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Author(s)	Fukuzawa, Karibu; Tateno, Ryunosuke; Ugawa, Shin; Watanabe, Tsunehiro; Hosokawa, Nanae; Imada, Shogo; Shibata, Hideaki
Citation	Oecologia, 196, 263-273 https://doi.org/10.1007/s00442-021-04914-x
Issue Date	2021-04-23
Doc URL	http://hdl.handle.net/2115/85066
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Type	article (author version)
Additional Information	There are other files related to this item in HUSCAP. Check the above URL.
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1 **Timing of forest fine root production advances with reduced snow cover in**
2 **northern Japan: Implications for climate-induced change in understory and**
3 **overstory competition**

4 Karibu Fukuzawa^{1*}, Ryunosuke Taten², Shin Ugawa³, Tsunehiro Watanabe⁴, Nanae
5 Hosokawa^{5,6}, Shogo Imada^{2,7}, Hideaki Shibata⁴

6 1) Nakagawa Experimental Forest, Field Science Center for Northern Biosphere, Hokkaido
7 University, 483 Otoineppu, Otoineppu, Hokkaido, 098-2501, Japan

8 2) Field Science Education and Research Center, Kyoto University, Oiwake-cho,
9 Kitashirakawa, Sakyo-ku, Kyoto, 606-8502, Japan

10 3) Faculty of Agriculture, Kagoshima University, 1-21-24 Korimoto, Kagoshima, 890-0065,
11 Japan

12 4) Field Science Center for Northern Biosphere, Hokkaido University, N9W9, Kita-ku,
13 Sapporo, Hokkaido, 060-0809, Japan

14 5) Graduate School of Environmental Science, Hokkaido University, N9W9, Kita-ku,
15 Sapporo, Hokkaido, 060-0809, Japan

16 6) Institute for Agro-Environmental Sciences, NARO, 3-1-3 Kannondai, Tsukuba, Ibaraki,
17 305-8604, Japan

18 7) Institute for Environmental Sciences, Ienomae, Obuchi, Rokkasho-mura, Kamikita-gun,
19 Aomori, 039-3212, Japan

20 **ORCID**

21 Karibu Fukuzawa 0000-0002-1490-2406

22 Ryunosuke Taten 0000-0001-8461-3696

23 Nanae Hosokawa 0000-0003-2336-0570

24 Hideaki Shibata 0000-0002-8968-3594

25 *Corresponding author: Karibu Fukuzawa, Nakagawa Experimental Forest, Field Science Center for Northern
26 Biosphere, Hokkaido University, 483 Otoineppu, Otoineppu 098-2501, Japan. E-mail: caribu@fsc.hokudai.ac.jp;
27 Tel: +81-1656-5-3216; Fax: +81-1656-5-3218

28 Author Contributions: Hideaki Shiba and Ryunosuke Taten conceived and designed the experiment. Karibu
29 Fukuzawa and Shin Ugawa developed methodology. Tsunehiro Watanabe, Nanae Hosokawa, Shogo Imada, and
30 Karibu Fukuzawa conducted fieldwork. Karibu Fukuzawa wrote the manuscript; other authors provided editorial
31 advice.

32 **Abstract**

33 To investigate the effect of reduced snow cover on fine root dynamics in a cool-temperate
34 forest in northern Japan because of decreases in snowfall at high latitudes due to global
35 warming, we monitored root length, production, and mortality before and after snow removal
36 with an in-ground root scanner. We measured root dynamics of both overstory deciduous oak
37 (*Quercus crispula*) and understory evergreen dwarf bamboo (*Sasa nipponica*), the two major
38 species in the forest. Snow removal advanced the timing of peak root production by a month
39 both in total and in *Sasa*, but not in oak. There was a significant interaction between snow
40 removal and plant form on root production; this indicates that enhanced *Sasa* root production
41 following snow removal might increase its ability to compete with oak. In contrast, snow
42 removal did not enhance root mortality, suggesting that the roots of these species tolerate soil
43 freezing. The earlier snow disappearance in the snow removal plot expanded the growing
44 season in *Sasa*. We speculate that this change in the understory environment would advance
45 the timing of root production by *Sasa* by extending the photosynthetic period in spring. We
46 propose that different responses of root production to reduced snow cover between the two
47 species would change the competitive interactions of overstory and understory vegetation,
48 influencing net primary production and biogeochemistry (e.g., carbon and nitrogen cycles) in
49 the forest ecosystem.

50 **Key words:** snow removal, soil freezing, fine root mortality, growing season, root scanner

51 **Introduction**

52 Fine roots (generally <2 mm in diameter) play a significant role in carbon (C) and nutrient
53 cycling in forest ecosystems owing to their rapid turnover, and contribute 30% to 40% of the
54 total net primary production of forests (Jackson et al. 1997; Tateno et al. 2004; Fukuzawa et al.
55 2013). Plants take up nutrients via their fine roots and supply organic matter, C and nutrients
56 to soils via root death and decomposition. Therefore, fine root dynamics, which we define as
57 the timing of fine root production and mortality, decomposition, and turnover, may influence
58 not only annual but also seasonal changes in C and nutrient dynamics in forest ecosystems,
59 though reports of these belowground processes are limited.

60 The response of ecosystem process in forests to global climate change has become a
61 focus of research. Decreases of snowfall at high latitudes due to global warming are expected
62 (IPCC 2014), and the consequent decreased snowpack, which insulates soil against frost, will
63 allow the soil to cool further and accelerate the soil freeze–thaw cycle during winter.

64 Increased soil inorganic nitrogen (N) content and stimulated soil microbial N mineralization
65 (ammonium production) under intensive freeze–thaw cycling have been shown in snow
66 removal studies and inter-translocation experiments in many snowy forest ecosystems
67 (Groffman et al. 2001a, b, 2011; Freppaz et al. 2008; Shibata et al. 2011, 2013; Zhou et al.
68 2011; Urakawa et al. 2014; Watanabe et al. 2019). Those studies identified the freezing death
69 of roots and soil microbes, which provide organic N, substrates for N mineralization, and the
70 consequent reduction of N uptake by plants due to reduced root biomass after snow removal.
71 Such root–microbe interactions are important in the forest N cycle (Sorensen et al. 2016).

72 Tierney et al. (2001) reported the promotion of fine root mortality during spring by snow
73 removal and compensatory fine root production during the following growing season in a
74 hardwood forest in the north-eastern USA. The timing of fine root production, rather than just
75 the amount, would be vital information for identifying the temporal dynamics of soil N
76 availability via changes in the timing of nutrient and water uptake caused by a decline in the
77 snowpack (Tierney et al. 2001; Cleavitt et al. 2008; Groffman et al. 2011). However, the
78 response of fine roots to reduced snowpack is poorly known, because reports are limited and
79 most studies have considered the freezing effect exclusively, despite multiple possible
80 responses of fine roots to reduced snow cover (e.g., extended growing season). In addition,
81 reports in snowy regions in East Asia where the climate is milder than the Arctic are lacking.

82 Finér et al. (2011) proposed that fine roots of understory vegetation should be taken into
83 account for precise estimation of the overall fine root dynamics in forest ecosystems. In cool-
84 temperate forest in northern Japan, coverage of the forest floor by dense understory dwarf
85 bamboo (*Sasa* spp.) is characteristic; it grew in 89% of all forested area on Hokkaido,
86 northernmost Japan (Toyooka, 1983), and has a larger fine root biomass than that of trees
87 (Fukuzawa et al. 2013, 2015). These facts suggest that understory *Sasa* is the major
88 component below the ground even in forest ecosystems. In natural forests where multiple tree
89 species co-exist, most studies have evaluated the overall fine root dynamics, because it is hard
90 to distinguish roots by species in image analysis. But if the fine root dynamics of different
91 individual species (e.g., oak and *Sasa*) or functional types which are defined as sets of species
92 with similar responses to the environment and with similar effects on ecosystem functioning
93 (e.g., deciduous overstory and evergreen understory species) can be determined, their
94 mechanisms and those of nutrient dynamics in forests with multiple species could be
95 identified more precisely under environmental change (e.g., decreased snowpack). Oak–*Sasa*
96 ecosystems are typical in secondary forests in eastern Hokkaido, Japan. This simple
97 ecosystem, with just two components, is suitable for identifying fine root dynamics of

98 different functional types.

99 Here we manipulated snow cover to expose roots to colder temperatures during winter
100 and investigated the effect on fine root dynamics by using scanner observation of fine roots
101 before and after snow removal in an oak–*Sasa* forest in northern Japan. We quantified the fine
102 root dynamics of the two species separately. We hypothesized that (1) decreased snow cover
103 causes the earlier disappearance of the snowpack, and the fine root responses to the extended
104 growing season (e.g., advanced or increased root production) differ between overstory
105 deciduous trees and understory evergreen plants; and that (2) intensive soil freezing due to
106 reduced snow cover causes more fine root mortality during winter, so subsequent fine root
107 production is altered in both species through compensatory root growth.

108 **Materials and methods**

109 **Study site**

110 We conducted the study in a cool-temperate, natural, deciduous broadleaved forest of the
111 Shibeche branch of the Hokkaido Forest Research Station, Field Science Education and
112 Research Center, Kyoto University, Japan (43°24.2' N, 144°38.5' E). The mean annual air
113 temperature and precipitation from 1986 to 2015 were 6.3 °C and 1189 mm at the
114 meteorological station 9 km south of the site (43°19.46' N, 144°36.8' E; Kyoto University
115 Forests 2016). The mean monthly air temperatures range from –9.0 °C in January to 19.8 °C
116 in August with minimum and maximum records of –31.7 °C in February and 36.0 °C in
117 August. The monthly precipitation ranges from 31 mm in February to 182 mm in September.
118 The mean annual maximum snow depth was 64 cm (range, 21 to 135 cm), in the late February
119 to the middle of March. The soil freezes from December to May. The soils of this study area
120 are characterized as Andosols (IUSS Working Group WRB 2015) with a clay-loam to loam
121 texture. We established study plots in October 2013 in a stand dominated almost 100% by
122 *Quercus crispula* with a diameter at breast height of ~30 cm. The understory layer is
123 completely covered with dense *Sasa nipponica* 80–100 cm tall.

124 **Snow removal**

125 We established snow removal (REM) and control (CON) plots with four replications each in
126 the stand. We set up each plot (5 m × 12 m) surrounding a target oak tree. The stand includes
127 east- and west-facing gentle slopes, so we set REM and CON plots evenly on both slopes
128 (Watanabe et al. 2019). In REM plots, we removed snowpack manually by shovel from late
129 December to late March during the winter of 2014–15. We left the bottom 10–20 cm of snow

130 in REM plots to minimize damage to the understory vegetation (e.g., *S. nipponica*), which
131 were laying down beneath the snowpack. Snowpack depth in REM and CON plots is shown
132 in Fig. 1 (Hosokawa et al. 2017; Watanabe et al. 2019).

133 **Environmental conditions**

134 We measured snowpack depth at three points in each plot by inserting meter sticks vertically
135 into the snow. The soil temperature at 0 cm depths of the mineral soil in each plot was
136 measured at 30-minute intervals by thermal sensors (TR-51 and TR-52, T & D Corp.,
137 Matsumoto, Japan and CO-UA-001, Onset Computer, Bourne, MA, USA). The frozen depth
138 of the soil was measured using frost tubes made from acrylic tubes filled with methylene blue
139 dye that were covered with polyvinyl chloride (PVC) tubes inserted into the soil in each plot.
140 Details of measurement of environmental conditions described above and of soil gravimetric
141 and volumetric water contents in the study area are reported in Watanabe et al. (2019).

142 **Root observation and image analysis**

143 We imaged roots using a before–after control–impact design (Tateno et al. 2019). We used an
144 A4-size flatbed document scanner to record fine roots (Dannoura et al. 2008). In October
145 2013 we built transparent acrylic rhizo-boxes (296 mm × 379 mm × 46 mm, 3 mm walls) in
146 which to set the scanner and installed them on site. One box was installed in the soil 2 m from
147 each oak tree. Although a large flat area may be a less natural environment in soil for root
148 growth than a cylindrical minirhizotron, the flatbed scanner captures a larger image than a
149 minirhizotron (Dannoura et al. 2008). Each box was installed vertically into the soil to allow
150 the soil profile to be scanned. We began scans in April 2014 to allow roots to regrow. From
151 April 2014 to November 2015 we set the scanner (GT-S630, Epson Corp., Tokyo, Japan) into
152 each rhizo-box on each observation date and scanned the soil profile in 24-bit color at 300-dpi
153 resolution. Scans were made every 1 to 1½ months during the growing season and every 2 to
154 3 months during the dormant season in 2014 (5 dates in total), and every 10 days from May to
155 July 2015 and monthly thereafter (13 dates in total).

156 A major constraint in root image analysis is the manual analysis of the images, which can
157 be very elaborate and time consuming. To minimize the image analysis work, we analyzed a
158 limited area measuring 5 cm wide from 1 to 9 cm below the surface. We analyzed only the
159 top layer because it is most strongly influenced by frost and has the most concentrated fine
160 roots. In the total 158 images captured, we measured the length and diameter of each
161 individual root in root image analysis software (Win Rhizotron 2015a, Regent Instruments
162 Inc., Quebec, QC, Canada). We classified brown (woody) roots as oak and white (herbaceous)

163 roots as *Sasa* (Fukuzawa et al. 2010). The understory at this site is nearly 100% *Sasa*, so we
164 regarded all non-woody roots as *Sasa*. All lengths were converted to root length density
165 (RLD: mm cm⁻² of image). The diameters of all the roots observed were less than 2 mm. We
166 defined fine root production as the sum of the length of new roots and the length extension of
167 existing roots in the images during each interval. We defined fine root mortality as the sum of
168 the length of roots that disappeared in the images during each interval. Annual fine root
169 production and mortality were the cumulative values of each interval in each year. We
170 standardized fine root production and mortality rates by dividing the respective absolute
171 values by the number of days in each interval (mm cm⁻² d⁻¹). We omitted data in one plot in
172 REM in June and August 2014 owing to a failure of image capture. We then calculated
173 proportional fine root production and mortality as the ratio of each in each interval to the
174 respective annual values.

175 **Statistical analysis**

176 We compared differences in proportional fine root production and mortality of all plants in
177 each interval among treatments by *t*-test after logit-transformation before analysis (Ashbeck
178 and Bell, 2016). If normality of the distribution was violated, we used the Wilcoxon rank sum
179 test. We compared RLD and the proportional and absolute fine root production and mortality
180 of all roots in each interval among the treatments using multiple testing in 2014 (*n* = 5) and
181 2015 (*n* = 13) based on the adaptive Benjamini–Hochberg procedure (Benjamini and
182 Hochberg 2000) to control the false discovery rate, as is used for repeated measures data and
183 is effective in the condition of high correlation (Stevens et al., 2017). In the procedure, we
184 assigned a *P* value that was ‘significant’ under a *q* value of 0.05.

185 We used a general linear mixed model (GLMM) with a gamma error distribution and a log
186 link to analyze the effects of treatment (snow removal), form (*Sasa* or oak), and occasion
187 (observation time) on RLD and on fine root production rate in 2014 (before treatment) and
188 2015 (after treatment). We specified treatment, form, occasion, and their interactions as fixed
189 effects and the plot (block) as a random effect. We used a general linear model (GLM) with a
190 gamma error distribution and an inverse link to analyze the effects of treatment, form, and
191 their interaction on annual fine root production and mortality in 2014 and 2015. We
192 determined the significance of each fixed effect using analysis of deviance (type II test). We
193 also compared annual fine root production and mortality of all plants, *Sasa*, and oak, and RLD
194 and fine root production and mortality rates of all plants in each observation interval between
195 treatments using the GLM. Analyses were performed in R software (v. 4.0.2; R Core Team

196 2020).

197 **Results**

198 **Snowpack depth and soil environment**

199 Snow removal decreased the snowpack throughout the winter, and the snowpack disappeared
200 a month earlier in REM than in CON (Watanabe et al. 2019; Fig. 1). The soil temperature
201 during the snowmelt season remained steady in CON but showed recurrent soil freezing–
202 thawing in REM (Watanabe et al. 2019; Fig. 2). However, soil temperature in REM remained
203 low (<5 °C), and reached 5 °C on the same date as in CON (22-Apr-2015).

204 **RLD and fine root production**

205 Root length density (RLD) showed a clear seasonal pattern, with an increase during the
206 growing season (June to October) and a slight decrease during the dormant season (Fig. 3).
207 There was no significant difference in total RLD between snow removal treatments either
208 before or after snow removal. The GLMM analysis showed significant effects of occasion in
209 both years and a significant effect of treatment × plant form in 2015 (the year of snow
210 removal, Table 1), as confirmed by the lower RLD in oak in REM (Fig. 3). No significant
211 treatment × occasion interaction was detected.

212 Root production had a clear seasonal pattern, with a unimodal peak in midsummer (early
213 June to November) in both treatments (Fig. 4). Before snow removal (2014), the temporal
214 pattern of root production was similar between snow removal treatments, with no significant
215 difference. There was little root production during winter. After snow removal, the timing of
216 the onset of root production did not differ significantly between snow removal treatments as
217 the onset was in early June, but thereafter root production was significantly higher in early
218 July and significantly lower in late August in REM than in CON (Fig. 4), indicating that snow
219 removal shifted root production earlier.

220 *Sasa* root production was higher in REM than in CON and peaked earlier in REM after
221 snow removal in 2015, although no early summer peak was observed in either treatment
222 before snow removal in 2014 (Figs. 2b, 5b). On the other hand, oak root production peaked in
223 August in both plots both before and after snow removal (Fig. 5c). The GLMM analysis
224 showed significant effects of occasion in both years and a significant effect of treatment ×
225 plant form in 2015 (Table 1), as confirmed by the higher root production in *Sasa* in REM (Fig.
226 5b). No significant treatment × occasion interaction was detected.

227 Total annual root production did not differ significantly between treatments either before or

228 after snow removal (Table 2). GLM showed no significant effect on annual root production
229 by snow removal, but the treatment \times plant form interaction was significant in 2015,
230 indicating that the snow removal effect differed among forms. In *Sasa*, root production was
231 higher in REM than in CON in 2015 (Fig. 5b; Table 2).

232 **Fine root mortality**

233 There was no significant difference in root mortality rate on each date between REM and
234 CON even after snow removal (Fig. 6). Proportional root mortality showed a seasonal trend of
235 high mortality during the dormant period (October to April) and low mortality during spring–
236 early summer (May to June; Fig. S1). There was no significant difference between treatments
237 for proportional root mortality on any date. Annual root mortality (total, *Sasa*, and oak) did
238 not differ significantly between treatments either before or after snow removal, and there was
239 no significant effect of snow removal, plant form, or their interaction on annual root mortality
240 (Table 2).

241 **Discussion**

242 **Advanced timing of peak fine root production by snow removal**

243 Snow removal advanced the timing of peak root production by a month, from late July to late
244 June and early July (Figs. 4, 5a). This result is consistent with our first hypothesis, that
245 decreased snow cover causes the earlier disappearance of the snowpack, and the roots respond
246 to the extended growing season (e.g., advanced root production depending on plant species).
247 The midsummer peak in CON was found in previous studies in a cool-temperate forest in
248 northern Hokkaido (Fukuzawa et al. 2013) or in boreal or cool-temperate forests in Alaska,
249 Canada, and north-eastern USA (Steele et al. 1997; Ruess et al. 1998; Tierney et al. 2003). On
250 the other hand, the advance of peak root production by snow removal was also reported in a
251 hardwood forest in the north-eastern USA, where Tierney et al. (2001) suggested the
252 possibilities of both exogenous (i.e., increased soil N availability) and endogenous (such as
253 compensatory effect) triggers in response to increased root mortality. At our site, the
254 similarity of soil environment (temperature, moisture, and NH_4^+ and NO_3^- availability) during
255 the subsequent growing season between the treatments (Watanabe et al. 2019) suggests that
256 exogenous factors were uniform among treatments, although it remains unclear whether
257 increased NH_4^+ availability during the snowmelt period influences N uptake by vegetation. In
258 addition, a compensatory effect is not likely, because root mortality was not affected by snow
259 removal at our site as discussed in *Fine root mortality was not increased by snow removal*

260 section.

261 The separation of root dynamics by plant type showed that the timing of peak root
262 production of *Sasa* was advanced and the amount increased (Fig. 5a, b), indicating that the
263 advance of root production is attributable to that of *Sasa* root production. In contrast, the
264 timing of oak root production did not change, and root production was lower in REM than in
265 CON (Fig. 5c). Being an evergreen perennial plant, *Sasa* is ready to initiate photosynthesis
266 while the overstory deciduous trees are leafless (Lei and Koike 1998); thus, not only the
267 belowground response but also the aboveground response to snow removal should be taken
268 into account. Root production is considered to peak after leaf production, less so in grasses
269 than in woody plants, owing to the difference in the reliance of their root growth on supply of
270 newly produced photosynthates (Steinaker et al. 2010). Abramoff and Finzi (2015) reported,
271 in a literature review, that average root growth lags behind shoot growth by several weeks in
272 boreal and temperate biomes, although it occurs before shoot growth in subtropical forests. In
273 CON, the peak of root production of *Sasa* was similar to that of oak (Fig. 5b, c). The pattern
274 of root production in *Sasa* in our study, despite its being a grass, would relate to its change
275 from gradual in early summer to intensive leaf expansion in midsummer, as suggested by a
276 study conducted in a cool-temperate forest covered with *Sasa senanensis* in northern Japan
277 (Fukuzawa et al. 2013).

278 At the same site, Tateno et al. (2019) suggested that increased aboveground production
279 and N uptake by *Sasa* in the growing season following snow removal could be due to the
280 production of more carbohydrates owing to the earlier onset of photosynthesis, because the
281 spring period before leaf flush of overstory trees is important for understory *Sasa* to get light
282 (Lei and Koike 1998). In their study, the onset of and seasonal change in its aboveground
283 biomass production and N in biomass were the same between treatments before July, but
284 differed gradually between treatments after July until midautumn with significant interaction
285 effect between treatment and occasion, indicating that shoot elongation and leaf expansion
286 would continue under favorable carbohydrate and nutritional conditions (Tateno et al. 2019).
287 On the other hand, snow removal advanced the timing of active root production by a month,
288 as evidenced by the significant difference between treatments in early July (Fig. 4). Although
289 there was no significant treatment \times occasion interaction in the GLMM analysis, we speculate
290 that this shift in root production and active N uptake is essential for producing further
291 aboveground parts because of the high uptake capacity of newly emerged roots (Volder et al.
292 2005) or the earlier initiation of N uptake in evergreen plants (Larsen et al. 2012). A positive
293 effect of snow removal on *Sasa* root production, as shown by the significant treatment \times plant

294 form interaction (Tables 1, 2), and increased aboveground production of *Sasa* (Tateno et al.,
295 2019) are the evidences for a tight interaction above and below ground in response to the
296 change of understory environment after snow removal.

297 **Limited effects on fine root production and timing of its onset by snow removal**

298 Snow removal did not substantially affect annual root production (Fig. 5; Tables 1, 2), in
299 contradiction of our hypothesis that root production increases through compensatory root
300 growth. Tierney et al. (2001) suggested the occurrence of compensatory root production after
301 an increase in root mortality due to soil freezing by snow removal in a hardwood forest in the
302 north-eastern USA. However, our results revealed that root mortality was not significantly
303 stimulated by snow removal, as discussed below, and so root production was not stimulated
304 either. On the other hand, there was a significant effect of snow removal \times plant form on
305 annual root production after the treatment (in 2015) in the GLM, indicating different effect on
306 *Sasa* and oak (Tables 1, 2). This positive effect on *Sasa* is consistent with the advance of root
307 production in *Sasa* by snow removal (Fig. 5b).

308 Root production was re-initiated in early June in both treatments (Fig. 4). In a boreal
309 forest in northern Sweden, soils remained frozen longer in spring in plots with snow removal
310 (Blume-Werry et al. 2016). At our site, in contrast, soil freezing ended earlier in spring in
311 plots with snow removal. This difference may be attributable to the milder winter climate at
312 our site than in the Arctic. Although the snowpack disappeared and the soil temperature began
313 to increase nearly a month earlier in the REM plots than in the CON plots, it remained low
314 ($<5\text{ }^{\circ}\text{C}$) in the REM plots while the snowpack melted because of the low air temperature
315 during early spring, and there was no significant difference between treatments after the
316 snowpack had disappeared in the CON plots (Fig. 2; Watanabe et al. 2019; Tateno et al. 2019).
317 The lower limit for active belowground physiological processes (e.g., root growth) is
318 considered to be $5\text{ }^{\circ}\text{C}$ (Kozłowski and Pallardy 1997), but has been reported to be 2.3 to
319 $4.2\text{ }^{\circ}\text{C}$, depending on the tree species, perhaps in relation to their natural elevation limits
320 (Schenker et al., 2014). However, a minor change in soil temperature in the range of lower
321 limit by the advance of snowmelt in our study did not influence the timing of the onset of root
322 production, and the timing would have occurred >1 month later at the onset of leaf expansion,
323 which was not changed by snow removal in either species (Tateno et al. 2019).

324 Soil moisture also regulates root production (Joslin et al., 2001) and it has been suggested
325 that loss of the snowpack will decrease later water availability for plants (Hardy et al. 2001).
326 However, Watanabe et al. (2019) reported that the soil gravimetric water content at our site

327 during the soil freezing period was higher in the snow removal plots than in the control plots
328 despite the removal of snowpack water, and suggested the upward movement of soil water
329 from deeper layers caused by an increase in capillary power among soil particles and ice
330 when the soil freezes; thus, after the soil thawed in spring, the soil volumetric water content in
331 the REM plots was consistent with that in the CON plots. Thus, the negative effect of snow
332 removal on soil moisture is not likely at our site.

333 **Fine root mortality was not increased by snow removal**

334 Snow removal did not increase root mortality either in total or by species (Fig. 6; Table 2).
335 We did not find any effects of snow removal, plant form, or their interaction on annual root
336 mortality, so snow removal does not affect the root mortality of either plant form (Table 2).
337 This result contradicts our second hypothesis that intensive soil freezing due to reduced snow
338 cover causes more root mortality during winter, and the results in a hardwood forest in the
339 north-eastern USA (Tierney et al. 2001) and in a Norway spruce forest in Germany (Gaul et al.
340 2008). In contrast, Repo et al. (2014) reported greater root longevity in plots with snow
341 removal in Norway spruce forest in Finland, suggesting that roots are not damaged by soil
342 freezing. Our site is located in a cold area in northern Japan with a small amount of snow and
343 thus regular soil frost. It is possible that the trees in this region, including *Q. crispula*, are
344 tolerant to soil freezing. Calme et al. (1994) suggested that red oak (*Quercus rubra* L.) is less
345 tolerant to soil freezing than are yellow birch and sugar maple in Canada, and Morin et al.
346 (2007) found variation in cold hardiness among three European oak species. These results
347 suggest that cold hardiness is species-dependent, even within oak. The leaves of the evergreen
348 *S. nipponica*, which is distributed in less snowy areas, have a shorter lifespan than those of
349 *Sasa* species distributed in heavily snowed areas in Japan, so a proportion of its leaves may
350 die during winter (Kayama and Koike 2018). But the distribution of *S. nipponica* corresponds
351 with a snow depth of <75 cm in this region, and this species is tolerant to cold temperatures,
352 because its shoots emerge below ground (Kayama and Koike 2018). Thus, *S. nipponica* also
353 might have a strategy to survive in frozen soil. The high tolerance of both species to soil
354 freezing might thus explain the lack of a significant increase in root mortality in our results.
355 But as Tierney et al. (2001) suggested, how roots are killed in frozen soil should be
356 investigated.

357 **Ecological implications**

358 Our separation of root dynamics by species can provide useful insight into belowground
359 responses to environmental change. In addition, technical innovations in the analysis of root

360 images will remove constraints on separation by species in forests with more species.

361 Our results highlight the distinct responses of understory *Sasa* and overstory oak to snow
362 removal, namely the earlier root production by *Sasa* but not oak. The importance of
363 understory vegetation in C and nutrient cycling in boreal and temperate forests is widely
364 recognized (Nilsson and Wardle 2005; Moore et al. 2007; Finér et al. 2011; Blume-Werry et
365 al. 2016). In cool-temperate forests in northern Japan, understory *Sasa* dwarf bamboo is a
366 major component of ecosystems, especially its roots, which comprise 60% to 80% of the total
367 root biomass (Fukuzawa et al. 2013, 2015). At our study site, *Sasa* roots accounted for 31%
368 of total root length density in CON and 52% in REM (data not shown), and *Sasa* root biomass
369 accounted for 35% of the total (Hosokawa et al. 2020), indicating that *Sasa* is a major
370 component of the root system in this forest, and that the change of root dynamics of *Sasa* by
371 reduced snow influences that of the whole forest ecosystem.

372 The change in the timing of peak root production might be attributable to the change in
373 the timing of the snow disappearance rather than in soil freezing itself, because there was no
374 significant increase in root mortality after snow removal. Reduced snow cover could change
375 root production in several scenarios. Our study is consistent with that of D'Imperio et al.
376 (2018), who suggested that increased snow accumulation reduces root production by reducing
377 the growing season length in an Arctic wetland in Greenland. In contrast, Kreyling et al.
378 (2012) reported a negative effect of reduced snowpack on aboveground parts and root
379 biomass of understory vegetation due to direct frost damage of roots and shoots in Sweden.
380 We found a positive effect in terms of the phenology of the understory vegetation. Therefore,
381 the difference in the response of roots to reduced snow would depend on plant tolerance to
382 freezing, the severity of freezing during winter, and the length of the subsequent growing
383 season for understory vegetation (Marumo et al. 2020). In our study, the high abundance of
384 the evergreen *S. nipponica*, which is tolerant to soil freezing, in a forest with mild soil
385 freezing would explain the positive response of the roots to reduced snow. Multiple
386 belowground responses to reduced snow cover might be possible, and further studies that
387 consider vegetation changes will be necessary.

388 Our results also support the importance of interactions between aboveground and
389 belowground organs and of C and N demand in the understory vegetation after the snowpack
390 change, as suggested by Tateno et al. (2019), who suggested N limitation for canopy trees
391 after snow removal due to increased N uptake by understory *Sasa*. Changes in competition for
392 resources between overstory trees and understory vegetation would change not only
393 productivity above and below ground but also ecosystem biogeochemical cycles under

394 climate change (Cleavitt et al. 2008; Groffman et al. 2011; Kreyling et al. 2012, 2015).

395 Uncertainties remain. First, we removed snow in only one winter and observed root
396 dynamics over just one year. Blume-Werry et al. (2016) suggested that the effects of short-
397 term and long-term snow removal are not the same, even though one extreme winter with
398 reduced snow cover can certainly alter root dynamics and aboveground responses. In addition,
399 although we detected a significant snow removal \times plant form interaction, which indicates a
400 positive effect on root production of *Sasa*, if aboveground production increased, root
401 production in the next year might increase further, because aboveground and belowground
402 production are linked (Aragao et al. 2009). Furthermore, root production may fluctuate
403 annually owing to variations in climate (e.g., snowpack, temperature, precipitation, solar
404 radiation; Xu et al. 2012). Thus, a long-term perspective on the effect of decreased snow on
405 root dynamics will be necessary.

406 Second, we investigated a simple ecosystem composed of oak and bamboo. Although
407 these are key species in cool-temperate forests in this region, the response of more species to
408 reduced snow cover needs to be investigated. Nevertheless, our study demonstrates distinct
409 responses of root dynamics to reduced snow cover between understory and overstory
410 vegetation and proposes changes in interactions between them under climate change.

411 **Conclusion**

412 Reduced snow cover did not change total root mortality or production but did advance the
413 timing of peak root production by a month in a cool-temperate forest composed of oak and
414 *Sasa*. The advanced patterns of both total and *Sasa* root production and the increased amount
415 in *Sasa* root production after snow removal suggest that *Sasa* root production governs the
416 total root production pattern, and highlights the importance of distinct responses among
417 functional type (i.e., overstory tree and understory bamboo) to decreased snow cover. We
418 propose that a change in the competitive interaction between trees and understory caused by
419 snow cover reduction would influence net primary production and biogeochemical cycles in
420 forest ecosystems under climate warming.

421 **Acknowledgements**

422 We thank Takayuki Yamauchi, Yasuyuki Shibata, Tomoyuki Nakagawa, Ken-ichi Ohta,
423 Yohichiro Kitagawa, Yasunori Kishimoto, and Makoto Fruta, the technical staff of the
424 Hokkaido Forest Research Station, Field Science Education and Research Center, Kyoto
425 University, for their great efforts in snow removal and maintenance of the study site; Michiko

426 Shimizu and Masataka Nakayama (Kyoto University) for their help with image analysis;
427 Sanae Yanagawa and students of the Graduate School of Environmental Science, Hokkaido
428 University, for their help with the field survey; Drs. Tomoki Oda, Takuo Hishi, Yoshiyuki
429 Inagaki, Kazuo Isobe, Megumi Kuroiwa, Toshizumi Miyamoto, Takahiro Sasai, Yuichi Suwa,
430 Hiroto Toda, and Rieko Urakawa, members of the RESIN-III (Regional and Comparative Soil
431 Incubation Study on Nitrogen Dynamics in Forest Ecosystems) project, for their valuable
432 comments; and Dr. Kazuya Kobayashi (Kyoto University) for help with the statistical analysis.
433 This study was supported in part by JSPS KAKENHI (25252026 and 17K07830).

434

435 **Declarations**

436 **Conflict of interest** The authors declare that they have no conflicts of interest.

437

438 **Availability of data and material** Root dynamics data are available at
439 http://db.cger.nies.go.jp/JaLTER/metacat/metacat/Shibecha_Shiranuka.1.10/jalter-en

440

441 **Author contribution statement** HS and RT conceived and designed the experiment. KF and
442 SU developed methodology. TW, NH, SI, and KF conducted fieldwork. KF wrote the
443 manuscript; other all authors provided editorial advice.

444

445 **References**

446 Abramoff RZ, Finzi AC (2015) Are above- and below-ground phenology in sync? *New*
447 *Phytol* 205:1054–1061

448 Aragao L, Malhi Y, Metcalfe DB, Silva-Espejo JE, Jimenez E, Navarrete D, Almeida S,
449 Costa ACL, Salinas N, Phillips OL, Anderson LO, Alvarez E, Baker TR, Goncalvez PH,
450 Huaman-Ovalle J, Mamani-Solorzano M, Meir P, Monteagudo A, Patino S, Penuela MC,
451 Prieto A, Quesada CA, Rozas-Davila A, Rudas A, Silva JA, Vasquez R (2009) Above-
452 and below-ground net primary productivity across ten Amazonian forests on contrasting
453 soils. *Biogeosciences* 6:2759–2778 doi: 10.5194/bg-6-2759-2009

454 Ashbeck EL, Bell ML (2016) Single time point comparisons in longitudinal randomized
455 controlled trials: power and bias in the presence of missing data. *BMC Med Res*
456 *Methodol* 16:43 doi:10.1186/s12874-016-0144-0

457 Benjamini Y, Hochberg Y (2000) On the adaptive control of the false discovery rate in
458 multiple testing with independent statistics. *J Educ Behav Stat* 25:60–83 doi:
459 10.3102/10769986025001060

460 Blume-Werry G, Kreyling J, Laudon H, Milbau A (2016) Short-term climate change
461 manipulation effects do not scale up to long-term legacies: effects of an absent snow
462 cover on boreal forest plants. *J Ecol* 104:1638–1648 doi:10.1111/1365-2745.12636

463 Calme S, Bigras FJ, Margolis HA, Hebert C (1994) Frost tolerance and bud dormancy of
464 container-grown yellow birch, red oak and sugar maple seedlings. *Tree Physiol* 14:1313-
465 1325 doi:10.1093/treephys/14.12.1313

466 Cleavitt NL, Fahey TJ, Groffman PM, Hardy JP, Henry KS, Driscoll CT (2008) Effects of
467 soil freezing on fine roots in a northern hardwood forest. *Can J For Res* 38: 82–91
468 doi:10.1139/x07-133

469 Dannoura M, Kominami Y, Oguma H, Kanazawa Y (2008) The development of an optical
470 scanner method for observation of plant root dynamics. *Plant Root* 2:14–18 doi:
471 10.3117/plantroot.2.14

472 D’Imperio L, Arndal MF, Nielsen CS, Elberling B, Schmidt IK (2018) Fast responses of root
473 dynamics to increased snow deposition and summer air temperature in an Arctic wetland.
474 *Front Plant Sci* 9 doi: 10.3389/fpls.2018.01258

475 Finér L, Ohashi M, Noguchi K, Hirano Y (2011) Fine root production and turnover in forest
476 ecosystems in relation to stand and environmental characteristics. *Forest Ecol Manag*
477 262:2008–2023 doi:10.1016/j.foreco.2011.08.042

478 Freppaz M, Celi L, Marchelli M, Zanini E (2008) Snow removal and its influence on
479 temperature and N dynamics in alpine soils (Vallée d’Aoste, northwest Italy). *J Plant*
480 *Nutr Soil Sci* 171:672–680 doi:10.1002/jpln.200700278

481 Fukuzawa K, Dannoura M, Kanemitsu S, Kosugi Y (2010) Seasonal patterns of root
482 production of Japanese oak seedlings and dwarf bamboo grown in rhizoboxes. *Plant*
483 *Biosyst* 144:434–439 doi: 10.1080/11263501003725971

484 Fukuzawa K, Shibata H, Takagi K, Satoh F, Koike T, Sasa K (2013) Temporal variation in
485 fine-root biomass, production and mortality in a cool temperate forest covered with dense
486 understory vegetation in northern Japan. *Forest Ecol Manag* 310:700–710 doi:
487 10.1016/j.foreco.2013.09.015

488 Fukuzawa K, Shibata H, Takagi K, Satoh F, Koike T, Sasa, K (2015). Roles of dominant
489 understory *Sasa* bamboo in carbon and nitrogen dynamics following canopy tree removal
490 in a cool-temperate forest in northern Japan. *Plant Species Biol* 30:104–115

491 doi:10.1111/1442-1984.12086
492 Gaul D, Hertel D, Leuschner C (2008) Effects of experimental soil frost on the fine-root
493 system of mature Norway spruce. *J Plant Nutr Soil Sci* 171:690–698
494 doi:10.1002/jpln.200700284
495 Groffman PM, Driscoll CT, Fahey TJ, Hardy JP, Fitzhugh RD, Tierney GL (2001a) Colder
496 soils in a warmer world: A snow manipulation study in a northern hardwood forest
497 ecosystem. *Biogeochemistry* 56:135–150 doi:10.1023/a:1013039830323
498 Groffman PM, Driscoll CT, Fahey TJ, Hardy JP, Fitzhugh RD, Tierney GL (2001b) Effects of
499 mild winter freezing on soil nitrogen and carbon dynamics in a northern hardwood forest.
500 *Biogeochemistry* 56:191–213 doi:10.1023/a:1013024603959
501 Groffman PM, Hardy JP, Fashu-Kanu S, Driscoll CT, Cleavitt NL, Fahey TJ, Fisk MC (2011)
502 Snow depth, soil freezing and nitrogen cycling in a northern hardwood forest landscape.
503 *Biogeochemistry* 102:23–238 doi:10.1007/s10533-010-9436-3
504 Hardy JP, Groffman PM, Fitzhugh RD, Henry KS, Welman AT, Demers JD, Fahey TJ,
505 Driscoll CT, Tierney GL, Nolan S (2001) Snow depth manipulation and its influence on
506 soil frost and water dynamics in a northern hardwood forest. *Biogeochemistry* 56:151–
507 174 doi: 10.1023/a:1013036803050
508 Hosokawa N, Isobe K, Urakawa R, Tateno R, Fukuzawa K, Watanabe T, Shibata H (2017)
509 Soil freeze-thaw with root litter alters N transformations during the dormant season in
510 soils under two temperate forests in northern Japan. *Soil Biol Biochem* 114:270–278
511 doi:10.1016/j.soilbio.2017.07.025
512 Hosokawa N, Fukuzawa K, Tateno R, Shibata H (2020) Effect of snow removal on the fine
513 root biomass dynamics and carbon and nitrogen concentrations of oak and dwarf bamboo
514 *Sasa* in eastern Hokkaido Japan. *J For Res* 25:405-412 doi:
515 10.1080/13416979.2020.1826622
516 IPCC (2014) *Climate Change 2014: Synthesis Report. Contribution of Working Groups I II*
517 *and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.*
518 IPCC, Geneva
519 IUSS Working Group WRB (2015) *World Reference Base for soil resources 2014*
520 *International soil classification system for naming soils and creating legends for soil*
521 *maps Update 2015 World Soil Resources Report 106* FAO Rome
522 Jackson RB, Mooney HA, Schulze ED (1997) A global budget for fine root biomass, surface
523 area, and nutrient contents. *Proc Natl Acad Sci USA* 94:7362-7366
524 doi:10.1073/pnas.94.14.7362

525 Joslin JD, Wolfe MH, Hanson PJ (2001) Factors controlling the timing of root elongation
526 intensity in a mature upland oak stand. *Plant Soil* 228:201–212 doi:10.2307/42951067

527 Kayama M, Koike T (2018) Growth characteristics of dwarf bamboo distributed in the
528 northern part of Japan. In: HPS Abdul Khalil (ed) *Bamboo: Current and Future Prospects*
529 Intec Open London doi:10.5772/intechopen.68541

530 Kozłowski TT, Pallardy SG (1997) *Physiology of tree plants* 2nd edn Academic San Diego

531 Kreyling J, Haei M, Laudon H (2012) Absence of snow cover reduces understory plant cover
532 and alters plant community composition in boreal forests. *Oecologia* 168:577–587 doi
533 10.1007/s00442-011-2092-z

534 Kreyling J, Schuerings J, Malyshev AV, Vogt L, Werner C, Jentsch A (2015) Nitrogen
535 leaching is enhanced after a winter warm spell but mainly controlled by vegetation
536 composition in temperate zone mesocosms. *Plant Soil* 396:85–96 doi:10.1007/s11104-
537 015-2587-1

538 Kyoto University Forests (2016) Meteorological observations in the Kyoto University forests
539 No. 16, Field Science Education and Research Center, Kyoto University, Kyoto City, p
540 63 (in Japanese)

541 Larsen KS, Michelsen A, Jonasson S, Beier C, Grogan P (2012) Nitrogen Uptake During Fall
542 Winter and Spring Differs Among Plant Functional Groups in a Subarctic Heath.
543 *Ecosystem Ecosystems* 15:927–939 doi: 10.1007/s10021-012-9555-X

544 Lei TT, Koike T (1998) Functional leaf phenotypes for shaded and open environments of a
545 dominant dwarf bamboo (*Sasa senanensis*) in northern Japan. *Int J Plant Sci* 159:812–
546 820 doi: 10.1086/297601

547 Marumo E, Takagi K, Makoto K (2020) Timing of bud burst of smaller individuals is not
548 always earlier than that of larger trees in a cool-temperate forest with heavy snow. *J For*
549 *Res* 25:285–290 doi:10.1080/13416979.2020.1753279

550 Moore PT, Van Miegroet H, Nicholas NS (2007) Relative role of understory and overstory in
551 carbon and nitrogen cycling in a southern Appalachian spruce–fir forest. *Can J For Res*
552 37:2689–2700 doi: 10.1139/X07-115

553 Morin X, Améglio T, Ahas R, Kurz-Besson C, Lanta V, Lebourgeois F, Miglietta F, Chuine I
554 (2007) Variation in cold hardiness and carbohydrate concentration from dormancy
555 induction to bud burst among provenances of three European oak species. *Tree Physiol*
556 27:817–825 doi: 10.1093/treephys/27.6.817

557 Nilsson MC, Wardle DA (2005) Understory vegetation as a forest ecosystem driver: evidence
558 from the northern Swedish boreal forest. *Front Ecol Environ* 3:421–428 doi:

559 10.1890/1540-9295(2005)003[0421:UVAAFE]2.0.CO; 2

560 R Core Team (2020) R: A language and environment for statistical computing. R Foundation
561 for Statistical Computing, Vienna, Austria. <https://www.r-project.org/>

562 Repo T, Sirkia S, Heinonen J, Lavigne A, Roitto M, Koljonen E, Sutinen S, Finer L (2014)
563 Effects of frozen soil on growth and longevity of fine roots of Norway spruce. *Forest*
564 *Ecol Manag* 313:112-122 doi:10.1016/j.foreco.2013.11.002

565 Ruess RW Hendrick RL Bryant JP (1998) Regulation of fine root dynamics by mammalian
566 browsers in early successional Alaskan taiga forests. *Ecology* 79:2706–2720 doi:
567 10.2307/176511

568 Schenker G, Lenz A, Körner C, Hoch G (2014) Physiological minimum temperatures for root
569 growth in seven common European broad-leaved tree species. *Tree Physiol* 34:302–313
570 doi:10.1093/treephys/tpu003

571 Shibata H, Urakawa R, Toda H, Inagaki Y, Tateno R, Koba K, Nakanishi A, Fukuzawa K,
572 Yamasaki A (2011) Changes in nitrogen transformation in forest soil representing the
573 climate gradient of the Japanese archipelago. *J For Res* 16:374-385 doi:10.1007/s10310-
574 011-0288-z

575 Shibata H, Hasegawa Y, Watanabe T, Fukuzawa K (2013) Impact of snowpack decrease on
576 net nitrogen mineralization and nitrification in forest soil of northern Japan.
577 *Biogeochemistry* 116:69–82 doi: 10.1007/s10533-013-9882-9

578 Sorensen PO, Templer PH, Christenson L, Duran J, Fahey T, Fisk MC, Groffman PM, Morse
579 JL, Finzi AC (2016) Reduced snow cover alters root-microbe interactions and decreases
580 nitrification rates in a northern hardwood forest. *Ecology* 97:3359-3368
581 doi:10.1002/ecy.1599

582 Steele SJ, Gower ST, Vogel JG, Morman JM (1997) Root mass net primary production and
583 turnover in aspen jack pine and black spruce forests in Saskatchewan and Manitoba
584 Canada. *Tree Physiol* 17:577–587 doi:10.1093/treephys/17.8-9.577

585 Steinaker DF, Wilson SD, Peltzer DA (2010) Asynchronicity in root and shoot phenology in
586 grasses and woody plants. *Glob Chang Biol* 16:2241–2251 doi: 10.1111/j.1365-
587 2486.2009.02065.X

588 Stevens et al. (2017) A comparison of multiple testing adjustment methods with block-
589 correlation positively-dependent tests. *Plos One* 12:e0176124 doi:
590 10.1371/journal.pone.0176124

591 Tateno R, Hishi T, Takeda H (2004) Above- and belowground biomass and net primary
592 production in a cool-temperate deciduous forest in relation to topographical changes in

593 soil nitrogen. *Forest Ecol Manag* 193:297-306 doi:10.1016/j.foreco.2003.11.011
594 Tateno R, Imada S, Watanabe T, Fukuzawa K, Shibata H (2019) Reduced snow cover
595 changes nitrogen use in canopy and understory vegetation during the subsequent growing
596 season. *Plant Soil* 438:157–172 doi:10.1007/s11104-019-04011-2
597 Tierney GL, Fahey TJ, Groffman PM, Hardy JP, Fitzhugh RD, Driscoll CT (2001) Soil
598 freezing alters fine root dynamics in a northern hardwood forest *Biogeochemistry*
599 56:175–190 doi: 10.1023/A:1013072519889
600 Tierney GL, Fahey TJ, Groffman PM, Hardy JP, Fitzhugh RD, Driscoll CT, Yavitt JB (2003)
601 Environmental control of fine root dynamics in a northern hardwood forest. *Glob Chang*
602 *Biol* 9:670–679 doi:10.1046/j.1365-2486.2003.00622.X
603 Toyooka H (1983) Sasa growing in Hokkaido as biomass resources. *Bamboo J* 1: 22–24 (in
604 Japanese)
605 Volder A, Smart DR, Bloom AJ, Eissenstat DM (2005) Rapid decline in nitrate uptake and
606 respiration with age in fine lateral roots of grape: implications for root efficiency and
607 competitive effectiveness. *New Phytol* 165: 493–501 doi:10.1111/j.1469-
608 8137.2004.01222.X
609 Watanabe T, Tateno R, Imada S, Fukuzawa K, Isobe K, Urakawa R, Oda T, Hosokawa N,
610 Sasai T, Inagaki Y, Hishi T, Toda H, Shibata H (2019) The effect of a freeze–thaw cycle
611 on dissolved nitrogen dynamics and its relation to dissolved organic matter and soil
612 microbial biomass in the soil of a northern hardwood forest. *Biogeochemistry* 142:319–
613 338 doi: 10.1007/s10533-019-00537-w
614 Xu X, Niu SL, Sherry RA, Zhou XH, Zhou JZ, Luo YQ (2012) Interannual variability in
615 responses of belowground net primary productivity (NPP) and NPP partitioning to long-
616 term warming and clipping in a tallgrass prairie. *Glob Chang Biol* 18:1648–1656 doi:
617 10.1111/j.1365-2486.2012.02651.X
618 Zhou WM, Chen H, Zhou L, Lewis BJ, Ye YJ, Tian J, Li GW, Dai LM (2011) Effect of
619 freezing-thawing on nitrogen mineralization in vegetation soils of four landscape zones
620 of Changbai Mountain. *Ann of For Sci* 68:943–951 doi: 10.1007/s13595-011-0100-4
621

622 **Figure legends**

623 Figure 1. Temporal patterns of (a) snowpack depth, (b) daily snowfall, and (c) soil frost depth
624 before, during, and after snow removal. —●— Control (CON); —○— snow removal (REM).

625 Values are means \pm SD ($n = 4$). ■ Period of snow removal. Details of environmental data can
626 be found in Watanabe et al. (2019).

627 Figure 2. Temporal fluctuations of soil temperature at soil surface (0 cm). Daily mean value
628 during (a) whole observation period and (b) snowmelt period. Gray square in *a*: period of
629 snow removal; blank square, period shown in *b*. Details of environmental data can be found in
630 Watanabe et al. (2019).

631 Figure 3. Temporal patterns of root length density (RLD): (a) total, (b) *Sasa*, and (c) oak
632 before and after snow removal. —○— Control (CON); —▲— snow removal (REM). Bars
633 represent SEM ($n = 4$). There was no significant difference ($P < 0.05$) between treatments on
634 any date for total roots. ■ Period of snow removal.

635 Figure 4. Temporal patterns of proportional fine root production. —○— Control (CON);
636 —▲— snow removal (REM). Values are means + SEM ($n = 4$). Significant differences between
637 treatments on each date are shown: ** $P < 0.01$, * $P < 0.05$. ■ Period of snow removal.

638 Figure 5. Temporal patterns of fine root production: (a) total, (b) *Sasa*, and (c) oak. —○—
639 Control (CON); —▲— snow removal (REM). Values are means + SEM ($n = 4$). There was no
640 significant difference ($P < 0.05$) between treatments on any date for total roots. ■ Period of
641 snow removal.

642 Figure 6. Temporal patterns of fine root mortality: (a) total, (b) *Sasa*, and (c) oak. —○— Control
643 (CON); —▲— snow removal (REM). Values are means + SEM ($n = 4$). There was no
644 significant difference ($P < 0.05$) between treatments on any date for total roots. ■ Period of
645 snow removal.

646

Table 1. Results of analysis of deviance for three factors (snow removal, occasion, and plant form) and their interactions after GLMM for root length density (RLD) and fine root production rate.

Factors	RLD		Fine root production rate	
	2014	2015	2014	2015
Snow removal treatment (T)	ns	ns	ns	ns
Occasion (O)	***	***	*	***
Form (F)	ns	ns	ns	ns
T × O	ns	ns	ns	ns
T × F	ns	**	ns	***
O × F	ns	ns	ns	ns
T × O × F	ns	ns	ns	ns

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, ns: not significant

Table 2. Annual length-based fine root production and mortality of total, *Sasa*, and oak in control (CON) and snow removal (REM) plots ($\text{mm cm}^{-2} \text{yr}^{-1}$) in 2014 (before snow removal) and 2015 (after snow removal). Mean and standard error of the mean (SEM, $n=4$) are displayed. *P* values for the comparisons between treatments in GLM and results of analysis of deviance after GLM for factors: snow removal treatment (T), plant form (F) and their interaction (T \times F) are displayed on the two right-hand columns.

Category	Year	CON		REM		<i>P</i>	Effects (GLM)
		Mean	SEM	Mean	SEM		
Production total	2014 (before)	3.54	1.38	2.95	0.80	0.72	T: ns
<i>Sasa</i>	2014 (before)	1.89	1.05	1.05	0.39	0.44	F: ns
oak	2014 (before)	1.65	0.67	1.29	0.40	0.66	T \times F: ns
Production total	2015 (after)	3.46	0.69	2.97	1.17	0.74	T: ns
<i>Sasa</i>	2015 (after)	0.63	0.19	1.88	0.94	0.18	F: ns
oak	2015 (after)	2.83	0.67	1.09	0.41	0.12	T \times F: *
Mortality total	2014 (before)	0.20	0.04	0.38	0.18	0.30	T: ns
<i>Sasa</i>	2014 (before)	0.19	0.04	0.18	0.05	0.83	F: ns
oak	2014 (before)	0.00	0.00	0.20	0.15	0.25	T \times F: ns
Mortality total	2015 (after)	1.04	0.59	2.39	0.76	0.30	T: ns
<i>Sasa</i>	2015 (after)	0.96	0.62	1.52	0.96	0.65	F: ns
oak	2015 (after)	0.07	0.07	0.87	0.50	0.30	T \times F: ns

* *P* < 0.05; ns: not significant

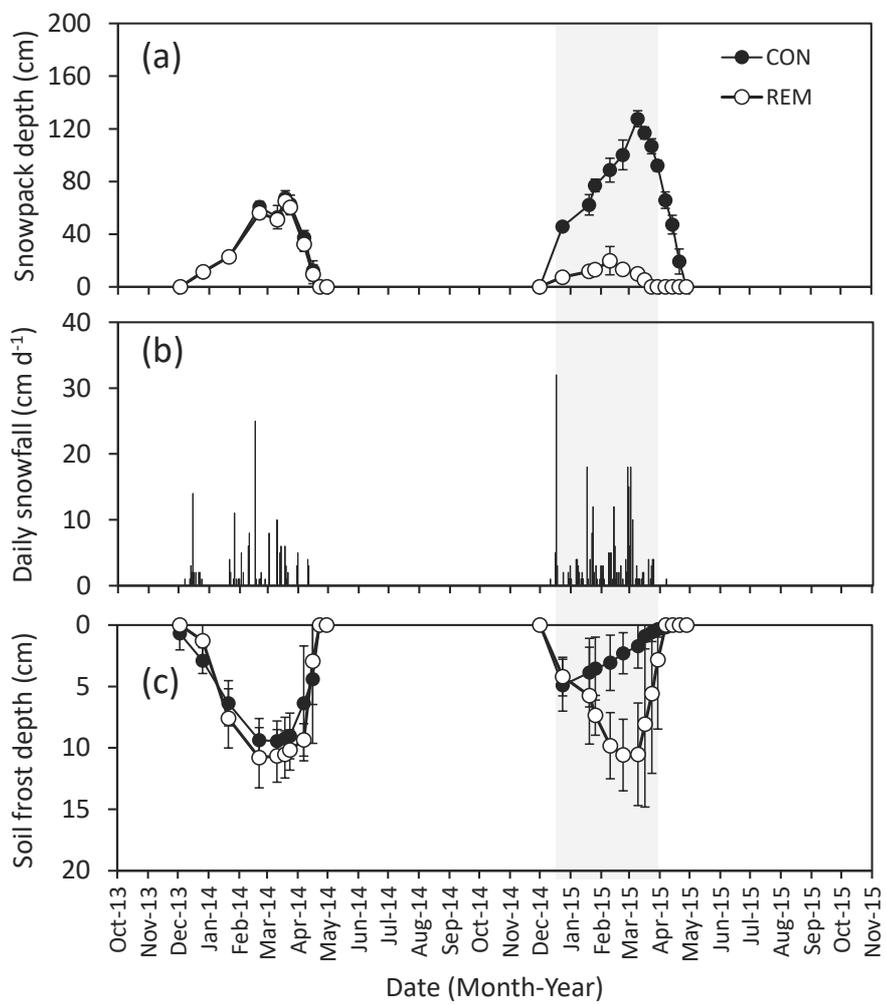


Fig. 1

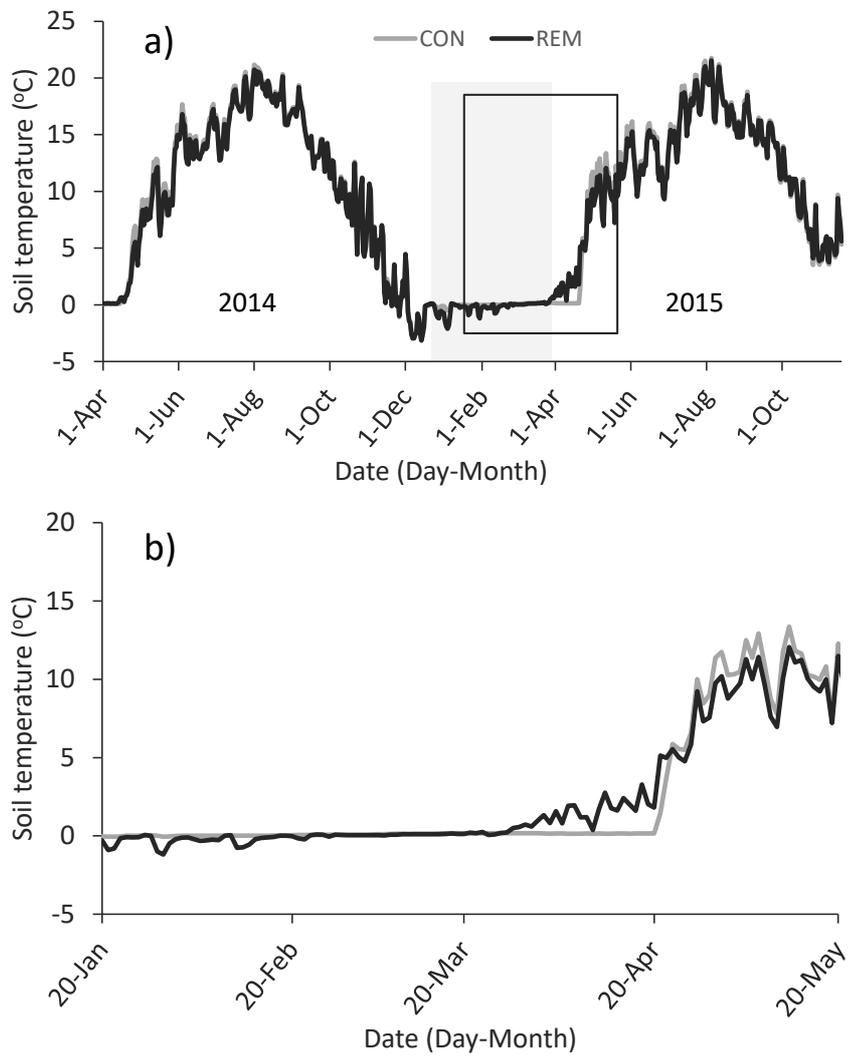


Fig. 2

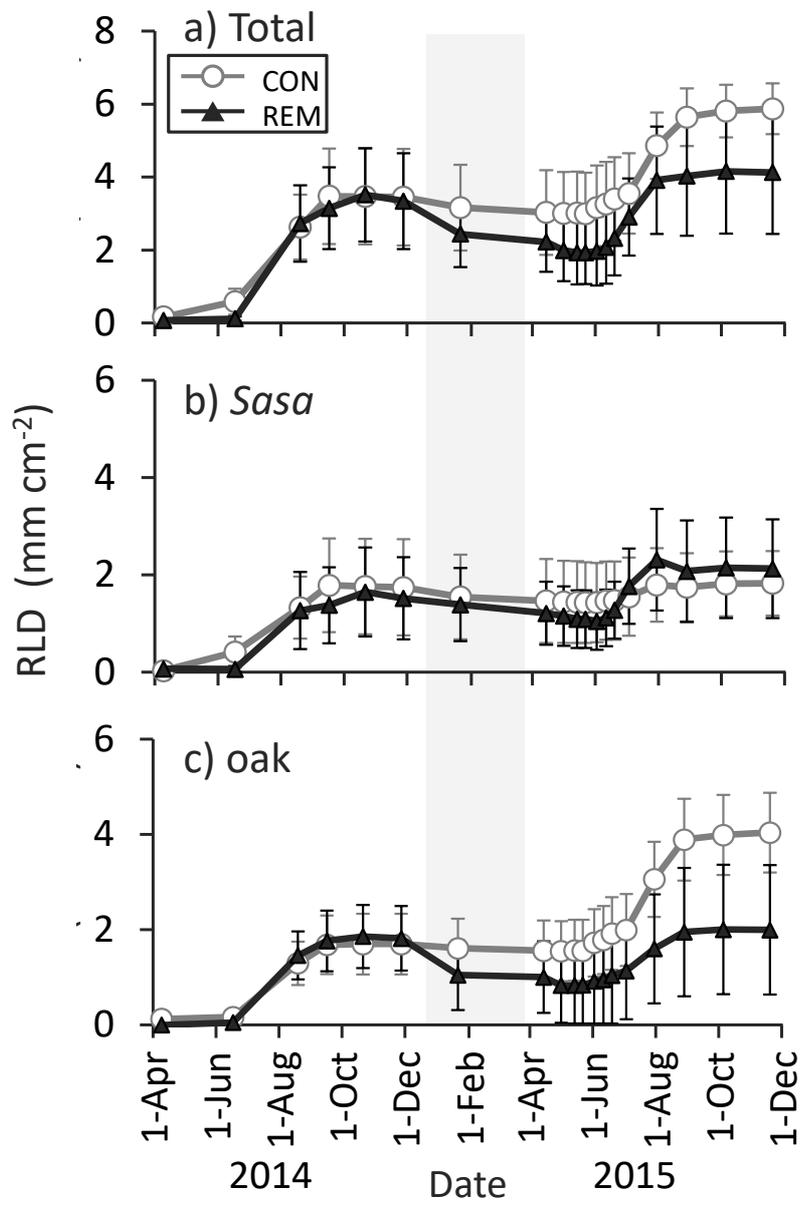


Fig. 3

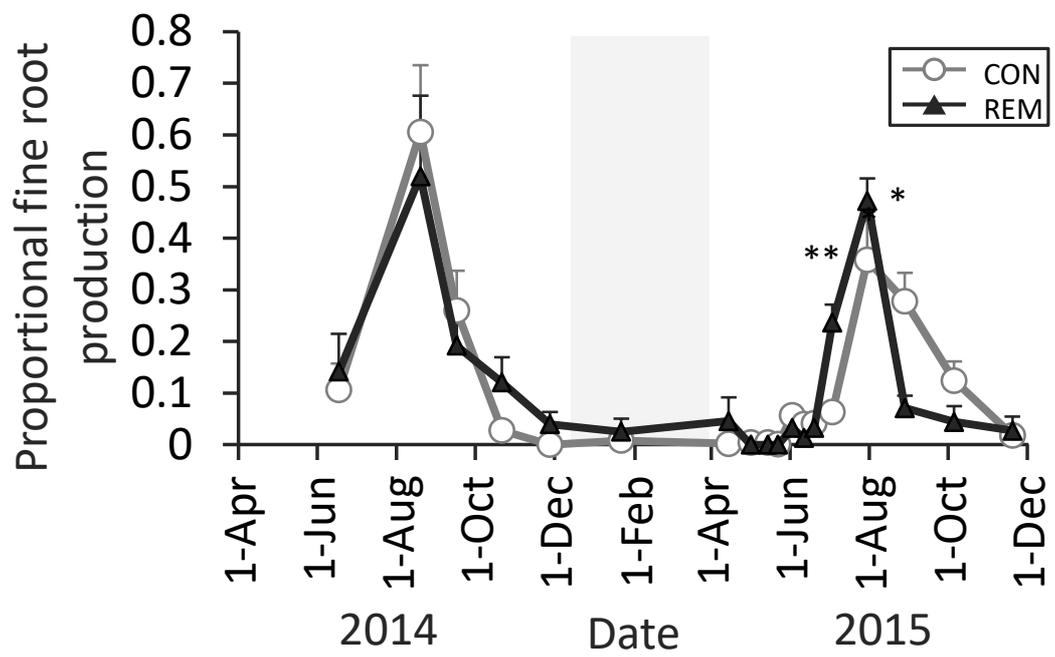


Fig. 4

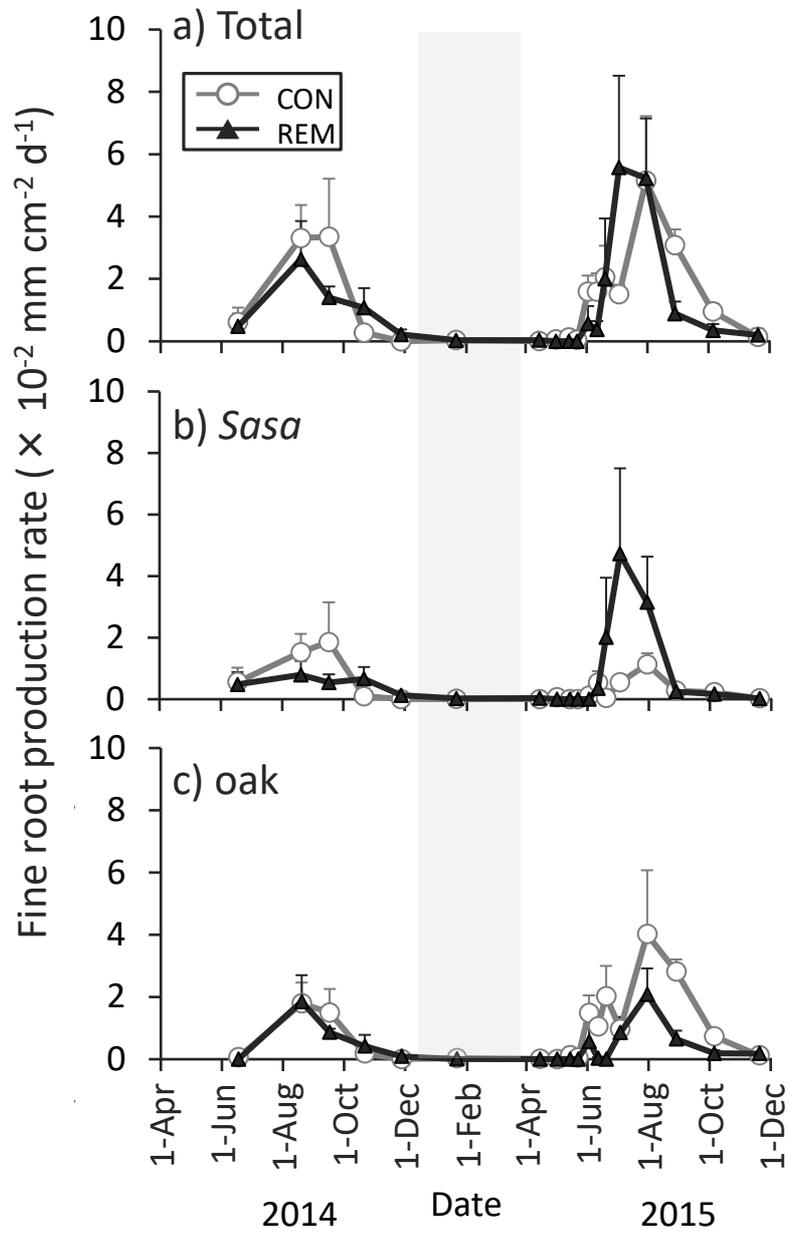


Fig. 5

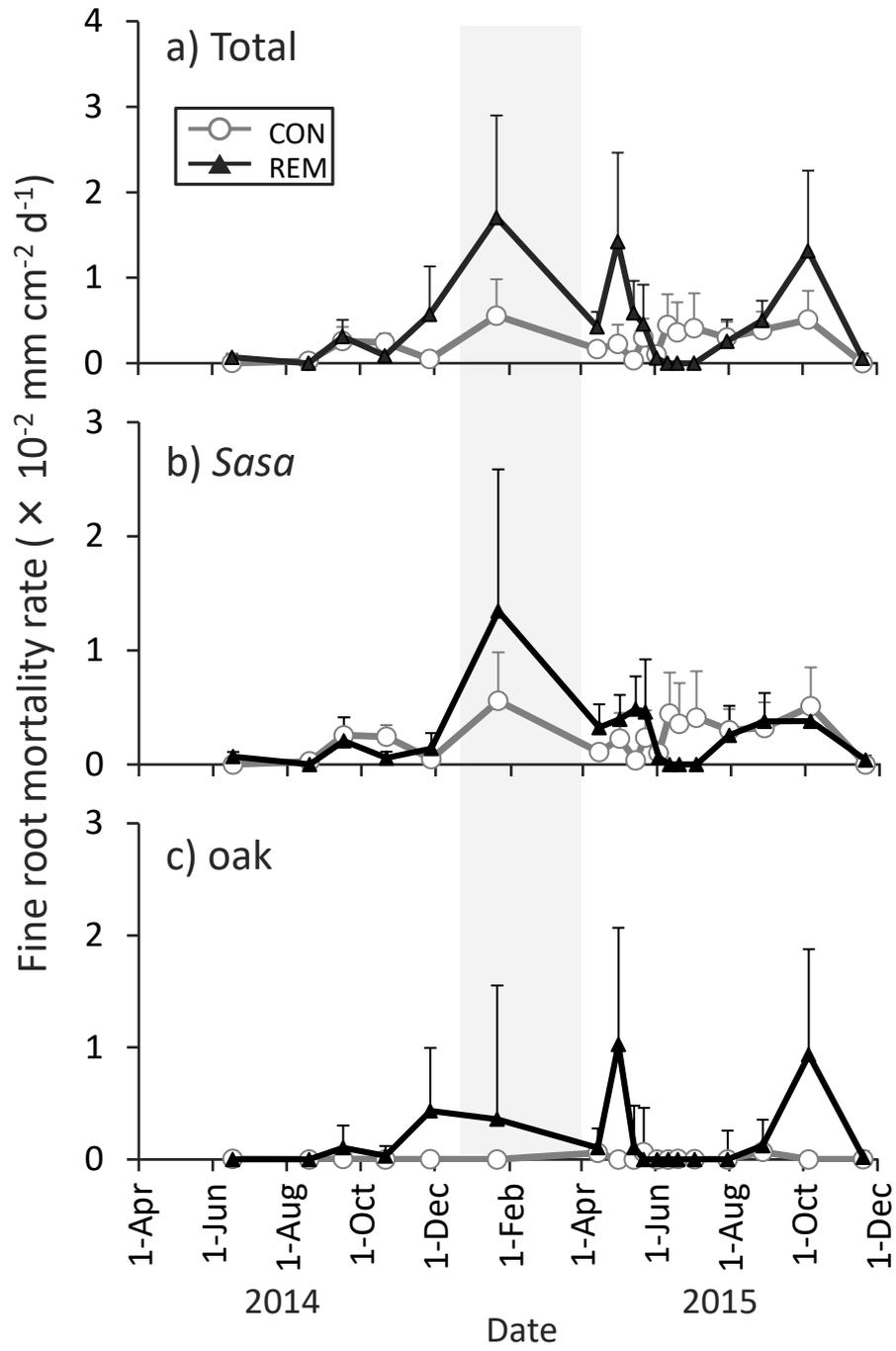


Fig. 6