

# Taller and larger: shifts in Arctic tundra leaf traits after 16 years of experimental warming

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## Abstract

Understanding plant trait responses to elevated temperatures in the Arctic is critical in light of recent and continuing climate change, especially because these traits act as key mechanisms in climate-vegetation feedbacks. Since 1992, we have artificially warmed three plant communities at Alexandra Fiord, Nunavut, Canada (79°N). In each of the communities, we used open-top chambers (OTCs) to passively warm vegetation by 1–2 °C. In the summer of 2008, we investigated the intraspecific trait responses of five key species to 16 years of continuous warming. We examined eight traits that quantify different aspects of plant performance: leaf size, specific leaf area (SLA), leaf dry matter content (LDMC), plant height, leaf carbon concentration, leaf nitrogen concentration, leaf carbon isotope discrimination (LCID), and leaf  $\delta^{15}\text{N}$ . Long-term artificial warming affected five traits, including at least one trait in every species studied. The evergreen shrub *Cassiope tetragona* responded most frequently (increased leaf size and plant height/decreased SLA, leaf carbon concentration, and LCID), followed by the deciduous shrub *Salix arctica* (increased leaf size and plant height/decreased SLA) and the evergreen shrub *Dryas integrifolia* (increased leaf size and plant height/decreased LCID), the forb *Oxyria digyna* (increased leaf size and plant height), and the sedge *Eriophorum angustifolium* spp. *triste* (decreased leaf carbon concentration). Warming did not affect  $\delta^{15}\text{N}$ , leaf nitrogen concentration, or LDMC. Overall, growth traits were more sensitive to warming than leaf chemistry traits. Notably, we found that responses to warming were sustained, even after many years of treatment. Our work suggests that tundra plants in the High Arctic will show a multifaceted response to warming, often including taller shoots with larger leaves.

**Keywords:** artificial warming, climate change, functional traits, International Tundra Experiment, ITEX, open-top chamber, passive warming, tundra

Received 27 March 2010; revised version received 26 June 2010 and accepted 4 July 2010

## Introduction

Plant growth may be limited by environmental factors, interactions with other plants, herbivores, and pathogens. In resource-poor High Arctic tundra, plants are primarily controlled by physical factors. The region's cold climate directly and indirectly influences many environmental factors that are important for plant growth, including air and soil temperatures, nutrient availability, and soil moisture (Shaver *et al.*, 2000). In recent decades, the climate of the Arctic has warmed significantly (Anisimov *et al.*, 2007; Hudson & Henry, 2009), and future climate change is expected to lead to pronounced effects on tundra plants (Callaghan *et al.*, 2005). Understanding the effects of environmental factors on plant performance is important for predicting plant responses to climate change.

Since 1990, the International Tundra Experiment (ITEX) has been assessing the responses of plant communities to climate change by (i) artificially warming ecosystems with small open-top chambers (OTCs; Henry & Molau,

1997) and (ii) following changes in unmanipulated control plots (Hudson & Henry, 2009). Short-term passive warming has led to surprisingly large leaf growth responses (e.g. mass, length, and width), given its relatively minor effect on temperature (1–2 °C; Henry & Molau, 1997; Arft *et al.*, 1999). The largest effects were observed after 2–3 years of warming, and by year 4, most treatment effects disappeared (Arft *et al.*, 1999; Stenström & Jónsdóttir, 2006). These authors posited that elevated temperatures stimulate plant investment in new tissue by exploiting stored resources; effects then diminish as plants exhaust their reserves. This hypothesis suggests that plants require a long-term increase in resource supply to sustain higher growth rates. If investments are in fact transient and short-term, predicting tundra responses to climate change should be relatively straightforward. However, plant responses to changes in environmental factors are rarely simple, and are characterized by lag times, slow responses, step-changes, and feedbacks (Shaver *et al.*, 2000).

Over the last decade, plant functional traits have become increasingly popular for characterizing

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vegetation responses to environmental factors (e.g. Poorter & Navas, 2003; Aranda *et al.*, 2005; Bassin *et al.*, 2009), and spatial environmental variation (e.g. Kudo *et al.*, 1999, 2001; Gross *et al.*, 2007), partly because consensus among researchers for a shortlist of the most important traits has been reached (Westoby *et al.*, 2002). The shortlisted traits have strong impacts on ecosystem processes (Cornwell *et al.*, 2008) and/or have strong predictive power of ecosystem response to environmental change (Chapin, 2003). In this study, we examined the intraspecific effects of long-term warming on several Arctic plants. We focused on leaf growth [size, specific leaf area (SLA), dry matter content, and plant height] and leaf chemistry (carbon and nitrogen) traits. We selected eight traits because of their importance in biomes around the world (Reich *et al.*, 1999; Díaz *et al.*, 2004; Wright *et al.*, 2004). Leaf size is important for leaf energy and water balance (Parkhurst & Loucks, 1972). SLA and leaf dry matter content (LDMC) are correlated with relative growth rate (e.g. Grime *et al.*, 1988; Garnier, 1992; Reich *et al.*, 1992). Increasing leaf size decreases SLA due to the proportionally greater investment in support and structural tissue required (Milla & Reich, 2007). Plant height is correlated with competitive ability with respect to light capture (Westoby *et al.*, 2002). Leaf carbon and nitrogen concentrations indicate nutrient availability, growth rates, photosynthetic rates, and forage quality (Bryant & Reichardt, 1992). Leaf carbon isotope discrimination (LCID,  $\Delta$ ) provides an integrated measure of the concentration of  $\text{CO}_2$  at the site of carboxylation within the leaf, which in turn depends on stomatal regulation, carboxylation capacity, and mesophyll conductance (Farquhar *et al.*, 1982) and  $\delta^{15}\text{N}$  can be used to qualitatively assess resource use and partitioning (Nadelhoffer *et al.*, 1996). Considering the importance of tundra leaf traits to climate-vegetation feedbacks (Chapin, 2003), accurately forecasting their responses to climate change is critical.

Climate change in the Arctic is expected to have substantial effects on plant distribution, abundance, and biodiversity (Callaghan *et al.*, 2005). To refine ecosystem-level consequences of these changes, studies that examine species-level trait responses to environmental factors are needed (Suding *et al.*, 2008). In this paper, we present leaf growth and chemistry traits for five High Arctic vascular species across three plant communities that were artificially warmed for 16 years. The questions we asked were (i) what are the intraspecific plant trait responses to long-term elevated temperature? and (ii) are the effects of long-term warming similar to the effects of short-term warming (e.g. Henry, 1997; Henry & Molau, 1997; Arft *et al.*, 1999), especially effects observed at our study site (Jones *et al.*, 1997, 1999; Tolvanen & Henry, 2001; Welker *et al.*, 2004)? Specifically, we test the hypotheses that long-term artificial

warming increases plant height and leaf size and carbon concentration, decreases SLA, dry matter content, nitrogen concentration, and LCID and alters the  $^{15}\text{N}/^{14}\text{N}$  ratio.

## Materials and methods

### Study site

Our 2008 study was conducted in the outwash plain adjacent to Alexandra Fiord (78°53'N, 75°47'W), on the eastern coast of Ellesmere Island, Nunavut, Canada (Fig. 1). The 8 km<sup>2</sup> plain is considered a polar oasis because it is well-vegetated compared with the surrounding polar desert and semidesert landscapes. At the site, hydrologic variability strongly affects plant communities (Muc *et al.*, 1989) and soil properties (Muc *et al.*, 1994). For a more detailed description of the study site and region, see Svoboda & Freedman (1994).

### Experimental design

The ITEX is a long-term collaboration of researchers examining the effects of climate warming on Arctic and alpine tundra (Henry & Molau, 1997). The network, which began in 1990, currently includes more than 20 sites that use OTCs to conduct standardized, small-scale artificial warming (1–2 °C) experiments. The collaboration has produced several tundra-wide

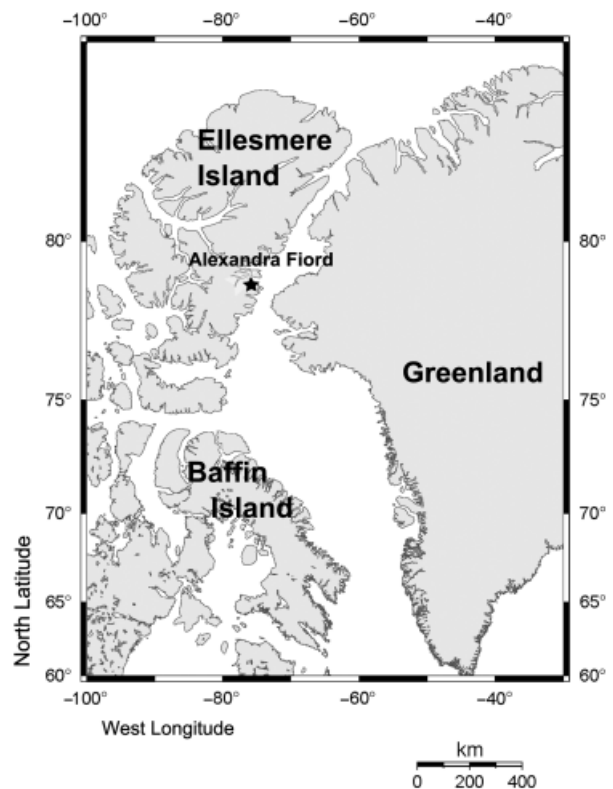


Fig. 1 Location of Alexandra Fiord (\*) on the east coast of Ellesmere Island in the Canadian High Arctic.

**Table 1** Environmental characteristics for experimental plots in three tundra plant communities at Alexandra Fiord during the 2008 growing season

Site	Treatment	Snow-free (day of year)	Moisture (% vol. water)	Nutrients ( $\mu\text{g N } 10 \text{ cm}^{-2} \text{ day}^{-1}$ )	Temperature ( $^{\circ}\text{C}$ )
Heath	CON	165 $\pm$ 1	13 $\pm$ 2	0.23 $\pm$ 0.03	<b>8.7 <math>\pm</math> 0.0</b>
	OTC	166 $\pm$ 1	12 $\pm$ 2	0.24 $\pm$ 0.05	<b>9.8 <math>\pm</math> 0.1</b>
Willow	CON	163 $\pm$ 1	18 $\pm$ 3	0.10 $\pm$ 0.03	<b>8.6 <math>\pm</math> 0.0</b>
	OTC	162 $\pm$ 1	18 $\pm$ 3	0.10 $\pm$ 0.02	<b>10.4 <math>\pm</math> 0.1</b>
Meadow	CON	165 $\pm$ 0	<b>49 <math>\pm</math> 2</b>	0.23 $\pm$ 0.07	9.0 $\pm$ 0.0
	OTC	164 $\pm$ 1	<b>44 <math>\pm</math> 2</b>	0.28 $\pm$ 0.09	Unavailable

Data are means  $\pm$  95% confidence intervals.

Significant differences ( $P < 0.05$ ) between treatments within sites are given in bold.

reviews of plant growth, reproduction, and phenology (Henry & Molau, 1997; Arft *et al.*, 1999), community composition and abundance (Walker *et al.*, 2006), and carbon flux (Oberbauer *et al.*, 2007), as well as dozens of other papers, including a Global Change Biology special issue (Henry, 1997).

The study was conducted in three plant communities that contained ITEX warming experiments (experiments were established in 1992). The communities were: Heath, dominated by evergreen shrubs; Willow, dominated by deciduous shrubs; and Meadow, dominated by wet sedges. The communities vary in snow melt timing, moisture status, soil nutrients, and temperature (Table 1). In 2008, plots were considered to be snow-free when  $>90\%$  of the ground surface was visible. Relative moisture status was measured six times during the growing season with a handheld probe (HydroSense<sup>®</sup> probe, Campbell Scientific Canada Corp., Edmonton, AB, Canada). Measurements were taken on days of year 169, 184, 198, 202, 216, and 226. Soil nitrogen flux (Willow: days 169–228; Heath: days 170–228; Meadow: days 178–228) was measured with ion exchange membranes (Plant Root Simulator<sup>™</sup> probes, Western Ag Innovations Inc., Saskatoon, Saskatchewan, Canada) and air temperature at 10 cm aboveground was monitored with weatherproof loggers from day 173 to day 226 at the Willow and Heath sites and from day 180 to day 226 at the Meadow site (HOBO<sup>®</sup> Pro Series<sup>™</sup>, Onset Computer Corp., Bourne, MA, USA).

Warmed and control plots were randomly located in each of the plant communities in 1992. OTCs made of transparent greenhouse fibreglass (SunLite<sup>®</sup> HP, Solar Components Corp., Manchester, NH, USA) passively warmed the vegetation. The OTCs were hexagonal, 0.5 m high, had inclined sides ( $60^{\circ}$ ), enclosed a surface of  $1.8 \text{ m}^2$  (although vegetation sampling was from the central  $1 \text{ m}^2$ ), and were left in place year round. Equal numbers of OTC and control (CON) plots were established in each community (Heath = 18, Willow = 10, Meadow = 10). During the winters of 1992–2008, snow cover in the lowland was deep enough to avoid snow-trapping by the OTCs, except for 1994. The OTCs have not affected spring snow melt timing (G. H. R. Henry, unpublished results). Artificial warming can cause other unintended side effects, such as increased temperature extremes; altered light, moisture, and gas concentrations; and problems with access by insects and other animals (Kennedy, 1995a,b; Marion *et al.*, 1997; Shen & Harte, 2000). However, the ITEX OTC approach has been validated as an analogue of regional

climate warming (Hollister & Webber, 2000) and remains the preferred method of passively warming tundra ecosystems (Wookey, 2008).

#### Leaf sampling and measurements

Leaves were harvested from July 22 to 25, 2008 (days 204–207) to coincide with maximum aboveground biomass. Five leaves of five key species were collected from all plots, where available (minimum of 50 leaves per species per treatment level per site). Plant species were relatively common in the site(s) from which they were harvested (see Supporting Information Table S1). Two species were sampled at all three sites, whereas three other species were sampled at one site (Table 2). To harvest individual leaves, five coin envelopes were haphazardly dropped into each plot. We selected the closest plant to each envelope that met a narrow set of phenological, reproductive, and vegetative criteria. For example, all *Cassiope* leaves were harvested from main branches that had two immature fruit. This standardization reduced the potential for sampling error because it limited within-plot variability.

Plant height (ground surface to tip of selected leaf) was recorded before harvesting. Stems were removed with a razor then leaves were immediately wet weighed and scanned (CanoScan LiDE 90, Canon Canada Inc., Mississauga, ON, Canada). For *Cassiope*, only photosynthetically active (green) leaves were included. Leaves were immediately dried at about  $40^{\circ}\text{C}$  for 72 h and then at  $60^{\circ}\text{C}$  for 24 h in the field. Before reweighing, leaves were dried at  $70^{\circ}\text{C}$  for 72 h in the lab. Data were collected for four leaf growth traits: height, size, SLA (area per unit dry mass), and LDMC (dry- to fresh-mass ratio).

To prepare the leaves for nutrient analyses, they were ground at  $4.0 \text{ m s}^{-1}$  for 20 s with a homogenizer (FastPrep FP120, Thermo Fisher Scientific Inc., Waltham, Massachusetts, USA). They were analyzed for  $\delta^{15}\text{N}$  ( $^{15}\text{N}/^{14}\text{N}$  ratio), LCID, leaf nitrogen concentration (%), and leaf carbon concentration (%) on a stable isotope ratio mass spectrometer (Delta Plus, Thermo Fisher Scientific Inc.) at the University of British Columbia's Pacific Centre for Isotopic and Geochemical Research (PCIGR, <http://pcigr.eos.ubc.ca>). LCID was calculated according to Farquhar *et al.* (1989). The carbon isotope composition of air  $\text{CO}_2$  ( $\delta_{\text{air}}$ ) was assumed to be  $-8.0\%$ .

**Table 2** Key plant species sampled from the three tundra plant communities in 2008

Scientific name	Family	Growth form	Sites	Selection criteria
<i>Dryas integrifolia</i> Vahl.	Rosaceae	Evergreen shrub	Heath, Willow, Meadow	Leaf = growth in 2008; mat >25 cm <sup>2</sup> ; flowering stem = mature flowers or more advanced, height >50 mm
<i>Salix arctica</i> Pall.	Salicaceae	Deciduous shrub	Heath, Willow, Meadow	Leaf = mature and flat, second from branch tip; branch = vegetative
<i>Cassiope tetragona</i> (L.) D. Don	Ericaceae	Evergreen shrub	Heath	Branch = on a main stem, new leaves in 2008; flowers = 2 immature
<i>Oxyria digyna</i> (L.) Hill	Polygonaceae	Forb	Willow	Leaf = mature; flowering stem = mature flowers or more advanced, height >75 mm
<i>Eriophorum angustifolium</i> ssp. <i>triste</i> Honck.	Cyperaceae	Sedge	Meadow	Leaf = oldest, >30 mm; no inflorescence stalk

### Statistical analyses

We used *t*-tests and Mann–Whitney tests to assess the effect of warming on all traits for all species. Some variables were transformed (log or reciprocal) to improve the normality of the residuals. Mann–Whitney tests were used when transformations failed to sufficiently improve the fit to a normal distribution. The effect of site for *Dryas* and *Salix* was tested with two-way ANOVAS. Again, transformations (log or reciprocal) were often necessary. For all analyses, we used R version 2.5.1 (R Development Core Team, 2007).

### Results

2008 was a typical year for snow cover, snow melt timing, and temperature (authors' personal observation). The three plant communities were warmed by 1–2 °C from day 173/180 to 226 (Table 1). Snow-free dates, moisture status, and nutrient flux at the Heath and Willow sites were not affected by warming. In 2008, snow melted about 3 days earlier at the Willow site than the Heath and Meadow sites. At the Meadow site, the soil of warmed plots was drier than the soil of control plots. The Heath site was slightly drier than the Willow site, whereas the Meadow site was the wettest during the 2008 growing season. Nutrient flux was similar at the Heath and Meadow sites, and lower at the Willow site.

Long-term artificial warming affected five of eight leaf growth and chemistry traits (Figs 2 and 3). For *Cassiope*, leaf size and plant height increased in response to warming; SLA, leaf carbon concentration, and LCID decreased. For *Salix*, warming increased leaf size and plant height at the Heath and Willow sites, and decreased SLA at the Willow site. The effect of site was significant for all three of these variables (two-way ANOVAS, *df* = 2, 70, *P* < 0.05). For *Dryas*, warming increased leaf size at the Heath and Willow sites, increased plant height at the Heath site, and decreased LCID at the Willow site. The effect of site was significant

for *Dryas* for leaf size and plant height (two-way ANOVAS, *df* = 2, 66, *P* < 0.05). There were no significant warming × site interactions for *Salix* or *Dryas*. Warming increased leaf size and plant height for *Oxyria* and decreased leaf carbon concentration for *Eriophorum*. Warming did not affect leaf nitrogen concentration, δ<sup>15</sup>N, or LDMC for any species. Mean values for all traits and species are presented in the Supporting Information (Table S1).

### Discussion

#### Trait responses to long-term warming

The most common responses to long-term warming were larger leaf size and increased plant height. However, the responses of both traits varied among sites: 11 of 12 species traits were affected at the Heath and Willow sites, whereas none of the traits were affected at the Meadow site. Short-term warming responses were also site-specific: *Salix* traits were responsive at Willow but not at Meadow (Jones *et al.*, 1999). Of the three sites, Meadow has the highest plant cover and biomass, as well as the tallest mean plant height, whereas the Heath and Willow sites had bare ground patches and more open cover (Walker *et al.*, 2006). Plants at the Heath and Willow sites are able to grow larger and taller with less competition for space compared with the Meadow site. Biome-wide predictions of trait responses to warming must, therefore, consider the influence of habitat heterogeneity.

SLA responses were also site-specific. *Cassiope* and *Salix* are the most common species at the Heath and Willow sites (with percent covers of 40% and 50%, respectively). Relative to the other sites, *Cassiope* grows the largest leaves at Heath, as does *Salix* at Willow. Warming led to a decrease in SLA for *Cassiope* at Heath and for *Salix* at Willow, likely because larger leaves

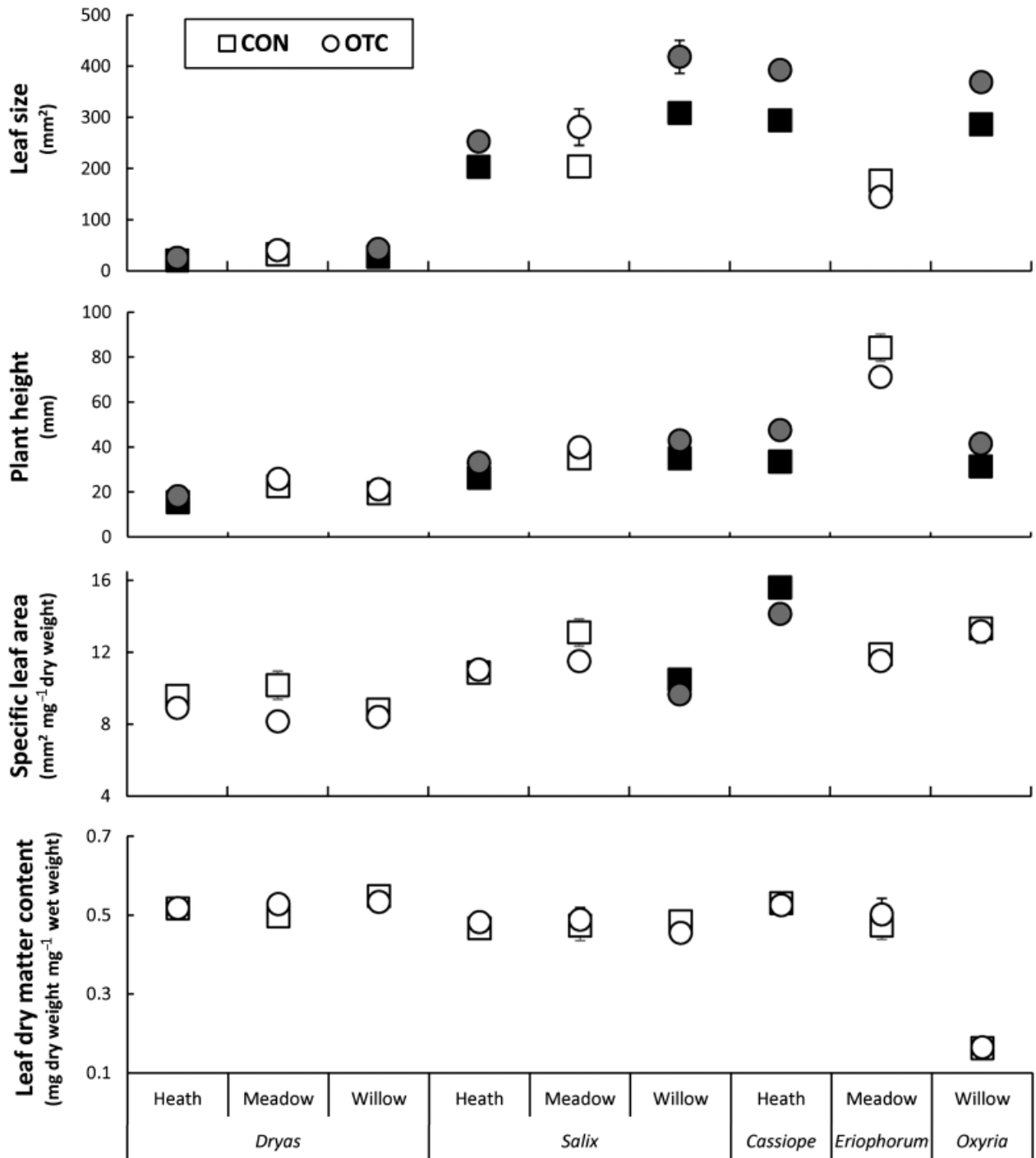


Fig. 2 Growth trait responses to warming. Data are means  $\pm$  standard errors. Significant differences between CONs and OTCs are represented by closed symbols. CON, controls; OTC, open-top chambers.

require substantial structural investments (Milla & Reich, 2007).

Warming affected the leaf carbon traits; leaf carbon concentration decreased for *Cassiope* and *Eriophorum*. Lower leaf carbon may be due to increased early season allocation belowground to roots (Sullivan & Welker,

2005) as plants respond to warming by accelerating their phenology (Arft *et al.*, 1999). Warming also decreased LCID for the two evergreen shrub species, *Cassiope* and *Dryas* (at the Willow site), indicating time-integrated lower CO<sub>2</sub> concentrations at the site of carboxylation (Farquhar *et al.*, 1982). There are two

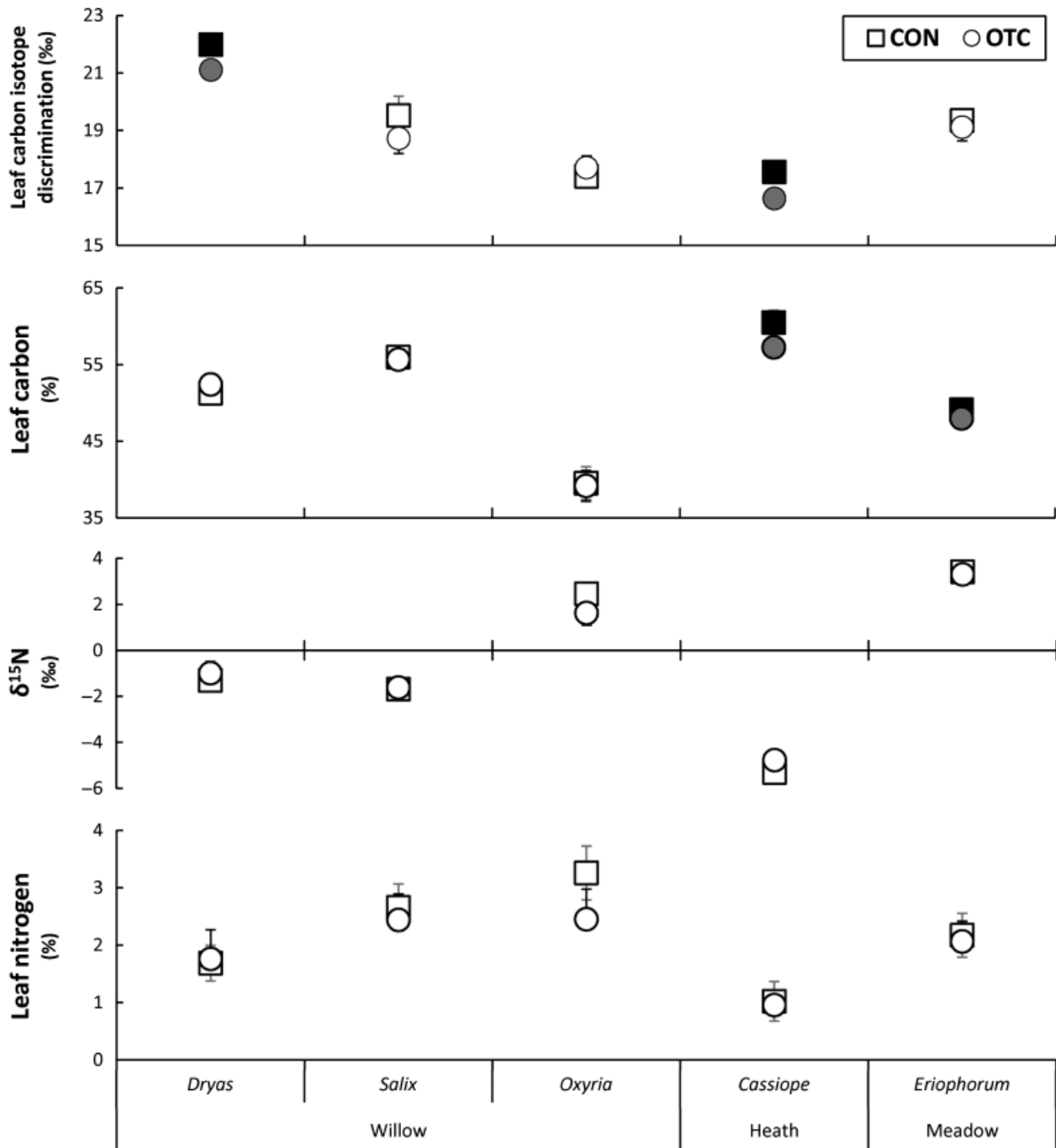


Fig. 3 Leaf chemistry responses to warming. Data are means  $\pm$  standard errors. Significant differences between CONs and OTCs are represented by closed symbols. CON, controls; OTC, open-top chambers.

possible contributions to this shift in LCID. First, higher temperatures under the warming treatments may have led to increased photosynthetic rates and higher water use efficiency (Day *et al.*, 2008). Second, OTCs elevate temperature, which may lead to a small decrease in the relative humidity of the air within the chambers (Marion *et al.*, 1997). Warmer leaves and drier air both increase vapour pressure deficit (VPD), which

is the force that drives water out of the leaves and into the atmosphere (Marion *et al.*, 1997). Plants may respond to increased VPD with lower stomatal conductance, which in turn leads to lower CO<sub>2</sub> at the site of carboxylation and reduced isotopic discrimination (Farquhar *et al.*, 1989). However, Jones *et al.* (1999) found no difference in stomatal conductance of *Salix* leaves in the warmed and control plots at the Willow and

Meadow sites. Understanding the relative importance of these mechanisms in response to warming will require further research because the effects of climate warming and OTCs on water relations and LCID are complex (Marion *et al.*, 1997). As well, whether climatic warming in the High Arctic will be accompanied by a similar decrease in relative humidity is an open question (Kattsov *et al.*, 2005; Anisimov *et al.*, 2007).

Leaf nitrogen concentration and  $\delta^{15}\text{N}$  were unaffected by warming. Tundra plant  $\delta^{15}\text{N}$  values typically vary from +2‰ (sedges) to -8‰ (evergreen shrubs) as plants competitively partition nitrogen at both the species- and plant functional type-levels (Nadelhoffer *et al.*, 1996). Interpretation of  $\delta^{15}\text{N}$  values remains challenging because the  $^{15}\text{N}/^{14}\text{N}$  ratio simultaneously assesses the contributions of multiple factors: N sources, rooting depth, mycorrhizal associations, and the forms of N taken up (Evans, 2001). Our results indicate that while species appear to have important differences in their N nutrition, long-term warming does not cause a dramatic shift in the pool of N that Arctic plant species use.

Plant functional types (PFTs) are the product of grouping species into categories based on their growth form, as well as other characteristics. The four PFTs for Arctic vascular plants are evergreen shrubs, deciduous shrubs, forbs, and graminoids. In this study, we sampled at least one species from each of the four Arctic PFTs. We found that the evergreen and deciduous shrubs responded most frequently to warming, while the forb and graminoid responded less frequently. Similarly, in a biome-wide synthesis, Walker *et al.* (2006) found that shrubs were most responsive to 4–6 years of warming. The increased height and larger leaves of certain PFTs, particularly the evergreen and deciduous shrubs, has led to the decreased cover of shade-intolerant cryptogam species in many tundra ecosystems (Walker *et al.*, 2006). Shifts in the traits of the PFTs in response to warming will change the competitive balance and ultimately translate into community change (Arft *et al.*, 1999).

We encourage the development of a trait-based approach for classifying Arctic plant species, rather than the continued reliance on the PFT categories. Arctic plants within each PFT do not necessarily respond similarly to warming as Arctic plants are individualistic (Chapin & Shaver, 1985). In our study, we found evidence in support of this; the responses of the evergreen shrubs, *Dryas* and *Cassiope*, were consistent for many, but not all of the traits. Given the variability of responses within each PFT, we suggest that traits be given more prominence in classifying Arctic vegetation. For many tundra species, trait data already exist (e.g. Chapin *et al.*, 1996; Arft *et al.*, 1999).

#### *Comparison of short- and long-term responses*

Our work indicates that plant growth traits may not be subject to internal resource depletion. Plant growth responses were still apparent after almost two decades of elevated temperatures. Arft *et al.*'s (1999) findings of transitory leaf growth responses to 4 years of warming were not supported by our work. Four species (*Cassiope*, *Dryas*, *Oxyria*, and *Salix*) from Alexandra Fiord were included in their meta-analysis and grew larger due to short-term warming. Here, we have shown that all four species sustained their increased leaf size and plant height in response to long-term warming. Our growth trait responses to long-term warming match the responses from several shorter-term experiments, including 2, 3, 3, and 5–7 year studies (Jones *et al.*, 1997, 1999; Suzuki & Kudo, 2000; Hollister *et al.*, 2005, respectively). Our study indicates that height and leaf size responses can be sustained over the long-term and are therefore not transitory. Moreover, this suggests that the results of some short-term growth trait studies may be indicative of sustained plant responses to longer-term warming.

A comparison of the short- and long-term effects of warming on SLA and LDMC is difficult, owing to a lack of short-term data. While other authors have found that SLA is rarely responsive to warming (Parsons *et al.*, 1994; Wookey *et al.*, 1995; Suzuki & Kudo, 1997), only a small number of species have been examined so far. To the best of our knowledge, no other study has examined LDMC in Arctic plants.

Leaf chemistry trait responses to warming have diminished over time at our site. Using similar designs and species, two previous studies examined leaf carbon concentration, leaf nitrogen concentration, leaf C/N, and LCID responses to warming at Alexandra Fiord. After 5 years of warming, 39% of leaf chemistry traits were affected (13/33 traits, 3 traits  $\times$  5 species  $\times$  1–3 tissue types; Tolvanen & Henry, 2001), after 9 years, 15% were affected (6/40 traits, 4 traits  $\times$  5 species  $\times$  1–2 tissue types  $\times$  3 sites; Welker *et al.*, 2004), and after 16 years, 20% (4/20 traits, 4 traits  $\times$  5 species) were affected. Based on the proportion of significant responses observed in these studies, it appears that leaf chemistry trait responses to warming decline over time.

The leaf chemistry responses match the results of several shorter-term studies from other polar sites (Sullivan & Welker, 2005; Day *et al.*, 2008), but differ from earlier work at our site. We found decreases in leaf carbon concentration in two species and no effect on leaf nitrogen concentration, whereas Tolvanen & Henry (2001) and Welker *et al.* (2004) found no effect on leaf carbon and decreases in leaf nitrogen.

We have found that (i) leaf size and height of several High Arctic plant species are sensitive to long-term

environmental change, (ii) growth trait responses can be site-specific, and (iii) short-term growth trait responses can be used to forecast long-term responses to warming. Over the last several decades, the Arctic has been warming rapidly (Anisimov *et al.*, 2007; Hudson & Henry, 2009). It is worth noting that the experimental responses that we have observed here are consistent with observations by Inuvialuit on Banks Island in the Canadian Arctic Archipelago, who report that in response to recent ambient warming, plants are becoming noticeably 'bigger, fresher, and greener' (Riedlinger, 2001). In a warming Arctic, plants will show multifaceted responses, often including taller shoots with larger leaves. Plant traits warrant further study because of their effects on climate-vegetation feedbacks.

## Acknowledgements

Funding was provided by the Government of Canada International Polar Year program, NSERC, ArcticNet, the Garfield Weston Foundation, and the Northern Scientific Training Program. We thank the Polar Continental Shelf Program and the Royal Canadian Mounted Police for logistical support. Will Brown, Eric Lamb, Steve Sciliano, and Sarah Trefry assisted in the field, and Kathy Gordon at the UBC PCIGR conducted the stable isotope analysis.

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### Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Table S1.** Means  $\pm$  95% confidence intervals for cover, growth traits and leaf chemistry traits for five Arctic tundra plant species in three plant communities at Alexandra Fiord, Nunavut, Canada. For several variables, not all species were sampled in all plots. For these cases, the reduced number of plots sampled are shown in brackets.

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