil depth and applied the paired T-test for comparison of means by diameter and depth.

4 RESULTS AND DISCUSSION

4.1 Fine root and EcM responses to warmer soil and higher nutrient availability

At Flakaliden, with a cold boreal climate, warmer soil temperature and longer growing season were expected to favour fine root growth and EcMs (measured as EcM short root tip numbers and mycelia production (studies **I** and **II**). Fertilization was also expected to activate fine root growth, but to reduce both the number of EcM short root tips and mycelia production as a response to decreased need to forage nutrients. EcM short root morphology, being highly sensitive to environmental changes (Ostonen et al. 1999), was hypothesized to respond to these changes (study **I**). According to the cost-benefit analysis (Eissenstat et al. 2000), fine roots should live longer in harsh environmental conditions, where their construction costs in terms of expended C are higher, compared to sites with more favourable temperature and water and nutrient availability conditions. Thus, both the warming and the fertilization treatments at Flakaliden were expected to shorten the fine root lifespan (study **II**). Accordingly, in the two natural Norway spruce stands in Finland (study **III**), trees growing in the south were anticipated to have faster fine root turnover than trees growing in the north. As the growing season is shorter and soil organic layer C:N -ratios were higher in the northern stand, the hypothesis was that more fine root production would be directed belowground than aboveground in the northern site compared to the southern site, in order to guarantee sufficient acquisition of nutrients. Thus, the C input into the soil via root litter would become higher along with higher latitude. The litter production data from these two sites was eventually augmented with data from four additional sites in Sweden (study **III**).

Fine root biomass was highest in the surface soil and decreased sharply towards deeper soil layers (study **I**), as reported also by many other investigators (Helmisaari et al. 2007, Finér et al. 2011, Makita et al. 2011). However, as the thickness of the organic layer affects the amount of fine root biomass in the organic layer (Borken et al. 2007), for comparing the treatments we unified the dissimilar thicknesses of the organic layer (from 0.5 to 7 cm) at Flakaliden by converting fine root biomass m^{-2} to fine root density (the amount of fine roots dm^{-3} of soil). The highest density of roots was in the organic layer (in all treatments) and the density of roots decreased exponentially towards the deeper soil layers (Figure 5). Soil warming treatment did not significantly change the fine root density in the organic layer (Figure 5), but in the mineral soil fine root biomass (<1 mm in D) was significantly higher at the depths of 10 - 20 cm ($P<0.05$) and 20 - 30 cm ($P<0.01$) in the warmed (WI + WFI) than in the non-warmed (FI + I) soil (Figure 6) (study **I**). A corresponding vertical response in warming experiments has also been reported by Lahti et al. (2005) and Johnson et al. (2006). Proliferation of roots downwards plus the higher soil temperature (enhanced mineralization and increased nutrient uptake capacity (BassiriRad 2000, Pregitzer & King 2005)), both vertically but also seasonally, should enable trees to improve N uptake especially deeper in the mineral soil. At Flakaliden this has been demonstrated on the basis of isotope analysis: needles of the warmed plots had a shift in the increased abundance of $\delta^{15}N$ compared to corresponding controls (also without any increase due to fertilization) (Strömgren 2001) and deeper soil layers had a significantly higher $\delta^{15}N$ abundance than upper soil layers (Högberg et al. 1996, Högberg 1997).

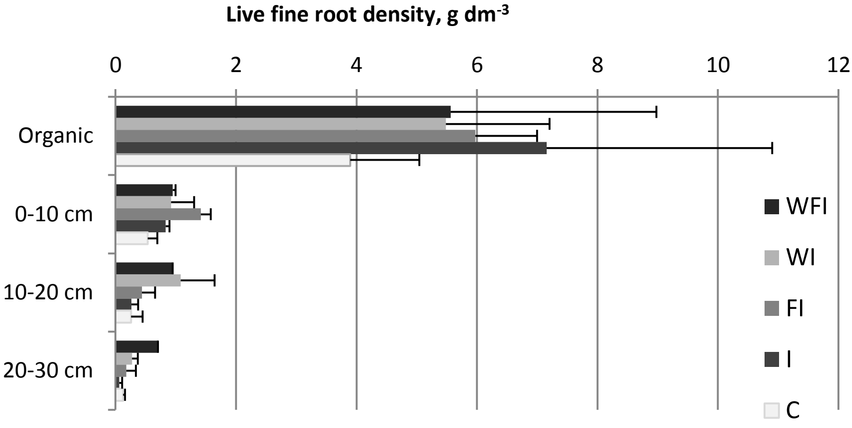

Figure 5 The density of living roots (<1 mm in D) of Norway spruce in different treatments and depths at Flakaliden (study **I**). Abbreviations: WFI = warming – fertilization – irrigation, WI = warming – irrigation, FI = fertilization – irrigation and I = irrigation. Bars indicate standard deviation.

The total fine root biomass was highest in both fertilization treatments (WFI vs. I $P<0.05$; FI vs. I $P = 0.07$), but as the trees in these plots were two times taller, it was necessary to take the aboveground part into account. After dividing the fine root biomass by ba, fertilized treatments were rather similar to the other treatments but the WI treatment stood out from the manipulation treatments by having more fine root biomass per ba (Figure 7), although not significantly ($P = 0.19$). The inclusion of the unmanipulated stands Flakaliden C, Kivalo and Olkiluoto in the comparison showed that the amount of fine root biomass per ba in the WI treatment was as high as in the low-fertility Kivalo site from northern Finland and in Flakaliden C (Figure 7). However, no statistical testing was done due to the lack of replicates and lower sampling depth at Olkiluoto (only one soil sample from 10 - 20 cm; due to the high stone content). Kivalo and Flakaliden are similar e.g. with regard to their N deposition and N mineralization (study **III**), Kivalo having somewhat harsher climate but Flakaliden having a higher C:N -ratio (Table 1). According to several publications the increased C allocation to the roots results from nutrient, especially N, deficiency (Ingestad & Ågren 1991, Ericsson 1995, Poorter et al. 2012), accompanied by changes in root morphology (Trubat et al. 2006, Ostonen et al. 2013) and/or increased production of mycorrhizal hyphae (Högberg et al. 2003, Lukac & Godbold 2011).

The analyses of MR images and short root morphology indeed showed that other temperature-induced changes than increased fine root biomass per ba had taken place in the WI treatment. The total fine root elongation, traced from the MR images (study **II**), was higher in the WI and I treatments compared to both fertilized treatments (Figure 8), but the differences were not statistically significant due to high variation between the tubes. In the warming treatment, concurrent increment of root elongation and higher fine root biomass in the mineral soil is possible only if the root D has decreased. The analysis of morphological traits (study **I**) validated this as the fine root D was significantly lower in the WI than in the other treatments. Correspondingly, in the fertilized plots the EcM short roots were the

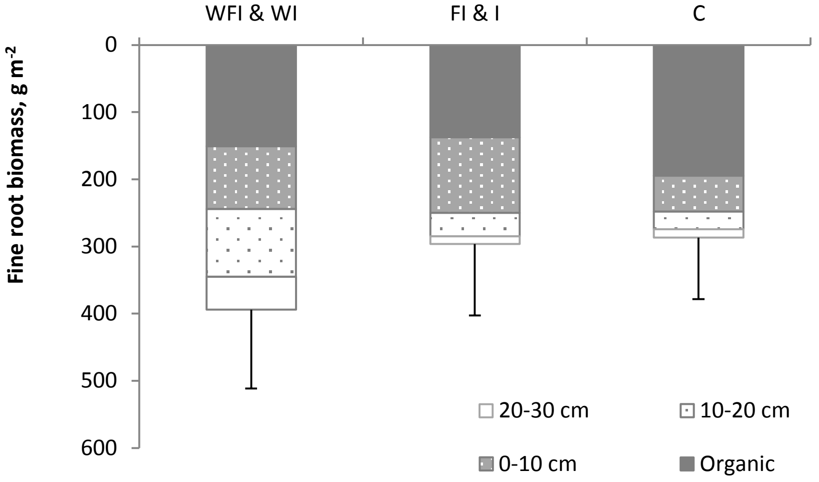

Figure 6 Norway spruce fine root biomass (<1 mm in D) in different soil layers in the warmed soil (treatments WFI, WI), non-warmed soil (treatments FI, I) (*P>0.05*) and in the control (C) at Flakaliden (study **I**).). Abbreviations: WFI = warming – fertilization – irrigation, WI = warming – irrigation, FI = fertilization – irrigation and I = irrigation. Bars indicate standard deviation of the treatment mean. Warmed n = 4, non-warmed n = 4, n = 2.

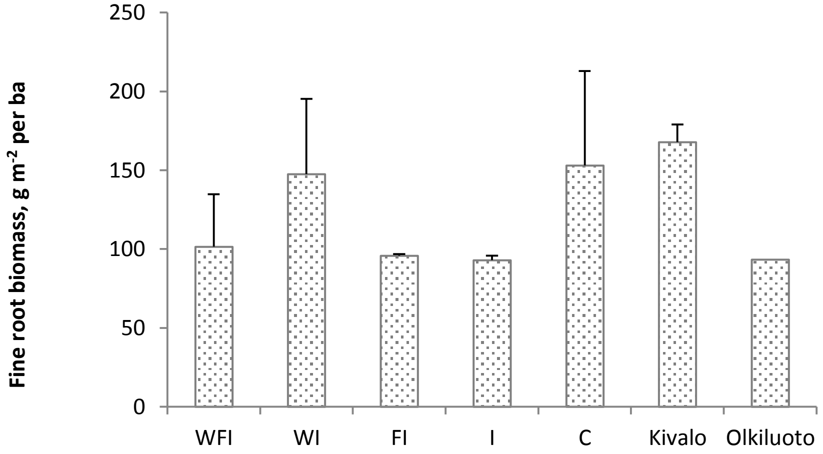

Figure 7 Spruce fine root biomass (<1 mm in D) per square meter (m^2) per stand basal area (ba) at Flakaliden (WFI, WI, FI and I) Kivalo and Olkiluoto (studies **I** and **III**). Abbreviations: WFI = warming – fertilization – irrigation, WI = warming – irrigation, FI = fertilization – irrigation and I = irrigation. Flakaliden n = 2, Kivalo n = 3, Olkiluoto n = 1.

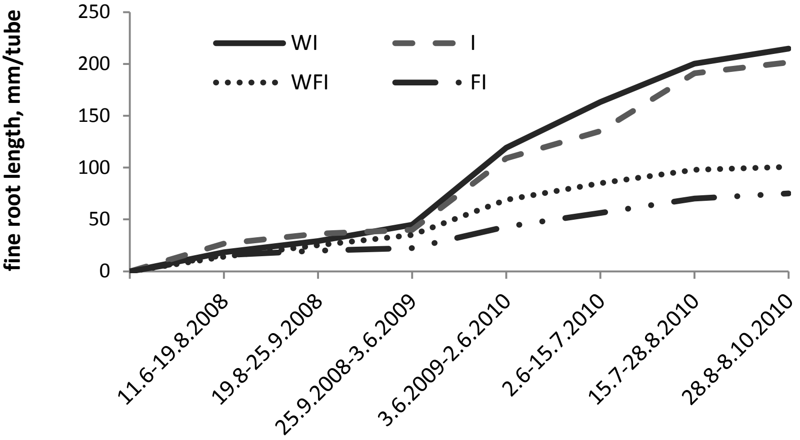

Figure 8 The cumulative total elongation of new fine roots during the study in different treatments at Flakaliden (study **II**). Abbreviations: WFI = warming – fertilization – irrigation, WI = warming – irrigation, FI = fertilization – irrigation and I = irrigation.

thickest and had the lowest RTD ($P<0.05$), leading to low SRL (study **I**). In the WI, the SRL of EcM short roots was significantly higher than in the other treatments; and this trait has been shown to be a good indicator of environmental changes (Ryser 2006, Björk et al. 2007), especially of nutrient availability (Hill et al. 2006, Trubat et al. 2006, Ostonen et al. 2007b). These changes in root growth and morphology reinforced the conclusion that in the WI the amount of nutrients was not adequate for spruce root uptake, to which the tree responded by increasing the absorbing root area. Thus, the increased fine root biomass in the mineral soil may have been not just a result of a longer growing season and more favourable temperature conditions as hypothesized, but a response to the necessity to acquire more nutrients from the soil where microbial activity has been attenuating due to depletion of the most labile C pools (Kirschbaum 2004, Eliasson et al. 2005, D'Orangeville et al. 2013) and/or decrease in litter quality (Hyvönen et al. 2007). At Flakaliden the microbial biomass in the WI treatment has indeed been shown to be lower than in the non-warmed treatments (Coucheney et al. 2013). According to Ueda et al. (2013), soil warming may also decrease soil nitrogen pools by preventing the soil from freezing.

EcM root tip frequency (no of tips g^{-1} fine root <1 mm in D) did not differ between the soil warming or fertilization treatments (study **I)**. The (profile) average number of EcM short root tips per mg of fine root (<1 mm in D) was 14.8 at Flakaliden C (study **I**), 6.9 at Kivalo and 4.5 at Olkiluoto (study **III**). However, after taking the ba into account the number of EcM short root tips per ba was twofold at Flakaliden compared to Kivalo, and 3.5-fold at Kivalo compared to Olkiluoto (Figure 9). The highest number of EcM root tips per ba was at Flakaliden, where the C:N -ratio of the organic layer was highest (Table 1), decreasing towards Kivalo and Olkiluoto ($R^2 = 0.72$, Figure 10). Our result is in a good agreement with the pattern described in a Finnish Norway spruce stand: the number of EcM

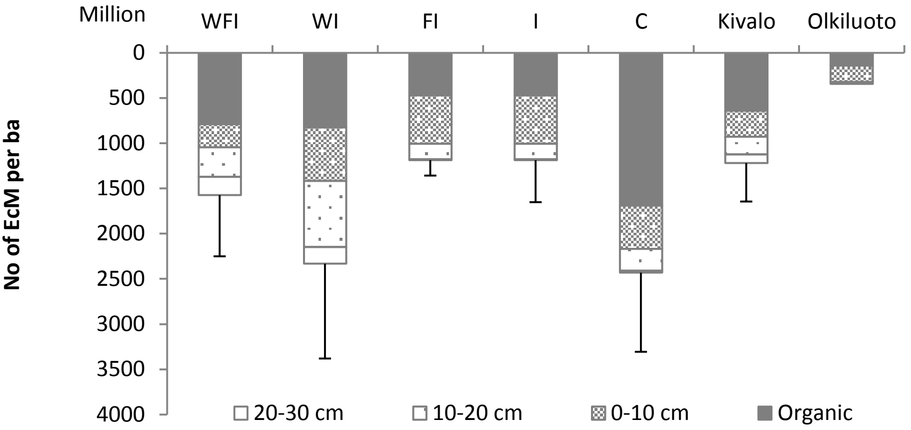

Figure 9 Number of ectomycorrhizal (EcM) short root tips (calculated from the roots <1 mm in D) per stand basal area (ba) at Flakaliden (WFI, WI, FI and I), Kivalo and Olkiluoto (studies **I** and **III**). Abbreviations: WFI = warming – fertilization – irrigation, WI = warming – irrigation, FI = fertilization – irrigation and I = irrigation. Bars indicate standard deviation of the treatment. Flakaliden n = 2, Kivalo n = 3, Olkiluoto n = 1.

short root tips:foliage biomass -ratio was positively correlated to the C:N -ratio in the organic layer (Helmisaari et al. 2009). Later, this same pattern was demonstrated on a larger scale: on a European latitude/fertility gradient the Norway spruce forests in Finnish Lapland had 4.5 to 11 times more EcM root tips per ba than roots in spruce stands growing in Estonia and Germany (Ostonen et al. 2011).

Fertilization has frequently been reported to decrease the fine root biomass (Lee et al. 2007, Wang et al. 2012), but as the below- and aboveground parts of a tree are inseparably intertwined, no deductions about belowground biomass or production should be made unless the aboveground part is included in the study, and *vice versa*. Optimally the stands in comparison are similar with regard to their age and tree density as well as climate conditions, but in the case of fertilizing or latitude/fertility gradients the difference in tree size/faster development becomes inevitable. Soil fertility also affects soil chemistry, microbial activity and mineralization *etc*, leading to differences in tree growth and developmental stages. The difficulty of separating the effects of tree ontogeny from the treatment effect has been regularly discussed (Gedroc et al. 1996, King et al. 1999, Coleman et al. 2004, Xie et al. 2012).

The effects of long-term fertilization on fine root biomass were studied at Flakaliden already before our study: Iivonen et al. (2006) studied the effect of 12 years of nutrient optimization on biomass, carbon, and nitrogen acquisition and allocation in Norway spruce. They detected a significant increase in biomass allocation to stumps and coarse roots (as well as to all aboveground organs except dead branched and cones) but no changes in the biomass of small and fine root biomass in the fertilization treatment compared to the control - indicating that a smaller amount of small and fine roots was sufficient to maintain a higher aboveground biomass (ba in the fertilized treatment was 2.5-fold compared to the

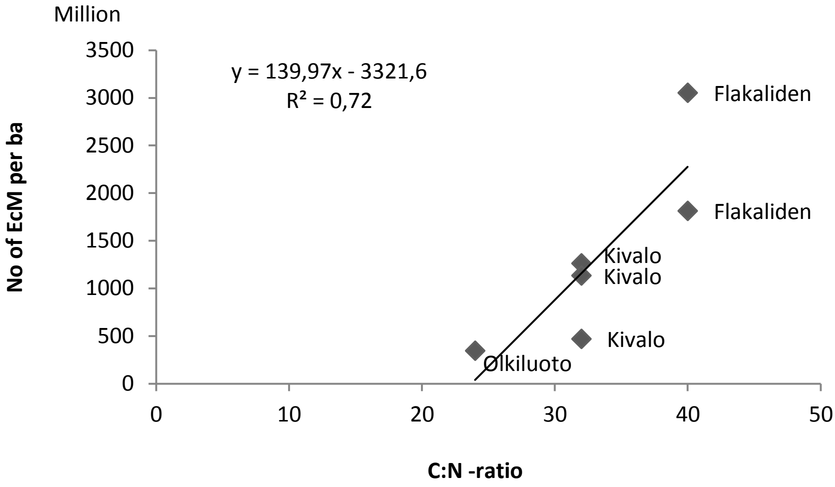

Figure 10 Number of ectomycorrhizal (EcM) root tips (calculated from the roots <1 mm in D) per stand basal area (ba) in relation to site C:N -ratio.

control). A similar trend has been observed by several authors (Keyes & Grier 1981, Gower et al. 1992, 1994, Vanninen & Mäkelä 1999, Helmisaari et al. 2009).

Our results from Flakaliden were rather similar: fine root biomass tended to be higher (*P = 0.071*) in the fertilized treatment (FI, 388 g m^{-2}) compared to the irrigated (I, 205 g m^{-2}) if only the belowground part was examined. However, after taking the twofold higher ba in the FI plots into account, the amount of fine root biomass in both fertilization treatments decreased to the same level as in the high-fertility Olkiluoto site and in I (Figure 7). Thus, at all these sites a smaller amount of fine roots was sufficient to maintain a higher aboveground biomass. The assorting of I into this group is somewhat surprising and no fully satisfying explanation can be provided. However, one possible explanation is that in the I the share of EcMB of total fine root biomass was considerably higher (54%) than in the other treatments (27 - 32%) (study **I**) implying that the quantity of absorbing roots in the I was approximately double that in the others. Furthermore, this short root area provides exudates which benefit mycorrhiza and microbes living in the rhizosphere (Priha et al. 1999).

Fine roots are so tightly connected with EcM that the results may sometimes differ from the expected. Phillips & Fahey (2007) for example found no changes in fine root biomass after several years of fertilization, although mycorrhizal colonization and microbial respiration were reduced due to fertilization. Similarly, the production of EcM mycelia at Flakaliden was only slightly increased by higher soil temperature (study **I**), which in case of suspected nutrient deficiency is a rather mild response, as several studies have shown that EcM mycelia growth and nutrient availability correlate negatively (Nilsson & Wallander 2003, Nilsson et al. 2005, Sims et al. 2007) and temperature generally leads to a positive response in microbial biomass (Pendall et al. 2004). Lack of water (Lehto & Zwiazek 2011) or photosynthetic products (Högberg et al. 2008) can diminish EcM mycelia production, but at least drought seems unlikely as all the treatments were irrigated. Possible explanations are that the incubation time of two years to the in-growth bags was too long as a growing season or one calendar year are regularly used (Nilsson et al. 2005, Wallander et al. 2010, Bahr et al. 2013), or that the trees responded predominantly via fine roots.

Overall, bigger trees had more fine roots as has been described in many stand succession papers (Paavilainen 1968, Liu et al. 2014), but the relation is smaller in the fertile sites. Until canopy closure, trees increase the foliage biomass and thus a relatively large root system is required to provide larger amounts of nutrients. After canopy closure C allocation to stem D and L growth continues (Mäkelä & Valentine 2001), but re-translocation of nutrients can satisfy much of the nutrient requirement at this stage (Helmisaari 1992a, b) and thus the amount of fine roots remains rather stable (Vogt et al. 1983, Helmisaari et al. 2002, Claus & George 2005). Later in the stand development, nutrient availability may again decrease as more and more nutrients are bound in the litter and humus (Grier et al. 1981, Sprugel 1984, Vanninen & Mäkelä 1999). In our study plots only the trees growing in the Olkiluoto, Kivalo and Flakaliden fertilized plots (WFI, FI) had reached canopy closure and should thus, if following the described pattern, have had lower amounts of fine root biomass per ba than trees before canopy closure. However, according to our limited data, fertility appears to be a more dominant factor in defining this relationship than the stand developmental stage.

At Flakaliden an increase in stem wood production (m^3 ha^{-1} yr^{-1}) was measured in the warmed plots after six seasons of soil warming (Strömgren & Linder 2002). However, ten years later the ba in the warmed (WI) plots was not higher than in the reference plots I and C, study **II**). Thus, the increased temperature may have enhanced the short-term mineralization rate, but the effect has dampened or vanished with time; a phenomenon also observed in other long-term soil warming experiments (Oechel et al. 2000, Luo et al. 2001, Melillo et al. 2002). A cause for this may be substrate limitation due to losses of labile C, population and community reorganization and/or the acclimatization of root or microbial respiration or both (Oechel et al. 2000, Luo et al. 2001, Strömgren 2001, Melillo et al. 2002, Coucheney et al. 2013).

4.2 Effect of temperature and nutrient availability on fine root turnover

Differences in ratios of live:dead fine root biomass indicate differences in fine root dynamics. In study **I**, we found that the ratios of live:dead fine root biomass tended to decrease with increasing soil depth and from the warmed plots to the non-warmed ones, with up to six-fold difference between the treatments. The increased live:dead -ratio may result from 1) increased production or 2) decreased mortality of fine roots or from 3) enhanced decomposition. Of these three reasons, the first two were investigated – and confirmed (studies **I** and **II**) but the latter could not be verified as we performed no measurements of the decomposition rate. However, there are indications that higher soil temperature may have enhanced decomposition at Flakaliden: Strömgren (2001) and Coucheney et al. (2013) observed an increased soil-surface CO_2 flux after short- and long-term soil warming at the same study site, but as the total CO_2 flux does not separate autotrophic and heterotrophic respiration, no direct conclusions of the decomposition rate could be drawn. However, on the basis of the data collected from Flakaliden, heterotrophic respiration has been modelled to increase 60% in the first year after the perturbation caused by heating cable installation and to decrease to 30% after a decade (Eliasson et al. 2005), possibly due to the reduced substrate availability. Generally, many reports support the positive relationship between temperature and decomposition (Van Cleve et al. 1990, Kirschbaum 1995, Kätterer et al. 1998, D'Orangeville et al. 2013,), although there is a lively discussion concerning the differences in decomposition rates between the different C pools (Fang et al. 2005, Fierer et al. 2005, Karhu et al. 2010).

Higher soil temperature and longer growing season affected fine root lifespan at Flakaliden (study **II**): fine root median lifespan (weeks) was significantly lower in both soil warming treatments than in the un-warmed ones: 48 and 58 in WFI and WI compared to 78 and 110 in FI and I, respectively, estimated with the regression model with Weibull error distribution. Nutrient addition gave an additive effect. The Kaplan-Meier survival function gave estimates of the median longevities very similar to those of the regression models (Figure 11), and both methods showed statistically significant (*P<0.01*) differences in the survival distributions between the treatments.

Majdi & Öhrvik (2004) studied the short-term effects of the same treatments on fine root survival at the same site and their results agreed with ours in the main part: both soil warming and nutrient addition increased the risk of mortality. However, in their study the risk of mortality in the interaction treatment was lower than in the WI of FI treatments, whereas in our study it was highest of all. It is possible that the response of WFI treatment on fine root survival has changed during the years, but their study period of one year only, or the different calculation methods used, may also have affected the results to some extent. King et al. (1999) also observed that the root length production and mortality of trembling aspen increased at elevated soil temperature, but that response was modified by soil N-availability. In the light of the suspicion of nutrient deficiency in the WI treatment, fine root lifespan in the WI treatment would have been expected to be higher – unless the response is more connected to the temperature increase itself (Pregitzer et al. 2000) than to temperature-related changes in nutrient availability. For example, higher temperature enhances autotrophic respiration (Burton et al. 2002, Melillo et al. 2011) and acclimatization does not always take place (Sowell & Spomer 1986, Weger & Guy 1991). Roots in a way respire themselves to death.

The mechanism behind the shorter root lifespan in a warmer environment has been suggested to be based on enhanced metabolism (respiration) which accelerates the rate at which root efficiency decrease with age, causing a decrease in optimal lifespan (Eissenstat & Yanai 2002). Similarly, enhanced nitrogen mineralization/nitrogen uptake by fine roots, and higher nitrogen concentration of fine roots (Peterjohn et al. 1994, 1998, Ryan et al.

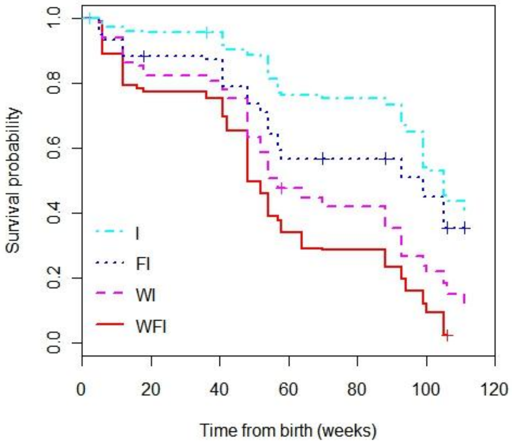

Figure 11 The Kaplan-Meier survival curves for Norway spruce fine roots monitored 11.6.2008 - 8.10.2010 at a depth of 0 - 25 cm (study **II**). All treatments differed significantly from each other, *P<0.01*. Abbreviations: WFI = warming – fertilization – irrigation, WI = warming – irrigation, FI = fertilization – irrigation and I = irrigation.

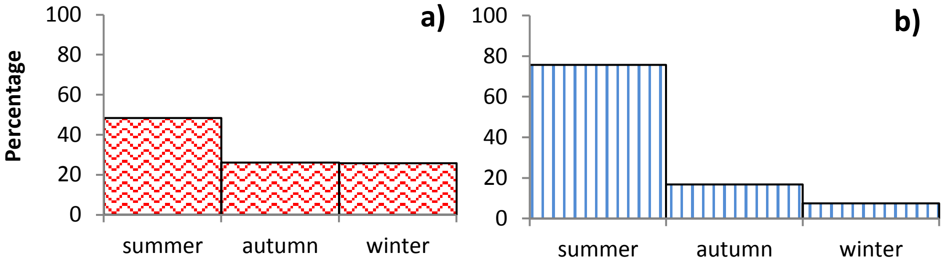

Figure 12 The percentage of new fine root growth during the first year in warmed (WFI, WI) (a) and non-warmed (FI, I) (b) treatments (study **II**). The distributions were significantly different (*P<0.01*). Summer period = 11.6 - 19.8.2008, fall period = 19.8 - 25.9.2008 and winter period = 25.9.2008 - 3.6.2009.

1996, Reich et al. 1998, BassiriRad 2000, Rustad et al. 2001, Widén & Majdi 2001, Burton et al. 2002, Bagherzadeh et al. 2008, Zhou et al. 2011), have been connected to enhanced metabolism and thus earlier senescence. However, if the temperature increment leads to soil drought or to the physiological acclimatization of fine roots (construction of fine roots with lower root amino acid and protein concentrations), the root metabolic capacity may also decrease (Burton et al. 2008).

In the natural Norway spruce stands in Finland the fine root median age was also younger in the southern stand (89 weeks), where the MAT was higher, than in the northern stand (97 weeks) (study **III**), but other changing variables than temperature were also involved between these sites. The decreasing fine root survival along with increasing temperature has been reported in several soil/air warming or latitude experiments (Hendrick & Pregitzer 1993, Forbes et al. 1997, Gill & Jackson 2000, Majdi & Öhrvik 2004, Bai et al. 2010, Kitajima et al. 2010, Finér et al. 2011), but as discussed by Eissenstat & Yanai (2002), Högberg & Read (2006) and McCormack & Guo (2014), there are many co-varying factors, such as soil fertility, moisture, growing-season length, herbivore & pathogen activity and the influence of solar irradiation on photosynthesis, which makes it difficult to distinguish the direct effects of temperature.

Obviously higher soil temperature lengthened the growing season and the active period in soil, as in the soil warming treatments (WFI & WI) 25% of the first year's total new root elongation had taken place outside the growing season (October-May) whereas the corresponding figure in the non-warmed treatments (FI & I) was 7% (Figure 12, study **II**). Majdi & Öhrvik (2004) reported related results from the same site: half of the annual root elongation occurred between October and June in the warmed plots compared to non-warmed ones at Flakaliden. However, soil warming did not lengthen the period of active photosynthesis correspondingly, or reflect chlorophyll fluorescence or needle starch content at Flakaliden (Bergh & Linder 1999), which may mean that the flux of photosynthetic products in these warmed plots has not been higher than in the non-warmed ones, regardless of the higher need for C due to the longer active period in soil in the warmed plots, possibly affecting fine root lifespan (Eissenstat & Yanai 1997, Anderson et al. 2003).

Belowground C availability varies during the year according to the photosynthetic activity and according to the changes in the aboveground-belowground sink strength, and due to this the survival times of fine roots formed in different seasons were expected to differ. If C allocated to fine roots mostly originates from current photosynthesis (Epron et al. 2011, Keel et al. 2012), the fine roots born outside the growing season may have had less C available for their construction, and thus weaker survival capability.

At all sites, the fine roots born during the first year of image collection were included in the survival analysis, and in Flakaliden, to avoid having too small cohorts, all treatments were pooled together. Both at Flakaliden ($P<0.05$) and at the Finnish sites the lifespan of roots appearing after the growing season and/or during the following winter was in most cases significantly lower than that of the roots born during the growing season (Figure 13) (studies **II** and **III**). In addition to low photosynthetic C availability for these roots, simply the stress derived from low winter temperatures, the mechanical damage caused by frost heaving or the impaired water uptake capacity of roots in cold soil in spring and early summer, when evapotranspiration is high (Repo et al. 2014), may have lowered the survival capacity. Just before the winter the C availability for the roots may be low due to competition: the aboveground parts compete for C for accumulating storages for winter dormancy and frost hardiness (Brüggemann et al. 2011).

A shift in the C allocation to the aboveground for a new needle cohort growth early in the summer and to the belowground late in the summer has been demonstrated (Högberg et al. 2010, Keel et al. 2012). However, only at Kivalo did the spruce roots born in the end of the summer have a significantly longer lifespan ($P<0.05$) than the roots born in other seasons. Most probably, the disparity in the correspondence in the growing season timing between northern and southern sites, and the unequal intervals between the image collections, are the best explanations for this.

There was no uniform pattern in the fine root turnover rate regarding the soil depth (Table 3). In the warming treatments at Flakaliden as well as in northern Finland, the fine root turnover was, surprisingly, faster in the mineral soil than in the soil surface, although significantly only in the WFI. In general, the opposite trend has been reported (Baddeley & Watson 2005, Joslin et al. 2006, Chen & Brassard 2013), although with some exceptions (López et al. 2001, McCormack et al. 2012). In the reference treatment I at Flakaliden and at Olkiluoto the fine root longevity was practically unchanged along the soil profile. In the latter site, there were no such distinct horizons as the soil is pedologically rather young after the last glaciation and land-up lifting (Tamminen et al. 2007), and therefore the organic layer was set as 5 cm thick. Bio- and cryoturbation may have been stronger there and thus affected fine root mortality more evenly along the soil profile. At Kivalo, the characteristic thick and dense moss layer of the HTM site type leads to rapid decrease in soil temperature, nutrient mineralization, oxygen availability and soil acidity (Sirén 1955), which may have caused unfavourable conditions for fine roots to grow in the mineral soil. However, with regard to Flakaliden no satisfactory explanation can be provided.

The MR method catches mostly fine roots with small D, and in Scandinavian conifer forests, the majority of the roots are ectomycorrhizal short roots. Practically all traced roots in both countries were <1 mm in D, and in the thickest D class (0.5 - 1 mm) there were only 2.6% and 3.4% of spruce fine roots in Flakaliden and in Finland, respectively (studies **II** and **III**). At Kivalo the mean fine root D was significantly ($P<0.01$) thinner than in Olkiluoto (0.27±0.08 and 0.32±0.10 mm, respectively, measured with the MR method), which is in agreement with earlier climate gradient studies in which Norway spruce EcM root tips were observed to be 2.1 times longer and significantly thinner in northern Finland than in Germany (Ostonen et al. 2011, 2013). In all treatments the trend was towards longer

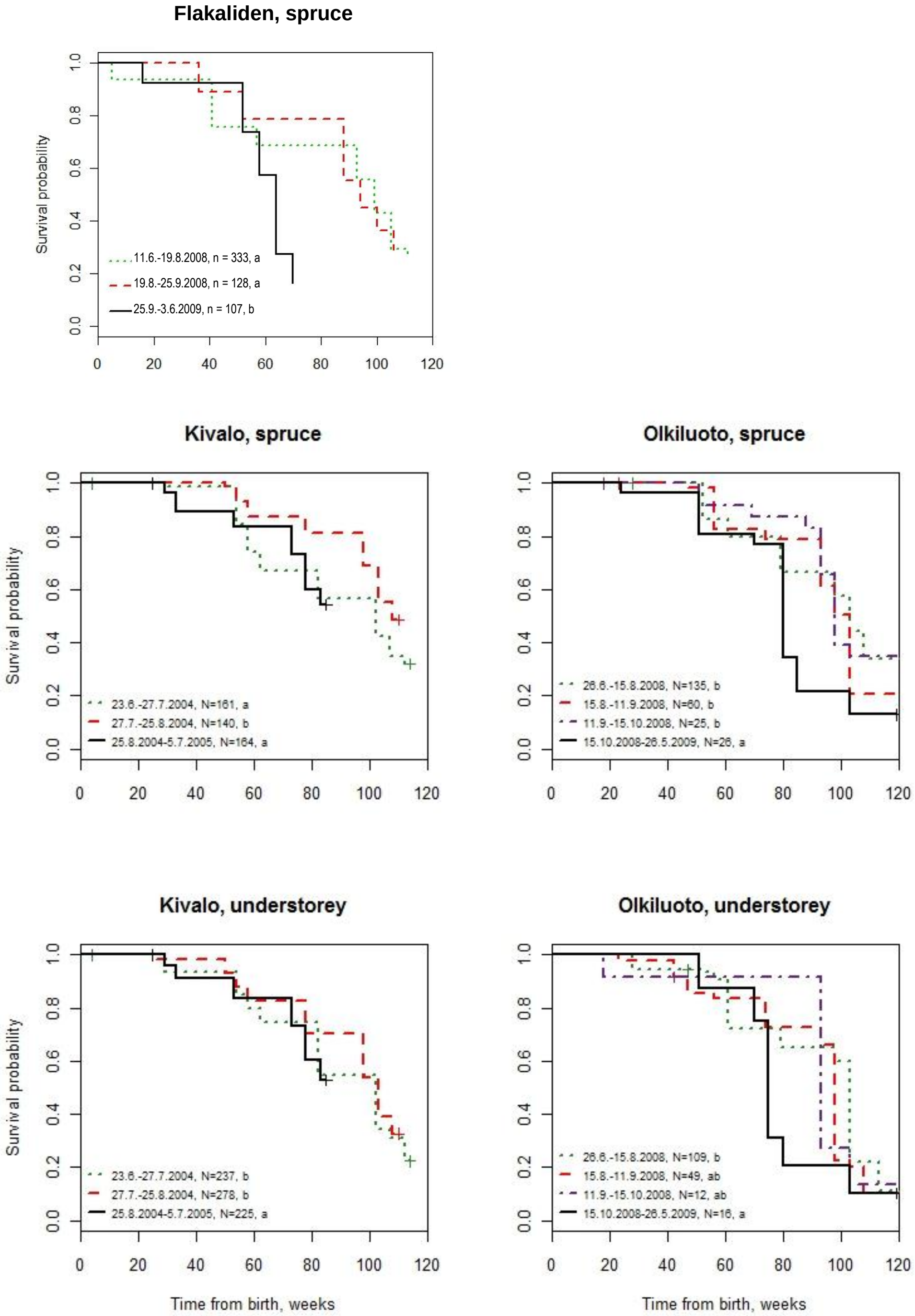

Figure 13 Survival curves of spruce and understory fine root cohorts born during the first year of image acquisition at Flakaliden, Kivalo and Olkiluoto (studies **II** and **III**).

Table 3 The median (±se) fine root lifespan (weeks) in different soil layers and diameter (D, mm) classes (studies **II** and **III**). The letters (a-b) indicate significant differences ($P<0.05$) between the topmost 5 cm and mineral soil within each treatment. Topsoil represents the uppermost five centimeters and mineral soil 5 - 25 cm depth. WFI = warming – fertilization – irrigation, WI = warming – irrigation, FI = fertilization – irrigation and I = irrigation, us = understory, ns = non-significant.

	WFI	WI	FI	I	Kivalo, spruce	Olkiluoto, spruce	Kivalo, us	Olkiluoto, us
Topsoil	71 ± 9^{a}	64 ± 6^{ns}	54 ± 12^{ns}	108 ± 17^{ns}	103 ± 3^{b}	89 ± 2^{ns}	104 ± 3^{b}	87 ± 2^{ns}
Mineral soil	45 ± 2^{b}	56 ± 3^{ns}	90 ± 13^{ns}	102 ± 5^{ns}	89 ± 3^{a}	89 ± 7^{ns}	77 ± 1^{a}	92 ± 11^{ns}
D <0.2	30 ± 4	32 ± 14	–	56 ± 9				
D 0.2 - 0.3	38 ± 2	44 ± 3	61 ± 11	99 ± 10^{c}				
D 0.3 - 0.4	57 ± 3	60 ± 3	86 ±11	126 ± 11				
D 0.4 - 0.5	64 ± 7	78 ± 9	90 ± 26	116 ± 22				
D >0.5	55 ± 18	95 ± 23	40 ± 23	–				

turnover with increasing D (Table 3), which supports the general rule of thumb that root lifespan correlates with diameter (Eissenstat & Yanai 2002), but also that the root survival may vary markedly among fine roots differing in D by only a few tenths of a millimeter (Wells & Eissenstat 2001): the median longevity of spruce fine roots at least doubled within a root D class of only a few millimeters (Table 3). Nevertheless, as the number of roots was rather low in some D classes, we did not use the turnover rates of D classes when calculating belowground litter production. Instead, we used the fine root turnover rates in the two soil depths: organic layer and mineral soil.

4.3 Norway spruce litter C input in different environmental conditions

Both Finnish Norway spruce stands and the reference treatment I at Flakaliden yielded approximately similar ratios between the above- and belowground litter production, the aboveground being slightly higher (Figure 14) with the difference that in Flakaliden the quantities were almost twofold lower than in Finland (Table 4). This was somewhat surprising as higher altitude Flakaliden resembled Kivalo by its climate, length of the growing season and ba (Table 1) and furthermore the soil fertility did not differ substantially between the sites: the C:N -ratio in the organic layer was higher at Flakaliden than at Kivalo (Table 1), but the net N mineralization rate and N deposition were the same at these sites (Andersson 2002, Kleja et al. 2008, Lindroos et al. 2008, Olsson et al. 2012). The tree density ha^{-1} at the sites was 2100, 939 and 667 at Flakaliden, Kivalo and Olkiluoto, respectively (study **II**, Smolander & Kitunen 2002, Aro et al. 2012). Aboveground litter production has been shown to correlate negatively with mean stem number, but stem number was not among the best predicting variables (Saarsalmi et al. 2007). The amount of litter production was converted to C input by assuming a C content of 50% of the litter dry mass (Table 4, Figure 14).

The highest foliage litter production was in the southern Finnish spruce stand whereas spruces growing in northern Sweden produced the lowest amount. The longer needle retention time in northern Finland compared to southern Finland (Ukonmaanaho et al. 2008) explains some of the difference in the foliage litterfall between the Finnish sites (Table 4), but no data of needle retention was available for comparison of Kivalo and Flakaliden. Furhermore the dissimilar crown form probably affected the amount of foliage litterfall: to diminish damages caused by heavy snow load, the northern spruce trees (*Picea abie*s 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 & Bergmann 1995). The mean aboveground spruce litter productions (2100 kg ha^{-}1 yr^{-1} in the north (Kivalo), 2400 kg ha^{-1} yr^{-1} in the south (Olkiluoto) and 1300 kg ha^{-1} yr^{-1} at Flakaliden I) 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 than Saarsalmi et al. (2007) 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. In our limited dataset, consisting of the Kivalo and Olkiluoto sites in Finland and four extra sites in Sweden (Flakaliden, Knottåsen, Asa and Tönnersjöheden (Kleja et al. 2008, partly Hansson et al. 2013a,b), Figure 2) latitude was not a particularly good predictor ($R^2 = 0.21$) (study **III**).

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

		BG	AG	BG:AG -ratio	BG % of total
Spruce	Kivalo	91	104	0.9	47
	Olkiluoto	83	121	0.7	41
	Flakaliden (I treatm.)	51	67	0.8	43
	Flakaliden (natural)	57	60	1.0	49
	Knottåsen	82	68	1.2	55
	Asa	84	101	0.8	45
	Tönnersjöheden	57	128	0.4	31
Understory	Kivalo	27	50		35
	Olkiluoto	10	21		32
	Flakaliden (natural)	41	32		56
	Knottåsen	50	33		60
	Asa	17	17		50
	Tönnersjöheden	1	24		4

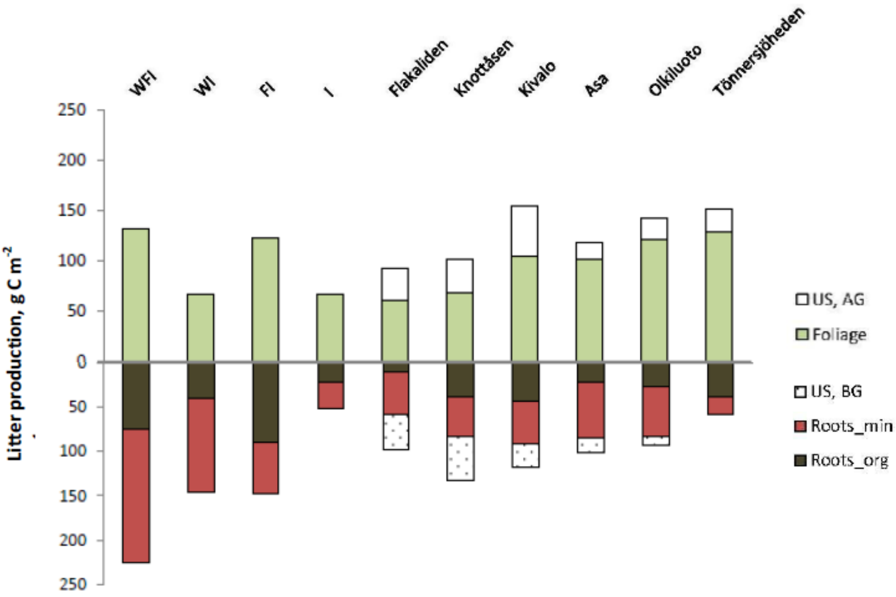

Figure 14 The annual litter production of Norway spruce (foliage, roots) above- and belowground (AG, BG) in different treatments (WFI, WI, FI, I) at Flakaliden in northern Sweden and the annual litter production of Norway spruce and understory (US) above- and belowground in six natural stands in Sweden and in Finland (studies **II** and **III**). WFI = warming – fertilization – irrigation, WI = warming – irrigation, FI = fertilization – irrigation and I = irrigation, org = organic layer, min = mineral soil.

The aboveground litter production experienced less drastic manipulation-induced changes: the highest foliage litterfall was as anticipated in the fertilized treatments (WFI, FI) (Figure 14) as the trees as well as the ba in these treatments were the largest (Table 1, study II). Furthermore, C stocks in the organic layer of these plots have been determined to be approximately twice as high as in the non-fertilized plots (Fröberg et al. 2013). Correspondingly, in the WI and I plots ba, amount of foliage litterfall and the C stock in the organic layer were well matched. In the Finnish stands the trend was similar to that seen at Flakaliden: the mean annual aboveground foliar litterfall was higher at Olkiluoto, where the trees and the ba were larger, than at Kivalo. However, in the Finnish stands the understory litter production was also estimated and after including this in the litter production, the total annual aboveground litter C input was almost equal at both sites (Figure 14). In the north, there was an abundant shrub vegetation consisting of bilberry (coverage 22%) and mosses (coverage 37%) (Nieminen & Smolander 2006), contributing one third to the aboveground litterfall in the north. At Olkiluoto, dwarf shrubs were practically absent and 58% of annual biomass (dry weight g m^{-2}) was produced by mosses (Haapanen 2010). The share of understory contribution to the aboveground litter production in the southern stand was 15%. Hansson et al. (2013b) described analogous, moss-dominated scarce understory vegetation in the fertile spruce stand in south-west Sweden.

At Flakaliden, high biomass in the mineral soil combined with the fast turnover rate led to high annual fine root production in the warmed plots (WFI, WI) (study **II**). In the WFI ba and foliage litterfall were also high, but in the WI the belowground litter production was 2.2-fold in relation to the foliage litterfall (Figure 14). In the fertilization treatments the corresponding ratios were 1.7 and 1.2 in the WFI and FI, respectively. As the ba in the fertilized plots was practically double compared to the non-fertilized ones (Table 1), it was not meaningful to compare the fine root litter production in these treatments to the reference treatment I. However, in the WI and I ba was almost the same, but nevertheless fine root litter production in the WI was three times higher than in the I (Figure 14).

At the Finnish spruce stands the annual belowground C input from fine root litter, both tree and understory, was higher at Kivalo than at Olkiluoto (Table 4), although at Olkiluoto the sampling depth was shallower due to the high stoniness. The share of understory fine root litter of the belowground litter production was 23% and 11% at the northern and southern sites, respectively. The C flux from spruce root litter (83 - 91 g C m^{-2} yr^{-1}, <1 mm in D) in the natural stands 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 & Andersson 2005, Lukac & Godbold 2010), 130 - 143 g C m^{-2} yr^{-1} (<2 mm in D, Majdi & Nylund 2001, Hansson et al. 2013b) and 276 g C m^{-2} yr^{-1} (<5 mm in D, van Praag et al. 1988).

At the Finnish stands the litter production by understory vegetation was also estimated and particularly in the northern site it contributed substantially to both below- and aboveground litter production (Table 4). The calculation of understory root litter production was based on root biomass less than 2 mm in D, whereas roots less than 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 understory litter production. The understory 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 understory 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, if calculated for understory roots <1 mm in D. Our understory fine root litter production of 10 and 27 g C m^{-2} yr^{-1} is close to the figures of 17 - 50 g C m^{-2} yr^{-1} reported by Kleja et al. (2008) and 37 g C m^{-2} yr^{-1} by Majdi & Andersson (2005).

C dynamics in the topsoil and in the mineral soil are different (Salomé et al. 2010) and are strongly affected by climate, tree species and litter decomposability (Prescott & Vesterdal 2013, Vesterdal et al. 2013). In the topsoil, mineralization is continuously stimulated by addition of fresh organic material (priming effect) (Fontaine et al. 2007), whereas in the deeper mineral soil the soil microbial biomass and activity are lower (Taylor et al. 2002), gradually diminishing the decomposition rate and the biodegradability of organic material with increasing soil depth (Fontaine et al. 2007). In the organic layer the litter input is a mixture of root and aboveground litter, whereas in the mineral soil litter originates mainly from root tissues but also from root exudates, dissolved OM, soil animals and through bioturbation from leaf litter. The results of some studies indicate that the root-originated residues increase SOM more effectively than the shoot-originated residues (Gregorich et al. 2001, Rasse et al. 2005, Uselman et al. 2012). Thus, it is of significance to investigate whether the ratio of the litter production and/or deposition in these different soil layers changes.

At Flakaliden, due to the increased fine root biomass in the mineral soil and the shortest fine root lifespans in the mineral soil of the warming treatments (WFI, WI), almost half (42 - 50%) of the total annual spruce litter C input ended up directly in the mineral soil whereas the corresponding percentage in the non-warmed plots was 22 - 25% (study **II**). In the Finnish natural stands the trend was identical: at Kivalo 25% and at Olkiluoto 28% of the spruce litter C input was set down in the mineral soil (study **III**). Thus, it can be speculated that if the increasing MAT increases the root litter input into the mineral soil, more C may be sequestered into the mineral soil. However, at the same time, many researchers have speculated that in the topsoil the C cycling will be enhanced due to the priming effect caused by the elevated CO_2 concentration and higher MAT (Phillips et al. 2012).

In Scandinavia nitrogen deposition is low compared to Central Europe (Högberg et al. 1998, Lindroos et al. 2007, Dise et al. 2011), and N availability limits the tree growth (Kukkola & Saramäki 1983, Linder & Flower-Ellis 1992). Therefore, the C:N -ratio well describes the nutrient availability and productivity of forests in northern Europe. The inclusion of data from four additional Norway spruce stands, Tönnersjöheden, Asa, Knottåsen and Flakaliden in Sweden (Kleja et al. 2008, partly by Hansson et al. 2013a,b), along a Scandinavian north-south gradient (Figure 2) allowed us to examine relations of belowground and aboveground litter production in relation to soil fertility (study **III**). For spruce, the total litter C input (including below- and aboveground) tended to decrease towards higher C:N -ratios ($R^2 = 0.59, P = 0.08$) (Figure 14a) whereas for the understory the trend was the opposite ($R^2 = 0.64, P = 0.06$) (Figure 15b). Regressing the ratio of total above- and belowground spruce litter production against the C:N -ratio of the organic layer of the sites revealed that the aboveground litterfall decreased significantly towards the higher organic layer C:N -ratio ($P<0.01$) and to a lesser extent towards the lower ba ($P<0.05$) (data not shown). The shift in allocation from aboveground to belowground did not follow tree age, latitude or the length of the growing season gradient ($P>0.05$), but rather the organic layer C:N -ratio gradient ($R^2 = 0.70, P<0.05$) (Figure 15c). The southernmost site, Tönnersjöheden, was the most fertile site (lowest C:N -ratio), and here the tree foliage litterfall was more than double compared to the belowground litter C input. At the less productive sites the share of belowground litter C input was almost equal to the aboveground input.

Thus, at the low fertility sites, relatively more C is allocated to the belowground. The result also supports the functional equilibrium hypothesis (Brouwer 1963), which states 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 proportion of litter C of root origin, and this may have an impact on C sequestration into the forest soil. Some studies have reported differences in root litter quality (Uselman et al. 2012), or decomposability (Vivanco & Austin 2006, Hansson et al. 2010, Freschet et al. 2013) compared with leaf litter, indicating longer mean residence times for the root litter than of leaf litter in the soil. This area needs further research, and if validated, should be taken into account in C cycle models.

In our study only the belowground litter C input from fine roots less than 1 mm in D was estimated which means that 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 root lifespan decreases towards the smaller D classes, as reported in several studies with broadleaf species (Wells & Eissenstat 2001, Wells et al. 2002, Anderson et al. 2003) and in our manipulation experiment (study **II**). Thus, the smaller D classes probably produce more fine root litter than was calculated with the estimated average lifespan of 86 - 97 weeks for roots <1 mm in D in this study (study **III**). As a result, the total belowground litter C input most probably exceeds the aboveground litter C input in the majority of boreal forests.

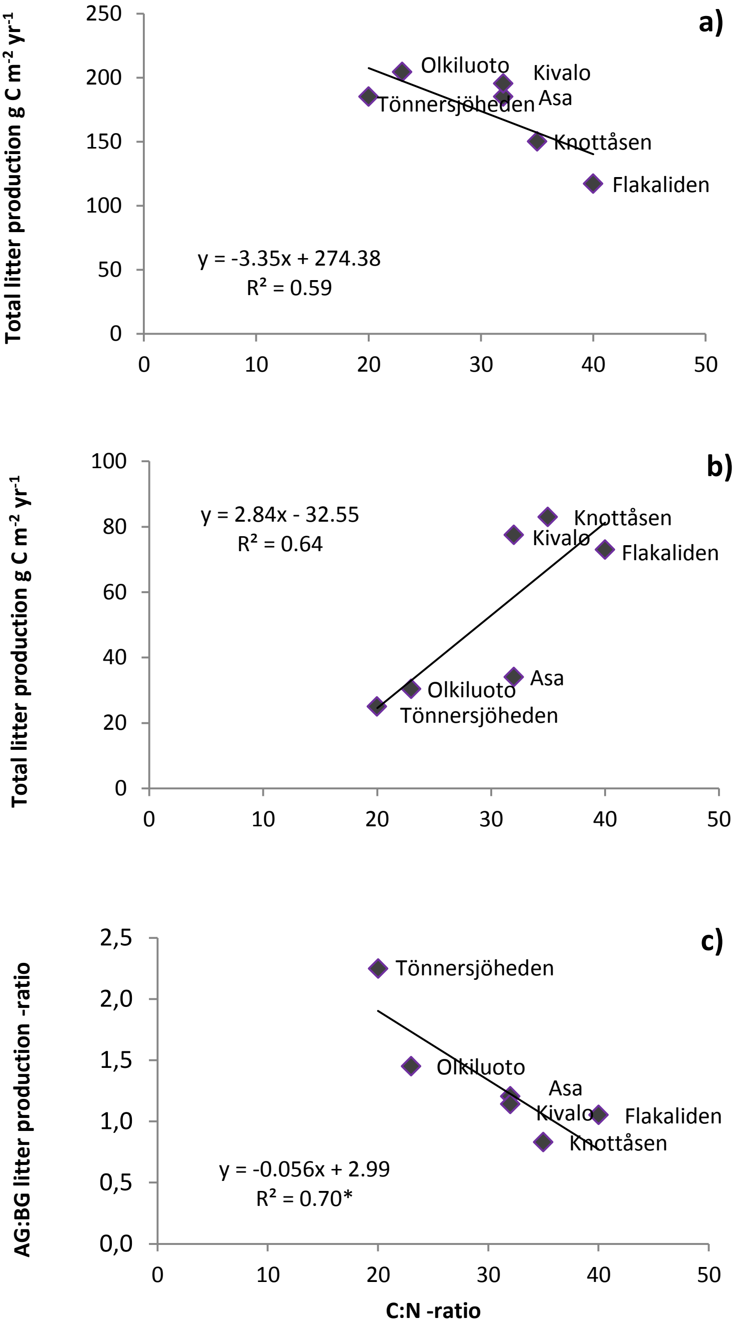

Figure 15 The total litter production of a) Norway spruce and b) understory, as well as c) tree aboveground (AG):belowground (BG) -ratio in relation to organic layer C:N -ratio. The original data from Flakaliden, Knottåsen and Asa was published in Kleja et al. (2008) and from Tönnersjöheden partly by Hansson et al. (2013a,b).

When reflecting all these results in relation to the on-going climate change, it must be kept in mind that increasing the soil temperature via cables buried into the soil is not necessarily a good proxy for the predicted mean annual air temperature (and CO_2) increase. The soil temperature increment of 5 degrees, even down to the 40 cm depth of mineral soil (study **I**), was an extremely strong manipulation. Sigurdsson et al. (2013) increased the air temperature by 3 °C for three years at Flakaliden and reported that tree growth was not affected unless extra nutrients were provided. Neither did elevated CO_2 cause increased tree growth. Air temperature, soil temperature and CO_2 elevation have been shown to increase root growth (Majdi & Öhrvik 2004, Zhao & Liu 2009, Lapenis et al. 2013, Pritchard et al. 2014) but in order to attain an increase in aboveground tree biomass, nutrient addition is required. Thus, the future climate with higher MAT (and soil temperature) and atmospheric CO_2 concentration may entail a greater litter C input into the soil compared to the current climate. However, the enhanced nutrient mineralization due to the higher soil temperature was not markedly increased, especially not from long-term manipulations. Thus great investments in forest fertilization would be needed to have substantial effects on aboveground forest growth in boreal forests with a few degrees higher MAT.

4.4 Carbon age of fine roots

In Finnish and Estonian sites, we investigated how the C age of fine root cellulose varies between stands, tree species, root D and soil depth by determining the natural abundance of ^{14}C in fine roots (study **IV**). In Sweden, at Flakaliden, we compared 1) the $\Delta^{14}C$ values of fine roots to the fine roots of known age, 2) the $\Delta^{14}C$ values of roots to the tree seedlings of know age, and 3) the ^{14}C values of fine roots sampled from the WI and I treatment plots of the long-term soil warming experiment to the fine root lifespans estimated with the MR method (study **V**).

In all the studied sites in Finland and in Estonia, the root mean ^{14}C values sampled from the soil cores exceeded the contemporary atmospheric mean of the sampling year – most in the less fertile Punkaharju and Mekrijärvi sites in Finland (by 60 - 170‰, i.e. 4 - 12 years) and less in the most fertile site at Voore (by 20 - 70‰, i.e. C age 3 - 8 years) (Table 5). If new fine roots are built mostly from recent photosynthetic products, this would imply that roots live longer in less fertile soil, which could in turn be related to the minimization of C costs (Eissenstat et al. 2000, Helmisaari et al. 2007) or nutrient losses through root mortality (Janssens et al. 2002).

Among conifer species growing at the same location (Punkaharju), spruce roots were expected to have younger root C than pine, because the organic layer in the spruce forests was more fertile than in the pine stands (Table 5). For the same reason, fine roots growing in the organic layer were expected to have younger C than roots growing in the mineral soil. Our limited data showed tendencies for pine to have older root C in the organic layer and spruce in the mineral layer. Likewise, the root C age tended to be less in organic soil than in mineral soil ($P = 0.103$, tested with pooled D and tree species data in Punkaharju) (Table 5). However, the same trend was found at Flakaliden (sampled with soil coring from I and WI plots): the ^{14}C age of the finest roots was higher in the mineral soil than in the organic soil (study **V**). The data in Voore and Mekrijärvi was incomplete for this comparison (Table 5).

The finest roots have higher N concentration (Pregitzer et al. 1995, Majdi & Andersson 2005) and turnover (Majdi & Andersson 20015) than thicker roots and were thus expected

Table 5 Mean $\Delta^{14}C$ and ^{14}C-derived age values (in parentheses max-min values) of soil core roots of all studied stands (study **IV**).

Stand	Species	Fertility	Sampling year	Soil depth	Root Ø (mm)	No. of sampl. (n)	Calc. root C age** (min-max) (yrs)
Voore	spruce	fertile	1996	mineral	< 0.5	3	3 (6 - 0)
					1.5 - 2	3	8 (11 - 4)
Punkaharju	spruce	fertile	1989	organic	< 0.5	3	6 (10 - 4)
					1.5 - 2	2	4 (5 - 3)
				mineral	< 0.5	2	11 (12 - 10)
					1.5 - 2	3	12 (14 - 11)
Punkaharju	pine	less fertile	1989	organic	< 0.5	3	7 (9 - 6)
					1.5 - 2	2	8 (9 - 6)
				mineral	< 0.5	2	8 (8 -7)
					1.5 - 2	3	10 (11 - 8)
Mekrijärvi	pine	less fertile	1986	mineral	< 0.5	2	5 (7 - 3)
					1.5 - 2	3	6 (11 - 2)

** Root C age calculated by finding the year at which the atmospheric $\Delta^{14}C$ value (Levin & Kromer 2004) corresponds to the root $\Delta^{14}C$ value (values rounded to nearest whole year).

to include younger C. At Flakaliden, root ^{14}C age increased by one or two years from this finest root cohort to slightly thicker (0.5 - 1 mm) roots and further by two years to the next cohort (1 - 2 mm in D), with significant differences ($P<0.05$) between the smallest and largest diameter group in the WI treatment when the data for both soil layers were combined (study **V**). At Finnish and Estonian sites, the 2 - 3 years difference in C age between the corresponding D classes was significant ($P<0.05$) only after pooling the data (Voore, Punkaharju and Mekrijärvi). The difference in the ^{14}C age of fine roots in these two D classes was more apparent in the fertile sites. An enhanced root turnover according to site fertility and/or decreasing root D is in agreement with several other studies which have used other methods than ^{14}C (Pregitzer et al. 1995, Hendricks et al. 1997, Johnson et al. 2000, Majdi & Öhrvik 2004, Chen & Brassard 2013).

There is a basis for assuming that the finest roots (<0.5 mm in D) are constructed from the most recent photosynthetic products (Gaudinski et al. 2001, Matamala et al. 2003, Trumbore et al. 2006)): fine roots less than 0.5 mm in D are mainly EcM root tips (Pregitzer et al. 2002, Ostonen et al. 2007b) and EcM root tips together with their mycorrhizal symbionts regenerate continuously and thus form a strong C sink (Bloomfield et al. 1996, Simard et al. 2003). However, our ingrowth core study at Flakaliden strongly contrasted with this assumption: At Flakaliden, living spruce fine roots (<0.3 mm in D) that had been growing into the ingrowth cores during summer 2009 and were thus at maximum three months old, had a mean ^{14}C value 94.7±36.5‰, which means 11±6 years older ^{14}C in cell wall cellulose than the ^{14}C concentration of the atmospheric ^{14}C of the study year 2009 (45±4, Levin & Kromer 2004) (study **V**). The number of replicates was only three bulk root samples from three ingrowth cores, but even one root has been used to gain the comparable result (Gaudinski et al. 2000). Furthermore, archive ingrowth core root samples from Finland have given an equal result (Sah et al. 2011): in the Punkaharju pine site the ^{14}C values of fine roots (1.5 - 2 mm in D) of the ingrowth cores exceeded the concurrent atmospheric level by 10 years, even though the maximum age of the root in the cores was two years. However, in some cases, the ^{14}C values of the ingrowth core roots were consistent with the atmospheric ^{14}C values of the sampling year (Sah et al. 2011).

In order to trace whether the old C in the newborn fine roots could be of soil origin, we sampled young seedlings from the Flakaliden, on the site that was harvested about ten years ago. If the young, naturally established saplings seeded from mature Scots pine trees left on the site or from surrounding Norway spruce forests would have had older C in their fine root cellulose than their actual age was, it would mean that the C must have been taken from soil (for example as amino acids, Nordin et al. 2001) . The results gave no support to this anticipation: the 8-years-old Norway spruce seedlings and the 4-years-old Scots pine seedlings had current or at maximum 1.3 year old ^{14}C in roots <0.5 mm in D and maximally two years old ^{14}C in the thicker roots (study **V**).

Finally, we analysed ^{14}C values of fine roots sampled from the WI and I treatment plots of the long-term soil warming experiment. As the fine root lifespan was significantly shorter in the WI than in the I (study **II**), in case of using the recent photosynthetic products for constructing fine roots, the ^{14}C age in the WI would be expected to be lower than in the I. There was a tendency for the WI to have younger ^{14}C in fine roots <0.5 mm in D in the organic layer than in the I (study **V**), but the difference was not significant (study **V**) and ^{14}C in the thicker roots did not differ between soil layers. The mean age of ^{14}C in fine roots 1 - 2 mm in D in both treatments was around 9 years (study **V**) which is in line with Solly et al. (2013) who reported rather similar ^{14}C ages (11 years) of roots less than 2 mm in D and recently, with Fröberg (2012) who reported that ^{14}C concentration in spruce fine roots from soil archives in Sweden fitted well with a one-pool steady-state model with a residence time of 8 years.

We compared the ^{14}C results to the median fine root lifespans from MR, which were one year and three months and two years in WI and I treatments, respectively (study **II**), 3 - 6 years younger than the ^{14}C age of the fine roots from soil cores. Similar and even greater differences in median lifespan from minirhizotrons and mean residence time using carbon isotopes have reported by several authors (Guo et al. 2008, Strand et al. 2008, Gaul et al. 2009). These differences between the two methods, MR lifespan and ^{14}C age, were statistically significant ($P = 0.013$, n = 4, study **V**). However, the trends in fine root survival analysis (MR) and fine root C age analysis (<0.5 mm in D) were parallel: fine root longevity (study **II**) was shorter and ^{14}C was younger in the warmed plots than in the reference plots (study **V**). Here, only fine roots <0.5 mm in D were compared as the thicker roots are practically absent around the MR tubes.

A main conclusion that can be drawn from the soil- and ingrowth core radiocarbon studies is that sometimes the ^{14}C values of the fine roots correspond well to the concurrent atmospheric level and sometimes not – for unknown reason. There are several possible interpretations to explain the high ^{14}C values in the roots, none of which is fully satisfying. Firstly, in the case of soil core roots, the roots may have lived significantly longer than the periods of a few years observed by MRs (studies **II** and **III**), or the scale of fine root lifespans is much wider than has been assumed. This explanation is, however, no valid in the ingrowth core studies, in which the maximum root age was known. Secondly, the root separation may have failed to separate the living fine roots from the dead ones. However, it is unconvincing that roots that have died ten years ago would look superficially young and fresh, especially when decomposition studies from boreal forests have showed that fine roots lost about half of their mass only in a few years (Lõhmus & Ivask 1995, McEnroe & Helmisaari 2001, Majdi 2007, Palviainen et al. 2008) and seven-year-old fine roots from a litterbag study were strongly decomposed (Hansson et al. 2010). Thirdly, in a plant there may be two or more C pools with different mean residence times (Luo 2003, Riley et al. 2009, Gaudinski et al. 2010, Keel et al. 2012). How and why the proportions of these pools vary in building new roots is not known, but Adams & Eissenstat (2014) recently demonstrated that the incorporation of current photosynthate into the structural carbon of roots continued after the roots were formed, showing that the root structural C pool is not derived solely from the photosynthate available at root initiation. A few studies have shown that after a severe disturbance plants may allocate long-lived storage C to produce new fine roots (Langley et al. 2002, Vargas et al. 2009), but never, even in the case of storage C, has the age of C been as much as a decade (Gaudinski et al. 2009). The organs that trees can utilize as primary C reservoirs include boles (Sakai & Sakai 1998), burls (James 1984), rhizomes (Lacey 1974), lignotubers (Mesleard & Lepart 1989), thick roots (Rodgers et al. 1995) or intermediate roots (Woods et al. 1959), but the remobilization of C in these storage organs as well as in other organs is not clear – it may be as dynamic as other plant resources such as N and P in stressed individuals (Langley et al. 2002). Taking into account aboveground disturbance such as fire, extreme weather or massive herbivore attack, the belowground C storages are more plausible than the aboveground storages.

One more dimension regarding C storage is that in deciduous species the use of storage C is a common practice to fuel winter- and spring root growth and bud break in the spring (McLaughling et al. 1980, Trumbore et al. 2002), but in conifers the capability to photosynthesize persists throughout the year if light and temperature do not restrict and thus there is less need for great storage. Nevertheless, the highest ^{14}C values were measured in maximally three months or two years old fine roots in Norway spruce (studies **IV** and **V**). The fourth interpretation is that trees growing in less fertile sites might deposit older C to their roots via organic N uptake (amino acids), which has been shown to contribute, at least to some extent, to plant N nutrition especially in the less fertile, northern sites (Nordin et al. 2001, Persson & Näsholm 2001, Kielland et al. 2007, Näsholm et al. 2009, Whiteside et al. 2012) – although our Norway spruce and Scots pine seedling studies did not support this (study **V**). We conclude that more research should be oriented towards improving our understanding of possible internal redistribution and uptake of C in trees.

5 CONCLUSIONS

In C cycle models the longevity of fine roots together with their mycorrhiza has for long been one of the factors causing greatest uncertainty. The fine roots contribute significantly to net primary production and their incorrect quantification may thus cause a great error. In this thesis the longevities of Norway spruce and understory fine roots were estimated with the MR method and the C input into the soil via below- and aboveground litter production was determined in three boreal Norway spruce stands – and for the regressions the data was augmented with four additional sites in Sweden. Long-term effects of temperature, nutrient availability and growing season length on fine root dynamics and litter production were investigated. Aboveground foliage and understory litter C input were also quantified and compared with the belowground. Furthermore, a contribution was made to the on-going discussion concerning determination of the age of C in fine roots by using the radiocarbon method, and the way in which the C age differed from the root age was analysed with the MR method.

Fine roots, and specifically EcM fine root tips (1st and 2nd order short roots), were shown to be highly adaptable to changes in environmental conditions. Both higher soil temperature and increased nutrient availability enhanced fine root turnover significantly and altered the EcM short root morphology compared to the non-warmed and/or unfertilized treatments. The shortest fine root lifespan was in the warming-fertilization combination treatment. Morphological changes in EcM short root and high fine root biomass per ba in the warming treatment showed that trees had increased the absorptive surface of EcM short roots, i.e. improved their ability to forage nutrients, whereas short root morphology in the fertilized plots gave no such indications. In the warming treatment the enhanced turnover of fine roots together with the increased fine root biomass deeper in the mineral soil led to threefold higher belowground fine root litter production compared to the reference treatment where the foliage litterfall and ba were the same. In fact, fertilization was the only treatment which increased the aboveground tree growth and litter production. Therefore, the observed increment in tree growth in the soil-warming plots at the same site a few years after the soil-warming initiation (Jarvis & Linder 2000) has been only a short-term response, ending after a few years. Our results indicate that without nutrient addition the increasing MAT alone will not be sufficient to increase forest growth, but could increase the fine root litter C input into the soil. Sigurdsson et al. (2013) reached the same conclusion regarding the aboveground forest growth at the same site after increasing air temperature and CO_2 concentration. Only the trees in the fertilized plots were mature with great foliage, ba and a high amount of fine root biomass. Thus, both the below- and aboveground litter production were greater in the fertilized treatments than in the unfertilized ones.

At natural Norway spruce stands in Finland fine root longevity was longer in the northern site than in the southern site, whereas there was no difference in the longevity of understory fine roots between these sites. When comparing the above- and belowground litter production at these sites, the proportion of aboveground litter increased more in the more fertile southern site – and the proportion of litter C input produced by understory diminished. 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. Overall, longer lifespan of fine roots, thinner roots, more fine root biomass per ba, and number of EcM root tips in the north compared to the south, all point to great adaptation of spruce to climatically harsh Nordic conditions to improve acquisition of nutrients.

The results demonstrate that Norway spruce fine root litter C input into the soil at least equals the aboveground input, which endorses the notable role of belowground litter production in the boreal forest C cycle. The shift in the litter production pattern from above- to belowground together with the higher contribution of understory vegetation in the less fertile sites may also have an impact on litter C quality and soil C storage and should be taken into account in C models.

The analysis of ^{14}C concentration in fine roots showed great variability in root C age regardless of the root age, and the root C age was in some cases several years older than the known root age. The 'old' C in the roots may have been storage C or have originated from the soil. In order to investigate this, we determined the root C age in fine roots of a few years old pine and spruce seedlings. At least the seedlings do not appear to take up substantial amounts of C from the soil by fine roots and mycorrhiza, as the C age in the fine roots was in all cases less than 2 years old (study **V**). However, treatment effects of fine root C age in the soil warming experiment were qualitatively pointing to the same direction as the MR results, fine roots having younger C and shorter longevity in the warming treatment compared to the reference. The fine root lifespan was around one and two years, and fine root C age 4.5 years and 6.5 years, in the warming and reference treatments, respectively. In future, focus should be targeted on determining the ecological conditions in which root growth uses stored or recycled C, as this may have a significant effect on terrestrial C budgets.

As demonstrated in this thesis, the below- and aboveground components of litter production are strongly connected and should always be studied in conjunction with each other. As rather small changes in the environmental conditions led to a substantial change in fine root dynamics and even in the relations of below- and aboveground litter production, more emphasis should be put on studying the belowground processes for obtaining holistic understanding of the role of roots in C budgets in boreal forests.

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