

***CASSIOPE TETRAGONA* AS A DENDROECOLOGICAL PROXY: A  
RETROSPECTIVE ANALYSIS OF EXPERIMENTAL WARMING IN THE ARCTIC  
TUNDRA**

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## Abstract

Annual stem growth and reproductive effort of the evergreen dwarf-shrub, *Cassiope tetragona*, exhibit a strong positive relationship to summer temperature and have been used in dendroclimatological analyses to reconstruct climate in the High Arctic through the application of transfer function equations. Retrospective analysis of the annual growth increments have also previously been used to examine the impact of short term warming in a few tundra sites. This thesis presents a full retrospective analysis approach to reconstruct the impact of long-term experimental warming in tundra communities at Alexandra Fiord (Ellesmere Island) from before the installation of open-top-chambers in 1992 to the present day, using a before-after-control-intervention design on growth and reproduction variables. We found a positive, significant effect of experimental warming on the stem growth of *C. tetragona* and revealed that phenology stages (such as bud break, flowering, and fruit production) take place significantly earlier in the warming plots in comparison to the control plots. Furthermore, the relationship between both July Average and August Maximum air temperature time series at Alexandra Fiord and the annual stem growth and reproductive chronologies from the control plots were used to construct summer air temperature models with good predictive abilities, explaining up to 68% of the variance.

We compared chronologies of *C. tetragona* samples from multiple International Tundra Experiment sites to investigate the extent to which growth and reproductive responses to experimental warming vary across the Arctic. An effect size analysis and linear mixed effects model was used to determine the fact that experimental warming has a significant and positive effect on plant growth, increasing annual stem growth by an average of 0.665 mm across the Arctic, with 60% of the overall variance in the stem growth data being explained by Region. This regional signal was also revealed in a Principal Components Analysis which included descriptive stem characteristics statistics at 23 circumarctic sites. These findings complement existing research about the warming effect of treatment on tundra plant growth and phenology, and provide novel information on the value of *C. tetragona* as a dendroecological proxy and the regional differences in *C. tetragona* growth and reproduction patterns.

## **Lay Summary**

We created annual timelines of stem growth, flower and bud production of Arctic white heather (*Cassiope tetragona*) to investigate the extent to which these characteristics are influenced by local climate, and in particular by the additional warming effect of open top greenhouses. On Ellesmere Island we found that stem growth and flowering of the plant was significantly increased by the warming experiments, and that flowering was taking place earlier in the summer inside the open top greenhouses than in plots outside the greenhouses. We also determined that these timeseries can be used to successfully reconstruct local summer air temperatures. Using samples from other Arctic field sites, we found that the effect of experimental warming increased stem growth at all field sites, although the differences in stem characteristics were greater between the regions than in the experimental plots.

## **Preface**

The research objective for this thesis was proposed by Dr Greg Henry (UBC), with whom I worked to design the sampling scheme and general statistical approach. In the field, I was assisted by Dr Zoe Panchen (UBC) in recording phenology stages of my tagged stem samples. Dr Lori Daniels (UBC) suggested the use of the Cybis CooRecorder and CDendro software packages, and I conducted my image processing in her Tree Ring Research Laboratory. Additionally, I was assisted by Hailey May in preparing my stems for scanning, and by Cristina Mace in counting flower and bud features on the samples collected in Alaska. Dr Greg Henry, Dr Shelly Rayback (University of Vermont) and Dr Lori Daniels acted as my thesis committee and provided regular feedback on my writing and statistical analysis. I was responsible for the writing of the thesis and conducted all of the analysis included therein.

The following researchers collected stem samples for this project from their respective field sites and will be listed as co-authors on any publication based on this research: Christian Rixen, Lærke Stewart, Bob Hollister, Jeremy May, Petr Macek, Sylvain Monteux and Johan Martinelli.

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## **List of Abbreviations**

- AGI: Annual Growth Increment
- BACI: Before-After-Control-Intervention
- ITEX: International Tundra Experiment
- OTC: Open Top Chamber
- RWI: Ring Width Index

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## **Dedication**

*To the wily little arctic fox who ran 3500 km from Svalbard to Ellesmere Island (Fuglei & Tarroux, 2019). Just like the writing of a thesis, a cross-polar migration is a marathon, and not a sprint.*

# Chapter 1: Introduction and Study Design

## 1.1 Introduction

Where instrumental climate records are unavailable, climate scientists commonly adopt a paleoenvironmental approach, interpreting physical and biological responses of environmentally sensitive indicators in order to reconstruct chronologies of climate change. There is a demand for terrestrial proxies which preserve an annual record, as most other paleo-indicators (such as lake-sediments, ice core isotope analysis and pollen samples) often lack fine temporal resolution, or represent environmental change on a larger scale. Dendroclimatology is the study of tree ring characteristics as a proxy of climate change, and allows for the exploration of the climate response of a number of individual species (Fritts, 1976). One such dendroclimatological proxy is the widespread evergreen dwarf-shrub, *Cassiope tetragona*, which exhibits a strong positive relationship to summer temperature change and has been used to develop climate reconstructions in the Arctic, where meteorological stations are sparsely distributed and data is temporally limited (McBean et al., 2005).

In this thesis, we draw on our current understanding of this proxy and undertake a retrospective approach to the effect of passive experimental warming in tundra communities at Alexandra Fiord on Ellesmere Island using the before-after-control-impact (BACI) design. In addition, we make a comparison of chronologies of experimentally warmed *C. tetragona* samples from multiple sites across the Arctic.

## 1.2 Literature Review

### 1.2.1 Climate Change in the High Arctic

The Arctic has been warming disproportionately in comparison to other global regions since the late 1970s, as a function of atmospheric warming and the exacerbation of major regional feedbacks, including the reduction of albedo and the thawing of permafrost – a phenomenon referred to as *Arctic amplification* (Serreze & Francis, 2006). Instrumental and proxy records indicate unprecedented warming of 1.06°C over the last century alongside a sea ice extent decrease

of  $-2.1 \pm 0.3\%$  decade<sup>-1</sup> in the Arctic Ocean between 1979-2010 (Tingley & Huybers, 2013; Cavalieri & Parkinson, 2012). Within the Canadian Arctic, models have projected a 5-10% decrease of Arctic terrestrial snow cover and sea ice per decade between 2020-2050 (Mudryk et al., 2018). It is estimated that, through the increase in the temporal range of the summer season and decreases in sea ice thickness, the Arctic Ocean has switched to a seasonal regime (similar to that of the Antarctic) (Haine & Martin, 2017), and models project longer ice-free seasonal periods in line with different emissions scenarios [i.e. an August-September ice free season following additional greenhouse emissions of  $800 \pm 300$  Gt, and a July-October ice free season following additional greenhouse emissions of  $1400 \pm 300$  Gt] (Stroeve & Notz, 2018).

Furthermore, the permafrost carbon feedback is predicted to contribute an additional 0.04–0.23°C warming under a scenario whereby 33-114 Gt carbon will be released from Arctic permafrost by 2100 (Schneider Von Deimling et al., 2012). However, estimates of the carbon stock and expected carbon release from Arctic and alpine permafrost landscapes remains uncertain and hindered by a lack of regional field data points, particularly in the High Arctic and Central Siberia (Hugeluis et al., 2014; Schurr et al., 2015).

The instrumental meteorological record for the High Arctic is spatially limited as monitoring stations are sparsely distributed, and are temporally constrained to the 20th-21st centuries, necessitating the use of paleoenvironmental proxy records and models to infer pre-instrumental climate variability (McBean et al., 2005). Multi-proxy analyses have been used to reconstruct multiple centuries' worth of temperature variability which reveal the unprecedented and rapid nature of 20<sup>th</sup> Century climate warming (e.g. Overpeck et al., 1997; Tingley & Huybers, 2013) . Moreover, proxy records are commonly used to help inform predictions of future environmental change (i.e. by examining past proxy-climate relationships and applying them to potential fossil fuel emissions projections) in global climate models that can be used to inform climate policy (i.e. IPCC 2013). Therefore, under such rapid rates of change, and considering the complexity of climate feedback systems, it is imperative to reconstruct past climate change so that we may better model future change. Considering the vulnerability of societal and ecological systems to Arctic

amplification, the disparity between demand for data and its limited availability remains a key motivation for polar research.

### **1.2.2 Ecosystem Response to Climate Change in the High Arctic**

There exists a close relationship between the regional distribution of vegetation and climate conditions in the High Arctic (Edlund & Alt, 1989; Gould et al., 2003; Walker et al., 2005). Conversions from shrub tundra to forest at the tree line and the expansion of tall shrubs are set to increase in both rate and in relative contribution to the albedo positive feedback in the Low Arctic (Chapin et al., 2005), with one estimate projecting a doubling of woody vegetation cover by the 2050s (Pearson et al., 2013). Another estimation suggests that this feedback could cause an increase in solar radiation absorption of 75% in winter (Sturm et al., 2005). Experimental warming generally increases sexual reproductive effort by tundra plants, and it is suggested that future warming will promote increased productivity and vegetation cover in the High Arctic (Klady et al., 2011). Furthermore, it is expected that warming summer temperatures and increased precipitation will alter biogeochemical processes in tundra ecosystems, for example by promoting greater carbon sequestration in tundra ecosystems and increasing soil microbe activity at the beginning of the growing season (Schaeffer et al., 2013). It is expected, therefore, that High Arctic landscapes and vegetational communities will change alongside climate warming, and contribute to enhanced climate feedback dynamics and other environmental state shifts.

There is an increasing drive to investigate the extent to which related environmental (and particularly micro-site) variables such as soil moisture and snow depth are contributing to plant growth and productivity, for example via changes in nutrient cycling, as this information will allow us to make more informed predictions of landscape change across different bioclimatic zones across the terrestrial Arctic (Elmendorf et al., 2012; Myers-Smith et al., 2015; Bjorkman et al., 2018). Many Arctic ecosystem studies published to date are site-specific. Furthermore, due to the complex and critically understudied relationships between tundra vegetation and climate change (Post et al., 2009), both regional and circumpolar landscape change is difficult to predict, though there are a growing number of synthesis studies aiming to explore tundra ecosystem responses to accelerated warming over different bioclimatic zones (i.e. Arft et al., 1999; Elmendorf et al., 2012,;

Oberbauer et al., 2013). However, the field sites included are often sparsely distributed and often exclude the Siberian Arctic.

To investigate the vegetation response to climate warming in tundra ecosystems, warming experiments have been established in a number of locations. One example of a coordinated, distributed multifactor warming experiment is the International Tundra Experiment (ITEX), which explores the relationship between climate change and vegetation change across multiple sites throughout the Arctic and in some alpine regions, providing a useful platform through which to investigate spatial variability between regions via identical and replicable warming methodologies (Henry et al., 2013). Since many ITEX sites were established in the 1990s, it would be useful to retrospectively evaluate the impact of warming experiments on shrubs from before the experimental plots were installed through to the present day to examine the magnitude of experimental warming on shrub growth, and to compare the magnitude of this response between different ITEX sites, which span a number of environmental gradients. The consideration of both local and regional scales in the analysis of warming experiments is important as it would be misleading to assume the existence of particular trends across the entirety of the High Arctic based on site-specific observations alone (Wiens, 1989; Post et al., 2009; Myers-Smith et al., 2015). Reflexively designed studies can provide useful insights into the terrestrial impact of Arctic amplification and differences in tundra ecosystem responses to experimentation across latitudes, vegetation types and bioclimatic zones. For example, Arft et al. (1999) compiled data from multiple ITEX sites and observed that vegetation in low and high Arctic sites exhibited differing reproductive strategies, whereby growth responses to warming were strongest at more southern latitudes, while seed-setting responses were strongest further north. Furthermore, experimental warming could be used in conjunction with paleoclimate research to investigate terrestrial responses to climate variability over the last 100 years.

Phenology is the study of the timing of life history stages of organisms, including the seasonal timing of flowering, fruiting and senescence in plant life, and has also been essential in clarifying our understanding of plant responses to Arctic amplification. In Arctic tundra ecosystems over the past century, we have observed earlier flowering and seed dispersal of many common Arctic plants

(Panchen & Gorelick, 2017), and it is theorised that there is a link between this change in reproductive patterns and warmer summer growing season temperatures, and at a higher magnitude of change than observed in temperate regions (Wookey et al., 1993; Panchen & Gorelick, 2015). Studies of phenology in tundra shrubs, therefore, are another useful gauge of ecosystem change in response to Arctic amplification, and are key to our understanding of species' responses to experimental warming in collaborations such as ITEX.

### **1.2.3 Proxy Studies in the High Arctic**

Paleoclimatological data are used to reconstruct historical climate change in areas with temporally limited instrumental records. While ultimately limited by summer growing conditions (Miller et al., 2010), biological paleoclimate proxy data provides a means to interpret long-term fluctuations through the biological growth and reproduction in the short summer season. This section of the literature review evaluates the effectiveness of the key biologically-derived proxies in the High Arctic.

#### **1.2.3.1 Paleolimnology**

Paleolimnology is the study of lake sediments in relation to historical environmental change. Lake sediments provide an archive of biogeochemical responses to climate change, often at an annual resolution and often covering centuries worth of environmental variability, for example through the presence of chlorophyll-*a* which is symptomatic of the trophic state of the lake, and through the analysis of fossils of organisms with clear environmental tolerance ranges (Smol & Douglas, 2007), and the thickness of annually resolved varves of sediment (Hardy et al., 1996). Variables that have been reconstructed through these techniques include annual air temperature anomalies, pH, ice cover, and habitat conditions. One example of a paleolimnology study on recent warming (2000-2012) in the Canadian High Arctic was the analysis of sediment characteristics in Lake Hazen (Ellesmere Island), whereby the authors used shifts in diatom community composition from largely benthic (shoreline) to planktonic (open-water) species alongside a recent decline in health of Arctic Char as a proxy of ice cover change in response to regional warming (Lehnerr et al., 2018).

It is possible to reconstruct long-term Arctic climate cooling of around  $-0.22 \pm 0.66^\circ\text{C}$  per millennia followed by rapid warming post-1950 (Kaufman et al., 2009). Furthermore, the climate response of thermokarst lakes to climate warming can be investigated through proxy analysis of diatom community composition changes, while oxygen isotope analysis ( $\delta^{18}\text{O}$ ) can be used to reconstruct snowmelt runoff into lakes (Bouchard et al., 2016). Additionally, metrics such as pH, water colour change and dissolved organic carbon composition can act as a proxy of permafrost degradation such as retrogressive thaw slumping (Bouchard et al., 2016; Lehnherr et al., 2018). While paleolimnology can detect general climate signals and represent the biotic response of lakes to events such as ice cover decrease (Smol & Douglas, 2007), the results represent lake-specific responses to climate and landscape processes (such as sediment run-off and thaw slumps) but are not a direct representation of local terrestrial plant communities.

### **1.2.3.2 Palynology & Macrofossil Analysis**

Similarly, palynology (the study of fossil pollen) and plant macrofossil research have both been used to reconstruct paleoenvironmental conditions in the Arctic. Pollen deposited in peat bogs, glacial ice and lakes aids in the reconstruction of succession, environmental conditions and their impact on processes such as peat accumulation, species dispersal and landscape change. Comparative analysis between modern pollen and  $^{14}\text{C}$ -dated records provides a regional overview of vegetation distribution change following deglaciation (Bigelow, 2003). Furthermore, our understanding of plant temperature tolerances and tundra vegetation community dynamics has been applied to reconstruct broad July average air temperature anomalies across millennia within the Eastern Canadian Arctic (Kerwin et al., 2004). However, limitations to this technique include the wind-blown transport of ‘exotic’ pollen (i.e. pine) from other regions and the relatively low pollen count from plant species in the High Arctic in comparison to other global regions (Gajewski et al., 1995; Gajewski 2006). Moreover, it is impossible to construct an annually delimited record of climate change through these methodologies.

### **1.2.3.3 Dendrochronology**

Dendrochronology is the study of tree rings, whereby annually resolved tree-ring chronologies may be compared with environmental data to understand environmental change over time (Fritts

1976), and is a tool that has been used to aid research in environmental science and ecosystem research, landscape management, archaeology, and basic climatology (Bräker 2002). When tree ring chronologies are calibrated against historical climate data, it is possible to develop transfer functions that use annual growth to reconstruct past climate variability, an approach known as **dendroclimatology**. Reconstructions of climate variation through this methodology are common below the treeline where it is possible to use boreal trees and classic dendrochronology techniques (Briffa et al., 1988). Tree rings are valuable proxies, as they exhibit annual resolution and represent a direct link between a terrestrial species and its response to the climate. Moreover, multiple trees from one site and across sites can be crossdated to establish a correct calendar dating and aid comparison among sites as part of a large scale spatial analysis. These characteristics provide the tools needed to infer climate change through the contemporary techniques established by Fritts (1976).

Due to the absence of trees north of the Arctic treeline, many have applied dendroclimatological methods to tundra shrub species in order to reconstruct annual climate variables. An initial investigation by Wilson (1964) on *Salix arctica* illustrated that annual growth responded positively to temperature, and that there was a negative association between age and annual growth rate. While this was influential as one of the first dendrochronology studies on an Arctic shrub, it should be noted that the reliability of the study was hindered by the fact that there were many false and incomplete rings. Similarly, the Arctic-Alpine dwarf-shrub *Empetrum hemaphroditum* has been utilised as a dendroclimatological proxy: the relationship between summer air temperature and annual growth allowed for the detection of a climate signal (1951-2004) across multiple sites, despite variations caused by local topography (Bär et al., 2008). However, the small sample size in these studies limits the reliable comparison of the relative growth rate between these shrubs in the High Arctic with other species and between study sites and at different latitudes.

However, a temperature signal cannot always be isolated, highlighting the need to consider the statistical relationships between annual growth and other environmental variables. While Wilson (1964) initially outlined a clear relationship between annual growth and temperature, Schmidt et al. (2006) employed mixed-model statistics to their *S. arctica* samples and found no significant

relationship between annual growth and summer temperature, instead finding a significant positive correlation between growth and early spring snow cover. Furthermore, a 74-year chronology was developed for the Arctic willow *Salix alaxensis*, indicating a positive relationship between annual ring widths and precipitation (Zalatan & Gajewski, 2006). Liang et al. (2012) found that *Juniperus pingii* var. *wilsonii* shrubs in the Tibetan Plateau displayed dominant sensitivity to moisture availability. Findings such as these exemplify the notion that shrub growth is not only a function of summer temperature.

Although tundra shrubs are sensitive to environmental variability, dendroclimatological studies of tundra shrubs in the Arctic are limited spatially and in number, largely due to logistical constraints including the cost of fieldwork in remote locations. Furthermore, a number of shrubs contain missing rings or rings that are too narrow or labour-intensive to accurately delineate on a large scale (Schmidt et al., 2006; Zalatan & Gajewski, 2006). Due to considerable uncertainty surrounding methodological reliability and potential spatial differences in shrub response, further studies are required to refine the process of analysis alongside comparative studies across the Arctic (Myers-Smith et al., 2011; Myers-Smith et al., 2015).

#### **1.2.4 *Cassiope tetragona*: a dendroclimatological proxy**

*Cassiope tetragona* is an evergreen dwarf-shrub common throughout Arctic and alpine areas and has been the focus of research refining its usage as a paleoclimate proxy. Unlike other dendrochronological proxies on shrubs as outlined in section 1.2.2.3, *C. tetragona* does not show clearly delineated growth-rings. Yet, it has been identified as a successful proxy of climate reconstruction in the High Arctic with a linear relationship between stem growth and air temperature (Callaghan et al., 1989; Johnstone & Henry, 1997; Rayback & Henry, 2005; Weijers et al., 2012). Callaghan et al. (1989) observed a repeating series of ‘wave-like’ patterns in the leaf size distribution whereby the shortest pairs of leaves on the stem represent the end of the growing season and the beginning of winter. The authors linked annual leaf length and changes in the climate through multiple regression analyses using local climate records. These findings led to the development of *C. tetragona* as a formal tool for paleoclimate reconstruction over the following three decades. As the plant is widespread in circumpolar regions, environmentally sensitive with

well-preserved annual growth increments, this species provides a promising solution to the issue of a lack of reliable terrestrial proxies in the High Arctic.

Havström et al. (1993) developed Callaghan's methodology by attempting to investigate the differences in annual changes in both leaf length *and* reproductive effort (flowering) using open-top-chambers (OTCs) to simulate warmed conditions. By including an element of geographical comparison, and by analysing the correlation values between annual stem growth and local summer air temperatures, it was speculated that the main control of growth at the upper distributional limits of the plant (Svalbard in the High Arctic) is summer temperature, in comparison to light and nutrient competition at the lower distributional limits (Abisko in the Low Arctic) (Havström et al., 1993). Havström et al. (1995) used the linear relationship between annual growth increments in *C. tetragona* and summer temperature to show that July temperatures were 0.7°C lower during the Little Ice Age at a site on Ellesmere Island. They compared annual growth between extant plants and plants released from a glacial front. A similar investigation by Molau (1997) in Swedish Lapland (in the Low Arctic) found that *C. tetragona* growth (as determined by leaf size) was more responsive to insolation than it was to summer temperature, as determined through a Before-After-Control-Intervention with pairwise sampling (BACIP) comparing the magnitude of change in and outside of OTCs, following methods outlined by Osenberg et al. (1994). While sample sizes in these studies were very small, they were influential in applying the proxy to summer air temperature reconstructions and investigating geographical variations in growth response.

While these early papers were significant in determining a link between climate and morphological characteristics such as leaf length and reproductive effort, the methodology was updated by Johnstone and Henry (1997). The authors introduced the measurement of leaf node distances to determine AGIs in a similar manner to the width measurement of tree-rings. By removing two adjacent rows of leaves, it is possible to determine 'wave-like' patterns in leaf node distances on the stem, which can be measured under the microscope. The smallest distance between scars represents the end of the growing season and thus, AGIs (the distance between the start and end of growing seasons) can be determined and measured in length. These lengths are plotted against

year - alongside counts of features such as aborted flower buds and flower peduncle scars (a proxy for reproductive effort). Using this approach, an uninterrupted chronology calibrated with air temperature through the use of transfer functions allowed for a climate reconstruction for the 20<sup>th</sup> century, which closely matched regional instrumental records and other proxy records (Rayback & Henry, 2006). Furthermore, this methodology has been paired with isotopic analysis. In an effort to detect the Arctic and North Atlantic Oscillations (AO & NAO), positive oscillation phases were reflected by enriched sample  $\delta^{18}\text{O}$  (associated with increased summer precipitation) and reduced  $\delta^{13}\text{C}$  (associated with lower stomatal conductance), measurements which were applied to a time-series using the internodal method (Welker et al., 2005). Ultimately, development of the internodal AGI method allowed for a more sophisticated tool through which to measure yearly change along the stem and allows for the longest chronologies (e.g. 100 years [Rayback & Henry, 2006]) among the methods used for AGI measurements in *C. tetragona*.

An alternative approach to the measurement of AGIs was developed by Rozema et al. (2009), who instead measured the distance between wintermarksepta, which are visible as a pinching-in of the darker pith along a longitudinal cross section of a stem. This approach achieves the same effect as the internodal methodology, although the cross-sectioning of the stem removes the possibility of analysis of reproductive effort and leaf length. Weijers et al. (2010) employed a similar approach to Rayback & Henry (2006) and found that their 169-year chronology calibrated with summer temperature correlated positively with the regional instrumental record. This approach has been used to analyse the response of *C. tetragona* to OTC warming, which recorded the warming of the local air temperature by 1.3°C after 2-3 years (Rozema et al., 2009). This could explain the lack of difference between OTC and control plots in Molau's 1997 study, which only considered the effects of experimentation between 1993-1995. Furthermore, Weijers et al. (2017) developed a 40-year chronology using wintermarksepta measurements and further demonstrated a strong association between *C. tetragona* growth and AO/NAO oscillations. *C. tetragona* stem growth (analysed through the wintermarksepta approach) has been included in ecological work across the circumpolar Arctic using multiple widespread tundra shrub species (i.e. Myers-Smith et al., 2011). Additional examples of the inclusion of *C. tetragona* wintermarksepta records include recent studies which have applied a novel dendroecological approach whereby plant recruitment

dynamics of vegetation communities at a site in east Greenland were reconstructed and calibrated with summer air temperature records (Büntgen et al. 2015; Büntgen et al. 2018).

The use of *C. tetragona* as a dendroclimatological proxy is still in its developmental stages and, as is the case with the other shrub-based proxies in the Arctic, is spatially limited. Studies investigating the difference in the climate signal across sites in the Arctic have determined that while regional signals can be determined, there are temporal variations in climate fluctuations and variations in site sensitivity to variables such as summer temperature, winter precipitation and moisture availability (Rayback et al. 2011; Rayback et al. 2012). There is also a considerable amount of intraplant variability in AGI lengths, suggesting the need for further investigations into microenvironmental processes and resource partitioning in *Cassiope* plants (Rayback & Henry 2005). There is a clear need for further research into the influence of branching in the growth patterns of *Cassiope*, in addition to more careful consideration of life history traits and the juvenile growth effect in stems. Furthermore, methods that have calibrated both growth and reproductive effort into their chronologies have proven to be time consuming and resource intensive, limiting the sample size in a number of studies. In this thesis, we attempt to improve these methods through the adaptation of contemporary dendrochronology software, Cybis CooRecorder and CDendro (Larsson 2016).

### 1.2.5 Synthesis

Due to the limited nature of the instrumental record of the Arctic, we must rely on spatially and temporally sparse proxies of historical climate. The dendroclimatological approach can be applied to Arctic shrub species which have been proven to act as annually resolved, climate-sensitive terrestrial proxies found commonly throughout the Arctic. *C. tetragona* is a newly developed proxy and therefore there are considerable knowledge gaps. For example, while Weijers et al. (2012) reconstructed seven years of OTC warming using *C. tetragona* shoot length, there has not yet been an effort to use the proxy to retrospectively investigate the impact of long-term warming experiments on stem growth and reproductive effort combined. Additionally, while studies to date have explored stem growth over a limited range of single sites, it is beneficial to empirically determine geographical difference in stem growth characteristics in multiple warming experiment

sites across the Arctic, along bioclimatic, vegetation and latitudinal gradients. This proxy is still in its developmental stages and the methodology is likely to be refined in conjunction with technological advances. By including phenology in this study, we investigate the potential to combine these two methodologies that are becoming increasingly common practise at tundra field sites, as comparison of the phenological and stem-growth response to experimental warming is a useful way to investigate the impact of the amplified effect of treatment. This study has the potential to further establish *C. tetragona* as a reliable tool to examine the effects of the rapid warming on plant growth and reproduction.

### 1.3 Research Questions and Hypotheses

The primary objective of this project is to further develop our understanding of the growth and reproductive responses of *Cassiope tetragona* to ambient and experimental climate warming and clarify our understanding of how the plant responds to accelerated climate warming across different geographical and bioclimatic zones. This objective was investigated through the use of classical dendroecology techniques and a synthesis of phenology observations taken at Alexandra Fiord between 1994 and 2018, and through a multivariate analysis of growth and reproductive chronologies representing both experimental and non-experimental circumpolar field sites. The research gaps outlined in section 1.2 are addressed through the investigation of the following research questions:

1. *What is the effect of long-term experimental and ambient warming on the growth and reproductive efforts of Cassiope tetragona, from before the establishment of the warming experiment to the present day at Alexandra Fiord?*

**Hypothesis:** Because we know the plant is sensitive to temperature variability, we expect that the growth and reproductive efforts of *C. tetragona* have been accelerated by experimental warming, and that there is likely to be a trend toward greater growth over time as the local climate at Alexandra Fiord warms.

2. *How does Cassiope tetragona's growth and reproductive response to experimental warming vary spatially across the Arctic?*

**Hypothesis:** We expect the growth and reproductive response to temperature enhancement to have been the greatest in the coldest sites; and that differences in growth and reproductive patterns will be related to the regional gradients in temperature.

## 1.4 Methods and Materials

### 1.4.1 Study Site

Alexandra Fiord (78°53' North, 75°55' West) on Ellesmere Island (Nunavut, Canada) is considered to be a High Arctic 'polar oasis', with relatively high plant productivity and a higher diversity in contrast to the surrounding 'polar desert', despite short and cool growing seasons (Freedman et al., 1994). Temperatures reach above freezing from May to mid-August, with peak temperatures occurring in June and July (Labine, 1994). As this is the longest running ITEX site (established in 1992), this study examines 27 years of experimental warming at multiple tundra plant communities containing *C. tetragona*. Other samples were obtained from ITEX researchers working at a number of other experimental and non-experimental sites across the Arctic (Figure 1.1). In addition, samples of *C. tetragona* from OTC and control plots at other ITEX sites were collected to examine regional differences along climatic gradients (Research Question 2).

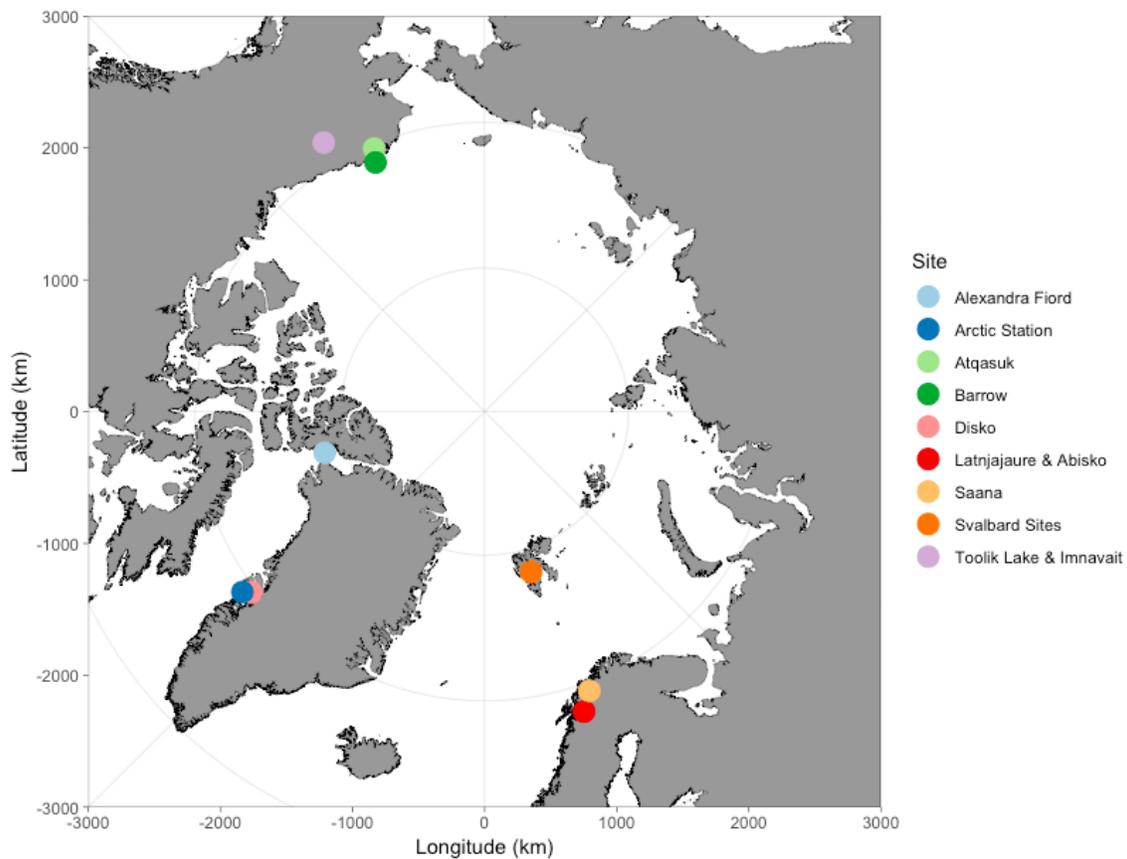


Figure 1.1 - Samples collected at field sites between July-September 2018. Sites that include OTCs: Alexandra Fiord, Atqasuk, Barrow, Toolik Lake, Imnavait Creek & Latnjajaure.

### 1.4.2 *Cassiope tetragona* Species Description

*Cassiope tetragona* (L.) D. Don (*Ericaceae*), or ‘Arctic white heather’, is an evergreen dwarf-shrub common in snowbeds and acidic soils throughout circumpolar and Alpine regions (Hulten, 1968). The plant is common throughout Arctic tundra ecosystems, particularly in mixed and dwarf-shrub heath vegetation communities (Bliss & Matveyeva, 1992), grows extensive branches to form sprawling mats, with stems often producing two or more bell-shaped flowers, which then form upright fruit capsules towards the end of the growing season (Sørensen, 1941; Aiken et al., 2007) and can live 100+ years (Rayback & Henry, 2006). As detailed by Callaghan et al. (1989), *C. tetragona* exhibits annual wave-like patterns in leaf length, with the shortest set of leaves representing the end of a growing season. This pattern is reflected by both the wave-like pattern between leaf scar internodes (Johnstone & Henry, 1997) and through the presence of wintermarksepta on a stem cross-section (Rozema et al., 2009). In a study at Alexandra Fiord, Nams & Freedman (1987) reported an annual shoot growth of 3.6 mm. In addition to the sensitivity to temperature and light as demonstrated by dendrochronological studies, *C. tetragona* also shows delayed phenological responses to experimentally delayed snowmelt and thus potentially decrease the overall growing season length for the plant (Mallik et al., 2011), though this prolonged snowpack could potentially serve to increase soil nitrogen availability and protect the shrub under projected deeper snow in the High Arctic (Blok et al., 2015).

### 1.4.3 Fieldwork Description

Field-based data collection included three components: phenology observations and stem harvests from Alexandra Fiord, and stem harvests from other ITEX sites. In 2018, at five experimental sites at Alexandra Fiord (named ‘Cassiope’, ‘Dryas’, ‘Vaccinium’, ‘Migration’, and ‘Annex’, see Table 1.1), phenology was recorded every three days by detailing the flowering stage of five tagged *C. tetragona* stems from different individual plants in each of the control and treatment plot pairs, and 2-3 randomly selected stems per plot that were temporarily tagged and harvested for dendrochronology analysis. The recorded stages were bud break, date of first mature flowers, flower senescence and fruit maturation, in line with phenology protocols followed by researchers at the site from 1994-2018. Additionally, in mid-July the prominent first leaves of the growing

season were marked on each tagged stem using water soluble acrylic paint and annual growth from those markers to the tip of the stem were recorded using digital callipers in the second week of August to obtain annual growth estimates for the tagged stems over the monitoring period. Together, these data provide information about the 2018 summer season growth rate and reproductive effort of *C. tetragona* in both OTC and control plots, allowing us to obtain average characteristics of plots from both long-term tagged stems and those selected for harvesting.

**Table 1.1 - Alexandra Fiord Site Descriptions**

Site Name	Soil Moisture	Vegetation Classification*	Dominant Plant Species
Cassiope	Dry-Mesic	Prostrate dwarf-shrub herb tundra	<i>C. tetragona</i> , <i>D. integrifolia</i> , <i>S. arctica</i>
Dryas	Mesic	Prostrate dwarf-shrub herb tundra	<i>D. integrifolia</i> , <i>Arctagrostis latifolia</i>
Vaccinium	Mesic	Dwarf-shrub, cushion plant	<i>V. uliginosum</i> , <i>D. integrifolia</i> , <i>C. tetragona</i> , <i>S. arctica</i>
Migration	Mesic-Wet	Deciduous shrub	<i>S. arctica</i> , <i>C. tetragona</i>
Annex	Mesic-Wet	Prostrate dwarf-shrub herb tundra	<i>C. tetragona</i> , <i>D. integrifolia</i> , <i>S. arctica</i>

[\*Walker et al., (2006)]

At the end of the growing season, three long, non-deformed stems were selectively harvested from three individual plants per OTC and control plot via a hierarchical sampling regime. We selected stems which would optimise the standard dendrochronology methodology, although we acknowledge that selecting only the dominant stems introduces selection bias. The stems were air-dried, stored in labelled paper bags and returned to the laboratory at the end of the field season. A number of samples were straightened via storage in plastic drinking straws. Following identical protocols, our collaborators collected long stems from *C. tetragona* plants in their OTC and control plots at the additional ITEX sites, stored them in airtight bags, and shipped them to UBC at the end of the field season. These stems were processed alongside the Alexandra Fiord samples to provide data for the analysis of Research Question 2.

#### 1.4.4 The BACI Design

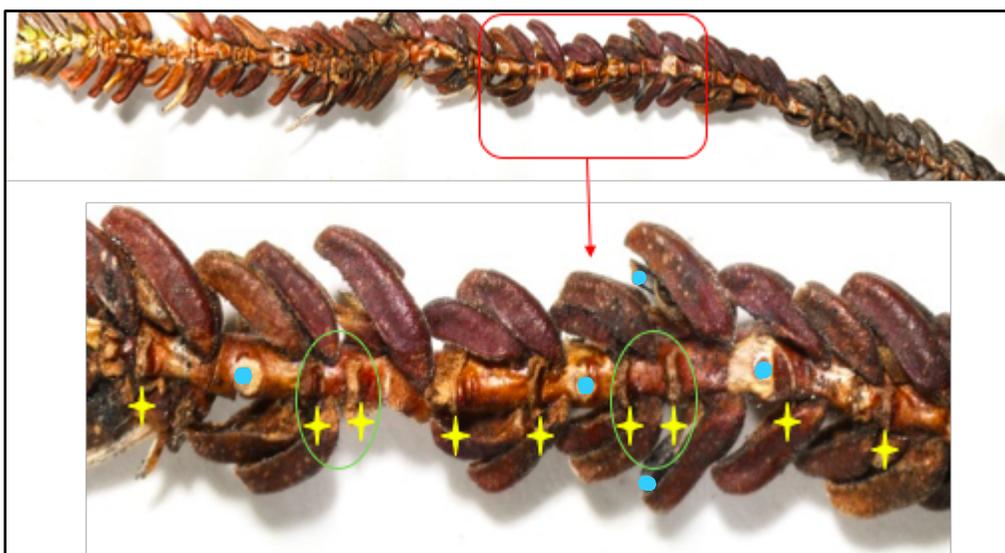
This research loosely follows a Before-After-Control-Intervention (BACI) research model. Designed by Green (1979), this methodology allows for the comparison of change in a system before and after a known impact. Furthermore, Stewart-Oaten & Bence (2001) coined the

‘Intervention Analysis’ approach, which applies the BACI approach to a time series attributed to a single site. BACI can be achieved by comparing the relative contribution of experimental warming on the growth of samples from OTC plots in comparison to those in unperturbed control plots. Additionally, as the OTC installation dates are known at each ITEX site, it is possible to use the BACI design (through Intervention Analysis) to compare growth parameters from before experimental warming to the present day. These parameters have been compared against *C. tetragona* growth in control plots. While Molau (1997), Rayback (2003) and Rozema et al. (2009) applied small-scale BACI analyses to single-site studies, there has not yet been an attempt to conduct a longer-term retrospective analysis on the impact of experimental warming on *C. tetragona* growth and reproduction metrics. Furthermore, we apply this research framework to samples from multiple sites across the Arctic, thus investigating potential geographical controls of stem growth.

#### **1.4.5 Laboratory Work - The Dendrochronology Approach**

Annual growth increments of samples were measured from the tip of the stem (representing 2018 summer growth) to the base. The stems were mounted to grooved wooden blocks and scanned to a high resolution (2400 dpi) to a computer using an Epson Perfection V800 Photo STD 4800 scanner. The measurements were taken by processing the stem image using the software Cybis CooRecorder (Larsson 2016). The shortest distance (or the shortest internode) between the leaf scars was taken to represent the end of the growing season and thus, the end of a year’s growth increment (Figure 1.2). Evidence of flowering are preserved stalks or pits where stalks once protruded from the stem, while aborted buds (which did not produce stalks and flower by the end of the growing season) are preserved on the stem as dry round mounds in close proximity to any flower peduncles which may be present for that given year. The aborted bud chronologies were included in this study as they are an additional expression of the plant’s reproductive effort and their abortion may be correlated with local climate conditions. Each annual stem growth increment was logged on a database alongside a count of aborted flower buds and flower peduncle scars, with their position on the stem recorded to match flowering patterns by year. The reproductive chronologies are expressed in this thesis as “Annual Flower Occurrence” (a standardised index of

# flowers per year) and “Annual Bud Occurrence” (a standardised index of # aborted buds per year). Cross-dating of the growth and reproductive chronologies was aided by the production of skeleton plots, following the methodology outlined by Stokes & Smiley (1968), and the analysis of covariance between annual growth increments of multiple samples, as described by Fritts (1976) and aided by the Cybis CDendro software. The cross-dated individual chronologies were then detrended and mean chronologies were built for each of the field sites and treatment types (see 1.4.6.2).



**Figure 1.2 - Scanned Image of a section of a stem sample. Leaf scars marked in yellow, shortest internode distances (end of a growing season) marked in green circles. Flower peduncle scars and stalks marked by blue circle.**

## **1.4.6 Statistical Processing**

### **1.4.6.1 Phenology**

To explore the relationship between phenology stages and air temperature at Alexandra Fiord over the observed period (1993-2018, although the chronology includes some missing years), we examined the range of dates from archived field records for the first occurrence of each of the following phenology stages: flower bud emergence, first flower, flower senescence, and the formation of immature upright fruit capsules. Spearman’s rank-order correlation analysis was used to determine the direction and strength of the relationship between these reproductive stages and summer air temperatures. Following this, simple ordinary least squares models were run using

flowering date as a response variable and mean June air temperature (following Panchen & Gorelick [2017]) as the explanatory variable to determine the extent to which the date of first flower emergence can be predicted by local climatic conditions (recorded from the Alexandra Fiord Meadow climate station, which is an automatic station recording daily air temperature 1.5 metres from the ground) within the vicinity of the experimental sites.

#### **1.4.6.2 Standardisation**

As described by Fritts (1976), standardisation of multiple dendrochronology time series is required to counter intra-sample variability in growth parameters caused by factors such as age and to aid comparison between chronologies, and is usually achieved by fitting the multiple tree ring chronologies to a detrending curve or straight line fit to produce an index against which multiple chronologies could be compared. The process of autoregressive standardisation was run through the `dplr` package in R (Bunn, 2008) to produce standardised, detrended chronologies by dividing the AGI measurements by the detrending curve. The chronologies were also pre-whitened to remove any low-order autocorrelation within the individual stem chronologies. The individual chronologies were averaged into master chronologies representing each site and treatment type through the use of Tukey's bi-weight robust mean (i.e. a robust, standardised index chronology which is not affected by the presence of outliers). The standardised index chronologies are herein referred to as Stem Length Index, Average Flower Occurrence and Average Aborted Bud Occurrence.

#### **1.4.6.3 Response Function Analysis and Calibration Modelling**

Response function analysis was completed through the use of `bootRes`, an R package that uses functions from the original `DendroClim` software, which indicates the highest responses of the growth and reproductive chronologies to various matrices and potential air temperature variables collected from 1988-2018 at Alexandra Fiord, split by month into average and maximum temperature values. This analysis identified suitable local climate time series with which to develop climate reconstruction models, which provide a good measure of the extent to which the growth and reproduction of the plant is sensitive to summer air temperature. In line with previous studies (Johnstone & Henry, 1997; Rayback & Henry 2005; Rayback & Henry 2006; Rayback et

al., 2012), the flowering and aborted bud chronologies were lagged backwards by 1 year (t-1) as bud formation in *C. tetragona* begins in the summer of the previous year (Sørensen 1941). The stepwise multiple linear regression model included the observed climate time series as the dependent variable, and the growth and lagged reproductive chronologies as explanatory variables. Growth-temperature transfer functions were identified through the predictive models to relate stem growth to summer temperature, a key step in the reconstruction of temperature changes over many years aided by the calculation of response functions between AGI measurements and available climate data for the study period. For example, Rozema et al. (2009) identified transfer functions using a model of recorded summer temperature against multiple parameters of plant growth to infer a temperature increase of 0.35°C for every extra 1 mm of stem growth. After plotting the modelled climate data alongside the observed climate data, we used verification tests (Coefficient of Estimation, Reduction of Error, Signs Test) to investigate the predictive skill of the selected model.

We also compiled monthly average surface air temperature data for June, July and August from 1992-2018, recorded using 'HOBO' temperature loggers which were placed in central positions in nine control and OTC plots in the Cassiope site. These chronologies were used to investigate the correlation of stem growth and reproductive characteristics of plants under experimental warming, as the air temperature data collected from the Meadow Station tower does not capture the amplified warming effect of treatment. Furthermore, we also built calibration models for the July and August average surface temperature data using the stem length and reproductive chronologies from the 'Cassiope' site treatment plots.

#### **1.4.6.4 Effect Size Analysis**

Effect size analysis is a mode of comparison between treatment and control variables within an experiment as a means to ascertain the scale and direction of change as a result of manipulation. It is an especially powerful mode of comparison between geographically different experimental sites because field protocols, length of experiment and site conditions differ, and it represents a standard metric of change, which can be classified as 'Negligible', 'Small', 'Medium' or 'Large', and both positive and negative. As such, this is a common statistical tool for meta-analysis studies, and is

prominent in a number of tundra ecology synthesis studies (e.g. Walker et al. 2006; Henry et al. 2013; Elmendorf et al., 2015).

#### **1.4.6.5 Linear Mixed Effects Model**

Growth and reproduction parameters for the experimental sites were compiled alongside local summer temperature records, from the UEA Climate Research Unit (CRU) 0.5° TS 4.03 monthly air temperature grid. These parameters were used to develop a linear mixed effects model to analyse the strength of the relationship between stem growth chronologies at each site and ascertain the influence of warming experiments on annual stem growth. The hierarchical nature of the linear regression model allowed for a division of the error terms by levels of the sampling hierarchy. We selected stem growth as the independent variable, with local July Average Temperature and Experiment (Control vs OTC) as fixed effects (explanatory) variables. Furthermore, 'Region' and 'Site' were included as random effects variables.

#### **1.4.6.6 Principal Components Analysis**

As an additional step for Research Question 2, Principal Components Analysis (PCA) was used as a means to conduct multivariate analysis on the growth and reproductive time series for each of the additional circumpolar sites. PCA operates by orthogonally transforming complex multivariate datasets and ranking the variables from the highest to lowest contributors of variance within the data. This process was used to identify 'clusters' of growth and flowering behaviour and investigate the extent to which this clustering is controlled by geographical differences, or environmental characteristics such as soil moisture. Furthermore, a bootstrap analysis was included to identify the statistical significance and strength of the contribution of each variable to either the primary or secondary principal components.

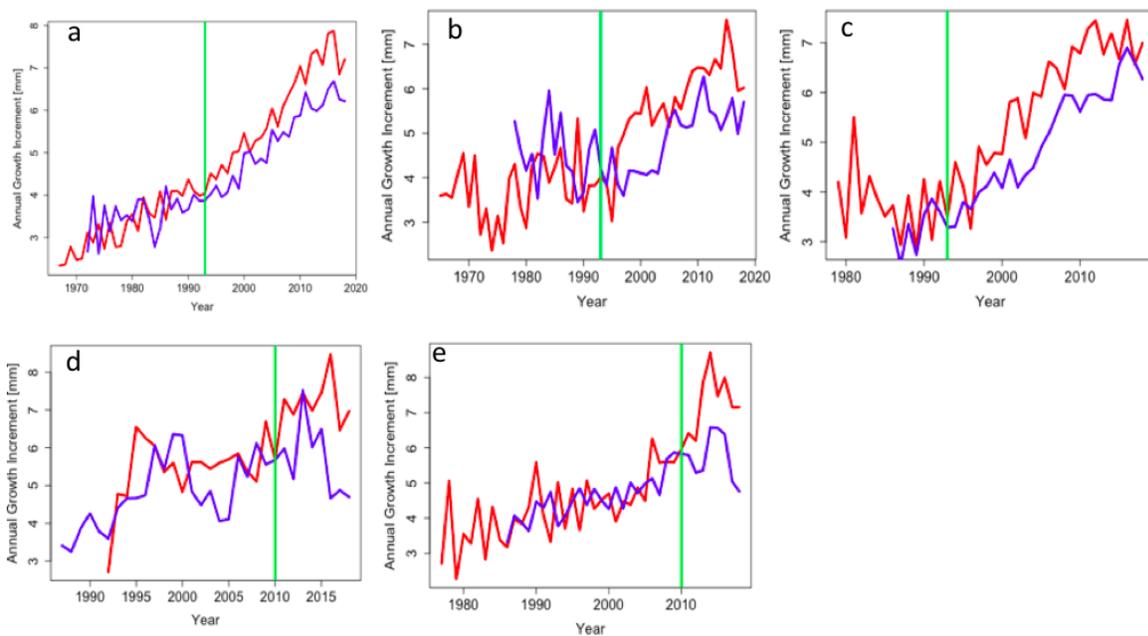
## Chapter 2: Analysis of the Alexandra Fiord Chronologies

### 2.1 Results

#### 2.1.1 Alexandra Fiord Stem Growth Chronologies

##### 2.1.1.1 Stem Growth Chronologies

Prior to standardisation, the individual raw stem annual growth increments were averaged into master chronologies. Overall, 210 *C. tetragona* stems were collected from Alexandra Fiord (control  $n = 98$ , treatment  $n = 112$ ), covering 50 control plots and treatment plots pairs (100 plots overall) at five long term sites: ‘Cassiope’, ‘Dryas’, ‘Vaccinium’, ‘Migration’ and ‘Annex’ (Table 2.1). The chronologies span the period between 1964 and 2018, with an average chronology length of 40 years. The longest stem (54 years) was collected at the Dryas Site, Treatment Plot 2.

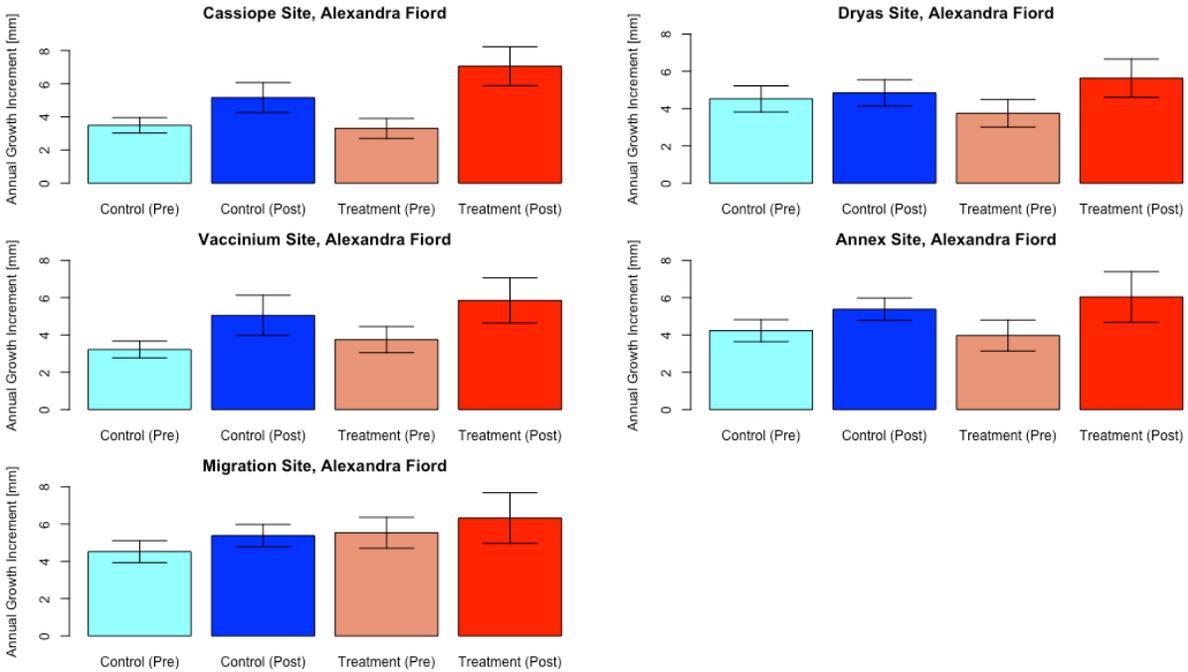


**Figure 2.1 - Annual chronologies of raw stem growth by treatment (red) and control (blue) averaged master chronologies by year. Onset of experimental warming marked by green. a) Cassiope Site, b) Dryas Site, c) Vaccinium Site, d) Migration Site, e) Annex Site.**

**Table 2.1 - Descriptive statistics for each of the control and treatment master chronologies**

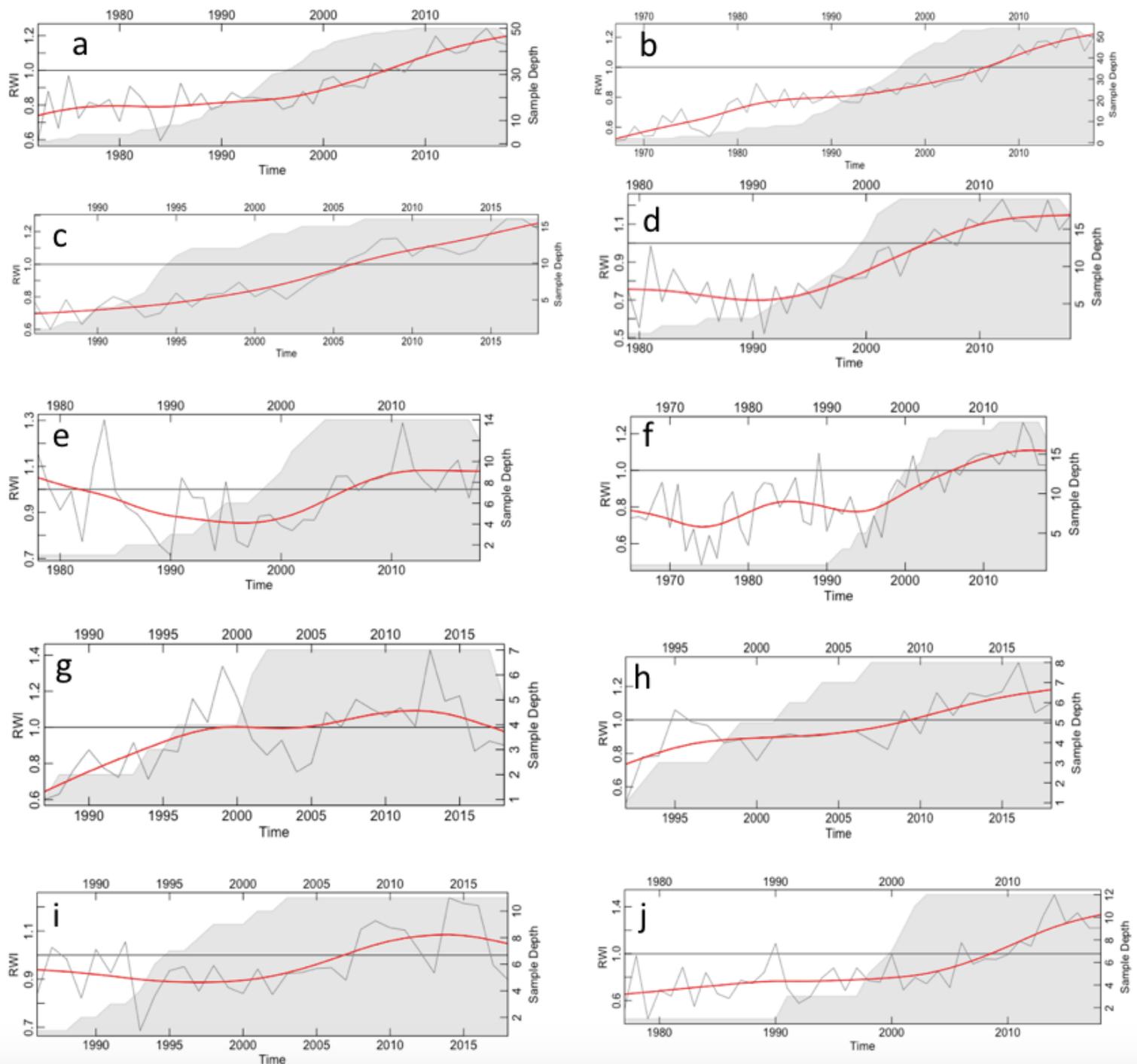
Site / Treatment	Chronology Length (Years)	Stems n =	Plots n =	Mean Interseries Correlation [ $\bar{r}$ ] (and SD)
Cassiope Control	42	50	18	0.23 (0.20)
Cassiope Treatment	52	54	18	0.29 (0.21)
Dryas Control	42	14	10	0.18 (0.24)
Dryas Treatment	54	19	10	0.12 (0.24)
Vaccinium Control	33	16	10	0.20 (0.22)
Vaccinium Treatment	40	19	10	0.14 (0.16)
Migration Control	32	7	6	0.27 (0.23)
Migration Treatment	27	8	6	0.11 (0.27)
Annex Control	33	11	6	0.03 (0.21)
Annex Treatment	42	12	6	0.19 (0.15)

The raw ring width (non-standardised) master chronologies generated for each site show increasing growth increments over both control and treatment plots. The mean stem growth between the control and treatment samples at all sites diverged after the implementation of the OTCs in 1992 (Cassiope, Dryas, Vaccinium) and 2010 (Migration, Annex), though a general positive (warming) trend is still evident among controls (Figure 2.1, Figure 2.2). However, these non-standardised chronologies are not detrended and the positive trend is likely influenced to some extent by the juvenile growth effect of the stems, whereby very young stems appear to grow more slowly and do not produce buds. This effect has not yet been quantified, although Rayback & Henry (2005) reported that is likely ~10-15 years before a *C. tetragona* plant is able to produce flowers. The mean difference in growth between the non-experimental (pre-OTC) and experimental (post-OTC) period was +1.16 mm for stems in the control plots, and +2.12 mm for stems in the treatment plots.



**Figure 2.2 - Plots of the cross-dated chronologies of annual growth of *C. tetragona* stem samples from control and warming treatment plots at the experimental sites at Alexandra Fiord, pre OTC and post OTC implementation (1992)**

When standardised and averaged into master chronologies, the time series (Figure 2.3) reveal a gradual increase in annual stem growth between 1965 and 2018, though with a more gradual incline than the raw chronologies (Figure 2.1) due to the removal of the juvenile growth trend. There appears to be a plateau in growth during the period 1990-2000, particularly evident in the control and treatment chronologies from the ‘Dryas’, ‘Migration’ and ‘Annex’ sites. The mean interseries correlation ( $\bar{r}$ ) is a measure of a common signal across individual stems within a chronology. This measure is low across the treatments and sites (ranging 0.033 - 0.29), though this is characteristic for the proxy as it exhibits considerable intra-plant variability. Autocorrelation (AR1) is the measure of similarity between steps along a time series and indicates some correlation between annual growth increments by time across the treatments and sites (0.182-0.422) (Table 2.2).



**Figure 2.3 - Detrended & standardised master annual stem growth index chronology, averaged using Tukey's biweight robust mean, plotted against a cubic smoothing spline (red line) of 20 years: a) Cassiope Control, b) Cassiope OTC, c) Vaccinium Control, d) Vaccinium OTC, e) Dryas Control, f) Dryas OTC, g) Migration Control, h) Migration OTC, i) Annex Control, j) Annex OTC. Shading represents the sample depth for each chronology.**

**Table 2.2 - Average annual growth increments and standard deviations (SD) in the pre- and during-experimental periods.**

Site / Treatment	Pre-Experiment AGI Mean (mm)	SD	During Experiment AGI Mean (mm)	SD
Cassiope Control	3.49	0.46	5.16	0.9
Cassiope Treatment	3.3	0.6	7.06	0.19
Dryas Control	4.52	0.7	4.84	0.71
Dryas Treatment	3.75	0.74	5.63	1.03
Vaccinium Control	3.22	0.45	5.05	1.08
Vaccinium Treatment	3.75	0.7	5.85	1.21
Migration Control	4.52	0.95	5.38	0.92
Migration Treatment	5.53	0.79	6.32	0.99
Annex Control	4.23	0.59	5.38	0.6
Annex Treatment	3.97	0.83	6.04	1.36

### 2.1.1.2 Before-After-Control-Intervention

The new BACI metrics proposed by Chevalier et al. (2018) were used to analyse aspects of the difference between the before- and during- experimental periods between control and treatment plots. *Control-Impact Contribution* represents the absolute value in the change in mean between the pre-experimental and experimental period, and between the treatment and control chronologies. If CI Contribution is positive, we would assume that the change in growth at treatment sites from the non-experimental to experimental periods is higher (and the impact stronger) than the change seen at the control sites. At each site at Alexandra Fiord, the CI contribution is positive, indicating that stem growth in the treatment sites is consistently more strongly impacted by warming than the ambient change seen in the control chronologies. The average CI contribution across sites was 9.02 mm, with the highest values at ‘Migration’ (9.36 mm) and ‘Cassiope’ (9.08 mm) and the lowest values at ‘Dryas’ (5.23 mm) and ‘Vaccinium’ (4.13 m) (Table 2.3).

The second metric, *Control-Impact Divergence*, is a measure of dissimilarity between the treatment and control chronologies, compared between the experimental and non-experimental period (Chevalier et al., 2018). Positive CI Divergence values provide evidence of divergence between the OTC and control plots since the date of establishment for the warming experiments.

At each site except ‘Dryas’ (CI Divergence = - 1.16 mm), CI Divergence was positive. The average CI Divergence across sites was 12.02 mm, though there was considerable variation across sites in this metric (‘Cassiope’ = 4.88 mm, ‘Vaccinium’ = 4.13 mm, ‘Migration’ = 40 mm, ‘Annex’ = 12.25 mm) (Table 2.3).

**Table 2.3 - Control-Impact Contribution & Control Impact Divergence Metrics for annual growth chronologies of *Cassiope tetragona* at Alexandra Fiord**

Site	CI Contribution (mm)	CI Divergence (mm)
Cassiope	9.08	4.88
Dryas	5.23	-1.116
Vaccinium	4.13	4.13
Migration	9.36	40.0
Annex	17.32	12.25
Average	9.02	12.02

Two-sample t-tests were also performed to determine the difference between the control and treatment stem growth chronologies at every site (**Error! Reference source not found.**). On average, across Alexandra Fiord, the difference between the treatment and control samples were larger during the experimental period (M = 9.08 mm) in comparison to the “before” / non-experimental period (M = 0.189 mm). At every site except Vaccinium, a two-sample t-test indicated this difference in means to be statistically significant at the  $p < 0.05$  level. This is strong evidence of the stems growing longer as a direct result of the amplified warming effect of treatment, although the effect obviously varies from site to site. Furthermore, these results reflect the CI Contribution metrics generated for each site, whereby there was a large divergence at all sites except the Vaccinium site.

### 2.1.2 Alexandra Fiord Phenology

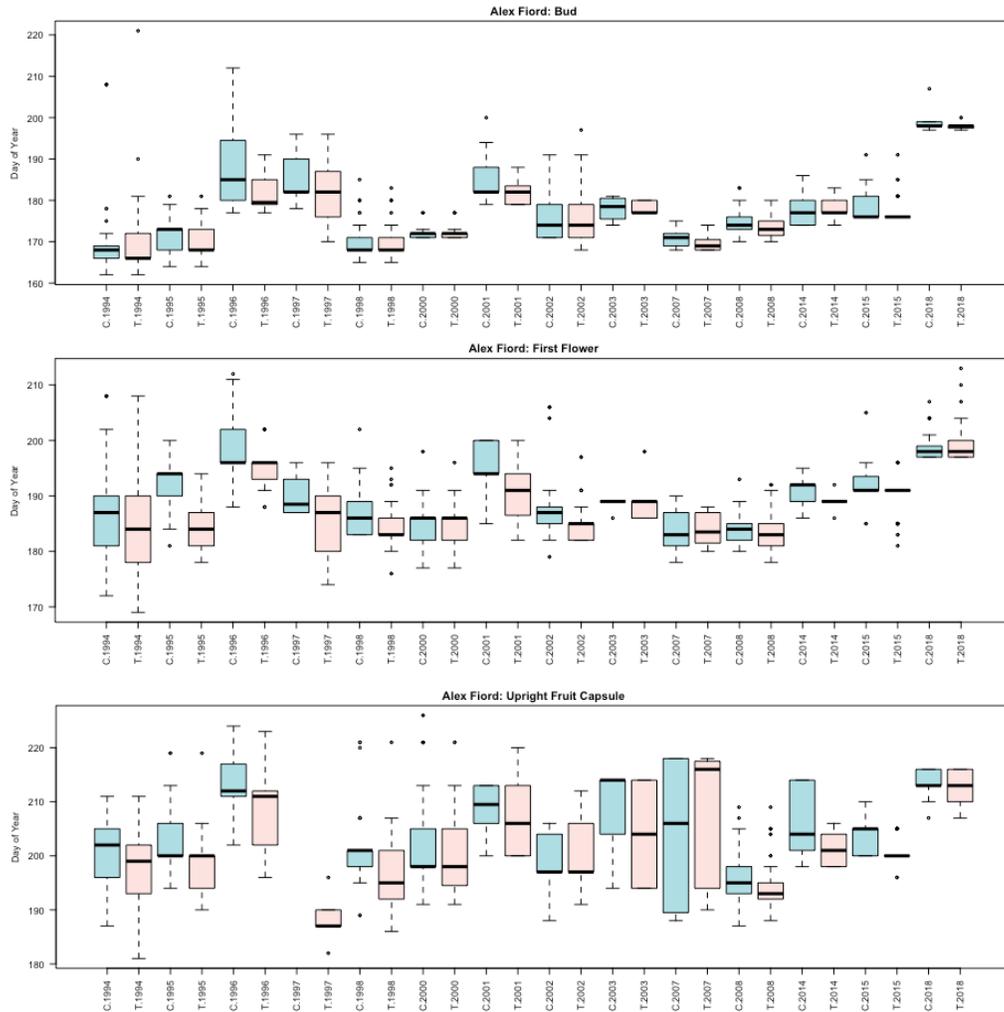
Two-sample t-tests were conducted to determine the difference between the date of phenology stages (bud-break, first flower, immature fruit capsule formation) across all control and treatment phenology measurements (averaged 1993-2018 phenology records collected at Alexandra Fiord at the Cassiope, Dryas and Vaccinium sites) (Table 2.4). At each phenology stage, there was a statistically significant effect at the  $p < 0.05$  level, with stages taking place between 1-2 days earlier in the treatment plots in comparison to the control plots.

**Table 2.4 - T-Tests for the annual average date of four phenology stages in and out of the OTCs at Alexandra Fiord (1993-2018)**

Phenology stage	Mean day-of-year in control plots	Mean day-of-year in warming treatment plots	T-value (Welch Two-Sample t-tests)	df
Bud Formation	177	175	4.6243**	792.71
Mature Flower	191	190	3.5337**	1030.7
Upright Fruit Capsule forms	203	201	2.97777**	713.25

*\*p < 0.05, \*\*p < 0.01*

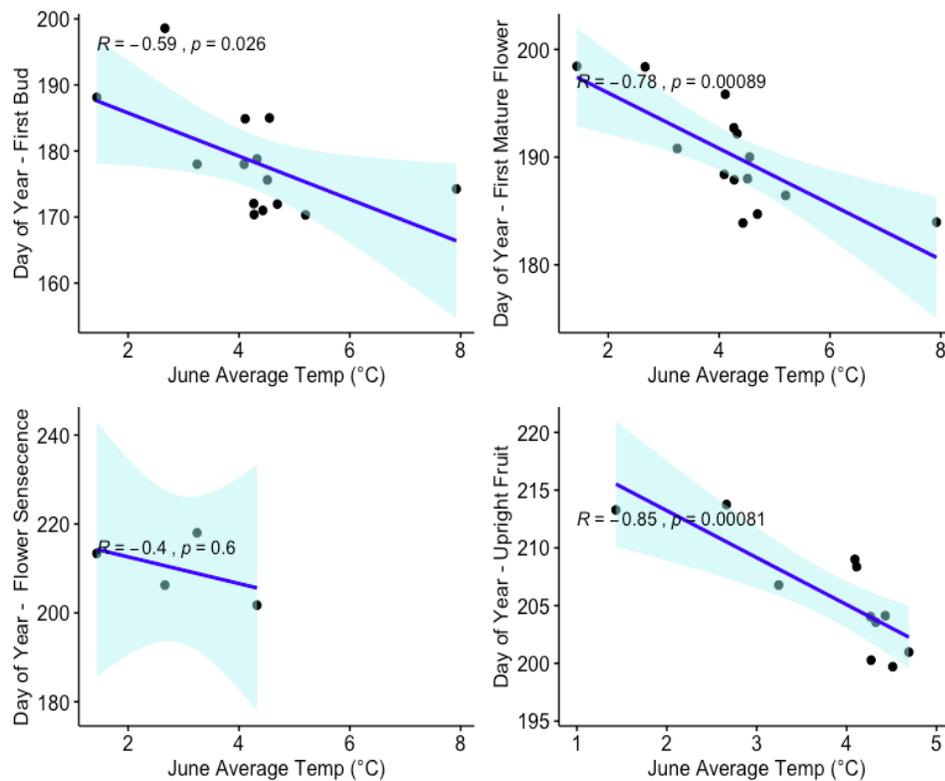
On average, bud break takes place two days earlier in the treatment plots than in the control plots ( $t = 4.62438^{**}$ ), first flowers appear one day earlier in the treatment plots than in the control plots ( $t = 3.5337^{**}$ ). Furthermore, formation of immature fruit capsules begins two days earlier in the treatment plots than in the control plots ( $t = 2.9777^{*}$ ). Thus, we can infer that the warming treatment is consistently triggering earlier reproduction across Alexandra Fiord, although this difference is only on average 1-2 days (up to 2.5% of the 80 day growing season). This relationship is found nearly every year (Figure 2.4), with earlier phenology stage dates in treatment plots than control plots.



**Figure 2.4 -Boxplots of the range of phenology stages by Day of Year. Control plots represented in blue, treatment plots represented in red.**

Using data from the control plots only, Spearman's rank-order correlation analysis was used to investigate the relationship between the timing of the reproductive stages between 1993 and 2018 and the average air temperature in June, measured from the Meadow climate station at Alexandra Fiord. The onset of first mature flowers ( $r = -0.78$ ,  $p = 0.009$ ) and the first immature upright capsules ( $r = -0.85$ ,  $p = 0.008$ ) exhibited a very strong negative relationship with June average air temperatures. Likewise, the timing of bud break exhibits a strong negative relationship with June average air temperature ( $r = -0.59$ ,  $p = 0.026$ ).

The onset of first mature flowers was used as a response variable in a simple ordinary least squares regression model using June average air temperature as an explanatory variable. This model predicted 52% of the variation in the timing of flowering averaged across all sites between 1993 and 2018 ( $\text{adj.}r^2 = 0.5211$ ,  $p = 0.002$ ). The same model was also applied using the first occurrence of immature upright fruit capsules as a response variable, with June average air temperatures predicting 70% of the variation in the timing of this reproductive stage ( $\text{adj.}r^2 = 0.7027$ ,  $p = 0.0002$ ).



**Figure 2.5 - Relationship between average timing of phenological stages and average June air temperatures.**

### 2.1.3 Alexandra Fiord Stem Chronology Characteristics

Pearson's product-moment correlation coefficient analysis was used to investigate the relationships between the stem growth, flower peduncle and aborted bud chronologies for the master treatment and control chronologies at the three long-term sites at Alexandra Fiord: 'Cassiope', 'Vaccinium' and 'Dryas' (expressed as standardised indices). Furthermore, in line

with previous findings (Johnstone & Henry, 1997; Rayback 2003; Rayback & Henry, 2005), the flower and aborted bud chronologies were lagged by one year (t-1), as they have been shown to be correlated highest with the previous years' summer air temperatures.

While relationship between annual stem growth and average flower occurrence (a standardised index of number of flowers per year, produced using the standardisation methods described in section 1.4.6.2) was positive at each of the long term sites at Alexandra Fiord (Figure 2.6), it was strongest at the 'Cassiope' site (control:  $r = 0.59$ ,  $p = 0.0031$ ; treatment:  $r = 0.62$ ,  $p = 0.000$ ). The 'Vaccinium' site showed a similarly strong positive correlation (control:  $r = 0.53$ ,  $p = 0.0035$ ; treatment:  $r = 0.41$   $p = 0.0035$ ). The 'Dryas' site treatment chronology also exhibited a strong positive correlation between the variables ( $r = 0.55$ ,  $p = 0.0004$ ).

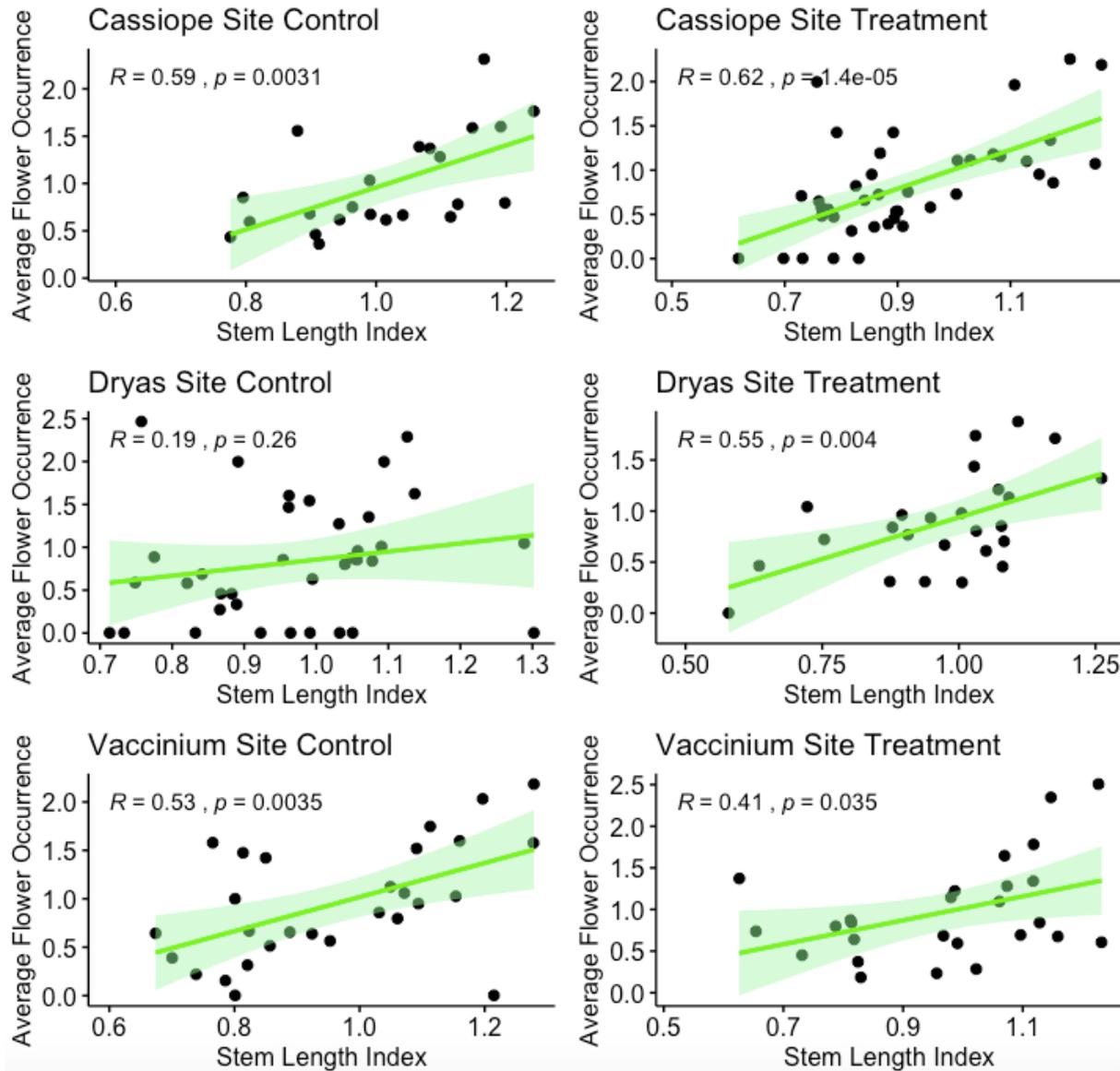
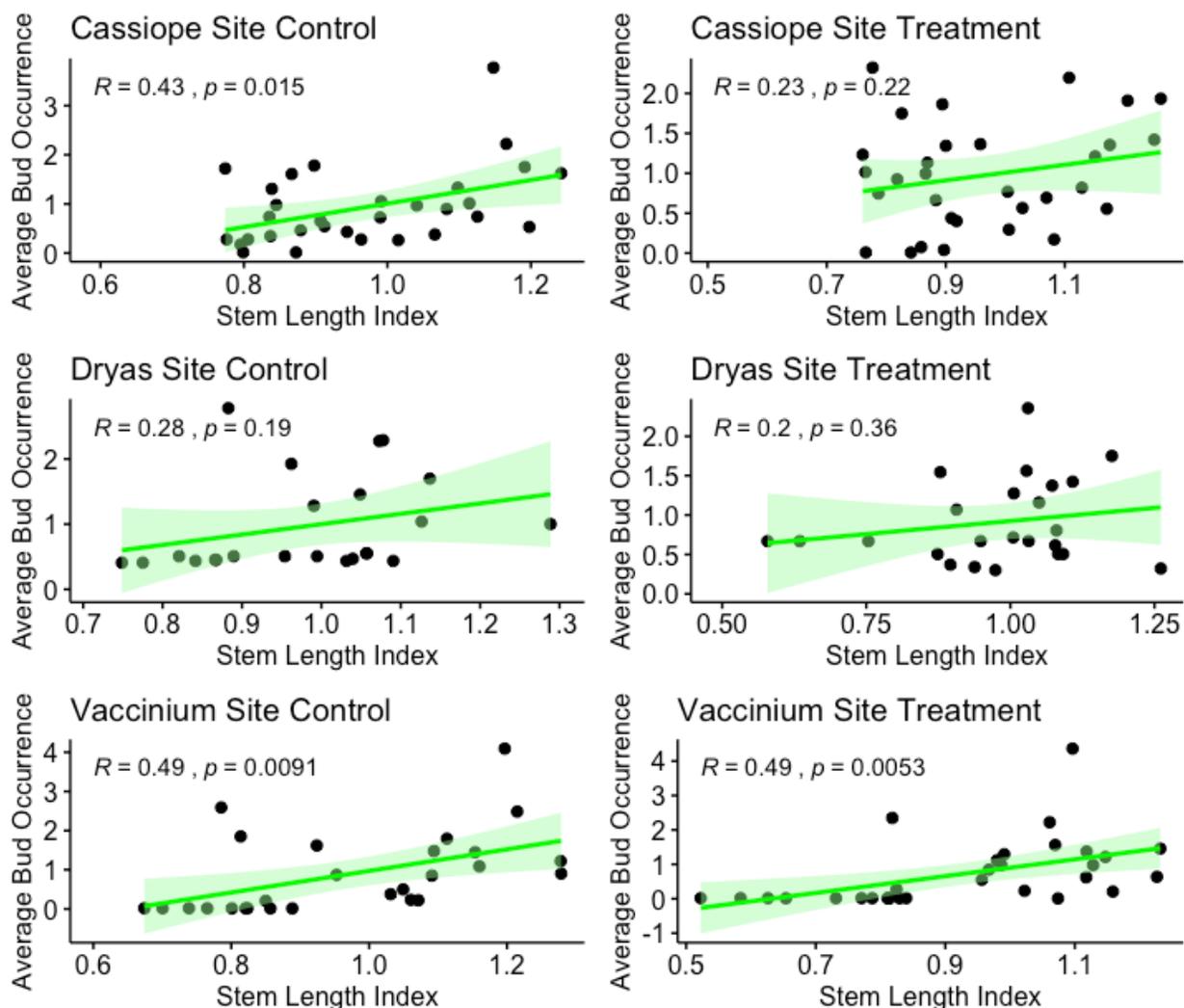


Figure 2.6 - Relationship between average annual flower occurrence and average stem growth ('ring width index') at the 'Cassiope', 'Vaccinium' and 'Dryas' sites at Alexandra Fiord 1964-2018.

The relationship between annual stem growth and average annual aborted bud occurrence was not as universally strong as was the relationship between stem growth and flowering, although there was at least a weak positive relationship at all of the long-term Alexandra Fiord sites (Figure 2.7). At each site, the control chronologies exhibited a slightly stronger relationship than the treatment chronologies. The strongest relationships were seen at 'Cassiope Control' ( $r = 0.43$ ,  $p = 0.015$ ), 'Vaccinium Control' ( $r = 0.49$ ,  $p = 0.0091$ ) and 'Vaccinium Treatment' ( $r = 0.49$ ,  $p = 0.0053$ ).



**Figure 2.7 - Relationship between average annual aborted bud occurrence and average stem growth ('ring width index') at the 'Cassiope', 'Vaccinium' and 'Dryas' sites at Alexandra Fiord 1964-2018.**

The interaction between annual aborted bud and flower occurrence (Figure 2.8) is of interest as these variables have previously been included in *C. tetragona* calibration models and correlations could determine whether to include an interaction term between the two chronologies, which would be interesting biologically as it may indicate a seed-setting strategy and allow us to build a fuller reproduction model than just including flowering and aborted buds as separate variables (Johnstone & Henry, 1997; Rayback 2003; Rayback & Henry, 2005; Rayback & Henry, 2006). There was a strong, positive and statistically significant relationship between the reproductive chronologies at the 'Cassiope' control ( $r = 0.59, p = 0.0032$ ) and treatment ( $r = 0.4, p = 0.024$ ) and

‘Dryas’ treatment ( $r = 0.57, p = 0.0039$ ) sites). Conversely, for the treatment and control ‘Vaccinium’ site chronologies, there was no strong or statistically significant correlation.

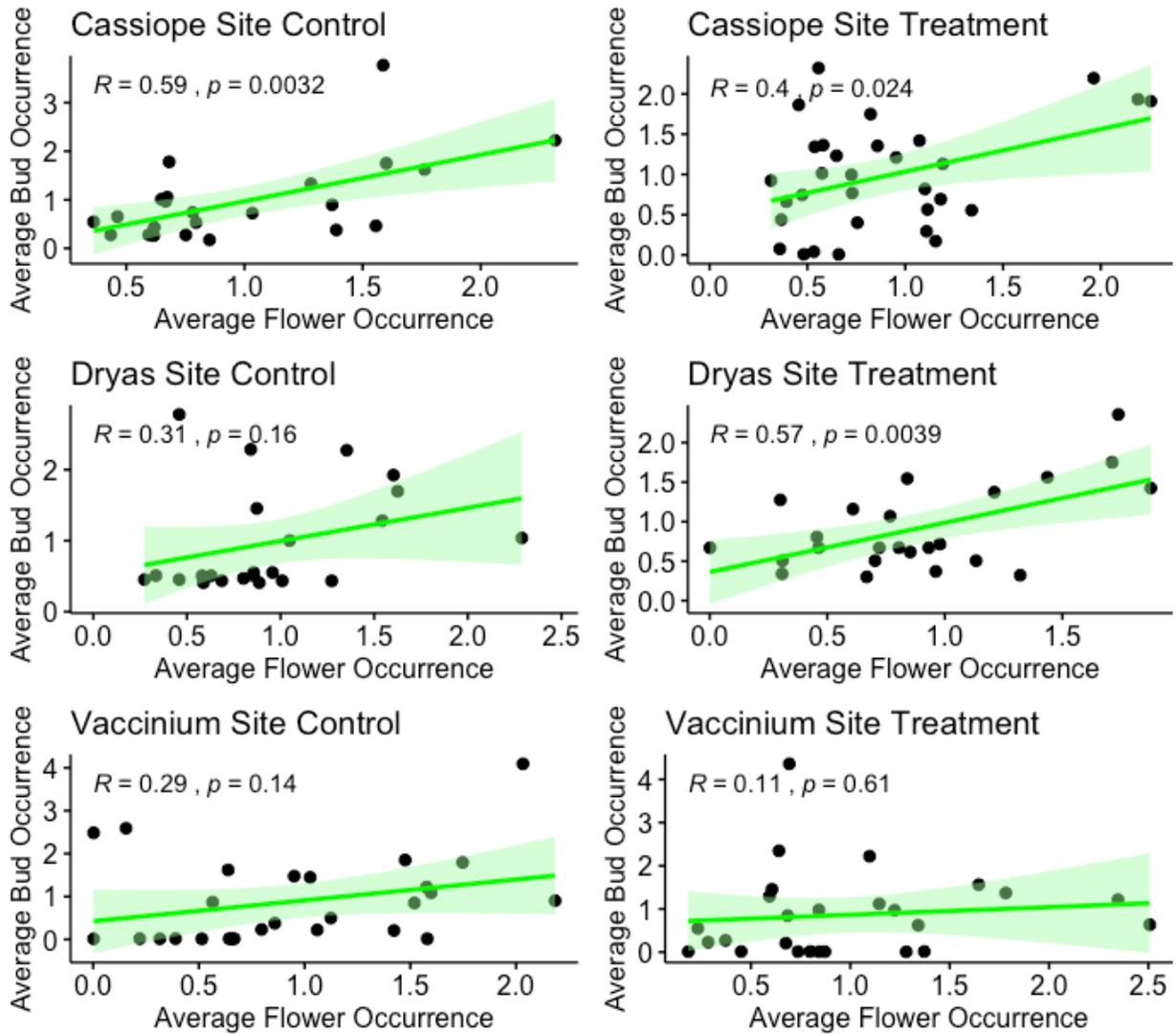


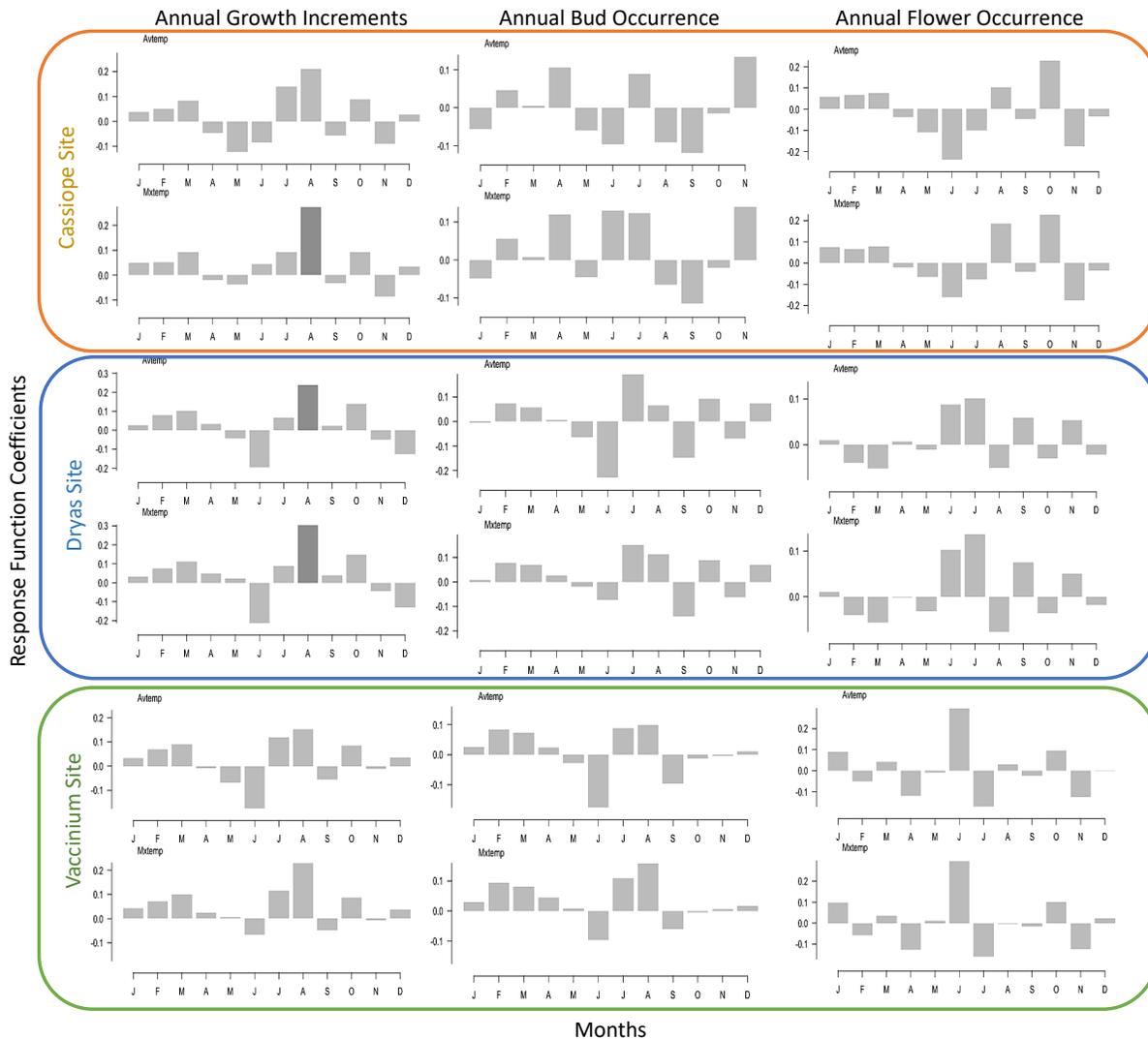
Figure 2.8 - Relationship between average annual flower occurrence and average aborted bud occurrence at the ‘Cassiope’, ‘Vaccinium’ and ‘Dryas’ sites at Alexandra Fiord 1964-2018.

## **2.1.4 Correlation of Climate, Growth and Reproductive Chronologies**

### **2.1.4.1 Response Function and Correlation Coefficients for Control Plots**

Response function coefficients were calculated for each month using stem growth and reproductive individual time series chronologies of the control plot chronologies as the dependent variable, and monthly average and maximum temperature values as explanatory variables. Cassiope site stem growth, flower peduncle and aborted bud chronologies exhibited few monthly significant response function coefficients ( $p < 0.05$  level) (Figure 2.9). Over the course of the year, there appeared to be a negative relationship between each of the chronologies in late spring and early summer (April - June), while the relationship between temperature and growth appeared positive, but low, over the course of winter. There were distinct peaks in summer (the June-August growing season) though the response function values remained below 0.3 for each of the chronologies.

The only significant response functions were for stem growth at the ‘Cassiope’ and ‘Dryas’ sites, for August maximum and August average air temperature. Furthermore, August maximum temperature consistently yielded the greatest response for each of the annual stem growth chronologies. Conversely, the highest response for the aborted bud chronologies was June average air temperature at all sites, while the optimal air temperature varied for flowering (t-1) across each of the sites (‘Cassiope’ = November Maximum [ $r = 0.15$ ], ‘Vaccinium’ = June Average [ $r = 0.31$ ], ‘Dryas’ = August Maximum [ $r = -0.106$ ]). Overall, while response function values were low across chronologies, aborted bud occurrence (t-1) seems to be influenced the most by average June temperatures, while stem growth appears to be influenced the most by the warmest days in August.



**Figure 2.9 - Response function analysis for stem, aborted bud and flower chronologies (columns) at three long term sites at Alexandra Fiord by monthly average and maximum air temperature (top and bottom rows for each site). Darker shaded bars signify statistical significance at the  $p < 0.05$  level.**

Pearson's Product Moment correlation analysis was also conducted for each month using stem growth and reproductive individual time series chronologies of the control plot chronologies as the dependent variable (Figure 2.10), and monthly average and maximum temperature values as explanatory variables to select the months appropriate for further examination in section 2.1.4.2. Annual growth increment chronologies responded most positively and significantly ( $p < 0.05$  level) to monthly mean and maximum air temperatures, and were most positively correlated for the July and August average and maximum air temperatures across each of the three sites. There

were only statistically significant relationships for the aborted bud chronologies for Cassiope Site average temperature June records, and Dryas Site July maximum temperature records. Finally, the only statistically significant relationships for the flowering chronologies were at the ‘Dryas’ (July average and maximum air temperature) and ‘Vaccinium’ sites (January, February and March average and maximum air temperatures).

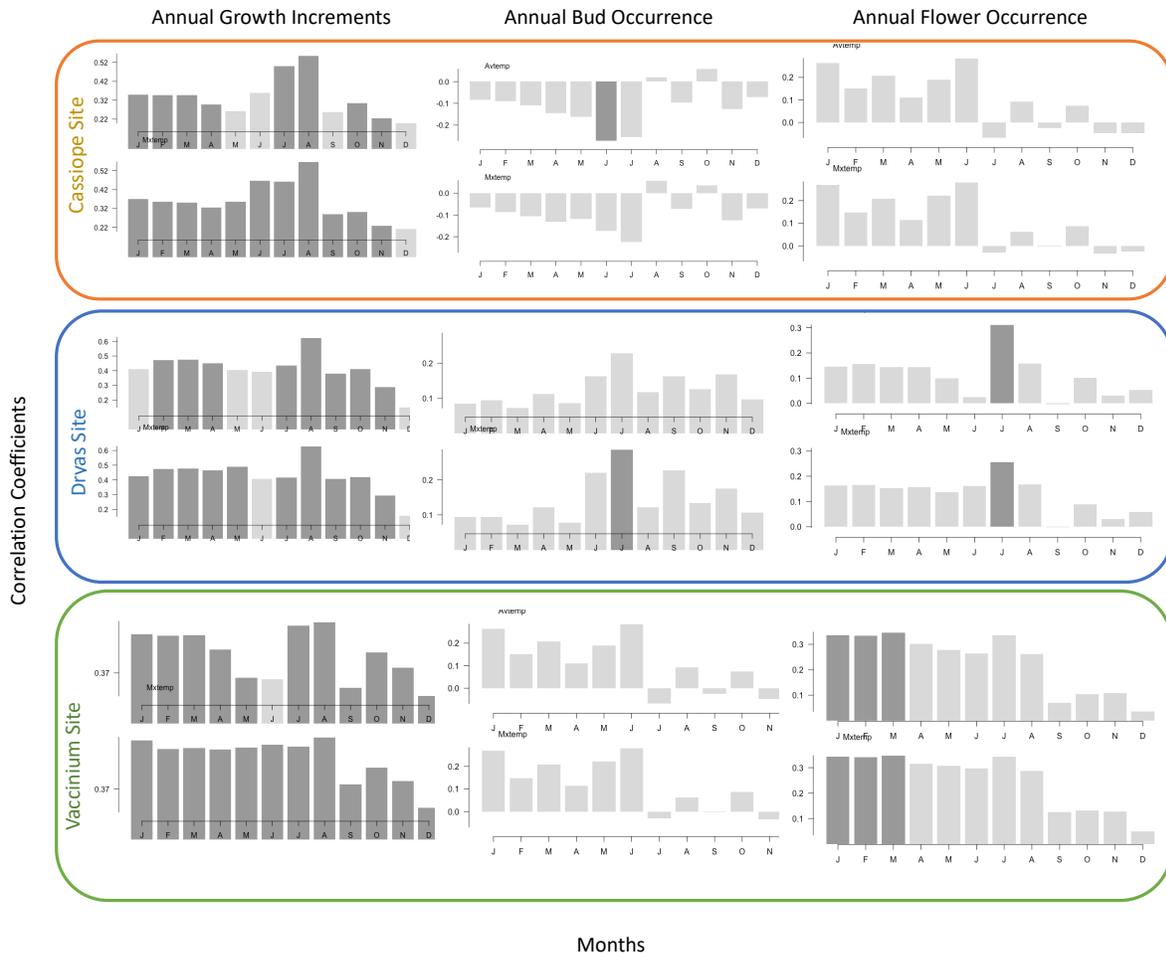
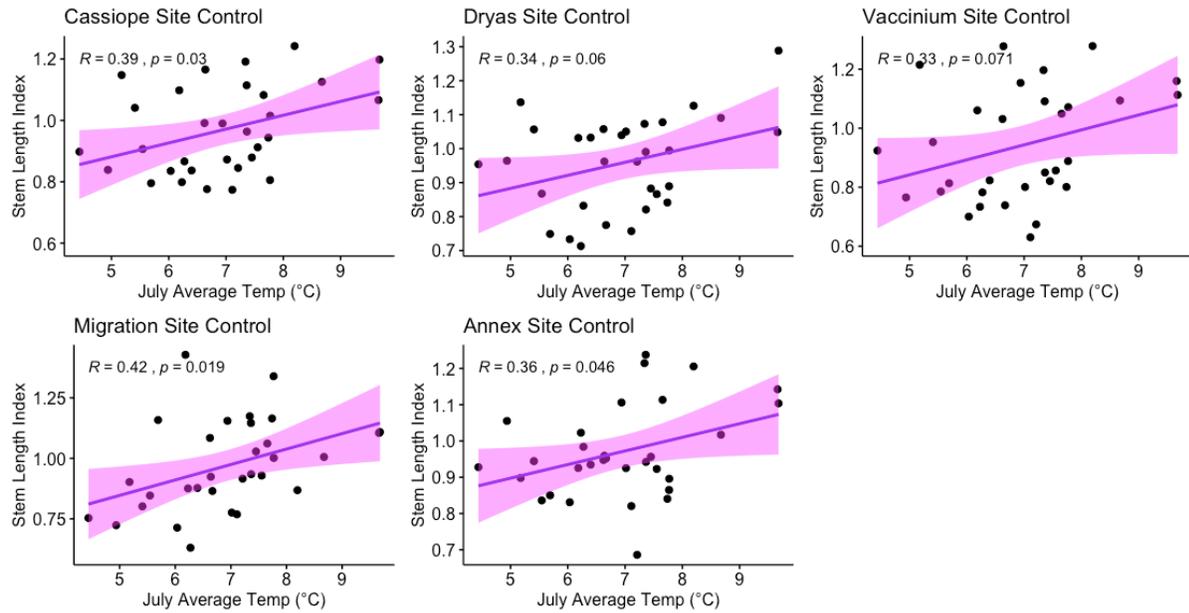


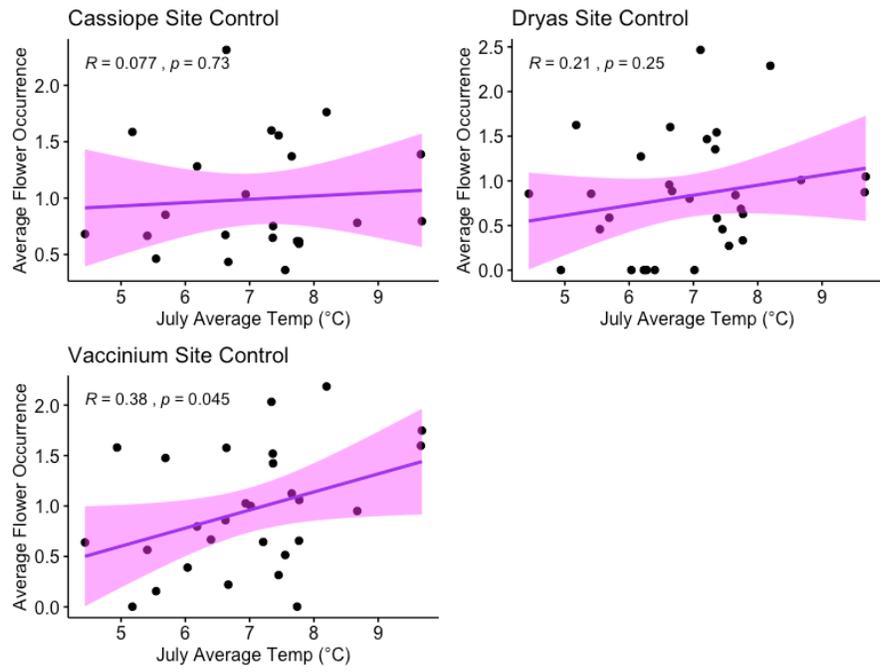
Figure 2.10 - Correlation analysis for stem, aborted bud and flower chronologies (columns) at three long term sites at Alexandra Fiord by monthly average and maximum air temperature (top and bottom rows for each site). Darker shaded bars signify statistical significance at the  $p < 0.05$  level.

#### 2.1.4.2 Climate Correlations across Sites

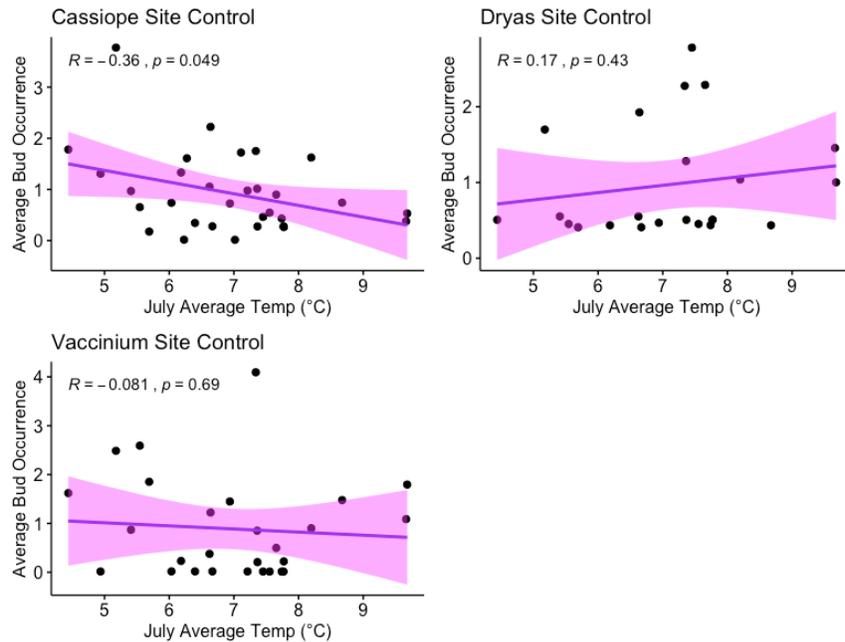
Correlation analysis is commonly used alongside response function analysis to explore the influence of climate indices on the physiological response of plants. Based on the response function and basic correlation analysis, it was decided that summer temperature was the optimal predictor of stem growth, flowering and the occurrence of aborted buds. The longest continuous record of air temperature at Alexandra Fiord is for July, so the July average air temperature time series was selected for Pearson's product-moment correlation analysis alongside the stem growth and reproductive chronologies for the control plots at each of the sites at Alexandra Fiord (flower and aborted bud occurrence lagged by -1 year). A positive relationship ( $r = 0.28-0.49$ ) was apparent across all sites, and was statistically significant at the  $p < 0.05$  level at 'Cassiope' ( $r = 0.46$ ,  $p = 0.048$ ), 'Vaccinium' ( $r = 0.34$ ,  $p = 0.058$ ) and 'Migration' ( $r = 0.49$ ,  $p = 0.0056$ ) (Figure 2.11). There was a weak relationship between July average air temperature and average annual flower count ( $r = 0.077-0.38$ ), and the only statistically significant relationship was between the two variables at the 'Vaccinium' site (Figure 2.12). There was a weak negative relationship between July average air temperature and average annual aborted bud occurrence at the 'Cassiope' ( $r = -0.36$ ,  $p = 0.049$ ) and 'Vaccinium' ( $r = -0.081$ ,  $p = 0.69$ ) sites (Figure 2.13). Meanwhile, there was a statistically insignificant weak positive trend at the 'Dryas' site.



**Figure 2.11 - Relationship between average annual stem growth 'Ring Width Index' in control plots and average July air temperatures at the 'Cassiope', 'Vaccinium' and 'Dryas', 'Migration' and 'Annex' sites at Alexandra Fiord.**



**Figure 2.12 - Relationship between average flower occurrence in control plots and average July air temperatures at the 'Cassiope', 'Vaccinium' and 'Dryas' sites at Alexandra Fiord**



**Figure 2.13 - Relationship between average aborted bud occurrence in control plots and average July air temperatures at the ‘Cassiope’, ‘Vaccinium’ and ‘Dryas’ sites at Alexandra Fiord**

### 2.1.4.3 Near-Surface Air Temperature Correlations at ‘Cassiope’ site

We also conducted correlation analysis using the near-surface air temperature data collected from the HOBO loggers at 10 cm from the ground at the Cassiope site (Table 2.5). While there was a positive relationship between near-surface air temperature and the stem and reproductive chronologies in the treatment plots, the correlations were unanimously weak and non-significant. However, the relationships between the July and August average near-surface air temperature and the stem length chronologies in the treatment plots were both high (July average:  $r = 0.69$ ,  $p = 0.0003$ ; August average:  $r = 0.62$ ,  $p = 0.001$ ). Likewise the relationship between July and August average near-surface air temperature and the flower occurrence chronologies in the treatment plots was very strongly correlated and statistically significant (July average:  $r = 0.54$ ,  $p = 0.008$ ; August average:  $r = 0.80$ ,  $p = 0.0004$ ). The aborted bud chronologies yielded negligible relationships through the correlation in both treatment and control plots for every monthly average timeseries.

**Table 2.5 - Correlation table for control & OTC plots at the ‘Cassiope’ Site comparing average annual stem length, flower and aborted bud occurrence alongside monthly average near-surface (10 cm) air temperatures.**

Plot Treatment / Monthly average	Chronology length (Years)	Stems n =	Correlation AGI & Average Surf. Temperature	Correlation Flower & Average Surf. Temperature	Correlation Aborted Bud & Average Surf. Temperature
Control – June Average	42	50	0.19	0.32	0.11
Treatment – June Average	52	54	0.32	0.30	0.08
Control – July Average	42	50	0.33	0.13	-0.37
Treatment – July Average	52	54	0.69**	0.54**	-0.01
Control – August Average	42	50	0.62*	0.22	-0.02
Treatment – August Average	52	54	0.62*	0.80**	0.16

\* $p < 0.05$ , \*\* $p < 0.01$

### 2.1.5 Reconstruction of Summer Temperature

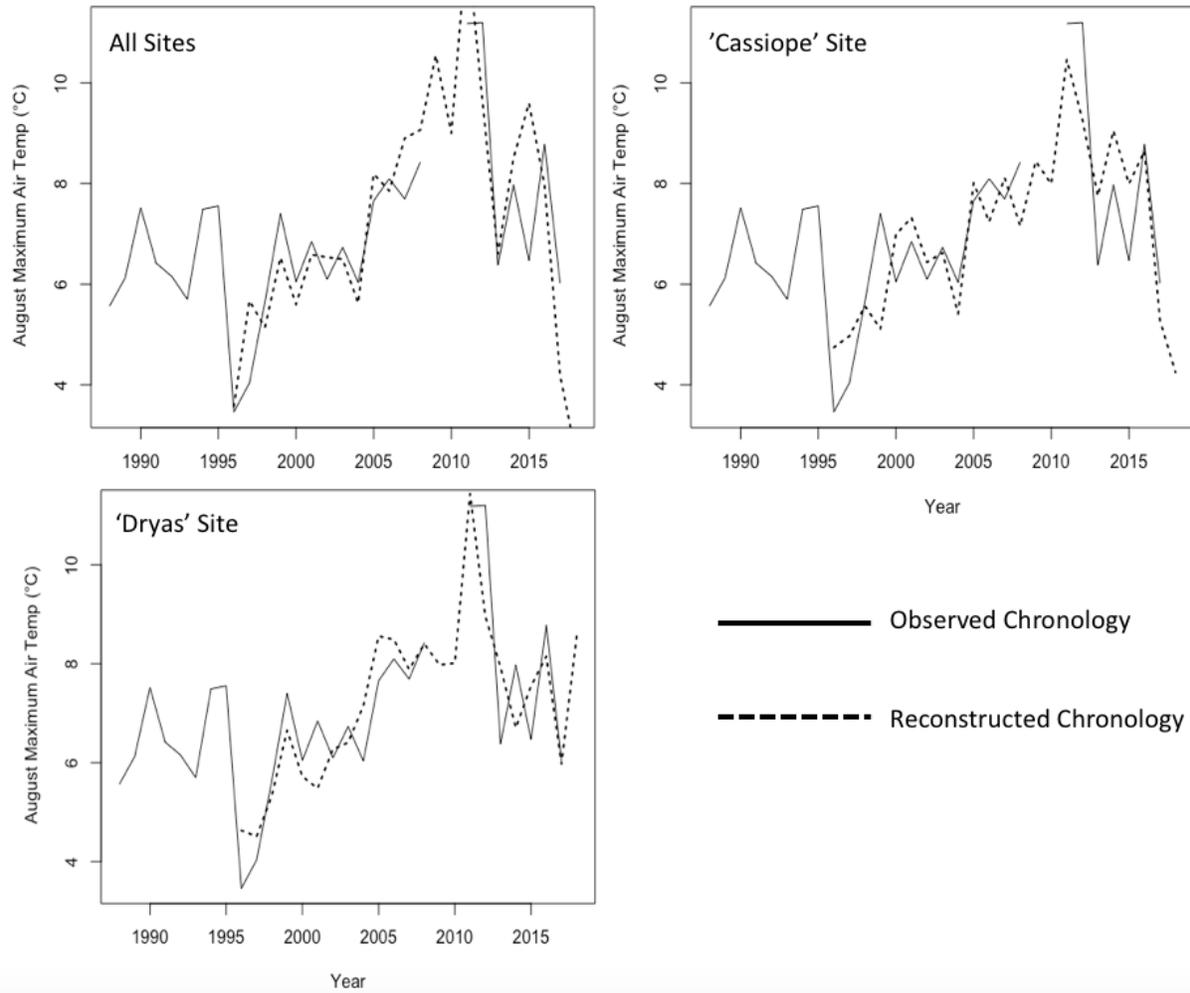
Based upon the response function and correlation coefficient analysis, it was determined that the summer months would be best suited for climate reconstruction via stepwise multiple linear regression. During model selection, models used a series of average and maximum annual air temperatures as the dependent variable and the standardised AGIs, and an interaction term of the standardised reproduction variables (aborted buds \* flower peduncles) as explanatory variables. Two models were compared; ‘August Maximum’, which was consistently the best (although incomplete) reconstructed climate variable across the sites at Alexandra Fiord, and ‘July Average’, which was the best complete climate record. While both records span the period of 1988-2018, ‘August Maximum’ is missing the years 2009 and 2010 due to climate station malfunctions. These models were run using combinations of growth and reproductive chronologies for all sites at Alexandra Fiord, and a master compilation of all control sites. Due to the low sample size included in their master chronologies, the ‘Migration’ (n = 7) and ‘Annex’ (n = 11) sites were excluded from this analysis. Additionally, based on the correlation analysis in section 2.1.4.3, we also built calibration models for the July and August average near-surface temperature data using the stem

length and reproductive chronologies from the ‘Cassiope’ site treatment plots. Furthermore, all models presented in this chapter met all ordinary least squares assumptions regarding normality, linearity and equal variance. All regression tables are listed in Appendix B.

#### **2.1.5.1 ‘August Maximum’ Model**

The ‘August Maximum’ model including all annual stem growth index and reproductive variables from the ‘Cassiope’, ‘Dryas’ and ‘Vaccinium’ sites performed well despite the high number of growth variables and reproductive interactive terms (see Appendix B for model tables). Adjusted for loss of degrees of freedom, the explanatory variables predicted 68% of the variation in August maximum air temperature ( $p = 0.029$ ). Furthermore, Pearson’s product-moment correlation analysis yielded a 94% correlation between the observed and reconstructed air temperature time series.

The model was applied to growth and reproductive variables from ‘Cassiope’ site only, which predicted 60% of the variation in August maximum air temperature ( $p = 0.001$ ). Pearson’s product-moment correlation analysis yielded an 83% correlation between the observed and reconstructed air temperature time series. Despite the low sample size included in the standardised master chronologies for the control plots ( $n = 14$ ), the model also performed well at the ‘Dryas’ site, explaining 69% of the variation in the observed air temperature record ( $p = 0.0001$ ). There was an 87% correlation between the observed and reconstructed air temperature time series. The ‘Vaccinium’ site chronologies were the only records to perform poorly using this model, explaining only 18% of the variation in the August maximum air temperature record ( $p = 0.1052$ ). As such, a reconstruction was not attempted for the chronologies at this site.



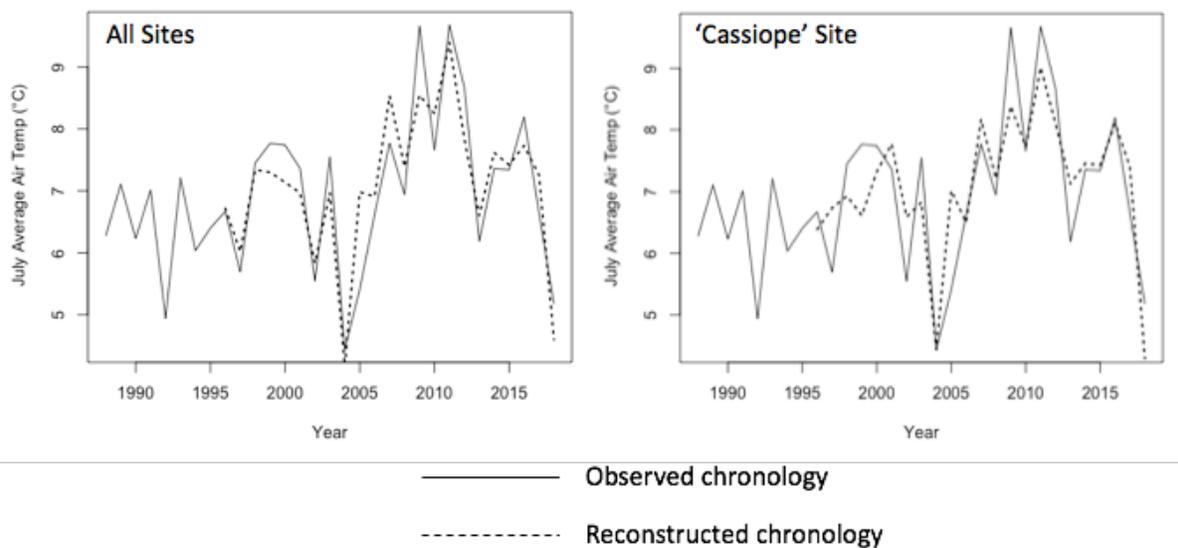
**Figure 2.14 - Comparison of the observed and reconstructed chronologies of August Maximum Air Temperature using growth and reproductive variables from all sites, 'Cassiope' site only, and 'Dryas' site only.**

### 2.1.5.2 'July Average' Model

The model calibration was repeated using the complete (1988-2018) July average air temperature data (see Appendix for model tables). The model included all stem growth and reproductive indices (a flower peduncle \* aborted bud interaction term), which predicted 53% of the variation in July average air temperature when adjusted for loss of degrees of freedom ( $\text{adj.}r^2 = 0.53$ ,  $p = 0.042^*$ ). Despite this, there was a significant correlation (89%) between the reconstructed and observed July average air temperature chronologies.

The iteration of the model applied to ‘Cassiope’ site growth and reproductive chronologies performed the best as a predictor of July average air temperature, explaining 61% of the variation in the observed chronology ( $\text{adj.}r^2 = 0.6123$ ,  $p = 0.0002$ ). Furthermore, there was a positive, strong correlation (83% \*\*) between the observed and reconstructed July average air temperatures.

Comparatively, the model performed poorly when applied to the ‘Vaccinium’ and ‘Dryas’ stem growth and reproductive chronologies, probably as a result of low stem sample size in the control plots for these two sites. At ‘Vaccinium’, only 23% of the variation in July average air temperature was captured by the model ( $\text{adj.}r^2 = 0.2136$ ,  $p = 0.043$ ), while at ‘Dryas’, the  $r^2$  value adjusted for loss of degrees of freedom was especially low at  $-0.009$  ( $p = 0.4578$ ). As a result, reconstructed chronologies for these two sites were not attempted.

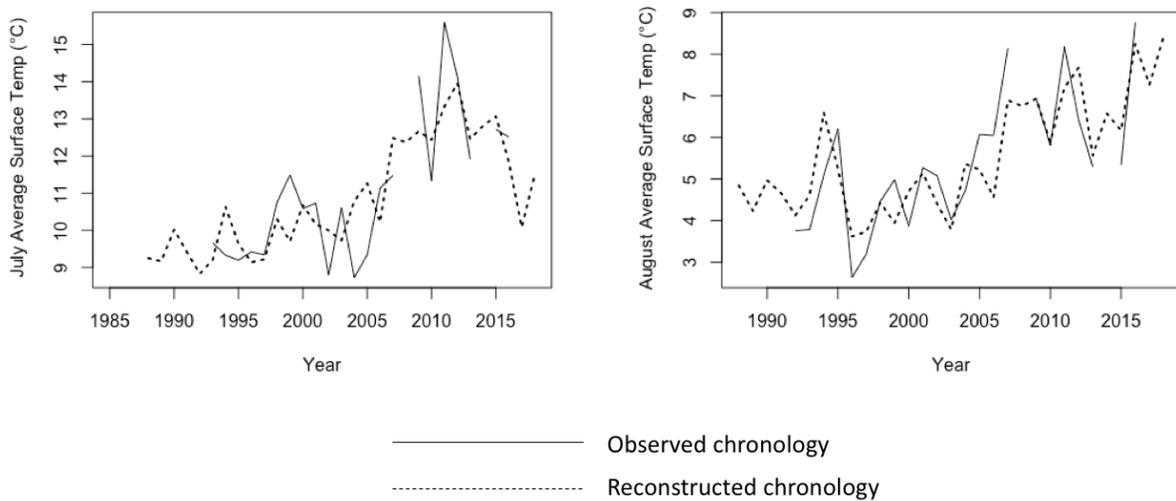


**Figure 2.15 - Comparison of the observed and reconstructed chronologies of July Average Air Temperature using growth and reproductive variables from all sites and ‘Cassiope’ site only.**

### 2.1.5.3 Near-Surface Air Temperature Treatment Models

The ‘July Average Surface Temperature’ model including the stem growth index and reproductive variables from the ‘Cassiope’ treatment plots performed well, with the explanatory variable predicting 54% of the variation in the average surface temperature data when adjusted for loss of

degrees of freedom ( $p = 0.001$ ). Likewise, Pearson’s product-moment correlation analysis yielded a 79% correlation between the observed and reconstructed surface temperature time series. Furthermore, the ‘August Near-Average Surface Temperature’ iteration of the model performed very well, with the explanatory variable predicting 65% of the variation in the average 10 cm temperature data when adjusted for loss of degrees of freedom ( $p = 0.001$ ). Likewise, Pearson’s product-moment correlation analysis yielded an 84% correlation between the observed and reconstructed surface temperature time series.



**Figure 2.16 - Comparison of the observed and reconstructed chronologies of July and August Average Surface Air Temperature using growth and reproductive variables in the ‘Cassiope’ treatment plots only.**

#### 2.1.5.4 ‘July Average’ Model Verification

As it was the most continuous reconstruction, we selected the July Average model using all growth and reproductive chronologies at Alexandra Fiord to be tested using classic dendroclimatology robust verification statistics. Only live stems were collected for this study, limiting the possible chronology length and as such, only one verification period was used. The Reduction of Error (RE) statistic was positive at 0.756, indicating very good agreement between the observed and reconstructed climate chronologies. Furthermore, the Coefficient of Efficiency (CE) was positive at 0.366, indicating strong agreement in the variances of the observed and reconstructed chronologies. The non-parametric signs test is used in dendroclimatology studies to tabulate the

number of ‘agreements’ and ‘disagreements’ between individual values in the observed and reconstructed chronologies, and for the selected model there were 23 ‘agreements’, and 0 ‘disagreements’. These verification statistics indicate a robust climate model with very good predictive skill.

## **2.2 Discussion**

### **2.2.1 Discussion of Methodology Updates**

The use of Cybis CooRecorder image analysis software (Larsson 2016) greatly improved the efficiency of the measurement of leaf scars, aborted buds and flower peduncles. In comparison to the previous method in which a manually operated calliper device was used to measure the internode distance between leaf scars, CooRecorder allowed us to save the coordinates of features on top of a high resolution scan of the stem, allowing for cross-validation of measurements between team members and for closer examination of the morphological features of the stem. The method was tested against the manually operated calliper method to ensure precision and repeatability, and allowed a greater number of processed stems than would be otherwise be possible using this method (otherwise  $n < 100$  stems could have been processed within the period of study). The Cybis CDendro software package is commonly used by dendrochronologists working with tree species, and we recommend it for the ease of cross-dating using correlation scores and skeleton plots.

In this study, we only selected live stems from the plots as we wanted to capture the current period of climate variability. As a result, the chronologies do not extend beyond the 1960s, capturing late 20th century ambient climate warming, the installation of the OTCs in the early-1990s, and the subsequent amplified warming effects in the treatment plots. For future studies following this design, we recommend collecting senesced stems to cross-date into an extended 20th century chronology to better capture the baseline climate variability in the pre-experimental period at the Alexandra Fiord sites.

### **2.2.2 Before – After – Control – Intervention Analysis**

Previous research on the effect of warming experiments on the growth of *C. tetragona* has yielded mixed responses of the physiological reaction to amplified warming treatment. Molau (1997) employed a simplified BACI analysis at a warming experiment in Latnjajaure (Sweden) and found no significant difference between treatment and control plots, despite an overall difference of 4.95 mm in average AGI length. However, their study only captured three growing seasons under

experimental conditions. Indeed, the results reported in 2.1.1.2 capture lags in divergence for a few years following OTC installation at Alexandra Fiord, while the overall divergence between post- and pre- experimentation is markedly high by the year 2018, with the average difference between treatment and control samples across all sites reaching 9.08 mm after 26 years of experimental warming. This annual stem growth lag (of 2-4 growing seasons after OTCs were installed) was also reported by Rozema et al. (2009), who noted significant divergence between OTC and control stems thereafter.

At most High Arctic sites, the warmer air temperature forced by the passive warming experiments do indeed cause a marked divergence in stem growth between control and treatment plots (Havström et al. 1993; Weijers et al., 2012; Rozema et al., 2009; Rayback 2003). It has been posited that in Low Arctic sites, stem growth is ultimately controlled by light availability and competition for nutrients (Havström et al., 1993; Molau 1997). While the influence of regional geography is investigated in the analysis of Research Objective 2, it is important to consider the other environmental drivers interacting with experimental warming. In this study, we found variable responses to experimental warming across the long term field sites at Alexandra Fiord. At two of the drier sites ('Cassiope' and 'Migration') the CI Contribution between OTC and control plots post-experimentation was the highest, twice the effect of the CI Contribution at the moist 'Vaccinium' site, and 'Dryas', which was heavily flooded in 2001 and again in 2010. In contrast, the control and treatment chronologies behaved similarly prior to the installation of OTCs. Ultimately, while BACI analysis at all sites display some level of divergence forced by experimental warming, indicating that these High Arctic plants are indeed sensitive to air temperature, the marked difference in response between the site supports the use of the new BACI metrics suggested by Chevalier et al. (2019) as they highlight the differences in site-specific population trends. This method could be used for a number of multi-factor experiments at ITEX sites, including shading, fertilisation, grazing, snow removal and snow fence experiments as it is highly likely that other site-specific factors influence plant growth and reproduction aside from just air temperature.

### 2.2.3 Phenology

The 26 years of phenology observations at the warming experiment at Alexandra Fiord indicated that reproductive stages in *C. tetragona* consistently take place earlier in the warmed plots in comparison to control plots, although only by an average of one or two days. Furthermore, annual phenology timings appear to closely relate to annual climate variability. The synchronous relationship between summer air temperature and reproductive behaviour reflects previous observations of earlier flowering and seed dispersal of Arctic plant species, which have been reported to exhibit a higher sensitivity to air temperature than observed in temperate regions (Panchen & Gorelick, 2015; Panchen & Gorelick, 2017; Wookey et al., 1993). The results reported in this thesis, therefore, indicate that *C. tetragona* is optimising warmer summer conditions (both in and out of the warming plots) to set seed earlier in the growing season. It would be useful to repeat this methodology for other plants with long-term phenology records at Alexandra Fiord and other sites to compare rates of phenology stage timing change, as such differences would have an impact on future vegetation community dynamics, including population shifts and competition for resources.

Previous ITEX research complements the effect of warming Arctic summer temperatures on the phenology response of *C. tetragona* observed at Alexandra Fiord through experimental warming (Arft et al., 1999). Oberbauer et al. (2013) found that there was a mixed response across ITEX sites as a result of highly variable summer air temperature records between sites, noting that the greatest predictors of the phenology response to air temperature variability are site conditions such as soil moisture characteristics. Furthermore, many ecologists have reported disparities between OTC observations and long-term non-experimental phenology observations, whereby warming experiment results appear to ‘underpredict’ temperature sensitivity of plants with regards to reproductive phenology, perhaps as a result of design issues with OTCs such as light and wind disruption and limited access for animals (Wolkovich et al., 2012; Marion et al., 1997). However, it is likely that the effect of OTC design on pollination and seed dispersal is minimal (Robinson & Henry, 2018). Our results certainly indicate a sensitivity of phenology timing to summer temperature, and a divergence between OTC and control plots, so it is likely that the OTCs are not significantly underpredicting temperature sensitivity of the reproductive phases of *C. tetragona*,

although the extent of any such disparity would be difficult to accurately quantify. However, our results indicate that OTCs are not interfering with phenology, as the ambient shifts from the control plots are the same as in the OTCs.

#### **2.2.4 Dendrochronology Analysis**

The inter-series correlation is characteristically low amongst the master chronologies at Alexandra Fiord. This has been explained in previous studies as a consequence of resource partitioning through the many branches of a *C. tetragona* plant and the influence of micro-environmental variability around the complex and heavily branched structure of an individual plant (Johnstone & Henry, 1997; Rayback & Henry 2005). Furthermore, the first-order autocorrelation was typically low for the stem length indices at all sites and suggests a direct relationship with annual summer temperatures, with little relation to previous years' growth conditions, as has been reported in previous studies (Johnstone & Henry, 1997; Rayback & Henry 2005; Rayback & Henry 2006; Rayback et al., 2012).

The annual stem growth chronologies were positively correlated with summer temperatures, and the flower and aborted bud chronologies were positively correlated with summer temperatures of the previous year. This lag is supported by the fact that bud formation begins during the growing season of the previous year (Sørensen 1941). Furthermore, the success of the July Average chronology is supported by the selection of July temperatures in most other studies using *C. tetragona* as a dendrochronological proxy (Rayback & Henry 2005; Rayback & Henry 2006; Rayback et al., 2012; Rozema et al., 2009; Weijers et al., 2010; Weijers et al., 2012; Weijers et al., 2017), especially considering July is in the middle of the growing season, and is also the month in which flowers bloom and begin to senesce after bud break in late June. Likewise, the negative response functions for the stem growth, aborted bud and flower chronologies during spring may be related to *C. tetragona*'s success as a snowpack species, as deeper and prolonged snowpack during a colder spring insulates the plant and could potentially increase soil nitrogen availability thus promoting stem growth (Blok et al., 2015). The similarity in chronology correlation to summer temperatures between Alexandra Fiord and other High Arctic field sites (such as Svalbard [i.e. Weijers et al., 2012] and North Greenland [i.e. Weijers et al., 2017]) are a useful benchmark

against which to investigate the spatial variability in *C. tetragona* growth patterns across the Arctic in Chapter 3 of this thesis, as the relationships indicated in this study somewhat contradict observations by Molau (1997), who observed no significant influence between summer temperatures and annual stem growth at a Low Arctic field site. As such, there are likely other variables at play in the Low Arctic, such as competition for light (Havström et al., 1993).

The July Average and August Maximum models explained amongst the highest percent variance in summer temperature of all of the models using *C. tetragona* as a dendrochronological proxy (Rayback & Henry 2005; Rayback & Henry 2006; Rayback et al., 2012; Rozema et al., 2009; Weijers et al., 2010; Weijers et al., 2012; Weijers et al., 2017). The high adjusted  $r^2$  values were complemented by the results of verification tests for the July Average Model (RE, CE, signs test) from which we can infer that the model has very high predictive ability. The success of the model could be attributed to the large number of stems samples processed, the inclusion of an interaction term between the aborted bud and flower chronologies, or simply a result of the shorter time series used in this study. We found that the success of the models varied between the field sites at Alexandra Fiord. While Rayback et al. (2011) sampled from different field sites across Ellesmere Island (and thus sites with slightly different regional environmental controls such as topography and local meteorological characteristics), the spatial variation apparent in the growth and reproductive chronologies at the different sites at Alexandra Fiord could likewise be explained by local environmental conditions such as soil moisture, community composition and even extreme events such as flash floods, that affected only the ‘Dryas’ site in 2001 and 2010 when a glacial stream overflowed its banks.

All of the stem growth chronologies were visually similar in trend, with rapidly increasing annual stem growth throughout the late 1980s-2018, preceded by either a slight decrease or plateauing of annual stem growth between the 1960s and early 1980s. This trend complements the reconstruction of temperatures in other studies, which observed a decline in High Arctic summer temperatures in the 1960s until a new period of more rapid warming from the early 1980s (Rayback et al., 2006). While the goal of reconstruction in this research was to indicate the extent to which the plant is sensitive to summer temperatures, it should be noted that modelled temperature

chronologies from this study extend the reconstruction of Alexandra Fiord temperatures into the 2010s, when in previous dendrochronology studies at the site they terminated in the late-1990s or early 2000s (Johnstone & Henry, 1997; Rayback & Henry 2005; Rayback & Henry 2006). The reconstruction tightly fits the observed summer temperature variation within the last three decades, in particular the period of very rapid warming (the Arctic amplification effect) between 2005 and 2012. The model also fairly accurately identifies peak warm years (i.e.  $>9^{\circ}\text{C}$  July average in 2011) and peak cold years (i.e.  $\sim 4^{\circ}\text{C}$  July average in 2004). The successful predictive skill of the model means there is no over- or under- estimation of years with extreme high or low temperatures as was noted by Weijers et al. (2010) and Rayback et al. (2012). Furthermore, the proxy can be used at Alexandra Fiord to capture the accelerated warming forced by the Arctic amplification effect, and does not experience the ‘divergence problem’, whereby other species used for dendrochronology studies fail to capture recent warming trends, perhaps as a result of drought-induced stress (D’Arrigo et al., 2008).

The direct relationship between air temperature warming and *C. tetragona* stem growth and reproduction supports the prediction that the shrub has the potential to increase in density, reproduce efficiently and expand into new areas as summer air temperature continues to climb in the High Arctic (Weijers et al., 2017). Furthermore, these results contradict the theory that shrub growth is restrained in High Arctic tundra environments under current temperature and nutrient regimes (Hollister et al., 2005; Hudson & Henry, 2010; Elmendorf et al., 2012a). However, any predictions are contingent on the physiological response to competition from other rapidly expanding species such as *S. arctica*. As such, we recommend that future dendrochronology studies consider species composition at sample sites as a factor, perhaps incorporating long term records of plant cover as annual proxies of competition.

## Chapter 3: Analysis of Circum-Arctic Growth and Reproduction

### Chronologies

#### 3.1 Results

##### 3.1.1 Multi-Site Stem Growth Chronologies

Prior to standardisation, the individual raw stem annual growth increments of *C. tetragona* stems from multiple tundra sites were averaged into master chronologies (Table 3.1). Overall, 136 control (including non-experimental) and 70 warming treatment stems were collected from twelve ITEX-affiliated field sites representing four circum-Arctic regions: Northern Scandinavia (Abisko & Latnjajaure in Sweden, Saana in Finland), Greenland (Disko Island & Arctic Station), Svalbard (Za Pyr, Elza, Skansbutka, AWS) and Alaska (Barrow, Atqasuk, Toolik Lake and Imnavait Creek), in addition to the samples collected on Ellesmere Island and analysed in Chapter 2. The average chronology length across these sites was 28 years (1990-2018). The longest stem (57 years) was collected at the Arctic Station site in Western Greenland. The mean interseries correlation ( $r_{bar}$ ) measures common signal of variability between individual stems, and ranged from 0.014-0.253 (average 0.14) across the sites included in the analysis, although this low score is characteristic of the proxy as explained in Chapter 2. Autocorrelation (AR1) ranged from 0.033-0.429 across the sites (average 0.19), indicating low correlation between yearly growth patterns amongst individual stems.

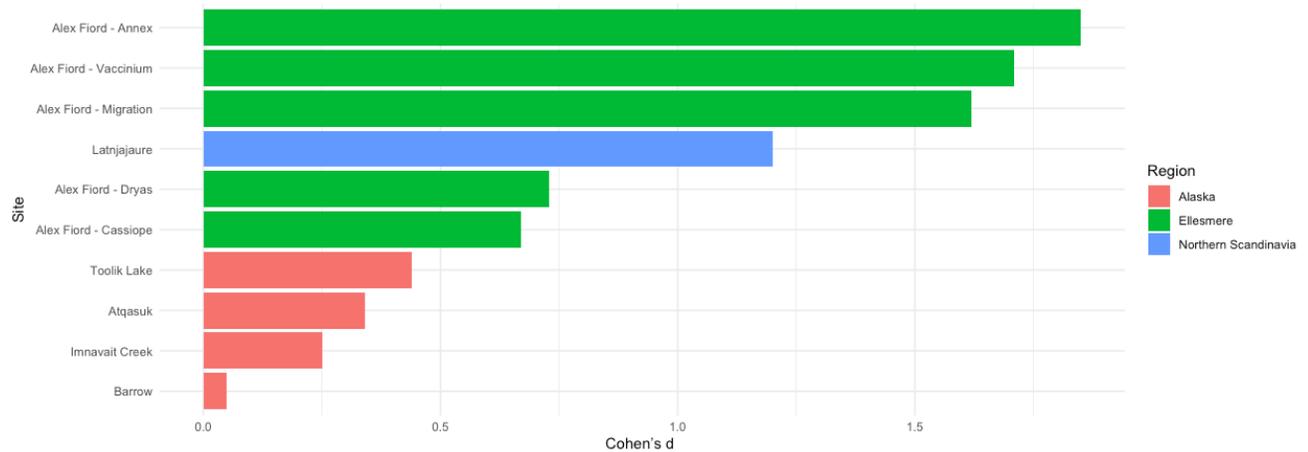
**Table 3.1 - Characteristics (inter-series correlation and autocorrelation) of annual growth increment chronologies for *C. tetragona* from multiple circum-Arctic field sites.**

Site	Region	Chronology length (Years)	Stems n =	Interseries Correlation	AR1
Abisko	Northern Sweden	34	7	0.075	0.429
Latnjajaure	Northern Sweden	16	10	0.125	0.038
Saana	Northern Finland	38	5	0.153	0.057
Elza	Svalbard	30	5	0.014	0.147
Za Pyr	Svalbard	25	10	0.149	0.184
AWS	Svalbard	26	3	0.008	0.157
Skansbukta	Svalbard	24	5	0.192	0.277
Imnavait Creek	Alaska	14	8	0.192	0.140
Barrow	Alaska	18	23	0.253	0.033
Toolik Lake	Alaska	16	12	0.153	0.143
Atqasuk	Alaska	22	14	0.226	0.301
Disko Bay	Western Greenland	42	16	0.209	0.233
Arctic Station	Western Greenland	57	18	0.063	0.296

While the chronologies presented in Chapter 2 were long enough to capture sufficient growth in both the pre- and mid- experimental periods, the lengths of the stems acquired from the other experimental field sites (Latnjajaure, Toolik Lake, Imnavait Creek, Barrow and Atqasuk) were not sufficient to conduct a full Before-After-Control-Impact analysis. We instead implemented Effect Size analysis as a means to compare the relative impact of experimental warming across the sites, using *Cohen's d* effect size as a comparison metric. This metric represents the difference between treatment and control chronologies for each site, divided by their standard deviation. Using Romano et al.'s (2006) effect size classification system, the impacts were categorised into 4 groups: Large, Medium, Small and Negligible (Table 3.2, Figure 3.1). The 'Vaccinium', 'Migration' and 'Annex' sites at Alexandra Fiord and the site at Latnjajaure in Sweden exhibited a 'Large' effect size: at each site annual stem growth in the warmed plots was over 1 standard deviation removed from those of the control plots - the difference induced by experimentation was visible and obvious. Likewise, the 'Cassiope' and 'Dryas' sites at Alexandra exhibited a 'Medium' effect size ( $d = 0.67$ ,  $d = 0.73$ ). In contrast, the Alaska experimental chronologies exhibited a clear, though 'Small' difference (average  $d = 0.27$ ), with Barrow only exhibiting a 'Negligible' effect size ( $d = 0.05$ ).

**Table 3.2 – Effect size Cohen’s *d* values and classifications for the circum-Arctic experimental field sites**

Site	Cohen’s <i>d</i> value	Effect Size
Alex Fiord - Cassiope	0.67	Medium
Alex Fiord - Dryas	0.73	Medium
Alex Fiord - Vaccinium	1.71	Large
Alex Fiord - Migration	1.62	Large
Alex Fiord - Annex	1.85	Large
Latnjajaure	1.20	Large
Toolik Lake	0.44	Small
Imnavait Creek	0.25	Small
Barrow	0.05	Negligible
Atqasuk	0.34	Small



**Figure 3.1 - Effect size Cohen’s *d* values and classifications for the circum-Arctic experimental field sites**

### 3.1.2 Multi-Site Stem Chronology Characteristics

Pearson’s product-moment correlation coefficient analysis was used to investigate correlations between the stem growth, flower peduncle and aborted bud chronologies for the master control chronologies at all of the circum-Arctic sites (Table 3.3). As explained in Chapter 2, the flower and aborted bud chronologies were lagged by one year (*t*-1) because previous studies have shown lagged reproductive chronologies to be correlated most strongly with previous year’s summer air

temperatures (Johnstone & Henry, 1997; Rayback 2003; Rayback & Henry, 2005). Unlike the sites at Alexandra Fiord, the relationship between annual stem growth and average flower occurrence was not universally positive at the other sites included in this analysis. The strongest statistically significant relationships between these two indices are apparent at Imnavait Creek ( $r = 0.61^*$ ), Barrow ( $r = 0.53^*$ ), Disko Bay ( $r = 0.52^*$ ) and Saana ( $r = 0.45^*$ ). The analysis yielded a number of non-significant negative trends, including AWS ( $r = -0.3$ ), Latnjajaure ( $r = -0.18$ ), Toolik Lake ( $r = -0.18$ ), and Abisko ( $r = -0.042$ ).

In contrast, the relationship between annual stem growth and average annual bud occurrence represented the strongest (and most consistently statistically significant) correlation of the three relationships tested as part of this analysis. The highest statistically significant relationships were apparent at Za Pyr ( $r = 0.62^{**}$ ), Skansbukta ( $r = 0.61^{**}$ ), Abisko ( $r = 0.58^{**}$ ), Disko Bay ( $r = 0.52^{**}$ ) and AWS ( $r = 0.48^*$ ). While not statistically significant, the other sites all had positive slopes, while only Elza showed a negligible trend ( $r = 0.00097$ ). For comparison, the correlations derived from the same indices from stems collected at Alexandra Fiord sites (Chapter 2) ranged  $r = 0.0091 - 0.49$ . The relationship between average annual aborted bud and flower occurrence was the weakest of the three included in this analysis, with only two moderate to strong, statistically significant correlations (Barrow  $r = 0.72^{**}$ ; Disko Bay  $r = 0.47^{**}$ ). Most of the other sites exhibited a weak positive or negligible relationship, with no statistical significance, while four sites exhibited a weak negative relationship with no statistical significance (Abisko  $r = -0.16$ , Latnjajaure  $r = -0.12$ , Skansbukta =  $-0.14$ ). In contrast, the same indices from stems collected at Alexandra Fiord sites (Chapter 2) exhibited a generally positive correlation ( $r = 0.11 - 0.59$ ).

**Table 3.3 - Correlation table for control sites comparing average annual stem length, flower and aborted bud occurrence.**

Site	Chronology length (Years)	Stems n =	Correlation AGI & Flower	Correlation AGI & Aborted Bud	Correlation Aborted Bud & Flower
Alex Fiord – Cassiope	42	50	0.59**	0.43*	0.59**
Alex Fiord - Dryas	42	14	0.19	0.28	0.31
Alex Fiord – Vaccinium	33	16	0.53**	0.49**	0.29
Alex Fiord – Migration	32	7	0.17	0.05	-0.08
Alex Fiord - Annex	33	11	0.53**	0.33	0.43*
Abisko	34	7	-0.042	0.58**	-0.16
Latnjajaure	16	10	-0.18	0.44	-0.12
Saana	38	5	0.45*	0.45*	0.084
Elza	30	5	0.1	0.001	0.15
Za Pyr	25	10	0.014	0.62**	0.077
AWS	26	3	-0.3	0.48*	0.054
Skansbukta	24	5	0.028	0.61**	-0.14
Imnavait Creek	14	8	0.61*	0.48	0.38
Barrow	18	23	0.53*	0.51*	0.72**
Toolik Lake	16	12	-0.18	0.38	-0.23
Atqasuk	22	14	0.49	0.37	0.32
Disko Bay	42	16	0.52**	0.51**	0.47**
Arctic Station	57	18	0.27*	0.21	0.31

\* $p < 0.05$ , \*\* $p < 0.01$

### 3.1.3 Correlation of Climate, Growth and Reproductive Chronologies

For the climate correlation analysis we used local July average temperatures (for direct comparison with the Alexandra Fiord climate correlations) derived from the UEA Climate Research Unit (CRU) 0.5° TS 4.03 monthly air temperature grid (Harris et al., 2014). These climate indices were paired with the detrended site master stem growth chronologies and analysed using Pearson's product-moment correlation analysis along with the reproductive chronologies for the control plots at each of the sites, with flower and aborted bud occurrence lagged by t-1 year (Table 3.4). A weak to moderate positive relationship between stem length and summer temperature was apparent across all sites with an average of  $r = 0.24$ , although the only statistically significant relationship was apparent at Disko Bay ( $r = 0.46^{**}$ ). The most positive non-significant trends were at the Svalbard sites (Elza  $r = 0.29$ , Za Pyr  $r = 0.26$ , AWS  $r = 0.28$ , Skansbukta  $r = 0.37$ ).

Likewise, a weak to moderate positive correlation between aborted bud occurrence and July Average temperature was apparent across all sites except Elza ( $r = -0.14$ ), although the only statistically significant correlations were exhibited at AWS ( $r = 0.48^*$ ) and Skansbukta ( $r = 0.48^*$ ). The relationships were negligible at the Alaska field sites (average  $r = 0.07$ ) and highest at the Svalbard field sites (average  $r = 0.3$ ). The relationships between average flower occurrence (t-1) and July average temperature were universally weak and statistically nonsignificant.

**Table 3.4 - Correlation table for control sites comparing average annual stem length, flower and aborted bud occurrence alongside July Average air temperature.**

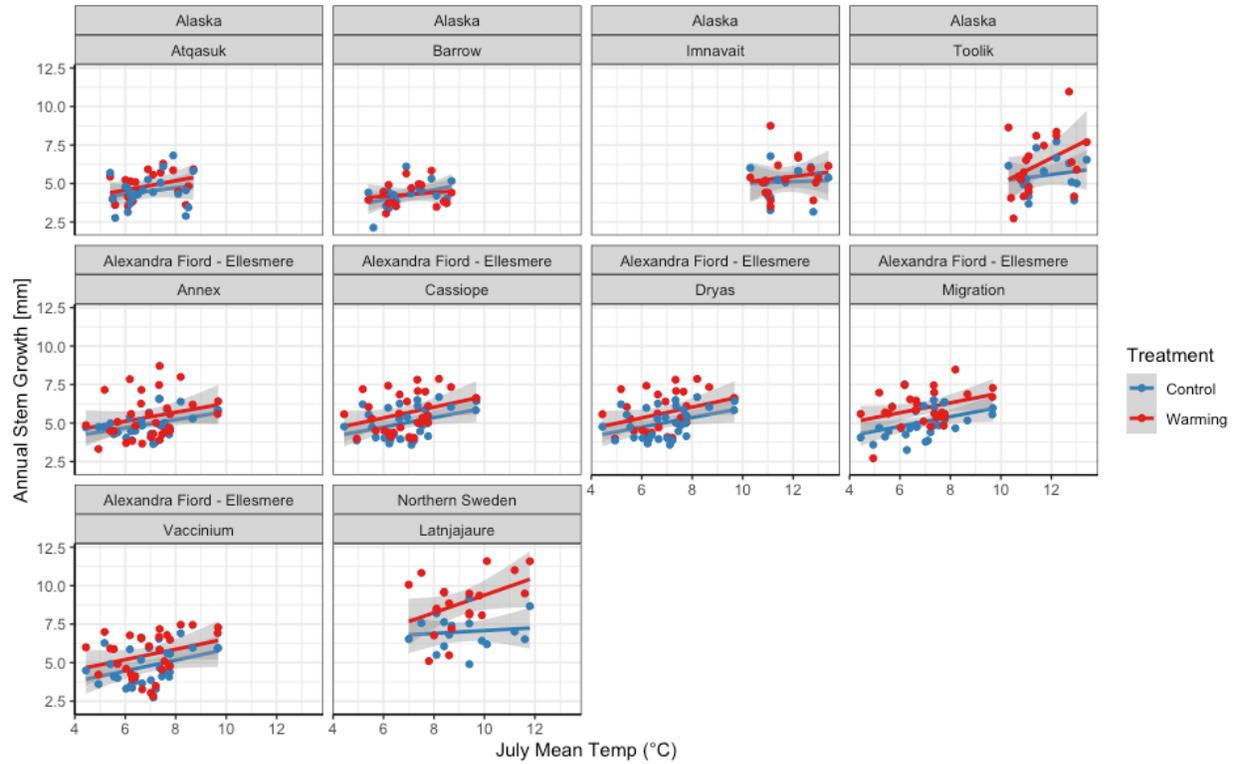
Site	Chronology (Years)	Stems n =	Correlation AGI & July Average Temperature	Correlation Flower & July Average Temperature	Correlation Aborted Bud & July Average Temperature
Alex Fiord – Cassiope	42	50	0.39*	0.077	-0.36*
Alex Fiord - Dryas	42	14	0.34	0.21	0.17
Alex Fiord – Vaccinium	33	16	0.33	0.38*	-0.081
Alex Fiord – Migration	32	7	0.42*	0.23	-0.07
Alex Fiord - Annex	33	11	0.36*	0.40*	0.26
Abisko	34	7	0.14	0.26	0.12
Latnjajaure	16	10	0.39	0.01	-0.20
Saana	38	5	0.05	0.29	-0.19
Elza	30	5	0.29	-0.14	0.24
Za Pyr	25	10	0.26	0.37	0.19
AWS	26	3	0.28	0.48*	0.12
Skansbukta	24	5	0.37	0.48*	-0.10
Imnavait Creek	14	8	0.29	0.08	0.19
Barrow	18	23	-0.20	0.10	0.18
Toolik Lake	16	12	0.18	0.04	0.34
Atqasuk	22	14	0.15	0.06	0.05
Disko Bay	42	16	0.46**	0.14	0.17
Arctic Station	57	18	0.07	0.13	0.18

\* $p < 0.05$ , \*\* $p < 0.01$

### 3.1.4 Linear Mixed Effects Model – Climate & OTCs

To model the impact of experimental warming versus ambient summer temperature on annual stem growth, we developed a linear mixed effects model using the lme4 package in *R* (Bates et al., 2012). The model included averaged master chronologies of the raw annual stem growth of samples collected at each of the experimental warming sites: Alexandra Fiord, Latnjajaure, Toolik Lake, Barrow, Innavaik Creek and Atqasuk. The stem growth chronologies were selected as the dependent variable, while we used average July air temperature derived from the UEA Climate Research Unit (CRU) TS 4.03 0.5° monthly air temperature grid, and control vs treated plot (as a class variable) as fixed effects. Region (Ellesmere Island, Alaska and Northern Sweden) and the six individual field sites were used as random effect class variables.

When compared to the null model (full model excluding the Experiment class fixed effect), the warming experiment included in the full model was found to significantly impact annual stem growth (Chi-square = 38.5,  $p = 5.393e-10$  \*\*\*), increasing it by 0.665 mm (SD = 0.10490) (see Appendix C; Figure 3.2). The Region class variable explained 60% of the overall variance in the stem growth data, while the Site class variable explained only 2% of the overall variance. The overall impact of the climate variable (contributing an additional 0.28 mm to annual average stem growth) was fairly minimal in comparison to the experimental variable, a result that supports the idea that stem growth retains a linear relationship to ambient warming, and that the plant is also very sensitive to experimental warming in at least three circumpolar regions. Furthermore, while Site characteristics did not greatly contribute to the variance apparent in the data, there appears to be a clear Regional signal amongst the control and treatment chronologies, which is visibly apparent in plots showing the relationship between annual stem growth and average July temperatures at each of the sites (Figure 3.2).



**Figure 3.2 - Scatter plots of annual stem growth against July Average Temperature, grouped by site and classified by treatment.**

### 3.1.5 Principal Component Analysis

Principal Component Analysis (PCA) was used to identify potential clusters of stem growth and reproductive effort characteristics between sites. For each of the control sites, we included the average, maximum and standard deviation scores of annual stem growth, aborted bud occurrence and flower occurrence. The eigenvalue analysis revealed that the first three principal components explained 36.5%, 25.3% and 18% of the overall variance in the data respectively (Figure 3.3).

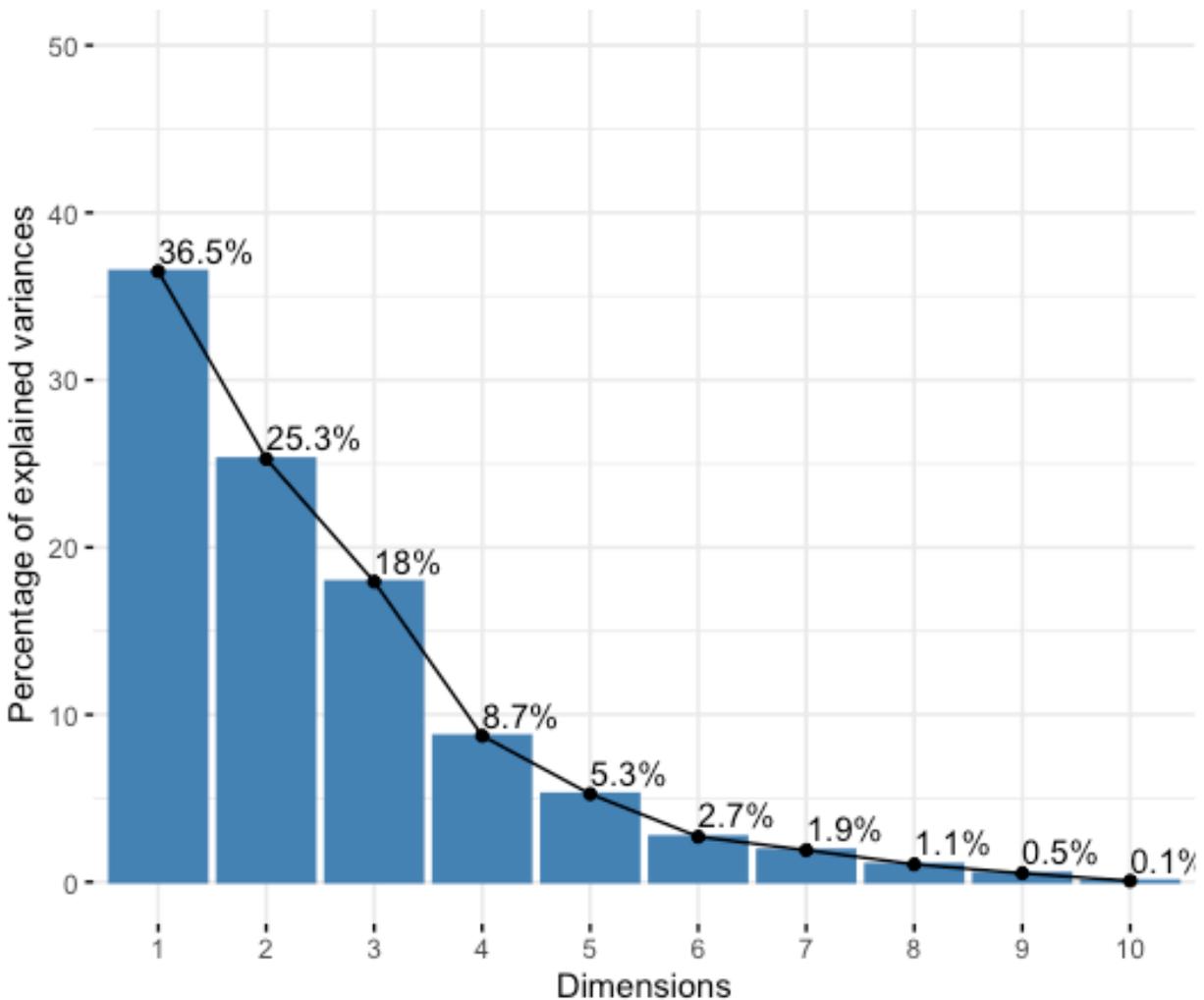
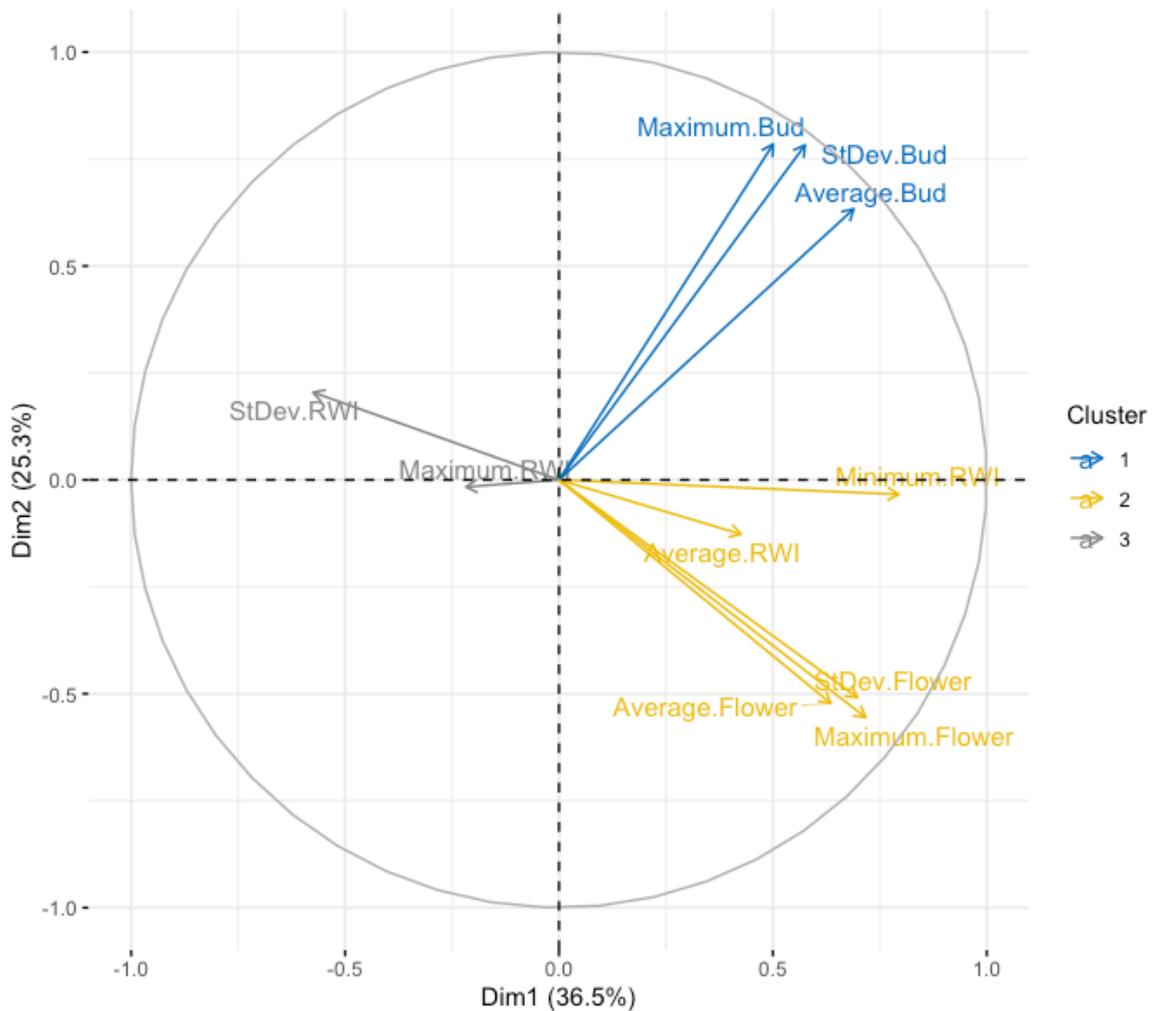


Figure 3.3 - Scree plot showing the % variance explained by each of the 10 principal components.

A bootstrap analysis was used to identify the statistically significant ( $p < 0.05$ ) factor loadings of the variables (

Table 3.5). PC1 was predominantly influenced by minimum annual stem growth (0.79), the maximum annual flowering (0.72), standard deviation of annual flowering (0.7) and average annual aborted bud occurrence (0.69). Meanwhile, PC2 was predominantly influenced by maximum annual aborted bud occurrence (0.78), the standard deviation of aborted bud occurrence (0.78) and average annual aborted bud occurrence (0.63). The contributing variables were coordinated into three distinct clusters aligned to the two Principal Components (Figure 3.4).



**Figure 3.4 - Cluster plot showing the relative contribution (correlations) of the variables to the PCA analysis.**

While there was no significant clustering by site or by a mesic/wet/dry classification, the analysis identified significant clustering by region as can be seen in Figure 3.5. The Alaska sites, for example, appear to be more strongly characterized by bud characteristics, while the Svalbard and

Northern Scandinavia sites appear to be more strongly characterised by the standard deviation and maximum annual stem growth.

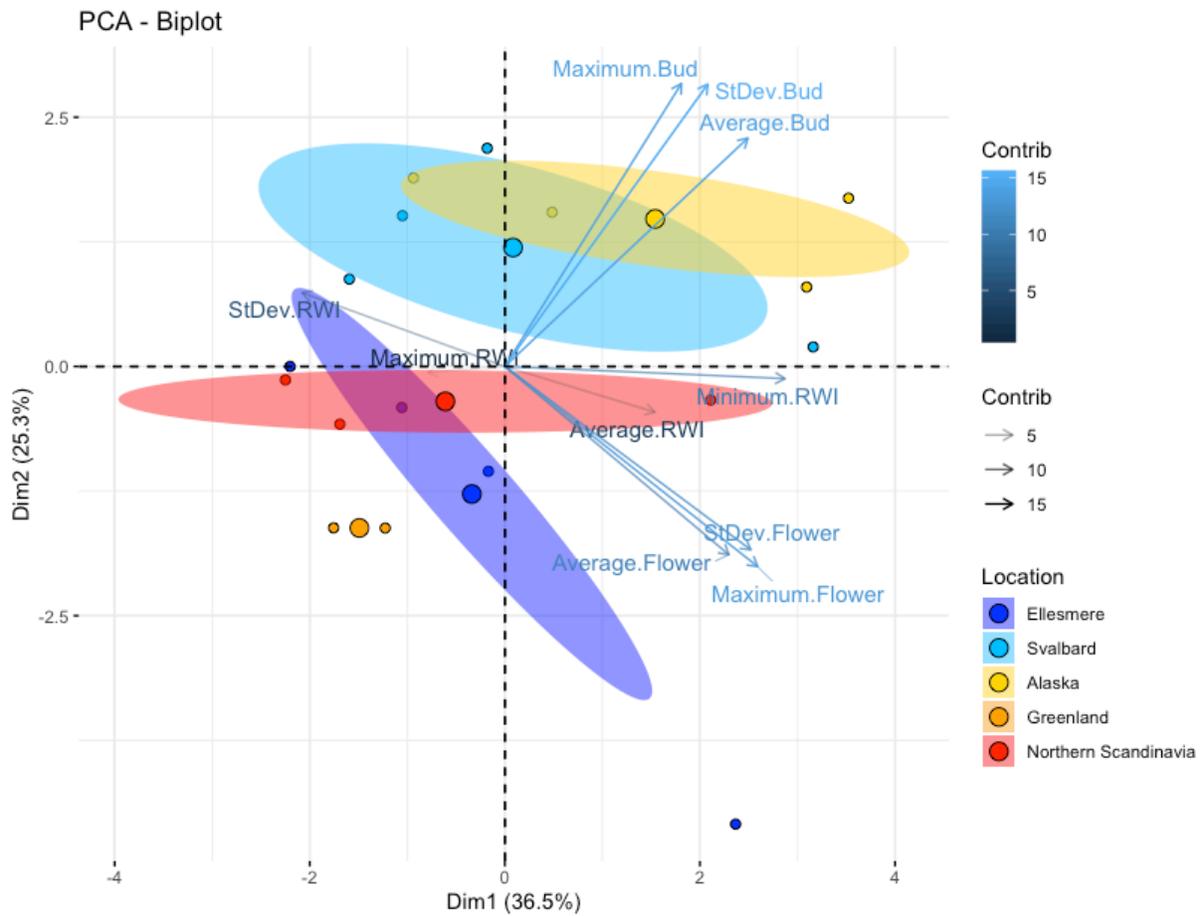


Figure 3.5 PCA Biplot showing clustering within ellipses by Arctic region (with 95% significance).

Table 3.5 : Bootstrap analysis for Principal Components 1 and 2.

PCA1 Variables	Correlation	<i>p</i> -value	PCA2 Variables	Correlation	<i>p</i> -value
Minimum RWI	0.794	0.0001	Maximum Bud	0.785	0.0001
Maximum Flower	0.717	0.001	StDev. Bud	0.783	0.0001
StDev. Flower	0.697	0.001	Average Bud	0.633	0.005
Average Bud	0.689	0.002	StDev. Flower	-0.509	0.031
Average Flower	0.635	0.005	Average Flower	-0.522	0.026
StDev. Bud	0.575	0.013	Maximum Flower	-0.555	0.017

Maximum Bud	0.501	0.034
StDev. RWI	-0.575	0.013

## 3.2 Discussion

### 3.2.1 Multi-Site Dendroclimatology Analysis

The dendrochronological characteristics of the stems collected at the circumpolar sites follow similar patterns to those exhibited by the Alexandra Fiord samples described in Chapter 2. For example, the interseries correlation was characteristically low amongst the master chronologies at each circumarctic site, as was also reported for each site at Alexandra Fiord. Again, this could be explained through the influence of resource partitioning between the branches of a *C. tetragona* plant, in addition to the influence of micro-environmental variability around and between plants within the same community (Johnstone & Henry 1997; Rayback & Henry 2005). Likewise, first-order autocorrelation was very low within the annual stem growth chronologies, as was also the case for the Alexandra Fiord sites. This indicates little relation between previous and current years of growth, and a more direct relationship with external factors such as the current year's summer air temperature (Johnstone & Henry, 1997; Rayback & Henry 2005; Rayback & Henry 2006; Rayback et al., 2012). It should be noted, however, that most of the chronologies included in this analysis were composed of fewer individual stems than the chronologies compiled at Alexandra Fiord.

The annual stem growth chronologies were mostly positively and strongly correlated with summer temperatures, though this relationship was only statistically significant at Disko Bay in Western Greenland (and notably only negligibly related at nearby Arctic Station). Meanwhile, the flower peduncle chronologies only exhibited a weak-moderate, non-significant relationship with July average temperature. Conversely, both the AWS and Skansbukta sites (Svalbard) exhibited a moderate and statistically significant relationship between annual aborted bud occurrence and July average temperature, while at other sites this relationship was effectively negligible. Although there was considerable inter-site variability, the relationships between the growth and reproductive chronologies and local summer air temperature were stronger at the High Arctic sites in comparison to the Low Arctic sites. Furthermore, the relationship between stem growth and

aborted bud occurrence was moderate to strong, and statistically significant at most of the High Arctic sites, while the relationship between stem growth and flower occurrence appears to have no latitudinal patterning.

A number of studies have hypothesised that High Arctic plants are more resistant to amplified growth as a result of accelerated climate warming (Arft et al., 1999; Hollister et al., 2005; Hudson & Henry, 2010; Elmendorf et al., 2012a). In this study, the stem growth response to a warming climate was not distinguishably stronger in the Low Arctic than the High Arctic, with some of the strongest growth-summer temperature correlations found in High Arctic sites (i.e. Ellesmere Island and Western Greenland). This result is comparable to other dendrochronology studies - for example, Havström et al. (1993) compared *C. tetragona* growth trends between sites in Ny Alesund (Svalbard) and Abisko (Sweden) and concluded that stem growth was more sensitive to air temperature increases in the High Arctic, while stem growth was more sensitive to light conditions, nutrient availability and competition for resources in the Low Arctic. More recently, Weijers et al. (2018) reported that dwarf shrub response to local summer temperature was relatively strong in the High Arctic in comparison to other plant functional types.

It has also been hypothesised that High Arctic plants show increased reproductive effort than those in the Low Arctic, and the use of both growth and reproductive chronologies in this multisite study provides an ideal lens through which to quantify fecundity of *C. tetragona* across the Arctic. In an early ITEX multisite synthesis, Arft et al. (1999) found that while flowering of multiple tundra shrub species took place significantly earlier as a result of passive warming experiments at all sites, the strongest reproductive trends were found in the High Arctic, compared to the higher growth and lower reproductive trends found in the Low Arctic. In our analysis, we found the highest correlations between stem growth and reproductive effort chronologies at Svalbard, Barrow, Alexandra Fiord and Disko - all classified as High Arctic. Furthermore, Klady et al. (2011) reported very high reproductive effort in warming experiments at Alexandra Fiord from a variety of tundra shrubs, explaining this behaviour as a strategy to colonise as many bare patches of exposed soil as possible within the growing season while flowering conditions are favourable. It appears the life history strategy of greater reproductive effort in *C. tetragona* in High Arctic sites

is supported by the results of our analysis. This may be partly explained by the lack of competition in the High Arctic in comparison to the Low Arctic: if the plant is competing against many other individuals in a more densely populated Low Arctic heath, it may invest its resources more heavily in stem growth and branching and produce fewer fruits.

### **3.2.2 Influence of Warming Experiments – Effect Size and Linear Mixed Effects Model**

Effect size analysis is a powerful tool for multi-site environmental analysis as it communicates the proportion of change as a result of experimental manipulation in a standardized fashion. Because some chronologies from the circumarctic sites did not extend far beyond the pre-experimental period, a BACI design was not feasible for this analysis. The largest effect sizes were found at the Alexandra Fiord field sites (High Arctic), and Latnjajaure (Low Arctic), while all of the effect sizes at the four Alaskan field sites, while positive, were either small or negligible. The results of the linear mixed effects model corroborated these findings, reflecting a universally linear positive relationship between experimental warming and stem growth at all sites. Indeed, this model estimates that passive warming experiments across the Arctic increase annual stem growth by 6.6 mm a year (at Alexandra Fiord this contribution ranged from 6.9 at the ‘Cassiope’ site to 14.78 at the ‘Annex’ site – indicating strong intra-site variability). Furthermore, the greatest variability in the stem growth - summer temperature relationship can be explained by regional differences (primarily Canadian High Arctic vs Alaskan Arctic vs Low Arctic mainland Scandinavia), with site-by-site differences only capturing 2% of the overall variability.

Many of the sites included in this analysis have been studied using other metrics of plant growth and reproductive change, such as long term observations of canopy height, biomass estimates and flower surveys. For example, Van Wijk et al. (2004) analysed changes in plant cover in Toolik Lake, and found that overall plant cover (including evergreen shrub cover) had not significantly increased under experimental warming conditions. While plant cover is not necessarily comparable to annual individual plant growth, our results indicate that in fact there has been a positive stem growth response to experimental warming, although the response seems to be somewhat dampened at the Alaska sites (including Toolik Lake). Likewise, Hollister et al. (2005) have noted that in Barrow and Atkasuk, the response to experimental warming was initially

strongest at Barrow whereas the long-term positive growth trend is highest at Atqasuk - as is reflected by the effect size analysis using *C. tetragona* stem growth chronologies presented in this chapter.

### 3.2.3 Principal Components

The strong regional signal captured in the linear mixed effects model is further corroborated by the results of the principal component analysis, in which 18 of the of the 24 control sites were significantly grouped into five distinct regional clusters: Alaska, Ellesmere, Greenland, Northern Scandinavia and Svalbard. There may be genetic precedent for these findings. In a multi-site study of the genetic structure of various tundra species, Eidesen et al. (2013) found the genetic structure of *C. tetragona* to fall within five distinct regional clusters: Beringia (East Russian Arctic & Alaska), Siberia, Central Canadian Arctic, Western Greenland / Eastern Canadian Arctic, and Eastern Greenland / Northern Scandinavia. These results were also reflected with similar genetic groups in an early study (Eidesen et al. 2007) and represent the same statistically significant regional clusters identified in our PCA analysis. It may be the case, therefore, that the highly regional growth and reproductive characteristics of *C. tetragona* may be informed by regional genotypic distributions. The dendrochronology growth and reproductive analysis methods could therefore be used to corroborate the genetic analysis which aims to identify spatial genetic clusters and borders, and reconstruct movement of Arctic shrub species (i.e. Abbott & Brochmann 2003).

While many have reported that soil moisture has a strong influence on plant response to warming (Elmendorf et al. 2012a; Bjorkman et al., 2018; Ackerman et al., 2017), the principal component analysis did not show any significant clustering via a soil moisture type classification. *C. tetragona* is a snowbed-adapted heather so all sites would likely have fairly similar soil moisture conditions, which may explain the lack of a relationship between soil moisture and plant growth and reproductive effort. However, there is still a need for further investigation of microsite conditions in tundra dendroecology as a means to explore site-specific heterogeneity (Myers-Smith et al., 2015; Weijers et al., 2015). Future dendroecology research should investigate the effect of factors such as microtopography, microclimate, soil moisture, snow depth, active layer depth and local

growing season windows on the strength and direction of a plant's response to accelerated climate warming.

## Chapter 4: Conclusion

### 4.1 Summary of Findings

This thesis aimed to sophisticate our understanding of *C. tetragona*'s growth and reproductive response to accelerated warming conditions across the Arctic. The updated dendrochronology methodology (in which stem growth measurement was conducted using image analysis software) increased efficiency and repeatability. For the first research question, we focused on five experimental field sites at Alexandra Fiord to investigate the effect of both experimental and ambient local warming over the last 30-40 years, comparing the plant's growth and reproductive patterns both before and after the establishment of open top warming chambers. We hypothesized that the stem growth and flowering of *C. tetragona* would accelerate under experimental warming conditions, and display a trend toward increased growth and reproduction as a result of ambient warming. At most sites, we observed a significant divergence in stem growth between warming and control plots shortly following the establishment of the passive warming structures, with the largest amplification of stem growth exhibited at the driest sites. Furthermore, though a phenology analysis, we found that since the installation of the warming experiment, the reproductive activity of *C. tetragona* takes place significantly earlier in the warmed plots. Finally, we found that annual stem growth and reproductive chronologies can be used to reconstruct July average temperatures to a high degree of success using a simple linear regression model function.

For our second research question, we investigated the extent to which *C. tetragona*'s growth and reproductive response to both ambient and experimental warming varied spatially across a number of long-term field sites across the Arctic. Despite theories that plants in the High Arctic are more resistant to warming summer temperatures than plants in the Low Arctic (Arft et al., 1999; Hollister et al., 2005; Hudson & Henry, 2010; Elmendorf et al., 2012a), we found that the most positive growth and reproductive responses to summer temperature were at the High Arctic sites, though a positive correlation between stem growth and summer conditions was exhibited across the Arctic. Through effects size analysis we found that while stem growth was amplified by experimental warming at all sites, the effect was greater at the High Arctic sites, in particular at Alexandra Fiord. We also found significant regional clustering in *C. tetragona*'s growth and

reproductive characteristics. This research helps to fill a vital research gap in *C. tetragona*'s role in dendroecology, as it provides a regional perspective to the use of the plant as a proxy for temperature variability and ecosystem change across a heterogeneously warming Arctic.

## 4.2 Future Directions

We have found that *C. tetragona* responds positively to experimental warming, although the extent of this change varies regionally. As it is possible to conduct similar dendroecological analysis on other common shrub species (Myers-Smith et al., 2015; Büntgen et al., 2015), it would be beneficial to apply the cross-site synthesis model adopted in Chapter 3 to other shrub species common within warming experiments, such as *D. integrifolia* and *S. arctica*. In Chapter 2, we called for a further consideration of microsite conditions as a means to explore site-specific heterogeneity in shrub growth and flowering characteristics (Myers-Smith et al., 2015; Weijers et al., 2015) – which could include a multivariate analysis taking into consideration environmental variables such as microtopography, active layer characteristics, and soil nutrient availability. Furthermore, we have identified that the regional clustering of *C. tetragona*'s growth and reproductive characteristics appears to mirror the regional clustering present in the plant's genetic structure (Eideson et al., 2007; Eideson et al., 2013). These analyses could be repeated using other shrub species to explore the extent to which genotypic distributions influence present-day growing season behaviours and Arctic vegetation change.

As a proxy of summer air temperature, we recommend the continued use of both stem growth and reproductive chronologies in the construction of predictive models. In addition, we recommend the use of Cybis CooRecorder and CDendro software (Larsson 2016) to streamline the dendrochronology process, from annual growth increment measurements, to cross-dating and standardization, to the generation of master chronologies. However, while the updated measurement methodology increased the amount of stem samples that could be included in our analysis, the sample size for some sites was very small – perhaps reducing the quality of the detrended master stem growth and reproductive chronologies. While we were able to cover a variety of circumarctic regions, there are still key regional gaps, including Siberia and the Western Canadian Arctic. As noted in Chapter 3, future analysis must take heterogeneity within individual

field sites into greater consideration. Furthermore, a better understanding of resource partitioning would help to streamline the dendrochronology methodology for the plant.

### **4.3 Concluding remarks**

As the environmental effects of warming in the Arctic continue to outpace those of other global regions (Serreze & Francis, 2006), it is imperative to develop proxy records of climate and ecosystem change to understand past and current rates of change, and to better predict future change. This thesis aimed to further develop our understanding of the growth and reproductive responses of *C. tetragona* to amplified climate warming, and our results have enhanced our understanding of how the plant responds differently to accelerated climate warming across different geographical and bioclimatic zones.

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## Appendices

### Appendix A

Table A.1 : Descriptive Statistics for the annual growth increments at sites at which OTCs were implemented in 1992

<b>Annual Stem Growth (mm / year)</b>	<b>Dryas Control</b>	<b>Dryas OTC</b>	<b>Vaccinium Control</b>	<b>Vaccinium OTC</b>	<b>Cassiope Control</b>	<b>Cassiope OTC</b>
<b>Mean (pre-OTC)</b>	4.52	3.75	3.22	3.75	3.49	3.3
<b>SD</b>	0.7	0.74	0.45	0.7	0.46	0.6
<b>Mean (post-OTC)</b>	4.84	5.63	5.05	5.85	5.16	7.06
<b>SD</b>	0.71	1.03	1.08	1.21	0.9	7.19

Table A.2: Descriptive Statistics for the annual growth increments at sites at which OTCs were implemented in 2010

<b>Annual Stem Growth (mm / year)</b>	<b>Annex Control</b>	<b>Annex OTC</b>	<b>Migration Control</b>	<b>Migration OTC</b>
<b>Mean (pre-OTC)</b>	4.23	3.97	4.52	5.53
<b>SD</b>	0.59	0.83	0.95	0.79
<b>Mean (post-OTC)</b>	5.38	6.04	5.38	6.32
<b>SD</b>	0.6	1.36	0.92	0.99

## Appendix B

**Table A.3 All Sites – August Max Regression Results**

	<i>Dependent variable:</i>
	Overall Rating
Dryas Site - Stem Length Index	9.868 (-2.618, 22.354)
Vaccinium Site - Stem Length Index	2.897 (-7.982, 13.776)
Cassiope Site - Stem Length Index	5.166 (-5.257, 15.588)
Cassiope Site - Bud Occurrence	0.131 (-3.480, 3.743)
Cassiope Site - Flower Occurrence	1.528 (-6.741, 9.797)
Vaccinium Site - Bud Occurrence	0.285 (-0.744, 1.314)
Vaccinium Site - Flower Occurrence	0.304 (-1.633, 2.241)
Dryas Site - Flower Occurrence	-2.701 (-8.882, 3.479)
Dryas Site - Bud Occurrence	-1.617 (-8.158, 4.924)
Cassiope Site - Bud & Flower Interaction	-1.388 (-5.892, 3.116)
Vaccinium Site - Bud & Flower Interaction	-0.540 (-1.329, 0.248)
Dryas Site - Bud & Flower Interaction	1.978 (-5.454, 9.411)
Constant	-8.426** (-14.060, -2.792)
Observations	20
R <sup>2</sup>	0.883
Adjusted R <sup>2</sup>	0.682
<i>Note:</i>	* p < 0.05 ** p < 0.01 *** p < 0.001

**Table A.4 Cassiope Site – August Max Regression Results**

	<i>Dependent variable:</i>
	Overall Rating
Cassiope Site - Stem Length Index	14.305*** (9.242, 19.368)
Cassiope Site - Bud Occurrence	0.011 (-2.253, 2.275)
Cassiope Site - Flower Occurrence	-0.055 (-2.813, 2.704)
Cassiope Site - Bud & Flower Interaction	-0.987 (-2.684, 0.711)
Constant	-6.219** (-11.052, -1.385)
Observations	20
R <sup>2</sup>	0.687
Adjusted R <sup>2</sup>	0.603
<i>Note:</i>	* p ** p *** p<0.01

**Table A.5 Dryas Site – August Max Regression Results**

	<i>Dependent variable:</i>
	Overall Rating
Dryas Site - Stem Length Index	14.067*** (9.676, 18.458)
Dryas Site - Bud Occurrence	-0.493 (-2.099, 1.113)
Dryas Site - Flower Occurrence	-0.842 (-3.234, 1.551)
Dryas Site - Bud & Flower Interaction	0.020 (-1.704, 1.743)
Constant	-5.330** (-9.168, -1.492)
Observations	20
R <sup>2</sup>	0.757
Adjusted R <sup>2</sup>	0.693
<i>Note:</i>	* p ** p *** p<0.01

**Table A.6 All Sites – July Average Regression Results**

	<i>Dependent variable:</i>
	Overall Rating
Dryas Site - Stem Length Index	3.555 (-5.720, 12.830)
Vaccinium Site - Stem Length Index	2.504 (-5.945, 10.952)
Cassiope Site - Stem Length Index	2.579 (-5.868, 11.025)
Cassiope Site - Bud Occurrence	-2.729* (-5.145, -0.314)
Cassiope Site - Flower Occurrence	-1.004 (-5.211, 3.202)
Vaccinium Site - Bud Occurrence	-0.321 (-1.119, 0.476)
Vaccinium Site - Flower Occurrence	-0.361 (-1.902, 1.180)
Dryas Site - Flower Occurrence	-0.099 (-3.624, 3.426)
Dryas Site - Bud Occurrence	0.238 (-3.570, 4.046)
Cassiope Site - Bud & Flower Interaction	0.805 (-1.410, 3.020)
Vaccinium Site - Bud & Flower Interaction	0.120 (-0.424, 0.664)
Dryas Site - Bud & Flower Interaction	0.376 (-3.784, 4.536)
Constant	1.150 (-3.488, 5.788)
Observations	23
R <sup>2</sup>	0.787
Adjusted R <sup>2</sup>	0.531
<i>Note:</i>	* p ** p *** p<0.01

**Table A.7 Cassiope Site – July Average Regression Results**

	<i>Dependent variable:</i>
	Overall Rating
Cassiope Site - Stem Length Index	7.303*** (3.972, 10.635)
Cassiope Site - Bud Occurrence	-2.276*** (-3.781, -0.772)
Cassiope Site - Flower Occurrence	-0.117 (-1.611, 1.377)
Cassiope Site - Bud & Flower Interaction	0.560 (-0.456, 1.575)
Constant	1.335 (-1.701, 4.371)
Observations	23
R <sup>2</sup>	0.683
Adjusted R <sup>2</sup>	0.612
<i>Note:</i>	* p ** p *** p<0.01

**Table A.8 Cassiope Site OTCs – July Average Surface Temperature Regression**

	<i>Dependent variable:</i>
	Overall Rating
Cassiope Site – Stem Length Index	7.481** (2.059, 12.904)
Cassiope Site – Flower Occurrence	3.470** (0.389, 6.552)
Cassiope Site – Bud Occurrence	1.302 (-0.558, 3.161)
Cassiope Site – Bud & Flower Interaction	-2.158** (-3.989, -0.327)
Constant	1.431 (-3.212, 6.073)
Observations	22
R <sup>2</sup>	0.629
Adjusted R <sup>2</sup>	0.542
<i>Note:</i>	* p ** p*** p<0.01

**Table A.9 Cassiope Site OTCs – August Average Surface Temperature Regression**

	<i>Dependent variable:</i>
	Overall Rating
Cassiope Site – Stem Length Index	0.309 (-3.618, 4.237)
Cassiope Site – Flower Occurrence	4.584*** (2.312, 6.856)
Cassiope Site – Bud Occurrence	0.785 (-0.509, 2.079)
Cassiope Site – Bud & Flower Interaction	-1.271* (-2.592, 0.049)
Constant	1.683 (-1.494, 4.859)
Observations	23
R <sup>2</sup>	0.712
Adjusted R <sup>2</sup>	0.648
<i>Note:</i>	* p ** p*** p<0.01

## Appendix C

**Table A.10 - Summary table for the linear mixed effects model.**

*Dependent variable:*

	Annual Stem Growth
July Average Temperature	0.280 <sup>***</sup> (0.035)
Experiment (Warming Treatment)	0.665 <sup>***</sup> (0.105)
Constant	3.404 <sup>***</sup> (0.932)
Observations	1080
Log Likelihood	-770.435
Akaike Inf. Crit.	1552.871
Bayesian Inf. Crit.	1577.976

*Note:* \* $p < 0.05$ ; \*\* $p < 0.01$ ; \*\*\* $p < 0.001$

Groups	Variance.
Site (Intercept)	0.0305
Region (Intercept)	2.3072
Residual	1.3355

*Number of obs: 485, groups: Site, 10; Region, 3.*