



HOKKAIDO UNIVERSITY

Title	Shifting snow and vegetation : How does tree canopy modify the response of understory plants to warming winter? [an abstract of dissertation and a summary of dissertation review]
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Degree Grantor	北海道大学
Degree Name	博士(環境科学)
Dissertation Number	甲第16527号
Issue Date	2025-06-30
Doc URL	https://hdl.handle.net/2115/95778
Rights(URL)	https://creativecommons.org/licenses/by/4.0/
Type	doctoral thesis
File Information	CAI_Yihan_abstract.pdf, 論文内容の要旨



学 位 論 文 内 容 の 要 旨/Dissertation Abstract

博士 (環境科学)

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学 位 論 文 題 名/Title of Dissertation

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)

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 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 act 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