Alpine Botany (2022) 132:329–336
https://doi.org/10.1007/s00035-022-00280-3

ORIGINAL ARTICLE

Bryophyte responses to experimental climate change in a mid-latitude forest-line ecotone

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Received: 10 December 2021 / Accepted: 21 February 2022 / Published online: 17 March 2022

Abstract
Climate change, such as warming, is a threat to mountain ecosystems in the forest-line ecotone. This influence could seriously affect bryophytes, because they easily lose their internal water at high temperatures. We conducted experimental warming using open-top chambers (OTCs) in a forest-line ecotone in central Japan and examined its influence on bryophyte cover. Six years after the experiment was initiated, the total bryophyte cover was not significantly different between the control and OTC treatments. However, the two dominant bryophyte species (*Pogonatum japonicum* and *Dicranum majus)* responded differently to the OTC treatment. The cover of *P. japonicum* significantly increased under the OTC treatment, while that of *D. majus* decreased to approximately 14% of the initial cover under the OTC treatment. These results could be explained by *D. majus* being better adapted to high-elevation climates than *P. japonicum.* The decline of *D. majus* cover was potentially further enhanced by the decrease in rainfall and fog within the OTCs. These are important water sources for *D. majus* because the species lacks water-conducting systems that enable mosses to absorb water from their substrates. As the OTCs in this study were tall (210 cm high), they may have blocked slanting rain and fog from reaching the plants, increasing water stress in *D. majus*. In contrast, *P. japonicum* develops water-conducting systems and may be less susceptible to the decrease in rainfall and fog. These results can aid future experimental studies in the mountains to elucidate the mechanisms underlying bryophyte responses to warming.

Keywords Climate warming · Elevation · Water absorption strategy · Open-top chamber · Japan

Introduction

Climate change, such as warming, is a major global driver of changes in vegetation (Sala et al. 2000; Gobiet et al. 2014). Shifts in vegetation due to global warming affect ecosystem processes, including net primary production (Xu et al. 2013), nutrient cycling (Wahren et al. 2005), biomass (Deane-Coe et al. 2015), and biological interactions (Roy et al. 2004). These changes are expected to be severe at high latitudes (Sala et al. 2000; Gobiet et al. 2014), because global warming substantially increases the temperature due to its feedback at the surface and the decreased albedo through melting snow and ice cover (Pithan and Mauritsen 2014). According to experimental warming studies in high-arctic and tundra ecosystems, plant groups respond differently to warming across time and space (Hollister et al. 2005; Walker et al. 2006; Hudson and Henry 2010; Elmendorf et al. 2012). In contrast to high-arctic and tundra ecosystems at high latitudes, the number of experimental warming studies conducted in mid-latitude regions is limited (Suzuki and Kudo 2000; Taguchi and Wada 2000; Wada 2000; Wada et al. 2002; Kudo and Suzuki 2003; Walker et al. 2006; Hoffmann et al. 2010; Kudo et al. 2010; Xu et al. 2012; Xu et al. 2012; Tanaka et al. 2013). This raises concerns when evaluating the influence of climate warming on vegetation

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in mid-latitude regions, because the responses of plant communities to warming depend on the initial conditions of their ecosystems and climates (Jónsdóttir et al. 2005).

Among the various types of mountain ecosystems at mid-latitudes, the forest-line ecotone (or subalpine–alpine ecotone) may be particularly vulnerable to climate warming. This is because both subalpine and alpine species coexist in this ecotone; thus, subalpine species can easily replace alpine species under elevated temperatures. For example, in central Japan, subalpine evergreen conifer trees (e.g., *Abies mariesii*) dominate the lower parts of the forest line, whereas Erman's birch (*Betula ermanii*) and the Japanese dwarf pine (*Pinus pumila*) dominate the upper parts. Climate warming might cause the dominant species in the upper parts to be replaced by those from the lower parts (Fujiwara et al. 1999; Horikawa et al. 2009). Such a replacement in dominant species from high-elevation to low-elevation species might result in substantial vegetation changes in this ecotone. However, to date, experimental warming in the forest-line ecotone (Danby and Hik 2007; Hoffmann et al. 2010) has been scarce (Tanaka et al. 2013).

Plant groups sensitive to warming are useful for examining possible changes in vegetation in a forest line. Bryophytes may be a suitable plant group for this purpose because of their sensitivity to changes in environmental conditions caused by climate warming, such as enhanced drought stress (Gignac 2001) and timing of the disappearance of snow beds (Hohenwallner et al. 2011). The sensitivity of bryophytes to these changes is attributed to their poikilohydric nature; that is, they lack the ability to actively regulate their water content to achieve homeostasis (Proctor and Tuba 2002). The water status of bryophytes depends on external environmental conditions; therefore, they easily lose their internal water at high temperatures, which increases their evaporation rates (He et al. 2016). The water deficit leads to a shorter period of photosynthetic activity, which can significantly reduce bryophyte diversity at elevated temperatures (He et al. 2016).

Previous studies have reported that bryophyte cover is more susceptible to experimental warming than other indices such as species richness (Sun et al. 2017; Alatalo et al. 2020; van Zuijlen et al. 2021), diversity (Alatalo et al. 2020), and evenness (van Zuijlen et al. 2021). Sun et al. (2017) conducted experimental warming in an ecosystem above the tree line, which revealed that the cover of forest bryophytes was more vulnerable to increased temperature than that of shrubland bryophytes owing to the adaptation of the forest bryophytes to a cooler and damper environment. These results imply that climate warming can cause significant changes in the cover of dominant bryophytes. Contrary to the expectation that bryophytes are vulnerable to warming, their responses to the warming effect varied from negative to positive in high-arctic and tundra ecosystems. Analyses of plant responses to experimental warming in tundra ecosystems revealed that the bryophyte cover decreased (Hollister et al. 2005; Jónsdóttir et al. 2005; Walker et al. 2006; Alatalo et al. 2020). However, other studies show an increase in bryophyte cover under experimental warming (Hudson and Henry 2010; Shortlidge et al. 2017) or no change (Jägerbrand et al. 2009, 2012). These varied responses of bryophytes to experimental warming warrant further studies investigating the influence of warming on bryophytes in various habitats.

In this study, we performed experimental warming in a forest-line ecotone to examine the response of bryophytes to increased temperature in a mid-latitude region (Japan). We hypothesized that the cover of low-elevation species would replace that of high-elevation species, considering that the high-elevation species are more susceptible to warmer climates. This examination contributes to an understanding of climate change on the dynamics of bryophytes in the forest-line ecotone at mid-latitudes.

Methods

Study sites

The experimental warming study was conducted in a forest-line ecotone (altitude of approximately 2570–2590 m) of Mt. Shoginokashira in central Japan (Fig. 1). This experiment aimed to examine the responses of vegetation, including bryophytes, to a warming climate. The study site is located in the Nishikoma Station at the Education and Research Center of Alpine Field Science of Shinshu University. The site experiences heavy snowfall, and packed snow covers the ground from November to June. The mean monthly temperature at the closest meteorological station (altitude of 2600 m) ranged from − 11.5 °C in December to 13.0 °C in August 2016 (Kobayashi et al. 2018). The vegetation around the study site comprises a mixed sparse forest of distorted deciduous broadleaf trees (*Betula ermanii* and *Sorbus matsumurana*) and subalpine conifers (*Abies mariesii* and *Abies veitchii*). The upper boundary of the study site is covered by a dense stand of dwarf alpine pines (*Pinus pumila*), while the lower part is covered by dense subalpine conifer trees. The forest floor is covered with shrubs, herbs, and bryophytes. The major shrub species are *Elliottia bracteata*, *Rhododendron pentandrum*, and *Vaccinium ovalifolium;* and the major herb species are *Maianthemum dilatatum*, *Solidago virgaurea* subsp. *leiocarpa*, and *Streptopus streptopoides* subsp. *japonicus*.

Two bryophyte species widely distributed in the study site are *Pogonatum japonicum* and *Dicranum majus.* They often coexist in the forest-line of subalpine forests, but their elevational distributions differ. In central Japan, *P. japonicum*

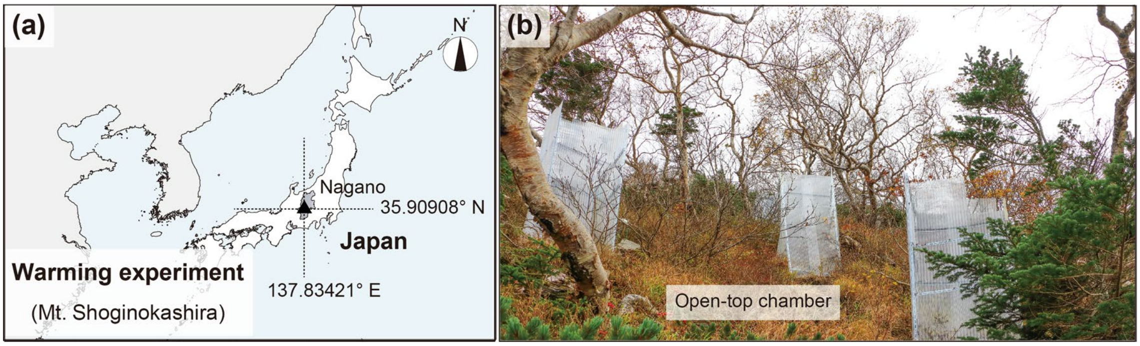


Fig. 1 Location of the study site, Mt. Shoginokashira in central Japan. **a** Location of Mt. Shoginokashira and (**b**) the experimental site and open-top chambers (OTCs)

dominates the upper-temperate to subalpine zone (Osada 1965), whereas *D. majus* dominates the subalpine to alpine zone (Takaki 1964). According to the elevational distributions of these species, *P. japonicum* and *D. majus* are considered low- and high-elevation species, respectively. Other bryophytes in the study site include common subalpine species such as *Brachythecium noesicum*, *Hylocomiastrum himalayanum*, *Hylocomium splendens*, *Pleurozium schreberi*, and *Rhytidiadelphus squarrosus*.

Experimental warming and bryophyte monitoring

In the study site, we commenced experimental warming in October 2010 using 10 open-top chambers (OTCs; each 105 cm long × 105 cm wide × 210 cm high). The chambers were made of clear corrugated polycarbonate panels and steel frames. These OTCs increase the temperature inside, thereby simulating climate warming (Suzuki and Nagaoka 2017). Five of the OTCs were used for the year-round OTC treatment, in which clear panels were installed throughout the year. The other five OTCs were used for the summer-time OTC treatment, in which clear panels were installed to the OTCs only during the summer season (late July to early October). One quadrat (55 cm × 55 cm) was set within each OTC (i.e., ten quadrats were under OTC treatment), and six quadrats (55 cm × 55 cm) were set outside the OTCs for the control treatment. All OTC and control plots (16 plots in total) were randomly placed within the study site. However, we changed the experimental design, because some OTCs had been damaged severely by heavy snow by 2013. In July 2013, we excluded four OTCs (one year-round and three summer-time). We also changed the remaining 4-year-round OTCs to the summer-time OTC treatment to avoid damage to OTCs during the winter. Thus, our experimental warming study was continued in 6 OTCs (two summer-time OTCs during 2010–2016, and 4 year-round OTCs until July 2013 which changed thereafter to summer-time) and 6 controls (12 quadrats in total).

The influence of OTCs on abiotic factors (temperature, humidity, water content of the soil, and relative light intensity) was examined, and the effects of OTCs are summarized as follows. The temperature was measured during 2010–2016 using data loggers (iButton [DS1920]; Maxim Integrated, San Jose, CA, USA) at 30 cm above ground level. The OTCs increased the temperature by 0.32 ± 0.12 °C during the summers of 2010–2016. In contrast, the OTC treatment did not enhance the temperature (− 0.01 ± 0.44 °C) during the other times of the year in 2010–2012 because the OTCs were buried under heavy snow. Relative humidity was also measured using data loggers (iButton [DS1923]; Maxim Integrated, San Jose, CA, USA) at 30 cm above ground level during July–September in 2013. The relative humidity decreased from 94.1 to 93.2% in OTC quadrats. The water content of soil was measured once in August 2013. The content was calculated by subtracting the dry weight of 100 g soil from that of wet weight. The OTC treatment decreased soil water content from 45.1 g to 38.1 g water/100 g soil. The relative light intensity was measured at soil surface (LI-190SA, Li-Cor, Lincoln, NE, USA). The average relative light intensities were 4.12% and 2.91% in the control and OTC treatments, respectively. Thus, the OTC treatment increased the temperature (+ 0.32 °C), whereas it decreased the relative humidity (− 0.9%). water content of the soil (− 7.0 g/100 g soil), and relative light intensity (− 1.21%).

Bryophyte cover in those 12 (6 OTC and 6 control) quadrats was recorded during September 2010–2016. In each quadrat, three types of bryophyte cover (total, *Pogonatum* [*P. japonicum*], and *Dicranum* [*D. majus*]) were measured using grids of two sizes (normal: 5 × 5 cm, fine: 1 × 1 cm). Both or either of the targeted species grew in the surveyed quadrats. The total cover included all the terrestrial bryophytes that grow in the area (i.e., the sum of the cover of *Pogonatum*, *Dicranum*, and the other species). The cover of *Rigodiadelphus robustus* was not included in the calculation of total cover, because this species often falls from the trees to the ground. The bryophyte cover was visually estimated for each grid cell (5 × 5 cm and 1 × 1 cm) and then averaged per plot. The cover of herbs and ferns on the ground was also recorded in 2010 and 2016.

Statistical analysis

The changes in total, *Pogonatum*, and *Dicranum* cover were chronologically plotted in 2010, 2012, 2014, and 2016 for the control and OTC treatments. The differences between these treatments were then examined using Bayesian methods. These methods are suitable for handling small sample sizes such as those in this study, because they are based on a Markov chain Monte Carlo simulation (McNeish 2016). For this model, we assumed that (1) the change in bryophyte cover in the control is expressed by a constant, and (2) the influence of the OTC treatment on bryophyte cover is expressed by a constant term. Based on these assumptions, the state equation (Eq. 1) and the observation equation (Eq. 2) for change in bryophyte cover are expressed as follows:

$$\log\mu[i,t] = \log\mu[i,t-1] + \alpha + \beta \times \mathrm{W} + \gamma \times \mathrm{IW} + \varepsilon_{\mu}[i,t-1], \quad (1)$$

$$\mathrm{Y}[i,t] = \mu[i,t] + \varepsilon_{\gamma}[i,t], \quad (2)$$

where $\mu[i, t]$ is the true value of bryophyte cover in quadrat i in surveyed year t; α expresses the change in bryophyte cover in the controls; β is the effect of the OTC treatment on the change in bryophyte cover; W expresses the presence/absence of the OTC treatment (W = 1 for the OTC treatment, W = 0 for the control treatment); γ is the effect of the initial OTC treatment during winter on the change in bryophyte cover; IW expresses the presence/absence of the initial OTC treatment in winter during 2010–2012 (IW = 1 for the OTC treatment, IW = 0 for the control treatment); ε_{μ} [i, t] is a process error in quadrat i reflecting the strength of the autocorrelation between the survey years; Y[i, t] is the observed bryophyte cover; and ε_{γ} [i, t] is the observational error in bryophyte cover in quadrat i in year t. In the model, ε_{μ} [i, t] and ε_{γ} [i, t] were assumed to follow a normal distribution with mean 0 and standard deviation σ_{μ} and σ_{γ}, expressed as Normal (0, σ_{μ}), and Normal (0, σ_{γ}), respectively.

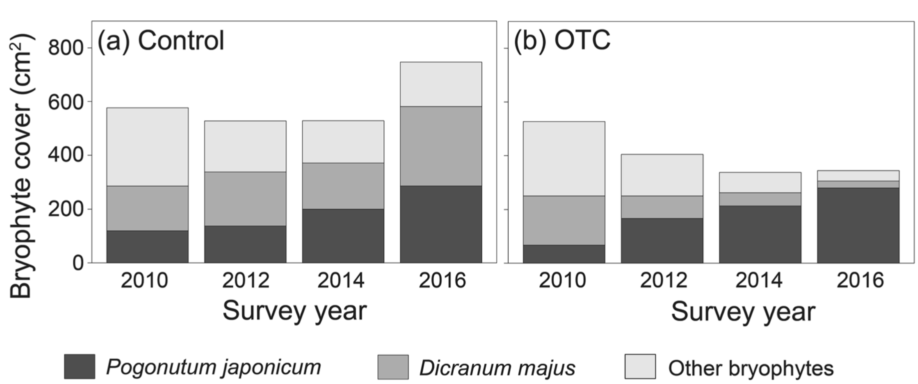
We then constructed a likelihood function for the parameters and examined the differences in α, β, and γ values based on a Bayesian 95% credible interval (quantiles between 2.5 and 97.5%). When the credible intervals of β and γ deviated from zero, the difference in the changes in cover between the control and OTC treatments was regarded as significant. To avoid the arbitrary selection of prior distributions, we adapted weakly informative prior distributions: a half-Cauchy distribution with mean 0 and standard deviation 5 for σ_{μ} and σ_{γ}; a normal distribution, Normal (0, 100), for α, β, and γ; and a uniform distribution with minimum 0 and maximum 1404 (maximum cover observed in the quadrats) for $\mu[i, t]$. Posterior estimates were visually examined for chain convergence with trace plots and a potential scale reduction factor (Gelman and Rubin 1992). The calculations were performed using Stan (Carpenter et al. 2017; Stan Development Team 2020) via the RStan interface of R version 4.0.3 (R Core Team 2021).

Results

Changes in vegetation cover

The changes in bryophyte cover during 2010–2016 are shown in Figs. 2 and 3 (Online Resource 1). The total bryophyte cover in the control and OTC quadrats in 2010 was 577 ± 199 cm^2 (average ± SD) and 527 ± 391 cm^2, respectively, and in 2016 was 747 ± 473 cm^2 and 344 ± 408 cm^2, respectively. The total cover after 6 years increased to 130% of its initial value in the control treatment, whereas it decreased to 65% of its initial value after the OTC treatment. The effect of OTC treatment (parameters β and γ) was not significant in the Bayesian model (Table 1). In 2010, the total cover of herbs and ferns in the control and OTC quadrats was 35 ± 50 cm^2 and 104 ± 245 cm^2, respectively, and in 2016 was 91 ± 164 cm^2 and 142 ± 256 cm^2, respectively. The average cover of herbs and ferns

Fig. 2 Changes in bryophyte cover in the control and OTC treatments during 2010–2016. **a** Control and (**b**) OTC treatments. The cover is the average of the values of each quadrat (control treatment: $n = 6$, OTC treatment: $n = 6$)



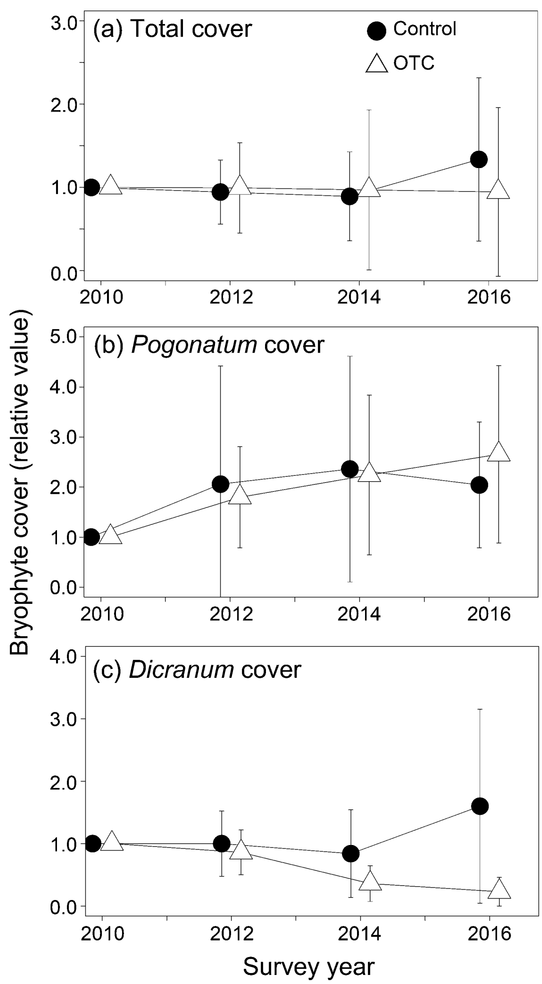


Fig. 3 Mean annual changes in the relative bryophyte cover per quadrat for 2010–2016. **a** Total cover, (**b**) *Pogonatum* cover, and (**c**) *Dicranum* cover. The bryophyte cover in 2010 was adjusted to 1.0. In the OTC quadrats, the *Dicranum* cover significantly decreased over time compared to that in the control quadrats, based on statistical models using a Bayesian framework

increased to 262% of its initial value during 2010–2016 in the controls, whereas the increase in the OTC quadrats was 137% of its initial value during the same period (Online Resource 1).

The two moss species exhibited different responses to the OTC treatment. The parameter α for *Pogonatum* cover was significant, but parameters β and γ were not significant. Thus, the *Pogonatum* cover increased over the 6 years of the experiment despite the OTC treatments. Notably, the rate of increase in the *Pogonatum* cover (i.e., the ratio of the final to initial cover) in the OTC plots (414%) was nearly double that in the control plots (238%). In contrast, the *Dicranum* cover increased to 179% of its initial value in the control treatment but considerably decreased to 14% of its initial value in the OTCs. The β value for the *Dicranum* cover was negative between the 2.5–97.5% quantiles (Table 1), indicating that the *Dicranum* cover significantly decreased due to the OTC treatment.

Discussion

Responses of bryophytes to experimental warming

The total cover of bryophytes did not change during the OTC experiment because of the opposite responses of the two dominant species to the OTC treatment. Our results support the implication that bryophytes do not respond to climate warming as a single plant group (Sun et al. 2017), which can partially explain the varied responses of bryophyte cover to experimental warming in previous studies.

The *Dicranum* cover in the OTC treatment significantly decreased after 6 years of the experiment. In contrast, the *Pogonatum* cover increased both under the control and OTC treatments, and the increase was larger in the OTC quadrats than in the control quadrats. The different responses of these two moss species could be attributed to their optimal growth environments related to their elevational distributions. The OTC treatment may have negatively affected *D. majus* because of the adaptation of the species to the cooler climate at higher elevations, whereas the same treatment may have had a considerable positive effect on the low-elevation species *P. japonicum*. In particular, the forest line corresponds to almost the upper boundary for the *P. japonicum* distribution in central Japan (Osada 1965), whereas *D. majus* is distributed up to the alpine area (Takaki 1964). Based on the elevational distribution, the increased temperature might be beneficial for the growth of *P. japonicum*, resulting in the increase of its cover through the OTC treatment. These results correspond to our hypothesis that the cover of the high-elevation species (*D. majus*) would significantly decrease in the OTC quadrat, while that of the low-elevation species (*P. japonicum*) would increase.

Nevertheless, considering that the increase in temperature was only 0.3 °C in the OTCs, other factors could have also affected the decrease in the *D. majus* cover. A possible factor could be a blocking effect of the OTCs against rainfall and fog. Rainfall and fog are specifically crucial for the survival of certain mosses, known as ectohydric mosses, that lack water-conducting systems to absorb water from their substrates (Glime 2017). However, the height of the OTCs (210 cm) may have physically blocked the slanting rainfall and fog from entering the OTCs, thus reducing the amount of water reaching the plants. Because *D. majus* is classified as an ectohydric moss (van der Wal et al. 2005), the decrease in rainfall and fog could have negatively affected the growth of this species.

In contrast to *D. majus*, *P. japonicum*, an endohydric moss, develops water-conducting systems (Glime 2017;

Table 1 Parameters assessed to determine the influence of the OTC treatment on bryophytes

α values					
Bryophyte type	Mean	SD	2.5%	97.5%	Effect
Total cover	0.04	0.10	−0.18	0.23	–
Pogonatum cover	0.25	0.12	0.00	0.48	Positive
Dicranum cover	0.01	0.15	−0.29	0.29	–
β values					
Bryophyte type	Mean	SD	2.5%	97.5%	Effect
Total cover	−0.06	0.16	−0.43	0.25	–
Pogonatum cover	0.13	0.19	−0.23	0.51	–
Dicranum cover	−0.52	0.26	−1.06	−0.03	Negative
γ values					
Bryophyte type	Mean	SD	2.5%	97.5%	Effect
Total cover	−0.70	0.38	−1.44	0.09	–
Pogonatum cover	−0.28	0.70	−1.59	1.18	–
Dicranum cover	0.01	0.44	−0.86	0.87	–

Quantiles of 2.5 and 97.5% for each variable were calculated using the Markov chain Monte Carlo method

SD standard deviation, α a constant that expresses the change in bryophyte cover in controls, β a constant that expresses the effect of the warming treatment on the change in bryophyte cover, γ a constant that expresses the effect of the winter warming treatment (2010–2012) on the change in bryophyte cover. – the effect was insignificant

Oishi 2018); hence, this species may have been less affected by the decrease in rainfall and fog in the OTCs. In our experiment, the soil water content in the OTCs was lower compared to that of the controls. Nevertheless, the water content in the OTCs was sufficient for the growth of *P. japonicum*; that is, the decrease in soil water content did not negatively affect the *Pogonatum* cover in the OTC quadrats.

Our results indicate that differences in the development of water-conducting systems in mosses could be related to the responses of the bryophytes to the warming experiment. Similar results were obtained in a previous study (Alatalo et al. 2014), wherein the authors suggested that acrocarpous species with more advanced water-conducting systems than pleurocarpous species can be less sensitive to drier conditions caused by experimental warming (Alatalo et al. 2014). Moreover, Oishi (2018) revealed that endohydric mosses have a higher ability to retain water during dry periods than ectohydric species. Therefore, considering these results, the development of water-conducting systems might provide a valuable perspective for understanding bryophyte responses to increased drought stress caused by climate warming.

Interaction between bryophytes and other plants

In addition to abiotic factors (temperature, rainfall, and fog), the changes in plant–plant interactions may have had an effect on the decrease in the *Dicranum* cover. However, in contrast to previous studies (Walker et al. 2006; Alatalo et al. 2020), the influence of these interactions on bryophytes is marginal or insignificant based on the changes in plant cover in the OTC quadrats. This is because the decrease in the *Dicranum* cover did not correspond to the increase in other plant covers in the OTC quadrats (Plot Nos. 6, 9, and 14 in Online Resource 1). Furthermore, the differences in light intensity between the control and OTC treatments were small, implying that shading by tree canopy had a negligible impact on the results of the OTC experiment. These findings indicate that the low influence of plant-plant interactions on the bryophytes were potentially related to the characteristics of the vegetation at the study plots. The plots were located under the canopy of dwarf alpine pines and subalpine conifers, where the cover of ferns and herbs was low throughout the OTC experiment (Online Resource 1). Hence, the competition between bryophytes and other vascular plants was perhaps weakened in our OTC experiment.

Conclusions

The results of this study do not contradict our hypothesis that an increase in temperature can negatively affect high-elevation species. However, further studies are required to validate the hypothesis, because these results may also be attributed to the decrease in the amount of rainfall and fog that reached the plants owing to the height of the OTCs. This influence is potentially considerably high for ectohydric mosses, which lack systems for conducting water from substrates.

This study has important implications for OTC experiments at high elevations. First, the measurement of the changes in rainfall and fog is necessary for elucidating the effects of OTC treatment on bryophytes. These measurements are particularly important when tall OTCs are used. Second, the differences in water absorption strategies of bryophytes (ectohydric vs. endohydric species) can affect their responses to increased drought stress caused by climate warming. Finally, considering that few studies are available on experimental warming at the forest-line ecotone in mid-latitude regions, our results are an important reference for future warming studies in this ecosystem.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00035-022-00280-3.

Acknowledgements The authors are grateful to Kiyotaka Hori for his contribution to bryophyte identification in 2010–2011; to Keiko Furukawa, Mitsunari Yakubo, and Taki Yabuta for their assistance with the bryophyte cover surveys; and to the staff and students at the Education and Research Center of Alpine Field Science, Shinshu University and the Sugadaira Research Station, University of Tsukuba for their assistance with the management and performance of the experimental warming in 2010–2016.

Author contributions TK and HK conceived and designed the experiment; RK, DM, and TK designed the open-top chambers used in this study; TK, HK, SNS, RK, and DM managed and performed the experiment; YO and TK surveyed the bryophyte cover; YO and SNS conducted the statistical analysis; YO interpreted the results and wrote early drafts of the paper; and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Funding This work was supported by Research and Education Funding for Japanese Alps Inter-Universities Cooperative Project, MEXT, Japan, and the Japan Society for the Promotion of Science—Grant-in-Aid for Young Scientists (B) (Grant Number 24710029).

Data availability All data generated or analyzed during this study are included in this published article and its supplementary information files.

Declarations

Competing interest The authors have no relevant financial or non-financial interests to disclose.

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