Global Change Biology

Global Change Biology (2011) **17**, 1611–1624, doi: 10.1111/j.1365-2486.2010.02319.x

Changes in high arctic tundra plant reproduction in response to long-term experimental warming

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Abstract

We provide new information on changes in tundra plant sexual reproduction in response to long-term (12 years) experimental warming in the High Arctic. Open-top chambers (OTCs) were used to increase growing season temperatures by 1–2 °C across a range of vascular plant communities. The warming enhanced reproductive effort and success in most species; shrubs and graminoids appeared to be more responsive than forbs. We found that the measured effects of warming on sexual reproduction were more consistently positive and to a greater degree in polar oasis compared with polar semidesert vascular plant communities. Our findings support predictions that long-term warming in the High Arctic will likely enhance sexual reproduction in tundra plants, which could lead to an increase in plant cover. Greater abundance of vegetation has implications for primary consumers – via increased forage availability, and the global carbon budget – as a function of changes in permafrost and vegetation acting as a carbon sink. Enhanced sexual reproduction in Arctic vascular plants may lead to increased genetic variability of offspring, and consequently improved chances of survival in a changing environment. Our findings also indicate that with future warming, polar oases may play an important role as a seed source to the surrounding polar desert landscape.

Keywords: Arctic tundra, climate change, long-term experimental warming, open-top chamber, reproductive biomass, seed germination, sexual reproduction, vascular plant reproductive effort and success

Received 8 June 2010 and accepted 4 July 2010

Introduction

Arctic ecosystems are strongly constrained by temperature (Billings & Mooney, 1968). As a result, even relatively small increases in temperature associated with climate warming are expected to have local and global implications greater than at other latitudes (Maxwell, 1992; IPCC 2001; ACIA 2004). Increases in air and soil temperatures predicted for high latitudes will contribute to decreases in the extent of regions underlain by permafrost (Anisimov & Nelson, 1997; ACIA 2004) and enhanced rates of nutrient cycling (Nadelhoffer *et al*., 1992; Eviner & Chapin, 2003). In the High Arctic, changes in nutrient mineralization rates will affect plant nutrient availability and subsequent uptake (Nadelhoffer *et al*., 1997; Rolph, 2003). Warming is also expected to advance spring snow melt, extending the growing season, advancing plant phenology and potentially enhancing plant reproductive success (RS) (Welker *et al*., 1997; Arft *et al*., 1999; Post *et al*., 2009). Short-term experimental warming studies have already demonstrated increases in vegetative biomass (Savile, 1972; Chapin *et al*., 1995; Arft *et al*., 1999; Walker *et al*., 2006) and, more recently, some long-term studies have shown increased biomass and changes in biodiversity in response to ambient warming, as well as an extended growing season (Hudson & Henry, 2009; Hill & Henry, 2010). These observations may indicate that with continued warming we can also expect enhanced tundra plant sexual reproduction (Arft *et al*., 1999).

In the High Arctic, primary constraints on plant reproduction include low air and soil temperatures, a restricted growing season and low soil nutrient availability (Billings & Mooney, 1968; Billings, 1987), limitations that have also been noted in Antarctica (Convey, 1996). In the Canadian High Arctic, bare ground predominates: approximately 49% of the land area ($\sim 1254 \times 10^6$ km^2), the majority of which is in the Arctic Archipelago, has <50% plant cover (Walker *et al*., 2005). Polar desert, the dominant High Arctic biotope, has <5% plant cover (Bliss, 1988). Polar oasis (PO), another High Arctic biotope, is characterized by ameliorated growing conditions that result in nearly continuous

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plant cover (Bliss, 1977; Freedman *et al*., 1994; Walker *et al*., 2005); however, this habitat comprises only about 6% of the Canadian Arctic Archipelago (Bliss, 1977; Freedman *et al*., 1994).

Changes in temperature associated with climate warming are expected to affect tundra plant sexual reproduction (Wookey *et al*., 1993; Arft *et al*., 1999; Welker *et al*., 2005), which will alter plant demographics (Walker & Chapin, 1987; Welker *et al*., 1997; Jones & Henry, 2003) and potentially the extent and rate of colonization (Arft *et al*., 1999; Bliss & Gold, 1999; Molau & Larsson, 2000; Larsson, 2002; ACIA 2004). As melting glaciers continue to recede and both growing conditions and colonization potential are enhanced, climate-mediated changes in tundra plant sexual reproduction, particularly in polar oases, will play an important role as a seed source for the surrounding barren polar desert landscape (Bliss, 1958; Svoboda & Henry, 1987). These changes in plant community dynamics will have important local and global implications, including increased forage availability for primary consumers in the Arctic, changes in permafrost thaw, and an altered global carbon budget, as increased plant cover affects both permafrost and carbon sequestration (ACIA 2004; Post *et al*., 2009). Changes in sexual reproduction of Arctic vascular plants may also have implications for genetic variability of offspring, including improved chances of survival in a changing environment (Steltzer *et al*., 2008; Stöcklin *et al*., 2009).

Environmental constraints affect plant reproductive effort (RE) – the investment in reproductive tissues and success (RS) – the final outcome of that investment (Molau, 1993; Molau & Shaver, 1997). Historically, asexual reproduction, or vegetative expansion, has played an important role in High Arctic plant community dynamics (Molau, 1993; Chambers, 1995; Molau & Shaver, 1997); increasingly, direct and indirect observations of plant response to warming indicate the need to understand changes in sexual reproduction. For example, in response to short-term warming observed increases in vegetative biomass (Savile, 1972; Arft *et al*., 1999; Rustad *et al*., 2001; Walker *et al*., 2006) may indicate the improvement of growing conditions and nutrient reserves that precede enhanced RE and RS. Indications are that temperature-driven restrictions on sexual reproduction of High Arctic vascular plants diminish with increased growing season temperatures; for example, indirect observations of increased seed weight, germinability and frequency and degree of seed set in response to warming (Wookey *et al*., 1993; Dormann & Woodin, 2002; Welker *et al*., 2005). However, the question of long-term effects remains unanswered.

The emergence of clear patterns of plant response to environmental perturbations may take place over a period of decades, and can be difficult to detect (Tilman, 1982; Epstein *et al*., 2004). Despite rapid rates of change forecasted for the Arctic, changes in active layer depth and nutrient mineralization rates, for example, are inherently limited (Nadelhoffer *et al*., 1997; Grogan & Chapin, 2000; Rolph, 2003). Nonetheless, experimental and observational studies have provided preliminary evidence that RE and RS are strongly influenced by temperature (Shaver & Kummerow, 1992; Henry & Molau, 1997; Bliss & Gold, 1999), and that both the direction and degree of plant response to warming are influenced by site conditions (Arft *et al*., 1999; van Wijk *et al*., 2004; Hollister *et al*., 2005a), species-specific responsiveness (Chapin *et al*., 1996) and time (Callaghan *et al*., 1999; Hartley *et al*., 1999; Epstein *et al*., 2000).

Here we investigate the effect of long-term experimental warming on High Arctic vascular plant RE (flower biomass) and RS (seed biomass, cumulative/rate of/peak germination) along a soil moisture and altitude gradient. We hypothesize that long-term warming has enhanced RE and RS relative to controls, producing flowers with higher biomass, and seeds that are heavier, germinate faster and have greater overall germination. However, we also expect that enhanced RE and RS will be sensitive to species-specific characteristics and site conditions: some species will not be as responsive to warming as others, and responses will vary by site. This study provides much needed information about long-term vascular plant response to experimental warming in the High Arctic, and the importance of habitat to measured responses.

Materials and methods

Site description

Our research was conducted at Alexandra Fiord, a coastal lowland situated on east-central Ellesmere Island (78°53′N, 75°55′W) (Fig. 1 inset). Our study sites included warming treatments distributed throughout six different vascular plant communities, located within a lowland PO and upland polar semidesert (PSD) at Alexandra Fiord. Warming was achieved using open-top chambers (OTCs) that passively warm air and soil temperatures by 1–3 °C during the growing season (Marion *et al*., 1997; Hudson & Henry, 2010), which is within general circulation model predictions for the Arctic (Maxwell, 1992; ACIA 2004). The six study sites varied by soil composition, soil moisture regime and plant community composition. Basic features of each site are given in Table 1, and are described in detail by others (see Muc *et al*., 1989, 1994; Henry *et al*., 1990; Freedman *et al*., 1994; Stenström *et al*., 1997; Walker *et al*., 2008; Hudson & Henry, 2010). The combination of lower elevation (0–100 m) and local topography in the PO (Fig. 1) contribute to favourable climatic conditions and slightly warmer temperatures, resulting in an extended growing

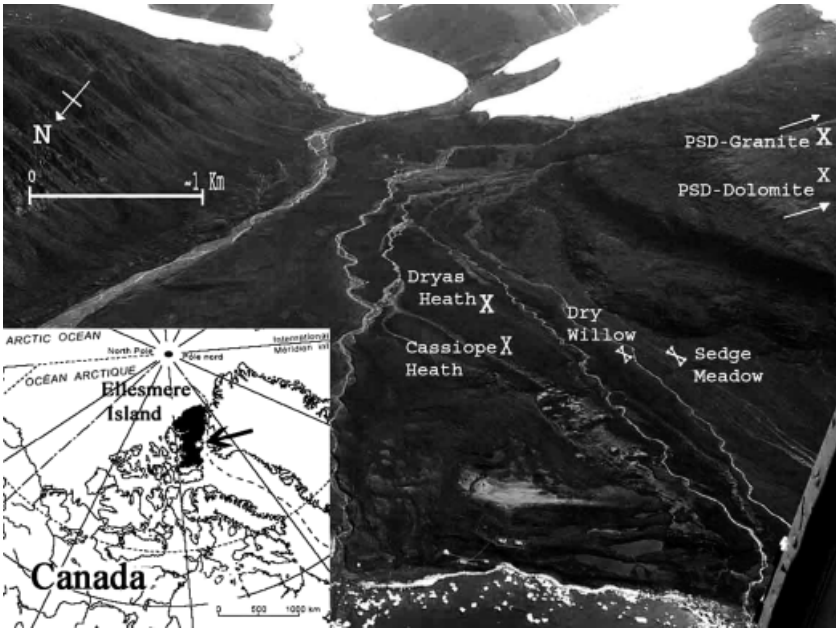

Fig. 1 Study site location (inset map) and aerial view of the study sites at Alexandra Fiord, east-central Ellesmere Island, Nunavut, Canada (78°53′N, 75°55′W). Sites are labelled with white Xs and abbreviated site names. The lowland polar oasis sites include the central cluster of Sedge Meadow, *Cassiope* Heath, *Dryas* Heath and Dry Willow sites. The upland polar semidesert (PSD) sites include PSD-Granite and PSD-Dolomite. Distance from the coast to the tip of the glacier is ~3 km (Photo: G. Henry).

season (24 h photoperiod light; ca. 65–80 days). These conditions permit the establishment of relatively dense vascular plant communities, with varying proportions of dwarf shrubs, forbs and graminoids, in which plant species diversity and productivity are higher than the surrounding polar desert landscape (Freedman *et al*., 1994).

Of the four sites within the PO, Sedge Meadow is dominated by graminoids (mostly sedges), soils are hydric, overlain by a thick organic layer and soil pH is 6.6–5.9 at greater depths (Walker *et al*., 2008). The *Cassiope* and *Dryas* Heath sites have similar species diversity and are dominated by evergreen dwarf shrubs, the former being *Cassiope tetragona* (L.) D. Don, and the latter *Dryas integrifolia* Vahl. Soil moisture regimes in both sites are mesic, soils are coarse mineral overlain by a thin organic layer (3–5 cm) and pH is ca. 4.9–5.4 (Walker *et al*., 2008). The plant community at Dry Willow is dominated by *Salix arctica* Pall., a deciduous dwarf shrub, and various graminoid and forb species, and generally has the highest species diversity of the four PO sites. Soils at Dry Willow are sandy–silty textured, with mesic–xeric soil moisture, pH 5.2–4.6 (Walker *et al*., 2008).

The two PSD sites are located ca. 500 m upland and southwest from the PO (Fig. 1). These sites are representative of a transition to polar desert: soil moisture conditions are largely xeric, but sufficient for cryptogamic crust development and associated sparse vascular plant communities. The growing season here tends to be shorter relative to the neighbouring PO, commencing later and finishing earlier (ca. 50–60 days; Bliss *et al*., 1994). These two sites are largely distinguished from each other by differences in soil type, which is reflected in pH and plant community composition: PSD-Granite is dominated by granitic parent material (pH 4.9–5.5) and PSD-Dolomite by dolomitic parent material (pH ca. 7.9) (Walker *et al*., 2008). This variation in soil type affects water- and nutrient-holding capacity, which in turn affects plant community composition and cover (ca. 5–40%, Table 1).

Experimental design

In 1992, warmed and control plots (1 m^2) were established at each of the four study sites in the PO at Alexandra Fiord, along a soil moisture gradient. The study sites in the PSD were established in 1993. Warming was achieved using OTCs, joined panels of 0.5 m high Sun-Lite HP® (1.0 mm thickness) fibreglass, which have a high solar transmittance in the visible wavelengths (86%) and low transmittance in the infrared range (<5%) (Marion *et al*., 1997). Forming a hexagon, panels were inclined to create a top diameter of 1.5 m, with a central monitoring area of 1 m^2. Some of the standard OTCs at the PSD-Dolomite site were replaced in 2000 (after 8 years) with smaller models (30 cm in height, 1 m diameter), in order to minimize wind damage; the smaller OTCs have a reduced monitoring area of 0.8 m^2; see Marion *et al*. (1997) and Hollister & Webber (2000) for detailed analysis and discussion of OTC design and effects on the physical environment. At each site, plots were located around randomly chosen individuals of the dominant plant species. Warming treatments were randomly assigned to plots (n = 6–10) at each site, with an equal number of warming and control plots per site. The value of n varied somewhat, depending on availability of plant species and samples (sample sizes are reported in Table 2).

Table 1 Generalized descriptions of study sites at Alexandra Fiord

Site characteristics	Polar oasis				Polar semidesert	
Plant community/site	Sedge Meadow	*Cassiope* Heath	*Dryas* Heath	Dry Willow	PSD-Granite	PSD-Dolomite
Plant cover	High (+ 100%)	High (80–100%)	High (80–100%)	High (80–100%)	Low (10–40%)	Low (5–30%)
Dominant growth forms and species	Graminoids, sedges (*Carex* spp.), mosses	Evergreen dwarf shrubs (*Cassiope tetragona*), forbs, mosses	Deciduous dwarf shrubs (*Dryas integrifolia*), graminoids	Deciduous dwarf shrubs (*Salix arctica*), graminoids, forbs	Dwarf shrubs (*Salix arctica, Dryas integrifolia*)	Dwarf shrubs (*Salix arctica, Saxifraga oppositifolia, Dryas integrifolia*), graminoids, forbs
Soil moisture	Hydric	Mesic	Mesic	Mesic–Xeric	Xeric	Xeric
Substrate	Thick organic layer overlying mineral soils	Glacial outwash sands and gravels	Glacial outwash sands and gravels	Glacial outwash sands and gravels	Granitic till	Weathered dolomite
Soil pH	6.6–5.9	4.9–5.4	ca. 5 (similar to *Cassiope* Heath)	5.2–4.6	4.9–5.5	ca. 7.9

Site descriptions extracted from Muc *et al.* (1994, 1989) and Walker *et al.* (2008).

Table 2 Sample sizes for reproductive effort (RE) and success (RS) of target species by site, showing control (C) and warming (W) treatment values; RE represents flower (F) biomass, RS seed (S) biomass and germination (G)

	Sedge Meadow			*Cassiope* Heath			*Dryas* Heath			Dry Willow			PSD-Granite			PSD-Dolomite		
	RE	RS		RE	RS		RE	RS		RE	RS		RE	RS		RE	RS	
Species	F	S	G	F	S	G	F	S	G	F	S	G	F	S	G	F	S	G
Dryas integrifolia	C4W2	C4W4	C6W5	C6W6	C6W6	C6W6	C6W6	C4W4	C6W6	C6W6	C4W3	C6W4						
Salix arctica	C4W2		C6W4	C6W6	C6W4	C6W5	C6W6		C6W6	C6W6	C4W4	C5W5	C6W6	C4W4	C3W3	C6W5	C3W4	C3W3
Papaver radicatum										C6W6	C4W4	C6W5						
Oxyria digyna										C6W6	C4W4	C6W6						
Festuca brachyphylla										C6W6	C4W4	C6W6						
Eriophorum angustifolium	C6W6		C7W7				C6W6	C4W4	C6W6									
Luzula arctica, L. confusa				C6W6		C6W6	C6W6		C6W6	C6W6	C4W4	C3W3						
Carex fuliginosa	C6W6	C4W3	C6W5				C6W4	C4W4	C6W6									

Field measurements

The primary criterion for selecting target species was the propensity to reproduce by seed. All species selected for this study reproduce sexually, although species-specific variability (Grime, 1977; Billings, 1987) and site-specific differences (Bliss, 1956; Grime, 1977) are inherent. Secondary selection criteria included abundance, site distribution and growth-form, allowing for as wide a range as possible to be incorporated (Arft *et al*., 1999). Target species used in this study are as follows: *D. integrifolia* Vahl., *S. arctica* Pall., *Papaver radicatum* Rothb., *Oxyria digyna* L. (Hill), *Luzula confusa* Lindeberg, *Luzula arctica* Blytt, *Festuca brachyphylla* Schult., *Eriophorum angustifolium* subsp. *triste* (Th. F.) Hultén (hereafter *E. angustifolium*), and *Carex fuliginosa* Schkuhr subsp. *misandra* (R.Br.) Nyman (hereafter *C. fuliginosa*). Detailed descriptions of target species are provided in Aiken *et al*. (1999) and Porslid & Cody (1980).

Plant sexual reproduction was measured as (a) investment in flowers and (b) and the outcome of that investment, referred to, respectively, as RE and RS (Molau, 1993; Molau & Shaver 1997). Flower biomass of the target species was harvested at peak production, between late July and early August 2004, from warmed and control plots in each of the six experimental sites at Alexandra Fiord. Two flower biomass subsamples were collected from different individuals whenever possible, and combined in labelled paper envelopes, but samples remained separated by target species, plot ($n = 1$–10), treatment (control vs. warming) and site (note that in all cases identification of individuals was not genetically based). In *S. arctica*, female flower biomass (current year catkin) was calculated without photosynthetic bract material. Seed harvests took place as close to the end of the growing season as possible (mid-August 2004), and seeds were harvested directly from parent plants in control and warmed plots, within each of the six vascular plant communities. Senescent inflorescences with seeds from two individuals of each target species were collected and combined in labelled paper envelopes, but samples remained separated by species, plot ($n = 1$–10), treatment (control vs. warming) and site. Biomass samples were air-dried in the field laboratory, and then oven-dried at 65 °C for 48 h just before weighing. Dried biomass samples were kept in desiccators until weighed. Seeds used in germination trials were air dried for 1 week in the field laboratory (~25 °C), then placed in cold storage at approximately 1 °C for 2 weeks, and afterwards exposed to a 1-month stratification period at −20 °C to simulate winter conditions (Baskin & Baskin 1998).

Seed biomass values were obtained by subsampling approximately 50 seeds per sample packet (by target species, plot, treatment and site); since subsampling priority was given to germination trials, corresponding seed biomass values were occasionally missing (Table 2), owing to insufficient quantities of surplus seed. Seed biomass samples included any attached protective material or dispersal mechanisms, such as awns or perigyna, with the exception of *Luzula* spp., in which perigyna were excluded. Biomass values were obtained using an analytical balance (accuracy ± 1 μg).

Snow melt across all sites was recorded as the day when a plot was 95% snow-free. Plots in the PO lowland were visited approximately daily, but only typically once per 3 days in the PSD.

Germination experiments

Subsamples of approximately 50 seeds were removed from sample packets, thereby representing a mixture of two harvested inflorescences (different individuals) per species, plot, treatment and site. Seeds were placed onto moist filter paper in 90 mm diameter Petri dishes; each Petri dish, containing one subsample of seeds, represented one species per plot, treatment and site (i.e. total seeds per Petri dish = ~50 seeds per species/plot/treatment/site). Seeds easily identified as lacking endosperm upon visual inspection were excluded (see Welker *et al*., 1997 for rationale). In an attempt to represent ideal germination conditions or 'potential' RS (Baskin & Baskin 1998; Graae *et al*., 2008), seeds were germinated in a greenhouse with temperatures ranging from 20 to 27 °C, and 24 h photoperiod full spectrum light (600 W, 90 000 lumens). Germination trials ran for 35 days (Baskin & Baskin 1998), during which time filter paper was kept moist and Petri plates were rotated to minimize systematic bias. Petri plates were checked a minimum of every 3 days for germination and germinants were discarded after being counted.

Four different aspects of RS were investigated: (1) seed biomass, (2) cumulative germination, (3) germination rate and (4) peak germination. The inclusion of three different measures of germination represents an effort to provide a more comprehensive view of germination response (Brown & Mayer 1988). Cumulative germination (%*G*) represents the germination potential of a given growing season, and was calculated as the total number of seeds germinating (G_T) from a given sample (i.e. Petri dish) during the germination trial period (35 days), divided by the total number of seeds (S_T) within a Petri dish, and then multiplied by 100: $\%G = (G_T/S_T) \times 100$. Germination rate was calculated using a modified Timson's Index (TI_m):$\Sigma G/t$ (Timson, 1965; Ungar, 1996). Timson's Index is routinely applied in the calculation of germination rate (Brown & Mayer, 1988; Baskin & Baskin, 1998), while the modification allows for measurement frequencies that occur less than daily (Khan & Ungar, 1984). This value was calculated by first obtaining average percent germination per 3-day interval, which was the maximum frequency that germinants were counted and removed from Petri plates. These averages were then summed as a progressive total of daily cumulative germination (ΣG) over the number of measurement increments in the trial period (Khan & Ungar, 1984), which in this study was 12 (i.e. eleven 3-day increments and one 2-day increment). The resultant value was then divided by the total number of days in the germination trial period (t). High TI_m values indicated multiple germination events early in the trial period. The maximum possible value of TI_m in this study was 34, with lesser values indicating lower and/or slower germination. Peak germination describes the maximum reproductive potential at a given time in the field (Baskin & Baskin, 1998), and was calculated as the maximum percent germination per 3-day interval during the 35-day germination trial per species, plot, treatment and site.

Statistical analysis

Species response variables were compared between treatments (warmed/control) and among sites, using general linear (PROC GLM) or generalized linear models (PROC GENMOD) in SAS® [version 8.2, SAS Institute Inc. (1999), Cary, NC, USA]. In all cases, results were considered significant when *P*-values ≤ 0.05. Where site by treatment (site × treatment) interactions were identified, *post hoc* comparisons were used to indicate differences between treatments within each site. Where there was no interaction between treatment and site, the main effects of treatment and site were assessed independently. Alpha levels were adjusted using a Bonferonni adjustment (Miller, 1981) for all *post hoc* comparisons. Assumptions for the error terms of GLM were tested using normality tests (Shapiro–Wilk, Kolmogorov–Smirnov, Cramer–von Mises, Anderson–Darling) and normality plots; equal variance was tested using Bartlett and Levene tests when a given species was available at only one site, otherwise residual plots were examined. The Bartlett test is more commonly used, but Levene's is quite robust to nonnormality and has high power (Conover *et al*., 1981). Rank-transformations were applied only when all other transformations failed to meet model assumptions. Where data could not be transformed to normality, PROC GENMOD was applied using a binomial (link = logit) distribution. In two cases, a zero-inflated normal distribution (i.e. left-truncated, mixture distribution) was fitted usingPROC LIFEREG.

For brevity's sake, species sample averages reported in tables include only those for which treatment effects were detected ($P \leq 0.05$), or had *P*-values ≤ 0.1. In addition, results of statistical testing provided here focus on treatment or site × treatment effects, such that not all site effects are reported, and *P*-values >0.1 are not specifically reported.

Sample means were reported with standard deviation (SD) whenever appropriate. Data were excluded from statistical analysis where $n<3$ (individuals/plots/treatment/site) and/or where all seeds failed to germinate (Table 2).

Results

RE

For all species except *D. integrifolia*, site × treatment interactions were not detected. *D. integrifolia* flower biomass showed a site × treatment interaction ($P = 0.0002$, GLM, log-transformed); using *post hoc* comparisons, differences between treatments were detected only at Sedge Meadow ($P = 0.0017$), with average flower biomass approximately twice that of the warming treatment (Table 3). *S. arctica*, the only species in sufficient abundance to be collected from all six sites, showed no treatment effects on RE. *P. radicatum*, *O. digyna* and *F. brachyphylla* availability was restricted to the Dry Willow site; neither *P. radicatum* nor *O. digyna* showed treatment effects on RE. Treatment effects on *F. brachyphylla* flower biomass were detected ($P = 0.0267$, GLM); on average flower biomass was higher

Table 3 Reproductive effort as flower biomass (g) per species in control (C) and warming (W) treatments by site at Alexandra Fiord

	Sedge Meadow		*Cassiope* Heath		*Dryas* Heath		Dry Willow	
Species	C	W	C	W	C	W	C	W
Dryas integrifolia†	0.033 ± 0.01	0.015 ± 0.004**	0.030 ± 0.01	0.023 ± 0.01	0.025 ± 0.004	0.033 ± 0.01	0.028 ± 0.01	0.026 ± 0.004
Festuca brachyphylla							0.015 ± 0.004	0.023 ± 0.006**
Luzula arctica, L. confusa			0.026 ± 0.02	0.030 ± 0.01**	0.017 ± 0.01	0.021 ± 0.01**	0.038 ± ± 0.01	0.061 ± 0.01**

Data are mean values ± SD.
$n = 26$ plots per treatment/site.
**$P \leq 0.05$.
†Site × treatment interaction was significant; *post hoc* comparisons were on site/treatment levels.

in the warming treatment (Table 3). *E. angustifolium* flower biomass was unaffected by warming. The data for *L. arctica* and *L. confusa* were combined for the analysis, owing to combination of samples during the collection stage and difficulties distinguishing seed coat morphologies: hereafter, the combined data will simply be referred to as *Luzula* spp. Treatment effects on *Luzula* spp. flower biomass were detected ($P = 0.0135$, GLM, log-transformed); average flower biomass was higher under the warming treatment (Table 3). *Carex fuliginosa* RE was unaffected by treatment.

RS

In general, long-term warming increased RS. Site × treatment interactions were only detected in *E. angustifolium*. Treatment effects were detected on *D. integrifolia* seed biomass ($P = 0.0100$, GLM): seeds from warmed conditions were, on average, heavier relative to ambient conditions (Table 4). At the *Dryas* Heath and Dry Willow sites, only *D. integrifolia* seeds from warmed plots germinated: these two sites were excluded from subsequent statistical analysis of germination effects. A treatment effect ($P < 0.0001$, GENMOD) was identified in *D. integrifolia* cumulative germination at the remaining sites (Sedge Meadow, *Cassiope* Heath), and average cumulative germination appeared to be enhanced by warming (Table 5). Despite seemingly large differences in sample averages, no treatment effect was detected on *D. integrifolia* germination rate; this may be partially attributable to extremely high variance. Peak germination differed by treatment ($P < 0.0001$, GENMOD) and average values were higher under warming conditions (Table 7).

Treatment effects on *S. arctica* seed biomass were detected ($P = 0.0012$, GLM, rank); average biomass was higher in warming vs. control plots (Table 4). All *S. arctica* seeds from PSD-Dolomite failed to germinate and these data were excluded from statistical analysis. *S. arctica* cumulative, rate of, and peak germination for the remaining sites differed between treatments (respectively, $P = 0.0071$, GENMOD; $P = 0.0006$, GLM; $P = 0.0332$, GENMOD), with sample averages higher under the warming treatment (Tables 5–7). Germination also differed between PSD-Granite and the PO lowland sites ($P < 0.05$). In all measures of RS, sample average *S. arctica* in the PSD was less than in the PO.

P. radicatum, *O. digyna* and *F. brachyphylla* availability was restricted to the Dry Willow site. *P. radicatum* seed biomass differed by treatment ($P = 0.0102$, GLM); seeds from the warming treatment were heavier on average (Table 4). Average *P. radicatum* cumulative germination under warming conditions was higher relative to the control at Dry Willow (Table 5), but there

Table 4 Reproductive success as seed biomass ($g \times 10^{-4}$) per species in control (C) and warming (W) treatments by site at Alexandra Fiord

	Sedge Meadow		*Cassiope* Heath		*Dryas* Heath		Dry Willow		PSD-Granite		PSD- Dolomite	
Species	C	W	C	W	C	W	C	W	C	W	C	W
Dryas integrifolia	2.2 ± 0.6	2.6 ± 0.8**	2.3 ± 0.6	3.4 ± 0.8**	2.1 ± 0.2	2.8 ± 0.5**	2.5 ± 0.9	2.8 ± 0.6**				
Salix arctica	2.8 ± 0.6	3.3 ± 0.1**	2.4 ± 0.3	3.1 ± 0.6**	1.8 ± 0.1	1.9 ± 0.5**	2.8 ± 0.4	2.9 ± 0.4**	1.1 ± 0.6	1.2 ± 0.5**	0.8 ± 0.3	1.4 ± 0.5**
Papaver radicatum							0.7 ± 0.9	1.2 ± 1.4**				
Oxyria digyna							8.0 ± 0.2	9.6 ± 0.2*				
Luzula arctica, L. confusa							0.8 ± 0.3	1.3 ± 0.3**				

Data are mean values ± SD.
$n = 36$ plots per treatment/site.
*$P \leq 0.1$; **$P \leq 0.05$.

Table 5 Reproductive success as total cumulative percent (%) germination per species in control (C) and warming (W) treatments by site at Alexandra Fiord

	Sedge Meadow		*Cassiope* Heath		*Dryas* Heath		Dry Willow		PSD-Granite		PSD-Dolomite	
Species	C	W	C	W	C	W	C	W	C	W	C	W
Dryas integrifolia	1 ± 2	24 ± 21**	2 ± 5	34 ± 23**	0	31 ± 24	0	33 ± 27				
Salix arctica	63 ± 30	76 ± 14**	42 ± 17	92 ± 5**	42 ± 22	79 ± 23**	58 ± 17	78 ± 20**	3 ± 5	5 ± 9**	0	0
Papaver radicatum							27 ± 20	55 ± 25*				
Festuca brachyphylla							1 ± 1	19 ± 14**				
Eriophorum angustifolium†	4 ± 6	24 ± 19**			13 ± 7	24 ± 14						

Data are mean values ± SD.
$n = 37$ plots per treatment/site.
*$P \leq 0.1$; **$P \leq 0.05$.
†Site × treatment interaction was significant; post-hoc comparisons were on site/treatment levels.

Table 6 Reproductive success as germination rate per species in control (C) and warming (W) treatments by site at Alexandra Fiord

	Sedge Meadow		*Cassiope* Heath		*Dryas* Heath		Dry Willow		PSD-Granite		PSD-Dolomite	
Species	C	W	C	W	C	W	C	W	C	W	C	W
Salix arctica	5.5 ± 3.1	8.1 ± 1.7**	4.0 ± 1.7	9.4 ± 0.4**	4.3 ± 2.2	8.2 ± 2.4**	4.8 ± 2.8	6.1 ± 3.9**	0.3 ± 0.5	0.5 ± 0.9**	0	0
Festuca brachyphylla							0	1 ± 0.8**				
Eriophorum angustifolium	0.1 ± 0.3	1.4 ± 1.1**			0.8 ± 0.5	1.3 ± 0.7**						

Data are mean values ± SD, calculated using a modified Timson's Index of germination velocity.
$n = 37$ plots per treatment/site.
**$P \leq 0.05$.

Table 7 Reproductive success as peak germination (%) per species in control (C) and warming (W) treatments by site at Alexandra Fiord

Species	Sedge Meadow		*Cassiope* Heath		*Dryas* Heath		Dry Willow		PSD-Granite		PSD-Dolomite	
	C	W	C	W	C	W	C	W	C	W	C	W
Dryas integrifolia	1 ± 2	8 ± 6**	2 ± 3	16 ± 13**	0	21 ± 17	0	13 ± 16				
Salix arctica	26 ± 17	39 ± 28**	22 ± 11	59 ± 12**	23 ± 15	38 ± 10**	28 ± 12	40 ± 9**	2 ± 3	4 ± 7**	0	0
Festuca brachyphylla							1 ± 1	8 ± 6**				
Eriophorum angustifolium†	1 ± 1	10 ± 8**			6 ± 4	8 ± 4						
Luzula arctica, L. confusa			8 ± 8	14 ± 12*	12 ± 9	9 ± 10*	0	7 ± 6*				

Data are mean values ± SD.
$n = 37$ plots per site.
*$P \leq 0.1$; **$P \leq 0.05$.
†Site × treatment interaction was significant; *post hoc* comparisons were on site/treatment levels.

was no statistically significant difference ($P = 0.0686$, GLM). Average *O. digyna* seed biomass was higher in the warming treatment (Table 4), but also not statistically so ($P = 0.0928$, GLM); no other measure of *O. digyna* RS was affected by treatment. *F. brachyphylla* showed no treatment effects on seed biomass, but cumulative, rate of, and peak germination differed between treatments (respectively, $P = 0.0143$, GLM, rank-transformed; $P = 0.0225$, GLM, log-transformed; $P = 0.0012$, GENMOD); average values of each measure of germination were higher under the warming treatment relative to the control at the Dry Willow site (Tables 5–7).

E. angustifolium seed biomass showed no treatment effects, but cumulative germination showed a site × treatment interaction ($P = 0.0495$, GENMOD); *post hoc* analysis showed treatment effects at Sedge Meadow ($P = 0.0050$). Average germination was higher in the warming treatment (Table 5). Germination rate was advanced ($P = 0.0063$, GLM, rank transformation), and on average was at a higher percentage throughout the germination trial in the warming relative to the control treatment (Table 6), particularly in the Sedge Meadow site. A site × treatment interaction was also detected in peak germination ($P = 0.0033$, GENMOD); *post hoc* analysis showed treatment effects at Sedge Meadow ($P = 0.0036$). Mean peak germination was higher under the warming treatment at both the Sedge Meadow and *Dryas* Heath sites (Table 7).

Treatment effects on *Luzula* spp. seed biomass were detected ($P = 0.0401$, GLM); average seed biomass was higher under the warming treatment (Table 4). *Luzula* spp. data from the Dry Willow site were excluded from analysis of cumulative germination because all seeds from control plots failed to germinate. No treatment effects were detected in any measures of RS, except in peak germination $P \leq 0.1$ ($P = 0.0937$, GENMOD) (Table 7). Sample averages of RS were higher under the warming treatment at *Cassiope* Heath and Dry Willow, but this trend was reversed at *Dryas* Heath, where germination was higher under ambient conditions.

There were insufficient *C. fuliginosa* seeds to measure seed biomass. The failure of all *C. fuliginosa* seeds at all sites to germinate, irrespective of treatment, may reflect the tendency of this species to reproduce via clonal (asexual) rather than sexual reproduction, thereby apportioning insufficient resources for successful germination. Alternatively, this species may have germination requirements that were unfulfilled in this experiment, such as physical abrasion and dormancy, or suppressed germination, as with chemical inhibition (Amen 1966; Baskin & Baskin 1998), or seeds were simply not fully matured at time of harvest.

In 2004, average snow melt was 2–3 days (24 h photoperiod) earlier in the warming treatment relative to the control, with the greatest differences identified in the PO (Fig. 2). Sedge Meadow had the earliest snow-free dates.

Discussion

Results of this study support our initial hypothesis – that long-term warming enhances RE and RS of tundra plants – and offer interesting insights into the possible mechanics and means of future change in the High Arctic. The influence of site on tundra plant reproduction was less than expected (e.g. Arft *et al*., 1999; van Wijk *et al*., 2004; Hollister *et al*., 2005a); this may indicate the overriding importance of temperature, relative to site-specific conditions, for the production of viable seed in High Arctic tundra plants. As predicted, plant response to warming varied by species, to the extent that broader generalizations at the level of functional group were possible, such as with the dwarf shrubs. In this regard, our findings were similar to those described by various meta-analyses (Arft *et al*., 1999; Walker *et al*., 2006). However, cross-comparison with other studies may not be entirely appropriate here, given, for example, that the vast majority of studies were conducted in the Low Arctic.

Changes in plant phenology in response to manipulation of environmental variables can provide critical insights into the constraints on an organism's growth (Murray & Miller, 1982). Short-term (1–3 years) application of warming treatments, for example, has been found to advance early-season phenophases, such as flowering (Hultén, 1968; Arft *et al*., 1999; Hollister *et al*., 2005b; Høye *et al*., 2007); such changes in turn can affect RS (Henry & Molau, 1997; Molau *et al*., 2005). In our study, enhanced RE and RS in warming relative to control treatments may indicate that via long-term experimental warming, both early - and late-season phenophases have been advanced (i.e. seed formation and ripening), resulting in enhanced plant sexual reproduction (Johnstone, 1995; Jones, 1995). Observed differences in sexual reproduction attributed to warming may affect the process of colonization in the High Arctic, depending on dispersal from the parent plant, and may potentially enhance survival of vascular plants in a changing environment, via increased genetic variability of offspring. Investigations into warming effects on *in situ* seedling survivorship in the High Arctic will help clarify the potential contribution to existing vegetation, and whether colonization via seed actually has the potential to occur at a faster rate than via vegetative expansion.

Observed differences in the frequency and magnitude of plant response in this study, particularly consistent detection of differences in shrub and graminoid RE or RS, suggest that under conditions of climate warming shrubs and graminoids in the High Arctic may be the first to colonize and establish areas of bare ground via enhanced sexual reproduction. Previous meta-analyses for other Arctic locations have shown, fairly consistently, positive responses to warming in whole plant and/or reproductive biomass of shrubs, herbaceous plants (Arft *et al*., 1999; Walker *et al*., 2006; Post *et al*., 2009) and graminoids, the latter particularly in the presence of herbivores (Post *et al*., 2009). The contribution of observed trends at other Arctic locations and the paucity of long-term experimental warming response data draw attention to the need for more long-term

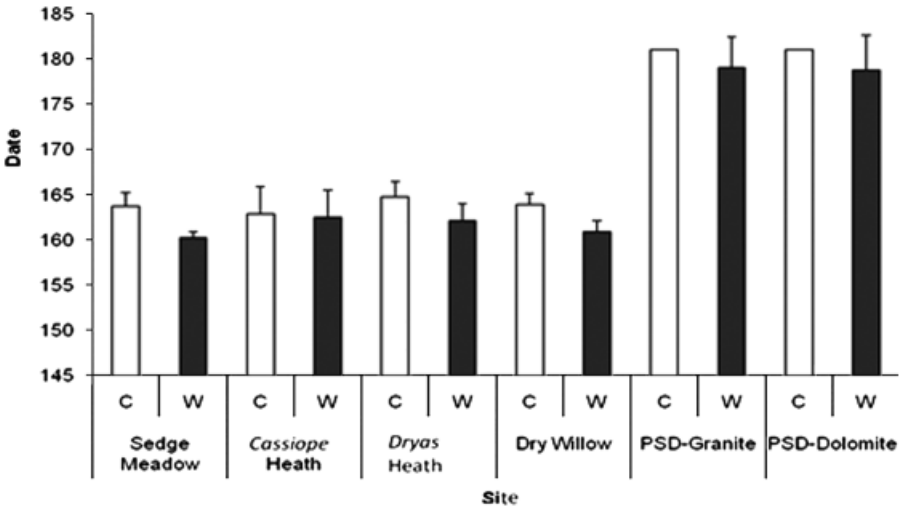

Fig. 2 Date of snow melt (January 1, 2004 = day 1) averaged (+ SD) across control (C) and warming (W) treatments within each polar oasis and polar semidesert (PSD) site at Alexandra Fiord, $n = 6–10$ plots/treatment/site.

research to verify or refute our findings; however, if the findings of other long-term studies prove to be in agreement with responses observed in this study, plant demographics in the High Arctic may indeed be altered under a climate-warming scenario, likely with shrubs and graminoids leading the way. This would support evidence from observations (Sturm *et al*., 2005) and experimental warming research (Walker *et al*., 2006), which show the expansion of shrub and graminoid abundance under warmed conditions.

The mechanisms responsible for observed differences in warming response among growth forms may be at least partly based on the means of vegetative tissue renewal; for example, dwarf shrubs such as *S. arctica* and *D. integrifolia* produce persistent woody tissue, which reduces the need for annual renewal of structural support, and reduces the influence of annual environmental variability. Despite annual renewal of structural support in graminoids, these growth forms typically invest quite heavily in a belowground system of roots and rhizomes (Billings, 1987). In this regard, graminoid nutrient storage is similar to that of shrubs, but with emphasis on the root rather than the shoot system. In contrast, forbs such as *P. radicatum* or *O. digyna* experience annual renewal of both vegetative and reproductive tissues. Application of cluster analysis to determine the plant traits that most influence ecosystem processes under conditions of rapid climate change in the Arctic, have shown that dwarf shrubs and graminoids with nonaerenchymatous roots were more closely linked with each other than with forbs (Chapin *et al*., 1996). These combined findings may indicate that functional group-specific responses to warming may be at least partly attributed to differences in nutrient storage and usage strategies (Chapin *et al*., 1996).

Other factors potentially influencing observed germination may be related to species-specific germination requirements and the artificial manner of germination (i.e. germination under greenhouse conditions). For example, this could include the absence of necessary conditions for breaking seed dormancy, such as physical abrasion or the presence of chemical stimulants like nitrate, or the presence of foreign bodies in Petri dishes, such as fungi, which produce certain enzymes and toxins that inhibit germination (Baskin & Baskin, 1998). Freshly matured seeds of most Arctic shrub, herb and many graminoid species are described as nondormant (Chapin & Shaver, 1985; Baskin & Baskin, 1998), but some tundra plants show specialized germination requirements that, if unaccounted for, can bias the outcome of germination trials (Chapin & Shaver, 1985; Baskin & Baskin, 1998). In this study, every effort was made to anticipate the germination requirements of target species, but in some cases it is possible that requirements were not sufficiently met, resulting in zero germination, as with *C. fuliginosa*. Development of flower primordia one to several years in advance of flowering is a selected adaptation (Mooney & Billings, 1961; Sørensen, 1941) that can also introduce variability to Arctic vascular plant performance in a given year, since it reflects the growth conditions of the previous growing season. In this sense, poor germination performance of a species in a given year may not necessarily indicate an overall inability to germinate or insensitivity to warming effects, but rather poor conditions for flower primordial development the previous growing season.

Despite some variability in functional group response to warming, site × treatment interactions across the range of species and sites tested were relatively infrequent; this ran counter to our initial hypothesis and expectations described in the literature (Arft *et al*., 1999; van Wijk *et al*., 2004; Hollister *et al*., 2005a). For example, Nosko & Courtin (1995) predicted that warming would result in increased rates of evapotranspiration and/or soil moisture deficits, ultimately diminishing plant response to warming in species poorly adapted to these conditions. In our study, fairly consistent positive responses to warming, largely irrespective of site and functional group, may indicate the relative importance of temperature compared with habitat quality for successful reproduction in High Arctic polar oases.

Abiotic characteristics such as soil moisture have been shown to affect plant growth and reproduction throughout the Arctic (Chapin & Shaver, 1985) and specifically at Alexandra Fiord (Jones, 1995). Observed germination success of *S. arctica* at PSD-Granite may suggest that site-specific differences in environmental conditions between the two PSD sites, such as soil moisture (Gold & Bliss, 1995), soil composition and pH (Bliss *et al*., 1994; Walker *et al*., 2008) determined the absolute presence or absence of germination (Miller, 1982; Chapin, 1983; Sheard & Geale, 1983). The observation that lighter seeds from PSD-Granite germinated, whereas heavier seeds from PSD-Dolomite did not, may be explained by the inverse relationship between soil moisture and diaspore mass (Baskin & Baskin, 1998; Dormann *et al*., 2002). In general, failure of *S. arctica* seeds from PSD-Dolomite to germinate may indicate that the role of temperature diminishes in importance relative to plant habitat quality beyond some abiotic and/or biotic threshold. In PSD sites, where vascular plant cover is limited (5–20%) (Walker *et al*., 2005), experimental warming research can provide information about potential future dynamics associated with bare-ground colonization (Svoboda & Henry, 1987); observed increases in RE and RS here may indicate the potential contribution of PSDs, in addition to polar oases, as a seed source for recruitment and colonization.

In the Arctic, the growth of some plant species begins even before the snow cover is completely gone (Billings & Mooney, 1968), allowing flower and seed maturation to begin as soon as critical light and temperature conditions are achieved (Chapin & Shaver, 1985). This adaptation indicates the potential importance of even hourly changes in the thermal microenvironment (Chapin & Shaver 1985), particularly where the photoperiod is 24 h light. Furthermore, it suggests the possibility that seemingly minor differences in snow melt date observed between warming and control treatments in this study, combined with overall warmer lowland growing season temperatures (Hudson & Henry, 2009) and specifically higher temperatures in warming treatments (Marion *et al*., 1997), could have been sufficient to enhance average RE and RS across the range of species and sites tested, as predicted by others (see Shaver & Kummerow, 1992; Wookey *et al*., 1993; Arft *et al*., 1999; Sandvik & Tøtland, 2000). Progressively earlier dates of snowmelt in warming treatments between 1993 and 2001 have been recorded at lowland sites within Alexandra Fiord (G. H. R. Henry, unpublished results).

Long-term changes in climate can also impact plant responses to warming. For example, forecasted increases in cloud cover (Chapin & Shaver, 1985; ACIA 2004) may result in diminished light quality, affecting plant growth and, consequently, production of viable seed (Olson & Richards, 1979). This effect can only be tested directly with multiannual data collection. Fluctuations in climate can also intensify or diminish challenges to tundra plant growth and reproduction, to the extent that among-year variation in phytomass can range from 15% to 40% in some alpine vascular plant communities (Walker *et al*., 1994). Fluctuating populations of pollinating insects (Kevan, 1972) and experimental influences, such as the date of seed harvest (Bliss & Gold, 1999), can also affect plant response in any given year. Changes in climate, such as increased cloud cover, resulting in a cooling effect, may be compensated for by an extended growing season, whereby even small increases in air or soil temperatures enhance reproduction by seed. The effect of warming observed in this study will benefit from further long-term, multiannual (consecutive), multispecies studies that can establish the contribution of interannual variability to observed differences in germination, as well as the influence of warming on the degree/extent of interannual variability in RE and RS.

Acknowledgements

This study was funded through grants from the Natural Sciences and Engineering Research Council of Canada and ArcticNet to G. H. R. H., and the Northern Student Training Program of Indian and Northern Affairs Canada to R. A. K. The authors would like to acknowledge Polar Continental Shelf Project and the Royal Canadian Mounted Police for logistical support. Many thanks to the following folks for field and lab support: K.-A. Down, S. Bogart, P. Brown. We would also like to thank the two anonymous reviewers for critiquing an earlier version of this manuscript.

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