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Timing of forest fine root production advances with reduced snow cover in northern Japan: Implications for climate-induced change in understory and overstory competition

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Abstract

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

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

Introduction

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

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

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

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

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

different functional types.

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

Materials and methods

Study site

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

Snow removal

We established snow removal (REM) and control (CON) plots with four replications each in the stand. We set up each plot (5 m × 12 m) surrounding a target oak tree. The stand includes east- and west-facing gentle slopes, so we set REM and CON plots evenly on both slopes (Watanabe et al. 2019). In REM plots, we removed snowpack manually by shovel from late 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)

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

Statistical analysis

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

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

2020).

Results

Snowpack depth and soil environment

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

RLD and fine root production

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

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

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

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

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

Fine root mortality

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

Discussion

Advanced timing of peak fine root production by snow removal

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

section.

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

At the same site, Tateno et al. (2019) suggested that increased aboveground production and N uptake by *Sasa* in the growing season following snow removal could be due to the production of more carbohydrates owing to the earlier onset of photosynthesis, because the spring period before leaf flush of overstory trees is important for understory *Sasa* to get light (Lei and Koike 1998). In their study, the onset of and seasonal change in its aboveground biomass production and N in biomass were the same between treatments before July, but differed gradually between treatments after July until midautumn with significant interaction effect between treatment and occasion, indicating that shoot elongation and leaf expansion would continue under favorable carbohydrate and nutritional conditions (Tateno et al. 2019). On the other hand, snow removal advanced the timing of active root production by a month, as evidenced by the significant difference between treatments in early July (Fig. 4). Although there was no significant treatment × occasion interaction in the GLMM analysis, we speculate that this shift in root production and active N uptake is essential for producing further aboveground parts because of the high uptake capacity of newly emerged roots (Volder et al. 2005) or the earlier initiation of N uptake in evergreen plants (Larsen et al. 2012). A positive effect of snow removal on *Sasa* root production, as shown by the significant treatment × 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 × 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 °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 °C (Kozlowski and Pallardy 1997), but has been reported to be 2.3 to
319 4.2 °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

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

Fine root mortality was not increased by snow removal

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

Ecological implications

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

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

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

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

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

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

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

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

Conclusion

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

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Declarations

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

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

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

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Figure legends

Figure 1. Temporal patterns of (a) snowpack depth, (b) daily snowfall, and (c) soil frost depth before, during, and after snow removal. −●− Control (CON); –○– snow removal (REM). Values are means ± SD (n = 4). ■ Period of snow removal. Details of environmental data can be found in Watanabe et al. (2019).

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

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

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

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

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

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 (mm cm^{-2} 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 × F) are displayed on the two right-hand colums.

Category		Year	CON		REM		*P*	Effects
			Mean	SEM	Mean	SEM		(GLM)
Production	total	2014 (before)	3.54	1.38	2.95	0.80	0.72	T: ns
	Sasa	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 × F: ns
Production	total	2015 (after)	3.46	0.69	2.97	1.17	0.74	T: ns
	Sasa	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 × F: *
Mortality	total	2014 (before)	0.20	0.04	0.38	0.18	0.30	T: ns
	Sasa	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 × F: ns
Mortality	total	2015 (after)	1.04	0.59	2.39	0.76	0.30	T: ns
	Sasa	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 × F: ns

* $P < 0.05$; ns: not significant

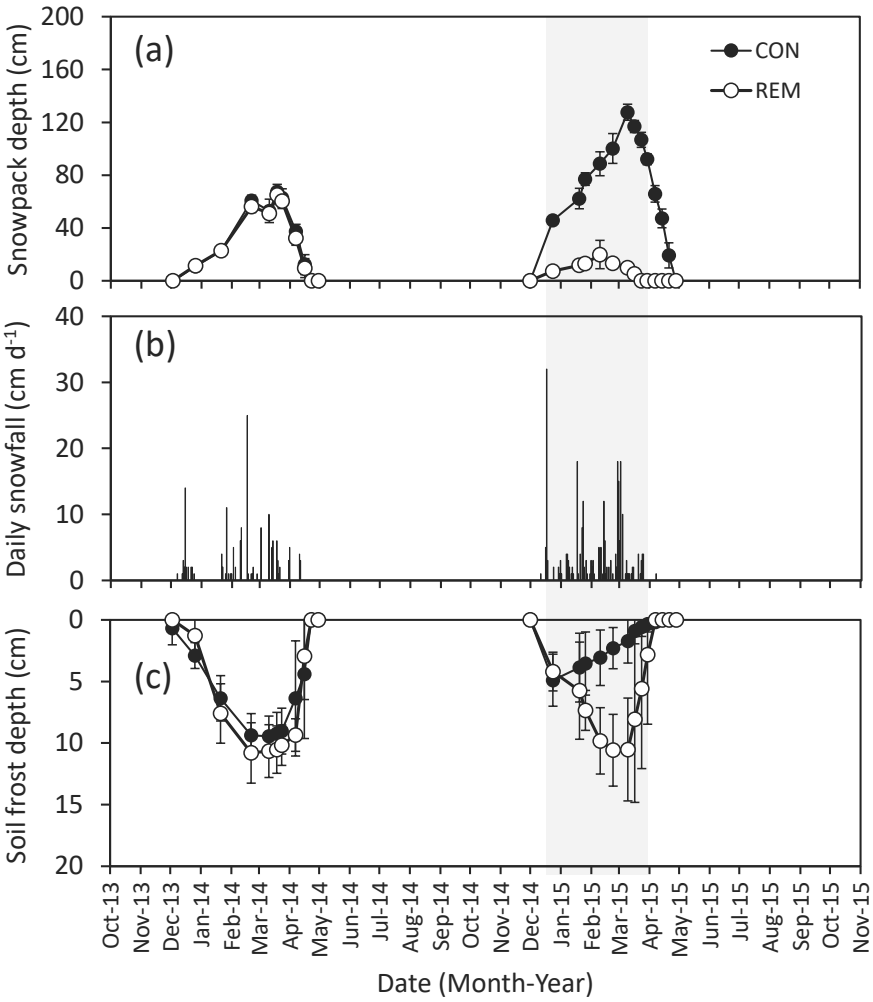
(a)
CON
REM
Snowpack depth (cm)
200
160
120
80
40
0
(b)
Daily snowfall (cm d-1)
40
30
20
10
0
(c)
Soil frost depth (cm)
0
5
10
15
20
Oct-13
Nov-13
Dec-13
Jan-14
Feb-14
Mar-14
Apr-14
May-14
Jun-14
Jul-14
Aug-14
Sep-14
Oct-14
Nov-14
Dec-14
Jan-15
Feb-15
Mar-15
Apr-15
May-15
Jun-15
Jul-15
Aug-15
Sep-15
Oct-15
Nov-15
Date (Month-Year)

Fig. 1

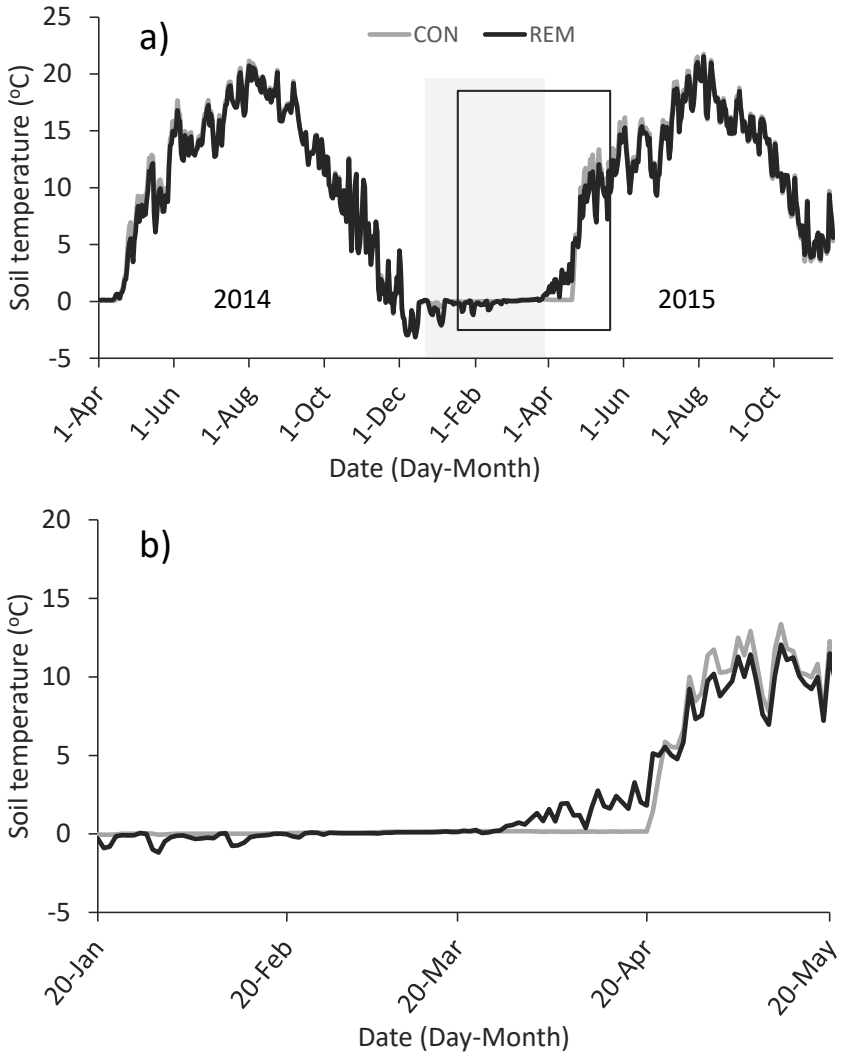
a)
CON
REM
Soil temperature (°C)
25
20
15
10
5
0
-5
2014
2015
1-Apr
1-Jun
1-Aug
1-Oct
1-Dec
1-Feb
1-Apr
1-Jun
1-Aug
1-Oct
Date (Day-Month)
b)
Soil temperature (°C)
20
15
10
5
0
-5
20-Jan
20-Feb
20-Mar
20-Apr
20-May
Date (Day-Month)

Fig. 2

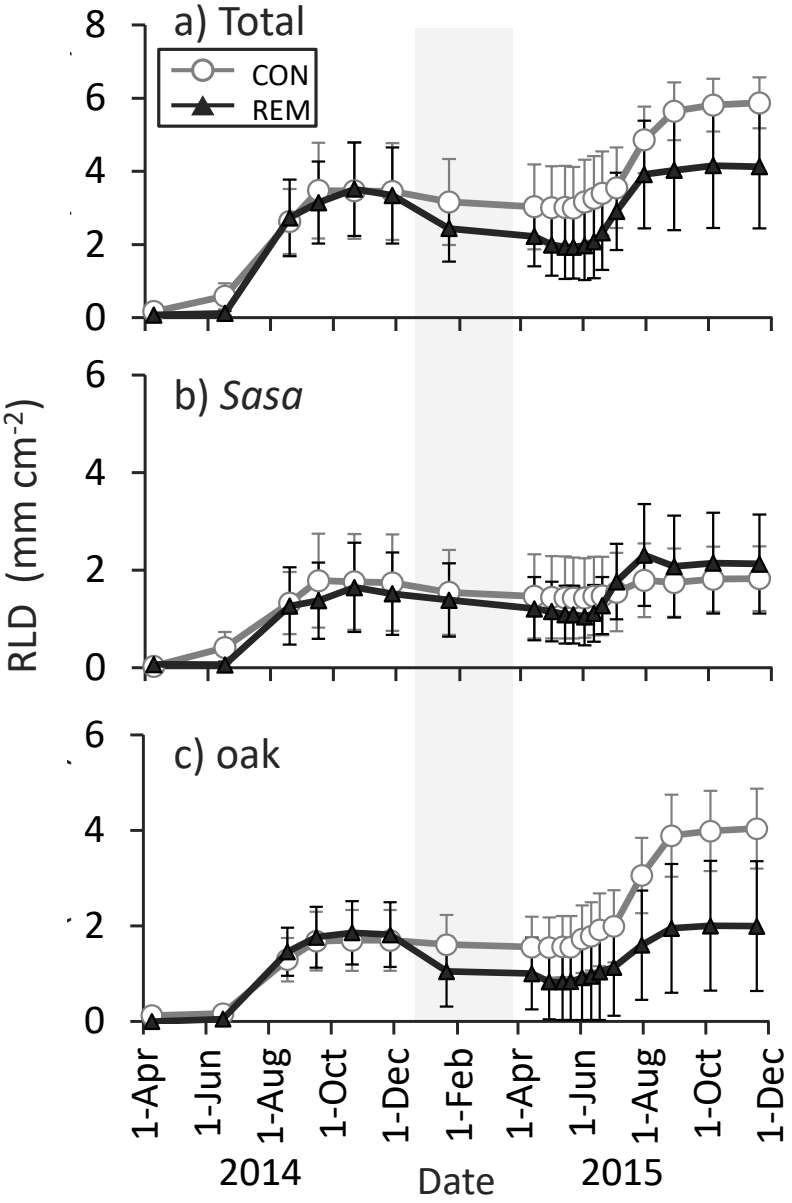
a) Total
CON
REM
b) Sasa
c) oak
RLD (mm cm-2)
0
2
4
6
8
1-Apr
1-Jun
1-Aug
1-Oct
1-Dec
1-Feb
1-Apr
1-Jun
1-Aug
1-Oct
1-Dec
2014
2015
Date

Fig. 3

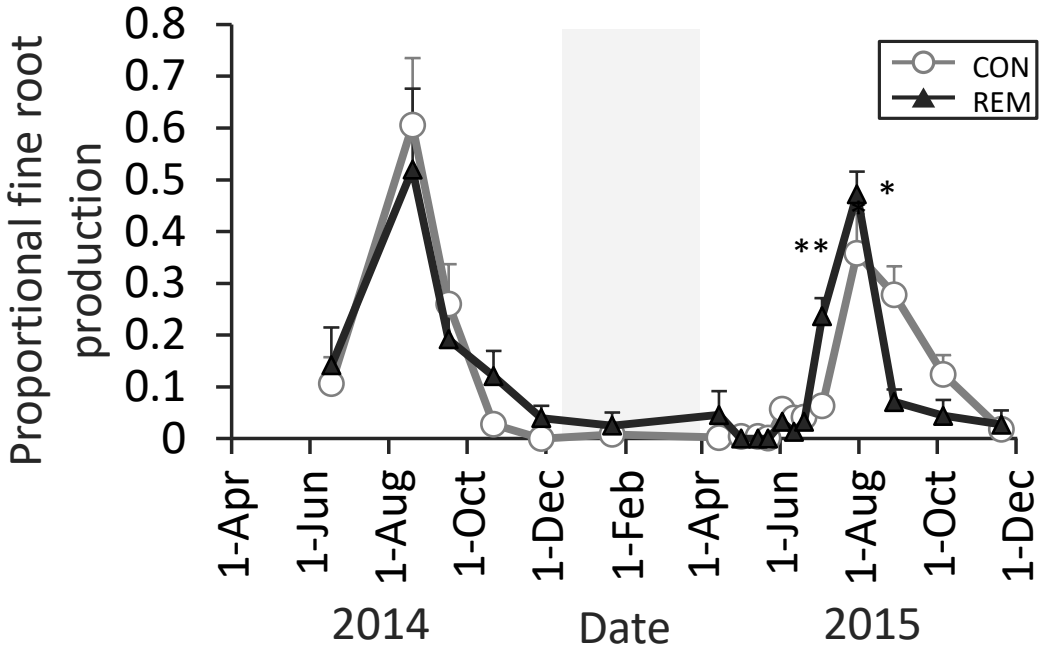
Proportional fine root production
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
CON
REM
**
*
1-Apr
1-Jun
1-Aug
1-Oct
1-Dec
1-Feb
1-Apr
1-Jun
1-Aug
1-Oct
1-Dec
2014
Date
2015

Fig. 4

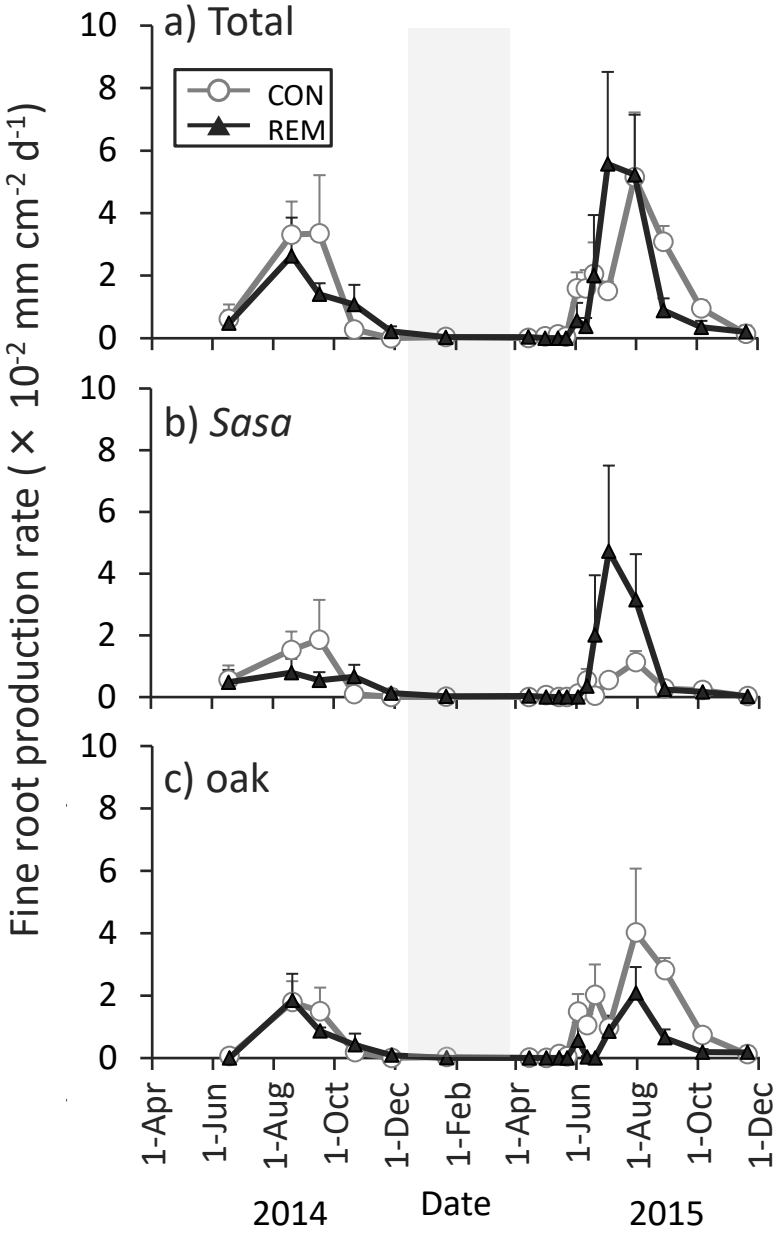
a) Total
CON
REM
b) Sasa
c) oak
Fine root production rate (× 10-2 mm cm-2 d-1)
0
2
4
6
8
10
1-Apr
1-Jun
1-Aug
1-Oct
1-Dec
1-Feb
1-Apr
1-Jun
1-Aug
1-Oct
1-Dec
2014
Date
2015

Fig. 5

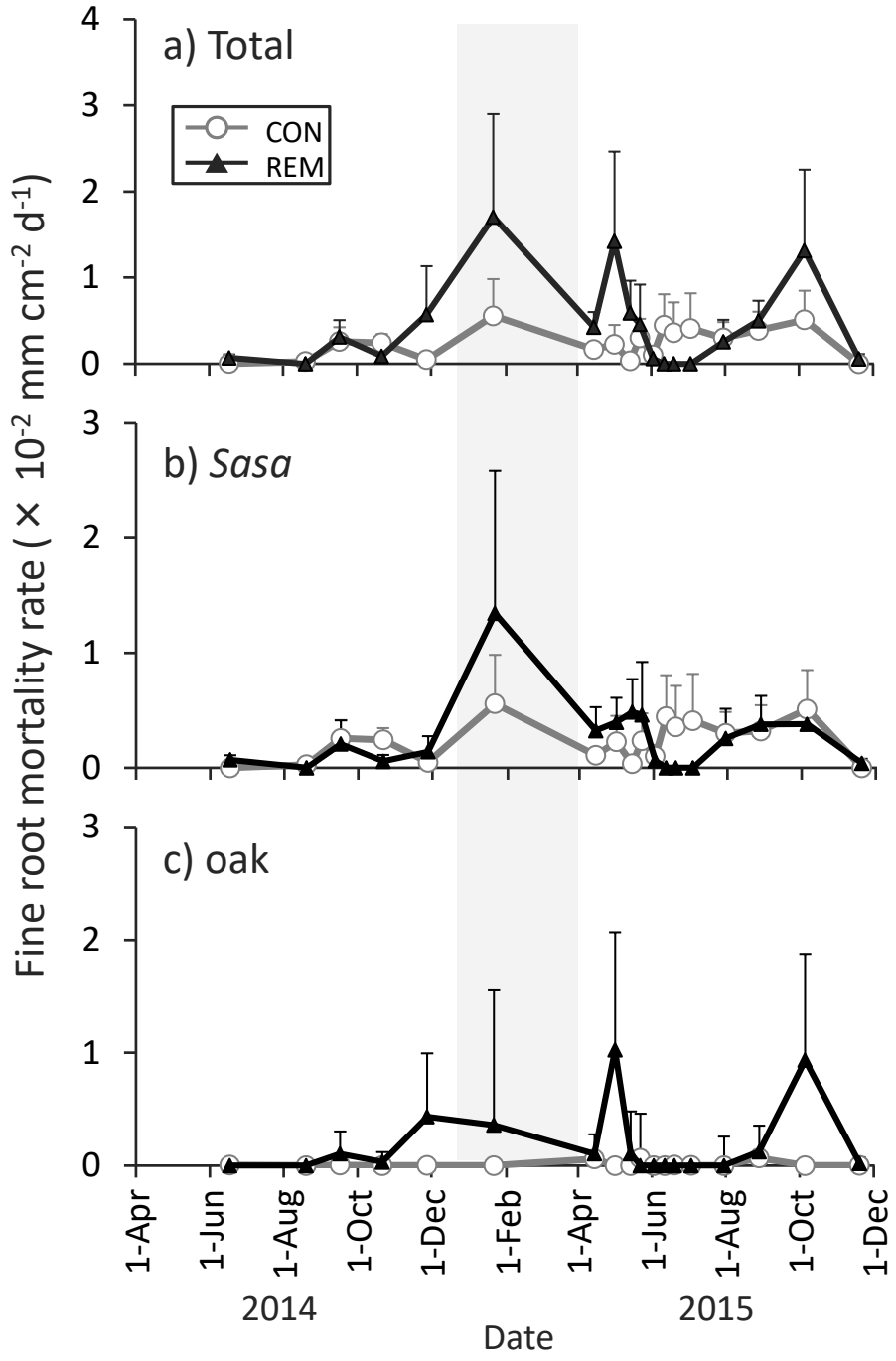
a) Total
CON
REM
b) Sasa
c) oak
Fine root mortality rate (× 10-2 mm cm-2 d-1)
0
1
2
3
4
1-Apr
1-Jun
1-Aug
1-Oct
1-Dec
1-Feb
1-Apr
1-Jun
1-Aug
1-Oct
1-Dec
2014
2015
Date

Fig. 6