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.
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.

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:

\[
\text{net radiation absorbed (} Q^* \text{)} = \text{evapotranspiration (} Q_{\text{LE}} \text{)} + \text{sensible heat flux (} Q_H \text{)} + \text{ground heat flux (} Q_G \text{)} + [\text{net energy flux by advection (} Q_v \text{)} + \text{net storage (} \Delta S \text{)}].
\]

Generally, \( Q_v \) and \( \Delta S \) 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

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net radiation absorbed (\( Q^* \)) = evapotranspiration (\( Q_{\text{LE}} \)) + sensible heat flux (\( Q_H \)) + ground heat flux (\( Q_G \)) + [net energy flux by advection (\( Q_v \)) + net storage (\( \Delta S \))].
dry winds (Dorrepaa 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).
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 Utqiagvik, 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 northermost 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; Dabro 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. 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.
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; Jaissie and Signareix 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 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 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). Nevertheless, a few studies have shown earlier root growth (Sullivan and Welker 2011).

Fig. 9. Inflorescence length of Carex aquatilis measured at the end of the summer at Atqasuk (triangles) and Utqiagvik (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).
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, although reindeer have been seen to lean in and graze the plants within). Invertebrates may be different from the long-term impacts (Hollister et al. 2005a; Rozema et al. 2007). 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).

Although reindeer have been seen to lean in and graze the plants within OTCs, it is also likely that there may be some effects on the short-term response 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; Birkenmoe et al. 2016). Observations at Alexandre Fjord 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 phytology 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 growth on a yearly basis 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 on 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, Gehrmann 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 and physiological processes 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 plot-level 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. 2005a, 2005b; 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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References


Jones, M.H., Bay, C., and Nordenhall, U. 1997. Effects of experimental warming on arctic willows (Salix spp.): a comparison of responses...


