Insect Pollination and Experimental Warming in the High Arctic

by

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B.Sc., The University of British Columbia, 2006

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

in

The Faculty of Graduate and Postdoctoral Studies

(Geography)

THE UNIVERSITY OF BRITISH COLUMBIA

(Vancouver)

April 2014

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Abstract

As climate change causes retreats in Arctic glaciers, it is important to understand the mechanics of growth and community change in Arctic plant communities. Arctic plants have been shown to respond to observed and experimental changes in temperature by altering their reproductive strategies, growth, and phenology. Researchers have used open-top chambers (OTCs) to experimentally alter the near-surface air temperatures of tundra plant communities over long periods of time, but these devices may exclude insect pollinators to flowers during crucial periods of pollen reception. Insect pollination in the context of OTCs and Arctic plants is therefore important to understand, but has been poorly researched. I altered pollination of _Salix arctica, Dryas integrifolia_, and _Papaver radicatum_ inside and outside of OTCs in a High Arctic shrub community, and conducted targeted insect netting to understand the dynamics of the visiting insect community. I also conducted bowl trapping inside and outside of OTCs to gauge their effect on insect availability to receptive flowers. OTCs altered the timing of flowering in Arctic plants, and significantly reduced the availability of pollinators to available flowers. However, I found that while both warming and pollination can alter flower and seed production in the study species, pollination is largely independent of OTC warming. Early-flowering species have the potential to be most affected by OTC-induced insect exclusion. The most common visiting insects were flies of the families Syrphidae and Muscidae, with occasional bumblebees (_Bombus polaris_). _Papaver radicatum_ was by far the most heavily-visited flower, and I showed that the Syrphidae visit the flower preferentially at low temperatures, likely for warmth as well as pollen. I discuss these results in context with the current literature on Arctic plant and insect communities, and make recommendations for future research.
Preface

• Chapters 2 and 3 are based on work conducted by Samuel Robinson and supervised by Dr. Greg Henry. I was responsible for field work, lab work, statistics, and writing.

• No publications have yet arisen from this.

• No approval was required from the UBC Research Ethics Board.
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This work was funded by the National Science and Engineering Research Council of Canada (NSERC), ArcticNet, Polar Continental Shelf Program (PCSP), the Northern Scientific Training Program (NSTP), the Canadian International Polar Year (IPY - CiCAT), and the University of British Columbia. Permission for research was granted from the Nunavut Department of Environment, and the use of the buildings at Alexandra Fiord was granted by the Royal Canadian Mounted Police (RCMP).

I foremost wish to thank Dr. Greg Henry for his help, advice, and encouragement during the last three years. Thank you to all of my field assistants who have helped me during the summers of field work, notably Christopher Greyson-Gaito, Doug Curley, Darcy McNicholl, Meagan Grabowski, and Matt Huntley. I thank Anne Bjorkmann for her statistical help and practical advice. Thank you to Fred Stride, for letting me continue to play in UBC Jazz Ensemble I throughout the past three years, and exercise a completely different part of my brain!

I thank my committee members, Dr. Elizabeth Elle and Dr. Roy Turkington, for their support and direction. I also thank Dr. Marwan Hassan for his support and encouragement.

Finally, I wish to thank my parents and my brothers for all of their love and support during my M.Sc. I can never thank you enough for how you’ve supported me.
Dedication

This work is dedicated to the memory of the people killed during the crash of First Air Flight 6560 on August 20, 2011, in Resolute Bay, Nunavut.
Chapter 1

Introduction

Pollination of flowering plants by insects (entomophily) in Arctic ecosystems is poorly understood. Visitation of flowers is beneficial for both the insects that visit them, as well as the plants, and is essential for fertilization and production of seeds in many plants. Climate change has already begun to alter plant community composition in the Arctic, and will continue to alter it into the next centuries. Understanding the speed and extent of these changes partially depends on their seed production. However, very few studies have been conducted that have identified changes in insect communities that the plants are associated with. In this literature review, I will examine the research that has currently been conducted on Arctic pollination biology, and the study of climate change effects on plant and insect communities. Finally, I will outline my specific research goals.

1.1 History of Pollination Ecology

1.1.1 Pollination in General

Pollination of plants has been examined since antiquity by natural philosophers such as Virgil (and certainly as much by agrarians), but Rudolf Camerarius (1665-1721) is generally credited with the first studies of the sexuality of plants (Faegri and Van der Pijl, 1979). However, Camararius only examined self-fertilization, and Joseph Köhruter (1733-1806) and Christian Sprengel (1750-1816) were the first to examine pollination of flowers by insects (Proctor et al., 1996), and found that many plants required insect pollinators to obtain full seed set (fully-formed, fertile seeds). Charles Darwin's work built on the concepts laid down by Köhruter and Sprengel in his observations of numerous floral structures and pollination techniques, and suggested a mechanism (natural selection) by which the structure of flowers could ultimately be controlled by their interactions with pollinators (Darwin, 1859, 1862). His work also lead to the general thesis that “nature abhors self-fertilization” (Waser and Ollerton, 2006). This hypothesis (“Darwin's Law”) continued to dominate literature on plant-pollinator interactions until the
1.2 Plant-Pollinator Interactions

1.1.2 Studies in Arctic Pollination Biology

After Darwin's publication of *Species* and *Orchids*, naturalists in the High Arctic such as Aurivillius noted that flowers such as *Pedicularis lanata* and *P. hirsute* appeared to be completely self-pollinating in stark contrast to "Darwin's Law (Kevan, 1973a). Other authors continued this trend into the 20th century (Warming, 1888; Mathiesen, 1921), and the hypothesis that stressed environments, such as the High Arctic, favoured self-fertilization continued. This was generally accepted until the work of Chernov (1966, 1985) and Hocking (1968) revealed that insect pollination was far more common than previously thought. Kevan (1972b) examined this in even greater detail by using acetate cones and netting to exclude pollinators, demonstrating dependence (and independence) of several pan-Arctic flowering plants on insect visitation. In recent years, plant-pollinator interactions in the High Arctic have seen an even greater interest in the scientific community, in the face of global climate change and an increased interest in networks and “connectivity in species interactions (Elberling and Olesen, 1999; Lundgren and Olesen, 2005; Hegland et al., 2009).

1.2 Plant-Pollinator Interactions

1.2.1 Benefits for Plants

It is well known that plants benefit from insect visitation. Visitation of flowers by insects, particularly bees and flies, has been shown to be essential to fertilization and fruit formation in many species. Many families of plants have self-incompatibility mechanisms that do not allow pollen from the same plant to fertilize itself (autogamy, or selfing). Transfer of pollen between individuals (heterogamy or outcrossing) can be facilitated either by wind or by pollinating animals such as insects. This outcrossing increases genetic variation within populations, meta-populations, and contributes to ongoing process of natural selection by allowing gene transfer. This is also important in the development of resilient genotypes which can withstand environmental change, and to avoiding the pairing of deleterious alleles (inbreeding) (Proctor et al., 1996). Pollinating insects are often a much more efficient mechanism because they direct pollen transfer directly to flowers, often to individuals of the same species, thus reducing the amount of pollen required by a plant to produce a successful mating. This has been found
1.2.2 Benefits for Insects

Plants are not the only beneficiary in this relationship. It has been argued that the pollen would have served as an attractant to the first pollinating insects, because it pre-dates angiosperm plants. It is one of the most nutrient-rich parts of a plant, and is commonly used by bees and other insects to rear their broods (Simpson et al., 1983). However, since it is energetically expensive to produce, many orders of plants have evolved nectaries to serve as an alternative attractant. The nectar produced by flowers represents a major source of energy for flower-visiting insects. Körruter was arguably the first to study its significance (and to discover that this was the source of honey) (Proctor et al., 1996), followed by (Darwin, 1862). More recently, Hocking (1968) compared nectar concentrations between the high and low Arctic (Churchill, NWT and Lake Hazen, NU) and found that northern flowers produce smaller quantities of high-concentration nectar. He also found that unlike more southern ecosystems, flowers compete for insect visitors rather than insects competing for nectar. Energetics also play a significant role in the plant-pollinator relationship. Heinrich (1983) writes about the role that optimal foraging plays in nectar and pollen feeding, and also how shelter by the flower contributes to the energy balance of pollinators. Hocking and Sharpin (1965) as well as Kevan (1975) show the corolla of heliotropic flowers such as *Dryas integrifolia* and *Papaver radicatum* act as parabolic reflectors, and suggest that added heat from this is an added attractant to pollinating insects.

1.3 High Arctic Ecosystems and Climate Change

1.3.1 The ITEX Program

Global climate change has been shown to have altered air temperatures and precipitation patterns over the past twenty years (Hinzman et al., 2005; Alexeev et al., 2012), and is predicted to have even larger effects on mean temperatures in Arctic regions over the next twenty years (Hassol, 2004; Stocker et al., 2013). This will have large effects on the structure and function of future plant communities (Walker et al., 2006), and has already been shown to be occurring (Hudson and Henry, 2009; Hill and Henry, 2011; Elmendorf et al., 2012a). It is well known that both insects (Downes, 1964;
Danks et al., 1994) and plants (Chapin, 1983; Jones et al., 1997; Klady et al., 2011) can dramatically change their behaviour and growth under higher temperatures. The International Tundra Experiment (ITEX) was created to monitor the changes in plant phenology, growth and reproduction across the Arctic resulting from passive warming using Open-Top Chambers (OTCs) (Marion et al., 1997; Henry and Molau, 1997). Part of the ITEX program also involves monitoring populations of larval Gynaephora groenlandica and G. rossii (Mølgaard and Morewood, 1996), but unlike the plant communities, no long term sampling scheme has been undertaken for other land-dwelling arthropods. Insects are also key indicators of environmental change (Danks, 1992), and as their populations should be expected to change with a warming Arctic, so should their interactions (both negative and positive) with Arctic plants.

1.4 Review of Arctic Pollination and Insect Studies

Table 1.1 provides a summary of some of the major works in Arctic pollination ecology to date. Below, I will briefly review the most recent work, and identify knowledge gaps that this work will operate in.

1.4.1 Confounding Effects of OTCs

Researchers have shown that OTCs can alter seed production in both high and low Arctic sites for Dryas octopetala (Alatalo and Totland, 1997; Welker et al., 1997). Stenström et al. (1997) noted latitudinal differences in the effect of experimental warming on seed set in Saxifraga oppositifolia, and suggest that warming by OTCs may reduce pollinator activity. Jones et al. (1997) also note that reduced seed set in OTC-warmed Salix arctica may be due to either reduced wind or insect pollination. However, the confounding effects of the OTCs on seed set are not well understood, and the confounding effect may alter predictions made for seed production in flowering plants in a warming High Arctic.

To quantify changes, observed pollination rates within the OTCs should be compared with control plots, but rates of background pollination are not well known across high Arctic plants. Bocher (1996) suggested that understanding this was necessary for the ITEX experiment to understand the degree of wind pollination and insect pollination that occurs within the OTCs. It has not been demonstrated that OTCs directly create a pollina-
### Table 1.1: Summaries of some key studies that have contributed to the modern study of Arctic pollination ecology

<table>
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<th>Author</th>
<th>Year</th>
<th>Location</th>
<th>Findings</th>
</tr>
</thead>
<tbody>
<tr>
<td>Y. Chernov</td>
<td>1963</td>
<td>Yugorski Peninsula, Russia</td>
<td>Found that many flowering plants depend on insect pollination for seed-set</td>
</tr>
<tr>
<td>B. Hocking</td>
<td>1968</td>
<td>Lake Hazen, Nunavut</td>
<td>Examined differences in pollination strategies between low and high Arctic flowering plants; found that high Arctic pollination networks tend to be pollinator-limited</td>
</tr>
<tr>
<td>L. Bliss</td>
<td>1971</td>
<td>Various</td>
<td>Reviewed all literature on plant reproduction in tundra ecosystems; described the characteristics of plant reproductive systems</td>
</tr>
<tr>
<td>P. Kevan</td>
<td>1972</td>
<td>Lake Hazen, Nunavut</td>
<td>Examined dependence on pollination in 13 Arctic flower plants; identified pollination deficits present as well as dependence on insect pollination in 5 species</td>
</tr>
<tr>
<td>H. Elberling &amp; J. Olesen</td>
<td>1999</td>
<td>Latnajaurje, Sweden</td>
<td>Examined the composition of an Arctic pollinating community; identified the predominance of Diptera as pollinators</td>
</tr>
<tr>
<td>R. Ring</td>
<td>2001</td>
<td>Alexandra Fiord, Nunavut</td>
<td>Examined abundance of insects inside and outside of OTCs in the context with the ITEX program; found differences in abundance in some insect families</td>
</tr>
<tr>
<td>R. Lundgren &amp; J. Olesen</td>
<td>2005</td>
<td>Uummannaq, Greenland</td>
<td>Conducted a network study on an Arctic pollinating community; found that insect and plant species were very closely linked</td>
</tr>
</tbody>
</table>
tion deficit, but it is implied any pollination deficit created is due to altering flowering phenology in relation to emergence of pollinating insects (Alatalo and Totland, 1997). Bliss (1958) showed historical rates of seed germination within Arctic plants, and other authors have shown that OTCs can change seed germination rates (Wookey et al., 1995; Klady et al., 2011). The mechanism for this is not understood, but has been suggested to be a combination of temperature alteration and changes in pollination rates.

1.4.2 Insect Community Composition

Ring (2001) completed pit-trap surveys that indicate lower numbers of insects are trapped in OTCs than in control plots, and has shown how this varies between taxa. However, actual visitation to flowers by insect taxa is not known, so it is difficult to say whether or not all pollinating taxa are excluded from OTCs (or attracted to them). Also, the temporal scale of measurement (collections were made weekly) was not appropriate for the scale of the ecosystem, which can undergo large changes in a phenology in only a matter of days. Identifying visitors to Family (or Genus) will help to assign degrees of pollination-importance to different taxa of insects, and ultimately help to better understand rates of seed set and plant establishment within OTCs. Some of this work has already been done at the ITEX site at Alexandra Fiord, Nunavut, and indicates that Hoverflies (Order: Diptera, Family: Syrphidae) may be responsible for a majority of the pollination in the High Arctic (Robinson, 2011), which was also observed by both Hocking (1968) and Kevan (1972b) at Lake Hazen Camp, Nunavut.

1.4.3 The Effects of Seasonality and Temperature

Levels of seed set have been found to be higher in late-blooming alpine flowers due to higher numbers of pollinators (Kudo, 1993). Earlier snowmelts, and hence earlier flowering times, in the High Arctic may have a similar effect on seed set, but this depends on the synchrony between insect emergence and flower emergence. Besides snowmelt timing, other environmental variables such as wind speed, cloud cover, and ambient temperature can control day-to-day variation of insect visitation in alpine zones (Kudo, 1993), and operates similarly in Arctic zones (Totland, 1994; Bergman et al., 1996). Typically, pollinating insects minimize their energy consumption by only visiting under energetically favourable conditions (Heinrich, 1975, 1983), which is usually visible in a diurnal cycle in mid-latitude ecosystems, but may not exist in the High Arctic where insects may be more opportunistic with re-
1.5. Conclusions

gards to visitation. It has also been noted that smaller insects are more affected by changes in temperature and insolation (Gilbert, 1985), and may be “released from summer limitations on feeding and growth as the High Arctic undergoes warming. Bergman et al. (1996) found that activities of bumblebees and butterflies were highly correlated with air temperature and incoming radiation, and that seed-set in bumblebee-pollinated plants was reduced during colder periods due to lack of visitation.

1.5 Conclusions

Other than the work of Bergman et al. (1996), almost nowhere else in the Arctic ecological literature has such a direct connection been made between weather, insects, and seed production in flowering plants. The shortness of the flowering season makes these connections very important for both flowering plants and their associated pollinators. There are few studies examining the diversity and numbers of insects during the flowering season (Ring, 2001), but few examining pollinating insects (Høye et al., 2013). Changes in pollination have been inferred in some species (Chapin, 1983; Stenström et al., 1997; Jones et al., 1997), but very few studies have explicitly determined levels of pollination (Kevan, 1972b), and none have examined pollination in the context of the ITEX program. Finally, long-term changes in the plant community have been observed (Walker et al., 2006; Hudson and Henry, 2009), but only recently has the importance of their respective pollination strategies been realized (Lundgren and Olesen, 2005). Insect communities may exhibit unpredictable responses because of individualistic changes in behaviour due to rising temperatures and lengthening growing seasons (Danks, 2004), highlighting the need for research that emphasizes how insect communities have changed along with plant communities. Insect communities, in general, are poorly sampled across the Canadian Arctic, and while changes in other ecosystem components (such as sea ice and snow melt) have been documented, changes in insect populations have not been studied.

1.6 Objectives

The work I have undertaken has multiple goals. Briefly:

- it aims to understand how OTCs interact with rates of pollination, in order to understand how reproductive changes within OTCs represent future warmed ecosystems.
1.6. Objectives

- it aims to understand the specific nature of a High Arctic insect community, with reference to insect taxonomy, seasonal timing, and its structure over the flowering season. This includes ambient bowl trapping and targeted netting, which will help to gauge the importance of specific groups of flower visitors.

- it aims to provide more accurate estimates of insect availability inside and outside of OTCs, and relate those to the dominant visitors found in the surrounding community.

These goals will provide a more accurate picture of how OTCs affect the flying insect community, the pollination regimes of Arctic plants, and how those two factors interact in the context of global change experiments.
Chapter 2

Pollen Limitation in Open-Top Chambers

2.1 Introduction

During the past decades, northern residents and the scientific community have witnessed large changes in Arctic plant communities (Hinzman et al., 2005; Elmendorf et al., 2012a). They have seen expansion into previously unoccupied areas (Tape et al. 2006; Morton et al., 2012), as well as changes in dominance and abundance within monitored communities (Elmendorf et al., 2012a). Climate change is predicted to bring greater changes to Arctic regions compared to mid-latitude regions, with mean air temperatures increasing 7-9° C by 2100, along with an increase in rainfall (Stocker et al., 2013). Many of these changes are already occurring (Graversen et al., 2008; Serreze et al., 2009; Alexeev et al., 2012). Plant community responses to climate change in the Arctic are not well understood, and vary highly depending on the region (Elmendorf et al., 2012b; Brochmann et al., 2013). Arctic plant communities can influence feedbacks to climate change (Wookey et al., 2009), such as CO$_2$ flux from the soil (Oechel et al., 2000; Lund et al., 2012) and the near-surface radiation budget (Blok et al., 2010; Myers-Smith et al., 2011).

Climate change in the High Arctic is predicted to be even more severe (Hassol, 2004; Stocker et al., 2013). Because of their isolation, sparse plant cover, and short growing season (8-12 weeks), High Arctic plant communities are studied far less than other ecosystems, and represent an area of large future changes and great uncertainty. For example, early snowmelt may result in an increased length of growing season, but only if mid-season droughts are offset by rain.

Since its inception in 1990, members of the International Tundra Experiment (ITEX) have studied the effects of climate warming on Arctic and alpine plant communities. The main experimental technique used by the ITEX is open-top chambers (OTC), which rely on a passive heating ef-
2.1. Introduction

fect by trapping incoming solar radiation and limiting convective heat loss (Marion et al., 1997; Hollister and Webber, 2000). OTCs increase the near-surface temperature over the snow-free season, and have been shown to drive changes in plant communities over a wide range of latitudes (Walker et al., 1999; Klanderud and Totland, 2005; Walker et al., 2006; Hudson and Henry, 2010; Klady et al., 2011). OTCs have also been shown to change the reproductive effort (flower numbers, seed numbers per flower) of Arctic plants (Stenström et al., 1997; Klady et al., 2011). These changes have usually been attributed to the effect of increased air temperature, but some authors have empirically found that OTCs decrease natural insect and wind pollination (Molau and Shaver, 1997; Stenström et al., 1997; Hollister and Webber, 2000).

Asexual reproduction plays a major role in the maintenance of Arctic plant communities (Billings and Mooney, 1968; Bell and Bliss, 1980), but dispersal into unvegetated areas is accomplished by sexual reproduction and seed dispersal. As glaciers recede due to prolonged warming, the process by which plants make and disperse their seeds is important to understand (Stenström et al., 1997; Bjorkman et al., 2013). Most Arctic plants have fairly robust pollination systems and are capable of producing at least some viable seeds by self-pollination. However, most of these plants increase seed-set when hand-pollinated or exposed to insect visitors, indicating that insect pollination is beneficial to plants (Stenström and Molau, 1992; Molau, 1993; Totland and Eide, 1999). The relative importance of wind, insect, and self-pollination in sexual reproduction are not well studied in the High Arctic. In light of this, it is important to understand how pollination influences seed production and viability in Arctic plants, and hence, their ability to colonize new areas.

The understanding of the mechanisms behind Arctic plant reproduction is at this point, mainly speculative. There are relatively few studies investigating the flower and seed production of Arctic plants under different pollination regimes, and even fewer examining how these regimes interact with warming. There are equally few studies examining how OTC warming and pollination interact with seed viability. Most studies use passive methods such as seed size, but few conduct actual germination trials because of the tedious nature of the experiment. To make accurate predictions about the state of plant reproduction and spread, it is necessary to quantify how the effect of warming interacts with any induced changes in the pollination regime. In this study, I investigate how pollination changes interact with OTC warming in three Arctic flowering plant species.
2.2 Methods

2.2.1 Site Description

The study was conducted at Alexandra Fiord, Ellesmere Island, Nunavut, in the Canadian High Arctic (Map in Figure 2.1). Alexandra Fiord is described as an “oasis in a polar desert” (Svoboda and Freedman, 1994a), and there are ITEX experimental sites located at seven distinct community types within the valley (Svoboda and Freedman, 1994b). For this study, I used the Xeric Shrub site, which is characterized by early snowmelt, peaty and sandy soils, and a deep active layer (Muc et al., 1989; Svoboda and Freedman, 1994a; Jones et al., 1997, 1999). *Salix arctica* is the most dominant plant at the site, followed by graminoids such as *Poa arctica* and *Festuca brachyphylla*.

2.2.2 Plant Species

Arctic Willow (*Salix arctica* (Pall)) is a woody, prostrate shrub present in the circumpolar tundra, and can be found across a large range of latitudes and ecological conditions (Dawson and Bliss, 1989b; Jones et al., 1997). Individual plants are dioecious and can exhibit differing growth patterns between sexes (Dawson and Bliss, 1989a; Jones et al., 1999). Inflorescences are dull red vertical catkins, with nectaries present on both male and female catkins. Catkins can have hundreds of individual flowers, and because flowers can produce multiple seeds a single female catkin can produce well over 500 seeds (this work). In the High Arctic *S. arctica* set their next year’s flower buds at the end of the snow-free season (late July-August), and bud break commences a few days after snow melt the following year. Along with *Saxifraga oppositifolia*, they are some of the earliest flowering plants at Alexandra Fiord (Kevan, 1990). Warming has been shown to advance their flowering phenology and their seed development (Jones, 1995; Jones et al., 1999). Both male and female plants produce nectar, and male plants also produce copious amounts of bright yellow pollen. The pollination strategies of other species in the genus *Salix* tend to be a mixture between wind and insect pollination (ambophily) (Tamura and Kudo, 2000; Totland and Sottocornola, 2001; Culley et al., 2002). *Salix arctica* is able to be wind-pollinated, but requires insect visitation for full seed-set (Kevan, 1972b; Peeters and Totland, 1999).

Mountain Avens (*Dryas integrifolia* (Vahl)) is a semi-evergreen dwarf shrub forming prostrate cushions, present in northern North America and Greenland (Porsild and Cody, 1980). It is closely related to its widespread sister species, *Dryas octopetala*, and there is some evidence of hybridization.
between the two species (Philipp and Siegismund, 2003). Like *S. arctica*, it produces flower buds during the autumn of the previous flowering season, but bud burst occurs later than *S. arctica* (Philipp et al., 1990). It produces white, 8-11 petalled perfect (bisexual) flowers with deep nectaries. Small proportions of male-only or female-only (unisexual) flowers have been noted by some workers (Molau and Mølgaard, 1996; Wada and Kanda, 2000). Some of the recorded unisexual flowers may be also due to flower herbivory by noctuid caterpillars such as *Sympistis nigrita* (Greg Henry, pers. comm.). The flowers are often visited by insects, and (Kevan, 1972b) has shown it to be dependent on insect pollination for full seed set. The flowers of *D. integrifolia* are heliotropic, and temperatures can be elevated in the flower corolla by 6-8°C, which can benefit both reproductive development within the flower as well as insects that bask or feed within the corolla (Hocking and Sharpin, 1965. Kevan, 1975. Krannitz, 1996). I used hand-held thermocouples to test temperature differences.

Arctic Poppy (*Papaver radicatum* (L.)) is an annual flowering forb, present across the circumpolar tundra and alpine zones. It produces yellow, cup-shaped perfect flowers in which the female parts are fused into a capsule which swells after fertilization. Warming has been shown to increase both plant biomass and flower production in *P. radicatum*, as well as accelerate flowering phenology (Lévesque et al., 1997; Mølgaard and Christensen, 1997). These changes are thought to be caused by an increased length of growing season rather than elevated temperature (Mølgaard and Christensen, 1997). Kevan (1975) found that air temperatures within the corolla could be elevated by approximately 7°C compared to ambient temperatures, but I found that temperatures were elevated by an average to 5°C.

### 2.2.3 Experimental Design

To test how OTCs interact with pollination, I manipulated pollen levels inside and outside of OTCs using the three aforementioned plant species. Treatment factors included Warming (2 levels: Warmed, Control) and Pollination (4 levels: Hand-pollinated, Net Excluder, Cloth Excluder, Control; explained below), with 10 replicates within each combination of factors. I tagged individual plants in both OTC and Control treatments, then randomly assigned Pollination treatment to them. The population size of flowering plants within OTCs at the Xeric Shrub site was limited, I could not conduct a 4-by-2 complete cross with sufficient replication, so I removed some levels of the experiment (Table 2.1). Because finding sufficient flowering plants outside of OTCs was not an issue, I was able to use all 4 levels of
2.2. Methods

Pollination (Hand pollinated, Net Excluder, Cloth Excluder, Control) outside the Warming treatments. The final structure of the experimental design is shown in Table 2.1.

Hand-pollination was conducted by taking pollen from the anthers of the same species of flowering plants using a small, soft paintbrush and transferring it to the receptive pistils of fully emerged flowers on treatment plants. I made an attempt to use pollen from plants both within and outside of OTCs randomly where possible, but this was sometimes limited because of advanced flowering phenology within OTCs or site characteristics. Net Excluders were used to exclude pollinators from individual flowers, using a 1mm nylon mesh attached using thin twist-ties. This mesh was intended to exclude pollinators without causing large changes to any wind-borne pollen load. Cloth Excluders were used to gauge the importance of self-pollination, using bags of 10µm cloth to exclude any wind-borne pollen from *D. integrifolia* and *P. radicatum* flowers. All Excluder bags were attached before the flowers were receptive to pollen, and removed once the flowers had senesced and were dispersing seeds. Cloth Excluders were not used on *S. arctica* because the species is dioecious and cannot be self-fertilized. Rain may have created some problems later in the season by washing pollen from late-season flowers (mainly *P. radicatum*), but this was confined to only a few days in late July to early August when most flowers were beyond pollen receptivity and had begun to senesce.

OTCs are hexagonal, plexiglass chambers approximately 1.5m across, designed to contain a 1-m² plot, and have been found to raise the ambient air temperature by 1-3°C. Molau and Mølgaard (1996) and Jones (1995) describe the use of OTCs used by the ITEX group, including construction and design of the chambers, and the efficacy of OTCs has been evaluated by Marion et al. (1997). In general, OTCs increase the near-surface air temperature during sunny days, and cause the date of snowmelt to advance. Hollister and Webber (2000) found that OTCs mimic an above-average warm summer, and during the summer of 2012, I found that the temperature was elevated by 1.79°C within the OTCs. During the summer of 2012, the temperature was elevated by 1.79°C. Ten OTC/control plot pairs were randomly assigned in 1992 when the treatments began, and four extra pairs were later added for monitoring CO₂ flux from the tundra.

To control for plant size, I sampled random plants from the site, collected size metrics (described in Equation 2.1 2.2 and 2.3), dried and weighed the sampled plants, and developed regression models to estimate above-ground biomass (AGB). Size metrics measured include: length of longest branch, width of largest leaf, mat length and width, rosette length and width.
2.2. Methods

In order to apply the Excluder bags before the flowers were receptive, plants were checked and pollination treatments were applied every day during the early growing season. After the majority of flowering was underway for each species and Excluder bags were in place, the plants were checked and pollinated using a paintbrush every 2 days. Once flowers had senesced and had begun to disperse their seeds, the entire floral head was collected and stored in individual envelopes. Some of the flowers failed to produce seeds, either due to flower abortion or being damaged by caterpillars. In some cases, I was able to see insect frass or the actual larvae, but this was not always the case.

Upon return from the field site in late August, seeds were stored in a freezer at -4°C for 27 weeks (September-March). Batches of seeds were weighed to the nearest 0.001g, counted, and a random sample from each flowering head was taken for germination, as numbers permitted (up to 100 seeds for *S. arctica*, 50 for *D. integrifolia* and *P. radicatum*). Germination trials took place in a greenhouse which provided 20 hours of light daily, and maintained temperatures from 15-25°C. Seeds were placed on filter paper in 10 cm petri dishes and kept moist with distilled water. Seeds were checked every 2 days from May 15 - June 14, 2013, and germinated seeds were removed from each dish and counted. I defined “germinated” as showing exposed cotyledons (*S. arctica*) or an exposed rootlet of >5mm (*D. integrifolia* and *P. radicatum*).

2.2.4 Statistical Analyses

To compare numbers of flowers produced per plant, I used Generalized Linear Models (GLM) with a Zero-Truncated Negative Binomial (ZTNB) distribution and a log-link function. This was necessary because the data did not fit assumptions of normality and heteroskedasticity for a traditional ANOVA model. Overdispersion in the data was too large to use a Poisson GLM, so I used a Negative Binomial GLM (Hilbe, 2011). A Zero-Truncated distribution (sometimes referred to as a “hurdle” model) was necessary because plants that failed to produce flowers could not receive pollination treatments, making it impossible for a treated plant to have zero flowers. Such models are described in Zuur et al. (2009) and Hilbe (2011). I selected the “best” model using Akaike’s Information Criteria (AIC), using second-order bias-corrected AIC to account for sample size (Burnham and Anderson, 2002; Anderson, 2008). AIC is considered a predictor of information entropy in a model, and is used to select the most parsimonious model (Anderson, 2008).

To examine the AGB:flower production relationship, I used Zero-Truncated
2.2. Methods

Negative Binomial GLMs. I included inferred AGB as a predictor to reduce any confounding effect of plant biomass on flower production. All predictor metrics were included in the original model, then AIC was used to determine the “best” model. Inferred biomass was calculated as follows for each species:

\[
\log B_{\text{salix}} = b_0 \log W + b_1 \log L + b_2 \log LB + b_3 \log L \times \log LB + \epsilon \quad (2.1)
\]

Where B = Above-ground biomass, W = Mat Width (cm), L = Mat Length (cm), LB = Longest Branch Length (cm), and \( \epsilon \) = error

\[
\log B_{\text{dryas}} = b_0 + b_1 \log W + b_2 \log L + \epsilon \quad (2.2)
\]

Where B = Above-ground biomass, W = Mat Width (cm), L = Mat Length (cm), and \( \epsilon \) = error

\[
\log B_{\text{papaver}} = b_0 \log W + b_1 \log L + b_2 \log LW + b_3 \log W \times \log LW + \epsilon \quad (2.3)
\]

Where B = Above-ground biomass, W = Rosette Width (cm), L = Rosette Length (cm), LW = Width of largest Leaf(cm), and \( \epsilon \) = error

To model the seed response across treatments, I used generalized linear mixed-effects models (GLMM), with seed response for each harvested flower nested within plant. GLMMs are relatively new in statistical literature, and are sensitive to the same assumptions that underlie both GLMs (Hilbe, 1994; Neuhaus and McCulloch, 2011) and linear mixed-effects models (LMM) (Laird and Ware, 1982; Pinheiro and Bates, 2000; Zuur et al., 2009). Bolker et al. (2009) gives an excellent overview of assumptions and fitting methods associated with GLMMs.

For each model, seed response was modeled using Pollination and Warming as Fixed Effects, with each individual plant as a Random Effect (necessary to avoid pseudoreplication). This structure of mixed model was repeated for the following responses:

- Seed Number
- Total Seed Mass (g)
- Average Seed Mass (Total Seed Mass/Seed Number) (g)
- % Germinability (Number Germinated/Number Sampled) \times 100
2.3. Results

All statistical analyses were done using R 3.0.2 (R Core Team, 2013). Binomial GLMs were fit using the base `stats` library, the zero-truncated GLMs were fit using the `VGAM` library (Yee, 2013), negative binomial GLMMs were fit using the `glmmADMB` library (Fournier et al., 2012), Gaussian, Poisson and binomial GLMMs were fit using the `lme4` library (Bates et al., 2013). The seed germination data were found to be highly overdispersed, and was modelled using a Markov-Chain Monte Carlo (MCMC) approach through the `MCMCglmm` library (Hadfield, 2010), which allows for overdispersion and is more robust than likelihood-based methods of parameter estimation.

Wald z-tests or t-tests of significant effects (i.e. \( p < 0.05 \)) are not reliable for small sample sizes in GLMs and are not defined for LMMs or GLMMs. Likelihood-ratio tests are also unreliable for small sample sizes, and their performance in a GLMM context is not well studied (Pinheiro and Bates, 2000; Bolker et al., 2009). I cite differences between the nested candidate models using \( \Delta AIC \), which is a measure of model parsimony. For citations of differences between candidate models, a negative \( \Delta AIC \) indicates that adding the term improves the model (Anderson, 2008). Table 2.6 contains an overview of flower response to pollination and warming.

2.3 Results

Using a handheld thermocouple probe, I found that temperatures were elevated by only 1°C on average within the corolla of *D. integrifolia*. However, the temperature within the corolla of *P. radicatum* was elevated by an average of 5°C.

2.3.1 Flower Response

*Salix arctica* exhibited no response in flower number to warming treatment (\( \Delta AIC = 1.23 \)). The effect of pollen was negligible both inside (\( \Delta AIC = 2.08 \), Figure 2.6.1) and outside the warming treatments (\( \Delta AIC = 2.64 \), Figure 2.7a). AGB was an important predictor of flower number (\( \Delta AIC = -6.22 \)), but the model was not improved by adding warming, pollination, or any higher-order combination of the terms.

*Dryas integrifolia* forms flower buds the previous year similar to *S. arctica*, but responded completely differently to warming treatment. Outside the warming treatments, pollen did not alter flower numbers (\( \Delta AIC = 2.73 \), Figure 2.7b). Flower number within warming treatments responded to pollen and showed an interaction between warming and pollination (\( \Delta AIC = -6.88 \)), where plants that were warmed but unpollinated produced the
2.3. Results

The greatest number of flowers per plant (Figure 2.6b). However, when I used inferred AGB as a covariate to correct for the size of the *Dryas* mats, a warming term improved the model (ΔAIC = -5.70), but pollination did not (ΔAIC = 0.69). This can be seen in Figures 2.6e and Figure 2.8 which shows that biomass influences flower production, but only if the plant is warmed.

*Papaver radicatum* also exhibited no response in flower number to pollination (ΔAIC = 12.56) or warming (ΔAIC = 1.95). AGB was found to improve AIC the most (ΔAIC = -15.36), but the model was not improved any further by adding warming, pollination, or any higher-order combination of the terms. Figures 2.6 and 2.7 show that the flower numbers and flower numbers per unit AGB for *P. radicatum* are very similar.

### 2.3.2 Seed Response

*Salix arctica* exhibited a dramatic response to pollination manipulation, increasing the number of seeds produced (ΔAIC = -4.28) and total biomass of seeds (ΔAIC = -1.2) when pollinated, while not increasing the overall seed size (ΔAIC = 22.40). Pollinated catkins produced an average of 100 more seeds inside and 145 more seeds outside the OTCs, compared to their unpollinated counterparts (Figures 2.9a, 2.10a). OTC warming did not affect seed number (ΔAIC = 2.02), nor did the interaction between warming and pollination, indicating that *S. arctica* may be generally subject to pollen limitation, but that this is not altered by OTCs (Figure 2.9a).

Pollination and OTC warming appears to have not altered germination in any important way, but this is difficult to interpret because of the very low germinability of *S. arctica* seeds (Figures 2.11, 2.12). I found a marginal effect of warming, pollen, and a warming:pollen interaction on seed germination in *S. arctica* using a MCMC approach to model fitting (ΔDIC = 1.08). However, the Deviance Information Criteria (DIC), a Bayesian analogue of AIC, showed very little difference between the full model (Warming + Pollen + Warming:Pollen) and the null model, indicating that the difference between candidate models is very small. Warming was only significant if high-order combinations of terms were included.

*Dryas integrifolia* did not change total seed number or biomass in response to OTC warming or pollination. For seed germination, warming, pollination, and a warming:pollen interaction were identified as being important (ΔDIC = -3.35). ΔDIC values between candidate models were small, but a MCMC modelling framework also identified the full model as having the best DIC score, although the interaction term was not significant (p_mcmc = 0.136). Outside the OTC treatments, pollen was important in predicting
2.4 Discussion

2.4.1 *Salix arctica*

Neither warming nor pollination altered flower production did not change in *S. arctica*. This is not surprising given that *S. arctica* produces flower buds the previous season.

Pollen addition was the main factor constraining production of seeds in *S. arctica*. I did not find evidence to suggest that OTCs alter seed production, or that they alter the pollination of *S. arctica* flowers. Jones et al. (1997) found that the ratio of seeds:flower in individual *Salix* catkins was decreased by OTCs, which they used to imply that pollination was reduced within the treatments. While not directly counting flower numbers per catkin, I recorded growth of the terminal shoot (length of catkin + length of stem) for each catkin, which has been shown to be a linear predictor of flower number (Jones, 1995). I found that neither warming nor pollination had any effect on the length of the terminal shoot (i.e. number of flowers per catkin), but Jones et al. (1999) has shown that this can vary from year-to-year and habitat-to-habitat. Pollen treatment did not alter the total number of catkins produced by *S. arctica*, because flower buds are grown at the end of the previous season.

*Salix arctica* germination was not largely affected by either pollination...
or OTC warming. Both inside and outside the OTCs, I found that all nested models had a very similar DIC, indicating that the effects of pollination and OTC warming are not largely important in germination. Much of this is probably due the inherently low germinability of *S. arctica* seeds. This also may be due to the sample size used, as well as the structure of the binomial GLMM required to analyze nested, overdispersed, binomial data. In the future, larger numbers of plants per level of treatment (>15) should be used if analyzing germination under a GLMM framework.

My low recorded germination rates for *Salix arctica* are consistent with other studies on germination (Bliss, 1958; Billings and Mooney, 1968; Dawson and Bliss, 1989a). However, Klady et al. (2011) tested seed germination across sites in the Alexandra Fiord Lowland, and recorded much higher germination rates for *S. arctica* (23%) than what were found in my study. This may have occurred for a few reasons: Klady et al. (2011) used a much shorter cold stratification period (1 month) before testing germinability, and used a longer photoperiod (24hrs). The length of stratification is more likely the cause of the difference between my treatments, because Dawson and Bliss (1989a) used a similar cold stratification period (-30°C for 18-24 weeks) to ours, and reported similar overall germination (2%). *Salix* seeds are also very small, on the order of 0.001 g per seed. The very small amount of endosperm along with each fruit means that viability decreases very quickly over time (Densmore and Zasada, 1983).

### 2.4.2 *Dryas integrifolia*

As a species, the reproductive responses of *D. integrifolia* have not been studied as much as its more widespread sister taxa *D. octopetala*.

I found that OTC warming increased flower production per unit AGB in *D. integrifolia*. This is most likely caused by a decreased rate of bud abortion in warmed plants. Wookey et al. (1993) also found that artificial warming treatments can stimulate flower production in *D. octopetala*, despite the fact that *Dryas* sets reproductive buds the previous year. They attribute this to a decreased rate of flower abortion and unsuccessful bud-burst within warmed treatments. Similarly, I found that warming treatments increased the Flower Production:AGB ratio for individual plants, whereas control plants produced approximately the same number of flowers per plant regardless of the biomass. Pollination treatments did not alter this relationship.

Although flower number responded to warming, I did not find any changes in seed number or seed mass resulting from OTC warming or pollination
2.4. Discussion

treatment. In this respect, my findings differ from the results of Welker et al. (1997) who found that OTCs increased both seed number and seed mass in *D. octopetala*. However, their between-site findings were very different, indicating that *D. octopetala* has a strong dependence on local environmental conditions. I found that that germinability of *D. integrifolia* was affected by OTC warming, pollination, as well as their interaction. Because I also found increased germinability in hand-pollinated plants outside OTCs, it is likely that seed viability is related to both warming and pollination. Because I found lower seed viability outside of the OTCs, it is not likely that OTCs are interfering with pollination in any significant way, and that the increased viability is caused by the elevated air temperatures.

My pollen treatments outside of the OTCs revealed that pollen addition increases germinability in *D. integrifolia*, but that exclusion of insect pollinators or wind has no large effect on germinability. Kevan (1972b) found that insect exclusion caused a reduction of seed-set in *D. integrifolia*, and that emasculated flowers were still capable of producing some seeds in an insect-free environment, although his sample size was small (1 plant, 5 flowers). I also found that *D. integrifolia* can produce seeds in the absence of pollinators. A possible explanation for this is that the flowers require small quantities of pollen relative to the amount of pollen they produce. Philipp et al. (1990) found that in *D. integrifolia* only 1% of the total pollen produced by a single flower was necessary to pollinate all of the stigmas on the flower. In this way, *D. integrifolia* can be thought of as a pollination “opportunist”: extra pollen enhances germinability, but it is not dependant on these external vectors.

2.4.3 *Papaver radicatum*

I found that experimental warming did not increase flower production, or flower production per unit AGB in *P. radicatum*. AGB was also not different between control and OTC for *P. radicatum*.

Seed number and seed mass were unaffected by either warming or pollination treatments. This indicates that the mating system of *P. radicatum* is fairly resistant to changes in pollination rates and ambient temperature. Kevan (1972b) found that *P. radicatum* exhibited no response in seed production to exclusion of pollinators, meaning that self-pollination is common in this system. At the level of the flower, the temperature effect of OTCs may be relatively small, because *P. radicatum* are capable of maintaining a high-temperature microclimate within their corolla by tracking the sun (Kevan, 1975).
2.4. Discussion

The germination response of *Papaver radicatum* is difficult to analyze. Because I did not exclude insects from hand-pollinated blossoms, I cannot exclude the possibility that the action of hand-pollination either imperfectly deposited pollen or damaged the stigmas, confounding a change in overall germinability. However, I believe that my treatments were not overly unrealistic, and conclude that the pollination system of *P. radicatum* is robust enough to not require large amounts of cross-pollination. Given that many plants at the edge of their range retain some degree of self-pollination, this is not surprising. I exclude germination conditions as a possible factor, because Olson and Richards (1979) found that final germination rates were not largely affected by temperature conditions. Karlsson and Milberg (2007) found that the time of seed collection was an important factor in seed germination. I did not find any effect of the day of seed collection through the season, most likely due to the short range of collection days late in the season.

In the control plants, germinability was reduced strongly by the selfing treatment ($p_{mcmc} < 0.001$), but not strongly altered by either hand-pollination or insect exclusion ($p_{mcmc} > 0.1$). This is more likely due to changes in temperature caused by the selfing treatments, rather any kind of self-incompatibility mechanism. *Papaver radicatum* is heliotropic, and temperatures can be strongly elevated within the corolla (Hocking, 1968; Kevan, 1975). Corbett et al. (1992) found that obstruction of flower petals can cause the blossoms to not track the sun, and have lower ovary temperatures, leading to smaller and fewer seeds. I suspect that this may have been the case with the selfing treatments, as the cloth required to exclude any wind-borne pollen necessarily covered the entire corolla, which probably caused a drop in temperature. While I did not find smaller seeds within the selfing treatment, it is conceivable that it may have altered germinability. The exclusion treatment (1mm net) is probably a more realistic estimate of self-fertilized seed production in *P. radicatum*, given that wind-pollination events are rare in *Papaver*.

OTCs do not strongly alter the magnitude of (seed) reproductive response of *P. radicatum*. Other species of *Papaver*, such as *P. somniferum*, are generally insect-pollinated or self-pollinated because of their sticky, dense pollen (Patra et al., 1992; Miller et al., 2005). *Papaver radicatum* is similar, but has much higher rates of self-pollination than lower-latitude *Papaver* species (Nordal et al., 1997). *Papaver radicatum* can be considered to be a complex of different subspecies (Solstad et al., 1999), so it is possible that individual subspecies could have slightly different responses to temperature and pollination. Year-to-year variability was also not considered within this
study, but can strongly influence both the timing and magnitude of flower production (Lévesque et al., 1997).

## 2.5 Conclusions

Many studies have shown that OTC warming can have variable effects on sexual reproduction in Arctic and alpine plants, but I found that OTC warming and changes in pollination are generally independent. Of the three plant species I examined:

- *Salix arctica* altered seed production in response to pollen levels, producing more seeds when hand-pollinated, and fewer when insect visitors were excluded.

- *Dryas integrifolia* produced more flowers per unit of AGB in OTC warming treatments, and displayed higher germinability in both warmed and pollinated treatments.

- *Papaver radicatum* reproductive output was not largely altered by OTC warming or pollen manipulation.

Seedling establishment is very rare in the Arctic, mainly due to low summer temperatures and low water availability for seedlings (Bell and Bliss, 1980). Establishment typically happens in climatic “windows” for long-lived species (Bliss, 1958; Eriksson and Fröborg, 1996). Almost all High Arctic plants can be thought of as stress tolerant *C*-selected species, *sensu* Grime (1977), or highly competitive *K*-selected species, *sensu* MacArthur (1967). Molau (1993) re-defined the systems of MacArthur (1967) and Grime (1977) in the context of tundra communities, which can be described in terms of their flowering phenology alone. Rather than *r* and *K*-selected, he defined “pollen-risking” and “seed-risking” strategies, which exist along a continuum of early-flowering to late-flowering, with corresponding rates of low selfing to high selfing. Examples of “pollen risking” strategists include *S. arctica* and *Saxifraga oppositifolia*, while “seed-risking” strategists include *P. radicatum*

With *Papaver radicatum*, a conflicting pattern emerges: a mid-season flowering plant that is apparently unaffected by selfing or pollination. This may be more of an artifact of the treatments used rather than an actual reflection of how the plants reproduce. *Papaver radicatum* is highly dependent on insolation to produce seeds (Corbett et al., 1992), and assumedly, to produce viable seeds. Kjellberg et al. (1982) found a similar pattern in *D. octopetala*. The 10µm cloths that I used to exclude wind-borne pollen
2.5. **Conclusions**

from the flowers of *P. radicatum* would also have had a shading effect within the corolla, which may have caused temperature to be confounded with selfing. This does not appear to have had a large effect in *D. integrifolia*. Unfortunately, there are relatively few methods to directly test rates of self-pollination aside from genetic analysis. If rates of insect visitation were to be continuously monitored over the season, it may be possible to indirectly assess how rates of visitation influence germination for *Papaver radicatum*.

Because of the tedious nature of germination studies, there is a lack of studies of seed germinability related to warming in the Arctic. Many studies simply use seed size as a proxy for germinability, but my results show that seed size is generally independent of germinability. Cooper et al. (2004) and Müller et al. (2011) suggest that greenhouse germination alone is insufficient to demonstrate germinability, and that field trials are necessary to measure the actual germination probabilities. To my knowledge, there are no studies on field trials of seed germination inside OTCs in the Arctic. Even though seedling establishment is rarer in the Arctic, it is still an important factor in many Arctic ecosystems (Freedman et al., 1982; Nordal et al., 1997), and its importance will continue to increase as glaciers retreat, creating new habitats for establishment.
2.6 Figures and Tables
2.6. Figures and Tables

Figure 2.1: Location of Alexandra Fiord, Ellesmere Island (78.882°N, 75.782°W). Source: James Hudson.
Figure 2.2: The Xeric Shrub site at Alexandra Fiord, with several ITEX OTCs visible. Many *Salix arctica* catkins (white, fluffy flowers) are dispersing seeds.
2.6. Figures and Tables

Figure 2.3: *Salix arctica* (Pall) ♂. Plants are dioecious, with male plants maturing earlier and producing copious amounts of pollen. Both male and female forms produce nectar.
Figures and Tables

Figure 2.4: *Dryas integrifolia* (Vahl). Their flowers are mainly complete (hermaphroditic), but some flowers are entirely staminate or pistillate. All forms of flowers have deep nectaries, and produce some of the largest volumes of nectar of all high Arctic flowers (Hocking, 1968). The flowers are moderately heliotropic.
Figure 2.5: *Papaver radicatum* (L.) All Papaveraceae lack nectaries, but produce large amounts of sticky, dense pollen. Their flowers are highly heliotropic, and the temperature within the bowl-shaped corolla can be significantly higher than the surrounding air. The fly basking in the corolla is a male *Phaonia* spp. (Diptera: Muscidae)
Figure 2.6: Flower output from hand-pollinated and warmed plants. Flowers per plant for a) *Salix arctica*, b) *Dryas integrifolia*, and c) *Papaver radicatum*. Flowers per gram AGB shown for d) *Salix arctica*, e) *Dryas integrifolia*, and f) *Papaver radicatum*. Letters a, b indicates ΔAIC >2 between candidate models.
Figure 2.7: Flower output from pollen-manipulated plants outside warming treatments. Flowers per plant are shown for a) *Salix arctica*, b) *Dryas integrifolia*, and c) *Papaver radicatum*. Flowers per gram AGB shown for d) *Salix arctica*, e) *Dryas integrifolia*, and f) *Papaver radicatum*. Pollination treatments are described in Methods. Letter a indicates indicates $\Delta AIC \approx 0$ between candidate models.
2.6. Figures and Tables

Figure 2.8: Flower output from warmed and control *D. integrifolia* plants as a function of above-ground biomass (AGB). All measurements are per plant.
Figure 2.9: Seeds per flower and seed mass per flower from hand-pollinated and warmed plants. Seeds per flower is shown for a) *Salix arctica*, b) *Dryas integrifolia*, and c) *Papaver radicatum*. Mass of seeds per flower is shown for d) *Salix arctica*, e) *Dryas integrifolia*, and f) *Papaver radicatum*. Letters a, b indicates $\Delta$AIC >2 between candidate models.
Figure 2.10: Seeds per flower and seed mass per flower from pollen-manipulated plants outside warming treatments. Flowers per plant are shown for a) *S. arctica*, b) *D. integrifolia*, and c) *P. radicatum*. Flowers per gram AGB shown for d) *S. arctica*, e) *D. integrifolia*, and f) *P. radicatum*. Letters a, b indicates $\Delta$AIC >2 between candidate models.
Figure 2.11: Average seed mass and germinability from hand-pollinated and warmed plants. Average seed mass is shown for a) *Salix arctica*, b) *Dryas integrifolia*, and c) *Papaver radicatum*. Seed germinability is shown for d) *S. arctica*, e) *D. integrifolia*, and f) *P. radicatum*. Letters a, b indicates $\Delta$AIC >2 between candidate models.
Figure 2.12: Average seed mass and germinability from pollen-manipulated plants outside warming treatments. Average seed mass is shown for a) *Salix arctica*, b) *Dryas integrifolia*, and c) *Papaver radicatum*. Seed germinability is shown for d) *Salix arctica*, e) *Dryas integrifolia*, and f) *Papaver radicatum*. Letters a, b indicates ΔAIC >2 between candidate models.
2.6. Figures and Tables

Table 2.1: Factors used in final design of experiment. A complete cross between Warming and Pollination was not possible due to the small number of plants available within the Warmed (OTC) treatments. Pollination treatments: Control plants were not altered. Pollinated plants were hand-pollinated. Excluded plants had 1mm mesh net Excluder bags placed over flowers to exclude pollinators. Selfed plants had 10µm cloth Excluder bags placed over flowers to exclude all external pollen. Selfing treatments were not applied to *S. arctica* because the plants are dioecious.

*Salix arctica*

<table>
<thead>
<tr>
<th>Pollination</th>
<th>Control</th>
<th>Pollinated</th>
<th>Excluded</th>
<th>Selfed</th>
<th>Total</th>
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<tbody>
<tr>
<td>Warming</td>
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<tr>
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<td>Total</td>
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*Dryas integrifolia*

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</tr>
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<td>Total</td>
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*Papaver radicatum*

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<th>Pollinated</th>
<th>Excluded</th>
<th>Selfed</th>
<th>Total</th>
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</thead>
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<tr>
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<td></td>
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<tr>
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<td>-</td>
<td>-</td>
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</tr>
<tr>
<td>Total</td>
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<td>10</td>
<td>10</td>
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Table 2.2: Models explaining flower number in response to warming and pollen manipulation. - indicates no important effect by any treatment factors. For specific AIC values, see Table A.2.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Flower#</th>
<th>Flower#</th>
<th>Biomass</th>
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<tbody>
<tr>
<td>Salix</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>OTC:pollen</td>
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<td></td>
</tr>
<tr>
<td>Salix pollen</td>
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<td></td>
<td></td>
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<td>Dryas</td>
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</tr>
<tr>
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<td>+Warming;Pollen</td>
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<tr>
<td>Papaver</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>OTC:pollen</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Papaver pollen</td>
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<td>-</td>
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</tbody>
</table>

Table 2.3: Models explaining seed number, mass, and germination in response to warming and pollen manipulation. - indicates no important effect by any treatment factors, while subscripted text indicates marginal effect ($\Delta$AIC<2). For specific AIC values, see Table A.3 and A.4.

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<td>Pollen</td>
<td>Pollen</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>OTC:pollen</td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Salix pollen</td>
<td></td>
<td>Pollen</td>
<td>-</td>
<td>Pollen</td>
</tr>
<tr>
<td>Dryas</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>Warming+Pollen</td>
</tr>
<tr>
<td>OTC:pollen</td>
<td></td>
<td></td>
<td>+Pollen;Warming</td>
<td></td>
</tr>
<tr>
<td>Dryas pollen</td>
<td></td>
<td>-</td>
<td>-</td>
<td>Pollen</td>
</tr>
<tr>
<td>Papaver</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>OTC:pollen</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Papaver pollen</td>
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</table>
Chapter 3

Effects of Open-Top Chambers on Flowering Patterns and Potential Insect Visitation

3.1 Introduction

Insects are key components of nearly all terrestrial ecosystems worldwide, acting as consumers, predators, parasites, and decomposers (Price, 1997; Schowalter, 2006), and their activities are well-known to contribute to ecosystem function (Holling, 1973; Losey and Vaughan 2006). Arctic insects are no less important (Strathdee and Bale, 1998), and act as consumers (Morewood and Ring, 1998), decomposers, predators (Oliver, 1963), parasitoids (Kukal and Kevan, 1987), and pollinators (Kevan, 1972b). Some authors indicate that the importance of insects in Arctic ecosystems is understated (Roslin et al., 2013; Gillespie et al., 2013). Insects represent the bulk of the total animal diversity of the Arctic (Chernov, 1995), but in general are not well studied.

As climate change increases air temperature and advances summer snow and ice melt in the Arctic, the structure and function of most ecosystems will be altered. This will be seen in a variety of ways, including increased net ecosystem production (Welker et al., 2000; Oberbauer et al., 2007; Lund et al., 2012), nutrient cycling (Epstein et al., 2000), changes in plant biomass (Hill and Henry, 2011), and timing of reproductive events (Wookey et al., 1993; Oberbauer et al., 2013). Animals will alter the timing of their reproduction, migration, and hibernation, notable examples being birds (Gaston et al., 2005), ungulates (Post and Forchhammer, 2008), and insects (Franzén and Ockinger, 2012). Niche-based models of range expansion are likely insufficient to represent actual transition, and experimental methods are necessary to predict responses to climate change (MacDonald, 2010;
3.1. Introduction

Van der Putten et al., 2010). Warming experiments such as those done by researchers involved in the International Tundra Experiment (ITEX) are an attempt to study the effect of climate change on plant communities, mainly using open-top chambers (OTCs). While these methods are generally sufficient to represent climate change scenarios in plant communities (Marion et al., 1997; Hollister and Webber, 2000), their effects on animals, specifically insects, are not well-quantified. Some authors have found that OTCs change the activity of soil and plant-dwelling insects (Ring, 2001; Dollery et al., 2006; Gillespie et al., 2013). It is generally assumed that the greater air temperatures within OTCs accelerates the growth and reproduction of these insects, given that the activities of insects are highly dependent on temperature (Danks et al., 1994; Danks, 2004). However, Moise and Henry (2010) suggest that plot-based manipulations are unrealistic for estimating animal effects within global change experiments, and others have implicated that OTCs exclude pollinating insects from plants during crucial parts of their flowering period (Jones et al., 1997; Stenström et al., 1997).

The detailed composition of plant-pollinator networks in the Arctic is not well known, except for a few studies (Mosquin and Martin, 1967; Kevan, 1972b; Olesen et al., 2008; Franzén and Öckinger, 2012). Changes to the network over the growing season are often unstudied, as the continuous monitoring of flowering plants and insects is tedious work. Most studies focus only on a single species of plant (Philipp et al., 1990, 1996; Stenström et al., 1997) or a single group of visiting insects (Kevan and Kevan, 1970; Richards, 1973; Pont, 1993). There are very few studies examining how climate change has altered plant-pollinator networks, and even fewer in the Arctic (Franzén and Öckinger, 2012; Høy et al., 2013). Dipterans (true flies) are often the dominant pollinator in Arctic plants (Mosquin and Martin, 1967; Elberling and Olesen, 1999; Robinson, 2011), but bumblebees (Bombus spp.) are often cited as being important pollinators (Richards, 1973; Lundberg and Ranta, 1980), as they can withstand fluctuations in air temperature, wind, and precipitation more readily. Furthermore, there have been no studies other than Ring (2001) that attempt to systematically quantify the effect of OTCs on ambient insect populations.

In this study I quantify the structure of a High Arctic plant-pollinator network, and examine the evolution of the interactions over the growing season. In particular, I examine how OTCs alter both the level of available flowers and the levels of available visiting insects over the course of the growing season. I discuss how well these OTC-induced changes may represent future ecological interactions, particularly plant-pollinator interactions. Finally, I examine the plant-visitor interaction rates, and show how differences
3.2 Methods

3.2.1 Flowering Community

The site and location are described in Chapter 2. The flowering plant community (non-graminoid) is composed primarily of *Salix arctica*, *Dryas integrifolia*, *Stellaria longipes* and *Papaver radicatum*, with a small number of *Draba lactea*, *Saxifraga oppositifolia*, *Saxifraga cernua*, *Saxifraga tricuspidata*, *Cassiope tetragona*, and *Pedicularis capitata* individuals. *Salix arctica*, *D. integrifolia*, and *P. radicatum* are described in Chapter 2.

*Stellaria longipes* Goldie subsp. *longipes* is a long-lived perennial that grows in a variety of habitats, and is a successful colonizer (Chinnappa et al., 2005). In primary successional sequences in the Arctic, *S. longipes* is often one of the first colonizers, along with *Salix arctica* and *Saxifraga oppositifolia* (Breen and Lévesque, 2006), but is also present in undisturbed communities. Flowers are small, 10-petaled, 5-7mm white flowers (Figure 3.1), and plants can be gynodioecious (female-only as well as bisexual flowers). Often their ratio of bisexual to female-only flowers changes from year-to-year or within the flowering season, depending on environmental conditions (Philipp, 1980). They are phenotypically very plastic, and can adapt to a large variety of environmental conditions due to their polyploidy and large genotypic variability (Dang and Chinnappa, 2007).

To gauge flower availability to insect visitors, I monitored flowers in plots over the growing season (14 Control, 14 OTC plots), counting all open blossoms with non-withered anthers and stigmas, where the petals had not yet begun to wither. This was done in both control and OTC plots, on the same days that insect sampling was conducted. Any receptive, open, non-graminoid flower was counted. Individual catkins of *Salix arctica* were counted as a single blossom.

3.2.2 Insect Community

To sample the overall flying insect community, I followed the CANPOLIN (2009) bowl trap protocol using sets of white, yellow, and blue bowls. These 15 cm plastic bowls were attached to the ground using metal tent pegs. Tent pegs were necessary because wind storms of up to 80 km/h occasionally occur in the valley. For the 15 treatment bowl traps, a single bowl was
3.2 Methods

placed in each of the 14 OTCs (one of the OTCs contained 2 bowls), the
colour of the bowl being systematically assigned along the length of the
site. For the control bowl traps, 5 of each colour was placed outside the
OTCs in a 140 m transect along the site, where bowl colour was repeated
systematically along the transect. This sampling procedure took place at
the xeric shrub community described in Muc et al. (1989) and Svoboda and
Freedman (1994a). I conducted insect sampling every two days, reducing
this to three days during the latter part of the season when insect activity
was visibly decreased, and no receptive flowers were available.

The bowls were filled with (unscented) soapy water during the morning of
the sampling days. The morning following the sampling day, the contents of
the bowls were poured through a 0.5 mm mesh strainer to catch arthropods
present in the bowls. Mites and Collembola may have escaped through this
size of mesh, but these were not the focus of my study.

Bowl traps do not give any information about taxa of insects that visit
flowers, so I conducted targeted netting of visiting insects along the site
outside the OTCs. Field workers walked a patrol route across the site,
capturing any visiting insects they saw on flowers. The length of time during
the patrol was recorded, and patrols were repeated over the course of the
day by different workers. Insects I failed to capture were identified as far as
visually possible (usually to Family).

All arthropods were stored in 70% ethyl alcohol and transported to the
lab at UBC in mid-August. Insects were pinned, identified, and labeled
as precisely as possible, usually to Genus (Chironomididae, Mycetophilidae,
Sarcophagidae, Tachinidae, and Ichneumonidae were only identified to Fam-
ily). Soft-bodied insects, minute insects, or arthropods such as spiders were
not identified, as they were rarely encountered on flowers, their abundances
were low, and their populations were considered to be beyond the scope of
the project.

3.2.3 Statistical Analyses

To test if the composition of flowers was different inside and outside of the
OTCs, I used non-metric multi-dimensional scaling (NMDS) to reduce the
dimensionality of my flower count data and a multivariate analysis of vari-
ance (MANOVA) to test for differences between OTC and control “flower
communities”. This was done using a permutation test of Bray-Curtis sim-
ilarity, which partitions variance between variables. For my analysis, I used
warming treatment and day of year as factors. Because there were many
plots that had no flowers and NMDS techniques are ill-suited for dealing
3.2. Methods

with “empty communities”, flower density for OTC and control was taken as an average of the 14 warmed and control plots. Days where no flowers were recorded in any plots were not used.

To test whether OTCs influence overall flower density at the plot scale, I used Generalized Estimating Equations (GEE). GEEs are described in Liang and Zeger (1986) and Hardin and Hilbe (2003), and are essentially a version of Generalized Linear Models (GLM) that allow for more elaborate correlation structures, such as between subject or between measurement period. In this case I used Plot as a grouping structure, and used an auto-regressive model of order 1 (AR-1) to model correlation between the same plot on different days.

Tests for day of maximum flowering were done in the following manner: the days of peak flowering for all non-zero plots were tallied, then a Student’s T-test of equal means was used to compare between warmed and control days. If the data did not meet the assumptions of a T-test, a non-parametric Kruskal-Wallis test of parameter equal distribution was used. I tested induced changes in day of first flower, the day of last flower, and the length of the flowering season (Day of Last Flower − Day of First Flower). If the day of first flower for a plot was on first day of observations, that plot was not used, and similarly if the day of last flower was on the last day of observations, that plot was also not used.

Similar to the examination of the flower community, I used MANOVA to test changes in insect catches between OTC and Control plots. All community analyses were done at the taxonomic level of Family, because this was the common level to which I was able to identify all specimens. I used counts of bowl-trapped insects as the “community” data, and compared change in catches from OTC and Control plots, between bowl colours, and across the length of the season. To examine the effect of OTCs on bowl-trap catches within a single family, I also used GEEs, with an AR-1 structure to model correlation between catch rates on different days.

Even though patterns of preference appear clear in terms of catch rates, these catch rates may be conflated by flower and insect abundance. In other words, if there were a higher number of receptive flowers available, or a larger number of insects present on that day, I would expect a higher catch rate. This can also be viewed in light of MacArthur’s “principle of equal opportunity”, where limited resources are used in proportion to their abundance (MacArthur, 1972). In order to examine the preference of flower visitors in relation to abundance, I scaled the catch rate by insect availability to examine the interaction rate (catch rate/bowl trap catches, used as an estimate of population size) for each group of pollinators. Interaction rates are
3.3. Results

not directly comparable between groups of pollinators because individual
groups of pollinators will be differentially attracted to bowl traps, but they
are roughly comparable within each group. The data met the assumptions of
simple linear regression once transformed, so I modeled interaction rates us-
ing flower availability, insolation and wind speed (air temperature was found
to be collinear with insolation). No *Bombus polaris* were caught in the bowl
traps, so I could not get any general estimates of abundance throughout the
season, so I used the catch rate instead of the interaction rate. I could not
transform the data to meet the assumptions of a linear model, so I compared
catch rates to individual variables using a Kendall rank-correlation test. I
realize that interspecific competition (Hocking, 1968) or facilitation (Heg-
land and Totland, 2005; Ghazoul, 2006) may occur between simultaneously
flowering plants, but a network study of this nature is complex and beyond
the scope of this work.

GEE computations were done using the *geepack* library (Halekoh et al.,
2006), NMDS and community analysis were done using the *vegan* library
(Oksanen et al., 2013), rank-order tests were done using the *Kendall* library
(McLeod, 2011), and the remainder was done in the *base* library in R (R
Core Team, 2013).

3.3 Results

3.3.1 Flower Availability

The flower community was significantly altered by OTC warming (p=0.05)
and date (p=0.004), but OTC warming explained only 4.4% of the variation,
while date explained 50.3%. This indicates that OTCs do alter the overall
composition of the flowering communities, but not nearly as much as day-
to-day changes over the season. Warming was only a significant predictor
if permutation tests were constrained by day of year, indicating that while
there are differences between OTC and control plots, these differences are
largely not detectable at the scale of the entire growing season. Figure 3.2
shows how the flower community changes over the course of the flowering
season using NDMS scores, which represents the composition of available
flowers in a multi-species space. The composition follows a clockwise arc as
the community progresses from *Salix* to *Dryas* to *Papaver-Stellaria*. Both
communities generally follow the same progression, but the warmed com-


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munity progresses faster.

Similar to other phenological studies (Wookey et al., 1993 Alatalo and
Totland, 1997; Jones et al., 1997), the timing of flower phenology was altered
3.3. Results

by the OTC treatments. The Day of First Flower (DFF) was significantly earlier in both *S. longipes* (p=0.05) and *P. radicatum* (p=0.0007) (Table 3.1), similar to the results of Mølgaard and Christensen (1997). Based on my past observations, and the findings of Hocking (1968) and Jones et al. (1997), I suspect that the day of first flower for *S. arctica* would also have been significantly earlier, but I was unable to begin surveys early enough in the season to formally test this.

In *S. arctica* ♀ (p=0.0005), and *D. integrifolia* (p=0.004), I found that experimental warming accelerated the Day of Peak Flowering (DPF) (Table 3.1). In *P. radicatum* and *S. arctica* ♂, I found changes in peak flowering were only marginally significant (p=0.09). In *S. longipes*, it was not shifted at all (p=0.41), but the senescence period was reduced. In other words, senescence occurred more quickly, but at approximately the same time of the season. The Day of Last Flower (DLF) was not altered in any species except for *S. arctica* ♂ (p=0.0008) and *D. integrifolia* (p=0.0002), in which it occurred earlier.

I found that the length of the flowering season of warmed plots was significantly shortened in *D. integrifolia*, and lengthened for *S. longipes* (marginally), and *P. radicatum*. Warmed plots had similar densities of *S. arctica* catkins (p=0.7, p=0.41) and *D. integrifolia* flowers (p=0.8) throughout the season. However, I found that warmed plots had a significantly higher flower density of *S. longipes* (p=0.002) and *P. radicatum* (p=0.02) (Figure 3.3).

### 3.3.2 Insect Community

#### General

The flying insect community was altered by OTC warming (p<0.001), bowl trap colour (p<0.001), and Day of Year (p<0.001). However, warming and bowl trap colour only accounted for only 3.2% and 2.8% of the variation, respectively, while day accounted for 50.4%. This indicates that while OTCs have an effect on the insect community composition, it is not very large in comparison to day-to-day variation over the growing season (see Figure 3.4a). To illustrate the seasonal trend better, I roughly divided the communities found in Control and OTC bowl traps into Early, Mid, and Late season (Figure 3.4b). In general, the insect community follows a clockwise pattern, but the variance is much more constrained during the peak of flowering (“Mid-Season”). The pattern becomes much more variable after the “Late Season”, especially in the OTC bowl traps.
3.3. Results

Using the bowl-trap data over the entire season, I found that OTCs tended to reduce bowl catch rates of all insect families sampled, including the dominant floral visitors ($p_{mcmc} < 0.001$), but not by a large amount on a per-bowl basis. However, this gives only a general sense of decreases, and does not address differences between families or genera. When I tested day-to-day bowl catch rates using a GEE, I found that OTCs significantly reduced the bowl catch rates ($p<0.0001$) for the five main families of insects observed, particularly for the Ichneumonidae, Noctuidae, and Syrphidae. This can be seen in Figures 3.5, 3.6, and Table 3.2, which show lower catches of all the dominant families of flying insects. In particular, Syrphidae catches were reduced by 80%. Ichneumonidae and Noctuidae were reduced by 70% and 50%, respectively. Finally, Dolichopodidae and Musidae were reduced by 25% and 20%, respectively.

Flower visitors

The most dominant flower visitors were flies (Diptera) in the families Syrphidae and Muscidae, followed by Bombus polaris (Hymenoptera: Apidae). Eupeodes curtus and Phaonia spp. were by far the most common visitors, followed by Platycneurus spp. and Drymeia spp. Bombus polaris, Melangyna arctica, and Eupeodes nigroventris were also found in abundance (Table 3.3).

In terms of hourly visitation rates, Muscidae were the dominant flower visitors during the early part of the flowering season (June to mid-July), while Syrphidae appeared more frequently during the late season (mid-July to August). Figure 3.7 displays the peaks in catch numbers graphically, and Muscidae seem to show a preference for D. integrifolia while Syrphidae seem to show a preference for P. radicatum (Table 3.4).

3.3.3 Interaction Rates

Syrphidae

Net catch rates (Catches/hr) of both Syrphidae and Muscidae on Dryas integrifolia were correlated with Muscid population (Kendall $\tau=0.24$, $p=0.02$) and Syrphid population (Kendall $\tau=0.55$, $p<0.0001$). The catch rate on all other flowering plants showed no relationship with insect population. Interaction rates (Net Catch Rate/Bowl Catch Rate) for Syrphidae were largely unaffected by overall floral density, except for P. radicatum ($p<0.0001$) and Stellaria longipes ($p=0.03$), which showed an increase in interaction rates at higher flower densities.
I also found that increased insolation tended to decrease Syrphidae interaction rates with \textit{P. radicatum} (p=0.02), implying that the Syrphidae seek out blossoms of \textit{P. radicatum} when insolation is lower, possibly for basking (Figure 3.9). Insolation and air temperature are correlated (r\textsuperscript{2}=0.39, p<0.0001), but I found that the model involving insolation was superior to the one involving air temperature (\textDelta AIC -4.1).

\textbf{Muscidae}

For the Muscidae, interaction rates were unaffected by overall floral availability, and tended to show comparable interaction rates at any surrounding density of flowers. Their interaction rates were also largely unaffected by wind speed and insolation.

\textit{Bombus polaris}

For \textit{Bombus polaris}, relatively few numbers of insects were netted in comparison to other pollinator clades (Figure 3.8). However, I found that similar to the Syrphidae, \textit{B. polaris} catches on \textit{P. radicatum} were positively influenced by overall flower density (p=0.02), but not by wind speed or insolation. I had too few observations to examine \textit{S. longipes} visitation by \textit{B. polaris}, and \textit{B. polaris} was not netted on the other dominant flower species, \textit{D. integrifolia} or \textit{S. arctica}. Figure 3.9 shows the interaction rate for \textit{Papaver radicatum} against flower density and insolation for both the Syrphidae and for \textit{Bombus polaris}.

\textbf{3.4 Discussion}

\textbf{3.4.1 Flower Availability}

During the summer of 2012, the OTC plots at the xeric shrub site were in their 21st year of continuous warming treatment. 2012 also represented one of the warmest years on record for the Canadian High Arctic, and also for Alexandra Fiord. Despite fairly consistent results across warmed Arctic sites (Klady, 2006; Elmendorf et al. 2012b; Oberbauer et al. 2013), interannual variability is an important component of studying Arctic ecosystems (Jones, 1995; Henry and Molau, 1997; Jones et al., 1997; Høye et al., 2007).

Some authors have examined “snapshot phenology” of plots during the peak flowering season (Wookey et al., 1995). Others have examined it at the plant scale over the season (Wookey et al., 1995; Stenström et al., 1997;
3.4. Discussion

Totland, 1999), but to my knowledge, there are no other Arctic studies that have examined flower availability at a plot scale continuously across an entire flowering season. However, several mid-latitude studies have examined flower availability at varying time scales (Holzschuh et al., 2007; Elliott, 2009). I found that OTCs altered flower availability in a variety of ways, but that generally differences between OTC and control plots were associated with the timing of flowering, and sometimes with overall density of flowers.

Because we did not arrive soon enough to begin measurements of *S. arctica*, I could not observe changes in the day of first flower or length of season. Hocking (1968) found that male plants tended to flower earlier than female plants. Other authors have found that OTC warming did not increase the day of first mature flower in plants of either sex of *S. arctica* (Jones et al., 1997), but this is subject to much interannual variation. I found that the OTC warming accelerated the day of peak flowering significantly in both male and female plants, which suggests that the day of first flower may also be earlier. The day of last flower was not altered, and overall flower density (per plot) was not altered, indicating that OTC warming affects the timing of flower production, but does not influence overall flower production in *S. arctica*.

OTC warming accelerated the phenological development of *Dryas integrifolia*. Other authors have reported similar results in *Dryas octopetala* (Wookey et al., 1993, 1995; Welker et al., 1997). My results were similar to results of the authors mentioned, in that the timing of first flower was not affected, but that advances in flowering became apparent soon after the early season. I also found that the day of last flower was advanced by six days in OTCs, and that overall flowering season was shortened by four days, indicating that visiting insects that rely on *D. integrifolia* may be forced to alter their diet under future scenarios.

OTC warming increased the per-meter flower density of *Stellaria longipes*, but did not alter the timing of flower production. *Stellaria longipes* has never been studied in the context of OTC warming, so these can be taken as preliminary predictions of future *S. longipes* flower densities, at least at similar xeric sites. This is relevant for the pollinator community, as *S. longipes* appears to be an important food source for the Syrphidae. Although I did not specifically examine feeding habits, I did observe large numbers of Diptera drinking nectar in the corolla of *S. longipes*. It produces large amounts of sweet nectar (Hocking, 1968), and Kevan (1973b) has shown that their nectar is a food source of parasitic wasps in the Arctic (Chalcididae, Braconidae, Ichneumonidae). To my knowledge, there is currently no literature on how *S. longipes* responds phenologically, structurally, or reproductively.
to induced warming, but this is an indication that it will likely respond positively under future warmed climates.

Warmed plots significantly shifted the flowering in *Papaver radicatum* earlier by six days on average, and showed an increased length of the overall flowering season by eight days. I also found that the overall density of *Papaver radicatum* flowers was increased in the warmed plots, but without measurements of plants per plot it is impossible to know whether this is from increased *P. radicatum* establishment, or rather increased reproductive effort. Klady et al. (2011) found that *P. radicatum* did not increase per-plant reproductive effort when experimentally warmed, which I also found in Chapter 2. My measurements were in flowers/m² while Klady et al. (2011) measured flower biomass/plant, but I suspect that some of the increase in flower density during the growing season is due to greater establishment in the warmed plots.

### 3.4.2 Insect Community

**Insects and OTCs**

While OTCs have been found to drive changes in Arctic plant communities by passive warming (Hudson and Henry, 2010; Elmendorf et al., 2012a), these changes are not expected to be seen to the overall insect community, because any accelerated emergence or feeding patterns of insects within OTCs would be dwarfed by the greater population of “unwarmed insects” from outside the chambers. Some authors have studied the behaviour of Hemiptera and larval Lepidoptera within OTCs, but this was only possible through use of a corral which confined the insects within the OTCs, and is essentially impossible to do with flying insects. Bocher (1996), Stenström et al. (1997), and Jones et al. (1997) all recognized that passive warming experiments such as OTCs may exclude insects from plants, and I have presented quantitative evidence to suggest that they were correct. Primarily this affects low-flying, medium-sized insects such as wasps and flies. I have observed flies and wasps encounter the angled plexiglass of the OTCs, right themselves after the collision, and fly away in a different direction after a short period. This appears to cause substantial reductions in catch rates, with an 80% reduction in Syrphidae catches and a 70% reduction in Ichneumonidae catches (see Results, and Table 3.2). However, the impacts of this exclusion are not well known. Of the five dominant insect families, I will review possible confounding effects found within OTCs that may be unrepresentative of future Arctic plant communities.
The reduction of Muscidae and Syrphidae is significant mainly in terms of reduction to pollination within OTCs. Both families of Diptera have been shown to be the dominant floral visitors in most Arctic regions (Kevan, 1972b; Pont, 1993), and their reduction in availability to plants within OTCs may provide unrealistic estimates of pollination rates within future ecosystems (Alatalo and Totland, 1997). However, reduction in visitation is more likely to affect the early season pollen-risk strategists such as *Saxifraga oppositifolia* (Molau, 1993), as plants that flower later tend to be associated with lower rates of self-incompatibility. I report similar results in Chapter 2, which indicates that late-flowering plants such as *P. radicatum* are fairly robust to changes in pollination.

The behaviour of other Arctic insects within warmed environments has been studied relatively little. Because Arctic insects are highly dependent upon their surrounding for thermoregulation (Danks, 1996, 2004), ground-dwelling invertebrates, particularly Arachnids, Collembola, Hemiptera, and larval Lepidoptera can be found in greater densities within OTCs (Richardson et al., 2002; Gillespie et al., 2013). They will stay inside of OTCs when given the opportunity, and Ring (2001) has found evidence that smaller Dipterans (Nematocera, Chironomidae, Empididae) also prefer OTCs. I found that OTCs influence the composition of the insect community on a day-to-day basis. In particular, larger insects such as Muscidae, Ichneumonidae, and Dolichopodidae are found less within OTCs. This is particularly important because Ichneumonidae and Dolichopodidae are ecologically important in many ecosystems as parasitoids and predators, respectively (Jervis and Kidd, 1986; Gelbić and Olejníc, 2011). In Arctic insect communities this is no less true. For example, at the Alexandra Fiord site, the dominant Lepidopteran grazer *Gynaephora groenlandica* is subjected to mortality rates of up to 95% due to Ichneumonid and Tachinid parasitoids (Kukal and Kevan, 1987).

From this, I imply that OTCs likely cause artificial trophic imbalances by excluding ambient predatory or parasitic insects, while promoting the activity of smaller soil, plant, or ground-dwelling insects. Because I was primarily interested in pollinating insects within OTCs, smaller unidentified arthropods such as Nematocera, small Braconidae, and Acari (Mites) were largely overlooked for the purpose of this study, but may be highly influential on the Hemiptera (Aphids) that feed on the plants within the OTCs. Dollery et al. (2006) have shown that OTC warming increases populations of soil-dwelling mites, Chironomid larvae, and plant-feeding aphids, while reducing Hymenopteran parasitoids. While not explicitly sampling for parasitoids, Gillespie et al. (2013) also found that aphids increased dramatically in the
first years that OTCs were present, but then were reduced to normal levels in later years. They attribute this to a corresponding increase in soil-dwelling predators such as mites and spiders, but it is uncertain if flying predators would increase their growth and phenology in the same way in future climate scenarios. Much of the emergence and life history of Dolichopodidae and other predatory Arctic insects is essentially unknown, and should be a topic of future study.

Flower-visiting Insects

Arctic flowering plants have relatively robust pollination strategies, and can produce seeds in absence of pollinating insects (Chapter 2). I suspect that the insects are more heavily dependent on the food and energy gained from flowers.

I found that the dominant visitors of flowers are overwhelmingly Diptera of the family Muscidae and Syrphidae, followed by the Bombus polaris (Hymenoptera: Apidae). While B. polaris is well-noted as an Arctic and alpine pollinating species (Bergman et al., 1996; Philipp et al. 1996), it is relatively uncommon in terms of actual catch rates. The per-visit efficacy of B. polaris compared to the common Arctic Syrphidae and Muscidae such as Euepeodes curtus or Phaonia spp. is not known, but is assumed to be higher in B. polaris simply due to body size and foraging behaviour (Sahli and Conner, 2007). While it is generally accepted that bees are more effective pollinators than flies (Herrera, 1987), visitation by flies can provide ample pollination, provided enough visitors are available (Mesler et al., 1980; Berenbaum et al., 2007), and this appears to be the case here. Other authors have identified that flies are often an over-looked component of many pollination systems (Larson et al., 2001; Kearns, 2001; Lundgren and Olesen, 2005), and I suggest that further study should be devoted to them, especially in Arctic and alpine ecosystems that are relatively free of bee pollinators.

I did not find evidence to suggest that S. arctica are dependent on insects for pollination, as I observed very low rates of visitation to female S. arctica plants. The female catkins are also capable of making seeds (albeit lower numbers) when insects are excluded from them (Chapter 2). However, insects may be more dependent on them for a source of food, as queens of Bombus polaris were observed gathering pollen from male S. arctica early in the season when no other pollen sources were available. The queens made no systematic attempt to visit female catkins, and concentrated their foraging on pollen-laden male catkins (>30 consecutive male catkins were visited, and approximately equal numbers of male/female catkins were available;
personal observation). By the time that Muscidae and Syrphidae emerge, *S. arctica* are largely senesced and non-receptive to pollen. It is possible that early-season visits are important for *S. arctica* (Molau, 1993), but I did not find large numbers of insects present that would facilitate pollination other than the occasional *B. polaris*.

I observed Syrphidae and Muscidae feeding from the deep nectaries of *D. integrifolia*, as well as feeding directly on the pollen from stamens. These represent an important food source for insect visitors, especially because they have some of the most nutrient-rich nectar of all Arctic flowering plants (Hocking, 1968), but without detailed observations it is difficult to assess whether pollen or nectar is the main attractant for the visiting insects. Hocking (1968) found that within the same plant species, nectar in Arctic flowers is much more concentrated at high latitudes, and that equal quantities were present in covered and uncovered flowers at high latitudes. He used this to show that between-plant competition for pollinators is higher in Arctic plants than in mid-latitude plants (Hocking, 1968). Kevan (1973a) views nectar in Arctic flowers as more of an attractant for Lepidoptera, and Chironomidae, but has noted that about 40% of the insects in the Arctic have been found imbibing nectar.

Catch rates on *D. integrifolia* scaled with insect abundance (bowl trap catches) for the Syrphidae and Muscidae. Large numbers of Muscidae visited *D. integrifolia*, most likely to forage for nectar and pollen reserves, as well as for warmth. However, I found that for both catch rates and interaction rates were not related to flower abundance for *D. integrifolia*, implying that their resources are not critical for their insect visitors.

The more likely attractant for most flower visitors is pollen and warmth. *Papaver radicatum*, does not produce nectar, yet I caught almost twice the number of visitors on *P. radicatum* than *D. integrifolia*. Some of this is due to timing of insect and flower emergence, but even at low densities, *P. radicatum* appear to be the most attractive blossom for insect visitors, especially the Syrphidae. Pollen production and availability in *D. integrifolia* and *P. radicatum* has not been quantified, but corolla temperatures of *D. integrifolia* are much less than *P. radicatum* (Kevan, 1972b, 1975). Kevan (1973a) discussed floral attraction in Arctic plants, and indicated that flower size is a key feature of insect attraction in Arctic plants because it is linked to both visual attraction and to the thermal regime within the corolla. I also found that interaction rates of *P. radicatum* with the Syrphidae decreased at higher rates of insolation, indicating that they likely visit the flowers at lower temperatures to gain thermal energy. This is contrary to the results of Totland (1994) who found that visitation rate was correlated with temper-
3.4. Discussion

atures. This is likely due to climatic differences between Alexandra Fiord, Nunavut and Mount Sandalsnut, Norway. Alexandra Fiord is in the High Arctic (78.9° N), and diurnal insolation and temperature are more constant than southern latitudes, even during the “night time”, whereas Mt. Sandalsnut (60.4° N) is subject to large variation in solar radiation and temperature over the course of the day.

I also found that interaction rates for Syrphidae and the catch rate for Bombus polaris tended to scale with abundance for flowers of P. radicatum, implying that they are limiting resources (sensu MacArthur (1972)) for these insects. Syrphidae are known to feed on pollen during the time of egg formation (Kevan, 1973a). Bombus polaris queens and workers forage for nectar pollen to provide for their brood, and have been shown to feed on all the flowers regarded in this study (Richards, 1973). Richards (1973) reported that the queens of B. polaris tended to visit Salix arctica and Saxifraga oppositifolia, while the workers visited Dryas integrifolia, Pedicularis capitata and Cassiope tetragona. Interaction rates for the Syrphidae with Stellaria longipes also scaled with floral abundance, implying they are also limiting resources. S. longipes is known to produce large amount of sweet-smelling nectar and pollen. However, the flowers are much smaller and shorter than the flowers of P. radicatum, making them less attractive. They also provide very little thermal benefits in comparison to P. radicatum. In this case, it is most likely that pollen (and possibly nectar) are limiting resources for the Syrphidae.

One of the reasons for the lack of B. polaris visits to anything but P. radicatum at my site may have been that the composition of available flowers at other sites was more attractive to B. polaris, but this is beyond the scope of my study. Other authors have found that insolation and air temperature tended to increase visitation in other Arctic species of Bombus (Lundberg, 1980; Bergman et al., 1996), but I failed to find any trend, possibly because I focused on overall patterns rather than diurnal patterns in visitation, as well as climatic differences between study sites. Both Bergman et al. (1996) and Richards (1973) found that Bombus queens were able to forage for longer at lower temperatures, simply because of the higher internal temperatures associated with their larger body size. I did not catch any queens of B. polaris. Because of the relatively small sample size of B. polaris netted (18 total), and the lack of overall population estimates, the relationship of between overall visitation and flower density is tenuous, and merits further study.
3.5 Conclusion

Flower production at a per-plot basis was altered strongly for most flowering plant species, and has implications for the structure of future plant-pollinator interactions. I demonstrate that:

- OTCs significantly change the structure of the flowering plant community on a day-to-day basis.
- The day of peak flowering for *Salix arctica* and *Dryas integrifolia* tended to be earlier in the warmed plots.
- The length of the overall flowering season was shorter for *Dryas integrifolia* and longer for *Papaver radicatum* in the warmed plots.
- Flower density was higher for *Stellaria longipes* and *Papaver radicatum* in the warmed plots.

Insect activity was also altered within OTCs, particularly for the dominant visitors. I show that:

- OTCs significantly change the structure of the flying insect community on a day-to-day basis, and likely exclude insect predators and parasites.
- Bowl-trap catches of nearly all groups of flying insects were significantly reduced over the growing season in the warmed plots.
- The most dominant insect visitors were Syrphidae and Musicidae, with a few *Bombus polaris*.
- Syrphid flies and *Bombus polaris* demonstrated temperature and availability-dependent visitation to *Papaver radicatum*. They tended to be caught at higher rates when flower density was high and temperatures were low.

OTCs have been shown to strongly alter the dynamics of flowering in Arctic plants (Wookey et al., 1993; Welker et al., 1997; Mølgaard and Christensen, 1997; Stenström et al., 1997; Alatalo and Totland, 1997; Klady et al., 2011), and similarly I found that OTCs alter the timing and magnitude of flowering in Arctic plants. While this is of interest in the context of future growth and range extensions, it is also of interest in the context of future ecological interactions. Climate change is expected to result in trophic mismatches (Post and Forchhammer, 2008; Post et al., 2009), including insect
3.5. Conclusion

outbreaks (Jepsen et al., 2008, 2011). It has been suggested that changes in insect emergence may result in plant/pollinator mismatches (Donnelly et al., 2011; Straka, 2012) and it is possible that mismatches could occur across the Arctic (Høye and Forchhammer, 2008; Hegland et al., 2009; Høye et al., 2013). However, the extent of this is not known, given that both insect and flower phenology in the Arctic tends to be related to snowmelt (Danks et al., 1994; Høye and Forchhammer, 2008; Ávila-Jiménez and Coulson, 2011; Oberbauer et al., 2013). Long-term records of insect emergence and phenology are lacking, especially in the Arctic, but Høye et al. (2013) have recently demonstrated that a phenological mismatch between Arctic plants and pollinators is indeed occurring, and show that the consequences are more severe for late-emerging flower visitors. Their observations do not include actual visitor observations, but are still valuable in terms of community data.

I found that *Papaver radicatum* flowers are a limiting resource to visiting *Bombus polaris* and Syrphidae. Additionally, I found evidence that Syrphidae visit flowers for warmth, as well as pollen resources. This adds quantitative evidence to the observations of Hocking and Sharpin (1965), Kevan (1975), Totland (1996), and others (Philipp et al., 1996; Danks, 2004) who identified flower microclimate as an important insect attractant along with scent, colour, and food resources. Considering that the corollas offer insects a food-laden microclimate on par with that of an OTC, it is no wonder that they seek out these blossoms! Lõve (1969), Kevan (1972a), and Mølgaard (1989) have studied how flower colour, temperature, and heliotropism are related in *P. radicatum*, but have not explicitly linked their studies to insect attraction. *Papaver radicatum*, and other similar heliotropic cup-shaped flowers, should be further studied at additional Arctic and alpine sites to understand how selection operates on warmth and colour.
3.6 Figures and Tables

Figure 3.1: *Stellaria longipes* Goldie subsp. *longipes* produce 5-7mm 10-petaled bisexual white flowers. They produce sweet smelling nectar and yellow pollen. They are visited by Diptera and occasionally *Bombus polaris*. 
Figure 3.2: NDMS ordination of flower communities over the growing season in warmed and control plots.
3.6. Figures and Tables

Figure 3.3: Daily flower densities for a) *Salix arctica* male, b) *Salix arctica* female, c) *Dryas integrifolia*, d) *Stellaria longipes*, and e) *Papaver radicatum*, in both warmed and control plots. 14 warmed and 14 control plots were monitored.
3.6. Figures and Tables

Figure 3.4: NDMS ordination of insect communities showing a) changes in NMDS scores over the season in warmed and control plots, and b) grouped into early, mid and late season communities. Abundances were averaged for each day between bowl colours, and split by warming treatment.
3.6. Figures and Tables

Figure 3.5: Daily bowl catches of a) Muscidae, b) Ichneumonidae, c) Dolichopodidae, d) Noctuidae, and e) Syrphidae over the flowering season in warmed (OTC) and control plots.
Figure 3.6: Total catch of all insects over the growing season in warmed (OTC) and control plots.
Figure 3.7: Hourly catch rate of a) Musidae, b) Syrphidae, and c) Bombus visitors on flowers of the four main plant species.
Figure 3.8: Total net catches of insect visitors outside of OTCs over the entire flowering season.
Figure 3.9: Factors influencing the *Papaver radicatum* interaction rate (Netting Catch Rate/Population Estimate) for the a,b) Syrphidae and c) *Bombus polaris*. P-value for *B. polaris* uses a Kendall rank-test ($r^2$ not defined).
Table 3.1: Results of tests for flower response to warming, along with p-values for tests of significant difference (Student’s T or Kruskal-Wallis). Changes in the day of first flower (DFF), peak flower (DPF), last flower (DLF), and season length (Len.) of all species are shown, as well as overall changes in density (Dens (flowers/m²)). For DFF, DPF, and DLF, numbers indicate how many days the event was shifted, with negative numbers indicating an earlier date. Len. represents the change in length of the flowering season.

<table>
<thead>
<tr>
<th>Plant Species</th>
<th>DFF</th>
<th>p</th>
<th>DPF</th>
<th>p</th>
<th>DLF</th>
<th>p</th>
<th>Len.</th>
<th>p</th>
<th>Dens.</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Salix arctica(♂)</td>
<td>n/a</td>
<td>n/a</td>
<td>-3.7</td>
<td>0.0008</td>
<td>-6.0</td>
<td>0.0008</td>
<td>n/a</td>
<td>n/a</td>
<td>-0.70</td>
<td>0.70</td>
</tr>
<tr>
<td>Salix arctica(♀)</td>
<td>n/a</td>
<td>n/a</td>
<td>-4.6</td>
<td>0.0005</td>
<td>-1.1</td>
<td>0.37</td>
<td>n/a</td>
<td>n/a</td>
<td>-3.22</td>
<td>0.41</td>
</tr>
<tr>
<td>Dryas integrifolia</td>
<td>-1.7</td>
<td>0.18</td>
<td>-3.7</td>
<td>0.004</td>
<td>-6.0</td>
<td>0.0002</td>
<td>-4.2</td>
<td>0.04</td>
<td>-0.97</td>
<td>0.80</td>
</tr>
<tr>
<td>Stellaria longipes</td>
<td>-4.8</td>
<td>0.05</td>
<td>-1.6</td>
<td>0.41</td>
<td>0.3</td>
<td>0.63</td>
<td>5.1</td>
<td>0.09</td>
<td>4.79</td>
<td>0.02</td>
</tr>
<tr>
<td>Papaver radicatum</td>
<td>-5.9</td>
<td>0.0007</td>
<td>-2.7</td>
<td>0.09</td>
<td>1.8</td>
<td>0.61</td>
<td>7.7</td>
<td>0.006</td>
<td>1.51</td>
<td>0.02</td>
</tr>
</tbody>
</table>
Table 3.2: Differences in average catches between Control and OTC Bowl Traps over the five most abundant insect families (all other families had overall numbers too low to test using a GEE). Numbers under Treatment are in catches per pay over the entire growing season.

<table>
<thead>
<tr>
<th>Group</th>
<th>Treatment</th>
<th>p-value</th>
<th>Total Catches</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Control</td>
<td>OTC</td>
<td></td>
</tr>
<tr>
<td>Diptera: Muscidae</td>
<td>58.33</td>
<td>47.25</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Hymenoptera: Ichneumonidae</td>
<td>25.27</td>
<td>7.14</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Diptera: Dolichopodidae</td>
<td>4.56</td>
<td>3.38</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Lepidoptera: Noctuidae</td>
<td>5.86</td>
<td>2.91</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Diptera: Syrphidae</td>
<td>2.18</td>
<td>0.42</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

Table 3.3: Abundance of netted insect species over the entire growing season.

<table>
<thead>
<tr>
<th>Order: Family</th>
<th>Species</th>
<th>♀</th>
<th>♂</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Diptera: Syrphidae</td>
<td><em>Eueodes curtus</em> (Hine, 1922)</td>
<td>180</td>
<td>0</td>
<td>180</td>
</tr>
<tr>
<td>Diptera: Muscidae</td>
<td><em>Phaonia</em> spp.</td>
<td>37</td>
<td>63</td>
<td>100</td>
</tr>
<tr>
<td>Diptera: Syrphidae</td>
<td><em>Platycheirus</em> spp.</td>
<td>34</td>
<td>0</td>
<td>34</td>
</tr>
<tr>
<td>Diptera: Muscidae</td>
<td><em>Drymeia</em> spp.</td>
<td>27</td>
<td>5</td>
<td>32</td>
</tr>
<tr>
<td>Hymenoptera: Apidae</td>
<td><em>Bombus polaris</em> Curtis, 1835</td>
<td>19</td>
<td>0</td>
<td>19</td>
</tr>
<tr>
<td>Diptera: Syrphidae</td>
<td><em>Melangyna arctica</em> (Zetterstedt, 1838)</td>
<td>12</td>
<td>0</td>
<td>12</td>
</tr>
<tr>
<td>Diptera: Syrphidae</td>
<td><em>Eueodes nigroventeris</em> (Fluke, 1933)</td>
<td>11</td>
<td>0</td>
<td>11</td>
</tr>
<tr>
<td>Diptera: Empididae</td>
<td><em>Rhamphomyia</em> spp.</td>
<td>3</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>Diptera: Culicidae</td>
<td><em>Aedes</em> spp.</td>
<td>1</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>Diptera: Syrphidae</td>
<td><em>Eueodes lapponicus</em> (Zetterstedt, 1838)</td>
<td>3</td>
<td>0</td>
<td>3</td>
</tr>
</tbody>
</table>
### 3.6. Figures and Tables

Table 3.4: All flower-insect interactions observed throughout the flowering season, ranked by frequency.

<table>
<thead>
<tr>
<th>Flowering Plant</th>
<th>Papaver radicatum</th>
<th>Dryas integrifolia</th>
<th>Stellaria longipes</th>
<th>Salix arctica ♀</th>
<th>Salix arctica ♂</th>
<th>Saxifraga tricuspidata</th>
<th>Cerastium alpinum</th>
<th>Draba lacera</th>
<th>Saxifraga nivalis</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Insect Visitor</strong></td>
<td></td>
<td></td>
<td></td>
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<td>0</td>
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<td><em>Boloria</em> chariclea</td>
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<td>0</td>
<td>0</td>
<td>0</td>
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<td>109</td>
<td>38</td>
<td>6</td>
<td>5</td>
<td>3</td>
<td>3</td>
<td>1</td>
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Chapter 4

Conclusions

Experimental studies on flower pollination in the High Arctic are rare (Kevan, 1972b), and very few of them deal explicitly with the topic of warming and pollination changes (Stenström and Molau, 1992). In this study, I experimentally altered pollination of flowering plants, and demonstrated that any pollination deficits induced by open-top chambers (OTCs) are likely to be insignificant in an Arctic ecosystem. *Salix arctica* demonstrated increased seed production with hand-pollination, and decreased seed production when insects were excluded, but OTCs do not appear to alter this in any significant way. Warming and pollination did not alter *S. arctica* germination rates significantly. *Dryas integrifolia* altered its flower production under warmed conditions, producing more flowers/g of above-ground biomass (AGB) when warmed. I also found that germination rates of *D. integrifolia* increased when pollinated outside of the warming treatments, or when warmed by an OTC, but that pollination and warming effects are not additive. *Papaver radicatum* proved resilient to changes in pollination and OTC warming, and did not alter its flower production, seed production, or germination rates in response to any treatment. By demonstrating this, I further validate the use of OTCs as a technique for studying climate change effects on reproduction in Arctic plant communities, and suggest that reproductive data from OTC-warmed Arctic plant communities are likely representative of future warmed climates.

The only exception to this may be early flowering self-incompatibly plants such as *Saxifraga oppositifolia*. (Stenström et al., 1997) showed that even minor changes in *S. oppositifolia* reproductive phenology occur at such early periods that pollination is reduced due to mismatches between pollinator emergence and flowering time. Other authors have implied that other early-flowering plants may be subjected to artificial pollen limitation within OTCs (Stenström and Molau, 1992; Jones et al., 1997). Both insect and flower emergence in Arctic ecosystems is generally tied to snowmelt rather than temperature (Molau, 1993; Walker et al., 1999; Totland and Alatalo, 2002; Dollery et al., 2006; Høye et al., 2007; Høye and Forchhammer, 2008), but Høye et al. (2013) identified that climate-induced changes in
phenology tend to shift phenology in late-flowering populations more than early-flowering populations.

I also examined the temporal structure of an Arctic plant-pollinator network, showing that the Syrphidae and the Muscidae constituted the most common floral visitors at the site, and that *Bombus polaris* plays a much reduced role (in terms of catches/hr). I showed that *Dryas integrifolia* does not appear to constitute a limiting resource for insect visitors, while *Papaver radicatum* is much more important to insect visitors, especially the Syrphidae. Using bowl-trapping, I demonstrated that OTCs significantly reduced catches of visiting insects, as well as other common flying insects. However, in the context of the results of experimental pollination manipulation, this reduction is probably not ecologically significant (except for early-flowering plants). Finally, I showed that OTC warming tended to shorten the flowering season for *D. integrifolia*, while lengthening the flowering season and increasing the flower density of *P. radicatum*. This implies that insect visitation could be enhanced later in the season under a future warmed climate, but much of this depends on the timing and duration of pollinator emergence.

Whether shifts in plant phenology will actually decouple Arctic plant-pollinator networks has yet to be seen, as most previous studies did not conduct actual netting or visitor observations, but used bowl or pit trap catch rates as a proxy for visitation. Bowl-trapping and pit-trapping are relatively easy ways to collect insects but yield no actual information on plant-insect interactions, and are more useful as a measure of relative population size. I did not find that insect population was a proxy of catch rates for any species except *Dryas integrifolia*, implying that visitation rates depend on other factors such as floral availability and environmental variables. Thus, future studies should examine actual visitation rates to better understand pollination rates, and avoid using bowl trapping rates as a “proxy of a proxy of pollination”.

Netting was not conducted inside of OTCs because of the danger it posed to the long-term study plants, the instrumentation present in the plots, as well as the inherent inaccuracy in comparing large area captures to small area captures. Measuring the actual visitation rate of insects to flowers inside and outside of OTCs is highly tedious work involving manually observing clusters of flower for long periods of time, recording visit rates of various insects. Video capture of visiting insects is a relatively new field, but has been used by some authors to investigate detailed insect visitation patterns (Steen and Thorsdatter, 2011; Lortie et al., 2012). I conducted time-lapse photography (5-second interval) of groups of flowers both inside and outside
the OTCs, using GoPro® HERO 1 cameras with an attached battery pack. These cameras were able to capture 12 hours of continuous data, and I conducted observations over the span of the growing season, concurrently with netting and bowl trapping. I have also devised an image-processing program that is able to determine threshold changes in intensity associated with dark-coloured insects landing on a brightly-coloured flower. The problem of flower motion due to wind is difficult to handle, but there are several classification schemes that may be able to handle this process. However, due to time constraints I was not able to complete an analyses of this method, and it is not part of this thesis.

In addition to monitoring plant-pollinator interactions, an effort should be made to further understand the ecology of Arctic insect communities, rather than solely descriptive studies. Aphids, midges, gall-wasps, stem-borers, leaf-miners, thrips, and caterpillars are all part of the Arctic herbivorous insect community, but their role has been far less studied than that of ungulate or avian grazers. Predatory flies and parasitic wasps most likely play a large role in regulating their populations (Kukal and Kevan, 1987). Spiders, in particular, are well-noted in Arctic arthropod collections (Leech and Ryan, 1972), but their ecological role has been studied to a very small extent. Hodkinson et al. (2001) links their activities to establishment and early plant community development, they form the base of the food web for many Arctic birds, and they are seen hunting insects throughout all parts of the snow-free season (personal observation). Clearly they play a role in the overall community, but this role is almost completely unstudied.

The effects of OTCs on plant growth and development are fairly well-established (Wookey et al., 1995; Jones et al., 1997; Welker et al., 1997; Molgaard and Christensen, 1997; Stenström et al., 1997), along with changes in community structure (Wookey et al., 1993; Hudson and Henry, 2010; Elmendorf et al., 2012a). However, changes in life history and population dynamics are not well understood in the context of OTC warming. As suggested by Cooper et al. (2004) and Müller et al. (2011), germination should be examined in the context of OTC warming to examine how induced warming changes rates of establishment. This is a key piece of ecological knowledge that has heretofore been unstudied. Seed germination studies in the context of Arctic warming often yield dissimilar results, which can be dependent on year-to-year and site-to-site variation (Molau and Shaver, 1997; Welker et al., 1997; Molau, 1997; Molgaard and Christensen, 1997; Müller et al., 2011; Klady et al., 2011). Milbau et al. (2009) found that seed germination occurred earlier, but not at higher rates, in warmed soils, implying that future seed establishment will take place earlier in the year.
Chapter 4. Conclusions

Depending on local moisture conditions, this has the potential to increase or decrease survival, as most seedling mortality occurs due to summer drought (Bliss, 1958; Bell and Bliss, 1980).

While changes to established plant communities are of great importance, new habitats will become available for colonization by plants as the Arctic warms, especially in the High Arctic. How these ranges will be colonized depends on reproduction and establishment by adjacent plants. In this way, it is important to understand the mechanisms that lead to establishment, including pollination, seed formation, and dispersal. Insects have the potential to alter patterns of pollination, especially in early-flowering plants. Thus, the continued study of plant-pollinator relationships is important to understanding aspects of future Arctic ecosystems.
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Bibliography


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Bibliography


## Appendix A

### Model Fitting

Table A.1: Model parameters used to infer Above-Ground Biomass (AGB).

<table>
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<tr>
<th>Model</th>
<th>Parameters</th>
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<td>$b_0=-5.02$, $b_1=0.82$, $b_2=0.50$, $b_3=0.98$</td>
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<td>Equation 2.3 (<em>Papaver radicatum</em>)</td>
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Table A.2: Likelihood criteria for flower production models. AIC$_c$ is AIC corrected for finite sample sizes (Burnham and Anderson, 2002). Terms in bold indicate the “best” model.

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<td>∆AIC$_c$</td>
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Table A.3: Likelihood criteria for seed production and seed mass models. Terms in bold terms indicate the “best” model.

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Table A.4: Likelihood criteria for seed mass and germination models. DIC is a Bayesian analogue of AIC used in Monte Carlo Markov Chain model selection. Terms in bold indicate the “best” model.

<table>
<thead>
<tr>
<th>Plant Species</th>
<th>Factors</th>
<th>Model Terms</th>
<th>Average Seed Mass</th>
<th>Germination Rate</th>
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<td></td>
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<td>AIC</td>
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<td>DIC</td>
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