

A review of open top chamber (OTC) performance across the ITEX Network

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Abstract

Open top chambers (OTCs) were adopted as the recommended warming mechanism by the International Tundra Experiment network in the early 1990s. Since then, OTCs have been deployed across the globe. Hundreds of papers have reported the impacts of OTCs on the abiotic environment and the biota. Here, we review the impacts of the OTC on the physical environment, with comments on the appropriateness of using OTCs to characterize the response of biota to warming. The purpose of this review is to guide readers to previously published work and to provide recommendations for continued use of OTCs to understand the implications of warming on low stature ecosystems. In short, the OTC is a useful tool to experimentally manipulate temperature; however, the characteristics and magnitude of warming varies greatly in different environments; therefore, it is important to document chamber performance to maximize the interpretation of biotic response. When coupled with long-term monitoring, warming experiments are a valuable means to understand the impacts of climate change on natural ecosystems.

Key words: Arctic, alpine, tundra, warming experiment, large-scale coordinated experiment

Introduction

Warming chambers have been used for many decades to study the impacts of rising temperature on vegetation. Interest in the impacts of warming on natural ecosystems increased greatly in the 1980s as researchers speculated on the potential effects of climate change across the globe.

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Fig. 1. Photographs of open top chambers. Images are of warming experiments at Utqiagvik, Alaska USA (upper left, photo credit: Robert Hollister); Latnja, Sweden (upper right, photo credit: Mario Rudner); Alexandra Fjord, Ellesmere Island Canada (lower left, photo credit: Cassandra Elphinstone); and Finse, Norway (lower right, photo credit: Kari Klanderud).



Different warming experiment designs have been employed over time spanning a variety of environmental gradients (Kennedy 1995; Shaver et al. 2000; Michelsen et al. 2012; Hanson and Walker 2020). Every warming mechanism has its own strengths and weaknesses. Open top chambers (OTCs, Fig. 1) were chosen as the recommended warming mechanism for low growing tundra vegetation by the International Tundra Experiment (ITEX) network because of their low cost, easy deployment, and relatively few experimental artifacts (Molau and Mølgaard 1996; Marion et al. 1997). Currently, OTCs are widely used in alpine and Arctic locations with low-stature vegetation (Henry et al. 2022). Many of the researchers using OTCs are members of the ITEX network, but many are not. While the OTCs are well suited for tundra environments, particularly at higher latitudes where diurnal contrasts in warming are small, they have been employed in other ecosystems with low-stature vegetation such as lower latitude meadows and peatlands. Over the past three decades, there have been hundreds of papers that have documented the impacts of OTCs on the physical environment and the organisms living in them. Here we review what has been learned about the impacts of OTCs on the physical environment and provide commentary on the interpretation of the biotic response to OTCs.

Diversity of OTCs

While somewhat standardized, the ITEX OTCs are not all the same and they vary in size from approximately 1 to 2 m² (Fig. 2). The materials used have varied over time, originally most of the OTCs deployed in North America were made of fiberglass, while OTCs deployed in Europe were made of plexiglass. Although these solid self-supporting materials are most commonly used, another approach utilized thin plastic wrapped around a solid metal frame (Day et al. 2008), and another modification is the use of semiflexible material wrapped into a cone (Schedlbauer et al. 2018; Parker et al. 2017, 2022). Other related approaches to experimental warming in tundra ecosystems have deployed plastic tents or greenhouses (Chapin and Shaver 1985; Havström et al. 1993; Wookey et al. 1993), although these do not clearly fall under the definition of OTC so they are not considered directly here. While there have not been detailed in situ studies of the difference in building materials, the common assumption is that the manufacturer's specifications apply and that most commercially available building materials for greenhouses are suitable. The materials are chosen to block wind and allow photosynthetically active wavelengths to pass through, although the various materials differ in their transmission of solar radiation. OTCs may need to be periodically cleaned

Fig. 2. Range of design dimensions for most commonly implemented hexagonal open top chambers (redrawn from Molau and Mølgaard 1996 and Hollister 1998). The size can vary, the corners are 120° angle, and can be braced with a bracket or the materials can be longer on one side and bent to a 60° angle.



to remove dirt and bird guano. Degradation of the materials over time is another potential issue, either through photodegradation, scratches by windblown snow or dust, or by staining from tannins at sites with periodic standing water. Different materials likely have different degradation rates.

Over time there have been a number of suggested improvements to the basic ITEX chamber design. These include increasing the height (Welshofer et al. 2018), addition of water filled pipes—providing thermal mass—to reduce fluctuations in the magnitude of heating throughout the day and night (Godfree et al. 2011), adding heating cables to ensure heating at low light levels (Sun et al. 2013), or adding small legs at each corner to allow air exchange (Delarue et al. 2011). Yet the basic ITEX OTC has remained one of the most commonly implemented field manipulations for examining vegetation response to warming, and it continues to be used in many tundra and non-tundra settings (Bokhorst et al. 2007; Aronson and McNulty 2009; Spence et al. 2014; Pugnaire et al. 2020; Bjorkman et al. 2020).

Physics of OTC warming

During the day, short-wave solar radiation is largely transmitted through the OTC walls, contributing to surface warming. By contrast, the OTC walls are more opaque to outgoing long-wave radiation, particularly in the infrared range of the electromagnetic spectrum (>700 nm wavelength), increasing the sensible heat of air inside the OTC. The increase in temperature is due to the absorption of solar radiation directly by the plant canopy and other exposed surfaces within the OTC (soil surface, exposed rock, or standing water) and the emission of long-wave radiation from these surfaces. The shape of the OTC was designed to increase the boundary layer and provide the opportunity for a warm "bubble" of air to develop over the surface, by greatly reducing wind speed and to reduce the loss of energy from air movement (advection). The panels also provide shelter from the wind reducing heat loss by convection, yet the open-top allows air to flow in and out and small eddies may form.

Because OTC performance varies both temporally and among locations, we recommend direct measurements of the physical environment in individual experiments to quantify net effects. To help understand the source of these variable impacts, it is useful to review the fundamental physics of energy balance. The equation for energy balance may be expressed as follows:

net radiation absorbed (Q^*) = evapotranspiration (Q_{LE}) + sensible heat flux (Q_H) + ground heat flux (Q_G)

+ [net energy flux by advection (Q_V) + net storage (ΔS)].

Generally, Q_V and $\triangle S$ are not included as they are considered to balance out over time. The OTC warming acts by blocking the wind and interfering with loss of energy from the surface through Q_V . Furthermore, the magnitude of these flows can then vary between wet and dry surfaces. Taken together, understanding the physics behind OTC warming can help understand the complex impacts of OTCs on air, leaf tissue, and soil temperatures (Fig. 3).

The impact of OTCs on humidity varies greatly between field locations (Sjögersten and Wookey 2002; Bokhorst et al.

2007). It is difficult to predict the impacts of OTCs on humidity without field observations, as humidity depends on vegetation, soil properties, and soil moisture, which are linked with landscape position and lateral movements of soil water. Plants and soils in the OTCs respond to the vapor pressure deficit (VPD). In many cases, air VPD increases inside OTCs as a function of increasing temperature and the subsequent increase in water holding potential of warmer air (Lamentowicz et al. 2016). In some locations VPD may remain the same or decrease inside the OTC presumably due to sheltering from



Fig. 3. Solar radiation and energy balance in and out of the open top chamber (OTC).



dry winds (Dorrepaal et al. 2004). At temperatures lower than 10 °C, VPD is generally at levels that do not constrain photosynthesis (Supplementary material 1) unless relative humidity is significantly below 50%.

Impacts on air and leaf temperatures

The OTCs provide passive warming; therefore, the magnitude of warming can vary greatly between locations (Fig. 4). Typically, warming is greatest around solar noon on a clear day with little wind and warming may be negligible when solar intensity is low (Fig. 5). At night temperatures within the OTC may also be cooler than outside the OTC due to radiative heat loss and reduced mixing and exchange with surrounding air (Dabros et al. 2010). The maximum potential intensity of warming is greatest near summer solstice, but in most locations, the variability of warming is more directly influenced by sky conditions and weather (Fig. 6; Hollister et al. 2006; Bokhorst et al. 2013; Schedlbauer et al. 2018). The effectiveness of OTCs at increasing air temperatures has been shown to be reduced at higher temperatures (Carlyle et al. 2011). Therefore, the net effect of OTCs can also be highly variable across time because the warming intensity of the OTCs depends on the ambient climate. This variability may better reflect future climate change than methods that increase temperature a constant amount.

Due to the nature of the warming, the daily range of temperatures is significantly greater in the OTC than the nearby ambient conditions (Fig. 6). This greater range is due to multiple factors, with the two main factors being reduction of wind and that the open top allows direct sunlight in part of the OTC (Hollister 1998). The greater range of temperatures and the general warming changes the number of freeze thaw **Fig. 4.** The average magnitude of open top chamber warming at Atqasuk, Alaska USA; Latnja, Sweden; Finse, Norway; and three sites at Alexandra Fjord, Ellesmere Island Canada. The dotted line represents the overall average. The daily course of warming was compiled for the summer months (June, July, and August) (unpublished data). The smoothness of the curve is a result of more years of observation (Atqasuk 1998–2021, Latnja 2020–2021, Finse 2019, Alexandra Fjord Cassiope and Willow 2008–2019, and Alexandra Fjord Dryas 2000–2019).



Fig. 5. The course of temperature and relative humidity over representative days in open top chambers (OTCs) (red dashed) and adjacent control plots (blue solid) (redrawn from Hollister 1998). Note, these readings are from a site with drier soils; in areas with higher moisture or standing water, relative humidity may be higher inside the OTCs and condensation may form on the inside of chamber walls (Bjorkman 2015).



events and other extreme temperatures experienced in the OTC (Bokhorst et al. 2013). The length of the growing season may be increased due to the warmer temperatures; however, snow accumulation inside the OTCs may negate the potential for earlier growth (see the Impacts on snow section) and the lack of OTC heating at night is likely to negate any differ-

ences in freeze events in the fall despite increasing average temperatures.

The OTC effect on temperature depends on where the temperature is measured. Warming is greatest near the ground surface in the center of the plot where direct sunlight enters the OTC (Hollister 1998); on average, at Northern latitudes,



Fig. 6. Change in the daily maximum, mean and minimum temperatures due to open top chamber warming. Points show average temperature differences from 1994–2018 at Utqiaġvik, Alaska USA; lines show the 2 week running mean for minimum (periwinkle), mean (grey) and maximum (magenta) daily temperatures (redrawn from Elmendorf and Hollister 2023).



the Northern half of the chamber warms slightly more than the Southern half, although throughout the daily cycle different regions in the chamber will warm more based primarily on what regions receive the most direct sunlight. Cross-site analyses benefit from standardized measurements. We therefore recommend studies employing OTCs deploy temperature sensors in the most commonly used location to date: halfway between the northernmost edge and center of the plot (or southernmost for Southern hemisphere sites), which will usually capture the largest magnitude of warming. Similarly, deployment of temperature sensors at the standardized (10-15 cm) plant height is recommended. At many sites the ground height is variable and the temperature sensor itself is more than a few cm long; therefore, an exact location is often not possible. The OTCs' effect on plant tissue and leaf surface temperatures have been found to be higher than the effect on the air temperatures (DeBoeck et al. 2012). The range of surface temperatures is greater within OTCs than in controls and results in higher maximum temperatures (Fig. 7; Healey et al. 2016; Lindwall et al. 2016) as well as lower temperatures due to shading (Jónsdóttir et al. 2005; Dabros et al. 2010). Elevated leaf temperatures have important consequences for plant water status through the increase in leaf to air VPD.

Impacts on snow

OTCs were designed to be installed year-round; however, many studies remove them in winter. In locations where the snowpack is lower than the height of the OTC, especially windswept regions with minimal snow cover, snow is trapped inside the OTCs and may accumulate; nevertheless, the warmer temperatures inside the OTCs tend to melt snow faster than the surrounding (Marion et al. 1997). However, without empirical evidence it is difficult to determine when snowmelt will occur within the OTC relative to the **Fig. 7.** Range of surface temperature observed by infrared photography of open top chamber (open red bars) and control (solid blue bars) plots (redrawn from Healey et al. 2016). The histogram represents surface temperatures observed in the Utqiagvik dry plots near mid-day on 4 August 2014; the spatial resolution was approximately 3 mm².



surroundings. At Alexandra Fiord (Ellesmere Island, Canada) and Finse (Norway), the combined effect of accumulated snow and warmer temperatures resulted in similar meltout days within the OTCs and ambient plots (Bjorkman et al. 2015; Klanderud personal observation). In sites with deeper snow inside the OTC, the soils under the OTC are more insulated from cold winter air and the soils are warmer during the winter compared to the ambient plots (Bokhorst et al. 2013; Bjorkman et al. 2015). The impacts of snow can be large and may vary greatly throughout the year and between years (Fig. 8). Greater snow accumulation in the OTCs has also the potential to increase water availability and nutrients, similar to snowfence manipulations (Rixen et al. 2022).

Impacts on soils and belowground properties

The impact of OTCs on soils varies greatly between locations and may result in higher soil temperatures within OTCs (Marion et al. 1997; Klanderud and Totland 2005; Bokhorst et al. 2013) as well as a cooling of the soil due to shading (Jónsdóttir et al. 2005; Dabros et al. 2010; Hollister et al. 2006; Dabros et al. 2010; Bokhorst et al. 2013), while some sites show no effect on soil temperatures (Hollister et al. 2006; Delarue et al. 2011; Buttler et al. 2015; Ma et al. 2022a). The impact on soil temperatures is complex, while air warming generally results in soil warming, reduced direct sunlight due to shading may offset increased air temperatures and the net result may be lower heat inputs into the soil, especially in landscapes with bare ground (see the Physics of OTC warming and Impacts on air and leaf temperatures sections). Cooling of the soil surface may be due to shading by the chamber walls or denser plant canopies reducing incoming radiation reaching the soil surface and thus reducing the warming effect (Klanderud and Totland 2005). It is also possible that vegetation changes inside the OTCs can impact the transfer of Fig. 8. Warming effect of the open top chambers (OTCs) (relative to control plots) at Atqasuk, Alaska USA and three sites at Alexandra Fjord, Ellesmere Island Canada. Lines represent the average daily temperature difference (OTC minus control) of each year, the thick blue line is a GAM-smoothed curve for the mean temperature difference across all years. Air temperatures were measured at a height of 10-15 cm. The OTCs are installed for the summer only at Atqasuk and remain in place year-round at Alexandra Fjord (redrawn from Bjorkman 2015 for the Dryas site and unpublished data compiled according to the methods in Bjorkman 2015); therefore, differences in air temperature above or within the snowpack during the winter at Atqasuk are due to differences in snow properties which vary greatly between years. At Alexandra Fjord, OTC impacts on above ground temperature greatly across the year and are greatest during the winter due to the insulative properties of the changed snow regimes.



heat from the air to the soil, similar to what has been suggested for shrubs (Blok et al. 2010), in particular a thicker moss layer may insulate the soil from ambient temperatures and incoming radiation (Lett et al. 2020). Furthermore, the lateral movement of soil water from outside the OTCs can negate any potential soil warming in moist, wet and flooded sites (Natali et al. 2011; Lindwall et al. 2016). The magnitude of difference may vary greatly throughout the year, for example, see differences in air temperature which may drive soil temperature (Fig. 8). While only a few OTC experiments have measured soil warming at depths of, or greater than, 20 cm (but see Hollister et al. 2006; Yang et al. 2015), it is generally assumed that warming effects diminish at greater soil depths due to the small size of the OTC and the hysteresis of surrounding soils. For this reason, soil temperature should be measured near the center of the plot. Warmer soils has resulted in increased depth of seasonal thaw under OTCs in Alaska (Welker et al. 2004; Hollister et al. 2006); increased thaw depth is particularly evident early in the season but may be swamped by the spatial diversity of thaw across the landscape (see Hinkel and Nelson 2003).

The OTCs tend to decrease soil moisture in drier sites, especially at the surface (Sjögersten and Wookey 2002; Bokhorst et al. 2013; van Zuijlen et al. 2022; Björnsdóttir et al. 2022; Jeanbille et al. 2022), although the effect is often not statistically significant and varies greatly depending on the soil moisture of the surroundings. However, in dry communities, a minor lowering in soil moisture near the surface may be enough to constrain plant performance (Hudson and Henry 2010; Dorji et al. 2013; Hollister et al. 2015). In moist and wet communities, the impact of the OTCs on soil moisture is often negligible (Hollister et al. 2006; Bernareggi et al. 2015), yet wet communities have also experienced drying in the OTCs (Scharn et al. 2021). Measurements of bare ground have shown increased soil moisture in OTCs due to reduced losses of soil water to the atmosphere (evaporation) as a result of reduced wind speed (Bernareggi et al. 2015; D'Imperio et al. 2017). It is also possible that changes in plant biomass may result in changes in evapotranspiration and soil moisture. Jeanbille et al. (2022) found decreased water content of the litter inside OTCs in some sites, whereas in other sites litter water content was higher in OTCs than in controls. In Latnjajare (Sweden), the OTCs are deployed over five plant communities following a soil moisture gradient (Scharn et al. 2021); here, only the warmed meadow (not heath) plots had a lower soil moisture content compared to ambient conditions. In particular for the dry and mesic meadow plots, the timing and magnitude of snowmelt drove the soil moisture differences between warmed and ambient plots (Scharn et al. 2021).

Studies on soil processes and the microbial communities have often found few direct impacts of the OTC (Lamb et al. 2011; Andresen et al. 2022; Jeanbille et al. 2022); however, there have been several studies that have documented changes in the microbial communities and soil processes in peatlands outside the tundra (Jassey et al. 2015; Delarue et al. 2015; Binet et al. 2017). The lack of a response in tundra is notable, given that warming has been shown to impact the quality of litter and thereby nutrient cycling (Cornelissen et al.



2007; Jeanbille et al. 2022) and impact the soil fauna (Dollery et al. 2006; Hågvar and Klanderud 2009). The reasons for a lack of response are unclear, but are likely due to the relatively low warming impact on soil temperatures, which decreases with depth, and may be masked by the heterogeneity of soils and vegetation. Furthermore, the rooting zones of the plants are likely to extend well beyond the chamber walls especially for plants with long rhizomes and underground stems, and below ground plant biomass has been shown to be less responsive to temperature than above ground biomass (Wang et al. 2016; Ma et al. 2022*a*, 2022*b*). Nevertheless, a few studies have shown earlier root growth (Sullivan and Welker 2005) and changing allocation patterns in response to warming (Björk et al. 2007; Hollister and Flaherty 2010; Yang et al. 2011).

Impacts on vegetation

The impacts of warming on tundra vegetation are the primary focus of the ITEX network and as such is described elsewhere; see Henry et al. 2022, this issue, for a review of OTC impacts on community composition, plant performance and carbon cycling. Here we focus on the robustness of using observations from the experimental manipulation to guide forecasts of vegetation change due to regional climate warming. Several studies have compared the response of plants in OTCs to that of a warmer year and in many cases found similar responses (Hollister and Webber 2000; Elmendorf et al. 2015; Bjorkman et al. 2020). Thawing degree days (daily temperatures above the lower threshold of 0 °C summed daily) have been shown to provide a reasonable prediction of plant responses irrespective of warming treatment (Hollister et al. 2005a), this is for instance true for inflorescence length of Carex aquatilis in Northern Alaska (Fig. 9). Comparisons of vegetation change due to warming by OTCs show similar patterns to regional warming and climate warming (Hollister et al. 2015; Elmendorf et al. 2015; Bjorkman et al. 2020). However, phenological development in OTCs has been shown to not advance as much as would be expected based on air temperatures (Hollister et al. 2005a; Oberbauer et al. 2013; Parker et al. 2017, 2022). Warming experiments across all biomes have been shown to under-predict phenological advance due to regional climate warming (Wolkovich et al. 2012). There is also evidence that OTC response may vary greatly depending on the season and year, these differences can be due to moisture available (Delarue et al. 2015; Jassey and Signarieux 2019), the responsiveness of plants has also been shown to be less during a warm year relative to a cold year (Barrett and Hollister 2016; Carbognani et al. 2016; but see Collins et al. 2021).

The explanation(s) for the differences between response to experimental warming and regional climate warming is not fully understood and there are likely a suite of reasons that vary between locations and species. Examining the differences between responses may further our understanding of the underlying mechanisms driving response to temperature. For example, the OTCs reduce wind, and sheltering from the wind can in itself drive vegetation change (Fitzgerald and Kirkpatrick 2017; Momberg et al. 2021). Also, the walls of the chambers may constrain seed rain and colonization of new **Fig. 9.** Inflorescence length of *Carex aquatilis* measured at the end of the summer at Atqasuk (triangles) and Utqiaġvik (squares) in OTCs (open red symbols) and ambient plots (closed blue symbols) graphed against thawing degree days measured from snowmelt until 15 August (redrawn and extended from Hollister et al. 2005a).



species, which may protect plants inside the OTCs from interactions with new immigrants (Yang et al. 2018).

The magnitude and quality of OTC warming may be significantly different from the warming experienced from climate change. The magnitude and timing of OTC warming varies by location and is generally on average less than 2 °C, this is a modest magnitude or warming that is less than some regions have already experienced due to climate change (IPCC 2022). The maximum temperatures experienced in warming experiments (including OTCs) may be outside the range normally experienced and the response to warming may diminish if the temperature optimum is exceeded (Elmendorf and Hollister 2023), it is possible that the maximum temperatures may negatively impact performance (Marchand et al. 2005; Shi et al. 2010). The potential decoupling of air and soil warming due to OTCs described above (see the Impacts on soils and belowground properties section) may also impact plant performance. The reduction of incoming photosynthetically active radiation (PAR) and other wavelengths relevant for plant development, such as far-red and ultraviolet radiation, varies within the OTC. Few studies report radiation measurements along with results from OTCs even though the reduced radiation and altered spectral composition, especially near the chamber walls, may impact plant production and change plant morphology in ways similar to shade experiments (May et al. 2022). Reductions of photosynthetic photon flux density as high as 16%-25% have been documented, the OTCs reduce light most when the sun is at a low angle, yet the open top allows direct sunlight and reductions are near zero at solar noon especially at lower latitude (Bokhorst et al. 2007; Lindwall et al. 2016; Schollert et al. 2017). It is also reasonable to assume that the vegetation response to warming may have built in lags and that the short-term response may be different from the long-term impacts (Hollister et al. 2005b; Rozema et al. 2009).

Cryptogam responses can vary greatly to OTC warming, with a dominant role for competition for light between cryptogams and vascular plants (Klanderud and Totland 2005; Wahren et al. 2005; Walker et al. 2006; Cornelissen et al. 2001; Day et al. 2008). In the few studied sites where mosses and lichens dominated, responses were highly species specific (Keuper et al. 2011; Dorrepaal 2007; Bokhorst et al. 2015, 2016). Moreover, this relationship can even be inverted in some habitats, for example, in Sphagnum dominated peatlands (Dorrepaal et al. 2006), often as a result of Sphagnum being a stronger competitor for nitrogen (Heijmans et al. 2002). Future studies may consider a specific focus on cryptogam communities with little to no vascular plants to better understand the moss and lichen response to climate warming without the influence of faster growing vascular plants.

Impacts on herbivores and pollinators

The impacts of OTCs on herbivores depend greatly on the species of interest. Large herbivores have often avoided OTCs, although reindeer have been seen to lean in and graze the plants within (personal observation IS Jónsdóttir at Endalen, Svalbard; EJ Cooper at Adventdalen and Ny Ålesund, Svalbard; RG Björk at Latnjajaure, Sweden). The presence of large herbivores can affect the outcome of passive warming from OTCs on plant communities. In West Greenland, herbivory by caribou and muskoxen has been observed to differentially influence the biomass response of plant functional groups to OTC-induced warming (Post and Pedersen 2008). After 7 years of study, grazed plots showed higher plant community stability and species diversity than ungrazed plots receiving the same warming treatment. The greater stability of grazed plots has been interpreted as the result of herbivore biomass exploitation mediating the effect of interspecific competition, which increases with warmer temperatures (Post 2013). The presence of small mammals such as lemmings and voles is patchy, although anecdotal evidence suggests that they may shelter in the OTCs. At Alexandra Fiord, OTCs were often covered with a screen to keep song birds from perching on the chamber walls and providing unwanted nutrient inputs and decimating the seed production. Juvenile snowy owls have also been observed to shelter in the OTCs on cool windy days.

Observations of insects are complex; for some species the chamber walls provide a deterrent, while other species seek out the chambers for shelter. Once in an OTC, activity is greater due to the lack of wind and warmer air temperatures (e.g., Gillespie et al. 2013; Birkemoe et al. 2016). Observations at Alexandra Fiord showed no impact of the OTC on insect pollination nor on wind pollinated species (Robinson and Henry 2018) whereas other sites have shown indications of potential pollen limitations in OTCs (Jones et al. 1997; Molau and Shaver 1997; Totland and Alatalo 2002; Totland and Eide 1999). OTCs have been used to demonstrate the link between timing of flowering and pollination in the High Arctic (Gillespie et al. 2016; Gillespie and Cooper 2022).

Items to consider

Robotic tram systems in close proximity to OTCs can provide continuous objective measurements of fundamental micrometeorological conditions present as well as biophysical properties of vegetation represented in nearby OTCs (Healey et al. 2014). Such implementations may help understand the different processes occurring at different scales across the heterogeneous landscape. Similarly, handheld instrumentation has also provided analysis of unique spectral characteristics linked with growth, development and phenology that are undetectable to the human eye (May et al. 2020). Our understanding of physiological impacts induced by OTCs has also been enhanced using thermal imaging technology (Healey et al. 2016). Surface tissue and underlying soil or moss temperatures are key determinants of metabolic activity and monitoring such phenomena is vital for comprehensive analysis of subtle, yet complex, interactions among permafrost, surface moss, cryptogamic crusts and soils, and tundra vegetation. Given the many factors and potential interactions between factors, we believe the use of OTCs is most effective when coupled with long-term monitoring.

As with any long-term experiment, it is important to clearly mark the plots with permanent robust markers and the corresponding precise GPS locations. Markers may include anchors that serve to retain the OTCs in position during high winds that occur at many study sites. How the OTCs are secured will depend on the location and the monitoring techniques deployed. Sometimes removal of the OTCs is desirable or necessary to facilitate measurement of the properties within. For example, measurement of vegetation solar spectral reflectance within the OTCs requires removal of the OTCs because of changes in the spectrum and amount of light transmitted through the chamber walls. Measurements of ecosystem trace gas fluxes within the OTCs creates a dilemma, should measurements be taken with the OTCs in place or with them removed. Measurements taken with the OTCs in place reflect the vegetation performance within the OTC environment that might include higher air and soil temperatures and lower light, while in cases where the focus is the vegetation potential it is preferable to remove the OTC to measure plant performance under the same environmental conditions.

While most experiments using OTC leave the OTCs in place year-round, many others remove them during the winter. It may be useful to deploy the OTCs during specific times of the year to ask specific questions. For example, Gehrman et al. (2022) deployed OTCs for late summer only use. Given that autumn is the season most neglected by summer-visiting researchers, autumn studies could help elucidate ecological activity and thermal sensitivities during the end of the growing season and during the onset of winter dormancy. However, there are caveats here related to the potential warming performance of OTCs at lower solar angles and shorter day lengths as the autumnal equinox approaches.



Finally, recent attempts have been made to scale up plotlevel observations from OTCs to biome-wide analyses using aerial or spaceborne observations (Westergaard-Nielsen et al. 2021). Therefore, it is important to clearly document the characteristics of the study site within the heterogeneity of the landscape and region to allow for comparison across sites and scaling of observations. The continued inclusion of remote sensing observations at a variety of scales will improve future monitoring of tundra plant responses to warming scenarios that have been projected to occur with climate change.

Recommendations and concluding remarks

It is important to document the impacts of the OTC on the physical environment at each study site. We have shown above that the impacts of OTCs vary greatly between locations in ways that are difficult to predict without empirical observations. Therefore, any observed biological response must be coupled with a clear understanding of the changes to the physical environment, including measurements at standardized locations throughout the season.

The OTC is a cost-effective robust method of in situ warming of ecosystems with low stature plants such as tundra environments. The response of tundra vegetation to OTC warming has been shown to be similar to that of interannual variability and latitudinal gradients (Elmendorf et al. 2015). However, as with any experimental manipulation, there are artifacts that may be problematic depending on the situation (Ettinger et al. 2019; Kimmel et al. 2021). The OTC may or may not provide a reasonable approximation of regional climate warming depending on the application. For example, the increased daily range of temperatures may be unrealistic, likewise air and soil warming may be decoupled. In many cases properly documenting the magnitude of warming both above-ground and below-ground may be enough to properly interpret the observations that the experiment was intended to examine. In other cases, it may be important to document other physical factors such as plant surface temperatures, PAR, wind speed, snow accumulation, nutrient inputs, or soil moisture. It may also be important to account for differences in herbivory or pollination. The small scale of the OTC makes it poorly suited to examine landscape dynamics such as permafrost degradation and changing migration patterns (Hegland et al. 2009; Post et al. 2009). Conversely, the small scale confers the advantage that OTCs can be deployed in contrasting landscape contexts, refining the process understanding necessary to underpin up-scaling such as interactions between microbes and plants (Jassey et al. 2015; Jeanbille et al. 2022; Klarenberg et al. 2022). Furthermore, the OTC does not require electricity and can be placed in remote locations.

In general, we recommend using the findings from OTC in conjunction with those of multiple years of observation. If the same patterns are observed in a warm year at ambient plot as observed in a warmed plot in a colder year, then the difference between warmed and control plot is mostly likely due primarily to temperature (Hollister et al. 2005*a*, 2005*b*; Hollister et al. 2015). In cases where the response to experimental warming and regional climate change are different, then the experiment may help elucidate biological processes that better our understanding of temperature relationships.

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Data availability

Most of the data presented in this study are continuations or redrawing of figures from published papers. All previously unpublished data are available from the corresponding author upon reasonable request.

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Competing interests

The authors declare there are no competing interests.

Supplementary material

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References

- Andresen, L.C., Bodé, S., Björk, R.G., Michelsen, A., Aerts, R. Boeckx, P., et al. 2022. Patterns of free amino acids in tundra soils reflect mycorrhizal type, shrubification, and warming. Mycorrhiza 32: 305–313. doi:10.1007/s00572-022-01075-4. 35307782.
- Aronson, E.L., and McNulty, S.G. 2009. Appropriate experimental ecosystem warming methods by ecosystem, objective, and practicality. Agric. For. Meteorol. 149: 1791–1799. doi:10.1016/j.agrformet.2009. 06.007.
- Barrett, R.T., and Hollister, R.D. 2016. Arctic plants are capable of sustained responses to long-term warming. Polar Res. 35: 25405. doi:10. 3402/polar.v35.25405.
- Bernareggi, G., Carbognani, M., Petraglia, A., and Mondoni, A. 2015. Climate warming could increase seed longevity of alpine snowbed plants. Alp. Bot. **125**: 69–78. doi:10.1007/s00035-015-0156-0.
- Binet, P., Rouifed, S., Jassey, V.E.J., Toussaint, M.-L., and Chiapusio, G. 2017. Experimental climate warming alters the relationship between fungal root symbiosis and sphagnum litter phenolics in two peatland microhabitats. Soil Biol. Biochem. 105: 153–161. doi:10.1016/j.soilbio. 2016.11.020.
- Birkemoe, T., Bergmann, S., Hasle, T.E., and Klanderud, K. 2016. Experimental warming increases herbivory by leaf-chewing insects in an alpine plant community. Ecol. Evol. 6: 6955–6962. doi:10.1002/ece3. 2398. PMID: 28725372.
- Bjõrk, R.G., Majdi, H., Klemedtsson, L., Lewis-Jonsson, L., and Molau, U. 2007. Long-term warming effects on root morphology, root mass distribution, and microbial activity in two dry tundra plant communities in northern Sweden New Phytologist, **176**: 852–873. doi:10.1111/ j.1469-8137.2007.02231.x.
- Bjorkman, A.D. 2015. Ph.D. Thesis. The University of British Columbia, Vancouver, Canada.
- Bjorkman, A.D., Elmendorf, S.C., Beamish, A.L., Vellend, M., and Henry, G.H.R. 2015. Contrasting effects of warming and increased snowfall on Arctic tundra plant phenology over the past two decades. Glob. Change Biol. **21**: 4651–4661. doi:10.1111/gcb.13051. PMID: 26216538.
- Bjorkman, A.D., Garcia Criado, M., Myers-Smith, I.H., Ravolainen, V., Jonsdottir, I.S. Westergaard, K.B., et al. 2020. Status and trends in Arctic vegetation: evidence from experimental warming and long-term monitoring. Ambio 49: 678–692. doi:10.1007/s13280-019-01161-6. PMID: 30929249.

- Björnsdóttir, K., Barrio, I.C., and Jónsdóttir, I.S. 2022. Long-term warming manipulations reveal complex decomposition responses across different tundra vegetation types. Arct. Sci. 8: 979–991. doi:10.1139/ as-2020-0046.
- Blok, D., Heijmans, M.M.P.D., Schaepman-Strub, G., Kononov, A.V., Maximov, T.C., and Berendse, F. 2010. Shrub expansion may reduce summer permafrost thaw in Siberian tundra. Glob. Change Biol. **16**: 1296– 1305. doi:10.1111/j.1365-2486.2009.02110.x.
- Bokhorst, S., Convey, P., Huiskes, A., and Aerts, R. 2016. Usnea antarctica, an important Antarctic lichen, is vulnerable to aspects of regional environmental change. Polar Biol. **39**: 511–521. doi:10.1007/ s00300-015-1803-z.
- Bokhorst, S., Huiskes, A., Aerts, R., Convey, P., Cooper, E.J. Dalen, L., et al. 2013. Variable temperature effects of open top chambers at polar and alpine sites explained by irradiance and snow depth. Glob. Change Biol. **19**: 64–74. doi:10.1111/gcb.12028.
- Bokhorst, S., Huiskes, A., Convey, P., and Aerts, R. 2007. The effect of environmental change on vascular plant and cryptogam communities from the Falkland Islands and the Maritime Antarctic. BMC Ecol. **7**: 15. doi:10.1186/1472-6785-7-15.
- Bokhorst, S., Phoenix, G.K., Berg, M.P., Callaghan, T.V., Kirby-Lambert, C., and Bjerke, J.W. 2015. Climatic and biotic extreme events moderate long-term responses of above- and belowground sub-Arctic heathland communities to climate change. Glob. Change Biol. 21: 4063–4075. doi:10.1111/gcb.13007.
- Buttler, A., Robroek, B.J.M., Laggoun-Défarge, F., Jassey, V.E.J., Pochelon, C. Bernard, G., et al. 2015. Experimental warming interacts with soil moisture to discriminate plant responses in an ombrotrophic peatland. J. Veg. Sci. 26: 964–974. doi:10.1111/jvs.12296.
- Carbognani, M., Bernareggi, G., Perucco, F., Tomaselli, M., and Petraglia, A. 2016. Micro-climatic controls and warming effects on flowering time in alpine snowbeds. Oecologia 182: 573–585. doi:10.1007/ s00442-016-3669-3.
- Carlyle, C.N., Fraser, L.H., and Turkington, R. 2011. Tracking soil temperature and moisture in a multi-factor climate experiment in temperate grassland: do climate manipulation methods produce their intended effects? Ecosystems **14**: 489–502. doi:**10.1007/s10021-011-9425-y**.
- Chapin, F.S., III, and Shaver, G.R. 1985. Individualistic growth response of tundra plant species to environmental manipulations in the field. Ecology **66**: 564–576. doi:10.2307/1940405.
- Collins, C.G., Elmendorf, S.C., Hollister, R.D., Henry, G.H.R., Clark, K. Bjorkman, A.D., et al. 2021. Experimental warming differentially affects vegetative and reproductive phenology of tundra plants. Nat. Commun. 12: 3442. doi:10.1038/s41467-021-23841-2.
- Cornelissen, J.H.C., Callaghan, T.V., Alatalo, J.M., Michelsen, A., Graglia, E. Hartley, A.E., et al. 2001. Global change and arctic ecosystems: is lichen decline a function of increases in vascular plant biomass? J. Ecol. 89: 984–994. doi:10.1111/j.1365-2745.2001. 00625.x.
- Cornelissen, J.H.C., Van Bodegom, P.M., Aerts, R., Callaghan, T.V., Van Logtestijn, R.S.P. Alatalo, J., et al. 2007. Global negative vegetation feedback to climate warming responses of leaf litter decomposition rates in cold biomes. Ecol. Lett. **10**: 619–627. doi:10.1111/j.1461-0248. 2007.01051.x.
- D'Imperio, L., Nielsen, C.S., Westergaard-Nielsen, A., Michelsen, A., and Elberling, B. 2017. Methane oxidation in contrasting soil types: responses to experimental warming with implication for landscapeintegrated CH ₄ budget. Glob. Change Biol. **23**: 966–976. doi:10.1111/ gcb.13400.
- Dabros, A., Fyles, J.W., and Strachan, I.B. 2010. Effects of open-top chambers on physical properties of air and soil at post-disturbance sites in northwestern Quebec. Plant Soil **333**: 203–218. doi:10.1007/s11104-010-0336-z.
- Day, T.A., Ruhland, C.T., and Xiong, F.S. 2008. Warming increases aboveground plant biomass and C stocks in vascular-plant-dominated Antarctic tundra. Glob. Change Biol. 14: 1827–1843. doi:10.1111/j. 1365-2486.2008.01623.x.
- De Boeck, H.J., De Groote, T., and Nijs, I. 2012. Leaf temperatures in glasshouses and open-top chambers. New Phytol. **194**: 1155–1164. doi:10.1111/j.1469-8137.2012.04117.x.
- Delarue, F., Buttler, A., Bragazza, L., Grasset, L., Jassey, V.E.J., Gogo, S., and Laggoun-Défarge, F. 2015. Experimental warming differentially affects microbial structure and activity in two contrasted moisture

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sites in a *Sphagnum*-dominated peatland. Sci. Total Environ. **511**: 576–583. doi:10.1016/j.scitotenv.2014.12.095.

- Delarue, F., Laggoun-Défarge, F., Buttler, A., Gogo, S., Jassey, V.E.J., and Disnar, J.-R. 2011. Effects of short-term ecosystem experimental warming on water-extractable organic matter in an ombrotrophic *Sphagnum* peatland (Le Forbonnet, France). Org. Geochem. **42**: 1016– 1024. doi:10.1016/j.orggeochem.2011.07.005.
- Dollery, R., Hodkinson, I.D., and Jónsdóttir, I.S. 2006. Impact of warming and timing of snow melt on soil microarthropod assemblages associated with *Dryas*-dominated plant communities on Svalbard. Ecography 29: 111–119. doi:10.1111/j.2006.0906-7590.04366.x.
- Dorji, T., Totland, Ø., Moe, S.R., Hopping, K.A., Pan, J.B., and Klein, J.A. 2013. Plant functional traits mediate reproductive phenology and success in response to experimental warming and snow addition in Tibet. Glob. Change Biol. **19**: 459–472. doi:10.1111/gcb.12059.
- Dorrepaal, E. 2007. Are plant growth-form-based classifications useful in predicting northern ecosystem carbon cycling feedbacks to climate change? J. Ecol. **95**: 1167–1180. doi:10.1111/j.1365-2745.2007.01294.x.
- Dorrepaal, E., Aerts, R., Cornelissen, J.H.C., Callaghan, T.V., and Van Logtestijn, R.S.P. 2004. Summer warming and increased winter snow cover affect *Sphagnum fuscum* growth, structure and production in a sub-Arctic bog. Glob. Change Biol. **10**: 93–104. doi:10.1111/j. 1365-2486.2003.00718.x.
- Dorrepaal, E., Aerts, R., Cornelissen, J.H.C., Van Logtestijn, R.S.P., and Callaghan, T.V. 2006. *Sphagnum* modifies climate-change impacts on subarctic vascular bog plants. Funct. Ecol. **20**: 31–41. doi:10.1111/j. 1365-2435.2006.01076.x.
- Elmendorf, S.C., and Hollister, R.D. 2023. Limits on phenological response to high temperature in the Arctic. Scientific Reports **13**: 208. doi:10.1038/s41598-022-26955-9.
- Elmendorf, S.C., Henry, G.H.R., Hollister, R.D., Fosaa, A.M., Gould, W.A. Hermanutz, L., et al. 2015. Experiment, monitoring, and gradient methods used to infer climate change effects on plant communities yield consistent patterns. Proc. Natl. Acad. Sci. U.S.A. 112: 448–452. doi:10.1073/pnas.1410088112.
- Ettinger, A.K., Chuine, I., Cook, B.I., Dukes, J.S., Ellison, A.M. Johnston, M.R., et al. 2019. How do climate change experiments alter plot-scale climate? Ecol. Lett. **22**: 748–763. doi:10.1111/ele.13223.
- Fitzgerald, N.B., and Kirkpatrick, J.B. 2017. Wind distortion in alpine and subantarctic plants is constant among life forms but does not necessarily reflect prevailing wind direction. Arct. Antarct. Alp. Res. 49: 521–535. doi:10.1657/AAAR0016-054.
- Gehrmann, F., Ziegler, C., and Cooper, E.J. 2022. Onset of autumn senescence in high Arctic plants shows similar patterns in natural and experimental snow depth gradients. Arct. Sci. 8: 744–766. doi:10.1139/ as-2020-0044.
- Gillespie, M.A.K., and Cooper, E.J. 2022. The seasonal dynamics of a High Arctic plant–visitor network: temporal observations and responses to delayed snow melt. Arct. Sci. 8: 786–803. doi:10.1139/as-2020-0056.
- Gillespie, M.A.K., Baggesen, N., and Cooper, E.J. 2016. High arctic flowering phenology and plant-pollinator interactions in response to delayed snow melt and simulated warming. Environ. Res. Lett. **11**: 115006. doi:10.1088/1748-9326/11/11/115006.
- Gillespie, M.A.K., Jónsdóttir, I.S., Hodkinson, I.D., and Cooper, E.J. 2013. Aphid–willow interactions in a high Arctic ecosystem: responses to raised temperature and goose disturbance. Glob. Change Biol. **19**: 3698–3708. doi:10.1111/gcb.12284.
- Godfree, R., Robertson, B., Bolger, T., Carnegie, M., and Young, A. 2011. An improved hexagon open-top chamber system for stable diurnal and nocturnal warming and atmospheric carbon dioxide enrichment. Glob. Change Biol. **17**: 439–451. Wiley Online Library. doi:10.1111/ j.1365-2486.2010.02276.x.
- Hågvar, S., and Klanderud, K. 2009. Effect of simulated environmental change on alpine soil arthropods. Glob. Change Biol. **15**: 2972–2980. doi:10.1111/j.1365-2486.2009.01926.x.
- Hanson, P.J., and Walker, A.P. 2020. Advancing global change biology through experimental manipulations: where have we been and where might we go? Glob. Change Biol. **26**: 287–299. doi:10.1111/gcb. 14894.
- Havström, M., Callaghan, T.V., Jonasson, S., and Havstrom, M. 1993. Differential growth responses of *Cassiope tetragona*, an Arctic dwarfshrub, to environmental perturbations among three contrasting high- and sub-Arctic sites. Oikos 66: 389. doi:10.2307/3544933.

- Healey, N., Oberbauer, S.F., Ahrends, H., Dierick, D., Welker, J. Leffler, A., et al. 2014. A mobile instrumented sensor platform for longterm terrestrial ecosystem analysis: an example application in an arctic tundra ecosystem. J. Environ. Inform. 24: 1–10. doi:10.3808/jei. 201400278.
- Healey, N.C., Oberbauer, S.F., and Hollister, R.D. 2016. Examination of surface temperature modification by open top chambers along moisture and latitudinal gradients in Arctic Alaska using thermal infrared photography. Remote Sens. 8: 54 1–19. doi:10.3390/ rs8010054.
- Hegland, S.J., Nielsen, A., Lázaro, A., Bjerknes, A.-L., and Totland, Ø. 2009. How does climate warming affect plant-pollinator interactions? Ecol. Lett. 12: 184–195. doi:10.1111/j.1461-0248.2008.01269.x.
- Heijmans, M.M.P.D., Klees, H., and Berendse, F. 2002. Competition between sphagnum magellanicum and eriophorum angustifolium as affected by raised CO2 and increased N deposition. Oikos 97: 415– 425. doi:10.1034/j.1600-0706.2002.970311.x.
- Henry, G.H.R., Hollister, R.D., Klanderud, K., Björk, R.G., Bjorkman, A.D. Elphinstone, C., et al. 2022. The International Tundra Experiment (ITEX): 30 years of research on tundra ecosystems. Arct. Sci. 8: 550– 571. doi:10.1139/as-2022-0041.
- Hinkel, K.M., and Nelson, F.E. 2003. Spatial and temporal patterns of active layer thickness at circumpolar active layer monitoring (CALM) sites in northern alaska, 1995–2000. J. Geophys. Res.-Atmos. 108: 8168. doi:10.1029/2001JD000927.
- Hollister, R.D. 1998. Response of Wet Meadow Tundra to Interannual and Manipulated Temperature Variation: Implications for Climate Change Research. Master's Thesis, Michigan State University, East Lansing, Michigan, USA.
- Hollister, R.D., and Flaherty, K.J. 2010. Above and belowground plant biomass response to experimental warming in northern Alaska. Appl. Veg. Sci. 13: 378–387. doi:10.1111/j.1654-109X.2010.01079.x.
- Hollister, R.D., and Webber, P.J. 2000. Biotic validation of small opentop chambers in a tundra ecosystem. Glob. Change Biol. 6: 835–842. doi:10.1046/j.1365-2486.2000.00363.x.
- Hollister, R.D., May, J.L., Kremers, K.S., Tweedie, C.E., Oberbauer, S.F. Liebig, J.A., et al. 2015. Warming experiments elucidate the drivers of observed directional changes in tundra vegetation. Ecol. Evol. 5: 1881–1895. doi:10.1002/ece3.1499.
- Hollister, R.D., Webber, P.J., and Bay, C. 2005a. Plant response to temperature in northern Alaska: implications for predicting vegetation change. Ecology 86: 1562–1570. doi:10.1890/04-0520.
- Hollister, R.D., Webber, P.J., and Tweedie, C.E. 2005b. The response of Alaskan Arctic tundra to experimental warming: differences between short- and long-term responses. Glob. Change Biol. **11**: 525–536. doi:10.1111/j.1365-2486.2005.00926.x.
- Hollister, R.D., Webber, P.J., Nelson, F.E., and Tweedie, C.E. 2006. Soil thaw and temperature response to air warming varies by plant community: results from an open-top chamber experiment in northern Alaska. Arct. Antarct. Alp. Res. **38**: 206–215. doi:10.1657/1523-0430(2006)38[206:STATRT]2.0.CO;2.
- Hudson, J.M.G., and Henry, G.H.R. 2010. High Arctic plant community resists 15 years of experimental warming. J. Ecol. **98**: 1035–1041. doi:10.1111/j.1365-2745.2010.01690.x.
- IPCC. 2022. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. *Climate Change 2022: Impacts, Adaptation, and Vulnerability.* Cambridge University Press, Cambridge, United Kingdom.
- Jassey, V.E.J., and Signarbieux, C. 2019. Effects of climate warming on *Sphagnum* photosynthesis in peatlands depend on peat moisture and species-specific anatomical traits. Glob. Change Biol. **25**: 3859–3870. doi:10.1111/gcb.14788.
- Jassey, V.E.J., Signarbieux, C., Hättenschwiler, S., Bragazza, L., Buttler, A. Delarue, F., et al. 2015. An unexpected role for mixotrophs in the response of peatland carbon cycling to climate warming. Sci. Rep. 5: 16931. doi:10.1038/srep16931.
- Jeanbille, M., Clemmensen, K., Juhanson, J., Michelsen, A., Cooper, E.J. Henry, G.H.R., et al. 2022. Site-specific responses of fungal and bacterial abundances to experimental warming in litter and soil across Arctic and alpine tundra. Arct. Sci. 8: 992–1005. doi:10.1139/ as-2020-0053.
- Jones, M.H., Bay, C., and Nordenhall, U. 1997. Effects of experimental warming on arctic willows (*Salix* spp.): a comparison of responses

from the Canadian High Arctic, Alaskan Arctic, and Swedish Subarctic. Glob. Change Biol. **3**: 55–60. doi:10.1111/j.1365-2486.1997.gcb135. **x**.

- Jónsdóttir, I.S., Magnússon, B., Gudmundsson, J., Elmarsdóttir, Á., and Hjartarson, H. 2005. Variable sensitivity of plant communities in Iceland to experimental warming. Glob. Change Biol. **11**: 553–563. doi:10.1111/j.1365-2486.2005.00928.x.
- Kennedy, A.D. 1995. Temperature effects of passive greenhouse apparatus in high-latitude climate change experiments. Funct. Ecol. 9: 340–350. [British Ecological Society, Wiley]. doi:10.2307/ 2390583.
- Keuper, F., Dorrepaal, E., Van Bodegom, P.M., Aerts, R., Van Logtestijn, R.S.P., Callaghan, T.V., and Cornelissen, J.H.C. 2011. A race for space? How Sphagnum fuscum stabilizes vegetation composition during longterm climate manipulations. Glob. Change Biol. 17: 2162–2171. doi:10.1111/j.1365-2486.2010.02377.x.
- Kimmel, K., Dee, L.E., Avolio, M.L., and Ferraro, P.J. 2021. Causal assumptions and causal inference in ecological experiments. Trends Ecol. Evol. **36**: 1141–1152. doi:10.1016/j.tree.2021.08.008.
- Klanderud, K., and Totland, Ø. 2005. Simulated climate change altered dominance hierarchies and diversity of an alpine biodiversity hotspot. Ecology **86**: 2047–2054. doi:10.1890/04-1563.
- Klarenberg, I.J., Keuschnig, C., Russi Colmenares, A.J., Warshan, D., Jungblut, A.D., Jónsdóttir, I.S., and Vilhelmsson, O. 2022. Long-term warming effects on the microbiome and *nifH* gene abundance of a common moss species in sub-Arctic tundra. New Phytol. 234: 2044–2056. doi:10.1111/nph.17837.
- Lamb, E.G., Han, S., Lanoil, B.D., Henry, G.H.R., Brummell, M.E., Banerjee, S., and Siciliano, S.D. 2011. A high Arctic soil ecosystem resists longterm environmental manipulations. Glob. Change Biol. 17: 3187– 3194. doi:10.1111/j.1365-2486.2011.02431.x.
- Lamentowicz, M., Słowińska, S., and Słowiński, M. 2016. Combining short-term manipulative experiments with long-term palaeoecological investigations at high resolution to assess the response of *Sphagnum* peatlands to drought, fire and warming. Mires Peat **18**: 1–17. doi:10.19189/MaP.2016.OMB.244.
- Lett, S., Teuber, L.M., Krab, E.J., Michelsen, A., Olofsson, J., Nilsson, M.-C., et al. 2020. Mosses modify effects of warmer and wetter conditions on tree seedlings at the alpine treeline. Glob. Change Biol. 26: 5754– 5766. doi:10.1111/gcb.15256.
- Lindwall, F., Svendsen, S.S., Nielsen, C.S., Michelsen, A., and Rinnan, R. 2016. Warming increases isoprene emissions from an Arctic fen. Sci. Total Environ. 553: 297–304. doi:10.1016/j.scitotenv.2016.02. 111.
- Ma, T., Parker, T., Fetcher, N., Unger, S.L., Gewirtzman, J., Moody, M.L., and Tang, J. 2022a. Leaf and root phenology and biomass of *Eriophorum vaginatum* in response to warming in the Arctic. J. Plant Ecol. 15: 1091–1105. doi:10.1093/jpe/rtac010.
- Ma, T., Parker, T., Unger, S., Gewirtzman, J., Fetcher, N., Moody, M.L., and Tang, J. 2022b. Responses of root phenology in ecotypes of *Eriophorum vaginatum* to transplantation and warming in the Arctic. Sci. Total Environ. **805**: 149 926. doi:10.1016/j.scitotenv.2021.149926.
- Marchand, F.L., Mertens, S., Kockelbergh, F., Beyens, L., and Nijs, I. 2005. Performance of high Arctic tundra plants improved during but deteriorated after exposure to a simulated extreme temperature event. Glob. Change Biol. 11: 2078–2089. doi:10.1111/j.1365-2486. 2005.01046.x.
- Marion, G.m., Henry, G.h.r., Freckman, D.w., Johnstone, J., Jones, G., Jones, M.h., et al. 1997. Open-top designs for manipulating field temperature in high-latitude ecosystems. Glob. Change Biol. 3: 20–32. doi:10.1111/j.1365-2486.1997.gcb136.x.
- May, J.L., Hollister, R.D., Betway, K.R., Harris, J.A., Tweedie, C.E., Welker, J.M., et al. 2020. NDVI changes show warming increases the length of the green season at tundra communities in northern Alaska: a fine-scale analysis. Front. Plant Sci. 11: 1174. doi:10.3389/fpls.2020. 01174.
- May, J.L., Oberbauer, S.F., Unger, S.L., Simon, M.J., Betway, K.R., and Hollister, R.D. 2022. Shading decreases and delays NDVI and flowering of prostrate Arctic shrubs. Arct. Sci. 8: 967–978. doi:10.1139/ as-2020-0043.
- Michelsen, A., Rinnan, R., and Jonasson, S. 2012. Two decades of experimental manipulations of heaths and forest understory in the subarctic. Ambio 41: 218–230. doi:10.1007/s13280-012-0303-4.

- Molau, U., and Mølgaard, P. 1996. International Tundra Experiment (ITEX) Manual. Second ed. Danish Polar Center, Copenhagen, Denmark.
- Molau, U., and Shaver, G.R. 1997. Controls on seed production and seed germinability in *Eriophorum vaginatum*. Glob. Change Biology, **3**: 80–88. doi:10.1111/j.1365-2486.1997.gcb130.x.
- Momberg, M., Hedding, D.W., Luoto, M., and le Roux, P.C. 2021. Species differ in their responses to wind: the underexplored link between species fine-scale occurrences and variation in wind stress. J. Veg. Sci. **32**: e13093. doi:10.1111/jvs.13093.
- Natali, S.M., Schuur, E.a.G., Trucco, C., Hicks Pries, C.E., Crummer, K.G., and Baron Lopez, A.F. 2011. Effects of experimental warming of air, soil and permafrost on carbon balance in Alaskan tundra. Glob. Change Biol. 17: 1394–1407. doi:10.1111/j.1365-2486.2010. 02303.x.
- Oberbauer, S.F., Elmendorf, S.C., Troxler, T.G., Hollister, R.D., Rocha, A.V., Bret-Harte, M.S., et al. 2013. Phenological response of tundra plants to background climate variation tested using the international tundra experiment. Phil. Trans. R. Soc. B **368**: 20120481. doi:10.1098/rstb. 2012.0481.
- Parker, T.C., Tang, J., Clark, M.B., Moody, M.M., and Fetcher, N. 2017. Ecotypic differences in the phenology of the tundra species *Eriophorum vaginatum* reflect sites of origin. Ecol. Evol. 7: 9775–9786. doi:10.1002/ece3.3445.
- Parker, T.C., Unger, S.L., Moody, M.L., Tang, J., and Fetcher, N. 2022. Intraspecific variation in phenology offers resilience to climate change for *Eriophorum vaginatum*. Arct. Sci. 8: 935–951. doi:10.1139/ as-2020-0039.
- Post, E. 2013. Erosion of community diversity and stability by herbivore removal under warming. Proc. R. Soc. B. **280**: 20122722. doi:10.1098/ rspb.2012.2722.
- Post, E., and Pedersen, C. 2008. Opposing plant community responses to warming with and without herbivores. Proc. Natl. Acad. Sci. U.S.A. 105: 12 353–12 358. doi:10.1073/pnas.0802421105.
- Post, E., Forchhammer, M.C., Bret-Harte, M.S., Callaghan, T.V., Christensen, T.R., Elberling, B., et al. 2009. Ecological dynamics across the arctic associated with recent climate change. Science **325**: 1355–1358. doi:10.1111/j.1365-2486.1997.gcb135.x.
- Pugnaire, F.I., Pistón, N., Macek, P., Schöb, C., Estruch, C., and Armas, C. 2020. Warming enhances growth but does not affect plant interactions in an alpine cushion species. Perspect. Plant Ecol. Evol. Syst. 44: 125530. doi:10.1016/j.ppees.2020.125530.
- Rixen, C., Høye, T.T., Macek, P., Aerts, R., Alatalo, J., Andeson, J., et al. 2022. Winters are changing: snow effects on Arctic and alpine tundra ecosystems. Arct. Sci. 8: 572–608. doi:10.1139/AS-2020-0058.
- Robinson, S.V.J., and Henry, G.H.R. 2018. High Arctic plants show independent responses to pollination and experimental warming. Botany 96: 385–396. doi:10.1139/cjb-2017-0200.
- Rozema, J., Weijers, S., Broekman, R., Blokker, P., Buizer, B., Werleman, C., et al. 2009. Annual growth of *Cassiope tetragona* as a proxy for Arctic climate: developing correlative and experimental transfer functions to reconstruct past summer temperature on a millennial time scale. Glob. Change Biol. 15: 1703–1715. doi:10.1111/j. 1365-2486.2009.01858.x.
- Scharn, R., Little, C.J., Bacon, C.D., Alatalo, J.M., Antonelli, A., Björkman, M.P., et al. 2021. Decreased soil moisture due to warming drives phylogenetic diversity and community transitions in the tundra. Environ. Res. Lett. 16: 064031. doi:10.1088/1748-9326/abfe8a.
- Schedlbauer, J.L., Fetcher, N., Hood, K., Moody, M.L., and Tang, J. 2018. Effect of growth temperature on photosynthetic capacity and respiration in three ecotypes of *Eriophorum vaginatum*. Ecol. Evol. **8**: 3711– 3725. doi:10.1002/ece3.3939.
- Schollert, M., Kivimäenpää, M., Michelsen, A., Blok, D., and Rinnan, R. 2017. Leaf anatomy, BVOC emission and CO₂ exchange of Arctic plants following snow addition and summer warming. Ann. Bot. **119**: 433–445. doi:10.1093/aob/mcw237.
- Shaver, G.R., Canadell, J.G., Chapin, F.S., Gurevitch, J., Harte, J., Henry, G., et al. 2000. Global warming and terrestrial ecosystems: a conceptual framework for analysis. BioScience 50: 871–882. doi:10.1641/ 0006-3568(2000)050[0871:GWATEA]2.0.CO;2.
- Shi, F.S., Wu, Y., Wu, N., and Luo, P. 2010. Photosynthetica **48**: 437–445. doi:10.1007/s11099-010-0058-8.
- Sjögersten, S., and Wookey, P.A. 2002. Spatio-temporal variability and environmental controls of methane fluxes at the forest-tundra eco-



tone in the Fennoscandian mountains. Glob. Change Biol. **8**: 885–894. doi:10.1046/j.1365-2486.2002.00522.x.

- Spence, L.A., Liancourt, P., Boldgiv, B., Petraitis, P.S., and Casper, B.B. 2014. Climate change and grazing interact to alter flowering patterns in the Mongolian steppe. Oecologia 175: 251–260. doi:10.1007/ s00442-014-2884-z.
- Sullivan, P.F., and Welker, J.M. 2005. Warming chambers stimulate early season growth of an Arctic sedge: results of a minirhizotron field study. Oecologia **142**: 616–626. doi:10.1007/s00442-004-1764-3.
- Sun, S.-Q., Peng, L., Wang, G.-X., Wu, Y.-H., Zhou, J., Bing, H.-J., et al. 2013. An improved open-top chamber warming system for global change research. Silva Fenn. 47: 1–11. doi:10.14214/sf.960.
- Totland, Ø., and Alatalo, J.M. 2002. Effects of temperature and date of snowmelt on growth, reproduction, and flowering phenology in the Arctic/alpine herb, *Ranunculus glacialis*. Oecologia **133**: 168–175. doi:10.1007/s00442-002-1028-z.
- Totland, Ø., and Eide, W. 1999. Environmentally-dependent pollen limitation on seed production in alpine *Ranunculus acris*. Ecoscience 6: 173–179. doi:10.1080/11956860.1999.11682518.
- van Zuijlen, K., Klanderud, K., Dahle, O.S., Hasvik, Å., Knutsen, M.S., Olsen, S.L., et al. 2022. Community-level functional traits of alpine vascular plants, bryophytes, and lichens after long-term experimental warming. Arct. Sci. 8: 843–857. doi:10.1139/as-2020-0007.
- Wahren, C.-H.A., Walker, M.D., and Bret-Harte, M.S. 2005. Vegetation responses in Alaskan Arctic tundra after 8 years of a summer warming and winter snow manipulation experiment. Glob. Change Biol. 11: 537–552. doi:10.1111/j.1365-2486.2005.00927.x.
- Walker, M.D., Wahren, C.H., Hollister, R.D., Henry, G.H.R., Ahlquist, L.E., Alatalo, J.M., et al. 2006. Plant community responses to experimental warming across the tundra biome. Proc. Natl. Acad. Sci. U.S.A. 103: 1342–1346. doi:10.1073pnas.0503198103.
- Wang, P., Heijmans, M.M.P.D., Mommer, L., van Ruijven, J., Maximov, T.C., and Berendse, F. 2016. Belowground plant biomass allocation in tundra ecosystems and its relationship with temperature. Environ. Res. Lett. 11: 055003. doi:10.1088/1748-9326/11/5/055003.

- Welker, J.M., Fahnestock, J.T., Henry, G.H.R., O'Dea, K.W., and Chimner, R.A. 2004. Co₂ exchange in three Canadian High Arctic ecosystems: response to long-term experimental warming. Glob. Change Biol. 10: 1981–1995. doi:10.1111/j.1365-2486.2004.00857.x.
- Welshofer, K.B., Zarnetske, P.L., Lany, N.K., and Thompson, L.A.E. 2018. Open-top chambers for temperature manipulation in taller-stature plant communities. Methods Ecol. Evol. 9: 254–259. doi:10.1111 /2041-210X.12863.
- Westergaard-Nielsen, A., Christiansen, C.T., and Elberling, B. 2021. Growing season leaf carbon:nitrogen dynamics in Arctic tundra vegetation from ground and sentinel-2 observations reveal reallocation timing and upscaling potential. Remote Sens. Environ. 262: 112512. doi:10.1016/j.rse.2021.112512.
- Wolkovich, E.M., Cook, B.I., Allen, J.M., Crimmins, T.M., Betancourt, J.L. Travers, S.E., et al. 2012. Warming experiments underpredict plant phenological responses to climate change. Nature 485: 494–497. doi:10.1038/nature11014.
- Wookey, P.A., Parsons, A.N., Welker, J.M., Potter, J.A., Callaghan, T.V., Lee, J.A., and Press, M.C. 1993. Comparative responses of phenology and reproductive development to simulated environmental change in sub-Arctic and High Arctic plants. Oikos 67: 490–502. [Nordic Society Oikos, Wiley]. doi:10.2307/3545361.
- Yang, Y., Halbritter, A.H., Klanderud, K., Telford, R.J., Wang, G., and Vandvik, V. 2018. Transplants, open top chambers (OTCs) and gradient studies ask different questions in climate change effects studies. Front. Plant Sci. 9: 1574. doi:10.3389/fpls.2018.01574.
- Yang, Y., Wang, G., Klanderud, K., and Yang, L. 2011. Responses in leaf functional traits and resource allocation of a dominant alpine sedge (*Kobresia pygmaea*) to climate warming in the Qinghai–Tibetan Plateau permafrost region. Plant Soil **349**: 377–387. doi:10.1007/ s11104-011-0891-y.
- Yang, Y., Wang, G., Klanderud, K., Wang, J., and Liu, G. 2015. Plant community responses to five years of simulated climate warming in an alpine fen of the Qinghai–Tibetan Plateau. Plant Ecol. Divers. 8: 211– 218. doi:10.1080 /17550874.2013.871654.