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Shifting snow and vegetation:

How does tree canopy modify the response of understory plants to warming winter?

積雪変化と植物：

樹冠は冬の温暖化に対する林床植物の応答をどのように改変するか

Yihan Cai

Primary advisor: Makoto Kobayashi

Field science center for Northern Biosphere

Co-advisors: Kentaro Takagi

Field science center for Northern Biosphere

Shunsuke Utsumi

Division of Biology, Department of Biological Science

Satoshi Suzuki

Field science center for Northern Biosphere

Abstract

Due to rising temperatures and shifting precipitation patterns, the dynamics of seasonal snow cover are changing on a global scale, influencing plant performance. Over the past three decades, researchers have accumulated knowledge about how plant performance responds to shifting snow cover across various climatic zones, ecosystem types, and plant functional types. However, there is still a lack of studies that have quantitatively analyzed plant performance in response to shifting snow cover and comprehensively capture variations in these responses. Such research is essential for identifying the specific regions, ecosystems, or plant functional types most vulnerable to these changes on a global scale. Meanwhile, for a better understanding of the conditions under which plant performance can be vulnerable to shifting snow cover, it is equally important to examine how the responses vary within ecosystems. Even within the same ecosystem, plants experience remarkably different environments due to variations in vegetation structure, topography, and soil. Plants inhabiting these diverse environments likely respond differently to shifting snow cover. This is particularly true in forest ecosystems, which possess clearest environmental heterogeneity due to their complex three-dimensional canopy structure in terrestrial ecosystems. Therefore, forest ecosystems would be the best model system to test how environmental heterogeneity within an ecosystem could influence plant performance in response to shifting snow cover.

In this thesis, I aimed to 1) quantify the responses of plant performance and vegetation cover to shifting snow cover and assess how these responses vary across climatic zones, ecosystem types, or plant functional types, and 2) advance our knowledge of how plants in different environments created by tree canopies respond differently to decreased snow cover. To achieve the goals of this thesis, I first performed a meta-analysis to examine how individual plant survival, growth, biomass, and vegetation cover respond to both decreased and increased snow cover. Then, I conducted a field manipulation experiment in a planted *Picea glehnii* forest (Teshio Experimental Forest, 45°03’N, 142°06’E) in northern Hokkaido, Japan, to examine how the tree canopy modifies the impacts of decreased snow cover on the abiotic environment, such as near-surface and soil temperatures in the understory, and on tree seedling performance, including phenology, survival, and growth. The experimental sites were established in both canopy gap and under canopy areas, with each including control and snow removal plots. Four dominant tree species in this region were planted, and snow removal manipulations were carried out to reduce snow cover duration over two experimental years.

The meta-analysis revealed that plant survival (-46.58 %), aboveground (-10.81 %) and belowground (-30.40 %) biomass showed a significant decrease in response to decreased snow cover. Almost all plant ecological variables s tended to increase with increased snow cover except for plant belowground growth (-13.37 %) and biomass (26.00 %). Through the subgroup analysis, plants in regions with thin snow and relatively low temperatures were found to be particularly vulnerable to decreased snow cover compared to regions with greater snow depth. In these regions, survival rate and aboveground biomass showed a significant decrease in response to reduced snow cover. On the other hand, even in areas with thin snow cover, plants in very warm regions exhibited a significant increase in aboveground length growth in response to decreased snow cover. Additionally, among all ecosystem types, only the tundra ecosystem showed a significant decrease in survival rate and aboveground biomass in response to reduced snow, while other ecosystems exhibited large variations in their responses. Lastly, I found that among all functional types, only woody species, such as tree seedlings and shrubs, showed significant decreases in survival and aboveground biomass in response

to reduced snow cover. Consequently, this meta-analysis quantified the responses of individual plant survival, growth, biomass, and vegetation cover to shifting snow cover and identified that plants in areas with thin snow cover and relatively low air temperature during the dormant season, plants in tundra ecosystems, and woody species are particularly vulnerable to decreased snow cover.

The field manipulation experiment revealed that snow interception by the tree canopy delayed snow cover establishment and advanced snowmelt. As a result, tree seedlings under the canopy experienced more severe temperature conditions despite the expected temperature-buffering effect of the tree canopy. During the snow cover formation period (early winter), the daily mean and minimum air temperatures (at 20 cm height from ground) were lower under the canopy than in the canopy gap. And during the snowmelt period (late winter), the daily minimum air temperature was lower in the snow removal plots than in the control plots under the canopy, whereas the daily mean air temperature was higher in the snow removal plots than in the control plots in the canopy gap. These differences in thermal conditions, influenced by both tree canopy and snow removal manipulation, led to significant variations in spring phenology, survival and growth of tree seedlings. For all four species, budburst and leaf-out were advanced by snow removal due to earlier heat accumulation. Furthermore, this advancement was more pronounced in the canopy gap than under the tree canopy. This may be due to the higher frequency of spring freezes and relatively lower heat accumulation in the snow removal plots under the canopy. Snow removal increased mortality across all four species, with evergreen conifers experiencing a greater increase in mortality under the canopy than in the canopy gap. Evergreen conifer species exhibited lower diameter growth in the snow removal plots compared to the control plots under the canopy, while no significant differences were observed in deciduous broad-leaved species or in the canopy gap by the end of the growing season. Overall, survival and growth were negatively affected by decreased snow cover, with greater impacts under the canopy, particularly for evergreen conifer species. The experiment highlighted the role of the tree canopy in shaping seedling responses to decreased snow cover. While the tree canopy is generally known to acts as a buffer and provide microrefugia for understory plants against macroclimatic changes during the growing season, the results indicate that snow interception by the tree canopy reduces the insulating effect of snow cover, leading to harsher winter conditions for seedlings beneath it. Additionally, since this experiment was conducted in a transition zone where vegetation is expected to shift from an evergreen conifer-dominated forest to a deciduous broad-leaved dominated forest, the findings suggest that decreased snow cover in this region may further accelerate this transition.

Overall, this thesis highlights the diverse responses of plant performance to shifting snow cover at both global and ecosystem scales. By understanding the variation in plant performance responses and identifying the factors driving this variation across different scales, we can pinpoint habitats and species vulnerable to winter climate change. Additionally, this knowledge enhances the accuracy of our predictions of ecosystem structure and function under future winter climate change, providing crucial information for effective management policies.

[Keywords] boreal forest, buffering, climate change, decreased snow, forest understory, insulation effect, meta-analysis, microclimate, phenology, plant performance, snow interception, tree seedling, winter climate change

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Chapter 1

General Introduction

1.1 Plant varied responses to climate change

Undoubtedly, human-induced global warming is exerting profound impacts on plants, leading to earlier phenological events (Cleland et al. 2007; Piao et al. 2019), shifts in species distributions (Kelly and Goulden 2008; Thuiller et al. 2008; Chan et al. 2024), and changing performance at the individual level (Rustad et al. 2001; Niu et al. 2014; Liang et al. 2016). These changes can alter the composition of plant communities (Walker et al. 2006; De Boeck et al. 2007; Elmendorf et al. 2014; Franklin et al. 2015; Harrison et al. 2019), as well as interactions between plants and other species (Penczykowski et al. 2017; Kudo and Cooper 2019; Burdon and Zhan 2020), and can lead to cascading influences on ecosystem processes, services, and overall ecological stability. While numerous studies have accumulated over the years, it has become increasingly clear that plant responses to climate change are not uniform (Lenoir 2020). For example, plant responses to climate change can vary across species (Klanderud 2008; Fisichelli et al. 2014). Even within the same species, individuals may respond differently depending on the location in which they grow (Rustad et al. 2001; Feeley et al. 2020). For instance, global-scale studies examining the effects of rising temperatures on plant productivity have revealed substantial variation in responses depending on geographic location (Rustad et al. 2001). More detailed analyses have demonstrated that plant responses to warming significantly differ across ecosystem types. Furthermore, even within the same location, variation in microenvironmental conditions and biotic interactions can lead to divergent responses (De Frenne et al. 2021; Kemppinen et al. 2024). For example, Xu et al. (2023) conducted a warming experiment on *A. pictum* seedlings in different light environments within a forest and showed that, even within the same ecosystem, plant biomass responses to rising temperatures varied depending on local light conditions. These findings indicate that plant responses to climate change are highly divergent and may initially seem unpredictable. However, by uncovering the underlying mechanisms driving the context dependency of these responses—such as differences among species, climate, or microenvironments—it becomes possible to interpret this variation systematically and identify

generalizable patterns across space. It is also important to note that the driver of context dependency can diverge across multiple spatial scales (Bütikofer et al. 2020). Recognizing and incorporating these scale-dependent effects is essential for improving the accuracy of predictions regarding biological responses to ongoing climate change. While there has been extensive research on the impacts of climate change on plants during the growing season—enabling researchers to identify the underlying factors driving variation in plant responses—much less attention has been given to its effects during the dormant season (Makoto et al. 2014; Bokhorst et al. 2016; Sanders-DeMott and Templer 2017), and even fewer studies have considered the context dependency of these responses.

1.2 Shift in snow cover regimes and its influence on plant

Warming trends are projected to be especially pronounced in high-latitude regions (Pithan and Mauritsen, 2014) and during the winter season (Xia et al., 2014), with substantial implications for ecosystems that rely on seasonal snow cover in mid- to high-latitude and mountainous regions (Bormann et al. 2018). In parallel, winter precipitation is undergoing notable changes, not only in total amounts but also in their timing and duration. Together, these changes in temperature and precipitation are reshaping snow cover dynamics across the globe, leading to regionally divergent trends: while snow cover is mainly decreased in most areas, it also showed the increasement in others (Williams et al., 2015; Gottlieb and Mankin, 2024). In regions with seasonal snow, the characteristics of snow cover—such as depth and duration—act as key drivers shaping both abiotic and biotic environments, thereby influencing plant performance and community composition (Rixen et al., 2022). In this section, I compile findings from previous studies to illustrate how snow cover regulates plant responses via its effects on abiotic and biotic conditions.

1.2.1 How snow cover control plant performance via abiotic factors

One of the most important attributes of snow is its role as a thermal insulator, decoupling near-surface air temperature and soil temperature from the air temperature above the snow (Zheng et al. 2018; De Frenne et al. 2021). A sufficiently thick snow cover can help maintain near-surface and soil temperatures close to 0°C, generally, preventing frost and freeze damage to understory plant and reducing the frequency of freeze-thaw cycles (Sanders-DeMott et al. 2017). These cold stresses can damage plant organs, such as leaves, winter bud, and root during winter (Cleavitt et al. 2008; Schaberg et al. 2008), influencing the survival and growth of the subsequent season (Kreyling et al. 2012; Martz et al. 2016; Girardin et al. 2022). Other than the insulation effect, snow cover can also control plant performance via its influence on soil moisture, soil nutrient, and light intensity. When snow melts in the spring, it provides a significant source of water to the soil (Uunila et al. 2006). In regions with limited access to water, such as deserts and semi-arid areas, snowmelt water is the primary source of moisture for plant to survive and growth in the subsequent growing season (Yin et al. 2020). In addition, snow cover can also reduce evaporation losses during the winter, leading to higher soil moisture levels and helping to prevent plants from winter desiccation (Neuner et al. 1999; Luoranen et al. 2022). Snow cover can also influence decomposition rates and nutrient availability in the soil (Schimel et al. 2004; Brooks et al. 2011). The absence of snow cover with increased freeze–thaw cycles can generally amplify the concentration of availability nitrogen to plants (Christopher et al. 2008, Zhao et al. 2022), however, whether plant can efficiently utilize the increased availability nitrogen also depends on plant phenological timing and the damages on the fine root (Sanders-DeMott et al. 2018; Makoto et al. 2022). Besides, snow cover can protect plants with their leaves still attached over winter from strong solar radiation, particularly in early spring, which can otherwise lead to photoinhibition when combined with low air temperatures (Neuner et al. 1999; Kitao et al. 2018). However, in regions with very long snow-covered durations, the persistent snow cover that blocks solar radiation can shorten the growing season, ultimately reduce plant growth and altering

community composition (Wipf and Rixen 2010). Accordingly, snow cover can control plant performance through its influence on the abiotic environment. Therefore, shifts in snow cover driven by climate change can significantly alter plant performance as the abiotic environments can change significantly with shifting snow cover (Song et al. 2018; Zhao et al. 2022; Rixen et al. 2022).

1.2.2 How snow cover control plant performance via biotic factors

Other than the abiotic factors, snow cover can also control plot performance via its influence on biotic interactions, such as herbivore and pathogen. Snow cover can act as a barrier that prevents large herbivores—such as reindeer, moose, caribou, and geese—from accessing vegetation beneath the snow (Penczykowski et al., 2017; Pedersen et al., 2021; Holtan et al., 2023). Consequently, thinner snow cover or earlier snowmelt can lead to increased herbivory pressure, resulting in greater feeding damage, reduced plant performance, and altered community composition (Christenson et al., 2014; Eischeid et al., 2023). On the other hand, snow cover can also provide shelter for small mammals, increasing their winter activity in the subnivium and potentially leading to more intense herbivory and plant damage (Guiden et al., 2018; Sanders-DeMott et al., 2017). Snow cover can also influence plant performance, distribution, and abundance through modifying their pathogens (Roy et al. 2004; Olofsson et al. 2011). Snow molds as one of the important groups of fungal pathogens have a particularly distinct relation with snow cover (Matsumoto 2009). Snow molds prefer deeper snow cover, which provides prolonged warm and moist conditions that facilitate their spread. This can reduce plant survival and performance in the following growing season (Barbeito et al. 2013; Moriana-Armendariz et al. 2022). However, since susceptibility to infection and plant resilience can be species-specific, the indirect influence of snow cover via pathogens may sometimes be difficult to predict (Roy et al. 2004). Accordingly, snow cover can determine plant performance through its influence on biotic factors. However, the influence of biotic factors can be difficult to predict because their relationship with plants is not always uniform and can range from positive to negative,

depending on environmental conditions (Roy et al. 2004; Guiden et al. 2018).

1.3 Plant responses to shifting snow cover at different spatial scales

As described above, snow cover influences various environmental factors surrounding plants and serves as a key determinant of plant performance. Over the past decade in particular, there has been a rapid increase in studies examining how changes in snow cover driven by climate change affect plant responses (Fig. 1-1), leading to a substantial accumulation of knowledge. In the following sections, I summarize this body of research by distinguishing between global and local scales, and highlight the remaining gaps in our understanding.

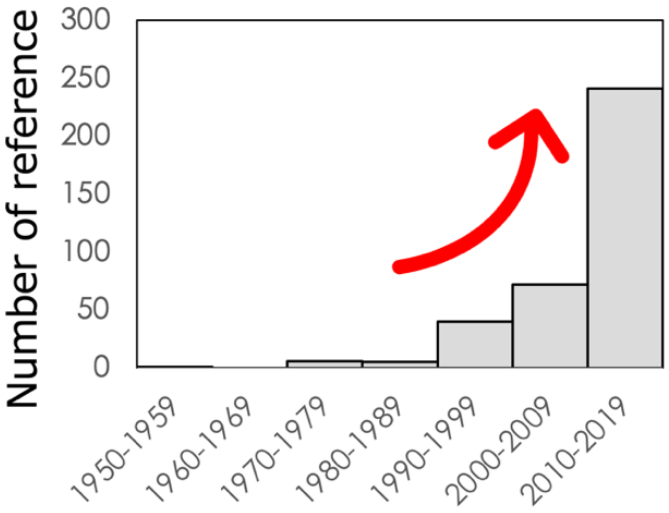


Fig. 1-1. Number of references on the responses of organisms to shifting snow cover.

1.3.1 Plant performance in response to shifting snow cover on a global scale and the remaining unknowns

Contributing to a growing body of research on how plant performance responds to changing

snow cover, we now have some comprehensive understanding (Wipf and Rixen 2010; Rixen et al. 2022; Slatyer et al. 2022). Especially in the recent review by Slatyer et al. (2021), which analyzed 365 original studies, including field manipulation experiments, natural snow gradients, and long-term monitoring, to investigate plant ecological responses to reduced snow depth and earlier snowmelt at various ecological levels—individual, population, and community. Their findings revealed that reduced snow cover led to negative responses, such as increased plant mortality, damage, and injury, in more than 50% of the referred studies (n = 23). Additionally, earlier snowmelt advanced plant phenology in more than 50% of the referred studies (n = 73). However, for other plant performance and life history parameters, studies reported mixed results—both positive and negative responses—with no clear trend dominating (i.e., no single response type accounted for more than 50% of the cases). The variation in plant ecological responses to decreased snow depth and earlier snowmelt can be partly explained by the plant characteristics, namely plant functional types and growth stages, with resistance and resilience to shifts in snow cover (Wipf and Rixen 2010; Osland et al. 2015). However, even within the same species, responses may vary across climates with different snow patterns and temperature conditions during the winter season (Wipf and Rixen, 2010; Henry et al., 2018), as well as across ecosystems where shifts in snow cover have varying levels of influence on the biotic and abiotic factors that control plant performance (Penczykowski et al., 2017; Zhao et al. 2022). However, studies attempting to explain the variation in plant performance in response to shifts in snow cover on a global scale are still lacking. Identifying factors that contribute to these variations quantitatively can help pinpoint vulnerable regions or plant types, enabling the development of more effective management strategies for shifting snow cover driven by winter climate change.

1.3.2 Plant performance in response to shifting snow cover at local scale

The knowledge gained from global-scale studies on plant responses to changes in snow cover contributes to understanding the broad impacts and trends of climate change. However, it is also

necessary to focus on plant responses at local scales, such as the different responses within an ecosystem. Plant responses within the ecosystems are strongly influenced by the environmental heterogeneities within the ecosystems. By considering these factors, we can gain valuable insights for developing more specific and effective climate change adaptation strategies for the local environment. Especially regarding environmental heterogeneity that driven by factors such as vegetation, topography, and soil is expected to have a distinct influence on how plants respond to climate change in ecosystems (Lenoir et al., 2017; De Frenne et al., 2021; Kenppinen et al., 2024). Given that forests account for the largest proportion of land area in regions with seasonal snow cover (Fig. 1-2), this dissertation will focus on the differences in ecological responses within forest ecosystems.

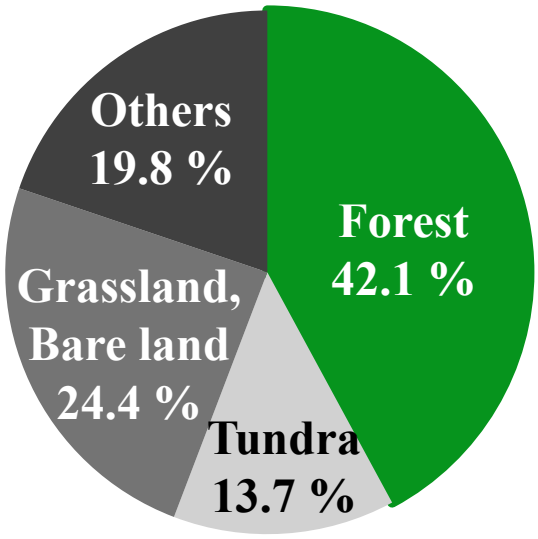


Fig. 1-2 Proportion of land area occupied by each ecosystem type in regions with seasonal snow cover.

1.3.2.1 Environmental heterogeneity during winter driven by tree canopy structure

Forest ecosystem has very evident environmental heterogeneity mainly due to their three-

dimensional canopy structure (Zellweger et al. 2020). The spatial heterogeneity of canopy structure leads to variability in the forest floor environment. In particular, areas below tree canopies and in canopy gaps formed by fallen trees or broken branches are among the most common and environmentally distinct microhabitats in forests (Muscolo et al. 2014). The tree canopy acts like a blanket, buffering against extreme cold events by reducing outgoing long-wave radiation (Safa et al., 2021; Rutter et al., 2023) and weaken wind speed (Geiger et al., 2009; De Frenne et al. 2021). Consequently, it moderates temperature by providing warmer minimum temperatures and reducing temperature fluctuations compared to canopy gaps (De Frenne et al. 2019; Zellweger et al., 2019).

However, tree canopy can intercept snowfall and reduce snow cover depth and duration below the canopy compared to the canopy gap (Varhola et al. 2010; Roth and Nolin 2018; Sun et al. 2022). This possibly cause lower minimum temperature and increased temperature fluctuations below the canopy compared to the canopy gaps. By compiling data from empirical studies that measured maximum snow depth both below the canopy and in canopy gaps or nearby open fields on a global scale (Fig. S1-3, *SI*), I found that forest canopies exhibit significant snowfall interception capacity, reducing snow cover by an average of 21.5 ± 3.8 cm globally (mean ± SE). When categorized by forest type—deciduous broadleaved, evergreen conifer, and mixed forests—significant snowfall interception by the tree canopy was detected only in evergreen conifer (21.8 ± 4.8 cm) and mixed forests (20.5 ± 4.9 cm), but not in deciduous broadleaved forests (17.7 ± 18.6 cm; Fig. 1-3). Furthermore, the difference in maximum snow depth was significantly positively correlated with canopy cover ratio (Fig. 1-4), indicating that denser canopies intercept more snowfall. Therefore, the understory environment during winter can vary considerably within forests due to horizontal spatial variation in canopy structure, especially between areas beneath the canopy and canopy gaps in forests with dense canopy cover.

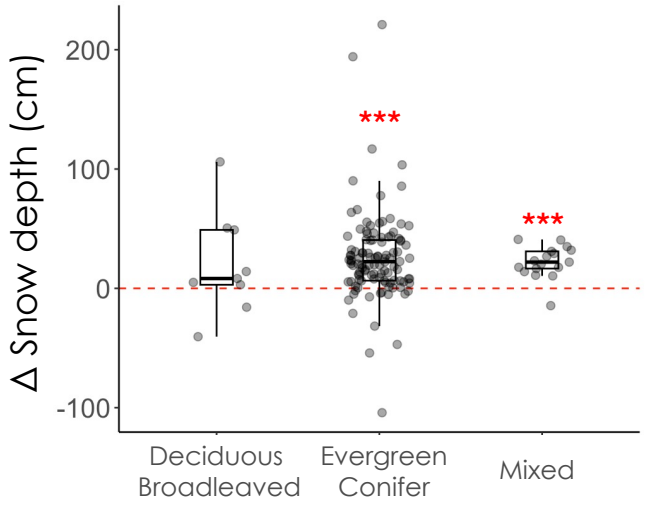


Fig. 1-3 Difference in maximum snow depth between below canopy and canopy gap (ΔSnow depth = Maximum snow depth in canopy gap or nearby open field − Maximum snow depth below canopy) in deciduous broadleaved, evergreen conifer, and mixed forests. Grey circles represent individual observations, and black lines within the boxes indicate median values. Asterisks denote significant snow interception capacity of the tree canopy as estimated by linear mixed-effects models.

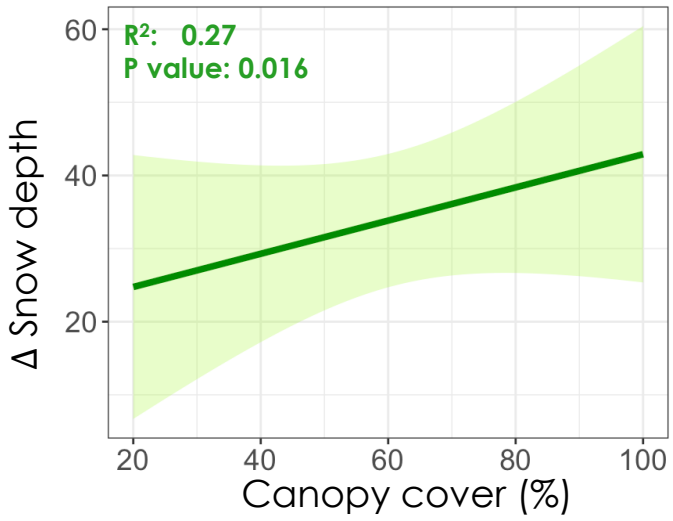


Fig. 1-4 The relationship between canopy cover and difference in maximum snow depth between below canopy and canopy gap (ΔSnow depth = Maximum snow depth in canopy gap or nearby open field − Maximum snow depth below canopy)

1.3.2.2 *How environmental differences could influence the responses of plant responses to decreased snow cover*

In forest ecosystems, decreased snow cover generally has a substantial impact on understory plants, such as reducing their survival rates, and can have both positive and negative effects on their growth during the growing season (Ishioka et al. 2013; Martz et al. 2016; Sanders-DeMott et al. 2017; Makoto et al. 2022). However, since the majority of studies have been conducted in relatively uniform environments, or even in common gardens, greenhouses, and laboratories, how environmental differences can influence plant responses to decreased snow cover remains largely unknown.

In forest ecosystems, the spatial differences of canopy structure may lead to varying environmental responses to decreased snow cover between different forest microsites. For example, below the tree canopy, where snow depth is generally thinner compared to the canopy gaps (Fig. 1-3), a decrease in snow cover would significantly impact near-ground air and soil temperatures. In contrast, in the canopy gaps, where snow depth is typically deeper and insulation effects are higher, the impact of the same level of snow reduction may be relatively smaller compared to that under the tree canopy. Thus, differences in initial conditions, such as snow depth, radiation, and temperature, suggest that the magnitude and nature of environmental changes resulting from decreased snow cover can also vary. As a result, plants within the forest may exhibit varying responses to these changes.

Generally, climate change prediction models tend to treat large areas uniformly; however, incorporating local variations can lead to more accurate predictions (Niittynen et al. 2020; De Frenne et al. 2021; Kemppinen et al. 2024). In particular, in forest ecosystems located in snowy regions, shifts in snow cover can significantly influence the performance of understory vegetation (Sutinen et al. 1999; Renard et al. 2016), including seedlings that will shape the future species composition of the forests (Lee and Schaffer-Morrison 2024). Therefore, examining how environmental differences, driven by canopy structure, influences seedling responses to decreased snow cover will provide valuable insights into the future structure of forest ecosystems.

1.4 *Main Objectives and Outline*

The overall aim of this PhD thesis aims to comprehensively understand plant responses to climate change–driven changes in snow cover by elucidating the underlying factors that influence these responses at both global and local scales. To be more precise, I aimed to: 1) quantify the responses of plant performance and vegetation cover to shifting snow cover and assess how these responses vary across climatic zones, ecosystem types, and plant functional types on a global scale; and 2) advance our knowledge of how plants in different environments driven by tree canopies respond to decreased snow cover within a forest ecosystem. These two objectives are addressed in **Chapter 2** and **Chapter 3**, respectively. In **Chapter 4**, I summarize and integrate the main findings of my PhD research.

Specifically, in **Chapter 2,** I performed a meta-analysis to examine how individual plant survival, growth, biomass, and vegetation cover respond to both decreased and increased snow cover. Also, I selected the potential drivers, such as climate conditions, ecosystem types, plant functional types, and the method of the treatment to explain the variation in plant responses to shifting snow regimes on the global scale.

In **Chapter 3**, I conducted a field snow removal manipulation to investigate how tree canopies influence the understory abiotic environment and understory plant performance in response to decreased snow cover.

In **Chapter 4**, I summarized and integrated the main findings of this PhD thesis, emphasizing the differences between drivers that shape plant responses to shifting snow cover at both global and local scales. Additionally, I discussed how these findings can inform management strategies to mitigate the potential negative effects of decreased snow cover on sub-boreal forests and provided suggestions for future research directions.

1.5 Supplemental information (*SI*)

1.5.1 Method

1.5.1.1 Data of snow cover depth

I conducted a Web of Science search on December 2024, using the following keywords: "snow*, AND forest*, AND canopy* OR overstory*, AND accumulation* OR interception* OR trapping* OR retention* OR capture*". This search produced 600 publications. Publications that did not show up in the Web of Science keyword search were not included in our analysis. 8 out of 600 publications were not able to access, even though I reach out to the corresponding authors. For the initial set of 592 publications, I excluded those 1) did not provide data of maximum snow depth measured in both below tree canopy and in canopy gap/open area, 2) only showed the value of maximum snow depth that were estimated based on models rather than empirical measurements. Following the established criteria, 51 publications were identified for inclusion in this analysis. Several of these publications reported data from multiple sites, resulting in a total of 85 sites being analyzed. The majority of these sites were located in the Northern Hemisphere, primarily in North America, Nordic countries, Western Europe, and parts of northern China and Japan.

For publications reporting more than one year of data for maximum SD and SMD, I averaged reported values across all years. For publications included only figures but not numeric values in their text or tables (i.e. Bewley et al. 2010; Hannula et al. 2016; Komarov and Sturm 2023), I extracted data from figures using WebPlot Digitizer (Version 4.7; Ankit Rohatgi, December, 2025).

1.5.1.2 Forest structural data

I extracted forest types and canopy cover data from the text or tables from each primary paper. The forest types included evergreen conifer forests (EC), deciduous broadleaved forests (DB),

and mixed forests composed of evergreen conifers and deciduous broadleaved species. For publications that only provided figures without numeric values in the text or tables, data were extracted from figures using WebPlot Digitizer (Rohatgi, 2022, Version 4.6).

1.5.1.3 Statistical analysis

All the statistical analyses were performed in R version 4.1.0 (R Development Core Team 2021). The individual difference in maximum snow depth between below-canopy and canopy gap (ΔSnow depth) at each site was calculated as the maximum snow depth in the canopy gap or nearby open field minus the maximum snow depth below the canopy. To calculate the average ΔSnow depth and test whether it significantly differed from zero, I used linear mixed-effects models implemented in the lme4 package (Bates et al., 2014), with the primary study set as a random effect. Tukey's HSD test was applied for post hoc comparisons when significant effects were detected. I also used linear mixed-effects models to examine the relationship between ΔSnow depth and canopy cover, with the primary study set as a random effect. In order to ensure normality of the residuals, I log-transformed the response variables before fitting the linear mixed models. Statistical significance was defined at $P < 0.05$.

1.5.2 Supplemental figures

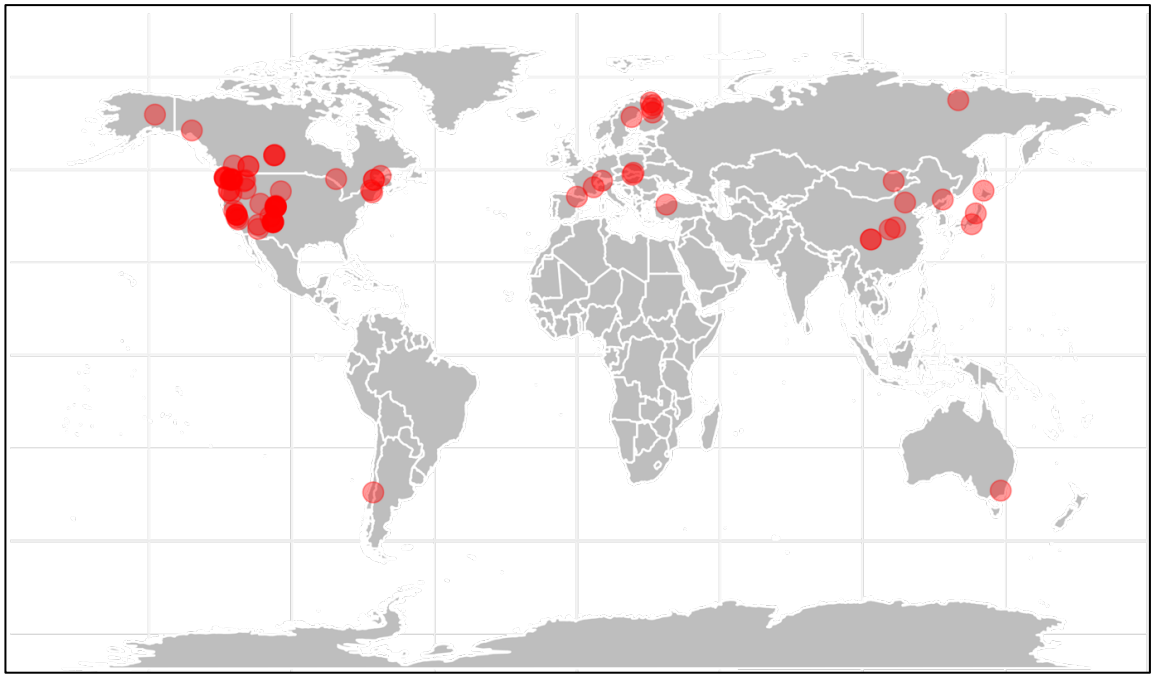


Figure S1-1. Map showing locations of 85 sites included in the analysis.







Chapter 2

Unveiling Responses of Plant Performance and Vegetation Cover to Shifting Snow Regimes: A Meta-Analysis

2

After

Cai, Y., Templer, P.H., Makoto, K. (*in press*). Unveiling Responses of Plant Performance and Vegetation Cover to Shifting Snow Regimes: A Meta-Analysis. *Climatic change*.

2.1 Abstract

Snow cover is a critical factor controlling plant performance, such as survival, growth, and biomass, and vegetation cover in regions with seasonal snow (e.g., high-latitude and high-elevation regions), due to its influence on the timing and length of the growing season, insulation effect during winter, and biotic and abiotic environmental factors. Therefore, changes in snow cover driven by rising temperatures and shifting precipitation patterns are expected to alter plant performance and vegetation cover. Despite the rapid increase in research on this topic in recent decades, there is still a lack of studies that quantitatively elucidate how plant performance and vegetation cover respond to shifting snow cover across snowy regions. Additionally, no comprehensive study has yet quantitatively examined these responses across regions, ecosystems, and plant functional types. Here, I conducted a meta-analysis synthesizing data from 54 snow cover manipulation studies conducted in both the field and laboratory across snowy regions to detect how plants performance and vegetation cover respond to decreased or increased snow cover. Our results demonstrate that plant survival, aboveground biomass, and belowground biomass exhibited significant decreases in response to decreased snow cover, with rates of survival having the greatest decrease. In response to increased snow cover, plant survival, growth, biomass and vegetation cover tended to increase, except for plant belowground length growth and biomass, which showed significant decreases. Additionally, our quantitative analysis of plant responses to changes in snow cover across regions, ecosystems, and plant functional types revealed that cold regions with thin snow cover, tundra and forest ecosystems, and woody species are particularly vulnerable to snow cover reduction. Overall, this study demonstrates the strong controls that snow cover exerts on plant performance, providing insights into the dynamics of snow-covered ecosystems under changing winter climatic conditions.

2.2 Introduction

Seasonal snow currently covers up to one-third of the Earth's terrestrial area (IPCC 2021; Slatyer et al. 2022). With rising air temperatures and region-specific shifts in precipitation patterns due to climate change (Dore 2005; Xia et al. 2014; Williams et al. 2015), shifts in the seasonal snow cover regime, including changes in snow cover duration influenced by shifts in snowmelt timing and the start of the snow-cover season, as well as changes in snow cover depth, are occurring worldwide (IPCC 2021; Notarnicola 2022; Mudryk et al. 2024). These changes include decreases in snow depth and duration in large parts of Europe and parts of North America, as well as increases in snow depth and duration in some parts of the Nordic countries – Sweden and Norway, the United States, and Russia (Gottlieb and Mankin 2024).

Snow cover is one of the most important factors that governs plant performance (e.g., survival, growth, biomass) and vegetation cover in snowy regions, due to its influence on the timing and length of the growing season and their insulation effects during winter (Wipf et al. 2009; Rixen et al. 2022). Changes in snow covers in turn could have significant implications for biodiversity (Niitynen 2018). For example, earlier snowmelt has been shown to lead to an earlier start and extension of the growing season, resulting in increased shrub growth (Francon et al. 2020). While in some cases, changes in snowmelt have been found to not necessarily affect the length of the growing season (Ishioka et al. 2014; Semenchuk et al. 2016). Also, later formation of winter snowpack, earlier snowpack melting, or thinner snowpack overall can reduce the insulation effects of snow and increase damages to both above- and belowground plant tissue, resulting in higher mortality and lower plant growth in the following growing season (Martz et al. 2016; Dimisch et al. 2018).

In addition, snow cover regime can also control plant performance through its impact on other biotic and abiotic environmental factors environmental factors (Rixen et al. 2022). For example, increased snowpack can provide refuge for small mammal herbivory, leading to increased damage and

negative effects on growth of tree seedlings and vegetation cover (Sanders-DeMott et al. 2018; Siewert and Olofsson 2021). On the other hand, large mammals, such as caribou and reindeer, tend to prefer areas with thinner snow, thereby the plants tend to be protected from these herbivores with increased snowpack (Pedersen et al. 2021; Holtan et al. 2023). In addition, snow cover is also associated with fungal pathogens (Olofsson et al. 2011). For example, outbreaks of snow mold—a group of fungal pathogens—are common during winters with prolonged snow cover (Matsumoto 2009). For abiotic factors, increased snowpack can significantly increase plant-available nitrogen in the soil (Zhao et al. 2022), which in turn boosts foliar nitrogen content (Li et al. 2016). This increase in nitrogen availability can enhance photosynthetic efficiency and positively affect plant growth (Pattison and Welker 2014). In addition, increased snowpack can also promote vegetation productivity through the increased available soil water during the following growing season (Peng et al. 2010; Zhao et al. 2022). Given the vital function of snow cover, it is essential to identify the magnitude and direction of change in plant performance to increased or decreased snow cover, which can cause cascading effects on vegetation cover and composition at both the ecosystem and regional scales (Wipf and Rixen 2010; Kreyling et al. 2012; Niittynen et al. 2020).

Over the past three decades, snow manipulation experiments have been conducted in both laboratory and field settings to understand how changes in snow cover impact plant performance and vegetation cover (Sanders-DeMott and Templer 2017). These studies, conducted across diverse regions with varying gradients of temperature and snowfall patterns, have involved a wide range of plant species from different ecosystem types (e.g., Bokhorst et al. 2015; Blume-Werry et al. 2016; Sanders-DeMott et al. 2018). By compiling the accumulated data, Slatyer et al. (2022) offered insights into the general directional trends in plant responses to reduced snow depth and earlier snowmelt. As a result, reduced snow depth was found to increase plant mortality and damage. In contrast, other response variables such as growth and biomass showed both increasing and decreasing trends under reduced snow depth and earlier snowmelt. While this study clarified the overall direction of plant

responses to global shifts in snow cover, particularly reduced snow cover, it provided limited insight into how these responses vary across climate zones, ecosystems, or plant functional types. Understanding such variation is essential for identifying vulnerable regions, ecosystems, and functional types, and improving the accuracy of models predicting the consequences of winter climate change on ecosystem functions.

The responses of plants to shifting snow cover could be influenced by the climate conditions, such as the snowfall and temperature patterns during the winter season. For example, decreased snow cover is expected to have a positive effect on plant growth in regions with thick and long-lasting snow cover since the growing season length is one of the limiting factors in these regions (Werner et al. 2019; Makoto et al. 2022). In contrast, decreased snow is expected to have negative effects on plant performance and vegetation cover in regions with relatively thin and short-lasting snowpacks with markedly low air temperatures, as these conditions can have frequent soil freeze-thaw cycles in winter and frost events for plants in late-spring (Krab et al. 2017; Henry et al. 2018; Zohner et al. 2020). Overall, understanding how climate influences plant responses to shifting snow cover can help identify regions most at risk from these shifts.

The responses of plant to shifting snow cover may also vary across plant functional types and growth stages. Previous studies revealed that increased snow depth and delayed snowmelt lead to no change or increases in vegetation cover of forbs and shrubs, but significant decreases in lichens and graminoids in Arctic and alpine ecosystems (Wipf and Rixen 2010). Additionally, Makoto et al. (2022) found that earlier snowmelt increased shoot growth in understory herbaceous plants, while no significant change was observed in the shoot growth of overstory trees. These differences in response direction or magnitude among plant functional types may be attributed to varying overwintering strategies, such as cold acclimation and hardiness (Sakai and Larcher 1987; Chang et al. 2020), the presence of overwintering organs, and the position of resting buds (Lubbe et al. 2021). In addition, growth stages can also respond differently to shifting snow cover. Mature trees are often expected to

be more resilient to winter cold stress compared to seedlings (Augspurger 2013; Osland et al. 2015). Additionally, seedlings covered by snow are more susceptible to snow-related effects than mature trees. For example, snow can control seedling survival and growth through its impact on spring phenology and pathogen infections of seedlings (Cheng and Igarashi 1988; Smull et al. 2019; Marumo et al. 2020; Makoto 2022). Overall, examining how plants respond to shifting snow cover across different plant functional types and growth stages can help identify which plant functional types and growth stages are most vulnerable to these shifts.

Even within the same species, plant responses to shifting snow cover may vary across ecosystems, such as tundra, forest, and grassland. Different responses in soil microclimates and physicochemical to shifting snow cover across ecosystems (Song et al. 2017; Zhao et al. 2022) could potentially lead to variations in plant performance and vegetation cover. For example, winter snow removal caused a significantly greater decrease in soil moisture in desert ecosystems compared to others, such as forest and cropland ecosystems (Zhao et al. 2022), which can affect plant water uptake and growth in the following growing season. In addition, the altered plant-herbivory interactions under shifting snow cover, which influence plant performance and vegetation cover, can also vary among different ecosystem types (Shimano and Masuzawa 1998; Koltz et al. 2022). Accordingly, the responses of plant performance and vegetation cover to shifting snow cover could also be varied across ecosystem types.

In this study, I aimed to quantify the responses of plant performance and vegetation cover to shifting snow cover across regions with different climatic conditions, ecosystems, and plant functional types and growth stages. In addition to these factors, I also examined the effects of methods applied for snow cover manipulation experiments on plant performance and vegetation cover in response to changed snow cover. To test these hypotheses, I conducted a quantitative meta-analysis, synthesizing data from 54 snow manipulation experiments. A total of 980 comparisons across eight response variables—survival rate, aboveground length or height growth, belowground length growth,

aboveground biomass, belowground biomass, total biomass, radial growth, and vegetation cover—were included.

2.3 Method

2.3.1 Data collection and compilation

I conducted a Web of Science search on May 10 and October 19, 2022 using the following keywords: "snow* OR freeze*", AND "climate change* OR winter warming* OR experimental warming*", AND "winter*", AND "sapling* OR seedling* OR plant* OR tree* OR vegetation*". This search resulted in 1618 publications. Publications that were not present in the Web of Science keyword search were not included in our analysis. To avoid bias in the selection of publications, I used the following criteria to determine whether to include a manuscript in our meta-analysis; only those studies that met all of these selection criteria were included: 1) The study involved a treatment that resulted in an increase or decrease in the depth and duration in snow in either field and laboratory settings. 2) The study included a control (or reference) and treatment. 3) The study included at least one response variable that indicated plant performance vegetation cover. 4) The mean, standard deviation, and sample size of the plant performance vegetation cover were reported or could be calculated from the data reported in the study.

Overall, our review of papers resulted in inclusion of 980 snow cover treatment and control pairs from 54 studies that met all four criteria and were included in our analysis (also see Supplemental Information (*SI*) 1). A total of 67 sites were represented across the 54 publications and were distributed across terrestrial ecosystems around the globe that experience seasonal snow-covered area (Fig. 2-1). The sites were classified into six climatic zones: polar, boreal, cool temperate, warm temperate, arid, and alpine zones (also see *SI* 2). If a single study reported more than one snow cover treatment (e.g., removing and adding different amounts of snow, using different snow manipulation

methods) or the same snow cover manipulation in different sites or targeting different plant species, I treated each comparison as a separate observation. For studies that measured plant performance and vegetation cover more than once in the same year, I averaged the reported values across all measurements within that year. And in this research, shifts in snow cover concluded both depth and duration since all snow manipulation experiments in the 54 studies consistently led to either a decrease in snow cover depth and duration or an increase in both (also see *SI* 3).

Survival, growth, and biomass, key indicators of plant performance, along with vegetation cover, were included as response variables in this study. Detailed definitions for each variable are provided in the supplemental material (also see *SI* 4; Table S2-1). Data for these variables, presented as paired control and treatment values, were extracted directly from the main text, tables, appendices, or figures. Numerical data from graphical visualizations were obtained using WebPlotDigitizer (Rohatgi, 2022, Version 4.6), a computer vision-based tool designed for such purposes. Each pair was classified as one of the following ecosystems: forest, shrubland, wetland, grassland, common garden, tundra, and desert, based on the descriptions provided in each study. Snow cover types were classified in one of six ways following Sturm and Liston (2021) (Table S2-2): (1) as thin snow cover with low air temperature, (2) thin snow cover with high air temperature, (3) moderate snow cover with low air temperature, (4) moderate snow cover with high air temperature, (5) heavy snow cover across all temperature, and (6) thin or no snow cover with very high air temperature. The location data from each study site were included in the Global Seasonal-Snow Classification, Version 1 (National Snow and Ice Data Center, https://nsidc.org/data/nsidc-0768/versions/1#anchor-1; accessed March 2023) in order to characterize each site as one of the six seasonal-snow cover types. The seasonal snow type classification and data complement were performed using R Studio (ver. 4.2.2.; R Studio, PBC, 2020). Plant functional types (PFTs) were categorized into deciduous broad-leaved (DB_tree), deciduous conifer (DC_tree), and evergreen conifer (EC_tree) trees, as well as deciduous (DE_shrub) and evergreen shrubs (EV_shrub), forbs, graminoids, and bryophytes/lichens. These categories were based

on life form, leaf shape, and phenology, as defined by Williams (2002). Growth stages were simply categorized as mature or seedling, and this classification was applied only to radial growth. Lastly, treatment methods were categorized based on whether the manipulation installed a heating system or not. For decreased snow cover treatments, I divided the studies into two categories: 1) *decreased snow* treatment, which includes experiments that used only shoveling or snow protection roofs, and 2) *decreased snow + warming* treatment, which includes experiments that used a heating system either alone or in combination with shoveling or snow protection roofs to reduce snow cover. Similarly, for increased snow cover treatments, I categorized the studies into: 1) *increased snow* treatment, for experiments that used snow fences or added snow from surrounding areas without additional heating, and 2) *increased snow + warming* treatment, for those using snow fences or added snow in combination with a heating system.

2.3.2 Statistical analysis

To assesses the effects of both decreased and increased snow cover on plant performance and vegetation cover, I used the natural logarithm of the response ratio ($\log_e$RR) as the standardized effect size metric (Hedges et al., 1999). The $\log_e$RR was selected for its ability to stabilize variance and ensure an approximately normal sampling distribution. The $\log_e$RR for each paired observation was calculated as:

$$\log_e RR = \log e \left(\frac{\overline{Xt}}{\overline{Xc}}\right) = \log_e (\overline{Xt}) - \log_e (\overline{Xc}) \quad (1)$$

where $\overline{Xt}$ and $\overline{Xc}$ are the means of plant performance or vegetation cover in snow cover treated and control groups, respectively. The variance associated with each $\log_e$RR was estimated as:

$$v = \frac{{S_t}^2}{n_t \overline{X_t}^2} + \frac{{S_c}^2}{n_c \overline{X_c}^2} \quad (2)$$

where S_t and S_c represent the standard deviation (SD) of the snow cover treated and control groups, respectively. And n_t and n_c denote the sample sizes (n). In the case where SD information was not provided in the papers, it was calculated from the standard error and sample size (n) using the following formula:

$$SD = SE\sqrt{n} \quad (3)$$

The weighting factor (w) of each observation was calculated as follows:

$$w = \frac{1}{v_i + \sigma^2_{pooled}} \quad (4)$$

where v_i is a variance of an individual study and σ^2_{pooled} is the pooled study variance, representing the pooled variance or between-study variance. I used mixed-effect models to estimate the overall weighted effect ($\log_e RR(w)$) for each response variable related to plant performance and vegetation cover. The models incorporated random effects to account for variations both between and within studies. Specifically, random effects were nested within primary studies, ensuring that observations from the same study were not treated as independent.. If the 95% confidence interval (CI) of $\log_e RR(w)$ that did not cross zero, shift in snow cover had a statistically significant effect on plant performance and vegetation cover. The $\log_e RR(w)$ and its 95 % CI were back-transformed as

($e^{logeRR(w)} - 1$) × 100 (%), demonstrating the percentage change. I also used mixed-effects models to test for potential differences across ecosystem types, plant functional types, snow cover types, growth stages, and treatment methods for response variables that included data from five or more primary studies. All statistical analyses were performed in R Studio (ver. 4.2.2.; R Studio, PBC, 2020) using the metafor package (Viechtbauer, 2010), with the rma.mv() function.

2.4 Result

2.4.1 Distribution of sites

Our selection criteria led us to include 54 publications from sites around the globe that experience seasonal snow cover, including North America (n = 22 publications), Europe (n = 33), Asia (n = 4), and Oceana (n = 1; Fig. 2-1). There were no studies or remarkably fewer studies that meet all the criteria conducted in South America, Central Asia, Eastern Europe and Tibetan plateau region. Studies were primarily conducted in tundra (n = 17) and forests (n = 17), followed by grasslands (n = 12), with only a few studies conducted in wetlands (n = 6), shrubland (n = 4), and deserts (n = 2). From the perspective of climatic zones, studies were primarily conducted in polar zone (n = 16), followed by boreal zone (n = 13), cool temperate zone (n = 15), and warm temperate zone (n = 12), with fewer studies in the alpine (n = 4) and arid (n = 3) zones, which include both desert and steppe climate. There was a significantly greater number of experiments included in our meta-analysis that included decreased snow (n = 57) compared to increased snow (n = 22).

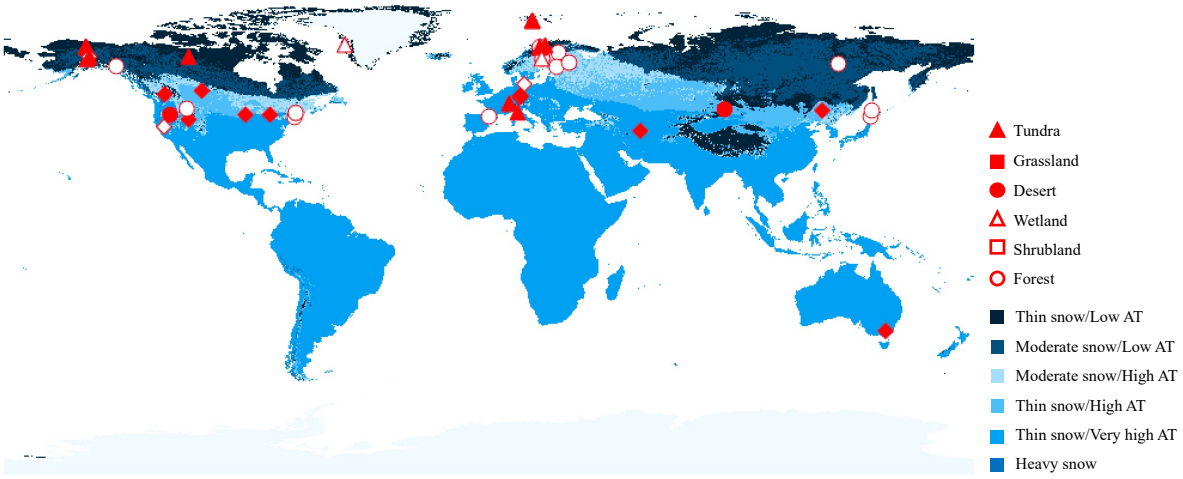


Fig. 2-1 Site locations of all studies included in the meta-analysis. Different shapes indicate each of the ecosystem types and different colors indicate the seasonal snow cover type.

2.4.2 Responses of plant performance and vegetation cover to shifting snow cover

Decreased snow cover significantly decreased survival rate by 46.58% ($P < 0.01$), aboveground biomass by 10.81% ($P < 0.05$) and belowground biomass by 30.40% (Fig. 2-2a, Table 2-S3; $P < 0.01$). Belowground length growth and total biomass decreased by 13.37 and 26.00 %, respectively, in response to decreased snow, however, these responses were not statistically significant ($P = 0.22$ and 0.14, respectively; Fig. 2-2a, Table 2-S3). When snow cover increased, plant performance and vegetation cover tended to increase, except for belowground length growth and belowground biomass, which decreased by 14.66 and 41.93% respectively ($P < 0.05$ and $P < 0.01$, respectively; Fig. 2-2b, Table 2-S3).

2.4.3 Drivers to explain the variation of plant performance and vegetation cover to decreased snow cover

The direction and magnitude of plant performance response to decreased snow cover varied across ecosystem types, plant functional types, snow cover types, and treatment methods (Fig. 2-3, 2-S1, 2-S2, 2-S3). For example, in response to decreased snow cover, plant survival decreased by 57.87% in tundra ecosystems (Fig. 2-3a, Table 2-S6; $P < 0.001$) and by 69.23% in regions with thin snow cover and low air temperature (Fig. 2-3c, Table 2-S6; $P < 0.001$). Additionally, survival of deciduous shrubs decreased by 55.08% ($P < 0.05$) and evergreen shrubs by 63.65% ($P < 0.01$) in response to decreased snow cover (Fig. 2-3b, Table 2-S6). Survival rates under *decreased snow* treatment decreased by 29.47% ($P < 0.05$) and under *decreased snow + warming* treatment by 81.98% (Fig. 2-5d, Table 2-S6; $P < 0.001$). In response to decreased snow cover, aboveground length or height growth increased by 51.06% in regions with thin snow cover and very high temperature (Fig. 2-3g, Table 2-S8; $P < 0.001$). Aboveground biomass decreased by 6.09% in response to decreased snow cover in tundra ecosystems (Fig. 2-3i, Table 2-S10; $P < 0.01$) and decreased by 12.53% in regions with thin snow cover and high air temperature (Fig. 2-3k, Table 2-S10; $P < 0.05$). In addition, aboveground biomass of deciduous broadleaved trees and deciduous shrubs decreased by 35.35% ($P < 0.05$) and 32% ($P < 0.001$), respectively, in response to decreased snow cover (Fig. 2-3j, Table 2-S10; $P < 0.001$). Aboveground biomass under *decreased snow* treatment decreased by 18.65% (Fig. 2-3l, Table S-S10; $P < 0.01$). Belowground length growth increased by 20.20% in shrubland ecosystems (Fig. 2-S1a, Table S2-12; $P < 0.01$) and 16.68% in regions with thin snow cover and very high air temperature (Fig. 2-S1c, Table 2-S12; $P < 0.05$). Furthermore, belowground length growth decreased by 27.65% under *decreased snow* treatment ($P < 0.001$) and increased by 18.20% under *decreased snow + warming* treatment (Fig. 2-S1d, Table 2-S12; $P < 0.05$). Belowground biomass decreased by 59.69% ($P < 0.001$) and 54.82% ($P < 0.001$) in tundra and desert ecosystems (Fig. 2-S1e, Table 2-S13), and by 59.48% ($P < 0.001$) and 23.56% ($P < 0.05$) in regions with thin snow cover and low and

high air temperatures (Fig. 2-S1g, Table 2-S13) in response to decreased snow. Also, belowground biomass of forbs decreased by 35.82% in response to decreased snow cover ($P < 0.01$, Table 2-S13, n =12). Radial growth in forest ecosystems declined by 6.75% in response to decreased snow cover (Fig. 2-S2a, Table 2-S14; $P < 0.05$). Radial growth in evergreen conifer trees decreased by 9.97% when snow cover decreased ($P < 0.001$); however, no significant response was observed in deciduous broadleaved trees (Fig. 2-S2b, Table 2-S14; $P > 0.05$).

In response to decreased snow cover, vegetation cover in forest ecosystems decreased by 38.93% (Fig. 2-S3a, Table 2-S15; $P < 0.001$), and by 23.39% ($P < 0.05$) and 29.73 % ($P < 0.05$) in regions with thin and moderate snow cover and high air temperature (Fig. 2-S3c, Table 2-S15). Conversely, vegetation cover in wetland ecosystems increased by 85.61% in response to decreased snow cover (Fig. 2-S3a, Table 2-S15; $P < 0.001$) and by 73.61% in regions with thin snow cover and low air temperature (Fig. 2-S3c, Table 2-S15; $P < 0.01$). Additionally, vegetation cover of deciduous shrubs decreased by 35.18% in response to decreased snow cover (Fig. 2-S3b, Table 2-S15; $P < 0.05$).

2.4.4 Drivers to explain the variation of plant performance and vegetation cover to increased snow cover

Survival rates, aboveground length or height growth, and aboveground biomass exhibited positive responses to increased snow cover across various ecosystem types, plant functional types, snow cover types, and treatment methods (Fig. 2-4). However, only a few responses were statistically significant. For example, survival rates of evergreen conifer trees increased by 95.46% in response to increased snow (Fig. 2-4b, Table 2-S7; $P < 0.01$). Additionally, aboveground length or height growth increased by 64.61% in wetland ecosystems (Fig. 2-4e, Table 2-S9; $P < 0.05$) and by 62.63% in regions with thin snow cover and high air temperatures (Fig. 2-4g, Table S2-9; $P < 0.05$) in response to increased snow cover. Furthermore, both aboveground length or height growth and aboveground

biomass in graminoids increased by 69.35% and by 53.65% in response to increased snow (Fig. 2-4f, j, Table 2-S11; $P < 0.001$ and $P < 0.01$).

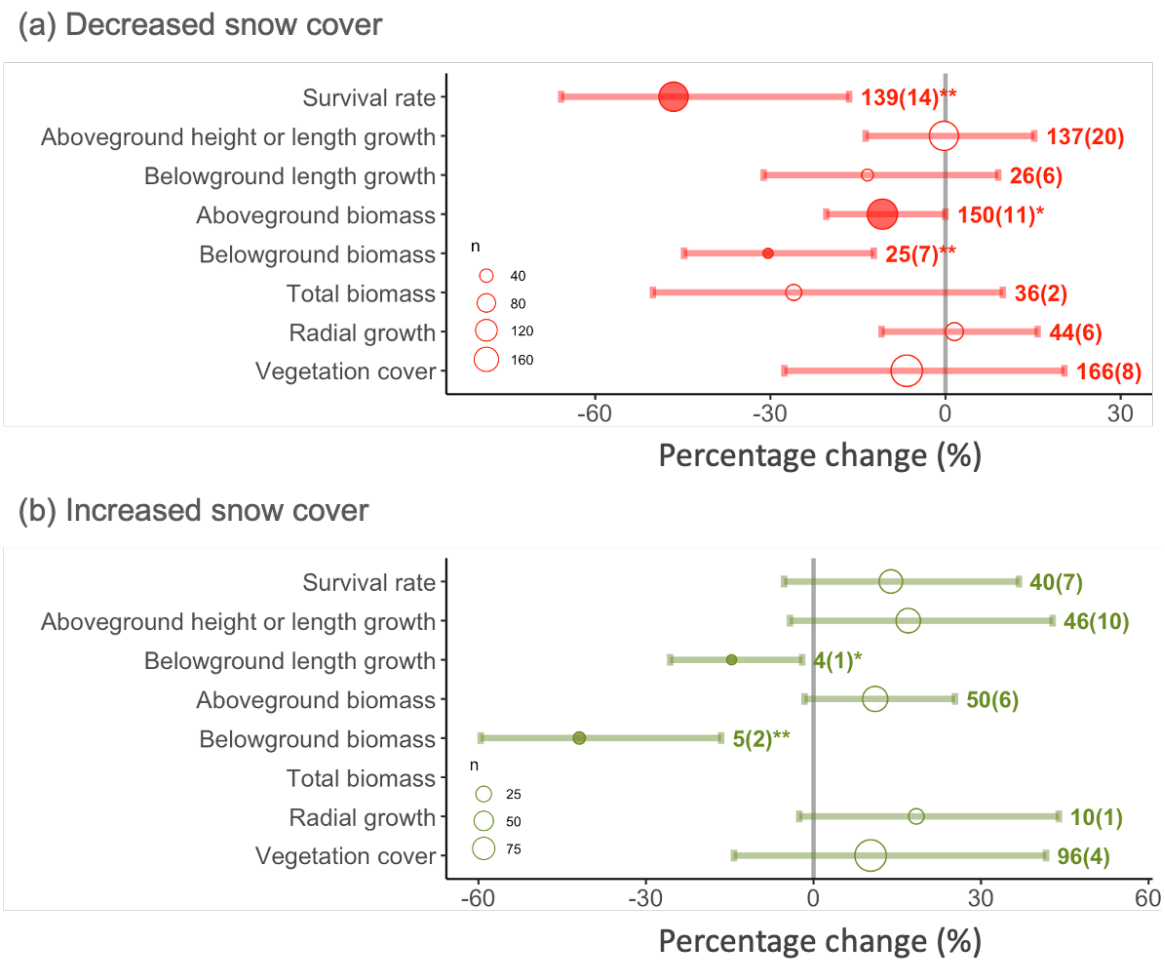


Fig. 2-2 Weighted response ratio of the plant performance and vegetation cover to both (a) decreased and (b) increased snow cover. Weighted effect size (logeRR(w)) of the plant response variables to decreased and increased snow cover. The 95% confidence intervals (CI) are shown. The 95% CI that does not cross zero indicates that decreased or increased snow cover have a statistically significant effect on the response variable (filled circles). The samples number of for each variable are shown next to the bar, with the number of studies shown in parentheses.

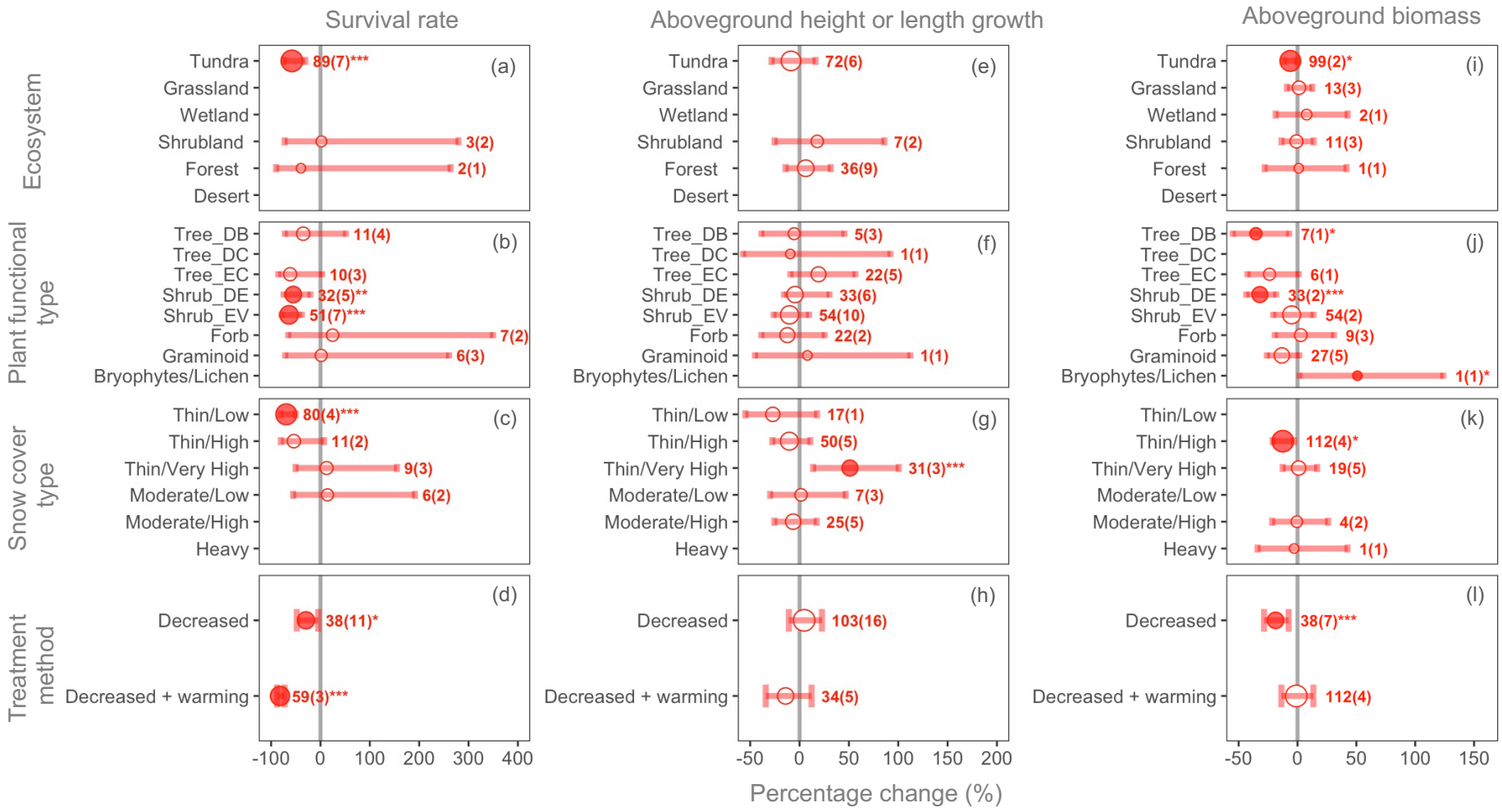

Survival rate
Aboveground height or length growth
Aboveground biomass
Ecosystem
Plant functional type
Snow cover type
Treatment method
Tundra
Grassland
Wetland
Shrubland
Forest
Desert
Tree_DB
Tree_DC
Tree_EC
Shrub_DE
Shrub_EV
Forb
Graminoid
Bryophytes/Lichen
Thin/Low
Thin/High
Thin/Very High
Moderate/Low
Moderate/High
Heavy
Decreased
Decreased + warming
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(i)
(j)
(k)
(l)
89(7)***
3(2)
2(1)
11(4)
10(3)
32(5)**
51(7)***
7(2)
6(3)
80(4)***
11(2)
9(3)
6(2)
38(11)*
59(3)***
72(6)
7(2)
36(9)
5(3)
1(1)
22(5)
33(6)
54(10)
22(2)
1(1)
17(1)
50(5)
31(3)***
7(3)
25(5)
103(16)
34(5)
99(2)*
13(3)
2(1)
11(3)
1(1)
7(1)*
6(1)
33(2)***
54(2)
9(3)
27(5)
1(1)*
112(4)*
19(5)
4(2)
1(1)
38(7)***
112(4)
-100
0
100
200
300
400
-50
0
50
100
150
200
Percentage change (%)

Fig. 2-3 Weighted response ratio of the plant ecological responses in response to decreased snow cover.

Weighted effect size (logeRR(w)) of the plant (a-d) survival, (e-h) aboveground length or height growth, and (i-l) aboveground biomass in the different (a, e, i) ecosystem types, (b, f, j) plant functional types, and (c, g, k) snow cover types, (d, h, l) treatment methods. The 95% confidence intervals (CI) are shown. 95% CI ranges that do not cross zero indicates that decreased snow cover has a statistically significant effect on the response variable (indicated with *). The numbers and numbers in parentheses represent sample sizes and study counts, respectively. In plant functional type, DB, DC, EC, DE and EV refer to deciduous broadleaved, deciduous conifer, evergreen conifer, evergreen, and deciduous, respectively. For snow cover types, Thin, Moderate, and Heavy indicate snow depth, while Low, High, and Vary High refer to air temperature conditions during dormant season. For treatment methods, *Decreased* refers to decreased snow only, and *Decreased + warming* refers to a combination of decreased snow and warming treatments.

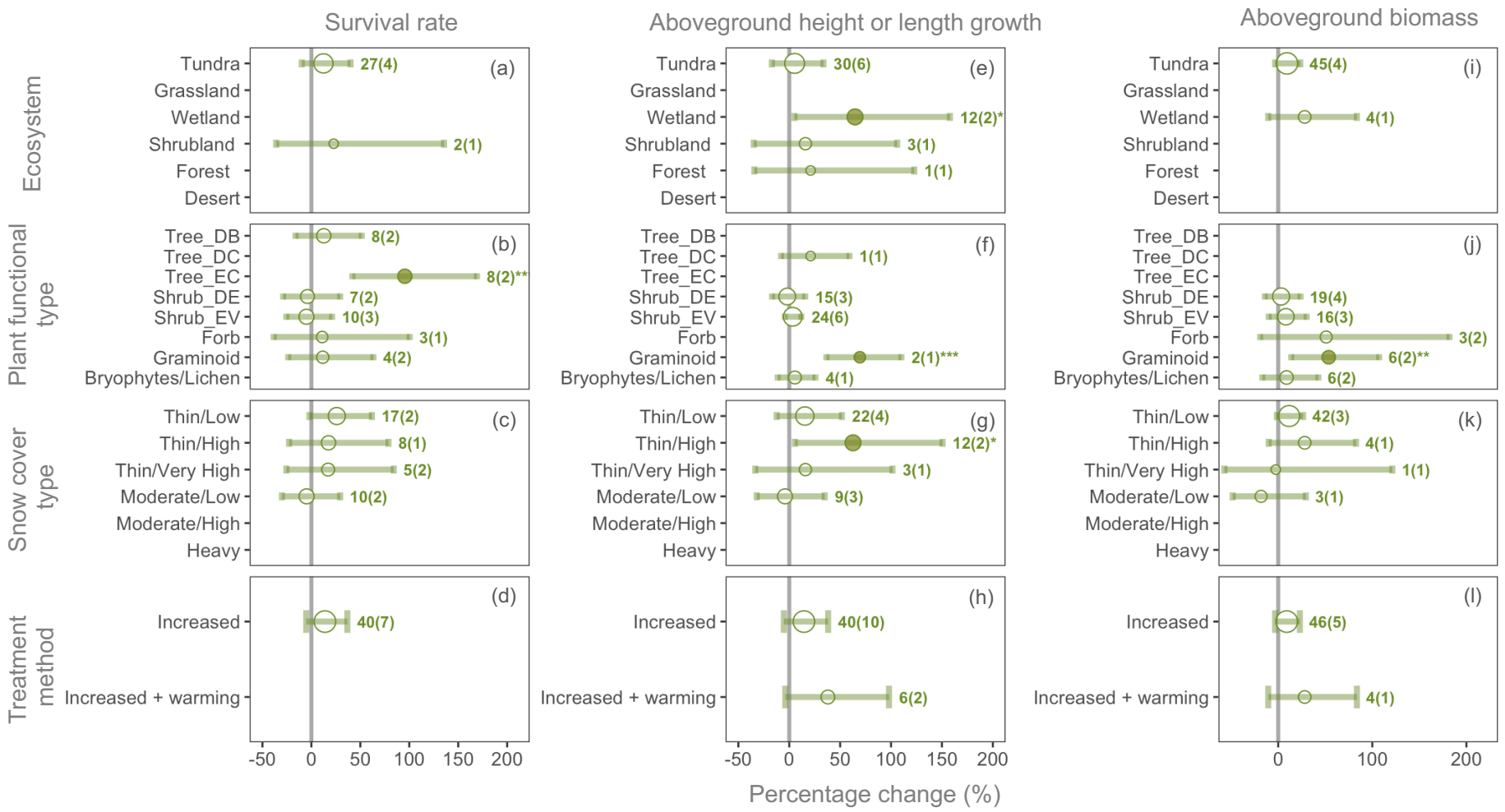

Survival rate
Aboveground height or length growth
Aboveground biomass
Ecosystem
Plant functional type
Snow cover type
Treatment method
Tundra
Grassland
Wetland
Shrubland
Forest
Desert
Tree_DB
Tree_DC
Tree_EC
Shrub_DE
Shrub_EV
Forb
Graminoid
Bryophytes/Lichen
Thin/Low
Thin/High
Thin/Very High
Moderate/Low
Moderate/High
Heavy
Increased
Increased + warming
27(4)
2(1)
8(2)
8(2)**
7(2)
10(3)
3(1)
4(2)
17(2)
8(1)
5(2)
10(2)
40(7)
30(6)
12(2)*
3(1)
1(1)
1(1)
15(3)
24(6)
2(1)***
4(1)
22(4)
12(2)*
3(1)
9(3)
40(10)
6(2)
45(4)
4(1)
19(4)
16(3)
3(2)
6(2)**
6(2)
42(3)
4(1)
1(1)
3(1)
46(5)
4(1)
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(i)
(j)
(k)
(l)
-50
0
50
100
150
200
Percentage change (%)

Fig. 2-4 Weighted response ratio of the plant response variables in response to increased snow conditions.

Weighted effect size (logeRR(w)) of the plant (a-d) survival, (e-h) aboveground length or height growth, and (i-l) aboveground biomass in the different (a, e, i) ecosystem types, (b, f, j) plant functional types, and (c, g, k) snow cover types, (d, h, l) treatment methods. The 95% confidence intervals (CI) are shown. 95% CI ranges that do not cross zero indicates that increased snow cover has a statistically significant effect on the response variable (indicated with *). The numbers and numbers in parentheses represent sample sizes and study counts, respectively. In plant functional type, DB, DC, EC, DE, and EV refer to deciduous broadleaved, deciduous conifer, evergreen conifer, evergreen, and deciduous, respectively. For snow cover types, Thin, Moderate, and Heavy indicate snow depth, while Low, High, and Vary High refer to air temperature conditions during dormant season. For treatment methods, *Increased* refers to increased snow only, and *Increased + warming* refers to a combination of increased snow and warming treatments.

2.5 Discussion

2.5.1 General responses of plant performance and vegetation cover to shifting snow cover

In this study, I quantitatively analyzed the effects of shifting snow cover on plant performances and vegetation cover in the snowy regions. I found that survival rate, aboveground and belowground biomass decreased significantly in response to decreased snow cover (Fig. 2-2a, Table 2-S3). Among all the response variables, survival rate exhibited the most significant decrease to decreased snow cover (Fig. 2-2a). Decreased snow cover, in combination with cold air temperatures, can intensify cold and drought stress, leading to increased plant mortality (Martz et al. 2016; Domisch et al. 2018). Interestingly, while aboveground biomass responded negatively to decreased snow cover, the responses of aboveground height or length growth were mixed, exhibiting both positive and negative trends (Fig. 2-2a). These results suggest a potential change in plant architecture, aligning with a previous study that indicated changes in plant architecture under shifting snow cover due to differing responses between primary and secondary growth (Addis and Bret-Harte 2019). For increased snow cover, plant performance and vegetation cover exhibited the trend toward increase as expected, except for belowground length growth and biomass, which showed significant decreases (Fig. 2-2b, Table 2-S3). The increased snow elevates soil moisture, so that plants no longer need to invest as much in roots, resulting in reduced root biomass and increased aboveground growth instead (Murphy et al. 2009; Yin et al. 2020). Also, increased snow cover and delayed snowmelt can increase plant-available nitrogen in the soil (Schimel 2004). As a result, plants may prioritize aboveground biomass growth to maximize their photosynthetic potential in response to reduced light availability.

2.5.2 Regions, ecosystems, and plant functional types that exhibit significant negative responses to decreased snow cover

In regions with thin snow cover, the effect of decreased snow cover on plant responses may shift from negative in cold climates—due to the loss of insulation—to more positive in warmer climates, where it can lead to a longer growing season (Fig. 2-3c, g, k, Fig. 2-S1c). In regions with thin snow cover and low air temperatures, reduced snow cover—especially a shorter snow cover duration, due to either delayed establishment or earlier snowmelt—can increase soil freeze-thaw cycles (Krab et al. 2017; Zhao et al. 2022). While a longer growing season from earlier snowmelt may potentially enhance plant growth (Myers-Smith et al. 2015; Ackerman et al. 2017), this positive effect is generally outweighed by increased cold and drought stress in regions with thin snow and low air temperature (Larsen et al. 2002; Callaghan et al. 2011). On the other hand, in regions with thin snow cover and relatively high air temperatures, the risk of cold damage may remain low even when snow cover decreases. Consequently, earlier snowmelt may lead to a longer growing season, potentially benefiting plant growth as I observed (Fig. 2-3g, Fig. 2-S1c).

Across ecosystem types, remarkable decreases in plant survival rate and above- and belowground biomass were detected in tundra ecosystem (Fig. 2-3a, i, Fig. 2-S1e), which largely overlaps with the region with thin snow cover and low air temperature. Radial growth and vegetation cover in forest ecosystems also exhibited clear decreases in response to decreased snow cover (Fig. S2-2a, Fig. 2-S3a). In forest ecosystems, snow plays an important role in protecting plant organs from cold damages. A reduction in snow cover can lead to cold damage to both aboveground and belowground organs (Blume-Werry et al. 2016; Sanders-DeMott et al. 2017), which may negatively affect plant growth and vegetation cover in the following spring. In addition, reduced snow cover is known to increase herbivory pressure by large mammals (Pedersen et al. 2021; Holtan et al. 2023), which may also contribute to a decrease in vegetation cover.

Across plant functional types, the significant decrease in plant survival, aboveground biomass and vegetation cover were mainly found in woody species, tree seedings and shrubs (Fig. 2-3b, j, Fig. 2-S3b). Woody species form resting buds near or above the soil surface, sometimes even above

snowpacks (Raunkiær 1934). Therefore, their winter buds would be exposed directly to frost and feeding damages when snow cover decreased. Meanwhile, herbaceous plants usually form their resting buds belowground under unfavorable conditions so that they can alleviate the frost stresses caused by decreased snow cover compared with the woody species (Lubbe et al. 2021). The negative responses of shrubs observed in this study contrast with previous findings, which reported positive effects of rising growing season temperatures on shrub performance and coverage (Walker et al. 2006; Myers-Smith et al. 2011), contributing to the ongoing shrubification of tundra ecosystems. These results highlight the need to further investigate the nonlinear effects of both winter and summer warming on shrub performance and coverage, as well as their subsequent impacts on the future structure of plant communities, ecosystem processes, and functions within tundra ecosystems.

2.5.3 *Treatment method*

Since the heating treatment can mitigate soil freeze-thaw cycles typically caused by reduced snow insulation, I expected positive plant responses to decreased snow cover under the combination of snow removal and heating treatment. However, for some plant performance parameters, the combination of snow removal and heating treatment showed a greater decrease in response to decreased snow cover compared to the snow removal treatment alone (Fig. 2-3d, h, Fig. 2-S1h). Under certain temperature conditions, the heating treatment could cause the soil to thaw during the day and refreeze at night, while the soil would remain frozen without the heating treatment (Ueda et al. 2013). Therefore, the heating treatment can increase the frequency of soil freeze-thaw cycles and lead to the establishment of ice encasement, which consequently has a negative effect on plant responses, as observed in this analysis and in previous studies (Höglind et al. 2010; Martz et al. 2016). Due to the lack of sufficient supporting data, such as the number of soil freeze-thaw events, I was unable to fully explore how treatment methods influence plant responses to shifting snow cover. Furthermore, it needs to be noted that the amount of snow added or removed from the treatment plots

varied considerably across studies, with snow addition ranging from approximately 10 to 130 cm depth and snow removal ranging from approximately 1 to 30 cm depth (see supplement datasheet). These substantial differences in snow manipulation may simply reflect local variation in climate change scenarios, but they could also stem from differing experimental methodologies. As difference in snow depth (calculated as snow depth in control minus snow depth in treatment; Fig. S2-4) can significantly influence the effect size of survival rate in response to decreased snow cover, the variation in the amount of added or removed snow is essential for accurately interpreting ecological outcomes and predicting how snow dynamics will influence ecosystems under future climate conditions (Rixen et al. 2022). Lastly, although changes in snow cover depth and duration may follow similar trajectories, their impacts on plant performance and vegetation cover may differ. Slatyer et al. (2022) found that reduced snow depth generally increased plant mortality, injury, and damage. They also found that earlier snowmelt had both positive and negative effects, suggesting that its impact on plant responses could largely depend on spring climatic conditions, such as cold spells. Therefore, it is crucial to account for the differences between changes in snow cover depth and duration when assessing the ecological consequences of shifting snow regimes.

2.5.4 Suggestions for future research

In recent years, a growing body of research has focused on plant responses to shifting snow cover (Sanders-DeMott and Templer 2017), enabling us to quantify these responses across regions, ecosystems, and plant functional types, and to identify those particularly vulnerable to decreased snow cover (Table 2-1). Here, I addressed several knowledge gaps to enhance our understanding of plant performance and vegetation cover responses to shifting snow regimes, while also identifying aspects that remain unclear. First, studies on how plant performance and vegetation cover respond to increased snow cover remained limited. Although I observed a general positive response pattern in plant performance and vegetation cover to increased snow cover, this could be driven by the

dominance of data from tundra ecosystems and regions with thin snow cover and cold winter temperatures (Fig. 2-4). The results may differ if studies from regions with higher winter temperatures and shorter baseline snow cover durations were included. Second, more research is needed to assess the long-term trends (Kreyling 2010). A previous study found significantly smaller negative effects of decreased snow on vegetation cover, fine root biomass, and shoot growth were observed in long-term manipulations compared to short-term ones (Blume-Werry et al. 2016). Therefore, further long-term manipulation studies are necessary to evaluate plant performance and vegetation cover to shifting snow cover for realistic predictions, especially in ecosystems dominated by long-lived species. Third, research that pays particular attention to the heterogeneities within ecosystems is also needed. As for the tundra ecosystem, several studies have already suggested that microtopography or microclimate (Niittynen et al. 2020; Heijmans et al. 2022), vegetation types or domain species (Addis and Bret-Harte 2019; Komarov and Sturm 2023), or even the presence of periglacial microtopography unique to the tundra ecosystem (Krab et al. 2017) mediate the impact of shifting snow cover on plant survival and growth. Similar situations could be expected in other types of ecosystems, especially in forest ecosystems with probably the highest environmental heterogeneity due to their complex three-dimensional vegetation structures (Muscolo et al. 2014; De Frenne et al. 2021). The investigation of these intricate environmental dynamics and their associated plant responses within ecosystems is crucial for advancing our comprehension and predictive capacity regarding biodiversity and ecological functions in the face of climate change across diverse ecosystem types (Zellweger et al. 2020; De Frenne et al. 2021). Lastly, more research is still needed to investigate the linear or non-linear response between above- and below-ground plant growth under both increased and decreased snow cover. According to our meta-analysis, the above- and belowground plant responses to a shifting snow cover were inconsistent with increased snow cover, namely increases in aboveground growth and reduction of belowground growth (Fig. 2-2b). As previous studies suggested, climate warming and its shifting snow regimens could potentially lead to different responses between the above- and belowground plant parts, such that plant aboveground would change their phenology or growth

immediately while plant belowground would remain unchanged (Blume-Werry et al. 2017; Liu et al. 2022). The non-linear responses between above- and belowground plant performances can change carbon allocation which could affect carbon sequestration and climate resilience (Liu et al. 2021).

Table 2-1 Regions (a), ecosystems (b), and plant functional types (c) that exhibit significant negative responses to decreased snow cover

(a) Vulnerable Regions	
Survival	Thin snow/Low AT, Thin snow/High AT
Growth	Thin snow/High AT
Biomass	Thin snow/Low AT, Thin snow/High AT
Vegetation Cover	Thin snow/High AT
(b) Vulnerable Ecosystems	
Survival	Tundra
Growth	Desert*, Forest
Biomass	Tundra, Desert*
Vegetation Cover	Forest
(c) Vulnerable Plant Function Types	
Survival	Shrub_DE, Shrub_EV
Growth	Tree_EC
Biomass	Shrub_DE, Tree_DB**, Forb
Vegetation Cover	Shrub_DE

In plant functional types, deciduous shrubs, evergreen shrubs, evergreen conifer trees, and deciduous broadleaved trees are abbreviated as Shrub_DE, Shrub_EV, Tree_EC, and Tree_DB, respectively.

* Only a small sample size for desert (n=2 sites only).

**Biomass of Tree_DE included data from seedlings.

2.6 Conclusion

In this study, I conducted a quantitative meta-analysis to examine the responses of plant performance and vegetation cover to shifting snow cover. Our findings revealed that decreased snow cover generally had significant negative effects on plant survival rate, aboveground biomass, and belowground biomass, with survival rate showing the most pronounced decline. In contrast, increased snow tended to have positive effects on plant performance and vegetation cover, except for belowground length growth and biomass, which exhibited significant decreases. This study also reveals the particularly vulnerable regions, ecosystems, and plant functional types when snow cover decreases, which includes regions with thin snow cover and low air temperature, tundra and forest ecosystems, and woody species. Through this study, I also identified key knowledge gaps in the current understanding of plant responses to snow cover changes. Further case studies are needed to explore plant performance and vegetation cover in response to increased snow cover across diverse ecosystems and regions with varying climatic condition, particularly in ecosystems with taller and denser vegetation, as well as in relatively warmer climate regions, to reduce potential biases. Moreover, future research should assess long-term trends in plant performance and vegetation cover, as well as to examine non-linear responses between above- and belowground variables and their impact on carbon sequestration and climate resilience.

2.7 Appendix

2.7.1 Supplemental information (*SI*)

2.7.1.1 Criteria for data screening (SI1)

For criteria 1, two studies were conducted in a laboratory setting (Domisch et al. 2018, 2019). The two laboratory experiments were conducted in a growth chamber with tree seedlings maintained at a stable air temperature. Control pots were covered with a 10 cm snow layer, completely covering the seedlings in them, while pots in the snow removal treatment had no snow. In field-based snow manipulation studies, various experimental methods were employed. To decrease snow cover, snow removal included manual methods such as shoveling, soil heating, canopy heating, and the installation of snow roofs. Conversely, to increase snow cover, techniques such snow fences, manually adding snow, and using open-top chamber systems were applied. Following Criteria 2, studies examining elevational gradients and comparing snowbeds with wind-exposed areas in mountain regions, or studies that recorded responses over multiple years at the same location where snow conditions differed, were not included, except for those where a clear control was indicated.

2.7.1.2 Classification of climatic zone (SI2)

The climatic zones were divided into polar, boreal, cool temperate, warm temperate, and arid zones (which include both desert and steppe) using the latitude and longitude data extracted from each study and the World Maps of the Köppen-Geiger Climate Classification (The World Bank, datacatalog.worldbank.org/search/dataset/0042325; accessed February 2023). Since the Köppen-Geiger Climate Classification system generally demonstrates lowland zones only and loses accuracy when it comes to high elevation sites (Kottek et al. 2006), I classified some studies as alpine zone when publications clearly described a site as being in an alpine region. The climatic zone classification was performed using QGIS except those classified as alpine zone (QGIS Geographic

Information System, QGIS Association, www.qgis.org, 2022).

2.7.1.3 Shifts in snow cover depth and duration (SI3)

Changes in winter snow depth and duration generally occur consistently, with both snow depth and duration often increasing or decreasing simultaneously (Hayhoe et al. 2007; Stewart 2009; Notaro et al. 2014). However, changes in snow depth and duration may not always align, leading to different ecological effects on plants. For example, snow depth can decrease due to rain-on-snow events, which causes ice encasement and results in no change in the overall snowpack duration compared to control conditions (Martz et al. 2016). It is also possible that snow depth increases due to rising temperatures and shifting precipitation patterns, however, overall snow duration might remain unchanged because of warmer spring temperatures. Among the 54 studies used in our meta-analysis, all snow manipulation experiments consistently led to either a decrease in snow cover depth *and* duration or an increase in both. Therefore, our analysis was designed to examine how plant performance and vegetation cover respond to shifts in snow cover, considering both depth and duration of snow.

2.7.1.4 Definitions of plant performance and vegetation cover (SI4)

Survival was calculated as a percentage, not as binary data. It is also important to note that the death of woody plants, especially shrubs, does not necessarily imply the death of the entire plant, but may only involve shoot mortality (e.g., Bokhorst et al. 2011; Martz et al. 2016; Saccone et al. 2017). Growth includes aboveground height or length growth (e.g., stem or shoot), belowground length growth (e.g., root or rhizome), and radial growth (e.g., stem or trunk) obtained from both one-time and repeated measurements. Biomass includes aboveground, belowground, and total biomass. Lastly, vegetation cover refers to vegetation abundance or relative abundance. Further explanation for each variable can be found in Table S2-1.

2.7.2 Supplemental figures

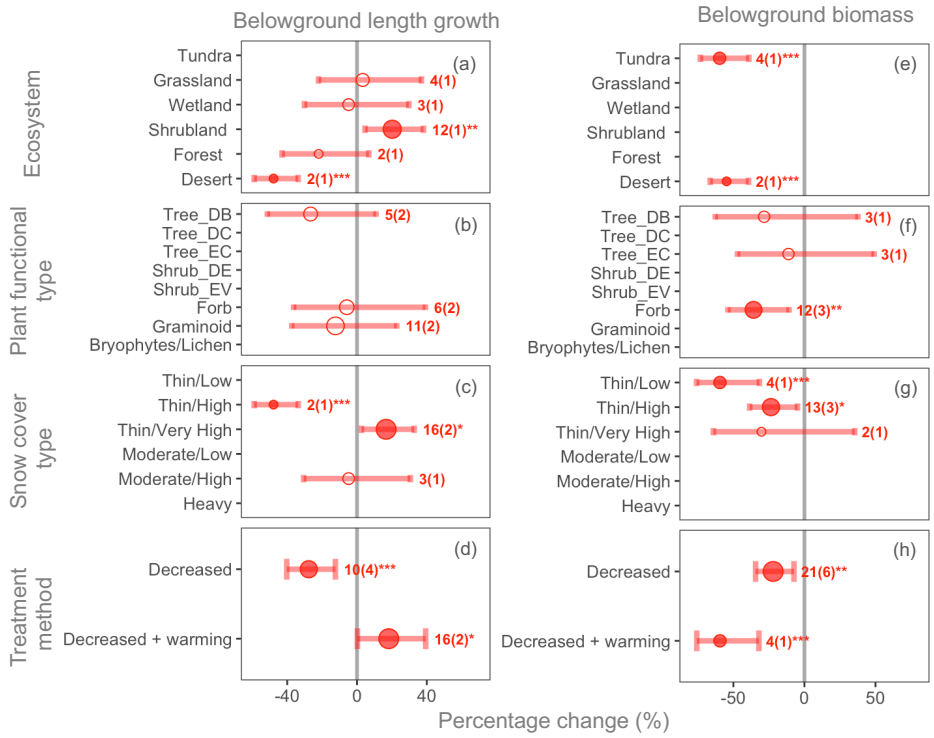


Fig. 2-S1 Weighted response ratio of the plant response variables in response to decreased snow cover. Weighted effect size ($\log_e$RR(w)) of the plant (a-d) belowground length growth and (e-h) belowground biomass in the different (a, e) ecosystem types, (b, f) plant functional types, (c, g) snow cover types, and (d, h) treatment methods. The 95% confidence intervals (CI) are shown. 95% CI ranges that do not cross zero indicates that decreased snow cover has a statistically significant effect on the response variable (indicated with *). The numbers and numbers in parentheses represent sample sizes and study counts, respectively. In plant functional type, DB, DC, EC, DE, and EV refer to deciduous broadleaved, deciduous conifer, evergreen conifer, evergreen, and deciduous, respectively. For snow cover types, Thin, Moderate, and Heavy indicate snow depth, while Low, High, and Vary High refer to air temperature conditions during dormant season. For treatment methods, *Decreased* refers to decreased snow only, and *Decreased + warming* refers to a combination of decreased snow and warming treatments.

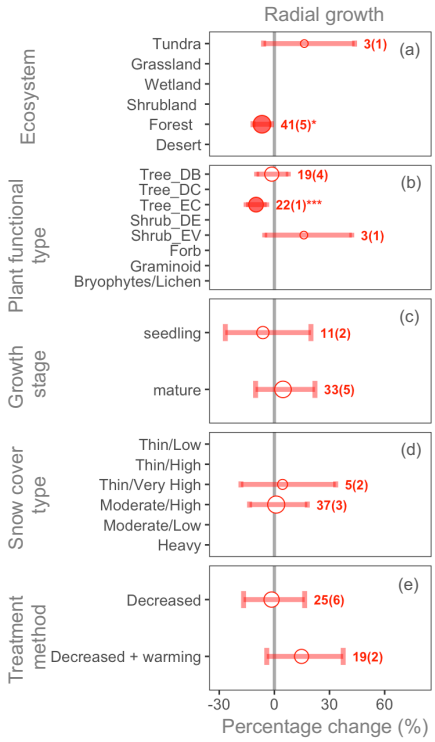


Fig. 2-S2 Weighted response ratio of the plant cover rate in response to increased snow cover. Weighted effect size ($\log_e RR(w)$) of the (a-e) plant radial growth in the different (a) ecosystem types, (b) plant functional types, (c) growth stages, (d) snow cover types, and (e) treatment methods. The 95% confidence intervals (CI) are shown. 95% CI ranges that do not cross zero indicates that decreased snow cover has a statistically significant effect on the response variable (indicated with *). The numbers and numbers in parentheses represent sample sizes and study counts, respectively. In plant functional type, DB, DC, EC, DE, and EV refer to deciduous broadleaved, deciduous conifer, evergreen conifer, evergreen, and deciduous, respectively. For snow cover types, Thin, Moderate, and Heavy indicate snow depth, while Low, High, and Vary High refer to air temperature conditions during dormant season. For treatment methods, *Decreased* refers to decreased snow only, and *Decreased + warming* refers to a combination of decreased snow and warming treatments.

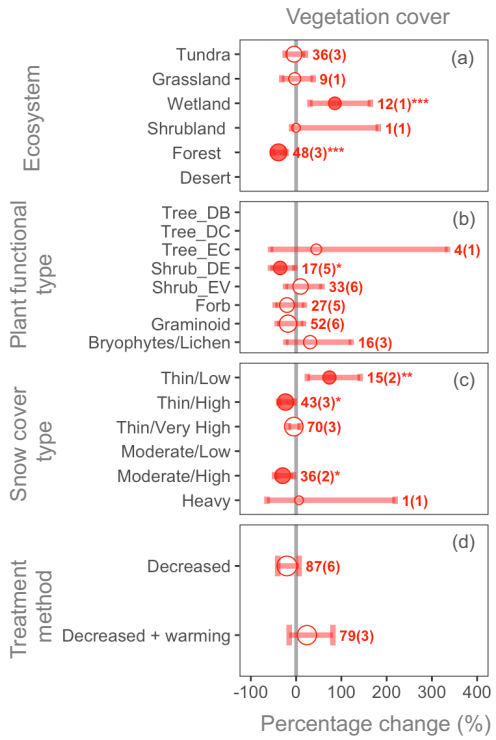


Fig. 2-S3 Weighted response ratio of plant radial growth in response to decreased snow cover. Weighted effect size ($\log_e RR(w)$) of the (a-e) vegetation cover in the different (a) ecosystem types, (b) plant functional types, (c) snow cover types, and (d) treatment methods. The 95% confidence intervals (CI) are shown. 95% CI ranges that do not cross zero indicates that decreased snow cover has a statistically significant effect on the response variable (indicated with *). The numbers and numbers in parentheses represent sample sizes and study counts, respectively. In plant functional type, DB, DC, EC, DE, and EV refer to deciduous broadleaved, deciduous conifer, evergreen conifer, evergreen, and deciduous, respectively. For snow cover types, Thin, Moderate, and Heavy indicate snow depth, while Low, High, and Vary High refer to air temperature conditions during dormant season. For treatment methods, *Decreased* refers to decreased snow only, and *Decreased + warming* refers to a combination of decreased snow and warming treatments.

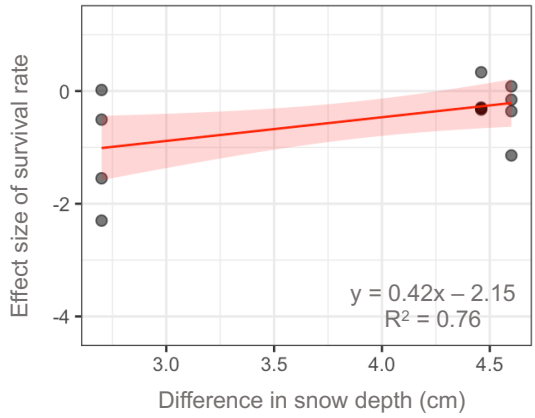


Fig. 2-S4 Relationship between change in snow depth (calculated as snow depth in control plot minus snow depth in treatment plot) and effect size of survival rate in response to decreased snow cover.

2.7.3 Supplemental tables

Table 2-S1. Definition of response variables

Response variables	
Survival (Individual plants)	Overwinter survival rate, survival rate over the subsequent growing season
Growth (Individual plant)	Rate of aboveground height or length, belowground length, or diameter change in the subsequent growing season
Biomass (Individual plant)	Rate of aboveground, belowground, and total biomass change in the subsequent growing season
Vegetation cover (Population)	Abundance or relative abundance measured during the snow-free period

Table 2-S2. Definition of moderator variables

Subgroup		Description
Snow Cover Type	Thin snow with low air temperature	Low air temperature, low precipitation, high wind speed. Snow depth is 0.2-0.8 m and CDM is higher than 125 ℃. Snowdrifts as exception range from 1 to over 8 m in depth.
	Moderate snow with low air temperature	Low air temperature, low precipitation, low wind speed. Snow depth is 0.3-1.3 m, up to 1.5m for heavy winters. CDM is higher than 125 ℃.
	Moderate snow with high air temperature	High air temperature, low precipitation, low wind speed. Snow depth is 0.5-3.0 m. CDM is lower than 125 ℃ and higher than 61 ℃
	Thin snow with high air temperature	High air temperature, low precipitation, high wind speed. Snow depth ranging from around 0.3 to more than 1 m outside the snowdrifts. CDM is lower than 125 ℃ and higher than 61 ℃.
	Heavy snow	High air temperature, high precipitation, both low and high wind speed. Snow depth ranges up to 8 m deep, with 2 m a valid average value.
	Thin snow/ no snow with very high air temperature	Very high air temperature, also include no snow area and only the snowfall from a single storm. Snow depth ranges from few cm to 1m and CDM is lower than 61 ℃.

CDM (cooling degree month) is calculated as the monthly mean air temperature approximately 2 m above the ground from the critical or threshold air temperature (10℃), only if monthly mean air temperature is higher than the critical or threshold air temperature. Snow cover type classified following the definition used in Sturm and Liston 2021.

Table 2-S3. Basic information of the study sites

Predictor variables	Unit	Range	Median	Mean (SD)
Mean annual temperature (MAT)	℃	-11.7 – 12.7	3.3	2.7 (5.4)
Annual precipitation (AP)	mm	140 - 2000	548.5	652.4 (381.9)
Latitude	°	-36.9 – 78.2	50.8	54.1 (16.0)
Minimum air temperature (Min AT)	℃	-45.2 - -1.3	-12.9	-14.1 (9.0)
Snow duration	days	38 - 240	195	174.2 (59.0)

SD; standard deviation

Table 2-S4. Weighted response ratios of the plant performance and vegetation cover to shifting snow cover.

	Mean	95 % lower	95 % higher	p value	Sample size	Study number
Decreased snow cover						
Survival rate	**- 0.627**	-1.074	-0.181	**< 0.01**	117	13
Aboveground height/length growth	-0.005	-0.150	0.139	0.941	135	20
Belowground length growth	-0.144	-0.373	0.086	0.117	26	6
Aboveground biomass	**-0.114**	-0.229	-0.000	< 0.05	150	11
Belowground biomass	**-0.362**	-0.594	-0.131	**< 0.01**	25	7
Total biomass	**-0.301**	-0.696	0.094	0.135	36	2
Radial growth	0.015	-0.116	0.147	0.821	44	6
Vegetation cover	-0.069	-0.323	0.185	0.595	166	8
Increased snow cover						
Survival rate	0.130	-0.054	0.313	0.166	40	7
Aboveground height/length growth	0.165	-0.013	0.342	0.070	48	11
Belowground length growth	**-0.159**	-0.297	-0.021	**< 0.05**	4	1
Aboveground biomass	0.105	-0.016	0.226	0.090	50	6
Belowground biomass	-0.544	-0.907	-0.181	**< 0.01**	5	2
Total biomass	-	-	-	-	-	-
Radial growth	0.169	-0.026	0.364	0.090	10	1
Vegetation cover	0.097	-0.154	0.348	0.447	96	4

The 95% confidence intervals (CIs) that do not include zero indicate that the altered snow cover, including depth and duration, have a statistically significant effect on the response variable (P-value < 0.05). These are indicated in bold.

Table 2-S5 Comparison of models for weighted response ratios of plant performance and vegetation cover to shifting snow cover

	Model 1	Model 2
Decreased snow cover		
Survival rate	332.11	1790.60
Aboveground height/length growth	126.58	1110.18
Belowground length growth	34.89	81.52
Aboveground biomass	117.98	460.64
Belowground biomass	39.42	50.42
Total biomass	51.04	111.87
Radial growth	-8.75	-5.60
Vegetation cover	403.04	657.47
Increased snow cover		
Survival rate	62.82	245.28
Aboveground height/length growth	54.29	127.67
Belowground length growth	-2.78	-4.78
Aboveground biomass	54.39	84.62
Belowground biomass	10.90	12.96
Total biomass	-	-
Radial growth	6.82	4.82
Vegetation cover	238.80	302.82

Model 1 account for variations both between and within studies and model 2 excluded within-study variation.

Table 2-S6. Weighted response ratios of the plant survival rate to decreased snow cover in different groups

	Sample size	P value	logeRR(w)	95 % low	95 % high
Ecosystem type					
Tundra	89	< 0.001	-0.865	-1.364	-0.365
Shrubland	3	0.977	0.019	-1.296	1.334
Forest	2	0.582	-0.504	-2.299	1.291
Seasonal snow cover type					
Thin/Low	80	< 0.001	-1.1786	-1.653	-0.704
Thin/High	11	0.072	-0.7753	-1.62	0.069
Thin/Very high	9	0.779	0.1175	-0.701	0.936
Moderate/Low	6	0.781	0.1328	-0.804	1.070
Plant functional type					
Tree_DB	11	0.319	-0.431	-1.279	0.417
Tree_EC	10	0.059	-0.952	-1.940	0.035
Shrub_DE	32	< 0.01	-0.800	-1.374	-0.227
Shrub_EV	51	< 0.001	-1.012	-1.553	-0.471
Forb	7	0.737	0.220	-1.064	1.503
Graminoid	6	0.981	0.015	-1.252	1.282
Snow cover treatment type					
Decreased	38	< 0.05	-0.349	-0.654	-0.045
Decreased + warming	59	< 0.001	-1.714	-2.133	-1.294

$\log_e$RR(w): weighted response ratio; 95% low, 95% high: 95% confidence ratio; p-value: statistical significance of the effect under snow decreasing regime conditions.

Table 2-S7. Weighted response ratio of the plant survival to increased snow cover in different groups

		Sample size	P value	logeRR(w)	95 % low	95 % high
Ecosystem type						
	Tundra	27	0.299	0.117	-0.103	0.337
	Shrubland	2	0.536	0.206	-0.446	0.857
Seasonal snow cover type						
	Thin/Low	17	0.071	0.231	-0.020	0.482
	Thin/High	8	0.451	0.161	-0.258	0.581
	Thin/Very High	5	0.494	0.158	-0.295	0.611
	Moderate/Low	10	0.750	-0.050	-0.358	0.258
Plant functional type						
	Tree_DB	8	0.430	0.119	-0.177	0.415
	Tree_EC	8	< 0.001	0.670	0.350	0.991
	Shrub_DE	7	0.787	-0.041	-0.340	0.258
	Shrub_EV	10	0.677	-0.052	-0.296	0.192
	Forb	3	0.728	0.105	-0.486	0.695
	Graminoid	4	0.571	0.110	-0.271	0.490
Snow cover treatment type						
	Increased	40	0.166	0.130	-0.054	0.313

$\log_e$RR(w): weighted response ratio; 95% low, 95% high: 95% confidence ratio; p-value: statistical significance of the effect under snow increasing regime conditions.

Table 2-S8. Weighted response ratio of the plant aboveground length or height growth to decreased snow cover in different groups

		Sample size	P value	logeRR(w)	95 % low	95 % high
Ecosystem type						
	Tundra	72	0.459	-0.091	-0.333	0.150
	Shrubland	7	0.478	0.165	-0.291	0.620
	Forest	36	0.574	0.061	-0.152	0.275
Seasonal snow cover type						
	Thin/Low	17	0.197	-0.316	-0.795	0.164
	Thin/High	50	0.315	-0.109	-0.322	0.104
	Thin/Very high	31	< 0.001	0.413	0.129	0.696
	Moderate/Low	7	0.935	0.015	-0.353	0.384
	Moderate/High	25	0.562	-0.067	-0.294	0.160
Plant functional type						
	Tree_DB	5	0.797	-0.057	-0.489	0.375
	Tree_DC	1	0.797	-0.098	-0.850	0.653
	Tree_EC	22	0.207	0.176	-0.097	0.449
	Shrub_DE	33	< 0.05	-0.047	-0.171	0.265
	Shrub_EV	54	0.291	-0.107	-0.305	0.091
	Forb	21	0.473	-0.132	-0.490	0.227
	Graminoid	1	0.826	0.076	-0.600	0.753
Snow cover treatment type						
	Decreased	103	0.577	0.045	-0.114	0.205
	Decreased + warming	34	0.265	-0.152	-0.419	0.115

$\log_e$RR(w): weighted response ratio; 95% low, 95% high: 95% confidence ratio; p-value: statistical significance of the effect under snow decreasing regime conditions.

Table 2-S9. Weighted response ratio of the plant aboveground length or height growth to increased snow cover in different groups

		Sample size	P value	logeRR(w)	95 % low	95 % high
Ecosystem type						
	Tundra	30	0.673	0.052	-0.187	0.290
	Wetland	12	< 0.05	0.498	0.050	0.947
	Shrubland	3	0.147	0.616	-0.428	0.723
	Forest	1	0.541	0.190	-0.420	0.801
Seasonal snow cover type						
	Thin/Low	22	0.306	0.143	-0.131	0.417
	Thin/High	12	< 0.05	0.486	0.054	0.919
	Thin/Very High	3	0.602	0.147	-0.406	0.700
	Moderate/Low	9	0.806	-0.043	-0.385	0.299
Plant functional type						
	Tree_DC	1	0.173	0.190	-0.084	0.464
	Shrub_DE	15	0.814	-0.020	-0.186	0.146
	Shrub_EV	24	0.398	0.034	-0.044	0.112
	Graminoid	2	< 0.001	0.527	0.311	0.743
	Bryophytes/Lichen	4	0.542	0.054	-0.120	0.229
Snow cover treatment type						
	Increased	40	0.162	0.135	-0.054	0.324
	Increased + warming	6	0.081	0.322	-0.040	0.683

$\log_e$RR(w): weighted response ratio; 95% low, 95% high: 95% confidence ratio; p-value: statistical significance of the effect under snow increasing regime conditions.

Table 2-S10. Weighted response ratio of the plant aboveground biomass to decreased snow cover in different groups

		Sample size	P value	logeRR(w)	95 % low	95 % high
Ecosystem type						
	Tundra	99	< 0.05	-0.063	-0.123	-0.003
	Grassland	13	0.821	0.012	-0.094	0.118
	Wetland	2	0.602	0.075	-0.206	0.355
	Shrubland	11	0.899	-0.009	-0.146	0.129
	Forest	1	0.951	0.011	-0.327	0.348
Seasonal snow cover type						
	Thin/High	112	< 0.05	-0.134	-0.237	-0.031
	Thin/Very high	19	0.898	0.010	-0.135	0.154
	Moderate/High	4	0.961	-0.006	-0.242	0.231
	Heavy	1	0.879	-0.030	-0.414	0.354
Plant functional type						
	Tree_DB	7	< 0.05	-0.436	-0.799	-0.074
	Tree_EC	6	0.059	-0.271	-0.553	0.010
	Shrub_DE	33	< 0.001	-0.386	-0.571	-0.200
	Shrub_EV	54	0.436	-0.052	-0.232	0.128
	Forb	9	0.822	0.028	-0.215	0.270
	Graminoid	27	0.077	-0.143	-0.301	0.016
	Bryophytes/Lichen	1	< 0.05	0.411	0.017	0.806
Snow cover treatment type						
	Decreased	38	< 0.001	-0.206	-0.334	-0.078
	Decreased + warming	112	0.881	-0.011	-0.147	0.126

$\log_e$RR(w): weighted response ratio; 95% low, 95% high: 95% confidence ratio; p-value: statistical significance of the effect under snow decreasing regime conditions.

Table 2-S11. Weighted response ratio of the plant aboveground biomass to increased snow cover in different groups

		Sample size	P value	logeRR(w)	95 % low	95 % high
Ecosystem type						
	Tundra	45	0.152	0.089	-0.033	0.211
	Wetland	4	0.177	0.248	-0.112	0.608
Seasonal snow cover type						
	Thin/Low	42	0.082	0.110	-0.014	0.235
	Thin/High	4	0.171	0.248	-0.107	0.603
	Thin/Very high	1	0.949	-0.027	-0.849	0.794
	Moderate/Low	3	0.390	-0.201	-0.660	0.258
Plant functional type						
	Shrub_DE	19	0.747	0.030	-0.153	0.213
	Shrub_EV	16	0.265	0.079	-0.106	0.265
	Forb	3	0.196	0.412	-0.213	1.037
	Graminoid	6	< 0.01	0.430	0.130	0.729
	Bryophytes/Lichen	6	0.537	0.085	-0.185	0.355
Snow cover treatment type						
	Increased	46	0.158	0.087	-0.034	0.207
	Increased + warming	4	0.177	0.248	-0.112	0.608

$\log_e$RR(w): weighted response ratio; 95% low, 95% high: 95% confidence ratio; p-value: statistical significance of the effect under snow increasing regime conditions.

Table 2-S12. Weighted response ratio of the plant belowground length growth to decreased snow cover in different groups

		Sample size	P value	logeRR(w)	95 % low	95 % high
Ecosystem type						
	Grassland	4	0.821	0.033	-0.249	0.314
	Wetland	3	0.756	-0.049	-0.358	0.260
	Shrubland	12	< 0.01	0.184	0.045	0.323
	Forest	2	0.121	-0.248	-0.562	0.066
	Desert	2	< 0.001	-0.651	-0.890	-0.411
Seasonal snow cover type						
	Thin/High	2	< 0.001	-0.651	-0.890	-0.411
	Thin/Very High	16	< 0.05	0.154	0.025	0.283
	Moderate/High	3	0.761	-0.049	-0.365	0.267
Plant functional type						
	Tree_DB	5	0.142	-0.309	-0.722	0.104
	Forb	6	0.763	-0.060	-0.451	0.331
	Graminoid	11	0.444	-0.132	-0.469	0.206
Snow cover treatment type						
	Decreased snow	10	< 0.001	-0.324	-0.515	-0.132
	Decreased snow + warming	16	< 0.05	0.167	0.003	0.332

$\log_e$RR(w): weighted response ratio; 95% low, 95% high: 95% confidence ratio; p-value: statistical significance of the effect under snow decreasing regime conditions.

Table 2-S13. Weighted response ratio of the plant belowground biomass to decreased snow cover in different groups

		Sample size	P value	logeRR(w)	95 % low	95 % high
Ecosystem type						
	Tundra	4	< 0.001	-0.909	-1.321	-0.496
	Desert	2	< 0.001	-0.795	-1.090	-0.499
Seasonal snow cover type						
	Thin/Low	4	< 0.001	-0.903	-1.426	-0.381
	Thin/ High	13	< 0.05	-0.269	-0.487	-0.050
	Thin/Very high	2	0.287	-0.360	-1.024	0.303
Plant functional type						
	Tree_DB	3	0.3167	-0.334	-0.988	0.320
	Tree_EC	3	0.6523	-0.119	-0.637	0.399
	Forb	12	< 0.01	-0.444	-0.773	-0.114
Snow cover treatment type						
	Decreased snow	21	< 0.01	-0.249	-0.421	-0.076
	Decreased snow + warming	4	< 0.001	-0.903	-1.419	-0.386

log_eRR(w): weighted response ratio; 95% low, 95% high: 95% confidence ratio; p-value: statistical significance of the effect under snow decreasing regime conditions.

Table 2-S14. Weighted response ratio of the plant radial growth to decreasing snow cover in different groups

		Sample size	P value	logeRR(w)	95 % low	95 % high
Ecosystem type						
	Tundra	3	0.162	0.151	-0.061	0.362
	Forest	41	< 0.05	-0.070	-0.124	-0.016
Seasonal snow cover type						
	Thin/Very High	5	0.727	0.044	-0.201	0.288
	Moderate/High	37	0.900	0.010	-0.145	0.165
Plant functional type						
	Tree_DB	19	0.746	-0.014	-0.102	0.073
	Tree_EC	22	< 0.001	-0.105	-0.167	-0.043
	Shrub_EV	3	0.150	0.149	-0.054	0.351
Snow cover treatment type						
	Decreased	25	0.857	-0.015	-0.183	0.153
	Decreased + warming	19	0.134	0.138	-0.042	0.318
Growth stage						
	Seedling	11	0.607	-0.065	-0.311	0.181
	Mature	33	0.559	0.046	-0.108	0.199

logeRR(w): weighted $\log_e$RR(w): weighted response ratio; 95% low, 95% high: 95% confidence ratio; p-value: statistical significance of the effect under snow decreasing regime conditions.

Table 2-S15. Weighted response ratio of the vegetation cover to decreased snow cover in different groups

		Sample size	P value	logeRR(w)	95 % low	95 % high
Ecosystem						
	Tundra	36	0.698	-0.046	-0.278	0.186
	Grassland	9	0.862	-0.031	-0.381	0.319
	Wetland	12	< 0.001	0.619	0.266	0.971
	Shrubland	1	0.997	-0.002	-0.104	1.035
	Forest	48	< 0.001	-0.493	-0.737	-0.249
Snow cover type						
	Thin/Low	15	< 0.01	0.552	0.221	0.882
	Thin/High	43	< 0.05	-0.267	-0.490	-0.043
	Thin/Very high	70	0.459	-0.052	-0.189	0.085
	Moderate/High	36	< 0.05	-0.353	-0.646	-0.060
	Heavy	1	0.911	0.063	-1.033	1.159
Plant functional type						
	Tree_EC	4	0.512	0.369	-0.832	1.469
	Shrub_DE	17	< 0.05	-0.434	-0.839	-0.028
	Shrub_EV	33	0.611	0.093	-0.266	0.453
	Forb	27	0.263	-0.225	-0.619	0.169
	Graminoid	51	0.266	-0.198	-0.546	0.151
	Bryophytes/Lichen	16	0.316	0.270	-0.257	0.797
Treatment Method						
	Decreased	87	0.126	-0.228	-0.521	0.064
	Decreased + warming	79	0.269	0.214	-0.166	0.595

$\log_e$RR(w): weighted response ratio; 95% low, 95% high: 95% confidence ratio; p-value: statistical significance of the effect under snow decreasing regime conditions.

Table 2-S16. Response ratio of the plant ecological responses to decreasing snow cover in field experiment and in lab setting.

		Sample size	logeRR(w)	95 % low	95 % high	P value
Aboveground height/ length growth						
	field	115	-0.033	-0.115	0.049	0.427
	lab	22	-0.087	-0.215	0.041	0.173
Aboveground biomass						
	field	136	-0.061	-0.114	-0.007	0.026
	lab	13	-0.392	-0.608	-0.176	0.002
Belowground length growth						
	field	23	0.104	-0.112	0.320	0.327
	lab	3	-0.354	-1.253	0.546	0.233
Belowground biomass						
	field	11	-0.549	-0.881	-0.217	0.004
	lab	14	-0.163	-0.455	0.130	0.251

2.7.4 reference used for meta-analysis

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E. Dorrepaal, R. Aerts, J.H.C. Cornelissen, R.S.P. Van Logtestijn, T.V. Callaghan	2006	Sphagnum modifies climate-change impacts on subarctic vascular bog plants	Functional Ecology	20	31-41
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S.Wipf, V. Stoeckli, P. Bebi	2009	Winter climate change in alpine tundra: plant responses to changes in snow depth and snowmelt timing	Climate Change	94	105–121
S. Wipf	2010	Phenology, growth, and fecundity of eight subarctic tundra species in response to snowmelt manipulations	Plant Ecology	207	53-66
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C. Preece, T.V. Callaghan, and G.K. Phoenix	2012	Impacts of winter icing events on the growth, phenology and physiology of sub-arctic dwarf shrubs	Physiologia Plantarum	146	460–472
J. Schuerings, C. Beierkuhnlein, K. Grant, A. Jentsch, A. Malyshev, J. Peñuelas, J. Sardans, and J. Kreyling	2013	Absence of soil frost affects plant-soil interactions in temperate grasslands	Plant and Soil	371	559–572
R. Gerdol, C. Siffi, P. Iacumin, M. Gualmini, and M. Tomaselli	2013	Advanced snowmelt affects vegetative growth and sexual reproduction of Vaccinium myrtillus in a sub-alpine heath	Journal of Vegetation Science	24	569–579

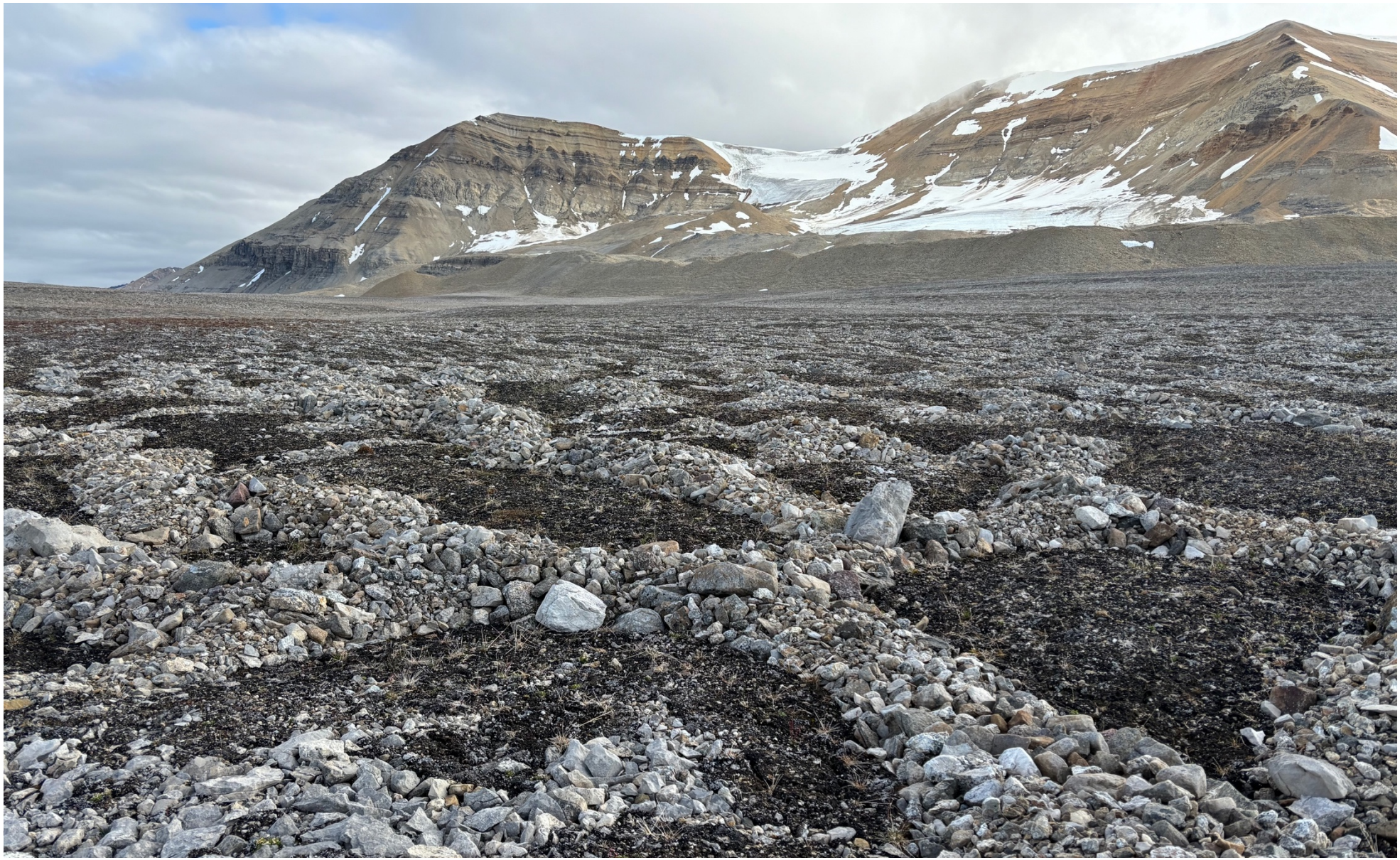
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T.Domisch, F.Martz, T.Repo, and P. Rautio	2018	Let it snow! Winter conditions affect growth of birch seedlings during the following growing season	Tree Physiology	39	544–555
C.T. Christiansen, M.J. Lafreniere, G.H.R. Henry, and P. Grogan	2018	Long-term deepened snow promotes tundra evergreen shrub growth and summertime ecosystem net CO2 gain but reduces soil carbon and nutrient pools	Global Change Biology	24	3508–3525

S. Bokhorst, L. Jaakola, K. Karppinen, G.K. Edvinsen, H.K. Mæhre, J.W. Bjerke	2018	Contrasting survival and physiological responses of sub-Arctic plant types to extreme winter warming and nitrogen	Planta	247	635–648
L. D'Imperio, M.F. Arndal, C.S. Nielsen, B. Elberling, I.K. Schmidt	2018	Fast Responses of Root Dynamics to Increased Snow Deposition and Summer Air Temperature in an Arctic Wetland	frontier in plant science	9	Article 1258
H.A.L. Henry, M.Abedi, C.L. Alados, K.H. Beard, L.H. Fraser, A.Jentsch, J.Kreyling, A. Kulmatiski, E.G. Lamb, W. Sun, M.R. Vankoughnett, S. Venn, C. Werner, I. Beil, I. Blindow, S. Dahlke, M. Dubbert, A. Effinger, H.W. Garris, M. Gartzia, T. Gebauer, M.A.S. Arfin Khan, A.V. Malyshev, J.Morgan, C. Nock, J.P. Paulson, Y. Pueyo, H.J. Stover, and X. Yang	2018	Increased Soil Frost Versus Summer Drought as Drivers of Plant Biomass Responses to Reduced Precipitation: Results from a Globally Coordinated Field Experiment	Ecosystems	21	1432–1444
D.M. Smull, N.Pendleton, A.R. Kleinhesselink, P.B. Adler	2019	Climate change, snow mold and the Bromus tectorum invasion: mixed evidence for release from cold weather pathogens	AoB PLANTS	11	
C.M. Werner, D.J.N. Young, H.D. Safford, T.P. Young	2019	Decreased snowpack and warmer temperatures reduce the negative effects of interspecific competitors on regenerating conifers	Oecologia	191	731–743
F.C. Lubbe and H.A.L. Henry	2019	Plant rhizome positioning in the soil and under litter: Trade-offs of frost T avoidance versus growth	Functional Ecology	41	125500

C.E. Addis and M.S. Bret-Harte	2019	The importance of secondary growth to plant responses to snow in the arctic	Functional Ecology	33	1050–1066
Y. Jinfei, Z. Xiaobing, Y. Benfeng, L. Yonggang, and Z. Yuanming	2020	Species-dependent responses of root growth of herbaceous plants to snow cover changes in a temperate desert, Northwest China	Plant and Soil	459	249–26
C.T. Maher, C.R. Nelson, A.J. Larson	2020	Winter damage is more important than summer temperature for maintaining the krummholz growth form above alpine treeline	Journal of Ecology	108	1074–1087
R.Weigel, H.A.L. Henry, I. Beil, G. Gebauer, G. Jurasinski, M. Klisz, E. van der Maaten, L. Muffler, J. Kreyling	2021	Ecosystem Processes Show Uniform Sensitivity to Winter Soil Temperature Change Across a Gradient from Central to Cold Marginal Stands of a Major Temperate Forest Tree	Ecosystems	24	1545–1560
A. Ósvaldsson, M.K. Chesler, and J.H. Burns	2021	Effects of snow on reproduction of perennial Thalictrum dioicum: Plants survive but seedlings fail to recruit with reduced snow cover	American journal of botany	109	406–418
T.Repo, T.Domisch, J. Kilpeläinen, and H.Mäkinen	2021	Soil frost affects stem diameter growth of Norway spruce with delay	trees	35	761–767
K. Makoto, P.H. Templer, A. Katayama, O. Seki, and K. Takagi	2022	Early snowmelt by an extreme warming event affects understory more than overstory trees in Japanese temperate forests	Ecosphere	13	e4182
R. Shakhmatov, S. Hashiguchi, T.C. Maximov, and A. Sugimoto	2022	Effects of snow manipulation on larch trees in the taiga forest ecosystem in northeastern Siberia	Progress in Earth and Planetary Science	9(3)	1–16





Chapter 3

How does tree canopy modify the response of understory plant to warming winter?

3.1 How tree canopy affects the impact of decreased snow cover on forest floor abiotic conditions

3.1.1 Abstract

Snow cover plays a vital role in shaping understory environment of forest, particularly in snowy regions. Decreased snow cover driven by climate change can increase temperature fluctuation and freeze event due to decreased insulation effect, lower soil water content due to decreased snowmelt water into soil, and increase light intensity in spring due to earlier snowmelt. However, the knowledge about how tree canopy can influence the response of understory environment to decreased snow cover remains limited. In this study, I conducted a snow manipulation experiment in both below canopy and in canopy gap to examined how tree canopy influences the impact of decreased snow cover on understory environment, especially focusing on temperature dynamics. The experiment was conducted in a *Picea glehnii*-planted forest in northern Hokkaido, Japan. I established five sites in both below the canopy and in the canopy gap, and set both control and snow removal plots in each site. In each site, I measured snow depth, snowmelt date, near ground air temperature, soil temperature, soil water content, and light intensity. Our results indicated that near-ground air temperature was lower in the snow removal plots only below the canopy during the snowmelt period. Additionally, I observed that near ground temperature was lower in the snow removal plots in both microsites during the snow cover establishment period. Since the near ground air temperature was lower below the tree canopy compared to the canopy gap because the tree canopy intercepted snowfall and delayed the establishment of snow cover, the snow removal plot below the canopy exhibited the coldest near ground temperature among the manipulation plots. These findings underscore that the understory environment can differ significantly between below the canopy and in the canopy gap when snow cover decreases, potentially leading to distinct responses in understory vegetation in each microsite.

3.1.2 Introduction

Snow cover is a key factor shaping the abiotic environment of the understory in forest ecosystems of snowy regions (Kreyling et al. 2012; Sanders-DeMott et al. 2017). One of its most critical functions is acting as a thermal insulator, decoupling below-snow temperatures from free-air temperatures. As a result, temperature fluctuations beneath the snowpack are much smaller than those in the air above (Groffman et al. 2001; Morgner et al. 2010). When snow cover is sufficient, temperatures beneath the snowpack can remain stable around 0°C throughout the winter (Pattison and Welker 2014; Sanders-DeMott et al. 2017). In contrast, when snow cover is insufficient, understory temperatures can drop below 0°C, leading to soil freezing in winter or increased freeze-thaw cycles in early winter and/or during snowmelt. These changes can significantly influence ecosystem processes and alter understory species composition (Gilliam et al. 2010; Kreyling et al. 2012; Makoto et al. 2014). Beyond its role in thermal dynamics, snow cover also regulates light availability on the forest floor (Rixen et al. 2022). By reflecting much of the incoming solar radiation, snow cover can protect understory vegetation from excessive light exposure that might otherwise cause photoinhibition in the early spring (Luoranen et al. 2022). Additionally, snowmelt timing strongly influences the timing of budburst and leaf-out in understory vegetation (Marumo et al. 2020) due to its effects on both forest floor temperatures and light conditions. These influences can, in turn, affect overall understory productivity (Rixen et al. 2022; Liu et al. 2023). Furthermore, snow cover is tightly linked to soil moisture, particularly during snowmelt (Hardy et al. 2001; Shibata et al. 2013), which plays a crucial role in regulating soil microbial activity and vegetation performance in the following growing season (Zhao et al. 2022).

Given the multiple roles of snow cover, its ongoing decline—driven by rising temperatures and shifting precipitation patterns across much of the Northern Hemisphere (IPCC 2021; Gottlieb and Mankin 2024)—is expected to bring profound changes to the understory environment. Previous studies have demonstrated that a decrease in snowpack can disrupt thermal buffering (Kreyling et al.

2013; Martz et al. 2016), alter solar radiation dynamics (Kunishima and Yoshimura 2025), and reduce moisture input (Makoto et al. 2014; Shibata 2016), collectively altering ecosystem dynamics (Makoto et al. 2014; Zhao et al. 2022) and influencing the performance of forest floor species in forest ecosystems (Kreyling et al. 2012; Kosolapova and Altshuler 2024). Although the general changes in abiotic factors in response to decreased snow have been studied in forest ecosystems, the variation in abiotic conditions and the potential differences in the effects of reduced snow within forests remain less explored.

Since tree canopy can intercept snow (Varhola et al. 2010; Sun et al. 2022), snow cover regimes, including the timing of snow cover establishment and melt, snow cover duration, and snow cover depth, are differ between the areas below tree canopy and in canopy gaps (Harpold et al. 2015; Bouchard et al. 2024), which are openings in the forest canopy created by falling trees and/or branches (Whitmore 1989). Typically, snow cover is thinner below the tree canopy compared to the canopy gaps. Additionally, the establishment of snow cover would be delayed, and snowmelt would occur earlier due to the interception effect. Consequently, distinct snow cover regimes are expected within forest ecosystems, leading to varied influences on the abiotic conditions of the forest floor. In addition to the snow interception effect, the tree canopy can also moderate the temperature below tree canopy by intercepting direct solar radiation, reducing wind speed, and absorbing long-wave radiation (Geiger 2009; De Frenne et al., 2021). Previous studies have highlighted the importance of the temperature buffering effect provided by tree canopy, which creates a cooler environment in summer and a warmer environment in winter, with less temperature fluctuation compared to canopy gaps (De Frenne et al. 2019; John et al. 2024). Overall, the abiotic conditions of the forest floor can vary within forest ecosystems due to both the temperature buffering effect of the tree canopy and the snow interception effect. Additionally, we lack knowledge about how the tree canopy modifies the influence of decreased snow cover on the abiotic conditions of the forest floor.

In this study, I aimed to examine how tree canopy modifies the influence of snow cover on

forest floor abiotic conditions, particularly winter temperature dynamics. Additionally, I investigated how tree canopy affects the impact of decreases in snow cover driven by climate change on these conditions. To address these questions, I established study sites both under the tree canopy and in canopy gaps within a *Picea glehnii*-planted forest in northern Hokkaido, Japan. Regarding temperature dynamics, I hypothesized that air and soil temperatures would be lower under the canopy than in canopy gaps, particularly in early winter during snow accumulation and in early spring during snowmelt. Furthermore, I hypothesized that snow removal would reduce air and soil temperatures in both microsites, resulting in harsher abiotic conditions under the tree canopy compared to the canopy gaps.

3.1.3 Methods

3.1.3.1 Sites establishment

The study sites are situated in *Picea glehnii* plantation forests (around 40 years old in 2022, mean diameter at breast height of 17.8 cm) in the Teshio Experimental Forest of Hokkaido University (45º03’N, 142º06’E, 66 m above sea level, Fig. 3.1-1a), northern part of Hokkaido in Japan. The study area is located within an ecotone between boreal and cool-temperate forest (Sato et al. 2023), whose vegetation is known to be drastic (Fisichelli et al. 2014, Hiura et al. 2019). By following the FAO classification, the soil type at this site was classified as Dystric Cambisol (Makoto et al. 2012). The mean monthly temperature ranges from −5.4 to 18.1 °C (January and July, respectively), and the annual precipitation is approximately 1000 mm (Naka et al. 2023). The maximum snowpack depth reaches up to 2 meters (Makoto et al., 2022). Although snowfall begins in November, continuous snow cover typically forms in early December and lasts until late April.

In July 2022, I established 10 sites, each measuring 10 × 20 m. Half of the sites were located

below the tree canopy, while the other half were clear-cut to artificially create canopy gaps (Fig. 3.1-1b). The experimental area was set in a planted forest to minimize environmental differences unrelated to tree canopy structure. Within each site, two 5 × 5 m plots were designated as control and snow removal plots, spaced 5 m apart. This resulted in four distinct plot types: control plot below the tree canopy (CC, n = 5), snow removal plot below the tree canopy (CS, n = 5), control plot in the canopy gap (GC, n = 5), and snow removal plot in the canopy gap (GS, n = 5) (Fig. 3.1-1c).

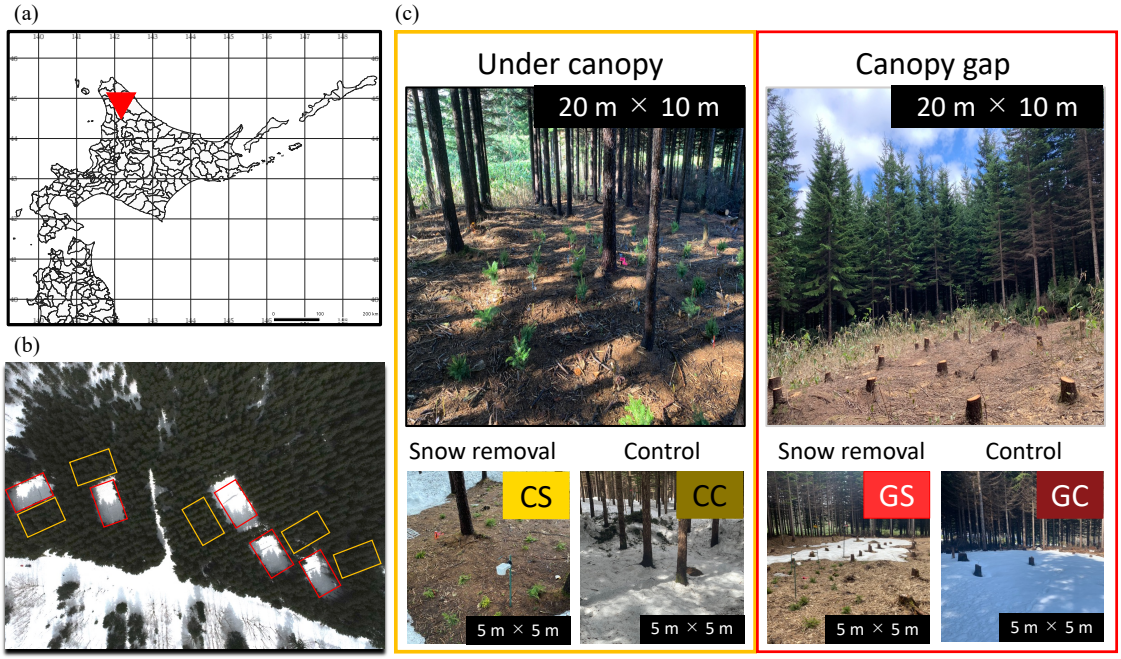


Fig. 3.1-1 Location and design. Location of study area (a). The position of study sites (an aerial photo of a 3-hectare area, taken using a drone at a height of 150 m) (b). Yellow and red rectangles represent under canopy and canopy gap, respectively. The condition of CC (under canopy control plot), CS (under canopy snow removal plot), GC (canopy gap control plot), and GS (canopy gap snow removal plot) taken during the early spring (c).

3.1.3.2 Snow removal manipulation

The analysis of average monthly (November) air temperature (Horokanai, Japan

Meteorological Agency, https://www.data.jma.go.jp/stats/etrn/index.php) and snow cover appearance data (long-term observations of snowpack and snowfall depth in the Uryu Experimental Forest (UREF), northern Japan; https://db.cger.nies.go.jp/JaLTER/metacat/metacat/JaLTER-Hokkaido-Kita.2.5/jalter) from 1977 to 2012 in the northern part of Hokkaido demonstrated that a 1 °C rise in air temperature can delay snow cover forming for approximately 4.9 d (Fig. 3.1-S1a). Additionally, an analysis of the average spring (March–May) air temperature data and date of snowmelt from 1996 to 2014 in the northern part of Hokkaido demonstrated that a 1 °C rise in air temperature may advance snowmelt for approximately 6.7 d (Fig. 3.1-S1b). In this study, I conducted snow removal based on the Representative Concentration Pathways (RCP) 6.0 scenario, which projects a global mean surface temperature increase of 2.2°C (with a likely range of 1.4 to 3.1°C) between 2081 and 2100 (IPCC 2021). Accordingly, I aimed to delay snow cover formation by approximately 11 days (ranging from 7 to 14 days) and advance snowmelt by approximately 15 days (ranging from 9 to 21 days). During the onset of winter, snow was removed immediately after the appearance of snow cover to delay snow cover forming. I repeated the snow removal manipulation to ensure the 11 days (ranging from 7 to 14 days) delay in snow cover forming compared with that of the control plot. Consequently, I conducted snow removal twice in December 2022 and 2023. To prevent snow removal process-induced damage to the tree seedlings, a 5 cm layer of snow cover was left undisturbed. In March 2023 and 2024, I removed snow to half the depth of the control plot to advance snowmelt by approximately 15 days (ranging from 9 to 21 days) compared to that of the control plots. All snow-removal activities were manually performed using shovels.

3.1.3.3 Environmental variables

Snow depth was measured weekly during the snow removal manipulation in December and after the manipulation in March. At other times, it was measured monthly. To obtain precise data on snowmelt, TLC200 time-lapse cameras (Brinno, Taiwan) recorded daily images of each plot until the

snow cover had completely disappeared.

Temperature and light data loggers (HOBO Pendant, Onset Computer, Bourne, MA, USA) were installed 20 cm above the ground in each plot. These air temperature loggers were set up in October 2022 to record air temperature and light intensity every 30 minutes.

Soil temperature data loggers (TR-5i, T&D Corporation, Nagano, Japan) were installed in each plot from late October to early November 2022, recording data every hour. Soil temperature was measured at a depth of 10 cm below the ground surface, as this depth is where the roots of understory vegetation typically develop in this region (Fukuzawa et al., 2006).

Soil moisture sensors (10HS, Onset Computer, Bourne, MA, USA) were also installed in each plot at a depth of 10 cm below the ground surface. These sensors, set up from late October to early November 2022, recorded soil moisture data every hour.

3.1.3.4 Statistical analysis

To examine the effects of tree canopy, snow removal, and their interaction on daily mean, minimum, and maximum air temperatures, daily mean soil temperature, daily mean soil moisture, daily mean light intensity, snow cover depth, and snowmelt date, linear mixed-effects models were applied using the 'lme4' package (Bates et al., 2015). For air temperature, soil temperature, soil moisture, and light intensity, the season was divided into four periods for analysis: beginning of winter when snow cover is establishing (November to December), middle winter when snow cover is fully established (January to February), end of winter when snow cover begins to melt below the tree canopy (March) and in the canopy gap (April), and the growing season. The sites and years were set as the random effect for all the models. All the response variables were log-transformed to ensure the normality. To examine the differences among manipulation plots, we performed a multiple comparison for all variables. I first calculated the estimated marginal means (EMMs) for the variables

of each plot using the 'emmeans' package (v.1.10.0, Lenth et al., 2024). Then, I conducted multiple comparisons using the pairs function and applied Bonferroni correction to account for the increased risk of Type I errors associated with multiple tests. Statistical significance was defined as $P < 0.05$, and all analyses were performed in R version 4.1.0 (R Development Core Team, 2021).

3.1.4 Results

3.1.4.1 Seasonal snow cover depth trends and snowmelt date

Both tree canopy and snow removal manipulation had the significant influences on snow cover depth in both first (*tree canopy*: $F_{1,636} = 71.71$, $P < 0.001$, *snow removal*: $F_{1,636} = 412.28$, $P < 0.001$) and second (*tree canopy*: $F_{1,445} = 167.20$, $P < 0.001$, *snow removal*: $F_{1,445} = 183.28$, $P < 0.001$) experimental year (Fig. 3.1-2). No interactive effect on snow cover depth was found in both years. Both tree canopy and snow removal manipulation had the significant influences on snowmelt date in both first (*tree canopy*: $F_{1,12} = 18.71$, $P < 0.001$, *snow removal*: $F_{1,12} = 42.11$, $P < 0.001$) and second (*tree canopy*: $F_{1,12} = 24.10$, $P < 0.001$, *snow removal*: $F_{1,12} = 98.45$, $P < 0.001$) experimental year. Snowmelt date differed significantly among manipulation plots, with the earliest occurring in the snow removal plots below the canopy, followed by the snow removal plots in the canopy gap, the control plots below the canopy, and the control plots in the canopy gap (Table 3.1-S1).

3.1.4.2 Temperature dynamics of forest floor

Diurnal air temperature fluctuations were observed in different periods (Fig. 3.1-3). During the beginning of winter and the end of winter (April), the remarkable air temperature rising was detected in the daytime with peak around noon (Fig. 3.1-3a. d). The fluctuations were also observed in the snow removal plots during the end of winter (March). Air temperature showed the decrease in

morning in the snow removal plots in both canopy gap and below canopy sites (Fig. 3.1-3c). No fluctuations in diurnal air temperature were observed during the snow cover fully established periods (Fig. 3.1-3b).

Daily mean and minimum air temperature were influenced by both tree canopy (*mean*: $F_{1,652}$ = 103.82, $P < 0.001$, *minimum*: $F_{1,489}$ = 103.85, $P < 0.001$) and snow removal manipulation (*mean*: $F_{1,652}$ = 103.82, $P < 0.001$, *minimum*: $F_{1,407}$ = 23.14, $P < 0.001$) at the beginning of winter. During this period, both the daily mean and minimum air temperature were higher in the canopy gap compared to below the canopy, and the daily minimum air temperature was higher in the control plots compared to snow removal plots in both microsites (Fig. 3.1-4a, e; Table 3.1-S3). When it comes to the middle of winter, only tree canopy was detected to have significant influence on both the daily mean and minimum air temperature (*mean*: $F_{1,439}$ = 330.97, $P < 0.001$, *minimum*: $F_{1,1205}$ = 388.06, $P < 0.001$). At the end of winter (March), the interactive effect was detected to significantly influence both the daily mean and minimum air temperature (*mean*: $F_{1,638}$ = 5.11, $P < 0.05$, *minimum*: $F_{1,643}$ = 6.98, $P < 0.01$), while the significant influence of both tree canopy ($F_{1,647}$ = 41.04, $P < 0.001$) and snow removal ($F_{1,460}$ = 18.20, $P < 0.001$) were only detected in the daily minimum air temperature. In this period, significant difference between control and snow removal plots was only detected in daily minimum air temperature below the canopy, with significantly higher minimum temperature (Fig. 3.1-4g; Table 3.1-S3). The significant influence of tree canopy on both the daily mean and minimum air temperature were detected (*mean*: $F_{1,491}$ = 8.12, $P < 0.01$, *minimum*: $F_{1,408}$ = 18.05, $P < 0.001$), while the significant influence of both snow removal ($F_{1,343}$ = 36.86, $P < 0.001$) and the interactive effect ($F_{1,478}$ = 8.71, $P < 0.01$) were only detected in the daily mean air temperature in the end of winter (April). And during this period, significant difference between control and snow removal plots was only detected in daily minimum air temperature below the canopy (Fig. 3.1-4d; Table 3.1-S3).

The soil temperature never dropped below 0°C in any of the manipulation plots during the whole season (Fig. 3.1-5). During the snow cover establishing period, only tree canopy had the significant

influence on the daily mean soil temperature ($F_{1,992} = 44.46$, $P < 0.001$, Fig. 3.1-5). Tree canopy, snow removal, and interactive effect all showed the significant influences on the daily mean soil temperature (Fig. 3.1-5) during the snow cover fully established (*tree canopy*: $F_{1,1772} = 641.22$, $P < 0.001$, *snow removal*: $F_{1,1772} = 69.54$, $P < 0.001$, *interactive effect*: $F_{1,1772} = 47.99$, $P < 0.001$) and snowmelt-below-canopy periods (*tree canopy*: $F_{1,921} = 191.95$, $P < 0.001$, *snow removal*: $F_{1,921} = 84.84$, $P < 0.001$, *interactive effect*: $F_{1,921} = 32.39$, $P < 0.001$). Accordingly, the significant differences of the daily soil temperature among manipulations were only detected between the control and snow removal plots in the canopy gap (Table 3.1-1). When it comes to the end of winter (April) period, the significant effect of snow removal ($F_{1,858} = 114.60$, $P < 0.001$) and its interactive effect with tree canopy ($F_{1,868} = 21.54$, $P < 0.001$) on the daily mean soil temperature were detected (Fig. 3.1-5). And the daily mean soil temperature was significantly higher in the snow removal plots compared to the control plots in both microsites, with greater differences in the canopy gap (Table 3.1-1).

3.1.4.3 Soil water content and light intensity

Through the whole season, soil water content was slightly higher in the snow removal plots compared to the control plots below the canopy, while almost no differences were detected between the snow removal plots and control plots in the canopy gap (Fig. 3.1-6, Table 3.1-2).

During the snow cover establishing period, only tree canopy ($F_{1,1382} = 329.50$, $P < 0.001$) showed the significant influence on the daily mean light intensity (Fig. 3.1-7). During the snowmelt-below-canopy period, snow removal ($F_{1,370} = 29.30$, $P < 0.001$) and its interactive effect with tree canopy ($F_{1,630} = 4.68$, $P < 0.05$) showed the significant influences on the daily mean light intensity (Fig. 3.1-7). The significant difference between the snow removal plots and control plots was only detected below the canopy, with greater daily mean light intensity in the snow removal plots (Table 3.1-3). Tree canopy ($F_{1,424} = 106.02$, $P < 0.001$), snow removal ($F_{1,459} = 58.42$, $P < 0.001$), and their

interactive effect ($F_{1,545} = 52.06$, $P < 0.001$) all showed the significant influence on the daily mean light intensity (Fig. 3.1-7). And the significant difference between the snow removal plots and control plots was only detected in the canopy gap, with greater daily mean light intensity in the snow removal plots (Table 3.1-3).

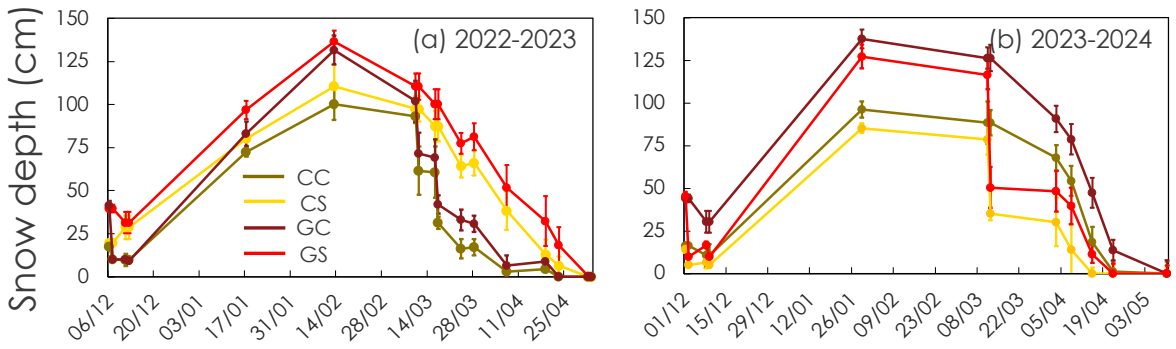


Fig. 3.1-2 Seasonal trends of snow cover depth in control plot below canopy (CC), snow removal plot below canopy (CS), control plot in canopy gap (GC), and snow removal plot in canopy gap (GS) in the first (a) and second (b) experimental year.

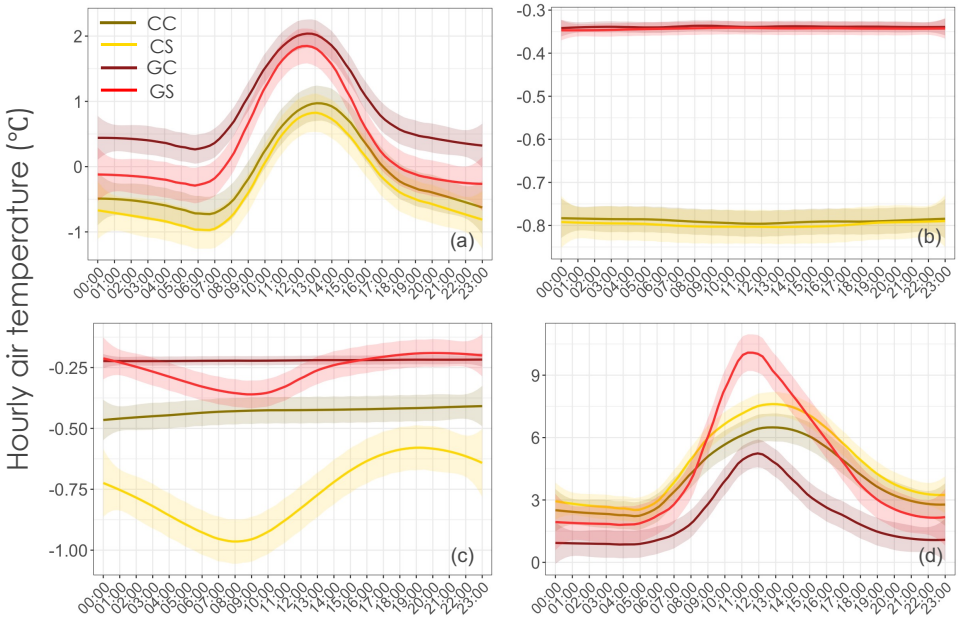


Fig. 3.1-3 The hourly air temperature in control plot below canopy (CC), snow removal plot below canopy (CS), control plot in canopy gap (GC), and snow removal plot in canopy gap (GS) at the beginning of winter (a), in the middle of winter (b), in the end of winter (March) (c), and in the end of winter (April) (d). Each panel shows temperature data averaged by hour across all days in the corresponding seasonal period. The lines were smoothed using the geom_smooth() function from the ggplot2 package in R (method = "loess"), and shaded areas represent 95% confidence intervals.

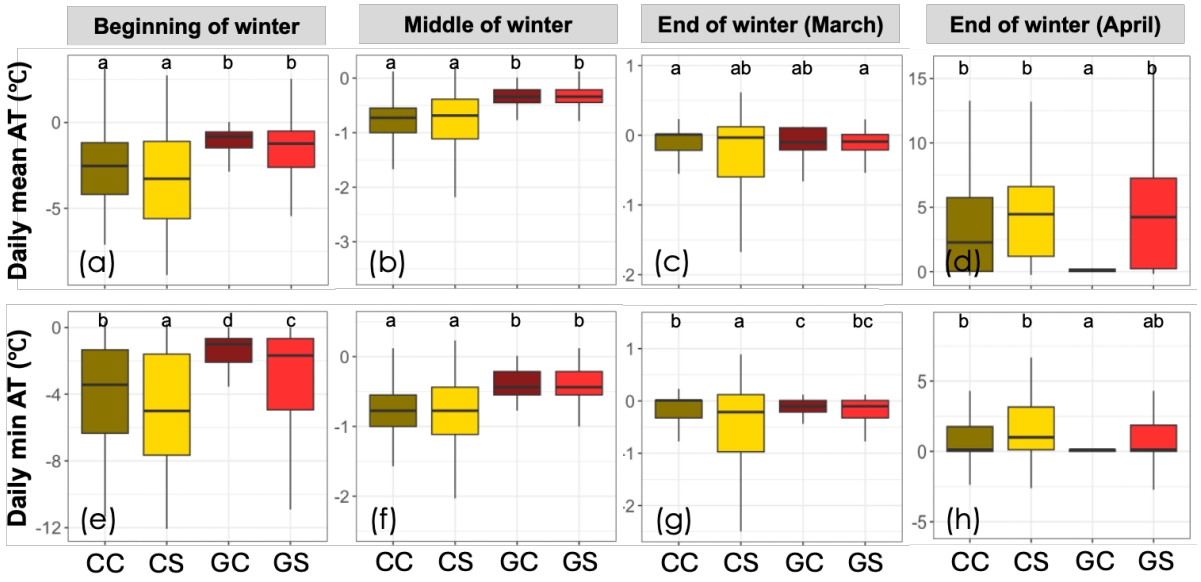


Fig. 3.1-4 Daily mean (a-d) and minimum (e-h) air temperature at the beginning of winter (a-e), in the middle of winter (b,f), in the end of winter (March) (c, g), and in the end of winter (April) (d, h) in control plot below canopy (CC), snow removal plot below canopy (CS), control plot in canopy gap (GC), and snow removal plot in canopy gap (GS).

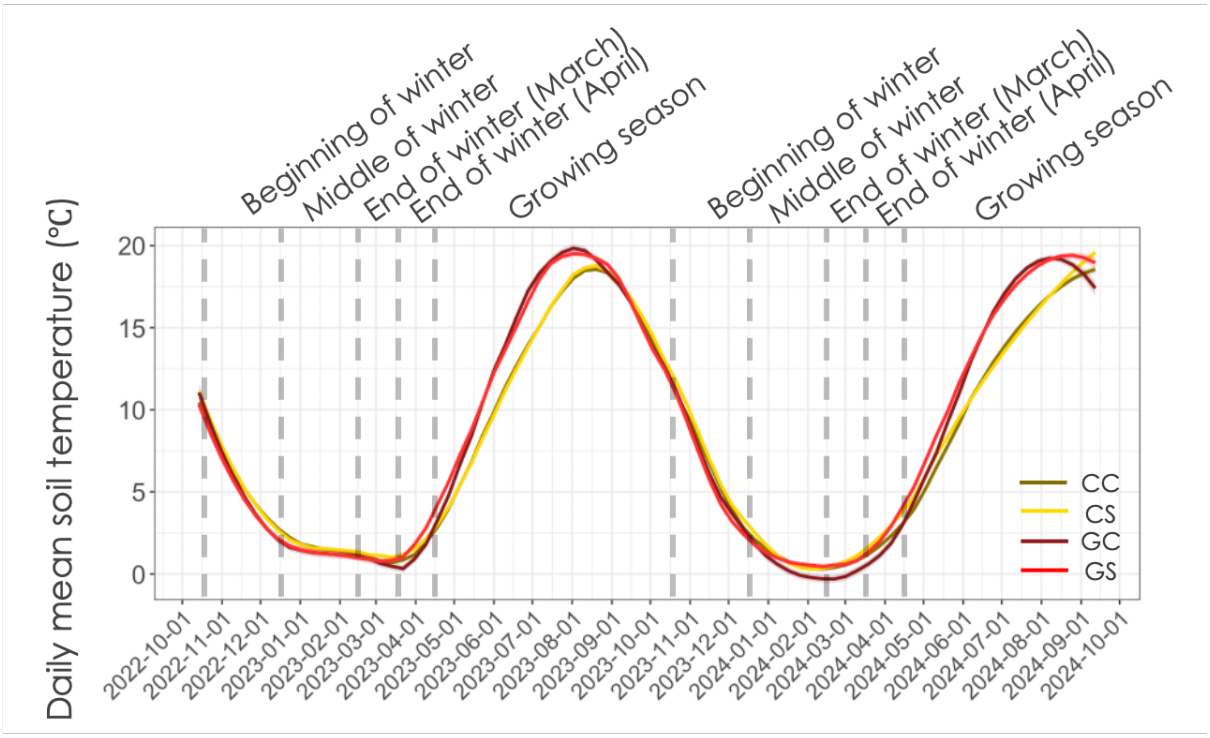


Fig. 3.1-5 Daily mean soil temperature in control plot below canopy (CC), snow removal plot below canopy (CS), control plot in canopy gap (GC), and snow removal plot in canopy gap (GS) during the two experimental years. The lines were smoothed using the geom_smooth() function from the ggplot2 package in R (method = "loess"), and shaded areas represent 95% confidence intervals.

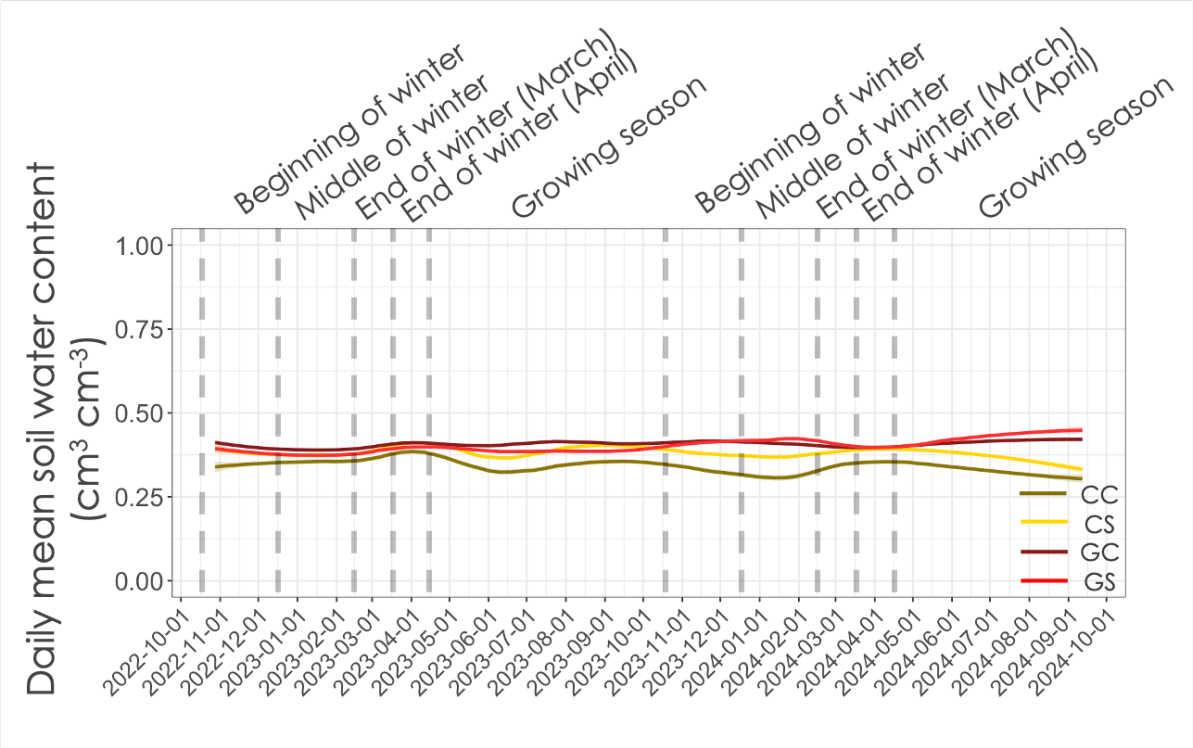


Fig. 3.1-6 Daily mean soil water content in control plot below canopy (CC), snow removal plot below canopy (CS), control plot in canopy gap (GC), and snow removal plot in canopy gap (GS) during the two experimental years. The lines were smoothed using the geom_smooth() function from the ggplot2 package in R (method = "loess"), and shaded areas represent 95% confidence intervals.

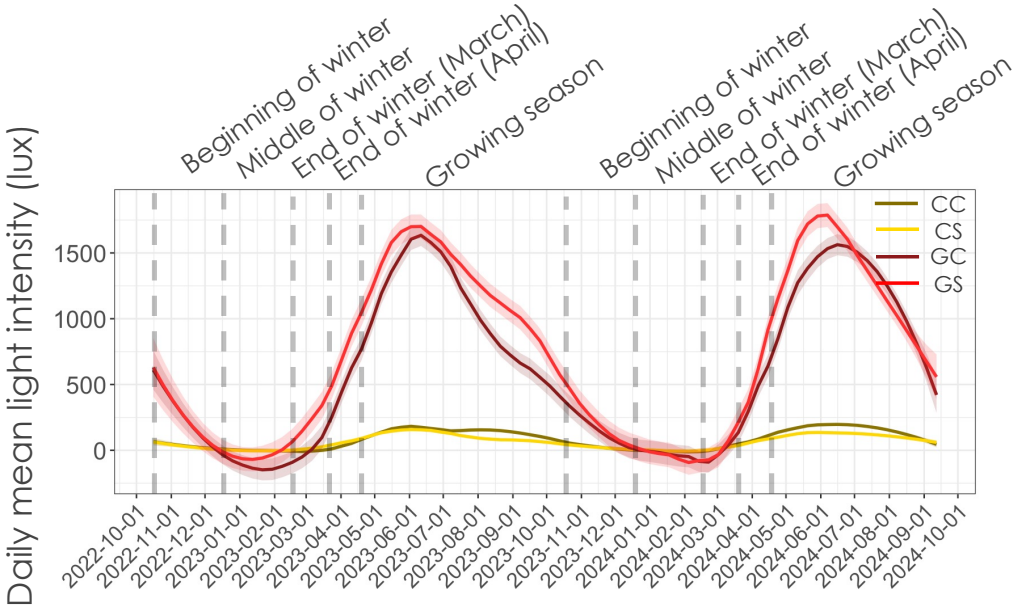


Fig. 3.1-7 Daily mean light intensity in control plot below canopy (CC), snow removal plot below canopy (CS), control plot in canopy gap (GC), and snow removal plot in canopy gap (GS) during the two experimental years. The lines were smoothed using the geom_smooth() function from the ggplot2 package in R (method = "loess"), and shaded areas represent 95% confidence intervals.

Table 3.1-1 The daily mean soil temperature (℃) among manipulations

	CC	CS	GC	GS
Beginning of winter	2.0 (0.1)b	1.9 (0.1)b	1.7 (0.1)a	1.8 (0.1)a
Middle of winter	1.4 (0.7)c	1.4 (0.7)c	1.0 (0.7)a	1.2 (0.7)b
End of winter (March)	1.0 (0.5)c	1.0 (0.5)c	0.7 (0.5)a	0.9 (0.5)b
End of winter (April)	2.0 (0.3)a	2.8 (0.3)b	1.5 (0.3)a	3.6 (0.3)c
Growing season	12.7 (0.3)a	12.7 (0.3)a	14.1 (0.3)b	14.1 (0.3)b

CC, CS, GC, and GS indicate control plots below canopy, snow removal plots below canopy, control plots in canopy gap, and snow removal plots in canopy gap, respectively. The alphabet demonstrates the results of the multiple comparisons, and the values in parentheses indicate the standard error.

able 3.1-2 The daily mean soil water content (cm^3 cm^{-3}) among manipulations.

	CC	CS	GC	GS
Beginning of winter	0.34 (0.01)a	0.37 (0.01)b	0.40 (0.01)c	0.40 (0.01)c
Middle of winter	0.35 (0.01)a	0.38 (0.01)b	0.40 (0.01)c	0.40 (0.01)c
End of winter (March)	0.36 (0.01)a	0.39 (0.01)b	0.40 (0.01)b	0.40 (0.01)b
End of winter (April)	0.38 (0.01)a	0.41 (0.01)c	0.40 (0.01)bc	0.40 (0.01)b
Growing season	0.33 (0.01)a	0.38 (0.01)b	0.41 (0.01)d	0.40 (0.01)c

CC, CS, GC, and GS indicate control plots below canopy, snow removal plots below canopy, control plots in canopy gap, and snow removal plots in canopy gap, respectively. The alphabet demonstrates the results of the multiple comparisons, and the values in parentheses indicate the standard error.

Table 3.1-3 The daily mean light intensity (lux) among manipulations

	CC	CS	GC	GS
Beginning of winter	13.7 (8.3)a	14.7 (8.2)a	102.7 (8.2)b	111.5 (8.5)b
Middle of winter	0.0 (0.0)a	0.1 (0.0)b	0.0 (0.0)a	0.0 (0.0)a
End of winter (March)	0.0 (2.3)a	11.9 (2.4)c	0.0 (2.4)ab	6.0 (2.4)bc
End of winter (April)	59.5 (72.5)a	82.9 (75.8)a	231.9 (75.0)a	936.3 (78.1)b
Growing season	101.1 (71.3)a	84.3 (71.4)a	1091.6 (71.3)b	1222.0 (71.4)c

CC, CS, GC, and GS indicate control plots below canopy, snow removal plots below canopy, control plots in canopy gap, and snow removal plots in canopy gap, respectively. The alphabet demonstrates the results of the multiple comparisons, and the values in parentheses indicate the standard error.

3.1.5 Discussion

3.1.5.1 The understory environment is cooler than the canopy gap during winter

Just as I expected, the mean and minimum daily air temperature during the dormant season were significantly lower below the canopy compared to the canopy gap, especially during the snow cover establishing and snowmelt periods (Fig. 3.1-4, Table 3.1-S3). Generally, it has been considered that tree canopy with the temperature buffering effect can prevent extreme cold event below the canopy during dormant season (De Frenne et al. 2019). However, in this region, I found that the snow interception effect provided by tree canopy can exceed the influence of temperature buffering effect provided by tree canopy, leading to cooler air temperature near the ground below tree canopy compared to canopy gap. The difference between our study and the previous meta-analysis (De Frenne et al. 2019) can be explained by several reasons. First, the meta-analysis included more studies conducted during the growing season than the dormant season. Consequently, the temperature offset primarily reflected patterns observed during the growing season, where mean and maximum temperatures were lower and minimum temperatures were higher under tree canopies, due to reduced direct solar radiation and wind speed compared to areas outside the forest (Potter et al. 2013; De Frenne et al. 2021). Second, a substantial portion of studies in the meta-analysis may have been conducted in regions without seasonal snow cover or with only thin snow cover. In these regions, the insulation effect provided by snow cover is nearly nothing, therefore, the buffering effect could exceed the snow interception effect.

Also, as I expected, snow removal lowered the daily minimum air temperature during the snow cover establishing period, leading to the coldest environment in the snow removal plots below the canopy (Fig. 3.1-4e, Table 3.1-S3). Interestingly, the influence of snow removal on the air temperature during the snowmelt period were different between the microsites (Fig. 3.1-4). Following our expectation, the daily minimum air temperature was lower in the snow removal plots compared to the

control plots during the snowmelt-below-canopy period (Fig. 3.1-4g), while the daily mean air temperature was higher in the snow removal plots compared to the control plots during the snowmelt-in-canopy-gap period (Fig. 3.1-4b). During the snowmelt-in-canopy-gap period, the temperature above snow cover can already be warmer than the temperature below snow cover that kept around 0 degree Celsius (Kelsey et al., 2021; Tyystjärvi et al., 2024). This reduction in air temperature near the ground surface due to decreased snow cover can negatively affect the performance of understory vegetation, including seed germination, survival, and growth (Sanders-DeMott et al. 2017; Slatyer et al. 2022), with downstream effects on vegetation composition, plant-herbivore interactions, and forest regeneration (Kreyling et al. 2012; Guiden et al. 2018). Although previous studies have acknowledged the negative effects of decreased snow cover on understory vegetation, few studies have considered variations in its impact on temperature dynamics, which could lead to different responses of understory vegetation to decreased snow cover within the forest ecosystem.

3.1.5.2 Unexpected soil temperature responses during growing season

Soil temperature did not go down below 0 degree Celsius in any of the manipulation plots even during the snow cover establishing and snowmelt periods where the soil surface was directly exposed to the air sometimes (Fig. 3.1-5). The relatively thick litter layer in the boreal forest due to the slow decomposition rate (Zhang et al. 2008) can partly explain this phenomenon since thick litter layer can act as an insulator to reduce soil temperature change to some extent (Mackinney 1929). As no soil freeze-thaw cycle was observed, we basically assume that the trends of the decreased snow cover in this region with heavy snow cover would not cause significant negative damages on plant belowground organs which can lead to decreased in both survival and growth (Groffman et al. 2001; Kreyling et al. 2012). Furthermore, the decoupling between air and soil temperatures could lead to asymmetrical responses in understory vegetation. In our case, significant cold damage is anticipated for aboveground organs, while belowground organs are expected to remain unaffected.

3.1.5.3 The responses of soil water content and light intensity to decreased snow cover

A slightly higher soil water content was observed in the snow removal plots compared to the control plots throughout the season below the canopy (Fig. 3.1-6, Table 3.1-2). This result is consistent with previous studies conducted in nearby regions, which reported higher soil water content under reduced snow cover depth and/or duration during winter season (Watanabe et al. 2019) and in the following growing season (Makoto et al. 2022). In general, decreased snow cover is expected to reduce soil water content, as it can lower unfrozen soil water content through increased soil freezing, reduce the amount of snowmelt water, and increase soil evaporation (Ohkubo et al. 2011; Wang et al. 2013). Due to the thick humus layer at the sites, soil freezing did not increase even under the snow removal manipulation (Fig. 3.1-5). Additionally, since our manipulation reduced only the duration of snow cover but not the total amount of snow, the input of meltwater might not have changed significantly. Therefore, I consider the slightly higher soil water content observed in the control plots beneath the canopy to be explained by initial variations across sites, along with occasional malfunctions in the sensors and/or data loggers.

Due to advanced snowmelt, higher daily mean light intensity was detected in the snow removal plots compared to the control plots in the canopy gaps (Table 3.1-3, Fig. 3.1-7). Light intensity was also higher in the canopy gaps than beneath the canopy due to the absence of tree canopy to intercept direct light (Table 3.1-3, Fig. 3.1-7; Muscolo et al. 2014). When understory plants are exposed to intense sunlight in combination with low temperature, the excess light energy can overwhelm the plant's capacity to process it, leading to damage in the photosynthetic machinery, particularly in Photosystem II (photoinhibition; Huner et al. 1993; Kitao et al. 2018). Therefore, the significantly greater light intensity in the snow removal plots increase the possibility of photoinhibition that can limit both growth and survival in understory vegetation (Germino and Smith 1999; Egerton et al. 2000). Especially for evergreen species that retain leaves throughout the winter, the combination of

high light and low temperatures in canopy gaps under global warming is more likely to cause increased damage to these species.

3.1.5.4 Future perspectives

In this study, our result suggested that the buffering effect of the tree canopy can be canceled out by its snow interception effect, resulting in colder conditions below the canopy compared to the canopy gap during winter in snowy region. However, to reach the general understanding of the relationships between tree canopy, snow cover, and understory temperature dynamics during winter season, it is crucial to separately assess their contributions to the temperature dynamics. This assessment will clarify individual and combined impacts of temperature buffering effect and snow interception capacity of tree canopy on understory temperatures and how these effects may shift with climate change during the dormant season. Also, both the buffering and snow interception effects can change significantly with climatic conditions (Zellweger et al., 2019; De Lombaerde et al., 2022; Sun et al., 2022; Meriö et al., 2023) and forest structure (De Lombaerde et al., 2022; Sun et al., 2022; Katsushima et al., 2023; Chen et al., 2024). For example, it is well-known that tree canopy with higher coverage can intercept more snow, therefore, cause thinner snowpack and/or shorter snow cover duration below tree canopy compared to the open area and gap (Dickerson-Lange et al. 2023; Bouchard et al. 2024). At the same time, greater canopy coverage can demonstrate higher temperature buffing effect (Chen et al. 2024). Additionally, when free-air temperatures are relatively low, both the snow interception and buffering effects tend to become more pronounced (De Frenne et al., 2019; Dickerson-Lange et al., 2021). Therefore, I can use global-scale datasets (for example, the SoilTemp database includes paired datasets of near-ground air temperature and soil temperature measured both below the tree canopy and in open areas, such as outside the forest or in canopy gaps) to examine how these factors interact in shaping below tree canopy temperature dynamics in regions with seasonal snow during winter in the future

3.1.6 Conclusion

This study examined how the tree canopy influences the effects of decreased snow cover on forest floor abiotic conditions, particularly near-ground temperature. By conducting a snow removal experiment both below the canopy and in the canopy gap of a Picea glehnii-planted forest in northern Hokkaido, Japan, I found that earlier snowmelt in the snow removal plots led to colder near-ground air temperatures below the canopy but not in the canopy gap. Additionally, I observed that near-ground temperatures were lower in the snow removal plots during the snow cover establishment period in both microsites. Consequently, the coldest near-ground air temperatures occurred in the snow removal plots below the canopy, as the tree canopy intercepted snow and delayed snow cover formation, further lowering temperatures. Overall, our study clarified that decreased snow cover affects the understory environment differently below the tree canopy and in the canopy gap, which may further lead to varying responses of understory vegetation to decreased snow cover between the two microsites.

3.1.7. Appendix

3.1.7.1 Supplemental figures

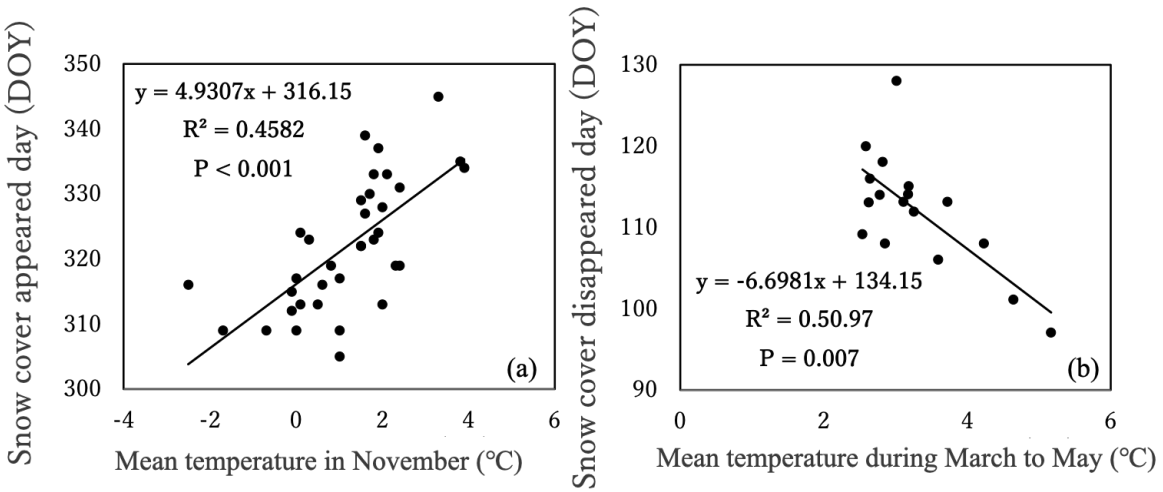


Fig. 3.1-S1 The relationships between mean temperature in November (Horokanai, Japan Meteorological Agency) and the date of snow cover appearance (long-term observation of snowpack and snowfall depth from Uryu Experimental Forest (Uryu Experimental Forest, Hokkaido University; JaLTER-Hokkaido-Kita.2.5) (a); the relationships between mean temperature from March to May and the date of snow cover.

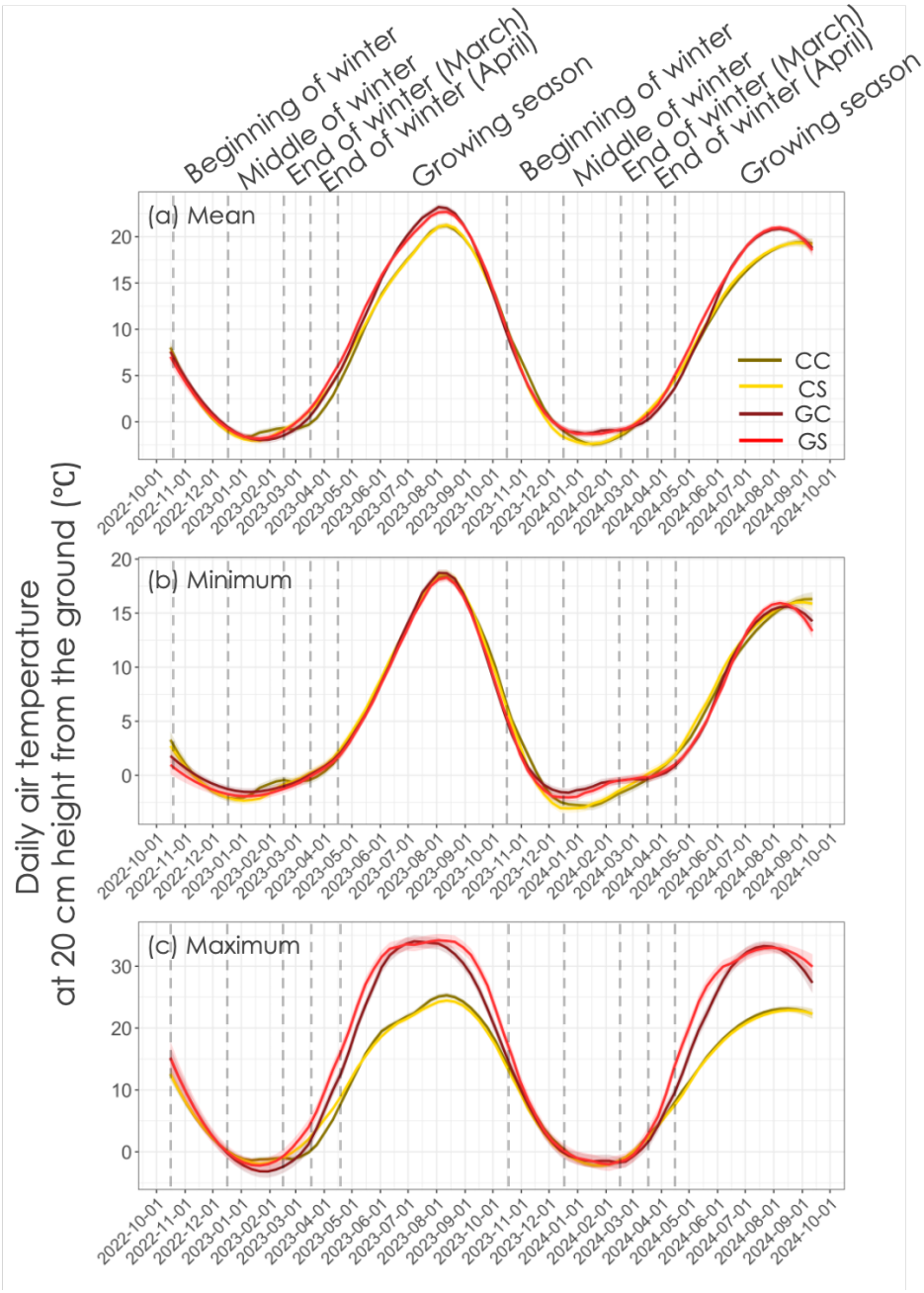


Fig. 3.1-S2 Daily mean (a), minimum (b) , and maximum (c) air temperature in control plot below canopy (CC), snow removal plot below canopy (CS), control plot in canopy gap (GC), and snow removal plot in canopy gap (GS) during the two experimental years. The lines were smoothed using the geom_smooth() function from the ggplot2 package in R (method = "loess"), and shaded areas represent 95% confidence intervals.

3.1.7.2 Supplemental Tables

Table 3.1-S1 Snowmelt date (DOY: day of year) among manipulations

	CC	CS	GC	GS
First year	109 (2)bc	96 (2)a	116 (2)c	105 (2)b
Second year	112 (1)c	102 (1)a	117 (1)b	107 (1)d

CC, CS, GC, and GS indicate control plots below canopy, snow removal plots below canopy, control plots in canopy gap, and snow removal plots in canopy gap, respectively. The alphabet demonstrates the results of the multiple comparisons, and the values in parentheses indicate the standard error.

Table 3.1-S2 Hourly air temperature (℃) among manipulations

	CC	CS	GC	GS
Beginning of winter	-0.1 (0.4)b	- 0.3 (0.4)a	0.7 (0.4)d	0.5 (0.4)c
Middle of winter	- 0.8 (0.1)a	- 0.8 (0.1)a	- 0.3 (0.1)b	- 0.3 (0.1)c
End of winter (March)	-0.4 (0.1)b	-0.8 (0.1)a	-0.2 (0.1)c	-0.2 (0.1)c
End of winter (April)	4.2 (1.0)b	5.8 (1.0)c	1.2 (1.0)a	4.7 (1.0)b
Growing season	15.9 (0.2)a	16.2 (0.2)b	17.6 (0.2)c	17.7 (0.2)d

CC, CS, GC, and GS indicate control plots below canopy, snow removal plots below canopy, control plots in canopy gap, and snow removal plots in canopy gap, respectively. The alphabet demonstrates the results of the multiple comparisons, and the values in parentheses indicate the standard error.

Table 3.1-S3 The daily mean, maximum (max), and minimum (min) air temperature (℃) among manipulations

		CC	CS	GC	GS
Beginning of winter	mean	-2.7 (0.3)a	-3.3 (0.3)a	-1.1 (0.3)b	-1.6 (0.3)b
	min	-4.0 (0.4)b	-4.8 (0.4)a	-1.4 (0.4)d	-2.7 (0.4)c
	max	-1.6 (0.3)a	-1.8 (0.3)a	-0.8 (0.3)b	-0.4 (0.3)b
Middle of winter	mean	-0.8 (0.1)a	-0.8 (0.1)a	-0.3 (0.1)b	-0.3 (0.1)b
	min	-0.8 (0.1)a	-0.9 (0.1)a	-0.3 (0.1)b	-0.3 (0.1)b
	max	-0.7 (0.1)a	-0.7 (0.1)a	-0.3 (0.1)b	-0.3 (0.1)b
End of winter (March)	mean	-0.2 (0.1)a	-0.1 (0.1)ab	-0.1 (0.1)ab	-0.1 (0.1)b
	min	-0.2 (0.1)b	-0.6 (0.1)a	-0.1 (0.1)c	-0.2 (0.1)bc
	max	-0.2 (0.2)a	-0.5 (0.1)b	-0.1 (0.2)a	-0.1 (0.2)a
End of winter (April)	mean	3.3 (0.5)b	4.3 (0.5)b	1.7 (0.5)a	4.6 (0.5)b
	min	1.3 (0.3)b	1.5 (0.3)b	0.5 (0.3)a	0.8 (0.3)ab
	max	6.5 (1.1)ab	7.7 (1.2)b	4.5 (1.2)a	13.3 (1.2)c
Growing season	mean	13.3 (0.4)a	13.3 (0.2)a	14.6 (0.4)b	14.6 (0.4)b
	min	9.8 (0.4)c	9.9 (0.4)d	9.4 (0.4)b	9.3 (0.4)a
	max	17.2 (0.6)a	17.0 (0.6)a	24.6 (0.6)b	26.0 (0.6)c

CC, CS, GC, and GS indicate control plots below canopy, snow removal plots below canopy, control plots in canopy gap, and snow removal plots in canopy gap, respectively. The alphabet demonstrates the results of the multiple comparisons, and the values in parentheses indicate the standard error.







Chapter 3.2

How tree canopy influences the spring phenological responses to decreased snow cover in four tree seedlings in a boreal forest

After

Cai, Y., Sawada, K., & Makoto, K. (2025). How Microclimate Influences the Spring Phenological Responses to Decreased Snow Cover in Four Tree Seedlings in a Boreal Forest. *scientific reports*, 15(10742). https://doi.org/10.1038/s41598-025-94523-y

3.2.1 Abstract

Heat accumulation and spring freeze, both strongly influenced by snow cover, are key factors regulating the onset of spring phenology. In forest ecosystems, decreased snow cover due to climate change may differently impact heat accumulation and the occurrence of spring freezes between canopy gap and under the tree canopy, leading to varied phenological responses. In this study, we examined how spring phenology of tree seedling responds to decreased snow cover across microsites and explored whether these responses are species-specific. We conducted a manipulation experiment in a planted forest in northern Hokkaido, Japan, establishing five canopy gap and five under canopy areas, each with control and snow removal plot. Four dominant tree species were planted in each plot. Snow removal significantly advanced budburst and leaf-out in both microsites, with a more pronounced effect observed in the canopy gap. Moreover, snow removal significantly advanced the budburst and leaf-out of all four species in the canopy gap, whereas only Abies sachalinensis showed significantly earlier budburst and leaf-out in the under canopy. Overall, our study demonstrated that projected winter warming led to a greater advancement of spring phenology in tree seedlings in canopy gap compared to under the canopy, with species-specific responses.

3.2.2 Introduction

Plant spring phenology is triggered by three major environmental cues, namely, heat accumulation (forcing), overwinter cold temperature accumulation (chilling), and photoperiod (Körner and Basler, 2010), which is highly sensitive to global warming (Fu et al., 2014; Piao et al., 2019). The general trend indicates that spring phenology typically advances under current rapid warming (Cleland et al. 2007; Vitasse et al. 2009), potentially leading to increased growth by an earlier onset and extending the length of the growing season (Augspurger 2008; Lee et a. 2024). However, the advancement of spring phenology does not necessarily occur in regions with decreased snow cover due to climate warming (IPCC 2021; Gottlieb and Mankin 2024). Earlier snowmelt can advance the timing of leaf-out in tree seedlings (Livensperger et al., 2016) because late-melting snowpacks, which keep near-surface temperatures lower than surrounding air temperatures, limit heat accumulation (Kelsey et al., 2021; Tyystjärvi et al., 2024). Conversely, early snowmelt can also delay leaf-out in tree seedlings (Sanders-DeMott et al., 2018) due to increased spring freeze events, which occur when plants are in a dehardening phase and vulnerable to freezes (Lenz et al., 2013; Chamberlain et al., 2019). Freeze damage can cancel the effect of an earlier onset of heat accumulation, diminishing or even reversing the advancement of spring phenology. Such varied spring phenological responses to decreased snow cover can be partly explained by the pattern of spring freeze occurrences under climate change when considered on a global scale (Liu et al., 2018; Zohner et al., 2020). Likewise, finer-scale microclimates, such as those influenced by forest structure that can outweigh the effects of macro-scale climate change on plant performance (Zellweger et al., 2020), also potentially resulting in greater variation in the spring phenological response of tree seedlings.

Forests are known to support diverse microclimates in the understory due to the structural complexity of the tree canopy (De Frenne et al., 2021). Given the significant differences in understory abiotic environment, such as solar radiation, air and soil temperature, and soil moisture

(Malcolm et al. 2001; Muscolo et al. 2014), forest microsites can be broadly categorized into under canopy and canopy gap (open areas). Snow cover typically appears later and melts earlier under the tree canopy than in canopy gaps due to the interception of snowfall by the canopy (Varhola et al. 2010; Roth and Nolin 2019). While the tree canopy acts as a buffer can moderate temperature fluctuations below the tree canopy to some extent (De Frenne et al. 2019; Chen et al. 2024), the shorter snow cover duration and thinner snowpack would cause more spring freeze events below the tree canopy (Fig. S1). Whereas, decreased snow cover can also lead to earlier start of heat accumulation (Kelsey et al. 2021). Because of the greater amount of direct solar radiation (Malcolm et al. 2001; Muscolo et al. 2014), the heat accumulation would be faster in the canopy gap even though the snow cover disappeared later (Fig. S1; Vitasse et al. 2021). In addition, decreased snow cover due to climate change would further increase the occurrence of spring freeze and accelerate the heat accumulation in both the under canopy and canopy gap, although the extent of these effects may vary between these microsites. As a result, decreased snow cover would lead to varied phenological responses across microsites, however, empirical research on how microclimates modulate spring phenological responses to decreased snow remains limited.

Furthermore, species-specific phenological timing (Chamberlain and Wolkovich 2021) is additional factor to consider. The timing of spring phonology can vary significantly among species (Augspurger 2013) due to the trade-off between the risk of damage from spring freezes events and resource accessibility and growing season length (Basler and Körner 2012; Chamberlain and Wolkovich 2021). For example, deciduous species generally exhibit earlier budburst and leaf-out compared to evergreen species (Panchen et al. 2014; Osada 2017), which may be because evergreen species with overwintering leaves can conduct photosynthesis in early spring while deciduous species without overwintering leaves must leaf-out as early as possible to start photosynthesis (Davi et al. 2011; Panchen et al. 2014). Under changing climate conditions, deciduous species that initiate spring phenology earlier may be more susceptible to increased spring freeze events due to decreased snow

cover. However, to the best of our knowledge, comprehensive studies have not been performed on the response of tree seedling spring phenology to decreased snow cover that consider both microclimate and species-specific flushing timings.

This study aimed to enhance our understanding of how microclimates within the forest ecosystem influence plant phenological responses to decreased snow cover and whether these responses are species-specific. I hypothesized that 1) decreased snow cover would advance spring phenology in canopy gap but result in no change or even a delay under the canopy and 2) late-flushing evergreen species would show clearer advancements in spring phenology in response to decreased snow cover compared to early-flushing deciduous species. To accomplish the goal, I conducted a manipulation experiment in a boreal forest in northern Hokkaido, Japan. I first established experimental sites in both the canopy gap, which were created by clear-cutting trees, and under the tree canopy. Since global warming has caused snow cover to appear later and disappear earlier, resulting in a shorter snow cover duration over the past few decades in this region (Makoto et al., 2022), I performed a snow removal experiment to delay snow cover appearance and advance snowmelt in both microsites. To examine how the flushing time of tree seedlings influences spring phenological responses to decreased snow, I selected two deciduous and two evergreen species that are dominant in this region and planted them in each manipulation plot. Since spring phenology can affect the growth and survival of tree seedlings by determining the start of the growing season and the likelihood of freeze damage (Forrest et al. 2010), understanding how the spring phenology of tree seedlings with different flushing timings in both canopy gap and under canopy areas can provide crucial insights into future tree regeneration.

3.2.3 Materials and Methods

3.2.3.1 Study site and experimental design and snow removal manipulation

For the site discretion, please refer to 3.1.2.1. In each plot, 20 tree seedlings from each of the four representative boreal mixed forest species (deciduous broadleaced: *Acer pictum* Thunb. Subsp. *Mono* (Maxim.) and *Quercus crispula* var. *crisp*, evergreen conifer: *Abies sachalinensis* and *Picea glehnii*, Fig. 3.2-1) were planted in October 2022 (1,600 tree seedlings). *A. pictum* and *Q. crispula* were brought from OSAKA NURSERY, and *A. sachalinensis* and *P. glehnii* were brought from SASAKI SANGYO Co., Ltd., both located in the Hokkaido region. Seedlings with heights ranging from approximately 20 to 40 cm were selected for plantation in the field to prevent ontogenetic differences in phenological responses (Vitasse 2013).

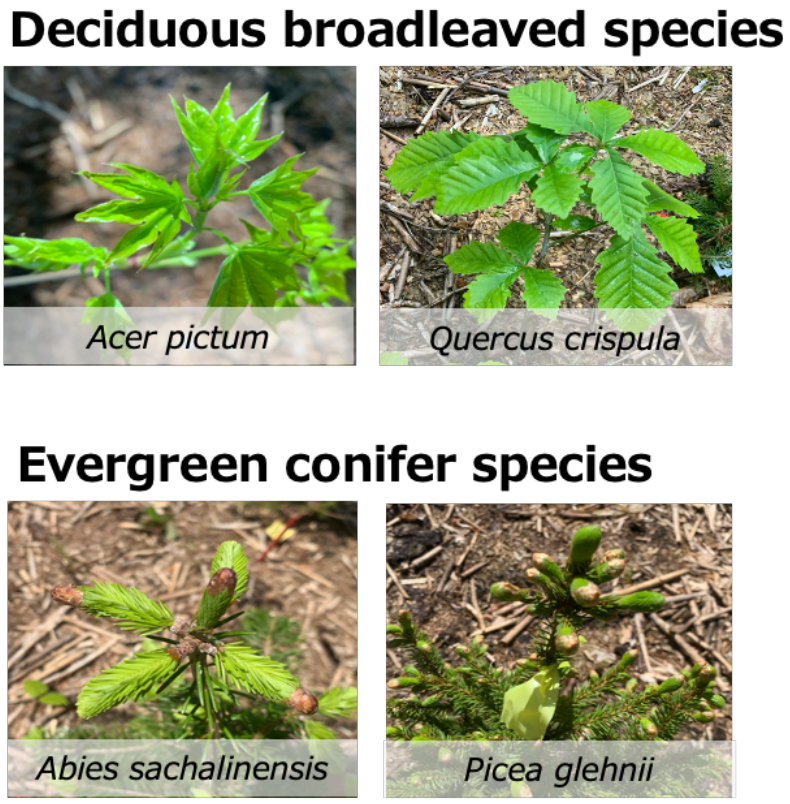


Fig. 1 Four species of tree seedings planted in each manipulation plot.

Snow was removed twice in December and once in March to reduce the snow cover duration following the local environmental change trend and based on the Representative Concentration Pathways (RCP) 6.0 scenario, which projects a global mean surface temperature increase of 2.2°C (with a likely range of 1.4 to 3.1°C) between 2081 and 2100 (IPCC 2021). The detail was mentioned in 3.1.3.2.

3.2.3.2 Phenology observation

Following the Biologische Bundesanstalt, Bundessortenamt und CHemische Industrie (BBCH) scale (Meier, 2001), I recorded budburst (BBCH stage 07, which is defined as the onset of sprouting or bud breaking) and leaf-out (BBCH stage 11, which is defined as first leaves unfolded) twice or thrice a week until the tree seedlings reached leaf-out in 2023 and 2024. I randomly selected 5 to 7 seedlings of each species from each manipulation plot at five sites to observe their phenology in 2023 (560 seedlings in the first stage). In 2024, I targeted all surviving seedlings for phenological observations (totally 1383 seedlings in the first stage). Tree seedlings that were browsed by mammals or had died before leaf-out were excluded. Consequently, a total of 460 and 957 seedlings were included in the subsequent analyses for 2023 and 2024, respectively.

3.2.3.3 Calculation of chilling, forcing, and spring freezes

Air temperature and light data loggers (HOBO Pendant, Onset Computer, Bourne, MA, USA) were installed in the centre of each plot and set up in October 2022 to record data every 30 min. To measure the air temperature experienced by the tree seedlings, data loggers were located 20 cm above the ground level. Chilling was recorded as days with daily mean temperatures between 0 and 5 °C from 1st November until leaf-out of individual seeding (Peaucelle et al. 2019). Growing degree days, which is used as a measure of heat accumulation (Reaumur, 1735), was calculated by

accumulating the average daily temperature above a base temperature of 5 °C according to previous studies (Clark et al. 2014). The accumulation of growing degree days starts from 1st January (Murray et al. 1989) and continues until leaf-out of individual seeding. The data did not accumulate when the mean daily temperature was below 5 °C. I started recording the spring freeze after snow removal manipulation in March until the end of May. Following budburst, -1.7 ℃ represented the threshold of soft freeze that can damage certain forest areas (Augspurger 2013) while -2.2 ℃ represented the threshold of hard freeze that can damage large forest areas (Schwartz et al. 2002). Following these criteria, I counted the number of soft- and hard-spring freezes that occurred in each plot.

3.3.3.4 Statistical analysis

I performed linear mixed-effects models (LMMs) to estimate the effects of tree canopy absence, snow removal, and their interaction on heat accumulation, chilling accumulation, and the number of soft and hard spring freeze ('lme4' package, Bates et al. 2015). The models included site and year as random effects. I also performed LMMs to estimate the effects of tree canopy absence, snow removal, and their interaction on budburst and leaf-out timing for each species. Species, site, and year were treated as random effects when analyzing budburst and leaf-out. All the response variables were log-transformed to ensure the normality. Multi-comparisons were performed for heat accumulation, chilling days, the number of soft and hard spring freeze, budburst, and leaf-out date. I initially calculated the estimated marginal means (EMMs) for the parameters ('emmeans' package, Lenth 2023), then, performed the multi-comparisons using the pairs function and applied Bonferroni correction to account for the increased risk of Type I errors associated with multiple tests. I also used a Bayesian generalized linear mixed model with a Gaussian family (Bayesian Regression Models using Stan, v.2.20.4, Bürkner 2017) to predict budburst and leaf-out dates for each species. The model included microsite (under canopy, canopy gap), treatment (control, snow removal), and their interaction as fixed effects, with site and year as random effects. The posterior distribution was

estimated based on a non-informative prior distribution using a flat uniform distribution across the parameter values of the Bayesian model using the Markov chain Monte Carlo (MCMC) method, which was implemented in RStudio using the package rstan, version 2.31 (Stan Development Team, 2022). Non-informative priors play a crucial role in objective Bayesian analysis (Shemyakin, 2014). For each model, I ran four chains, each with 10,000 iterations, among which 2,000 were warm-up iterations. I considered the effects to be statistically significant if the lower and upper 95% confidence intervals did not cross zero. The Bayesian generalized linear mixed models were all convergent (Rhat < 1.1). All statistical analyses were conducted using R software, v.4.1.0 (R Development Core Team 2021).

3.2. 4 Results

3.2.4.1 Chilling accumulation, heat accumulation, and late spring freeze events

The number of soft spring freeze occurred greater in snow removal plots compare to control plots, however, the significancy was only detected in the under canopy ($P < 0.05$; Fig. 3.2-2a), but not in the canopy gap ($P = 0.67$; Fig. 3.2-2a). The number of hard spring freeze also occurred greater in snow removal plots compared to control plots, however no statistical significance was detected ($P > 0.05$; Fig. 3.2-2b). Heat accumulation started earlier in the snow removal plots compared to the control plots in both the under canopy and the canopy gap (Fig. 3.2-3). And snow removal had the significant positive effect on heat accumulation (10-days summed) in both the under canopy and canopy gap, leading to greater heat accumulation in snow removal plots compared to the control plots since the late April (e.g. DOY 111: $F_{1,17} = 11.94$, $P < 0.01$; Fig. 4). Although heat accumulation (10-days summed) began earlier under canopy than in the canopy gap due to the earlier snowmelt, the heat accumulation in the canopy gap significantly surpassed that under canopy once the snow cover disappeared from the canopy gap (e.g. DOY 141: $F_{1,18} = 13.428$, $P < 0.01$; Fig. 3.2-3). Chilling

accumulated significantly greater below tree canopy compared to canopy gap ($F_{1,283} = 7.57$, $P < 0.01$; Fig. 3.2-S3).

3.2.4.2 Differences in spring phenology response to reduced snow between the canopy gap and under canopy areas

The absence of tree canopy had significant negative effect on budburst ($F_{1,1381} = 34.98$, $P < 0.001$) and leaf-out ($F_{1,1381} = 43.79$, $P < 0.001$), leading to the earlier budburst and leaf-out in the canopy gap compared to the under canopy (Fig. 3.2-4, Table 3.2-1). The snow removal also had significant negative effect on budburst ($F_{1,1380} = 106.98$, $P < 0.001$) and leaf-out ($F_{1,1379} = 97.77$, $P < 0.001$), leading to the earlier budburst and leaf-out in the snow removal plots compared to the control plots (Fig. 3.2-4, Table 3.2-1). In addition, significant interactions between the absence of tree canopy and snow removal were detected for the budburst ($F_{1,1380} = 4.35$, $P < 0.05$) and leaf-out ($F_{1,1380} = 8.03$, $P < 0.01$), indicating that snow removal advanced budburst and leaf-out more in canopy gap compared to the under canopy (Fig. 3.2-4, Table 3.2-1).

3.2.4.3 Species-specific responses

Significant differences in budburst and leaf-out dates were observed among the species ($F_{1,1380} = 732.3$, $P < 0,001$; Fig. 3.2-5). Specifically, *A. pictum* exhibited the earliest budburst and leaf-out, followed by *Q. crispula*, *A. sachalinensis*, and *P. glehnii*. The absence of tree canopy had significant negative effect on budburst and leaf-out of *Q. crispula* (leaf-out: $F_{1,250} = 6.72$, $P < 0.05$), *A. sachalinensis* (budburst: $F_{1,397} = 50.59$, $P < 0.001$; leaf-out: $F_{1,396} = 44.01$, $P < 0.001$), and *P. glehnii* (budburst: $F_{1,350} = 120.50$, $P < 0.001$; leaf-out: $F_{1,351} = 82.27$, $P < 0.001$), leading to the earlier budburst and leaf-out in canopy gap compared to under canopy, except for budburst of *Q. crispula* ($F_{1,251} = 3.52$, $P = 0.062$; Table 3.2-2). On the other hand, the absence of tree canopy had the

significant positive effect on budburst of *A. pictum* ($F_{1,366} = 2.03$, $P < 0.01$; Table 3.2-2), leading to the later budburst in canopy gap compared to under canopy. Snow removal had a significant negative effect on the budburst (*A. pictum*: $F_{1,367} = 11.56$, $P < 0.001$; *Q. crispula*: $F_{1,252} = 15.38$, $P < 0.01$; *A. sachalinensis*: $F_{1,397} = 92.11$, $P < 0.001$; *P. glehnii*: $F_{1,350} = 31.93$, $P < 0.001$) and leaf-out (*A. pictum*: $F_{1,367} = 10.45$, $P < 0.01$; *Q. crispula*: $F_{1,251} = 12.61$, $P < 0.01$; *A. sachalinensis*: $F_{1,397} = 69.02$, $P < 0.001$; *P. glehnii*: $F_{1,351} = 35.42$, $P < 0.001$) of all four species (Table 3.2-2, Fig. 3.2-5). Additionally, significant interactions between the absence of tree canopy and snow removal were detected for the budburst and leaf-out of *A. sachalinensis* (budburst: $F_{1,391} = 6.39$, $P < 0.05$; leaf-out: $F_{1,350} = 8.44$, $P < 0.01$) and *P. glehnii* (budburst: $F_{1,397} = 6.04$ $P < 0.01$; leaf-out: $F_{1,351} = 7.67$, $P < 0.01$), indicating that snow removal advanced budburst and leaf-out more pronouncedly in canopy gap compared to the under canopy (Table 3.2-2). By conducting the multi-comparison, I found significant earlier budburst in the snow removal compared to the control plot for *Q. crispula* ($P < 0.01$), *A. sachalinensis* ($P < 0.001$), and *P. glehnii* ($P < 0.001$) in canopy gap, however only *A. sachalinensis* ($P < 0.001$) showed significant earlier budburst in snow removal plot also in the under canopy (Fig. 3.2-5a). Likewise, I found significant earlier leaf-out in the snow removal compared to the control plot for all four species ($P < 0.05$), however only *A. sachalinensis* ($P < 0.001$) showed significant earlier leaf-out in snow removal plot also in the under canopy (Fig. 3.2-5b).

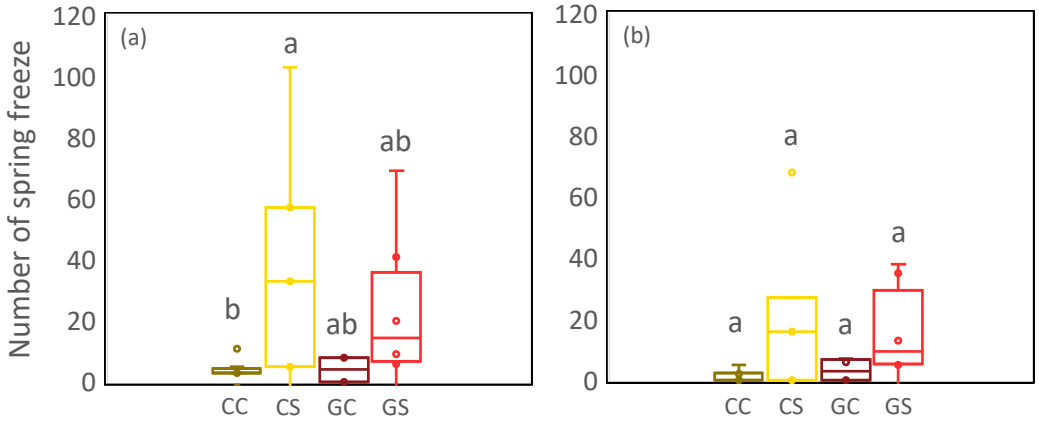


Figure 3.2-2 The number of soft (a) and hard (b) spring freezes in under canopy control plot (CC), under canopy reduced snow plot (GS), canopy gap control plot (GC), and canopy gap reduced snow plot (GS) in 2023 (a) and 2024 (b). The median (horizontal line), first and third quartiles (box edges), and the maximum and minimum values were shown in the figure. Different letters indicate statistically significant differences among the manipulation plots.

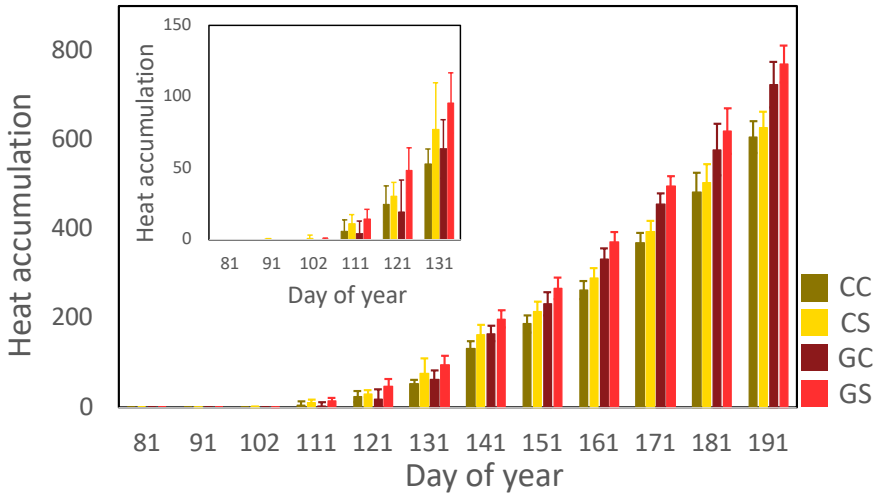


Fig. 3.2-3 10-days summed heat accumulation (growing degree hours) in under canopy control plot (CC), under canopy snow removal plot (CS), canopy gap control plot (GC), and canopy gap snow removal plot (GS). The small figure is an enlargement of the day of year (DOY) period from 91 to 131.

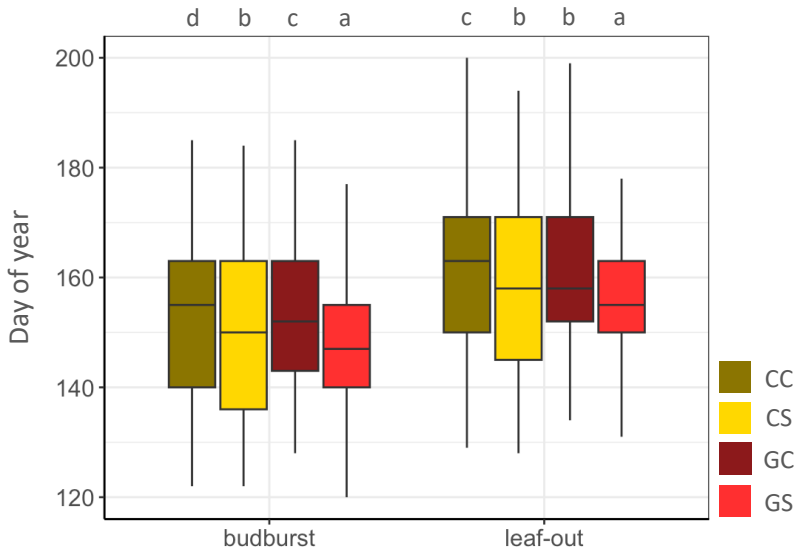


Fig. 3.2-4 Budburst and leaf-out date in under canopy control plot (CC), under canopy reduced snow plot (GS), canopy gap control plot (GC), and canopy gap reduced snow plot (GS) when considering all four species together in 2023 (a) and 2024 (b). The median (horizontal line), first and third quartiles (box edges), and the maximum and minimum vales were showed in the figure. Different letters indicate statistically significant differences among the manipulation plots.

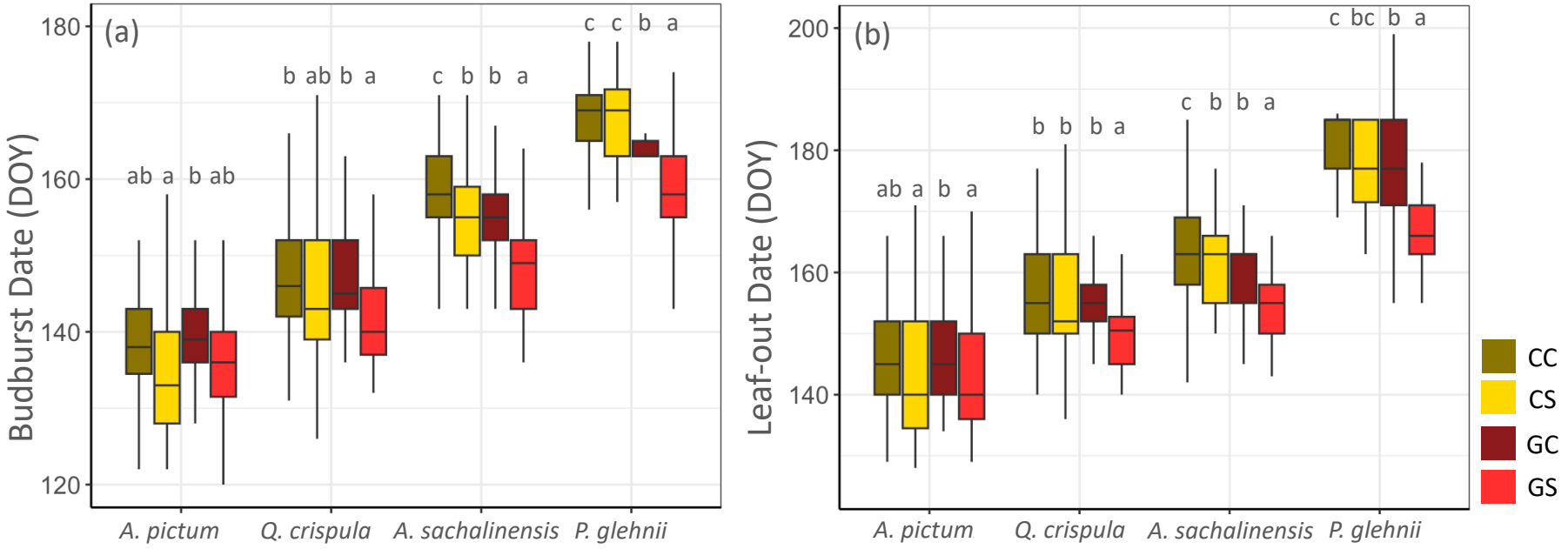


Fig. 3.2-5 Budburst (a) and leaf-out (b) of A. pictum, Q. crispula, A. sahalinensis, and P. glehnii in under canopy control plot (CC), under canopy reduced snow plot (GS), canopy gap control plot (GC), and canopy gap reduced snow plot (GS) in 2023 (a) and 2024 (b). The median (horizontal line), first and third quartiles (box edges), and the maximum and minimum vales were showed in the figure. Different letters indicate statistically significant differences among the manipulation plots.

Table 3.2-1 Results of mixed-model ANOVA on timing of budburst and leaf-out including all species.

	Absence of tree canopy			Snow removal			Absence of tree canopy× Snow removal		
	df	F	*P*	df	F	*P*	df	F	*P*
Budburst	1,1381	34.98	**< 0.001**	1,1380	106.98	**< 0.001**	1,1380	4.35	**< 0.05**
Leaf-out	1,1381	43.79	**< 0.001**	1,1379	97.77	**< 0.001**	1,1380	8.03	**< 0.01**

Bold value indicates the significance of the effects.

Table 3.2-2 Results of mixed-model ANOVA on timing of budburst and leaf-out for each species.

		Absence of tree canopy			Snow removal			Absence of tree canopy× Snow removal		
		df	F	*P*	df	F	*P*	df	F	*P*
Budburst	*A. pictum*	1,366	4.62	**< 0.01**	1,367	11.56	**< 0.001**	1,364	0.0080	0.93
	Q. crispula	1,251	3.52	0.062	1,252	15.38	**< 0.01**	1,249	0.56	0.46
	A. sachalinensis	1.397	50.59	**< 0.001**	1,397	92.11	**< 0.001**	1,397	6.39	**< 0.05**
	P. glehnii	1.350	120.50	**< 0.001**	1,350	31.93	**< 0.001**	1,350	8.44	**< 0.01**
Leaf-out	*A. pictum*	1,366	2.03	0.15	1,367	10.45	**< 0.01**	1,364	0.34	0.56
	Q. crispula	1,250	6.72	**< 0.05**	1,251	12.61	**< 0.01**	1,253	2.11	0.15
	A. sachalinensis	1,396	44.01	**< 0.001**	1,397	69.02	**< 0.001**	1, 397	6.04	**< 0.05**
	P. glehnii	1,351	82.27	**< 0.001**	1,351	35.42	**< 0.001**	1,351	7.67	**< 0.01**

Bold value indicates the significance of the effects.

3.2.5 Discussion

Our study clarified that the absence of tree canopy can advance budburst and leaf-out (Table 3.2-1, Fig. 3.2-4, 3.2-5). Snow cover disappeared later, and the onset of heat accumulation occurred later in the canopy gap compared to the under canopy (Fig. 3.2-3). However, once the snow cover had completely disappeared, heat accumulation in the canopy gap exceeded that in the under-canopy (Fig. 3.2-3), driven by higher air temperatures resulting from direct solar radiation (Fig. 3.2-S2; Muscolo et al. 2014). This explained the earlier budburst and leaf-out in the canopy gap (Fig. 3.2-4; Vitasse et al. 2021). As the tree canopy absorbs red light, seedlings growing beneath the canopy experience a lower red/far-red ratio compared to those in the canopy gap (Turnbull and Yates 1993). The reduction in red light may weaken the perception of day length (Zohner and Renner 2015), potentially leading to a delayed onset of spring phenology below tree canopy (Fig. 3.2-4). Additionally, since insufficient chilling accumulation delays the onset of spring phenology by increasing the amount of forcing temperature required for leaf-out (Beil et al. 2021; Chamberlain and Wolkovich 2021), it can be expected that budburst and leaf-out would have occurred even earlier in the canopy gap if chilling accumulation had been greater (Fig. 3.2-S3). Alternatively, it could simply be that, although chilling accumulation was lower in the canopy gap, it was still sufficient to meet the requirement for seedlings to become increasingly sensitive to warmth. Furthermore, I found that the decreased snow cover can advance budburst and leaf-out in both the under canopy and canopy gap, with significantly greater advancement in the canopy gap (Table 3.2-1, Fig. 3.2-4), consistent with our first hypothesis. Snow removal would advance the onset of heat accumulation and in both the canopy gap and the under canopy compared to the control. As more direct solar radiation reaches the canopy gap, while the tree canopy intercepts solar radiation (De Frenne et al., 2021), I expected that snow removal would accelerate heat accumulation, with a more pronounced effect in the canopy gap. However, our results did not support this expectation, as the effect of snow removal on the heat accumulation was similar in two microsites (Absence of tree canopy × Snow removal: $P > 0.05$; Fig. 3.2-3). Unlike heat

accumulation, wIe found that the significantly greater number of spring freezes in the snow removal plots compared to the control plots in the under canopy, but not in the canopy gap (Fig. 3.2-2a). The increased spring freeze events elevate the risk of freeze damage to plants in the dehardening phase, when they are particularly vulnerable to freezing, and partially diminish the advancement of spring phenology (Lenz et al., 2013; Chamberlain and Wolkovich 2021). This likely explains the more pronounced advancement of budburst and leaf-out in the snow removal plots in the canopy gap compared to the under canopy (Table 3.2-1). However, it should be noted that the contribution of both spring freezes and heat accumulation due to decreased snow cover can vary depending on the interannual variations in spring temperature dynamics and regional climate differences. Spring temperature dynamics vary from year to year. If the spring temperatures are extremely low, decreased snow cover would lead to more spring freezes. In this case, the effect of increased spring freezes may outweigh the effects of faster heat accumulation, resulting in delayed spring phenology. Furthermore, the risk of spring freezes varies globally and is expected to increase in Asia and Europe under climate change (Liu et al. 2018; Zohner et al., 2020). Therefore, in these regions, the effects of spring freezes may outweigh those of heat accumulation, leading to delayed spring phenology under decreased snow cover. Additionally, it is important to investigate how altered spring phenology may influence the performance of tree seedlings in the subsequent growing season. Advanced budburst and leaf-out can enhance plant survival and growth by increasing carbon assimilation in early spring (Lee and Ibáñez 2021; Lee et al. 2024). However, increased spring freeze events may have carry-over negative effects on the survival and growth of tree seedlings (Chamberlain and Wolkovich 2021). As the next generation of the forest ecosystem, it is crucial to examine how altered spring phenology, resulting from decreased snow cover, may influence the recruitment of tree seedlings across different microsites.

In addition, I also observed species-specific spring phenological responses to decreased snow cover between the canopy gap and the under canopy (Table 3.2-2, Fig. 3.2-5). Contrary to our

second hypothesis, early-flushing species *A. pictum* and *Q. crispula* also showed the significant advancement of leaf-out in response to decreased snow cover in the canopy gap, similar to late-flushing species *A. sachalinensis* and *P. glehnii* (Fig. 3.2-5b). However, *A. sachalinensis* was the only species that showed a significant advancement of budburst and leaf-out in the snow removal plot compared to the control plot in the under canopy (Fig. 3.2-5). The lack of significant responses in *A. pictum* and *Q. crispula* to decreased snow cover under the canopy is likely explained by the timing of spring freezes, which coincide with their dehardening and flushing phases, making their winter buds and/or leaves vulnerable to damage (Chamberlain et al. 2019), thus negating the effect of faster heat accumulation. On the other hand, *A. sachalinensis*, with its relatively late leaf-flushing timing, can avoid freeze damage to swollen winter buds, which likely explains its significant advancement of spring phenology in response to decreased snow cover, even under the canopy. Overall, our study demonstrated that spring phenological responses to decreased snow cover in two microsites can be species-specific, which partially explained by the species-specific phenological timings. However, it is important to note that snow removal did not have a significant effect on the leaf-out of *A. pictum* and *Q. crispula* based on the results of the Bayesian generalized linear model (Table 3.2-S1, 3.2-S2). This suggests that the two-year field experiment may have been insufficient to fully capture the patterns in phenological responses to decreased snow cover across microsites with varying abiotic conditions (e.g., thermal and light dynamics influencing phenological responses [Ward et al. 2018; Vitasse et al. 2021]) or to disentangle the underlying mechanisms driving these responses. Therefore, long-term observations that account for interannual variability in climatic conditions are needed to develop a more comprehensive understanding of how microclimates influence the phenological responses of understory vegetation to decreased snow cover, as well as the mechanisms underlying these responses.

Lastly, although I did not consider the effects of browsing damage on spring phenology, it may be a significant negative factor that delays the timing of spring phenology (Guiden et al. 2018).

Reduced snow can make it easier for herbivores, such as deer and rodent, to locate tree seedlings (Giroux et al. 2016), increasing the risk of browsing on winter bud, which can delay budburst (Quiring and McKinnon 1999; Carroll and Quiring 2003). Given the range expansion and increased population of deer, along with their associated browsing damage in Japan—particularly in the Hokkaido region where I conducted our research (Takatsuki 2009)—a comprehensive study that incorporates the effects of herbivory is needed for more accurate predictions of seedling spring phenology in response to decreased snow.

3.2.6 Conclusion

Our study showed that in a boreal forest ecosystem, decreased snow cover can advance the budburst of tree seedlings in both under canopy and canopy gap with more pronounced advancement in the canopy gap. The varied influence of decreased snow cover on the occurrence of freeze events in spring between canopy gap and under canopy may explain the difference of spring phenological responses to decreased snow between these microsites. Moreover, while the decreased snow cover caused significant advancement on budburst and leaf-out in the canopy gap for all four species, only *A. sachalinensis* showed the significant earlier budburst and leaf-out in the snow removal plot compared to the control plot also in the under canopy. Overall, our study demonstrated the varying responses of spring phenology to decreased snow cover across microsites and species. However, further research is needed to confirm the trends observed in this study and to examine how shifts in spring phenology due to decreased snow affect tree seedling performance in the subsequent season.

3.2.7 Appendix

3.2.7.1 Supplemental figures

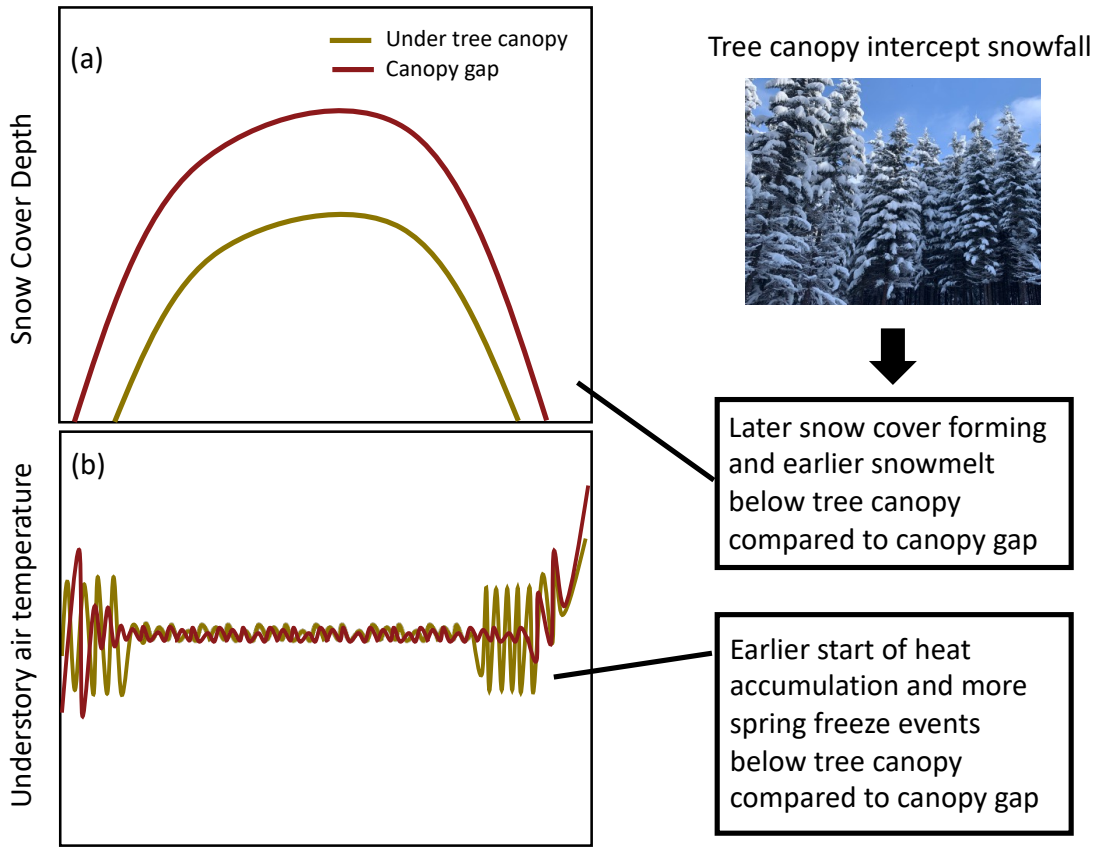


Fig. 3.2-S1 Schematic illustration of the effects of tree canopy on snow cover depth/duration (a) and understory air temperature dynamics (b).

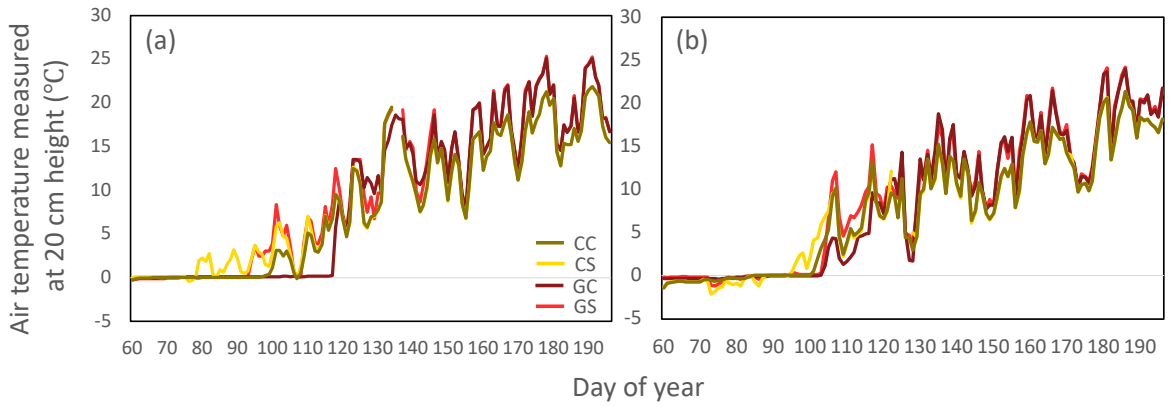


Fig. 3.2-S2 Mean daily air temperature measured at 20 cm height in under canopy control plot (CC), under canopy reduced snow plot (GS), canopy gap control plot (GC), and canopy gap reduced snow plot (GS) in 2023 (a) and 2024 (b).

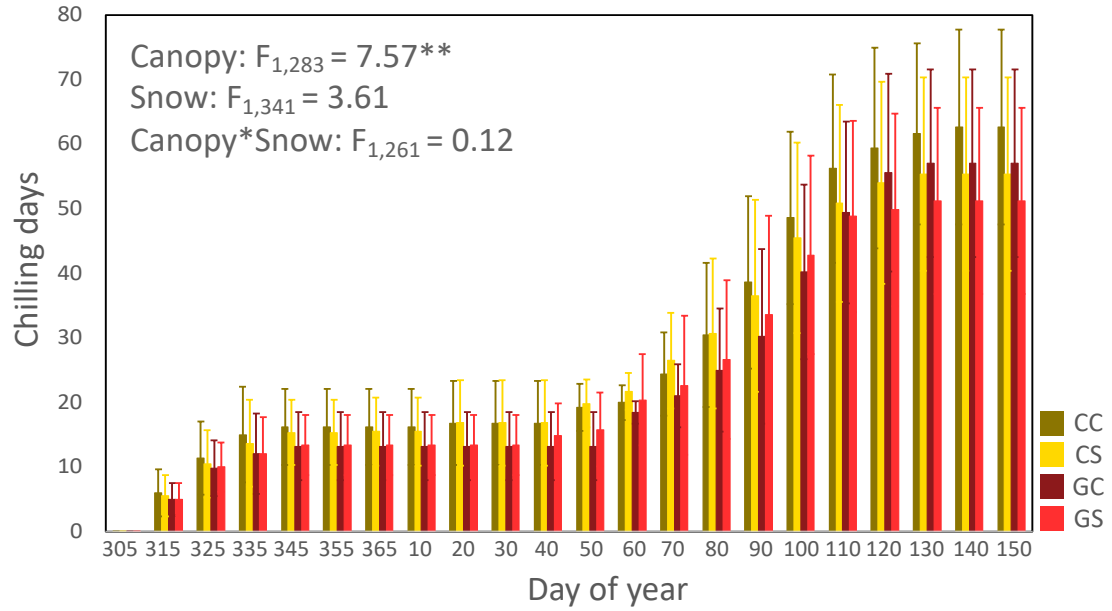


Fig. 3.2-S3 Number of chilling days in under canopy control plot (CC), under canopy snow removal plot (CS), canopy gap control plot (GC), and canopy gap snow removal plot (GS). Chilling accumulated faster below tree canopy compared to canopy gap ($F_{1, 283}$ = 7.57, P < 0.01).

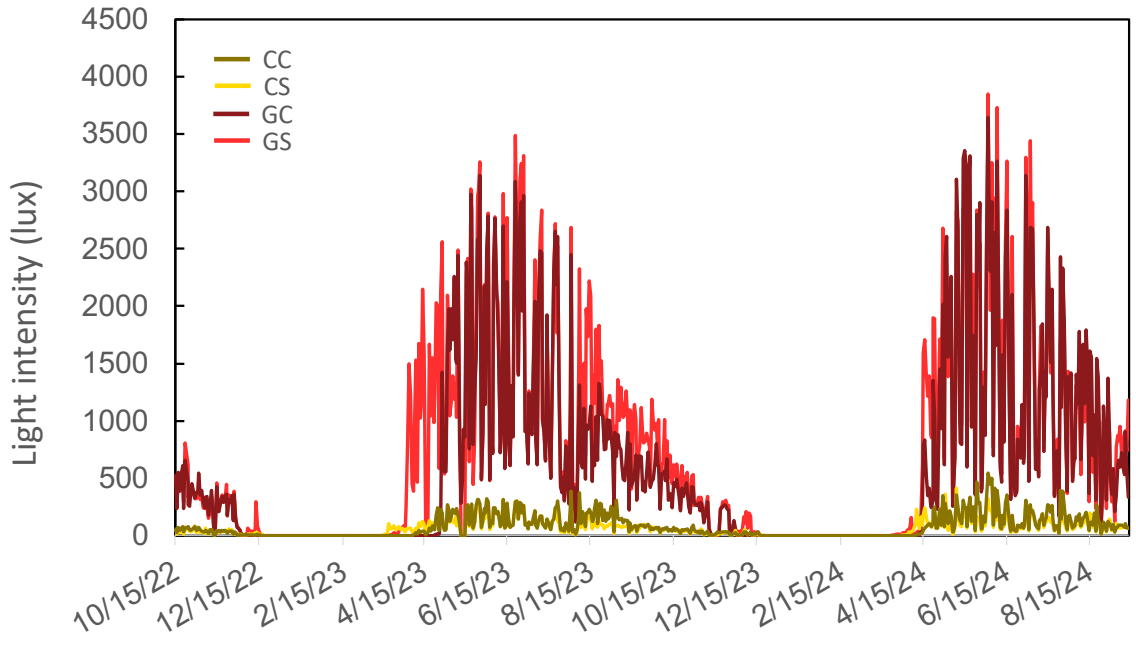


Fig. 3.2-S4 The dynamics of light intensity in under canopy control plot (CC), under canopy snow removal plot (CS), canopy gap control plot (GC), and canopy gap snow removal plot (GS).

3.2.7.2 Supplemental tables

Table 3.2-S1 Summary of the Bayesian generalized linear model showing the effects of tree canopy, snow removal manipulation, and their interactions on the timing of budburst and leaf-out.

	Tree canopy				Snow removal				Tree canopy×Snow removal			
	Estimate	Error	l-95% CI	u-95% CI	Estimate	Error	l-95% CI	u-95% CI	Estimate	Error	l-95% CI	u-95% CI
Budburst	- 1.91	0.58	**-3.03**	**- 0.77**	0.66	0.66	**-4.74**	**-2.12**	- 1.90	0.85	**- 3.58**	**- 0.20**
Leaf-out	- 2.01	0.63	**-3.25**	**-0.78**	-3.24	0.73	**-4.64**	**-1.81**	-2.73	0.93	**-4.57**	**-0.93**

The effects are statistically significant if the lower (l) and upper (u) 95% confidence intervals (CIs) do not cross zero. Bold values indicate that the effects are significant.

Table 3.2-S2 Summary of the Bayesian generalized linear model showing the effects of tree canopy, snow removal manipulation, and their interactions on the timing of budburst and leaf-out of each species.

		Tree canopy				Snow removal				Tree canopy×Snow removal			
		Estimate	Error	l-95% CI	u-95% CI	Estimate	Error	l-95% CI	u-95% CI	Estimate	Error	l-95% CI	u-95% CI
Budburst	*A. pictum*	2.04	1.33	-0.54	4.64	-2.84	1.39	**-5.49**	**-0.11**	-0.33	1.91	-4.13	3.27
	Q. crispula	-1.52	1.66	-4.76	1.71	-3.68	1.80	**-7.27**	**-0.16**	-1.81	2.47	-6.63	3.08
	A. sachalinensis	-2.88	0.76	**-4.38**	**-1.38**	-4.24	0.96	**-6.13**	**-2.38**	-2.80	1.18	**-5.09**	**-0.50**
	P. glehnii	-5.01	0.81	**-6.61**	**-3.41**	-1.78	1.01	-3.73	0.20	-3.35	1.23	**-5.76**	**-0.96**
Leaf-out	*A. pictum*	2.04	1.41	-0.71	4.84	-2.40	1.45	-5.24	0.41	-1.38	2.00	-5.29	2.55
	Q. crispula	-1.45	1.62	-4.60	1.50	-2.39	1.72	-5.80	1.05	-3.28	2.41	-7.82	1.48
	A. sachalinensis	-2.62	0.79	**-4.17**	**-1.07**	-3.49	0.97	**-5.43**	**-1.58**	-2.90	1.21	**-5.27**	**-0.52**
	P. glehnii	-5.67	1.18	**-7.94**	**-3.36**	-2.91	1.46	**-5.79**	**-0.18**	-4.61	1.74	**-8.06**	**-1.14**

The effects are statistically significant if the lower (l) and upper (u) 95% confidence intervals (CIs) do not cross zero. Bold values indicate that the effects are significant.





Chapter 3.3

Do tree canopies provide microrefugia for tree seedlings under decreased snow cover?

After

Cai, Y. & Makoto, K. (submitted). Do tree canopies provide microrefugia for tree seedlings under decreased snow cover? *Ecosystems.*

3.3.1 Abstract

Decreased snow cover generally reduces insulation, increasing freeze events and drought stress, which can negatively affect tree seedling survival and growth. However, few studies have examined how tree canopy influences seedling responses to reduced snow cover. Previous research suggests that tree canopy modifies the effects of decreased snow on understory temperature and spring phenology, leading to colder temperatures under the canopy and earlier leaf-out in canopy gaps. Since both factors influence seedling survival and growth, the responses may differ between microsites. To test this, I conducted a two-year snow removal experiment in a planted *Picea glehnii* forest, comparing seedling survival and growth between below canopy and canopy gap microsites. I hypothesized that (1) survival would decline with snow removal, particularly below the canopy, and (2) growth would increase in canopy gaps but decrease below the canopy due to reduced snow cover. Five sites were established in each microsite, with both control and snow removal plots at each site. Four dominant tree species were planted, and seedling survival and growth were recorded. Our results showed snow removal increased mortality of *Q. crispula* and *P. glehnii* only below the canopy, and increased mortality of *A. sachalinensis* in both microsites with greater increase under the canopy compared to the canopy gap. Snow removal showed the significantly negative effect on shoot and near ground diameter growth of *A. sachalinensis* and *P. glehnii* below the canopy, but not in the canopy gap. While no significant influence of snow removal was detected on the growth of *A. pictum* and *Q. crispula*. These findings confirmed our expectation that understory plant can respond differently to decreased snow even within the forest. Also, the results indicate that tree canopy, by intercepting snowfall, can reduce the insulating effect provided by snow cover, resulting in a harsher environment for understory vegetation during winter. Overall, our results highlight the importance of integrating

vegetation-driven environmental heterogeneity into assessments of plant responses to climate change.

3.3.2 Introduction

Global warming, combined with shifting precipitation patterns, decreases seasonal snow cover duration and/or depth worldwide (IPCC 2021; Gottlieb and Mankin 2024). Forests, particularly those in snow-dominated regions, are highly sensitive to these changes in snow cover. Reduced snowpack alters air and soil temperature regimes, increasing the frequency of frost events and freeze-thaw cycles (Groffman et al. 2001; Campbell et al. 2005). Such changes can have cascading effects on seedling performance, ultimately influencing forest composition and ecosystem functions (Kreyling 2014; Sanders-DeMott et al. 2017). The previous studies generally detected the negative responses of seedling performance, such as decrease in survival (Drescher and Thomas 2013; Guiden et al. 2018) and growth (Martz et al. 2016; Domisch et al. 2018). Although many previous studies have investigated the effects of decreased snow cover, most were conducted in common gardens, greenhouses, or nearby open fields adjacent to forests, all with uniform environmental conditions (Drescher and Thomas 2013; Martz et al. 2016; Sanders-DeMott et al. 2017, but see Guiden et al. 2018 that also tested how forest canopy composition influence seedling responses to decreased snow cover).

Forests likely exhibit the most diverse environmental heterogeneity, owing to their three-dimensional canopy structure (Zellweger et al. 2020; De Frenne et al. 2021). Specifically, horizontal heterogeneity can result in significant variations in snow cover depth and duration, even within the same forest (Varhola et al. 2010; Sun et al. 2022). These differences are most pronounced between areas beneath the tree canopy and those in canopy gaps, which are primarily formed by tree mortality or branch fall due to natural disturbances (Muscolo et al. 2014). Snow cover tends to be thinner, accumulate later, and melt earlier under the tree canopy compared to canopy gaps (Chapter 3-1), particularly in evergreen forests, where foliage remains during winter (Harpold et al. 2015; Roth and Nolin 2019). Consequently, understory temperatures below the canopy can drop more sharply and

frequently than in canopy gaps due to reduced snow cover insulation (Chapter 3-1). Moreover, it has become evident that the tree canopy modulates the response of understory temperature to decreased snow cover: earlier snowmelt leads to lower understory temperatures beneath the canopy but has no such effect in canopy gaps (Chapter 3-1). Given that the response of understory temperature to decreased snow cover can vary across microsites within the forest, it is reasonable to expect that the seedlings inhabiting in these areas will also exhibit different responses.

Here, I assess how seedling survival and growth respond differently to decreased snow cover under the tree canopy and in canopy gaps. To address this, I established two hypotheses. First, we hypothesized that decreased snow cover would enhance seedling growth in spring in canopy gaps but not under the tree canopy. Second, we hypothesized that decreased snow cover would reduce seedling survival and growth under the tree canopy, but not in canopy gaps. To test these hypotheses, I conducted a snow manipulation experiment at two microsites, under the tree canopy and in canopy gaps, within a planted *Picea glehnii* forest in northern Hokkaido, Japan.

3.3.3 Material and Methods

3.3.3.1 Site description, experimental design, and snow removal manipulation

For site description and seedling planting information, please refer to Sections 3.1.3.1 and 3.2.3.1. Seedlings with heights ranging from approximately 20–40 cm were selected for field planting to minimize the effects of initial variation in tree size. For details on the snow removal manipulation, please refer to Section 3.1.3.2.

3.3.3.2 Frequency of temperatures crossed 0°C

Using both air temperature at seedling height and soil temperature data (see Section 3.1.3.3), I

calculated the frequency of temperature fluctuations across 0°C throughout the winter period (November to April).

3.3.3.3 Mortality and growth of seedlings

Seedling mortality was recorded in June and September of 2023 and 2024 for each individual seedling (0: alive; 1: dead). Shoot length was measured in June and September 2024 for all surviving evergreen conifer seedlings. Additionally, diameter near the ground (D0) was measured in October 2022, and in June and September of both 2023 and 2024 for all surviving seedlings. Growth in shoot length and D0 was calculated as the difference between the current and the previous measurement.

3.3.3.4 Statistical analysis

In order to understand the interactive effects of tree canopy and decreased snow cover on seedling mortality of each species, I constructed a generalized linear mixed model with a binomial error structure ('lme4' package in R; Bates et al. 2015). Seedling mortality of each species in June and September in both experimental years were used as the response variable, and experimental site (n = 5) was set as a random effect. Additionally, to examine the interactive effects of tree canopy and decreased snow cover on seedling growth of each species, I constructed linear mixed models ('lme4' package in R; Bates et al. 2015). Seedling D0 and both spring and annual shoot growth of each species in June and September across both experimental years were used as the response variables, with the experimental site (n = 5) set as a random effect. Furthermore, to examine the interactive effect of tree canopy and decreased snow cover on frost number, I also constructed a linear mixed model with the frequency of air temperature crossings at 0°C at seedling height (ATC_0) used as the response variables, and with the experimental site set as a random effect. I did not test the frequency

of soil temperature crossing at 0°C since soil temperature did not drop below 0°C in any of the treatment plots during the two-year experimental period (Fig. 3.1-5). In order to ensure normality of the residuals, I log-transformed the response variables before fitting the linear mixed model. Statistical significance for the fixed effects was tested using Type III sum of squares via the anova function ('car' package in R; Fox and Weisberg 2019), which is appropriate for models with interactive terms, allowing us to assess each effect after adjusting for others. Multiple comparisons were performed for D0 growth and shoot growth of each species and the frost number across the four manipulation plots. First, I calculated the estimated marginal means (EMMs) for the parameters ('emmeans' package in R; Lenth 2023), then performed the pairwise comparisons using the pairs function and applied Bonferroni correction to account for the increased risk of Type I errors associated with multiple tests. Statistical significance was defined at $P < 0.05$, and all analyses were performed in R version 4.1.0 (R Development Core Team 2021).

3.3.4 Results

3.3.4.1 Frequency of temperatures crossed 0°C

Both absence of tree canopy ($F_{1,17} = 5.40$, $P = 0.03$) and snow removal ($F_{1,17} = 25.15$, $P < 0.001$) had significant effects on the frequency of ATC_0. The frequency of ATC_0 was significantly higher in the snow removal plots compared to the control plots in both microsites, with slightly higher frequency of ATC_0 in the snow removal plot under the tree canopy compared to the canopy gap (Fig. 3.3-1).49

3.3.4.2 Mortality of tree seedlings

Snow removal and its interaction with absence of tree canopy had significant influence on the mortality of *Q. crispula* seedlings recorded in September 2023 (snow removal: $\chi^2 = 5.40$, $P = 0.02$;

snow removal × absence of tree canopy: $\chi^2 = 8.29$, $P = 0.004$), June 2024 (snow removal: $\chi^2 = 5.44$, $P = 0.02$; snow removal × absence of tree canopy: $\chi^2 = 5.07$, $P = 0.02$), and September 2024 (snow removal: $\chi^2 = 6.34$, $P = 0.01$; snow removal × absence of tree canopy: $\chi^2 = 6.27$, $P = 0.01$; Table 3.3-1, Fig. 3.3-2). For the mortality of *A. sachalinensis* seedlings, the significant effect of absence of tree canopy and snow removal were detected in September 2023 (absence of tree canopy: $\chi^2 = 11.93$, $P < 0.001$; snow removal: $\chi^2 = 6.70$, $P = 0.01$), June 2024 (absence of tree canopy: $\chi^2 = 19.34$, $P < 0.001$; snow removal: $\chi^2 = 23.34$, $P < 0.001$), and September 2024 (absence of tree canopy: $\chi^2 = 16.13$, $P < 0.001$; snow removal: $\chi^2 = 21.93$, $P < 0.001$; Table 3.3-1, Fig. 3.3-2). For the mortality of *P. glehnii* seedlings, the significant effect of absence of tree canopy, snow removal, and their interaction were detected in June 2024 (absence of tree canopy: $\chi^2 = 12.17$, $P < 0.001$; snow removal: $\chi^2 = 10.27$, $P = 0.002$; snow removal × absence of tree canopy: $\chi^2 = 4.83$, $P = 0.03$), and September 2024 (absence of tree canopy: $\chi^2 = 19.34$, $P < 0.001$; snow removal: $\chi^2 = 23.34$, $P < 0.001$; snow removal × absence of tree canopy: $\chi^2 = 0.22$, $P = 0.01$; Table 3.3-1, Fig. 3.3-2).

3.3.4.3 Growth of tree seedlings

Snow removal had significant influence on spring shoot growth of *A. sachalinensis* seedlings ($F_{1,290} = 4.46$, $P = 0.04$; Table 3.3-S1), while no significant difference between the snow removal plots and the control plots were detected in both under the tree canopy and in the canopy gap (Fig. 3.3-3a). Also, absence of tree canopy ($F_{1,284} = 388.87$, $P < 0.001$), snow removal ($F_{1,284} = 16.17$, $P < 0.001$), and their interaction ($F_{1,284} = 9.08$, $P = 0.003$) all had significant influence on annual shoot growth of *A. sachalinensis* and seedlings (Table 3.3-S1). For *P. glehnii* seedlings, absence of tree canopy (spring: $F_{1,271} = 74.17$ $P < 0.001$; annual: $F_{1,231} = 210.69$, $P < 0.001$), snow removal (spring: $F_{1,271} = 4.87$, $P = 0.03$; annual: $F_{1,231} = 6.76$, $P = 0.01$), and their interaction (spring: $F_{1,271} = 19.47$, $P < 0.001$; annual: $F_{1,231} = 23.56$, $P < 0.001$) all had significant influence on both spring and annual shoot growth (Table 3.3-S1). Multiple comparison also showed the significant lower annual shoot growth of *A.*

sachalinensis seedlings and both spring and annual shoot growth of *P. glehnii* seedlings in the snow removal plots compared to the control plots only below the tree canopy, but not in the canopy gap (Fig. 3.3-3).

Significant influence of snow removal on the growth of diameter near the ground (D0) of *A. sachalinensis s*eedlings was detected in September 2024 ($F_{1,283} = 12.25$, $P < 0.001$; Table 3.3-S2), while no significant difference between the snow removal plots and the control plots were detected in both under the tree canopy and in the canopy gap (Fig. 3.3-4b). For *P. glehnii* seedlings, significant influence of snow removal on the D0 growth was detected in September 2024 ($F_{1,256} = 4.68$, $P = 0.03$) and significant influences of the interaction between snow removal and absence of tree canopy on the D0 growth were detected in June 2024 ($F_{1,267} = 9.98$, $P = 0.002$) and September 2024 ($F_{1,256} = 22.51$, $P < 0.001$; Table 3.3-S2). Multiple comparison also detected the significantly greater D0 growth of *P. glehnii* seedlings in the snow removal plots compared to the control plots only in the canopy gap in June 2024 (Fig. 3.3-4a) and the significantly lower D0 growth of *P. glehnii* seedlings in the snow removal plots compared to the control plots only in the canopy gap in September 2024 (Fig. 3.3-4b).

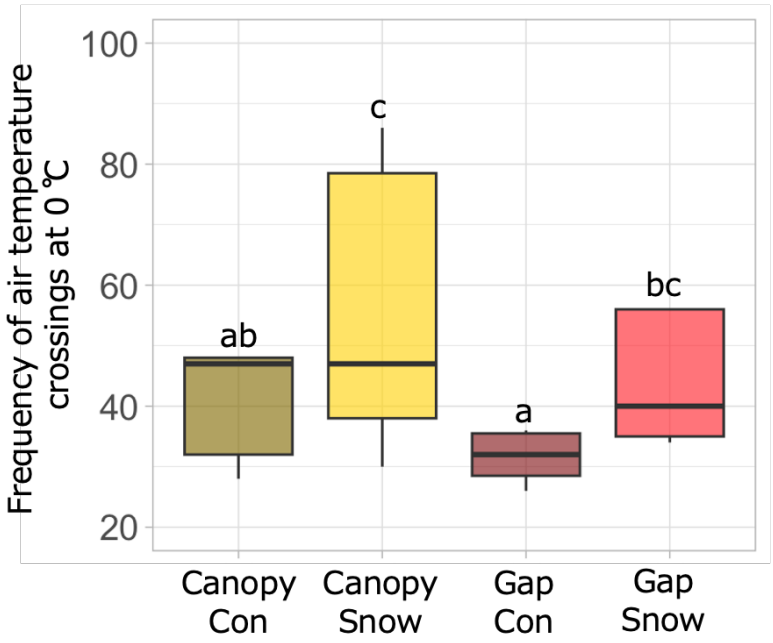


Fig. 3.3-1 Frequency of air temperature experienced by seedlings crossings at 0℃ across control plot under tree canopy, snow removal plot under tree canopy, control plot in canopy gap, and snow removal plot in canopy gap. "Con" denotes control plots, and "Snow" denotes snow removal plots. Lowercase letters indicate the results of multiple comparisons

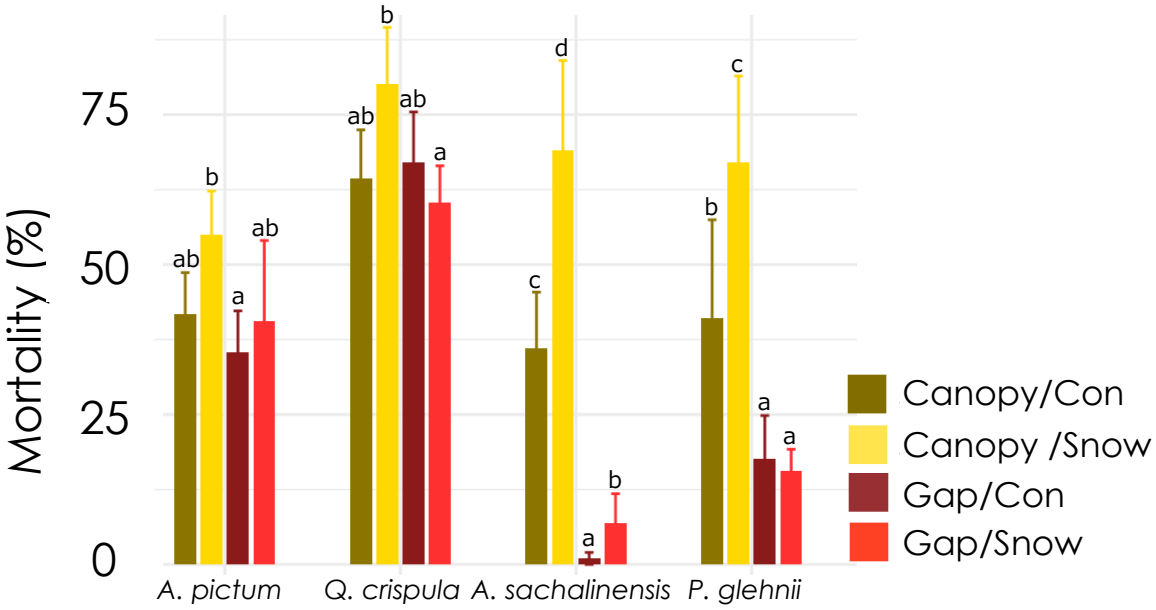


Fig. 3.3-2 Mortality of tree seedling recorded in September 2024. Canopy/Con, Canopy/Snow, Gap/Con, and Gap/Snow indicated control plot under tree canopy, snow removal plot under tree canopy, control plot in canopy gap, and snow removal plot in canopy gap, respectively.

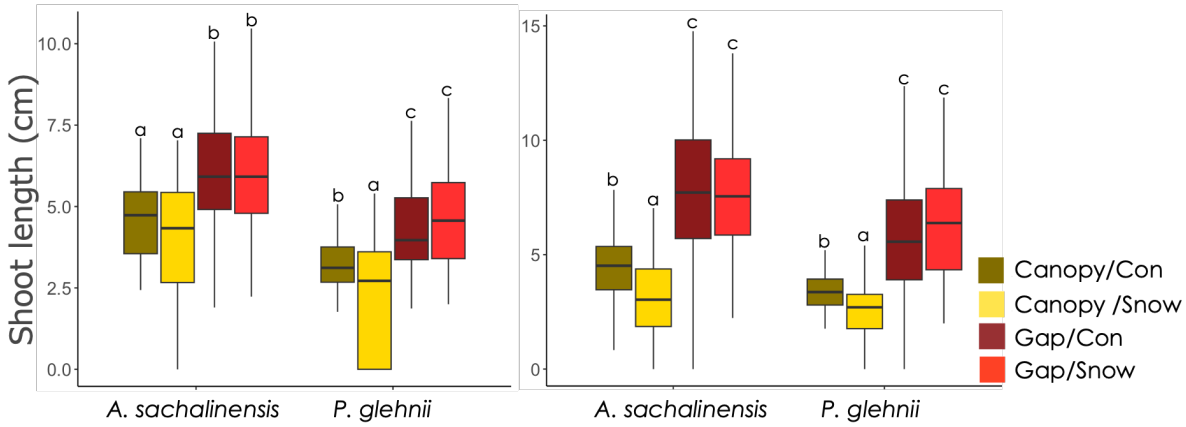


Fig. 3.3-3 Shoot growth of seedlings measured in June 2024 (a) and in September 2024 (b). Canopy/Con, Canopy/Snow, Gap/Con, and Gap/Snow indicated control plot under tree canopy, snow removal plot under tree canopy, control plot in canopy gap, and snow removal plot in canopy gap, respectively.

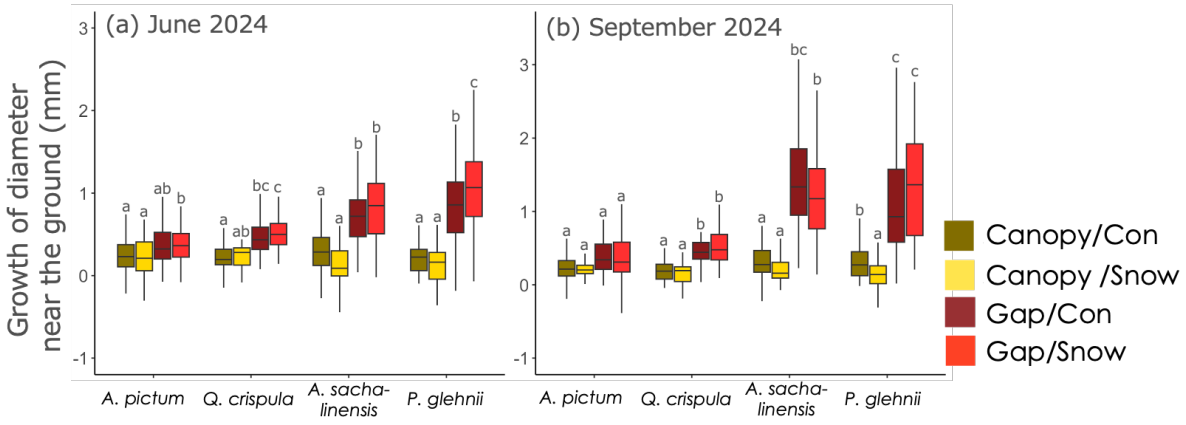


Fig. 3.3-4 Growth of diameter near the ground of seedlings measured in June 2024 (a) and in September 2024 (b). Canopy/Con, Canopy/Snow, Gap/Con, and Gap/Snow indicated control plot under tree canopy, snow removal plot under tree canopy, control plot in canopy gap, and snow removal plot in canopy gap, respectively.

Table 1 Summary of generalized linear mixed models (GLMMs) with the effects of microsites, snow cover treatment, and their interactions effect on death of each tree species in June and September of 2023 and 2024.

Season	species	Absence of tree canopy			Snow removal			Absence of tree canopy:Snow removal		
		χ^2	df	P value	χ^2	df	P value	χ^2	df	P value
Jun.23'	*A. pictum*	1.55	1	0.21	2.05	1	0.15	0.14	1	0.71
	Q. crispula	1.52	1	0.22	1.48	1	0.22	0.89	1	0.35
	A. sachalinensis	3.55	1	0.06	0.28	1	0.60	0.43	1	0.51
	P. glehnii	1.35	1	0.24	0.16	1	0.69	0.20	1	0.66
Sep.23'	*A. pictum*	1.92	1	0.17	0.07	1	0.79	0.56	1	0.45
	Q. crispula	0.20	1	0.66	**5.40**	**1**	**0.02**	**8.29**	**1**	**0.004**
	A. sachalinensis	**11.93**	**1**	**< 0.001**	**6.70**	**1**	**0.01**	0.79	**1**	0.37
	P. glehnii	2.75	1	0.10	0.48	1	0.49	0.14	1	0.71
Jun.24'	*A. pictum*	0.84	1	0.36	2.11	1	0.15	0.97	1	0.33
	Q. crispula	0.01	1	0.93	**5.44**	**1**	**0.02**	**5.07**	**1**	**0.02**
	A. sachalinensis	**19.34**	**1**	**< 0.001**	**23.34**	**1**	**< 0.001**	0.22	1	0.64
	P. glehnii	**12.17**	**1**	**< 0.001**	**10.27**	**1**	**0.002**	**4.83**	**1**	**0.03**
Sep.24'	*A. pictum*	0.84	1	0.36	3.76	1	0.06	0.66	1	0.42
	Q. crispula	0.15	1	0.70	**6.34**	**1**	**0.01**	**6.27**	**1**	**0.01**
	A. sachalinensis	**16.13**	**1**	**< 0.001**	**21.93**	**1**	**< 0.001**	0.22	1	0.64
	P. glehnii	**19.34**	**1**	**< 0.001**	**23.34**	**1**	**< 0.001**	**0.22**	**1**	**0.01**

3.3.5 Discussion

3.3.5.1 Seedling mortality and growth responded differently to decreased snow cover between microsites

I expected greater growth in the snow removal plots compared to the control plots in the canopy gap because advanced leaf-out can increase carbon assimilation in early spring (Augspurger 2008; Lee and Ibáñez 2021). However, contrary to our expectations, seedlings did not exhibit significantly greater growth in the snow removal plots compared to the control plots in the canopy gap (Fig. 3.3-3a, 3.3-4a). The only exception was the D0 growth of *P. glehnii*, which was greater in the snow removal plots than in the control plots in the canopy gap (Fig. 3.3-4a). One possible explanation is that air temperatures remained too low during early spring for most seedlings to effectively perform photosynthesis (Ensminger and others 2004).

Partially consistent with our hypothesis, snow removal significantly increased the mortality of seedlings only under the tree canopy, but not in the canopy gap for *Q. crispula* and *P. glehnii* seedlings (Table 3.3-1). Although snow removal significantly increased the mortality of *A. sachalinensis* seedlings in both microsites, the highest mortality was found in the snow removal plots under the tree canopy (Fig. 3.3-2). Also, snow removal significantly decreased the growth of seedlings only under the tree canopy, but not in the canopy gap for both evergreen conifer species (Fig. 3.3-4, 3.3-S2). These results can be related with the different responses of daily minimum temperature measured at seedings height to decreased snow cover between microsites (Fig. 3.1-4). At the beginning of winter, the daily minimum temperature measured at seedings height was lower in the snow removal plots compared to the control plots in both microsites. However, it needs to be noted that as the daily minimum temperature measured at seedings height is lower under the tree canopy compared to the canopy gap at the first place, the daily minimum temperature measured at seedings height was significantly lower in the snow removal plots under the tree canopy compared to that in the

canopy gap (Fig. 3.1-4). Additionally, at the end of winter (March), snow removal only significantly decreased the daily minimum temperature measured at seedings height under the tree canopy, but not in the canopy gap (Fig. 3.1-4). Taken together, these results suggest that in the snow removal plots, the duration of exposure to sub-zero air temperatures without the insulating effect of snow cover was longer under the tree canopy than in the canopy gap. In addition, although the significancy was not detected, the frequency of ATC_0 was highest in the snow removal plots under the tree canopy (Fig. 3.3-1). Consequently, seedlings in the snow removal plots under the tree canopy were likely subjected to greater cold stress than those in the canopy gap, which may explain why the markedly higher mortality and reduced growth performance were observed only in the snow removal plots under the tree canopy. However, it is important to note that the snow removal treatment also decreased the air temperature experienced by seedlings at the beginning of winter and significantly increased the frequency of ATC_0 in the canopy gap (Fig. 3.1-4, Fig. 3.3-1), which indicates that seedlings in the snow removal plots in the canopy gap also experienced greater cold stress compared to those in the control plots. Nonetheless, as seedlings in the canopy gap had access to sufficient light during the growing season (Ritter and others 2005; Muscolo and others 2014), I believe that light availability, rather than decreased snow cover, primarily governs seedling survival and growth in the canopy gap. This is consistent with a previous study suggesting that light availability plays a more pivotal role in seedling growth than warming (Xu and others 2023).

Almost no significant effects of snow removal or its interaction with canopy cover on the growth of deciduous broadleaved seedlings were detected (Table 3.3-S2, Fig. 3.3-4). However, it is reasonable to expect that deciduous broad-leaved seedlings would be more vulnerable to cold damage from snow removal, especially in spring, due to their earlier leaf-out timing compared to evergreen conifer seedlings (Panchen and others 2014; Cai and others 2025). One possible reason why I did not detect a negative effect of snow removal on the growth of deciduous broad-leaved seedlings may be the influence of biotic factors such as herbivory and bacterial infections. I observed substantial

damage caused by both large mammal and insect herbivory, as well as bacterial infections, across all manipulation sites on both *A. pictum* and *Q. crispula* seedlings (Fig. 3.3-S3). These biotic stresses may have masked the potential impact of snow removal, resulting in no clear differences in growth for these species.

3.3.5.2 Implication

It is well-known that low temperatures, combined with strong solar radiation in open spaces, can increase desiccation and photoinhibition and result in greater mortality, particularly for evergreen species that retain their leaves during the dormant season (Egerton and others 2000; Luoranen and others 2022). Contrary to these earlier findings, both mortality and growth in our study showed little difference between control and snow removal plots within canopy gaps (Table 3.3-1, Fig. 3.3-2). Unlike a previous study conducted in a large-scale clear-cut area where substantial photoinhibition was observed (Kitao et al. 2018), our research was conducted in relatively small canopy gaps surrounded by mature *Picea glehnii* trees. This residual canopy likely reduced the intensity of direct solar radiation within the gaps, thereby helping to protect evergreen seedlings from desiccation and photoinhibition. Thus, retaining part of the canopy as sheltering trees may help the survival and growth of planted evergreen conifer seedlings in this region, even under ongoing reductions in snow cover due to climate change.

Recent trends suggest that tree canopy, through their temperature-buffering effect, can provide microrefugia for understory plants and slow their range shifts under climate change (Lenoir and others 2017; Zellweger and others 2019). However, our results indicate that tree canopy may not necessarily serve as a buffer under climate change condition during winter season in the snowy region. In these regions, the snow interception effect would exceed the temperature-buffering effect of tree canopy, resulting in more severe environment for understory species (Fig. 3.3-S1). In addition, climate change

has been shown to drive a directional shift in forests, from boreal conifer-dominated to cool-temperate broadleaf-dominated forests, in regions where our experiment was conducted (D'Orangeville and others 2016; Hiura and others 2019; Brice and others 2020). Especially in northern Hokkaido, hotter and drier summers associated with global warming (Reich and others 2022), combined with the high density of dwarf bamboo species in canopy gaps (Fukuzawa and others 2015), may make the area under the tree canopy a more favorable habitat for the regeneration of evergreen conifer species. It was assumed that, under such environmental conditions, evergreen conifer seedlings would show a preference for regenerating under the tree canopy. However, the results of this study suggest that both the survival and growth rate of evergreen conifer seedings would significantly decline under the tree canopy when snow cover decreases. Therefore, the dominance shift from evergreen conifer-dominated forests to broadleaf-dominated forests is expected to accelerate in this region, especially under continued climate warming and reduced winter snow accumulation.

3.3.6 Conclusion

By conducting a snow removal experiment under the tree canopy and in the canopy gap in a planted evergreen conifer forest in northern Hokkaido, I found that seedling mortality and growth responded differently to decreased snow cover between the microsites. For *Q. crispula* and *P. glehnii*, seedling mortality only significantly decreased under the tree canopy in response to increased snow cover, while no significant change occurred in the canopy gap. For *A. sachalinensis*, seedling mortality increased in both microsites with decreased snow cover, with the significantly highest mortality observed in the snow removal plots under the tree canopy. Additionally, the growth of evergreen conifer seedlings significantly decreased only under the tree canopy, not in the canopy gap. Overall, these results highlight that understory plant responses to decreased snow cover within a forest ecosystem are not uniform and can vary depending on environmental heterogeneity induced by the

tree canopy.

3.3.7 Appendix

3.3.7.1 Supplemental figure

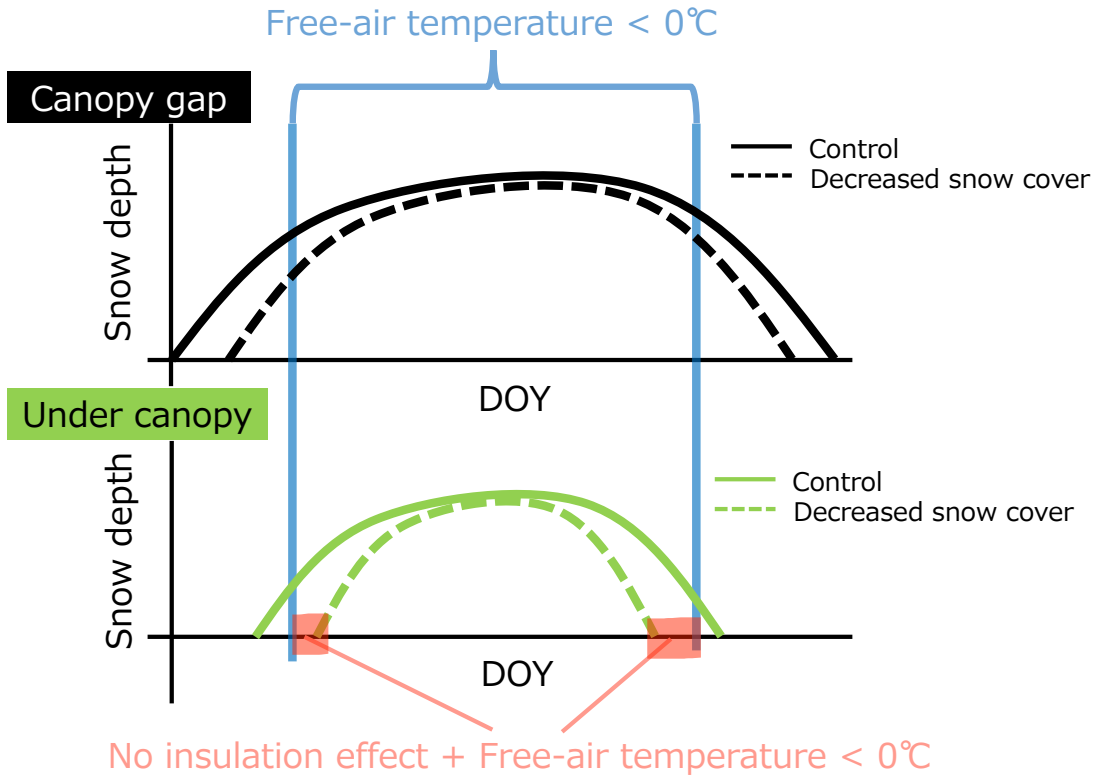


Fig. 3.3-S1 The conceptual diagram illustrates how soil temperature and understory air temperature experienced by seedlings differ between canopy gaps and areas under the tree canopy when snow cover is reduced.

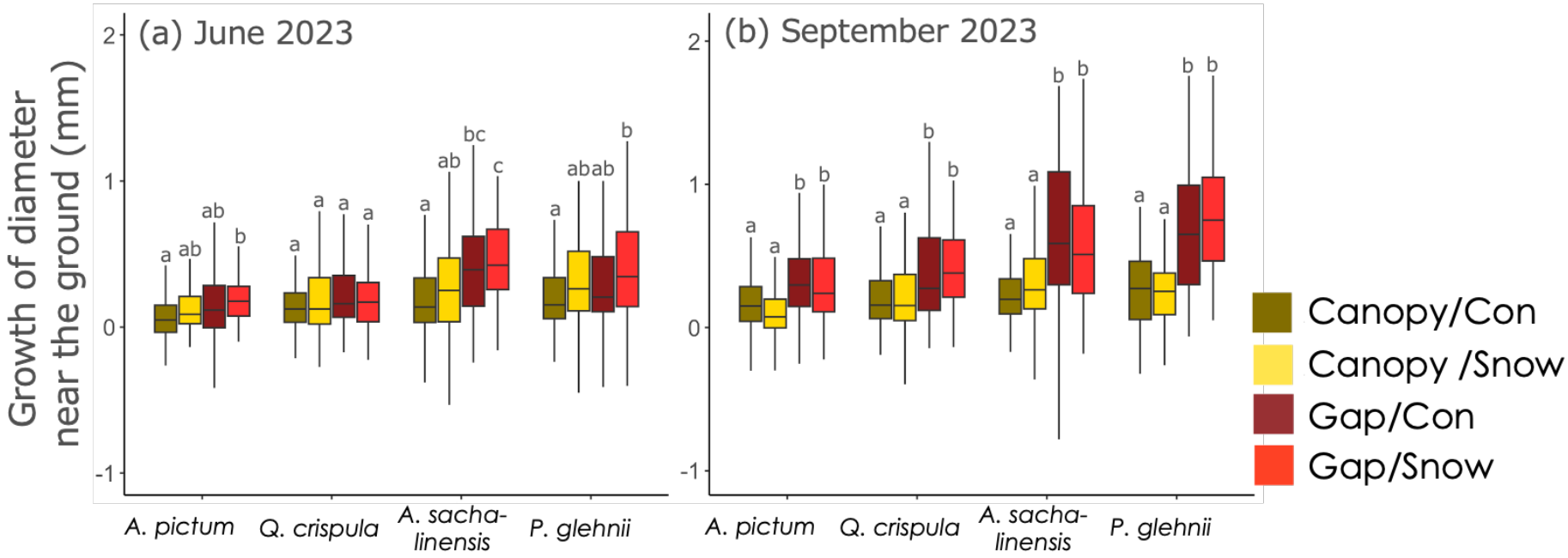


Fig. 3.3-S2 Growth of diameter near the ground of seedlings measured in June 2023 (a) and in September 2023 (b). Canopy/Con, Canopy/Snow, Gap/Con, and Gap/Snow indicated control plot under tree canopy, snow removal plot under tree canopy, control plot in canopy gap, and snow removal plot in canopy gap, respectively.

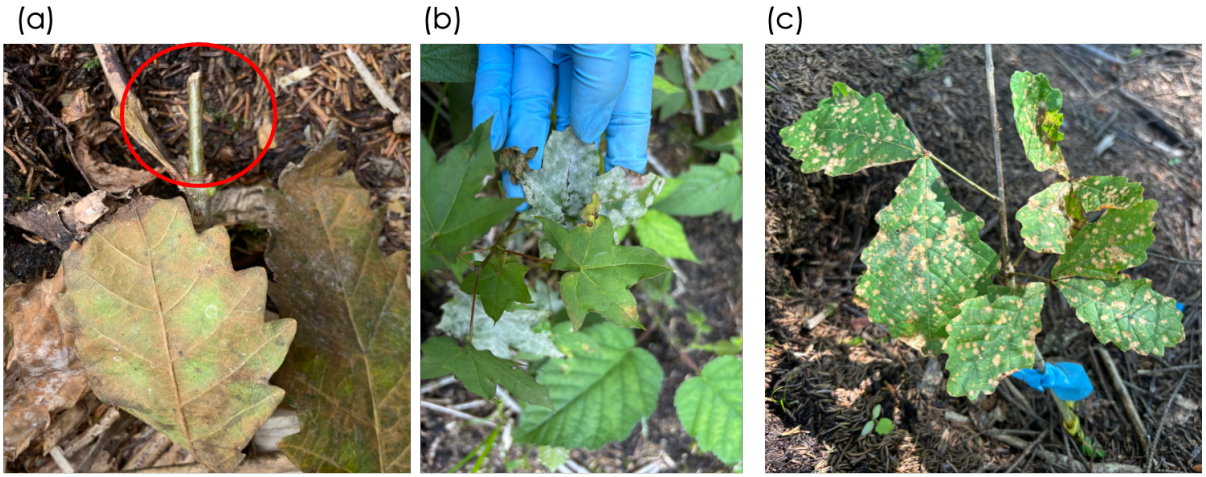


Fig. 3.3-S3 Biotic factors affecting deciduous broadleaved species: apical bud of *Q. crispula* browsed by deer (a); pathogen infection in *A. pictum* (b) and *Q. crispula* (c).

3.3.7.2 Supplemental tables

Table 3.3-S1 Summary of linear mixed models (LMMs) with the effects of microsites, snow cover treatment, and their interactive effect on spring and annual shoot growth of evergreen conifer seedlings

		Absence of tree canopy			Snow removal			Absence of tree canopy:Snow removal		
Variable	Species	df	F	P value	df	F	P value	df	F	P value
Spring shoot growth	*A. sachalinensis*	**1,290**	**45.05**	**< 0.001**	**1,290**	**4.46**	**0.04**	1,290	1.16	0.28
	P. glehnii	**1,271**	**74.17**	**< 0.001**	**1,271**	**4.87**	**0.03**	**1,271**	**19.42**	**< 0.001**
Annual shoot growth	*A. sachalinensis*	**1,284**	**388.87**	**< 0.001**	**1,284**	**16.17**	**< 0.001**	**1,284**	**9.08**	**0.003**
	P. glehnii	**1,231**	**210.69**	**< 0.001**	**1,195**	**6.76**	**0.01**	**1,214**	**23.56**	**< 0.001**

Table 3.3-S2 Summary of linear mixed models (LMMs) with the effects of microsites, snow cover treatment, and their interactive effect on relative growth of diameter near the ground of each tree species in June and September 2023, and June 2024.

Season	species	Absence of tree canopy			Snow removal			Absence of tree canopy:Snow removal		
		df	F	P value	df	F	P value	df	F	P value
Jun.23'	*A. pictum*	**1,347**	**10.83**	**0.001**	**1,347**	**5.65**	**0.02**	1,347	0.02	0.90
	Q. crispula	1,337	0.91	0.34	1,337	0.01	0.94	1,337	0.56	0.46
	A. sachalinensis	**1,357**	**31.16**	**< 0.001**	1,357	2.67	0.10	1,357	0.42	0.52
	P. glehnii	**1,353**	**4.28**	**0.04**	**1,353**	**6.26**	**0.01**	1,353	1.02	0.31
Sep.23'	*A. pictum*	**1,357**	**48.60**	**< 0.001**	1,357	3.16	0.08	1,357	0.29	0.59
	Q. crispula	**1,325**	**37.66**	**< 0.001**	1,325	0.94	0.33	1,325	1.05	0.31
	A. sachalinensis	**1,318**	**66.69**	**< 0.001**	1,315	0.90	0.34	1,317	2.64	0.11
	P. glehnii	**1,312**	**110.67**	**< 0.001**	1,311	1.87	0.17	1,311	1.91	0.17
Jun.24'	*A. pictum*	**1,228**	**17.36**	**< 0.001**	1,228	0.28	0.60	1,228	1.34	0.25
	Q. crispula	**1,130**	**27.27**	**< 0.001**	1,130	1.75	0.19	1,121	0.52	0.47
	A. sachalinensis	**1,290**	**96.89**	**< 0.001**	1,289	0.10	0.75	1,289	1.84	0.18
	P. glehnii	**1,247**	**174.46**	**< 0.001**	1,254	2.75	0.10	**1.267**	**9.98**	**0.002**
Sep.24'	*A. pictum*	**1,220**	**11.97**	**< 0.001**	1,220	0.23	0.63	1,220	1.23	0.27
	Q. crispula	**1,122**	**25.43**	**< 0.001**	1,122	0.01	0.95	1,122	0.76	0.38
	A. sachalinensis	**1,283**	**247.80**	**< 0.001**	**1,283**	**12.25**	**< 0.001**	1,283	0.026	0.87
	P. glehnii	**1,256**	**192.88**	**< 0.001**	**1,256**	**4.68**	**0.03**	**1,256**	**22.51**	**< 0.001**






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Chapter 4

General Discussion

4.1 Plant responses to shifting snow cover on different scales

In this thesis, I asked two major questions at both the global and ecosystem scales to investigate the consequences of plant responses to shifting snow cover and discussed the underlying mechanisms behind the different plant responses at both scales. In Chapter 2, I conducted a meta-analysis to quantitatively assess how plant survival, growth, and vegetation cover respond differently to both decreased and increased snow cover across regions with varying climates, ecosystems, and plant functional types. This study enabled us to identify high-risk regions and species types that are particularly vulnerable to reduced snow cover under climate warming. Specifically, plants inhabiting areas with shallow snow cover and relatively cold winter temperatures, those in tundra ecosystems, and woody species—particularly shrubs—were classified as high-risk (Fig. 1). Shrubs provide food resources not only for various animals (Thomas 1990; Cadieux et al. 2005; Christie et al. 2015; Webber et al. 2022), the shrub berries also provide food service for human beings, particularly for Indigenous peoples whose traditional livelihoods in the high-latitude regions rely on these resources (Fediuk et al. 2002; Weber 2022). Therefore, the decline in shrub performance under reduced snow cover may have cascading effects on both ecological interactions and cultural ecosystem services in these vulnerable regions. However, since snow depth and the timing of snowmelt are largely influenced by local factors such as vegetation structure (Essery et al. 2004; Grünberg et al. 2020; Mazzotti et al. 2023) and topography (Litaor et al. 2008; Niittynen et al. 2020a; Tyystjärvi et al. 2024), it is likely that some areas could serve as microrefugia so that shrubs can persist despite broader regional declines in snow cover.

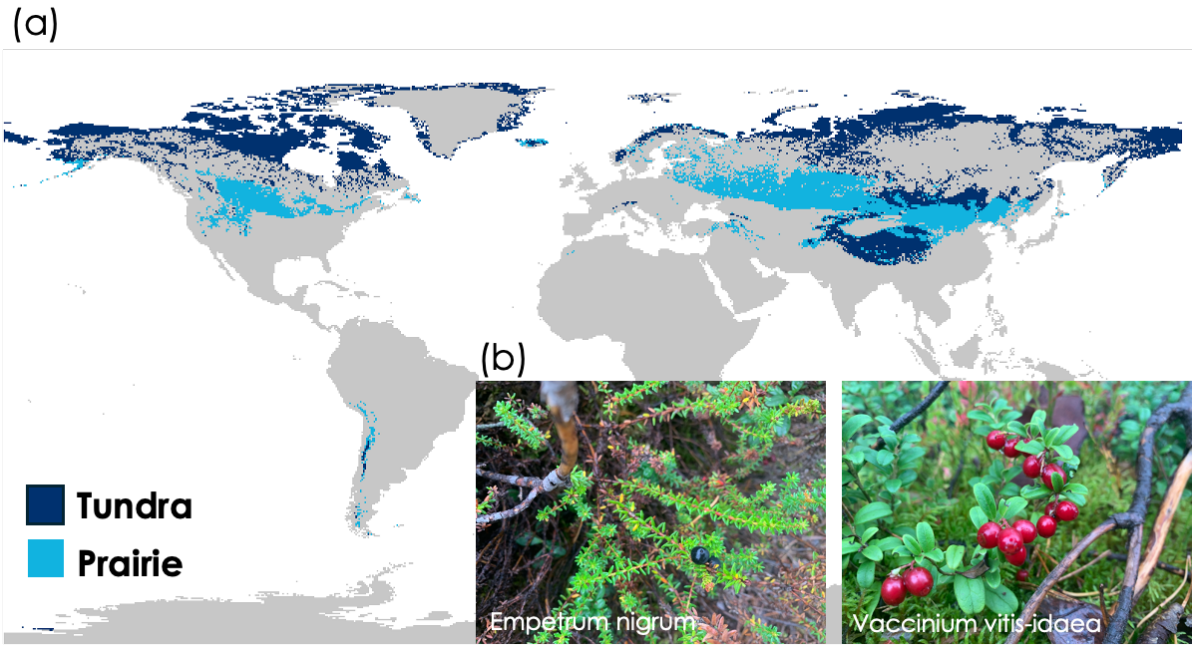


Fig. 1 The vulnerable regions (a) and species (example; b) to decreased snow cover based on the result of the meta-analysis (Chapter 2). Tundra and Prairie represented the regions with thin snow cover and low air temperature and thin snow cover with high air temperature based on the definition of Sturm and Liston 2021.

On the local scale, I chose forest ecosystem with the most heterogeneous environment across the ecosystem types due to their three-dimensional canopy structure (Zellweger et al. 2020), to asked how the environmental variation driven by tree canopy can influence the responses of understory vegetation to decreased snow cover (Chapter 3). Through the field manipulation experiment, I confirmed that the environmental heterogeneity driven by tree canopy in the forest can shape plant responses to decreased snow cover, especially for evergreen species. Particularly, the significant decrease in survival and growth of evergreen conifer seedlings under the canopy would substantially influence the regeneration and alter future species composition in the natural forests in this region. This shift could also have cascading effects on biodiversity, carbon sequestration, and ecosystem resilience. Therefore, forest management practices should consider these microclimate effects,

possibly by adjusting thinning practices or preserving certain canopy structures to buffer against extreme winter conditions.

Throughout this research, it became evident that plant responses to shifting snow cover are influenced by both global-scale climate patterns and local environmental conditions. Global climate trends, such as changes in temperature and precipitation, have widespread effects, while local factors, such as vegetation, topography, and soil properties, can significantly alter plant responses (Niittynen et al. 2020b; De Frenne et al. 2021; Kemppinen et al. 2024). For example, I found that while seedlings show vulnerable responses to decreased snow cover on the global scale (Chapter 2), the effect of snow cover reduction varied depending on local factors, such as canopy cover (Chapter 3). By considering both global and local scales, I can gain a more detailed understanding of how plants adapt to climate change. Additionally, integrating global climate trends with local observations allows for more accurate predictions of how climate change will impact plant species in specific regions or ecosystems. While I could not directly compare the relative influence of global versus local factors on plant responses, this study highlights the importance of examining plant responses across multiple spatial scales to fully capture the complex interactions between these factors.

4.2 Future studies

4.2.1 Use global data to clarify can tree canopy provide microrefugia

According to previous studies, tree canopy buffers free-air temperatures, providing cooler maximum temperatures and warmer minimum temperatures (De Frenne et al., 2019; De Pauw et al., 2022). Under climate change, the rate of temperature rise is slower under the tree canopy compared to free-air temperatures (Zellweger et al. 2020; Kašpar et al. 2021). Due to this, tree canopy is expected to act as a microrefugia, offering a more stable and protective environment for understory plants in the face of climate change (De Freene et al. 2021; De Lombaerde et al. 2022). In contrast, the results of

our study suggest that tree canopy does not necessarily provide microrefugia during winter in snowy regions (Chapter 3). In our case, the snow insulation effect outweighed the temperature buffering effect provided by the tree canopy. However, whether the tree canopy can provide microrefugia during winter in snowy regions largely depends on the balance between the temperature buffering effect and the snow interception effect. Therefore, further studies are necessary to clarify under what conditions the temperature buffering effect outweighs the snow interception effect, and when the opposite occurs. Accordingly, in future studies, I could use SoilTemp, a global database of near-surface temperature (Lembrechts et al., 2020; Lembrechts et al., 2021), to clarify under what conditions tree canopy can provide microrefugia for understory vegetation during winter in regions with seasonal snowfall.

In addition, I need to distinguish the temperature buffering effect from the snow interception effect in order to better examine the controlling factors for each. Distinguishing these two effects helps us understand their individual and combined roles in shaping the forest microclimate, enabling more precise predictions of temperature dynamics and plant responses under future climate conditions. As a starting point, I can conduct simple temperature measurements to separate the effects. The measurements should be taken at four positions as one set: above and below the snow cover in both the canopy gap area (Gap_Temp_{above} and Gap_Temp_{below}) and the area under the canopy ($Canopy_Temp_{above}$ and $Canopy_Temp_{below}$; Fig. 2). Then the temperature buffering effect (°C) and the snow interception effect (°C) can be calculated as follows:

$$\text{Buffering effect (°C)} = Canopy_Temp_{above} - Gap_Temp_{above} \quad (1)$$

$$\text{Snow interception effect (°C)} = Canopy_Temp_{below} - Gap_Temp_{below} - \text{Buffering effect} \quad (2)$$

By conducting these measurements in forests with various environmental conditions, I can identify

the driving factors of the temperature buffering effect and snow interception effect.

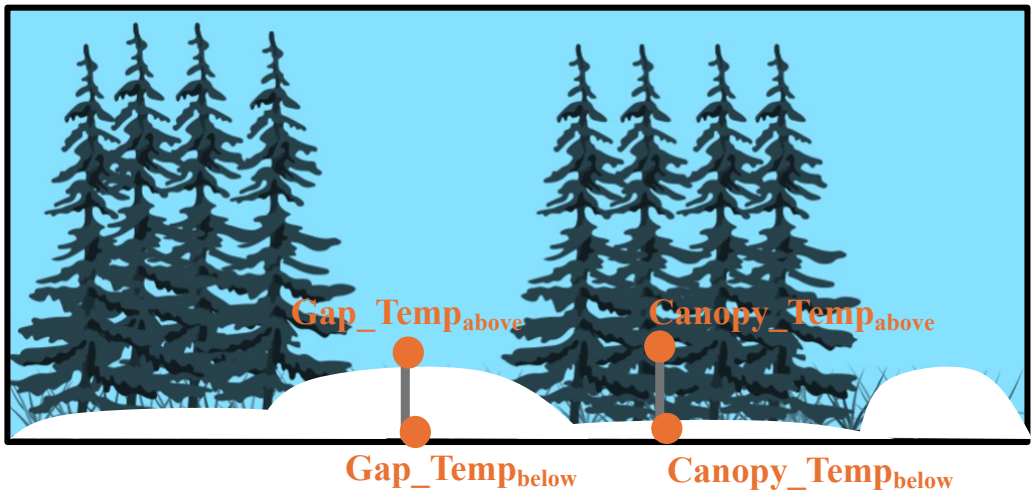


Fig. 2 Separation of the temperature buffering effect and snowfall interception effect

4.2.2 Greater impact from large mammal herbivory or decreased snow cover?

In Chapter 3, I observed a notably high rate of browsing by large mammals, primarily deer (*Cervus nippon yesoensis)*, in this region. Winter bud damage caused by deer browsing reached nearly 50% in *A. pictum* and 70% in *Q. crispula* seedlings (Chapter 3-3, Fig. S4). Additionally, over 50% and 80% of seedlings showed leaf damage in July and September, respectively (Fig. 3). In recent decades, the continued increase in deer populations across the entirety of Hokkaido has been observed (Fig. 4; Kaji et al. 2000; Uno et al. 2009). The browsing of seedlings and saplings is one of the main factors suppress forest regeneration (Rooney 2001; Takatsuki 2009). Therefore, particularly for deciduous broad-leaved species that showed the high browsing damages rate, further studies are needed to disentangle the effects of decreased snow cover and deer herbivory in order to determine which factor has a greater impact on seedling performance. Moreover, snow cover during winter typically provides physical protection for seedlings against deer browsing. However, as snow cover declines, winter bud

damage by deer is expected to increase. Consequently, it is also important to investigate whether the combination of reduced snow cover and intensified deer browsing exerts a synergistically negative effect on seedling performance.

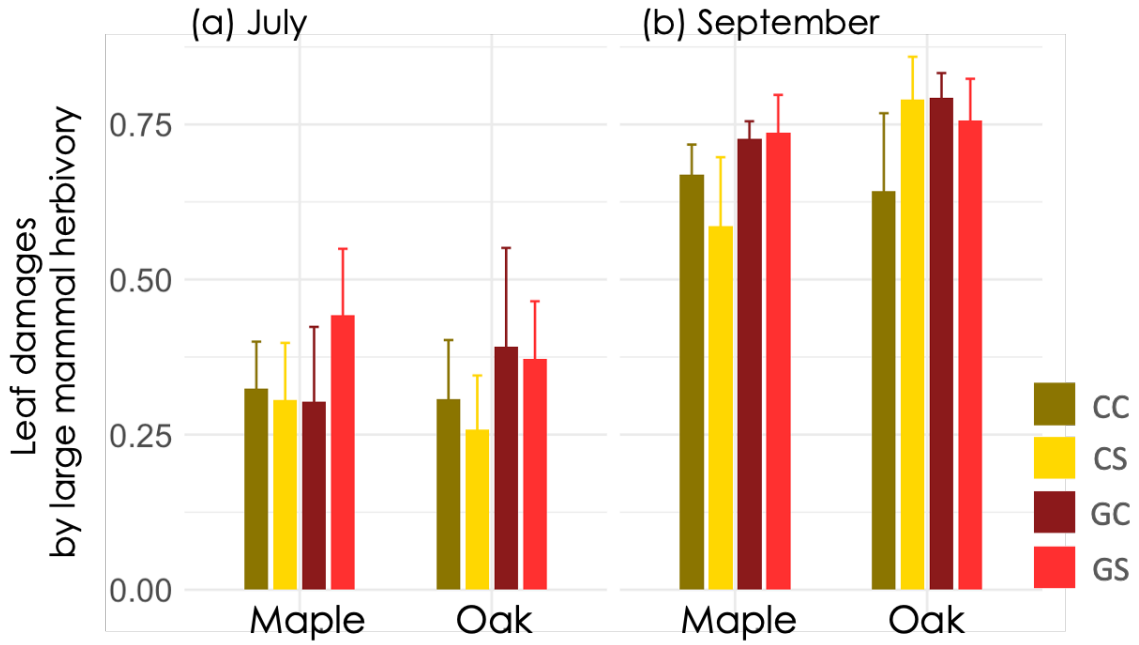


Fig. 3 The ratio of the leaf damages by large mammal herbivory, mainly deer in CC (under canopy control), CS (under canopy snow removal), GC (canopy gap control), and GS (canopy gap snow removal) in July (a) and September (b).

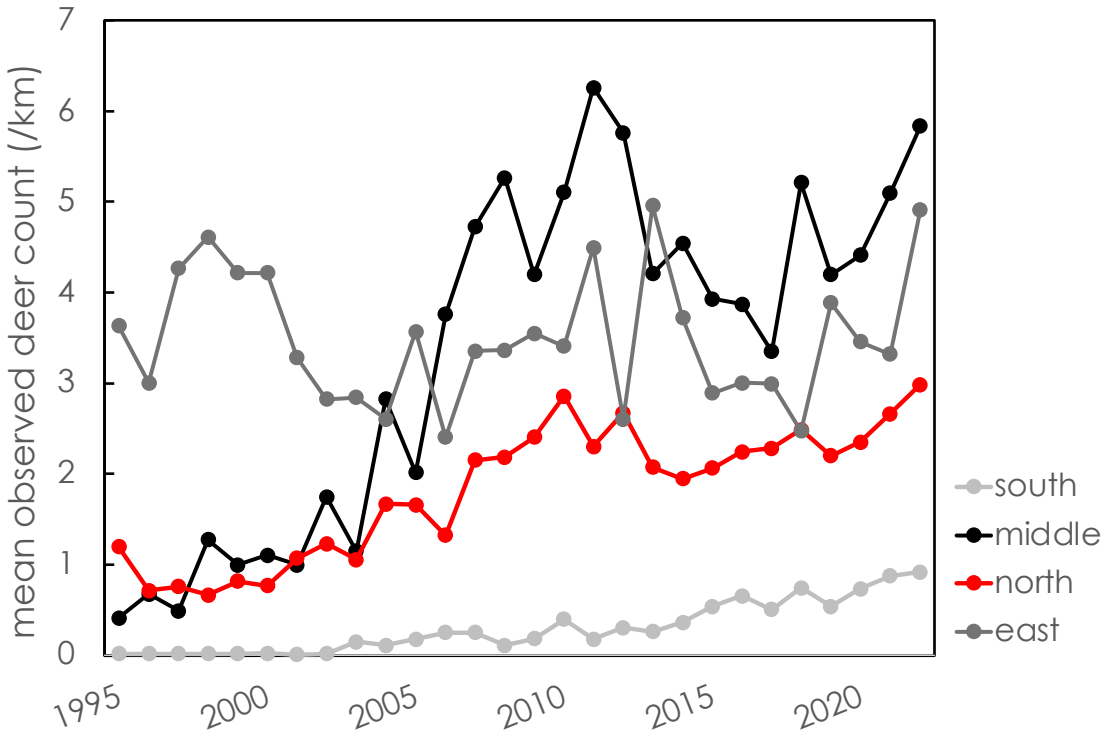


Fig. 3 Trend in average observed deer per kilometer across four regions in Hokkaido (1993–2022) based on the data provided Hokkaido Research Organization (Ueno and Yamaguchi 2023, in Japanese).

4.2.3 Dormant to growing seasons: Investigating the impacts of seasonal warming on plant responses

In this study, I focused solely on the influence of winter warming during the dormant season on seedlings. However, the effects of global warming are also significant during summer, the growing season. Although seedlings in the canopy gap showed no significant response to decreased snow cover in winter, summer warming is expected to cause more intense drought and heat stress in these open areas (Davis et al., 2019; Finocchiaro et al., 2024). In contrast, while seedlings under the canopy showed significant declines in response to winter warming, the drought and heat stress associated with summer warming would likely be buffered by the tree canopy (John et al. 2024). A comprehensive study that considers both seasons would provide valuable insights into whether summer and/or winter

warming are the primary limiting factors for plant performance under global warming conditions, and how these effects may be modified by tree canopy structure. In addition, it could reveal potential interactions between winter and summer warming—for instance, whether damage sustained during winter warming makes plants more vulnerable to the stresses of summer warming.

4.3 General conclusion

To conclude, this PhD study aimed to enhance our understanding of how shifting snow cover influences plant performance at both global and ecosystem scales by employing meta-analysis and field manipulation experiments. Our findings clearly identified the regions, ecosystems, and plant functional types most vulnerable to decreased snow cover—namely, areas with thin snowpack and low winter air temperatures, tundra ecosystems, and shrubs. Overall, woody plants inhabiting high-latitude regions experienced more significant negative impacts from snow cover reduction than those in other regions. Moreover, the field manipulation experiment demonstrated that plant performance in response to decreased snow cover is significantly influenced by local factors, such as environmental heterogeneity driven by canopy cover in forest ecosystems. This was particularly evident in the evergreen conifer species studied. These results highlight the critical role of local-scale factors—tree canopy structure, in this case—in shaping plant responses to climate change. In sum, this research underscores the need to consider both large-scale patterns and fine-scale environmental variability to better predict the ecological consequences of shifting snow cover on plant performance under global warming.

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Chapter 1

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