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Effects of snow manipulation on larch trees in the taiga forest ecosystem in northeastern Siberia

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Abstract

Changes in winter precipitation (snow) may greatly affect vegetation by altering hydrological and biochemical processes. To understand the effects of changing snow cover depth and melt timing on the taiga forest ecosystem, a snow manipulation experiment was conducted in December 2015 at the Spasskaya Pad experimental larch forest in Eastern Siberia, which is characterized by a continental dry climate with extreme cold winters and hot summers. Variables including soil temperature and moisture, oxygen and hydrogen isotope ratios of soil moisture and stem water, foliar nitrogen and carbon contents and their isotopes, phenology, and soil inorganic nitrogen were observed at snow removal (SNOW−), snow addition (SNOW+), and CONTROL plots. After snow manipulation, the soil temperature at the SNOW− plot decreased significantly compared to the CONTROL and SNOW+ plots. At SNOW− plot, snowmelt was earlier and soil temperature was higher than at other plots during spring because of low soil moisture caused by less snowmelt water. Despite the earlier snowmelt and higher soil temperature in the SNOW− plot in the early growing season, needle elongation was delayed. Leaf chemistry also differed between the CONTROL and SNOW− plots. The needle nitrogen content in the SNOW− plot was lower in the middle of July, whereas no difference was observed among the three plots in August. The soil inorganic nitrogen content of each plot corresponded to these results. The amount of soil ammonium was lower in the SNOW− plot than in the other plots at the end of July, however, once production started in August, the amount of soil ammonium in the three plots was comparable. Extremely low soil temperatures in winter and freeze–thaw cycles in spring and dry soil condition in spring and early summer at the SNOW− plot may have influenced the phenology and production of soil inorganic nitrogen.

Keywords: Boreal forest, Taiga, Larch, Snow manipulation, Permafrost, Stable isotopes, Phenology, Nutrient, Soil moisture

1 Introduction

Snow plays an important role in the ecosystems of the Northern Hemisphere (Chapin et al. 2000; Vavrus 2007). Snow cover acts as an insulator in winter and regulates the water and nutrient balance, thereby influencing material cycling in summer (Aerts et al. 2004; Kreyling et al. 2012; Freppaz et al. 2018). As stated in the IPCC

Fifth and Sixth Assessment Reports, the snow covered area is declining as the southern boundary turns into a snow free area (Vaughan et al. 2013; Douville et al. 2021). Because of global warming, snow-covered areas are expected to decrease and precipitation events are expected to become less frequent and intense (Huntington 2006; Deser et al. 2010; Callaghan et al. 2011).

Although a general decrease in the depth of snow cover is expected because of the decrease of snowfall, in arctic and subarctic regions snow depth may increase. According to simulation models by Park et al. (2014), snow depth is expected to increase in Siberia by 0.99 mm per

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year. This modeled trend is in accordance with observations from the central and western Siberia regions of Russia (Bulygina et al. 2009, 2011). Snow cover depth and duration have a major effect on ecosystems through their influence on the soil water balance and thermal regimes, nutrient availability, and duration of the growing season (Schimel et al. 2004; Grippa et al. 2005; Lorienty et al. 2018). Additionally, changes in snow depth and density have a significant influence on the soil temperature (Zhang 2005; Callaghan et al. 2011). In continuous permafrost regions, deeper snow cover can lead to a significant increase in mean annual ground temperatures, a reduction in the winter freezing depth, and an increase in soil moisture in spring and summer (Morse et al. 2012; Johansson et al. 2013; Park et al. 2015; Karjalainen et al. 2019). Such phenomena were observed in Eastern Siberia in 2004–2007 with heavy summer rainfall and winter snowfall (Iijima et al. 2010). Interannual variations in snow cover conditions (timing, duration, density, and thickness) also have a strong influence on long-term ground temperatures in cold regions (Aerts et al. 2004). During winter and early spring, arctic soil temperatures mainly depend on the properties of snow cover and regional climate, and even small changes in snow cover can have a strong impact on soil frost frequency and intensity (Walker et al. 1999). In addition to the soil temperature, an increase in snow cover may cause soil subsidence and waterlogging in permafrost regions with a high ice content (Nauta et al. 2015). In high-latitude ecosystems, snowmelt timing controls not only hydro-meteorological processes, but also many biological processes such as plant phenology and productivity. There are many case studies of snow manipulation experiments exploring the effects of changing depths of snow cover (e.g., Wipf and Rixen 2010).

Snow cover affects soil moisture in the early growing season because approximately half of the snow water equivalent (SWE) infiltrates into the soil after snow melt (Sugimoto et al. 2003). Increased water availability, especially during the early growing season, can positively affect boreal tree growth (Zhang et al. 2019), whereas large amounts of soil moisture may lead to overwetting conditions (Iwasaki et al. 2010; Tei et al. 2013), resulting in reduced gross primary production (Kotani et al. 2019). In subarctic bogs, phenology observed by earlier flowering dates was reported in an experiment with an open top chamber (Aerts et al. 2004). On the other hand, earlier snow melt, followed by cold air temperatures in spring, reduced productivity in Arctic Alaskan tundra (Stow et al. 2004) and boreal forests in northeastern Siberia (Kirdyanov et al. 2003). Models with coupled hydrological and biogeochemical processes (such as CHANGE) have also shown that deeper snow cover causes larger

net ecosystem exchange because of higher soil moisture, especially during dry years (Park et al. 2011).

Figure 1 is a schematic diagram of the effects of changes in snow depth on boreal forest or tundra ecosystems. Snow influences length of growing season, soil moisture, and N availability (Fig. 1). Because an increase in snow cover depth causes lower thermal conductivity, leading in higher soil temperatures. This can stimulate the decomposition of soil organic matter, resulting in increased nitrogen availability, as generally described (Schimel and Clein 1996; Hardy et al. 2001; Robinson 2002; Aerts 2006; Wipf and Rixen 2010). However, such effects are diverse and depend on ecosystem types, which is associated not only with climatic conditions but also with vegetation, litter quality and quantity, microbial composition, and plant N demand (Li et al. 2016). Although nitrogen production and uptake by plants during winter are relatively well studied in temperate forests (Andresen and Michelsen 2005; Ueda and Tokuchi 2013), the number of studies in boreal and tundra ecosystems is still limited (Cooper 2014; Koyama and Kielland 2019). Kielland et al. (2006) described how earlier and deeper snow packs in forest ecosystems allow microbial activity to continue during winter in Alaska, which was previously presumed to be biologically inactive due to a negative soil temperature. They also observed that winter (non-growing season) nitrogen mineralization accounted for approximately 40% of the annual flux, which was significantly higher than previously reported. Moreover, deeper snow cover causes higher soil nitrogen availability, which leads to increased plant N uptake, foliar nitrogen content, photosynthesis rates (Leffler and Welker 2013), leaf area index (Pattison and Welker 2014), and plant production (Wahren et al. 2005).

Frost damage is another factor associated with a decrease in snow cover depth. Thin snow cover may cause freeze–thaw cycles in winter and have a negative effect on plant production. The experimental removal of snow cover has produced direct frost damage, followed by a 50% reduction in understory vegetation coverage (Kreyling et al. 2012). Indirectly, soil frost and frequent freeze–thaw cycles in the absence of snow cover during winter and spring can cause a decrease in nitrogen availability (Feng et al. 2007; Frechette et al. 2011), an increase in nitrogen and phosphorus leaching (Fitzhugh et al. 2001), and root damage, which disrupts nutrient uptake (Cleavitt et al. 2008). Forests with deeper organic layers have a lower possibility of soil frost damage during winter, even if the snow cover is less deep (Hardy et al. 2001).

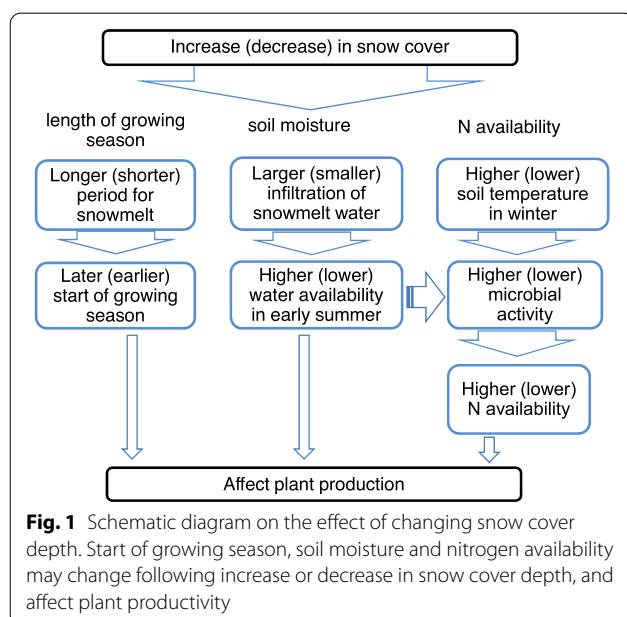
Although there have been many reports on snow manipulation experiments on tundra ecosystems, few reports have been published on forest ecosystems. This is because snow cover manipulation in forests is

complicated by snow shoveling, unlike in tundra, where snow fences can be easily used to manipulate snow cover. In temperate and boreal forests, most snow manipulation experiments have been conducted in regions with expected reductions in snow, for example, North America and Scandinavia, and were mainly focused on the snow removal treatment (e.g., Groffman et al. 2001). Snow removal experiments in forested areas have shown a strong effect of snow cover on ecosystem processes, such as heat and moisture fluxes, nutrient dynamics, and changes in phenology and diversity (Groffman et al. 2001; Frechette et al. 2011; Kreyling et al. 2012; Comerford et al. 2013; Drescher and Thomas 2013; Martz et al. 2016; Watanabe et al. 2019). Because of direct frost damage to the root system, there have been many reports on the reduced ability of plants to uptake water and nutrients (Pilon et al. 1994; Cleavitt et al. 2008; Blume-Werry et al. 2016). A decrease in nutrient availability from shallower snow cover due to leaching or impaired microbial activity has also been reported (Fitzhugh et al. 2001). Moreover, Frechette et al. (2011) observed decreases in foliar N and photosynthetic activity through spring snow removal in a Canadian boreal forest ecosystem. In a northern hardwood forest in Japan, soil ammonium increases following the enhancement of soil freeze–thaw cycles in winter because DON and DOC availability for soil microbes increase (Watanabe et al. 2019). Other effects have also been observed, such as reductions in the terminal shoot length of sugar maple trees in the U.S. (Comerford et al. 2013), a decrease in the coverage of understory plants in Swedish boreal forests (Kreyling et al. 2012), and reductions in sapling survival in forests in Canada and

northern Finland (Drescher and Thomas 2013; Martz et al. 2016). These effects have negative implications for biomass production. As described above, there are many publications on Alaska and European boreal and temperate forest ecosystems; however, no snow manipulation experiments have been conducted for taiga (deciduous conifer larch forests) in northeastern Siberia, which is a globally typical forest ecosystem because of its extremely large area.

Eastern Siberia is a vast territory covered by taiga, characterized by deciduous conifer larch trees (*Larix gmelinii* and *L. cajanderi*) which grow on permafrost (Archibold 1995). This region experiences extreme cold winters, short and hot summers, and an extremely dry climate (Tei et al. 2017; Tei and Sugimoto 2018). Because of the vast coverage area of larch forests worldwide (approximately 40% of boreal forests), the response of larch forests is extremely important. Changes in snow cover depth and snow water equivalent (SWE) in this region affect soil moisture considerably. For larch trees, soil moisture derived from snowmelt water is extremely important in the early summer season when photosynthesis activity is highest (Sugimoto et al. 2002, 2003). It is also expected that larch trees will be affected by changing snow cover and the related processes described above. There have been no reports of snow manipulation experiments for larch forests in northeastern Siberia, conditions with extremely low winter temperature and extremely dry climate. The objective of this research is to observe the responses of larch trees to changes in snow cover using snow manipulation experiments.

We conducted a snow manipulation experiment in December 2015 by manually removing snow from the snow removal plot (SNOW−) using shovels and adding the removed snow to the snow addition plot (SNOW+). The snow was transported with heavy duty bags. The aim of this study is to examine (1) whether snow cover manipulation affects soil temperature under extreme cold winter and short spring, and (2) whether it alters the start of the growing season. Deeper snow cover causes longer period of snowmelt (Fig. 1); however, soil thaw rate in spring depends on the soil temperature, which is strongly affected by soil moisture (or ice) content. We also investigate (3) when the nitrogen production starts, and (4) whether soil moisture affects the nitrogen availability. Notably, soil moisture is extremely important for larch forest in northern Siberia, because of the small amount of annual precipitation (238 mm). Therefore, not only water availability but also N availability for plants are also expected to be affected by soil moisture. Such dynamic effects will cause a change in tree production. As no direct measurements of changes in production are conducted in this study, we instead employ the following



approaches: (1) needle elongation measurements as a proxy for the growing season length, which can be used as a proxy for production change; (2) soil nutrient availability and foliar nitrogen content, which can also be used as a proxy for the photosynthesis rate, and effects on production. We also use (3) water isotopes to investigate the origin of soil moisture and carbon isotope to know photosynthetic physiology and carbon allocation trends.

2 Methods

2.1 Site description

The experiment was conducted at Spasskaya Pad Scientific Forest Station (62° 25' N, 129° 62' E, elevation 220 m above sea level) of the Institute for Biological Problems of Cryolithozone, Siberian Branch of the Russian Academy of Sciences (Fig. 2). The station is located 20 km northwest of Yakutsk, Sakha Republic, Russian Federation (Fig. 2). Deciduous conifers (*Larix cajanderi* and *L. gmelinii*) are the dominant species in the study area. The forest floor is covered by various plant species, including deciduous shrub *Arctous alpina* and evergreen shrubs *Vaccinium vitis-idaea* and *Arctostaphylos uva-ursi*, and many grass species. This region is characterized by an intense continental climate with severe cold winters and hot dry summers with an extreme range of monthly mean temperatures from +19 °C in July to −40 °C in January. The average annual mean precipitation is 238 mm (from 1971 to 2000) and the average maximum snow cover depth is 34 ± 7 cm (from 1959 to 2015), according to observations at Yakutsk station of the Hydrometeorological Center of Russia.

2.2 Experimental design

During the summer of 2015, three 20 m × 20 m (400 m²) experimental plots for snow addition (SNOW+), snow removal (SNOW−), and no treatment (CONTROL) were established (Fig. 2c). Snow cover at the SNOW− plot was manually removed using shovels and transported to the SNOW+ plot using heavy duty bags on December 17–21, 2015. At the time of manipulation, the snow depth was 24 cm. After transporting the snow, the SNOW− plot had approximately 1 cm of snow cover remaining, and the snow cover depth of the SNOW+ plot did not change because of compaction of existing snow cover by the added snow. Soil temperature and soil moisture observations were conducted from 2015 to 2016 summer. In spring, the snow depth and snowmelt timing were recorded using automatic time-lapse cameras. During the growing season, needle elongation and thaw layer thickness were measured manually.

2.3 Hydrometeorological observations

Air temperature and precipitation were observed using an automatic weather observation system (WXT520, Vaisala, Vantaa, Finland) installed at a height of 15 m (the top of the canopy). Soil moisture was observed with dielectric permittivity probes with data loggers (HS10 with EM50 data logger, Decagon Devices, Pullman, Washington, USA) installed at five depths of 0.01, 0.1, 0.2, 0.3 and 0.5 m at the SNOW− and SNOW+ plots. Measurements began on June 4, 2015. Soil temperature measurements began on July 15, 2015, using thermistors (TMC-HD with U-12-008 data loggers (HOBO, Onset Computer Corporation, Bourne, Massachusetts, USA) at six depths of 0.1, 0.2, 0.4, 0.6, 0.8, and 1 m for SNOW− and SNOW+ plots. The date of snowmelt was determined at all treatment plots using images from a time-lapse camera according to the date at which 50% of the ground surface was visible.

2.4 Needle elongation and samplings

In order to reach the sunlight branches, we used young larch trees. Three typical young larch trees (2–4 m height) were selected from each treatment plot for needle elongation measurement and sampling for foliar chemistry analysis (C and N contents, and their isotopic compositions). For each tree, three branches were marked, and the elongation of 3–9 randomly selected needles was measured at each branch using digital calipers (totally 38–55 replications at each plot). Each tree was located more than 4.8 m from the edge of the plot and each plot was 8 m apart. Needle length measurements were conducted seven times from May 8 to July 8, 2016. Data was presented as percentage of the final length of needles observed on the last day of the observation (July 8). Needles were also sampled on June 17, July 16, and August 20, 2016, and current year shoots were sampled on August 20, 2016 for C and N contents and isotope analyses. Dried needles and shoots were ground and analyzed with an elemental analyzer—mass spectrometer online system (Flash EA 1112 and Delta V, Thermo Fisher Scientific, Massachusetts, USA). The analytical accuracy (reproducibility) was 0.3% and 0.2% for C and N content, respectively, and less than 0.2‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

2.5 Isotopic analyses of stem water and precipitation

To analyze the isotopic composition of stem water, we selected branches from mature trees. Tree branches from two mature larch trees (reaching stand height) at each treatment plot were sampled from 4 to 6 m height using an extendable tree pruner. Bark and cambium

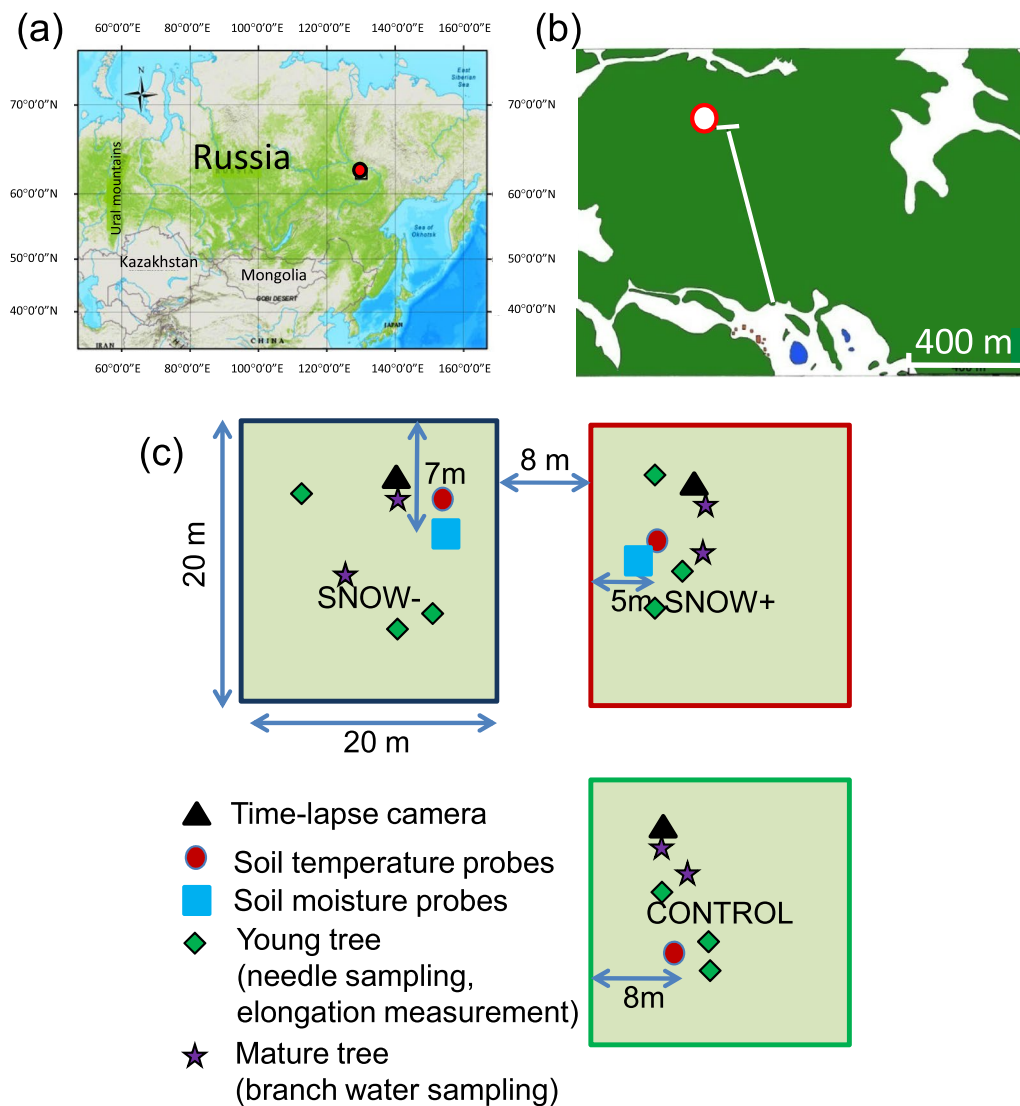


Fig. 2 Maps of Eastern Eurasia with the locations of Yakutsk, Spasskaya Pad Forest Station, and experimental sites. Maps of **a** Yakutsk (62° 03' N, 129° 71' E), **b** Spasskaya Pad Scientific Forest Station (62° 14' N, 129° 37' E) with green and white areas indicating forest and grassland respectively, and red circle marking experimental sites, and **c** schematic maps of snow manipulation experimental sites. Purple stars show the mature sample larch trees used for stem sampling and green diamonds are young larch trees used for needle elongation observations and needle chemistry sampling

were removed and the remaining xylem was cut into 1 cm pieces, stored in glass vials, and stored at -18°C prior to extraction. Branch samples were collected on May 14, May 27, June 7, June 15, July 16, and August 12, 2015, and on May 29, June 17, July 15, and August 14, 2016. Water was extracted from the stem cryogenically on a vacuum distillation line and stored in glass vials at 5°C prior to analysis. Rain samples were collected during rain events in situ using a simple rain collector. Snow cover samples were collected on December 16–19, 2015, using a metal cylinder (12 cm diameter).

The water samples were analyzed using an online system (GasBench equipped with MAT253, Thermo Fisher Scientific, Massachusetts, USA). Analytical accuracy (reproducibility) was 0.1 and 0.2‰ for $\delta^{18}\text{O}$ and δD , respectively. Delta values are defined by

$$\delta^{18}\text{O} \text{ (or } \delta\text{D}) = (R_{\text{sample}}/R_{\text{SMOW}} - 1) \times 1000 (\text{‰}),$$

where R_{sample} and R_{SMOW} are isotope ratios ($\text{H}_2^{18}\text{O}/\text{H}_2^{16}\text{O}$ or $\text{HDO}/\text{H}_2\text{O}$) of sample and standard (Vienna Standard Mean Ocean Water).

2.6 Soil inorganic nitrogen

For the soil inorganic N analysis, four soil core samples were collected from all treatment plots on July 16 to 18, July 22 to 25, and August 13 to 15, 2016, at four depths (organic layer, 0–10, 10–20, and 20–50 cm). Roots were removed from the soil samples, and soil N was immediately extracted from 4 g of soil sample by 40 ml of 2 M KCl solution and mixed on a shaker (40 min). The solution and soil particles were then separated using a centrifuge and filtrated with a 0.45 μm syringe filter. The extracts were stored at $-18\text{ }^{\circ}\text{C}$ prior to analysis, and ammonium and nitrate concentrations in the extracted samples were analyzed using a continuous flow spectrophotometer autoanalyzer (Bran & Luebbe, Norderstedt, Germany).

2.7 Statistical analyses

Statistical significance was analyzed using the Student's *t* test for needle length difference among treatments and between consecutive dates. One-way Analysis of Variance with post-hoc Tukey test was used for needle chemistry analyses. Data were compared among treatments and consecutive dates based on a significance level of $p < 0.05$.

3 Results

3.1 Hydrometeorological conditions during the experiment

Table 1 shows the monthly averages of air temperatures and precipitation during warm periods (April to September) as a 7-year average (2010–2016) and for 2015 and 2016. The air temperature of the years before and after snow manipulation (2015 and 2016, respectively) was close to the 7-year average, except for April 2015 ($-6.3\text{ }^{\circ}\text{C}$) and September 2016 ($7.9\text{ }^{\circ}\text{C}$), which were colder and warmer than the 7-year average (-0.6 and $4.7\text{ }^{\circ}\text{C}$), respectively. Total precipitation during the warm period in 2015 and 2016 was mostly similar to the 7-year average (119, 109, and 109 mm, respectively); however, June 2015 showed a larger amount of rainfall, and August 2015 and September 2016 received smaller amounts of rain than the 7-year average. Before snow manipulation on December 17–21, 2015, the snow density was 106 kg/m^3 with snow water equivalent (SWE) of 25 mm.

Before snow manipulation, soil temperatures of all three plots exhibited no significant difference, except for lower values at 0.1 m and 0.2 m depth at CONTROL from October to December (Fig. 3). After manipulation, the soil temperature in the SNOW– plot rapidly decreased and became significantly lower than those in the SNOW+ and CONTROL plots. The maximum difference between SNOW– and CONTROL was $5.8\text{ }^{\circ}\text{C}$ at 0.1 m on December 30, 2015, and the difference

decreased with an increase in depth. The difference between SNOW+ and CONTROL was $3.7\text{ }^{\circ}\text{C}$ at 0.1 m on the same date. At the end of March, as the daytime air temperature increased, the soil temperature started to increase simultaneously for all treatments. No significant difference in soil temperature was observed among the three plots during the period from March 24 to April 18, 2016. However, after snowmelt started on April 19 at the SNOW– plot (Fig. 4a, b), the soil temperature of all monitored soil depths (from 0.1 to 1 m) became higher than the soil temperature at the CONTROL plot at corresponding depths. This may be caused by a difference in soil moisture, as described below. The observed difference in soil temperature continued until the end of the observation period. The soil temperature difference between SNOW+ and CONTROL was much smaller than that between SNOW– and CONTROL after snowmelt. The soil temperature at 0.1 m depth in the SNOW– plot exceeded $0\text{ }^{\circ}\text{C}$ on April 27 (8 days after snowmelt), and exhibited diurnal fluctuations for 12 days (until May 10), decreasing to almost $0\text{ }^{\circ}\text{C}$ during nighttime (Fig. 4a), which indicates diurnal freeze–thaw cycles. However, soil temperature at 0.1 m depth in the SNOW+ plot only exceeded $0\text{ }^{\circ}\text{C}$ on May 16 (20 days after snowmelt), and showed diurnal variations with minimum soil temperatures at or below $0\text{ }^{\circ}\text{C}$ for only seven consecutive days (until May 23).

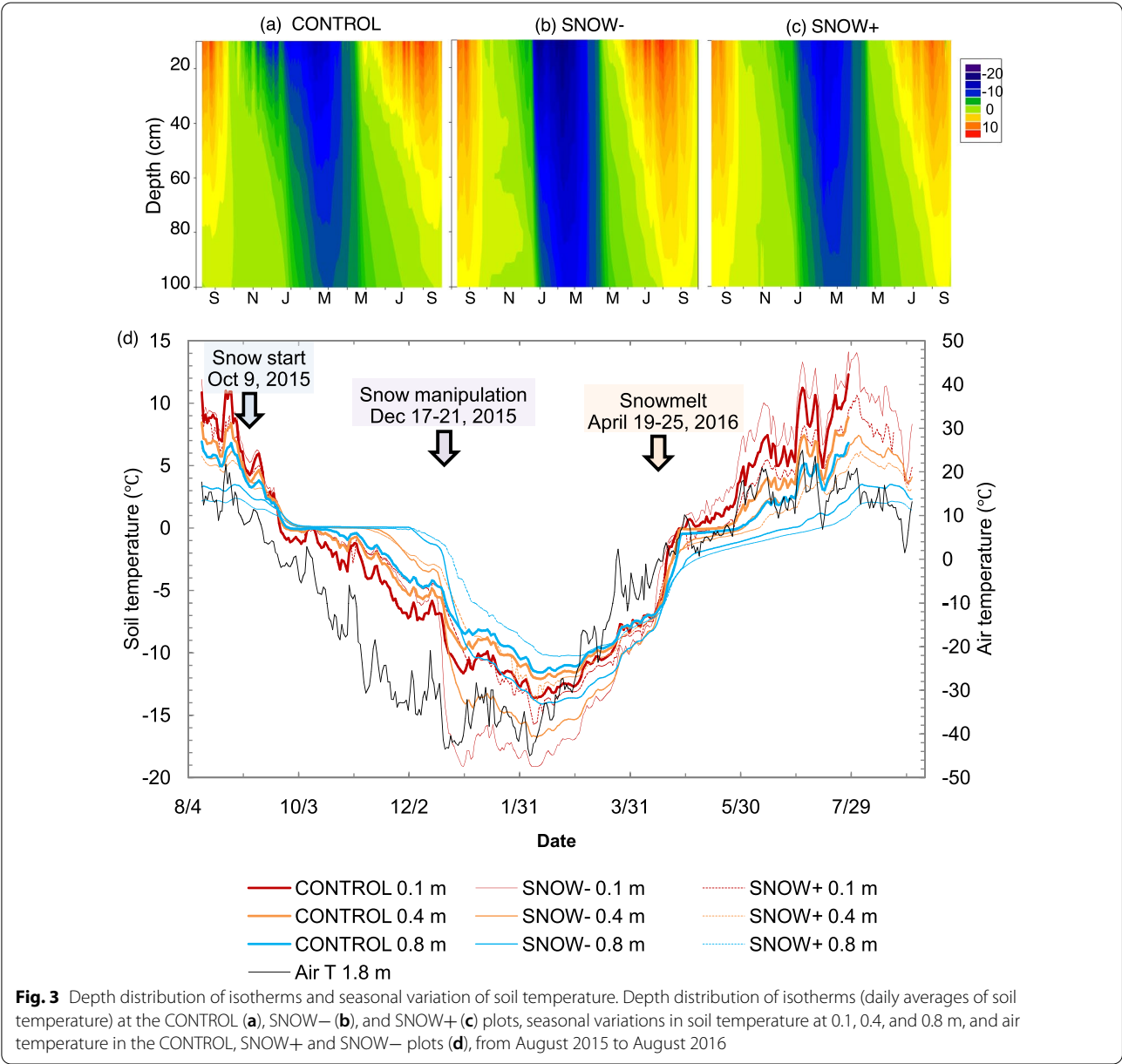
Before snow manipulation, there was no significant difference in the average soil thaw depth between SNOW+ ($58 \pm 13\text{ cm}$) and SNOW– ($61 \pm 13\text{ cm}$) plots ($n = 441$) on July 7, 2015 (data not shown), indicating similar soil properties between the two plots. However, the spatial variability of soil thaw depth showed a dependency on understory vegetation. Under patches of deciduous shrubs with broader leaves (*Arctous alpina*), the thaw depth was shallower than that under patches of evergreen shrubs (*Vaccinium vitis-idaea*, *Arctostaphylos uva-ursi*) and grasses due to shading by the higher leaf area.

After snow manipulation, in the summer of 2016, thaw depth was measured only for designated subplots (9 m^2) with a dominant type of understory plant (deciduous shrub, evergreen shrub, grasses). On July 26, 2016, SNOW– subplots had the deepest average thaw depth, whereas SNOW+ subplots were the shallowest, and CONTROL subplots exhibited intermediate thaw depths. The average thaw layer depths of the three subplots were $84 \pm 9\text{ cm}$ for SNOW–, $72 \pm 6.7\text{ cm}$ for SNOW+, and $77 \pm 5.3\text{ cm}$ for CONTROL (data not shown). As the soil thawed in the summer of 2016, soil moisture was higher at SNOW+ than SNOW– in the surface soil layers (0.1 m and 0.3 m) (Fig. 4c) due to the infiltration of snowmelt water.

Table 1 Monthly air temperature and precipitation

Month	Air temperature (°C)			Precipitation (mm)			Precipitation δ18O (‰)	
	7-year ave	2015	2016	7-year ave	2015	2016	2015	2016
Apr	− 0.6	− 6.3	0.3	1.7	0.1	0.1	–	–
May	8.1	6.2	7.0	10.8	12.6	10.7	–	− 18.1
Jun	14.8	13.8	15.9	24.1	45.2	27.7	–	− 15.1
Jul	19.9	18.5	17.6	32.7	28.8	41.8	− 10.0	− 14.5
Aug	14.5	15.5	13.2	25.3	13.6	27.4	− 13.4	–
Sep	4.7	4.3	7.9	14.1	18.4	1.1	–	–

Monthly data in 2015 and 2016 and the 7-year average from 2010 to 2016, and δ¹⁸O (‰) values of precipitation in 2015 and 2016 observed at Spasskaya Pad during the warm period (April to September) were shown



3.2 Snowmelt timing and needle elongation

Figure 6 shows the growth of needles of young larch trees, which is a percentage of the needle length on July 8, 2016 in each plot. Needle lengths on June 16 were 103, 99.2, and 101% in the SNOW–, SNOW+ and CONTROL plots, respectively, indicating that needles were already mature on June 16. The snowmelt date was the earliest in the SNOW– plot (April 19), followed by the CONTROL plot (April 23), then SNOW+ plot (April 25), as shown in Fig. 5. Leaf opening in young larch trees in all three plots had already started on May 8, 2016, at the beginning of the observation period (Fig. 6). Despite the earlier snowmelt, SNOW– plot needles exhibited delayed elongation, with shorter length (7.4%) than those in the CONTROL (14.1%) and SNOW+ (12.7%) plots on May 8 (Fig. 6). This situation continued until May 30.

In the period between May 30 and June 16, there was a different situation. Needle length in the SNOW– plot increased significantly from May 30 (64.9%) to June 16 (103%), while only small differences were observed from May 30 (83% for both SNOW+ and CONTROL) to June 16 (99.2 and 101% for SNOW+ and CONTROL), although the differences were not statistically significant. In the early growing season, elongation of needle length in the SNOW– plot was delayed, and continued until the later stages.

3.3 Stem water isotopic composition

Before snow manipulation, in the summer of 2015, the $\delta^{18}\text{O}$ of larch stem water showed clear seasonal variations and no difference was observed among the three plots (Fig. 7a). The $\delta^{18}\text{O}$ values were highest in May (-13.6‰), with a sharp decrease in June (-21.3‰), followed by an increase in July (-16.5‰) and August (-18.6‰). After snow manipulation, in the summer of 2016, the $\delta^{18}\text{O}$ values of larch stem water showed clear differences (Fig. 7b). The $\delta^{18}\text{O}$ of the SNOW– plot exhibited the highest values throughout summer (-18.5‰), with only a slight increase of 1.3‰ from June to August. CONTROL and SNOW+ plots exhibited similar values that were lower than those of SNOW– in early summer, but almost equal to those of SNOW– (-18.1‰) in August. As shown in Table 1 and Fig. 8, summer rainfall has higher $\delta^{18}\text{O}$ values (-18 to -10‰) than snow cover (approximately -30‰); thus, the decreased $\delta^{18}\text{O}$ in all plots in June 2015 and in SNOW+ and CONTROL plots in 2016 resulted from the uptake of infiltrated snowmelt water with extremely low $\delta^{18}\text{O}$ values, as previously described by Sugimoto et al. (2002).

3.4 Carbon and nitrogen contents and isotopic ratios

From June to August 2016, the needle C content of young trees and their $\delta^{13}\text{C}$ values exhibited decreasing

trends among all three plots, although no statistically significant differences were observed (Fig. 9a, b). In addition, current year shoots and needles on them of young larch trees at SNOW+ plots showed lower $\delta^{13}\text{C}$ values ($-30.8 \pm 0.7\text{‰}$ and $-30.6 \pm 0.8\text{‰}$) than the SNOW– plot ($-29.9 \pm 0.5\text{‰}$ and $-29.9 \pm 0.3\text{‰}$), although this difference was not statistically significant (Fig. 10). However, we suppose that the soil moisture difference between SNOW– and SNOW+ plots may have caused the higher $\delta^{13}\text{C}$ at SNOW–, as we will discuss later.

Needle N content at SNOW– decreased drastically from June 17 ($1.4 \pm 0.2\%$) to July 16 ($1.2 \pm 0.1\%$), whereas the average values at SNOW+ and CONTROL decreased slightly. Then, on August 20, the N content in all plots increased, especially in the SNOW– plot (Fig. 9c). The observed needle $\delta^{15}\text{N}$ values ranged from -6.2 to -2.1‰ , revealing large variability among individual trees. Needle $\delta^{15}\text{N}$ values of most trees exhibited an increasing trend from June 17 to August 20, excluding the two cases out of the three trees in the SNOW– plot. In the SNOW+ and CONTROL plots, the increase in $\delta^{15}\text{N}$ values from June to August was 0.8‰ (Fig. 9d).

3.5 Soil inorganic nitrogen

Soil inorganic N exhibited temporal and spatial variations at the study site (Fig. 11). Inorganic N mostly comprised ammonium at the site. A low concentration of ammonium was found in the SNOW+ plot in the middle of July (Fig. 11a). At the end of July (Fig. 11b), the concentration of ammonium increased in the SNOW+ and CONTROL plots. These results agree to our previous study. Soil inorganic N was small in the beginning of summer, and increased quickly after cumulative degree day of the soil temperature at 20 cm reached $300\text{ °C}\cdot\text{days}$ (Popova et al. 2013). On the other hand, at the end of July, a low concentration of ammonium was observed at the SNOW– plot (Fig. 11b), and at the end of August concentration of ammonium in the SNOW– plot finally increased (Fig. 11c).

4 Discussion

4.1 Soil temperature

In our experiment, after snow manipulation, winter soil temperature in the SNOW– plot quickly decreased when compared with that in the SNOW+ and CONTROL plots (Fig. 3). The absence of a snowpack at the SNOW– plot during the coldest period in winter reduced the effect of snowpack insulation and we expect a higher thermal conductivity of the ground surface, including the snowpack, enabling winter cold waves to cool the deep soil layer. Therefore, because of the lower snowpack depth and higher thermal conductivity, the SNOW– plot had lower

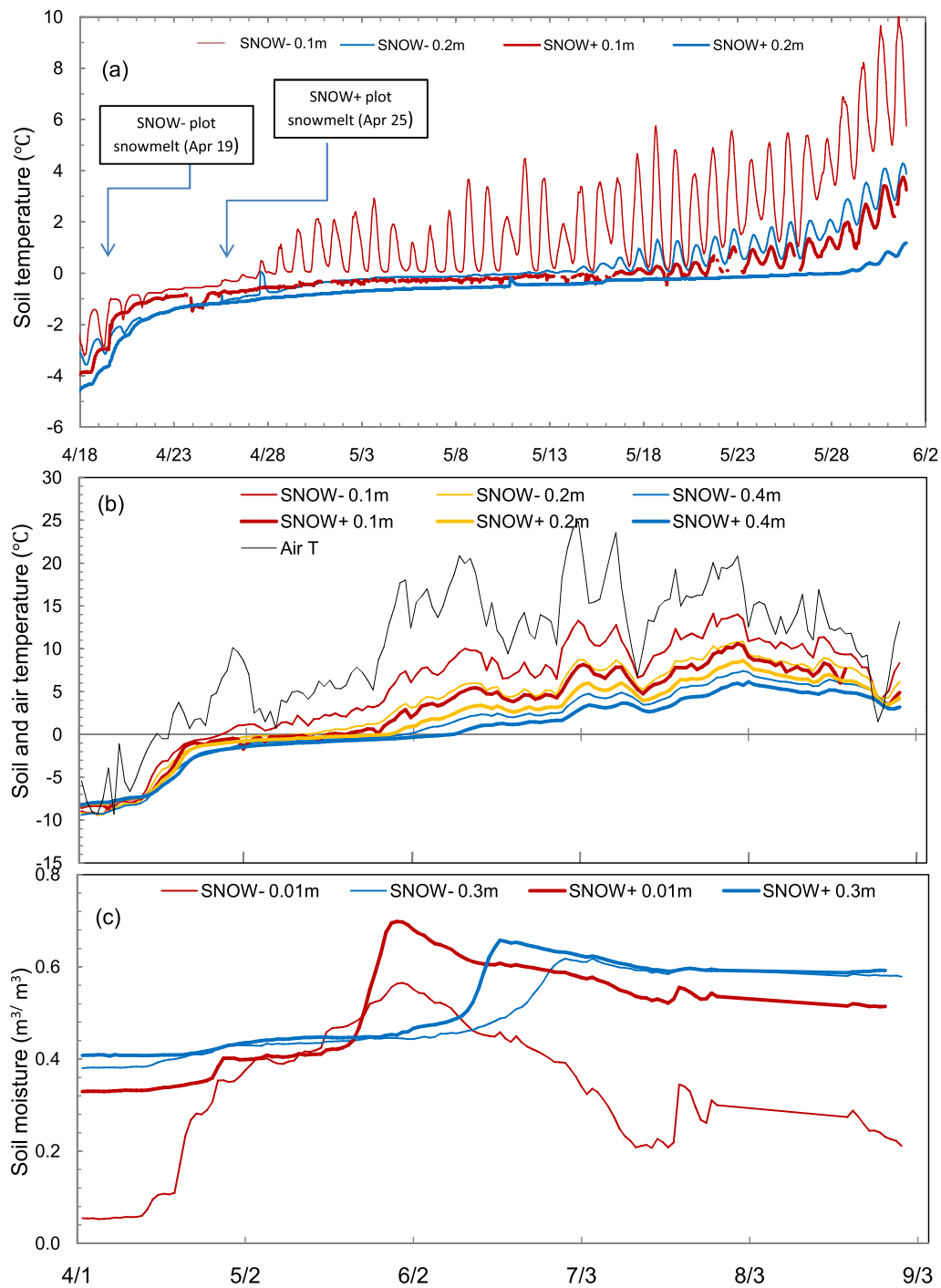


Fig. 4 Soil and air temperature, and soil moisture in spring–summer 2016. **a** Hourly soil temperature at 0.1 m and 0.2 m depth from April 18 to May 30, 2016; **b** daily average air and soil temperature at 0.1, 0.2, and 0.4 m depth, and **c** soil moisture at 0.01 m and 0.3 m depth from April to August in 2016 for SNOW– and SNOW+ plots. SNOW– and SNOW+ plots data are represented by thin and thick lines, respectively

soil temperatures until March, when air temperature rose substantially.

The SNOW+ plot showed higher soil temperatures than the CONTROL plot until mid-January, however, during the period from mid-January to March, the soil

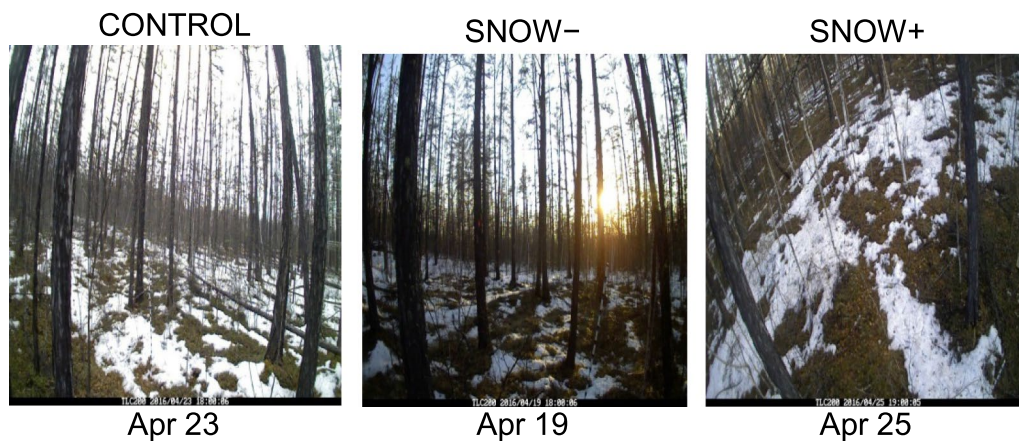


Fig. 5 Snowmelt timing observed by time-lapse cameras at CONTROL, SNOW–, and SNOW+ plots. Date of snowmelt was determined by a criteria of 50% ground surface appearance. Snowmelt dates were April 23, April 19, and April 25 for CONTROL, SNOW–, and SNOW+ plots, respectively

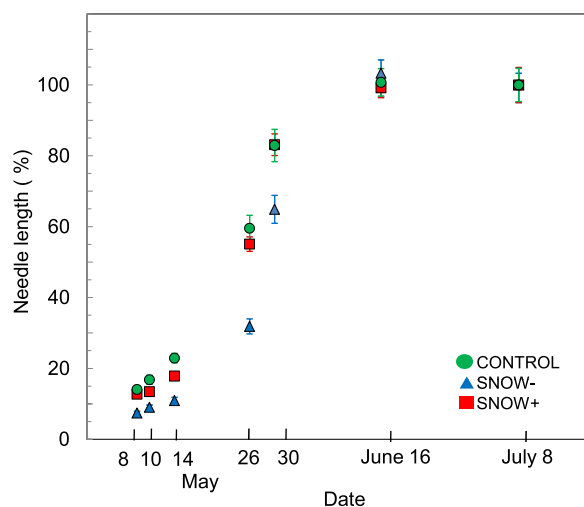


Fig. 6 Growth of needle length in young larch trees in spring–summer 2016. Growth is shown as percentage of needle length at final observation date (July 8) in each plot. Average lengths at final observation date were 18.4, 21.1 and 25.1 mm for the CONTROL, SNOW– and SNOW+ plots respectively. Markers are averages and bars are standard errors in the CONTROL (green circle), SNOW– (blue triangle), and SNOW+ (red square) plots observed on May 8, 10, 14, 26, and 30, June 16, and July 8, 2016.

temperature was similar in SNOW+ and CONTROL (Fig. 3). The similarity may have been caused by compaction of the snowpack. After manipulation, the observed snow depth at SNOW+ was 24 cm, which was similar to that before manipulation, because the snow density was doubled by adding snow from the SNOW– plot. Generally, cold regions such as Yakutsk have lower snow density (108 kg/m^3 in winter and 161 kg/m^3 in spring, as measured in 2015 at the experimental site), which

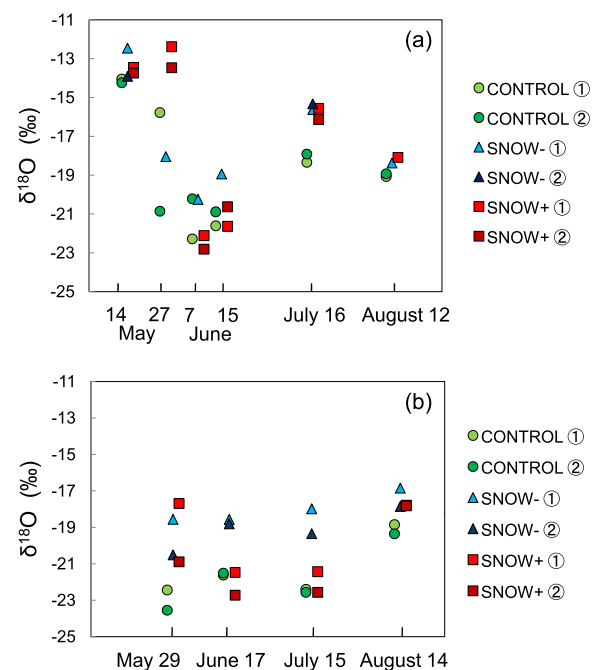
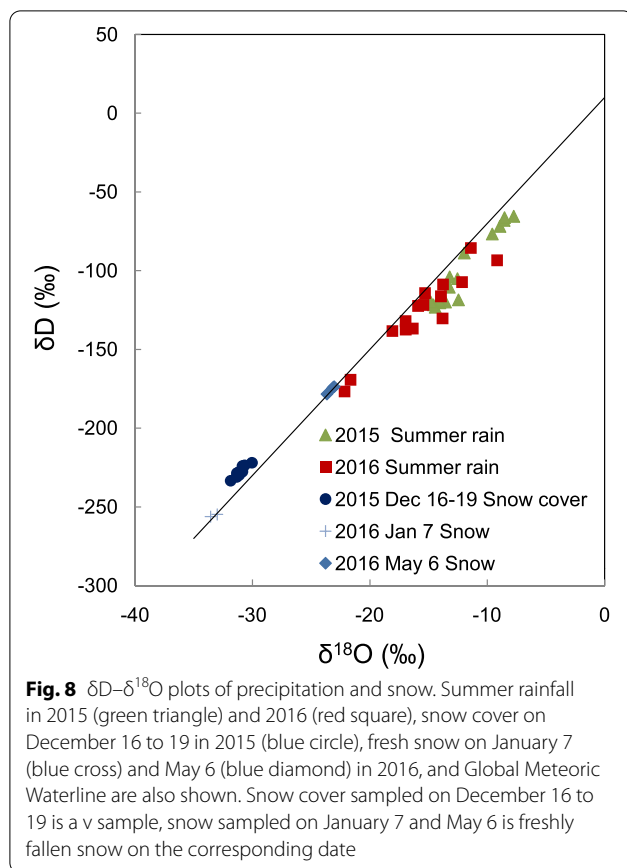


Fig. 7 The $\delta^{18}\text{O}$ values of stem water of larch trees. The $\delta^{18}\text{O}$ values observed in **a** 2015 and **b** 2016 in the CONTROL (green circle), SNOW– (blue triangle), and SNOW+ (red square) plots are shown. “1” or “2” after plot name indicates duplicate sampling

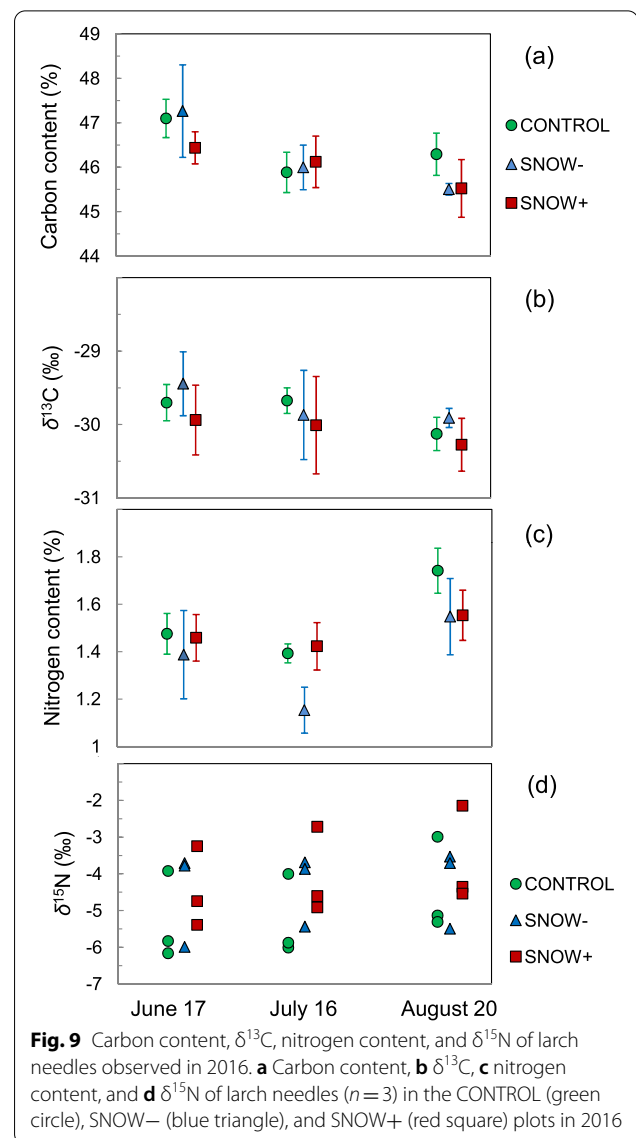
suggests a lower thermal conductivity of the ground surface, including the snowpack. Conversely, we expect larger snow density observed at the SNOW+ plot correspond to a larger thermal conductivity. Thus, compaction of the snowpack may impair the insulation effect of the snowpack (Zhang 2005).



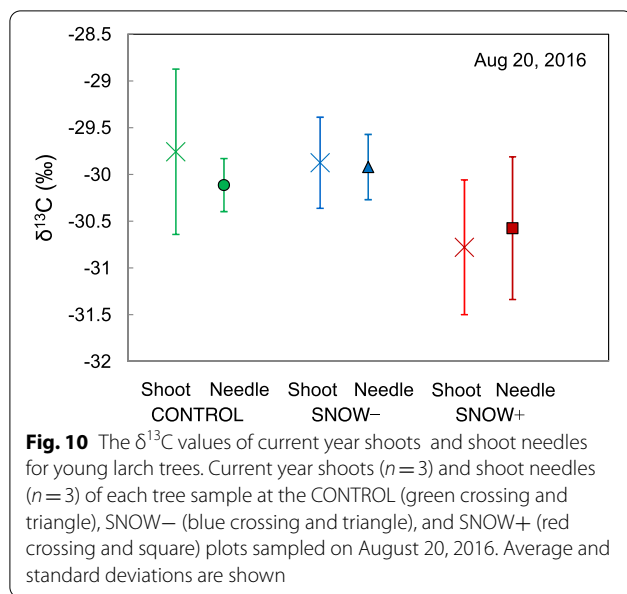
4.2 Length of growing season

The SNOW–plot experienced earlier snowmelt (April 19) than the SNOW+ and CONTROL plots (April 25 and 23), as shown in Fig. 5. However, contrary to the schematic diagram shown in Fig. 1, the SNOW–plot did not exhibit earlier needle opening, with delayed needle elongation (Fig. 6). Needle opening started before the first day of our observation (May 8, 2015). During the period from May 8 to May 30, needle length in the SNOW–plot was significantly shorter than that in the SNOW+ and CONTROL plots, where needle elongation continued until May 30. On the other hand, needles at the SNOW–plot continued to elongate until June 16. Clearly, needle elongation took longer at the SNOW–plot. One of the possible reasons for this is the dry conditions (Fig. 1). The limited water supply at the SNOW–plot during early summer may also be a factor influencing slower needle elongation (Fig. 4c). In the following subsection, we discuss the influence of soil moisture.

In contrast to these findings, previous studies have found that earlier snowmelt leads to a longer growing season. According to satellite and ground observation data, Barichivich et al. (2013) showed that photosynthesis activities in northern ecosystems are enhanced by



the longer growing season, especially by earlier snowmelt and an earlier spring. Moreover, Sutinen et al. (2015) conducted a snow manipulation experiment and showed that soil frost in spring caused a delay in needle and shoot growth in Norway spruce. These results, which have generally been attributed to earlier snowmelt resulting in a longer growing season, seem inconsistent with ours. In our study, SNOW– treatment had a higher soil temperature in spring, but the dry soil condition in the SNOW–plot may cause this. The small amount of precipitation (approximately 238 mm per year) at our study site (Yakutsk) may explain the difference between our study and previous research. Another possibility not explicitly shown in Fig. 1 is that frost damage of fine roots caused by freeze–thaw cycles

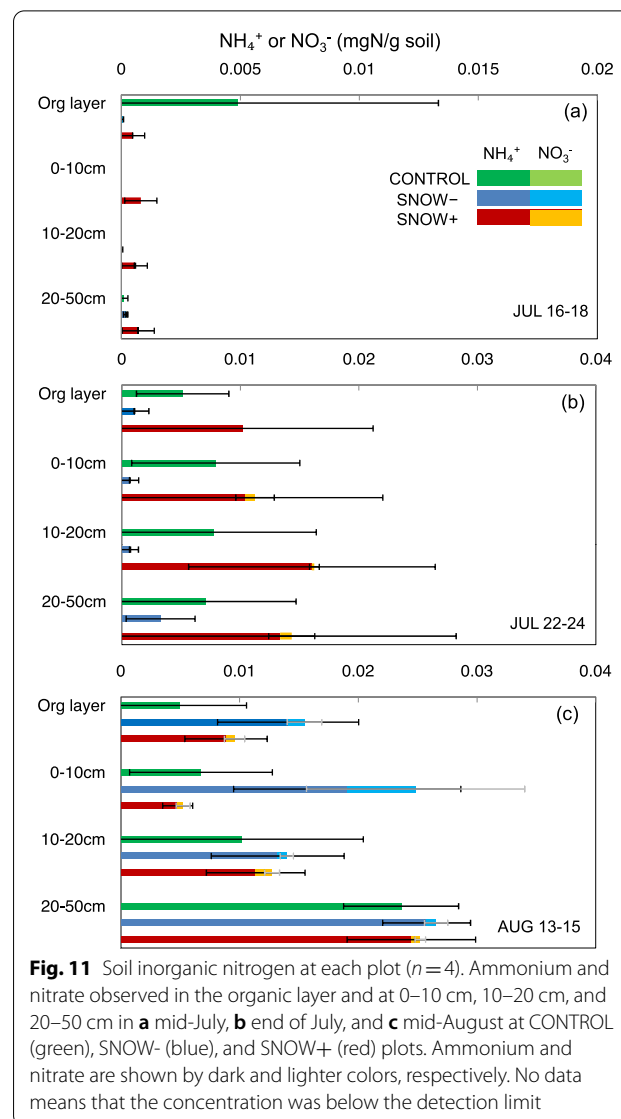


in spring (Fig. 4a) might cause a delay in needle elongation (Fig. 6) through a decline in water and nutrient uptake.

4.3 Soil moisture

In 2015 and 2016 at Spasskaya Pad, the precipitation values agreed with the 7-year average (Table 1). Therefore, our experiment was conducted in typical dry conditions, with no “overwetting” conditions in the forest after the snowmelt in 2016 spring. The origin of water in the soil can be determined using water isotope values (Sugimoto et al. 2002). Infiltration of larger amounts of snowmelt water in SNOW+ and CONTROL plots than in the SNOW- plot was recorded by the $\delta^{18}\text{O}$ values of stem water (Fig. 7b). This means that trees in the SNOW- plot were unable to use snowmelt water, which has lower $\delta^{18}\text{O}$ values (Fig. 8). During summer, rainwater with high $\delta^{18}\text{O}$ values recharged the soil, and in August, all plots showed similarly high $\delta^{18}\text{O}$ values (Fig. 7). As seen in Fig. 4c, soil moisture in the SNOW- plot increased gradually from early summer. In our study area, which is in a continental dry climate, larch trees show high photosynthetic activity in the early growing season, because snowmelt water can be used by plants (Sugimoto et al. 2002). Snow removal treatment thus shows negative effect on tree growth.

Another proxy for soil moisture is the $\delta^{13}\text{C}$ values of current year shoots because C used for the production of current year shoots is mainly photosynthesized during the growing season (Kagawa et al. 2006; Li and Sugimoto 2018). In the SNOW- plot, the $\delta^{13}\text{C}$ values of current year shoots were relatively higher than those in the SNOW+ and CONTROL plots, which suggests



dry conditions in the SNOW- plot, however, these values were not statistically significant because of the small number of samples (Fig. 10).

Delayed elongation of needles in SNOW- plot may be caused by the dry soil condition in the SNOW- plot.

4.4 Nitrogen availability

As shown in Fig. 9c, on June 17 and July 16, needle N content in the SNOW+ and CONTROL plots showed similar values, whereas that at SNOW- showed a large deviation on June 17, and the value on July 16 was significantly lower than those at the SNOW+ and CONTROL plots. The results show that N uptake by trees at the SNOW- plot was insufficient in the first half of summer. However, on August 20, needle N content in the

SNOW– plot increased to a value comparable to those of the SNOW+ and CONTROL plots. Similar trends were also observed in the soil inorganic N data, as shown in Fig. 11. As most roots of larch trees are distributed in the soil layer within 50 cm depth (Kajimoto et al. 2007; Sugimoto personal communication), foliar N contents are compared with the observed soil inorganic N data.

Low concentration of soil inorganic N were observed at the SNOW+ plot on July 16 to 18 (Fig. 11a) and increased rapidly at the end of July (Fig. 11b), whereas that of the SNOW– plot only increased in August (Fig. 11c). Therefore, these results indicate that N availability in the SNOW– plot was low until mid-July, which may have led to lower needle N content in the SNOW– plot during this period. Subsequently, trees in the SNOW– plot used soil inorganic N at the end of July and in August, and the needle nitrogen content in the SNOW– plot in August increased to roughly the same as that in the SNOW+ and CONTROL plots (Fig. 9c). It should be noted that the soil temperature at the SNOW– plot was higher than those at the SNOW+ and CONTROL plots during the growing season (Fig. 4). Foliar $\delta^{15}\text{N}$ at the SNOW+ and CONTROL plots (Fig. 9d) showed a gradual increase from June to August. Because soil organic matter in the deeper layer generally has higher $\delta^{15}\text{N}$ values than plant tissue or atmospheric nitrogen depositions (Craine et al. 2015), observed increases in foliar $\delta^{15}\text{N}$ (Fig. 9d) correspond to the use of soil N.

There are several possible reasons for the delayed increase in soil inorganic N availability at the SNOW– plot. One may be the freeze–thaw cycles in the SNOW– plot during the period from April 28 (the day when the soil temperature exceeded 0 °C) to May 8 (the day when the soil temperature stopped decreasing to 0.1 °C or lower during the night) (Fig. 4a), which may damage the microbial biomass in the soil and plant roots. Another reason may be the dry soil conditions in the first half of the summer (Figs. 4c, 7b). Under dry soil conditions, inactive microbial decomposition may lead to less available N at the SNOW– plot, and the inactive uptake of N by plants causes low N contents in the needles. As described already, climate of study site (near Yakutsk) shows extremely low winter temperature, therefore extremely low soil temperature at the SNOW– plot might affect the soil microbes and plant roots.

At the SNOW+ plot, increase in snow depth did not significantly alter winter soil temperature. This may be because of compaction of added snow, which leads to snow density double, compared to the CONTROL plot, resulting in the decreased thermal conductivity. Besides, additional snow provided sufficient soil moisture in the early growing season, and the start of production of soil

inorganic N in the SNOW+ plot was earlier than in the SNOW– plot.

We could not estimate the effect of doubled snow density on the ecosystem. In the natural condition, snow density was much lower than the observed density in our SNOW+ treatment. This would affect the soil temperature and consequently N availability.

4.5 Comparison with other regions

Our study site is located in a continuous permafrost zone with an extreme continental subarctic climate. It has extremely cold long winters with a small amount of snowfall and dry and hot short summers. Compared to other regions, it is a rather complex study area because it is as cold as high arctic tundra but as dry as alpine tundra, and contains abundant forests. Groffman et al. (2001) proposed a hypothesis whereby global warming will cause less snow cover during winter and therefore less thermal insulation, which will lead to the “colder soils in a warmer world” phenomenon. They conducted a snow removal experiment in a northern hardwood forest in the US and reported only mild soil freezing (−4 °C) in winter, indicating a greater potential for freeze–thaw cycles during winter. Active growth of soil microbes during winter and/or the snowmelt period was reported following snow reduction experiments in northern forests (Groffman et al. 2001; Durán et al. 2014; Sorensen et al. 2016; Watanabe et al. 2019). On the other hand, at our site, the soil in the CONTROL plot was frozen for more than 3 months and the soil temperature was below −14 °C. Moreover, the soil temperature at the SNOW– plot was less than −19 °C soon after snow removal (Fig. 3). Such low temperatures could cause mechanical or cellular root damage. In our experiment, the production of soil ammonium at the SNOW– plot was delayed until the end of July (Fig. 11c). The low soil temperature at the SNOW– plot observed during winter might damage not only the roots but also the soil microbes. In addition, freeze–thaw cycles in spring (Fig. 4a) may also damage soil microbes.

Owing to these problems, snow removal in the experiments caused a delay in needle elongation during the early growing season. It has previously been reported that low spring soil temperatures affect the ecosystem. In a boreal forest in Finland, the bud burst of Norway spruce was delayed for 2 weeks in a spring frost experiment, in which insulation by 15 cm of hay was applied, resulting in prolonged soil frost (Sutinen et al. 2015). This indicates that spring soil frost affects the length of the growing season. In our experiment, we observed that earlier snowmelt at the SNOW– plot did not hasten needle flushing, but slowed needle elongation, although the

soil temperature was higher than that at the CONTROL plot. This result contradicts the diagram illustrated in Fig. 1, where shorter period for snowmelt caused an earlier start of the growing season. Our results showed the later start of growing season, despite the shorter period of snowmelt and higher soil temperature. Our study site is characterized by extremely low air temperature and dry conditions in winter, as well as a short snowmelt season. Therefore, it is very important for plants to obtain water, instead of warming the soil during the needle flushing period.

In the present study, we observed soil inorganic N only in summer season. Additional studies to investigate soil microbial activity, especially during winter and spring, are required in the future.

5 Conclusions

A snow cover manipulation experiment was conducted in December 2015 at the Spasskaya Pad Scientific Forest Station in the Eastern Siberia taiga forest ecosystem. The snow removal (SNOW-) plot showed a more significant effect of manipulation than the other plots. Soon after the manipulation, the SNOW-plot showed extreme cold soil temperature. Needle elongation was delayed in the SNOW-plot, despite earlier snowmelt and a higher soil temperature during the growing season. Production of soil inorganic N was also delayed in the SNOW-plot, and the larch needle N content was lower than that in other plots until July. Soil ammonium at the SNOW-plot was eventually produced in August, which resulted in a comparable needle N content to the other plots. Dry soil conditions in the SNOW-plot, during the snowmelt period and early growing season, caused higher soil temperature, and also caused freeze-thaw cycles in spring, resulting in soil N production.

The study duration was only 1 year, however, we observed a clear response of larch trees to snow cover changes, including changes in phenology (needle opening and elongation). Moreover, longer experiments may cause changes to the ecosystem, such as photosynthesis and production. It is also difficult to predict possible scenarios for long-term ecosystem change because other factors, such as overwetting or permafrost degradation, should also be assessed.

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Authors' contributions

RS conducted the experiments and wrote the manuscript, and SH analyzed the soil inorganic N. TM organized all processes for field works and AS

designed the experiments, and wrote the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials

Please contact author for data requests.

Declaration

Competing interests

The authors declare no competing interests.

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References

- Aerts R (2006) The freezer defrosting: global warming and litter decomposition rates in cold biomes. *J Ecol* 94(4):713–724. <https://doi.org/10.1111/j.1365-2745.2006.01142.x>
- Aerts R, Cornelissen JHC, Dorrepaal E, van Logtestijn RSP, Callaghan TV (2004) Effects of experimentally imposed climate scenarios on flowering phenology and flower production of subarctic bog species. *Glob Change Biol* 10(9):1599–1609. <https://doi.org/10.1111/j.1365-2486.2004.00815.x>
- Andresen LC, Michelsen A (2005) Off-season uptake of nitrogen in temperate heath vegetation. *Oecologia* 144(4):585–597. <https://doi.org/10.1007/s00442-005-0044-1>
- Archibald OW (1995) Ecology of world vegetation. Chapman & Hall, London
- Barichivich J, Briffa KR, Myneni RB, Osborn TJ, Melvin TM, Ciais P, Piao SL, Tucker C (2013) Large-scale variations in the vegetation growing season and annual cycle of atmospheric CO₂ at high northern latitudes from 1950 to 2011. *Glob Change Biol* 19(10):3167–3183. <https://doi.org/10.1111/gcb.12283>
- Blume-Werry G, Kreyling J, Laudon H, Milbau A (2016) Short-term climate change manipulation effects do not scale up to long-term legacies: effects of an absent snow cover on boreal forest plants. *J Ecol* 104(6):1638–1648. <https://doi.org/10.1111/1365-2745.12636>
- Bulygina ON, Razuvaev VN, Korshunova NN (2009) Changes in snow cover over Northern Eurasia in the last few decades. *Environ Res Lett*. <https://doi.org/10.1088/1748-9326/4/4/045026>
- Bulygina ON, Groisman PY, Razuvaev VN, Korshunova NN (2011) Changes in snow cover characteristics over Northern Eurasia since 1966. *Environ Res Lett*. <https://doi.org/10.1088/1748-9326/6/4/045204>
- Callaghan TV, Johansson M, Brown RD, Groisman PY, Labba N, Radionov V, Barry RG, Bulygina ON, Essery RLH, Frolov DM, Golubev VN, Grenfell TC, Petrushina MN, Razuvaev VN, Robinson DA, Romanov P, Shindell D, Shmakin AB, Sokratov SA, Warren S, Yang DQ (2011) The changing face of arctic snow cover: a synthesis of observed and projected changes. *Ambio* 40:17–31. <https://doi.org/10.1007/s13280-011-0212-y>
- Chapin FS, McGuire AD, Randerson J, Pielke R, Baldocchi D, Hobbie SE, Roulet N, Eugster W, Kaschke E, Rastetter EB, Zimov SA, Running SW (2000) Arctic and boreal ecosystems of western North America as components of the climate system. *Glob Change Biol* 6:211–223. <https://doi.org/10.1046/j.1365-2486.2000.06022.x>
- 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-Revue Canadienne De Recherche Forestiere 38(1):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(1):261–269. <https://doi.org/10.1007/s00442-012-2393-x>
- Cooper EJ (2014) Warmer shorter winters disrupt arctic terrestrial ecosystems. In: Futuyma DJ (ed) Annual review of ecology, evolution, and systematics, vol 45. Annual review of ecology evolution and systematics. Annual Reviews, Palo Alto, p 271–+
- Craine JM, Brookshire ENJ, Cramer MD, Hasselquist NJ, Koba K, Marin-Spiotta E, Wang E (2015) Ecological interpretations of nitrogen isotope ratios of terrestrial plants and soils. *Plant Soil*. <https://doi.org/10.1007/s11104-015-2542-1>
- Deser C, Tomas R, Alexander M, Lawrence D (2010) The seasonal atmospheric response to projected arctic sea ice loss in the late twenty-first century. *J Clim* 23(2):333–351. <https://doi.org/10.1175/2009jcli3053.1>
- Douville H, Raghavan K, Renwick J, Allan RP, Arias PA, Barlow M, Cerezo-Mota R, Cherchi A, Gan TY, Gergis J, Jiang D, Khan A, Pokam Mba W, Rosenfeld D, Tierney J, Zolina O (2021) Water cycle changes. In: Masson-Delmotte V, Zhai P, Pirani A, Connors SL, Péan C, Berger S, Caud N, Chen Y, Goldfarb L, Gomis MI, Huang M, Leitzell K, Lonnoy E, Matthews JBR, Maycock TK, Waterfield T, Yelekci O, Yu R, Zhou B (eds) Climate Change 2021: the physical science basis. Contribution of working group I to the sixth assessment report of the intergovernmental panel on climate change. Cambridge University Press, United Kingdom and New York
- Drescher M, Thomas SC (2013) Snow cover manipulations alter survival of early life stages of cold-temperate tree species. *Oikos* 122(4):541–554. <https://doi.org/10.1111/j.1600-0706.2012.20642.x>
- Durán J, Morse JL, Groffman PM, Campbell JL, Christenson LM, Driscoll CT, Fahey TJ, Fisk MC, Mitchell MJ, Templer PH (2014) Winter climate change affects growing season soil microbial biomass and activity in northern hardwood forests. *Glob Change Biol*. <https://doi.org/10.1111/gcb.12624>
- Feng XJ, Nielsen LL, Simpson MJ (2007) Responses of soil organic matter and microorganisms to freeze-thaw cycles. *Soil Biol Biochem* 39(8):2027–2037. <https://doi.org/10.1016/j.soilbio.2007.03.003>
- Fitzhugh RD, Driscoll CT, Groffman PM, Tierney GL, Fahey TJ, Hardy JP (2001) Effects of soil freezing disturbance on soil solution nitrogen, phosphorus, and carbon chemistry in a northern hardwood ecosystem. *Biogeochemistry* 56(2):215–238. <https://doi.org/10.1023/a:1013076609950>
- Frechette E, Ensminger I, Bergeron Y, Gessler A, Berninger F (2011) Will changes in root-zone temperature in boreal spring affect recovery of photosynthesis in *Picea mariana* and *Populus tremuloides* in a future climate? *Tree Physiol* 31(11):1204–1216. <https://doi.org/10.1093/treephys/tp102>
- Freppaz M, Pintaldi E, Magnani A, Viglietti D, Williams MW (2018) Topsoil and snow: a continuum system. *Appl Soil Ecol* 123:435–440. <https://doi.org/10.1016/j.apsoil.2017.06.029>
- Grippa M, Kergoat L, Le Toan T, Mognard NM, Delbart N, L'Hermitte J, Vicente-Serrano SM (2005) The impact of snow depth and snowmelt on the vegetation variability over central Siberia. *Geophys Res Lett*. <https://doi.org/10.1029/2005gl024286>
- 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. *Biogeochemistry* 56(2):135–150. <https://doi.org/10.1023/a:1013039830323>
- Hardy JP, Groffman PM, Fitzhugh RD, Henry KS, Welman AT, Demers JD, Fahey TJ, Driscoll CT, Tierney GL, Nolan S (2001) Snow depth manipulation and its influence on soil frost and water dynamics in a northern hardwood forest. *Biogeochemistry* 56(2):151–174. <https://doi.org/10.1023/a:1013036803050>
- Huntington TG (2006) Evidence for intensification of the global water cycle: review and synthesis. *J Hydrol* 319(1–4):83–95. <https://doi.org/10.1016/j.jhydrol.2005.07.003>
- Iijima Y, Fedorov AN, Park H, Suzuki K, Yabuki H, Maximov TC, Ohata T (2010) Abrupt increases in soil temperatures following increased precipitation in a Permafrost Region, Central Lena River Basin, Russia. *Permafrost Periglacial Process* 21(1):30–41. <https://doi.org/10.1002/ppp.662>
- Iwasaki H, Saito H, Kuwao K, Maximov TC, Hasegawa S (2010) Forest decline caused by high soil water conditions in a permafrost region. *Hydrol Earth Syst Sci* 14(2):301–307. <https://doi.org/10.5194/hess-14-301-2010>
- Johansson M, Callaghan TV, Bosio J, Akerman HJ, Jackowicz-Korczynski M, Christensen TR (2013) Rapid responses of permafrost and vegetation to experimentally increased snow cover in sub-arctic Sweden. *Environ Res Lett*. <https://doi.org/10.1088/1748-9326/8/3/035025>
- Kagawa A, Sugimoto A, Maximov TC (2006) Seasonal course of translocation, storage and remobilization of C-13 pulse-labeled photoassimilate in naturally growing *Larix gmelinii* saplings. *New Phytol* 171(4):793–804. <https://doi.org/10.1111/j.1469-8137.2006.01780.x>
- Kajimoto T, Osawa A, Matsuura Y, Abaimov AP, Zyryanova OA, Kondo K, Tokuchi N, Hirobe M (2007) Individual-based measurement and analysis of root system development: case studies for *Larix gmelinii* trees growing on the permafrost region in Siberia. *J for Res* 12:103–112. <https://doi.org/10.1007/s10310-006-0259-y>
- Karjalainen O, Luoto M, Aalto J, Hjort J (2019) New insights into the environmental factors controlling the ground thermal regime across the Northern Hemisphere: a comparison between permafrost and non-permafrost areas. *Cryosphere* 13(2):693–707. <https://doi.org/10.5194/tc-13-693-2019>
- Kielland K, Olson K, Ruess RW, Boone RD (2006) Contribution of winter processes to soil nitrogen flux in taiga forest ecosystems. *Biogeochemistry* 81(3):349–360. <https://doi.org/10.1007/s10533-006-9045-3>
- 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-Struct Funct* 17(1):61–69. <https://doi.org/10.1007/s00468-002-0209-z>
- Kotani A, Saito A, Kononov AV, Petrov RE, Maximov TC, Iijima Y, Ohta T (2019) Impact of unusually wet permafrost soil on understory vegetation and CO₂ exchange in a larch forest in eastern Siberia. *Agric for Meteorol* 265:295–309. <https://doi.org/10.1016/j.agrformet.2018.11.025>
- Koyama LA, Kielland K (2019) Black spruce assimilates nitrate in boreal winter. *Tree Physiol* 39(4):536–543. <https://doi.org/10.1093/treephys/tpy109>
- Kreyling J, Haei M, Laudon H (2012) Absence of snow cover reduces understory plant cover and alters plant community composition in boreal forests. *Oecologia* 168(2):577–587. <https://doi.org/10.1007/s00442-011-2092-z>
- Leffler AJ, Welker JM (2013) Long-term increases in snow pack elevate leaf N and photosynthesis in *Salix arctica*: responses to a snow fence experiment in the High Arctic of NW Greenland. *Environ Res Lett*. <https://doi.org/10.1088/1748-9326/8/2/025023>
- Li F, Sugimoto A (2018) Effect of waterlogging on carbon isotope discrimination during photosynthesis in *Larix gmelinii*. *Isot Environ Health Stud* 54(1):63–77. <https://doi.org/10.1080/10256016.2017.1340886>
- Li WB, Wu JB, Bai E, Guan DX, Wang AZ, Yuan FH, Wang SQ, Jin CJ (2016) Response of terrestrial nitrogen dynamics to snow cover change: a meta-analysis of experimental manipulation. *Soil Biol Biochem* 100:51–58. <https://doi.org/10.1016/j.soilbio.2016.05.018>
- Loranty MM, Abbott BW, Blok D, Douglas TA, Epstein HE, Forbes BC, Jones BM, Kholodov AL, Kropp H, Malhotra A, Mamet SD, Myers-Smith IH, Natali SM, O'Donnell JA, Phoenix GK, Rocha AV, Sonnentag O, Tape KD, Walker DA (2018) Reviews and syntheses: changing ecosystem influences on soil thermal regimes in northern high-latitude permafrost regions. *Biogeochemistry* 15(17):5287–5313. <https://doi.org/10.5194/bg-15-5287-2018>
- Martz F, Vuosku J, Ovaskainen A, Stark S, Rautio P (2016) The snow must go on: ground ice encasement, snow compaction and absence of snow differently cause soil hypoxia, CO₂ accumulation and tree seedling damage in boreal forest. *PLoS ONE*. <https://doi.org/10.1371/journal.pone.0156620>
- Morse PD, Burn CR, Kokelj SV (2012) Influence of snow on near-surface ground temperatures in upland and alluvial environments of the outer Mackenzie Delta, Northwest Territories. *Can J Earth Sci* 49(8):895–913. <https://doi.org/10.1139/e2012-012>
- Nauta AL, Heijmans MMPD, Blok D, Limpens J, Elberling B, Gallagher A, Li BX, Petrov RE, Maximov TC, van Huissteden J, Berendse F (2015) Permafrost collapse after shrub removal shifts tundra ecosystem to a methane source. *Nat Clim Change* 5(1):67–70. <https://doi.org/10.1038/nclimate2446>
- Park H, Iijima Y, Yabuki H, Ohta T, Walsh J, Kodama Y, Ohata T (2011) The application of a coupled hydrological and biogeochemical model (CHANGE) for modeling of energy, water, and CO₂ exchanges over a larch forest in eastern Siberia. *J Gerontol Ser A Biol Med Sci*. <https://doi.org/10.1029/2010jd015386>

- Park H, Sherstiukov AB, Fedorov AN, Polyakov IV, Walsh JE (2014) An observation-based assessment of the influences of air temperature and snow depth on soil temperature in Russia. *Environ Res Lett*. <https://doi.org/10.1088/1748-9326/9/6/064026>
- Park H, Fedorov AN, Zheleznyak MN, Konstantinov PY, Walsh JE (2015) Effect of snow cover on pan-Arctic permafrost thermal regimes. *Clim Dyn* 44(9–10):2873–2895. <https://doi.org/10.1007/s00382-014-2356-5>
- Pattison RR, Welker JM (2014) Differential ecophysiological response of deciduous shrubs and a graminoid to long-term experimental snow reductions and additions in moist acidic tundra, Northern Alaska. *Oecologia* 174(2):339–350. <https://doi.org/10.1007/s00442-013-2777-6>
- Pilon CE, Cote B, Fyles JW (1994) Effect of snow removal on leaf water potential, soil-moisture, leaf and soil nutrient status and leaf peroxidase-activity of sugar maple. *Plant Soil* 162(1):81–88. <https://doi.org/10.1007/bf01416092>
- Popova AS, Tokuchi N, Ohte N, Ueda MU, Osaka K, Maximov TC, Sugimoto A (2013) Nitrogen availability in the taiga forest ecosystem of northeastern Siberia. *Soil Sci Plant Nutr* 59(3):427–441. <https://doi.org/10.1080/00380768.2013.772495>
- Robinson CH (2002) Controls on decomposition and soil nitrogen availability at high latitudes. *Plant Soil* 242(1):65–81. <https://doi.org/10.1023/a:1019681606112>
- Schimel JP, Clein JS (1996) Microbial response to freeze-thaw cycles in tundra and taiga soils. *Soil Biol Biochem* 28(8):1061–1066. [https://doi.org/10.1016/0038-0717\(96\)00083-1](https://doi.org/10.1016/0038-0717(96)00083-1)
- Schimel JP, Bilbrough C, Welker JA (2004) Increased snow depth affects microbial activity and nitrogen mineralization in two Arctic tundra communities. *Soil Biol Biochem* 36(2):217–227. <https://doi.org/10.1016/j.soilbio.2003.09.008>
- Sorensen PO, Templer PH, Finzi AC (2016) Contrasting effects of winter snow-pack and soil frost on growing season microbial biomass and enzyme activity in two mixed-hardwood forests. *Biogeochemistry* 128:141–154. <https://doi.org/10.1007/s10533-016-0199-3>
- Stow DA, Hope A, McGuire D, Verbyla D, Gamon J, Huemmrich F, Houston S, Racine C, Sturm M, Tape K, Hinzman L, Yoshikawa K, Tweedie C, Noyle B, Silapaswan C, Douglas D, Griffith B, Jia G, Epstein H, Walker D, Daeschner S, Petersen A, Zhou LM, Myneni R (2004) Remote sensing of vegetation and land-cover change in Arctic Tundra Ecosystems. *Remote Sens Environ* 89(3):281–308. <https://doi.org/10.1016/j.rse.2003.10.018>
- Sugimoto A, Yanagisawa N, Naito D, Fujita N, Maximov TC (2002) Importance of permafrost as a source of water for plants in east Siberian taiga. *Ecol Res* 17(4):493–503. <https://doi.org/10.1046/j.1440-1703.2002.00506.x>
- Sugimoto A, Naito D, Yanagisawa N, Ichiiyanagi K, Kurita N, Kubota J, Kotake T, Ohata T, Maximov TC, Fedorov AN (2003) Characteristics of soil moisture in permafrost observed in East Siberian taiga with stable isotopes of water. *Hydrol Process* 17(6):1073–1092. <https://doi.org/10.1002/hyp.1180>
- 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>
- Tei S, Sugimoto A (2018) Time lag and negative responses of forest greenness and tree growth to warming over circumboreal forests. *Glob Change Biol* 24(9):4225–4237. <https://doi.org/10.1111/gcb.14135>
- Tei S, Sugimoto A, Yonenobu H, Yamazaki T, Maximov TC (2013) Reconstruction of soil moisture for the past 100 years in eastern Siberia by using delta C-13 of larch tree rings. *J Geophys Res-Biogeosci* 118(3):1256–1265. <https://doi.org/10.1002/jgrg.20110>
- Tei S, Sugimoto A, Liang MC, Yonenobu H, Matsuura Y, Osawa A, Sato H, Fujinuma J, Maximov T (2017) Radial growth and physiological response of coniferous trees to arctic amplification. *J Geophys Res-Biogeosci* 122(11):2786–2803. <https://doi.org/10.1002/2016jg003745>
- Ueda MU, Tokuchi N (2013) Effects of winter buds on winter nitrogen uptake and allocation in *Pinus densiflora* saplings. *J for Res* 18(6):462–465. <https://doi.org/10.1007/s10310-012-0371-0>
- Vaughan DG, Comiso JC, Allison I, Carrasco J, Kaser G, Kwok R, Mote P, Murray T, Paul F, Ren J, Rignot E, Solomina O, Steffen K, Zhang T (2013) Observations: cryosphere. In: Stocker TF, Qin D, Plattner G-K, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM (eds) *Climate change 2013: the physical science basis. Contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change*. Cambridge University Press, Cambridge, United Kingdom and New York
- Vavrus S (2007) The role of terrestrial snow cover in the climate system. *Clim Dyn* 29(1):73–88. <https://doi.org/10.1007/s00382-007-0226-0>
- Wahren CHA, Walker MD, Bret-Harte MS (2005) Vegetation responses in Alaskan arctic tundra after 8 years of a summer warming and winter snow manipulation experiment. *Glob Change Biol* 11(4):537–552. <https://doi.org/10.1111/j.1365-2486.2005.00927.x>
- Walker MD, Walker DA, Welker JM, Arft AM, Bardsley T, Brooks PD, Fahnestock JT, Jones MH, Losleben M, Parsons AN, Seastedt TR, Turner PL (1999) Long-term experimental manipulation of winter snow regime and summer temperature in arctic and alpine tundra. *Hydrol Process* 13(14–15):2315–2330. [https://doi.org/10.1002/\(sici\)1099-1085\(199910\)13:14<15%3c2315::aid-hyp888%3e3.0.co;2-a](https://doi.org/10.1002/(sici)1099-1085(199910)13:14<15%3c2315::aid-hyp888%3e3.0.co;2-a)
- Watanabe T, Tateno R, Imada S, Fukuzawa K, Isobe K, Urakawa R, Oda T, Hosokawa N, Sasai T, Inagaki Y, Hishi T, Toda H, Shibata H (2019) The effect of a freeze-thaw cycle on dissolved nitrogen dynamics and its relation to dissolved organic matter and soil microbial biomass in the soil of a northern hardwood forest. *Biogeochemistry* 142:319–338. <https://doi.org/10.1007/s10533-019-00537-w>
- Wipf S, Rixen C (2010) A review of snow manipulation experiments in Arctic and alpine tundra ecosystems. *Polar Res* 29(1):95–109. <https://doi.org/10.1111/j.1751-8369.2010.00153.x>
- Zhang TJ (2005) Influence of the seasonal snow cover on the ground thermal regime: an overview. *Rev Geophys*. <https://doi.org/10.1029/2004rg000157>
- Zhang XL, Manzanedo RD, D'Orangeville L, Rademacher TT, Li JX, Bai XP, Hou MT, Chen ZJ, Zou FH, Song FB, Pederson N (2019) Snowmelt and early to mid-growing season water availability augment tree growth during rapid warming in southern Asian boreal forests. *Glob Change Biol* 25(10):3462–3471. <https://doi.org/10.1111/gcb.14749>

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