ECOLOGICAL AND EVOLUTIONARY CONSEQUENCES OF EXPERIMENTAL AND NATURAL WARMING IN THE HIGH ARCTIC TUNDRA

by

Anne Donahey Bjorkman

B.A., Cornell University, 2004

M.Sc., The University of British Columbia, 2009

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF

THE REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

in

THE FACULTY OF GRADUATE AND POSTDOCTORAL STUDIES

(Geography)

THE UNIVERSITY OF BRITISH COLUMBIA

(Vancouver)

January 2015

Abstract

Recent increases in global temperatures are having substantial and often unpredictable consequences for the earth's biota. Species' responses to environmental change depend on 1) the ability of individuals to adjust *in situ* through phenotypic plasticity, 2) the rate at which evolutionary adaptation can occur, and 3) the ability of individuals to colonize newly suitable habitat through migration or propagule dispersal. Temperatures in the Arctic are increasing faster than anywhere else, yet our understanding of the consequences of climate change in the Arctic lags behind that of temperate ecosystems.

In this thesis, I ask whether plant phenology has advanced in response to 21 years of experimental and ambient warming at Alexandra Fiord, Ellesmere Island, Canada. While experimental warming led to earlier flowering in three out of four species, flowering dates in the control plots were unchanged or delayed despite more than 1 °C of ambient warming over the 21-year period, likely due to concurrent delays in snowmelt. This suggests that the effects of altered snowmelt patterns can counter the effects of warmer temperatures, even generating phenological responses opposite to those predicted by warming alone.

I then use reciprocal transplant experiments to test for evidence of evolutionary adaptation in two plant species to differing environmental conditions between two spatially proximate habitat types and in response to 18 years of experimental warming treatments. Results were consistent both with substantial phenotypic plasticity in response to site-to-site and year-to-year variability, and with evolutionary adaptation to site and treatment conditions. Differences across natural habitats

were stronger than those across experimental treatments. This indicates that plastic and genetic responses to climate change are likely to play an important role in structuring future Arctic plant communities.

Finally, I test the hypothesis that warming will confer a fitness advantage to "pre-adapted" southern immigrants relative to native populations. Despite experimental conditions 3-5 °C warmer than the historical average, local populations leafed-out earlier and attained greater maximum size than foreign populations in two of three species, suggesting that the success of southern immigrants may be limited by a lack of adaptation to novel non-climatic environmental conditions even when temperatures are suitable.

Preface

Part of the introduction to this thesis (Chapter 1) is adapted from an essay I wrote for the journal *Arctic*:

Bjorkman, A.D. 2013. Ecological and evolutionary consequences of experimental warming in a high Arctic tundra ecosystem. *Arctic*. 66(4): 512-515.

Outside contributions to this thesis are as follows:

Chapter 2 utilizes data from a long-term ecological experiment founded in 1992 by Dr. Greg Henry. These experiments were initiated with the goal of investigating the effect of experimental warming on plant phenology (among other responses). I contributed to five years of this data collection (2009-2013). Sarah Elmendorf formulated the idea for the Bayesian analysis, and she and I together developed the models. Alison Beamish contributed data for *Dryas integrifolia* in 2012 and assisted with the preliminary analyses. I conducted the final analyses and wrote the manuscript, with inputs from Sarah Elmendorf, Alison Beamish, Greg Henry, and Mark Vellend.

Greg Henry, Mark Vellend and I conceived the idea for Chapter 3. I executed the experiment, analyzed the data, and wrote the manuscript, with inputs from Mark Vellend and Greg Henry.

I conceived the idea for Chapter 4, with guidance from Greg Henry and Mark Vellend. I executed the experiment, analyzed the data, and wrote the manuscript, with inputs from Greg Henry and Mark Vellend.

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Acknowledgements

First and foremost I want to express my undying gratitude to five amazingly wonderful summer field crews: Sarah Desrosiers, Erin Alexiuk, Knut Kitching, Sam Robinson, Emily McNaughton, Breanne Johnson, Meagan Grabowski, Matt Huntley, Chris Greyson-Gaito, Darcy McNicholl, Doug Curley, Sean Kearnan-Carbonneau, Dannie Piezas, and Véronique Demers. This thesis quite literally would not have been possible without them. Special thanks go to Breanne Johnson and Chris Greyson-Gaito, who stuck with me for a second or third year of Arctic gardening adventures. Additional huge thanks go to Robert Björk, Ulf Molau, Per Larsson, Bob Hollister and Rob Slider for help with seed collecting in Alaska and Sweden. I am also grateful for field help from my fellow graduate students: Kim Bryson, Marc Edwards, Xanthe Walker, Ali Beamish, Amanda Guy, Sam Robinson, Ali Cassidy, and Noémie Boulanger-Lapointe. Additional thanks go to my fellow Biodiversity officemates: Emily Drummond, Jenny McCune, Heather Kharouba and Tanis Gieselman, for enlightening discussions and frequent fun.

Both of my supervisors, Greg Henry and Mark Vellend, have been incredibly supportive throughout my PhD. Thanks to Greg for making all this possible, and for sharing with me just a small portion of his vast Arctic knowledge. Thanks to Mark for lightning-fast response times, and for encouraging me to keep going until I got it right. I also thank my committee members, Loren Rieseberg and Sally Aitken, as well as Amy Angert for helpful discussions about experimental design and interpretation of results.

Field work in the high Arctic requires a huge amount of logistical support. I am indebted to the wonderful group at the Polar Continental Shelf Program (Tim, Glenn, Jodi, Mike, Wally, George) for keeping things running smoothly and for twice-daily radio entertainment.

I thank Sarah Elmendorf for teaching me most of what I know about fancy statistics (or at least setting me on the right track), and for being a help and inspiration throughout my PhD. I am also grateful to Gavin Shaddick and Rick White at UBC for their statistical advice.

I am grateful for financial support I received through a UBC Four-Year Fellowship, a BRITE fellowship through the Biodiversity Research Centre at UBC, the Jimmy Grewal Memorial Scholarship awarded by UBC, and the Jennifer Robinson Memorial Scholarship awarded by the Arctic Institute of North America. Additional research funding was provided to Dr. Henry by the Natural Science and Engineering Research Council of Canada (NSERC), ArcticNet, the Polar Continental Shelf Program (PCSP), the Northern Science Training Program (NSTP) of Aboriginal Affairs and Northern Development Canada, and the Canadian International Polar Year (IPY – CiCAT). I additionally thank the RCMP for use of the buildings at Alexandra Fiord, the Nunavut Department of the Environment for providing research permits, and the Qikiqtani Inuit Association for permission to conduct research on Inuit owned land.

Finally, I thank my family and friends for their unwavering support. I am particularly grateful to my husband, Hannes Dempewolf, who did much more than his fair share of cooking and dishes during the “home stretch” of this thesis (which lasted nearly a year), and to my parents, Roxanne Donahey and Tom Bjorkman, for just about everything.

Dedication

This thesis is dedicated to Alexandra Fiord, in the hopes that her endless glaciers, majestic wildlife, and ice-choked waters will endure for millennia to come.

Chapter 1: Introduction

1.1 Brief overview

1.1.1 Global environmental change

Over the past century, global average temperatures have increased by 0.78 °C (IPCC 2013), with the rate of change during the last 50 years nearly twice that of the whole 100-year period (Bernstein et al. 2007). With this increase in temperature have come corresponding changes in global precipitation trends and the earth's landscape: global sea levels are increasing at a rate of 3.1 mm per year, summer Arctic sea ice has shrunk by 7.4% per decade, and snow cover has declined in both hemispheres (Bernstein et al. 2007). Widespread consequences of these changes for the world's biota have already been observed. Numerous studies have demonstrated substantial changes in phenology (the timing of life events; Parmesan and Yohe 2003, Root et al. 2003, Menzel et al. 2006, Ovaskainen et al. 2013) and shifts in abundance and distribution (Parmesan et al. 1999, Parmesan 2006, Chen et al. 2011) correlated with climate change. These changes are likely to become even more pronounced in the future, as temperatures are expected to continue increasing for at least the next several decades (IPCC 2013).

1.1.1.1 Climate change in the Arctic

Climate change is occurring faster in the Arctic than anywhere else on the planet (Weller et al. 2005). While global average temperatures have increased by 0.78 °C over the past century (IPCC 2013), temperatures in the Arctic have risen by 2 °C over the past 50 years alone, and are expected to rise an additional 4-7 °C by the end of the 21st century (Weller et al. 2005, Stocker et al. 2013). This rapid increase in temperature is expected to have wide-ranging implications for

Arctic ecosystems, including changes in biodiversity, ecosystem functioning, and nutrient cycles (Callaghan et al. 2005). Despite this rapid change, however, the responses of Arctic species to climate change are less well understood than those of temperate species, due in part to the paucity of long-term ecological records in the Arctic (Post et al. 2009, Post and Høye 2013).

1.1.2 Plasticity, adaptation, and migration

Based on our understanding of the ecological effects of environmental change, biologists have identified three major ways in which species can respond to changing environments: phenotypic plasticity, evolutionary adaptation, and migration of individuals or propagules (Holt 1990, Davis et al. 2005, Aitken et al. 2008, Anderson et al. 2012a). The relative importance of each of these processes will depend on a number of factors, including the rate of climate change, characteristics of the population itself (e.g., population size, strength of biotic interactions, dispersal ability) and genetic constraints within the population (e.g., genetic diversity, heritability, and mutation rates; Aitken et al. 2008). If the magnitude or rate of climate change exceeds the ability of individuals to respond plastically or for populations to adapt to new conditions, they may become extirpated in their current range (Davis and Shaw 2001, Shaw and Etterson 2012). If these species are additionally unable to disperse to new areas of suitable habitat as the climate changes, they face the risk of extinction (Thomas et al. 2004).

Here I review the phenotypic, genetic, and range shifts observed in response to both historical and recent changes in climate. I first discuss species' responses to environmental change globally, and then specifically in Arctic tundra ecosystems. I then present the objectives for the research conducted as part of this thesis. Finally, I discuss the significance of my research for understanding Arctic species' responses to current and future climate change.

1.2 Species' responses to climate change

1.2.1 Phenotypic changes

The most widely observed phenotypic changes in response to climate change have been in the timing of life events (i.e., phenology) for animal and flowering plant species (Walther et al. 2002, Parmesan 2006). Bradley et al. (1999) identified advances in arrival date or first bloom date for 19 bird and plant species in Wisconsin over 61 years. Four out of six frog species in central New York now call 10-13 days earlier than they did 100 years ago (Gibbs and Breisch 2001). Menzel and Fabian (1999) documented a Europe-wide change in plant growing season length by 10.8 days; species now begin spring growth (i.e. leaf unfolding) an average of 6 days earlier while senescence occurs 4.8 days later than in the 1960's. In the Rocky Mountains, yellow-bellied marmots now emerge from hibernation 38 days earlier than they did 23 years prior, an apparent response to warmer spring temperatures (Inouye et al. 2000). One global meta-analysis estimated an average across-taxa advance in spring events of 2.3 days per decade (Parmesan and Yohe 2003).

The concurrence of phenological shifts with changes in temperature can have important consequences for fitness. Several studies have documented higher fitness in species whose phenologies track changes in climate relative to non-responsive species (Both et al. 2006, Møller et al. 2008, Willis et al. 2008, Cleland et al. 2012). Many factors could account for reduced fitness in either non-responsive or overly responsive species, including temporal mismatches between plants and their pollinators or between animals and their food source (Visser and Both 2005, Thomson 2010, Høye et al. 2013), exposure to detrimental weather conditions such as

freezing or drought (Franke et al. 2006, Inouye 2008), or increased susceptibility to herbivores (Pilson 2000).

Phenotypic changes unrelated to phenology have also been observed, though these are much less frequently documented. The average body size of woodrat populations in New Mexico decreased by 15% over the 8-year study period, coincident with increased warming (Smith et al. 1998). A similar trend has been observed in passerine birds in Israel (Yom-Tov 2001) and England (Yom-Tov et al. 2006), while increases in body size were observed in Alaskan shrew populations (Yom-Tov and Yom-Tov 2005). Experimental warming of plants has been shown to lead to larger annual shoot growth (Suzuki and Kudo 1997) and increased specific leaf area (Hartman and Nippert 2013), though responses vary by species.

1.2.1.1 Phenotypic changes: evolution or plasticity?

Despite the large number of species showing phenotypic responses to climate change, the degree to which evolutionary adaptation plays a role in driving these responses is largely unknown. The majority of documented responses to warming have been attributed to phenotypic plasticity, though this assumption is rarely tested (Gienapp et al. 2008). Phenotypic plasticity is the "flexibility" that allows an individual to respond to changing environmental conditions by modifying its behavior, phenology, morphology, or physiology (Schlichting 1986, Walther et al. 2002, Bradshaw and Holzapfel 2006).

While phenotypic plasticity is important for allowing individuals to respond to environmental change, the amount of plasticity possible is limited, and in many cases potential costs of

plasticity have been identified (DeWitt et al. 1998). In some situations, plasticity might accelerate evolutionary change (Behera and Nanjundiah 1995), for example by allowing populations to persist while sufficient genetic mutations accumulate to allow adaptive evolution (Crispo 2008). However, plasticity could also slow down evolution in response to gradual selective pressures, as the effective strength of selection is reduced (Ancel 2000, Crispo 2008). In addition, the sensory and regulatory mechanisms responsible for detecting and manifesting plasticity could be energetically costly (DeWitt et al. 1998, Ghalambor et al. 2007). Finally, the magnitude of temperature change over the next century may exceed the limits of plasticity for many species to maintain positive population growth (Jump and Peñuelas 2005, Gienapp et al. 2008).

The likely limit to phenotypic plasticity highlights the importance of understanding the relative contributions of plastic and genetic changes in driving the responses of species to climate change observed thus far. However, experimental or genetic studies are rarely undertaken to determine whether phenotypic changes might include an evolutionary component (Gienapp et al. 2008). In a meta-analysis of trait shifts in response to warming temperatures, only three of 105 studies provided genetic evidence for adaptation (Parmesan and Yohe 2003, Gienapp et al. 2008). Many studies have claimed to show evidence of microevolutionary responses to environmental heterogeneity, but these are often based entirely on phenotypic data (Gienapp et al. 2008). Thus, while numerous studies have demonstrated shifts in phenology and other traits in response to climate change, the role of evolutionary adaptation in driving these responses is still largely unknown.

1.2.2 Evolutionary adaptation

Where the role of evolutionary adaptation in species' responses to climate change is directly investigated, evidence is mixed. Even when evolutionary changes are detected, it is often unclear whether these changes are directly in response to climate change, or whether correlated changes (e.g., loss of habitat, pollution) could be driving the response (Merilä and Hendry 2014). Furthermore, evidence of genetic change does not always mean that this change is adaptive. Evolution could also be due to neutral or maladaptive genetic changes, for example through genetic drift or inbreeding (Lande 1976).

Perhaps the best evidence for relatively rapid evolutionary changes comes from studies of plants and insects (Merilä and Hendry 2014). Bradshaw & Holzapfel (2001) compared lab-reared populations of pitcher-plant mosquitoes collected over a 25-year period and found that the critical photoperiod of northern populations had shifted towards that of more southern populations, thus lengthening the breeding season for these populations. Evolution in response to a drought was detected after only a few generations in the annual plant *Brassica rapa*; a common garden experiment with seeds from 1997 and 2004 demonstrated that 2004 populations flowered 1.9 to 8.6 days earlier than their pre-drought ancestors (Franks et al. 2007). In recent reviews, the vast majority of studies that investigated a genetic component to phenotypic shifts in plants and terrestrial invertebrates found evidence of evolutionary adaptation in response to environmental change, usually in addition to plastic changes (Schilthuizen and Kellermann 2014).

Few studies have demonstrated evidence of evolutionary adaptation in other taxa, but some examples do exist. Réale et al. (2003) determined that evolutionary adaptation in response to

spring warming accounted for 13% of the observed shift in parturition date for Yukon red squirrels over 10 years (62% was a result of phenotypic plasticity). In a classic study of microevolutionary change, Grant and Grant (1995) documented significant changes in gene frequencies as a result of drought-induced changes in food availability and interspecific competition after just one year. However, eleven additional studies in mammals found that recent phenotypic changes were due primarily to phenotypic plasticity (Boutin and Lane 2014). Shifts in egg laying date and the timing of migration in birds have been shown to be highly plastic traits, but whether evolutionary adaptation has also played a role in recent phenological changes remains largely uninvestigated (Charmantier and Gienapp 2014).

1.2.3 Range shifts

Range shifts, either through the movement of individuals or through the dispersal of propagules, have been widely discussed in the ecological literature. Some of the most compelling evidence for this process comes from paleoecological studies revealing substantial historical range shifts in conjunction with warming or cooling temperatures (Davis 1983a, Huntley and Webb 1989, Huntley 1990, Williams et al. 2004). Tree species, in particular, have been tracked by measurements of pollen composition and abundance over time. In their study of post-glacial movements of tree species in North America during the Holocene, Huntley & Webb (1989) estimated that tree species' ranges moved northward at rates between 100 and 200 meters per year, a range similar to that estimated by other paleoecological studies (Davis 1981).

Range shifts have already been documented in response to contemporary climate trends. The majority of these shifts have been in mobile species (Parmesan 2006). In one of the earliest

studies to document shifts associated with current climate trends, Parmesan (1996) identified a significant latitudinal and altitudinal shift in the current range of Edith's checkerspot butterfly in western North America compared to historical records. Population extirpation rates at the southern edge of the species' range were greater than at the northern edge, thus providing evidence that a warming climate was driving these trends.

Subsequent studies of species' range shifts have identified similar trends throughout the globe. In another study of Lepidoptera, Parmesan et al. (1999) reported that 63% of evaluated butterfly species in the UK had experienced northward range shifts, while only 3% had shifted southward. Thomas and Lennon (1999) identified an average northward range shift of 18.9 km for bird species in Britain. In a meta-analysis of data from 1,700 species worldwide, Parmesan & Yohe (2003) described an average northward range shift of 6.1 km (or 6.1 m upward in elevation) per decade across all species. A subsequent study estimated rates of latitudinal shifts at 16.9 km/decade, or 11.0 m/decade in elevation (Chen et al. 2011). In both cases, the rate of the shift varied widely by species, indicating that not all species are responding equally to warming temperatures.

Range shifts specifically in plants have also occurred, but are less frequently observed than those for animals (Shaw and Etterson 2012, Zhu et al. 2012). Many alpine plant species show evidence of movement upward in elevation, both in Europe (Grabherr et al. 1994, Wipf et al. 2013) and North America (Kelly and Goulden 2008, Savage and Vellend 2014), but a recent meta-analysis of western North America plant species found the opposite pattern – 63% of species shifted downward in elevation despite warming across the study area (Harsch and Hille Ris Lambers

2014). Similarly, an analysis of latitudinal range shifts in 92 tree species found evidence of the expected northward shift in only 20% of species, while a majority experienced range contractions (Zhu et al. 2012).

While substantial evidence, both historical and current, indicates that range shifts are a critical component of species' responses to climate change, several factors might hinder future poleward movements. Firstly, potential migration pathways have been considerably fragmented by human land use, especially through agriculture and residential settlement (McCarty 2001), potentially leading to barriers to species dispersal and migration. As species will need to track changes in climate at speeds 100 times those of historical migrations (Davis 1989, Aitken et al. 2008), these barriers could represent a substantial obstacle to dispersal. Finally, even if dispersal is not limited, a variety of local factors can prevent the successful establishment of propagules in a new environment (Davis and Shaw 2001). While gene-flow between populations or species has been shown to promote adaptation to novel environments (Lewontin and Birch 1966, Rieseberg et al. 2003), it can also lead to outbreeding depression if populations are locally adapted to environmental conditions (Edmands 2007, Frankham et al. 2011, Sexton et al. 2011, Schiffers et al. 2013, Aitken and Whitlock 2013). For example, a lack of adaptation to photoperiod, soil type, moisture regime, or biotic interactions could slow or inhibit the immigration of novel species or genotypes even when climatic conditions are suitable (Davis et al. 1998, 2005, Visser 2008, Van der Putten et al. 2010, Alberto et al. 2013). Thus, evolutionary adaptation to novel environmental conditions other than climate may be necessary for the successful establishment of an immigrant species (Davis et al. 2005, Anderson et al. 2012a).

1.2.4 Predicting responses

Predictions of ecological and evolutionary responses to climate change involve tremendous uncertainty. The ultimate outcome will depend largely on two factors: (1) the rate and magnitude of environmental change (Burger and Lynch 1995), and (2) constraints on species' responses to this change. Some characteristics may be useful in predicting which species will migrate, adapt, or become extinct. For example, species with short generation times and large population sizes (and, relatedly, high genetic diversity) might best be able to adapt to changing conditions (Lande and Shannon 1996, Stockwell et al. 2003, Berteaux et al. 2004, Smith and Donoghue 2008), though this can also depend on the nature of the environmental change (Rosenheim and Tabashnik 1991, Lande and Shannon 1996). Furthermore, traits related to dispersal ability, generation time and offspring number, and the degree of ecological generalization might influence the speed at which the range of a species will shift (Angert et al. 2011), although thus far such traits have had only low predictive ability when describing recent range shifts (Angert et al. 2011).

Expert opinion on the relative importance of evolution and migration is divided. Parmesan (2006) proposed that, while local microevolutionary processes will undoubtedly occur, there is little historical evidence that climatic changes following the last ice age have resulted in novel phenotypes or speciation events. In particular, she highlights the lack of empirical evidence for evolution in the absolute climate tolerances of species, a necessary factor in allowing a species to persist *in situ*. Conversely, Davis et al. (2005) maintain that the focus on migration and corresponding de-emphasis on evolution is misguided. They suggest that many predicted migratory responses actually involve an evolutionary component. Selection can act in

conjunction with migration; for example, individuals with the greatest dispersal ability will be most likely to establish and reproduce in a novel environment, therefore passing on that dispersal ability to their offspring. Therefore, they conclude that, while perhaps less visible, evolutionary processes will be an equally important component of species' responses to future environmental change.

1.2.5 Responses to climate change in Arctic plant species

As elsewhere, visible changes in response to warming in the Arctic are already underway. Unfortunately, in contrast to temperate systems, relatively few long-term records of ecological change in Arctic systems exist (Post and Høye 2013). Recent syntheses of plant community composition data have shown that some functional groups, particularly shrubs and graminoids, have responded positively to warming over the past few decades, while others, including lichens, have declined (Callaghan et al. 2011, Elmendorf et al. 2012b). Despite these general trends, specific responses to warming varied according to temperature and moisture conditions at each site, indicating that not all tundra ecosystems respond similarly to warming (Elmendorf et al. 2012b, 2012a).

Phenological changes have also been observed in Arctic ecosystems, both in response to experimental and ambient climatic warming. Substantial advances (14.5 days on average) in flowering, emergence and breeding dates were observed for plant, arthropod and bird species at Zackenberg, Greenland between 1996 and 2005 (Høye et al. 2007). These phenological advances were likely driven at least in part by changes in the timing of snowmelt, which advanced by 14.6 days over the same time period. A recent meta-analyses of changes in plant phenology across the

Arctic observed only moderate changes in flowering time, however, perhaps due to varying climatic trends at the different study locations (Oberbauer et al. 2013).

Evidence of shifts in Arctic species' ranges in response to climate change is also mixed. Shrubs have increased in abundance in areas experiencing substantial warming (Sturm et al. 2001, 2005), but the evidence for changes in spatial distribution is less clear. Little or no forest expansion into tundra was observed in areas of northern Canada and Sweden, despite significant warming in both regions (Masek 2001, Van Bogaert et al. 2011). However, a recent global meta-analysis found that just over half of surveyed sites showed evidence of northward treeline advancement (Harsch et al. 2009), including in some Arctic sites.

Experimental warming studies can also contribute to our understanding of how Arctic species respond to warmer temperatures. Multi-year warming experiments have led to changes in nutrient availability and net primary production (Chapin et al. 1995), shifts community composition (Walker et al. 2006, Elmendorf et al. 2012a), greater plant size (Hudson et al. 2011) and canopy height (Chapin and Shaver 1996, Hollister et al. 2005b), increased relative growth rate (Campioli et al. 2013), advanced phenology (Arft et al. 1999), and enhanced reproductive effort and seed-set (Wookey et al. 1993), though some studies have also demonstrated remarkable stability in response to warming for some species (Chapin and Shaver 1996, Campioli et al. 2013) or plant communities (Hudson and Henry 2010).

Despite some evidence that Arctic plants are changing in response to warming temperatures, very little is known about the mechanisms behind these changes. Classical studies of Arctic

species have demonstrated that, although individual populations show a high degree of phenotypic plasticity, adaptation to local conditions is also prevalent (Mooney and Billings 1961, Billings and Mooney 1968, Billings 1974). Several studies of local adaptation in Arctic populations have found evidence of genetic differences over space and time (McGraw and Antonovics 1983, Bennington et al. 1991, Vavrek et al. 1991, McGraw 1993, Bennington et al. 2012), suggesting that substantial genetic diversity exists among populations of Arctic species. This genetic diversity could become important as environmental conditions change, as adaptation from standing genetic variation is likely to be faster than evolution through the occurrence of novel mutations (Barrett and Schulter 2008).

1.3 Research objectives

In this thesis, I seek to explore the roles that phenotypic plasticity, evolution, and range shifts may play in influencing Arctic plant species' responses to future climate warming. In Chapter 2, I investigate whether the timing of flowering and seed maturation have advanced in response to 21 years of experimental and ambient climatic warming in two habitat types. In Chapter 3, I use reciprocal transplant experiments between the above-mentioned experimental warming and control treatments in both habitat types to determine whether adaptation to warming has occurred in two common forb species. I additionally ask whether local adaptation to environmental conditions in the two different habitat types is apparent despite their close proximity (~500m). In Chapter 4, I ask whether experimental warming confers an adaptive advantage to "immigrant" populations from southern latitudes over local populations despite potentially novel non-climatic environmental conditions (e.g., photoperiod or edaphic factors).

1.3.1 Introduction to study system

Alexandra Fiord (78°53`N, 75°55`W) is located on the eastern side of Ellesmere Island, Nunavut, Canada (Figure 1.1). The Alexandra Fiord lowland is a polar oasis (warmer and more productive than the surrounding polar desert; Freedman et al. 1994) bounded on two sides by low mountains, to the south by the Twin Glacier, and to the north by Alexandra Fiord Bay. The lowland itself is approximately 8 km^2 and is characterized by a mosaic of different plant communities (Muc et al. 1989). Chapters 2 and 3 of this thesis were conducted in both a mesic and dry habitat at the site.

Figure 1.1: Location of Alexandra Fiord, Ellesmere Island, Canada (78°53`N, 75°55`W)

The research in this thesis makes use of a long-term warming experiment begun in 1992 by Dr. Greg Henry as part of the International Tundra Experiment (ITEX; Henry and Molau 1997). Open-top warming chambers (OTCs; Figure 1.2) were erected in several habitat types at Alexandra Fiord, Ellesmere Island, and the phenological responses of the dominant species in each plot have been tracked over the past 21 years of the experiment. These open-top chambers warm the air and soil by approximately 1-3 °C relative to the control plots.

Figure 1.2: Experimental warming plots (open-top chambers) at the dry site at Alexandra Fiord. The yellow flowers are rooted poppy (Papaver radicatum).

All three experiments reported in this thesis focus on two species, *Oxyria digyna* (mountain sorrel) and *Papaver radicatum* (rooted poppy). These species were chosen because they are

abundant in both the mesic and dry habitat types at Alexandra Fiord, they are widespread throughout the Canadian Arctic, and they reproduce readily by seed. Three additional species, *Arctagrostis latifolia* (wideleaf polargrass), *Dryas integrifolia* (mountain-avens), and *Salix arctica* (Arctic willow) were included in at least one experiment.

1.3.1.1 Prior research in this system

The long-term experimental warming plots at Alexandra Fiord have already facilitated several analyses of changes in community composition and plant traits. Hudson and Henry (2010) analyzed changes in community composition after 15 years (1992-2007) of experimental warming at the mesic site (an evergreen-shrub heath community). They found subtle increases in bryophyte cover and decreases in lichen cover, but no effect of warming on overall plant cover, canopy height, or species diversity. In contrast to the relative stability in community composition, species traits have shifted in response to warming. Hudson et al. (2011) found evidence of increased leaf size, plant height, and specific leaf area in at least one species and habitat type. Klady et al. (2011) found evidence of enhanced reproductive effort and reproductive success in response to warming for several species; shrubs and graminoids were particularly responsive.

Two recent studies have also assessed changes in biomass and community composition over time in response to ambient (natural) climatic warming at Alexandra Fiord. Hudson and Henry (2009) found evidence of significant increases in biomass in a heath community over a nearly 30 year period (1981-2008), concurrent with regional warming. They also observed evidence of significant increases in bryophyte and evergreen shrub abundance, while other plant growth

forms and species diversity did not change. Hill and Henry (2011) assessed changes in a wet sedge tundra habitat at Alexandra Fiord over the same ~30-year period (1980-2005) and found a similar pattern of increasing aboveground and root biomass. Sedges (*Carex spp*. and *Eriophorum angustifolium*) and the dwarf deciduous shrub *Salix arctica* were the most responsive species. As in the Hudson and Henry (2009) study, species diversity did not change over time.

1.4 Significance of research

The Arctic is warming faster than any other region on earth, and yet our understanding of the current and likely future effects of climate change on Arctic species lags behind that of temperate systems (Post et al. 2009). Due to the paucity of long-term datasets in Arctic regions, extremely few studies have been able to identify changes in Arctic ecosystems over more than a few years of warming (Post and Høye 2013). In recent years, several studies have attempted to identify long-term changes in species composition and phenology (Høye et al. 2007, Elmendorf et al. 2012b, Oberbauer et al. 2013), but have not identified the mechanisms behind these changes. In particular, the role of evolution in influencing the responses of Arctic species to recent climatic warming has rarely been studied. The capacity to adapt in response to increasing temperatures will likely be particularly important for Arctic species; while temperate species might be able to persist by tracking their optimal climate northward, areas of suitable habitat for many Arctic species (given their current genetic makeup) could disappear altogether (Derocher et al. 2004). Thus, the ability of Arctic species to adapt to warming, as explored in Chapter 3, could have important implications for the persistence of these species in the future. Furthermore, while it is often proposed that warming will facilitate the successful northward migration of southern, warm-adapted genotypes and species (Davis and Shaw 2001, Aitken et al. 2008, Norberg et al.

2012, Anderson et al. 2012a), empirical tests of this are extremely rare (Chapter 4). If southern populations have an adaptive advantage over northern populations under warmer temperatures, future climatic warming will likely facilitate the northward migration of warm-adapted populations and species. Conversely, if a lack of adaptation to local conditions other than temperature limits the success of southern immigrants, evolution – either of local populations to novel climatic conditions or of immigrant populations to novel environmental conditions – may again be key in structuring future Arctic communities.

Changes in the plant community will undeniably have widespread effects, including an impact on animal species that use vegetation for food and cover, and on Arctic indigenous communities that traditionally depend on these plant and animal species (Weller et al. 2005). An enhanced understanding of the ecological and evolutionary processes at work in Arctic plant communities can help us to better predict, and possibly even influence, the future of ecosystems in the Arctic under global climate change.

Chapter 2: Contrasting effects of experimental and ambient warming on phenology over two decades in two Arctic tundra plant communities

2.1 Synopsis

The timing of phenological events can have substantial consequences for an individual's fitness. Recent changes in climate have led to significant shifts in phenology, with many studies demonstrating advanced phenology in response to warming temperatures. The rate of climate change is especially high in the Arctic, but this is also where we have relatively little information about the phenological changes occurring and the processes driving these changes. In order to understand how Arctic plant species are likely to respond to future changes in climate, we monitored flowering phenology in response to both experimental and ambient (non-experimental) warming for four widespread species in two habitat types over 21 years. We additionally used snowmelt and temperature records from the same time span to determine which environmental variables are most closely associated with changes in flowering time. While flowering occurred earlier in response to experimental warming, all four species showed no change or a delay in flowering over the 21-year period in the control plots, despite more than 1 °C of ambient warming over the study period. This counterintuitive result was likely due to significantly delayed snowmelt over the study period (0.1-0.3 days/year), which in turn may have been due to increased winter snowfall. The timing of snowmelt was a strong driver of flowering phenology for all species, and especially for the earliest flowering species, while spring temperature was significantly related to flowering time only for the later-flowering species. Despite significantly delayed flowering phenology over the course of the study, the timing of

development of mature seeds showed no significant change over time. This suggests that, while delayed snowmelt leads to later flowering, warmer temperatures promote more rapid seed development. The results of this study highlight the importance of understanding the specific environmental cues that drive species' phenological responses as well as the complex interactions between temperature and precipitation when forecasting phenology over the coming decades. As demonstrated here, the effects of altered snowmelt patterns can counter the effects of warmer temperatures, even to the point of generating phenological responses opposite to those predicted by warming alone.

2.2 Introduction

Synchronization between temporal changes in environmental conditions and phenological events is of fundamental importance to an individual's lifetime fitness (Fox 1989, Stenseth and Mysterud 2002, Berteaux et al. 2004). As phenology is often driven by temperature (Rathcke and Lacey 1985), recent climate warming has led to considerable shifts in phenology across ecosystems and taxa (Parmesan and Yohe 2003, Root et al. 2003, Parmesan 2006, Menzel et al. 2006, Høye et al. 2007, Oberbauer et al. 2013, Ovaskainen et al. 2013). In Europe, 78% of 561 plant and animal species studied demonstrated phenological advances over the last three decades of the 20th century (Menzel et al. 2006). Similarly, a global meta-analysis spanning decades to centuries of observations of plant and animal spring phenology found significant advancement in 62% of species studied (Parmesan and Yohe 2003).

Reduced fitness as a result of out-of-sync phenology has also been demonstrated for both plant and animal species. Studies have demonstrated reduced fitness as a result of mismatches between

plants and their pollinators (Thomson 2010, Høye et al. 2013) or animals and their food source (Visser and Both 2005), increased susceptibility of plants to frost damage (Inouye 2008) or herbivores (Pilson 2000), and a failure to reach reproductive maturity before the onset of winter (Molau 1993, Berteaux et al. 2004) or other seasonal events such as drought (Franke et al. 2006).

Both species and individuals within species differ in their ability to track changes in climate, which can have important implications for community composition and population dynamics (Diez et al. 2012). Differential fitness between species within a community can lead to shifts in species abundance. For example, bird species whose phenology did not track changes in temperature experienced significant population declines, while those that exhibited altered phenology corresponding with changing temperatures experienced little or no decline (Both et al. 2006, Møller et al. 2008). Similar findings have been reported for plants (Willis et al. 2008, Cleland et al. 2012).

Changing temperatures could also lead to evolutionary changes in phenologically relevant traits within a species or population if sufficient heritable variation for these traits exists (Berteaux et al. 2004, Davis et al. 2005, Anderson et al. 2012b). Furthermore, if different populations of the same species respond differently to climate change – either due to genetic differences between populations or to site-specific differences in the magnitude of warming (Primack et al. 2009, Diez et al. 2012) – it could lead to a reduction or increase in gene flow between these populations (Fox 2003). Thus, phenological shifts can lead to changes not only in the abundance and distribution of species, but also in the genetic makeup of those species.

Arctic tundra ecosystems provide a particularly compelling setting for investigations of phenological responses to climate change, as warming is happening faster in the Arctic than anywhere else on the planet (Weller et al. 2005, IPCC 2013). Thus, we might expect to see the most rapid changes in phenology and substantial evidence of the consequences of out-of-sync phenologies in Arctic systems (Høye et al. 2007). In contrast to temperate systems, where increasing spring temperatures is generally considered the primary driver of advancing plant phenology (Cleland et al. 2006), Arctic and alpine phenology is substantially influenced by the timing of snowmelt (Billings and Bliss 1959, Billings and Mooney 1968 but see, Thórhallsdóttir 1998, Wielgolaski and Inouye 2013). Thus, changes in winter precipitation may be as or more important than temperature in driving future phenological changes. Future temperature increases are predicted with relatively high confidence, but current projections of precipitation change are much less certain and could be much more variable over space and time (Weller et al. 2005). The most recent projections predict an Arctic-wide increase in winter precipitation (Bintanja and Selten 2014). This could lead to very different phenological patterns than would be observed as a response to changing temperatures alone.

Even when the timing of snowmelt is held constant, temperature changes may affect species differently depending on whether they are relatively early- or late-flowering. Early-flowering subalpine plant species in the Rocky Mountains, for example, showed greater advances in response to warming than late-flowering species (Dunne et al. 2003). Winter snowpack might also have an effect on plant phenology through a mechanism other than through timing of snowmelt, for example through freezing damage when the snowpack is too low (Inouye and McGuire 1991) or by the volume of water released during snowmelt (Høye et al. 2013).

Furthermore, because tundra species form leaf and flower buds in the summer prior to flowering (Billings and Mooney 1968), temperatures during the previous summer of growth might affect flowering in the current summer. Finally, increases in winter (rather than spring) temperatures have been found to be important in delaying phenology in some alpine species, likely due to a delay in chilling requirements (Yu et al. 2010, Cook et al. 2012).

While long-term records of phenology are common in temperate ecosystems, very few such records exist for Arctic regions (Post and Høye 2013). Short-term monitoring of phenological responses to experimental warming has demonstrated that Arctic plants flower earlier when warmed (Arft et al. 1999, Hollister and Webber 2000, Hollister et al. 2005a), but this may not accurately represent species' responses to long-term experimental warming or to ambient warming (Chapin et al. 1995, Hollister et al. 2005b, Wolkovich et al. 2012). A ten-year study of plant and animal phenology at Zackenberg, Greenland showed a substantial advance in phenology for many species – up to 30 days in some cases (Høye et al. 2007) – likely driven, at least in part, by earlier snowmelt over the same period. Whether these patterns are true of the high Arctic in general, however, is not known. An 18-year study compiled from multiple species and sites across the Arctic found mixed responses to ambient temperature variation during that time (Oberbauer et al. 2013). Neither study specifically examined seed maturation phenology, however, which can be as important as flowering time to plant fitness (Molau 1993).

Here we ask whether flowering time and seed maturation have advanced for four common Arctic plant species in response to both experimental and ambient (natural) warming in two distinct tundra habitat types over a period of 21 years. This study represents the longest record of Arctic

plant species' phenological responses to both experimental and ambient warming to date. We also examine changes in the timing of snowmelt and in winter and spring temperatures over the same time period. We use this comprehensive data set to test 1) whether flowering phenology and seed-set have advanced a) in response to experimental warming and b) over time; 2) whether these changes vary by habitat type or species; and 3) what environmental drivers are most closely related to changes in flowering phenology for each species?

We additionally present an improved method for analyzing interval-censored and right-censored phenological data. While most prior studies have used the date at which a phenological event is first observed as a response variable, this will necessarily late-bias the actual date of the event when phenological monitoring occurs at discrete intervals throughout the growing season. In addition, if the monitoring intervals vary from year to year or within the same year, failure to account for these differences would lead to late-biased estimates of phenological events for those years, species, or events that were sampled less frequently (Miller-Rushing et al. 2008). Conversely, if phenological monitoring has become more intensive over time, failure to account for sampling frequency would lead to early-biased estimates and a false trend of phenological advancement over time. Finally, end-of-season events, such as seed maturation, can be strongly early-biased if monitoring ends before all individuals have reached that stage. Here we use Bayesian hierarchical modeling with interval-censored and right-censored response variables to account for uneven sampling frequency, ensuring that the patterns presented here reflect actual changes in phenology and not statistical artifacts of variation in sampling effort or duration of monitoring.

We predict that both the timing of snowmelt and spring temperature will be related to flowering time across all species. Therefore, if ambient warming at our Arctic field site has been as rapid as elsewhere in the Arctic, and if this warming has led to earlier snowmelt, we would expect strong and consistent advances in flowering time and seed maturation across sites, species, and treatments. However, if the timing of snowmelt has not changed, or if warmer winter temperatures have led to a delay in chilling requirements, we would expect only a slight advancement or no advancement in flowering time in response to warmer temperatures.

2.3 Methods

2.3.1 Study site and species

Alexandra Fiord (78°53`N, 75°55`W) is located on the central eastern coast of Ellesmere Island, Canada. The Alexandra Fiord lowland is a ~8 km^2 area of heterogeneous tundra habitat bounded on two sides by low mountains, to the south by the Twin Glacier, and to the north by the fiord. Although the surrounding area is dominated by polar desert due to very low precipitation levels (Freedman et al. 1994), the Alexandra Fiord lowland itself is considered a polar oasis and supports a relatively diverse assemblage of species and habitats due in part to spatial variation in soil conditions and to a strong moisture gradient created by glacial runoff (Muc et al. 1989, Freedman et al. 1994).

The study presented here was conducted in two common habitat types, a mesic heath community dominated by the evergreen shrubs *Dryas integrifolia* (mountain-avens) and *Cassiope tetragona* (Arctic white heather), and a dry sandy creek bank dominated by graminoids and the deciduous dwarf shrub *Salix arctica* (Arctic willow). Two of the four focal species – *D. integrifolia* and

Papaver radicatum (rooted poppy) – are abundant in both habitat types. *Oxyria digyna* (mountain sorrel) and *S. arctica* also occur in both habitats, but phenological observations were conducted only at the dry site. These four species were chosen because they are abundant at our field site and are widespread throughout the Canadian Arctic and subarctic (Porsild and Cody 1980). The distribution of *O. digyna* is circumpolar and spreads as far as the alpine areas of the southwestern United States (Mooney and Billings 1961, Billings et al. 1971).

2.3.2 Experimental design

In 1992, 20 plots were established at both the dry and mesic sites. These experimental plots, along with those in several other habitats at Alexandra Fiord, were the first to be established as part of the International Tundra Experiment (ITEX). In 1993, an additional 18 plots were created at the mesic site. Half of the plots were experimentally warmed using clear-sided, open-topped chambers, according to the established ITEX protocol (Henry and Molau 1997; available online at http://www.geog.ubc.ca/itex/library/). Within each experimental plot, between 2-5 individuals of each study species were chosen randomly and tagged for long-term monitoring (Table 2.1). When a tagged individual died, a replacement individual of that species was chosen haphazardly in the plot, and the date of re-tagging was recorded. Comprehensive phenological monitoring was conducted for *P. radicatum* and *O. digyna* between 1993 and 2013, for *D. integrifolia* between 1993-2009 and 2012-2013, and for *S. arctica* between 1995-2009 and 2012-2013. From 1995-2009 only 12 plots were monitored at the mesic site. Site access constraints prevented monitoring in 1999 and 2006.

Table 2.1: Number of tagged individuals of each species at each site, and the total number of years each species was surveyed between 1993 and 2013. As not all individuals flower in every year, the total number of observations in a given year is somewhat less than the total number of individuals. The total number of unique individuals across the entire study is somewhat more than the total number of individuals observed at any moment in time, as a new plant was selected whenever a tagged individual died.

Species	**Number of Individuals**		**No. of Years Surveyed**
	Dry Site	Mesic Site	Total
Dryas integrifolia	49	107	17
Oxyria digyna	59	--	19
Papaver radicatum	60	72	19
Salix arctica	80	--	15

Phenological monitoring was generally conducted every three days, but in some years the time between sampling was 6 days or more at the end of the growing season (after most plants had already flowered, but before seed maturation). The day of the year on which the first mature flower was observed was recorded for every tagged individual in every plot. A "mature" flower was defined as visible pollen (*O. digyna* and male *S. arctica*) or a receptive stigma (female *S. arctica*), or when the corolla was fully open (*P. radicatum* and *D. integrifolia*). We also recorded the date at which mature (dispersing) seeds were first observed for each species. Because seed dispersal in *D. integrifolia* occurs very late in the season, usually after monitoring has ended, we instead used the formation of a seed capsule as an estimate of seed maturation date. Seed maturation in *S. arctica* was observed only for female individuals.

Climate stations were established in both sites; shielded copper-constantan thermocouples measured air temperatures at 10 cm above ground level in four plots of each treatment in order to assess the warming effect of the OTC's. The thermocouples were attached to a data logger (CR10, Campbell Scientific Canada Corp.) and temperatures recorded every five minutes.

Ambient air temperatures (1.5 m) were measured at a third climate station located ~250 m from the mesic and dry sites. Winter temperature (average temperature from day 225 of the previous year to day 150 of the current year), previous summer temperature (average temperature of days 150-225 of the previous year), and spring temperature were derived from temperature measurements at this climate station, as it provided the most consistent long-term temperature record. Because different species flower at different times during the spring, spring temperature was defined as the average temperature between day 150 (~beginning of snowmelt) to the day (averaged across all years) at which 75% of the monitored reproductive individuals had flowered. Day 150 was used as the start date for calculating spring temperature to reduce correlation with date of snowmelt and because snow cover substantially buffers plants from air temperature fluctuations that occur while they are still covered by snow (Jones 1999, Groffman et al. 2001). Snow-depth sensors were also installed in four plots at each site to record snowmelt rates each spring. Early analyses of these data demonstrated no change in snowfall over time (Hudson and Henry 2009), but due to electronic malfunctions in some years we were not able to reconstruct a full time-series of snow depth data from these sensors. Thus, we also provide an estimate of total winter snow accumulation in each year based on winter snowfall data recorded at the Environment Canada weather station at Eureka, approximately 240 km northwest of Alexandra Fiord.

In addition to phenological monitoring, the timing of snowmelt in each plot (defined as the day on which the plot became 90% snow-free) was recorded in every year except 2009, when we arrived at the site after all snowmelt had occurred. In 1993, 1994, 1997, 2004 and 2012, some plots were already snow-free upon our arrival (in all cases except 1994, fewer than half the plots

were already snow-free). In total, across all years, 20% of plot-level snowmelt dates were unobserved. Because these data were not missing at random (i.e., early-snowmelt plots and early-snowmelt years were most likely to be missing), simply excluding these values would bias yearly average snowmelt dates to appear later than they actually were. Thus, we modeled snowmelt dates as an interval censored response variable, where the upper interval bound was the first date a given plot was observed to be already snow-free and the lower bound was five days prior to the single earliest snowmelt date observed in each site across all years (= day 150 at the mesic site and day 140 at the dry site). We included predictor variables of total winter snowfall at the Eureka weather station (~240 km to the northwest), early spring (day 120-150) mean temperature at Alexandra Fiord, treatment (warmed/control) and site, with random effects of plot and year*site. A regression of true (observed) vs. model-predicted snowmelt dates had an R^2 value of 0.87.

2.3.3 Statistical analyses

We used Bayesian hierarchical modeling with an interval censored response variable in order to account for the varying intervals between survey dates. Censored observations are common in survival analyses (Ibrahim et al. 2005), but appropriate analytic techniques developed in these fields have rarely been applied to phenology studies. Typically, researchers either assume the first day a phenological event occurred was the first day on which it was observed to occur (which will lead to late-biased estimates of flowering time), or the midpoint between sampling days (which systematically underestimates the variance). Both adjustments have the potential to introduce artifacts, particularly when the sampling interval is not consistent over time. We defined the upper interval bound as the day on which flowering was actually observed for a

given individual and the lower interval bound as the closest preceding survey date on which a plant was observed not to be flowering. Thus, the actual date of flowering is known to occur somewhere between the lower and upper bounds, and the associated uncertainty is incorporated into the model. For those individuals that reached the seed maturation stage before monitoring ended, lower and upper bounds were assigned as described above. If an individual did not reach the seed maturation stage before the end of monitoring, the lower bound was defined as the last day on which monitoring was conducted and no ripe seeds were observed. Individuals that showed signs of herbivory, fungus, or aborted/unfertilized flowers were excluded from the analysis.

An additional advantage of Bayesian modeling is the ability to obtain credible intervals for any derived parameter of interest. Thus, we were able to determine whether changes in phenology differed significantly between species and between habitat types, as well as model differences in flowering time and seed maturation for each species in each treatment, habitat type, and year.

We used three primary models in order to determine 1) the direction and magnitude of the treatment (warming) effect for each species in each habitat type, 2) the change in flowering date and seed maturation date over time (control plots only) for all species within each habitat type, and 3) the environmental variables most correlated with flowering time for each species (control and warmed treatments together). Flowering responses to variation in snowmelt were partitioned (Fitzmaurice et al. 2011, see chapter 14) into responses due to spatial variation in snowmelt (differences among plots within a year) and temporal variation in snowmelt (differences in mean snowmelt date across years). Gap-filled snowmelt dates per plot (as described above) were used

only for calculating the yearly mean snowmelt date (temporal variation component). Estimates of the relationship between flowering time and spatial variation in snowmelt were based only on observed snowmelt dates per plot.

All models included a random effect of plot to account for nonindependence of plants measured within the same plot, and a random effect of year to account for nonindependence of plants measured within the same year. The year random effect also ensures that changes in phenology over time are not driven by differences in the number of individuals that flower in each year. For the third model, environmental variables (winter temperature, spring temperature, previous summer temperature, and timing of snowmelt per plot and per year) were incorporated into the model at the level at which they were measured (e.g., temperature variables at the year level, plot-level snowmelt dates at the plot level). No pair of environmental variables were correlated at greater than 0.23 (Pearson's correlation coefficient). We refer to environmental covariates as "significant" in the text when the 95% credible interval for the corresponding parameter in the fitted models did not overlap zero. We used noninformative priors for all coefficients.
All models were conducted in JAGS (v. 3.4.0) called from R (v. 3.0.3) using the programs *rjags* and *R2jags*. Convergence was assessed using the Gelman-Rubin diagnostic (Gelman and Rubin 1992) available in the *coda* package.

2.4 Results

Temperatures have increased substantially at Alexandra Fiord over the past two decades (Figure 2.1a-b). Winter temperatures increased the most consistently, at a rate of 0.52 °C per decade (R^2 = 0.234, *p=0.026*). Spring temperatures (days 150-200) also increased, but with slightly greater

among-year variation than annual temperatures (0.52 °C per decade; $R^2 = 0.181$, *p=0.055*). Over the same time period, winter snowfall at Eureka (~240 km northwest of Alexandra Fiord) increased by 10.9 cm per decade ($R^2 = 0.189$, *p=0.049*), though again with considerable year-to-year variation (Figure 2.1c).

The date of snowmelt was significantly delayed over the study period in both sites (Figure 2.1d), although there was again large among-year variation. Snowmelt at the mesic site was delayed by 0.15 days/year (*p<0.001* for the "year" term in a linear mixed model analysis with a plot random effect), and by 0.14 days/year at the dry site (*p<0.0001* for the "year" term in a linear mixed model analysis with a plot random effect). If predicted as well as observed snowmelt values are included in the analysis, the delayed snowmelt trend becomes even stronger (0.16 days/year at the mesic site and 0.30 days/year at the dry site; *both p-values <0.0001*). Overall, snowmelt occurred significantly earlier at the dry site than at the mesic site (3.09 days earlier for observed values only, or 3.96 days earlier if predicted snowmelt values are also included; *both p-values <0.0001*), and there was a slight but not significant effect of treatment on snowmelt (0.7 days earlier in the warm treatment; *p=0.180*, or 0.99 days earlier in the warm treatment (*p=0.120*) if predicted snowmelt values are included).

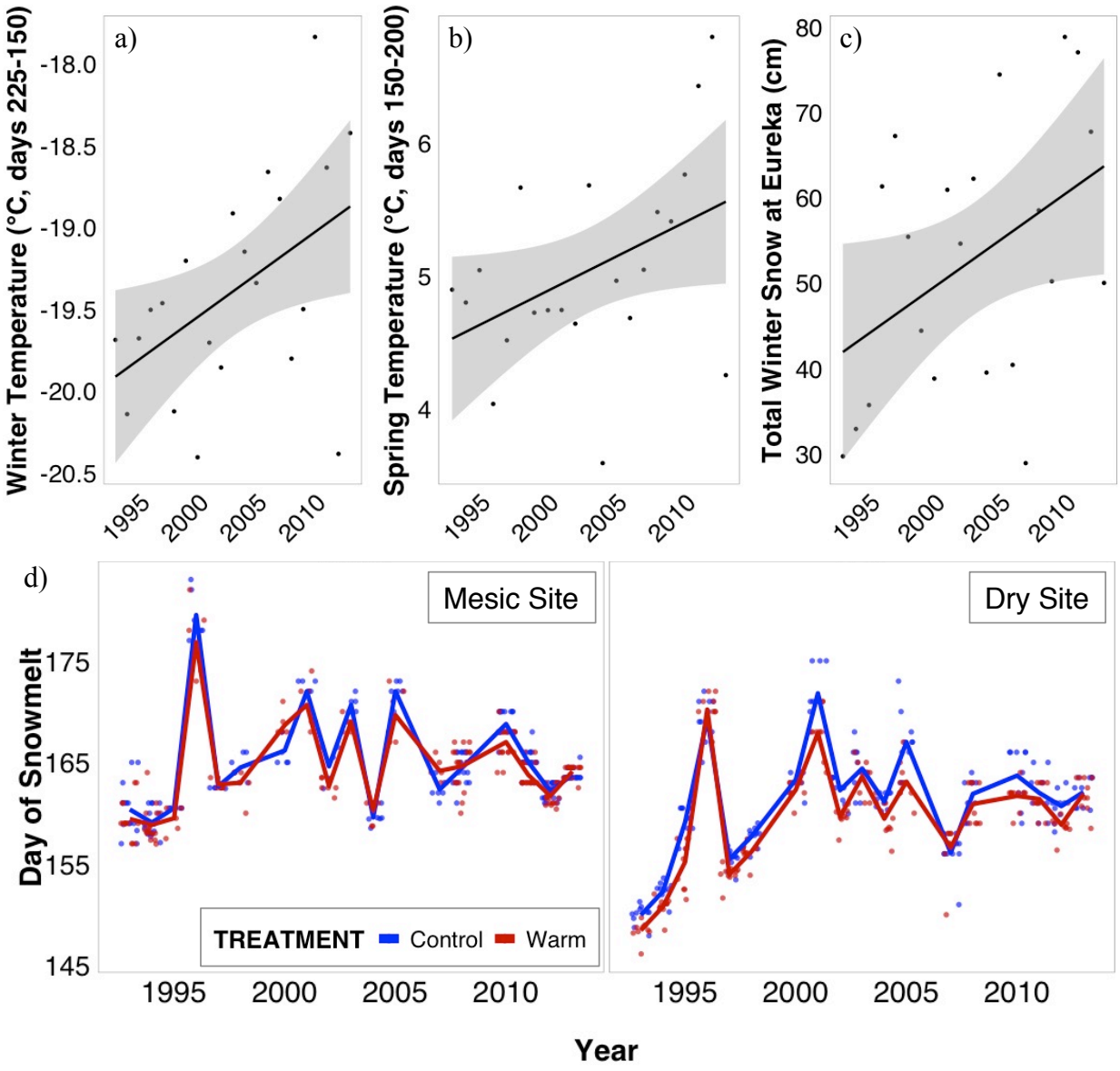

Figure 2.1: Change in winter temperature (a) and spring temperature (b) at Alexandra Fiord, and in total winter snowfall at Eureka (c), and mean date of snowmelt (day of the year), where points are snowmelt dates in each plot and lines are means per treatment, per year (d) over the past two decades.

Three of the four species flowered significantly earlier in the experimental warming treatment than in the control plots, as expected. However, the magnitude of the response varied by species and site (Figure 2.2a, Table A.1). *P. radicatum* flowered 2-5 days earlier in the warm treatment at the dry site, but did not respond significantly to warming at the mesic site. *S. arctica* did not

flower significantly earlier in the warm treatment. Experimental warming also led to earlier seed development for three of the four species (Figure 2.2b), but the effect was significant only for *D. integrifolia* at the mesic site (1.5-7 days earlier) and *P. radicatum* at the dry site (2.7-10 days earlier). In contrast, warming delayed seed dispersal in *S. arctica* by 1-10 days.

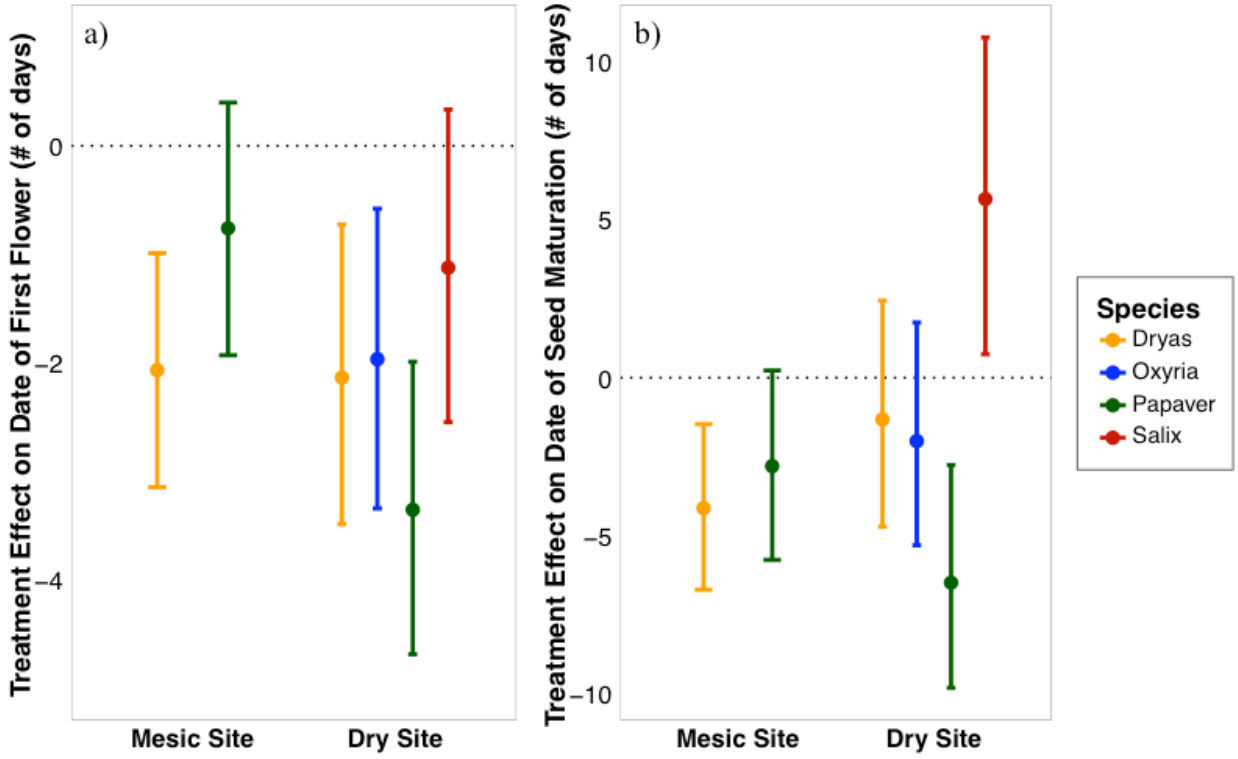

Figure 2.2: Modeled difference, in number of days, in flowering time (a) and seed maturation/dispersal (b) between the control and warmed treatment for each species across all years. Negative values (below the zero line) indicate earlier flowering in the warm treatment. Point estimates and 95% credible intervals are derived from a Bayesian hierarchical model including random effects for plot and year.

Despite more than 1°C of ambient (non-experimental) warming over the two decades of observation, none of the four species show the expected trend of earlier flowering over time in the control plots (Figure 2.3, Table A.1). In fact, one species (*D. integrifolia*) showed significantly delayed phenology over time at the dry site (0.58 days/year, CI range = 0.06 to

1.11). Both *P. radicatum* and *O. digyna* also demonstrated delayed phenology, though 95% credible intervals for the slope of change over time overlapped zero for both species. The flowering time of the other species, *S. arctica*, remained constant over the study period. The magnitude of the time trend varied between the two habitat types. The delay in flowering time was greater at the dry site than at the mesic site for at least one species; at the beginning of the study, flowering of *D. integrifolia* occurred significantly earlier at the dry site than at the mesic site (mean = 8.5 days earlier, CI range = 1.3 to 15.8 days) while at the end of the study there were no significant differences between the two sites (mean = 2.4 days earlier, CI range = -5.7 to 10.4 days). *P. radicatum* showed a similar pattern of more rapid change in the dry site than in the mesic site, but the difference between sites was not significant. Similar trends were observed in the warm treatment (Figure A.2).

Differences in individual species' flowering-time responses also led to significant changes in the period of co-flowering over the course of the study. At the start of the study *S. arctica* and *D. integrifolia* did not flower at significantly different times (mean = 3.6 days earlier for *S. arctica*, CI range = -4.5 to 11.7 days), but by the end of the study *D. integrifolia* flowered an average of 13.3 days later than *S. arctica* (CI range = 4.9 to 21.7 days).

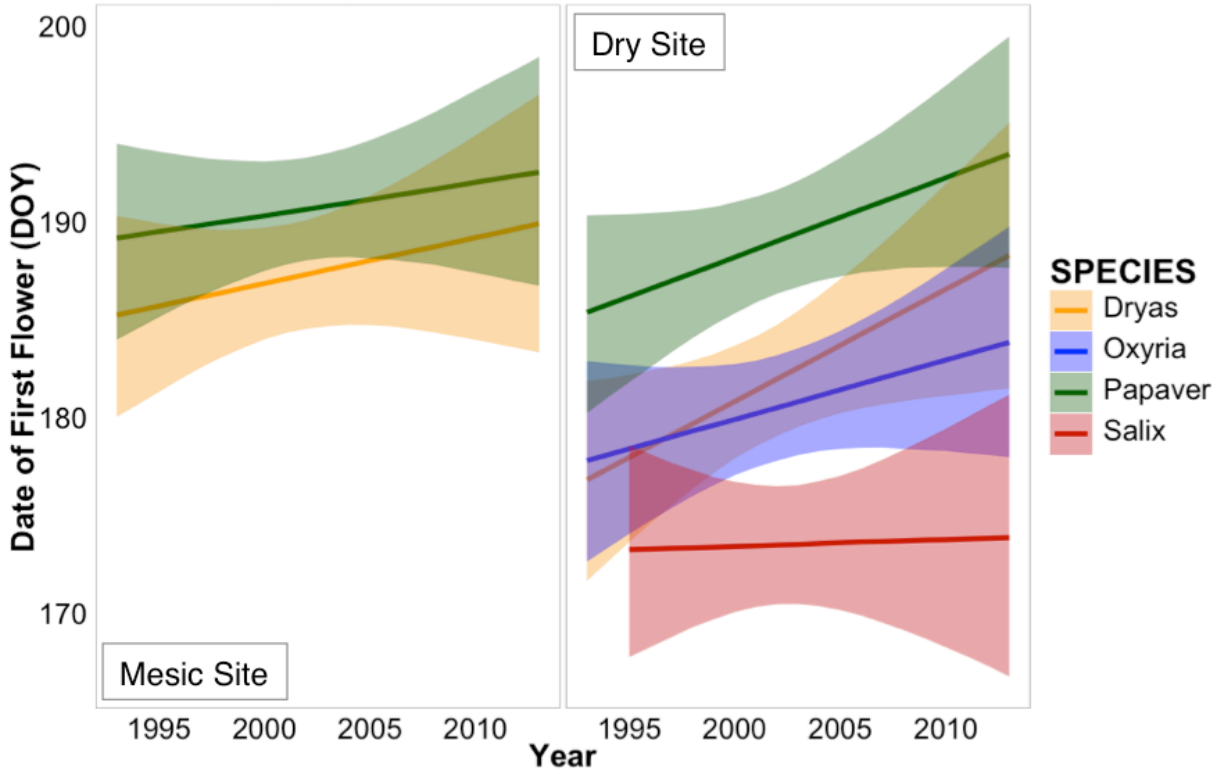

Figure 2.3: Change in flowering time (+/- 95% credible intervals) in the control plots over the duration of the study. Flowering in *Salix* includes both male and female plants. Modeled results are from a Bayesian hierarchical model with random effects for plot and year. Slopes were allowed to vary by species and site as well as the interaction between the two.

Despite delayed flowering times for at least one species, the timing of seed maturation remained relatively constant over the study period (Figure 2.4, Table A.1). In no case was the slope of the trend over time significantly different from zero.

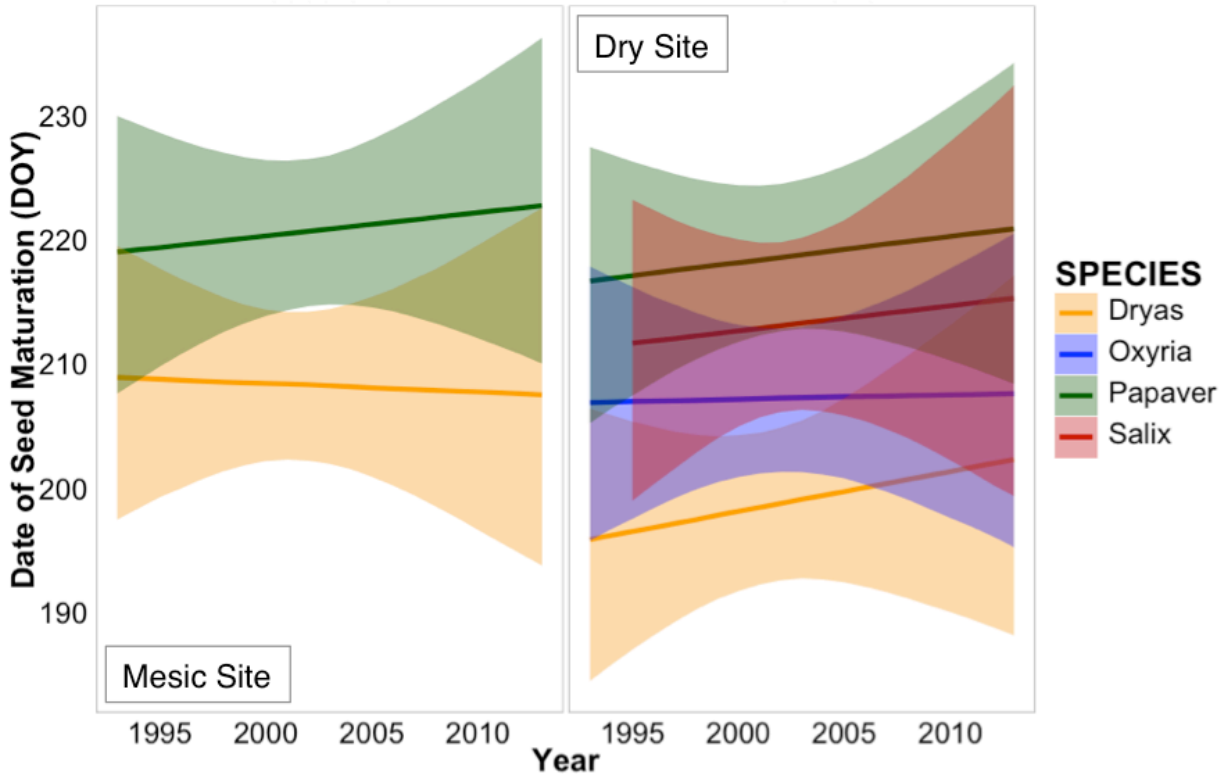

Figure 2.4: Change in predicted date of seed maturation (+/- 95% credible intervals) in the control plots over the duration of the study. Seed development, rather than dispersal, is shown for *Dryas* as dispersal usually occurs late in the season after observations have ceased. Seed maturation for *Salix* is for female plants only. Modeled results are from a Bayesian hierarchical model with random effects for plot and year. Slopes were allowed to vary by species and site as well as the interaction between the two.

Date of snowmelt was significant in explaining flowering time for every species (Figure 2.5, Table A.1). Flowering time was significantly delayed when snowmelt was later, regardless of whether the delay in snowmelt was due to landscape positioning of a particular plot (spatial variation) or the late snowmelt years (temporal variation). Flowering time of *D. integrifolia*, *O. digyna* and *P. radicatum* was negatively related to spring temperature (i.e., warmer spring temperatures led to earlier flowering), but not for *S. arctica*. Winter temperature was positively related to flowering time for *P. radicatum*, indicating that warmer winter temperatures led to

later flowering in this species. The temperature of the previous summer was not a significant predictor of flowering time for any species.

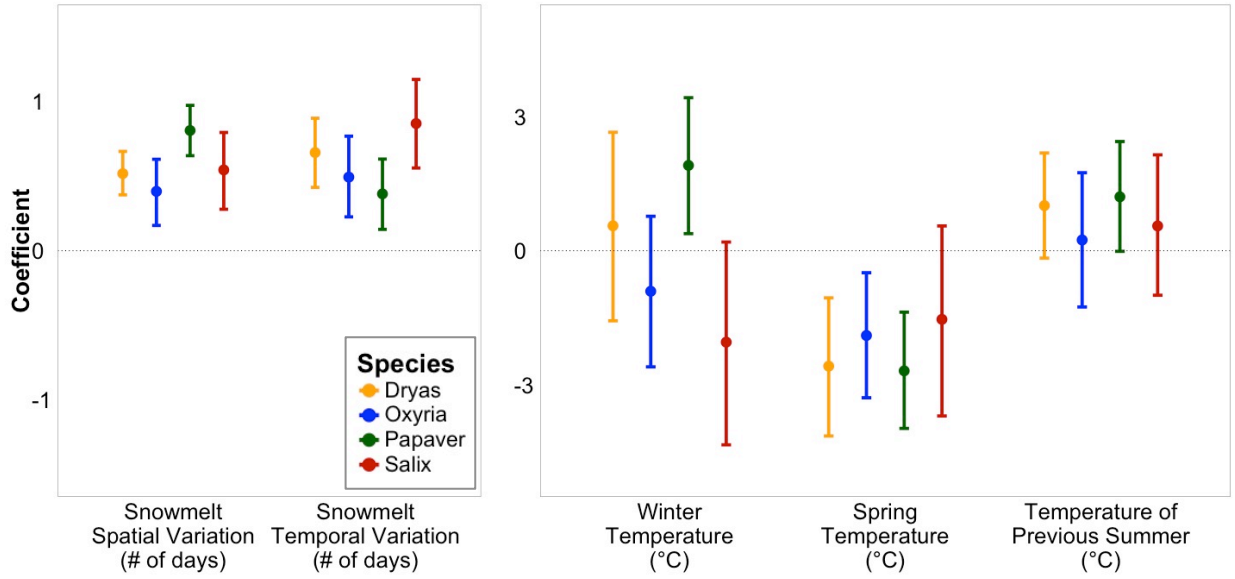

Figure 2.5: Coefficients from a Bayesian hierarchical model of flowering time in both treatments (+/- 95% credible intervals). Coefficients represent the slope of the relationship between flowering time and the different environmental variables for each species. Positive coefficients indicate a positive relationship between that variable and flowering time. Model coefficients reflect the effect of each variable (e.g., a one-day delay in snowmelt leads to a ~one-day delay in flowering for *S. arctica*) in the presence of all other variables in the model (including site, species and treatment, not shown).

2.5 Discussion

The results of this study are in marked contrast to many prior studies demonstrating recent phenological change. As expected, experimental warming led to significantly earlier flowering phenology across species and habitat types. Despite more than 1 °C of ambient warming over the 21 years of the study, however, flowering phenology in the control plots remained constant or was delayed over time for all four species observed. The timing of seed maturation did not change significantly over the study period, indicating that warmer temperatures may lead to the

more rapid development of mature seeds and at least partly mitigate the effects of delayed flowering.

The contrasting responses to experimental and ambient warming are likely due to disparate effects of warming on the timing of snowmelt. While experimental warming led to slightly (though not significantly) earlier snowmelt, snowmelt in the control plots was delayed in one of the habitat types and showed no change in the other. This may have been due to increased winter snowfall over the study period (likely an indirect effect of atmospheric warming; Bintanja and Selten 2014), as winter snow accumulation increased substantially at the nearest weather station between 1993 and 2013. However we are unable to confirm that increases in snowfall have also occurred at our study site due to a lack of long-term data. Delayed phenology could also be explained by a delay in chilling requirement (Yu et al. 2010), but as winter temperature was a significant predictor of flowering time for only one species (*P. radicatum*) this is likely not the primary driver here.

The disparity between phenological responses to experimental warming and the observed temporal trend in phenology concurrent with ambient warming highlights the importance of interpreting phenological responses to experimental warming with care. Several studies have demonstrated advanced phenology in response to experimental warming (Arft et al. 1999, Hollister et al. 2005a) and these experimental responses can sometimes underestimate true responses to climate warming (Wolkovich et al. 2012). The results from our study, however, indicate that responses to experimental warming can actually overestimate the phenological advances we are likely to see with climate warming, as they do not sufficiently account for

altered precipitation or other environmental changes that occur simultaneously with warming temperatures. The significant influence of snowmelt timing on phenology emphasizes the importance of understanding potential precipitation changes in Arctic ecosystems in order to accurately predict flowering phenology.

Phenological responses to ambient warming differed among species within the same habitat type. These differences are likely due in part to the different environmental variables driving flowering phenology in each species. Date of snowmelt was significantly and strongly related to flowering time for all species, suggesting that the timing of snowmelt is consistently a critical driver of flowering phenology in Arctic and alpine species, as has been previously shown (Inouye and McGuire 1991, Inouye et al. 2002, Wielgolaski and Inouye 2013). The relationship between snowmelt and flowering was especially strong for *S. arctica*, the earliest-flowering species, which typically flowers only ~15 days after snowmelt. Conversely, spring temperature was most strongly negatively related to flowering time for the two species, *D. integrifolia* and *P. radicatum*, that flower later in the summer, generally 20-30 days after snowmelt. This suggests that species are likely to differ in their responses to future climatic changes depending on whether they are early-flowering (and thus driven primarily by the timing of snowmelt) or late-flowering (and thus temperature-driven). Studies of temperate plants typically find that early-flowering species are more responsive to changes in temperature than late-flowering species (Rathcke and Lacey 1985, Mazer et al. 2013). This pattern has been attributed to positive physiological effects of warmer temperatures early in the season (i.e., more rapid development) but a negative physiological effect of extreme heat at mid-summer (Sherry et al. 2007). Plants at our study site show the opposite relationship to temperature; that is, early-flowering plants

respond almost exclusively to the timing of snowmelt, while later-flowering plants flower earlier when temperatures are warmer, even after accounting for the effect of differences in snowmelt. This implies that temperatures at our field site have not yet reached levels detrimental to plant development.

Further illustrating the complexity of snowmelt-temperature interactions, the most snowmelt-sensitive species (*S. arctica*) was the only species to show no evidence of a delayed flowering trend over the course of the study period - despite a delay in snowmelt over the same period - while the two temperature-sensitive species flowered later - despite an overall warming trend. This seeming paradox is likely due to a combination of factors. First, observations for *S. arctica* at the dry site are available only from 1995; thus there are no data for this species in the early-snowmelt years of 1993 and 1994. Secondly, several years (including 2004 and 2013) were warm early in the spring, leading to early or normal snowmelt, but then colder shortly after snowmelt. In these years, the snowmelt-driven species, *S. arctica*, responded to the early snowmelt and flowered early, while the temperature-driven species, *P. radicatum* and *D. integrifolia*, responded to the colder spring temperatures and flowered late. Thus a combination of cold springs in some years and later snowmelt in others likely led to the overall pattern of delayed flowering in these two species. Such interactions can also have substantial consequences for plant fitness; several studies have shown that early snowmelt can be beneficial in a warm year (likely due to the longer growing season) but can be detrimental if early snowmelt increases the likelihood of spring freezing events and frost damage (Inouye et al. 2002, Wipf et al. 2009). As species vary in their responses to changes in snowmelt (Walker et al. 1999, Wipf et al. 2009), these differences can lead to substantial shifts in community composition (Walker et al. 1999).

The differing phenological responses among species could have important implications for future shifts in species composition at this site. A failure to optimally track climate warming has been shown to lead to reduced fitness in several other species (Both et al. 2004, Cleland et al. 2012) and can lead to changes in species' abundances (Møller et al. 2008) and distributions (Chuine and Beaubien 2001). In high Arctic ecosystems, where the growing season is only 6-8 weeks long, delayed flowering could have serious implications for reproductive fitness if seeds do not reach maturity before the onset of winter (Molau 1993). Despite the delay in flowering time observed here, however, the timing of seed-set was not delayed. This could indicate that warmer temperatures at least partly make up for the delayed spring by promoting the rapid development of mature seeds.

While the lack of a delay in seed maturation suggests that species at this site are not yet experiencing truncated seed development, there are several other potential implications of the observed shifts in flowering time. One much-discussed consequence of changing phenology is the potential effect on the relationships between plants and their pollinators, which play a role in the fertilization of three of the four study species (Robinson 2014). The significant delay in flowering time but lack of change in seed maturation date suggests that the duration of an individual flower (i.e., length of time that any given flower has available pollen) has shortened for at least one species. Conversely, because phenological trends differed among species and sites, the between-species flowering interval actually increased over the study period (*S. arctica* flowering remained constant while *P. radicatum* and *D. integrifolia* were delayed). A similar pattern was observed in montane meadows of the southern Rocky Mountains, where differing

phenological trends in different habitat types led to a divergence in flowering time among sites, with potentially negative consequences for pollinators due to the resulting mid-summer gap in pollen availability (Aldridge et al. 2011). If no such gap occurs, however, a prolonged window of flowering might also be beneficial for generalist pollinators.

Differing phenological responses between the two habitat types could also have important implications for gene flow between populations in each habitat (Fox 2003). While in the early years of the study *D. integrifolia* at the dry site flowered significantly earlier than at the mesic site, the change in flowering over time was also greater at the dry site, so that by the end of the study period plants in both sites flowered concurrently. This difference could be due to differences in topography at the two sites and, as a result, differences in snowmelt trends, or to differences in soil moisture. The different responses could also be due to genetic differences between populations at the two sites (Weis and Kossler 2004). A reciprocal transplant study involving populations of *O. digyna* and *P. radicatum* from both habitat types found evidence of local adaptation in these populations despite their close proximity to each other (~500 m; see Chapter 3). Whether the same is true for *D. integrifolia* is not known, but the differential responses to climate warming at the two sites could lead to increased gene flow and thus increased genetic similarity between the populations of this species.

2.6 Conclusions

The results of this study are a striking contrast to most prior studies of phenological responses to climate change in temperate systems. Furthermore, the only other long term study of phenology in the high Arctic demonstrated dramatic advances in flowering over the decade (1996-2005) of

observation (Høye et al. 2007). In contrast, all four species in our study demonstrated unchanged or delayed flowering, despite significant ambient warming at the site over the 21-year period. Changes in flowering time varied by species and by habitat type, indicating that no single prediction will accurately describe future phenological changes for all species and locations. The timing of snowmelt, however, is a universally important driver of phenology in Arctic and alpine ecosystems (Billings and Bliss 1959, Billings and Mooney 1968, Wielgolaski and Inouye 2013). Our study thus highlights the importance of considering changes in both temperature and snowfall, as well as the interaction between the two, when predicting future phenological trends. Future work should focus on better understanding the fitness consequences of phenological changes in Arctic species and the resulting effects on tundra plant communities.

Chapter 3: Evolutionary and plastic responses of Arctic plants to experimental and natural environmental change in two contrasting habitats

3.1 Synopsis

Global environmental change is widely predicted to lead to altered species distributions and abundances. Species can respond to environmental changes through phenotypic plasticity, evolutionary adaptation, or dispersal to areas of suitable habitat. Plasticity and adaptation may be the only options for the persistence of some tundra species, as warming in high Arctic and alpine areas may eliminate the range of environmental conditions currently occupied by these species altogether. The potential for Arctic species to adapt to rapidly changing conditions is largely unknown. Warming experiments throughout the Arctic have demonstrated substantial responses in plant growth and phenology in Arctic species with warmer temperatures, but whether these responses represent plastic or evolutionary changes has never been tested. Here, we use reciprocal transplant experiments to test for evidence of evolutionary adaptation in two common Arctic plant species, mountain sorrel (*Oxyria digyna*) and rooted poppy (*Papaver radicatum*), to differing environmental conditions between two spatially proximate but distinct habitat types. We additionally test for evidence of genetic change in response to 18 years of experimental warming treatments in these same two habitats and species. In both cases, our results are consistent with evolutionary adaptation to site and treatment conditions, as well as substantial phenotypic plasticity in response to varying site and year-to-year conditions. Our results indicate that plastic and genetic responses to global climate change are likely to play an important role in determining the future of Arctic plant communities.

3.2 Introduction

As global atmospheric carbon concentrations continue to rise, polar areas are predicted to see higher rates of environmental change than anywhere else on the planet. Mean annual temperatures in these regions are projected to rise by 4-7 °C over the next century, along with substantial but less well-understood changes in precipitation and solar radiation via increased cloud cover (Weller et al. 2005, IPCC 2013).

Species can respond to climate change in one of three ways: individuals might acclimate to changing conditions through phenotypic plasticity, populations might evolve through adaptive genetic change, or species might migrate poleward, tracking their optimal climate (Holt 1990, Davis et al. 2005, Gienapp et al. 2008, Aitken et al. 2008). If species are not capable of plastic, adaptive, or migratory responses, they face the threat of extinction.

Polar and alpine species are in a unique situation in that they are already at the edge of their potential ranges; in other words, the climatic conditions suitable for these species might disappear from the earth altogether rather than shifting upward or poleward. Thus, phenotypic plasticity and evolutionary adaptation may be particularly important for the persistence of these species. While phenotypic plasticity is an important mechanism through which organisms can respond to environmental variability through space and time, there are limits to how much plasticity is possible (DeWitt et al. 1998). For this reason, it has been suggested that plasticity itself will not be sufficient to allow organisms to respond to the magnitude of environmental change expected to occur over the next century (Gienapp et al. 2008, Visser 2008).

Although many studies have demonstrated that organisms are showing phenotypic responses to climate change (Parmesan and Yohe 2003, Cleland et al. 2006), exceedingly few studies differentiate between plastic and evolutionary responses (Gienapp et al. 2008). Those studies that do investigate evolutionary shifts over time are often unable to separate climate change from other correlated changes (e.g., habitat loss, pollution, disturbance) as the driver of these shifts (Merilä and Hendry 2014, Franks et al. 2014). Furthermore, while rapid evolution has been demonstrated primarily in organisms with short generation times (Franks et al. 2007, Whitney and Gabler 2008, Strauss et al. 2008), Arctic species may be less capable of such rapid evolution, as they typically have long generation times (Berteaux et al. 2004), may be pollination-limited, and often have high rates of self-fertilization (Molau 1993, 1997).

Several studies of plant species in the low Arctic have shown evidence of local adaptation in populations across latitudinal gradients of hundreds (Shaver et al. 1986, Bennington et al. 2012) or dozens (McGraw and Antonovics 1983) of kilometers. Evidence of evolutionary change over time has also been demonstrated. For example, Vavrek et al. (1991) compared plants from modern populations of the sedge *Carex bigelowii* with those grown from seeds extracted from a ~200 year old seed bank and found evidence of temperature-related genetic differences between the historic and current populations. Cottongrass (*Eriophorum vaginatum*) seeds from a seedbank of unknown age (but likely <100 years old) were genetically distinct from the modern population growing at the same location (McGraw 1993).

While these studies suggest that among-population genetic diversity contributes to local adaptation over space and time in Arctic species, nearly all of these studies investigate genetic differences between spatially distinct populations or over many decades or centuries of time. Given the rate of climate change predicted for the Arctic (increases of 4-7 °C within the century; IPCC 2013), selective pressures due to warming and the other environmental changes associated with increased carbon emissions will likely be even stronger than in the past century.

Several experimental studies of Arctic plant species have shown substantial phenotypic and phenological changes in response to warming. Four years of experimental warming at multiple locations throughout the Arctic led to earlier flowering time and increased growth across many sites and species (Arft et al. 1999). Longer-term studies in particular localities have also demonstrated advanced flowering, increased leaf size, and increased plant height for individuals in experimental warming treatments relative to controls (Welker et al. 1997, Henry and Molau 1997, Hudson et al. 2011 and Chapter 2). Whether these changes are purely plastic responses to warming, or whether evolutionary adaptation has also played a role, has never been investigated although this kind of experiment has been identified as an ideal system to assess evolutionary responses to warming (Anderson et al. 2012a).

Our objectives for this study were twofold. First, we asked whether two Arctic plant species show evidence of evolutionary adaptation to environmental differences between nearby populations. We then investigated whether these same species show evidence of evolution over time in response to 18 years of experimental warming. While many studies of evolutionary adaptation in response to climate change have been unable to distinguish between correlated

drivers of evolution (Merilä and Hendry 2014), our experimental system permits testing for adaptation specifically to warmer temperatures. By assessing the phenotypic and evolutionary responses of species to existing spatial and recent temporal environmental variation, we can begin to understand the potential of these species to respond to future environmental change.

3.2.1 Study system

Alexandra Fiord (78°53`N, 75°55`W, Ellesmere Island, Canada; see Svoboda and Freedman 1994) provides an ideal Arctic setting to answer these questions. The Alexandra Fiord lowland contains substantial environmental heterogeneity due to variation in microtopography and soil moisture (Muc et al. 1989). Two species (*Papaver radicatum* and *Oxyria digyna*, both perennial forbs) occur in both a mesic and a dry habitat at the site, providing a natural environmental gradient over which adaptation to environmental conditions may occur. Furthermore, passive warming experiments have been maintained in both of these habitats since 1992. Plants in experimentally warmed plots have significantly larger leaf size and plant height (Hudson et al. 2011), and they flower significantly earlier (see Chapter 2) than plants in control plots in at least one of the two habitat types. Thus, this study system presents a unique opportunity to assess plastic vs. evolutionary responses to experimental warming.

3.2.2 Hypotheses and predictions

We conducted a series of reciprocal transplant experiments – one between the dry and mesic habitat types as well as two transplant experiments between the experimental treatments (warmed and control), one in each habitat type – to determine whether adaptation to environmental variation over space and time has occurred at this site. If local selection within

each habitat is strong enough to overcome the homogenizing effect of gene flow between them, we would expect to see evidence of local adaptation (Kawecki and Ebert 2004) to the environmental conditions at each site.

Similarly, if evolution in response to 18 years of experimental warming has occurred within the warming experiments, we would expect to find evidence of local adaptation to conditions within each treatment (i.e., warmed and not warmed). As Arctic plants often have the capacity to grow larger under more favorable (e.g., warmer) conditions than they do in their native environment (Mooney and Billings 1961, Billings and Mooney 1968, Arft et al. 1999), we would expect plants from both control and warm treatments to perform better under warmed conditions. In this case, evidence of adaptation to warming would be indicated by an additional advantage of plants transplanted from the warm treatment over plants transplanted from the control treatment into the warmed treatment. We would additionally expect plants from the warm treatment to have lower fitness relative to those from the control treatment when planted into the control treatment.

One potential consequence of climate change is a lengthening of the growing season (i.e., the number of snow-free days with mean temperature above 0 °C), either via earlier snowmelt and/or warmer spring temperatures, or via additional warm days in the fall. Thus, selection might favor genotypes that can take advantage of a longer growing season, either through earlier "leaf-out" (leaf bud unfolding) or through later fall senescence. We therefore expect to see evidence of earlier spring phenology (leaf-out date) and delayed fall senescence for plants from the warm treatment. Fall senescence can be determined by temperature, photoperiod, deterministic leaf age (Shaver and Kummerow 1992, Starr et al. 2000, Oberbauer et al. 2013) or even soil moisture

(Billings and Mooney 1968). It is not known which of these contribute to senescence in our study species, but if senescence were a response to photoperiod, we would not expect a transplant destination effect on individuals from the same source population, as photoperiod does not vary between the treatments or habitats.

3.2.3 Maternal effects

As with the majority of transplant studies, we are unable to entirely exclude the possible influence of maternal or epigenetic effects on offspring phenotype (Roach and Wulff 1987, Bossdorf et al. 2008). In order to minimize the potential influence of maternal environmental effects on our results, we included seed mass as a covariate in all models. Seed mass is commonly used as an estimate of maternal seed provisioning (Dlugosch and Parker 2008, Angert et al. 2008, McLane and Aitken 2012), especially in slow-growing perennial species for which the time required to generate new seed from plants grown in a common environment is prohibitive. Henceforth, we describe among-population differences, after controlling for seed mass, as being genetically based.

For population-specific seed mass means and a more thorough discussion of maternal environmental effects, see Appendix B.1.

3.3 Methods

3.3.1 Study site

Alexandra Fiord (78°53`N, 75°55`W) is located on Ellesmere Island, the northernmost island in the Canadian Arctic Archipelago. The Alexandra Fiord lowland is an 8 km^2 glacial outwash

plain bounded to the north by the fiord, to the east and west by ~750 m high plateaus, and to the south by a large glacier (part of the Prince of Wales ice cap). Although the region is considered polar desert due to very low precipitation levels (Freedman et al. 1994), there is a strong soil moisture gradient in the lowland. The vegetation consists of several different distinct plant communities, which vary along this moisture gradient (Muc et al. 1989).

This study was conducted in two distinct habitat types: a mesic heath community dominated by *Cassiope tetragona*, an evergreen dwarf shrub, and a dry sandy creek bank dominated by a deciduous dwarf shrub, *Salix arctica*, and several species of graminoids. The two sites are approximately 500 m apart and are separated by a small stream. The two focal species, rooted poppy (*Papaver radicatum* Rottb.) and mountain sorrel (*Oxyria digyna* (L.) Hill; hereafter referred to as *Papaver* and *Oxyria*), occur in both habitat types, though both tend to be more abundant at the dry site. Snowmelt generally occurs earlier at the dry site than at the mesic site. Between 1993 and 2013, long-term monitoring plots at the dry site became snow-free an average of 3-4 days earlier than at the mesic site (see Chapter 2). The mesic site is 0.82 °C warmer (+/- 0.04 °C; at 10 cm height) than the dry site on average over the year, likely due to deeper snowpack in winter, but during the early growing season (June) the dry site is slightly warmer than the mesic site (0.35 °C, +/-0.08 °C) possibly due to earlier snowmelt.

Oxyria is wind-pollinated (Billings 1974) while *Papaver* is insect pollinated (Robinson 2014); both species are self-fertile. The rate of selfing vs. outcrossing is not known, but a recent study at the site suggests that *Papaver* has higher germination rates when outcrossed rather than self-fertilized (Robinson 2014). Both species germinate readily from seed under controlled conditions

(Klady et al. 2011); *Oxyria* also spreads by underground rhizomes (Mooney and Billings 1961). The maximum life span of *Oxyria* individuals has been recorded as 13 years in the Austrian Alps and 17 years in the Scandinavian subarctic (Erschbamer and Retter 2004), but the life span of high Arctic populations is unknown. The maximum lifespan of *Papaver* ranges between 8 and 30 years (Lévesque et al. 1997, Jónsdóttir 2011).

Papaver is an early-successional species frequently found growing amongst rocks where there is very little substrate and in very dry conditions. It is often one of the first species to establish at the glacier foreland (Jones and Henry 2003), though it frequently occurs in undisturbed habitats as well. *Oxyria* is not typically associated with early successional habitats in the high Arctic but it does occur across a broad range of alpine and Arctic habitats; its distribution spans 47 degrees of latitude (Mooney and Billings 1961).

3.3.2 Warming experiment

In 1992, experimental plots were established in these two plant communities as part of the first site in the International Tundra Experiment (ITEX; Molau and Mølgaard 1996, Henry and Molau 1997, Hudson and Henry 2010). Half of the experimental plots were warmed using open-top chambers (OTC's), which passively warm the air inside (Marion et al. 1997). Between 1995 and 2011, experimentally warmed plots were 2.14 and 1.56 (+/- 0.04) °C warmer than the control plots at the dry and mesic sites, respectively, averaged over the entire year, as measured by temperature loggers (HOBO loggers, Onset Computer Co., U.S.A.) placed at 10 cm height in a subset of plots. The warming effect of the OTC's was greater during the winter than during the summer, likely due to a snow-trapping effect. Winter temperatures (September-May) were 3.01

and 2.38 °C warmer in OTCs than in control plots, while growing season temperatures (June-August) were 1.78 and 0.91 °C warmer in control plots at the dry and mesic sites, respectively. Despite the snow-trapping effect of the OTC's, snowmelt occurs slightly, though not significantly, earlier in the warmed plots (see Chapter 2; Table B.2).

Data on the timing of phenological events as well as other phenotypic measurements have been collected for tagged individuals of a number of species in nearly every year since 1992 (see Chapter 2).

3.3.3 Experimental design

During the summer of 2010, we collected seeds from every flowering individual of both species in every experimental plot in each of the two habitats. The total number of maternal plants sampled was n=77 for *Oxyria* and n=115 for *Papaver* at the mesic site, and n=147 for *Oxyria* and n=122 for *Papaver* at the dry site. Seeds were collected when they reached maturity (just before seed dispersal occurred); collection dates ranged from the 29th of July (day 210) to the 17th of August (day 229).

All seeds were allowed to dry at ambient temperatures for four weeks and were then weighed in groups of 10 to determine an average seed weight per family. Seeds were stored over the winter at 2°C. In early June 2011, seeds were planted into seed trays at Alexandra Fiord and germinated in Flowerhouse® RowHouse™ cold frame greenhouses. Seed trays were filled with soil collected from the site and sifted and homogenized during the previous summer.

In mid-July, seedlings were transplanted into newly established experimental plots in both sites in order to avoid compromising the long-term experimental plots. These plots were grouped together directly next to the original experimental area in each habitat type. Due to variable seed counts, germination rates, and seedling survival rates (40-100%) per family, between 4-20 individuals from 33-49 families were planted into the between-treatment and between-habitat experimental plots in an incomplete randomized block design (Table 3.1). Families were approximately evenly divided between "destination" treatments and sites.

Table 3.1: Total number of families (mothers) per species planted in each experimental site. The average number of individuals from each family is shown in parentheses.

Species	Mesic (between-treatment)	Dry site (between-treatment)	Between-habitat
Oxyria digyna	45 (11.6)	49 (14.3)	42 (14.1)
Papaver radicatum	33 (13.3)	45 (12.5)	41 (12.2)

During the summers of 2012 and 2013, all plants in the experiment were observed at 3-day intervals, and the timing of first new leaf and first mature leaf was recorded. In addition, we recorded the number of leaves and measured maximum leaf width and plant diameter at peak season (early-mid July) and at the end of the season (early August) for every individual (Figure 3.1). We used a subset of plants outside the experimental plots to determine the relationship between these measurements and true leaf area, as measured by scanning the leaves into the ImageJ (v. 1.48; http://imagej.nih.gov/ij/) program.

Figure 3.1: A *Papaver radicatum* individual at the mesic transplant site.

We determined that true leaf area was highly predictable based on these three measurements, according to the equations:

Oxyria: Leaf Area = 59.26 + 0.42 * Leaf Width * Plant Diameter * (# of Leaves / 2)

Papaver: Leaf Area = 70.00 + 0.41 * Leaf Width * Plant Diameter * (# of Leaves / 2)

Plant diameter is defined as the maximum distance, tip-to-tip, between two opposite leaves (see Figure 3.1). For individuals with only one leaf, the number of leaves was not divided by two as

this would underestimate total leaf area for these plants. The R^2 values for regressions of measured leaf area against true leaf area were 0.94 for *Papaver* and 0.96 for *Oxyria*.

In 2013 only, we also recorded the presence/absence of senescing leaves during the second round of measurements in order to determine whether these plants had reached the end of their growing season. We additionally recorded the date of snowmelt for each plot. A plot was considered snow-free when it was 90% bare. Plants that did not produce any new leaf buds at any point in 2013 were considered dead.

Although we do not have a direct estimate of fitness components other than survival (even after three summers of growth only one plant flowered), plant leaf area/size is often highly correlated with reproductive fitness (Samson and Werk 1986), and is a commonly used correlate of plant success for perennial species (Rehfeldt et al. 2002, Mimura and Aitken 2010, McLane and Aitken 2012). While this may affect some of our conclusions about which species do and do not show evidence of local adaptation *per se*, it does not affect an overall conclusion that significant source-population effects represent an evolutionary response to environmental differences.

3.3.4 Statistical analyses

All analyses were conducted using generalized linear (survival and senescence) or linear (phenology and leaf area) mixed models in the lme4 package (Bates 2010) in R (version 3.1.1). "Source" treatment or site and "destination" treatment or site were included as fixed effects, along with seed weight as a covariate to account for a possible maternal effect of differential seed provisioning. For those response variables measured in both years (leaf-out date and leaf

area), a factor term for "year" was included as a fixed effect. Family (mother) and plot were included as random effects, with a random slopes term for "destination treatment" for each family and a random slopes term for "year" for each plot. Survival and senescence were modeled with a binomial error distribution because they represent binary (yes/no) data. Continuous response variables were transformed as necessary (square-root or reciprocal transformations) to meet the assumptions of homogeneity and normality of errors. Values reported in the results are back-transformed to the original data scale.

The significance of each variable was determined by comparing nested models with likelihood ratio tests. First, non-significant random effects were dropped from the model (cutoff p-value = 0.1), followed by non-significant fixed effects (cutoff p-value = 0.05). We used a higher cut-off value for random effects because testing on the boundary in this way is likely to underestimate their significance (Zuur et al. 2009, Bates 2010). All analyses were also run separately with fixed effects for snowmelt, the interaction between snowmelt and source treatment/site, and the interaction between snowmelt and transplant treatment/site as covariates (2013 only), but as including snowmelt did not alter any of the results presented here, we do not show these analyses.

3.4 Results

Ambient temperatures varied substantially between the two years of measurements. Spring and early summer (day 150-200) temperatures were, on average, 2.5 °C warmer in 2012 than in 2013 (6.8 °C in 2012 vs. 4.3 °C in 2013; at 1.5 m height). Snowmelt occurred earlier in 2012 than in 2013, and earlier in the dry site than in the mesic site (Table B.2).

3.4.1 Between-habitat transplant experiment

Survival was extremely high for both species (83-90% for *Oxyria* and 97-100% for *Papaver*; Figures 3.2 and 3.3) across all source and transplant sites. There were no significant differences in survival between sites for either species. The "source site" effect was significant for nearly every other response variable for both species in the between-habitat experiment. *Oxyria* plants that originated from the mesic site leafed-out earlier than plants from the dry site at the dry site, but later at their home (mesic) site (Figure 3.2a, Table B.3). Despite their earlier phenology, however, these from-mesic-to-dry plants had the smallest leaf area of all source-destination combinations. Plants that originated from the dry site were consistently larger than those from the mesic site, regardless of transplant site (Figure 3.2c, Table B.3).

In 2013, plants from the mesic site were significantly more likely to have senesced by early August than plants from the dry site, regardless of their transplant site (Figure 3.2b, Table B.3). Although senescence was recorded only in 2013, an examination of the change in leaf area between the first (peak season) and second (end of season) measurements in 2012 shows that *Oxyria* plants from the mesic site were more likely to decline in leaf area between the two measurement periods than plants from the dry site ($p=0.03$), thus consistent with the results from 2013. Overall, plants leafed-out earlier and were larger in 2012 than in 2013.

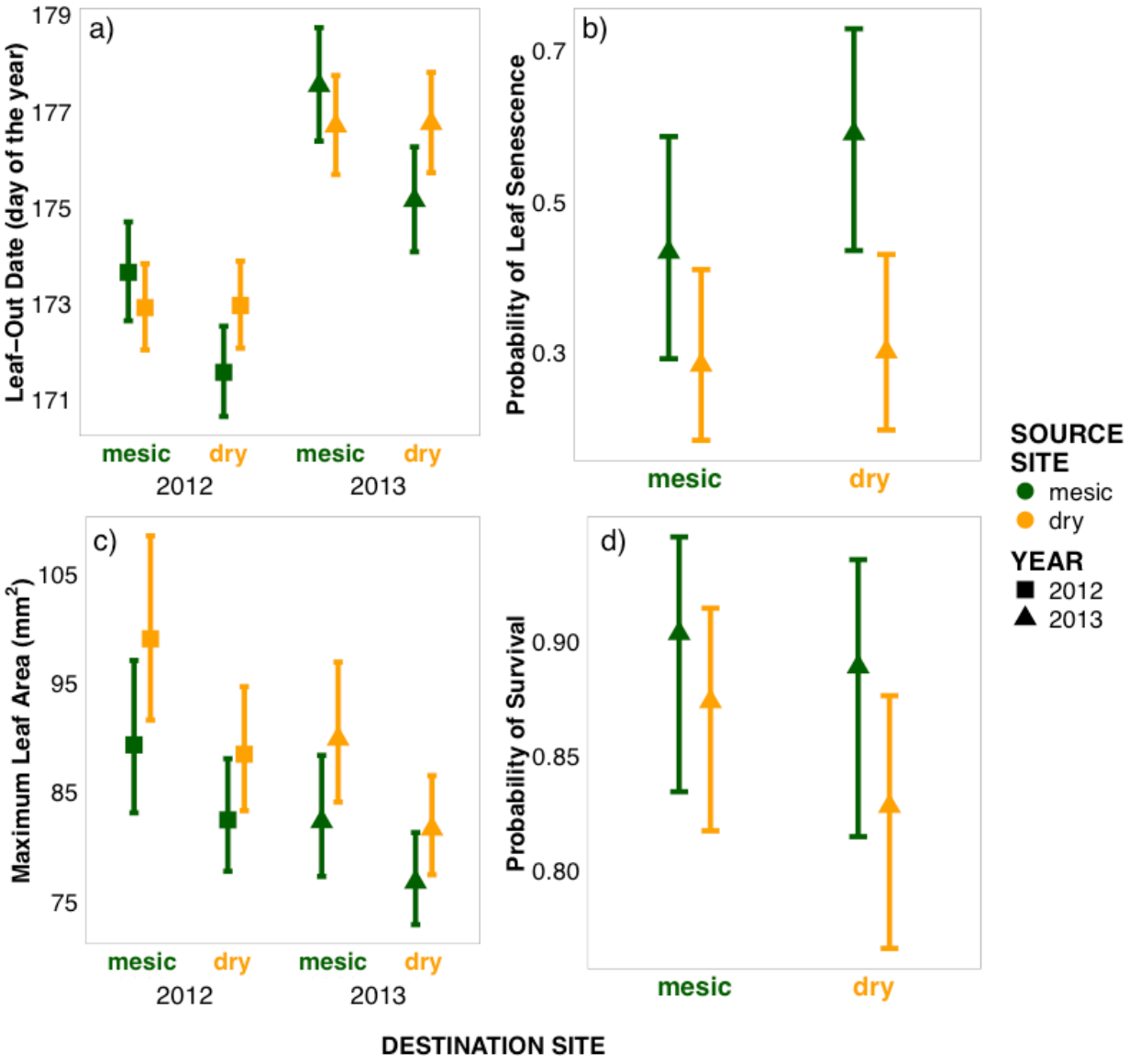

Figure 3.2: *Oxyria* in the between-habitat transplant experiment: a) day at which the first mature leaf was observed, b) probability of leaf senescence by mid-August (2013 only), c) maximum leaf area in 2012 and 2013, and d) probability of survival at the end of 2013. Points are predicted means from a linear mixed model; bars are 95% prediction intervals on the fixed effects of this model. Seed weight was significant in the model for maximum leaf area; therefore the values shown above are the predicted values of maximum leaf area at mean seed weight. The correlation between seed weight and plant size was slightly negative over both populations.

Leaf-out date for *Papaver* plants at the dry site showed a significant source treatment effect, such that plants from the dry site leafed-out earlier than plants from the mesic site (Figure 3.3a, Table

B.3). As with *Oxyria*, plants from the mesic site also senesced before plants from the dry site, regardless of their transplant site (Figure 3.3b, Table B.3). This indicates that dry-to-dry *Papaver* plants have an extended growing season relative to any other source-destination combination, as these individuals were also the first to leaf-out in the spring. As *Papaver* does not senesce in the same way that *Oxyria* does (leaves turn yellow but do not dry up), the same comparison to 2012 data was not possible.

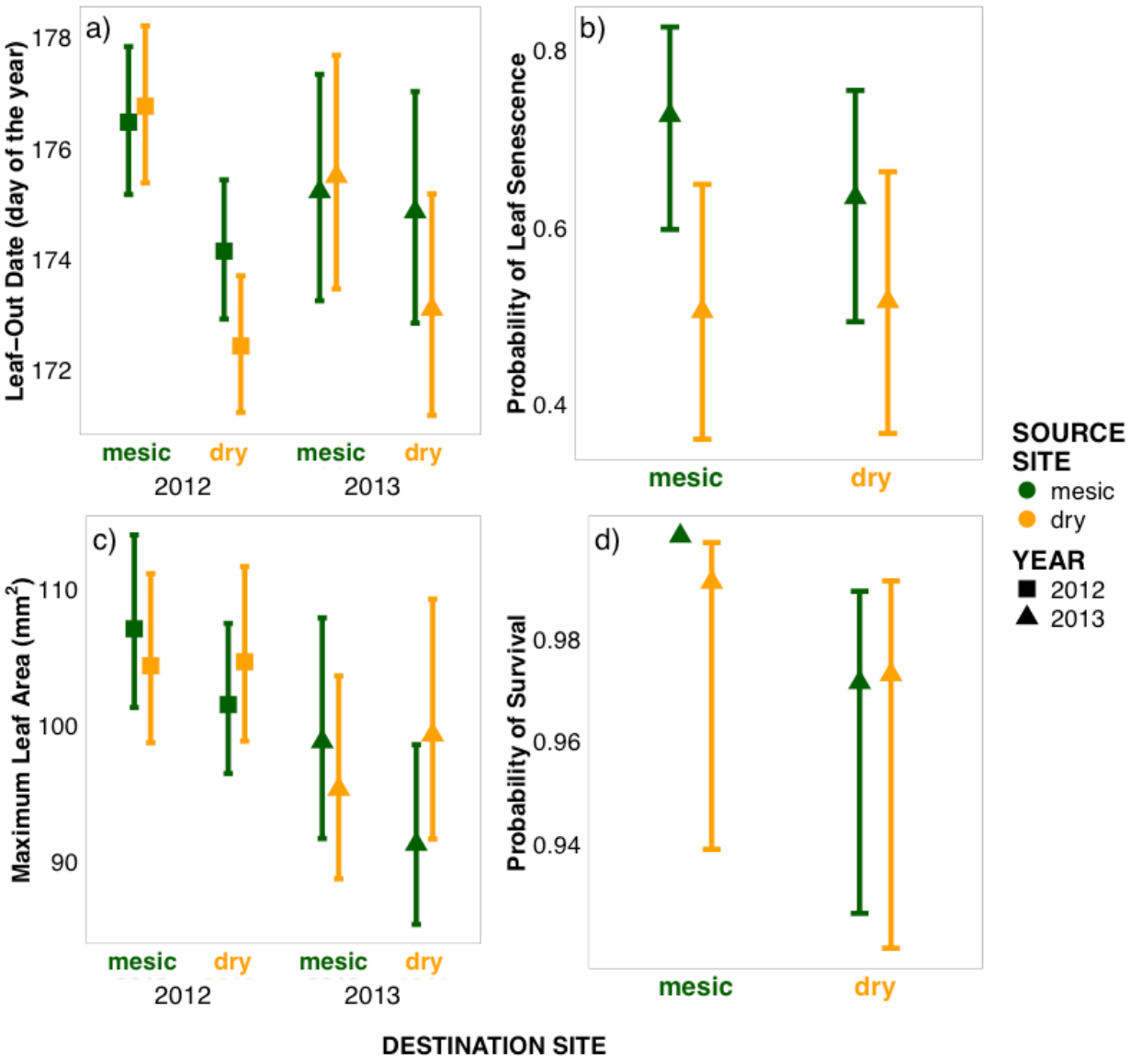

Figure 3.3: ***Papaver*** **in the between-habitat transplant experiment, a) day at which the first mature leaf was observed (leaf-out), b) probability of leaf senescence by mid-August (2013 only), c) maximum leaf area in 2012 and 2013, and d) probability of survival at the end of 2013. Points are predicted means from a linear mixed model; bars are 95% prediction intervals on the fixed effects of this model. A year * destination site interaction term was marginally significant (*** $p=0.06$ ***) in the model predicting leaf-out but was included in the predicted values shown in the graph for visualization purposes. Survival of mesic-at-mesic individuals was 100%, thus error could not be estimated.**

Maximum leaf area of *Papaver* also varied between the two source sites and transplant sites, and the interaction between source site and destination site was highly significant ($p<0.001$; Figure

3.3c, Table B.3). Plants from both source sites were larger at their "home" site and smaller at their "away" site in both years. Overall, plants were larger in 2012 than in 2013.

3.4.2 Between-treatment transplant experiments

Survival was again very high for both species in both treatments and at both sites (91-96%). *Oxyria* survival was slightly lower in the warmed plots than in the control plots at both sites, but the differences were not significant (Table B.4).

Phenological and leaf area responses varied substantially between species, sites, and years. The magnitude of the OTC treatment effect was generally reduced in 2013 compared to 2012, with some exceptions. Despite the variability between years, several response variables showed consistently significant source treatment and transplant treatment effects across both years of measurement.

Oxyria plants originating from the warm treatment at the dry between-treatment transplant site leafed-out significantly earlier than plants from the control treatments in both years. There was also a significant transplant treatment effect, such that plants in warmed plots leafed-out earlier than plants in control plots, in 2012 but not in 2013 (Figure 3.5a, Table B.4). Plants from the warm treatment at the dry site also senesced earlier than plants from the control treatment in 2013, though the difference was only marginally significant ($p=0.054$; Figure 3.5b, Table B.4). The change in leaf area between the first (peak season) and second (end of season) measurements in 2012 shows that *Oxyria* plants from the warm treatment were more likely to decline in leaf area between the two measurement periods than plants from the control treatment

(*p=0.029*), consistent with the senescence results from 2013. Despite significant source treatment effects for both first mature leaf and leaf senescence, only "year" was a significant predictor of maximum leaf area; plants overall were larger in 2012 than in 2013 (*p<0.0001*, Table B.4).

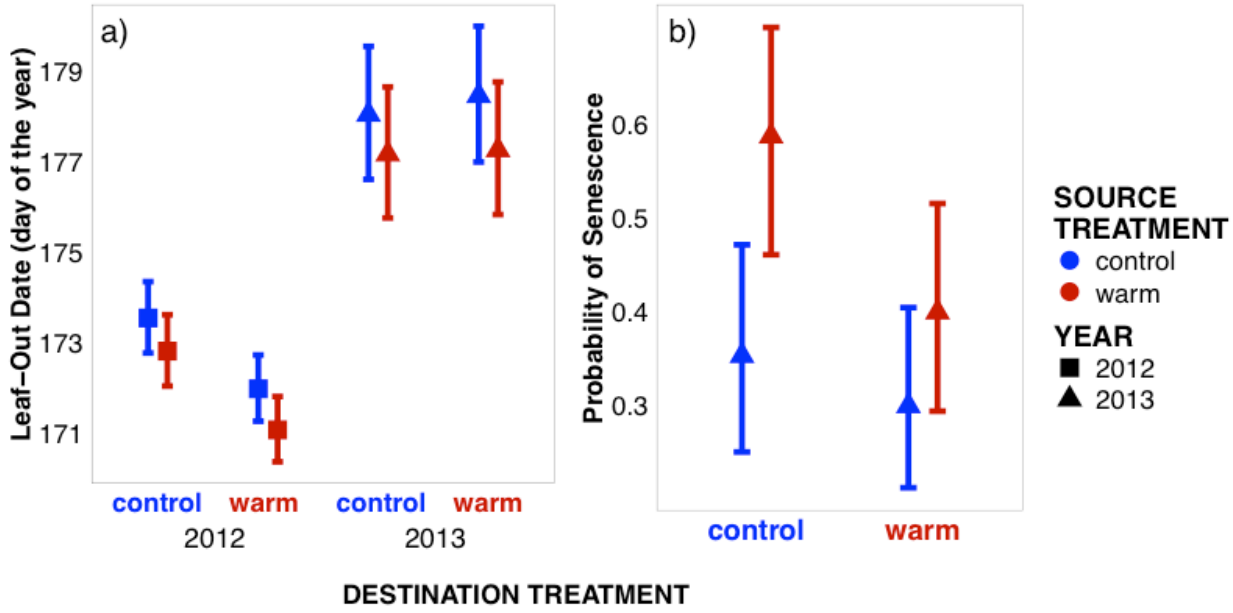

Figure 3.4: Day of first mature leaf (a) and probability of senescence by the first week of August (2013 only) (b) for *Oxyria* plants at the dry between-treatment transplant site. Points are predicted means from a linear mixed model (first mature leaf) or generalized linear mixed model (senescence) for each year and treatment; bars are 95% prediction intervals.

In contrast to the patterns for *Oxyria* seen at the dry between-treatment site, neither source treatment nor transplant treatment was significant for any response variable for *Oxyria* at the mesic between-treatment site. Leaf-out occurred slightly earlier in the warm treatment than in the control treatment in 2012, but not in 2013. Overall plants leafed-out significantly earlier in 2012 than in 2013, but were larger in 2013 than in 2012 (not shown, Table B.4).

For *Papaver*, plants in the warm treatment leafed-out significantly earlier than plants in the control treatment, but only at the mesic site. Plants originating from the warm treatment also leafed out significantly earlier than plants originating from the control treatment at this site, although the magnitude of the difference between source treatments was larger in 2012 than in 2013 (Figure 3.6a, Table B.4). Maximum leaf area also differed significantly with both source treatment and transplant treatment in both years, such that plants from and in the warm treatment were significantly larger than plants from and in the control treatment. In contrast to the leaf-out response, however, the magnitude of the difference between source treatments did not differ between 2012 and 2013 (Figure 3.6b, Table B.4). There were no significant differences between source or transplant treatments for leaf senescence in 2013 (Table B.4).

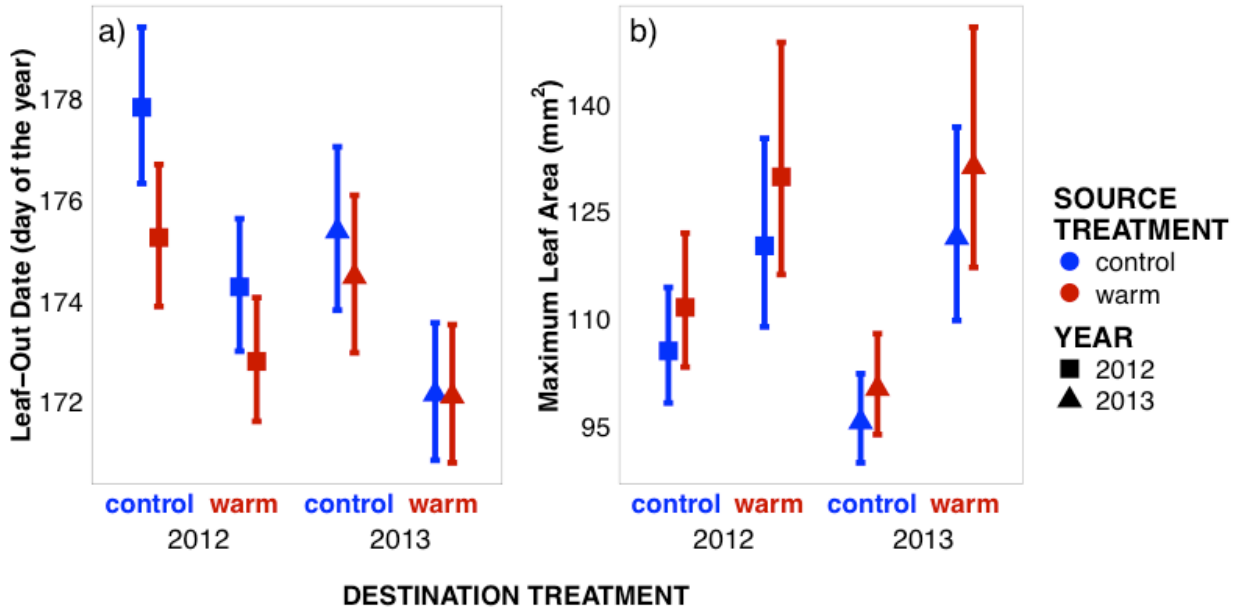

Figure 3.5. Day of first mature leaf (a) and maximum leaf area (b) for *Papaver* at the mesic between-treatment transplant site in 2012 (squares) and 2013 (triangles). Points are predicted means from a linear mixed model for each year and treatment; bars are 95% prediction intervals.

There were no significant source treatment effects for *Papaver* at the dry site. Plants in the warm treatment leafed out significantly earlier than those in the control treatment, but there were no significant differences in maximum leaf area. Both date of mature leaf and maximum leaf area varied significantly by year; plants leafed-out earlier and were larger in 2012 than in 2013 (not shown, Table B.4).

A random effect for family was significant in nearly every model, even when there was no significant source treatment effect, indicating that individuals of the same family are more similar to each other than to other families.

3.5 Discussion

Our results provide evidence of local adaptation to spatial environmental variation for at least one species, as observed in many previous studies (Leimu and Fischer 2008, Hereford 2009), and, more strikingly, of evolutionary responses to less than two decades of experimentally imposed environmental change. The results of the between-habitat transplant experiment suggest strong genetic differentiation between populations of both *Oxyria* and *Papaver* in contrasting environments over a short physical distance (~ 500m). These genetic differences have likely evolved over thousands of years. In addition, reciprocal transplants within the warming experiments provide the first evidence to date of significant, albeit modest, evolutionary responses to 18 years of experimental warming in the field. Although we cannot fully rule out an influence of maternal environmental effects, they are unlikely to account for the differences observed in this study (Weiner et al. 1997, Zas et al. 2013). Seed weight was significant in only one model, and the direction of the relationship between seed weight and plant size was slightly

negative – opposite from the expected direction if seed provisioning confers an early advantage to seedlings.

3.5.1 Phenotypic responses to spatial environmental variation

Results for *Papaver* in the between-habitat transplant experiment indicate local adaptation (Kawecki and Ebert 2004). As expected, *Papaver* plants from the dry site at the dry site leafed-out earlier and were larger than plants from the mesic site at the dry site (see Figure 3.3). At the mesic site, plants from both source sites leafed-out at the same time, but plants from the mesic site were slightly larger than those from the dry site. Assuming that plant size is indeed correlated with fitness (Samson and Werk 1986), this "home site advantage" pattern is indicative of local adaptation within each population (Kawecki and Ebert 2004).

The significant "source site" effect for *Oxyria* in the between-habitat transplant experiment suggests genetic differentiation among populations of this species as well, but the direction of this effect was not always indicative of local adaptation. Plants from the dry site leafed-out at the same time in both destination sites, in spite of the earlier snowmelt at the dry site, while plants from the mesic site leafed-out earlier than plants from the dry site when planted at the dry site, but not when planted at the mesic site (see Figure 3.2). These same mesic-to-dry plants were also the smallest of any source-destination combination, indicating that earlier leaf-out did not confer an advantage in this case. In addition, plants from both source sites were larger overall at the mesic site. This latter difference is not unexpected given the more stressful conditions (drier soils, colder winters, etc.) at the dry site. In contrast to our expectation, however, *Oxyria* plants from the dry site were larger than plants from the mesic site at the mesic site. Possible

explanations for this pattern include relaxed selection at the mesic site due to the less stressful conditions, a change in environmental conditions at the mesic site in the recent past (such that the local population is now maladapted), or that small plant size might be adaptive in some conditions rather than a reflection of low fitness (Dudley 1996). Maternal environmental effects might also be associated with a pattern such as this, but as discussed above, the correlation between seed weight and plant size was actually slightly negative for this species, making this an unlikely explanation.

Although genetic differentiation among populations was indicated by significant source-site effects in both species, plasticity also accounts for substantial phenotypic variation. Plants from the same source population generally varied in both phenology and size depending on the destination site they were planted into. In addition, differences between the two years were in some cases as large as the differences between source and destination sites. *Oxyria* was especially responsive to year-to-year differences; *Oxyria* plants leafed-out up to four days earlier in 2012 than in 2013, while the largest between-site difference within the same year was only two days. *Papaver* did not leaf-out significantly earlier in 2012, but plants of both species were significantly larger in 2012 than in 2013. The large trait differences between years are likely due to the much warmer temperatures in 2012 relative to 2013.

3.5.2 Phenotypic responses to experimental environmental change

Plants within the between-treatment transplant experiments also demonstrated slight but significant differences that suggest evolutionary change in response to experimental warming. As predicted, warming induced plants from both source treatments to leaf out earlier (significant for

Oxyria at the dry site and *Papaver* at the mesic site) and to grow larger (*Papaver* at the mesic site). Plants *from* the warm treatment also developed mature leaves earlier (*Oxyria* at the dry site) and were larger (*Papaver* at the mesic site) than plants from the control treatment, suggestive of genetic differences between the two populations.

Not all results were as predicted by the hypothesis of adaptive evolution in response to experimental warming. Plants from the warm treatment also attained larger sizes in the control treatment than plants from the control treatment (*Papaver* at the mesic site). This unexpected result may be due to the unusually warm ambient temperatures in the year of planting (2011) and the first year of measurements (2012). In fact, 2012 was the warmest spring on record by a margin of 0.5 °C (with 2011 being the second-warmest year, again by a margin of more than 0.5 °C). Thus, the temperature in the control treatment in 2012 was as warm as the average temperature that the "warmed" population experienced during the previous 20 years. Spring temperatures in 2013 were again relatively cool, but as many arctic species set leaf and flower buds in the previous year of growth (Billings and Mooney 1968), there may be a lag before the differential effects of growing season temperature are observed.

In contrast to our prediction that warmed plants would senesce later in order to take advantage of the extended growing season, *Oxyria* plants from the warm treatment at the dry transplant site senesced significantly earlier than those from the control treatment. There was no significant effect of destination treatment. The earlier senescence in plants from the warm treatment may be due to the fact that they also leafed-out earlier, and suggests that fall senescence in this species may be a genetically controlled response of deterministic leaf age rather than a response to

temperature or photoperiod (Sorenson 1941, Shaver and Kummerow 1992). In contrast to *Oxyria*, *Papaver* individuals demonstrated no significant differences in timing of fall senescence by treatment in either site, suggesting that senescence in *Papaver* may instead be a response to photoperiod.

Phenotypic plasticity again accounted for much of the overall variation in phenology and plant size observed for both years and in both treatments. As in the between-habitat experiment, there were large differences between years in timing of leaf-out and plant size. *Oxyria* plants in the warm treatment at the dry transplant site leafed-out approximately six days later in 2013 compared to 2012. *Papaver* plants at the dry site also leafed-out earlier in 2012 than in 2013, but the same pattern was not observed for *Papaver* at the mesic transplant site. Individuals of *Papaver* at both the dry and mesic sites demonstrated a significant plastic response to the warming treatment; plants in the warm treatment leafed-out earlier than plants in the control treatment.

The phenological differences between years were again likely due to the large differences in temperature between the two years, and demonstrate the high degree of plasticity in response to temperature in both species. Responses were particularly variable within the between-treatment transplant experiments, where the average warming effect of the OTCs during the growing season was smaller than the ambient temperature difference between the two years during that same time period. As evidence of adaptation may vary depending on year-to-year conditions (Kawecki and Ebert 2004, Leimu and Fischer 2008), this may account at least partially for the varying results between years in the between-treatment transplant sites, where treatment

differences are entirely temperature-dependent. In contrast, results in the between-habitat experiment – where spring/summer temperature does not differ substantially between the two sites – were much more consistent between years.

3.5.3 Implications for understanding responses to climate change

Genetic differentiation between the dry and mesic populations, as well as significant variation among seed families, indicates substantial heritable genetic variation within the larger Alexandra Fiord meta-populations of both species. In addition, the between-treatment reciprocal transplant experiment suggests that evolutionary responses to experimental warming have occurred after only 18 years, despite what is presumably substantial gene flow among treatments. Ambient climatic warming over the 18 years of the experiment (>1 °C) may also have contributed to the relatively modest evolutionary differences between warmed and control plots, as plants in the control treatment were also subjected to warm temperatures relative to previous decades during this time. Thus, the results presented here may represent a conservative estimate of the evolutionary response to warming for these species.

Even for those species or response variables without a significant source-population effect, a significant family random effect in nearly every model implies that there is a substantial amount of heritable genetic variation within the larger population (Banta et al. 2007, Bolker et al. 2009(see supplementary material)). This variation could become important as the environment continues to change. A family-by-treatment random effect was also significant on several occasions, even in the absence of a source-population effect (e.g., for *Papaver* at the dry

between-treatment transplant site). This is indicative of genetic variation for plasticity in response to warming (Banta et al. 2007), upon which we might expect future selection to act.

The dramatically different growing-season temperatures between the two years of measurement provided a fortuitous natural experiment. Large differences in leaf-out date between the two years demonstrate substantial plasticity in this trait. Furthermore, we observed no evidence of detrimental effects (e.g., reduced size) of warming on individuals of either species, even though temperatures in 2012 reached record highs and the additional warming of the OTCs created temperatures 3-4 °C warmer than the mean temperature of the previous two decades. This is consistent with laboratory studies demonstrating that the optimal growing temperatures of many Arctic and alpine tundra species are in fact substantially higher than what they generally experience in the field (Mooney and Billings 1961, Arft et al. 1999). Thus, future tundra plant communities may be shaped not only by which species can withstand increased temperatures, but also by which species can best compete – both with other local species (Arft et al. 1999, Klanderud 2005, Aerts et al. 2006, Crawford 2008) and with immigrant species (Klanderud and Birks 2003, Callaghan et al. 2004) – for newly available resources.

In contrast to the highly variable timing of leaf-out between treatments and sites, the markedly fixed timing of senescence could indicate that, while Arctic plant species may be able to take advantage of warmer temperatures and potentially earlier snowmelt in the spring through phenotypic plasticity, evolutionary adaptation may be necessary for plants to extend their growing season into the fall (see also Starr et al. 2000). There was never a significant

destination-site or destination-treatment effect for senescence in either species, though there were significant source-site and source-treatment effects for both species.

While most species distribution models predicting the range of species under future climate change assume no evolution in these populations (Pearson and Dawson 2003, Lavergne et al. 2010), the results of these experiments suggest that, in general, evolution in response to climate change may be considerably underestimated (Davis et al. 2005). We found that even long-lived perennial species can undergo evolutionary change in response to less than 20 years of warming and selective pressures are sufficiently strong to cause genetic differentiation in populations only 500 m apart. This study thus provides important evidence of the capacity for both plastic and evolutionary responses to promote the persistence of Arctic plants in the face of future climate change.

Chapter 4: Climate adaptation is not enough: warming does not facilitate success of southern populations at northern latitudes in an Arctic tundra ecosystem

4.1 Synopsis

Rapidly rising temperatures are expected to cause poleward shifts in suitable climate space for many species. If local populations cannot respond to increased temperatures through phenotypic plasticity, they may become maladapted to the warmer conditions in their current locations. Many researchers have hypothesized that northern populations might be "rescued" by gene flow from southern, warm-adapted populations, or will otherwise be replaced by the immigration of southern species tracking their optimal climate northward. However, these predictions rely on the assumption that warmer temperatures will allow southern immigrants to establish and prosper in an otherwise novel environment. Conversely, a lack of adaptation to environmental conditions other than temperature – for example photoperiod, biotic interactions, or edaphic conditions – might limit the success of southern immigrants despite hospitable climatic conditions. Here we test the hypothesis that warmer temperatures at northern latitudes will confer a fitness advantage to southern immigrants relative to native populations. We established a series of experimentally warmed and non-warmed common garden plots with plant populations collected from sites at different latitudes in the Arctic. In most cases, plants from the local population leafed-out earlier and obtained a greater maximum size than foreign individuals, regardless of treatment. This implies that environmental conditions other than climate are likely to have an important influence on the establishment of novel populations and species at more northerly latitudes.

Evolutionary adaptation, either of the resident populations to warming temperatures, or of the immigrant populations and species to novel biotic and abiotic conditions, is likely to play an important role in determining the future structure of these communities.

4.2 Introduction

Current and projected increases in global temperatures are predicted to have widespread consequences for the distribution and abundance of organisms (Parmesan 2006). As temperatures increase, areas of suitable climate will shift poleward and upward in elevation for many species (Loarie et al. 2009, Burrows et al. 2014). If the degree of climate warming exceeds the ability of individuals to respond through phenotypic plasticity, local populations will become maladapted to the novel climatic conditions in their current range (Anderson et al. 2012a), and evolutionary adaptation may be necessary for the *in situ* persistence of these populations (Aitken et al. 2008, Shaw and Etterson 2012, Alberto et al. 2013).

When species' distributions span a broad latitudinal range, it is often proposed that gene flow may "rescue" northern populations by introducing warm-adapted genotypes from the south (Aitken et al. 2008, Norberg et al. 2012, Anderson et al. 2012a). It is similarly projected that climate warming will lead to northward range shifts of "pre-adapted" southern species (Davis and Shaw 2001, Walther et al. 2002, Thuiller et al. 2008, Morin and Thuiller 2009). Both of these projections rely on the assumption that warmer temperatures will facilitate the establishment and success of warm-adapted immigrants at northern latitudes, though this assumption has only rarely been tested (but see Wilczek et al. 2014). While populations of many species show evidence of local adaptation (Leimu and Fischer 2008, Hereford 2009), including

adaptation to climate (Jump and Peñuelas 2005, Savolainen et al. 2007), the relative importance of climate vs. other environmental factors in driving local adaptation is largely unknown (Aitken and Whitlock 2013). If local adaptation is not driven primarily by climate but rather by non-climatic conditions (Davis et al. 1998, 2005, Alberto et al. 2013) southern immigrants may not be pre-adapted to site conditions further north as the climate warms, and gene flow from southern populations could instead lead to reduced in the northern population (Edmands 2007, Frankham et al. 2011, Sexton et al. 2011, Schiffers et al. 2013, Aitken and Whitlock 2013).

In this study, we test the hypothesis warming will confer an advantage to immigrants from southern, warm-adapted populations at northern latitudes relative to resident individuals, and that this advantage will outweigh the potential disadvantages due to differences in photoperiod or other novel edaphic or biotic factors. We collected seeds or ramets from several foreign and local populations of three widely-distributed Arctic plant species, planted them into both passively warmed and non-warmed (control) treatments at our high Arctic field site, Alexandra Fiord on Ellesmere Island (78.9° N, 75.9° W), and followed the survival, phenology, and growth of all individuals over two summers. We recorded phenology in addition to survival and growth because changes in the timing of life events have been shown to have important consequences for plant success (Willis et al. 2008, Cleland et al. 2012), particularly in the relatively short Arctic growing season (Molau 1993, Berteaux et al. 2004).

If populations are locally adapted to climate, individuals from populations from warmer areas should have higher fitness (here defined as survival and plant size) in the experimentally warmed treatment than in the control treatment. These warm-adapted populations should also have higher

fitness than local populations in the warmed treatment if the warming effect creates temperature conditions that resemble those at the population's home site. Conversely, if local conditions other than climate hinder the successful establishment and growth of foreign populations even under warmer temperatures, we would expect to see higher fitness in the local populations in both warm and control treatments. This study is one of the first to directly investigate the establishment potential of immigrant populations under a realistic future warming scenario and the natural environmental conditions that an immigrant individual would actually experience.

4.3 Methods

4.3.1 Species and site characteristics

The main experimental site, Alexandra Fiord (AF; 78.9° N, 75.9° W), is located on the eastern coast of Ellesmere Island in the Canadian High Arctic. The AF lowland is an 8 km^2 mosaic of dwarf-shrub tundra and wet sedge meadow, bounded to the east and west by high plateaus, to the south by the Twin Glacier, and to the north by the fiord. This area is considered a "polar oasis" due to the relatively mild conditions compared to the polar desert areas that dominate the high Arctic (Freedman et al. 1994). Although large herbivores (muskoxen and caribou) do occasionally pass through, large mammal herbivory at the site is generally very low, and has likely been low for at least 100 years (Henry et al. 1986). Snow geese are only occasionally seen at the site, and small animal herbivory, particularly by Arctic hares, lemmings, and the caterpillar *Gynaephora groenlandica* is more common but still generally low compared to most low Arctic sites. For a complete overview of the ecology of Alexandra Fiord and nearby areas, see Svoboda and Freedman (1994).

4.3.2 Seed and ramet collection

Our study focused on three species -- two forbs, mountain sorrel (*Oxyria digyna* (L.) Hill) and rooted poppy (*Papaver radicatum* Rottb. ssp. *radicatum*), and one grass, wideleaf polargrass (*Arctagrostis latifolia* (R. Br.) Griseb.). These species were chosen because they are widely distributed and relatively abundant across the Arctic, grow readily from seeds (*O. digyna* and *P. radicatum*) or ramets (*A. latifolia*), and have been focal species of the International Tundra Experiment (ITEX; Henry and Molau 1997) since 1992. In addition, *O. digyna* has been studied extensively along its latitudinal range, which stretches from alpine areas of the southwestern United States to the northern tip of Ellesmere Island (Mooney and Billings 1961, Billings et al. 1971).

For our common garden experiment at the Alexandra Fiord site, we collected seeds (*Oxyria digyna* and *Papaver radicatum*) or ramets (*Arctagrostis latifolia*) from local (AF) populations of all three species. "Foreign" populations were collected from 6 additional sites across the high and low Arctic, though not every species was available at every location (Table 4.1). Seeds of *O. digyna* were additionally collected from Latnjajuare, Sweden (68.35° N), Barrow, Alaska (71.30° N), and Sverdrup Pass, Ellesmere Island (79.12° N). Seeds of *P. radicatum* were collected at Resolute Bay, Cornwallis Island (74.72° N), and ramets of *A. latifolia* were collected at Resolute Bay and Sverdrup Pass (Table 4.1, Figure 4.1).

In order to test whether nearby sub-populations growing in a warmer microclimate would have the same adaptive advantage as foreign populations from southern latitudes, we additionally collected seeds of *O. digyna* and *P. radicatum* from the Twin Glacier site approximately 2 km to

the south. Plants at the Twin Glacier site are exposed to the same general weather patterns and biotic interactions to which AF populations are exposed, but grow in a microclimate that is ~0.5° C warmer during the growing season (Labine 1994, Bean 2002, Edwards 2012). Both snowmelt and flowering phenology are typically advanced at the Twin Glacier edge relative to other areas of the Alexandra Fiord lowland (Woodley and Svoboda 1994). Despite earlier snowmelt, the total growing season length of the Twin Glacier population is shorter than that of populations experiencing later snowmelt, likely due to the earlier onset of senescence as a consequence of water limitation (Billings and Mooney 1968, Bliss 1971, Woodley and Svoboda 1994).

4.3.3 Source population site conditions

If the distribution of Arctic species is driven primarily by mean annual temperature or growing season length, we would expect to see a clear south-to-north pattern of fitness if physical distance between the site of origin and the AF common garden site is roughly equal to climatic distance for these two variables. With the exception of Resolute Bay, mean annual temperatures (MAT) and growing season length at each source population site follow a south-to-north pattern, with the Latnjajuare (Sweden) population at the warmest and Sverdrup Pass at the coldest extremes (Table 4.1). Long-term (1960-1990) monthly 0.5°x0.5° gridded climate data (available at http://www.ipcc-data.org/observ/clim/get_30yr_means.html) for Resolute Bay indicate that its MAT is approximately 1 °C warmer than AF, but recent data (1990-2009) from local weather stations indicate that AF is in fact 0.9 °C warmer, on average, than Resolute.

Table 4.1: Latitude and temperature variables for each population. Mean annual temperature (MAT), 1960-1990 is 0.5°x0.5° gridded mean annual surface air temperature from the East Anglia Climatic Research Unit. MAT 1990-2009 is local climate station air temperatures provided by collaborators at each site (~1.5m height). Days above 0 °C is a count of the number of days with mean diurnal temperature above 0 °C at each site, averaged over the 1990-2009 period, and represents an estimate of potential growing season length. Latnjajaure, Sweden is abbreviated to Latnja. The common garden experimental site, Alexandra Fiord, is indicated by grey shading.

	Latnja	Barrow	Resolute Bay	Twin Glacier	Alexandra Fiord	Sverdrup Pass
Latitude	68.35° N	71.30° N	74.72° N	78.86° N	78.87° N	79.12° N
MAT, 1960-1990	-3.7 °C	-12.4 °C	-17.0 °C	n.a.	-18.8 °C	-20.8 °C
MAT, 1990-2009*	-2 °C	-11.2 °C	-15.4 °C	n.a.**	-14.5 °C	-16.1 °C
Days above 0 °C	145 ± 3	103 ± 4	74 ± 3	n.a.	91 ± 1	86 ± 2

*Because temperature data were not recorded at all local weather stations in every year, MAT 1990-2009 values for the foreign populations were calculated based on the relative temperature difference between the foreign site and the AF site only in those years for which temperature data were collected at both locations.

**MAT was not available for the Twin Glacier site but temperature data collected during the growing season (June-August) over several years indicate that this site is approximately 0.5 °C warmer than AF.

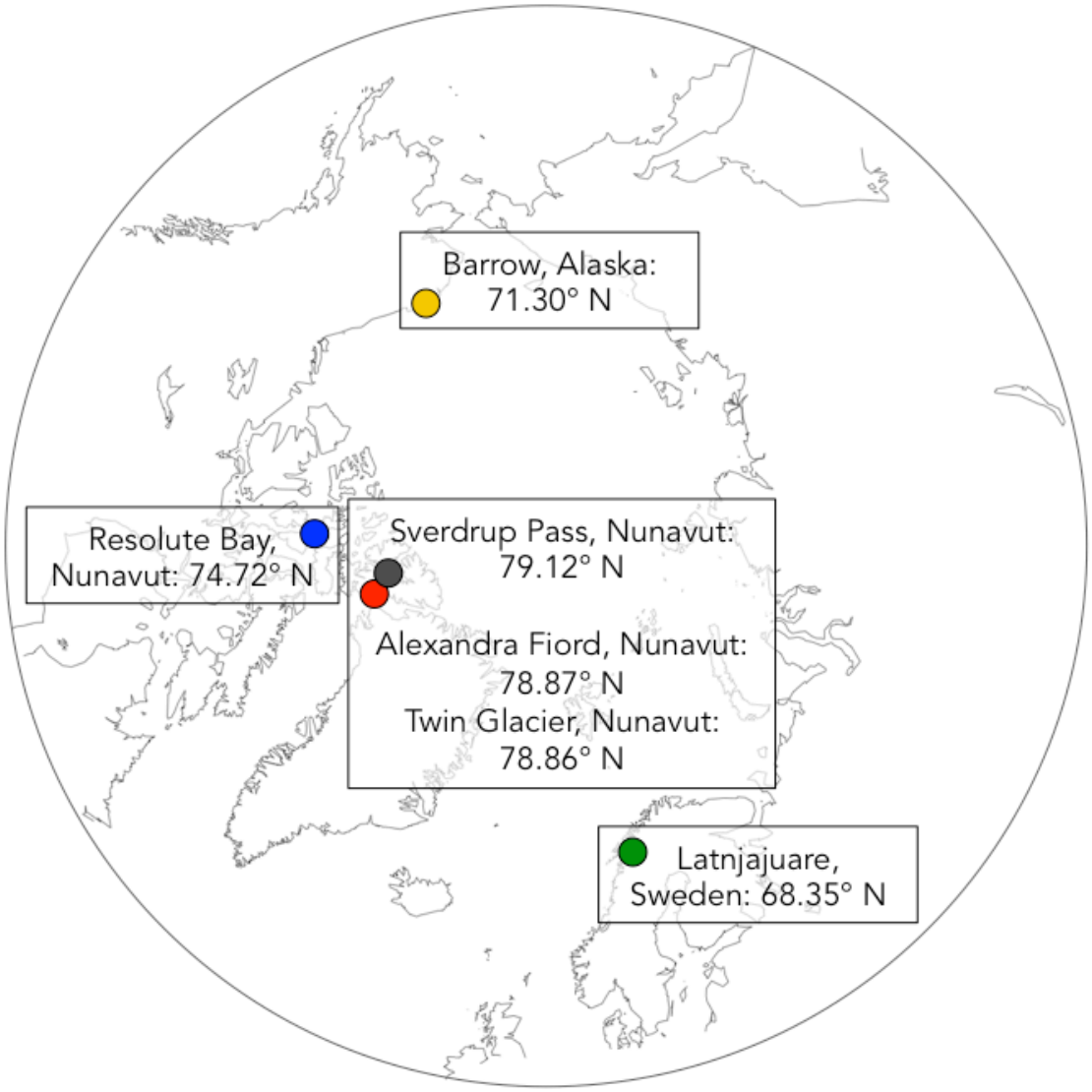

Figure 4.1: Seed and ramet collection locations and latitudes.

In sum, *O. digyna* was well represented by five distinct populations that span a large latitudinal and temperature gradient. The other two species, *P. radicatum* and *A. latifolia*, were collected from only three populations, the southernmost of which (Resolute Bay) is actually slightly cooler than AF. Thus, our analyses of *O. digyna* allowed a strong test of our predictions of patterns

across a latitudinal and temperature gradient, while analyses of *P. radicatum* and *A. latifolia* were more confined to a general test of local adaptation.

4.3.4 Experimental design

We collected seeds from 40 individuals (mothers) of *O. digyna* and *P. radicatum* spaced at least 2 meters apart at the Alexandra Fiord, Twin Glacier, Sverdrup Pass, and Resolute Bay sites in 2009. Latnjajuare and Barrow populations were collected by collaborators using the same criteria. Seeds from Barrow were collected in 2010. All seeds were collected just before seed dispersal at each site in order to minimize differences between populations due to seed ripeness. Seeds were air-dried and stored at 2 °C for 9-21 months. We measured average seed mass for each family (i.e., all seeds from the same mother) in order to estimate the maternal environmental effect of differential seed provisioning for each family and population.

Ramets of *A. latifolia* were collected from three sites in 2009 and transported live to the University of British Columbia, where they were planted into a common growth chamber environment (Conviron E-15, Controlled Environments, Inc., Winnipeg, MB, Canada). In the spring of 2010 and 2011, ramets were separated and replanted in the growth chambers, such that each genotype was represented by 2-6 clones by the summer of 2011.

In early June 2011, seeds of *O. digyna* and *P. radicatum* were germinated in Flowerhouse® RowHouse™ (www.flowerhouses.com) cold frame greenhouses to promote germination and initial establishment. Seed trays were filled with soil collected from Alexandra Fiord the previous summer and coarse-sifted to remove roots. Seedlings were planted into common

garden plots at Alexandra Fiord in mid-July, and each individual was marked. Ramets of *A. latifolia* were transported from Vancouver and planted directly into the common garden plots at AF. Half of the common garden plots were passively warmed (2-3 °C relative to control plots) using open-top chambers (OTCs). Plots were arranged along a moisture gradient so that we could test whether soil moisture differentially affected each population's performance. For more detail on the experimental set-up and a discussion of the OTC effect, see Appendix C.1.

Germination and survival of seedlings was variable between populations, and thus the number of families and number of individuals per family planted into the experimental site was also unequal (Table 4.2). A total of 1062 *O. digyna*, 719 *P. radicatum*, and 127 *A. latifolia* individuals were planted.

Table 4.2: Total number of families of each population for each species (bold numbers). In parentheses is the average number of individuals per family for each population. NA indicates that no individuals were collected at that site for that species. Latnjajaure, Sweden is abbreviated to Latnja.

Species	Latnja	Barrow	Resolute Bay	Twin Glacier	Alexandra Fiord	Sverdrup Pass
O. digyna	**18** (8.8)	**18** (7.4)	n.a.	**22** (17.4)	**22** (14.6)	**11** (6)
P. radicatum	n.a.	n.a.	**22** (12.2)	**18** (11.5)	**21** (11.6)	n.a.
A. latifolium	n.a.	n.a.	**21** (2.6)	n.a.	**21** (2.4)	**12** (1.8)

Temperature loggers (HOBO© Pro Series™, Onset Computer Corp., Bourne, MA, USA) were placed at a height of 10 cm in three warmed and three control plots during the peak growing season (late June-mid July) in both 2012 and 2013. We also measured soil moisture (using a handheld HydroSenses© probe, Campbell Scientific Canada Corp., Edmonton, AB, Canada) in every plot in mid-July in both years (Figure C.1). Soil moisture values were scaled and centered

within each year as the between-year variation in soil moisture was not of interest. The date of snowmelt was recorded for every plot in 2013 but not in 2012, as we arrived at the site after most snowmelt had already occurred.

4.3.5 Phenology and performance measurements

In order to assess plant performance, we measured survival, growth, and phenology for every individual throughout the growing season. Although not a direct component of plant fitness, phenology was recorded in addition to survival and growth because changes in the timing of life events can have enormous consequences for plant performance. In two recent multi-species studies, those species whose phenologies best tracked changes in climate had significantly better performance (Cleland et al. 2012) and more stable population sizes (Willis et al. 2008) than non-responsive species. Optimal vegetative and reproductive phenology is particularly important in Arctic species, where the relatively short Arctic growing season means that mismatches between phenology and temporal environmental patterns can lead to substantially reduced fitness (Berteaux et al. 2004). Individuals that flower too late in the summer, for example, may not have time to set seed before winter returns (Molau 1993).

In order to assess plant phenology and performance, we surveyed plants at the site every three days during the growing season (mid June through early August) of 2012 and 2013. We recorded the date of first mature leaf appearance (leaf-out date) for every individual, considering a leaf mature when the emerging leaf bud unfolded. We additionally measured each *O. digyna* and *P. radicatum* plant twice (2012) or three times (2013) during the summer in order to estimate maximum leaf area for each plant. Leaf area was estimated based on measurements of leaf width

and plant diameter using an equation developed from a separate sample of individuals (non-experimental plants) that were measured by hand and then harvested and scanned using ImageJ to measure total plant leaf area. The relationship between total leaf area and field leaf measurements was determined using multiple linear regression according to the equations:

O. digyna: Leaf Area = 59.26 + 0.42 * Leaf Width * Plant Diameter * (# of Leaves/2)
P. radicatum: Leaf Area = 70.00 + 0.41 * Leaf Width * Plant Diameter * (# of Leaves/2)

Plant diameter was defined as the maximum distance, tip-to-tip, between two opposite leaves. For individuals with only one leaf, the number of leaves was not divided by two as this would underestimate total leaf area for these plants. The R^2 value for a regression of measured leaf area against true leaf area was greater than 0.95 for both species. We used the maximum of the two (2012) or three (2013) leaf area measurements in each year as an estimate of overall plant size for each individual. Individuals of *A. latifolia* were measured only once during the summer, at the end of the growing season. As each individual produced multiple ramets, we summed the lengths of the longest leaf of each ramet as an index of overall plant size for each individual. We also determined plant height by measuring the tallest single leaf per individual.

In 2013 only, we also recorded the presence/absence of senescence for *O. digyna* and *P. radicatum* in the last round of measurements in early August. Senescence of leaves marks the end of the growing season for that individual, and differences in the timing of senescence can help to reveal varying patterns of growth among populations. A leaf was considered senesced if it had dried up (*O. digyna*) or turned yellow (*P. radicatum*). Survival of every individual was

recorded at the end of 2013. Plants that did not have a leaf bud at any point during the 2013 growing season were considered dead.

Due to the slow growth and long time to reproductive maturity of many Arctic plant species (including the three studied here), we use overall survival and plant size as proxies for fitness components, as plants did not flower during the two years of observation. Plant size has been shown to be highly correlated with reproductive fitness in many species (Samson and Werk 1986) and is commonly used as a measure of performance in slow-growing perennial species (Rehfeldt et al. 2002, Mimura and Aitken 2010, McLane and Aitken 2012).

4.3.6 Statistical analyses

We used generalized linear mixed models with a binomial error distribution to determine the effect of population, treatment, and seed weight on survival and senescence. Family and plot were included as random effects in the model, with a random slope term for family x treatment. We used linear mixed models to analyze differences in leaf-out date and maximum leaf area, with fixed effects of population, treatment, initial seed weight and year. Random effects for family x treatment, plot x year, and individual were also included in these models. The significance of each term was determined by comparing nested models using likelihood ratio tests. Non-significant random effects were dropped first (cutoff p-value = 0.1), followed by fixed effects (cutoff p-value = 0.05). The significance of soil moisture in predicting maximum leaf area was determined in a separate model of the same structure. All analyses were conducted using the lme4 package in R (v. 3.0.2).

For *O. digyna* we were also interested in understanding differences in growth over the entire growing season. We analyzed this pattern of growth using a linear mixed effects model with both (in 2012) or all three (in 2013) measurements on each individual as a response variable. Time of measurement was included as a fixed effect along with population and treatment and interactions between all three. In 2013 an additional quadratic term for time of measurement was included to account for non-linear patterns in plant growth. Random effects for individual (to account for repeated measures on individuals) and for plot were also included. Due to the different number of measurements in 2012 and 2013, years were analyzed separately.

Seed weight was included in every model for *O. digyna* and *P. radicatum* as a covariate to account for potential differences in seed provisioning by each mother, which could affect offspring performance. For long-lived, slow-growing perennial species, time constraints often prevent growing all populations in a common garden for one or more generations to minimize these maternal effects. Thus, the potential influence of maternal seed provisioning is frequently assessed using seed mass instead (Dlugosch and Parker 2008, Angert et al. 2008, McLane and Aitken 2012).

4.4 Results

Survival, leaf phenology, and size all varied significantly by source population in at least one species. In most cases, the local (AF) population had the greatest survival and growth regardless of treatment, while phenology followed a latitudinal pattern. There were also large differences between the two years, both in absolute measurement values and in the relative effect of the warming treatment. Growing season temperatures (June to early August) were 3 °C colder in

2013 than in 2012; 2012 was the warmest summer recorded at Alexandra Fiord since continuous records began in 1989. The average summer warming effect of the OTCs (average daily temperature difference between days 173 and 200) was 3.7 °C in 2012 and 2.8 °C in 2013 (Figure C.2).

4.4.1 Mountain sorrel (*Oxyria digyna*)

The strongest among-population differences were found for *O. digyna*, which spans the largest sampled latitudinal and temperature range of the three study species. Both phenological variables (date of leaf-out and leaf senescence) followed a clear latitudinal trend (Figures 4.2a-b, Table C.1), with northern populations leafing out only five days after snowmelt and southern populations up to ten days after that, regardless of treatment. Leaf-out date was significantly earlier for all populations in the warmed treatment in 2012 but not in 2013. Northern populations were also more likely to senesce by early August than southern populations, although the effect was not significant ($p=0.08$).

In contrast to the latitudinal gradient in phenology, both survival and growth of *O. digyna* demonstrated a pattern of home-site advantage, with the local (Alexandra Fiord and Twin Glacier) populations demonstrating the highest survival and growth. Foreign populations decreased in both survival and leaf area with increasing distance from their own home site, regardless of treatment (Figures 4.2c-d, Table C.1). Plants from Latnjajaure, the southernmost site, were significantly smaller in 2013 than in 2012.

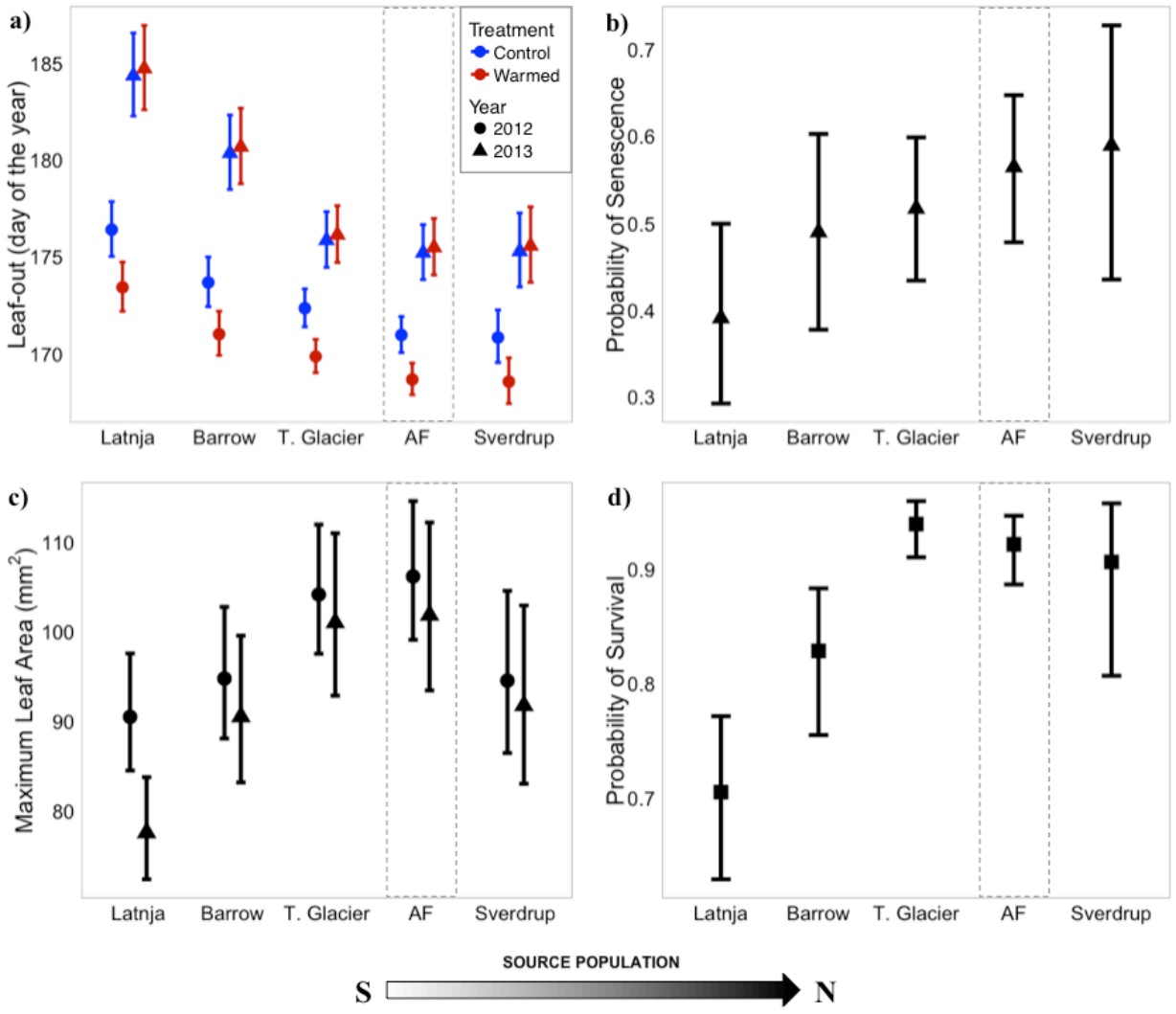

Figure 4.2. Day of first mature leaf in both years and treatments (a), probability of senescence by early August (2013 only) (b), maximum leaf area in both years (treatments combined) (c) and probability of survival at the end of 2013 (d) for *Oxyria digyna*. Populations are ordered from south to north along the x-axis; dashed lines indicate the "home" (AF) population. Points are predicted values from a generalized linear (survival and senescence) or linear (leaf area and first mature leaf) mixed model; error bars are 95% credible intervals. Latnja = Latnjajaure, T. Glacier = Twin Glacier, AF = Alexandra Fiord.

Analyses of *O. digyna* leaf area revealed a significant population-by-soil moisture interaction ($p<0.001$). Plants from Latnjajuare and Sverdrup Pass were larger in dry plots than in mesic plots, while all other populations showed the reverse relationship (Barrow and Twin Glacier) or

no relationship (AF) to soil moisture. The variable effect of soil moisture on leaf area did not change the overall size relationship among populations. Plants from Latnjajuare and Sverdrup were smaller than plants from AF even at their optimal soil moisture.

Populations of *O. digyna* also differed significantly in their patterns of growth (population x time $p < 0.001$ in both years). In both years, plants from southern latitudes continued to grow throughout the summer and reached or maintained their maximum size in early August, while northern plants reached their maximum size in mid-late July and then began to decline (leaf senescence). Treatment was also significant in predicting the pattern of growth in 2012 and marginally significant in 2013 (2013 treatment $p=0.03$; Figure 4.3, Table C.2). In 2012 only there was a significant interaction between time of measurement and treatment ($p < 0.001$), such that individuals in the warmed treatment were larger than those in the control treatment in mid-July but smaller in early August, indicating that warmed plants reached their peak size and then began to senesce earlier than plants in the control treatment. The overall treatment effect also differed between years; plants in the warmed treatment were generally larger than those in the control plots in 2012 (at peak size) but smaller in 2013.

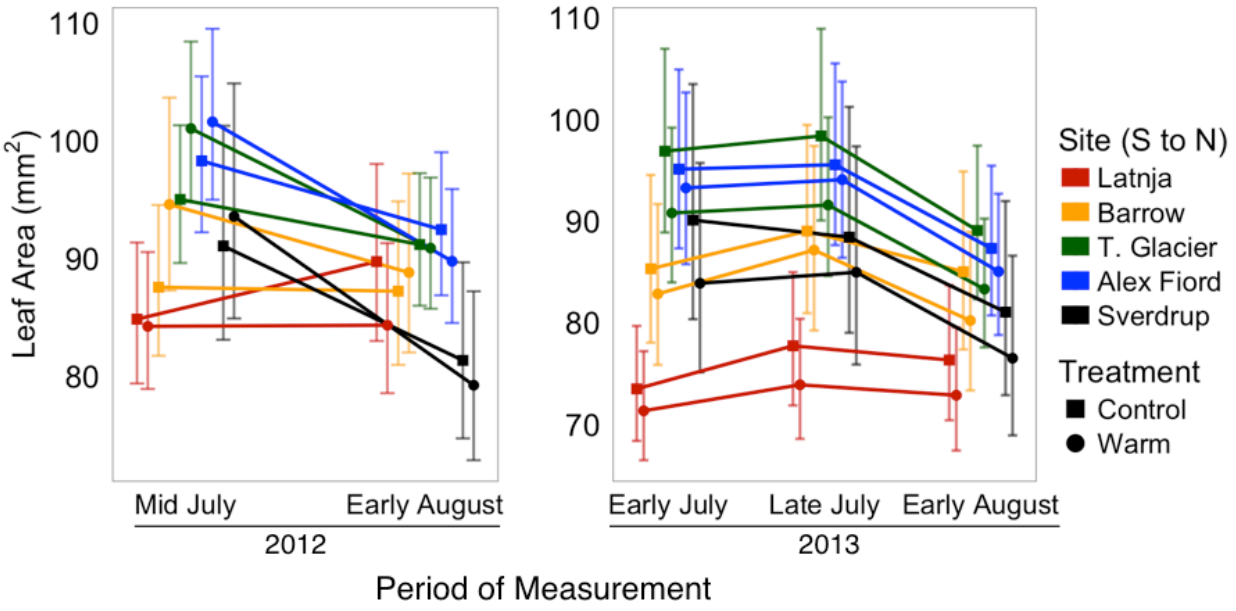

Figure 4.3. Leaf area (mm^2) of *O. digyna* throughout the 2012 and 2013 growing seasons. Individuals were measured twice in 2012 and three times in 2013. Points are predicted means (± 95% CI) for each measurement period from a linear mixed effects model with linear and quadratic (2013 only) terms for time.

4.4.2 Rooted poppy (*Papaver radicatum*)

Survival was universally high for *P. radicatum* (94-99%); thus, there were no significant differences in survival among populations or between treatments. Leaf-out date differed significantly by source population and treatment, as well as an interaction between the two (Figure 4.4a, Table C.1). The Alexandra Fiord population did not respond to treatment, while the other two populations did.

Similar to *O. digyna*, leaf area for *P. radicatum* was largest for the local (AF) or near-local (Twin Glacier) populations and smallest for the foreign population (Resolute Bay; Figure 4.4b, Table C.1). In contrast to *O. digyna*, however, *P. radicatum* demonstrated a consistently significant treatment effect in both years, such that leaf area was greater in the warming treatment (though

this was most noticeable in the Twin Glacier population). Leaf area of the AF population did not vary by treatment but did vary by year.

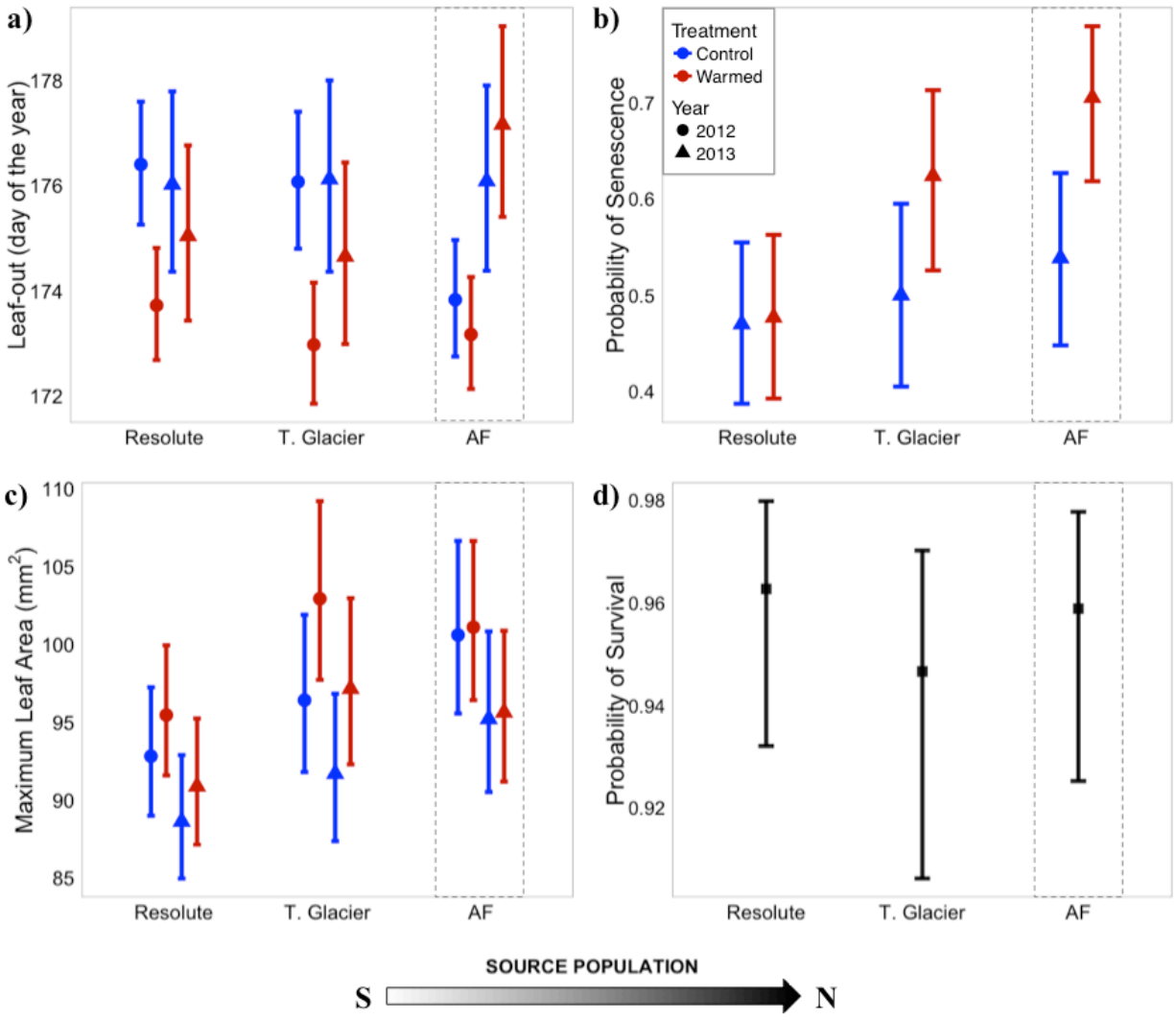

Figure 4.4. Date of first mature leaf (a) probability of senescence (b) maximum leaf area (mm^2) (c) and survival (d) for *P. radicatum* in control (blue) and warmed (red) treatments. Populations are ordered from south to north along the x-axis; dashed lines indicate the "home" (AF) population. Points are predicted values from a generalized linear (survival and senescence) or linear (leaf area and first mature leaf) mixed model; error bars are 95% credible intervals. T. Glacier = Twin Glacier, AF = Alexandra Fiord.

Senescence of *P. radicatum* occurred significantly earlier in the warm treatment than in the control treatment (*p=0.007*); although the effect was much more pronounced for the AF and Twin Glacier populations than for Resolute, an interaction term was nearly significant *(p=0.07*).

4.4.3 Wideleaf polargrass (*Arctagrostis latifolia*)

Survival of *A. latifolia* was also high (99-100%) across all populations and treatments, and did not differ significantly by either factor (not shown). As seen for *P. radicatum*, leaf-out date differed significantly by population and treatment, as well as an interaction between the two (Figure 4.5a, Table C.1). Again, the AF population did not respond significantly to treatment, while both other populations did.

Overall plant size (summed leaf length; Figure 4.5b, Table C.1) and height (single tallest leaf; not shown) of *A. latifolia* varied significantly by population and treatment. The Resolute Bay population reached greater overall size and height than the AF population, but only in the warmed treatment. Neither overall size nor height of the AF population varied significantly by year or treatment.

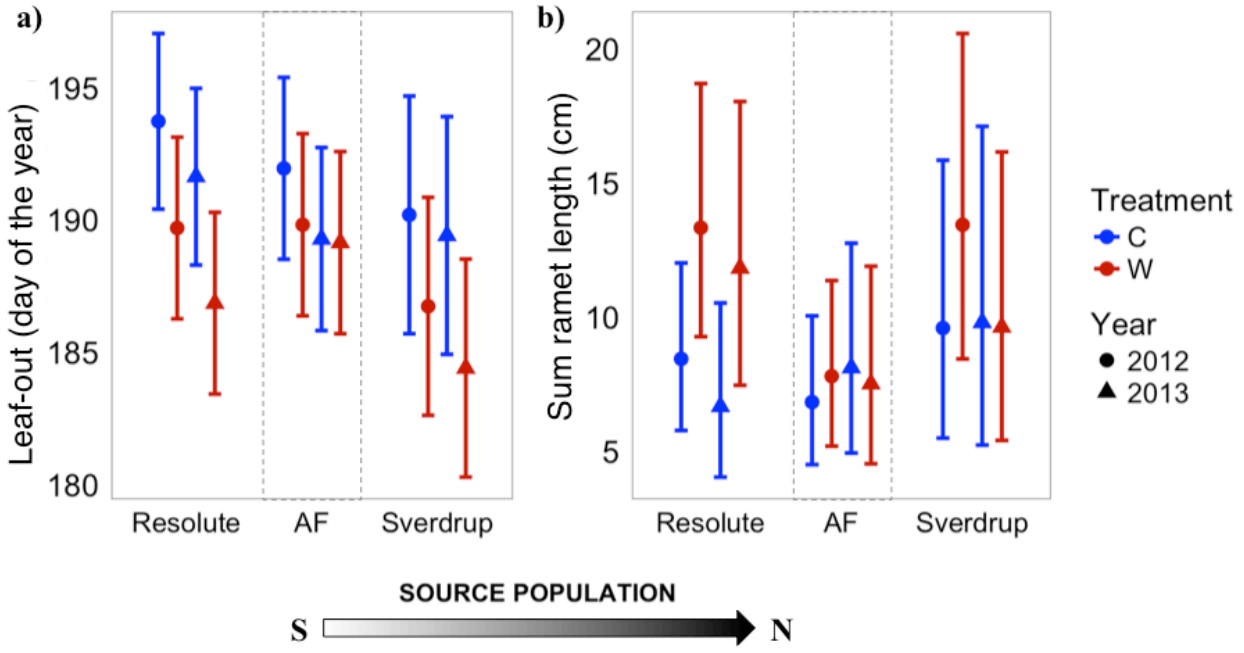

Figure 4.5. Date of first mature leaf (a) and summed ramet length (an estimate of overall plant size, in cm) (b) for *A. latifolia* in control (blue) and warmed (red) treatments. Populations are ordered from south to north along the x-axis; dashed lines indicate the "home" population. Points are predicted values from a linear mixed model; error bars are 95% credible intervals. AF = Alexandra Fiord.

4.4.4 Maximum size and seed weight

Although maximum size can also be influenced by local adaptation (e.g., when small stature confers an adaptive advantage), several studies have demonstrated that genetic constraints on plant size are more likely to exist in high Arctic than in low Arctic populations (Billings and Mooney 1968 and references therein). Thus, our finding that local (high Arctic) populations were larger than low Arctic populations is almost certainly due to better performance and not genetically controlled differences in size.

Seed weight was not a significant predictor in any model for either *O. digyna* or *P. radicatum*, suggesting that the potential maternal effect of seed provisioning did not likely have a large influence on the patterns shown here.

4.5 Discussion

The results of our study do not generally support the prediction that southern populations will perform better under experimental warming at higher latitudes. Local populations had higher survival and/or grew larger than foreign populations in nearly every case, and, with one exception (*A. latifolia*), regardless of treatment. This result indicates that local populations have a "home-site advantage" even under warmer conditions, and suggests that environmental factors other than climate may hinder the success of southern immigrants in the Arctic. This is one of the first studies to directly evaluate the performance of southern immigrants at northern latitudes given a realistic scenario of future climate warming.

The general advantage of local populations over foreign populations in two of the three study species, regardless of treatment and regardless of the geographic location of those foreign populations, points to the likely considerable importance of local adaptation to factors other than temperature. Even in 2012, the warmest summer ever recorded at Alexandra Fiord since 1989, the local populations performed better than all foreign populations for two of the three species (including *O. digyna*, the best-represented species). This pattern held even in the warmed plots, where the combination of experimental warming and the record atmospheric temperature and predominantly clear sky conditions in 2012 led to warming-treatment temperatures more than 5 °C warmer than the mean ambient temperature of the previous two decades. This result contrasts

somewhat with a recent study of *Arabidopsis thaliana* populations in Europe, in which the northernmost population demonstrated lower fitness than a more southern population at the northern site, presumably due to elevated temperatures in the present relative to historical means (Wilczek et al. 2014).

While it is often predicted that gene flow from warm-adapted, southern populations will "rescue" northern populations as temperatures increase (Norberg et al. 2012, Anderson et al. 2012a), the results of our experiment suggest that southern genotypes may actually be maladapted to non-climatic local conditions at northern latitudes. This finding also has important implications for the implementation of assisted gene flow, in which warm-adapted, southern genotypes are deliberately introduced to northern populations in order to promote their adaptation to increasing temperatures (Kreyling et al. 2011, Weeks et al. 2011, Aitken and Whitlock 2013). Assisted gene flow is already underway in some areas (O'Neill et al. 2008), and has been proposed as a potential conservation strategy in several others (Broadhurst et al. 2008, Vitt et al. 2009). The reduced fitness of southern populations in a northern environment even under warmed conditions, as observed here, suggests that assisted gene flow from southern populations might actually negatively impact native populations, at least in the short term (Frankham et al. 2011, Aitken and Whitlock 2013).

The importance of local adaptation to non-climatic conditions demonstrated here also has implications for the immigration of novel species to northern latitudes. While many plant and animal species have already exhibited northward shifts of 6-17 kilometers per decade (Parmesan and Yohe 2003, Chen et al. 2011), projected rates of climatic change will likely require future

shifts of hundreds of kilometers or more (Davis 1989, Malcolm et al. 2002). Range shifts over such large physical distances increase the likelihood that immigrant species will face environmental conditions substantially different from those at their site of origin (Davis et al. 2005, Alberto et al. 2013). Our results suggest that a lack of adaptation to local conditions at these locations may hinder the successful establishment of immigrants even when climatic conditions are suitable.

The Twin Glacier population in our study provides an interesting comparison of the importance of adaptation to small-scale variation in climate. Although some gene flow likely does occur between the Twin Glacier and AF populations, as they are only ~2 km apart, genetic differentiation has been found to occur over much shorter physical distances at the AF site (see Chapter 3). This standing genetic variation could be of key importance as climate change progresses (Jump and Peñuelas 2005 and references therein). In our study, the ~0.5 °C warmer Twin Glacier populations performed similarly to the AF populations in the control plots. However, the Twin Glacier *P. radicatum* population responded positively to the warming treatment, while the AF population did not. In fact, the mean size of the Twin Glacier *P. radicatum* population in the warming treatment was slightly (though not significantly) larger than that of the AF population. The differential response to warming between the two "local" populations in our study could indicate that an important source of warm-adapted genes is likely to come from areas of warmer microclimate within the same general region, rather than from populations far to the south (Crawford 2008, Hof et al. 2011). These regional populations are already adapted to the local photoperiod, herbivores, and many other environmental factors, and thus may have an advantage over southern immigrants.

4.5.1 Patterns in phenology and growth

Two clear patterns emerged from the analyses of phenological and growth responses. Firstly, plant size and survival predominantly demonstrated evidence of home-site advantage, such that both populations from farther north and those from farther south performed poorly relative to the local populations. Secondly, phenological variables (leaf-out date and leaf senescence) followed a latitudinal trend, with individuals from northern populations leafing out and senescing earlier than those from southern populations.

The strong latitudinal pattern of phenology has been observed in other species (e.g., Johnsen et al. 1996, Raven et al. 1999) and suggests that a combination of factors, which may include a differential response of populations to photoperiod (Mooney and Billings 1961), as well as variation in speed of response to springtime snowmelt (Wipf 2010), are important determinants of plant performance and can be equally or even more important than climate. Such among-population differences are often explained by differences in required heat accumulation for dormancy release (Campbell and Sugano 1979, Johnsen et al. 1996), although in our study the effect of experimental warming on leaf-out dates was inconsistent, and varied by population and year.

The delay in leaf development of southern populations relative to northern populations (up to 10 days for *O. digyna*) is likely at least partly responsible for the smaller size of individuals from southern populations. Experimental warming did not always cause earlier leaf-out, but when it did it nearly always led to greater plant size as well (relative to the same population in the control

treatment), suggesting that earlier leaf-out is usually advantageous. As asynchrony between environmental events and phenological responses can have strong negative consequences for plant growth and fitness, plants that can respond quickly to seasonal cues will have the most time for growth and reproduction (Stinson 2004, Andrés and Coupland 2012). This is particularly true in the high Arctic, where the growing season is only 6-10 weeks long; a delay of 10 days can be nearly a fifth of the growing season.

The timing of fall senescence also affects plant success, as fall freezing events that occur before the plant has fully hardened could be extremely detrimental (Taschler and Neuner 2004, Inouye 2008). Southern populations of *O. digyna* showed fewer signs of leaf senescence at the end of the growing season than local populations, which may have contributed to the lower survival rate for southern populations. Among-population differences in leaf phenology of *Papaver radicatum* and *Arctagrostis latifolia* were also significant but less pronounced, likely because of the much smaller distance between the populations' home sites. As both fall senescence in response to photoperiod and dormancy release in response to spring warming are heritable traits (Shaver and Kummerow 1992, Prock and Körner 1996, Fracheboud et al. 2009, Andrés and Coupland 2012), these results highlight the likely important role that evolutionary adaptation will play in these species as the climate warms.

Environmental factors unrelated to latitudinal gradients also played a role in plant success in our study. Soil moisture was significant in predicting plant size for two populations of *O. digyna*. In addition, populations of *O. digyna* and *P. radicatum* from Sverdrup Pass and Resolute Bay, respectively, also demonstrated reduced fitness at AF, even though plants from these sites

experience similar photoperiods and growing-season lengths. This indicates that limits to the successful immigration of warm-adapted populations or species to a novel site are likely to exist even when the sites of origin and destination do not differ in day-length or growing-season duration (Davis et al. 1998, Van der Putten et al. 2010).

Despite substantial warming caused by the experimental treatment in both years (3.7 °C in 2012 and 2.8 °C in 2013), responses to warming were moderate in comparison to among-population differences, and varied by species and year. Experimental warming led to earlier leaf-out dates and slightly larger plant size for *O. digyna* in 2012, but all populations were equally responsive to warming, suggesting that moderately warmer temperatures will not confer an advantage to southern, warm-adapted populations of this species. Warming led to a significant advance in leaf-out date for the southernmost population of *P. radicatum*, but individuals from this population still did not grow as large as the local populations, indicating that factors other than a spring phenology response limits the success of this species at the transplant site. Only *A. latifolia* demonstrated the expected pattern, in which the southern population (Resolute Bay) grew larger than the local population in the warming treatment. However, as temperatures at Resolute Bay are not warmer than those at AF, it is not clear why this population responded positively to warming. As all individuals of *A. latifolia* were grown in a common environment for 2 years and were split twice before planting at AF, it is unlikely that any non-genetic effects of environmental differences at the source sites could affect the experimental results, but there could have been differential responses to the growth chamber environment.

4.6 Conclusions

The results of our study have important implications for our understanding of how Arctic species will respond to climate change. Many species distribution models are based on the prediction that species will track their optimal climate northward (Davis et al. 1998, Pearson and Dawson 2003). Similarity, it is often proposed that northward gene flow will promote adaptation to warming conditions at northern latitudes (Davis and Shaw 2001, Norberg et al. 2012, Anderson et al. 2012a). Conversely, the predominant trend in our study was that of local-population advantage. This highlights the importance of local adaptation to environmental factors in addition to climate when considering how species will respond to future warming, and suggests that evolution, either of local populations to novel climatic conditions or of foreign populations and species to novel environmental conditions, will play a critical role in these responses.

Chapter 5: Conclusion

The unprecedented rise in greenhouse gas emissions over the past century has led to rapid increases in global temperatures (IPCC 2013). The effects of rising temperatures on the world's biota are already apparent through altered phenology (Menzel and Fabian 1999, Parmesan and Yohe 2003, Parmesan 2006), shifting abundances and distributions (Parmesan and Yohe 2003, Parmesan 2006, Chen et al. 2011), and even extinction (Parmesan 2006, Pounds et al. 2006). Temperatures in the Arctic are increasing faster than anywhere else on the planet, with projected increases of 4-7 °C by the end of the 21st century (Weller et al. 2005, Stocker et al. 2013), and yet our understanding of how Arctic species are affected by climate change lags behind that of many temperate systems (Post et al. 2009, Post and Høye 2013). In this thesis, I sought to improve our understanding of the ecological and evolutionary consequences of climate change in Arctic tundra ecosystems by observing responses of several Arctic plant species to both experimental and natural warming. In this final chapter, I will briefly summarize and synthesize the key results and discuss the broader implications of these findings. I will address some of the limitations of this research and discuss directions for future research, both specifically within this study system and more generally in the field of climate change ecology.

5.1 Summary

In Chapter 2, I presented an analysis of the longest record of Arctic plant phenology to date. I found that, while experimental warming led to earlier flowering in all four species, flowering dates in the control plots remained unchanged or were delayed despite more than 1 °C of ambient warming over the 21-year period. This seemingly contradictory result was likely due to

significant delays in snowmelt dates, possibly as a result of increased winter snowfall (Bintanja and Selten 2014). Despite the delay in flowering for at least one species, the timing of seed maturation was not significantly delayed, indicating that warmer temperatures may speed the development of seeds and thus mitigate the effects of later flowering.

In Chapter 3, I explored whether long-term (18-year) experimental warming has led to evolutionary adaptation in two widespread forb species (*Oxyria digyna* and *Papaver radicatum*) in both a mesic and dry habitat. Although warming experiments have been identified as an ideal system in which to observe plant evolutionary responses to warming (Anderson et al. 2012a), this research represents the first time, to my knowledge, that such a study has been undertaken. Both species showed some evidence of genetic differences between warmed and control populations in at least one habitat type, though not always in the direction predicted by local adaptation. Substantial ambient warming over the 18-year period as well as unusually warm temperatures in the first two years after planting (2011 and 2012), may have contributed to the somewhat unexpected results.

In a complimentary experiment, I asked whether the same two forb species show evidence of local adaptation to environmental conditions in the mesic and dry habitats, despite their close proximity (~500 m apart) and what is likely substantial gene flow between the populations at each site. Local adaptation has been demonstrated in many species (Leimu and Fischer 2008, Hereford 2009), including over very small spatial scales (Lenssen et al. 2004). The general view of Arctic plants, however, has been that low genetic diversity often precludes adaptation at the local scale (Shaver et al. 1979, McGraw 1995, Hewitt 1996, Ehrich et al. 2007, but see

Bennington et al. 2012), although genetic differentiation is frequently observed at larger scales (Mooney and Billings 1961, Billings et al. 1971, Heide 2005). Conversely, both species in my experiment showed evidence of genetic differences between mesic and dry populations, and *P. radicatum* showed evidence specifically of local adaptation (i.e., each population performed best at its home site).

In Chapter 4, I tested the hypothesis that warming will confer an advantage to "pre-adapted" southern populations over local (northern) populations. While projections of future range shifts often rely on the assumption that warming will facilitate the establishment and success of warm-adapted immigrants at northern latitudes (Davis et al. 1998, Walther et al. 2002), this assumption has rarely been tested (but see Wilczek et al. 2014). In my study, local populations leafed-out earlier and attained greater maximum size than foreign populations in nearly every case, even under conditions 3-5 °C warmer than the historical average at this site.

5.2 General conclusions

The results presented in this thesis contribute to our understanding of how Arctic plant species respond to warming. Several key themes emerge. Firstly, the finding that flowering time at Alexandra Fiord has remained constant or been delayed over the past two decades despite more than 1 °C of warming (Chapter 2) illustrates the importance of considering the indirect effects as well as the direct effects of atmospheric warming on phenology. Temporal trends can differ substantially even within the high Arctic; at Zackenberg, Greenland (74º28' N, 20º34' W), several species of plants, insects and birds showed remarkable advances in phenology concurrent with warming between 1996 and 2005 (Høye et al. 2007). This markedly different pattern

highlights the importance of considering local processes when predicting phenological responses to climate change, as variation in microtopography and microclimate, as well as larger-scale interactions between changes in temperature and precipitation, could lead to ecological surprises.

Individual plant phenological responses to among-year and between-treatment variation in temperature (Chapters 2, 3 & 4) imply substantial phenotypic plasticity in phenological traits in Arctic species. Furthermore, no detrimental consequences of warming were observed despite a warming effect that was 3-5 °C higher than the historical mean for Alexandra Fiord populations (Chapter 3 & 4). This suggests that many Arctic species are remarkably plastic in their responses to temperature fluctuation, and can withstand temperatures much greater than those they have historically experienced (Mooney and Billings 1961, Arft et al. 1999).

In addition to substantial plasticity in these populations, evidence of local adaptation to varying environmental conditions in the dry and mesic habitat types (Chapter 3) and of the differential response to warming between the Alexandra Fiord and Twin Glacier *P. radicatum* populations (Chapter 4) suggests that genetic differences are also common within the AF meta-populations of these species. This standing genetic variation could facilitate evolutionary adaptation in response to warming temperatures in the future (Barrett and Schulter 2008), particularly if the magnitude of temperature increase exceeds the ability of many individuals to respond plastically (DeWitt et al. 1998, Visser 2008).

Evidence of the importance of local adaptation is also readily apparent in the marked differences among populations transplanted to Alexandra Fiord from southern latitudes (Chapter 4). The

failure of warmer temperatures to facilitate the success of "warm-adapted" populations suggests that a lack of adaptation to local environmental conditions other than temperature may limit the success of southern immigrants at northern latitudes, even when climatic conditions are suitable. The limitations to northward expansion suggested by these experimental results do not suggest that range shifts in response to warming are unlikely to occur. On the contrary, such shifts were a common response to historic changes in climate (Webb 1981, Davis 1983b, Huntley and Webb 1989, Williams et al. 2002) and have already been observed in response to contemporary climate warming (Parmesan and Yohe 2003, Chen et al. 2011). Instead, my results highlight the importance of adaptation to environmental conditions other than (or rather, in *addition* to) climate, and suggest that evolutionary adaptation to novel conditions will likely have to occur in concert with the northward movement of species and genotypes, as was likely the case for historical range shifts as well (Davis et al. 2005).

The importance of adaptation to non-climatic conditions could have important implications for management efforts seeking to maintain species or populations through assisted colonization or assisted gene flow. For example, introducing "warm-adapted" genotypes from southern populations in an effort to facilitate adaptation to warming in northern populations could instead lead to maladaptation in the target population if the populations differ in adaptation to photoperiod, biotic interactions, or other factors (Aitken and Whitlock 2013). Instead, a potential source of warm-adapted alleles could come from sub-populations that exist in relatively warm microhabitats within the range of the larger population, as these sub-populations would be "pre-adapted" to local conditions in addition to warmer temperatures (Crawford 2008, Hof et al. 2011). In fact, Alexandra Fiord itself could become a source of warm-adapted genotypes to

nearby high Arctic locations, as temperatures at Alexandra Fiord are generally milder than those of surrounding areas (Freedman et al. 1994).

5.3 Addressing the influence of maternal effects

The original experimental protocol for the experiments presented in chapters three and four called for growing field-collected seed in a climate-controlled common garden environment (i.e., environmental growth chambers) until flowering was initiated, and then using seed produced from these common garden individuals in the field experiments. This is a frequent first step when conducting common garden and reciprocal transplant experiments in plants, as it (at least in theory) reduces the non-genetic variation between individuals due differences in growing environment (Roach and Wulff 1987). Thus, phenotypic differences between experimental individuals can be attributed to genetic differences rather than differences related to the maternal environment (Alexander and Wulff 1985, although maternal effects can persist for more than one generation; Roach and Wulff 1987). Despite growing field-collected *Papaver* and *Oxyria* seeds in growth chamber environments for over two years (equivalent to four summer seasons), however, only a handful of individuals of each species successfully flowered and set seed. Experiments were instead conducted directly with field-collected seed, and seed mass was included as a covariate in all analyses to control for the potential influence of maternal seed investment.

Future efforts to conduct reciprocal transplants with Arctic species should take into account the challenges of growing Arctic species under controlled conditions. Growth chambers in which humidity in addition to light and temperature can be controlled may improve efforts to stimulate

flowering. In addition, growth chambers that can cool below 6 °C (the lower limit for the chambers I used) may better simulate Arctic conditions. Mooney and Billings (1961) successfully stimulated flowering in Alaskan populations of *O. digyna* with "nighttime" temperatures of 1.7 °C and 24-hour light.

5.4 Measuring fitness in Arctic plants

My conclusions in the third and fourth chapters are somewhat tempered by the failure of field-grown plants to reach reproductive maturity even after three summers of growth. Observations were continued for a fourth summer (2014; data not included in this thesis) but still only a handful of individuals produced flowers. Thus, while I was able to collect abundant data on phenology, growth, and survival, the relationship between these three measurements and true fitness (as measured by reproductive success) is not known.

Lack of a reproductive fitness metric is a common problem in studies of long-lived perennial plants that take several years to reach reproduction (Rehfeldt et al. 2002, Mimura and Aitken 2010, McLane and Aitken 2012). Thus, with the exception of an extensive literature on tree species valuable in forestry, many studies of local adaptation and evolution in plants are conducted solely on annual or short-lived perennial species, potentially leading to a large bias in the evolutionary literature. Follow-up studies of reproductive fitness in experiments involving perennial species could help to fill this gap. For example, Bennington et al. (2012) surveyed transplant sites 30 years after their establishment, and found stronger evidence for local adaptation than was initially reported.

Monitoring of all the experiments presented here will continue at least until 2016. Thus, future estimates of reproductive fitness may be possible.

5.5 Future work

5.5.1 What are the consequences of changes in the timing of life events for plant performance?

While multiple studies have provided strong evidence that species are responding differently to recent environmental change (Diez et al. 2012, Chapter 2) the consequences of these shifts are often not known. Comparing shifts in phenology with changes in abundance and reproductive effort would help to elucidate some of the consequences of these changes (Willis et al. 2008, Cleland et al. 2012). In our study system, plant cover data has been collected in each plot at 5-year intervals since 1995, providing a method for assessing the relationship between shifts in phenology and changes in abundance. In addition, flower counts are conducted annually in every plot, and in many years data on the number of flowers for each tagged plant (i.e., the same individuals for which phenology has been observed) was also recorded. These data would allow a strong assessment of changes in reproductive effort over time, which could then be correlated with shifts in phenology.

5.5.2 Does altered phenology lead to changes in the duration of overlap between species and sites? How might this affect pollinator activity?

Differential shifts in flowering time can lead to shorter, longer, or bimodal flowering windows, with potential consequences for pollinators (Aldridge et al. 2011). Despite the potentially important effects of phenological mismatches, however, concurrent assessments of plant and

pollinator phenology are only rarely undertaken (Hegland et al. 2009, Miller-Rushing et al. 2010, Høye et al. 2013). Furthermore, it is often unknown whether pollinators respond to different environmental cues than the plants they pollinate (Hegland et al. 2009). At Alexandra Fiord, future work could combine observations of flowering duration (Chapter 2) with an assessment of pollinator activity, as has been recently explored at this site (Robinson 2014).

5.5.3 Will gene flow from southern populations promote adaptation to climate change in northern populations?

The results of Chapter 4 demonstrate that immigrants from southern populations do not have an advantage over local populations under warmer conditions. This implies that the immigration of "pre-adapted" species and genotypes from the south might be limited by environmental conditions other than climate. Given sufficient time, gene flow and selection might eventually lead to the expected "evolutionary rescue," but empirical evidence of this phenomenon is lacking (Anderson et al. 2012a, Aitken and Whitlock 2013). Future experiments could assess the fitness not only of local vs. southern genotypes under experimentally warmed conditions, but also of hybrids created by experimentally simulating gene flow between the populations. If some hybrids demonstrate greater fitness than either parent, it would indicate that gene flow – in concert with natural selection – could facilitate the persistence of northern populations as the climate warms.

5.5.4 What is the relative importance of climate versus other environmental conditions in driving local adaptation?

Many populations show evidence of local adaptation (Leimu and Fischer 2008, Hereford 2009), but while adaptation to climate is clearly common (Jump and Peñuelas 2005, Savolainen et al. 2007), the frequency and relative importance of adaptation to climate versus other environmental conditions is largely unknown (Aitken and Whitlock 2013). Future research could begin to disentangle the influence of climate and other environmental variables through controlled experiments in which only one variable is manipulated at a time. A better understanding of the roles of climate and other factors in driving local adaptation would be beneficial not only to our general understanding of ecological processes, but could also inform attempts to model future range shifts and/or to choose source populations for assisted colonization or assisted gene flow.

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Appendices

Appendix A

Supplementary material for Chapter 2

A.1 Warming effect of the open-top chambers throughout the year

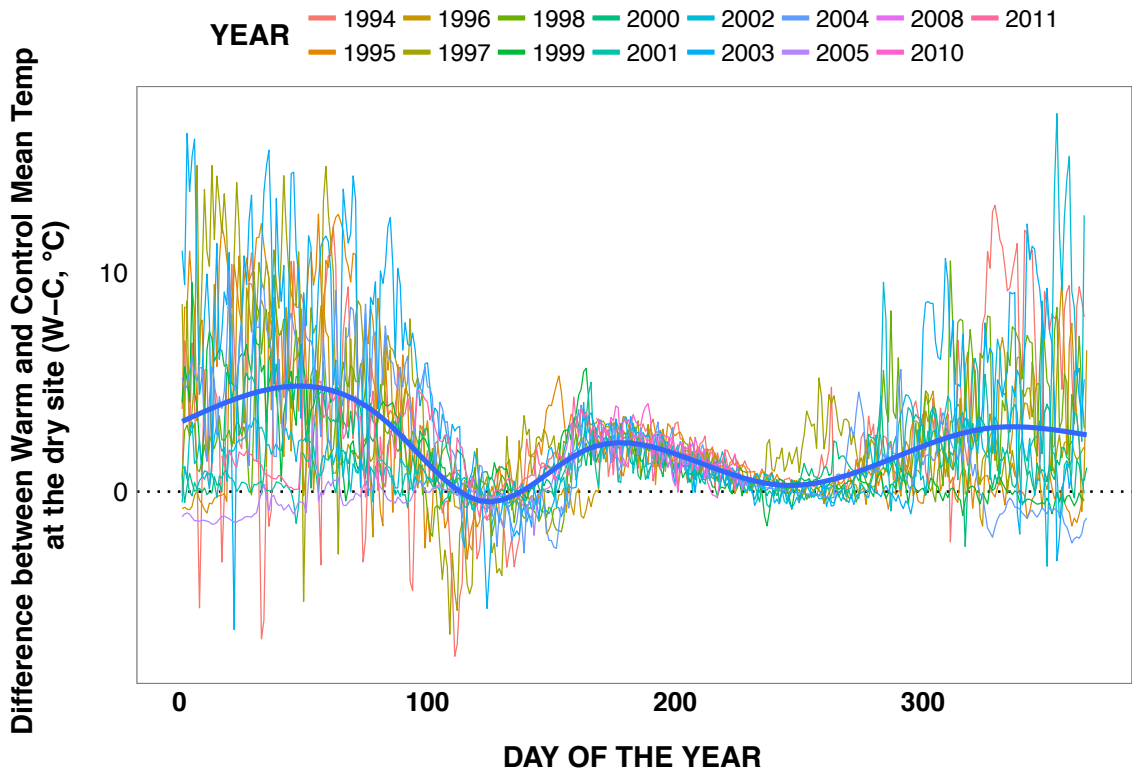

Figure A.1: Warming effect in the OTCs (relative to control plots) at the dry site. Coloured thin lines are the temperature difference (warm minus control) in each year; the thick blue line is a GAM-smoothed curve for the mean temperature difference across all years. Numbers above the zero line indicate warmer temperatures in the warming treatment than in the control treatment.

A.2 Coefficients from Bayesian models

Table A.1: Coefficients from Bayesian models predicting the effect of treatment on flowering and seed maturation phenology, the trend over time in flowering and seed maturation phenology, and the relationship between flowering and environmental variables for each species. Bold numbers indicate mean values for which the 95% credible interval does not overlap zero.

		Mean	SD	2.50%	25%	50%	75%	97.50%
Treatment Effect								
Flowering								
Dryas	Mesic Site	**-2.07**	0.55	-3.15	-2.44	-2.07	-1.70	-0.99
	Dry Site	**-2.14**	0.71	-3.49	-2.62	-2.15	-1.68	-0.73
Oxyria	Mesic Site	NA	NA	NA	NA	NA	NA	NA
	Dry Site	**-1.97**	0.71	-3.35	-2.45	-1.97	-1.48	-0.58
Papaver	Mesic Site	-0.76	0.59	-1.93	-1.16	-0.76	-0.36	0.40
	Dry Site	**-3.36**	0.69	-4.69	-3.82	-3.37	-2.90	-1.99
Salix	Mesic Site	NA	NA	NA	NA	NA	NA	NA
	Dry Site	-1.12	0.73	-2.55	-1.63	-1.12	-0.63	0.33
Seed Maturation								
Dryas	Mesic Site	**-4.12**	1.34	-6.70	-5.03	-4.13	-3.23	-1.47
	Dry Site	-1.32	1.81	-4.71	-2.56	-1.38	-0.14	2.44
Oxyria	Mesic Site	NA	NA	NA	NA	NA	NA	NA
	Dry Site	-2.00	1.78	-5.29	-3.24	-2.06	-0.85	1.75
Papaver	Mesic Site	-2.79	1.53	-5.76	-3.84	-2.80	-1.78	0.23
	Dry Site	**-6.47**	1.78	-9.80	-7.67	-6.56	-5.35	-2.76
Salix	Mesic Site	NA	NA	NA	NA	NA	NA	NA
	Dry Site	**5.65**	2.55	0.75	3.93	5.65	7.33	10.75
Time Trend								
Flowering								
Dryas	Mesic Site	0.24	0.26	-0.28	0.06	0.24	0.41	0.76
	Dry Site	**0.57**	0.27	0.05	0.39	0.57	0.75	1.10
Oxyria	Mesic Site	NA	NA	NA	NA	NA	NA	NA
	Dry Site	0.30	0.25	-0.19	0.13	0.30	0.47	0.79
Papaver	Mesic Site	0.17	0.24	-0.31	0.00	0.17	0.33	0.65
	Dry Site	0.41	0.24	-0.06	0.25	0.41	0.57	0.89
Salix	Mesic Site	NA	NA	NA	NA	NA	NA	NA
	Dry Site	0.04	0.32	-0.59	-0.17	0.03	0.24	0.66

		Mean	SD	2.50%	25%	50%	75%	97.50%
Seed Maturation								
Dryas	Mesic Site	-0.06	0.57	-1.17	-0.44	-0.07	0.32	1.10
	Dry Site	0.34	0.57	-0.74	-0.05	0.34	0.72	1.51
Oxyria	Mesic Site	NA	NA	NA	NA	NA	NA	NA
	Dry Site	0.03	0.53	-0.98	-0.32	0.02	0.38	1.10
Papaver	Mesic Site	0.19	0.53	-0.83	-0.16	0.19	0.55	1.26
	Dry Site	0.22	0.52	-0.79	-0.13	0.21	0.56	1.27
Salix	Mesic Site	NA	NA	NA	NA	NA	NA	NA
	Dry Site	0.20	0.71	-1.15	-0.28	0.19	0.67	1.66
Environmental Predictors								
Flowering								
Dryas	Snowmelt (spatial)	**0.52**	0.08	0.37	0.46	0.51	0.57	0.67
	Snowmelt (temporal)	**0.66**	0.12	0.42	0.58	0.66	0.74	0.89
	Winter Temperature	0.56	1.07	-1.57	-0.15	0.56	1.26	2.65
	Spring Temperature	**-2.58**	0.80	-4.14	-3.10	-2.58	-2.04	-1.05
	Temp of Previous Summer	1.01	0.60	-0.17	0.62	1.01	1.40	2.18
Oxyria	Snowmelt (spatial)	**0.40**	0.11	0.17	0.32	0.40	0.48	0.61
	Snowmelt (temporal)	**0.49**	0.14	0.23	0.40	0.49	0.59	0.77
	Winter Temperature	-0.91	0.85	-2.60	-1.46	-0.91	-0.34	0.77
	Spring Temperature	**-1.89**	0.72	-3.29	-2.37	-1.89	-1.43	-0.49
	Temp of Previous Summer	0.24	0.76	-1.26	-0.26	0.24	0.75	1.74
Papaver	Snowmelt (spatial)	**0.81**	0.09	0.64	0.75	0.80	0.86	0.97
	Snowmelt (temporal)	**0.38**	0.12	0.14	0.30	0.38	0.46	0.61
	Winter Temperature	**1.91**	0.77	0.38	1.41	1.92	2.41	3.42
	Spring Temperature	**-2.68**	0.66	-3.97	-3.13	-2.68	-2.25	-1.37
	Temp of Previous Summer	1.20	0.62	-0.01	0.79	1.20	1.61	2.44
Salix	Snowmelt (spatial)	**0.54**	0.13	0.28	0.45	0.54	0.63	0.79
	Snowmelt (temporal)	**0.85**	0.15	0.55	0.75	0.85	0.95	1.15
	Winter Temperature	-2.04	1.15	-4.34	-2.80	-2.03	-1.28	0.19
	Spring Temperature	-1.53	1.08	-3.69	-2.23	-1.52	-0.81	0.55
	Temp of Previous Summer	0.55	0.80	-1.00	0.00	0.55	1.08	2.14

A.3 Change in flowering time over time in both the warmed and control plots

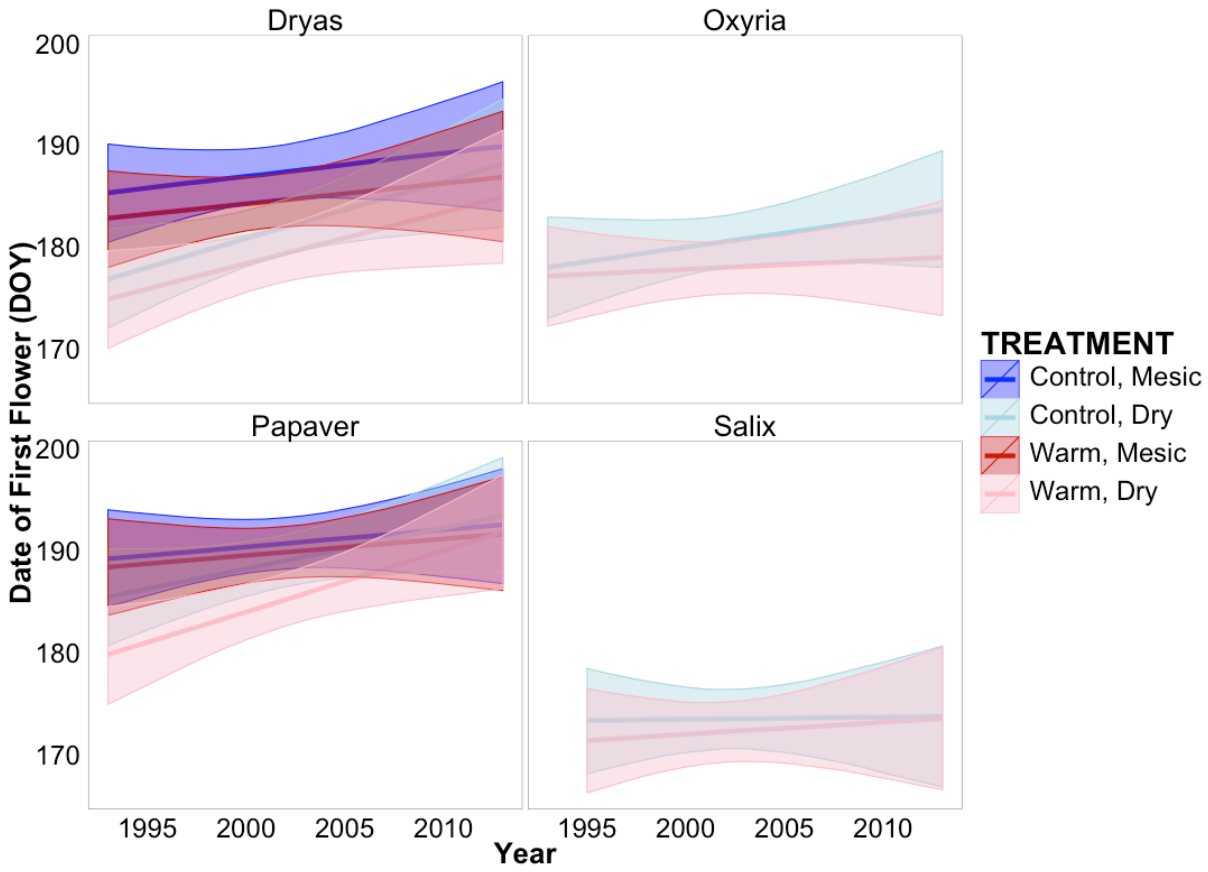

Figure A.2: Change in flowering time (+/- 95% credible intervals) in both treatments over the duration of the study. Flowering in *Salix* includes both male and female plants. Modeled results are from a Bayesian hierarchical model with random effects for plot and year. Slopes were allowed to vary by species, site, and treatment, as well as interactions between the three.

Appendix B

Supplementary material for Chapter 3

B.1 About maternal effects

The importance of maternal environmental effects on offspring performance has been widely debated (Roach and Wulff 1987, Weiner et al. 1997). Some studies have found a significant effect of maternal environment on offspring performance, primarily through differential seed provisioning (Zas et al. 2013). When seed weight was included as a model covariate, as in our study, the effect of maternal environment was strongly reduced. In an experimental study of the influence of maternal environment on offspring size and fitness in *Centaurea maculosa*, seed weight was weakly positively correlated with offspring growth, but only in the initial few weeks of growth (Weiner et al. 1997). The authors concluded that, while variation in seed size due to maternal plant was large, this variation was a genetically-controlled individual plant effect and not an environmental effect.

Although some studies have demonstrated a weak but significant effect of maternal warming on offspring germination (Zhang et al. 2012), a study of seed germination at Alexandra Fiord found no significant differences in germination between *Oxyria* and *Papaver* seeds collected from warmed and control plots (Klady et al. 2011). It should be noted that many of the studies of maternal effects through seed provisioning were performed on species with seeds far larger than *Oxyria* and especially *Papaver*. A single *Papaver* seed weighs, on average, 0.13 mg (imagine, for example, the seeds on a poppy-seed bagel), and an *Oxyria* seed 0.95 mg (Table B.1). In comparison, the average seed weight in the study by Zas et al. (2013) was 66.7 mg.

Table B.1: Seed weight per 10 seeds, in grams. Weight is the average of 2-3 weighing trials of 10 seeds each. Seeds from the warm treatments were marginally heavier for *Oxyria* at the mesic site (*p=0.02*) and the dry site (*p=0.04*) and for *Papaver* at the dry site (*p=0.04*) but not at the mesic site (*p=0.96*). Overall, *Oxyria* seeds from the dry site were heavier than those from the mesic site (*p<0.001*) but *Papaver* seeds from the mesic site were slightly heavier than those from the dry site (*p=0.05*).

	Site	Treatment	Mean	Minimum	Maximum
OXYRIA	mesic	Control	0.00765	0.00403	0.01185
	mesic	Warm	0.00906	0.00497	0.01320
	dry	Control	0.01011	0.00720	0.01495
	dry	Warm	0.01128	0.00643	0.01447
PAPAVER	mesic	Control	0.00135	0.00085	0.00165
	mesic	Warm	0.00136	0.00050	0.00225
	dry	Control	0.00119	0.00055	0.00150
	dry	Warm	0.00136	0.00080	0.00180

One limitation of using seed weight as a covariate to account for maternal environmental differences is that seed weight itself can be a genetically-controlled trait, in which case including seed weight as a covariate in our models would underestimate the true source-population effect. Because we germinated these seeds in a common, controlled environment and planted them into the experimental sites only as seedlings, we would have missed any treatment- or site-level differences in germination and initial establishment.

B.2 Environmental conditions in the mesic and dry sites at Alexandra Fiord

Table B.2: Temperature and snowmelt values in the mesic and dry habitats in 2012, 2013, and the long-term (1993-2011) average, as well as the treatment (warming – control) effect in both habitats. Spring temperature is the average temperature of days 150-200, winter temperature is the average temperatures of days 225-365 of the year before and 1-149 of the present year. Temperatures were measured at 1.5 m height. Snowmelt values were observed in each plot; a plot was considered snow-free when less than 10% of the plot area remained covered by snow. For the long-term average snowmelt dates, missing values were imputed (see methods in Chapter 2).

		Spring Temp	Winter Temp	Snowmelt (DOY)	Treatment Effect on Temperature (W-C)	Treatment Effect on Snowmelt (W-C)
2012	mesic	6.8 °C	-20.4 °C	~163 (?-164)	NA	NA
	dry			all plots <162		
2013	mesic	4.3 °C	-18.4 °C	164 (163-165)		-0.1 days
	dry			162.2 (159-165)		0.1 days
Long-term (1993-2011)	mesic	5.0 °C	-19.4 °C	165.5	1.6 °C	-0.8 days
	dry			160.8	2.1 °C	-1.7 days

B.3 Significance of model terms for between-habitat transplant experiment

Table B.3: Significance of terms in the (generalized) linear mixed models predicting differences in survival, date of leaf-out, maximum leaf area, and leaf senescence in the between-habitat transplant experiment for each species. Significance of the fixed effects terms (* p<0.001, ** p<0.01, * p<0.05, . p<0.1) was determined by comparing nested models using a chi-squared likelihood ratio test. Random effects were considered significant at p≤0.1.**

	Fixed Effects							**Significant Random Effects**
	Source Site	Transplant Site	Source x Transplant	Source x Year	Transplant x Year	Year	Seed Mass	
Oxyria								
Survival				na	na	na	.	Plot, Family
Leaf-out			**			***		Plot x Year, Family x Site
Max Leaf Area	**	*				***	* (-)	Plot, Family x Site
Senescence	**			na	na	na		Plot, Family
Papaver								
Survival				na	na	na		none
Mature Leaf			**		.			Plot x Year, Family
Max Leaf Area			***			***		Plot x Year, Family
Senescence	**			na	na	na		Plot

B.4 Significance of model terms for between-treatment transplant experiments

Table B.4: Significance of terms in the (generalized) linear mixed models predicting differences in survival, date of leaf-out, maximum leaf area, and leaf senescence in the between-treatment transplant experiment for each species at each site. Significance of the fixed effects terms (* p<0.001, ** p<0.01, * p<0.05, . p<0.1) was determined by comparing nested models using a chi-squared likelihood ratio test. Random effects were considered significant at p≤0.1.**

	Fixed Effects							**Significant Random Effects**
	Source Treat	Transplant Treat	Source x Transplant	Source x Year	Transplant x Year	Year	Seed Mass	
OXRYIA								
Mesic Site								
Survival		.		na	na	na	.	none (GLM used instead)
Leaf-out		.						Plot x Year, Family
Max Leaf Area						*		Plot x Year, Family x Treatment
Senescence		.		na	na	na	*	Plot, Family
Dry Site								
Survival		.		na	na	na		none (GLM used instead)
Leaf-out	*				*			Plot x Year, Family
Max Leaf Area			.			***		Plot x Year, Family
Senescence	**	.		na	na	na		Plot, Family
PAPAVER								
Mesic Site								
Survival				na	na	na		none (GLM used instead)
Leaf-out		***		*				Plot x Year, Family
Max Leaf Area	*				**			Plot x Year, Family x Treatment
Senescence				na	na	na		Plot, Family

Dry Site	Fixed Effects							Significant Random Effects
	Source Treat	Transplant Treat	Source x Transplant	Source x Year	Transplant x Year	Year	Seed Mass	
Survival				na	na	na		none (GLM used instead)
Leaf-out		**				***		Plot x Year, Family x Treatment
Max Leaf Area						***		Plot x Year, Family x Treatment
Senescence				na	na	na		Plot, Family

Appendix C

Supplementary data for Chapter 4

C.1 Experimental set-up

We established experimental common garden plots in a natural plant community along a short moisture gradient in the Alexandra Fiord lowland in 2010. Both *O. digyna* and *P. radicatum* are more abundant at the drier end of the moisture gradient, while *A. latifolia* is more abundant at the mesic end. Plots were arranged along the moisture gradients so that we could experimentally determine whether soil moisture differentially affects each population's performance.

In order to create a passive warming treatment, we established a total of 27 clear-sided, open-top chambers (OTCs) along with 27 non-warmed control plots. Open-top chambers are commonly used to simulate climate warming; these particular OTCs follow the design used in the International Tundra Experiment (ITEX) network (Marion et al. 1997, Henry and Molau 1997). The chambers passively warm the air inside by 1.5-3 °C while minimizing (but not eliminating) effects on soil moisture and gas concentrations. OTCs do frequently create a snow-trapping effect, especially in areas of relatively little snowfall, which leads to warmer winter temperatures but does not cause later snowmelt (Marion et al. 1997 see Chapter 1).

Despite substantially warmer summer and winter temperatures, OTCs at a nearby long-term experimental warming site increased the length of the growing season (as measured by the number of days with mean temperatures above 0 °C) by only 3.6 (+/- 1.2) days. This is at least partially due to a snow-trapping effect over the winter, which precludes much earlier snowmelt despite warmer temperatures. Although this is not an intended effect of the OTCs, it in fact

simulates a likely consequence of climate change: projections of future warming in the Arctic predict warmer temperatures throughout the year but especially in the winter, which in turn will lead to increased winter precipitation in the form of snow (Weller et al. 2005, Bintanja and Selten 2014). Thus, although temperatures will increase, the date of snowmelt may not shift significantly. We have already seen evidence of this pattern at Alexandra Fiord, where the mean temperature has increased by more than 1° C over the past two decades but the date of snowmelt shows no temporal trend or even occurs slightly later, depending on the habitat type (Hudson and Henry 2009 and Chapter 1 of this thesis).

OTCs also only minimally extend the growing season into the fall. This is likely due to the rapid reduction of light and onset of colder temperatures that occurs in the high Arctic in mid-late August. While the rapid decline in daylight that occurs during this period will not change with climate warming, increased fall temperature may be underrepresented by the OTCs.

C.2 Soil moisture in each treatment at the experimental site in 2012 and 2013

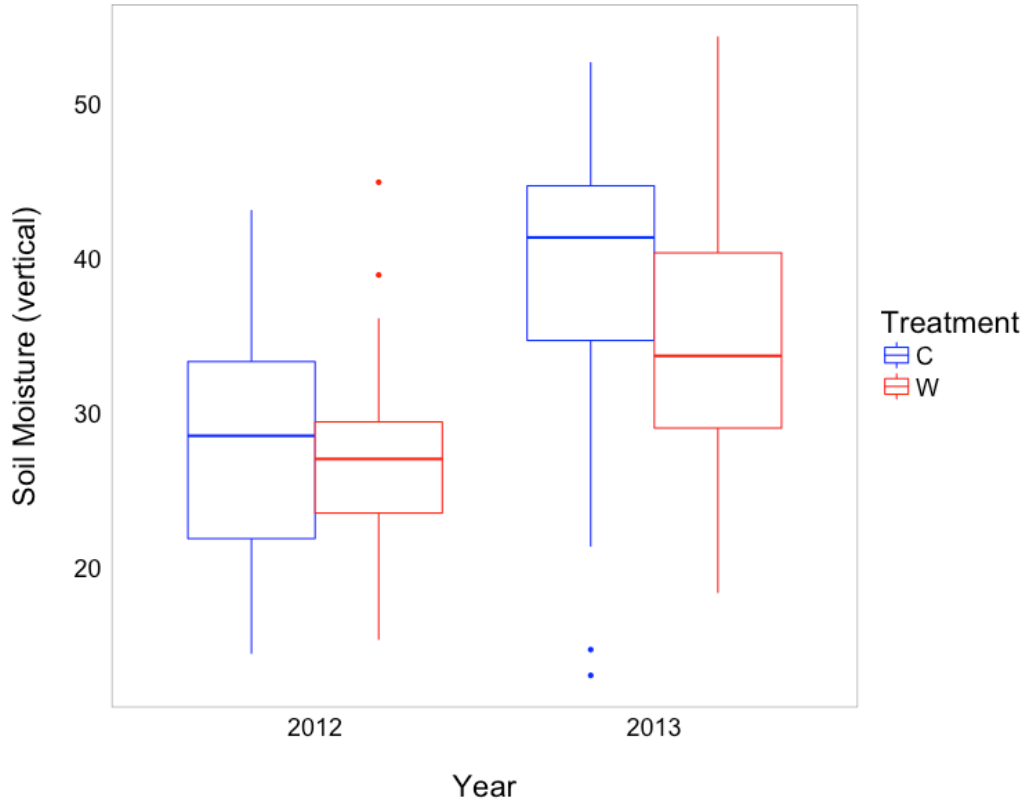

Figure C.1: Soil moisture (to a depth of 12 cm) in both treatments in mid-July of both years, as measured with a Hydrosense soil moisture probe.

C.3 Temperature and treatment effect at the experimental site in 2012 and 2013.

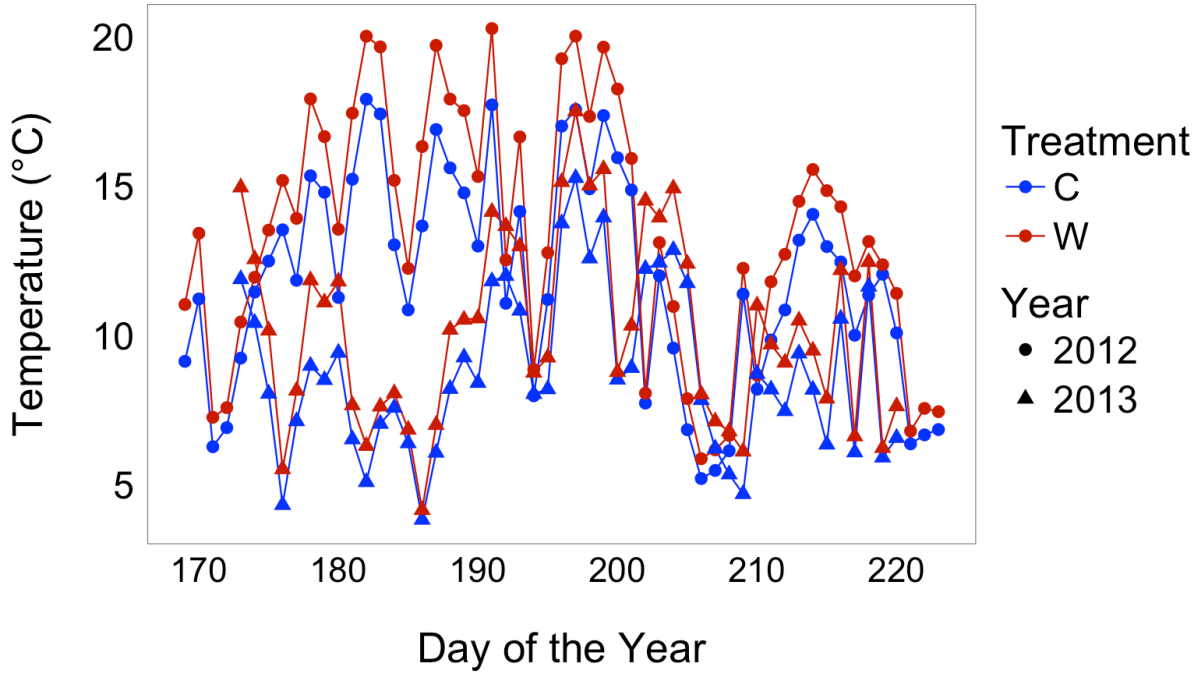

Figure C.2: Temperature (measured at 10 cm height) in warmed and control treatments in 2012 and 2013 at the experimental site. Early summer temperatures were substantially cooler in 2013 (triangles) than in 2012 (circles).

C.4 Significance for model terms in the latitudinal gradient transplant experiment

Table C.1: Significance of terms in the (generalized) linear mixed models predicting differences in survival, date of leaf-out, maximum leaf area, and leaf senescence among populations of all three species in the latitudinal transplant experiment. Significance of the fixed effects terms (* p<0.001, ** p<0.01, * p<0.05, . p<0.1) was determined by comparing nested models using a chi-squared likelihood ratio test. Random effects were considered significant at p≤0.1.**

	Fixed Effects							**Significant Random Effects**
	Source Site	Treatment	Year	Source x Treatment	Source x Year	Treatment x Year	Seed Mass	
OXYRIA								
Survival	***		na	.	na	na		(none)
Mature Leaf					***	***		Family, Individual, Plot x Year
Max Leaf Area					***	***		Individual, Plot x Year
Senescence	.		na		na	na		Family, Plot
PAPAVER								
Survival			na		na	na	.	(none)
Mature Leaf				**	***	.	.	Family, Individual, Plot x Year
Max Leaf Area	**	*	***					Family, Individual, Plot x Year
Senescence		**	na	.	na	na		(none)
ARCTAGROSTIS								
Survival			na		na	na		(none)
Mature Leaf	*	*	*					Individual, Plot x Year
Plant Size		*			*			Individual, Plot x Year
Maximum Height				**				Family, Individual, Plot x Year

Table C.2: Significance of terms in the (generalized) linear mixed models predicting differences in pattern of growth among populations of *Oxyria digyna* in the latitudinal transplant experiment. Significance of the fixed effects terms (* p<0.001, ** p<0.01, * p<0.05, . p<0.1) was determined by comparing nested models using a chi-squared likelihood ratio test. Random effects were considered significant at p≤0.1. Q denotes a quadratic term in the model, L a linear term. Quadratic terms were included only in 2013, when all plants were measured three times during the growing season.**

	Fixed Effects						**Significant**
	Source Site	Treatment	Time	Source x Treatment	Source x Time	Treatment x Time	**Random Effects**
OXYRIA							
Growth, 2012					***	***	Individual x Time, Plot
Growth, 2013		*	*** (Q)		*** (L)		Individual x Time (Q), Plot