The Effect of Experimental Warming on Plant-Pollinator Relationships in the Low Arctic

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Introduction

Although the impacts of climate change are globally distributed, they are especially pronounced in polar regions. Phenology, or the timing of recurring life cycle events, of low arctic tundra plant communities has shifted earlier over the last several decades in response to higher temperatures and earlier snowmelt (Linderholm, 2006; Oberbauer et al., 2013; Khorsand Rosa et al., 2015). Despite this trend, the basic reproductive ecology of tundra plant communities is still not well understood. A key component of this reproductive ecology is the integrity of the plant-pollinator network. If insect pollinators and plants exhibit disparate responses to changing patterns of seasonality, it is possible for a phenological mismatch to occur. Phenological responses of insects and plants have implications for the fitness of both functional groups as the climate continues to warm. It is also critical to test which floral visitors effectively pollinate which plant species, to provide further insight into ecosystem response to climate change.

Materials and methods

We used the open top chamber (OTC) warming method employed by the International Tundra Experiment (Hollister and Webber, 2000). OTCs are roofless plexiglass structures that increase the ambient temperature of the area within the chamber by approximately 2° C. Fieldwork was conducted at Toolik Field Station (TFS) on the North Slope of Alaska. We established a total of 128 research plots between two field sites, 12 km away from each other. At each site, 64 plots were evenly split between moist acidic tundra and dry heath tundra. At each moist and dry site, 16 OTCs and 16 control plots were established. We conducted a phenology survey of 34 plant species twice a week at each site to determine onset and duration of flowering (anthesis), as well as floral density. We also conducted systematic floral visitor observations (each observation lasting 5 minutes) to monitor pollinator activity. We performed a pollen limitation experiment to exclude pollinators from 4 plant species to determine the mating system of each species and assess the role of pollinators in fruit production. We quantified nectar production to understand how warming may affect floral rewards. Finally, we conducted pollen counts from voucher specimens to determine the effectiveness of different pollinators.

Study questions

(1) Which plant species attract the most floral visitors?
(2) Do floral visitation rates (measured by number of landings on flowers) correspond to number of pollen grains found on bodies of floral visitors?
(3) Which plant species require insect visitation to produce fruit and which are self-compatible?

Results

Order	n	Range [min, max]	Mean pollen count (SD)	% of total landings
Hymenoptera (Bees, ants, wasps)	19	[0, 674]	80.16 **(a)** (181.95)	20%
Lepidoptera (butterflies, moths)	10	[0, 88]	10.00 **(b)** (27.42)	7%
Diptera (flies, mosquitoes)	41	[0, 28]	3.88 **(b)** (7.12)	72%

Table 1. Mean pollen count differed significantly among insect orders [Kruskal-Wallis test, $\chi^2(2) = 15.62$, $p < .001$]. Mean pollen count for Hymenoptera was significantly higher than for Diptera [Mann-Whitney pairwise comparisons, $U = 150$, $p < .001$] and Lepidoptera [$U = 148.5$, $p = .01$], while mean pollen count for Diptera did not differ significantly from that of Lepidoptera [$U = 185.5$, $p = .64$]. Different letters indicate significant difference at $\alpha = 0.01$.

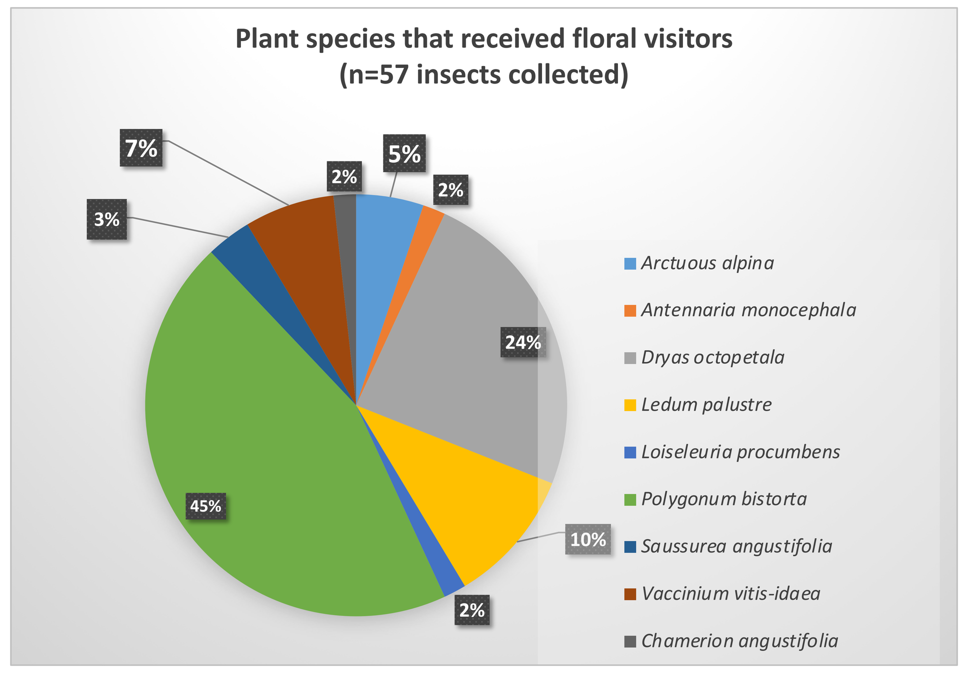

Figure 2. Plant species that had highest visitation rates based on voucher collection assembled during fieldwork.

	Mean date of peak anthesis (DOY), SE	Duration of flowering season (days)
Control	168.13, 0.34	48
Experimental	168.22, 0.33	55 *

Table 2. Phenology survey results from biweekly observations at Toolik Lake and Imnavait Creek.
* indicates significance between control and treatment at $\alpha = 0.05$.

Picture 1. OTCs and control plots at site 1, Toolik Lake.

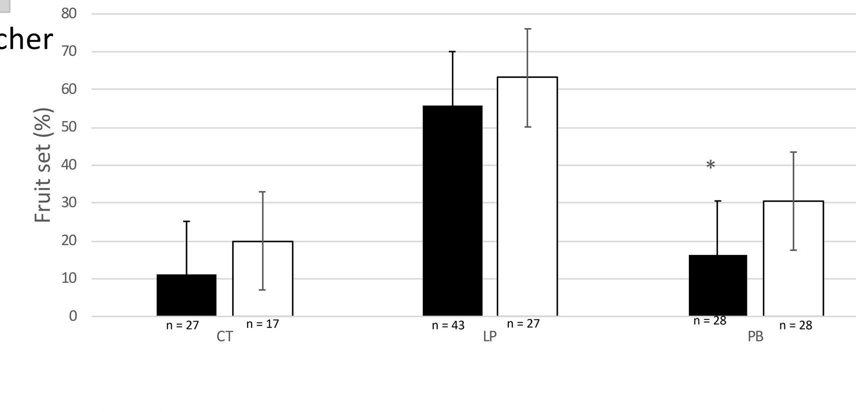

Figure 3A. Fruit set in treatment (bag) and open (control) plants. CT = *Cassiope tetragona,* LP = *Ledum palustre*, PB = *Polygonum bistorta.* Fruit set (%) is the proportion of fruit to flowers.
* indicates significance between treatment and control at $\alpha = 0.01$.

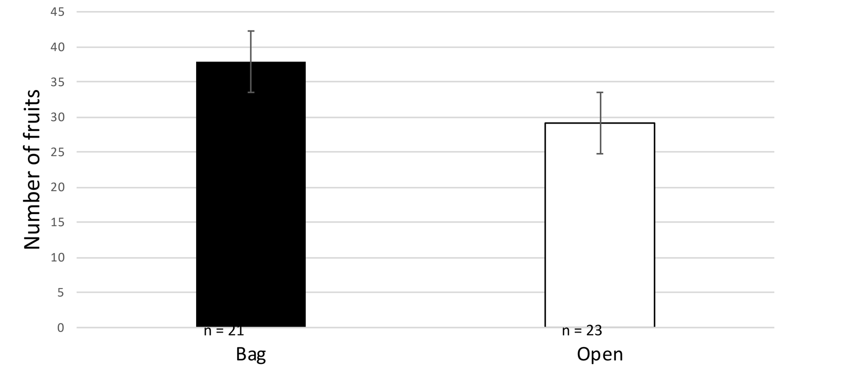

Figure 3B. Fruit set in treatment (bag) and open (control) *Dryas octopetala* plants. These fruit were quantified by counting seeds, as *D. octopetala* produces only one terminal flower head per plant. There was no significant difference in fruit set observed.

	Mean volume (μL), SE	Mean nectar quality (%Brix), SE
Experimental	6.79, 0.29	16.56, 1.39
Control	4.14, 0.39	16.40, 1.63
p-value, Z-value	<0.0001, 2.43	> 0.05, 0.96

Picture 2. *Vaccinium uliginosum* (Ericaceae).

Table 3. Comparison of nectar volume and quality in warmed and control populations of *Vaccinium uliginosum.* Warming significantly increased volume of nectar, but not nectar quality (% sucrose).

Key findings

- Nectar volume was significantly higher in plants exposed to the warming treatment, but there was no difference in nectar quality
- *Polygonum bistorta* received the highest proportion of floral visitors based on observations of flower landings
- *P. bistorta* exhibited a significant decrease in fruit set in the visitor-exclusion treatment compared to the control
- Order Diptera plays a disproportionate role in floral visitation
- Order Hymenoptera collects significantly more pollen, particularly bumblebees, suggesting that they are effective pollinators of tundra forbs
- Floral density was significantly higher in the warming treatment compared to the control (1.67x higher)
- Flowering lasted significantly longer in the warming treatment compared to the control

Discussion and implications

Our study provides novel results providing insight into the reproductive ecology of the Alaskan tundra plant community in the context of a changing climate. Order Diptera visits significantly more flowers than other taxa. However, order Hymenoptera carries significantly more pollen, suggesting that Hymenoptera are the most effective pollinators of tundra forbs, despite accounting for only 20% of recorded landings. Plant reproductive output is species-specific; our results show that species such as *Cassiope tetragona*, *Ledum palustre*, and *Dryas octopetala* are self-compatible and don't require insects to produce fruit. *P. bistorta* exhibited a significant difference between open and experimental treatment, suggesting that insects play a crucial role in this species' reproduction. This species was also found to receive the most visitors proportionally than any other species present in the ecosystem. These results suggest that, if subject to a phenological mismatch with its pollinators, reproductive output of *P. bistorta* could decrease throughout the tundra. The nectar findings with respect to *Vaccinium uliginosum* suggest that warming will increase nectar production in this species in the future, though the sucrose quality of nectar may not change. Warmed individuals may offer more nectar as a reward for pollinators, but with a potential physiological trade-off, a topic that merits further study. The Arctic is changing rapidly, warranting continued research on plant-pollinator phenology and natural history.

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