

1 Title: Fine root longevity and below- and aboveground litter production in a boreal *Betula pendula*
2 forest ☆

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12

13 **Abstract**

14 1. Fine root turnover plays a critical role in carbon and nutrient cycling in forest ecosystems. In this study,
15 we focused on the most abundant deciduous species in Nordic countries, silver birch (*Betula pendula*
16 Roth) and its fine root dynamics, including the amount of litter produced by fine roots as well as by
17 aboveground vegetation.

18 2. The minirhizotron method was used to quantify fine root longevity of silver birch and understory fine
19 roots and rhizomes in northern Finland. Fine root biomass per basal area and ectomycorrhizal short root
20 numbers per mg were also quantified. The fine root litter production was estimated by fine root biomass
21 and longevity, and then compared with the aboveground litter collected with litter traps.

22 3. Birch fine root biomass was 1.4-fold higher than that of understory fine roots and rhizomes (234 ± 22 ,
23 $171 \pm 19 \text{ g m}^{-2}$ respectively). Fine root longevity of birch (372 days) was significantly ($P < 0.05$) shorter
24 than that of understory vegetation (643 days). The birch fine root longevity was positively related to root
25 diameter and soil depth. Hazard analysis showed that thicker roots, long roots, roots produced late in
26 the growing season, and roots growing deeper in the soil had relatively lower mortality hazard compared
27 to the reference data. The total annual soil C input, including both birch and understory, was 283 g C m^{-2}
28 yr^{-1} . The proportion of understory annual C input was 35% of the total. Total annual belowground C
29 input was 1.4-fold greater than that of aboveground.

30 4. Our study indicated that the total annual belowground litter production was greater than that of the
31 aboveground litter in a boreal deciduous forest stand. Therefore, more emphasis should be put to
32 quantify the C cycling of both above- and belowground parts of different tree species as well as
33 understory in boreal forests.

34 Keywords: Carbon; Minirhizotrons; Survival analysis; Fine root longevity; Silver birch; Understory.

36 **1 Introduction**

37 Fine roots with their symbionts play a key role in water and nutrient absorption, and significantly
38 contribute to forest soil carbon (C) as a result of their fleeting lifespan (Gill and Jackson, 2000;
39 Clemmensen et al., 2013). For a long time, aboveground litter was assumed to be the main C input to
40 the soil, whereas the belowground litter C input was less in focus. Fine root biomass comprises only <
41 5% of total forest biomass, although fine root production is estimated to constitute about one third of
42 annual net primary production (NPP) on a global scale (Vogt et al., 1996; Jackson et al., 1997). Both
43 below- and aboveground litter production vary as a function of different terrestrial biomes, genetics,
44 climate, soil nutrients, and other soil environmental factors (Vogt et al., 1986; Jackson et al., 1996;
45 Pregitzer et al., 2000; Brassard et al., 2009). The boreal forest (50–70 °N), accounting for only 15% of
46 the global land area, is one of the largest biomes of the world. Due to ongoing global warming, boreal
47 forest under serious environmental stress may be an even more fragile ecosystem than forests in more
48 southern biomes and can easily switch from a sink to a net C source as a result of minor temperature
49 changes (Ashton et al., 2012).

50 Fine root biomass and turnover are the main contributors to belowground C input (Lukac, 2012).
51 Generally, not many references have separated fine roots into tree species roots and understory
52 vegetation roots (Finér et al., 2011). As the understory vegetation in boreal forests contributes to almost
53 35% of the total fine root biomass (Finér et al., 2011), the high portion of understory vegetation can
54 affect the result of fine root turnover (Helmisaari et al., 2002; Hansson et al., 2013; Leppälammii-
55 Kujansuu et al., 2014a; Bhuiyan et al., 2017). At the same time, fine root longevity (turnover time) varies
56 as a function of mycorrhizal colonization types, soil nutrient status, soil temperature, root chemistry, root
57 diameters, and tree species (Matamala et al., 2003; Noguchi et al., 2005; Leppälammii-Kujansuu et al.,
58 2013; Adams and Eissenstat, 2015; Kubisch et al., 2016).

59 Due to the seasonally shed leaves, deciduous trees may contribute more to forest annual litter
60 production than conifers (Gobat et al., 2004). The broadleaf litter is more decomposable and richer in N

61 and cellulose but contains less lignin than conifer litter (Lukac and Godbold, 2011). However, within a
62 zone of similar climate and soil fertility, most of the previous studies indicated that deciduous forests
63 have similar or even lower aboveground litter input compared to coniferous forests (Alriksson and
64 Eriksson, 1998; Sigurthardottir, 2001; Smolander et al., 2005; Olsson et al., 2012). Steele et al. (1997)
65 reported that the ratio of fine roots NPP to total NPP (both above- and belowground) is higher in
66 coniferous than in deciduous forests in the boreal biome. A more recent study reported no clear
67 correlations between tree species and the belowground litter input (Augusto et al., 2015).

68 Because of their economic importance, boreal conifers have been the targets of intensive research for
69 some decades, recently also with respect to fine root turnover (Finér et al., 2011; Leppälammil-Kujansuu
70 et al., 2013, 2014a; Helmisaari et al., 2015; Bhuiyan et al., 2017). Some commercially important
71 deciduous tree species, such as beech, aspen and maple have attracted research interest during the
72 past decades in Europe and North America (Tierney et al., 2001; Lukac et al., 2003; Meier and
73 Leuschner, 2008; Pregitzer et al., 2010; Beyer et al., 2013), but only a few Betulaceae species have
74 been investigated with regard to their fine root dynamics and C input, especially in the hemi-boreal or
75 boreal vegetation zone (Hansson et al., 2013; Varik et al., 2015; Ostonen et al., 2017).

76 Finland, the most forested country in Europe, supports primarily boreal coniferous forests, with a short
77 growing season and a limited variety of tree species. Norway spruce and Scots pine are the two main
78 coniferous species in Finland, whereas the main broad-leaved tree species is silver birch (*Betula*
79 *pendula* Roth.), the standing volume of which comprises 16% of Finnish forest (Luque and Vainikainen,
80 2008). Studies of fine root dynamics of silver birch from the northern latitudes are scarce, although a
81 few studies have been investigated in hemi-boreal forests. Hansson et al. (2013) measured silver birch
82 fine root longevity and biomass in southern Sweden and Varik et al. (2015) investigated silver birch C
83 budgets in Estonia, whereas the Kivalo experimental site (our study) is a typical Finnish northern boreal
84 forest.

85 We used minirhizotron (MR) method to estimate fine root longevity in a northern boreal silver birch stand,
86 and used it together with the fine root biomass to determine the amount of fine root litter production. The
87 belowground litter production was compared with the aboveground litterfall, which was collected for
88 three years. The aims of this study were (1) to determine the fine root longevity and biomass of silver
89 birch and understory in northern Finland, (2) to compare the amounts of above- and belowground litter
90 production of silver birch and the understory, and (3) to compare fine root longevity and litter C input of
91 the silver birch stand to those of the adjacent Norway spruce stand as they were originally a same
92 Norway spruce stand (Leppälammii-Kujansuu, et al. 2014a).

93 **2 Materials and Methods**

94 *2.1. Site description*

95 Kivalo (66°20' N, 26°40' E), located in northern Finland, represents a typical forest of the southern
96 Lapland region. This site type based on Cajander (1949) is *Hylocomium–Myrtillus* type (HMT). The
97 most abundant shrub in the site is *Vaccinium myrtillus* (42%), with 4% of other dwarf shrubs, grasses
98 and herbs covering 23% of the whole area, and the field layer is abundantly covered by mosses
99 (Nieminen and Smolander, 2006). The average thickness of the organic layer is 4.4 cm, and the
100 stoniness of mineral soil is around 25%. More detailed soil characteristics are presented in Table 1. This
101 study site was a single tree species stand of *Betula pendula* Roth., commonly known as silver birch or
102 warty birch. The site was originally dominated by Norway spruce, which was clear-cut and burned in
103 1926, and a tree species experiment was established on this site. Three 25m×25m replicate study plots
104 were established in the naturally regenerated silver birch-dominated stand. The adjacent spruce stand
105 was planted in 1930, and became a Norway spruce dominated stand. The fine root longevity and above-
106 and belowground C input of Norway spruce have been published by Leppälammii-Kujansuu et al.
107 (2014a). For more information on the site and soil characteristics, see Smolander and Kitunen (2002).

108

109

110 **Table 1**

111 General soil characteristics of the Kivalo birch site were measured in 2000 (Smolander and Kitunen,
112 2002). The C:N ratio of the organic layer is derived from Smolander and Kitunen, (2011). Mean length
113 of the growing season (> 5 °C, MLGS) was calculated from the data collected from 1981 to 2011, based
114 on the dataset of the Finnish Meteorological Institute.

Site and stand characteristics	Birch
Soil pH	4.3
Soil type	Podzol
Organic layer	Mor
Organic layer C:N	30
Stem density (ha ⁻¹)	1003
Basal area (m ² ha ⁻¹)	21
Mean stem diameter (cm)	17
Mean height (m)	15.5
Stem volume (m ³ ha ⁻¹)	153
Mean annual precipitation (mm)	517
Mean annual temperature (°C)	0.7
Mean length of the growing season (days yr ⁻¹)	112

115

116 *2.2. Root biomass*

117 Roots were sampled in August 1999, when a total of 60 cores were taken from the three replicate plots
118 (20 cores, 40 mm in diameter from each plot). Each core was sorted for the organic layer and mineral
119 soil layer, and the mineral soil layer was subdivided into 0-10, 10-20, and 20-30 cm layers. Since only
120 one plot had roots in the 20-30 cm mineral soil layer, the data of the third layer was excluded. The
121 maximum depth of mineral soil was 34 cm. The root samples were transported directly back to the
122 laboratory and stored in a freezer at -18 °C. After thawing, the roots in the soil cores were manually
123 rinsed using sieve nets and the attached soil particles were carefully removed. The roots were then
124 sorted into birch and understory roots by observation under a microscope. Based on the color, elasticity,
125 and morphology of the roots, they were then sorted as dead or living. There is no fresh tissue (white or
126 light brown color) in the middle of the dead roots; instead, there is dark decaying tissue, sometimes with
127 hollows. In addition, we sorted birch roots into different diameter (D) classes: < 1 and 1-2 mm, and
128 understory (mostly dwarf shrubs) roots and rhizomes by D < 2 mm, although over 90% of understory

129 roots and rhizomes had $D < 1$ mm. Similarly to Norway spruce and Scots pine in Finnish boreal forests
130 (Helmisaari et al. 2009), the silver birch fine roots in our study are the roots < 1 mm in D . The stoniness
131 of each stand was taken into consideration when calculating the dry mass of fine roots in the mineral
132 soil layers by using the stoniness index (Viro 1952, Tamminen, 1991). In cases in which the lowest
133 layer of the soil core did not reach down to a depth of 20 cm, the fine root biomass was extrapolated to
134 include the full 10 cm layer.

135 Ectomycorrhizal (EcM) short roots were counted from 10% of the total birch fine root biomass. Ostonen
136 et al. (2013) demonstrated that in boreal birch forest at least 97% of short roots were colonized by EcM
137 fungi, and we therefore assumed that in our samples 100% of first-order fine roots were EcM colonized
138 short roots.

139 *2.3. Minirhizotrons method: filming and image analysis*

140 Fine root longevity was measured using the MR method (Bates, 1937). Compared to other methods of
141 estimating fine root production, the MR method is more reliable on the basis of previous studies
142 (Hendricks et al., 2006, Addo-Danso et al., 2016). In the spring of 2003, three MR observation tubes
143 were installed vertically in each of the three replicate plots in the silver birch stand. The diameter (D) of
144 the tubes was 5 cm and their length varied depending on the soil depth. During 2004–2006, a total of
145 2838 images were collected, three times in 2004 (June 22, July 27, Aug 25), four times in 2005 (July 6,
146 Aug 4, Sept 1, Sept 27), and four times in 2006 (May 30, July 6, Aug 10, Sept 11). The images were
147 taken by a stick-like camera with a drawer-carriage wheel so that each image size was restricted to a
148 size of 1.1×2 cm. The survival time of fine roots was recorded using the WinRHIZOTron MF 2015a
149 software. We followed the lifecycle of 1210 roots from a total of 11 sessions, including 970 birch roots
150 and 240 understory roots and rhizomes. The roots were manually classified as birch roots and
151 understory roots. We marked the birch 1st and 2nd order root tips as ‘short roots (Ostonen et al., 2007,
152 Ostonen et al., 2013)’, to differentiate them from the birch long roots. Each root segment was marked
153 as a single root because of the difficulty of tracing by root orders higher than order two (Treseder and

154 Allen, 2000, Luo et al., 2004). Also, we did not separate higher root orders when tracing the roots, as
155 the roots in the images were often covered by soil or grew outside the image, which made it difficult to
156 determine the root orders. On the other hand, as new roots grow and develop continuously, the original
157 root orders will change to higher root orders, leading to replicated work for determining the orders.

158 The diameters, lengths, and depths of roots were automatically recorded by the program. Based on the
159 living status of roots as judged by their color and morphological properties, all the roots were classified
160 as 'dead', 'alive' and 'gone' (Hendrick and Pregitzer, 1993). Generally, the shrunk and dark-colored roots
161 which had no newborn branches were defined as 'dead'; while the white or light brown roots with solid
162 structure were marked as 'alive'; and the missing roots, the roots growing back to the soil or out of
163 images, and the invisible roots totally covered by mycelia, were defined as 'gone'. Tracing of the roots
164 began from the second session, since the birth time of existing roots in the first session was unknown.

165 2.4. Above- and belowground litter production

166 The aboveground foliage litter was collected during 1999–2002 with 12 conical traps, which were
167 systematically placed on each plot. The funnel-shaped trap had a collecting area of 0.5 m², placed 1.5
168 m above the ground. The litter was collected twice a month during Oct 1999–Oct 2002, except during
169 the season of snow cover. After collection, all the aboveground litter samples from the same plot were
170 combined. The samples were air-dried and sorted into different classes, such as leaves, branches and
171 twigs, cones, bark, flowers, etc. The aboveground understory biomass was collected by a cylinder (236
172 mm in D). The locations of 103 sample points were systematical along the birch plots. The annual shoots
173 were separated from vascular plants for annual shoots mass. The aboveground understory litter
174 production was estimated by annual shoots mass plus one-third of mosses and lichens annual living
175 biomass. Samples were dried in the oven at 60 °C and then weighed (Nieminen and Smolander 2006).

176 We assumed a constant carbon fraction of 50% of dry matter. The belowground fine root litter production
177 was calculated as fine root biomass multiplied by fine root turnover rate. The fine root turnover rate is

178 commonly defined as the times fine root biomass is replaced in one year (Hendrick and Pregitzer, 1992),
179 and we calculated it by the inverse of median fine root longevity (yr).

180 *2.5. Data analysis*

181 *2.5.1. Survival analysis*

182 Because not all the roots died during the observation period, fine root longevity was calculated as the
183 median longevity when half of the fine roots were dead (Andersson and Majdi, 2005). The still living
184 roots on the final session were considered as 'right censored' (Guo et al., 2008a). We used the non-
185 parametric survival function (surv function) in RStudio Version 1.0.153 to estimate the roots from all
186 cohorts by different criteria, as shown in Table 2. This improved function was more practical than
187 previous Kaplan-Meier (KM) functions (Kaplan and Meier, 1958), because it considered equal longevity
188 variances on the basis of different classifications (Leppälammil-Kujansuu et al., 2014a). The survival
189 curves (Fig. 4) were also produced by RStudio, while other figures are made by OriginPro 8.6. In addition,
190 in order to compare our results with other references, a parametric regression model called Weibull error
191 distribution (Weibull, 1951) was employed to examine the root median longevity by using the SurvReg
192 function in RStudio Version 1.0.153. Moreover, the statistical analysis of variable classes was examined
193 by one-way ANOVA with IBM SPSS statistics 24.

194 *2.5.2. Risk analysis*

195 One way to predict the mortality risks of different indicators for root longevity is Cox proportional hazards
196 regression analysis. The hazard regression ratio, the so-called age-specific rate, explains the mortality
197 rate at the specific time t (Cox, 1972; Allison, 1995; Cantor, 1997). Classification of the cohorts is
198 described in Table 2. A positive parameter estimate value indicates a hazard ratio > 1 , which implies an
199 increasing risk of death, and *vice versa*. If the parameter estimate is 0, this means that the hazard ratio
200 is equal between two groups. In this case, we also excluded the understory roots because of their high

201 'right censored' roots number. For more research on the use of Cox proportional hazards regression of
 202 fine root longevity, see Wells and Eissenstat, (2001), Wells et al., (2002), and Gu et al., (2017).

203 **Table 2**

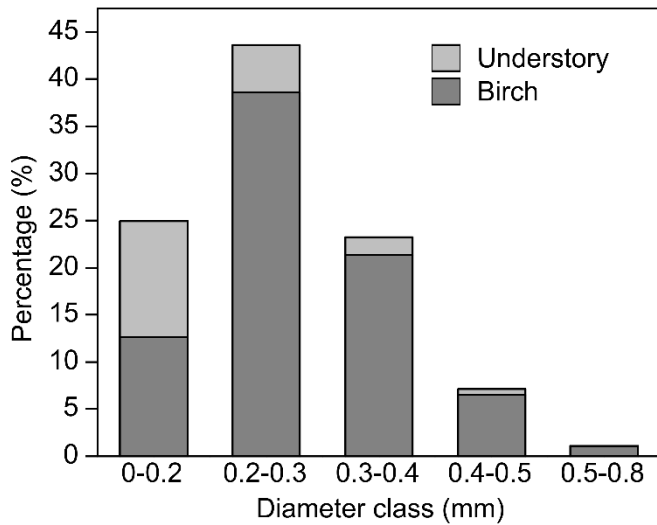
204 The variable description used to predict relationships of different factors with root longevity. Short roots
 205 were defined as the 1st and 2nd order roots without secondary development, as described by Ostonen
 206 et al. (2013).

Variable	Coding and description	207
Diameter	1= 0-0.2 mm, 2= 0.2-0.3 mm, 3= over 0.3 mm	208
Root class	1= short roots, 2= long roots	
Year	Birth year of the roots. 1=2004, 2=2005, 3=2006	
Season	The birth time of roots, 1= early growing season (June to August), 2= late growing season (September to October). One observation date was May 30 th , this observation was classified as the early growing season.	209 210
Depth	Soil depth at which roots were born, 1=top soil (0-5 cm), 2= mineral soil (5-20 cm)	211

212 **3. Results**

213 *3.1. Fine root morphology*

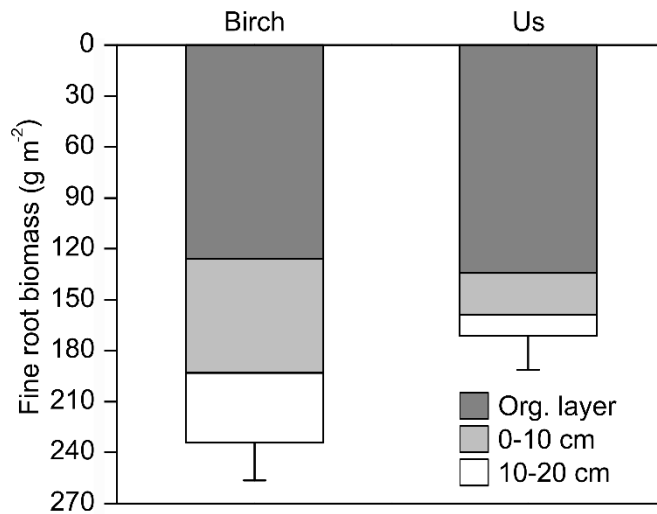
214 The fine root D varied between 0.03 and 0.75 mm in the MR measurements (Fig.1). Most of the fine
 215 roots (92%) were less than 0.4 mm in D (Fig.1). Only 1% of fine roots were in the D range of 0.5-0.75
 216 mm. The mean understory fine root D (0.17 ± 0.01 mm) was significantly ($P < 0.05$) thinner than that of
 217 birch (0.26 ± 0.01 mm). The majority (62%) of understory fine roots were less than 0.2 mm in D, whereas
 218 about half (48%) of birch fine roots were 0.2-0.3 mm in D (Fig.1).



219

220 **Fig. 1.** Diameter class distribution of birch fine roots and understory fine roots

221 *3.2 Fine root biomass and ectomycorrhizal short roots*



222

223 **Fig. 2.** Birch and understory (Us) fine root biomass (g m^{-2}) (mean \pm S.E.) in the organic layer and two
 224 mineral soil layers.

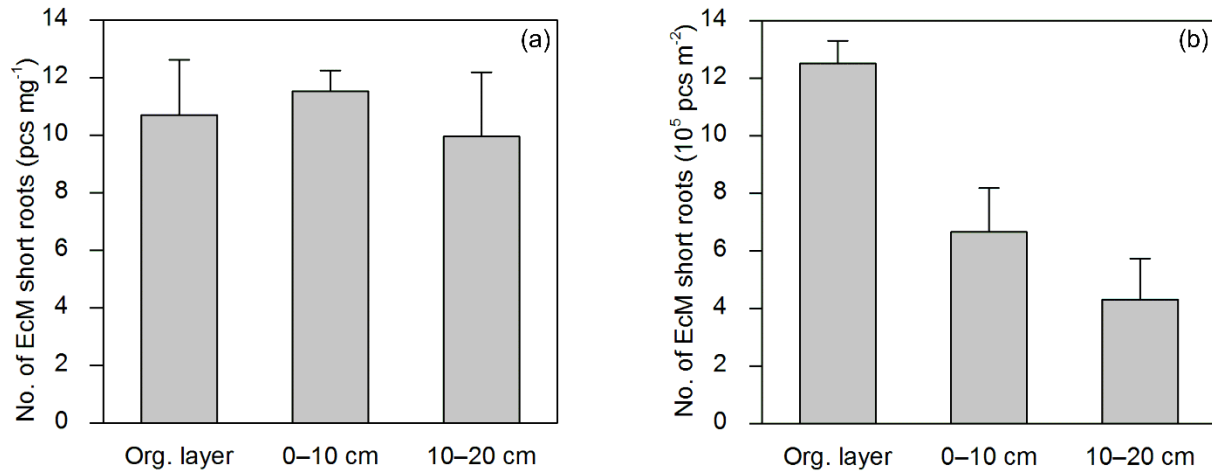
225 Birch fine root ($< 1 \text{ mm}$ in D) biomass ($234 \pm 22 \text{ g m}^{-2}$) was 1.4 times higher than that of understory

226 rhizomes ($171 \pm 19 \text{ g m}^{-2}$, Fig. 2). When thicker fine roots ($< 2 \text{ mm}$ in D) were included, birch fine root

227 biomass was $402 \pm 41 \text{ g m}^{-2}$. Shrub fine roots and rhizomes comprised 72% of the understory fine roots

228 ($< 2 \text{ mm}$ in D) biomass. Understory roots were mostly (around 80%) located in the organic layer, and in

229 this layer their biomass (134 g m^{-2}) was slightly higher than that of birch (126 g m^{-2} , Fig. 2a). Birch had
230 54% of its fine roots biomass in the organic layer. Only one of the three plots had fine roots in the 20-30
231 cm mineral soil layer, and therefore we excluded this layer in the results.



232

233 **Fig. 3.** The number of EcM short roots (a) per mg of living fine roots ($< 1 \text{ mm}$), (b) per m^2 based on fine
234 root biomass. Error bars represent S.E.

235 The number of EcM short roots per fine root weight unit did not vary significantly in the different soil
236 layers: there were 11 ± 2 , 12 ± 1 , and 10 ± 2 short roots mg^{-1} of fine roots in the organic layer and in the
237 0-10 cm and 10-20 cm mineral soil layers, respectively (Fig. 3a). The EcM short root number decreased
238 gradually from the organic layer to the deep soil. The total EcM short root number of the organic layer
239 was almost threefold higher than that of the 10-20 cm soil layer. The total short roots number colonized
240 by EcM in both the organic layer and mineral soil was 2.34 million m^{-2} .

241 3.3. Fine root longevity

242 80% of total traced roots were birch roots, and 68% of fine root elongation was by birch (Table 3). The
243 measured birch roots were over twofold longer than the understory roots. 730 of the 970 birch roots
244 were short roots. 41% of fine roots were still alive at the end of the observation period; the other fine
245 roots were either gone or dead (Table 3). The number of living and dead roots of understory were similar.

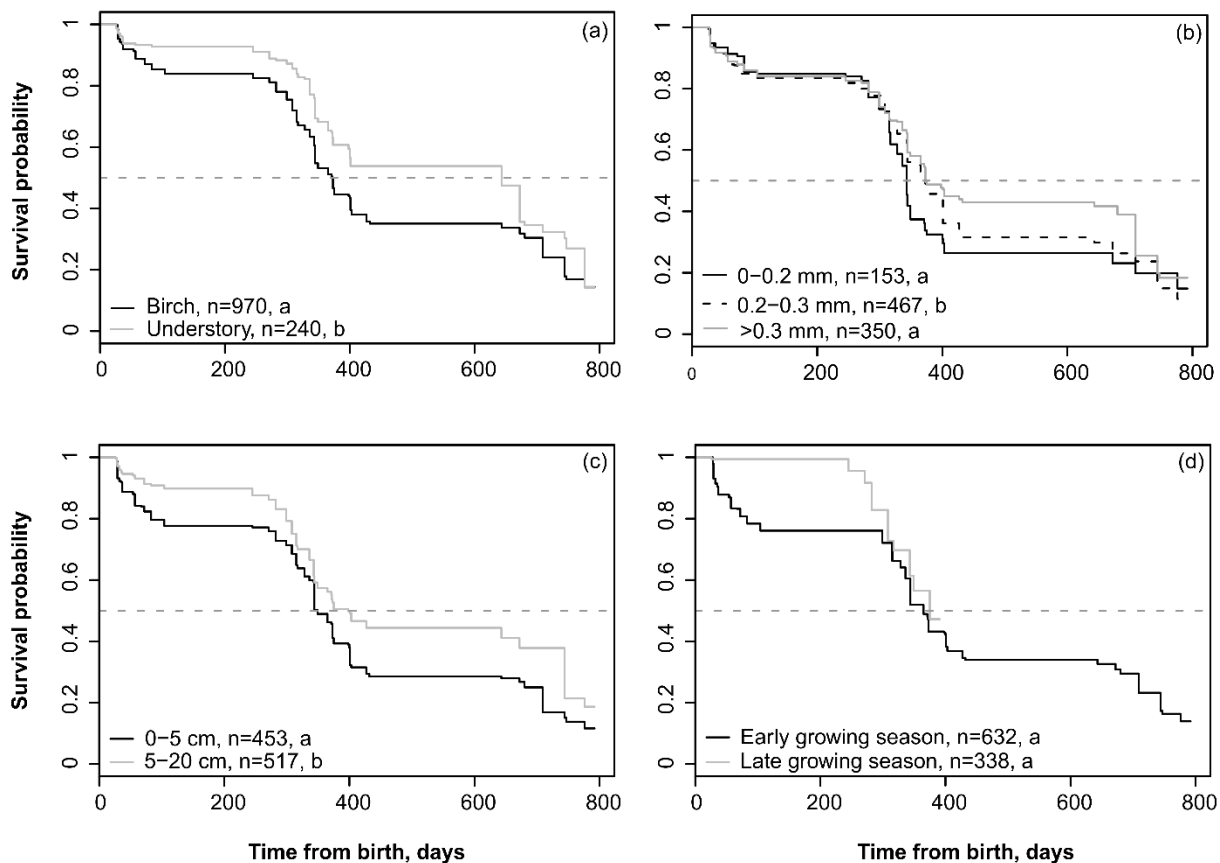
246 **Table 3**

247 Birch and understory root and rhizome number and elongation distributions at the end of the study. (a)
 248 The average number of fine roots, and (b) the fine root elongation sum (mm/tube) in roots and rhizomes
 249 of different living status.

	Understory	%	Birch	%	Tot.	%
(a) Alive	116	48	381	39	497	41
Dead	118	49	498	51	616	51
Gone	6	3	91	9	97	8
Tot.	240	20	970	80	1210	
(b) Alive	103.2	55	183.8	46	287.0	49
Dead	77.9	42	172.7	43	250.6	43
Gone	6.1	3	42.4	11	48.5	8
Tot.	187.2	32	398.9	68	586.1	

250

251



252

253 **Fig. 4.** Kaplan-Meier survival curves of fine roots and rhizomes during 2004–2006 (11 sessions in total),
254 between (a) birch and understory, (b) diameters, (c) depths, and (d) seasons. The dashed gray line
255 represents the median survival probability, identifying the corresponding median survival time on the x-
256 axis. The different letters a, b indicate the significant ($P < 0.05$) differences between different classes.

257 We estimated the longevity mainly using the KM regression estimation. Fine root longevity of birch (372
258 days) was significantly ($P < 0.05$) shorter than that of understory vegetation (643 days), and the root
259 turnover rates of the two species were 1.06 and 0.57, respectively (Fig. 4a). Due to the limited number
260 of understory vegetation fine roots and rhizomes, we only analyzed birch root longevity by root diameter,
261 soil depth and season (Fig. 4b-d). The birch fine root longevity was positively related to root diameter
262 and soil depth. The fine root longevity of coarser (0.2-0.3 mm in D) roots was significantly ($P < 0.05$)
263 longer than that of thinner D (0-0.2 mm) roots (Fig. 4b). Birch fine roots in the upper mineral soil layer
264 had a significantly ($P < 0.05$) shorter longevity compared to those in the deeper layer: 349 and 398 days,
265 respectively (Fig. 4c).

266 The comparisons of median longevities between different root morphology characteristics obtained
267 using KM and Weibull estimations differed slightly (Table 4). The variations of Weibull were less than
268 those of KM, and the majority of the Weibull values were slightly higher than the KM values.

269

270 **Table 4**

271 Comparisons of median longevity (median days \pm S.E., by 95% of confidence limits) of different birch
 272 root diameters, soil depths, season, and between birch and understory using two different regression
 273 models: Kaplan-Meier (KM) and Weibull. Different letters a, b indicate the differences between root
 274 classes ($P < 0.05$).

	KM (days)	Weibull (days)
Diameter		
0-0.2 mm	343 (336-349) ^a	339 \pm 25
0.2-0.3 mm	343 (349-401) ^b	372 \pm 18
> 0.3 mm	373 (371-432) ^a	416 \pm 23
Depth		
0-5 cm	349 (344-373) ^a	340 \pm 15
5-20 cm	398 (372-643) ^b	439 \pm 23
Season		
Early-growing	365 (356-374) ^a	354 \pm 13
Late-growing	375 (NA) ^a	463 \pm 32
Birch	372 (349-375) ^a	383 \pm 12
Understory	643 (400-672) ^b	493 \pm 32

275

276 In the year 2006, a diameter of > 0.3 mm in D, birth season and soil depth significantly influenced the
 277 birch fine root longevity ($P < 0.05$) (Table 5). The roots > 0.3 mm in D, the long roots, the roots born in
 278 the late growing season and the roots in the deeper (5-20 cm) layer had a relatively lower mortality
 279 hazard (13-30%) compared to the reference data (Table 5). However, the roots born in 2006 had a 3.2-
 280 fold higher mortality hazard than those born in 2004, due to the shorter observation time (Table 5).

281

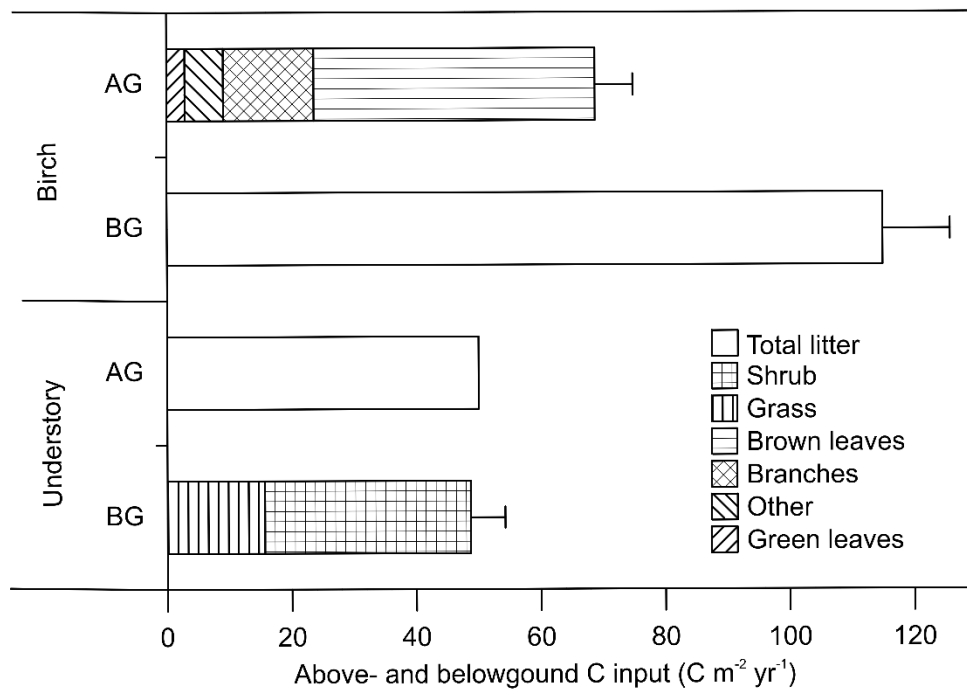
282 **Table 5**

283 Results of Cox proportional hazards regression analysis for variables of root longevity for birch roots during 2004–
 284 2006. The hazard ratio is only reported for the significant results ($P < 0.05$). Bold numbers represent significant
 285 results.

Factors	df	Parameter estimate	SE	χ^2	P	Hazard ratio
Year (ref.2004)	2	-	-	39.805	< 0.001	-
2005	1	1.115	0.107	1.153	0.283	-
2006	1	1.173	0.191	37.581	< 0.001	3.232
Diameter (ref.0-0.2 mm)	2	-	-	8.010	0.018	-
0.2-0.3 mm	1	-0.214	0.124	3.015	0.083	-
> 0.3 mm	1	-0.362	0.128	7.941	0.005	0.696
Root class	1	-0.184	0.107	2.976	0.085	-
Season	1	-0.143	0.054	7.033	0.008	0.867
Depth	1	-0.346	0.092	14.233	< 0.001	0.707

287

288 **3.4. Above- and belowground litter C production**



289

290 **Fig. 5.** The annual above- (AG) and belowground (BG) C input distributions of understory vegetation
291 and birch. Understory aboveground data includes both grasses and shrubs (Nieminen and Smolander,
292 2006), whereas these groups were separated in the belowground data. The other aboveground litter
293 included twigs, cones, bark, flowers, etc.

294 The total annual C input of the Kivalo birch stand, including both birch and understory, was 283 g C m⁻²
295 yr⁻¹. The belowground annual C input was higher than that of the aboveground, 58% and 42% of the
296 total, respectively (Fig. 5). The proportion of understory rhizomes C input comprised 35% in total (Fig.
297 5).

298 For understory, the above- and belowground C inputs were almost equal, at 49 and 50 g C m⁻² yr⁻¹,
299 respectively (Fig. 5). Shrub and grass roots and rhizomes consisted of 67% and 33% of the total
300 understory belowground C input, respectively (Fig. 5). For birch, the belowground C input was 1.7-fold
301 higher than that of aboveground C (Fig. 5). Birch brown leaves comprised the highest proportion (66%)
302 of AG, followed by branches (21%), other litter (9%) and green leaves (4%) (Fig. 5).

303 **4. Discussion**

304 *4.1. Fine root morphology, biomass and ectomycorrhizal short roots*

305 Silver birch fine root biomass per basal area in our study in northern Finland was somewhat higher than
306 that recorded in more southern forests. The fine root biomass ($D < 1$ mm) was about half of that of < 2
307 mm in D (Helmisaari et al., 2007; Leppälammı-Kujansuu et al., 2014a). On the basis of this relation, the
308 birch fine root biomass per stand basal area in our boreal site was estimated to be around twofold higher
309 than fine root biomass of roots of < 2 mm in D in SW Sweden on a hemi-boreal site (Hansson et al.,
310 2013). In another study established on a chronosequential series of silver birch stands in the temperate
311 zone, the fine root biomass per basal area varied from 66.8 to 86.2 g m⁻² ba⁻¹ (Varik et al., 2015), which
312 was much lower than ours (111.4 g m⁻² ba⁻¹), even with a criterion of $D < 2$ mm. Thus, studies on boreal
313 (this study), hemi-boreal (Hansson et al., 2013) and temperate (Varik et al., 2015) birch forests, support

314 the conclusion that the fine root biomass (< 1mm) per basal area gradually decreases from north to
315 south. According to Ostonen et al., (2017), the absorptive short root biomass of birch per basal area
316 remarkably increased along a climate gradient from southern temperate to northern boreal forest stands
317 in Europe, whereas the absorptive short roots in boreal forests were generally thinner and longer, with
318 higher tissue density, than those in temperate forests. In a root morphology study of 50 tree species,
319 Gu et al., (2014) showed that the root diameter has strong correlation with cortex thickness, the thinner
320 roots generally have thinner cortex, with higher absorptive capacity.

321 This study showed that the birch roots had more EcM short roots per root weight unit than spruce roots
322 in the adjacent stand (Leppälampi-Kujansuu et al., 2014a). This result was also confirmed by an earlier
323 study (Ostonen et al., 2007) at the same site. The higher number of EcM short roots per root weight unit
324 indicates that the Kivalo birch may also have a higher short root surface area per root weight unit, and
325 lower root tissue density than spruce, which means that birch has a more efficient foraging system than
326 spruce (Ostonen et al., 2007).

327 *4.2. Fine root longevity and litter production*

328 Fine root longevity was significantly affected by species (trees and understory), diameter and fine root
329 depth (Fig. 4, $P < 0.05$). At Kivalo, located in the boreal forest zone with a low annual average soil
330 temperature, the longevity of boreal forest species roots is normally longer, and roots are distributed
331 more widely in order to satisfy the demand for nutrients. The fine roots living in favorable soil conditions
332 (warm, moist, fertile soil) generally have a shorter longevity compared with roots in harsh soil conditions
333 (Majdi and Öhrvik, 2004; Helmisaari, et al., 2009b; Leppälampi-Kujansuu et al., 2013). The nutrient and
334 water content and microbial biomass gradually decrease with increasing soil depth, and the fine roots
335 living in the deeper soil layers may have longer longevity, as was confirmed by this study.

336 The diameter of birch fine roots also had positive correlations with root longevity in this study (Table 3).
337 Most of the birch fine roots belong to the 0.2-0.3 mm D class, whereas understory fine roots were in the
338 0-0.1 mm D class. We found a significant increase ($P < 0.05$) in the root longevity from D (0.2-0.3 mm)

339 to D (> 0.3 mm). However, there were no significant differences ($P > 0.05$) of fine root longevity between
340 D (0-0.2 mm) and D (0.2-0.3 mm) classes, this may be due to the fine root functional type: we would
341 consider most of these roots (0-0.3 mm in D) as absorptive roots. The thinner fine roots of the same
342 species tend to have a shorter longevity, which is in agreement with most of the fine root survival studies
343 in both boreal and temperate forest zones (Baddeley and Watson, 2005; Hansson et al., 2013;
344 McCormack et al., 2015; Liu et al., 2016; Gu et al., 2017). We defined the fine roots as the roots under
345 1 mm in D, but these roots still differ in functional and structural characteristics (Guo et al., 2008b). In
346 fact, Betulaceae roots less than 1 mm in D can contain roots up to the 5th order (Guo et al., 2008b). The
347 fine roots higher than the 3rd order are called transport fine roots, which have more woody tissue and
348 fewer absorption functions (Gu et al., 2014; McCormack et al., 2015). Short roots were defined as the
349 first- and second-order roots without secondary thickening, which is the most active part of the root
350 system (Ostonen et al., 2007; Ostonen et al., 2013). Thus, we analyzed the short roots separately and
351 estimated that they have a relatively shorter lifespan. Eissenstat et al. (2000) also reported that higher
352 order fine roots generally have longer longevity than first order roots without laterals. The first order
353 roots are thinner and contain more N in their tissue, indicating that they participate more in N uptake
354 (Pregitzer et al., 2002). Hitherto, only a few studies of fine root longevity have classified roots by orders
355 (Guo et al., 2008b; McCormack et al., 2015). Thus, root longevity studies by diameter classes may still
356 be globally the most widely used method. A combination of diameter-based and a functional
357 classification (orders, absorptive/transport roots, including the separation of ectomycorrhizal short roots)
358 may be a meaningful classification for fine roots of different tree species.

359 We found that the fine roots which were born earlier in the growing season (June to August) had a
360 significantly ($P < 0.05$) higher mortality hazard compared to roots born late in the growing season
361 (September to October). Aboveground parts such as leaves grow most in the early growing season
362 (McCormack et al., 2014), and thus are important aboveground C and nutrient sinks in spring and
363 summer. During the late growing season, the aboveground growth has gradually stopped (and leaves

364 have entered the stage of senescence), but roots continue growing. A study in a birch-aspen mixed
365 temperate forest confirmed that roots can grow for about one month longer than leaves (Du and Fang,
366 2014). Thus, the fine roots born in the late growing season may acquire more nutrients compared to
367 those born in the early growing season. Roots born in the late growing season having a longer lifespan
368 have also been reported from the temperate region (Eissenstat and Yanai, 1997; Anderson et al., 2003;
369 Gu et al., 2017), but in a sub-tropical pine plantation Guo et al. (2008a) found that roots born in winter
370 and spring had a longer lifespan than roots born in summer and autumn. In boreal forests, the roots
371 born in autumn may have more nutrients available (especially N) because of the higher rate of broad-
372 leaved litter decomposition in late summer. The better nutrient acquisition may increase fine root
373 longevity (Eissenstat and Yanai, 1997). One explanation to this phenomenon is that fine roots born in
374 the late growing season may have lower winter mortality, as confirmed by studies in north Sweden
375 boreal forest and northeastern China temperate forest (Andersson and Majdi, 2005, Gu et al., 2017).

376 Different tree species can have very different root longevities, but there are still many open questions
377 concerning the relationships between fine root morphology, physiological traits and longevity among
378 species (Augusto et al., 2015). Varying environmental factors such as soil temperature, moisture and
379 fertility may also contribute to fine root longevity (Huck et al., 1987, Eissenstat and Yanai, 1997, Majdi
380 and Öhrvik, 2004). The results showed that birch in our study had a shorter fine root lifespan than spruce
381 in the adjacent stand (Leppälampi-Kujansuu et al., 2014a). Even if these two stands were originally
382 established on the same site, after 70 years the birch stand had a lower soil C:N ratio and higher pH
383 compared to the spruce stand (Smolander and Kitunen, 2002). Studies from the hemi-boreal zone have
384 made similar observations: Saetre et al. (1997) reported deciduous (birch) litterfall to induce a higher
385 pH value and higher topsoil base saturation, leading to a high richness of vascular understory species
386 and a low amount of mosses in a deciduous mixed forest.

387 Hitherto, there are only a few studies of birch fine root longevity, especially in the boreal forest zone.
388 Some of the previous studies did focus on Betulaceae, but using sequential coring and ingrowth bags

389 (Yuan and Chen, 2010, Varik et al., 2015, Sun et al., 2015). Addo-Danso et al. (2016) indicated that the
390 variable methodologies can lead to great differences in the accuracy of the results, and the MR method
391 should be more accurate and efficient than the other methods. We found only one study using the MR
392 method which had compared fine root longevity between the three main boreal tree species (Scots pine,
393 Norway spruce and silver birch) in SW Sweden (Hansson et al., 2013). However, the birch fine root
394 longevity of trees in SW Sweden was over twofold longer than that of birch trees in northern Finland,
395 and the authors found no differences in fine root longevity between coniferous and deciduous tree
396 species or between tree species and understory vegetation (Hansson et al., 2013). These different
397 results were probably caused by the fact that the authors did not determine the root as dead until it had
398 disappeared (i.e. dead and decomposed) while we separated roots to dead and living. The high
399 proportion of censored roots (which lived until the final observation) in the study by Hansson et al. (2013)
400 may also influence the root longevity result, whereas we had only a few such roots. Another study in
401 north-eastern China used the sequential coring and ingrowth bags method to estimate the longevity of
402 white birch, and found that birch fine root longevity in the 82-year-old *Betula platyphylla* stand was 445
403 days (Sun et al., 2015), which is approximately 70 days longer than in our study. Considering the fact
404 that the annual air temperature in north-eastern China (0.5 °C) is close to that of Kivalo, and the stand
405 ages of the two stands are similar, the results may be comparable.

406 With the same site and environmental conditions, we found that the lifespan of understory fine roots in
407 the birch stand was consistent with the understory of the adjacent spruce stand (Leppälammi-Kujansuu
408 et al., 2014a). Furthermore, the understory fine root and rhizome lifespan was significantly ($P < 0.05$)
409 longer than that of tree species, which has been confirmed by only a few studies (Finér and Laine, 1998;
410 Hansson et al., 2013; Leppälammi-Kujansuu et al., 2014a; Huang et al., 2016). Several studies have
411 estimated longevity differences between trees and understory (Hansson et al., 2013; Leppälammi-
412 Kujansuu et al., 2014a; Huang et al., 2016), but most of these references were about coniferous tree
413 species, the fine roots of which have been shown to live longer than those of deciduous trees.

414 All the shrub and grass fine roots were combined as understory fine roots due to the difficulty of
415 identification on the MR analysis screens. However, shrub fine roots generally have a longer lifespan
416 than grasses due to the higher concentration of soluble phenolics in shrub fine roots (Peek et al., 2005;
417 Rodriguez et al., 2007; Huang et al., 2016). Therefore, researchers need to pay careful attention to the
418 arbitrary combination of shrub and grass vegetation in the future, which may lead to erroneous results
419 of longevity and annual productivity of understory.

420 *4.3. Above- and belowground annual C input*

421 Overall, the total annual soil C input in the birch stand was only slightly higher than that of the spruce
422 stand (Leppälammil-Kujansuu et al., 2014a), with a higher belowground and lower aboveground annual
423 litter input. Altogether 58 % of the annual total litter C input was from belowground in our birch stand, in
424 comparison to 43% in the spruce stand (Leppälammil-Kujansuu et al., 2014a). The main differences
425 between birch and spruce stands were in the longevity: the birch forest had a lower fine root longevity
426 compared to spruce. The shorter fine root longevity may be related to site fertility, as indicated by a
427 lower C:N ratio in the birch stand. The relationship between site fertility and fine root longevity has earlier
428 been confirmed by Majdi (2001) and Leppälammil-Kujansuu et al., (2014b).

429 The amount of above- and belowground litter input has also been shown to vary along latitude gradients.
430 Based on the shorter fine root longevity and a larger amount of fine root biomass in northern stands
431 (Varik et al., 2015; Ostonen et al., 2017), we may conclude that the belowground annual litter input is
432 higher compared to the aboveground in the northern boreal biome than in more southern areas. The
433 results of Kleja et al., (2008) from Swedish Norway spruce stands agree with this; the total below- and
434 aboveground litter production ratios of two northern stands (61–64 °N) were 1.1 and 1.3, whereas the
435 ratio of the southern stand (57 °N) was 0.9.

436 **5. Conclusions**

437 At our study site in the northern boreal forest zone, the silver birch fine root longevity was significantly
438 shorter than that of understory fine roots and rhizomes. The fine roots born in the late growing season

439 had a relatively smaller mortality hazard than those born in the early growing season. The annual
440 understory C input of above- and belowground litter was almost equal, comprising one third of the total
441 soil C input, whereas the belowground litter C input of birch was 1.7-fold higher than that of the
442 aboveground. The high ratio between below- and aboveground C input indicate that soil carbon in the
443 northern boreal deciduous forests may be relatively more of below- than aboveground origin. Future
444 studies on soil C input in the boreal forest zone should consider both understory and tree species,
445 above- and belowground.

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