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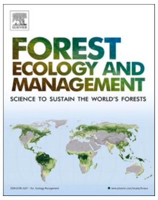

Distinct patterns of below- and aboveground growth phenology and litter carbon inputs along a boreal site type gradient

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ABSTRACT

Forest ecosystem productivity is strongly linked to site nutrient availability, which is influenced by litter inputs and their decomposition rates. Fine roots and mycelia are key contributors in belowground soil carbon (C) accumulation, but studies have seldom reported how belowground litter C input is related to site types in boreal forests. In this study, three mature and one young *Pinus sylvestris* forests along a site type gradient in southern Finland were chosen for measurements of fine root biomass, fine root longevity, below- and aboveground growth phenology and annual litter input from tree and understorey vegetation. Site types were distinguished by understorey vegetation composition, which indicated the site fertility. Fine root biomass per tree stand basal area decreased significantly from nutrient-poor to nutrient-rich sites, the nutrient-poor sites with longer fine root longevity resulted in an equal belowground litter input with the nutrient-rich site. Above- and belowground annual litter inputs were 131–236 and 70–91 g m^{-2} $year^{-1}$, respectively. Aboveground litter increased with site fertility, resulting into belowground litter having a decreasing trend from 37% to 23% of total litter inputs with increasing site fertility. Ectomycorrhizal mycelia and understory production contributed 8–13% and 18–41% of belowground production, respectively. Contribution of understorey vegetation to the belowground litter C input was lower than that of trees at xeric and sub-xeric sites but equaled to that of trees at the mesic site. Our study showed distinct dimensions of below- and aboveground litter inputs influenced by site types. Moreover, we emphasize that the belowground C inputs from ectomycorrhizal mycelia and the understorey in addition to those of trees should always be considered in C balances and C reporting in boreal conifers.

1. Introduction

Globally, terrestrial living vegetation and soil carbon (C) stock is approximately three times greater than atmospheric C stock (Falkowski et al., 2000). Soil C accumulation is affected by C input from aboveground (AG) and belowground (BG) litter, root exudates, and by C output via heterotrophic respiration and leaching of dissolved organic carbon. Knowledge of the linkages and relative contributions of BG and AG plant C inputs to stable soil C stock has been insufficient but in great demand for decades (Wardle et al., 2004). Fine root turnover and production account for 22–33% of net primary production (NPP) of global forests (Jackson et al., 1997; McCormack et al., 2015). Fine root turnover is the major contributor to BG litter (Lukac, 2012), along with other litter inputs of mycelia, root exudates, microbes, and soil fauna. In European boreal forests, the forest site type is classified by understorey vegetation composition which indicates the site fertility (Cajander, 1949; Lahti and Väisänen, 1987; Pohjanmies et al., 2020). The forest productivity differs among site types, and therefore site types are widely

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used in classifying boreal forests. Important relations of plants and soil should also be studied using site type classification as framework (Högberg et al. 2017). In previous studies, BG C input of boreal forests accounted for 31–66% of total soil C input (Ding et al., 2019; Hansson et al., 2013a, 2013b; Kleja et al., 2008; Leppälammi-Kujansuu et al., 2014a), but neither site type effect nor root associated mycelia C input were examined in previous studies.

In the N-limited condition of boreal forests, ectomycorrhizal (EcM) fungi and soil microorganisms can be considered competitors for this limiting resource, which constrains tree growth and thus forest productivity (Högberg et al., 2017). In return, more C is allocated to roots, and fine roots produce more biomass in infertile sites compared to relatively fertile sites (Helmisaari et al., 2007; Kalliokoski et al., 2010; Leppälammi-Kujansuu et al., 2014a; Ostonen et al., 2011; Vanninen and Mäkelä, 1999). Forests in harsh conditions, such as at high latitudes or in nutrient-limited sites, typically contain thin-root-diameter species that may have faster turnover rates to acquire maximum of nutrients and respond rapidly to unfavorable conditions (Eissenstat et al., 2015; Ma et al., 2018). These fine roots can be differentiated according to morphological and functional differences: absorptive roots have primary development with the function of nutrient and water absorption; whereas transport roots have secondary development with the function of transporting and partly storing nutrients (McCormack et al., 2015). Besides these differences, the transport roots are more tolerant to severe conditions such as low temperatures or summer droughts, therefore they survive for a longer time compare to absorptive roots (Ding et al., 2020). Moreover, growth phenology of fine roots is not synchronized with that of shoots at high latitudes (Abramoff and Finzi, 2015; Ding et al., 2020), with a ca. 50% longer growing period for roots (Blume-Werry et al., 2016).

Besides roots, soil fungi play pivotal roles in the decomposition of organic litter, in acquiring various mineral ions and in regulating forest C and N cycling in boreal and temperate forests (Clemmensen et al., 2013; Godbold et al., 2006; Read and Perez-Moreno, 2003). EcM mycelia biomass has been reported to peak at the same time (autumn) and in the same quantities (125–200 kg ha^{-1}) as fine root biomass (FRB) in south-west Sweden (Wallander et al., 2001). Only a few studies (e.g. Nilsson et al., 2005; Kalliokoski et al., 2010; Sterkenburg et al., 2015) have reported the EcM mycelia production of natural site types. The significance of C stored in EcM fungi stresses the importance of evaluating root and fungi interactions in the C cycling of different forest site types and under different environmental conditions (Wallander et al., 2013).

For decades, studies on litter input to soil have focused mostly on annual litter inputs of AG (including foliage, twigs, cones and understorey) but less on BG (including fine roots, mycorrhizal mycelia and root exudates). BG litter input forms more effective and stable soil organic carbon than AG litter due to the more rapid formation of rhizosphere microbial community than in bulk soil (Sokol and Bradford, 2019). Furthermore, a study carried out along a fertility gradient in the boreal zone reported that BG root-derived C inputs were more important than AG litter C inputs in controlling organic matter accumulation in the soil (Kyaschenko et al., 2019). Linking whole-tree AG and BG C allocation and fluxes could comprehensively increase our understanding of forest C cycling and sequestration. However, few empirical studies specifically link the annual inputs of boreal AG and BG litter, and most of the studies were conducted in Finland and Sweden (Ding et al., 2019; Hansson et al., 2013a; Ilvesniemi et al., 2009; Kleja et al., 2008; Leppälammi-Kujansuu et al., 2014a). Leppälammi-Kujansuu et al., (2014a) concluded that, in Norway spruce sites, the AG/BG annual litter production ratio was negatively related with the C:N ratio and concluded that nutrient-poor forests have a higher share of BG than AG in litter inputs. The main components of BG and AG litter are fine roots and foliage, but their decomposition rates vary, and they release stable C to the soil after different time lags. A modelling study in Fennoscandian conditions showed that forest productivity decreases from south to north due to decreasing temperatures and the increasing relative C allocation from foliage to fine roots (Mäkelä et al., 2016).

In this study, our primary aim was to determine the FRB, fine root longevity (FRL), root morphology traits, above- and belowground growth phenology and mycelia production on different site types dominated by the same tree species, Scots pine (*Pinus sylvestris* L.). Secondarily, we aimed to compare the values between BG and AG litter inputs and to evaluate the importance of understorey vegetation and EcM mycelia for these inputs. Thus, we hypothesized that (1) fine root morphology, (2) fine root longevity, and (3) fine root and mycelia production varies between different site types. In addition, we hypothesized that (4) the proportion of BG litter of total litter (AG + BG) varies between site types (indicated by understory species richness). As additional indicators of site type, we used a common site index, soil pH as well as organic layer thickness, to test our hypotheses.

2. Materials and methods

2.1. Site description

The study sites were selected according to a site-type classification system developed in Finland (Cajander, 1949; Pohjanmies et al., 2020), which uses understorey vegetation (called later as understorey) as an indicator of edaphic and climatic conditions. The three mature sites were named after their site type, CT- Calluna type (xeric heath forest), VT- Vaccinium vitis-idaea type (sub-xeric heath forest), and MT- Vaccinium myrtillus type (mesic heath forest). A fourth site represented a young stand named CTY, adjacent to the mature CT forests on the same site type. If not specifically explained, CTY and CT share the same site background information. Each site had three plots (30 m × 30 m), on which forest floor and soil characteristics were investigated in May 2016 (Table 1, Table 2). VT site was a part of the UN-ECE ICP Forests Level II monitoring network (International Cooperative Programme on the Assessment and Monitoring of Air Pollution Effects on Forests) (Merilä et al., 2014) and the MT site was the intensive ecosystem study site of SMEARII (Hari and Kulmala, 2005). All sites were situated within a circle of radius 4 km. The soil temperature and moisture (Fig. S1) were recorded at MT using a Philips KTY81-110 temperature sensor and Campbell TDR100 Time-Domain Reflectometer, respectively, using a data logger placed 2–5 cm below the organic layer's surface. The data were downloaded from the AVAA database (https://smear.avaa.csc.fi/). During the study years 2014–2017, monthly mean soil temperature was usually highest in August without notable year-to-year differences (Fig S1). Soil temperature at CT and VT (Fig. S2) between Oct 2017 and Sep 2018 were measured by thermometers (iButton DS1921G-F5, Maxim/Dallas, USA) placed at 5 cm (CT) or 3.5 cm (VT) from the organic layer's

Table 1
Soil characteristics.

Site	CTY	CT	VT	MT
Soil type	Ferric podzol	Ferric podzol	Ferric podzol	Haplic podzol
Organic layer				
Thickness (cm)	2.8	4.0	4.2	4.5
pH	3.4	3.8	3.4	3.5
N%	1.2	0.8	1.1	0.9
C:N	33.1	32.8	30.8	33.0
Mineral soil				
pH	5.0	4.6	4.4	4.5
N%	0.17	0.15	0.19	0.22
C:N	14.8	12.9	15.1	13.6
Mineral soil texture				
Stoniness (%)	21.1	21.1	13.1	46.5
Sand (%)	93.9	92.3	89.4	82.7
Silt and clay (%)	6.1	7.4	10.6	17.3

Note: The soil type classification is according to World Reference Base (WRB) for Soil Resources.

Table 2
Stand characteristics. The southern forest site types based on understorey vegetation (Cajander, 1949; Pohjanmies et al., 2020) and habitat types indicating soil fertility and soil moisture conditions. Tree characteristics apply to the main tree species i.e. Scots pine.

Site	CTY	CT	VT	MT
Location	61° 50′N, 24° 17′E	61° 50′N, 24° 17′E	61° 52′N, 24° 13′E	61° 51′N, 24° 17′E
Forest type	Calluna	Calluna	Vitis-idaea	Myrtillus
Habitat type	Xeric	Xeric	Sub-xeric	Mesic
Stem basal area (m^2 ha^{-1})	11.4	16.4	25.1	18.3
Stand age (yr)	21	73	96	54
Mean DBH[1] (cm)	2.8	26.2	27.1	17.8
Mean height (m)	3.3	20.1	23.6	17.1
Stem density (no. ha^{-1})	18,433	407	422	684

[1] Abbreviated for diameter at breast height.

surface.

The stand information is described in Table 2. Nine subsamples of the organic layer and nine subsamples from the upper mineral soil were taken systematically from each of the three plots per site with a steel cylinder (D = 58 mm). The dwarf shrub species consisted of *Vaccinium vitis-idaea*, *Vaccinium myrtillus*, *Calluna vulgaris*, and *Empetrum* spp. whereas mosses consisted of *Pleurozium schreberi*, *Dicranum* spp., *Brachythecium* spp., *Sphagnum* spp., *Polytrichum commune* and *Ptilium crista-castrensis*. Lichens *(Cladonia* spp.) occurred only at CT, CTY, and sparsely in VT. Compared to the poorer sites (CT/CTY), VT and MT were more abundant in mosses, herbs and grass species.

The soils of all sites were acid and podzolic with a thin mor organic layer, relatively high C:N ratios and coarse-textured mineral soil (Table 1). The fine fraction (silt + clay) content of the mineral soil gradually increased from poor towards more fertile sites on the site type gradient (Table 1). This indicates the increasing nutrient-holding and water-holding capacities of mineral soil (Heiskanen et al., 2018).

2.2. *Aboveground litter production*

Aboveground litter production consists of tree litter (needles, branches, cones, bark, other) and understorey plant litter (dead parts of lichens, mosses, dwarf shrubs, herbs, other). The AG litter of trees and understorey from CTY was not collected due to the high density and low height of the Scots pine seedlings.

2.2.1. *Tree litter production*

Funnel-shaped traps (trap area of 0.5 m^2) were used in collecting tree litterfall at VT and MT. At VT, tree litter was collected by 12 traps located systematically and collected every two weeks during the snow-free season (May 2013 to November 2016) and once before spring. The traps were placed 1.5 m above the forest ground. At MT, 20 traps were randomly distributed at the height of 0.6 m above ground. There, the litterfall samples were collected every month from 1997 to 2008 and originally published by Ilvesniemi et al., (2009). The tree litterfall (needle and total) data in CT was predicted using liner models (No.1 LF_{needle} and No. 5 LF_{total}) based on the annual litterfall production and long-term climate data of 34 Scots pine stands located throughout Finland (Starr et al., 2005).

2.2.2. *Understorey litter production*

The annual aboveground litter production of understorey vegetation was estimated by sorting the annual growth of different plant groups at CT site and by literature estimates (Lehtonen et al., 2016) on the ratio between the annual growth and the total biomass of VT and MT sites.

Vegetation samples of aboveground biomass were collected using a frame (square 30 cm × 30 cm) systematically placed along two transects on each plot. The aboveground plant biomass was harvested from the squares, excluding tree seedlings. We used earlier data on 28 understorey samples at VT (July 2002) and collected 36 new samples at MT (July 2015) and nine new samples at CT (August 2018). The biomass samples were sorted by species. The whole aboveground biomass of annual species represents their annual growth. Current-year growth for perennial understorey species was sorted from the samples at CT. The samples were oven dried at 60 °C for over 48 h and weighed.

At VT and MT, the annual litterfall of dwarf shrubs, grasses, mosses and herbs was estimated using the shares of 37%, 33%, 42% and 100% of the total biomass, respectively, according to the turnover rates reported by Lehtonen et al., (2016). At CT, we used the estimate of 30% for the annual litterfall of dwarf shrubs (Merilä et al., 2014) and 20% for reindeer lichens (*Cladina* spp.) according to their growth rate (Helle et al., 1983) and the length of annual growths measured from our own lichen samples. The annual litterfall for mosses was estimated according to average annual growth from our own biomass samples. Annual growths were sorted from the upper part of the gametophytes with the aid of species-specific morphological characteristics.

2.3. *Fine root morphology*

First-, second- and fourth- order root segments were selected from each study site. In September 2015, three soil-core samples (0–10 cm) were taken from each plot using an auger (50 cm in height, 5 cm in diameter, the same auger in the later sampling procedures). Several root branches with 18–30 absorptive roots were washed and sorted from each sample. The fresh root segments were scanned using WinRHIZO^{TM} Pro 2003b (Regent Instruments Inc., Quebec, Canada) to measure root diameter, length and project area. Due to the low mass of each root segment, a combination of three root samples was dried in petri dishes at 65 °C for 48 h and weighed. Root traits such as specific surface area (SSA), specific root length (SRL) and root tissue density (RTD) were calculated according to Ostonen et al. (1999, 2007a).

2.4. *Above- and belowground growth phenology*

The aboveground growth (stems, shoots and needles) phenology was predicted by a dynamic growth model called 'carbon allocation sink source interaction' (CASSIA), which estimated the growth and seasonal dynamics of the different organs using measured factors such as photosynthesis and environmental factors *in situ* (Schiestl-Aalto et al., 2015). The BG root growth phenology was estimated from mini-rhizotron (MR) image analysis. The production percentage was calculated using the accumulated growth of the previous interval period divided by the sum of whole year's growth within each site. For BG production percentage, the first value of each year represents the period from the previous year's late autumn to the current year's early spring as there were no root measurements during that period. In order to parallel the AG growth of pine trees, the understorey root growth was not included.

2.5. *Fine root mass*

Nine soil samples per site were taken in July 2013 at CTY, CT and VT. Fifteen soil samples were taken from MT in June 2011 using an auger, and thereafter the MR tubes were installed into these holes. For each soil sample, the organic layer was separated and the mineral soil was divided into layers of 0–10, 10–20 and 20–30 cm. All the samples were stored at −18 °C before laboratory analysis. Roots were wet sieved and carefully washed free of soil. According to the color, elasticity and morphology of the roots (Persson, 1983), they were divided by species (pine, understorey plants) and by living status with the help of a dissecting microscope. More specific sorting criteria can be found in Persson (1983), Makkonen & Helmisaari (1998) and Persson & Stadenberg (2010). Pine roots were grouped into diameter classes of: <1mm, 1–2 mm, >2 mm. All understorey roots were selected under 1 mm in diameter. The sorted root samples were oven dried at 65 °C for over 48 h and weighed. The

FRB in mineral soil was corrected using the corresponding stoniness index of each mineral soil layer (Viro, 1952; Tamminen, 1991).

2.6. Ectomycorrhizal mycelia production

EcM mycelia production was determined by 'mycelial in-growth bags', the fine mesh allowing fungal ingrowth while tree roots are prevented from penetrating into the bags (Wallander et al., 2001, Wallander et al., 2013). The EcM mycelia biomass was quantified from ergosterol levels in quartz sand filled in triangle-shaped ingrowth mesh bags (8 × 8 × 11 cm, 90 μm mesh size). Each mesh bag was filled with 10 ml (ca. 16.7 g) of acid washed quartz sand (grain size 0.2 mm). In May 2014, five ingrowth mesh bags were buried at the interface between the organic horizon and the mineral soil of each site. In September 2014, three bags (referred to 'summer bags') were collected and replaced with new bags. In May 2015 all the bags (3 'winter bags' and 2 'whole-year bags') were collected and the experiment was repeated as in the previous year. The mesh bags were stored in a freezer at −20 °C until further analysis.

On opening the bags, the sand from the mesh bags was pooled for each plot and period. The fungal content in the sand (5 g, wet weight; later corrected for the water content) was further estimated by analyzing the content of the fungal biomarker ergosterol (erg) according to Bååth, (2001), and by using the conversion factor of 3 μg ergosterol mg^{-1} fungal biomass (Wallander et al., 2001). Two to four replicates were analyzed from each sample. One outlier out of 85 samples analyzed was removed, due to exceptionally high values.

The field incubation time exceeding one growing season leads to over-estimate of mycelia production (Wallander et al., 2013). Therefore, we compared the summer bags (4 months' incubation time) plus winter bags (8 months' incubation time) to one-year bags (12 months' incubation time) to minimize the error.

The EcM mycelia production ($G_{em,}$ kg ha^{-1}) was calculated using the EcM mycelia biomass ($c_{em,}$ μg g^{-1}) analysed from the bags, as follows:

$G_{em} = c_{em}\ \rho soil\ d\ f,$

where ρsoil is the quartz soil density (1.67 g/cm^3) in the bag (volume of 10 cm^3), d is the soil depth where mean of the EcM mycelia biomassis located (10 cm) and f is a factor (0.1) for unit transformation, as 1 kg $ha^{-1} = 0.1 \times \mu g\ cm^{-3}$.

2.7. Fine root turnover and belowground litter input

Fine root growth and longevity were monitored using the MR method. In June 2011, we installed five MR-transparent acrylic tubes (internal D of 5 cm, external D of 6 cm, length of 45 cm) vertically in each of the three subplots of MT, and in July 2013, we installed three similar tubes vertically in each subplot of CT, CTY and VT. Images were taken by an MR camera (BTC-2; Bartz Technology, Santa Barbara, USA) immediately after tube installation. The MR images were taken 22 times altogether during the four growing seasons (2013–2017) for CT, CTY, VT and 17 times during three growing seasons (2013–2016) for MT (Table S1). The VT site was harvested by clear-cutting in May 2017, therefore the data after clear-cutting was excluded. We captured continuous images (size 1.1 × 2 cm, Fig S3) from one side of the tube. In total, 4180, 5456, 4131, and 4284 images were analyzed for CTY, CT, VT and MT, respectively. WinRHIZO TRON 2015a software (Regent Instruments Inc., Quebec, Canada) was used to trace the root longevity, root diameter, root length and root surface area. We marked the first-order roots which sometimes later became second-order roots as 'absorptive roots' to distinguish them from 'transport' roots using morphological differences (Fig. S3). Absorptive root tips are also called EcM short roots (Helmisaari et al., 2009; Ostonen et al., 2011), with a typical dichotomous root branching system, whereas the transport fine roots have wider stele, and grow faster and deeper than absorptive roots. Roots present in the first session were excluded since the true birth times of these roots were uncertain. The roots still alive in the last observation session were treated as 'right-censored' in survival analyses. Median fine root longevity was estimated by two methods: primarily the non-parametric Kaplan-Meier (Kaplan and Meier, 1958) method using the 'survfit' and 'survreg' functions in "survival" package of R software (Therneau, 2016), and secondarily the regression model using Weibull error distribution (Weibull, 1951). If <50% of roots had died at the end of observation (survival probability >50%), median longevity could not be estimated using Kaplan-Meier functions, and thus Weibull regression was fitted to the data estimation. To compare the FRL differences between sites, the "survminer" package was used (Kassambara et al., 2017).

Fine root litter production (g m^{-2} $year^{-1}$) was calculated by FRB (pine, understorey) divided by Weibull regression estimated median fine root longevity (year) on each site and for each species. The AG and BG annual litter C input was assumed to be 50% of the annual AG and BG litter dry mass. The annual C input of EcM mycelia was assumed to be 45% of dry mass of ergosterol production (Taylor et al., 2003).

2.8. Statistical analysis

Statistical analyses were performed with R software (R Core Team; R version 3.5.3; RStudio version 1.1.463). Results were compared using one-way ANOVA if the data was normally distributed. If the data did not meet the criteria, a Kruskal-Wallis test was performed. Paired *t*-test was used to compare two groups, such as consecutive years or seasons in fungal biomass. We detected the relationships between fine root longevity, EcM mycelia production, litter production and the various soil and stand variables with the linear regression model. For all statistical tests, a significance level of 0.05 was used.

3. Results

3.1. Fine root morphology

Morphological and chemical traits significantly ($P < 0.05$) varied between absorptive (first- and second-order) and transport (fourth-order) roots; only root C% was similar between root types (Table S2). Moreover, the MR root morphology data showed that the CTY site had significantly ($P < 0.05$) thinner and shorter pine absorptive roots and its understorey roots had less surface area compared to the mature sites (Table S3). In the mature sites, the understorey root diameter in MT was significantly ($P < 0.05$) thicker than that of CT and VT (Table S3)

3.2. Above- and belowground growth phenology

The growth phenology was decoupled between BG and AG growth of Scots pine at MT. The peak of total aboveground growth at the MT site was in June-July but root growth peaked either at the same time (2015, Fig. 1A) or later than the AG growth (in September 2014, 2016, Fig. 1A). The root growth period lasted longer than that of AG growth (Fig. 1). The root phenology was roughly following the same trend of variations between sites during the same year, but the peak time was earlier in 2015 than in the other years (Fig. 1).

3.3. Fine root mass

Pine and understorey FRB gradually decreased from organic layers to deep mineral soil layers at all sites except in CTY, with its extremely thin organic layer (Fig. 2). Ratios of understorey FRB to total pine and understorey FRB were between 28 and 65%. With pine, the proportion of dead fine roots of total (living + dead) mass varied between 52 and 62%, which was higher than with understorey (34–51%). VT had the highest proportion of dead roots for both pine and understorey.

Along with increasing fertility, FRB (<1 mm) per stand basal (ba) area decreased from the least fertile site CT, to the most fertile site MT (Fig. 3). Trees at CTY were clearly younger than at the other sites

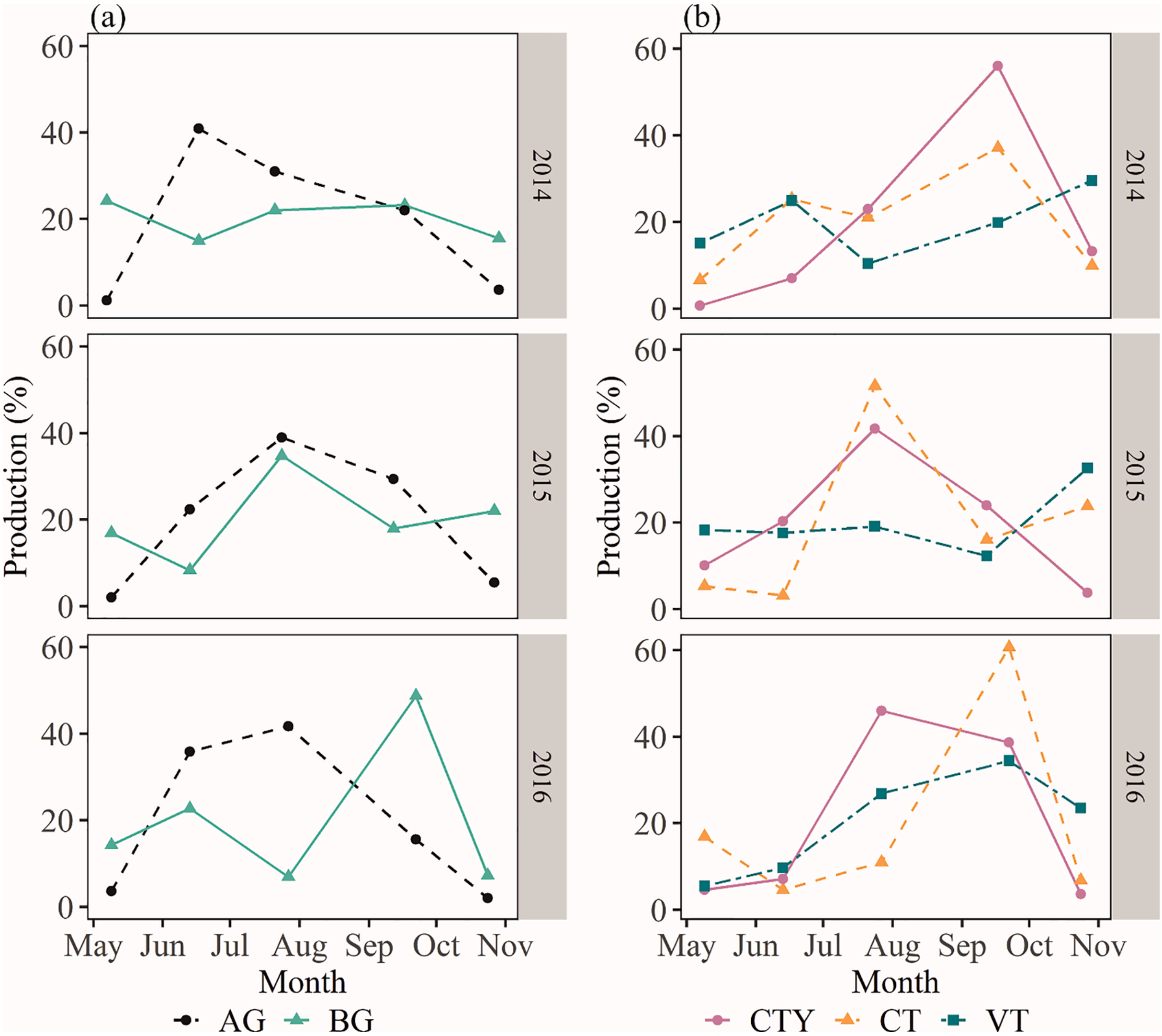

Fig. 1. The Scots pine growth phenology of (a) above- and belowground production percentage of MT site (b) belowground production percentage of CTY, CT and VT sites. The whole-year accumulation is 1 for belowground, but <1 of aboveground since the minor growth during winter was excluded.

(Table 2), but the CTY FRB/ba of pine was higher than that of VT and MT. Per basal area, there were no significant differences ($P > 0.05$) in the biomass of transport roots (diameter 1–2 mm) along the site type gradient (Fig. 3).

3.4. *Ectomycorrhizal mycelia production*

The range of EcM mycelia growth at all sites was 0.14–0.50 μg erg. g^{-1} (dry weight) DW of sand during the summer months (May-September) and 0.06–0.13 μg erg. g^{-1} DW of sand during the autumn and winter months (September-May) (Fig. S4). Neither the two summers nor the two winters differed, but the summer and winter ergosterol content displayed significant statistical contrasts ($t = 6.65$, $df = 11$, $P < 0.001$, Fig. S4a).

The annual EcM mycelia production was estimated in two ways, by summing up the summer and the winter production, and directly from the whole-year-bags. These two methods of calculation did not differ statistically (Fig S4b). The mean value of the whole-year bags was slightly higher than that of summed values (0.35 vs. 0.31 μg erg. g^{-1} DW of sand), but as the summer and the winter bags were able to trace the seasonal variation better with less variation, we choose to use the summed values when reporting the annual EcM mycelia production.

The summer, winter and the summed EcM mycelia production increased with site fertility (Fig. 4). However, EcM mycelia production did not differ statistically along the site type gradient at any time (Fig. 4). Summer production ranged between 8.7 and 16.8 g m^{-2}, whereas winter production was 4.2–5.5 g m^{-2}. The summed annual EcM mycelia production for CTY, CT, VT and MT were 11.8, 17, 19.7, and 20.5 g m^{-2}, respectively. The summed annual EcM mycelia production (same as summer + winter production) correlated significantly with the thickness of the organic layer ($R^2 = 0.95$–0.97, $P < 0.05$, Fig. S5). The annual soil C input from EcM mycelia, as 45% of summed annual EcM fungal production, was 5.3, 7.7, 8.9 and 9.2 g C m^{-2} for CTY, CT, VT and MT, respectively.

3.5. *Fine root longevity and litter C input*

When we pooled the root longevity data of all sites together, there were significant differences ($P < 0.01$) between pine and understorey species; pine root tips and long roots, and roots in organic layer and mineral soil (Fig. S6). FRL of the understorey was 3.5 times longer than that of pine, FRL of pine long roots was over two times longer than that of root tips, FRL of pine roots in the organic layer was 1.4 times longer than in the mineral soil (Fig. S6a–c). Conversely, FRL of understorey was longer in mineral soil than in organic layer (Fig. S6d).

The Kaplan-Meier survival function estimated FRL with a difference

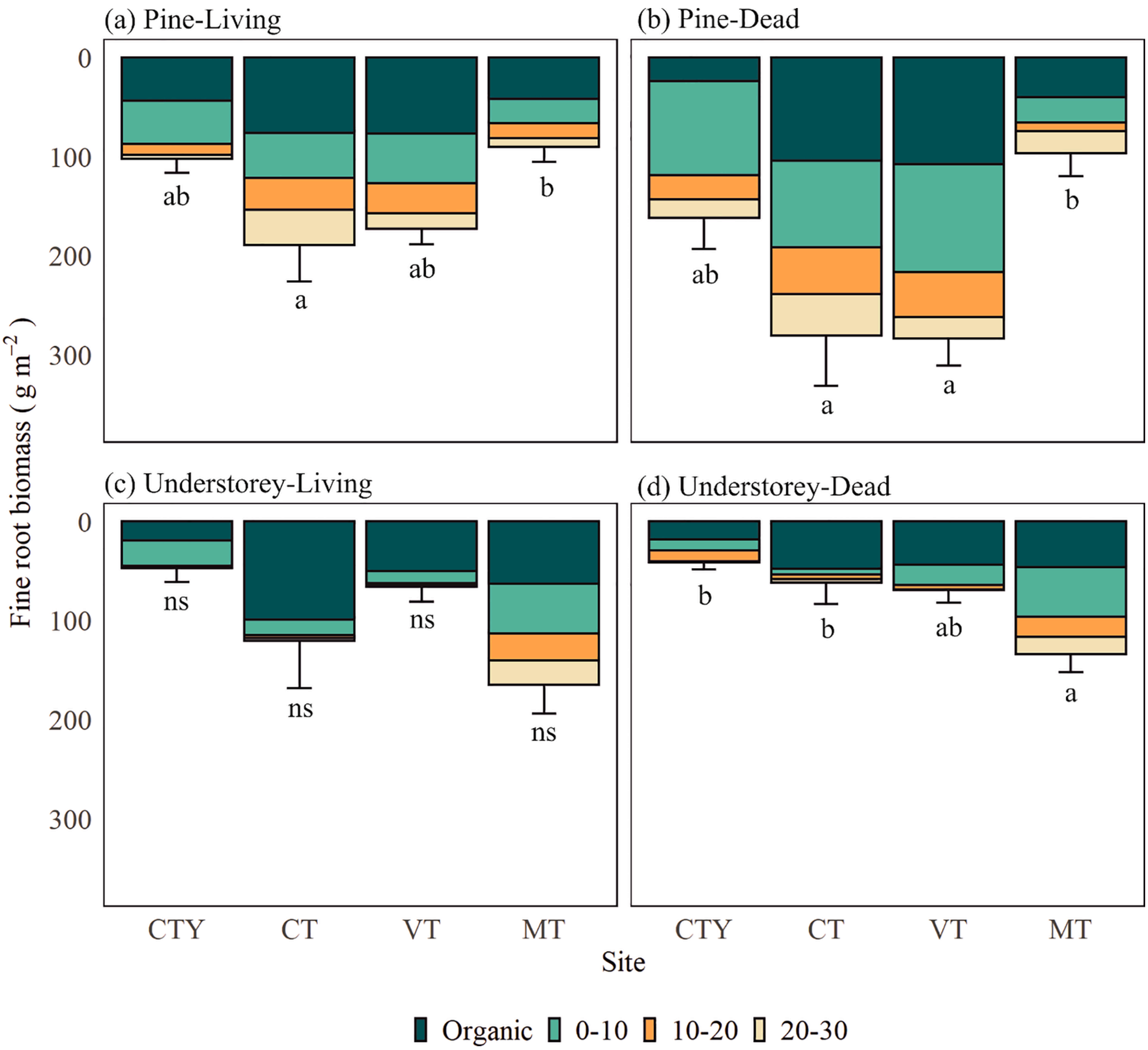

Fig. 2. Fine root (<1 mm in diameter) (a) biomass of pine; (b) dead mass of pine; (c) biomass of understorey and (d) dead mass of understorey along a site fertility gradient (CTY, CT, VT, MT) in southern Finland. The bar values represent mean + SE (N = 3), the letters a-b indicate significant (P < 0.05) differences between sites, ns indicates non-significant.

range of 5-364d compared to Weibull regression models, and major differences were mainly in long-lived roots (Table 3) which did not reach to 50% of mortality until the final session. Pine FRL was highest on the poorest site, CT (Table 3). Pine FRL in VT and MT were significantly ($P < 0.05$) lower than in CT, whereas there were no significant differences between VT and MT (Table 3). In addition, we found that FRL of both pine root tips and understorey roots was significantly positively correlated to pH in the organic layer ($R^2 = 0.97$, $P < 0.05$, Fig. S5). The higher the pH of the organic layer, the longer FRL the trees may have.

Total annual litter (BG + AG) increased along the site type gradient as the C inputs were 206.2, 276.2, and 307.1 g m^{-2} year^{-1} for CT, VT and MT, respectively. Fungal mycelia production only consisted 8–13% of total annual BG litter C input. The AG litter C input increased with increasing site fertility and the AG understorey litter C input did not vary much (49.4–53.8 g m^{-2} year^{-1}) between sites (Table 4). The AG litter C input was 1.7–3.3 fold higher than that of BG across sites. The share of BG litter C inputs increased with decreasing site fertility (Table 4). The BG C litter input of understorey vegetation was lower than that of pine at VT and CT, but almost equal to that of pine at MT.

4. Discussion

4.1. Fine root morphology

Supporting our results, absorptive roots have been reported to have smaller diameter and length but higher SRL (Guo et al., 2008; Zadworny and Eissenstat, 2011) and higher N concentration than transport roots (Zadworny et al., 2015). Ostonen et al., (2007b) showed that SRL was an important indicator to soil nutrient availability as it has been shown to decrease significantly with increasing fertilization. Our sites did not vary significantly in first-order root morphology, which does not support our first hypothesis, as site type was not clearly related to fine root morphology. Thinner fine roots with higher SRL have higher absorption efficiency as the first-order root SRL tended to decrease (with root diameter increase) from poor to fertile sites, although without statistically significant differences. In line with our results, Zadworny et al., (2015) proved that there were no compatible root morphology differences between sites with contrasting fertility of *Quercus robur* (L.) in central Poland. Along a naturally developed *Betula pendula* forests in southern Finland, SRL decreased on a gradient from nutrient-poor to nutrient-rich stands, whereas coniferous stands exhibited no consistent

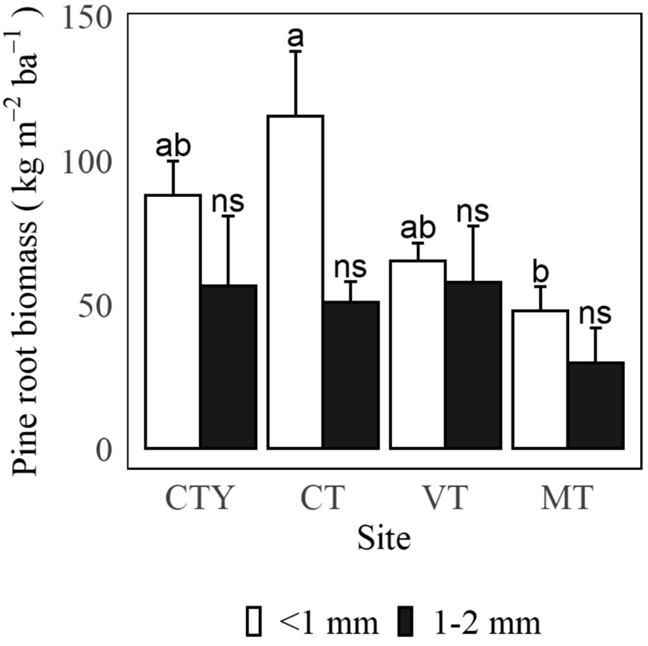

Fig. 3. Pine root biomass per stand basal area (g m^{-2} ba^{-1}) by different root diameter classes (<1mm, 1–2 mm). Error bars indicate standard error (N = 3). Ba indicates stand basal area. The letters a and b indicate the significant differences ($P < 0.05$) among sites of different diameter levels, ns indicates non-significant.

trend (Kalliokoski et al., 2010).

The roots studied in the young stand were significantly thinner and shorter, with a smaller surface area compared to mature stands, probably due to the more competitive root growth environment. Our results are agree with those from an age sequence of 6–47 year old Scots pine stands, where the stand age was positively connected with fine root length, surface area and root tips density per tree (Jagodziński and Kałucka, 2011).

4.2. *Fine root biomass, turnover and mycelia production*

Our fine root biomass of mature forests decreased from nutrient-poor to nutrient-rich sites. Fine root biomass in boreal forests has been reported to be related to stand and site characteristics such as dominating tree species (Finér et al., 2007, Hansson et al., 2013b), stand basal area (Helmisaari et al., 2007), stand age (Makkonen and Helmisaari, 2001, Finér et al., 2007), latitude/temperature (Leppälammi-Kujansuu et al., 2014a), and nutrient availability (Leppälammi-Kujansuu et al., 2013). Although the sites were closely located and had the same dominant tree species, they varied in tree size and stand density. Thus, expressing the results per stand basal area enabled us to minimize the size and density differences. Confirming the third hypothesis, FRB/ba decreased significantly from poor to fertile sites. In addition to the mature sites, FRB calculated per m^2 ground (Fig. 2) or per tree basal area (Fig. 3) was also relatively high on our young and infertile site, supporting our third hypothesis.

The BG biomass values did not include EcM mantle, but some of the mantle was attached tightly to fine roots and included in FRB. The proportion of EcM mantle biomass was reported to be 12–28% of attached EcM root tissue in conifers (Hobbie and Colpaert, 2003; Ostonen and Lõhmus, 2003). Some sand adhered tightly to the EcM mantle, which might result in an overestimate of fine root biomass. Based on Helmisaari et al., (2007), the ash content of fine roots was always <6%, suggesting that the possible mineral particle effect on root biomass was minor.

The understorey roots and rhizomes consisted 28–65% of total FRB in our study comparable to reported 47% of total FRB (D < 2 mm) (Helmisaari et al., 2007). Understorey species are known to have more superficial roots and rhizomes than conifer roots (Makkonen and Helmisaari, 2001, 1998). In our study, however, the understorey FRB in MT was evenly distributed to deeper mineral soil (down to 30 cm) compared to other sites. This may be due to the extremely high soil stoniness at MT (46.5 compared to 13.1–21.1 in other sites) and severe competition with pine roots in the upper soil.

Fine root longevity significantly differed between pine and understorey, and between root types as shown by previous studies in boreal forests (Ding et al., 2019; Leppälammi-Kujansuu et al., 2014a). Information on FRL on a site type gradient was scarce and the results are inconsistent (Eissenstat and Yanai, 1997; Nadelhoffer, 2000). Within Scots pine sites, we found that the poorest site, CT, had the longest FRL, and relative fertile sites VT and MT had shorter FRL, though these not exactly follow the fertility gradient as hypothesized. Eissenstat & Yanai (1997) suggested that low resources of nutrients lead to longer lifespans. Fertilization experiments have confirmed this: after nutrient addition in *Picea abies* forests, fine root mortality increased significantly and resulted in shorter FRL (Andersson and Majdi, 2005; Majdi, 2001), with similar effects on *Pinus ponderosa* stands (Johnson et al., 2000).

We showed that FRL of pine root tips and understorey rhizome correlated significantly with organic layer pH. In coniferous forests, soil acidity increases due to decomposition of needles and nutrient uptake. The most infertile site, CT, had the highest pH of 3.8, and the other sites had lower pH values of 3.4–3.5. Previous studies have demonstrated that higher soil acidity is related to high fine root turnover rate and high Al^{3+} concentration in the deeper soil, which restricted roots in shallower soil layers (Godbold et al., 2003; Lukac and Godbold, 2011).

We observed that for Scots pine, thinner roots that emerged on a nutrient-poor site or in a young stand (such as CTY and CT) may build more FRB and have longer lifespans, and thus rely more on absorption ability by themselves, instead of the massive EcM mycelia expansion observed on thicker roots on nutrient-richer sites (VT and MT). Based on our results, roots in nutrient-limited/young forests tend to allocate more C to BG with thin and long-lived fine roots, also with the least EcM production, but roots in more suitable conditions may allocate less C to BG and even deliver part of the C to build EcM fungi. According to Surplus Carbon Hypothesis by Prescott et al., (2020), EcM associations are likely to be a result of C the plant has in surplus, rather than reflecting the plant's need for nutrients. Our dense fertile MT site has a large total needle mass with a likely greater total amount of photosynthates produced than on a less fertile site. A larger part of photosynthates can be used for aboveground growth when nutrients are less limiting, probably leading into less C transport into the root system. Using the data gathered on the MT site, Schiestl-Aalto et al., (2019) estimated that 6% of annual photosynthetic production is allocated to mycorrhizal fungi.

On our sites, EcM mycelia production increased with site fertility, which is in agreement with other studies of natural boreal forests (Kalliokoski et al., 2010; Ostonen and Lõhmus, 2003; Sterkenburg et al., 2015). Studies have demonstrated that EcM production is reduced in N-fertilized forests (Högberg et al., 2011; Nilsson and Wallander, 2003), but natural fertility differences cannot be directly compared with fertilization results. Sterkenburg et al., (2015) state that high N-availability in boreal natural forests without artificial N addition resulted in a maximum of EcM fungi, whereas artificial N addition limited EcM growth. Our results on a natural fertility gradient in areas with low atmospheric N deposition agreed with this result.

Finally, seasonal and annual EcM mycelia production was closely related to the thickness of the organic layer (Fig. S5). Mycelia emanating from pine distal roots are generally located in the humus layer. Mycorrhiza fungi has been reported to be most abundant in the humus layer, regardless of the soil fertility levels (Sterkenburg et al., 2015). Therefore, the thickness of humus is understandably positively correlated to seasonal EcM biomass and annual production. Our results for

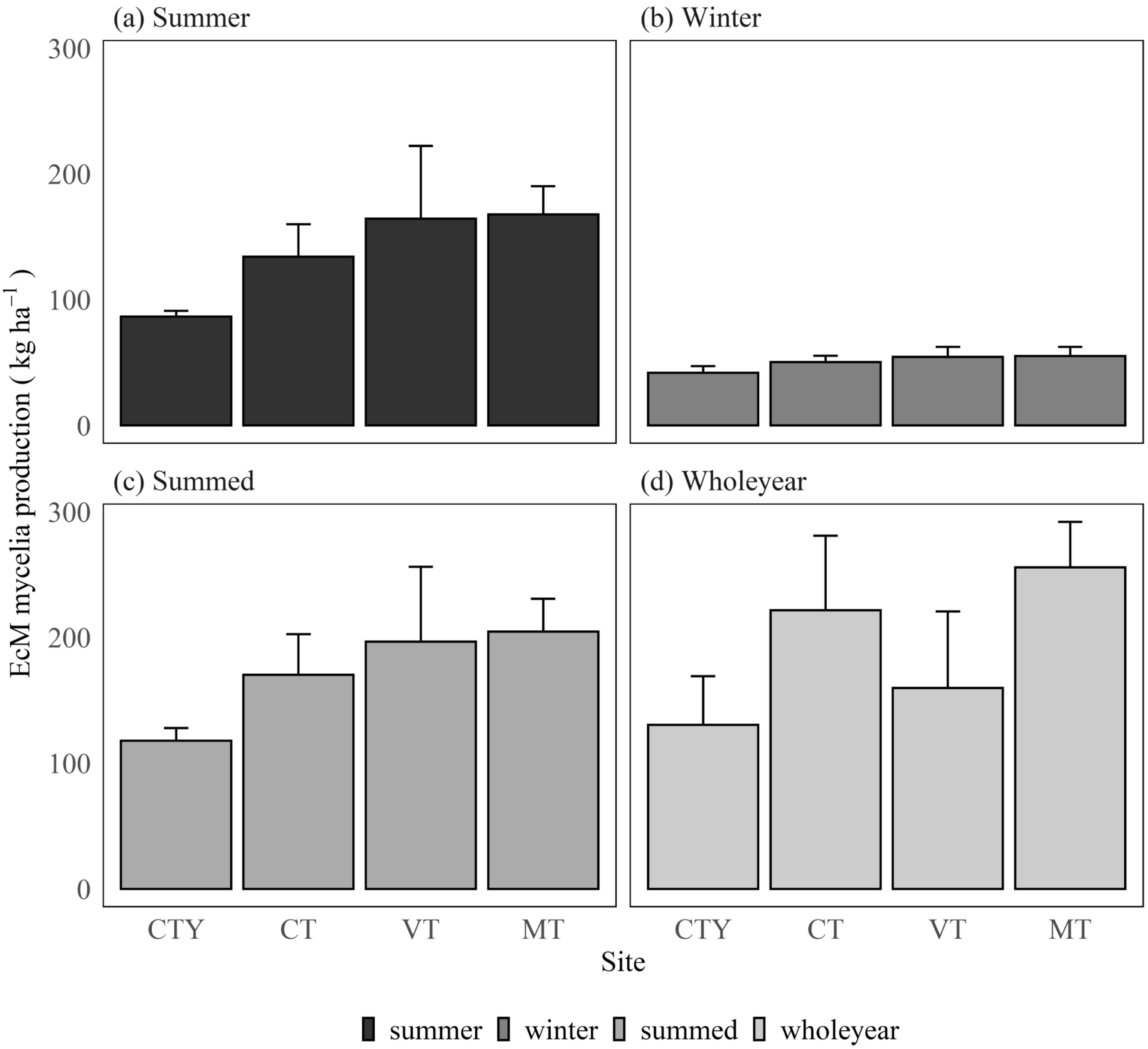

Fig. 4. The EcM mycelia production of (a) summer (May-September), (b) winter (September-May), (c) summing up the summers and the winters, and (d) whole-year bags. The values represented mean + SE (N = 3).

Table 3
Fine root median longevity (days) at different sites by Kaplan-Meier estimation and by Weibull error distribution regression model (mean ± SE).

Sites	N	CTY	CT	VT	MT
Kaplan-Meier					
Pine	2520	324^c (318–328)	881^a (769-NA)	367^b (364–417)	487^b (417–530)
Understorey	2226	831^c (769-NA)	NA^a (1301-NA)	1088^c(942-NA)	NA^b(1088-NA)
Pine roots					
Tips	1831	318^c (280–328)	867^a (412-NA)	326^c (324–364)	417^b (417–487)
Long roots	689	480^b (448–614)	927^a (776-NA)	942^a (942-NA)	965^a (576-NA)
Organic layer	631	517^a (411–622)	769^a (409–1094)	324^a (324-NA)	487^a (410-NA)
Mineral soil	1889	321^c (280–328)	881^a (734-NA)	367^b(364–417)	480^b (417–530)
Weibull					
Pine	2520	340 ± 8	710 ± 51	494 ± 26	509 ± 21
Understorey	2226	931 ± 39	1870 ± 296	724 ± 47	1032 ± 119
Pine roots					
Tips	1831	324 ± 7	598 ± 52	333 ± 18	436 ± 19
Long roots	689	525 ± 36	865 ± 104	1147 ± 165	893 ± 105
Organic layer	631	460 ± 35	576 ± 53	491 ± 54	614 ± 60
Mineral soil	1889	329 ± 8	962 ± 124	495 ± 30	482 ± 22

Note: Kaplan Meier estimation (95% of confidence in the parenthesis, the NA means the data is skewed). N indicates number of roots. The groups of tips, long roots, organic layer, mineral soil all belong to pine roots. Organic and mineral layers were separated according to organic layer thickness of each site. The different letters a-c indicate significant differences ($P < 0.05$) between sites.

Table 4

Annual below- and aboveground litter C input (g m^{-2} $year^{-1}$) of pine and understory species.

		Belowground							Aboveground					BG/Tot. (%)
	Pine	Us	EcM	BG Tot.	Needles	Others	Pine Tot.	Dwarf Shrub	Lichen	Moss	Others	UsTot.	AG Tot.	
CTY	55.7	9.1	5.3	70.1	*	*	*	*	*	*	*	*	*	*
CT	47.7	20.1	7.7	75.5	44.0	33.0	77.0	36.3	13.1	4.5	0	53.8	130.7	37
VT	66.1	16.3	8.9	91.3	77.3	58.2	135.5	16.4	0	27.9	5.1	49.4	184.9	33
MT	32.6	28.9	9.2	70.7	111.5	74.3	185.8	30.2	0.2	15.9	4.5	50.6	236.4	23

Note: Us abbreviated for understorey, EcM abbreviated for ectomycorrhizal mycelia, asterisks indicated the missing data we did not measure. Annual fungal production estimated by summing up summer and winter production. The data of aboveground tree litterfall of MT was from Ilvesniemi et al., (2009). CT tree needle and total litterfall was predicted based on models from Starr et al., (2005). VT tree litterfall was empirically collected 2013–2016 for this study.

annual EcM mycelia production varied between 118 and 205 kg ha^{-1}, which was comparable to that of mixed-coniferous forests in south-west Sweden of 125–200 kg ha^{-1} (Wallander et al., 2001). The whole-year growth bags did not significantly differ from those sequentially harvested, but they tended to have slightly greater EcM mycelia production, except in the VT site. The reason for the contradiction in the VT site might be caused by dead mass formed and decomposed (higher turnover rate) of hyphae in the whole-year bags compared to the sequential harvests with shorter incubation time (4–8 months).

4.3. *Above- and belowground C input*

Supporting our fourth hypothesis, the share of total C (pine and understorey) allocation to root litter decreased with increasing site fertility from 37% to 23% (CT, VT to MT; Table 4). The amount of AG C input (131–236 g m^{-2} $year^{-1}$) increased with site fertility but BG C inputs (71–91 g m^{-2} $year^{-1}$) did not follow the same pattern. Previous studies showed Norway spruce to have a higher BG C input (93–132 g m^{-2} $year^{-1}$) and a lower AG C input (92–153 g m^{-2} $year^{-1}$) compared to Scots pine in this study, which resulted in a relatively high BG share (40–57%) of Norway spruce total C input (Kleja et al., 2008; Leppälammi-Kujansuu et al., 2014b). Scots pine were reported to have three times faster needle turnover rate compared to spruce (Reich et al., 1996), therefore Scots pine with low needle biomass has a high AG litter production. The amount of AG tree litter production, 77–186 g m^{-2}C $year^{-1}$, was in accordance with an earlier range reported for Scots pine 67–170 g m^{-2}C $year^{-1}$ (Ukonmaanaho et al., 2008). AG litter production was positively related to site fertility as reported in previous studies (Leppälammi-Kujansuu et al., 2014b; Norris et al., 2013).

In our study, the share of BG litter of pines did not increase along the fertility gradient as AG did. As a result, the share of BG to total litter input decreased with site fertility. On the other hand, the BG of the understorey, which mainly consisted of ericaceous dwarf shrubs, showed the highest BG C input at the most fertile MT site. Here the dominant species were deciduous *Vaccinium myrtillus* and *Vaccinium vitis-idaea,* which spread with extensive rhizomes and may have 5–10% of the total biomass in fine roots (Frolov et al., 2020). In these plants, the coverage of the shoots (leaves) seems to regulate the amount of fine roots since root-to-shoot ratio was found to be constant after various N-additions (Palmroth et al., 2014). Although understorey vegetation represents a relatively minor component of the total biomass of boreal forests, it plays an important role in the annual C input to the soil in boreal forest (Lehtonen et al. 2016).

5. Conclusion

We quantified the carbon inputs from above- and belowground vegetation components in boreal forests dominated by Scots pine. Quantifying soil C and nutrient inputs by separating above- and belowground litter provides valuable empirical data for terrestrial C cycle models. Ilvesniemi et al., (2009) reported that soil organic layer of the MT site contained 1680 g C per m^2. Aboveground litter C accumulates on the top of the organic layer from where the C compounds will slowly move downwards during decomposition. On the contrary, belowground litter C input is larger in the mineral soil. Root litter was reported to have 2–10 times slower decomposition rate than leaves in boreal forests (Kyaschenko et al., 2019). Therefore, the variation of soil organic matter depends more on root-related litter inputs and turnover than on those from aboveground, but unfortunately the belowground litter is seldom quantified. In N-limited and infertile boreal forest ecosystems, the forest NPP was mainly hampered by the low N-supply caused by slow root and fungal decomposition and root-derived C supplied to mycelia (Kyaschenko et al., 2019). Also, low nutrient supply to root and fungal decomposers have resulted into less fertile sites having smaller productivity but a stronger belowground C sink (Clemmensen et al., 2014, 2013). The low decomposition rate of belowground litter may be caused by the high chitin of distal EcM roots (Freschet et al., 2013), or the high values of condensed tannins and non-lignin C compounds (Adamczyk et al., 2019; Sun et al., 2018). Further studies should strive to determine the unsolved belowground questions such as root exudates inputs and their decomposition as well, and how they add to the C fluxes and nutrient cycling.

CRediT authorship contribution statement

Yiyang Ding: Conceptualization, Formal analysis, Data curation, Software, Investigation, Visualization, Writing - original draft. **Jaana Leppälammi-Kujansuu:** Conceptualization, Investigation, Supervision. **Maija Salemaa:** Investigation. **Pauliina Schiestl-Aalto:** Investigation, Methodology. **Liisa Kulmala:** Investigation. **Liisa Ukonmaanaho:** Investigation. **Pekka Nöjd:** Investigation. **Kari Minkkinen:** Investigation. **Naoki Makita:** Investigation. **Peter Železnik:** Investigation. **Päivi Merilä:** Investigation, Resources. **Heljä-Sisko Helmisaari:** Conceptualization, Investigation, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.119081.

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