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Plant Responses to Natural and Experimental Variations in Temperature in Alpine Tundra, Southern Yukon, Canada

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Abstract

Substantial climate warming is predicted for high latitude regions and may have large impacts on tundra communities. As part of the International Tundra Experiment, this study characterized plant responses to natural and experimental variations in temperature at a subarctic, alpine tundra site. Non-destructive measures of plant reproduction and growth were monitored annually for four target species (*Dryas octopetala*, *Lupinus arcticus*, *Polygonum viviparum*, and *Salix arctica*) from 1999 to 2008. Plants were exposed to 8 years of an experimental warming treatment using open-topped chambers (OTCs). Temperatures in OTCs tended to be warmer at midday but cooler at night, with little net daily warming. OTCs had relatively little effect on plant responses, except for positive effects on reproductive characteristics of *D. octopetala* and *P. viviparum.* All target species except *L. arcticus* showed significant annual variations in vegetative and reproductive characteristics. Non-destructive measures used to monitor plant performance were significantly related to actual growth and reproductive output in most cases. Plant community composition did not show experimental effects nor were there consistent trends in composition over the 10 years of the study. Results of the study highlight individualistic species responses and the resilience of the plant community to observed temperature variations at this site.

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Introduction

It is now widely acknowledged that anthropogenic activities are having a profound impact on the earth's climate (Solomon et al., 2007). Global mean annual temperatures have increased by approximately 0.13 °C per decade over the last 50 years (Solomon et al., 2007), although the magnitude of this increase varies across the globe. In the Arctic, mean annual temperatures have increased by an average of 0.40 °C per decade between 1966 and 2003, with rates of up to 2 °C per decade in some regions (McBean et al., 2004). Observations of the intensity of recent arctic warming are supported by paleoclimate records, which suggest that arctic temperatures in the latter half of 20th century were the highest they had been in the preceding 2000 years (Kaufman et al., 2009).

While arctic and alpine plants are adapted to cold temperatures (Bliss, 1962), in general they are still living below their temperature optima (Tieszen et al., 1981) and even small increases in temperature can yield significant increases in growth and reproduction. Common responses of tundra plants to increased temperatures include advances in phenological events (Arft et al., 1999; Stenström and Jónsdóttir, 2006) and increases in the growth and reproduction of individual species (e.g. Chapin and Shaver, 1985; Arft et al., 1999; Kudernatsch et al., 2008). Species often respond differently to the same temperature changes (Chapin and Shaver, 1985), which can lead to changes in the composition of tundra plant communities (Walker et al., 2006; Wilson and Nilsson, 2009). For example, woody shrub species have shown increases in cover at arctic and alpine sites in response to both regional (Wilson and Nilsson, 2009) and experimental warming (Walker et al., 2006). In some cases, increased shrub dominance has caused lower-canopy species abundance to decline, leading to decreases in species diversity in response to experimental warming (Hollister et al., 2005b; Walker et al., 2006). However, it is difficult to predict a general pattern of tundra plant responses to climate warming. Observed responses are often context-dependent (Shaver et al., 2000), and in many regions little to no information on plant responses to temperature changes is available. One objective of research networks such as the International Tundra Experiment (ITEX) has therefore been to improve our ability to detect general patterns of plant responses to climate change by conducting similar studies across a wide range of tundra habitats (Molau and Mølgaard, 1996).

Field studies of plant responses to temperature typically involve plants and/or plant communities being subjected to an experimental warming treatment and then compared to those growing under ambient conditions (e.g. Hollister et al., 2005b; Stenström and Jónsdóttir, 2006). However, studies using experimental warming can often be more powerful when they are integrated with observations of plant responses to natural temperature variation (Hollister and Webber, 2000; Dunne et al., 2004). Comparative studies allow researchers to better assess the effects of temperature on plants in the context of other environmental factors that also influence plant traits (Hollister et al., 2005a).

This study examines plant responses to 10 years of interannual temperature variation and 8 years of experimental warming at a high-latitude, alpine tundra site. It is one of few studies of plant responses to temperature conducted in high-latitude alpine tundra (see also Gugerli and Bauert, 2001; Klanderud and Tøtland, 2005; Jägerbrand et al., 2009) and aims to improve under-representation of this region in global assess-

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ments of tundra responses to climate variation. Tundra responses to climate variation are also of local importance in the study area, as alpine regions in southern Yukon provide important calving and post-calving habitat to woodland caribou (Northern Mountain population), for which some populations are declining (Farnell et al., 1998). Assessing and predicting changes in plant communities that may affect caribou forage availability is an important element of predicting the long-term viability of these sensitive populations, which are a main target for ecosystem conservation in the region.

The main objectives of this study are: (1) to test the effects of an experimental warming treatment and natural temperature variation on the growth and reproduction of individual target plant species, and (2) to assess whether experimental warming or natural climate variations over a 10-year period have affected plant community composition within this alpine tundra ecosystem. In addition, we also collected data to test whether the non-destructive measurements used in this and other ITEX studies were likely to be good indicators of actual leaf growth or reproductive output.

Methods

STUDY AREA

We conducted this study in alpine tundra located in the upper catchment of the Wolf Creek drainage basin (60°33′47″N, 135°07′51″W; elevation 1526 m), approximately 20 km southeast of Whitehorse, Yukon Territory, Canada. The geologic makeup of the area is primarily sedimentary rock, mostly composed of limestone, sandstone, and siltstone (Janowicz, 1999). Soils at the site are mesic with a large gravel and rock component and are overlain with a 2- to 5-cm-deep organic layer in vegetated areas. The study area is in the zone of sporadic/discontinuous permafrost (Brown et al., 2001), and permafrost may be present at the site but the active layer is greater than 1 m deep. The climate is subarctic and characterized by large seasonal variations in temperature, low precipitation, and low relative humidity (Wahl et al., 1987). Mean annual temperature measured at a nearby alpine climate station (Janowicz, 1999) was −1.6 °C with mean temperatures of 9.5 °C in the summer snow-free period (June–August) and −11.3 °C during the winter (December to February). The Whitehorse area receives an average of 300 mm of precipitation annually, with approximately 50% falling as snow (Environment Canada, 2009). Vegetation at the site is characteristic of dwarf-shrub heath tundra (Bliss and Matveyeva, 1992). Common plant species include mat-forming shrubs such as *Dryas octopetala*, *Salix arctica*, and *S. reticulata*; the forb *Lupinus arcticus*; graminoids (e.g. *Carex* spp., *Festuca* spp.); lichens; and mosses. The site has a south-southeast aspect and a gentle slope (1 to 3°). More details on the study site, including a list of all vascular species encountered, can be found in Pieper (2009).

EXPERIMENTAL DESIGN

The experimental design for this study consisted of long-term observations of vegetation in permanent control plots, paired with experimental manipulations designed to increase growing season temperatures in treated plots. Study plots were laid out in a randomized block design with 20 plots arranged in 5 blocks and two replicates of each treatment per block. The effect of the slight slope at the site was not known at the outset of the experiment and blocks were arranged parallel to the slope contours to account for potential slope effects. Plots of 1 m × 1 m were permanently marked and spaced approximately 8 to 10 m apart. The study was carried out from 1998 to 2008.

The experimental manipulation used open-topped chambers (OTCs) that were constructed as truncated cones similar to those outlined in the ITEX protocol (Molau and Mølgaard, 1996). For the first three years of the study (1998–2000), experimental plots were equipped with an alternative type of rectangular, open-topped chamber. After these years, temperature increases were not apparent in the treated plots, and in 2001 the original chambers were replaced with OTCs. Initial measurements indicated that the OTC design provided a moderate warming effect. The OTCs were constructed of flexible pipe rings with narrow, angled wooden slats connecting lower and upper rings to create a truncated cone. The frame was covered with clear vinyl sheeting that provided a barrier to wind and transmitted ~95% of photosynthetically active radiation. The OTC walls were 40 cm tall and angled 60° to the ground, with an inside basal area of 1.72 m^2, and a top opening of 0.85 m^2. The OTCs sat directly on the ground surface, but variations in surface microtopography occasionally resulted in gaps of up to approximately 5 cm between the bottom of the OTC frame and the ground surface. OTCs were placed on the experimental plots for the duration of the growing season (late May to early September) each year from 2001 to 2008. Open-topped chambers of similar designs have been shown in previous studies to increase mean daily and monthly surface temperatures in tundra environments by 1 to 4 °C, while minimizing unwanted secondary effects on factors such as soil moisture and relative humidity (e.g. Marion et al., 1997; Hollister and Webber, 2000).

Near-surface air and soil temperatures were monitored in four control and four treated plots for the duration of the study. Monitored plots were selected in a stratified random fashion such that each block had at least one monitored plot and blocks with two monitored plots had one of each treatment type. Temperatures were recorded hourly using waterproof temperature probes attached to data loggers (HOBO™ 4-Channel External Input, Onset Computer Corporation, Bourne, Massachusetts, U.S.A.). In each plot, a pair of temperature probes was positioned in each of the north and south halves of the plot, with one probe in each pair measuring air temperature 5 cm above the ground surface, and the other measuring temperature at 5 cm below the ground surface. Soil temperature probes were inserted vertically into the soil to minimize soil and vegetation disturbance, with the conductive end of the probe fully buried within the soil. Above-ground probes were shielded from direct sunlight by white PVC tubes and open at each end to allow air flow.

TARGET SPECIES AND PLANT MEASUREMENTS

Four common plant species were selected for repeated, non-destructive measurements of growth and reproduction: *Dryas octopetala* L. (mountain aven), *Salix arctica* Pall. (arctic willow), *Polygonum viviparum* L. (syn. *Bistorta vivipara* (L.) S.F. Gray) (alpine bistort), and *Lupinus arcticus* S. Wats. (arctic lupine). The first three species listed are identified as main target species of the ITEX program (Molau and Mølgaard, 1996) and have been studied at many arctic (e.g. Wookey et al., 1995; Jones et al., 1997) and alpine sites (Bauert, 1993; Welker et al., 1997; Arft et al., 1999). *Lupinus arcticus* is endemic to northwestern North America and is common throughout most of the Yukon Territory (Cody, 2000), including the Wolf Creek study area.

Dryas spp. are dominant dwarf shrubs at many arctic and alpine tundra sites (Murray, 1997), and *Dryas octopetala* is abundant at the Wolf Creek site. *Dryas* often spreads laterally to

TABLE 1

Summary of annual measurements collected for the four target species in the Wolf Creek study.

Species	Vegetative Characteristics	Reproductive Characteristics
Dryas octopetala	Average leaf length (n = 5/plant) (mm)	Inflorescence peduncle length (mm)
Lupinus arcticus	Length of longest petiole (mm)	Number of inflorescences/plant
	Length of longest leaflet on longest petiole (mm)	
Polygonum viviparum	Width of the largest leaf (mm)	Length of the bulbil-producing section of the rachis ('bulbil section'; mm)
	Number of leaves	Length of the flower-producing section of the rachis ('flower section'; mm)
Salix arctica	Annual stem increment (mm)	Length of catkin (mm)
	Length of longest leaf (mm)	

form dense mats and reproduces sexually via plumed achenes that are dispersed by the wind (Welker et al., 1997). *Salix arctica* is a deciduous dwarf shrub that occurs in many arctic and alpine habitats in North America (Hultén, 1968). Plants can reproduce asexually via clonal ramets, or by seed. *Salix arctica* is dioecious, and physiological differences between sexes have been found previously (Jones et al., 1999), so male and female plants were monitored separately. *Polygonum viviparum* is a perennial rhizomatous forb found in a variety of habitats throughout the circumpolar North (Hultén, 1968). Reproductive structures of *Polygonum viviparum* are situated on a terminal inflorescence with flowers occupying the topmost section and vegetative bulbils for asexual reproduction located below. While mature seeds have been found (Bauert, 1993), sexual reproduction in this species is thought to be quite uncommon (Law et al., 1983). *Lupinus arcticus* is a nitrogen-fixing, perennial forb found in boreal to tundra habitats (Hultén, 1968). Plants grow in clonal clumps with one to several racemose inflorescences emerging from a rosette of basal leaves. Each raceme bears 10 to 20 flowers that yield legumes containing 5 to 10 seeds (Hultén, 1968).

Selection, marking, and measurement of individuals of each target species followed procedures outlined in the ITEX manual (Molau and Mølgaard, 1996). When available, four ramets or clones (herein 'plants') of each species were marked per plot. Ideally one plant from each quarter of a plot was marked, but if a quarter did not contain a plant of a certain species, plants were selected to be as far as possible from another of the same species in a quarter. In some instances fewer than four plants of a species were present in a plot. Selected plants were marked with a metal tag attached to a wire wrapped loosely around the base of the plant. In the years after initial plant selection, plants that had died or were lost due to tag displacement were recorded as such and another plant was randomly selected.

Non-destructive measurements of vegetative and reproductive characteristics were recorded for each species in mid- to late July annually from 1999 to 2008 (Table 1). The selection of measurement variables was based on established ITEX protocols (Molau and Mølgaard, 1996), with the exception of *L. arcticus*, which is not an ITEX species. Measurements for this species were similar to those laid out for other forbs studied in ITEX. Leaf dimensions were the predominant measure used to indicate vegetative productivity of target species (Table 1). For *D. octopetala*, the lengths of the five leaves closest to the tag were measured and an average leaf length was calculated for each plant. For *L. arcticus*, the leaf with the longest petiole was selected for measurement and the length of the petiole and the longest leaflet of the divided leaf were measured. For *P. viviparum* and *S. arctica*, the largest leaf width and length, respectively, on a plant were measured. Plant parts of any species that had been damaged by herbivory were encountered rarely and were excluded from analysis.

For most species, inflorescence length was used to indicate reproductive output (Table 1). For both *D. octopetala* and *S. arctica*, measurements were made on the inflorescence closest to the tag that was associated with an individual ramet. For *L. arcticus*, the total number of inflorescences arising from a marked rosette was recorded, while *P. viviparum* generally produced only a single inflorescence per ramet. *P. viviparum* inflorescences were divided into the section of the rachis that produced bulbils (herein 'bulbil section') and the section that produced flowers (herein 'flower section') and the length of each section was measured separately. Collection of target species data was often completed after male *S. arctica* catkins had fallen off so only female catkin data were included in the analyses; females accounted for nearly 70% of the *S. arctica* plants that were marked. Reproductive output was further assessed by counting the number of inflorescences of each vascular plant species in each of the 1 m^2 plots.

Leaves and seeds of target species were collected to assess the ability of non-destructive plant measurements to represent actual variations in leaf size and production of seeds or propagules. For these collections, non-destructive measurements consistent with the annual measurements were made on the plants before destructive samples were collected. Samples were collected from plants growing at the study site but outside the experimental plots using systematic sampling along two randomly oriented, 60 m transects. At each 2 m mark along a transect, samples were collected from the closest plant of each target species.

Leaves from 51 plants of each target species were collected on 16 July 2008 and processed to obtain measures of leaf area and dry mass. Leaf samples were stored in plastic bags and photocopied within 16 hours, and the photocopies of leaf outlines were later used to estimate leaf area (cm^2) using a digital scanner and the software WinFolia v. 2007b (Regent Instruments, Quebec City, Canada). After being copied, leaves were dried at 60 °C for 48 hours and weighed to measure dry mass (mg).

Inflorescences from up to 40 plants of each target species were collected on 6 August 2008 and 12 August 2009. Only inflorescences with ripe fruits were sampled. Fruits of an inflorescence were considered ripe based on the following criteria: (a) seed plumes on *D. octopetala* inflorescences had opened from the initial twisted stage, (b) *P. viviparum* inflorescence stalks had at least one visible bulbil, and (c) *S. arctica* catkins had more than one swollen ovary. Our observations indicated that the swelling of ovaries in *S. arctica* was largely dependent on fertilization, and that once there was clear swelling of ovaries on an inflorescence, additional time did not cause additional changes in the total number of swollen ovaries. Reproductive output of *L. arcticus* was not assessed because the variable timing of fruit maturation within individual inflorescences prevented collection of all seeds or fruits on a plant. Sampled inflorescences were stored in plastic bags and refrigerated overnight, and then transferred into envelopes and

dried at 30 °C for 72 hours. Once dry, inflorescences were stored in the freezer (−8 °C) for two to three months until they were processed. Sample sizes varied considerably between years and species, and years were consequently pooled in our analyses to maintain reasonable sample sizes.

Seed viability of *D. octopetala* and *S. arctica* was assessed based on the number of filled seeds and percent seed germination under controlled conditions. Dormancy-breaking techniques were not required for *Dryas* (Bliss, 1958) or *Salix* seeds (Densmore and Zasada, 1983), but plumes and hairs were removed, respectively. To test germination, seeds from each inflorescence were placed on filter paper in a Petri dish and moistened as needed with deionized water. Dishes were randomly arranged under fluorescent lights (18 hours light, 6 hours dark) and kept at approximately 20 °C. Germinated seeds were counted and removed daily. A seed was considered to have germinated when the radicle was approximately twice the length of the seed. Germination trials ended when newly germinated seeds were not found for five consecutive days. Once trials were complete, seeds that did not germinate were sliced open to assess whether the seed contained an embryo (i.e. was filled).

No seeds of *P. viviparum* were found and bulbil production was used to assess reproductive output for this species. Bulbils had already started to disperse when inflorescences were collected so we used the number of bulbil scars present on the rachis to represent the number of bulbils produced. Bulbils still attached were used to estimate mean mass per bulbil (mg) for each inflorescence.

COMMUNITY COMPOSITION

Species composition was measured in each study plot in mid- to late July at 5-year intervals (1998, 2003, 2008) using a point-intercept method (Molau and Mølgaard, 1996). We used a 1 m × 1 m frame strung with fine, waxed string to form a grid of 100 string intersections spaced at 10 cm intervals. A long pin with a diameter of 1.6 mm was lowered at each string intersection and each live plant part that intersected the pin was recorded. It was common for a species to register >1 intersection per pin drop. The number of intersections with a species in a plot was summed to represent the raw species abundance in that plot. Species present in a plot but not intersecting the pin were also noted to better assess species richness. Vascular plants were identified to species, while lichens and mosses were recorded as growth-form categories. Species not identifiable in the field were given a pseudonym and a sample was collected for later identification. The point frame quadrat was carefully relocated on the plots each year so that differences in contacts recorded between sampling times reflected changes in community composition that occurred in the plot over time.

DATA ANALYSIS

Plots were treated as replicates in this study (n = 10/treatment) and within-plot samples were averaged to obtain a single plot value for each variable and sample year prior to analysis. Target species data rarely satisfied the assumptions of parametric statistical tests and were rank transformed prior to analyses (Conover and Iman, 1981). For the most part, this did not change statistical conclusions. A P-value of 0.05 was used to assess significance. All statistical analyses were performed using SPSS v. 17.0 (SPSS Inc., Chicago, Illinois, U.S.A.) unless otherwise stated.

All data were quality checked for possible errors. Loggers that repeatedly recorded very high (>50 °C) or very low (<−20 °C) temperatures were deemed unreliable and were not used in our analyses. Most of the remaining temperature records (>99%) were within the range of −10 °C and 30 °C.

Interannual temperature variation during the 10 years of this study was represented by annual growing degree days (GDD), which provide an integrated measure of heat accumulation through the growing season (Maxwell, 1992). GDD were calculated by subtracting a base temperature from the hourly air temperature and then averaging those hourly values across a full 24-hour period to get the GDD for that day (Molau and Mølgaard, 1996). A base temperature of 5 °C was used, as recommended in the ITEX protocols (Molau and Mølgaard, 1996) and applied in other subarctic, alpine sites (e.g. Wipf, 2010). Negative hourly values were set to zero. Annual GDD values were based on air temperatures measured in control plots from snowmelt (27 April to 7 June depending on the year) until 31 August. Snowmelt date was estimated from snow-depth sensors at a nearby alpine climate station (Janowicz, 1999). Snowmelt data were missing for 2000. Assessment of OTC effects on GDD was based on temperature data from 1 June to 31 August because OTCs were not always put up immediately following snowmelt. Temperature data from the study site were incomplete for 1999, 2007, and 2008 and we estimated missing data based on calibration with data from the Whitehorse International Airport (Environment Canada, 2009; r^2 = 0.842; n = 7; P < 0.001; $GDD_{Wolf\ Creek} = 0.637 \times GDD_{Airport} - 100.84$). Additional information on July temperatures recorded in OTCs and controls is available in Pieper (2009).

We examined diurnal patterns in temperature between treatment types using hourly temperature means in July from the warmest (2004) and coolest (2008) summers during the study period. We estimated the temperature deviation between treatment types by subtracting hourly temperatures in the control plots from hourly temperatures in the OTCs (ΔT; °C). These hourly temperatures were mean values of all plots within a treatment type (n = 4 control plots/year; n = 3 OTCs in 2004, 4 OTCs in 2008). Temperature data were more complete for July than for either June or August which allowed us to use data from more plots than were used for the comparison of GDD between treatment types. Days in July in a given year were used as replicates (n = 31) to generate mean values for each hour in a 24-hour day. Temperature analyses focused on data from July, as that is the period of peak plant productivity (Johnson and Tieszen, 1976) and also the time when plant measurements were made. We also calculated the percentage of nights in each year and month (June, July, August) that exhibited average cooling in OTCs relative to controls.

The first step in our analyses of plant variables was to test whether the blocking of plots in the experimental design had a significant effect on plant measurements. We tested for effects of blocking on target species data in single years using one-way ANOVA on pre-treatment data (1999) and two-way ANOVA on 2008 data to test for a Block × Treatment interaction. There was a significant effect of the interaction for only one measure (flower section length of *P. viviparum*; P = 0.002) and when we examined the data for this measure from other randomly selected years (2004, 2007) there were no significant block effects (P > 0.05). We therefore concluded that blocking the plots had no significant effects on plant measurements and the remaining analyses were run as a completely randomized design.

We used two-way ANOVAs to detect differences between treatment types and year (Molau and Mølgaard, 1996). Fixed

factor ANOVAs were used for GDD data, and repeated measures ANOVAs were used for target species data and inflorescence counts. Year was the repeated factor and Treatment was a fixed factor in all repeated measures analyses. Inflorescence counts were standardized by dividing annual counts by the average raw abundance of a species obtained from the point-intercept sampling in order to account for differences in inflorescence numbers caused by variations in species abundance. ANOVAs performed on absolute counts of inflorescences did not yield different results from those based on standardized counts and are not presented here.

Multivariate analysis of variance (MANOVA) was used to account for potential correlation between vegetative measures made on the same plant. There is evidence that vegetative and reproductive measurements respond differently to experimental warming (e.g. Jones et al., 1997; Arft et al., 1999), so vegetative and reproductive characteristics of a species were considered separately. Type III SS and Pillai's statistic were used to assess the significance of MANOVA tests. Significant MANOVA results were followed by repeated measures ANOVA to determine which measurements were different. We used Tukey's honestly significant difference test (Zar, 1999) to examine Year or Year × Treatment differences when ANOVA results were significant.

We used correlation analyses to test for relationships between annual plant measurements and GDD. These analyses were run using plant data (target species measurements and inflorescence counts) and GDD that were each averaged across control plots within a year. Since data were from control plots only we included data for 1998–2008. Correlation analyses on inflorescence counts were carried out using both standardized and absolute counts. GDD in 2004 were abnormally high due to a very hot June so we used Spearman's rank correlation to reduce the influence of this outlier year. We used regression analyses on collected leaf and inflorescence samples to determine how well variations in leaf and inflorescence morphology predicted variations in leaf mass or area, and seed production or germination, respectively.

For the analysis of community composition, point-intercept data for each species were relativized by the total number of intersections in a plot to focus the analyses on changes in relative species composition (Will-Wolf et al., 2006). Rare species were left in the data set. Outlier analysis revealed one plot that was an outlier in all three years (average distances greater than 2.0 SD from the mean of all plots), and likely represented a local microenvironment and community that was distinct from the remaining plots. Because including this plot in the ordination compressed and distorted the ordination of the remaining plots, the outlier was removed from our analyses of community composition. Species richness, Pielou's evenness, and Shannon-Weiner diversity were calculated using the relative abundance data for vascular plants in each plot using PC-Ord version 5.19 (MjM Software Design, Gleneden Beach, Oregon, U.S.A.). We used repeated measures ANOVA to determine if there were differences in diversity measures between years and treatment type.

Multivariate analysis of community composition examined the relative dissimilarity in composition between plots using Bray-Curtis (Sørensen) distances calculated from relative species abundance data (McCune and Grace, 2002). Distances were calculated between plots within the same year and between the same plots for each of the five-year intervals (1998 to 2003 and 2003 to 2008). We used repeated measures ANOVA on calculated distances of the latter to determine if there were differences in the amount of change between the two 5-year intervals and treatment types. A significant Interval × Treatment interaction would indicate that composition had changed directionally more in experimental plots than in controls (Price and Waser, 2000).

We used non-metric multidimensional scaling (NMS; Kruskal, 1964) to show the arrangement of plots based on species composition and to explore patterns in community composition over time. NMS is an iterative ordination technique that positions entities based on ranked distances between plots and avoids the assumption of multivariate normality and linear relationships among variables (McCune and Grace, 2002). It provides the best fit of n entities (plots) in k dimensions that minimizes the stress on the final configuration, where the stress value indicates how well the distances in the associated ordination represent the distances between plots in n-dimensional space (McCune and Grace, 2002). The ordination was run with a random starting configuration in the auto-pilot mode of PC-Ord. Two hundred fifty runs with real data were completed. A Monte Carlo test using 250 runs with randomized data was used to determine the optimal number of ordination axes and to indicate whether NMS extracted stronger axes than expected by chance. Solutions were considered stable if the final instability was less than 10^{-4} (McCune and Grace, 2002). The ordination was performed using vascular species data for all three sample years together. Treatment types were overlaid to show potential differences between treatments, and successional vectors were used to indicate whether vascular species composition changed directionally between sampling times.

While the point-frame method is among the more objective methods of collecting abundance data (Bonham, 1989), systematic differences among observers may have biased results. To assess the potential impact of observer bias on our results, community measurements were collected independently by each of two observers for five plots in 2008. Using these data, we applied a non-parametric test using a blocked multi-response permutation procedure (MRBP; Biondini et al., 1988) to determine if there were differences in community composition as estimated by the two observers. MRBP was carried out on point-frame data using Euclidean distances (Mielke, 1991). When doing MRBP one must consider whether or not to align the medians within a block to zero. Alignment was not used here because our aim was to determine an exact match between groups (observers) (McCune and Grace, 2002).

Results

TEMPERATURE

The OTCs had no significant effect on GDD for the treatment period of 2001 to 2008 (Treatment: $F = 0.001$; df = 1, 21; $P = 0.971$; Year × Treatment: $F = 0.261$; df = 5, 21; $P = 0.929$), although there were significant differences in GDD between years ($F = 7.147$; df = 6, 21; $P < 0.001$; Fig. 1). GDD at the study site was 53% higher in 2004 than the mean for 2001 to 2008 due to unusually high June temperatures (Environment Canada, 2009). We also found no significant effects of OTCs on average mean, minimum, or maximum July temperatures in any year for either air or soil ($0.01 \leq F \leq 1.09$; df = 1, 30; $P > 0.05$), although differences were significant between years ($2.90 \leq F \leq 16.17$; df = 6, 30; $P < 0.05$). Average daily mean, minimum, and maximum temperatures in June were also not different between treatment types ($0.003 \leq F \leq 4.311$; df = 1, 3 to 5; $P > 0.10$).

Despite the absence of OTC effects on average temperatures, calculations of hourly temperature deviations between OTCs compared to controls showed clear diurnal patterns in OTC effects. Temperature deviations between OTCs and controls were often positive during midday and negative at night, suggesting that

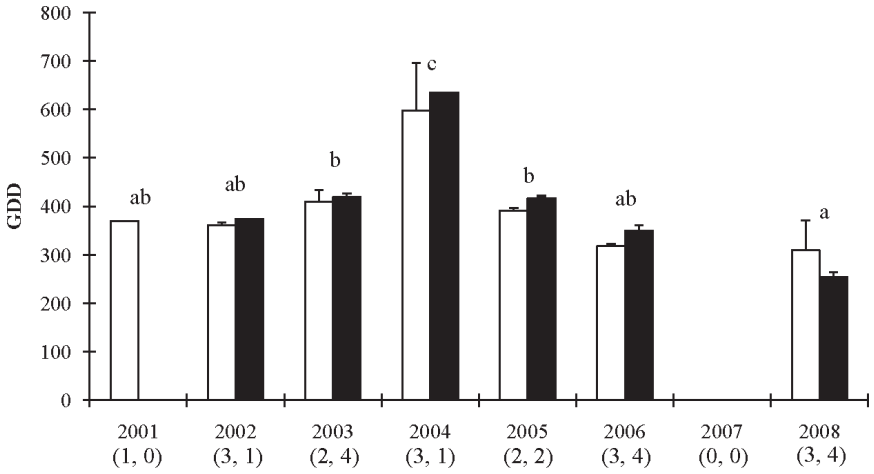

FIGURE 1. Total growing degree days (GDD) from 1 June to 31 August for 2001 to 2008 in control plots (open bars) and open-topped chambers (OTCs) (solid bars). Values are means + SE. Sample size (control, OTC) is indicated below the years. Years that do not share a letter are significantly different ($P \leq 0.05$). There was no significant difference between treatment types. Data were missing for 2001 (OTC) and 2007 (both treatments).

OTCs generally had a warming effect during the day and a cooling effect at night (Fig. 2). In 2004, the warmest summer in the study period, average hourly air temperatures were close to 1.5 °C warmer in experimental plots at midday, while nighttime temperatures showed no net warming or cooling. In 2008, the coolest summer in the study period, average air temperatures showed a nonsignificant trend of being slightly higher in OTCs at midday, while average temperatures in OTCs were up to 0.9 °C cooler at night. Soil temperatures showed a smaller range of temperature deviations between OTCs and controls, but largely followed the same pattern as air temperatures (Fig. 2). Relatively large fluctuations in air temperature deviations (0.7 to 1.0 °C) as observed at hours 15 and 19 in 2004 were unexpected, but may have been due to shading of the temperature probes by the OTC frame. Cooler nighttime air temperatures in OTC plots compared to controls were observed in most years, but were most frequent in 2008 when over half of the days in June and August showed evidence of nighttime cooling (Table 2). Incidences of nighttime cooling in soil temperatures were most common in the relatively cool years of 2006 and 2008 (Table 2).

VEGETATIVE GROWTH

Analyses of vegetative traits of target species indicated no significant effects of the OTC treatments on leaf or stem characteristics (Table 3), although leaves of *D. octopetala* and leaves and stem increments of *S. arctica* showed a tendency to be longer in OTCs than in control plots (Fig. 3). All target species except *L. arcticus* showed significant variation in vegetative characters between years (Table 3). *Dryas octopetala* produced significantly longer leaves in 2007, but otherwise leaf lengths remained fairly constant during the study period (Fig. 3, A). *Polygonum viviparum* leaf widths showed a trend of increasing width over the study period, and leaf numbers were also higher in the final three years of the study (Fig. 3, C and D). The aboveground shoots of *P. viviparum* die back each year to a

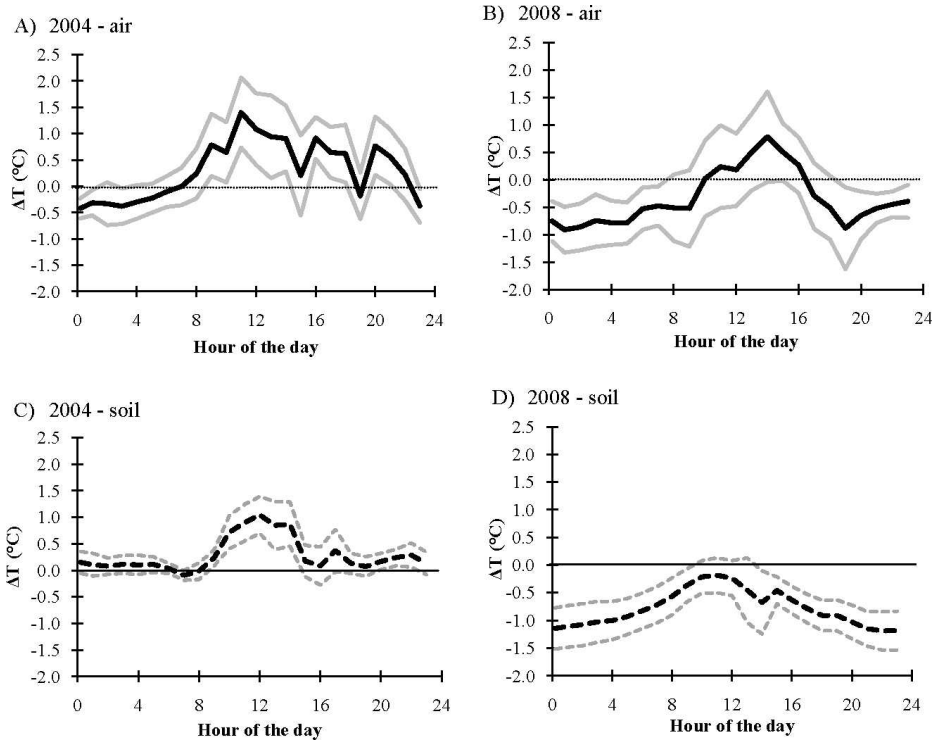

FIGURE 2. Diurnal patterns of air (solid lines) and soil (dashed lines) temperature deviations (ΔT) between OTCs and control plots averaged for all days in July in a warm year (2004; A and C) and a cool year (2008; B and D) (n = 31). Deviations are control plot temperatures subtracted from OTC temperatures so that positive or negative values indicate that treated plots were warmer or cooler, respectively, than controls. Black lines represent means, and gray lines indicate the 95% confidence interval around the means. Temperature deviations are significantly different from zero if the entire confidence interval is above or below zero.

TABLE 2

Percentage of nights that exhibited average cooling in OTC plots relative to control plots. A night was considered to show a cooling effect if the average temperature difference between OTC and control plots was < − 0.5 °C or < −1.0 °C during the hours from 2100 to 0400 inclusive. Data were incomplete for 2001 and 2007.

		< −0.5 °C		< −1.0 °C	
Year	Month	Air	Soil	Air	Soil
2002	June	0.0	0.0	0.0	0.0
	July	0.0	0.0	0.0	0.0
	August	6.5	0.0	0.0	0.0
2003	June	0.0	0.0	0.0	0.0
	July	0.0	0.0	0.0	0.0
	August	41.9	0.0	32.3	0.0
2004	June	0.0	12.9	0.0	12.9
	July	38.7	6.5	0.0	0.0
	August	74.2	38.7	32.3	9.7
2005	June	22.6	12.9	12.9	6.5
	July	64.5	32.3	45.2	16.1
	August	61.2	77.4	45.2	29.0
2006	June*	82.6	95.7	43.5	95.7
	July	71.0	100	32.3	80.7
	August	58.1	100	25.8	16.1
2008	June+	69.2	92.3	57.7	84.6
	July	45.2	67.7	22.6	38.7
	August	96.8	35.5	77.4	19.4

* Based on 23 days

+ Based on 26 days

belowground perennial rhizome, making it difficult to assign trends over time to the aging of individual ramets or genets. *Salix arctica* stem growth also varied significantly among years, and stems in 2001 and 2004 were more than 60% shorter than the study average (Fig. 3, E and F).

Despite significant annual variation, vegetative characteristics of target species were not significantly correlated with variations in GDD in current or previous years (Spearman's $\rho < 0.5$, $P > 0.2$, $n = 9, 8$; data not shown). An exception was the number of leaves of *P. viviparum*, which showed a weak negative correlation with GDD in the current year (Spearman's $\rho = 0.58$, $P = 0.10$, $n = 9$). Relationships between target species measurements and other temperature variables (mean June and July temperatures) were also not significant (data not shown). Exploratory analysis examining correlations between target species measurements and other climate variables (e.g., total snowfall, mean January temperature, total summer precipitation) measured at the Whitehorse airport (Environment Canada, 2009) indicated that leaf lengths of *D. octopetala* and *S. arctica* were negatively related to total summer precipitation in the current and previous year, respectively ($r = -0.640$ and -0.718 for *D. octopetala* and *S. arctica*, respectively; $P < 0.05$; $n = 10$).

Annual measurements of leaf lengths or widths showed significant positive relationships with leaf area and dry mass (Table 4). Leaf or leaflet lengths of *D. octopetala* and *L. arcticus* predicted 65 to 80% of the observed variation in leaf area and dry mass. These relationships were somewhat weaker for *P. viviparum* and *S. arctica*, and predicted between 40 and 70% of the variation in leaf area and dry mass (Table 4).

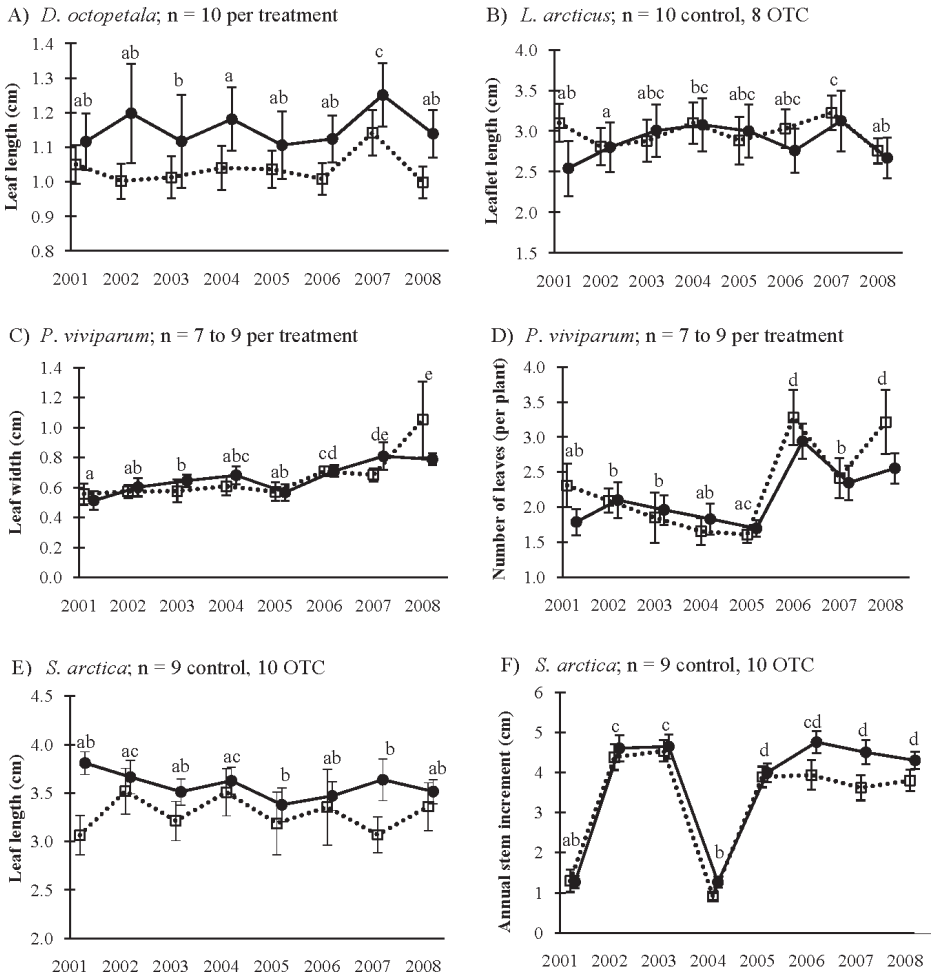

FIGURE 3. Annual variation in leaf measurements (A–E) and current year stem lengths (F) of target species from the Wolf Creek study site from 2001 to 2008 in control plots (open squares) and OTCs (solid circles). Values that share a letter indicate years that were not significantly different ($P \leq 0.05$). Points are mean values ±SE (sample sizes indicated in the panel caption) and have been staggered along the *x*-axis to increase readability.

TABLE 3

Summary of results of repeated measures (M)ANOVAs indicating differences in the vegetative (top) and reproductive (bottom) responses to the OTC treatment and years of four target species. Significant results ($P \leq 0.05$) are in bold.

Species	Measurement	Variation	*F*	df	*P*
L. arcticus	Leaflet and petiole length (MANOVA)	Year	2.702	14, 3	0.224
		Treatment	1.098	2, 15	0.359
		Year × Treatment	0.980	14, 3	0.587
S. arctica	Leaf length and annual stem increment (MANOVA)	Year	17.097	14, 4	**0.007**
		Treatment	1.822	2, 16	0.194
		Year × Treatment	1.035	14, 4	0.543
D. octopetala	Leaf length	Year	2.974	7, 126	**0.006**
		Treatment	1.082	1, 18	0.312
		Year × Treatment	0.716	7, 126	0.659
P. viviparum	Leaf width	Year	3.489	7, 42	**0.005**
		Treatment	1.272	1, 6	0.303
		Year × Treatment	1.508	7, 42	0.191
	Number of leaves	Year	5.582	7, 42	**<0.001**
		Treatment	1.562	1, 6	0.258
		Year × Treatment	0.969	7, 42	0.466
S. arctica	Leaf length	Year	1.680	7, 119	0.120
		Treatment	3.553	1, 17	0.077
		Year × Treatment	1.178	7, 119	0.320
	Annual stem increment	Year	55.027	7, 119	**<0.001**
		Treatment	3.844	1, 17	0.067
		Year × Treatment	1.800	7, 119	0.093
D. octopetala	Peduncle length	Year	2.483	7, 126	**0.020**
		Treatment	6.124	1, 18	**0.024**
		Year × Treatment	2.154	7, 126	**0.043**
L. arcticus	Number of inflorescences	Year	1.370	7, 112	0.225
		Treatment	0.173	1, 16	0.683
		Year × Treatment	0.370	7, 112	0.552
P. viviparum	Length of bulbil section	Year	9.560	7, 42	**<0.001**
		Treatment	10.834	1, 6	**0.017**
		Year × Treatment	11.290	7, 42	0.279
	Length of flower section	Year	6.631	7, 42	**<0.001**
		Treatment	0.025	1, 6	0.879
		Year × Treatment	1.054	7, 42	0.409
S. arctica	Catkin length	Year	2.796	7, 98	**0.011**
		Treatment	0.623	1, 14	0.443
		Year × Treatment	1.285	7, 98	0.266

REPRODUCTIVE MEASURES

Analysis of treatment and year effects on reproductive characteristics indicated that *D. octopetala* sometimes produced longer peduncles and *P. viviparum* usually produced longer bulbil sections in experimental plots compared to controls (Table 3; Fig. 4, A and C). A significant Year × Treatment interaction for *D. octopetala* peduncle lengths (Table 3) also indicated that interannual variation in peduncle lengths was only significant in control plots (control: $F_{year} = 3.063$; df = 1, 18; $P = 0.007$; OTC: $F_{year} = 1.033$; df = 1, 18; $P = 0.416$). Catkin lengths of *S. arctica* varied significantly among years (Table 3), being shortest in 2001, 2005, 2006, and 2008 (Fig. 4, B). The number of *L. arcticus* inflorescences averaged 1.23 ± 0.15 (mean ± SE) inflorescences/plant and did not vary significantly between treatments or years (Table 3).

None of the variables that showed significant interannual variation were significantly correlated with variations in June or July mean temperatures at the site, or with climate variables measured at the Whitehorse airport. However, peduncle lengths of *D. octopetala* were weakly and negatively correlated with previous year's GDD ($r = -0.643$, $P = 0.09$, $n = 8$), while flower lengths of *P. viviparum* were positively correlated with current year's GDD ($r = 0.600$, $P = 0.09$, $n = 9$). Additionally, *P. viviparum* in 2004 showed pronounced decreases and increases in the lengths of bulbil and flower sections, respectively (Fig. 4, C and D)., The mean length of *Polygonum* flower sections was nearly five times greater in 2004 than the 10-year mean, and the length of the bulbil section was 93% less than the 10-year mean. This pattern was apparent in both control and treated plots. None of the reproductive measurements on other target species showed strong responses to the unusually warm summer of 2004 (Fig. 4).

Inflorescence counts indicated that the evergreen shrub *D. octopetala* produced the most abundant flowers at the site (averaging 37.5% of total inflorescences/year), followed by deciduous shrubs *Salix reticulata* (15.1%) and *S. arctica* (8.6%), forbs *P. viviparum* (7.7%) and *L. arcticus* (6.1%), and the graminoid *Hierochloe alpina* (4.2%). Another graminoid, *Festuca altaica*, generally had few inflorescences (1.5%), but was notable for having one year of very high flower production (7.6%) during the study. The rank abundance of inflorescences generally followed the pattern of species abundances measured by point-intercept sampling, with *D. octopetala* having the highest mean proportion of species hits (32.0%), followed by *S. arctica* (14.8%), *S. reticulata* (13.5%), and *L. arcticus* (8.2%). *Polygonum viviparum*, however, produced flowers in disproportion to its relative abundance of 1.2% (Fig. 5).

TABLE 4

Summary of results of simple regression analyses of allometric relationships between leaf dimension (cm) and leaf area (cm^2) or dry mass (g) (top) and between lengths of reproductive structures (cm) and numbers or average dry mass (g) of reproductive units (seeds, bulbils, ovaries) (bottom). Data are from four target species from the Wolf Creek study site from July 2008 and 2009 (leaf data from 2008 only). Relationships that are significant ($P \leq 0.05$) are in bold and regression equations are included.

Species	Independent variable	Dependent variable	r^2	*n*	*P*	Regression equation
D. octopetala	Leaf length	Leaf area	**0.804**	49	**<0.001**	y = 0.720x − 0.380
	Leaf length	Dry mass	**0.712**	47	**<0.001**	y = 0.006x − 0.002
L. arcticus	Leaflet length	Leaf area	**0.777**	44	**<0.001**	y = 3.842x − 3.405
	Leaflet length	Dry mass	**0.652**	35	**<0.001**	y = 0.035x − 0.028
P. viviparum	Leaf width	Leaf area	**0.682**	51	**<0.001**	y = 2.861x + 0.058
	Leaf width	Dry mass	**0.415**	32	**<0.001**	y = 0.013x + 0.004
S. arctica	Leaf length	Leaf area	**0.468**	51	**<0.001**	y = 0.984x − 0.477
	Leaf length	Dry mass	**0.521**	40	**<0.001**	y = 0.009x − 0.007
D. octopetala	Peduncle length	# of seeds	0.000	41	0.949	
	Peduncle length	# of filled seeds	0.047	41	0.173	
	Peduncle length	% germination	0.051	41	0.157	
P. viviparum	Bulbil length	# of bulbils	**0.844**	35	**<0.001**	y = 9.452x − 1.532
	Bulbil length	Average bulbil mass	0.002	35	0.793	
S. arctica	Catkin length	# of swollen ovaries	**0.308**	51	**<0.001**	y = 6.189x − 1.683
	Catkin length	# of total seeds	**0.217**	51	**<0.001**	y = 37.238x − 114.272
	Catkin length	# of filled seeds	**0.191**	40	**0.005**	y = 34.694x − 115.500
	Catkin length	% germination	**0.123**	40	**0.026**	y = 6.535x − 10.720
	# swollen ovaries	# of total seeds	**0.339**	51	**<0.001**	y = 4.175x − 52.288
	# swollen ovaries	# of filled seeds	**0.320**	40	**<0.001**	y = 4.237x − 75.384

Two species, *D. octopetala* and *P. viviparum*, produced significantly more inflorescences per unit abundance in OTC plots compared to controls (Table 5; Fig. 5, A and C). Although five of the seven most commonly flowering species showed significant annual variation in inflorescence counts (Table 5), species within a growth form did not show the same pattern of annual variation. For example, while both forb species had fairly high interannual variation, *L. arcticus* inflorescences showed an increasing trend over time while *P. viviparum* inflorescences showed a decreasing trend and peak flowering of each species occurred in different years (Fig. 5, B and C). Inflorescence counts of *F. altaica* showed a significant year effect (Table 5) that was driven by a large increase in flowering in 2005 (Fig. 5, G).

Inflorescence counts that were standardized by average abundance were not significantly correlated with GDD in the current or previous year for any species (Spearman's $\rho < 0.6$, $P > 0.1$, $n = 10$ current year, 9 previous year). However, absolute inflorescence counts of *L. arcticus* and *S. reticulata* were positively

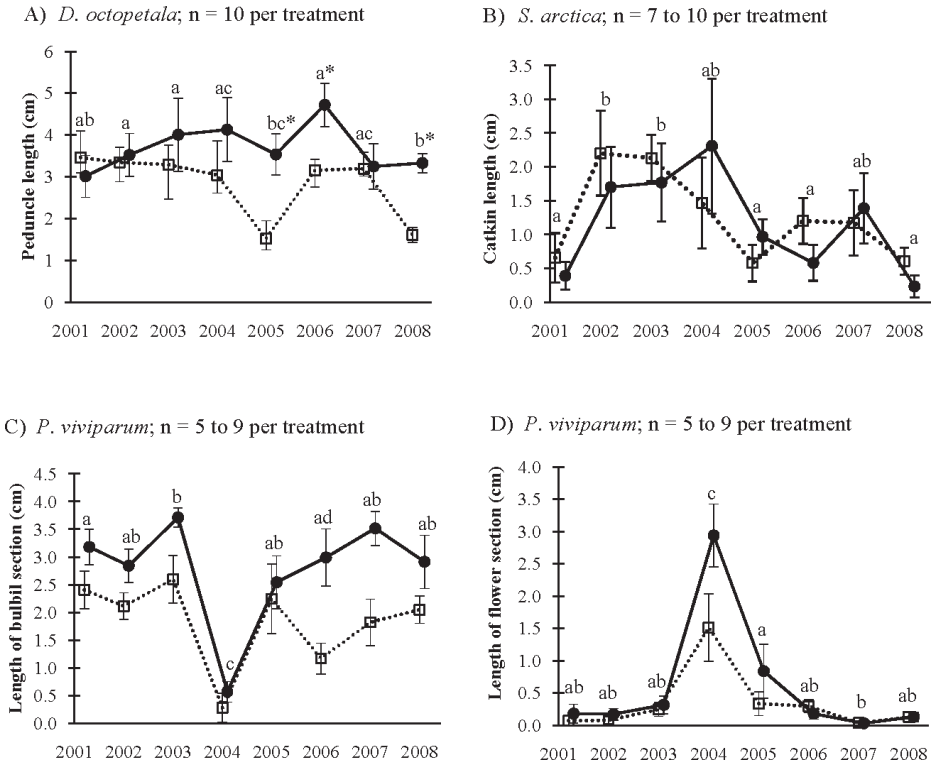

FIGURE 4. Lengths of reproductive structures of target species from 2001 to 2008 in controls (open squares) and OTCs (closed circles). Treatment effects were significant for (A) and (C). Values that share a letter indicate years that were not significantly different ($P \leq 0.05$). For *Dryas octopetala*, years where values were significantly different between treatment types are indicated (*). Points are mean values ±SE (sample sizes indicated in panel caption) and have been staggered along the *x*-axis to increase readability.

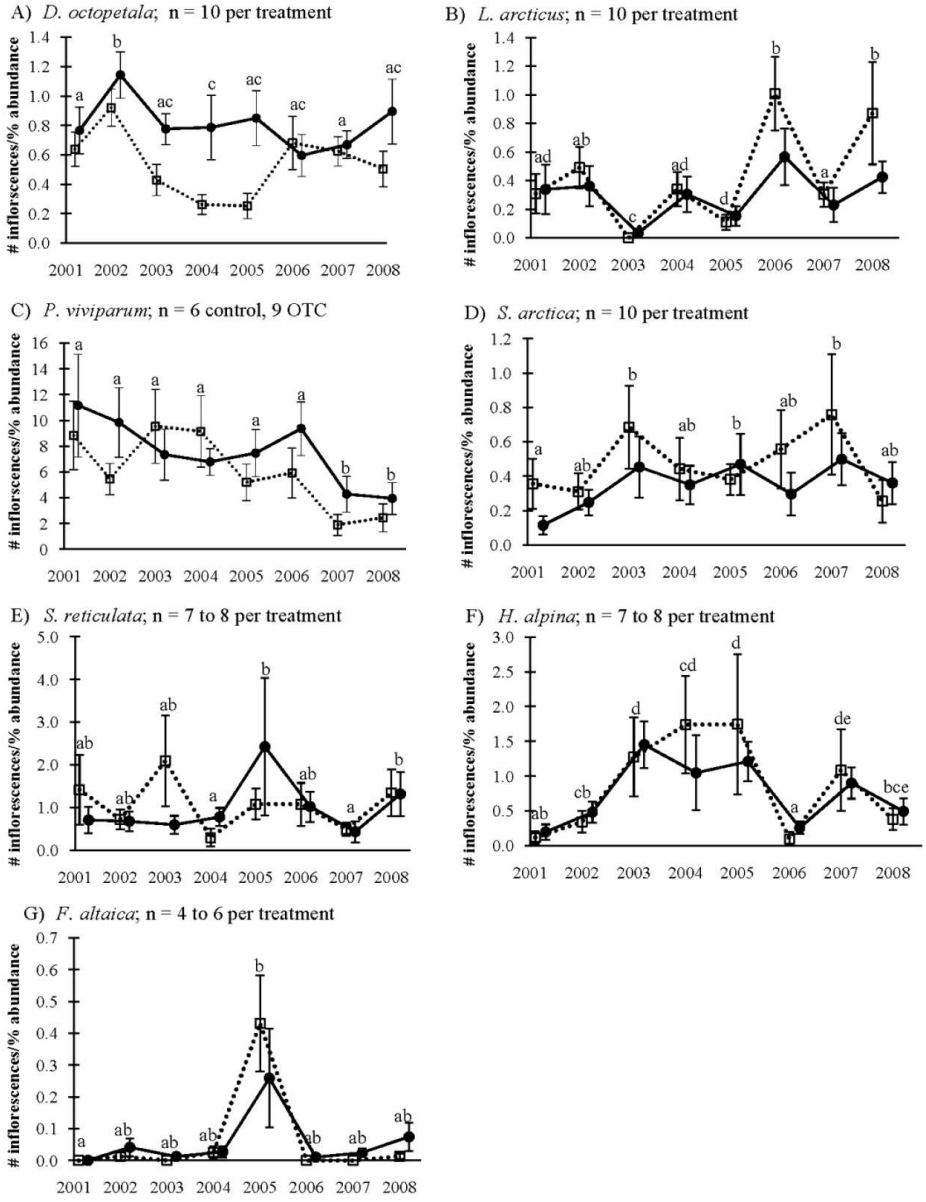

FIGURE 5. Numbers of inflorescences per unit average abundance of common species from 2001 to 2008 at the Wolf Creek site for control and OTC plots. Values that share a letter indicate years that were not significantly different ($P \leq 0.05$). Treatment effects were significant for (A) and (C). Points are mean values ± SE (sample sizes in panel caption) and are staggered along the *x*-axis.

and negatively correlated, respectively, with GDD in the current year (Spearman's $\rho = 0.62$ and -0.76, respectively, $P < 0.05$, $n = 10, 8$).

Annual, non-destructive measurements of reproductive output were significantly related to measured reproductive output for two of three sampled species. Catkin lengths of *S. arctica* were positively related to the numbers of swollen ovaries, total and filled seeds, and percent seed germination, but the proportion of variance explained was relatively low (Table 4). For *P. viviparum*, bulbil section length was strongly and positively related to the number of bulbil scars, but not to average mass per bulbil (Table 4). *Dryas octopetala* peduncle lengths showed no significant relationship with the total number of seeds, number of filled seeds, or percent seed germination of an inflorescence. Reproductive output of *L. arcticus* was not assessed.

COMMUNITY COMPOSITION

Of the three diversity indices calculated, only species richness changed significantly between years and none of the measures differed between treatment types. In total, 40 vascular plant species were found in the study plots, with mean species richness per plot (±SE) ranging from 12.4 ± 0.6 in 1998 to 13.3 ± 0.6 in 2008. Mean Pielou's evenness per plot was 0.68 ± 0.02 each year and mean Shannon-Wiener diversity per plot was 1.72 ± 0.06.

Multivariate ordination of vascular plant composition showed that OTC and control plots were interspersed, indicating that there were no clear differences in composition between treatments (Fig. 6). The NMS ordination required 51 iterations to produce a stable, 2-dimensional solution that captured 90.5% of the compositional variation in the data, with each axis expressing around 45%. Final stress was 13.66, suggesting that the graph was a reasonable representation of composition patterns in the data (McCune and Grace, 2002). Time sequence overlays on the ordination plot showed that, although species composition changed from 1998 to 2008, changes were not unidirectional, nor were they consistent across plots or treatments (Fig. 6). Some plots changed in one direction from 1998 to 2003 and then changed back along a similar direction, making composition in 2008 more similar to that in 1998 than in 2003, while others were more similar between 1998 and 2003 (Fig. 6). The ANOVA on distances between years revealed no interaction between treatment

TABLE 5

Summary of results of repeated measures ANOVAs on the number of inflorescences per unit average abundance of common vascular plant species from the Wolf Creek site. Results indicate differences associated with years (repeated factor) and OTC treatment (fixed factor). Data are from 2001 to 2008. Tests were carried out using ranked values. Significant results ($P \leq 0.05$) are in bold.

Species	Variation	F	df	P
L. arcticus	Year	8.955	7, 126	**<0.001**
	Treatment	0.470	1, 18	0.502
	Year × Treatment	0.517	7, 126	0.820
P. viviparum	Year	4.817	7, 63	**<0.001**
	Treatment	24.586	1, 9	**0.001**
	Year × Treatment	1.387	7, 63	0.226
D. octopetala	Year	4.928	7, 126	**<0.001**
	Treatment	4.660	1, 18	**0.045**
	Year × Treatment	1.741	7, 126	0.105
S. arctica	Year	1.589	1, 126	0.145
	Treatment	0.157	1, 18	0.697
	Year × Treatment	0.900	7, 126	0.509
S. reticulata	Year	2.070	7, 84	0.056
	Treatment	0.094	1, 12	0.764
	Year × Treatment	0.935	7, 84	0.484
H. alpina	Year	6.430	7, 77	**<0.001**
	Treatment	0.800	1, 11	0.390
	Year × Treatment	0.391	7, 77	0.905
F. altaica	Year	2.477	7, 42	**0.032**
	Treatment	0.566	1, 6	0.480
	Year × Treatment	0.869	7, 42	0.539

type and time interval ($F = 0.259$; df = 1, 17; $P = 0.613$). Results of the MRBP indicated that different observers in 2008 produced marginally significant differences in their estimates of community composition for the same plots ($A = 0.012$; $P = 0.054$).

Discussion

TEMPERATURE

In this study the deployment of OTCs did not have a significant effect on GDD or average monthly or daily July temperatures. Differences in temperature between treatment types were only apparent when hourly data were considered and the average degree of warming observed did not exceed 1.5 °C. Both positive and negative effects of the OTCs on hourly temperature means were observed, and mean daily warming was often masked by nighttime cooling which was present in most years. Thus, the net effect of the OTCs at Wolf Creek appears to have been an increase in the daily amplitude of temperature variation, rather than the intended net warming effect.

Patterns of nighttime cooling similar those seen in this study have been previously reported (Gugerli and Bauert, 2001; Stenström and Jónsdóttir, 2006). The mechanism behind nighttime cooling is unclear, but may relate to the pooling of cool air in the chambers at night when solar radiation is at a minimum. The OTCs are constructed to block winds and increase the near-surface boundary layer to reduce air mixing during the day and trap sensible heat (Marion et al., 1997). At night, these conditions may also create cooling by reducing the mixing of air in the OTCs with surrounding, potentially warmer air. Our results are consistent with other observations of nighttime cooling at alpine sites (Gugerli and Bauert, 2001; Stenström and Jónsdóttir, 2006) and may indicate a general limitation of large OTC chambers to produce significant warming at more exposed, alpine tundra sites. The degree of warming achieved by OTCs is dependent on other climate variables such as solar radiation, cloud cover, and wind speed (Marion et al., 1997) and thus the efficacy of OTCs may be site specific. Indeed, our comparison of diurnal warming patterns indicates that OTCs used in this study were more effective at

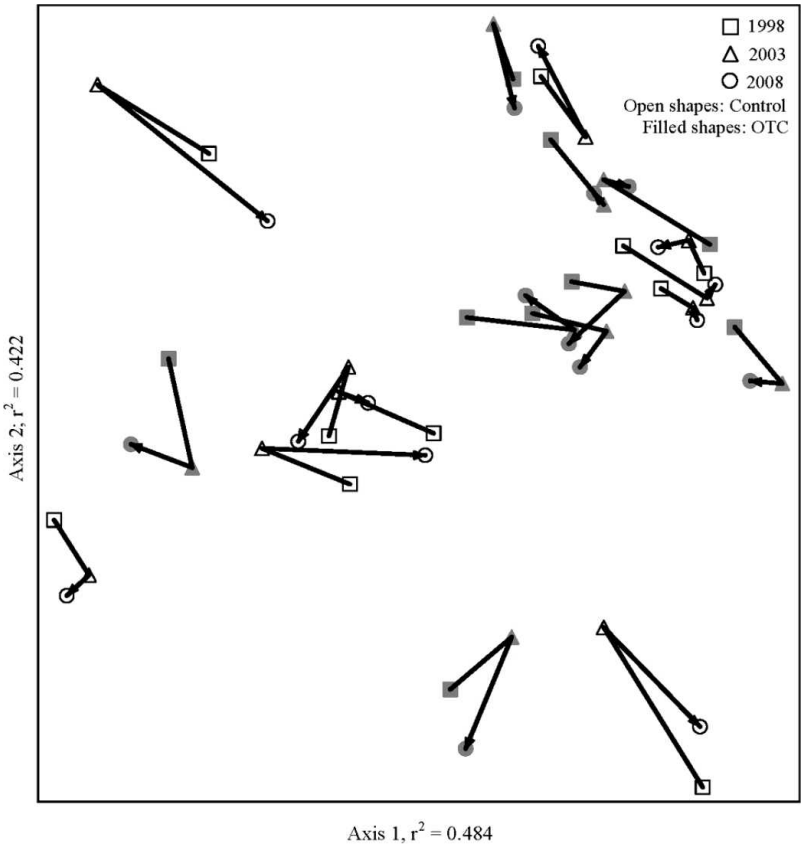

FIGURE 6. Non-metric multidimensional scaling (NMS) ordination of 19 study plots (10 control, 9 OTC) over three years (1998, 2003, 2008). The solution is 2-dimensional ordination with a final stress of 13.66. The r^2 value for an axis is a post-hoc representation of the proportion of variance expressed on that axis. Treatment type is indicated using open (control plots) or filled (OTCs) symbols. Symbols connected by lines represent the same plot measured in each of the three years with the arrow head pointing to 2008.

warming in a warm, sunny year (2004) than in a cool, cloudy one (2008). Overall, the low degree of warming found in this study may be due to a combination of high winds and relatively large OTC size that reduced the ability of the OTC to trap sensible heat during the day (Marion et al., 1997).

Experimental plots experienced warming and cooling relative to controls, but the magnitude of each was small. It seems likely that only the most sensitive plant variables would be responsive to such small deviations. While temperatures were not very different between treatment types, there was substantial interannual variation in temperature recorded across the 10 years of the study. Theoretically, examining responses to experimental warming and natural temperature variation simultaneously may provide a more accurate assessment of plant responses to warming (Dunne et al., 2004). Because of the relatively minor effects of OTCs on temperature and high interannual variation, we would expect plants in this study to show stronger responses to interannual variation than to the OTC treatment.

SPECIES RESPONSES

There were no significant vegetative responses to the experimental treatment for any of the target species. There was a non-significant trend for leaf lengths of *D. octopetala* and leaf lengths and annual stem increments of *S. arctica* to be greater in OTCs compared to controls. Positive, non-significant responses of vegetative traits to OTC treatments have been reported previously for both species (Jones et al., 1997; Welker et al., 1997), suggesting that weak responses to OTCs are masked by larger variability in response to other factors. In this study, vegetative traits of *L. arcticus* and *P. viviparum* showed no apparent responses to the OTCs. Responses of other perennial forbs to experimental warming have indicated increases in both vegetative and reproductive measurements in OTCs compared to controls (e.g. Molau, 2001; Kudernatsch et al., 2008), but non-significant effects of OTCs have also been reported (Hollister et al., 2005a). Although the OTC effects on temperature were small at this site, weak responses of plant vegetative traits to the warming treatment are consistent with these traits also showing little correlation with annual variations in climate. Despite significant annual variation in measured vegetative traits for nearly all species, patterns of growth were not strongly linked to GDD or other temperature variables. The lack of significant differences in vegetative metrics between treatment types or correlations with annual temperature indicate that vegetative growth of target species is relatively insensitive to temperature variations within the range observed in this study.

Plant responses to changes in temperature may be constrained by interactions with other factors, such as moisture (Körner, 2003). Previous experiments using open-topped chambers have found little to no detectable effects of OTCs on soil moisture (Jonasson et al., 1993; Marion et al., 1997). Soil moisture was not considered in this study, but since temperatures were not significantly different between treatment types we think it unlikely that soil moisture was greatly affected by the experimental treatment. If drought stress was an important control of plant growth in this study, we would have expected to see opposite plant responses to the warm, dry summer of 2004 in comparison to the cool, wet summer of 2008. However, highly individualistic responses of plants to annual climate variation prevent a conclusive assessment of the role of moisture and temperature interactions in controlling plant productivity at this alpine site. Negative correlations of *Dryas* and *Salix* leaf lengths with summer precipitation suggests that "bad weather" conditions associated with a rainy year may outweigh the potential benefits of reduced drought stress.

Overall, plant reproductive traits were more responsive to temperature than were vegetative traits, which is consistent with previous work (Welker et al., 1997; Gugerli and Bauert, 2001; Hollister et al., 2005a). However, species varied in the degree to which reproductive responses were consistent between the experimental treatment and interannual variation. Although peduncle lengths of *D. octopetala* and bulbil section lengths of *P. viviparum* were significantly longer and inflorescences were more numerous in OTCs compared to controls, only flower section lengths of *P. viviparum* were significantly related to annual variations in temperature. Since the warming effect of the chambers was minor, significant responses to the treatment may have been driven by another factor being manipulated by the chamber. Wind speed is often lower in OTCs compared to control plots (Kennedy, 1995; Marion et al., 1997) and protection from the wind may play a larger role than temperature in providing an improved environment for plants within OTCs (Marion et al., 1997). This secondary effect of OTCs may be especially important at windy alpine sites like Wolf Creek. In contrast to *Dryas* and *Polygonum*, reproductive characteristics of both *S. arctica* and *L. arcticus* appeared to be largely unresponsive to temperature variations within the observed range.

Although *P. viviparum* bulbil and flower section lengths were not strongly correlated with annual variation in GDD over the study period, these metrics showed large responses to the unusually warm summer conditions in 2004. The large reduction in bulbil section length in response to the atypically warm conditions of 2004 is opposite to what would be predicted from the significantly higher bulbil section lengths observed in the OTC treatment. These opposing responses suggest that bulbil production of *P. viviparum* may exhibit complex and non-linear responses to temperature. Given that bulbil section length is positively related to the number of bulbils (Table 4), and the number of bulbils is negatively related to the number of flowers (Bauert, 1993), the results observed here suggest that variations in temperature may lead to tradeoffs between sexual and asexual reproduction in *P. viviparum* (Law et al., 1983). For example, the total length of *P. viviparum* inflorescences was not affected by the warm conditions of 2004, but allocation to bulbils decreased and allocation to flowers increased. However, successful seed set in *P. viviparum* is very rare because of the abortion of young sporophytes in the flowers (Diggle et al., 2002). Thus, increases in flower production at the detriment of bulbil production may lead to overall decreases in the reproductive output of this species.

Inflorescence counts of common species at the study site indicated a range of individualistic species responses to annual variations in temperature or other factors. Absolute, but not relativized inflorescence counts of *Lupinus arcticus* and *Salix reticulata* were significantly related to GDD. Consequently, relationships between absolute numbers of inflorescences and GDD may have actually been a product of annual changes in species cover with GDD. We were unable to measure this relationship directly because abundance was only measured at 5-year intervals.

Only one species, *Festuca altaica*, showed a clear change in inflorescence production in response to the anomalously warm conditions in 2004. The strong increase in flowering of *F. altaica* in 2005 likely represents a lag response to warm conditions in 2004 associated with the preformation of floral buds. Floral preformation is common in arctic and alpine species (Bliss, 1962) and has been found in a subantarctic species of *Festuca* (Walton, 1982).

Repeated measurements made on the same plants require that measurements be non-destructive but these measures are irrelevant

to understanding plant ecology unless they are related to some aspect of plant survival, growth, or reproduction. We found that the annual leaf measurements used here and derived from the ITEX manual (Molau and Mølgaard, 1996) were strongly related to leaf area and leaf mass. Thus, the non-destructive leaf measurements appear to be reasonable indicators of plant growth processes such as light capture and photosynthetic capacity (Wright et al., 2004). Likewise, metrics of inflorescence lengths for *P. viviparum* and *S. arctica* were significantly related to reproductive output in terms of bulbil or seed production. However, these relationships were considerably weaker for *Salix* than *Polygonum*, and the reproductive trait measured for *D. octopetala* (peduncle length) was unrelated to seed production or viability. Consequently, it is unclear whether the observed increases in *Dryas* peduncle lengths in OTCs indicate any actual effects on reproductive output. These results underscore the importance of collecting data that links non-destructive metrics with variables that directly reflect plant performance before interpreting the ecological significance of measured plant responses.

COMMUNITY COMPOSITION

The OTC treatments did not result in a significant difference in plant community composition over the 10 years of this study. This is in contrast to several previous studies that have generally found decreases in species richness, increases in shrubs and graminoids, and decreases in lichens and bryophytes in response to experimental warming over two to seven growing seasons (Cornelissen et al., 2001; Hollister et al., 2005b; Walker et al., 2006). However, the absence of a community response to the OTC treatment in this study is consistent with the relative insensitivity of annually measured plant traits to the warming treatment and the relatively modest effects of OTCs on air and soil temperatures.

Our analyses suggest that community composition did change over the 10 years of this study, but the changes were not unidirectional. This is perhaps unsurprising as communities routinely change year to year in response to interannual variation (Shaver et al., 2001) and such variation is likely to mask any trends over time. Epstein et al. (2004) simulated an increase in temperature of 3 °C over 50 years for low arctic Alaska and found that changes in community composition that are driven by climate forcing, as opposed to natural variation, will likely not be observable for 15 or 20 years after initial sampling. This suggests that studies monitoring community change need to span multiple decades in order to capture the effects of temperature increases against background variation. Nevertheless, the variable and individualistic responses of both species and traits to temperature variations in this study provide little consistent evidence on which to base predictions of long-term, directional change in community composition at this site. Annual variations in most of our plant measurements appear to be driven by factors other than direct temperature effects, suggesting that the tundra community at Wolf Creek is resilient to short-term temperature changes within the range observed in this study.

While the point-frame method for assessing species cover is less subjective than other methods (Bonham, 1989), there were marginally significant differences in the measurement of species abundance between observers in 2008. These differences were largely due to differences in how observers classified ground cover into plant litter or standing dead material associated with a specific plant species. These differences among observers between years likely contributed to a portion of the observed variation in composition between sampling years.

CONCLUSIONS

Results of this study are consistent with a large body of literature that suggests that plants in arctic and alpine ecosystems respond individualistically to temperature (Chapin and Shaver, 1985; Dormann and Woodin, 2002). Species within a growth form did not show similar vegetative or reproductive responses to temperature variation at Wolf Creek. Responses of target species also differed from those observed at other sites, which makes generalizing about plant responses to temperature across the Arctic very difficult, and perhaps even inadvisable (Van Wijk et al., 2004). We also found that similar traits within a single species, such as leaf length and stem length in *Salix arctica*, can exhibit different responses to temperature. Responses to temperature that are species-, site-, and trait-specific restrict our ability to reliably predict future impacts of climate warming on tundra plants and plant communities.

The experimental OTC treatment applied in this study was not a strong test of whether or not plants are responsive to temperature. Warming by the OTCs was variable within days and years and the observed midday warming that occurred in the OTCs was relatively modest. Consequently, the degree of net warming attained was likely insufficient to stimulate measurable responses in many traits. However, by also examining the effects of annual temperature variations on plants, we were still able to gain a better understanding of the role of temperature in regulating the growth and reproduction of several target species. Plants in this study showed relatively few responses that could be clearly linked to temperature variations observed over the 10 years of the study. The unusually warm summer of 2004 did stimulate large responses from variables that were otherwise unresponsive, but this was only evident in three traits within two species. Taken together, these results suggest that temperature is not a strong factor that directly limits plant performance at Wolf Creek. Instead, temperature may act indirectly to shape plant responses via its influence on other factors. Consistently warmer temperatures over several years may yield larger responses due to changes in growing season lengths or nutrient cycling (Wilson and Nilsson, 2009).

One of the greatest obstacles in understanding responses to temperature is in the complex network of indirect effects from interactions among environmental factors and species (Shaver et al., 2000). The magnitude of plant responses to increased temperatures may be smaller than expected if growth is principally limited by the availability of other resources (Dormann and Woodin, 2002). Resources such as nutrients and moisture often limit plant growth in arctic and alpine environments (Körner, 2003), and studies that manipulated both temperature and nutrients have commonly found stronger responses to nutrient addition than to experimental warming (Chapin and Shaver, 1985; Robinson et al., 1998; Dormann and Woodin, 2002; Van Wijk et al., 2004). Increases in temperature may affect plants indirectly by affecting other factors such as nutrient availability or uptake (Nadelhoffer et al., 1997).

Based on the results of this study, decadal changes in plant community composition at this site can be expected to be small and slow as variable and individualistic species responses to climate variations may generate resilience to change at the community level. A high degree of warming such as that seen in 2004 may yield some direct responses to temperature, but for the most part, temperature variations may be more important in their indirect effect on plant species and communities at this site. Temperature is only one of many environmental variables projected to change with global warming (Solomon et al., 2007), and there are many ways it can interact with the abiotic and biotic components of an ecosystem. Our ability to predict responses of

tundra vegetation to climate change is likely to require a consideration of multiple environmental factors and a better understanding of the wide spectrum of species responses to environmental change.

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References Cited

Arft, A. M., Walker, M. D., Alatalo, J. M., Bret-Harte, M. S., Dale, M., Diemer, M., Gugerli, F., Henry, G. H. R., Jones, M. H., Hollister, R. D., Jónsdóttir, I. S., Laine, K., Lévesque, E., Marion, G. M., Molau, U., Mølgaard, P., Nordenhäll, U., Raszhivin, V., Robinson, C. H., Starr, G., Stenström, A., Stenström, M., Totland, Ø., Turner, P. L., Walker, L. J., Webber, P. J., Welker, J. M., and Wookey, P. A., 1999: Responses of tundra plants to experimental warming: meta-analysis of the international tundra experiment. *Ecological Monographs*, 69: 491–511.

Bauert, M. R., 1993: Vivipary in *Polygonum viviparum*: an adaptation to cold climate? *Nordic Journal of Botany*, 13: 473–480.

Biondini, M. E., Mielke, P. W. J., and Berry, K. J., 1988: Data-dependent permutation techniques for the analysis of ecological data. *Vegetatio*, 75: 161–168.

Bliss, L. C., 1958: Seed germination in arctic and alpine species. *Arctic*, 11: 180–188.

Bliss, L. C., 1962: Adaptations of arctic and alpine plants to environmental conditions. *Arctic*, 15: 117–144.

Bliss, L. C., and Matveyeva, N. V., 1992: Circumpolar arctic vegetation. *In* Chapin, F. S., III, Jefferies, R. L., Reynolds, J. F., Shaver, G. R., and Svoboda, J. (eds.), *Arctic Ecosystems in a Changing Climate: an Ecophysiological Perspective*. San Diego, California: Academic Press, Inc., 59–89.

Bonham, C. D., 1989: *Measurements for Terrestrial Vegetation*. New York: John Wiley & Sons, Inc.

Brown, J., Ferrians, O. J., Heginbottom, J. A., and Melnikov, E. S., 2001: Circum-arctic map of permafrost and ice conditions. Boulder, Colorado: University of Colorado, National Snow and Ice Data Center for Glaciology.

Chapin, F. S., III, and Shaver, G. R., 1985: Individualistic growth response of tundra plant species to environmental manipulations in the field. *Ecology*, 66: 594–576.

Cody, W. J., 2000: *Flora of the Yukon Territory*. 2nd ed. Ottawa, Canada: NRC Research Press.

Conover, W. J., and Iman, R. L., 1981: Rank transformations as a bridge between parametric and nonparametric statistics. *The American Statistician*, 35: 124–129.

Cornelissen, J. H. C., Callaghan, T. V., Alatalo, J. M., Michelsen, A., Graglia, E., Hartley, A. E., Hik, D. S., Hobbie, S. E., Press, M. C., Robinson, C. H., Henry, G. H. R., Shaver, G. R., Phoenix, G. K., Jones, D. G., Jonasson, S., Chapin, F. S., Molau, U., Neill, C., Lee, J. A., Melillo, J. M., Sveinbjornsson, B., and Aerts, R., 2001: Global change and arctic ecosystems: is lichen decline a function of increases in vascular plant biomass? *Journal of Ecology*, 89: 984–994.

Densmore, R., and Zasada, J., 1983: Seed dispersal and dormancy patterns in northern willows: ecological and evolutionary significance. *Canadian Journal of Botany*, 61: 3207–3216.

Diggle, P. K., Meixner, M. A., Carroll, A. B., and Aschwanden, C. F., 2002: Barriers to sexual reproduction in *Polygonum viviparum*: a comparative developmental analysis of *P. viviparum* and *P. bistortoides*. *Annals of Botany*, 89: 145–156.

Dormann, C. F., and Woodin, S. J., 2002: Climate change in the Arctic: using plant functional types in a meta-analysis of field experiments. *Functional Ecology*, 16: 4–17.

Dunne, J. A., Saleska, S. R., Fischer, M. L., and Harte, J., 2004: Integrating experimental and gradient methods in ecological climate change research. *Ecology*, 85: 904–916.

Environment Canada, 2009: Canada's National Climate Archive. Station ID#: 2101300, <http://www.climate.weatheroffice.gc.ca>.

Epstein, H. E., Calef, M. P., Chapin, F. S., III, and Starfield, A. M., 2004: Detecting changes in arctic tundra plant communities in response to warming over decadal time scales. *Global Change Biology*, 10: 1325–1334.

Farnell, R., Florkiewicz, R., Kuzyk, G., and Egli, K., 1998: The status of *Rangifer tarandus* caribou in Yukon, Canada. *Rangifer Special Issue*, 10: 131–137.

Gugerli, F., and Bauert, M. R., 2001: Growth and reproduction of *Polygonum viviparum* show weak responses to experimentally increased temperature at a Swiss alpine site. *Botanica Helvetica*, 111: 169–180.

Hollister, R. D., and Webber, P. J., 2000: Biotic validation of small open-top chambers in a tundra ecosystem. *Global Change Biology*, 6: 835–842.

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.

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. *Global Change Biology*, 11: 525–536.

Hultén, E., 1968: *Flora of Alaska and Neighboring Territories: a Manual of the Vascular Plants*. Stanford, California: Stanford University Press.

Jägerbrand, A. K., Alatalo, J. M., Chrimes, D., and Molau, U., 2009: Plant community responses to 5 years of simulated climate change at a subarctic-alpine site. *Oecologia*, 161: 601–610.

Janowicz, J. R., 1999: Wolf Creek research basin—Overview. *In* Pomeroy, J. W., and Granger, R. J. (eds.), *Wolf Creek Research Basin: Hydrology, Ecology and Environment*. Saskatoon, Saskatchewan, Canada: National Hydrology Institute, 121–130.

Johnson, D. A., and Tieszen, L. L., 1976: Aboveground biomass allocation, leaf growth, and photosynthesis patterns in tundra plant forms in arctic Alaska. *Oecologia*, 24: 159–173.

Jonasson, S., Havstrom, M., Jensen, M., and Callaghan, T. V., 1993: In situ mineralization of nitrogen and phosphorus of arctic soils after perturbations simulating climate change. *Oecologia*, 95: 179–186.

Jones, M., Macdonald, S., and Henry, G., 1999: Sex- and habitat-specific responses of a high arctic willow, *Salix arctica*, to experimental climate change. *Oikos*, 87: 129–138.

Jones, M. H., Bay, C., and Nordenhäll, 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. *Global Change Biology*, 3: 55–60.

Kaufman, D., Schneider, D., McKay, N., Ammann, C., Bradley, R., Briffa, K., Miller, G., Otto-Bliesner, B., Overpack, J., Vinther, B., Arctic Lakes 2k Project Members, 2009: Recent warming reverses long-term Arctic cooling. *Science*, 325: 1236–1239.

Kennedy, A. D., 1995: Simulated climate change: are passive greenhouses a valid microcosm for testing the biological effects of environmental perturbations? *Global Change Biology*, 1: 29–42.

Klanderud, K., and Tøtland, O., 2005: Simulated climate change altered dominance hierarchies and diversity of an alpine biodiversity hotspot. *Ecology*, 86: 2047–2054.

Körner, C., 2003: *Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems*. Berlin: Springer.

Kruskal, J. B., 1964: Nonmetric multidimensional scaling: a numerical method. *Psychometrika*, 29: 115–129.

Kudernatsch, T., Fischer, A., Bernhardt-Romermann, M., and Abs, C., 2008: Short-term effects of temperature enhancement on growth and reproduction of alpine grassland species. *Basic and Applied Ecology*, 9: 263–274.

Law, R., Cook, R. E. D., and Manlove, R. J., 1983: The ecology of flower and bulbil production in *Polygonum viviparum*. *Nordic Journal of Botany*, 3: 559–565.

Marion, G. M., Henry, G. H. R., Freckman, D. W., Johnstone, J., Jones, G., Jones, M. H., Levesque, E., Molau, U., Molgaard, P., Parsons, A. N., Svoboda, J., and Virginia, R. A., 1997: Open-top designs for manipulating field temperature in high-latitude ecosystems. *Global Change Biology*, 3(Suppl. 1): 20–32.

Maxwell, B., 1992: Arctic climate: potential for change under global warming. *In* Chapin, F. S., III, Jefferies, R. L., Reynolds, J. F., Shaver, G. R., and Svoboda, J. (eds.), *Arctic Ecosystems in a Changing Climate: an Ecophysiological Perspective*. London, United Kingdom: Academic Press, Inc., 11–34.

McBean, G., Alekseev, G., Chen, D., Førland, R., Fyfe, J., Groisman, P. Y., King, R., Melling, H., Vose, R., and Whitfield, P. H., 2004: Arctic Climate: Past and Present. *In Arctic Climate Impact Assessment Scientific Report: Cambridge: Cambridge University Press, 21–60.*

McCune, B., and Grace, J. B., 2002: *Analysis of Ecological Communities*. Gleneden Beach, Oregon: MjM Software Design.

Mielke, P. W. J., 1991: The application of multivariate permutation methods based on distance functions in the earth sciences. *Earth-Science Reviews*, 31: 55–71.

Molau, U., 2001: Tundra plant responses to experimental and natural temperature changes. *Memoirs of the National Institute of Polar Research Special Issue*, 54: 445–466.

Molau, U., and Mølgaard, P., 1996: *ITEX Manual.* 2nd ed. Copenhagen: Danish Polar Center.

Murray, D. F., 1997: Systematics of the ITEX species. *Global Change Biology*, 3(Suppl. 1): 10–19.

Nadelhoffer, K. J., Shaver, G. R., Giblin, A., and Rastetter, E. B., 1997: Potential impacts of climate change on nutrient cycling, decomposition, and productivity in arctic ecosystems. *In* Oechel, W. C., Callaghan, T. V., Gilmanov, T., Holten, J. I., Maxwell, B., Molau, U., and Svensbjörnsson, B. (eds.), *Global Change and Arctic Terrestrial Ecosystems*. New York: Springer-Verlag, 349–364.

Pieper, S., 2009: Alpine plant responses to natural temperature variation and experimental warming treatments in southern Yukon. MSc thesis, Biology Department, University of Saskatchewan, Saskatoon, Canada, 95 pp.

Price, M., and Waser, N., 2000: Responses of subalpine meadow vegetation to four years of experimental warming. *Ecological Applications*, 10: 811–823.

Robinson, C. H., Wookey, P. A., Lee, J. A., Callaghan, T. V., and Press, M. C., 1998: Plant community responses to simulated environmental change at a high arctic polar semi-desert. *Ecology*, 79: 856–866.

Shaver, G. R., Canadell, J., Chapin, F. S., III, Gurevitch, J., Harte, J., Henry, G., Ineson, P., Jonasson, S., Melillo, J., Pitelka, L., and Rustad, L., 2000: Global warming and terrestrial ecosystems: a conceptual framework for analysis. *Bioscience*, 50: 871–881.

Shaver, G. R., Bret-Harte, M. S., Jones, M. H., Johnstone, J., Gough, L., Laundre, J., and Chapin, F. S. I., 2001: Species composition interacts with fertilizer to control long-term change in tundra productivity. *Ecology*, 82: 3163–3181.

Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, A., Tignor, K., and Miller, H., 2007: *Climate Change 2007: the Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge and New York: Cambridge University Press.

Stenström, A., and Jónsdóttir, I. S., 2006: Effects of simulated climate change on phenology and life history traits in *Carex bigelowii*. *Nordic Journal of Botany*, 24: 335–371.

Tieszen, L. L., Lewis, M. C., Miller, P. C., Mayo, J., Chapin, F. S., III, and Oechel, W., 1981: An analysis of processes of primary production in tundra growth forms. *In* Bliss, L. C., Heal, O. W., and Moore, J. J. (eds.), *Tundra Ecosystems: A Comparative Analysis*. Cambridge: Cambridge University Press, 285–356.

Van Wijk, M. T., Clemmensen, K. E., Shaver, G. R., Williams, M., Callaghan, T. V., Chapin, F. S., III, Cornelissen, J. H. C., Gough, L., Hobbie, S. E., Jonasson, S., Lee, J. A., Michelsen, A., Press, M. C., Richardson, S. J., and Rueth, H., 2004: Long-term ecosystem level experiments at Toolik Lake, Alaska, and at Abisko, northern Sweden: generalizations and differences in ecosystem and plant type responses to global change. *Global Change Biology*, 10: 105–123.

Wahl, H. E., Fraser, D. B., Harvey, R. C., and Maxwell, J. B., 1987: *Climate of Yukon*. Ottawa, Canada: Environment Canada, Atmospheric Environment Service, Climatological Studies Number 40.

Walker, M. D., Wahren, C. H., Hollister, R. D., Henry, G. H. R., Ahlquist, L. E., Alatalo, J. M., Bret-Harte, M. S., Calef, M. P., Callaghan, T. V., Carroll, A. B., Epstein, H. E., Jonsdottir, I. S., Klein, J. A., Magnusson, B. O., Molau, U., Oberbauer, S. F., Rewa, S. P., Robinson, C. H., Shaver, G. R., Suding, K. N., Thompson, C. C., Tolvanen, A., Totland, O., Turner, P. L., Tweedie, C. E., Webber, P. J., and Wookey, P. A., 2006: Plant community responses to experimental warming across the tundra biome. *Proceedings of the National Academy of Sciences of the U.S.A.*, 103: 1342–1346.

Walton, D. W. H., 1982: Floral phenology in the South Georgian vascular flora. *British Antarctic Survey Bulletin*, 55: 11–25.

Welker, J. M., Molau, U., Parsons, A. N., Robinson, C. H., and Wookey, P. A., 1997: Responses of *Dryas octopetala* to ITEX environmental manipulations: a synthesis with circumpolar comparisons. *Global Change Biology*, 3: 61–73.

Will-Wolf, S., Geiser, L. H., Neitlich, P., and Reis, A. H., 2006: Forest lichen communities and environment—How consistent are relationships across scales? *Journal of Vegetation Science*, 17: 171–184.

Wilson, S. D., and Nilsson, C., 2009: Arctic alpine vegetation change over 20 years. *Global Change Biology*, 15: 1676–1684.

Wipf, S., 2010: Phenology, growth, and fecundity of eight subarctic tundra species in response to snowmelt manipulations. *Plant Ecology*, 207: 53–66.

Wookey, P. A., Robinson, C. H., Parsons, A. N., Welker, J. M., Press, M. C., Callaghan, T. V., and Lee, J. A., 1995: Environmental constraints on the growth, photosynthesis and reproductive development of *Dryas octopetala* at a high arctic polar semi-desert, Svalbard. *Oecologia*, 102: 478–489.

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J. H. C., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J., Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., Midgley, J. J., Navas, M.-L., Niinemets, Ü., Oleksyn, J., Poorter, H., Poot, P., Prior, L., Pyankov, V. I., Roumet, C., Thomas, S. C., Tjoelker, M. G., Veneklaas, E. J., and Villar, R., 2004: The worldwide leaf economics spectrum. *Nature*, 428: 821–827.

Zar, J. H., 1999: *Biostatistical Analysis.* 4th ed. Upper Saddle River, New Jersey: Prentice-Hall, Inc., 663 pp.

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