Author(s): Tapani Repo, Timo Domisch, Jouni Kilpeläinen & Harri Mäkinen

Title: Soil frost affects stem diameter growth of Norway spruce with delay

Year: 2021

Version: Published version

Trees
https://doi.org/10.1007/s00468-020-02074-8

ORIGINAL ARTICLE

Soil frost affects stem diameter growth of Norway spruce with delay

Tapani Repo[1,3] · Timo Domisch[1] · Jouni Kilpeläinen[1] · Harri Mäkinen[2]

Received: 4 August 2020 / Accepted: 19 December 2020

Abstract

Key message **A lack of snow cover and increased soil freezing may not only have short-term impacts on trees but longer-lasting lagged effects on radial growth.**

Abstract Soil temperature and soil frost intensity are affected by the depth of insulating snow cover and the timing of snowmelt which are predicted to change by climate warming. This may increase tree growth if there is less soil freezing or decrease growth if there is no insulating snow cover, but frost temperatures still exist. Previously, we showed that the changes in soil frost by snow manipulations in a ~ 50-year-old stand of Norway spruce [*Picea abies* (L.) Karst.] in eastern Finland in two winters (2005/2006 and 2006/2007) led to short-term changes in physiology, morphology, and the growth of the shoots and roots. The treatments were: (1) control with natural insulating snow accumulation and melting; (2) snow removal during winter; and (3) snow removal in winter and insulation at the top of the forest floor in late winter to delay soil thawing. In this study, we examined the lagged effects of those treatments by radial trunk increment cores during the nine-year recovery period after the termination of the treatments. Annual ring width index (AWI) was calculated for each year by normalization of the ring width in the respective year in proportion to the ring width in the last year (2005) before the treatments. No differences in AWI were found between the treatments before or during the snow manipulation period. However, differences started to appear 1 year after the treatments were finished, became significant 4 years later in 2011 and lasted for 3 years. The radial increment was lower in the treatment with snow removed than in the control and in the treatment with insulation to delay soil thawing, but there were no differences between the latter two treatments. The results indicate that a lack of snow cover may not only have short-term impacts but longer-lasting consequences on the radial growth of trees. The positive effects of prolonged growing season by the increasing summer temperatures on forest growth predicted for the boreal region may therefore not be fully realised due to the negative effects of decreased snow cover and increasing soil freezing.

Keywords Climate change · Snow manipulation · Soil freezing · Tree growth

Introduction

The length of the seasonal snowy period and snowpack thickness have declined due to the climate warming in boreal and at high elevations in temperate areas (Liston and Hiemstra 2011; Pederson et al. 2011; Morán-Tejeda et al. 2016) Further reductions in snow-covered areas are predicted in northern latitudes and mountainous areas due to a predicted shift in precipitation from snow to rain (Rasmus et al. 2004; Reinmann et al. 2019). Because snow is an effective insulator, the changes in snow cover and the timing of snowmelt will have implications on soil temperature and soil frost intensity (Sutinen et al. 2008, 2009a). As frost temperatures are also likely to occur in the future in midwinter in northern latitudes (Petoukhov and Semenov 2010), thinner and more compact snowpack may result in lower subnivean temperatures, and therefore deeper or longer-lasting soil frost than in the current climate (Isard and Schaetzl 1998; Groffman et al. 2001; Henry 2008; McCabe and Wolock 2010).

Communicated by Vospernik.

✉ Tapani Repo
tapani.repo@luke.fi

1 Natural Resources Institute Finland (Luke), Natural Resources, P.O. Box 68, 80100 Joensuu, Finland

2 Natural Resources Institute Finland (Luke), Production Systems, Tietotie 2, 02150 Espoo, Finland

3 Natural Resources Institute Finland (Luke), Yliopistokatu 6, 80100 Joensuu, Finland

Published online: 13 January 2021

Soil freezing and delayed soil thawing may damage fine roots and increase their mortality thus affecting the growth of trees (Tierney et al. 2001, 2003; Repo et al. 2014; Sutinen et al. 2014). Evapotranspiration of trees, particularly conifers, is high in spring due to high solar irradiance, temperature fluctuation and wind (Sakai 1968; Tranquillini 1982). Frozen soil inhibits water uptake, potentially causing severe water stress and injuries to trees (Bonan and Shugart 1989; Harrison et al. 2020). Although tree roots may tolerate short-term low temperatures in their frost-hardy state (Bigras et al. 2001), mild but long-lasting soil freezing may damage fine roots (Tierney et al. 2001, 2003; Comerford et al. 2013; Sutinen et al. 2014). In a snow manipulation study in New Hampshire (U.S.), adverse impacts of reduced snowpack and increased soil freezing on the physiology of sugar maple (*Acer saccharum* Marsh) were accompanied by 40% reduction in aboveground woody biomass increment, averaged across the 6 years from the start of the experiment (Reinmann et al. 2019). According to the model simulations for Finland, Solantie (2003) concluded that the productivity of boreal forests depends on snow depth and soil frost depth accordingly, such that an increase of one centimeter in mean maximum soil frost depth in winter decreases the annual productivity by 0.1 m^3ha^{-1}. Long-lasting soil frost has been found to reduce the shoot growth of Scots pine (*Pinus sylvestris* L.) saplings and mature Norway spruce (*Picea abies* (L.) Karst.) trees (Repo et al. 2007, 2008; Sutinen et al. 2015), as well as to induce death of annual shoots or the whole seedling, depending on snow cover and species (Martz et al. 2016; Domisch et al. 2018, 2019). Similarly, in European mountainous areas, exceptionally low winter temperatures combined with thin snowpack have resulted in large-scale yellowing and loss of needles in Scots pine and Norway spruce, accompanied by canopy dieback and tree mortality (Kullman 1989, 1991; Camarero et al. 2015). On the other hand, the radial growth of Scots pine reacted positively to midwinter precipitation in northern Finland, which contributed to the mean snow depth preventing the direct effects of low temperatures on roots over the winter (Helama et al. 2013). Moreover, early snowfall and soil cooling in the fall may lead to reduced photosynthate storage and reduced growth in the following summer (Carlson et al. 2017).

Delayed snow melting and soil frost affect soil temperatures and therefore limit tree establishment and shorten the growth period of several tree species. Accordingly, the radial growth of Scots pine correlated better with the soil temperature than the air temperature in April (Nikolaev et al. 2009; Helama et al. 2013). Likewise, northern conifers showed delayed cambial activity due to the delayed snowmelt at the beginning of the growing season (Vaganov et al. 1999; Kirdyanov et al. 2003; Macias Fauria et al. 2008). Helama et al. (2013) and Franke et al. (2017) reported that snow cover during the current year's April and May correlated negatively with the annual radial increment of Scots pine. Similar results have also been reported for mountain pine (*Pinus uncinata* Ram.) in the Spanish Pyrenees (Sanmiguel-Vallelado et al. 2019). On the other hand, abundant soil moisture from spring snowmelt may promote tree growth on xeric sites (Walsh et al. 1994; Pederson et al. 2011; St. George 2014; Watson and Luckman 2016). In our previous studies, soil freezing and its delayed thawing led to changes in the physiology, morphology, and growth of the shoots and roots of ~ 50-year-old Norway spruce (Repo et al. 2011, 2014; Jyske et al. 2012; Sutinen et al. 2015). Soil frost even led to the death of some trees. In terms of the number of new tracheids, the annual radial increment and intra-annual wood formation were reduced by delayed soil thawing during the post-treatment growing seasons (Jyske et al. 2012). In addition to such short-term effects, increased soil freezing may have longer-term effects which may limit tree growth and affect longer-term growth pattern, but they are not known well.

We aimed to study the lagged effects of soil freezing on radial growth of ~ 50-year-old Norway spruce in the same stand that was previously used for short-term intensive monitoring of shoot and root responses. The radial increment of trees was assessed during the nine-year recovery period after the termination of the soil frost treatments. We hypothesized that snow cover removal and delayed soil thaw would not have only immediate impacts on the radial growth of stems, but would also have long-lasting, lagged effects, and reduce tree growth over several years.

Materials and methods

The soil frost experiment was carried out in a Norway spruce stand in eastern Finland (N 62° 42′, E 29° 45′, 84 m asl). The stand with spruce as the only tree species was regenerated in 1958 on a medium fertile site, classified as a *Myrtillus* site type (MT) (Cajander 1949). Soil texture in the uppermost mineral layers was 66% sand, 23% silt, 9% coarse sand and 2% clay. The thickness of the organic layer was approximately 5 cm. In 2006, the average height of the trees was 17 m, the stand volume 211 $m^3\ ha^{-1}$ and the basal area 25.4 $m^2\ ha^{-1}$. Typically, Norway spruce has a superficial root system, with the mean rooting depth of 21 cm in the pole stage stand of the MT type (Kalliokoski et al. 2008). The stand had been managed by thinning in 1999 and 2014 in accordance with the recommendations for private forests (Rantala 2011).

The experimental design was a randomized complete block design with three treatments in three blocks, rendering nine plots. Each plot was 12 × 12 m in size with a transition zone of 5 m between the plots. The soil frost treatments with snow manipulations were carried out in two winters, 2005–2006 and 2006–2007. In the control treatment (CTRL), snow accumulated and thawed naturally. In the OPEN and FROST treatments, snow was removed during the winter after every snowfall, and the soil temperature was therefore lower, with the soil freezing more deeply than in CTRL (Table 1). In OPEN, soil thawing in spring took place in accordance with the natural pattern but without snow cover. To delay soil thawing in spring in the FROST treatment, the soil surface was insulated with a 15 cm layer of hay set between plastic sheeting when the air temperature increased above 0 °C at the end of March. The insulation was removed in July. The minimum soil temperatures decreased approximately to − 15 °C at the depth of 5 cm without the snow cover but remained at − 4 °C with the snow cover (Table 1). When the air temperature increased permanently above 0 °C and snow melt commenced, soil temperature started to increase first in CTRL, some days later in OPEN and with several weeks delay in FROST (Repo et al. 2011, 2014; Jyske et al. 2012). The soil remained frozen even at the depth of 90 cm for two months in OPEN after the air temperature had increased permanently above 0 °C (unpublished data). Snow removal and insulation of the forest floor affected the level and dynamics of soil water content in spring and early summer in 2006 and 2007, being typically lower in OPEN and FROST than CTRL (Repo et al. 2014). In addition, due to slow soil thawing in FROST, soil water content increased more slowly and reached the maximum later in the growing season in FROST than OPEN and CTRL where the volumetric soil moisture content decreased below 10% in July and August. The maximum snow cover ranged from 40 to 60 cm depending on year. The experiment and the treatments were described in detail previously (Maljanen et al. 2010; Repo et al. 2011, 2014; Jyske et al. 2012; Sutinen et al. 2015).

Table 1 The minimum air temperatures (at height 1.3 m) and soil temperatures at different depths in two winters with snow manipulations, and the respective monthly mean values in June, in a ~ 50-year-old stand of Norway spruce in eastern Finland

Treatment	Depth, cm	Minimum temperature in winter, °C		Mean temperature in June, °C	
		2005/2006	2006/2007	2006	2007
CTRL	5	− 4.1	− 3.6	10.4	13.2
	15	− 1.4	− 2.3	8.8	11.9
	50	− 0.3	− 0.7	6.8	10.1
OPEN	5	− 15.4	− 14.8	8.8	13.0
	15	− 10.7	− 11.3	6.9	11.7
	50	− 5.7	− 6.4	4.4	9.7
FROST	5	− 14.8	− 14.2	0.1	10.3
	15	− 11.5	− 12.1	0.0	8.9
	50	− 5.7	− 6.5	− 0.1	6.0
Air		− 31.0	− 31.9	14.8	15.8

CRTL refers to control, OPEN to the treatment where snow was removed during the winter and FROST the same as OPEN, but the soil surface was insulated from the end of March to July in both years

In December 2016, 11 years after the start of the experiment with snow manipulations, increment cores were taken at breast height (1.3 m) from five randomly selected trees left after thinning in 2014 on each plot. The ring widths of the cores were measured with 0.01 mm accuracy and visually cross-dated to ensure that each individual ring is assigned its exact year of formation. The rings formed between 1994 and 2016 were included in the analyses, i.e., 13 years before the treatment onset, two treatment years and 9 years after the end of the treatments. The annual ring-width index (AWI) was calculated for each year by dividing the ring widths of a tree by the width in 2005, i.e. the last year before the start of the soil frost treatments (Trt). The treatment effects on AWI were statistically tested by using the linear mixed model (procedure MIXED in IBM SPSS Statistics v25, IBM Co., Armonk, New York, US):

$$\mathrm{AWI} = \mu + \mathrm{Trt} + \mathrm{Year} + \mathrm{Trt} \times \mathrm{Year} + \mathrm{Block} + \mathrm{Plot} + \mathrm{Tree} + \epsilon$$

where Trt, Year, and their interaction are fixed effects, Block, Plot, and Tree are random effects, μ is a constant, and ε is an error term. A logarithmic transformation ($\ln(x + 1)$) was applied for AWI. The correlation of the residuals over time was described by a heterogeneous ARH1 covariance structure. The significance of the difference between the treatments in different years was tested using Bonferroni-corrected significance levels. The distribution of the residuals was checked using graphics, and the time correlation structure was selected based on Akaike's information criterion.

Results

The 'Year' and its interaction with the treatment had significant effects on AWI (Table 2). There were no significant differences in the average AWI between the plots before the

Table 2 The result of the linear mixed model on the effects of soil frost treatments (Trt) and calendar year (1994–2016) on the annual ring width index (AWI) of stems with snow manipulations in two winters (2006 and 2007) in a ~ 50-year-old stand of Norway spruce. The trees were cored in 2016

Effect	Degrees of freedom		*F*	*P* value
	df1	df2		
Year	22	348	66.3	< 0.0001
Trt	2	2.1	0.09	0.92
Year × Trt	44	346	1.89	< 0.001

onset of the treatments (Fig. 1). Moreover, no significant differences in the radial growth of the sample trees were found between the treatments during the snow manipulation period (2006 and 2007). In 2007, the mean (± SE) annual ring widths were 2.19 (± 0.14) mm, 1.79 mm (± 0.17) mm, and 1.88 (± 0.12) mm in CTRL, FROST, and OPEN respectively. The differences between the treatments started to appear in 2008 but only became significant in 2011, i.e. 4 years after the completion of the treatments (Fig. 1). In that year, the mean annual ring widths were 1.74 (± 0.14) mm, 1.67 mm (± 0.25) mm, and 1.18 (± 0.08) mm in CTRL, FROST, and OPEN respectively. In 2011, AWI was significantly lower in OPEN than CTRL and FROST ($P = 0.009$ and $P = 0.005$ respectively), but the difference between CTRL and FROST was not significant. The difference lasted for two more years (P values 0.154 and 0.071 in 2012, and 0.053 and 0.033 in 2013 respectively) until 2013 and then disappeared.

Discussion

In line with our hypothesis, altered snowpack and the consequent change in soil frost condition (lower soil temperatures, deeper soil frost, and delayed soil frost thawing) considerably reduced radial growth over several years after the actual snowpack manipulation. In the previous study of the same experiment, we found minor effects immediately after the treatments on radial growth (Jyske et al. 2012). According to that study, the timing of radial increment and tracheid differentiation was delayed in FROST after the first treatment winter but not after the second, when the total number of new tracheids remained slightly lower in FROST and OPEN than in CTRL. The results of this study indicate that severe soil frost would have not only minor short-term impacts but lagged effects after several years for the condition of trees and therefore for radial growth, too. If severe soil frost was to be repeated in several consecutive years, we assume that the effects on radial growth would be cumulative (cf. Reinmann et al. 2019).

Snow cover affects soil conditions in multiple ways (Groffman et al. 2006; Sutinen et al. 2008, 2009a). In the treatments without snow cover, the minimum soil temperatures in winter were below -10 °C in the layer where most of the roots of Norway spruce are located but remained above -5 °C in the CTRL treatment with snow cover (Table 1, Repo et al. 2011). Deep soil freezing led to delayed soil thawing in spring in FROST and in deep soil layers of OPEN, too. A low soil temperature and decreased soil water content resulting from soil freezing, together with a missing snow cover in winter and spring, may have caused a shortage of water for trees at the beginning of the growing season. This may have caused stem embolism and reduced xylem conductivity, which have been found to increase shoot and needle dieback (Tranquillini 1982). This probably also explains the delayed growth onset of roots and shoots, and reduced shoot growth in FROST during the post-treatment growing seasons of this experiment (Repo et al. 2014; Sutinen et al. 2015).

Although in the short-term freezing tests, fine roots may tolerate lower temperatures than measured in the upper soil layers of this experiment (Bigras et al. 2001), even mild

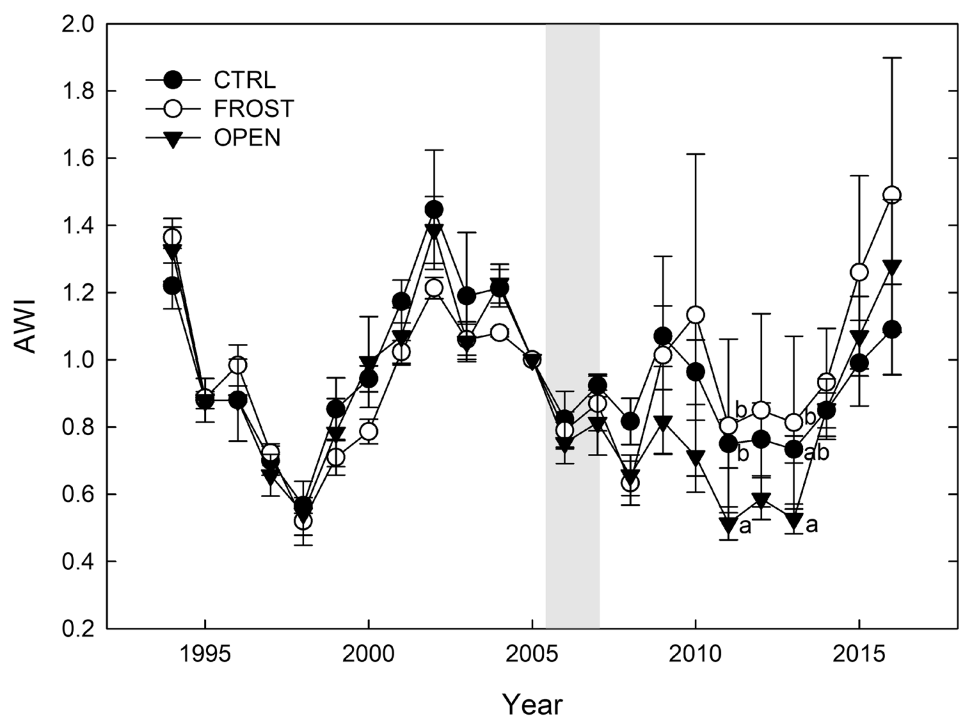

Fig. 1 The mean ring width index (AWI) (± standard error) of stems in a ca. 60-year-old stand of Norway spruce sampled for the increment cores in 2016. Snow manipulations took place in two winters, 2006 and 2007 (gray bar), resulting in different soil frost conditions. In OPEN and FROST, snow was removed in winter, but in FROST, the soil surface was insulated in spring to delay soil thawing. CTRL refers to the treatment without snow manipulations. The different small-case letters indicate significant differences among the treatments by years. AWI is the ring width for each year in proportion to the ring width in 2005

long-term soil freezing has been found to cause damage (Tierney et al. 2001, 2003; Sutinen et al. 2014). However, no remarkable increase in fine root mortality was observed by minirhizotron imaging in our study plots, which may be partly due to the limited scope of the imaging tubes for the whole root system of the large trees (Repo et al. 2014). Previously, delayed snowmelt in a study in Finnish Lapland caused a delay in soil thaw and the infiltration of melting water into the soil (Sutinen et al. 2009b). However, this snowmelt liquid water was found in the root zone area and even in the roots before soil temperature rose notably above 0 °C (Sutinen et al. 2009a), suggesting that in field conditions with thick snow cover water availability is not a limiting factor for growth onset in spring.

The soil water content increased with soil thawing in FROST in the latter part of the growing season. This happened because the soil melt took place later in FROST than OPEN and CTRL, in addition to reduced evaporation from the soil surface due to the insulation cover in FROST (Repo et al. 2011). A higher soil moisture content may have compensated for the negative effects of soil freezing, and shortage of water for the growth of roots and shoots at the beginning of the growing season. This enhanced the recovery from the stress of delayed soil thawing, and even favored the compensatory root growth in FROST compared with CTRL and OPEN (Repo et al. 2014). This may have been reflected as the better radial growth in FROST than OPEN, even several years after the treatments. In the last two years, AWI increased in all treatments, which may be explained by thinning in 2014 which was projected similarly in all plots.

The effects of the physiological and morphological changes observed in the aboveground parts during the post-treatment growing seasons on the long-term radial growth remain speculative. There were differences in the starch content and electrical impedance of needles but no differences in the soluble sugar content among the treatments in the post-treatment growing seasons (Repo et al. 2011). For the starch content of needles, FROST differed from the other two treatments in 2006, and CTRL from the other two treatments in 2007. Therefore, no clear conclusion can be made of the relation between the starch content and lagged decline in radial growth in OPEN. In addition, shoot elongation, the needle cross-sectional area, and the number of healthy buds were reduced after the treatments, but only in FROST (Sutinen et al. 2015). However, the effects of soil freezing are primarily projected onto roots, either directly through a low temperature and/or mechanical stress, or indirectly via microorganisms. The absence of snow cover with a consequent increase in soil freezing and delayed soil thawing may induce damage in roots, mycorrhizas, and counteracting microorganisms (Groffman et al. 2001; Tierney et al. 2003). Therefore, the growth rhythm of fine roots may be affected by lagged soil thawing as found here in the FROST treatment but not in the OPEN treatment with approximately similar soil freezing pattern in winter (Repo et al. 2014). In the long-term, those changes may have impacted the resources allocation and growth between roots and shoots, but in this study the impacts were not found in trunk diameter growth in FROST but in OPEN only. One reason could be that the compensatory root growth in FROST alleviated that effect in comparison to OPEN (Repo et al. 2014). In addition, spatial variation in soil properties and increased nutrient availability of roots by soil freezing may mediate the tree growth response (Cleavitt et al. 2008; Sanders-DeMott et al. 2018), but these relationships have yet to be evaluated. Future studies are needed to determine whether sublethal soil freezing induces shifts in carbon allocation and increased growth of fine roots and mycorrhizas at the expense of stem diameter growth.

In the boreal region, empirical results indicate that climate warming has already enhanced forest growth (Pretzsch et al. 2014; Henttonen et al. 2017), and model predictions forecast a future increase in some regions (e.g. Xia et al. 2014; Kellomäki et al. 2018). However, our results suggest that climate warming, which increases soil frost severity, may initiate physiological responses and damage that result in an overall decline in tree growth rates (cf. Reinmann et al. 2019; Harrison et al. 2020). Thus, the positive effects on forest growth via a longer growing season as a consequence of increasing temperatures may not be fully realised due to the negative effects of winter warming.

Author contribution statement The original idea for the study is given by Repo. All authors contributed to the data analysis and the preparation of the manuscript.

Acknowledgements We thank Eija Koljonen, Urho Kettunen, and the other staff working at the laboratory of the Natural Resources Institute Finland (Luke), Joensuu for their technical assistance in the field experiment, and Raino Lievonen for sampling and measuring the increment cores. We are grateful to the UPM forest company for their permission to use their forest in the study. This study was funded by the Natural Resources Institute Finland (Luke) (project 41007-00004000) and the Academy of Finland (decision no. 311455).

Funding Open Access funding provided by Natural Resources Institute Finland (LUKE).

Complaince with ethical standards

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

References

Bigras FJ, Ryyppö A, Lindström A, Stattin E (2001) Cold acclimation and deacclimation of shoots and roots of conifer seedlings. In: Bigras FJ, Colombo SJ (eds) Conifer Cold Hardiness. Kluwer, Dordrecht, pp 57–88

Bonan GB, Shugart HH (1989) Environmental factors and ecological processes in boreal forests. Ann Rev Ecol Syst 20:1–28. https://doi.org/10.1146/annurev.es.20.110189.000245

Cajander AK (1949) Forest types and their significance. Acta For Fenn 56:1–71. https://doi.org/10.14214/aff.7396

Camarero JJ, Gazol A, Sancho-Benages S, Sangüesa-Barreda G (2015) Know your limits? Climate extremes impact the range of Scots pine in unexpected places. Ann Bot 115:917–927. https://doi.org/10.1093/aob/mcv124

Carlson KM, Coulthard B, Starzomski BM (2017) Autumn snowfall controls the annual radial growth of centenarian whitebark pine (*Pinus albicaulis*) in the Southern Coast Mountains, British Columbia, Canada. Arc Antarc Alp Res 49:101–113. https://doi.org/10.1657/AAAR0016-033

Cleavitt NL, Fahey TJ, Groffman PM, Hardy JP, Henry KS, Driscoll CT (2008) Effects of soil freezing on fine roots in a northern hardwood forest. Can J For Res 38:82–91. https://doi.org/10.1139/X07-133

Comerford DP, Schaberg PG, Templer PH, Socci AM, Campbell JL, Wallin KF (2013) Influence of experimental snow removal on root and canopy physiology of sugar maple trees in a northern hardwood forest. Oecologia 171:261–269. https://doi.org/10.1007/s00442-012-2393-x

Domisch T, Martz F, Repo T, Rautio P (2018) Winter survival of Scots pine seedlings under different snow conditions. Tree Physiol 38:602–616. https://doi.org/10.1093/treephys/tpx111

Domisch T, Martz F, Repo T, Rautio P (2019) Let it snow! Winter conditions affect growth of birch seedlings during the following growing season. Tree Physiol 39:544–555. https://doi.org/10.1093/treephys/tpy128

Franke AK, Bräuning A, Timonen M, Rautio P (2017) Growth response of Scots pines in polar-alpine tree-line to a warming climate. For Ecol Manage 399:94–107. https://doi.org/10.1016/j.foreco.2017.05.027

Groffman PM, Driscoll CT, Fahey TJ, Hardy JP, Fitzhugh RD, Tierney GL (2001) Colder soils in a warmer world: A snow manipulation study in a northern hardwood forest ecosystem. Biogeochem 56:135–150. https://doi.org/10.1023/A:1013039830323

Groffman PM, Hardy JP, Driscoll CT, Fahey TJ (2006) Snow depth, soil freezing, and fluxes of carbon dioxide, nitrous oxide and methane in a northern hardwood forest. Glob Ch Biol 12:1748–1760. https://doi.org/10.1111/j.1365-2486.2006.01194.x

Harrison JL, Sanders-DeMott R, Reinmann A, Sorensen PO, Phillips NG, Templer PH (2020) Growing-season warming and winter soil freeze/thaw cycles increase transpiration in a northern hardwood forest. Ecology 101:e03173. https://doi.org/10.1002/ecy.3173

Helama S, Mielikäinen K, Timonen M, Herva H, Tuomenvirta H, Venäläinen A (2013) Regional climate signals in Scots pine growth with insights into snow and soil associations. Dendrobiol 70:27–34. https://doi.org/10.12657/denbio.070.003

Henry HAL (2008) Climate change and soil freezing dynamics: historical trends and projected changes. Clim Chang 87:421–434. https://doi.org/10.1007/s10584-007-9322-8

Henttonen HM, Nöjd P, Mäkinen H (2017) Environment-induced growth changes in the Finnish forests during 1971–2010 – an analysis based on National Forest Inventory. For Ecol Manage 386:22–36. https://doi.org/10.1016/j.foreco.2016.11.044

Isard SA, Schaetzl RJ (1998) Effects of winter weather conditions on soil freezing in southern Michigan. Phys Geogr 19:71–94. https://doi.org/10.1080/02723646.1998.10642641

Jyske T, Manner M, Mäkinen H, Nöjd P, Peltola H, Repo T (2012) The effects of artificial soil frost on cambial activity and xylem formation in Norway spruce. Trees 26:4–419. https://doi.org/10.1007/s00468-011-0601-7

Kalliokoski T, Nygren P, Sievänen R (2008) Coarse root architecture of three boreal tree species growing in mixed stands. Silva Fenn 42:189–210. https://doi.org/10.14214/sf.252

Kellomäki S, Strandman H, Heinonen T, Asikainen A, Venäläinen A, Peltola H (2018) Temporal and spatial change in diameter growth of boreal Scots pine, Norway spruce, and birch under recent-generation (CMIP5) global climate model projections for the 21st century. Forests 9:118:1–24. https://doi.org/10.3390/f9030118

Kirdyanov A, Hughes M, Vaganov E, Schweingruber F, Silkin P (2003) The importance of early summer temperature and date of snow melt for tree growth in the Siberian Subarctic. Trees 17:61–69. https://doi.org/10.1007/s00468-002-0209-z

Kullman L (1989) Cold-induced dieback of montane spruce forests in the Swedish Scandes – a modern analogue of paleoenvironmental processes. New Phytol 113:377–389. https://doi.org/10.1111/j.1469-8137.1989.tb02416.x

Kullman L (1991) Cataclysmic response to recent cooling of a natural boreal pine (*Pinus sylvestris* L.) forest in northern Sweden. New Phytol 117:351–360. https://doi.org/10.1111/j.1469-8137.1991.tb04917.x

Liston GE, Hiemstra CA (2011) The changing cryosphere: Pan-Arctic snow trends (1979–2009). J Clim 24:5691–5712. https://doi.org/10.1175/JCLI-D-11-00081.1

Macias Fauria M, Helle T, Niva A, Posio H, Timonen M (2008) Removal of the lichen mat enhances tree growth in a northern Scots pine forest. Can J For Res 38:2981–2993. https://doi.org/10.1139/X08-135

Maljanen M, Alm J, Martikainen PJ, Repo T (2010) Prolongation of soil frost resulting from reduced snow cover increases nitrous oxide emissions from boreal forest soil. Bor Environ Res 15:34–42. http://hdl.handle.net/10138/233016

Martz F, Vuosku J, Ovaskainen A, Stark A, Rautio P (2016) The snow must go on: ground ice encasement, snow compaction and absence of snow differently cause soil hypoxia, CO_2 accumulation and tree seedling damage in Boreal forests. PLoS One 11(6):e0156620. https://doi.org/10.1371/journal.pone.0156620

McCabe GJ, Wolock DM (2010) Long-term variability in Northern Hemisphere snow cover and associations with warmer winters. Clim Change 99:141–153. https://doi.org/10.1007/s10584-009-9675-2

Morán-Tejeda E, López-Moreno JI, Stoffel M, Beniston M (2016) Rain-on-snow events in Switzerland: recent observations and projections for the 21st century. Clim Res 71:111–125. https://doi.org/10.3354/cr01435

Nikolaev AN, Fedorov PP, Desyatkin AR (2009) Influence of climate and soil hydrothermal regime on radial growth of *Larix cajanderi* and *Pinus sylvestris* in Central Yakutia, Russia. Scand J For Res 24:217–226. https://doi.org/10.1080/02827580902971181

Pederson GT, Gray ST, Woodhouse CA, Betancourt JL, Fagre DB, Little JS, Watson E, Luckman BH, Graumlich LJ (2011) The unusual nature of recent snowpack declines in the North American Cordillera. Science 333:332–335. https://doi.org/10.1126/science.1201570

Petoukhov V, Semenov VA (2010) A link between reduced Barents-Kara sea ice and cold winter extremes over northern continents. J Geophys Res 115:D21111. https://doi.org/10.1029/2009JD013568

Pretzsch H, Biber P, Schutze G, Uhl E, Rotzer T (2014) Forest stand growth dynamics in Central Europe have accelerated since 1870. Nat Commun 5:1–10. https://doi.org/10.1038/ncomms5967

Rantala S (ed) (2011) Finnish forestry practice and management. Metsäkustannus, Helsinki, 271p

Rasmus S, Räisänen J, Lehning M (2004) Estimating snow conditions in Finland in the late 21st century using the SNOWPACK-model with regional climate scenario data as input. Ann Glaciol 38:238–244. https://doi.org/10.3189/172756404781814843

Reinmann AB, Susser JR, Demaria EMC, Templer PH (2019) Declines in northern forest tree growth following snowpack decline and soil freezing. Glob Ch Biol 25:420–430. https://doi.org/10.1111/gcb.14420

Repo T, Sutinen S, Nöjd P, Mäkinen H (2007) Implications of delayed soil frost thawing on the physiology and growth of Norway spruce. Scand J For Res 22:118–127. https://doi.org/10.1080/02827580701231795

Repo T, Lehto T, Finér L (2008) Delayed soil thawing affects root and shoot functioning and growth in Scots pine. Tree Physiol 28:1583–1591. https://doi.org/10.1093/treephys/28.10.1583

Repo T, Roitto M, Sutinen S (2011) Does the removal of snowpack and the consequent changes in soil conditions affect the physiology of Norway spruce needles? Environ Exp Bot 72:387–396. https://doi.org/10.1016/j.envexpbot.2011.04.014

Repo T, Sirkiä S, Heinonen J, Lavigné A, Roitto M, Koljonen E, Sutinen S, Finér L (2014) Effects of soil frost on fine root growth and longevity of Norway spruce. For Ecol Manag 313:112–122. https://doi.org/10.1016/j.foreco.2013.11.002

Sakai A (1968) Mechanism of desiccation damage of forest trees in winter. Contr Instit Low Temp Sci B 15:15–35. https://doi.org/http://hdl.handle.net/2115/20265

Sanders-DeMott R, Sorensen PO, Reinmann AB, Templer PH (2018) Growing season warming and winter freeze–thaw cycles reduce root nitrogen uptake capacity and increase soil solution nitrogen in a northern forest ecosystem. Biogeochem 137:337–349. https://doi.org/10.1007/s10533-018-0422-5

Sanmiguel-Vallelado A, Camarero JJ, Gazol A, Morán-Tejeda E, Sangüesa-Barreda G, Alonso-Gonzáles E, Gutiérrez E, Alla AQ, Galván JD, López-Moreno JI (2019) Detecting snow-related in radial growth of *Pinus uncinata* mountain forests. Dendrochronol 57(125622):1–10. https://doi.org/10.1016/j.dendro.2019.125622

Solantie R (2003) On definition of ecoclimatic zones in Finland. Fin Meteor Inst Reports No. 2003:2: 1–44

St. George S (2014) An overview of tree-ring width records across the Northern Hemisphere. Quat Sci Rev 95:132–150. https://doi.org/10.1016/j.quascirev.2014.04.029

Sutinen R, Hänninen P, Venäläinen A (2008) Effect of mild winter events on soil water content beneath snowpack. Cold Reg Sci Technol 51:56–67. https://doi.org/10.1016/j.coldregions.2007.05.014

Sutinen R, Vajda A, Hänninen P, Sutinen M-L (2009a) Significance of snowpack for root-zone water and temperature cycles in subarctic Lapland. Arc Antarc Alp Res 41:373–380. https://doi.org/10.1657/1938-4246-41.3.373

Sutinen R, Äikää O, Piekkari M, Hänninen P (2009b) Snowmelt infiltration through partially frozen soil in Finnish Lapland. Geophysics 45:27–39

Sutinen S, Roitto M, Lehto T, Repo T (2014) Simulated snowmelt and infiltration into frozen soil affected root growth, needle structure and physiology of Scots pine saplings. Bor Environ Res 19:281–294. http://hdl.handle.net/10138/228600

Sutinen S, Roitto M, Repo T (2015) Vegetative buds, needles and shoot growth of Norway spruce are affected by experimentally delayed soil thawing in the field. For Ecol Manag 336:217–223. https://doi.org/10.1016/j.foreco.2014.10.029

Tierney GL, Fahey TJ, Groffman PM, Hardy JP, Fitzhugh RD, Driscoll CT (2001) Soil freezing alters fine root dynamics in a northern hardwood forest. Biogeochem 56:175–190. https://doi.org/10.1023/A:1013072519889

Tierney GL, Fahey TJ, Groffman PM, Hardy JP, Fitzhugh RD, Driscoll CT, Yavitt JB (2003) Environmental control of fine root dynamics in a northern hardwood forest. Glob Ch Biol 9:670–679. https://doi.org/10.1046/j.1365-2486.2003.00622.x

Tranquillini W (1982) Frost-drought and its ecological significance. In: Lange OL, Nobel PS, Osmond CB, Ziegler H (eds) Physiological plant ecology II. Springer, Berlin, pp 379–400

Vaganov EA, Hughes MK, Kirdyanov AV, Schweingruber FH, Silkin PP (1999) Influence of snowfall and melt timing on tree growth in subarctic Eurasia. Nature 400:149–151. https://doi.org/10.1038/22087

Walsh SJ, Butler DR, Allen TR, Malanson GP (1994) Influence of snow patterns and snow avalanches on the Alpine treeline ecotone. J Veg Sci 5:657–672. https://doi.org/10.2307/3235881

Watson E, Luckman BH (2016) An investigation of the snowpack signal in moisture-sensitive trees from the Southern Canadian Cordillera. Dendrochronol 38:118–130. https://doi.org/10.1016/j.dendro.2016.03.008

Xia J, Chen J, Piao S, Ciais P, Luo Y, Wan S (2014) Terrestrial carbon cycle affected by non-uniform climate warming. Nat Geosci 7(3):173–180. https://doi.org/10.1038/ngeo2093