Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Effects of frozen soil on growth and longevity of fine roots of Norway spruce

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ARTICLE INFO

Article history: Received 15 August 2013 Received in revised form 31 October 2013 Accepted 6 November 2013 Available online 30 November 2013

Keywords: Carbon sequestration Climate change Production volume Root turnover Snow manipulation Soil freezing

ABSTRACT

Frozen soil is predicted to change in the boreal areas with climate warming. We studied growth, longevity and mortality of fine roots at different levels of frozen soil in winter followed by a delayed soil thawing in spring in a 47-year-old stand of Picea abies (L. Karst.) in the boreal zone. The treatments, repeated over two winters, were: (i) natural insulating snow accumulation and melting (CTRL), (ii) snow removed during winter (OPEN), and (iii) as OPEN in winter but soil thaw delayed by insulation at the top of the forest floor (FROST). Short and long roots were monitored at different depths by minirhizotron imaging at onemonth intervals from May to October in the 2 years during and 2 years after the treatments, to assess standing length (SSL), production volume (SPV) and mortality. A survival function estimate was calculated according to the nonparametric maximum likelihood estimate for interval censored data, and the mean and median root longevities were calculated as with a Kaplan-Meier estimate. CTRL and OPEN did not differ for SSL and SPV but they differed in FROST where compensatory growth occurred in the follow-up seasons. The mean longevity ranged from 276 to 305 days for short roots and from 425 to 464 days for long roots, being higher in OPEN than CTRL and FROST, and higher in the deeper soil layers than near the soil surface. The mean and median longevities were largely the same for short roots but the means were 80–100 days higher for long roots. We conclude that the winters with deep soil freezing are not detrimental for fine roots of Norway spruce, insofar as soil thawing will not prolong the growing season. The longer lifetime in OPEN suggests declining carbon flux into the soil following winters with deeply frozen soil.

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1. Introduction

Frozen soil is common in the boreal zone and its occurrence is affected by the depth of insulating snow cover. Thin or no snow cover exposes soil for freezing that proceeds faster in the uppermost soil layers where most of the roots of trees are located. Soil freezing affects roots, microorganisms and biogeochemical processes, and consequently can affect the carbon cycle and allocation in the forest ecosystems (Groffman et al., 2001, 2011; Tierney et al., 2001; Cleavitt et al., 2008; Gaul et al., 2008). The occurrence of frozen soil is predicted to change as a result of climate warming because of changes in snow cover, seasonal precipitation and their geographic distributions (Groffman et al., 2001; Poutou et al., 2004; Ruosteenoja et al., 2005; IPCC, 2007; Räisänen, 2008). Areas with thin or no snow cover with deeply frozen soil in the present climate may have less frozen soil in future (Venäläinen et al., 2001; Kellomäki et al., 2010). The opposite to this trend, however, may occur in areas where deep snow cover with shallow soil freezing in the present climate prevents the enhancement of more frozen soil in future (Groffman et al., 2001; Isard and Schaetzl, 1998; Henry, 2008; Kellomäki et al., 2010). Simulation studies for boreal forests forecast large spatial variability in the timing of soil warming in spring after winters with thin snow cover in the future climate (Mellander et al., 2005).

Fine roots of trees are the primary objects of stress derived from soil freezing, especially in the boreal zone with long winters. Stress may be due to direct effects of low temperatures on roots in winter, mechanical damage by frost heaving or by the impaired water uptake capacity of roots in cold soil in spring and early summer when evapotranspiration demand is high. The consequences of soil freezing may appear during the follow-up growing season in the periodicity of shoot and root growth, production and turnover due to resource production and allocation between shoots and roots. There is variation in the growth rhythm of roots during the vegetation period, which is suggested to be due to antagonistic interrelation of growth between roots and shoots, and root turnover and mortality, the main determinants of carbon flux into the soil (Lyr







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^{0378-1127/\$ -} see front matter @ 2013 Elsevier B.V. All rights reserved. http://dx.doi.org/10.1016/j.foreco.2013.11.002

and Hoffman, 1967). The effects of frozen soil on tree roots and their linkages with shoot responses have been studied by laboratory and field experiments (Groffman et al., 2001; Mellander et al., 2004; Gaul et al., 2008; Repo et al., 2005, 2007, 2008, 2011). Soil freezing after snow removal increased root mortality in a northern hardwood forest (New Hampshire, United States) dominated by American beech (Fagus grandiflora), sugar maple (Acer saccharum Marsh.) and yellow birch (Betula alleghaniensis Brit.) (Groffman et al., 2001; Tierney et al., 2001), and in a Norway spruce stand in SE Germany (Gaul et al., 2008). Increased fine root mortality in the New Hampshire experiment was explained by mechanical damage to roots in frozen soil, not by the low soil temperature (-4 °C) per se. Increased soil freezing and fine root mortality led to an earlier peak in fine root production during the follow-up growing season and increased fine root turnover, but these changes were not large enough to significantly alter fine root biomass (Groffman et al., 2001; Tierney et al., 2001). In a mature stand of Norway spruce in SE Germany, enhanced fine root production in the snow removal plots almost compensated for the fine root losses caused by low temperatures in winter (-5.5 °C in organic layer) (Gaul et al., 2008). In that study, the snow removal treatment was characterised by a significant reduction in root longevity, indicating a faster fine root turnover. In the same stand as this study, we observed delayed starch accumulation in needles (Repo et al., 2011) and delayed formation of new tracheid cell in trunks by late soil thawing (Jyske et al., 2012). Delayed soil thawing was found to cause changes in several physiological attributes of above-ground organs and in the growth of fine roots and root tip formation (Bergh and Linder, 1999; Mellander et al., 2004; Repo et al., 2005, 2008).

Fine roots form the most important component contributing to below-ground carbon pools and fluxes (defined by growth, production and turnover) in forest ecosystems, in addition to their key roles in nutrient uptake and retention. Up to 75% of the annual net primary production can be allocated to fine roots whose turnover rate is high, thus supplying significant amounts of carbon into soil (Finér et al., 2011 and the references therein). There is still much uncertainty over how fine root turnover depends on environmental regimes across the range of tree species (McCormack et al., 2013). The main reason is that fine root longevity (inverse of turnover) is difficult to assess accurately and depends on several factors, like assessment method, species, site, soil regimes, soil depth, root diameter and branching order (Tierney et al., 2001; Andersson and Majdi, 2005; Hendricks et al., 2005; Majdi et al., 2005; Satomura et al., 2007; Guo et al., 2008a,b; Persson and Stadenberg, 2010; Finér et al., 2011). Minirhizotron imaging (MR) is one method for this purpose. The estimates of fine root longevity by MR for boreal trees range from 280 to 770 days with a mean of 406 days (Finér et al., 2011; Andersson and Majdi, 2005; Majdi and Andersson, 2005; Børja et al., 2009). The order of roots is not usually considered in the longevity estimation but all fine roots are treated as a homogenous pool in spite of a highly heterogeneous population with a variety of lifespans (Trumbore and Gaudinski, 2003; Guo et al., 2008a,b). There are studies on root longevity, mortality and growth of temperate tree species by frozen soil and its variation with soil depth (Tierney et al., 2001; Gaul et al., 2008). However, there are no such studies in the boreal zone, even though the consequences of frozen soil on fine root turnover, and carbon fluxes accordingly, may be more considerable if the frozen period increases, reaches deeper soil layers and extends longer to the growing season. Such knowledge is needed for prediction of carbon balance in the present and future warmed climate conditions.

We aimed to study how frozen soil during dormancy season and its delayed thawing in spring affects Norway spruce fine roots in a 47-year-old stand growing in the boreal zone. We compared the standing length, production volume, mortality, mean and median longevity of fine roots (first and higher order roots separately) at different soil depths as assessed by minirhizotron imaging. The data covered winters with different soil freezing treatments and the follow-up period without the treatments. We hypothesised that more soil freezing with delayed thawing leads to a reduction in fine root production and longevity, which are compensated with new growth in favourable conditions during the follow-up seasons after the stress.

2. Materials and methods

2.1. Experimental set-up

The snow manipulation study was established in a 47-year-old stand of Norway spruce in the boreal coniferous zone in Eastern Finland (62°36'N, 29°43'E, 84 m a.s.l.). The site is a mesic heath forest with medium fertility (till soil). The forest type is *Myrtillus* (MT) according to the Finnish classification system (Cajander, 1949). The field layer is sparse due to the dense tree stand and poor light conditions. However, the most frequent species are Vaccinium myrtillus, Vaccinium vitis-idaea, Luzula pilosa and Deschampsia flexuosa. The ground layer is almost continuous. The most abundant species are Hylocomium splendens. Pleurozium schreberi. Dicranum maius and Brachythecium spp. The thickness of the organic layer is approximately 5 cm. The average height of the trees was 17 m, the stand density 864 trees per hectare, the stand volume $211 \text{ m}^3 \text{ ha}^{-1}$ and the basal area $25.4 \text{ m}^2 \text{ ha}^{-1}$. The ground was cleared of harvesting residue before the start of the experiment in autumn 2005 (for more details of the site characteristics see Maljanen et al. (2010), Repo et al. (2011) and Jyske et al. (2012)).

Different soil freezing conditions were obtained by snow manipulations over the two winters of 2005/06 and 2006/07. The experiment was set up with three treatments and three replicate plots (12×12 m for each) with a transition zone of 5 m between the plots. Treatments with three replicate plots for each were: (i) CTRL with natural snow accumulation and melting, (ii) OPEN with snow removed during winter, and (iii) FROST that was the same as OPEN but the soil surface was insulated with a 15 cm layer of hay set between plastic sheeting in late March (week 13) to delay soil thawing. Insulation was removed in July on weeks 29 and 27 in 2006 and 2007 respectively. Snow removal to the transition zone between the plots was undertaken within 2 days after each snowfall. Air temperature on the site was logged at a height of 2 m. Soil temperature at depths of 5, 15 and 50 cm (105T thermocouple, Campbell Scientific, Shepshed, UK) and volumetric soil moisture content at a depth of 15 cm (CS615, Campbell Scientific, Shepshed, UK) were logged in the middle of each plot. Snow depth was monitored manually in the winters of 2005/06 and 2006/07 in the middle of the CTRL plots. The dates for soil freezing at different depths were defined as dates when the daily mean soil temperature decreased below 0 °C. Soil thawing at different depths was defined as dates when the daily mean soil temperature rose above 0 °C for at least seven consecutive days.

2.2. Minirhizotron imaging

The growth of fine roots was monitored for 4 years from 2006 to 2009, including soil freezing manipulations in first 2 years and for 2 years thereafter, by minirhizotron (MR) imaging (Bartz BTC-100X Camera System, Bartz Technology Company, Santa Barbara, United States). The imaging took place at roughly one-month intervals in the snow-free season from the end of April to the beginning of October. Twenty-seven acrylic MR tubes (outer and inner diameters of 60 and 50 mm, respectively) were installed in the soil in

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