



Vegetative buds, needles and shoot growth of Norway spruce are affected by experimentally delayed soil thawing in the field



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ABSTRACT

Climate change may increase air temperature and decrease snowpack in the boreal zone. Due to declined insulating snow cover, tree roots may be exposed to too low soil temperatures that may be reflected in shoot growth. We studied the effects of soil freezing and delayed thawing on vegetative buds, needles and shoots in a 47-year-old boreal stand of Norway spruce (*Picea abies* L. Karst). The treatments in two winters of 2005/06 and 2006/07 were: (i) natural snow accumulation and melting (CTRL), (ii) artificial snow removal during winter (OPEN), and (iii) the same as OPEN, but the ground was insulated in early spring to delay soil thawing (FROST). More soil freezing occurred in OPEN and FROST than CTRL, and soil thawing was delayed in FROST as compared to the two other treatments. The formation of new buds, and consequently the number of new shoots were reduced in FROST. The shoot elongation was reduced and the needle cross-sectional area was smaller in FROST compared to OPEN and CTRL. As the soil temperature in both OPEN and FROST was the same during winter, the wintertime soil frost could not be the reason for the changes. Instead, the delayed soil thawing and warming towards summer seemed to hamper the root function and thus reduced the growth of above ground part of the trees. Timing of soil warming in spring appeared to be an important factor for the vegetative bud formation and shoot growth. Thus, on sites prone to soil frost and low soil temperatures, forest management practices should be planned for a proper stand development.

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1. Introduction

Accumulation of snow protects the soil from freezing during winter and keeps the soil moist during spring. Climate change towards warmer winter temperatures may lead to thin or missing snow cover in many areas in the boreal zone, but the low below-zero temperatures will presumably not disappear in future. Lack of snow or only thin snow cover may lead to more extensive and longer lasting soil freezing in areas where it is uncommon in the present climate (Groffman et al., 2001; Mellander et al., 2005; Henry, 2008). Globally, satellite data have shown about 10% reduction in the extent of snow cover over the past 40 year, and current climate change models predict these trends to continue (Houghton et al., 2001). The model simulations for boreal forests have shown large spatial variations in the snow depth and consequently in the timing of soil warming in spring (Solantie, 2000; Mellander et al., 2005; Wu et al., 2012).

The sensitivity of conifer roots to low wintertime soil temperatures has seasonal variation and depends on age of the roots, spe-

cies and geographical location of the trees (Sutinen et al., 1998; Bigras and Dumais, 2005). Too low soil temperatures may damage roots by cellular dehydration (Sutinen et al., 1996) or mechanically by soil movements (de Chantal et al., 2007; Sutinen et al., 2014). In the field studies with sugar maple (*Acer saccharum* Marsh.), yellow birch (*Betula alleghaniensis* Brit.) and Norway spruce (*Picea abies* L. Karst) snow was removed for some winter months by shoveling. This caused low soil temperatures (around -5.5 C) and consequently induced increased root mortality. However, the root growth recovered during the follow-up growing season (Tierney et al., 2001; Gaul et al., 2008). As a result of soil freezing to almost -6 C, electrolyte leakage increased in roots of sugar maple which led to a reduced terminal shoot growth in next growing season (Comerford et al., 2013). In the above studies the soil thawing occurred more or less simultaneously both in the snow manipulation and the control plots.

When soil thawing was delayed to the summer months (June and July) and when the soil temperature was under or close to 0 C, the changes in physiology and growth were observed in the above and below ground organs of Scots pine (*Pinus sylvestris* L.) and Norway spruce. Sap flow and stomatal conductance decreased and photosynthetic recovery was delayed in 20-year-old Scots pine

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(Mellander et al., 2004, 2008). Furthermore, the delayed soil thawing delayed starch accumulation in needles (Repo et al., 2011), delayed formation of new tracheid cells in trunks (Jyske et al., 2012) and hampered the fine root formation and increased root mortality in 47-year-old Norway spruce in Eastern Finland (Repo et al., 2014). The laboratory experiments have shown negative impacts of delayed soil thawing on needle physiology as well as on growth of fine roots and root tip formation in Scots pine saplings (Repo et al., 2005, 2008). Earlier studies have shown that low above zero temperatures in soil, for example 5 °C during spring or early growing season are not warm enough for proper function of trees, and thus affect physiology of the needles, decrease shoot and root growth, and in some cases delay bud burst in both broad-leaved and conifer seedlings (Lyr, 1996; Iivonen et al., 1999; Repo et al., 2004).

There are no comprehensive studies on how soil freezing in winter and its delayed thawing in spring affects anatomy and morphology of vegetative buds and needles, or on growth of the new shoots in mature conifer species in the northern latitudes. The recent studies have shown that the length growth of primordial shoot of Norway spruce in boreal areas, like central part of Finland (middle boreal zone), starts around mid-April without any visible signs in the buds (Sutinen et al., 2012) and continues as visible shoot elongation from late May/early June up to early July (Bronson et al., 2009). In spruce species with predetermined growth pattern, the formation of the new buds for the next years' growth starts already after mid-May and continues through the summer up to mid-September in Central and North Europe (Cannel and Willet, 1975; Svobodová et al., 2000; Sutinen et al., 2006). Thus, the primordial shoot growth and the initial phases of new bud formation take place at the time when soils are expected to be affected by climate warming in spring and early summer. Our aim was to study how the increased soil freezing in winter and delayed soil thawing up to the summer affects the bud development in spring, the formation of new vegetative buds, as well as shoot growth, anatomy and morphology of buds and needles of Norway spruce trees.

2. Materials and methods

2.1. Experimental set-up

A snow manipulation experiment was conducted in a 47-year-old (in 2005) stand of Norway spruce (forest type Myrtillus (MT), Cajander, 1949) in the boreal conifer zone near the city of Joensuu, Finland (62°36'N, 29°43'E) during two winters in 2005/06 and 2006/07. The average height of the trees was 17 m, the stand density 864 trees per hectare, the stand volume 211 m³ ha⁻¹ and the basal area 25.4 m² ha⁻¹. The soil was glacial till and the pedological soil type ferric podzol. The organic matter content in the organic horizon was 70.8% and in the uppermost mineral soil layer (3–10 cm) 9.0%.

The experiment had three treatments and three replicate plots (size 12 × 12 m with a transition zone of 5 m between plots) for each treatment. The replicate plots were located rectangularly around the data logger in the middle of the study area. The treatments were: (1) snow accumulated and thawed according to the natural rhythm (CTRL), (2) snow was removed throughout the winter by shoveling (OPEN), (3) the same as OPEN, but the ground was insulated with a layer of hay (ca. 15 cm) between plastic sheeting in late March (week 13) to delay soil thawing (FROST). The insulation was removed on July 21, 2006 and July 4, 2007 when soil temperature in FROST rose permanently above 0 °C.

Air temperature at a height of 2 m, soil temperature at the depths of 5, 15 and 50 cm (105T thermocouple, Campbell Sci-

tific, Shepshed, UK) and volumetric soil moisture content at the depth of 15 cm (CS615, Campbell Scientific, Shepshed, UK) were logged in each plot. Snow depth on the CTRL plots was monitored. For more details of the study design see Maljanen et al. (2010), Repo et al. (2011) and Jyske et al. (2012).

2.2. Sampling and analysis

Three trees were randomly selected from the middle of each plot in order to monitor the time of bud burst, and sampling for shoot growth assessments as well as anatomical and morphological studies of buds and needles. Bud burst was monitored by binoculars from the apical buds of the main shoot and of the branches in the third whorl from the top in 2006 and 2007. Bud development was followed twice a week from late May until bud burst was completed. The bud development was classified to three developmental phases as follows (Slaney et al., 2007): *A* = dormant, no visible signs of bud swelling, *D* = a short brush of new needles visible, bud scales abscising, but a "hat" of bud scales remains on the top of the new shoot, *E* = a longer brush of needles visible, all bud scales disappeared.

Branches were sampled with the telescopic secateurs at the height of 1–3 m from the top of the trees for studying growth of shoots as well as anatomy and morphology of buds and needles. The needles grown in 2006 were sampled between 28 June and 1 July, 2007 (at the age of about one year), and the needles grown in 2007 between 3 and 11 September, 2007 (at the age of four months). In both sampling times the needles were fully matured (cf. Sutinen et al., 2006). Five needles from each tree per plot (i.e. total of 27 trees) were sampled from the upper side of the branch from the middle of side shoots, and put to the test tubes containing fixative solutions (2% glutaraldehyde in cacodylate buffer, 0.05 M in summer and 0.07 M in autumn, pH 7.0). Cross-sectional samples (length 0.5–1 mm) were cut within two days at 3 mm from the tips from every five needles in a drop of a fixative mentioned above, and subsequently prepared as described in Sutinen et al. (1990). The cross-sections (1.5 μm thick) of each sample were sectioned on an LKB 2128 Ultratome (Bromma, Sweden), double-stained with 1% toluidine blue and 1% p-phenylene diamine (Kivimäenpää et al., 2004) and digitally photographed (Leica CD Camera, Switzerland) under a light microscope (Leica DM2500, Germany). The cross-sectional area of the needle and the area of the central cylinder was measured from digital images photographed at ×10 objective magnification (Fig. 1a) whereas sclerenchyma, phloem and xylem tissues were measured from images photographed at ×20 objective magnification (Fig. 1b). The measurements were made by using Adobe Photoshop (version 6.0, Adobe Systems Nordic AB, Kista, Sweden).

For stereomicroscopic analysis of the buds and for measurements of shoot length in 2006 and 2007, one branch of each tree was sampled in April 2007 and 2008. The analyses were done from the second whorl of each branch (Fig. 2). Three previous-year side shoots (C1-shoot) were cut from each branch, and the length of three current year shoots (C-shoot) from every three C1-shoots were measured with a ruler. Thus at maximum, the length of nine C-shoots was measured from the base of the node between the previous and current year's growths up to the location of lowermost bud scales of the terminal bud (Fig. 2). In total, 152 C1-shoots (81 in 2006 and 71 in 2007) and 427 C-shoots (243 in 2006 and 184 in 2007) were measured.

All terminal buds (243 buds in 2006 and 182 buds in 2007) and whorl buds (428 buds in 2006 and 279 buds in 2007) formed into the C-shoots were counted and scored for their healthy and numbers (Fig. 2). The buds were cut longitudinally into two halves and their condition was analysed under a stereomicroscope as follows: healthy bud (Fig. 3a), the primordial shoot was eaten (Fig. 3b), the bud was malformed (Fig. 3c) and the bud was dwarfed with

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