Experimental warming differentially affects vegetative and reproductive phenology of tundra plants

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Rapid climate warming is altering Arctic and alpine tundra ecosystem structure and function, including shifts in plant phenology. While the advancement of green up and flowering are well-documented, it remains unclear whether all phenophases, particularly those later in the season, will shift in unison or respond divergently to warming. Here, we present the largest synthesis to our knowledge of experimental warming effects on tundra plant phenology from the International Tundra Experiment. We examine the effect of warming on a suite of season-wide plant phenophases. Results challenge the expectation that all phenophases will advance in unison to warming. Instead, we find that experimental warming caused: (1) larger phenological shifts in reproductive versus vegetative phenophases and (2) advanced reproductive phenophases and green up but delayed leaf senescence which translated to a lengthening of the growing season by approximately 3%. Patterns were consistent across sites, plant species and over time. The advancement of reproductive seasons and lengthening of growing seasons may have significant consequences for trophic interactions and ecosystem function across the tundra.
High latitudes and elevations are warming much faster than the global average, with Arctic models suggesting between 3–5 °C of warming in spring and 7–13 °C in autumn by the end of the century. One consequence of this warming is altered plant phenology, including both the initiation and/or duration of vegetative and reproductive phenophases. Changes in tundra plant phenology have considerable implications for plant–pollinator interactions, herbivory, productivity, and carbon and energy balances. Despite this, we still lack a broad understanding of how warming influences the timing of multiple plant phenophases, particularly later in the season and whether all phenophases will respond in unison, or whether divergent responses to warming across phenophases will change the relative timing and duration of phenological events. This is especially true for the tundra, which is among the least studied biomes for plant phenology responses to climate change. Therefore, an improved understanding of how warming influences tundra plant phenology across multiple phenophases is crucial to predicting how tundra ecosystems will function in a warmer world.

There are numerous potential scenarios for how and why plant phenophases may respond distinctively to a warming climate. Reproductive and vegetative phenophases may differ in response to warming temperatures due to differences in plant-level physiology and co-evolutionary drivers (Fig. 1, tissue-type response scenario). For example, leaves and flowers utilize different physiological mechanisms to prevent frost damage and allow for sensitive responses to early spring temperature cues. Supercooling is the primary mechanism shown to prevent frost damage in reproductive structures of tundra plants, while extra-organ freezing or freezing tolerance is most common in leaves. Differing evolutionary mechanisms may also play a role, as flowering has likely co-evolved with pollinators while leaf phenology is influenced by herbivore pressure. In particular, species with early season pollinators (i.e., spring-flowering species) have shown higher phenotypic plasticity and ability to advance flowering with warming than later flowering species. Variable temperature sensitivity of leafing and flowering phenophases might also reflect selection for lower temporal overlap with interspecific competitors or herbivores or higher overlap with cross-pollinating conspecifics. Differential responses of flowering and leaf phenology can have consequences across trophic levels, highlighting the need for experimental comparisons of warming effects on both reproductive and vegetative phenophases.

Early and late season phenophases may also differ in their responses to warming (Fig. 1, early-late response scenario) if they are co-limited by different non-temperature variables such as snowmelt, and/or photoperiod. Broadly, long-term remote sensing and in situ monitoring suggest that early season (spring) phenophases will advance with warming, while general patterns for late season (autumn) phenophases, primarily leaf senescence, remain unresolved. The lack of resolution in late season phenological responses is due to several factors including conflicting evidence on patterns and drivers of senescence, and fewer studies overall for autumnal phenophases. Asynchronous shifts in early and late season phenophases may result in the lengthening or contracting of the growing, flowering, and/or fruiting seasons, while general patterns for late season (autumn) phenophases, primarily leaf senescence, remain unresolved. The lack of resolution in late season phenological responses is due to several factors including conflicting evidence on patterns and drivers of senescence, and fewer studies overall for autumnal phenophases. On the other hand, the start and end of plant phenophases (growth, flowering, and fruiting periods) may shift in concert because of fixed periodicity in phenophase duration (unison response scenario). Thus the net impacts of warming on both the timing and duration of tundra plant phenology require further investigation.

In addition to distinct responses among plant phenophases, overall plant sensitivity to warming can vary across spatial and temporal gradients in climate and resource availability, which can result in amplified or saturating phenology responses under certain conditions. For example, warming can dry out surface soils and increase the rate of snowmelt, potentially creating abiotic stress and shifting the timing of plant growth and phenology, especially for shallow-rooted or non-vascular plant species. At colder, high latitude sites, the thermal sums required to trigger phenological events may be lower than at warmer, lower latitude sites and thus phenological responses to the same amount of temperature change may be stronger at higher latitudes or in colder years at a given site. Finally, initial plant responses may differ from long-term responses to warming, as many tundra plants use stored resources from previous growing seasons to initiate growth or flowering, and these lag effects can delay responses.

Experimental warming manipulations, including passive open-top chambers (OTCs) are a widely used method to isolate the influence of warming temperatures on plant phenology. Plant phenology can be influenced by external cues such as temperature, snowmelt, and day length, and internal physiological cues such as a deterministic leaf or flowering longevity that may be phylogenetically constrained. Experimental approaches are necessary in order to disentangle these multiple, in some cases interacting, drivers and develop clear predictions of plant phenology responses to a warming climate. However, as with most experimental manipulations, in situ studies of plant phenology are limited in terms of species coverage, spatial extent, time period, and inclusion of multiple phenophases.

We address these limitations through a synthesis of data from the International Tundra Experiment (ITEX) covering 18 sites and 46 OTC warming experiments across Arctic, sub-Arctic, and alpine ecosystems with observations between 1 and 20 years in duration on six plant phenophases (green up, flowering, end of flowering, fruiting, seed dispersal, and leaf senescence). To our knowledge, this is this largest synthesis of experimental warming effects on tundra phenology to date, consolidating knowledge at the biome level, and providing experimental evidence of warming impacts across all major plant phenophases.

We ask the following questions:

1. What is the overall magnitude (number of days) and direction (advance or delay) of plant phenology shifts in response to warming?
2. Does warming differentially affect reproductive and vegetative phenology?
3. Does warming shorten, lengthen, or have no effect on the duration of growth, flowering, and fruiting/seed maturation periods?
4. How do plant responses to warming vary across spatial and temporal gradients in resource availability and ambient climate?
5. Are plant responses to warming sustained over time?

We hypothesize that warming will: (1) Differentially affect reproductive and vegetative phenophases and/or early and late season phenophases (tissue-type, early-late response scenarios, Fig. 1). (2) Shift both the timing and duration of growth, flowering, and fruiting periods. (3) Have stronger effects at higher latitudes and in colder years due to higher plant temperature sensitivity in colder climates. (4) Have stronger effects in dry sites due to interactions between warming and soil water stress and when chambers are deployed year-round due to increased thermal sums and earlier snowmelt. (5) Show enhanced plant responses over time due to initial lag effects of warming on phenology in many tundra species.
Here we show that experimental warming causes: (1) larger phenological shifts in reproductive versus vegetative phenophases and (2) advanced reproductive phenophases and green up but delayed leaf senescence which translates to a lengthening of the growing season by ~3%. Patterns are generally consistent across sites, plant species, and over time, with factors such as ambient climate and soil moisture having minor influences on plant phenological responses to experimental warming. Together, our findings highlight that that climate warming will not simply advance all phases of tundra plant phenology but rather that responses depend on plant tissue type and whether phenophases occur early or late in the growing season. The advancement of species’ reproductive seasons and lengthening of species’ growing seasons may have potentially significant consequences to trophic interactions and ecosystem function.

**Results**

**Experimental warming effects.** We found an effect of experimental warming on five out of six phenophases. Estimated shifts in OTC vs control plots did not overlap zero (based on 90% Bayesian CIs) for green up, flowering, end of flowering, seed dispersal, and leaf senescence (Table 1 and Fig. 3). Four of these phenophases (flowering, end of flowering, seed dispersal, and leaf senescence) showed significant responses to experimental warming. Green up showed a significant increase in the spring phenophase, while flowering showed a significant increase in both the spring and autumn phenophases. End of flowering showed a significant increase in the autumn phenophase, and leaf senescence showed a significant decrease in the autumn phenophase. Seed dispersal did not show any significant changes.

**Fig. 1 Potential scenarios of plant phenology responses to warming.** Phenophases are represented by images, and their timing reflected by their relative position on the line from spring to autumn. The arrows above images show the direction and magnitude (arrow thickness) of changes in timing for each phenophase in response to warming. Green, yellow, and brown horizontal bars reflect the length (duration) of the growth, flowering, and fruiting periods, respectively. Ambient signified no warming (i.e., control). Unison response scenario: all phenophases shift in the same direction (earlier) by an equal magnitude. The timing of phenology is shifted but there is no change in the duration of phenophases. Early-late response scenario: early (spring) and late (autumn) season phenophases shift in different directions (earlier, later) with the same magnitude. The timing of phenology is shifted and the duration of growth, flowering, and fruiting periods are lengthened. Tissue-type response scenario: all phenophases shift in the same direction (earlier) but reproductive phenophases shift by a greater magnitude than vegetative phenophases. The timing of phenology is shifted and the duration of the flowering and fruiting periods are shortened. The first response scenario describes an example of phenology having fixed periodicity where all phenophases shift in concert in response to warming. The second and third scenarios describe examples of distinct responses to warming between early vs. late season or vegetative vs. reproductive phenology, which can result in either a lengthening or shortening of vegetative and/or reproductive periods. This is not an exhaustive list but rather three hypothetical scenarios out of numerous possible plant phenology responses to warming. All botanical illustrations of Cassiope tetragona by Jane G. Smith.
Estimated shifts of green up and leaf senescence in response to OTC warming were in opposing directions supporting an early-late response scenario (Fig. 1). These differences reflect a lengthening of species’ growing seasons by 1.5 ± 0.6 days (Bayesian CIs 90% [0.58, 2.52], 95% [0.38, 2.75]) (Supplementary Fig. 1). Flowering also shifted slightly more than the end of flowering; however, there was no change in the length of species’ flowering periods based on Bayesian CIs (90% [−0.78, 1.94], 95% [−1.04, 2.24]). Posterior distributions for fruiting and seed dispersal overlapped entirely suggesting no change in the length of species’ fruiting periods (Fig. 3).

Interactions with spatiotemporal factors. While warming effects varied substantially among phenophases, within a phenophase, responses were fairly stable across latitudes, moisture regimes, site climate windows, and over time. Spatiotemporal covariates

| Model parameter | Phenophase       | Estimate (days) | Std. error | 90% eti low | 90% eti high | 95% eti low | 95% eti high |
|-----------------|-----------------|-----------------|------------|-------------|--------------|-------------|--------------|
| OTC             | Green up        | −0.731          | 0.480      | −1.558      | −0.033       | −1.789      | 0.108        |
| OTC             | Flowering       | −2.437          | 0.612      | −3.477      | −1.503       | −3.724      | −1.330       |
| OTC             | End of flowering| −1.877          | 0.569      | −2.788      | −0.992       | −3.031      | −0.760       |
| OTC             | Fruiting        | −2.581          | 1.875      | −5.600      | 0.100        | −6.572      | 0.947        |
| OTC × Soil moisture | Seed dispersal | −2.902          | 1.399      | −5.187      | −0.702       | −5.737      | −0.179       |
| OTC × OTC period | Flowering       | 1.313           | 0.657      | 0.231       | 2.294        | 0.044       | 2.495        |
| OTC × Site T    | Seed dispersal  | −0.880          | 0.525      | −1.790      | −0.063       | −1.984      | 0.065        |

Model parameter signifies the effect of treatment (OTC = difference in days between OTC-CTL) and the interaction of treatment (OTC ×) with a spatiotemporal (st) predictor. The interaction of OTC warming with other factors was examined for years of warming, latitude, soil moisture, OTC deployment period, and site mean climate anomaly; only those interactions where estimates did not cross zero based on 90% Bayesian credible intervals are shown (complete model results can be found in Supplementary Tables 3-6). For the soil moisture interaction, the model parameter signifies the difference in days between moist and dry sites, respectively, showing flowering occurred later in OTCs at moist sites. For the OTC period interaction, the model parameter signifies a difference in days between year-round and summer only OTCs, respectively, and sites where OTCs that were deployed in the summer only had later flowering. For the Site interaction, the model parameter signifies the difference in days between OTC and CTL plots per degree (°C) in Site T based on species’ climate windows, with earlier seed dispersal in OTC plots for species whose dispersal periods coincide with warmer ambient site temperatures.

and leaf senescence) also did not overlap zero at the 95% Bayesian CIs (Table 1). All reproductive phenophases shifted earlier, with 2.4 ± 0.6 days advancement for flowering, 1.9 ± 0.6 days advancement for end of flowering, and 2.9 ± 1.4 days advancement for seed dispersal. Vegetative phenophases shifted both earlier and later, but with a lesser magnitude than reproductive phases supporting a tissue-type response scenario (Fig. 1), with 0.7 ± 0.5 day advancement for green up and a 0.8 ± 0.4 day delay in leaf senescence (Table 1). There was more variation in species’ responses for reproductive than vegetative phenophases, as evidenced by wider posterior estimates and confidence intervals for seed dispersal, flowering, and end of flowering versus green up and leaf senescence (Table 1 and Fig. 3). Fruiting showed no consistent response to warming and varied strongly by site and overall (Fig. 3 and Supplementary Table 4).
Observed patterns were relatively consistent across sites, plant species, and over time, and spatiotemporal factors such as ambient climate and soil moisture had fairly minor influences on overall responses to experimental warming (Fig. 4 and Table 1). Taken together these patterns suggest that climate warming will likely advance most tundra plant phenology, but delay senescence, and shorten the time period between leaf emergence and flowering. Deciphering the effects of warming temperatures on plant phenology using only observational data can be challenging due to inherent correlations in environmental drivers, yet very few studies have assessed phenology responses to experimental warming at this spatial and temporal scale (see ref. 70). In addition, our estimates are likely very conservative, as actual levels of climate warming in the Arctic are predicted to reach 3–5°C the magnitude of warming achieved in OTCs.

Reproductive phenophases shifted by a greater magnitude than vegetative phenophases in response to experimental warming (Fig. 3 and Table 1) suggesting that tundra phenology responses to warming may be specific to plant tissue-type (Fig. 1. Tissue-type response scenario). Flowering, end of flowering, and seed dispersal had the strongest responses to warming, while phenological shifts in green up and leaf senescence were only ~1/3 the magnitude of those in reproductive phenophases. However, deciphering the mechanisms driving these differences is difficult and requires physiological approaches which are beyond the scope of this study. Previous work addressing these questions has generated mixed results. There is some evidence that reproductive tissues may be less vulnerable to spring frost than vegetative tissues and may thus respond more strongly to changing climate due to lower risk of adverse side effects. However, other work suggests that flowers are more sensitive than leaves to spring frost, likely due to the longer life span of leaves versus flowers in perennials which requires more structural investment in vegetative tissues. Alternatively, co-evolution with pollinators may influence the higher flowering sensitivity in response to warming, as earlier flowering species may receive higher pollinator visitations, but also risk higher chances of frost damage. Differential vegetative and reproductive responses to climate are poorly understood and require additional study to link processes at the individual plant scale to ecosystem-level patterns in plant phenology.

Discussion
Our findings demonstrate measurable shifts in the timing of plant phenology for green up, flowering, end of flowering, seed dispersal, and leaf senescence in response to experimental warming across the tundra biome (Fig. 3 and Table 1). Specifically, we observed advances in leaf green up and reproductive phenology of 0.7–2.9 days and delays in leaf senescence of 0.8 days in response to an average of 1.4°C of warming (0.5–2.3°C). Furthermore, we find evidence of both Tissue-type and Early-late response scenarios to warming (Fig. 1). Broadly, reproductive phenophases shifted earlier and by a larger magnitude than vegetative phenophases with experimental warming (Fig. 3), and divergent responses of green up and leaf senescence suggest a lengthening of species’ vegetative growing seasons (Fig. 3 and Supplementary Table 4).

Fig. 3 Effects of experimental warming on phenology. Reproductive phenophases shifted with a greater magnitude than vegetative phenophases to experimental warming. Density plots of modeled estimates of treatment effects for the difference (in days) in phenophase timing for plants growing in OTC versus control (CTL) plots. Colors designate each of the 6 measured phenophases. Estimates are shown on the x axis and phenophases are plotted vertically including data from all sites, years, and species as modeled using Eq. 2. Black vertical lines denote zero difference (no change) in the timing of phenology between OTC and CTL plots while red and gray dashed lines denote the 90% and 95% Bayesian credible intervals, respectively. Peaks to the left of black lines indicate an advancement, while peaks to the right of black lines indicate a delay, of that phenophase in response to warming. Created using the ggplot2 package (v 3.3.2) in R.
We also observed divergent responses of green up and leaf senescence to experimental warming (Fig. 3 and Table 1). This partially supports the idea that early and late season phenophases respond differently to warming (Fig. 1, early-late response scenario) with the exception of seed dispersal, which also advanced. Despite far less consensus on autumn phenophases, a meta-analysis of remote sensing and in situ studies suggested a weak delay in fall senescence with climate warming at the global scale, contrasted with strong advancement in spring green up. Our results differ from these patterns as we find a relatively small, but similar magnitude (0.7 and 0.8 days), shift for both green up and leaf senescence with experimental warming, leading to a lengthening at both the beginning and end of species’ growing seasons. Inconsistencies between previous work and this study may be due to differences in temperate/boreal and arctic biomes and the fact that observational studies do not isolate the influence of temperature alone. In line with our findings, a recent review of Arctic studies showed that green up and flowering tend to advance while leaf senescence is either unchanged or delayed in response to experimental warming. We provide further evidence that leaf senescence is delayed in response to warming in the tundra, helping to resolve this undecided pattern. It is important to note, however, that the shifts we observed were at the average species level, which can differ from the community and ecosystem-level responses, as only a subset of species in the community were sampled at each site. Variation in species’ responses to warming can enhance the likelihood of observing an increase in growing season length at the community or ecosystem level and does not necessarily mean that species’ annual life cycles are being extended.

Divergent responses of green up and leaf senescence lead to a lengthening species’ (vegetative) growing seasons in response to warming. However, we found similar magnitude shifts in the start and end of reproductive phenophases, suggesting no change in the duration of species’ flowering or fruiting periods (Fig. 3 and Table 1). Our estimates predict an increase in species’ growing season lengths by approximately 1.5 days (Fig. 3 and Supplementary Fig. 1), which reflects a 2.5–3.75% increase in the 40–60 day average length between leaf green up and senescence across all sites in this study (Supplementary Table 5). If generalizable across the tundra biome, this level of change could have nontrivial impacts on global carbon (C) stocks, as growing season length is highly correlated with GPP in the Tundra biome. Indeed, modeling studies have shown that a 1-day increase in growing season length can lead to significant increases in annual GPP at mid to high latitudes in the northern hemisphere. However, other work has highlighted that gains in production due to an extended growing season do not necessarily translate into enhanced C storage, as autumnal and winter warming are also associated with higher CO2 fluxes from plant and soil respiration over northern latitudes. Finally, differential allocation of biomass and phenology above versus below

![Fig. 4 Interactions with spatiotemporal factors.](image-url)
Plant responses to experimental warming were mostly consistent across gradients of resource availability, climate, and time as we only found three interactions between spatiotemporal factors and experimental warming (Table 1). This highlights that experimental warming can be considered a robust approach to test phenology responses to climate change across multiple species, latitudes, and microclimates. However, we did find interactive effects between experimental warming and soil moisture, OTC deployment period, and site-level climate for flowering and seed dispersal (Fig. 4 and Supplementary Fig. 2). Specifically, flowering responses to experimental warming were stronger in dry sites than in moist sites (Fig. 4), suggesting that warming effects may be enhanced when soil moisture is low and plants are experiencing water stress. This is similar to our finding that flowering was further advanced in sites where OTCs were left on year-round (Fig. 4) as OTCs can cause earlier snowmelt, increased thermal sums, and drier soils than those where OTCs are deployed during the summer only. Indeed, in sites where chambers are deployed year-round, snowmelt was advanced by an average of 1.02 days in OTCs versus with control plots (Supplementary Table 7), suggesting that experimental warming may also influence phenology through its effects on snowmelt. However, we only had snowmelt information for a subset of the sites in this study (Supplementary Table 2), and therefore more information is needed to fully assess the interaction(s) between experimental warming and snowmelt on tundra phenology. Overall, our results suggest that warming effects on phenology may be enhanced at dry versus moist sites, and for year-round versus summer warming, with important implications for a predictably drier and more variable tundra biome.

We found no evidence that latitude or inter-annual climate variability influenced phenology responses to experimental warming (Supplementary Table 3). However, seed dispersal responses varied by site-level climate, whereby species with warmer climate windows (ambient temperatures during their seed dispersal period) at a particular site, had enhanced responses to experimental warming (Supplementary Fig. 2). In other words, seed dispersal was advanced in warmed compared to control plots overall, and this was further enhanced for species whose dispersal periods coincide with the warmest times of the year. This is the opposite of our initial prediction that plant responses to warming would be weaker in warmer climates or warmer years. However, the two previous studies found decreased effects of warming in warmer climates/years for early season phenophases (green up and flowering) only, while the pattern we observed was for late-season phenophases (seed dispersal) only. This suggests that interactive effects of ambient and experimental warming may differ for early vs. late season phenophases, which is intuitive as OTCs will have accumulated higher thermal sums towards the middle and end of the growing season. Finally, phenology shifts observed in our study were consistent over time. We found that plant response to experimental warming did not increase or decline over the years, despite many important processes that can shift species’ responses on longer timescales, such as lag effects, local adaptation, thermal acclimation, and changes in resource availability. Barrett and Hollister similarly found that overall responses of tundra plants to experimental warming were consistent for 17–19 years at two sites in Northern Alaska. On the other hand, a meta-analysis of reported phenological rates of change from 1992 to 2019 on up to six plant phenophases (green up, flowering, ending of flowering, fruiting, seed dispersal, and leaf senescence; Table 3). OTCs are made of fiberglass in either cone or hexagon shape (~1.5–2 m in diameter, however, materials used and chamber size can vary slightly across sites based on plant species being monitored and landscape characteristics. OTCs in this study increased plot level air temperature by 0.5 and 2.3 °C (Supplementary Table 1). Because sites measured the degrees of warming achieved in OTCs at different time periods we are unable to accurately estimate phenology which we are aware, consolidating knowledge across this critical yet understudied biome, and generating an improved understanding of the influence of warming temperatures independent from other environmental drivers. We demonstrate that experimental warming creates measurable and consistent impacts on tundra plant phenology, including shifts between 0.7 and 2.9 days earlier and 0.8 days later for the 0.5–2.3 °C of warming achieved in OTC experiments. In addition, divergent shifts in leaf green up and senescence led to a 1.5-day increase in species’ growing season lengths, or ~3% of the average 50 days growing season length, given this modest level of warming. We consider these estimates to be on the low end of potential shifts in phenology, as much higher levels of warming (~3–13 °C) are expected in the Arctic by the end of the century. Our work incorporates all major plant phenophases across the growing season, including the beginning and ending phases of leaf, flowering, and fruiting phenology, uniquely testing the impact of warming on both the timing and duration of tundra plant phenology. Our results suggest a lengthening of species’ growing seasons, and stronger shifts in reproductive versus vegetative phenophases overall. These patterns support a type I response that responses of tundra plant phenology to warming are related to both tundra tissue-type and whether an event is early or late in the growing season. We found interactive effects of soil moisture and ambient climate for flowering and seed dispersal, but plant responses to experimental warming did not vary meaningfully across latitude, inter-annual climate, or over time. We provide robust estimates of plant responses to warming across 18 sites, over 100 species, 6 phenophases, and observations between 1 and 20 years in duration. Thus, our study incorporates very large spatial and temporal scales, both of which are crucial in order to estimate accurate effect sizes of global change drivers, and to scale up to predict net ecosystem-level responses. Incorporating these improved phenology estimates into process-based models will generate more accurate predictions of changes in global carbon budgets, albedo, and ecosystem processes in response to climate warming.

We suggest several ways to improve future research and decipher the potential drivers and ecosystem-level consequences of phenology responses to warming across the tundra: (1) Directly testing the physiological cues of vegetative versus reproductive phenology through growth chamber or field manipulations (warming leaves/flowers only), (2) co-measuring individual plant phenology alongside timing of pollinators and assessing outcomes on plant reproductive fitness (seed production and viability), (3) monitoring phenology at the plant community level, where all members (not just dominant or charismatic species) are recorded. (4) Using a gradient of experimental warming treatments (extreme, moderate, mild) to understand the consequences of more severe warming and limits of linearity of responses to temperature and (5) measuring the relationship between changes in phenology and ecosystem C fluxes using in situ plot-level measurements and biomass estimates and/or site-level Eddy covariance.

Methods
Experimental design. We compiled a data set of phenology observations from long-term open-top chamber (OTC) warming experiments and paired control plots within the International Tundra Experiment (ITEX). These data reflect the most up-to-date records from 18 sites and 46 experimental locations within these sites (i.e., subsites) in this network (Table 2 and Fig. 2), across the Arctic, sub-Arctic, and alpine ecosystems with observations from 1992 to 2019 on up to six plant phenophases (green up, flowering, ending of flowering, fruiting, seed dispersal, and leaf senescence; Table 3). OTCs are made of fiberglass in either cone or hexagon shape (~1.5–2 m in diameter, however, materials used and chamber size can vary slightly across sites based on plant species being monitored and landscape characteristics. OTCs in this study increased plot level air temperature by 0.5 and 2.3 °C (Supplementary Table 1). Because sites measured the degrees of warming achieved in OTCs at different time periods we are unable to accurately estimate phenology.
Table 1 18 sites and 46 subsites included in this study and the number of species, years, and phenophases that were included from each site.

| Site Subsites | Spp | Years | Latitude | Longitude | Phenophases |
|---------------|-----|-------|----------|-----------|-------------|
| Alexandra Fiord, NU, Canada 8 | 7 | 20 | 78.83 | −75.80 | G, F, EOF, FR, SD, S |
| Endalen, Svalbard 3 | 6 | 4 | 78.18 | 15.76 | F, EOF, SD |
| Adventalen, Svalbard 2 | 8 | 1 | 78.16 | 16.10 | G, F, EOF, SD |
| Utqiaġvik, AK, USA 2 | 40 | 20 | 71.28 | −156.60 | G, F, EOF, FR, SD |
| Atqasuk, AK, USA 2 | 28 | 16 | 70.45 | −157.40 | G, F, EOF, FR, SD |
| Toolik Lake, AK, USA 3 | 19 | 8 | 68.63 | −149.60 | G, F, EOF, SD |
| Inninait Creek, AK, USA 1 | 7 | 3 | 68.62 | −149.32 | G, S |
| Latnjajaure, Sweden 4 | 8 | 5 | 68.33 | 18.50 | G, F, EOF, SD |
| Kangerlussuaq, Greenland 3 | 7 | 2 | 67.02 | −50.72 | G, F, FR |
| Daring Lake, NT, Canada 2 | 3 | 19 | 65.87 | −111.53 | F, EOF, FR, SD |
| Healy, AK, USA 1 | 5 | 6 | 63.88 | −149.25 | G, S |
| Faroe Islands, Denmark 1 | 1 | 4 | 62.06 | −6.95 | F, EOF |
| Finne, Norway 3 | 4 | 3 | 60.61 | 7.50 | F, EOF |
| Jakobshorn, Switzerland 1 | 22 | 1 | 46.77 | 9.86 | G, F, EOF, S |
| Val Bercla, Switzerland 1 | 12 | 2 | 46.47 | 9.58 | F, EOF |
| Gavia Pass, Italy 2 | 3 | 5 | 46.34 | 10.49 | F, FR, SD |
| Niwot Ridge, CO, USA 6 | 19 | 6 | 40.06 | −105.59 | G, F, EOF, S |
| White Mountains, CA, USA 1 | 1 | 1 | 37.5 | −118.17 | F |

Sites are ordered by latitude (highest to lowest).

G green up, F start of flowering, EOF end of flowering, FR fruiting, SD seed dispersal, S leaf senescence.

Table 2 Total number of observations, species, sites, subsites, and years, as well as unique species × subsite × year × treatment combinations (replicates) for each of six plant phenophases.

| Phenophase | Total observations (i) | Spp | Sites | Subsites | Years | Replicates (r) | Replicates (r) climate models |
|------------|------------------------|-----|-------|----------|-------|----------------|-----------------------------|
| Green up   | 30,361                 | 71  | 11    | 28       | 27    | 1760           | 1526                        |
| Start of flowering | 30,011 | 107 | 16    | 44       | 28    | 2782           | 2400                        |
| End of flowering | 22,177 | 80  | 13    | 33       | 28    | 2108           | 1846                        |
| Fruiting   | 17,274                 | 53  | 6     | 18       | 28    | 1470           | 1320                        |
| Seed dispersal | 8292    | 48  | 9     | 22       | 28    | 770            | 692                         |
| Leaf senescence | 17,077 | 61  | 10    | 25       | 27    | 1414           | 1264                        |

Models were run separately for each phenophase and climate models had slightly lower replicate numbers due to limits on infilling of daily climate data (see “Climate data” section).

phylogenetic conservation, estimate of future scenarios3,9,5. Individual(s) responsible for

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shifts per degree of warming, however, the range of warming achieved is well within

the projected climate warming for tundra ecosystems, providing a realistic, though

likely conservative, estimate of future scenarios5,9. Individual(s) responsible for
data collection at each site also classified each experimental location (subsite) into

one of three soil moisture classes: dry, containing roughly <20% gravimetric water
content (GWC); moist 20-60% GWC; or wet >60% GWC46 (Supplementary

Table 2). When possible, sites recorded the first date(s) in each growing season

where plots were snow-free to provide information on snowmelt timing in and out

of warming chambers (Supplementary Table 2). Because snowmelt occurs before

OTC deployment at summer-only sites, we only test the effect of OTCs on snow-
melt for year-round sites (Supplementary Table 7).

Plant species monitored at each site followed criteria as defined in the ITEX

manual34, including prioritizing one or more of the following circumpolar main
target species: Carex aquatilis, Cassiope tetragona, Dryas integrifolia, Dryas

ocotopetala, Eriophorum vaginatum, Oxystipa digyna, Bistorta vivipara, Ranunculus

nivalis, Saxifraga crustulosa, Salix arctica, Salix herbacea, Salix polaris, Salix reticulata,

Saxifraga oppositifolia, Silene acaulis. Fifteen of the 18 sites included one or more of these

circumpolar species, while three sites included one or more dominant tundra plant

species present at their sites but not on this list (Supplementary Table 7).

Phenology data. Phenology measurements were taken using a common protocol

outlined in the ITEX manual34, yet sites included slightly different phenology
definitions across subsites and species (e.g., flower open vs. bud break), and we

included whichever phenophase definition was most commonly measured at a
given site for each species across all years. We then grouped these measurements

across all sites and categorized them as one of the six standardized phenophases

above. All site and species-specific phenology definitions can be found in Sup-

plementary Methods 2. We assumed that male and female flowering time did not

differ for dioecious species and we did not separate deciduous and evergreen

species’ leaf phenology as evergreen species in the Arctic (mostly heath shrubs) also

undergo leaf color change which can be monitored in the same way as deciduous

species30. In addition, preliminary analyses showed that evergreen and deciduous

species did not differ significantly in their timing of leaf phenology overall or in

response to OTC warming (Supplementary Table 3).

Sites years, and species varied in census intervals, which can cause bias in the

actual estimates of phenological events. For example, if a phenological event is

considered to occur on the date it was recorded, this may induce a late-biased

estimate. Taking the midpoint between sampling intervals is one way to account

for this uncertainty, however, this underestimates the variance in the data set

(reviewed in ref. 32). Therefore, for every phenology event date recorded (day

of year, i.e., DOY), we assigned a prior-visit date, which was the most recent recorded

visit in the same plot and year prior to the recorded phenology date of interest. For

any given observation, if the prior visit could not be assigned with this method (i.e.,

for data where the phenological event had already occurred by the first visit date:

green up 3885 observations, flowering 469 observations, end of flowering 144

observations, other phenophases <25 observations), we took the minimum prior-

visit date for each species across all years and then subtracted 3 weeks from that
date as a conservative estimate with a minimum of 100 (green up) and 120 (flowering,
end of flowering). In addition, missing data can bias effect sizes and therefore

we discarded any species × subsite × year combination (green up and leaf

senescence only) where more than 20% of the total observations were missing. We

then used interval-censored models (see below) to account for inconsistencies in

plot monitoring intervals across sites, where the actual date of the phenological

event is estimated to occur between the recorded DOY and the assigned prior visit.

All species names were updated and standardized using The Plant List (2013, v 1.1)

via the package Taxonstand (v 2.3) in R (v 3.6.1)36.

Climate data. We compiled daily mean air temperatures (T_{mean}°C) over all

measurement years from local weather stations at or near each site (Supplementary

Table 1). We averaged these daily temperatures over phenophase-specific climate
windows for each species at a given site (SiteTmean). Any missing climate data were infilled from ERA515 using the methodology described in Kittel et al.15. If model selection failed to pick a best model using this method, we used the long-term (multi-year) method to infill (see ref. 98, Appendix B). We allowed for no more than five days of the climate windows to be infilled. Because we used these conservative infilling cutoffs, some site-years were dropped from the climate data set and climate interaction models had slightly lower replicate counts than all other models (Table 3). Second, we calculated site-year temperature anomalies (Site-yearTmean) as the difference between the SiteTmean over all measurement years and the SiteTmean in each measurement year (both averaged over the phenophase-specific climate windows). Climate windows included the 30 days prior to the average of each species’ phenophase occurred at a given site across all years. For example, if the average flowering date for species i at site j across all measurement years 1 to k was DOY 180, then the SiteTmean would be the average daily air temperature from DOY 150–180 at site j across all measurement years, and the Site-yearTmean would be the difference between the SiteTmean and the average daily air temperature for the same window (DOY 150–180) in each measurement year at site j.

Statistical modeling. We used a two-step hierarchical modeling approach to test the effects of OTC warming on plant phenology. First, for each phenophase, we estimated the mean DOY and variation in each treatment (OTC or control) × species × subsite × year combination (hereafter replicate, r) using interval-censored regression models. Prior to regression, we discarded any non-adjacent year combinations that did not have at least two observations in both OTC and control treatments and removed outliers where the difference in OTC vs. control was greater than 4 standard deviations from the mean for that phenophase. We also standardized the data for each phenophase by calculating the midpoint between prior visit and DOY values for each observation, and subtracting the mean, and dividing by the standard deviation of the midpoints. Next, for each phenophase, we estimated the mean DOYs (μr) and standard errors (σr) by fitting an intercept-only model (interval-censored) to the data for each replicate (Supplementary Methods 1, Eq. 1). Interval-censored models assume the (unobserved) DOY on which each phenophase occurred is a random sample from a normal distribution with mean μr and variance σr2 (section) in the survreg function of the survival (v 3.2.7) package in R99,100.

For each group (species, site, year within site, and subsite within site), the group mean (μg) and the average standard error at the species x subsite x treatment level across all measurement years as the standard error (σg).

Second, we used Bayesian hierarchical modeling with default (non-informative) priors in the R package brms (v 2.14.4)101 to estimate the effects of OTC warming on phenology across sites, subsites, species, and years. We used the following model structure to answer questions about mean treatment effects (Q1–3):

\[ \mu_r \sim N(\mu, \sigma_\mu) \]

(3)

where the response is the previously estimated replicate level mean DOY (μr) and associated standard errors (σr) which are incorporated into a joint response variable using the resp.se function in brms (Eq. 2). Treatment (Trt) is an indicator variable for replicates measured in OTCs (1) or control (0), with random effects of treatment grouped by species (s), site (k), year within site (y), and subsite within site (i). We used default brms (i.e., non-informative) uniform flat priors (−∞, ∞), for the global intercept (α) and slope (β), and half student-t priors with 3 degrees of freedom and scale = 10 for the variance components σα and σβ and all group-level variances σαg and σβg.

For each group, species, site, year within site, and subsite within site, the group level coefficients (σαg, σβg) and their correlation (ραβ) were modeled using a multivariate normal distribution with means of zero and standard deviation Sαg,σβg which is the variance-covariance matrix of each varying intercept and slope and their correlation ραβ. Finally, we modeled the correlation matrix Rραβ using an LKJ-correlation prior distribution with θ parameter = 1, which constrains the correlation term uniformly between −1 and 1. See Supplementary Methods 1 for full model parameterization.

For questions about variation in treatment effects over space, time, and ambient climate (Q4 and 5), we used the same model structure but with an additional fixed interaction term between treatment and one of six spatiotemporal (predictor of site interest: (1) Years of warming (continuous, replicate level-τ) calculated as a number of years from the start of the experiment at each site/subsite, (2) latitude (continuous, site level-β), (3) water availability ((categorical: dry/moist/wet) based on gravimetric water content (GWC), subsite level-γ), (4) OTC deployment period (seasonal, year level-δ), (5) site mean temperature (continuous, site level-λ), and (6) site-year temperature anomaly (continuous, site-year level-μ) (Eq. 3). We included both climate predictors in the same model using a group means centering approach (described in van de Pol and Wright13) with two interaction terms to distinguish spatial (site-μ) and temporal (site-year-λ) influences of temperature on OTC warming (see “Climate data” section). See Supplementary Methods 1 for full model parameterization.

\[ \mu_r \sim N(\alpha_0 + \alpha_{\beta_g} + \alpha_{\gamma_g} + \alpha_{\delta_g} + \alpha_{\lambda_g} + \alpha_{\mu_g} + \beta_{Trt} + \beta_{\gamma_g} + \beta_\gamma + \gamma_{Trt} + \gamma_\gamma + \delta_{Trt} + \delta_\delta + \lambda_{Trt} + \lambda_\lambda + \mu_{Trt}) \]

(3)

Models were run separately for each phenophase (Table 3) and each model was run with two chains of 10,000 iterations (warm-up 5000 iterations, no thinning) MCMC sampling (brms default). We checked for convergence of chains for all parameters both visually with trace plots and with the Gelman–Rubin convergence statistic103. Trace plots showed that chains mixed well and converged to stationary distributions for all parameter estimates. Gelman–Rubin convergence statistics for parameter estimates of all models were less than 1.1. We calculated Bayesian credible intervals (CIs 90, 95%) for all fixed model parameters in the R package BayesPlot (v 0.9.0)104, using the equal tailed interval (eti) method and consider modeled parameter estimates to demonstrate an effect on the response variable when Bayesian CIs did not cross zero.

For question 3, to determine whether experimental warming will alter the duration of plant phenoperiods, we calculated the difference between posterior distributions of green up and leaf senescence, flowering and end of flowering, and fruiting and seed dispersal for species’ growth, flowering, and fruiting periods respectively and also calculated Bayesian CIs for each of these estimates. Because most fruits in this data set are dehiscent, and flowering is most often defined as the first seed development (Supplementary Methods 2), we defined the flowering period as the length of time between flowering and seed dispersal. It is important to note, however, that not all sites, species, years included each of these paired phenophases (see Supplementary Data 7d–e for replicates per phenophase). Finally, we extracted model intercepts from treatment-only models (Eq. 2) to estimate the average DOY when each phenophase occurred across all sites, species, and years and the average number of days between starting and ending phenophases as a baseline with which to compare treatment responses.

Disclaimer. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Reporting summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability. All data used in this analysis can be found at https://github.com/cour10eye/brace/OTC_synthesis_analysis.git. Figures 3, 4 and Supplementary Figs. 1, 2 of this manuscript have associated raw data. The complete data set is also archived in the Polar data Catalog https://doi.org/10.21963/I3215.

Code availability. All analysis code can be found at https://github.com/cour10eye/brace/OTC_synthesis_analysis.git107.

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Author contributions
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Competing interests
The authors declare no competing interests.

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