

CASSIOPE TETRAGONA AND CLIMATE CHANGE
IN THE CANADIAN HIGH ARCTIC:
EXPERIMENTAL STUDIES AND RECONSTRUCTION OF PAST CLIMATE FOR
ELLESMERE ISLAND, NUNAVUT, CANADA

by

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Abstract

This research examines the responses of the circumpolar, evergreen, dwarf-shrub, *Cassiope tetragona* (L.) D. Don (Ericaceae) (arctic white heather) to experimental warming and natural climatic variability through dendrochronological techniques. The study's goals were: (1) to quantify *C. tetragona* growth and reproductive responses prior to and during experimental temperature enhancement, (2) to reconstruct 20th century climate for Alexandra Fiord and central Ellesmere Island based on *C. tetragona* chronologies, (3) to conduct a comparative analysis of my climate reconstruction with other climate proxies from northern North America.

In 1992, permanent open-top chambers (OTCs) were established in heath tundra plant communities at Alexandra Fiord, Ellesmere Island. The OTCs raised the growing season temperature by 1.3°C. Using dendrochronological techniques, the responses of *C. tetragona* prior to (1986-1991) and during (1992-1998) the experimental warming were investigated. *Cassiope tetragona* exhibited a strong reproductive response, but weak growth response to the experimental warming. The results confirm that reproductive development in high arctic plants is more sensitive to the thermal environment than vegetative growth, and, summer temperatures are critical to tundra ecosystems for successful reproduction.

Secondly, dendroclimatological analysis of *C. tetragona* was used to reconstruct past summer temperature for Alexandra Fiord and central Ellesmere Island. Three *C. tetragona* populations were sampled at Alexandra Fiord (78° 52'N, 75° 47'W) and one at Hot Weather Creek (79° 58'N, 84° 28'W). Two growth and two reproduction chronologies were developed for each sampling site. The 95-year long reconstruction (1899-1994) of August-September average air temperature for Alexandra Fiord was the longest *C. tetragona*-based proxy record and explained 51% of the dependent climate variance. A second reconstruction of August-September average air temperature based upon chronologies from Alexandra Fiord and Hot Weather Creek explained 66% of the dependent climate variance. The reconstructions revealed an increase in summer temperature from the 1920s-1960s, a cooling period from the 1960s-1970s, and finally, a second increase in summer temperature beginning in the 1980s. Other arctic climate proxies support this study's conclusions. Finally, correlation analysis revealed that high summer Arctic

Oscillation index values are associated with unfavorable growing season conditions, resulting in reduced growth and reproduction in *C. tetragona* populations on Ellesmere Island.

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1. Introduction

1.1. Climate Change in the Arctic

From the time of Louis Agassiz and his contemporaries, Quaternary scientists have been interested in piecing together and understanding the complex record of past climate change. Accumulating evidence from many scientific disciplines has shown that the Northern Hemisphere has experienced repeated major climatic changes, as well as shorter and more abrupt fluctuations (Smol *et al.* 1991). In the Northern Hemisphere, high latitude sites have been identified as crucial reference points for environmental monitoring as they are especially sensitive to climatic change (Roots 1989; Douglas and Smol 1994). Research based on paleoclimatic and instrumental data from the Arctic has demonstrated that climate change during the twentieth century was anomalous in terms of the rate and magnitude. Paleoclimatic records from arctic sites suggest that temperatures have increased at an unprecedented rate since the end of the Little Ice Age (c. 1850), with many arctic regions experiencing both the coldest (end of Little Ice Age) and the warmest (1990s) temperatures for at least four hundred years and possibly several millennia (Jacoby and D'Arrigo 1989; Bradley 1990; Koerner and Fisher 1990; D'Arrigo and Jacoby 1992; 1993; Lamoureux and Bradley 1996; Overpeck *et al.* 1997; D'Arrigo *et al.* 1999; Hughen *et al.* 1999; Bradley 2000). At the close of the twentieth century, analysis of instrumental climate records from Arctic Canada revealed that the decade of 1989-1998 and the summer of 1998 were the warmest ever recorded (Meteorological Service of Canada, National Archive and Data Management, Environment Canada, 2002). For the twenty-first century, General Circulation Models (GCMs) predict continued significant climate change in association with anthropogenic and natural forcing factors. The greatest temperature increases were forecast for the Arctic (IPCC 1996; 2001). Thus, in order to understand current and future climate change in the Arctic, proxy records are necessary to gain a full understanding of how climate has varied in the past (Bradley and Jones 1993).

1.2. Proxy Climate Data

Paleoclimatic research and the resulting climate proxies provide the necessary perspective to understand past climate variability. Proxy data provide a means through which: (1) reference conditions can be determined, (2) natural climatic variability can be assessed, and (3) future climatic conditions and their impacts might be inferred (Smol and Douglas 1996). Understanding the unique spatial and temporal variability of arctic climate during the past 100-150 years is crucial to understanding current and future climate change, as well as its potential impact on arctic tundra ecosystems. However, as the instrumental record is short and geographically sparse, and only a limited number of high-resolution climate proxies exist for Arctic Canada (Hardy and Bradley 1997), new research is needed to fill the geographic gaps and to supplement existing paleoclimatic studies.

1.3. Arctic Vegetation and Climate Change

Previous studies indicate that arctic plant growth and reproduction are directly and indirectly limited by a range of environmental variables, including temperature (Bliss 1956; 1962; Billings and Mooney 1962; Chapin 1983; Henry *et al.* 1986; Shaver *et al.* 1986; Billings 1987; Shaver and Kummerow 1992). It is believed the future impact of climate change on the abiotic and biotic components of the arctic tundra ecosystem as predicted by GCMs will be substantial (Maxwell 1992; IPCC 2001). Increasing temperature would directly and indirectly impact arctic tundra vegetation through changes in geophysical feedback mechanisms and biogeochemical cycles (Swift *et al.* 1979; Chapin 1984; Oeschel and Billings 1992; Smith 1993; Robinson *et al.* 1998; IPCC 2001). Experimental studies offer one way to understand the response of arctic plant growth and reproduction to current and future climate change.

1.3.1. *Cassiope tetragona*

Cassiope tetragona (L.) D. Don (Ericaceae) (arctic white heather) is an evergreen, dwarf-shrub with a circumarctic distribution (Polunin 1959; Hultén 1968; 1971). Well-established individuals are long-lived, surviving for up to 100+ years (personal observation). It

is an important component of high and mid-arctic vegetation communities including, low shrub-heath, dwarf-shrub heath and mixed heath communities (Bliss and Mateyeva 1992). The species typically forms loose, prostrate cushions of monopodial stems (Sørensen 1941). Along the length of the stem, two alternating sets of opposite leaves form which are photosynthetic for three to ten years and may remain attached to the stem for periods up to and beyond 20 years (Callaghan *et al.* 1989; personal observation). *Cassiope tetragona* produces white, pendulous, bell flowers which form fruits with multiple seeds (Sørensen 1941). However, reproduction in *C. tetragona* is often unsuccessful due to unfavorable environmental conditions which lead to heavy flower and fruit abortion (Molau 1983) and a low number of seedlings (Freedman *et al.* 1982; Havstrom *et al.* 1993).

Cassiope tetragona is characterized by its slow growth and by its longevity. The species' short- and longer-term response to growing season conditions, both natural and ameliorated, have been investigated in several studies (Nams 1982; Callaghan *et al.* 1989; Havström *et al.* 1993; 1995; Johnstone 1995; Johnstone and Henry 1997; Molau 1997; 2001). The results of field experiments investigating the vegetative growth and reproductive responses to short-term temperature enhancement were equivocal. While the species has the potential to respond positively to increases in growing season temperature, it did not do so at all sites nor for all vegetative growth and reproductive variables (Nams 1982; Nams and Freedman 1987b; Havström *et al.* 1993; 1995b; Johnstone 1995; Bliss *et al.* 1997; Molau 1997; 2001). However, results from temperature enhancement studies are typically based on five years or less of experimental warming data and these indicated that longer-term investigations are needed.

In previous research, retrospective analysis of *C. tetragona* growth and reproduction was used to investigate and to reconstruct the species' response to past climate conditions for relatively long time periods (Callaghan *et al.* 1989; Havström *et al.* 1993; 1995; Johnstone and Henry 1997). Retrospective analysis is based upon modified dendrochronological and dendroclimatological techniques (Callaghan *et al.* 1989; Johnstone and Henry 1997). The results from previous studies indicated that its high arctic populations responded significantly to summer growing season temperature (Callaghan *et al.* 1989; Havström *et al.* 1993; 1995; Johnstone and Henry 1997). In addition, retrospective analysis was used to reconstruct average July temperature and July growing degrees for periods of up to 35 years (Havström *et al.* 1995; Johnstone and Henry 1997). Given the success of previous climate reconstructions using *C.*

tetragona growth and reproduction as predictors, and the possibility that the species can live for over 100 years, there is great potential for reconstructing past climate of high-resolution and moderate duration for high arctic sites where few or no instrumental or proxy data are yet available.

1.4. Research Framework

The first part of the thesis reports the results from a warming experiment conducted at Alexandra Fiord, Ellesmere Island, Canada as part of the International Tundra Experiment (ITEX). The purpose of the warming experiment was to investigate the current response and the potential future effects of recent and predicted climate change on *C. tetragona* growth and reproduction. Plants from a high arctic population were subjected to a short-term (7 years) temperature enhancement experiment using passive, open-top greenhouses. The retrospective analysis technique was used to reconstruct the growth and reproductive responses of the *C. tetragona* population to temperature both prior to (1986-1991) and during (1992-1998) the warming experiment (Chapter 2).

In the second part of the thesis, past summer temperature was reconstructed and analyzed for two sites on Ellesmere Island, Canada. Using modified dendrochronological techniques, chronologies of *C. tetragona* growth and reproduction were constructed for three sites at Alexandra Fiord and for one site at Hot Weather Creek. Through dendroclimatological analysis, *C. tetragona* chronologies were related to instrumental climate records from Alexandra Fiord (1980-1996) and the Eureka High Arctic Weather Station (1948-1996), Ellesmere Island, and used to reconstruct past growing season temperature for Alexandra Fiord (1899-1996) (Chapter 3) and for central Ellesmere Island (1948-1996) (Chapter 4). The temperature reconstructions for Alexandra Fiord and central Ellesmere Island were compared with instrumental climate data and other climate proxies from the Canadian Arctic, including tree-ring, lake varve sediments, ice core melt records and fresh water diatoms. Lastly, the chronologies developed for the Lowland and Hot Weather Creek sites were compared with the Arctic Oscillation index for the period 1948-1996 (Chapter 4). A summary and conclusions are presented in Chapter 5.

2. Retrospective analysis of the growth and reproductive response of *Cassiope tetragona* to experimental warming

2.1. Introduction

2.1.1. Climate Change in the Arctic

General circulation models (GCMs) of the Earth's atmosphere predict significant climate change at high latitudes within the first half of the twenty-first century due to the effects of anthropogenically enhanced greenhouse gases in the atmosphere (Maxwell 1992; IPCC 1996; 2001). The GCMs predict mean annual global surface air temperature will rise by 1.4–5.8 °C (IPCC 2001). However, the greatest temperature increase is forecast for the Arctic; 4.0–7.5 °C in summer and 2.5–14.0 °C in winter (Carter *et al.* 2000; IPCC 2001). While it is thought that predicted future warming in the circumpolar north will vary on both an areal and temporal basis, the direct and indirect impacts on the abiotic and biotic components of arctic tundra ecosystems will be substantial and will continue for centuries (Maxwell 1992; IPCC 2001). In fact, there is strong evidence that climate change has already had an impact on the Arctic including: increases in air temperature (Jones *et al.* 1999; Serreze *et al.* 2000) and precipitation (Groisman *et al.* 1991; Groisman and Easterling 1994; Georgiyevskii 1998), decreases in sea ice thickness and extent (Cavalieri *et al.* 1997; Wadhams 1997; Parkinson *et al.* 1999; Johannessen *et al.* 1999; Rothrock *et al.* 1999; Serreze *et al.* 2000), reduction in snow-cover extent (Brown 2000; Serreze *et al.* 2000), retreat of glaciers and ice caps (Koerner and Lundegaard 1996; Dowdeswell *et al.* 1997), changes in ocean circulation and temperature (Carmack *et al.* 1995; Maslanki *et al.* 1996; McPhee *et al.* 1998), deepening of the active layer and change in the distribution and temperature of permafrost (Halsey *et al.* 1995; Weller 1998; Weller and Lange 1999; Osterkamp *et al.* 2000).

General circulation models predict that increased temperatures will lead to alterations in geophysical feedback mechanisms impacting surface energy and water balances in the Arctic (Smith 1993; Robinson *et al.* 1998; IPCC 2001). Decreasing sea ice and snow cover due to the greenhouse effect would lead to a reduced surface albedo, increasing the absorption of solar radiation and terrestrial net radiation (Maxwell 1992; IPCC 2001). Increased net radiation

would, in turn, result in a positive feedback loop with further ice and snowmelt associated with the dissemination and storage of warmth in the atmosphere and ocean. Furthermore, GCMs forecast a decrease in the thickness and the retreat northward of the continuous permafrost boundary, as well as associated deepening of the active layer (Kane *et al.* 1992; Maxwell 1992; IPCC 2001). Changes in arctic permafrost would strongly affect the surface and subsurface hydrological regime of the Arctic (Kane *et al.* 1992; Osterkamp *et al.* 2000). Most general circulation models predict an increase in net annual precipitation throughout the circumpolar north, although the models' conclusions are far from uniform (Maxwell 1992; Stewart 2000; IPCC 2001). Greater cyclonic activity in winter combined with warmer winter temperatures should produce greater snowfall (Maxwell 1992). However, predicted spring and summer warming is expected to result in earlier snowmelt and a prolonged growing season (Barry 1982; IPCC 2001).

Future warming in the Arctic would likely lead to biogeochemical changes in tundra ecosystems. Increased temperature and variable soil moisture may increase microbial activity, thus stimulating decomposition and nutrient mineralization (Swift *et al.* 1979; Gates *et al.* 1992; Kane *et al.* 1992; Waelbroeck 1993; Groisman *et al.* 1994). Net trace gas fluxes between the atmosphere and tundra ecosystems are also hypothesized to change. Accelerated decomposition rates associated with permafrost loss and a deepening active layer could result in the increased release of carbon dioxide into the atmosphere from previously buried and frozen organic soils (Billings *et al.* 1982; Billings 1987a; Oeschel and Billings 1992; Oechel *et al.* 1993; McKane *et al.* 1997a and b). The influence of potentially anthropogenically-induced climate change on these biogeochemical and other geophysical factors will ultimately impact terrestrial tundra ecosystems

Predicted temperature increase is expected to directly affect tundra plant growth and phenology, while ecosystem functioning will be indirectly mediated by nutrient and moisture changes (Chapin *et al.* 1995; Harte and Shaw 1995; Wookey *et al.* 1995). Tundra plant species will respond individually to environmental changes in temperature, light and nutrients (Chapin *et al.* 1997; Callaghan *et al.* 1998). However, their interactions and cumulative response will dictate plant community composition and diversity on micro- and meso-scales, in addition to propelling future landscape-scale changes (Chapin and Shaver 1985; Henry *et al.* 1986; Wookey *et al.* 1993; Chapin *et al.* 1995; Henry and Molau 1997; Press *et al.* 1998). Given the

complexity and uncertainty inherent in predicting tundra ecosystems responses to climate change, the importance of defining precise relationships between climatic controls and ecosystem components becomes that much more critical (Kielland and Chapin 1992; Maxwell 1992; Wookey *et al.* 1995).

2.1.2. Simulated Environmental Change

The appeal of arctic ecosystems "...small vegetation stature, low species diversity and fine grained environmental variation..."(Chapin and Shaver 1985) has proven alluring to scientists interested in the effects of various environmental factors on ecosystem structure and function (Wookey *et al.* 1993). Furthermore, field-based experiments enable researchers to assess the ecological impacts of specific abiotic environmental factors within the context of an otherwise natural ecosystem (Chapin and Shaver 1985; Wookey *et al.* 1993). Over the past two decades, field experiments designed to determine plant responses to environmental change and to examine limiting factors have been conducted in various arctic ecosystems (e.g., Chapin and Shaver 1985; McGraw 1985; Henry *et al.* 1986; Shaver *et al.* 1986; Grulke *et al.* 1990; Havström *et al.* 1993; Oeschel *et al.* 1993; Wookey *et al.* 1993; 1995; Parsons *et al.* 1994; Chapin *et al.* 1995; Henry and Molau 1997; Welker *et al.* 1997; Press *et al.* 1998; Robinson *et al.* 1998; Arft *et al.* 1999).

The International Tundra Experiment (ITEX), begun in the early 1990s, was initiated in response to predictions made by GCMs of significant climate change in high latitude ecosystems (Henry and Molau 1997). ITEX provides a structure for international, collaborative, long-term research on plant and community responses to climate change throughout the circumpolar north and in high altitude mountain ranges (Molau 1993). The multi-site experiment employs a common temperature manipulation to examine variability in response of arctic and alpine species to increased warmth across climatic and geographic gradients of tundra ecosystems (Henry and Molau 1997; Arft *et al.* 1999). The studies are a combination of annual monitoring of the phenology, growth and reproduction of plant species, and simple field experiments designed to simulate predicted climate change (Henry and Molau 1997). Initial results from the ITEX study have provided ecologists with a preliminary understanding of the nature of plant variation in response to warming experiments across broad geographic and

climatic gradients (Henry 1997; Arft *et al.* 1999). Two recent ITEX studies focused on the growth and reproductive variability within and between populations of *Cassiope tetragona* (arctic white heather), one of the ten key ITEX species (Johnstone 1995; Molau 1997).

2.1.3. Experimental Warming and *Cassiope tetragona*

Previous studies which examined the responses of high arctic *C. tetragona* plants to experimental warming yielded mixed results. A two-year warming experiment of *C. tetragona* plants at a high arctic site at Ny-Ålesund, Svalbard, Norway, showed strong correlations between vegetative growth and summer climate conditions (Havström *et al.* 1993). The conclusions from this experimental warming study suggested that northern populations of *C. tetragona* are limited primarily by temperature and should respond positively to an increase in average summer temperature (Havström *et al.* 1993). An early study at Alexandra Fiord, Ellesmere Island, Canada, also resulted in a positive annual growth response in stem length to experimental warming after one growing season (Nams 1982). However, in these early investigations, greenhouse temperatures were raised by approximately 3-5 °C. More recent studies completed under the auspices of ITEX raised growing season temperatures by 1-3 °C, an increase that coincides more closely with recent GCM predictions for the high arctic (Maxwell 1992; Marion *et al.* 1997; IPCC 2001).

A two-year study of *C. tetragona*, conducted by Johnstone (1995) at Alexandra Fiord produced mixed results. At one of the Alexandra Fiord lowland study sites, annual shoot elongation was positively affected by experimental warming while at the second site it was not (Johnstone 1995). A three- and a five-year study at the sub-arctic ITEX site in Latnjajaure, northern Swedish Lapland resulted in no significant response of annual stem elongation to increased temperature (measured as total degree days above 0 °C for the growing season) (Molau 1997; 2001). The absence of a vegetative growth response to short-term experimental warming parallels results from research on other arctic evergreen species, such as *Saxifraga oppositifolia* L. (Stenström *et al.* 1997), *Diapensia lapponica* L. (Molau, unpublished data), and *Dryas octopetala* L. (Welker *et al.* 1993; but see Welker *et al.* 1997; Wookey *et al.* 1993).

In addition to investigating the vegetative response, several studies also examined the reproductive response of *C. tetragona* to experimental warming. The reproductive success of *C. tetragona* is highly sensitive to climate conditions of the previous and current year (Bliss *et al.* 1977; Nams and Freedman 1987b). In the aforementioned two-year study at Alexandra Fiord, increased temperature resulted in a strong positive response in the production of flowers and buds and an increase in seed viability (Johnstone 1995). Nams (1982) also observed a greater number of buds produced on experimentally warmed *C. tetragona* plants. The reproductive response of other high arctic evergreen species such as *Dryas octopetala* also showed a significant increase in flower production, seed set, seed weight and seed viability following favorable growing season conditions (Wookey *et al.* 1993; 1995). Strikingly, Havström *et al.* (1995) found no significant warming effect (temperature raised by 2.5-5 °C) on *C. tetragona* flowering frequency after four years of treatment at two subarctic sites near Abisko, Sweden. While observations of *C. tetragona* plants under experimental warming treatments appear to indicate an increase in reproductive success, the results are equivocal.

2.1.4. Retrospective Analysis of *Cassiope tetragona*

Dendrochronology is the study of the patterns of annual tree-ring widths (Fritts 1976). The technique facilitates the identification and reconstruction of common patterns of ring-width variation among trees within a region and allows for the identification of the exact calendar year of each ring (Fritts 1976). Precisely dated tree-ring chronologies may extend backwards in time for hundreds to thousands of years providing retrospective information on small- and large-scale fluctuations in climate, environmental disturbances and ecological relationships, depending on the chronology quality and research objectives (Fritts 1976; Cook and Kariukstis 1990).

The dendrochronological proxy technique was later modified by Callaghan *et al.* (1989) and Johnstone and Henry (1997) for use with *C. tetragona* to reconstruct ecological relationships and climate. Callaghan *et al.* (1989) outlined a retrospective analysis technique that used the pattern in leaf-lengths along the *C. tetragona* plant stem to delimit annual growth. They were able to develop growth chronologies of up to 20 years for three sites, two located in northern Swedish Lapland and one on Svalbard, Norway. By investigating the relationship between growth and climate using dendrochronological techniques, Callaghan *et al.* (1989)

developed climate response functions that explained up to 74% of the variance in the measured growth variables. More recently, Johnstone and Henry (1997) determined that patterns in the positioning of leaf nodes in adjacent leaf rows on the plant's stem were analogous to the patterns in leaf-length. Using this modified technique, they were able to date annual growth increments and generate longer chronologies (up to 35 years). Johnstone and Henry (1997) generated one reproductive and two growth chronologies that were significantly and positively correlated with June and July temperatures. Flower production was the most sensitive variable to summer climate conditions with climate response functions explaining up to 84% of the variation in the flower chronology (Johnstone and Henry 1997). These investigations indicate that retrospective analysis of *C. tetragona* could provide valuable information on past production and the long-term variability of the plants' vegetative growth and reproductive variables.

2.1.5. Research Objectives

In this chapter, the three objectives were: (1) to construct two vegetative growth and two reproductive chronologies which cover the period prior to and during the establishment of an experimental warming treatment; (2) to investigate the short-term trends and inter-annual variability of reproduction and growth for the pre-treatment and treatment periods and; (3) to evaluate the response of the variables to natural climatic variation and experimental warming. The pre-treatment period was defined as the period of time (1986-1991) prior to the initiation of the warming experiment in the summer of 1992 at Alexandra Fiord, Ellesmere Island. The treatment period was defined as the period of time from July 1992 to late August 1998 when the plants were harvested.

2.2. Methods

2.2.1. Species Characteristics

Cassiope tetragona is a long-lived, evergreen, dwarf shrub with a wide geographical range. The species has a circumpolar distribution, found at the highest latitudes to the

subarctic, with extensions into some alpine regions (Polunin 1948; 1959; Böcher *et al.* 1968; Hultén 1968; 1971). Throughout its range, it is a component of low shrub-heath, dwarf shrub-heath and mixed heath communities (Böcher 1954; 1959; 1963; Gjaerevoll and Bringer 1965; Igoshina 1969; Rønning 1969; Beschel 1970; Chepurko 1972; Thompson 1980; Bliss and Matveyeva 1992). The species may occur on well-drained heath tundras and fellfields with moderate snow cover in winter (Polunin 1959; Nams and Freedman 1987a; Muc *et al.* 1989). It may also occur at the base of raised beach ridges or on steep slopes where snow persists into the growing season as snowbeds, particularly in the high arctic (Porsild 1920; 1955; Polunin 1948; Holmen 1960; Brassard and Beschel 1968; Tikhomirov and Gavriluk 1969; Brassard and Longton 1970; Barrett and Teeri 1973; Bliss *et al.* 1977; Webber 1978; Nams and Freedman 1987a; Muc *et al.* 1989). It is also found within the shelter of rocks and in ice wedge depressions and crevices (Polunin 1959; Bliss and Matveyeva 1992; personal observation).

Cassiope tetragona forms loose prostrate cushions of stems that radiate outward in a centrifugal manner from a central root mass (Figure 2.1). The species initially grows monopodially with upright stems that later form wildly entangled and creeping shoots (Havström *et al.* 1993). The individual genets of *C. tetragona* are generally long-lived and can grow to cover an area of about one square metre (Crawford 1989; Havström *et al.* 1993). Personal observations of large genets in the Canadian Low Arctic revealed a large central zone of dead biomass encompassed by a circle of live stems and photosynthetic leaves.

The plant produces white pendulous bell flowers extending from the axils of the topmost leaves on the stem. Buds form the summer prior to flowering, remaining protected beneath the leaf at the base of the node until the following summer. Following flower opening and petal drop, a darkly-colored capsule on the end of the peduncle is revealed (Callaghan *et al.* 1989; Johnstone 1995). Seed dispersal is thought to take place either in winter or early spring as all capsules have dehisced prior to snowmelt (Molau, 1997). However, a truncated growing season due to unfavorable environmental conditions can lead to heavy flower and fruit abortion (Molau 1997).

Cassiope tetragona produces two alternating sets of opposite leaves along the stem forming four distinct rows (Figure 2.2). The imbricate leaves are deeply grooved and scale-like with stomata restricted to the curled margins of the abaxial leaf surface (Callaghan *et al.* 1989;



Figure 2.1. *Cassiope tetragona* (L.) D. Don (Ericaceae) growing in the lowland of Alexandra Fiord, Ellesmere island, Canada. Note the white pendulous bell flowers, usually visible in July.

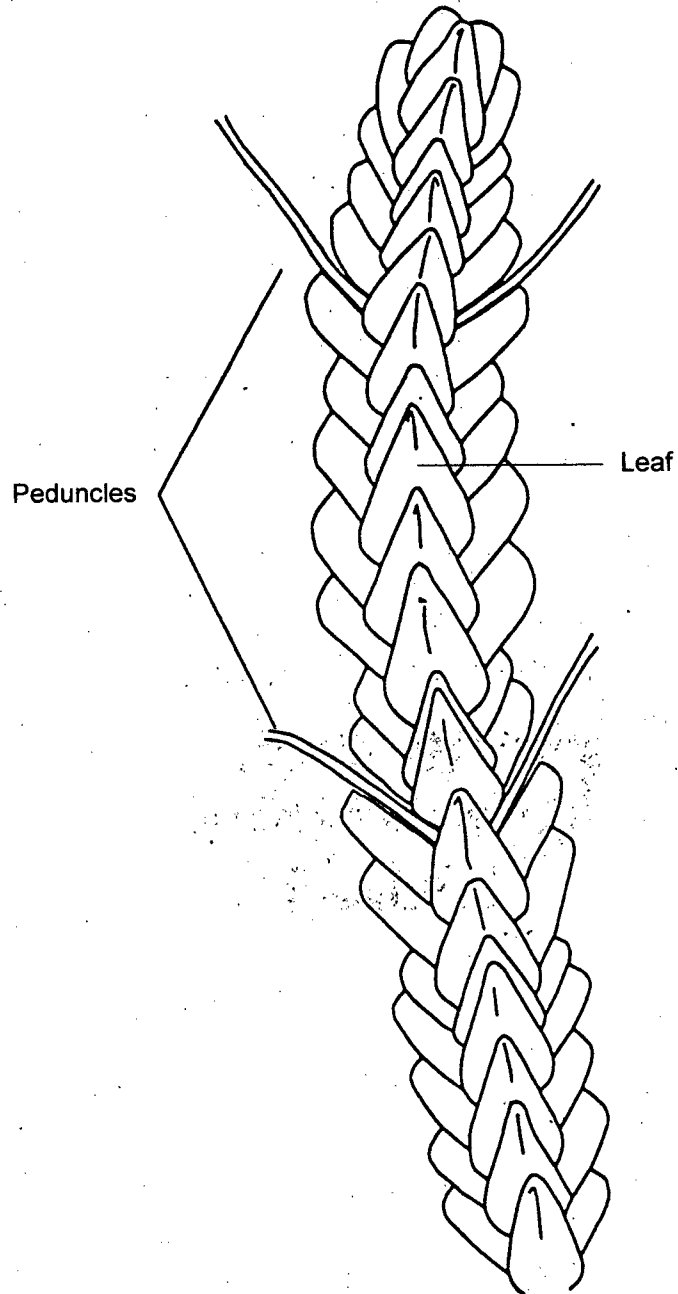


Figure 2.2. Schematic diagram of *Cassiope tetragona* leaf morphology and flower peduncles from Alexandra Fiord, Ellesmere Island, Canada (Figure adapted from Johnstone and Henry 1997).

Havström *et al.* 1993). The leaves of the species remain photosynthetic for three to ten years (Sørensen 1941; Molau 1997; personal observation). Later, the green leaves change color to yellow or red and then brown with death (Callaghan *et al.* 1989; personal observation). The dead leaves remain attached to the stem for at least 20 years and up to 100 years (Callaghan *et al.* 1989; Havström *et al.* 1993; Johnstone and Henry 1997; personal observation). Several species of microfungi are known to colonize the dead leaves, but this does not appear to affect the persistence of the leaves attached to the stem (Holm 1975). In addition, the green leaves contain flavonoids (Denford and Karas 1975) and phenols (Harborne and Williams 1973), making them unpalatable to caribou, muskox and other grazing species (Nams 1982; Callaghan *et al.* 1989; Henry and Gunn 1990; Johnstone and Henry 1997; Ferguson *et al.* 2001; personal observation). Wave-like patterns in leaf-length along individual stems are apparent on most plants. Small leaves produced in the spring and autumn of each year frame larger leaves formed during the summer (Warming 1908). The smaller leaves delimit an annual growth increment. Measurement of individual leaves allowed Callaghan *et al.* (1989) and Havström *et al.* (1993; 1995) to identify and date individual annual growth increments. Later, Johnstone and Henry (1997) found the pattern in the positioning of leaf nodes in adjacent leaf rows was analogous to patterns in leaf length. As leaf scars remain visible along the full length of a shoot even after long periods of time, Johnstone and Henry (1997) were able to use this pattern to measure and date annual growth increments (Figure 2.3). Their modified technique allowed for the generation of longer growth chronologies (Johnstone and Henry 1997) than the leaf-length method used by Callaghan *et al.* (1989) and Havström *et al.* (1993; 1995).

2.2.2. Study Area

Field work was carried out at Alexandra Fiord, Ellesmere Island (78° 53'N, 75° 55'W) during the summer of 1998. Ellesmere Island is located in the Queen Elizabeth Islands of Arctic Canada, an archipelago of about 1.3 million square kilometers (Bradley 1990). Alexandra Fiord lies on the eastern coast of central Ellesmere Island incising the Johan Peninsula and opening out onto Buchanan Bay and the Kane Basin (Figure 2.4). The triangular-shaped lowland, 8 km² in area, is a gently sloping, post-glacial, outwash plain. To the east and west, the lowland is bound by bare upland plateaus (approximately 500-700 m a.s.l.) of Arcane granite and Paleozoic dolomitic rock (Sternberg and Stone 1994). Two glacial tongues from the Prince of

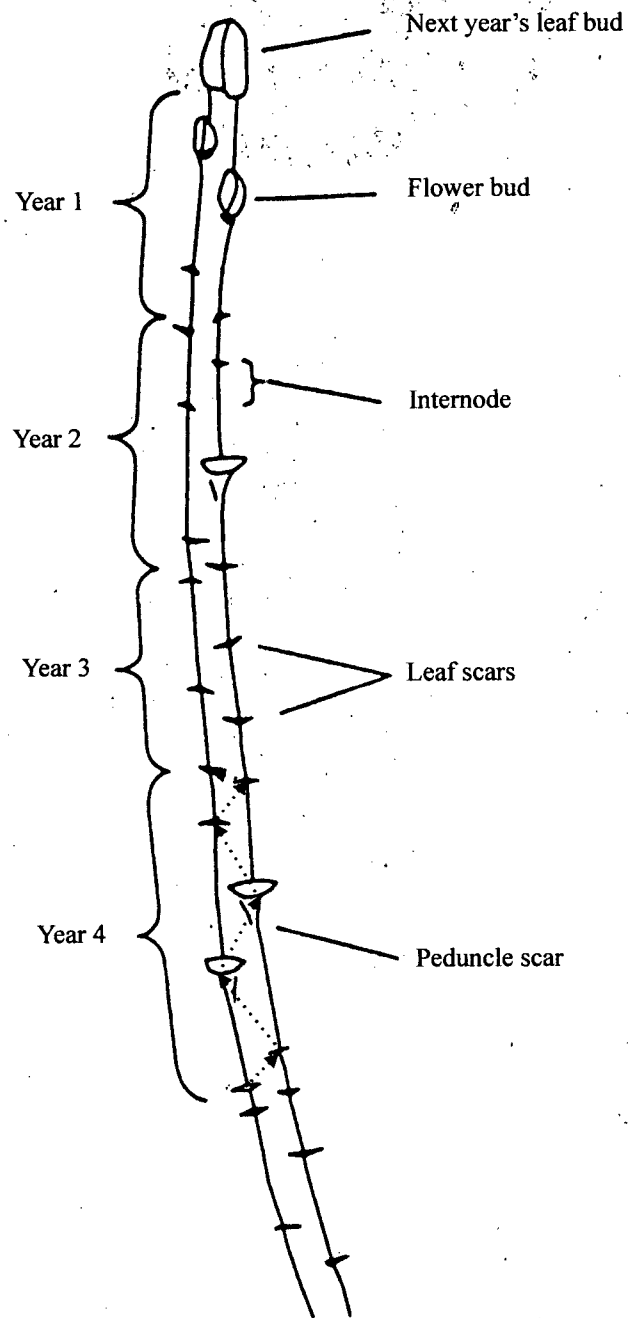


Figure 2.3 Schematic diagram of a *Cassiope tetragona* stem with leaves removed showing the leaf scars, flower peduncle scars, flower buds and internodes (Figure adapted from Johnstone and Henry 1997). Dotted line with arrows in Year 4 indicates the direction of measurement between internodes for one annual growth increment.

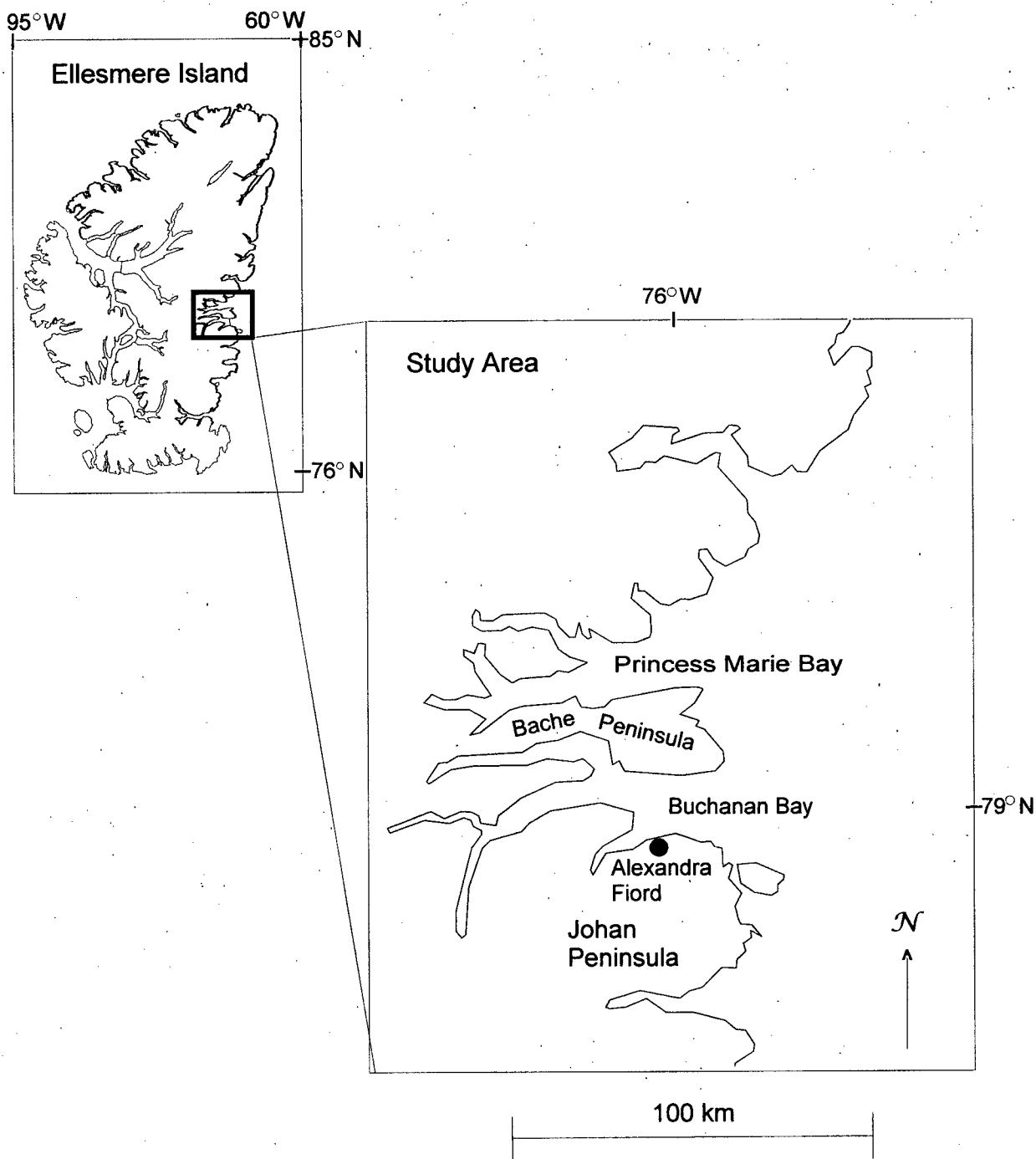


Figure 2.4 Map showing the location of Alexandra Fiord (78° 53' N, 75° 55' W) on the eastern central coast of Ellesmere Island, Nunavut, Canada.

Wales Ice cap form the southern apex while the northern base of the triangle meets the waters of Alexandra Fiord. The lowland topography consists of a river and several stream courses, granitic rock outcrops, sorted polygons, frost boils, raised beach ridges and erratics. Microtopographic variation includes hummocks and hollows, as well as smaller scattered boulders.

Most of the surrounding terrestrial landscape around the Alexandra Fiord lowland is classified as polar desert (vascular plant cover < 5%) or polar semi-desert (vascular plant cover 5-20%) (Bliss 1975; 1977; Bliss and Matveyeva 1992). Communities of semi-closed and closed vegetation are locally rare in the Queen Elizabeth Islands, Canada (Bliss and Matveyeva 1992). At Alexandra Fiord, 12 distinct plant communities comprised of closed to semi-closed vegetation occur over greater than 90% of the lowland (Muc *et al.* 1989) (Figure 2.5). Heath communities dominated by *C. tetragona* and *Dryas integrifolia* M. Vahl cover over 50% of the lowland (Nams and Freedman 1987a; Muc *et al.* 1989). *Cassiope tetragona* occupies a wide range of habitats within the lowland including late-lying snowbeds, well-drained heath tundra and fellfields (Muc *et al.* 1989).

2.2.3. Climate Conditions

According to the climate classification of the Canadian Arctic Archipelago by Maxwell (1981), Alexandra Fiord lies within the Northern Region along with the High Arctic Weather Station at Alert (85° N). However, climate variables during the summer months are more strongly correlated with those at the High Arctic Weather Station at Eureka (Labine 1994). The mean summer air temperature (June-August) of the Alexandra Fiord lowland is approximately 3.2 °C (Coastal station, 1980-1998) with a mean annual precipitation of approximately 100-200 mm (Freedman *et al.* 1983; Labine, 1994; C. Labine, personal communication, 2000). The contribution of two synoptic factors, the Greenland high-pressure system and the arctic circumpolar vortex, results in high levels of incoming radiation during the summer at Alexandra Fiord (Alt and Maxwell 1990; Labine 1994). The Greenland semi-permanent high-pressure system helps to maintain clear skies at Alexandra Fiord. Warmer temperatures in June and July are partly the result of the adiabatic drying and warming of air flow off the Arctic Ocean as it crosses interior mountain ranges before descending at Alexandra Fiord (Alt and Maxwell 1990;

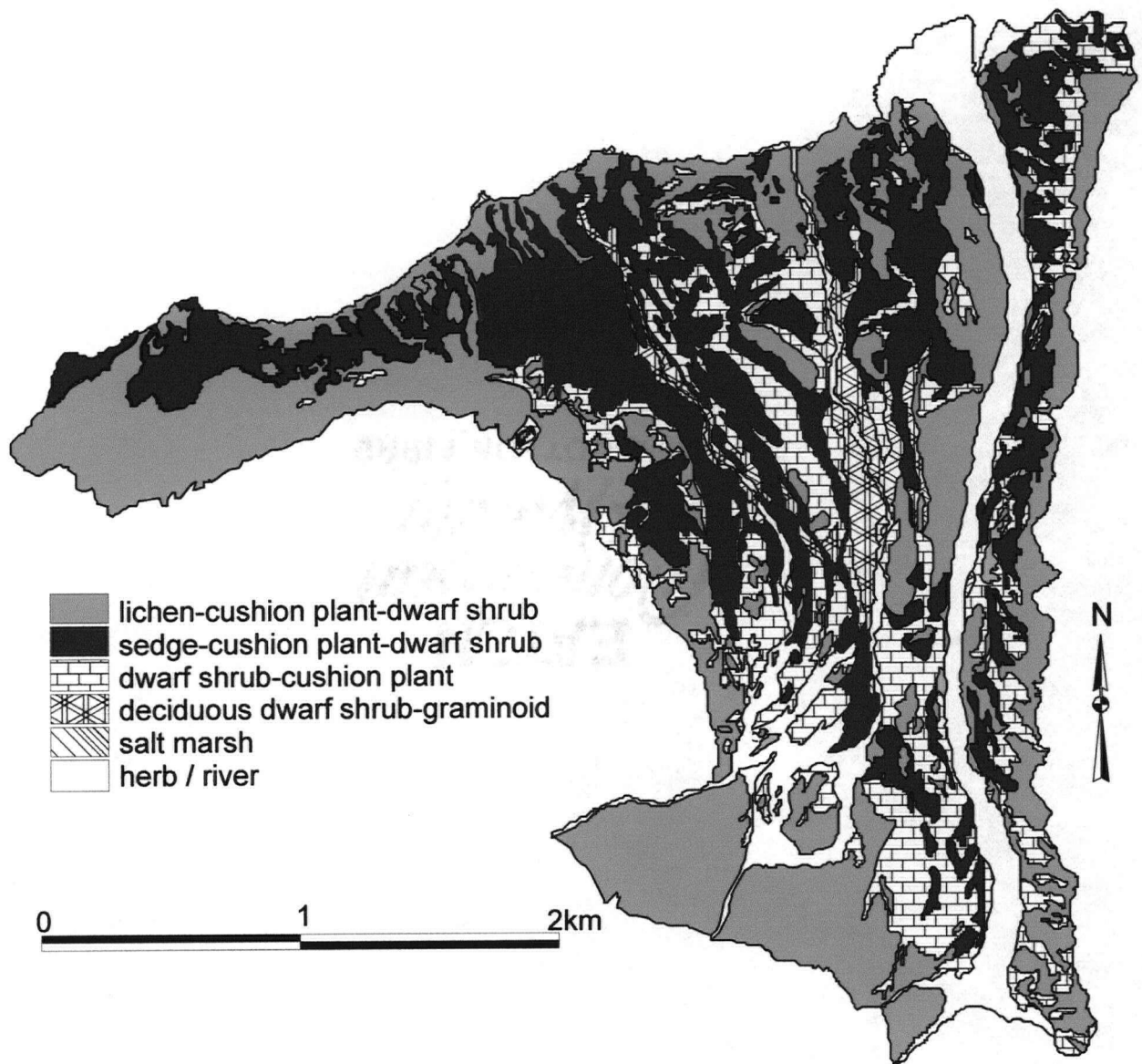


Figure 2.5. Plant communities of the Alexandra Fiord lowland (Figure adapted from Muc *et al.* 1989). Map digitized by D. Bean, 2003.

Labine 1994). Warmer winter conditions are maintained in the region by the prevailing airflow from the open waters of northern Baffin Bay and associated storm activity responsible for the later date of sea ice consolidation (Maxwell 1981; Labine 1994). Despite low mean summer precipitation values (10-60 mm), the lowland's hydrological budget is supplemented throughout most of the summer by a large influx of glacial and snow meltwater as well as water produced by the annual thaw of the active layer. The presence of the two synoptic factors, the unique topographical configuration of the lowland and subsequent low albedo levels, result in summer air and soil temperatures warmer than those of the surrounding uplands. Such factors combine to create a veritable thermal polar oasis (Labine 1994).

2.2.4. Study Site

During the summer of 1992, several sites were selected in the lowland for a long-term temperature manipulation experiment (Figure 2.6). The site selected for the current study is classified as a dwarf shrub-cushion plant community type for the Alexandra Fiord lowland (Muc *et al.* 1989). The community is dominated by *D. integrifolia*, with *C. tetragona*, *Carex misandra* (R. Br.) Nyman, *Eriophorum angustifolium* subsp. *angustifolium* Honck., *Luzula confusa* Lindeberg, *Papaver radiculatum* Rottb. and *Arctagrostis latifolia* (R. Br.) Briseb. subsp. *latifolia* also present. The site is underlain by soils characterized by alluvial sands and gravel topped by a thin layer of humus and organic litter (Muc *et al.* 1994). The topography slopes gently ($<2^\circ$) with a slight northern exposure (Johnstone 1995).

2.2.5. Experimental Temperature Manipulation

Experimental warming began at the *Dryas*-dominated community site (Dryas ITEX) in June 1992. Open-top hexagonal-shaped greenhouses or open-top chambers (OTCs) were established to increase the ground surface temperature (Marion *et al.* 1997). The sides of the open-top chambers are inwardly inclined (60° with respect to the horizontal), which allows transmittance of solar radiation and traps convective heat (Marion *et al.* 1997). The open-top chambers (OTCs) are approximately 60 cm high with a top diameter of 1.5 m. The chambers are constructed of 1.0 mm thick Sun-Lite HP® (Solar Components Corporation, Manchester,

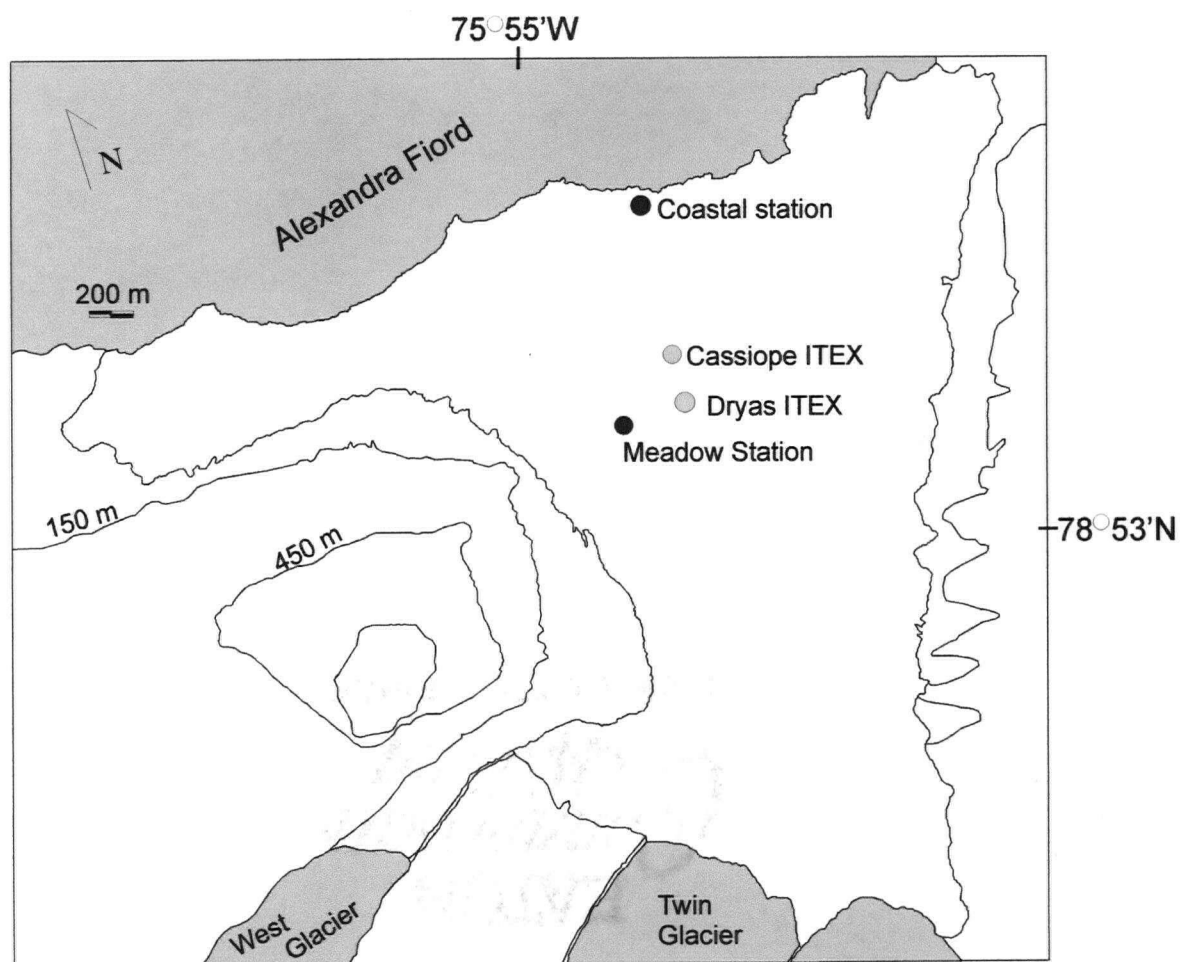


Figure 2.6 Map showing the locations of the Cassiope and Dryas ITEX sites, and the Coastal and Meadow automated weather stations in the lowland at Alexandra Fiord, Ellesmere Island.

NH, USA) fiberglass material designed for solar applications (Marion *et al.* 1997). While the open-top chambers do increase air temperature, side effects such as altered light, moisture and gas exchange are minimized (Marion *et al.* 1997). The fiberglass has a high solar transmittance of visible wavelengths (86%) and low transmittance of infrared (<5%) (Marion *et al.* 1997). At Alexandra Fiord, open-top chambers were left in place year round.

In June 1992, 14 treatment and 14 control plots were established within the *Dryas* ITEX site. Plot locations were selected in order to include individuals of the target ITEX species, including *C. tetragona*. The size of the control plots approximates that of the treatment plots (circa 1.8 m²) (Johnstone 1995). The control and open-top chamber plots were placed a minimum of three metres apart in order to reduce interference with normal snowpack conditions. At the establishment of the treatment, four plot pairs were randomly designated for future destructive sampling. One *C. tetragona* plant per plot was tagged in 1992 for later destructive sampling.

2.2.5.1. ITEX Thermocouple Data

Year-round temperature data have been collected at the *Cassiope* ITEX site since the summer of 1992. The *Cassiope* site is approximately 200 metres north of the *Dryas* site on the lowland. At the *Dryas* site, continuous growing season temperatures were only available for July 1995. Therefore, surface temperature (-3 cm) data from the *Dryas* ITEX site were only used in a Pearson's product moment correlation analysis with temperature data from the *Cassiope* ITEX site for the month of July 1995. Between 1992 and 1994 at the *Cassiope* site, there were seven treatment and seven control plots instrumented for temperature measurement using copper/constantan thermocouples. Beginning in July 1995, the number of treatment and control replicates was increased to nine plot pairs at the site. During the period 1992 to mid-summer 1995, three soil thermocouples (-3 cm) per treatment plot were placed along a south-to-north transect (Marion *et al.* 1997). One thermocouple was located in the center of the open-top chamber with the other two sited immediately beneath the top edge of the chamber on the north and south sides (Marion *et al.* 1997). Beginning in mid-July of 1995, the three soil thermocouples were moved to the center of each treatment plot in order to measure a single profile of air (+10 cm), near surface (0 cm) and soil (-10 cm) temperature. Measurements were

taken every five minutes and averaged hourly, with daily outputs of data. In addition, snow depth was measured daily over two control and two open-top chamber plots at the *Cassiope* site. Snow depth was measured with ultrasonic depth gauges (UDGO1, Campbell Scientific, Logan UT, USA) (Marion *et al.* 1997).

In order to assess the magnitude of the temperature response to the open-top chambers for the period 1992-1998, two-factor repeated measures analyses of variance (ANOVA-R) were carried out ((M)ANOVA procedure, SYSTAT 1992). Temperature response magnitude was examined for the months of May, June, July, August, and September, as well as the seasonal period of June-August. In addition, the temperature response magnitude during two-week periods in the months May, June, July, August and September was examined. In the ANOVA-R, both treatment and years were considered fixed effects (Model I) (Hicks 1993; Johnstone *et al.* 1996). Data used in the ANOVA-R met the assumptions of parametric statistics, including a normal distribution of errors and homogeneity of error variances.

2.2.6. Coastal Station Climate Data

Beginning in the summer of 1980, meteorological data on daily weather conditions were collected at Alexandra Fiord through the use of permanent, automatic, meteorological stations (Labine 1994). Climate data used in this thesis were recorded by two autostations, one located in the middle of the Alexandra Fiord lowland (Meadow station, 30 m a.s.l., 1989-1998) (G. Henry, unpublished) and a second station located 1 km away on an ancient, uplifted beach ridge (Coastal station, 10 m a.s.l., 1980-1998) (Labine 1994; C. Labine, unpublished) (Figure 2.6). The autostations measured all or several of the following variables: air (150 cm above surface), surface (0 cm) and soil temperatures (-2 cm), relative humidity, incoming global solar radiation, and wind speed and direction (300 cm). Air temperature and relative humidity were measured using a Campbell Scientific 207 sensor. The relative humidity sensor was a Phys-Chemical Model PCRC-11 polysulfonated styrene chip and the temperature sensor was a Fenwall UUT51J1 thermistor. Soil and surface temperatures were measured with Campbell Scientific 101 thermistor probes which use the Fenwall UUT51J1 thermistor as well. Incoming solar radiation was measured using a Li-Cor LI200S silicon pyranometer. Sensors used for wind speed and direction were 014A Met-One three-cup anemometers and Met-One 024A wind

vanes, respectively at the Coastal station. At the Meadow station, wind speed and direction were measured by a Wind Sentry set. Beginning in 1993, snowdepth was measured daily with ultrasonic depth gauges (UDG01, Campbell Scientific, Logan, UT, USA). A Campbell Scientific CR10 Micrologger monitored all sensors. The scan rate for each sensor was every five minutes with daily outputs of data. Average monthly air temperature data (1986-1998) recorded at the Coastal station were used to calculate average air temperature departures (relative to the 1980-1998 mean from the Coastal station) for Alexandra Fiord.

Remarkably, given the year-round environmental conditions of a high arctic site and the lack of instrument maintenance for nine months of the year, there was only one period of interrupted data collection at the Meadow station site (July 1992 – May 1993) since its start date in June 1989. There were a greater number of data gaps in the Coastal station data set from 1980-1985, but these were due to the lack of viable meteorological equipment in the early 1980s suitable for operation in the high arctic. Data are nearly continuous at the Coastal station from 1985 onward. Other gaps in the Coastal station data set due to instrumental reading errors do exist, but they are infrequent and of short duration (e.g., <1-2 months). Data gaps from 1989 onward in the Coastal station set were estimated using the Meadow station data set and linear regression. Gaps in the Coastal station data set between the years 1980-1989 were estimated using data from the High Arctic Weather Station (H.A.W.S.) at Eureka, Ellesmere Island (D. Bean, personal communication, 2002).

2.2.7. Plant Sampling and Measurement

At the *Dryas* ITEX site, *C. tetragona* plants were collected from the destructive plots on August 18, 1998. Unfortunately, the plants in the control and open-top chamber treatments were small in stature, and the stem lengths were short. Unavoidably, the lengths of the chronologies developed for this site were shorter than desired. Following harvest, the collections were air-dried for three days and then stored in sealed paper envelopes.

In the laboratory, between five and seven stems per plant were selected for measurement. Plants with multiple branching stems were excluded from the data set, as were stems that were irretrievably broken in transit. Stems were specifically selected for their length,

and when possible, for live green leaves and leaf buds at the tip of the shoot. In order to remove bends in the stems resulting from drying and storage, stems were placed in a lukewarm water bath for five to ten minutes. The stems were then inserted into 1 cm diameter glass tubes and allowed to dry overnight. Following drying, two adjacent rows of leaves along the stem were removed by hand with fine tweezers under a microscope. During the process, care was taken to leave any peduncles and flower buds in place.

Measurement was carried out under a dissecting microscope (10X to 30X magnification) using a manually operated caliper system (designed by J. Svoboda, University of Toronto, 1992). The measurement device is composed of a digital caliper attached to a computer, and a location marker mounted on a solid wooden base. Samples of *C. tetragona* stems were placed in glass tubes (1 cm diameter) and inserted into a holder attached to the base of the device. Internode scars found along a *C. tetragona* stem may be positioned precisely in relation to the location marker beneath the microscope. The glass tube is pushed past the location marker allowing the operator to measure accurately the distance from the base of one internode to the next. The internode lengths were measured from the base of the stem to the tip of the shoot (Figure 2.3). The number, location and size of flower buds and the number and location of flower peduncles were noted during the measurement process.

2.2.8. Retrospective Growth and Reproduction Analysis

Four variables of annual growth and reproduction for the sampled *C. tetragona* plants were measured and recorded including: annual stem elongation, number of leaves, number of flower buds, and number of flower peduncles. By following the wave-like distribution patterns in internode lengths, as first described by Johnstone (1995), annual growth increments were determined. Annual stem elongation was measured as the sum of the internode lengths with the terminus of each year's growth delimited by the shortest internode length at the end of each wave-series (Figure 2.7) (Johnstone 1995). Each year of growth is referred to as an annual growth increment (AGI). Annual leaf production was calculated by counting the total number of leaf scars within the two rows measured for each year. The number of flower buds and peduncles produced each year were calculated in the same way as the number of leaves.

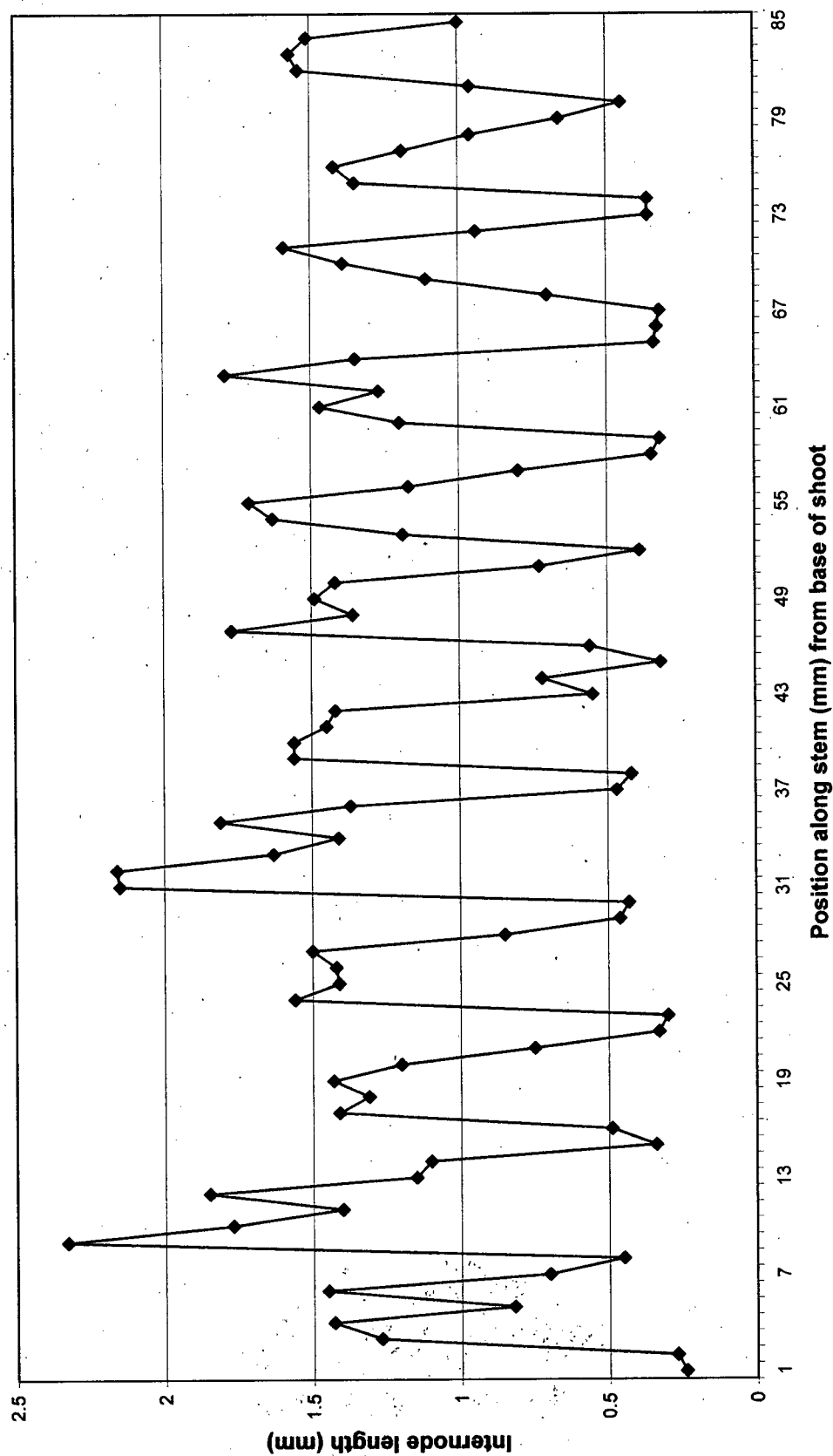


Figure 2.7. Internode lengths plotted against position along an 11 year portion of a *Cassiope tetragona* stem sampled at Alexandra Fiord, Ellesmere Island. Note the wave-like oscillations in internode lengths, with minimum lengths indicating the termination of annual growth.

2.2.8.1. Cross-dating and Skeleton Plots

Cross-dating, the cornerstone of dendrochronology, ensures the proper placement in time of individual annual growth increments by matching common patterns of yearly growth (Fritts 1976). In cross-dating, the assumption is made that environmental conditions affect the annual growth of a species. The effect may be observed in the width of a tree-ring, for example. The environmental factors produce synchronous variations in annual increment sequences over long periods of time and across large number of individuals within a wide geographic region. Using the technique of skeleton plotting, a process of graphically representing annual increment variations, synchronous growth patterns can be matched within-plant and between-plants to create a site chronology and, ultimately, to establish a precise calendar year for each growth increment.

In this study, the data series for each stem was cross-dated by hand using skeleton plots of annual growth increments (Stokes and Smiley 1968). Three to seven stems per plant were cross-dated. The stems from the treatment and control plants were maintained in two separate groups for cross-dating purposes. Both the treatment and control groups covered the time span from 1986 to 1998. The chronology based on the number of flower peduncles covered the time span 1986-1997, as flowers buds formed in 1998 would not produce flowers until the following summer. The cross-dating software COFECHA, available in the Dendrochronological Program Library, was used to detect measurement and cross-dating errors in the measured annual increment series (Holmes 1983; Holmes *et al.* 1986; Grissino-Mayer *et al.* 1992; Holmes 1994; Grissino-Mayer 2002). However, due to the short length of most of the series, 13 or fewer years, COFECHA analysis was only marginally useful.

2.2.8.2. Standardization

In dendrochronological studies, the purpose of standardization is to remove trends in the annual growth increment series and to allow the resultant standardized values of individual plants to be averaged together into a mean-value function by adjusting the series for differences in growth rates (Fritts 1976; Cook *et al.* 1990). The process of standardization involves fitting the observed annual growth increment series to a straight line or curve and calculating an index

value of the observed annual increment divided by the expected value (Fritts 1976; Veblen *et al.* 1991). Standardization results in a time series of annual growth increment indices with a defined mean and relatively constant common variance over the time series (Fritts 1976; Cook *et al.* 1990). This process allows for the calculation of an average annual growth increment chronology without the average being dominated by faster growing stems (Veblen *et al.* 1991).

In this study, the horizontal line standardization method was used to calculate indices for the individual time series (Cook and Holmes 1986), as the removal of the age-related growth trend was not the goal as it is in most tree-ring studies. Standardization with a horizontal straight line does not detrend the series and remove the “biological growth trend,” but rather it enhances the detection of deviations from average growth and reproduction rates (Veblen *et al.* 1991). In particular, horizontal standardization was employed in order to detect the growth and reproductive responses of *C. tetragona* to the temperature manipulation.

Two vegetative growth (annual growth increment, number of leaves) and two reproductive (number of flower buds, number of flower peduncles) chronologies were produced for both the control plots and the OTC treatment. All chronologies were estimated using the horizontal straight-line standardization method: Each stem was standardized using:

$$\frac{x - \bar{x}}{SD} \quad (2.1)$$

where x is the yearly measurement value, \bar{x} is the average measurement of the variable for the stem and SD is the standard deviation of the variable for the individual stem time series. Following standardization, the individual stem chronologies were averaged together using the arithmetic mean to form master chronologies for each of the four variables measured.

2.2.9. Before-After-Control-Impact-Paired-Comparison Analysis

Through the use of the retrospective analysis technique in this study, a modified Before-After-Control-Impact-Paired-Comparison (BACIP) methodological approach was feasible (Osenberg *et al.* 1994; Underwood 1994). In most experimental studies, treatment plots are

established and their responses compared to untreated controls. In the current study, annual growth and reproductive variables were measured and dated for the period prior to the establishment of the warming experiment, thus providing a baseline estimate of these variables. Furthermore, as prior studies of *C. tetragona* populations have shown (Callaghan *et al.* 1989; Havström *et al.* 1993; 1995; Johnstone and Henry 1997), sufficiently long records (25-35 years) of vegetative growth and reproduction can be reconstructed. Using retrospective analysis techniques, it was possible to determine the natural temporal variability of the measured variables prior to treatment. Retrospective analysis techniques were also used to measure the vegetative growth and reproductive effort of the control and treatment plants during the experimental period without annual monitoring and measurement. This technique facilitated the comparison of the measured annual variables from plants in the treatment plots with those from plants in concurrent control plots. In addition, the technique allowed the treatment period control and OTC plant variables to be compared with the same variables measured retrospectively for the period prior to treatment.

2.2.10. Graphical Representation of Indices

Each standardized master chronology was presented as a time series in order to examine patterns of annual departures from a mean of zero. The control and treatment chronologies were graphed separately for the period 1986-1998 (1986-1997 for number of flower peduncles). In addition, four standardized individual plant chronologies per treatment were graphed together for each of the growth (annual growth increment, number of leaves) and reproductive (number of flower buds, number of flower peduncles) variables. This representation facilitated a visual assessment of the synchronicity of departures from the mean across individual plants within the same treatment.

2.2.11. Mean Correlation Technique

The mean correlation technique was used to estimate the signal and noise within groups of standardized time series (indices) by measuring the common variability within and between plants (Briffa and Jones 1990). A correlation matrix was calculated for each of the 16 variables,

divided into control and open-top chamber treatments and into pre- and treatment periods, to show the relationships between all series of indices for the individual plant stems (Briffa & Jones 1990). In the matrix, correlation coefficients were calculated within-plants and between-plants. The correlation matrix grand mean, the mean of all correlations among different stems (both within- and between-plants) was defined first. It is defined as

$$\bar{r}_{tot} = \frac{1}{N_{tot}} \sum_{i=1}^t \sum_{\substack{l=i \\ l \neq i}}^t \sum_{j=1}^{c_i} r_{ilj} \quad (2.2a)$$

where

$$N_{tot} = \frac{1}{2} \left(\sum_{i=1}^t c_i \right) \left[\left(\sum_{i=1}^t c_i \right) - 1 \right], \quad (2.2b)$$

where \bar{r}_{tot} is the correlation matrix grand mean, N_{tot} is the total number of correlations summed, $i = 1$ to t plants, $l = i = 1$ to t plants, $j = 1$ to c_i stems, and r_{ilj} is the correlation coefficient among time series.

Then, an estimate of the within-plant signal was calculated by averaging the correlation coefficients between series of indices from the same plant over all plants (Briffa & Jones 1990). This within-plant signal is defined as

$$\bar{r}_{wt} = \frac{1}{N_{wt}} \sum_{i=1}^t \left[\sum_{j=2}^{c_i} r_{ij} \right], \quad (2.3a)$$

where

$$N_{wt} = \sum_{i=1}^t \frac{1}{2} c_i (c_i - 1), \quad (2.3b)$$

where \bar{r}_{wt} is the mean within-plant correlation coefficient, N_{wt} is the total number of within-plant correlations summed, $i = 1 - t$ plants, $j = 2 - c_i$ stems, and r_{ij} is the within-plant correlation coefficient.

Finally, the between-plant signal, \bar{r}_{bt} , was calculated. It was defined as the mean inter-series correlation calculated between all possible pairs of indexed series drawn from different plants (Briffa & Jones 1990). It is denoted as

$$\bar{r}_{bt} = \frac{1}{N_{bt}} (\bar{r}_{tot} N_{tot} - \bar{r}_{wt} N_{wt}) , \quad (2.4a)$$

where

$$N_{bt} = N_{tot} - N_{wt} , \quad (2.4b)$$

where \bar{r}_{bt} is the mean between-plant correlation coefficient, and N_{bt} is the total number of correlations summed minus the total number of within-plant correlations summed.

The between-plant signal, \bar{r}_{bt} , is thought to reveal the relative influence of a large-scale factor, such as climate, on plant growth or reproduction (Fritts 1976). The within-plant noise is calculated by subtracting \bar{r}_{wt} from 1. Finally, between-plant noise is calculated by subtracting \bar{r}_{bt} from \bar{r}_{wt} .

2.2.12. Pearson's Product Moment Correlation Coefficient

In order to understand the relationships among the growth and reproduction variables within their respective control and open-top chamber treatments, simple correlation coefficients between the standardized master chronologies were calculated using Pearson's product-moment

correlation coefficients (Correlation procedure, SYSTAT 1992). As the two vegetative and two reproductive variables for the control and open-top chamber treatment were divided into pre-treatment (1986-1991) and treatment (1992-1998) time periods, 16 chronologies were used in the correlation analysis.

To understand the constancy of the relationships among the two growth and two reproductive variables between plants within the control and open-top chamber treatment, Pearson's correlation coefficients were calculated. Individual plants were separated into control and open-top chamber treatment groups for comparison and further divided into their respective pre-treatment (1986-1991) and treatment (1992-1998) time periods. Sixty-four chronologies were used in the correlation analysis.

2.2.13. Repeated Measures Analysis of Variance and Multiple Analysis of Covariance

In order to assess the growth and reproductive response of *C. tetragona* plants to the warming treatment, two-factor with repeated measures on one factor analysis of variance (ANOVA-R) and analysis of covariance (ANCOVA-R) were carried out. In the repeated measures analysis of covariance (flower buds only), the average of the pre-treatment period flower bud measurements was used as the covariate. Plants were maintained within control and open-top chamber treatment groups for comparison, and further divided into the pre-treatment (1986-1991) and treatment (1992-1998) time periods. For this part of the study, the vegetative and reproductive chronologies used were cross-dated, but were not standardized with a horizontal line. Each annual value represents the arithmetic average measurement from all stems per plant. When the data met the assumptions of parametric statistics, including normal distribution and homogeneity of variance, a two-factor repeated measures analysis of variance was used ((M)ANOVA and (M)ANCOVA procedure, SYSTAT 1992). In the ANOVA-R and ANCOVA-R, both treatment and years were considered fixed effects (Model I) (Hicks 1993). Years were classified as fixed effects in this analysis as summer seasons, particularly in the Arctic, are discrete and short events separated by long winters (Johnstone *et al.* 1996). Data which did not meet parametric assumptions, including the number of buds and number of peduncles, were ranked and the ranks transformed to approximate a normal distribution using a Blom transformation (SAS 1985; Conover and Iman 1981). Repeated measures analysis of

variance and repeated measures analysis of covariance were performed on the transformed data sets ((M)ANOVA procedure, SYSTAT 1992). The vegetative and reproductive variables from the control and open-top chamber treatments were presented in bar graphs for the period 1986-1998 (1986-1997 for number of peduncles).

2.2.14. Correlation Analysis of the Standardized Chronologies and Climate Variables

The relationship between the standardized growth and reproduction chronologies and microclimate at Alexandra Fiord was evaluated using Pearson's product-moment correlation coefficients. Maintained within the respective control or open-top chamber treatments and the pre-treatment and treatment time periods, correlation coefficients were calculated for the growth and reproductive chronologies and average air temperature for the previous year (year C-1) and the current year (year C). Air temperature readings were recorded by the Coastal automated weather station at Alexandra Fiord. The readings were daily averages recorded at 1.5 metres above ground level. While other automated stations are in operation at Alexandra Fiord, the Coastal station has the longest data set, 1980 - 1998, covering the pre-treatment time period in this study (Labine 1994; C. Labine, unpublished data). No surface temperature data were available from the Coastal station. Average air temperature used in the correlation analysis was calculated as a monthly average. In addition, average air temperature was used to calculate thawing degree days for the months of May to September, inclusive. Thawing degree days were calculated as the sum of daily average air temperature above 0 °C for each month. For the correlation analysis, thawing degree days were calculated for individual summer months (e.g., June).

As an additional investigation, Pearson's product-moment correlation coefficients were calculated comparing the treatment period (1992-1998) standardized growth and reproductive chronologies with surface temperature for the previous year (year C-1) and the current (year C). Surface temperature data were recorded by thermocouples placed inside the open-top chambers and the control plots at the *Cassiope* ITEX site beginning in mid-July 1992. Data recorded by the central thermocouple (-3 cm) from 1992-1995 were considered as surface temperature readings. For the period 1995-1998, data were derived from the centrally-located surface (0 cm) thermocouples. Average thermocouple surface temperature was calculated as monthly averages

(e.g., June) and as a 15-day biweekly average. The biweekly averages were calculated for the months of May to September, inclusive. Correlation coefficients calculated for the previous year (year C-1) and the current year (year C), were based upon six years of thermocouple data for the months January to July and seven years of data for the months August to December. In addition, correlation coefficients calculated for the previous year (year C-1) were based upon six years of data from October to December.

2.3. Results

2.3.1. Local Climate Characteristics at Alexandra Fiord, 1986-1998

2.3.1.1. Coastal Station, Alexandra Fiord

June-August average air temperature departures for the period 1986-1998 at Alexandra Fiord indicated that the growing seasons of 1986, 1996, 1992, 1989, 1987, and 1997 were cool. (Figure 2.8). The summer of 1986 was the coldest growing season on record, followed by the summer of 1996. During the same period, the summer growing seasons of 1998, 1995, 1990, 1994, 1988, 1993 and 1991 were warm at Alexandra Fiord. The summer of 1998 was the warmest growing season (1986-1998). Average air temperature departures for the period 1986-1998 indicated that the months of June and July 1986, May 1989, August 1996, and September 1997 were the coldest for the period 1986-1998 at Alexandra Fiord (Figure 2.9). In contrast, May and August 1995, June and September 1998 and July 1988, were the warmest months for the same period.

2.3.1.2. Cassiope ITEX Site, Alexandra Fiord

Pearson's product-moment correlation analysis confirmed the strong similarity in surface temperature regime (-3 cm) between the *Dryas* and *Cassiope* ITEX sites. For the month of July 1995, temperatures in the control plots at the *Dryas* and *Cassiope* ITEX sites were significantly different from zero and positively correlated ($r = 0.87$; $n = 31$; $P < 0.01$). Temperatures recorded

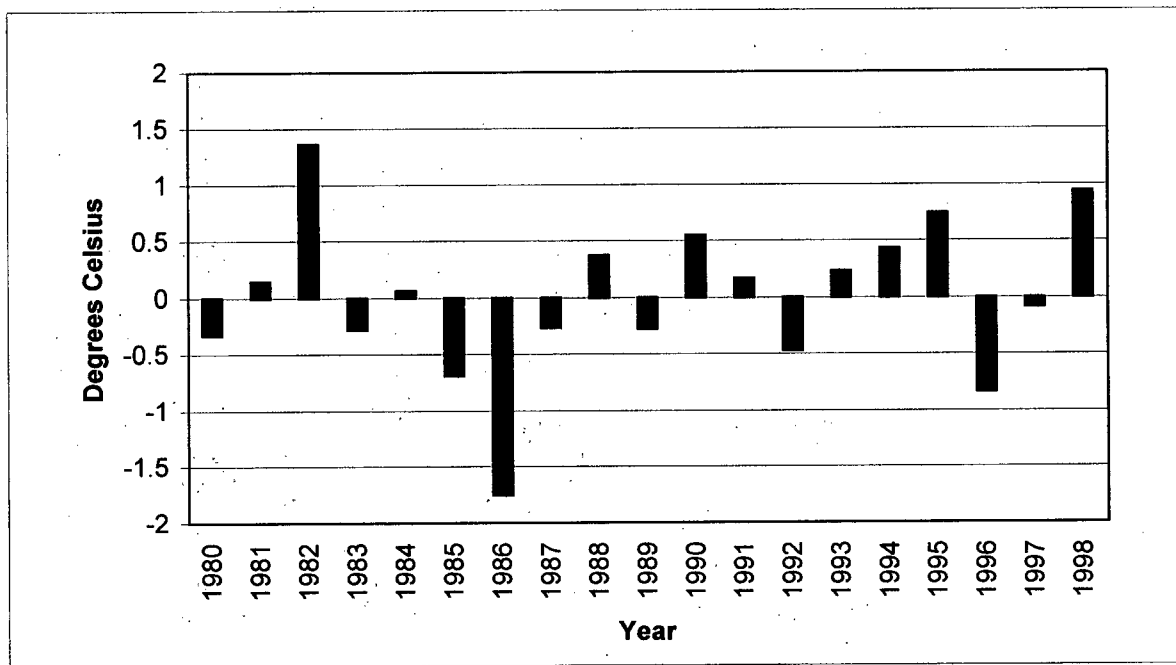


Figure 2.8. June-August average air temperature (°C) departures for Alexandra Fiord relative to the 1980-1998 mean from the Coastal station, Alexandra Fiord, Ellesmere Island.

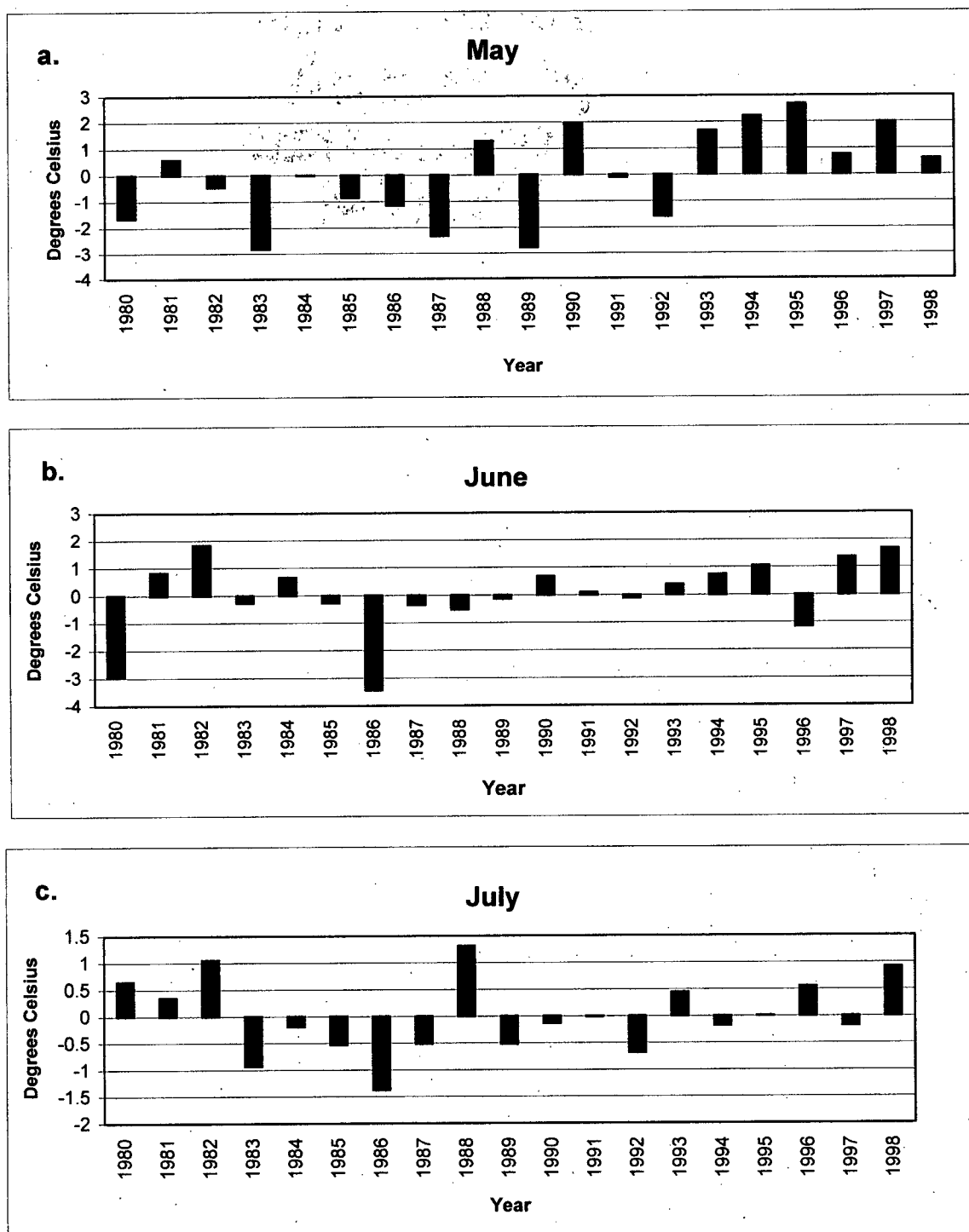


Figure 2.9. (a.) May, (b.) June, (c.) July average air temperature (°C) departures for Alexandra Fiord relative to the 1980-1998 mean from the Coastal station, Alexandra Fiord, Ellesmere Island.

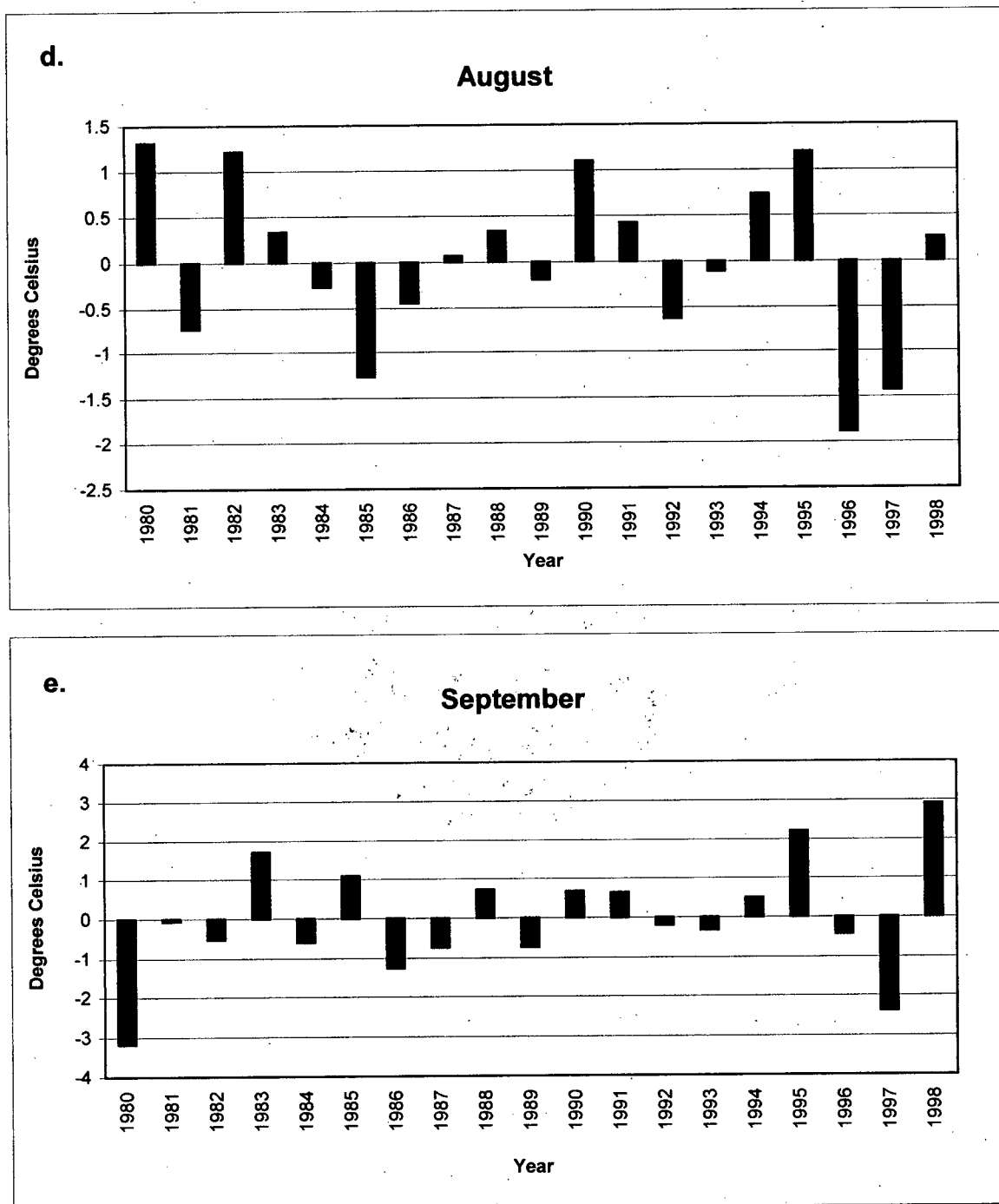


Figure 2.9. (d.) August and (e.) September average air temperature (°C) departures for Alexandra Fiord relative to the 1980-1998 mean from the Coastal Station, Alexandra Fiord, Ellesmere Island.

in the open-top chambers were also significantly different from zero and positively correlated ($r = 0.90$; $n = 31$; $P < 0.01$).

For the period 1995-1998, measurements of temperature in the control plots indicated that average monthly surface temperature (0 cm) was warmer than air temperature (10 cm) for the months of June, July, August and September (Figure 2.10 a). The average temperature difference between the surface (0 cm) and the air (10 cm) was greatest in July ($+2^{\circ}\text{C}$), followed by September ($+1.78^{\circ}\text{C}$), August ($+0.61^{\circ}\text{C}$) and June ($+0.45^{\circ}\text{C}$). Average surface temperature for the month of May was -1.15°C colder than the air temperature. Measurements of temperature in the open-top chamber plots for the period of 1995-1998 showed that average monthly surface temperature (0 cm) was warmer than air temperature (10 cm) for the months of July ($+0.35^{\circ}\text{C}$), August ($+0.15^{\circ}\text{C}$) and September ($+2.61^{\circ}\text{C}$) (Figure 2.10 b). During the months of May and June, average monthly surface temperature was -1.8°C and -2.15°C colder, respectively, than air temperature inside the open-top chambers.

At the *Cassiope* ITEX site, the magnitude of temperature response was significantly affected by the open-top chambers in September only ($P=0.028$) (Tables 2.1-2.6). However, among-year variation was significant for several months, including: May ($P=0.001$), June ($P=0.001$), August ($P = 0.001$), September ($P=0.028$), and the seasonal period of June-August ($P=0.000$). During the month of May, surface temperature showed a significant 'year X treatment' interaction, indicating that treatment cannot be evaluated independently of time. A comparison of average monthly surface temperature (0 cm) in the control and open-top chamber plots for the period 1995-1998, showed that the open-top chambers are cooler in May (-1.29°C) and June (-1.94°C), but warmer in July ($+0.23^{\circ}\text{C}$), August ($+0.30^{\circ}\text{C}$) and September ($+0.93^{\circ}\text{C}$) than the control plots (Figure 2.10). Similarly, the magnitude of temperature responses during two-week periods throughout the summer months were not significantly affected by the open-top chamber treatment, except in the month of September ($P=0.037$) (Appendix I). However, among-year variation was significant for two-week periods in May, June, July, August and September (Appendix I).

During the winter months from the previous September (year C-1) to the current May (year C), snowpack was generally thicker above the open-top chambers than above the control plots (Figures 2.11-2.13). From 1992-1998 snow pack depth measured above the open-top

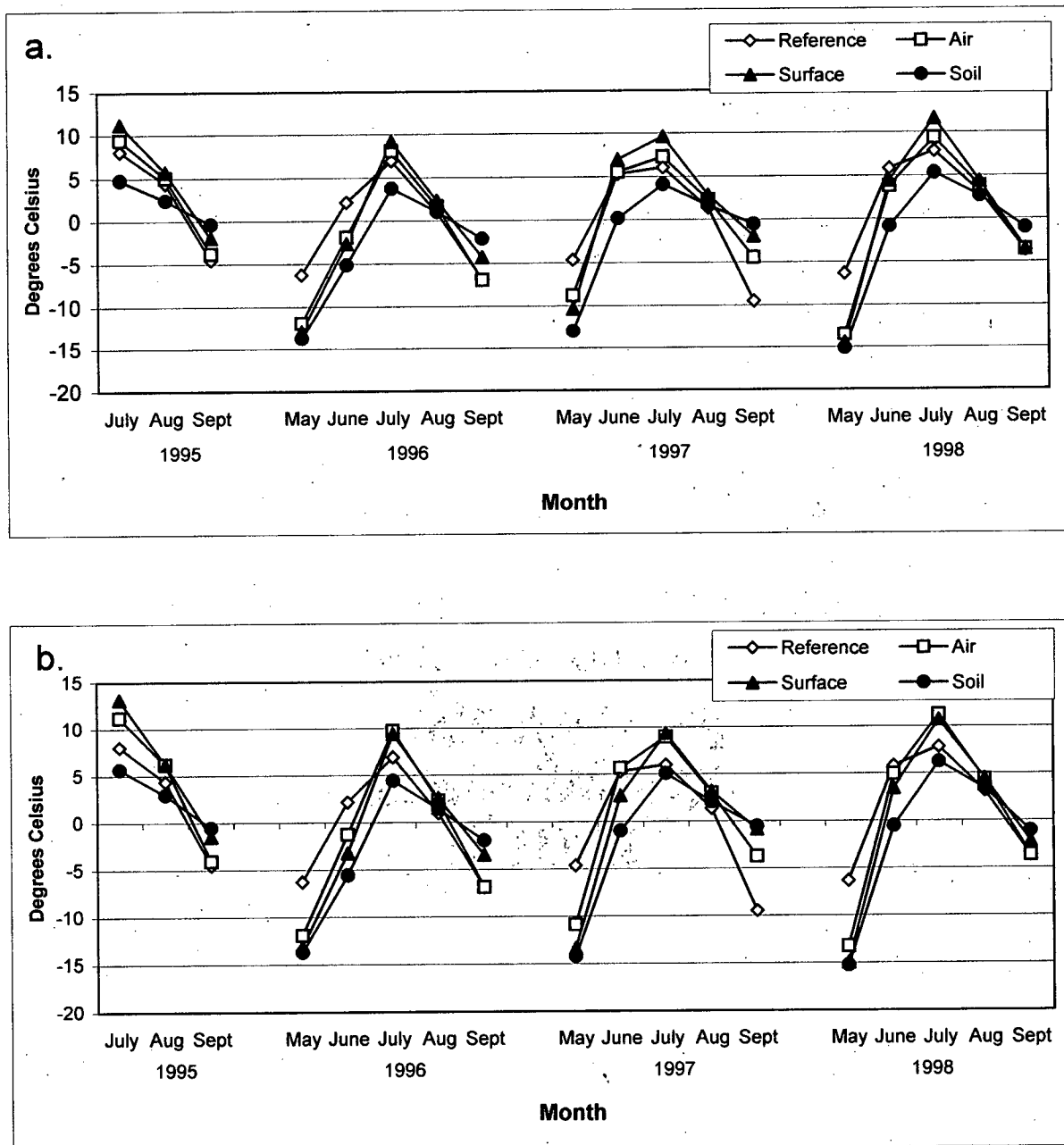


Figure 2.10. Comparison of summer growing season mean air, surface and soil temperatures measured in the Cassiope ITEX (a) control and (b) open-top chamber (OTC) plots for 1995-1998. Temperatures measured include +1.5 m (reference), +10 cm (air), 0 cm (surface) and -10 cm (soil).

Table 2.1. Effects of treatment and year on average May surface temperature measured in 7 open-top chambers and 7 control plots at the Cassiope ITEX site from 1993-1998. Effects were analyzed using a two-factor repeated measures analysis of variance. Year and treatment were considered fixed effects.
* P<0.05, ** P<0.01, *** P<0.001, ns = not significant.

1993-1998	Source of Variation	df	SS	MS	F	Probability
	Treatments	1	0.823	0.823	0.653	0.446 ns
	Error	7	8.823	1.260		
	Year	5	60.751	12.150	11.639	<0.001 ***
	Year x Treatment	5	35.594	7.119	6.820	<0.001 ***
	Error	35	36.536	1.044		
	Total	53	132.881			

Table 2.2. Effects of treatment and year on average June surface temperature measured in 7 open-top chambers and 7 control plots at the Cassiope ITEX site from 1993-1998. Effects were analyzed using a two-factor repeated measures analysis of variance. Year and treatment were considered fixed effects.
* P<0.05, ** P<0.01, *** P<0.001, ns = not significant.

1993-1998	Source of Variation	df	SS	MS	F	Probability
	Treatments	1	1.587	1.587	0.267	0.641 ns
	Error	3	17.844	5.948		
	Year	5	131.539	26.308	14.073	<0.001 ***
	Year x Treatment	5	11.156	2.231	1.194	0.359 ns
	Error	15	28.041	1.869		
	Total	29	190.167			

Table 2.3. Effects of treatment and year on average July surface temperature measured in 7 open-top chambers and 7 control plots at the Cassiope ITEX site from 1993-1998. Effects were analyzed using a two-factor repeated measures analysis of variance. Year and treatment were considered fixed effects.
* P<0.05, ** P<0.01, *** P<0.001, ns = not significant.

1993-1998	Source of Variation	df	SS	MS	F	Probability
	Treatments	1	11.530	11.530	3.462	0.122 ns
	Error	5	16.654	3.331		
	Year	5	35.466	7.093	2.033	0.108 ns
	Year x Treatment	5	7.676	1.535	0.440	0.816 ns
	Error	25	87.209	3.488		
	Total	41	158.535			

Table 2.4. Effects of treatment and year on average August surface temperature measured in 7 open-top chambers and 7 control plots at the Cassiope ITEX site from 1992-1998. Effects were analyzed using a two-factor repeated measures analysis of variance. Year and treatment were considered fixed effects.
* P<0.05, ** P<0.01, *** P<0.001, ns = not significant.

1992-1998	Source of Variation	df	SS	MS	F	Probability
	Treatments	1	9.906	9.906	4.847	0.079 ns
	Error	5	10.219	2.044		
	Year	6	48.489	8.082	7.789	<0.001 ***
	Year x Treatment	6	7.177	1.196	1.153	0.357 ns
	Error	30	31.127	1.038		
	Total	48	106.918			

Table 2.5. Effects of treatment and year on average September surface temperature measured in 7 open-top chambers and 7 control plots at the Cassiope ITEX site from 1992-1998. Effects were analyzed using a two-factor repeated measures analysis of variance. Year and treatment were considered fixed effects.
* P<0.05, ** P<0.01, *** P<0.001, ns = not significant.

1992-1998	Source of Variation	df	SS	MS	F	Probability
	Treatments	1	16.875	16.875	11.451	0.028 *
	Error	4	5.895	1.474		
	Year	6	32.782	5.464	10.005	<0.001 ***
	Year x Treatment	6	5.481	0.914	1.673	0.238 ns
	Error	24	13.106	0.546		
	Total	41	74.139			

Table 2.6. Effects of treatment and year on average June-August surface temperature measured in 7 open-top chambers and 7 control plots at the Cassiope ITEX site from 1993-1998. Effects were analyzed using a two-factor repeated measures analysis of variance. Year and treatment were considered fixed effects.
* P<0.05, ** P<0.01, *** P<0.001, ns = not significant.

1993-1998	Source of Variation	df	SS	MS	F	Probability
	Treatments	1	3.702	3.702	1.314	0.289 ns
	Error	7	19.715	2.816		
	Year	5	115.634	23.127	11.651	<0.001 ***
	Year x Treatment	5	11.093	2.219	1.118	0.369 ns
	Error	35	69.474	1.985		
	Total	53	219.618			

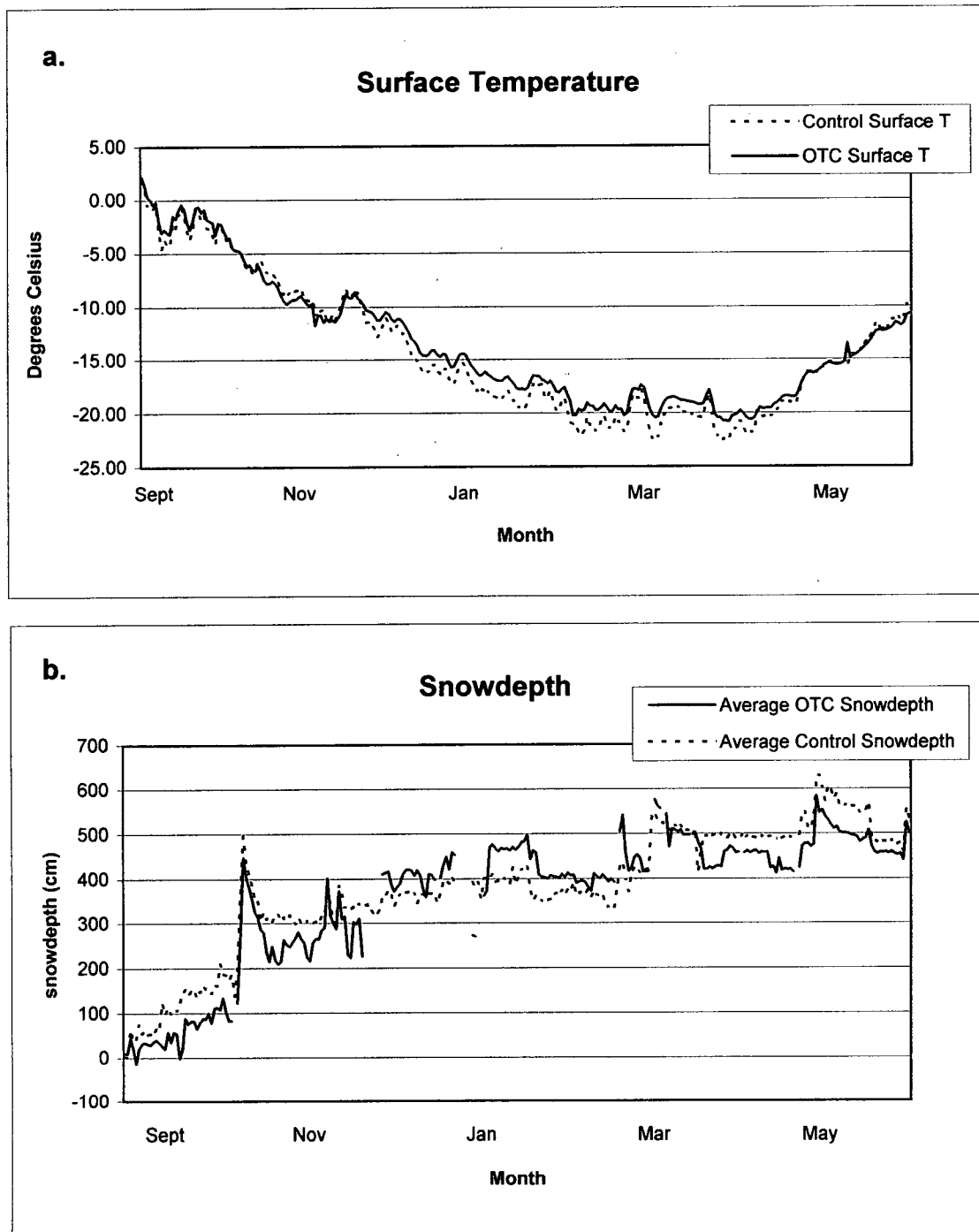


Figure 2.11. (a.) Comparison of average surface temperature and (b.) average snowdepth in the control and open-top chamber (OTC) plots for the winter (September - May) of 1995-1996. Some snowdepth data may be missing due to measurement errors.

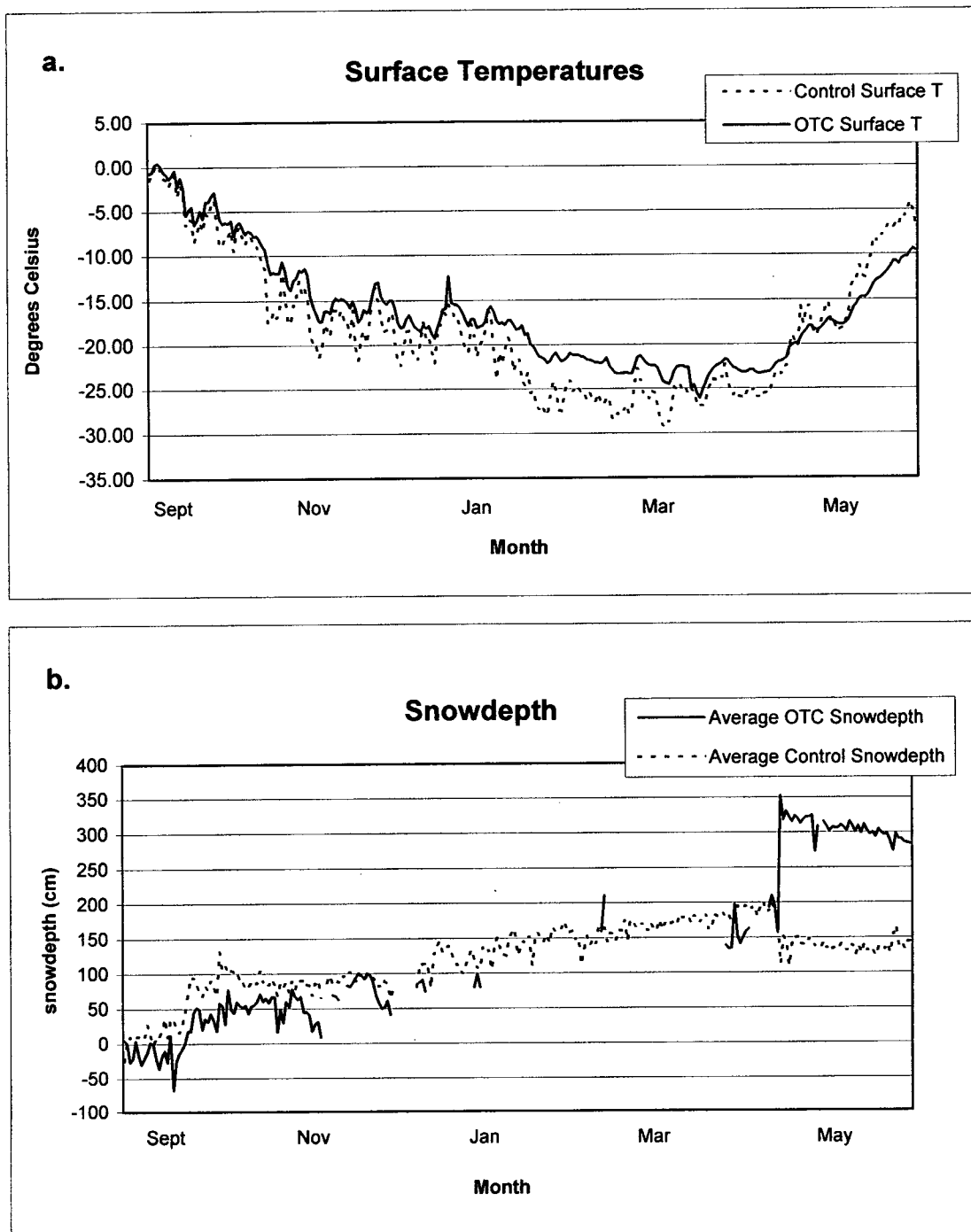


Figure 2.12. (a.) Comparison of average surface temperature and **(b.)** average snowdepth in the control and open-top chamber (OTC) plots for the winter (September - May) of 1996-1997. Some snowdepth data may be missing due to measurement errors.

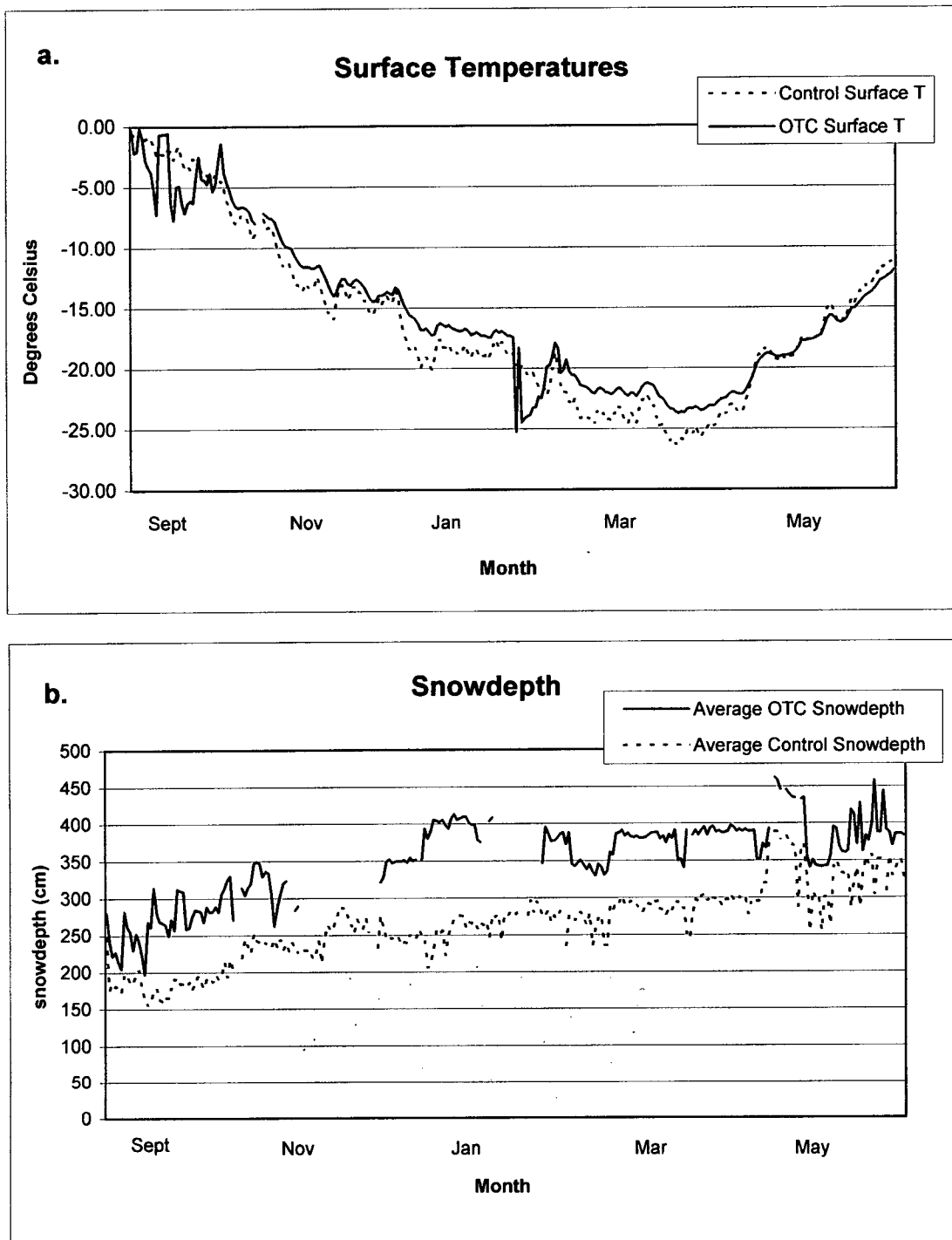


Figure 2.13. (a.) Comparison of average surface temperature and **(b.)** average snowdepth in the control and open-top chamber (OTC) plots for the winter (September - May) of 1997-1998. Some snowdepth data may be missing due to measurement errors.

chambers at the *Cassiope* ITEX site was, on average, +6 cm deeper than above the control plots. It appears that the open-top chambers act as snow-traps at Alexandra Fiord. However, it is important to note that snowpack depth changes due to drifting and blowing snow over the course of a winter (e.g., see Figure 2.12b). For the winters of 1995-1998, surface temperatures (0 cm) within the open-top chambers were warmer than in the control plots (Figures 2.11-2.13). For the winter months of September (year C-1) to May (year C), surface temperatures in the open-top chambers were +0.69°C (1995-1996), +1.75°C (1996-1997) and +0.71°C (1997-1998) warmer than in the control plots. Warmer surface temperature in the open-top chamber plots may be due to thicker snowpack.

2.3.2. Chronology Characteristics

A total of 12 stems representing four control plants and 22 stems representing four treatment plants were measured to produce two growth (annual growth increment and number of leaves) and two reproductive (number of flower buds and number of flower peduncles) chronologies (Table 2.7). The common time interval covered by all plants within both treatments was 1986-1998, except for the number of peduncles chronology which covers the period 1986-1997. The mean stem age for control plants was 13.5 years, with a mean stem length of 45.09 ± 26.85 mm (mean \pm SD). The longest control stem measured 105.63 mm with an age of 21 years. For treatment plants, the mean stem age was 15.68 years with a mean stem length of 52.15 ± 21.22 mm (mean \pm SD). The longest and oldest treatment stem measured were 122.77 mm and 33 years, respectively. The means and standard deviations were calculated with unstandardized data.

2.3.2.1. Control Plants

Visual analysis of the chronologies for annual stem elongation and annual production of leaves in the control treatment revealed that, in general, single plants responded individually to inter-annual environmental conditions for the period 1986-1998 (Figure 2.14 a and b). However, from 1996-1998, annual growth increments and leaf production values for individual plants did respond in unison. Examination of the standardized master chronologies of the two

Table 2.7. Descriptive statistics of *Cassiope tetragona* growth and reproduction variables in the control and warming treatment plots at Alexandra Fiord, Ellesmere Island, Canada. The table is divided into the full (1986-1998), pre-treatment (1986-1991) and treatment (1992-1998) periods. Numbers are means \pm standard deviation (SD). AGI = annual growth increment. lvs = leaves. peds = flower peduncles.

Full Period (1986-1998)	Control	Warming Treatment
Sample Size	4 plants	4 plants
Number of stems measured per plant	2-4 stems	4-7 stems
Total number of stems measured	12 stems	22 stems
Interval years	1986-1998	1986-1998
Mean stem length	45.09 \pm 26.85 mm	52.15 \pm 21.22 mm
Longest stem	105.63 mm	122.77 mm
Mean stem age	13.5 years	15.68 years
Oldest stem	21 years	33 years
Pre-treatment Period (1986-1991)		
Mean AGI	3.69 \pm 1.69 mm/yr	3.76 \pm 1.69 mm/yr
Mean # of Leaves*	10.28 \pm 2.88 lvs/yr	10.44 \pm 3.12 lvs/yr
Mean # of Flower Buds	0.16 \pm 0.37 buds/yr	0.15 \pm 0.41 buds/yr
Mean # of Flower Peduncles	0.16 \pm 0.37 peds/yr	0.23 \pm 0.53 peds/yr
Treatment Period (1992-1998)		
Mean AGI	3.51 \pm 1.69 mm/yr	3.53 \pm 1.70 mm/yr
Mean # of Leaves*	9.92 \pm 2.90 lvs/yr	10.70 \pm 3.28 lvs/yr
Mean # of Flower Buds	0.14 \pm 0.35 buds/yr	0.25 \pm 0.51 buds/yr
Mean # of Flower Peduncles**	0.21 \pm 0.45 peds/yr	0.43 \pm 0.70 peds/yr

* Mean annual leaf production estimates (mean \pm SD) are for four leaf rows on a stem. Mean annual flower bud and flower peduncle production estimates are for 2 of 4 leaf rows on a stem.

** Treatment period for average number of flower peduncles is 1992-1997.

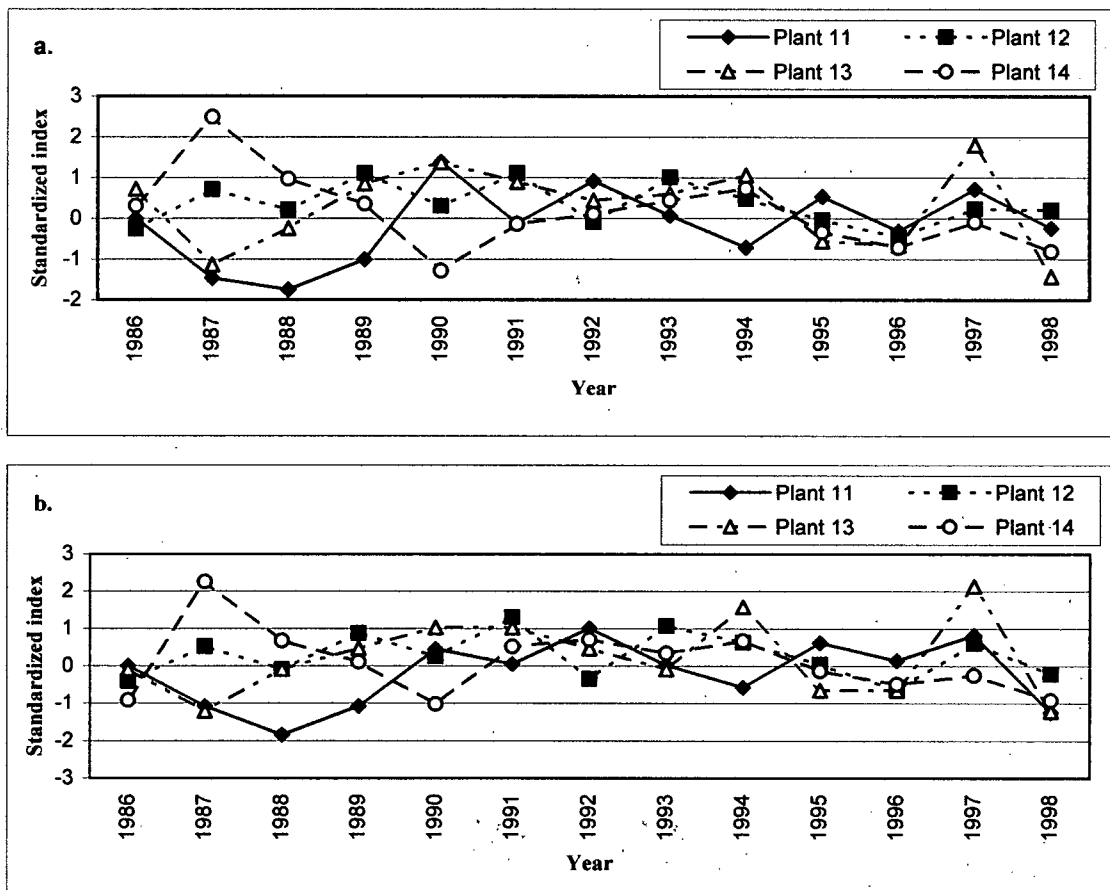


Figure 2.14. (a.) Standardized annual growth increment and (b.) standardized number of leaves indices for individual plants in the control plots at the Dryas ITEX site at Alexandra Fiord, Ellesmere Island, 1986-1998.

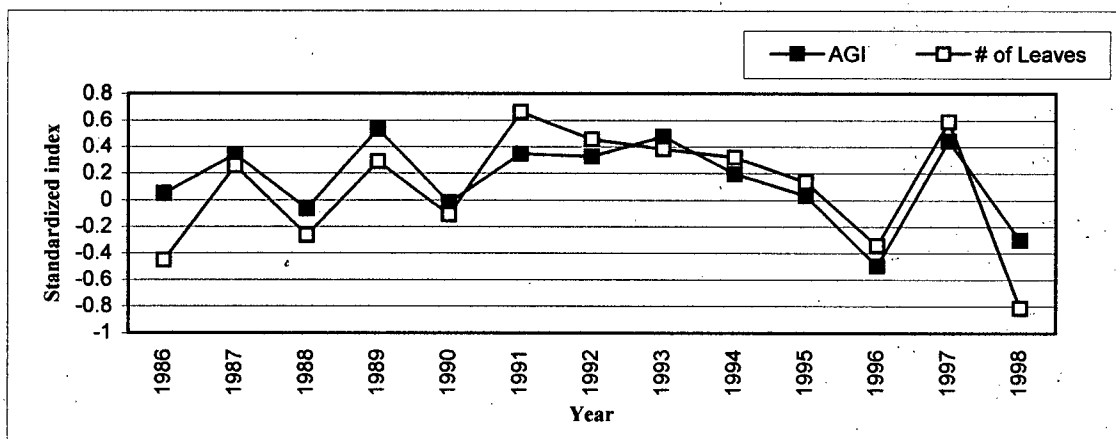


Figure 2.15. Standardized master chronology values for annual growth increments (AGI) and number of leaves in the control plots at the Dryas ITEX site, Alexandra Fiord, Ellesmere Island, 1986-1998.

growth variables showed closer unison of response to environmental conditions (Figure 2.15). Both master chronologies responded negatively in 1996, the second coldest growing season year on record at Alexandra Fiord.

Similarly, the chronologies for number of flower buds and number of flower peduncles in the control treatment showed individual plants did not respond in unison to inter-annual environmental conditions (Figures 2.16 a and b). The only consistent similarity between the individual control plants was the depressed state of flower bud and flower peduncle formation from 1986-1998. The generally depressed state of reproduction was punctuated occasionally by a positive departure by one or two plants. The standardized master chronologies for the two reproductive variables also revealed little unison in response (Figure 2.17).

2.3.2.2. Experimentally Warmed Plants

Examination of the chronologies for annual stem growth and annual production of leaves for individual plants in the open-top chambers revealed an individualistic response to inter-annual environmental conditions (Figure 2.18 a and b). However in 1987 and 1996, three plants responded negatively to colder summer temperatures, while in 1990 and 1994 three plants responded positively to warmer summer temperatures at Alexandra Fiord. Unlike the control master chronologies for vegetative growth, the treatment master chronologies did not respond in unison to inter-annual environmental factors. However, the treatment master chronologies for vegetative growth did respond positively in 1990 and 1994 and negatively in 1992, 1993 and 1997 (Figures 2.19).

The chronologies for annual production of flower buds and flower peduncles for individual plants in the open-top chamber treatment also revealed a general lack of unison in response to inter-annual environmental conditions (Figure 2.20 a and b). However during the first year of the warming treatment in 1992, the individual plants responded positively and/or remained above the zero mean. Then in 1993, the individual plant chronologies responded negatively, falling below the zero mean. Most of the individual plant chronologies rebounded positively in 1994. A similar pattern was evident in the standardized master chronologies for number of flower buds and number of flower peduncles (Figure 2.21).

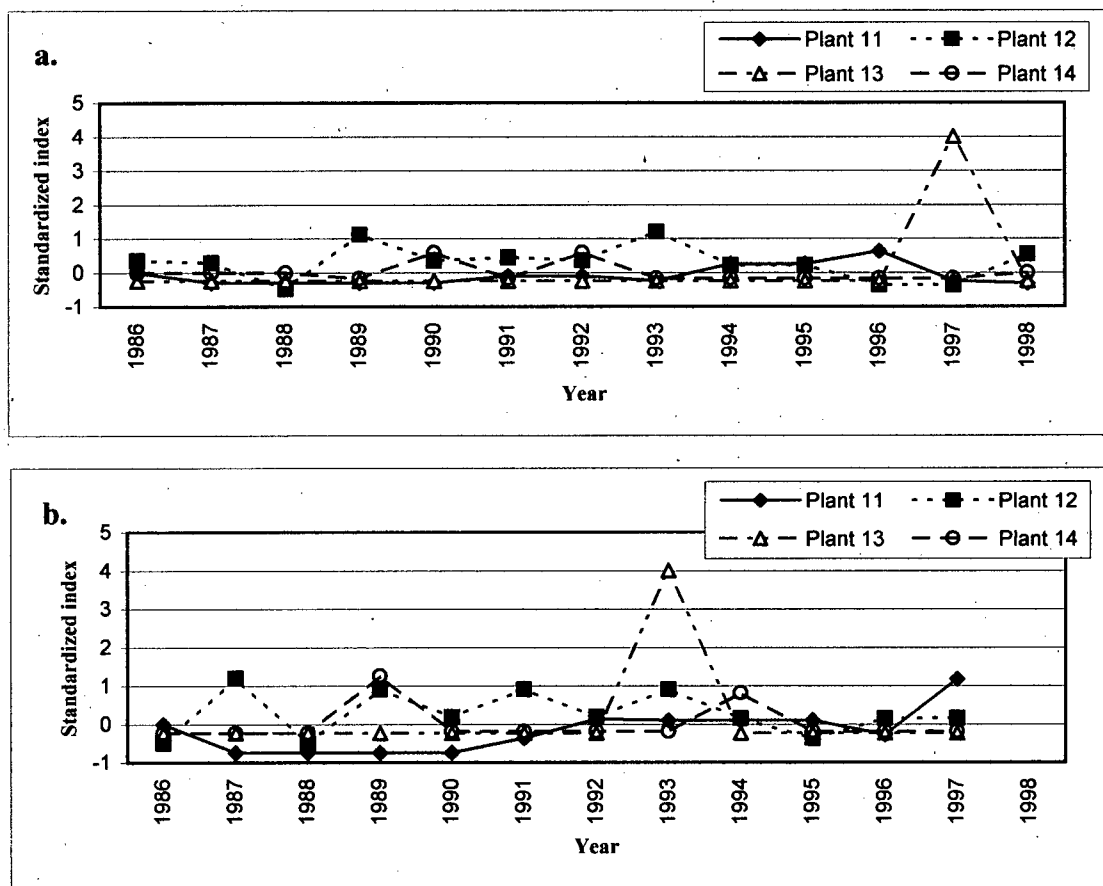


Figure 2.16. (a.) Standardized number of flower buds and (b.) standardized flower peduncle indices for individual plants in the control plots at the Dryas ITEX site at Alexandra Fiord, Ellesmere Island, 1986-1998. Note that number of flower peduncle indices end in 1997

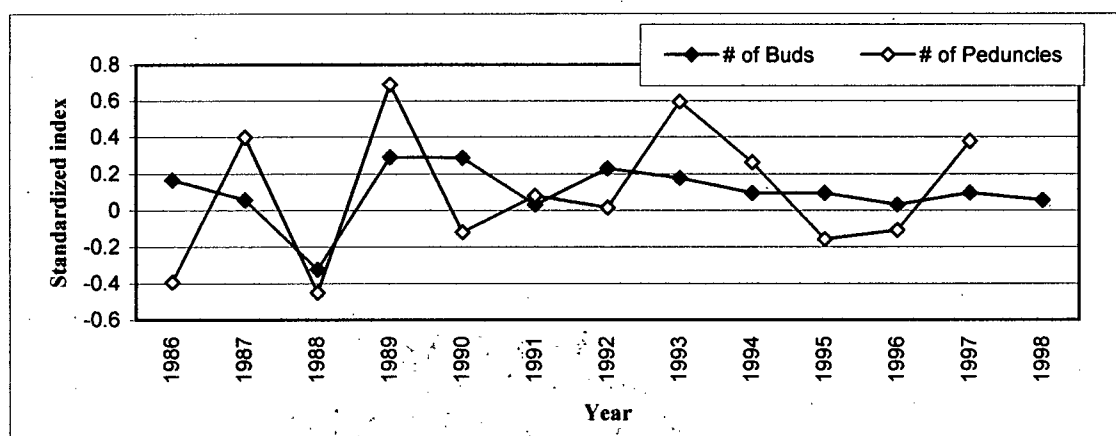


Figure 2.17. Standardized chronology values for number of flower buds and number of flower peduncles in the control plots at the Dryas ITEX site at Alexandra Fiord, Ellesmere Island, 1986-1998. Note that the standardized number of flower peduncles chronology ends in 1997.

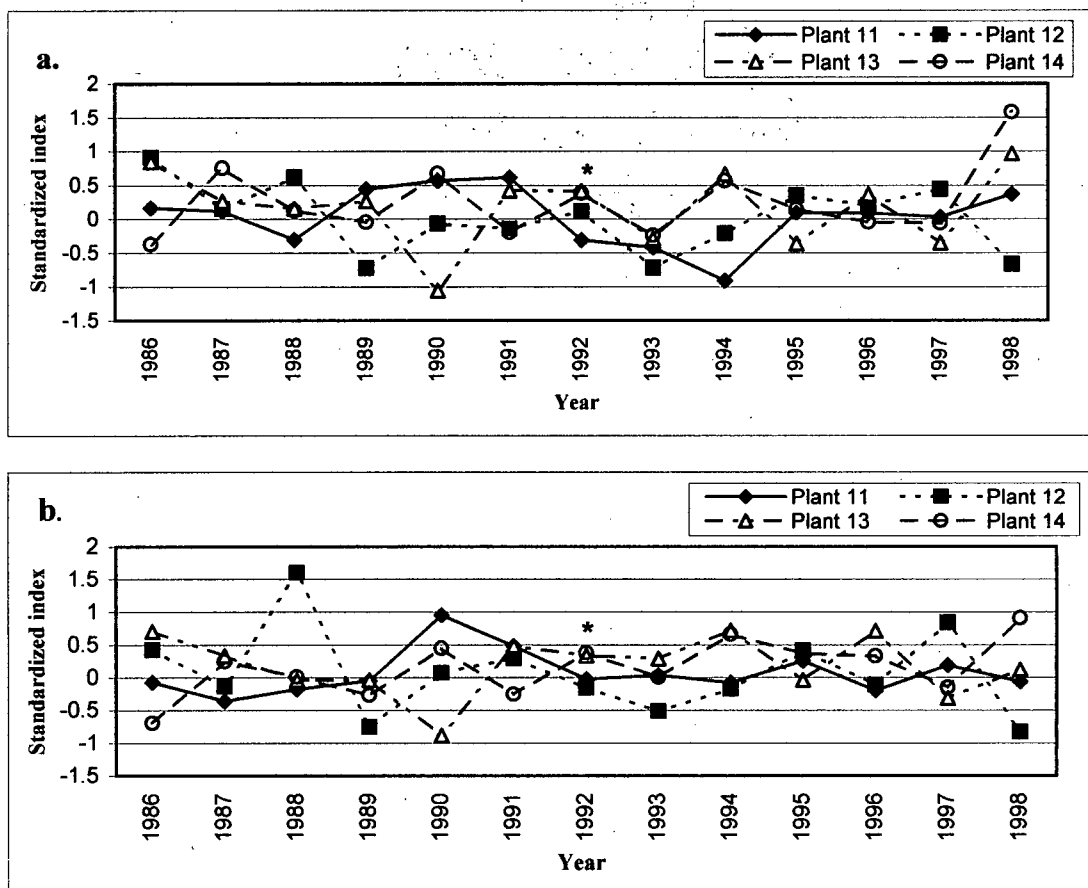


Figure 2.18. (a.) Standardized annual growth increment (AGI) and (b.) standardized number of leaves indices for individual plants for the open-top chamber (OTC) treatment at the Dryas ITEX site at Alexandra Fiord Ellesmere Island, 1986-1998. The warming treatment (OTC) was established in 1992, indicated by an asterix.

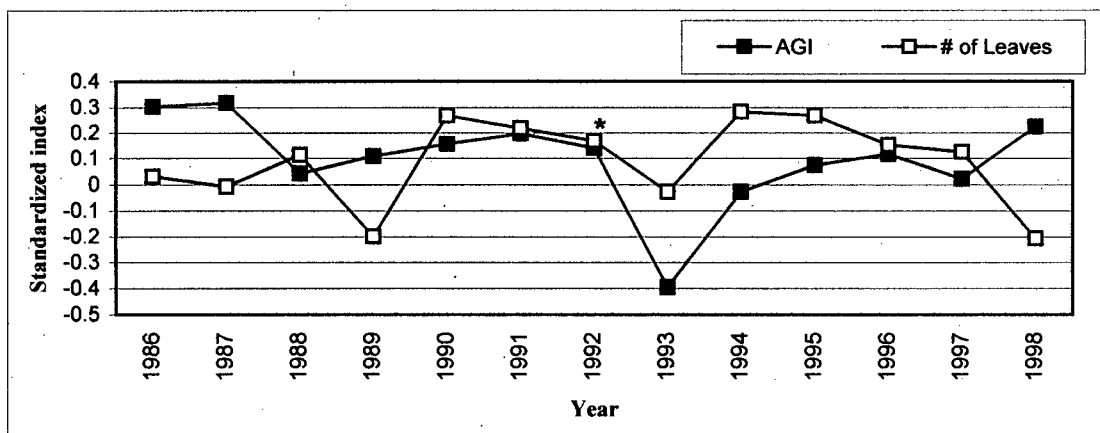


Figure 2.19. Standardized chronology values for annual growth increment (AGI) and number of leaves for the open-top chamber (OTC) treatment at the Dryas ITEX site, Alexandra Fiord, Ellesmere Island, 1986-1998. The warming treatment (OTC) was established in 1992, indicated by an asterix.

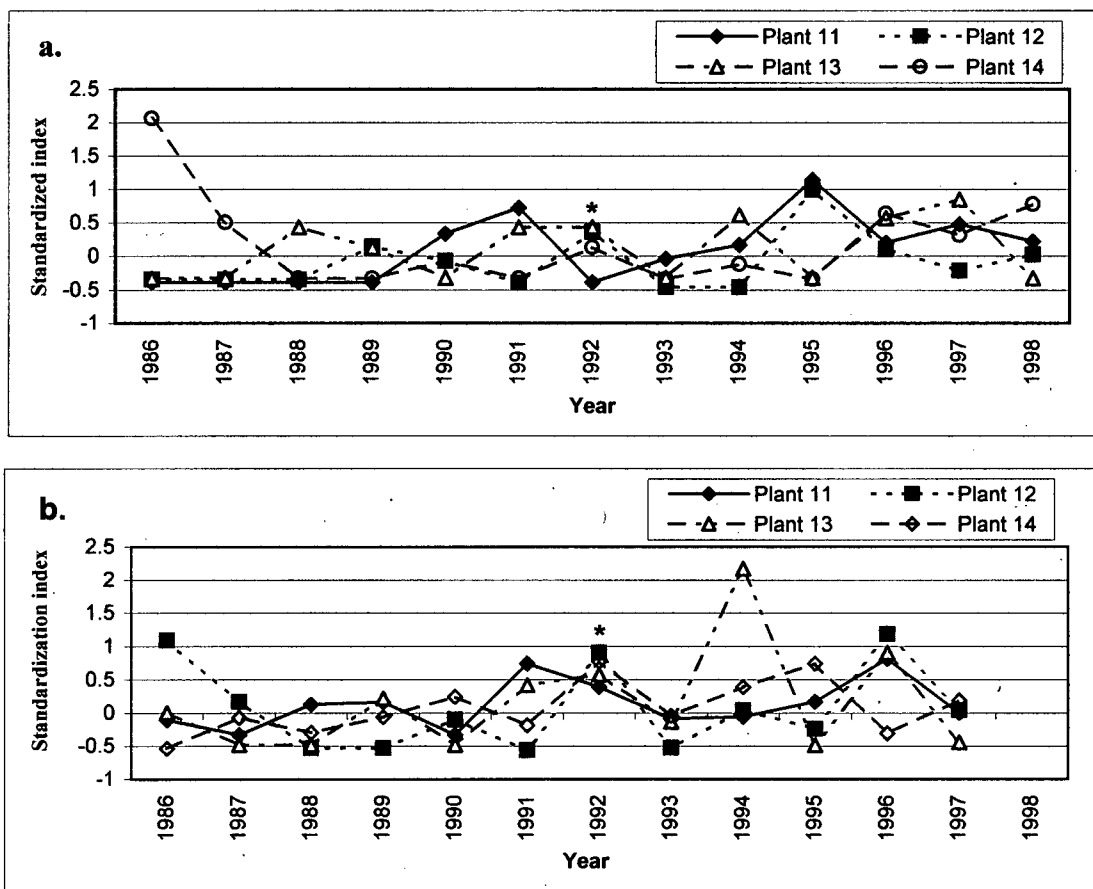


Figure 2.20. (a.) Standardized chronology values for the number of flower buds and (b.) standardized number of flower peduncle indices for individual plants in the open-top chamber (OTC) treatment at the Dryas ITEX site at Alexandra Fiord, Ellesmere Island, 1986-1998. The warming treatment (OTC) was established in 1992, indicated by an asterisk. Note that the number of flower peduncle indices end in 1997.

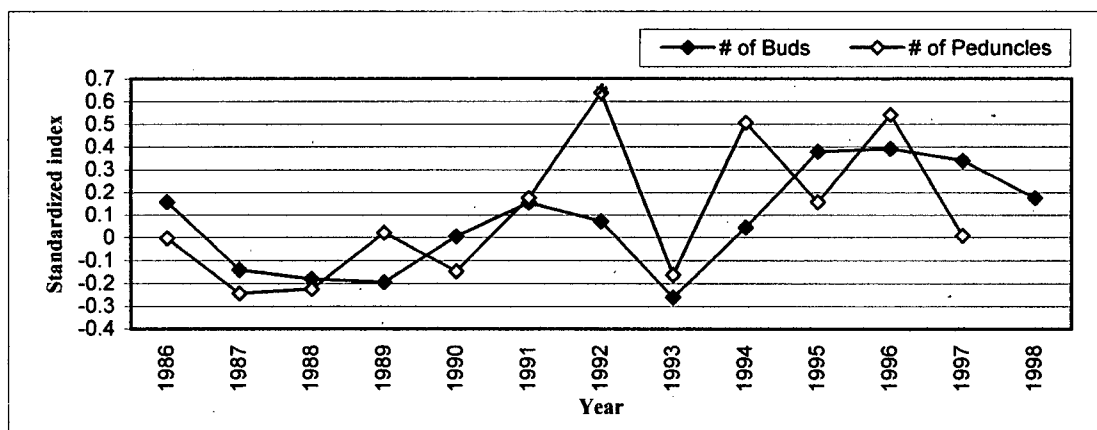


Figure 2.21. Standardized chronology values for the number of flower buds and number of flower peduncles in the open-top chamber (OTC) treatment at the Dryas ITEX site at Alexandra Fiord, Ellesmere Island, 1986-1998. The warming treatment (OTC) was established in 1992, indicated by an asterisk. Note that the number of flower peduncles chronology ends in 1997.

2.3.3. Mean Correlation Technique

Measurement of the signal strength revealed that the growth and reproductive variables in both the control and open-top chamber treatments, and for both pre-treatment (1986-1991) and treatment (1992-1998) periods, exhibited the highest level of variation due to differences among stems within the same plant ($1 - \bar{r}_{wt}$, within-plant noise or stem-chronology source) (Table 2.8). Variation attributed to difference among plants ($\bar{r}_{wt} - \bar{r}_{bt}$, plant-chronology source) and variation common to all plants (\bar{r}_{bt} , between-plant source) within a group were close to negligible.

2.3.4. Pearson's Correlation Coefficients Comparing Standardized Chronologies

2.3.4.1. Individual Plants

Simple Pearson's product-moment correlation coefficients calculated between the standardized chronologies for each individual plant for the current (year C) and previous year (year C-1) resulted in few strong and consistent relationships across treatments and time periods (Table 2.9 a and b). The correlations between the chronologies for annual stem elongation and annual production of leaves for the current year (year C) were the only strong relationships across all plants, treatments and time periods. Nearly all correlations between annual growth increments and number of leaves were positive and significant ($n = 6$ for pre-treatment period 1986-1991; $n = 7$ for treatment period 1992-1998; $P < 0.05$) (Tables 2.9 a and b).

2.3.4.2. Master Chronologies

Comparison of the simple Pearson's product-moment correlation coefficients generated between the standardized master chronologies resulted in no consistent significant relationships across treatments and time periods (Table 2.10). The correlations between chronologies for annual stem elongation and number of leaves, and between annual stem elongation and number of flower buds for the current year (year C) were positive, but were not all significantly different

Table 2.8. Measurement of the two growth and two reproductive chronologies' signal strength using the mean correlation technique (Briffa and Jones 1992). Chronologies are grouped by control and warming treatment (OTC) and into pre-treatment (1986-1991) and treatment periods (1992-1998). OTC = open-top chamber treatment.

	Control		Warming Treatment	
	Pre-treatment 1986-1991	Treatment 1992-1998	Pre-treatment 1986-1991	Treatment 1992-1998
Mean Correlation	Annual Growth Increment			
\bar{r}_{bt}	-0.06	0.07	-0.04	-0.01
$\bar{r}_{wt} - \bar{r}_{bt}$	0.20	0.03	0.02	0.01
$1 - \bar{r}_{wt}$	0.87	0.90	1.00	1.00
Number of Leaves				
\bar{r}_{bt}	-0.03	0.11	-0.03	0.00
$\bar{r}_{wt} - \bar{r}_{bt}$	0.07	0.08	0.04	-0.08
$1 - \bar{r}_{wt}$	0.96	0.82	1.00	1.00
Number of Buds				
\bar{r}_{bt}	-0.01	-0.05	-0.05	0.00
$\bar{r}_{wt} - \bar{r}_{bt}$	-0.04	0.01	0.21	0.00
$1 - \bar{r}_{wt}$	1.00	1.00	0.83	1.00
Number of Peduncles*				
\bar{r}_{bt}	-0.03	0.02	-0.01	0.02
$\bar{r}_{wt} - \bar{r}_{bt}$	0.01	0.00	-0.02	0.03
$1 - \bar{r}_{wt}$	1.00	0.99	1.00	0.96

* Treatment period for number of flower peduncles chronology is 1992-1997.

\bar{r}_{bt} is the between-plant signal.

$\bar{r}_{wt} - \bar{r}_{bt}$ is the between-plant noise.

$1 - \bar{r}_{wt}$ is the within-plant noise.

Table 2.9 a. Pearson's correlation coefficients showing relations between the standardized growth and reproductive chronologies of individual plants for the current year (year C) and previous year (year C-1). Table is divided into control and open-top chamber (OTC) treatments for the pre-treatment period, 1986-1991. n = 6 years for current year (year C) variables. n = 5 when previous year (year C-1) or lagged variables are included in the correlation.

Control 1986-1991

Plant #	A/A2	A/L	A/L2	A/B	A/B2	A/P	A/P2	A2/L	A2/B	A2/P	L/L2
11	0.295	0.948 **	0.225	0.125	0.000	0.125	0.000	0.556	0.977 **	0.977 **	0.453
12	-0.629	0.943 **	-0.618	0.779	-0.635	0.808	-0.795	-0.472	-0.313	-0.775	-0.416
13	0.272	0.970 **	0.548	0.000	0.000	0.000	0.000	0.273	0.000	0.000	0.544
14	0.250	0.960 **	-0.048	-0.522	-0.043	-0.076	-0.716	0.002	0.070	0.143	-0.262

Plant #	L/B	L/B2	L/P	L/P2	L2/B	L2/P	B/B2	B/P	B/P2	B2/P	P/P2
11	0.420	0.000	0.420	0.000	0.927 **	0.927 **	0.000	1.000 **	0.000	0.000	0.000
12	0.692	-0.367	0.768	-0.633	-0.394	-0.765	-0.454	0.722	-0.741	-0.320	-0.927 **
13	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
14	-0.563	0.190	-0.213	-0.726	0.038	0.175	-0.602	-0.381	0.959 **	-0.150	-0.240

OTC 1986-1991

Plant #	A/A2	A/L	A/L2	A/B	A/B2	A/P	A/P2	A2/L	A2/B	A2/P	L/L2
11	0.314	0.704	0.629	0.707	0.476	0.228	0.467	0.630	0.833 *	0.188	0.415
12	-0.099	0.899 *	-0.644	-0.754	-0.111	0.183	0.544	-0.277	-0.026	0.156	-0.587
13	-0.253	0.947 **	-0.074	0.584	-0.341	0.512	-0.771	-0.311	-0.674	-0.802	-0.131
14	-0.793	0.937 **	-0.905 *	0.832 *	0.548	0.607	-0.601	-0.582	-0.822 *	-0.663	-0.706

Plant #	L/B	L/B2	L/P	L/P2	L2/B	L2/P	B/B2	B/P	B/P2	B2/P	P/P2
11	0.813 *	0.322	0.072	0.322	0.854 *	0.714	0.799	0.489	-0.154	0.845 *	-0.595
12	-0.641	-0.063	-0.271	0.185	0.498	-0.259	0.051	-0.116	-0.661	0.122	0.583
13	0.466	-0.532	0.479	-0.594	-0.517	-0.809	-0.245	0.544	-0.919 **	0.238	-0.642
14	0.621	0.322	0.657	-0.318	-0.913 *	-0.534	0.847 *	0.291	-0.723	-0.252	-0.157

Significance levels indicated by: * = p < 0.05; ** = p < 0.01 for non-zero correlation test.

A = AGI (year C), A2 = AGI (year C-1), L = Leaf (year C), L2 = Leaf (year C-1), B = Bud (year C), B2 = Bud (year C-1), P = Peduncle (year C), P2 = Peduncle (year C-1).

Table 2.9 b. Pearson's correlation coefficients showing relations between the standardized growth and reproductive chronologies of individual plants for the current year (year C) and previous year (year C-1). Table is divided into control and open-top chamber (OTC) treatments for the treatment period, 1992-1998. $n = 7$ for correlation coefficients between current year (year C) chronologies for annual growth increments, number of leaves and number of flower buds. $n = 6$ when previous year (year C-1) or lagged variables are included in the correlation. For correlation coefficients between annual number of flower peduncles and another current year (year C) variable, $n = 6$. $n = 5$, when previous year (year C-1) annual production of flower peduncles are included in the correlation.

Control 1992-1998

Plant #	A/A2	A/L	A/L2	A/B	A/B2	A/P	A/P2	A2/L	A2/B	A2/P	L/L2
11	-0.514	0.948 *	-0.291	-0.534	0.776 *	0.657	-0.608	-0.523	-0.034	-0.427	-0.295
12	0.046	0.963 **	-0.143	0.826	0.275	0.723	0.576	-0.003	0.151	-0.356	-0.187
13	-0.284	0.944 *	-0.439	0.716	0.000	0.081	0.322	-0.314	-0.622	0.197	-0.510
14	0.319	0.965 **	0.387	0.000	0.418	0.698	-0.329	0.527	0.000	0.379	0.552

Plant #	L/B	L/B2	L/P	L/P2	L2/B	L2/P	B/B2	B/P	B/P2	P/P2	
11	-0.287	0.914 *	0.575	-0.632	-0.204	-0.186	-0.139	-0.718	0.495	0.639	-0.945 *
12	0.678	0.158	0.591	0.634	0.013	-0.497	0.335	0.645	0.303	0.067	0.026
13	0.715	0.000	-0.238	0.477	-0.468	0.200	0.000	-0.250	-0.250	0.000	-0.250
14	0.000	0.373	0.765	-0.188	0.000	0.132	0.000	0.000	0.000	-0.250	-0.250

OTC 1992-1998

Plant #	A/A2	A/L	A/L2	A/B	A/B2	A/P	A/P2	A2/L	A2/B	A2/P	L/L2
11	0.148	0.353	-0.049	0.551	0.560	0.548	0.342	-0.499	-0.611	0.356	-0.886 *
12	0.193	0.873	0.319	0.605	-0.069	0.429	-0.048	0.150	0.058	0.370	0.021
13	-0.936 *	0.884 *	-0.724	0.487	-0.973 **	0.981 **	-0.789	-0.843	-0.627	-0.872 *	-0.902 *
14	-0.535	0.840	-0.548	-0.168	-0.521	0.545	-0.486	-0.220	-0.431	0.190	-0.341

Plant #	L/B	L/B2	L/P	L/P2	L2/B	L2/P	B/B2	B/P	B/P2	P/P2	
11	0.729	-0.470	-0.538	0.273	-0.394	0.785	0.099	0.035	-0.219	0.954 **	-0.194
12	0.415	-0.274	0.018	0.345	0.244	0.744	-0.218	0.065	-0.227	0.650	-0.458
13	0.116	-0.924 *	0.852 *	-0.781	-0.196	-0.637	-0.476	0.440	-0.572	-0.919 **	-0.741
14	-0.144	-0.898	0.322	0.055	-0.163	0.228	0.028	-0.647	-0.074	0.005	-0.455

Significance levels indicated by: * = $p < 0.05$; ** = $p < 0.01$ for non-zero correlation test.

A = AGI (year C), A2 = AGI (year C-1), L = Leaf (year C), L2 = Leaf (year C-1), B = Bud (year C), B2 = Bud (year C-1), P = Peduncle (year C), P2 = Peduncle (year C-1).

Table 2.10. Pearson's correlation coefficients showing relations between the standardized growth and reproductive chronologies. Table is divided into the control and open-top chamber treatments, and into pre-treatment (1986-1991) and treatment (1992-1998) time periods. OTC = open-top chambers. n = 6 for the pre-treatment period (1986-1991), and n = 7 for the treatment period (1992-1998) for correlations between current year (year C) master chronologies for annual growth, number of leaves and number of flower buds. n = 5 and n = 6 for the pre-treatment and treatment periods, respectively, when previous year (year C-1) variables are included in the correlation. n = 5 for the pre-treatment period and n = 6 for the treatment period for correlations between current year (year C) flower peduncle chronologies and another variable. n = 4 and n = 5 for the pre-treatment and treatment periods, respectively, when previous year (year C-1) flower peduncle chronologies are included.

Control 1986-1991											
A/A2	A/L	A/L2	A/B	A/B2	A/P	A/P2	A2/L	A2/B	A2/P	L/L2	
-0.927 **	0.794	-0.868 *	0.474	-0.515	0.993 **	-0.934 **	-0.814 *	-0.118	-0.753	-0.668	
L/B	L/B2	L/P	L/P2	L2/B	L2/P	B/B2	B/P	B/P2	B2/P	P/P2	
0.314	0.039	0.595	-0.7	-0.266	-0.849 *	-0.717	0.663	-0.191	-0.561	-0.849 *	
OTC 1986-1991											
A/A2	A/L	A/L2	A/B	A/B2	A/P	A/P2	A2/L	A2/B	A2/P	L/L2	
0.187	0.01	0.141	0.262	0.857 *	-0.055	0.723	0.176	-0.241	-0.641	-0.271	
L/B	L/B2	L/P	L/P2	L2/B	L2/P	B/B2	B/P	B/P2	B2/P	P/P2	
0.739	-0.038	0.031	0.406	0.287	0.734	0.145	0.630	0.316	-0.096	-0.318	
Control 1992-1998											
A/A2	A/L	A/L2	A/B	A/B2	A/P	A/P2	A2/L	A2/B	A2/P	L/L2	
-0.088	0.969 **	-0.079	0.838 *	0.260	0.835 *	0.169	-0.233	0.285	-0.012	-0.254	
L/B	L/B2	L/P	L/P2	L2/B	L2/P	B/B2	B/P	B/P2	B2/P	P/P2	
0.678	0.063	0.751	0.202	0.376	-0.013	0.646	0.785	0.138	0.480	-0.042	
OTC 1992-1998											
A/A2	A/L	A/L2	A/B	A/B2	A/P	A/P2	A2/L	A2/B	A2/P	L/L2	
-0.218	0.749	0.245	0.949 **	0.277	0.67	-0.401	-0.746	0.081	-0.616	-0.194	
L/B	L/B2	L/P	L/P2	L2/B	L2/P	B/B2	B/P	B/P2	B2/P	P/P2	
0.562	-0.42	0.682	-0.633	0.479	-0.187	0.508	0.433	-0.098	-0.18	-0.902 **	

Significance levels indicated by: * = $p < 0.05$; ** = $p < 0.01$ for non-zero correlation test. A = AGI (year C), A2 = AGI (year C-1), L = Leaf (year C), L2 = Leaf (year C-1), B = Bud (year C), B2 = Bud (year C-1), P = Peduncle (year C), P2 = Peduncle (year C-1).

from zero ($n = 6$ for the pre-treatment period 1986-1991; $n = 7$ for the treatment period of 1992-1998; $P < 0.05$ and $P < 0.01$). Correlations between annual stem elongation for the previous year (year C-1) and number of peduncles for the current year (year C) were negative, but not significantly different from zero ($P > 0.05$). Correlations between annual production of leaves produced for the current year (year C) and number of flower buds and number of flower peduncles produced for the current year (year C) were positive. These correlations were also not significantly different from zero ($P > 0.05$). Lastly, correlation coefficients between the chronologies for number of flower peduncles for the current year (year C) and the number of flower buds for the current year (year C) were positive, but not significantly different from zero ($P > 0.05$).

2.3.5. Repeated Measures Analysis of Variance and Analysis of Covariance

Results from two-factor repeated measures analysis of variance showed that the length of the annual growth increment of *C. tetragona* was not significantly affected by the warming experiment between 1992-1998 (Table 2.11, Figure 2.22 a). Annual variations in local environmental conditions did not affect yearly stem elongation. Analysis of the annual growth increments for the period prior to the establishment of the open-top chamber treatment (1986-1991) revealed the two populations exhibited a consistent community wide response to annual variation in the environment.

Similarly, the number of leaves produced per year was not significantly affected by the open-top chamber treatment from 1992-1998 (Table 2.12; Figure 2.22 b). In addition, the collective response of this vegetative growth variable to local environmental conditions was uniform from 1986-1991 (Figure 2.16 b). However, annual leaf production was strongly affected by year-to-year differences in environmental factors, both prior to ($P = 0.001$) and during ($P = 0.001$) the open-top chamber treatment.

There was a significant warming effect of the open-top chambers on the number of buds produced per year after 1992 ($P = 0.039$) (Table 2.13). A repeated measures analysis of covariance using the pre-treatment period (1986-1991) values as the covariate, confirmed the

Table 2.11. Effects of treatment and year on length of annual growth increment of *Cassiope tetragona* for the pre-treatment (1986-1991) and treatment (1992-1998) periods. Effects were analyzed using a two-factor repeated measures analysis of variance.

1986-1991	Source of Variation	df	SS	MS	F	Probability
	Treatments	1	0.834	0.834	0.275	0.619
	Error	6	18.177	3.029		
	Year	5	2.380	0.476	0.542	0.743
	Year x Treatment	5	4.968	0.994	1.132	0.365
	Error	30	26.34	0.878		
	Total	47	52.699			

1992-1998	Source of Variation	df	SS	MS	F	Probability
	Treatments	1	0.378	0.378	0.346	0.578
	Error	6	6.553	1.092		
	Year	6	4.722	0.787	1.219	0.319
	Year x Treatment	6	8.078	1.346	2.086	0.079
	Error	36	23.237	0.645		
	Total	55	42.968			

* = $P < 0.05$. ** = $P < 0.01$. *** = $P < 0.001$.

Table 2.12. Effects of treatment and year on number of leaves produced by *Cassiope tetragona* for the pre-treatment (1986-1991) and treatment (1992-1998) periods. Effects were analyzed using a two-factor repeated measures analysis of variance.

1986-1991	Source of Variation	df	SS	MS	F	Probability
	Treatment	1	3.810	3.810	0.356	0.573
	Error	6	64.295	10.716		
	Year	5	25.129	5.032	7.319	0.000 ***
	Year x Treatment	5	7.378	1.476	2.146	0.087
	Error	30	20.625	0.688		
	Total	47	121.237			

1992-1998	Source of Variation	df	SS	MS	F	Probability
	Treatment	1	0.152	0.152	0.106	0.756
	Error	6	8.589	1.432		
	Year	6	50.018	8.336	8.229	0.000 ***
	Year x Treatment	6	9.114	1.519	1.500	0.206
	Error	36	36.468	1.013		
	Total	55	104.341			

* = $P < 0.05$. ** = $P < 0.01$. *** = $P < 0.001$.

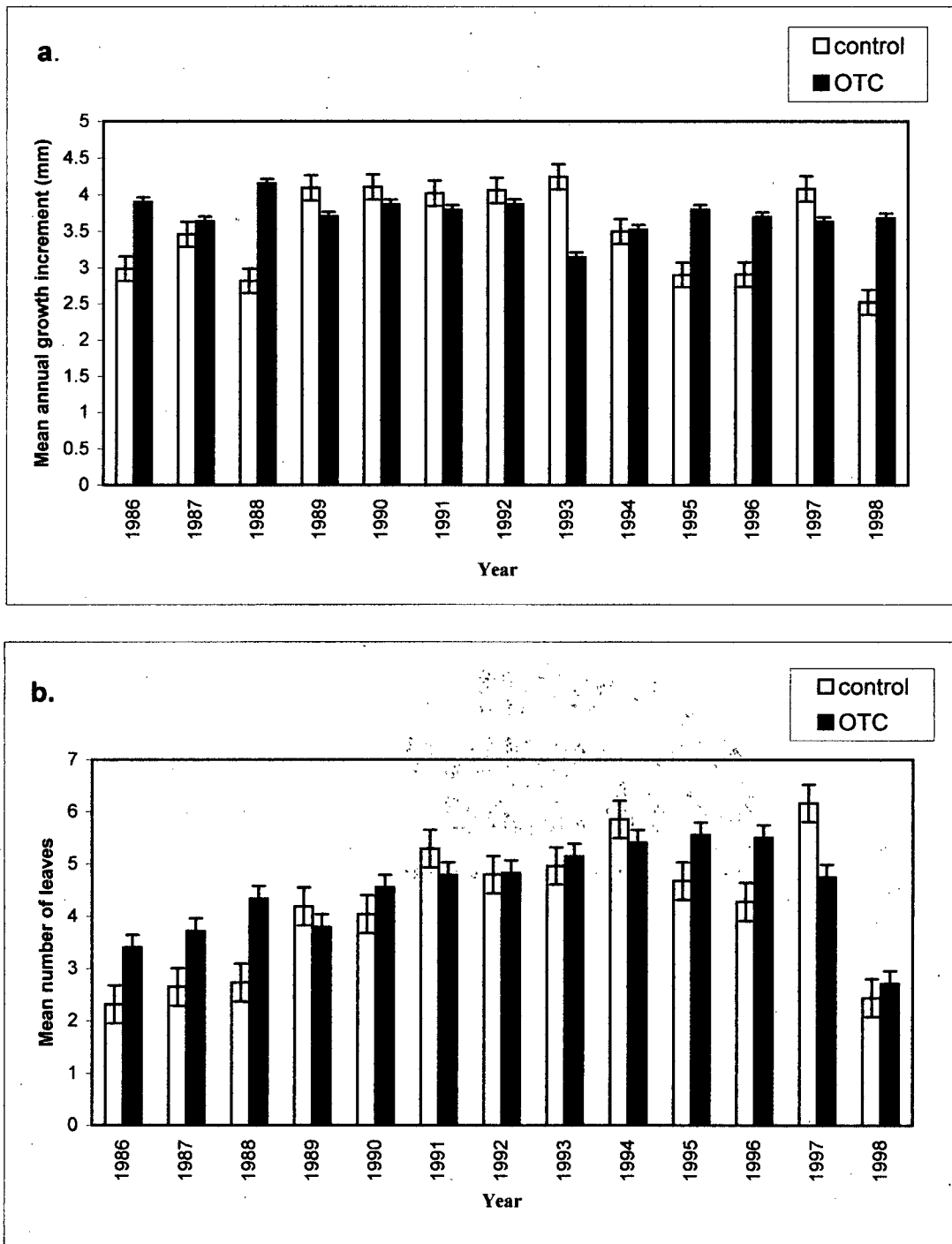


Figure 2.22. (a.) Comparison of mean annual growth increment and (b.) mean number of leaves produced per year for *Cassiope tetragona* in the control and open-top chamber treatment (OTC) plots, 1986-1998. Warming experiment began in 1992. $n = 4$. Error bars indicate one standard error.

Table 2.13. Effects of treatment and year on number of flower buds produced by *Cassiope tetragona* for the pre-treatment (1986-1991) and treatment (1992-1998) periods. Effects were analyzed using a two-factor repeated measures analysis of variance. Data were ranked and the ranks transformed using a Blom transformation.

1986-1991	Source of Variation	df	SS	MS	F	Probability
	Treatment	1	0.815	0.815	0.562	0.482
	Error	6	8.712	1.452		
	Year	5	1.626	0.325	0.585	0.712
	Year x Treatment	5	0.336	0.067	0.121	0.987
	Error	30	16.692	0.556		
	Total	47	28.181			

1992-1998	Source of Variation	df	SS	MS	F	Probability
	Treatment	1	3.545	3.545	6.966	0.039 *
	Error	6	3.054	0.509		
	Year	6	4.404	0.734	0.947	0.474
	Year x Treatment	6	3.911	0.652	0.841	0.546
	Error	36	27.894	0.775		
	Total	55	42.808			

* = $P < 0.05$. ** = $P < 0.01$. *** = $P < 0.001$.

Table 2.14. Effects of treatment and year on number of flower buds produced by *Cassiope tetragona* for the treatment period (1992-1998). Effects were analyzed using a two-factor repeated measures analysis of covariance. The pre-treatment period (1986-1991) values were used as the covariate. Data were ranked and the ranks transformed using a Blom transformation.

1992-1998	Source of Variation	df	SS	MS	F	Probability
	Treatment	1	1.773	1.773	9.76	0.026 *
	Covariate	1	2.145	2.145	11.84	0.019 *
	Error	5	0.908	0.182		
	Year	6	2.159	0.36	0.537	0.776
	Year x Treatment	6	4.575	0.762	1.137	0.365
	Year x Covariate	6	7.781	1.297	1.934	0.108
	Error	30	20.113	0.67		
	Total	55	39.454			

* = $P < 0.05$. ** = $P < 0.01$. *** = $P < 0.001$.

effect of the open-top chambers ($P = 0.026$) (Table 2.14). Annual flower bud production on treatment plants increased dramatically in 1994 compared with the control plants, and remained high throughout the treatment period (Figure 2.23 a). Retrospective analysis showed no significant difference in the plants' production of flower buds prior to establishment of treatment (Table 2.13). There also appeared to be no effect on flower bud production due to yearly differences in environmental conditions either prior to or during the experimental warming.

Lastly, the number of flower peduncles produced per year was significantly affected by the experimental warming treatment from 1992-1997 ($P = 0.03$) (Table 2.15). The increase in flower peduncle production was seen immediately in 1992 after only one summer of warming (Figure 2.23 b). The effect of the warming was visible throughout the treatment period (1992-1997). Analysis of the annual flower peduncle production during the period prior to the establishment of the open-top chamber treatment (1986-1991) confirmed a consistent reproductive response of the sampled plants to the prevailing environmental conditions.

2.3.6. Correlations Between Standardized Chronologies and Climate

2.3.6.1. Thermocouple Surface Temperature, 1992-1998

The correlation coefficients for the control growth and reproductive variables revealed a consistent negative relationship with extremely cold surface temperatures from October (year C-1) to April (year C) (Table 2.16). Eight of the correlations during the winter period were significantly different from zero ($n = 6$ for the months of January-July; $n = 7$ for months August-December; $P < 0.05$ to $P < 0.01$). In contrast, the correlation coefficients relating annual stem growth and the production of flower buds and flower peduncles to surface temperatures within the open-top chambers during the winter months were mostly positive, although only one was significantly different from zero (for flower buds: $n = 6$ for months of January-July, $n = 7$ for months August-December; for flower peduncles: $n = 5$ for months of January-July, $n = 6$ for months August-December; $P > 0.05$) (previous October, $P < 0.05$). The correlation coefficients for annual leaf production in the open-top chamber treatment were negative from October (year C-1) to April (year C).

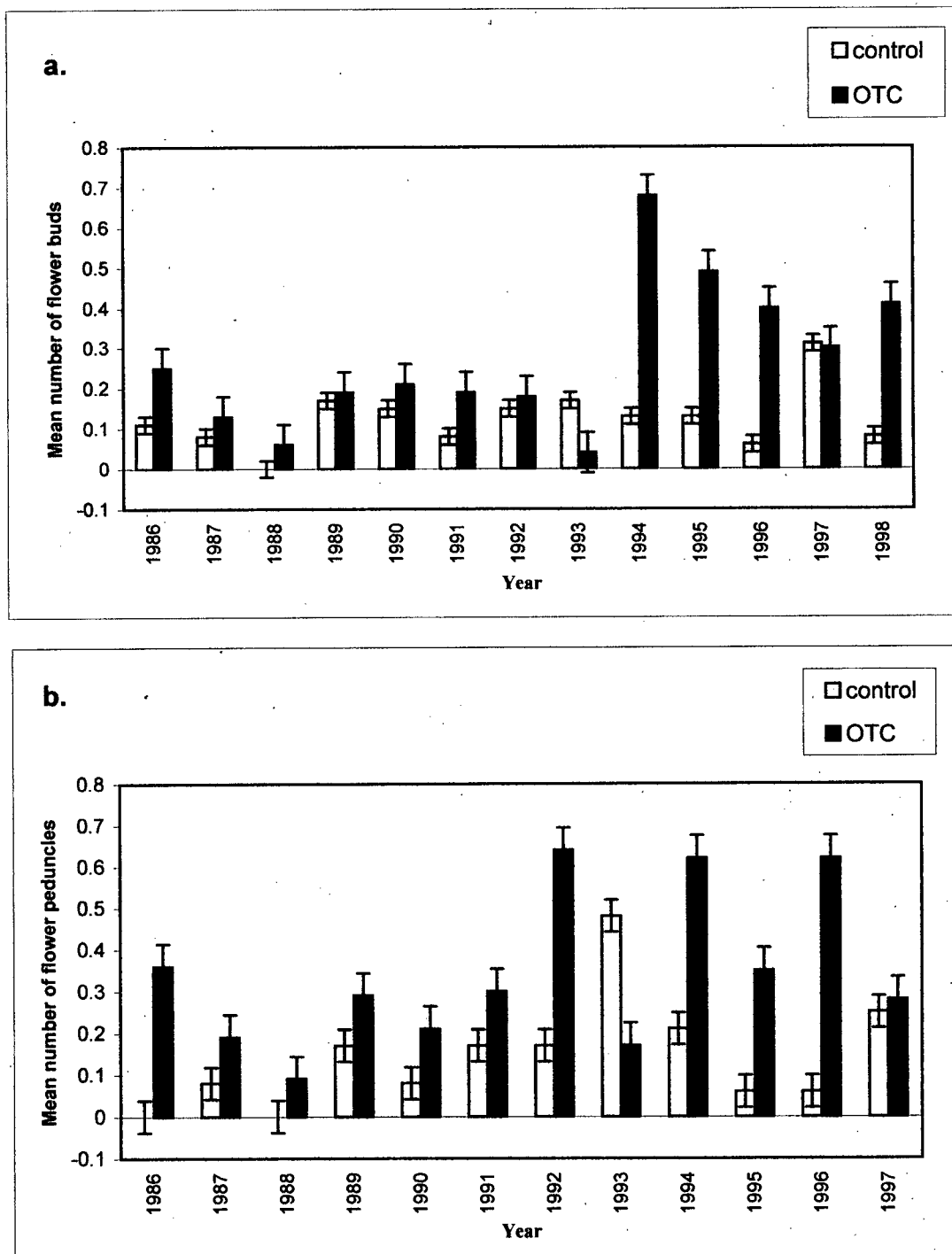


Figure 2.23. (a.) Comparison of the mean number of flower buds and (b.) the mean number of flower peduncles produced per year for *Cassiope tetragona* in the control and open-top chamber treatment (OTC) plots, 1986-1998. Warming experiment began in 1992. $n = 4$. Error bars indicate one standard error.

Table 2.15. Effects of treatment and year on number of flower peduncles produced for *Cassiope tetragona* for the pre-treatment (1986-1991) and treatment (1992-1997) periods. Effects were analyzed using a two-way repeated measures analysis of variance. The data were ranked and the ranks transformed using a Blom transformation.

1986-1991	Source of Variation	df	SS	MS	F	Probability
	Treatment	1	1.925	1.925	2.789	0.156
	Error	5	3.451	0.69		
	Year	5	2.487	0.497	0.835	0.538
	Year x Treatment	5	1.006	0.201	0.337	0.885
	Error	25	14.898	0.596		
	Total	41	23.767			
1992-1997	Source of Variation	df	SS	MS	F	Probability
	Treatment	1	6.172	6.172	8.395	0.027 *
	Error	6	4.411	0.735		
	Year	5	2.508	0.502	0.799	0.559
	Year x Treatment	5	7.303	1.461	2.326	0.067
	Error	30	18.84	0.628		
	Total	47	39.234			

* = $P < 0.05$. ** = $P < 0.01$. *** = $P < 0.001$.

Table 2.16. Pearson's correlation coefficients relating average thermocouple surface temperature for the previous (year C-1) and current (year C) year to control or open-top chamber (OTC) master chronologies for annual growth increment (AGI), number of leaves, number of flower buds and number of flower peduncles for the treatment period of 1992-1998.

Control 1992-1998										OTC 1992-1998									
Average Thermocouple Surface Temperature										Average Thermocouple Surface Temperature									
Year	Month	Annual Growth Increment	Number of Leaves	Number of Buds	Number of Peduncles	Month	Annual Growth Increment	Number of Leaves	Number of Buds	Number of Peduncles	Year	Month	Annual Growth Increment	Number of Leaves	Number of Buds	Number of Peduncles			
(year C-1)	October	-0.526	-0.319	-0.654	-0.007	October	0.124	-0.132	-0.384	0.915 *	(year C)	January	-0.915 *	-0.631	0.029	0.497			
	November	-0.885 *	-0.685	-0.949 **	-0.434	November	0.651	-0.423	0.334	0.558		February	-0.699	-0.246	-0.144	0.732			
	December	-0.584	-0.518	-0.838 *	-0.094	December	0.594	-0.617	0.342	0.174		March	-0.753	-0.350	0.344	0.370			
	April	-0.804	-0.636	-0.841 *	-0.704	April	0.621	-0.253	0.796	0.078		May	0.669	-0.253	0.796	0.078			
	May	0.669	0.758	0.352	0.790	May	-0.889 *	0.972 **	0.025	0.682		June	0.784	0.118	-0.524	-0.406			
	June	-0.358	-0.630	-0.344	-0.366	June	0.523	-0.258	0.138	-0.323		July	-0.358	-0.258	0.138	-0.323			
	August	0.156	-0.028	0.516	-0.311	August	-0.129	0.259	-0.316	-0.135		August	0.156	0.259	-0.316	-0.135			
	September	0.871 *	0.782 *	0.957 **	0.558	September	-0.636	0.309	-0.397	-0.571		September	0.871 *	0.309	-0.397	-0.571			

* = $P < 0.05$, ** = $P < 0.01$.

Note, because thermocouples were not put into place in the open-top chambers and control plots before late July 1992, there were no temperature measurements to compare with growth and reproduction for the period January-July 1992. Thus, for the months January-July, $n = 6$, and for the months August-December, $n = 7$. In addition, as the number of flower peduncles chronology is one year shorter for the treatment period (1992-1997) than the other growth and reproduction chronologies, $n = 5$ for the months of January-July and, $n = 6$ for the months August-December.

During May and June, the growth and reproductive variables in the control plots changed sign, and were positively correlated with spring and early summer temperatures (Table 2.16). At the biweekly time scale, the surface temperatures during the last two weeks of May were important for flower peduncle development in the control treatment ($P < 0.05$) (Table 2.17). Stem elongation ($P < 0.05$) and flower bud production ($P < 0.01$) were positively influenced by warm temperature in the first two weeks of June (Table 2.17).

In May, the relationships of the four treatment variables with increased surface temperature were mixed (Table 2.16). Annual stem elongation was negatively related ($P < 0.05$) while annual leaf production was positively related ($P < 0.01$) to temperatures in May. Increasing temperatures in the last two weeks of May appeared to adversely affect stem elongation ($P < 0.01$) in the open-top chamber treatment (Table 2.16). The two reproductive variables in the open-top chamber treatment were positively related to May temperatures, but negatively to June temperatures (Table 2.16).

By mid to late summer, the surface temperatures in the control plots were negatively correlated with the growth and reproduction of *C. tetragona* (Table 2.16). Annual flower buds production was the exception, with a positive association with surface temperatures in August. The positive response by flower buds ($P < 0.01$) to surface temperatures continued into September. Annual growth increments ($P < 0.05$), the number of leaves ($P < 0.05$) and number of flower peduncles were positively associated with September temperature as well. Any remaining warmth in the final two weeks in September was particularly beneficial to stem elongation ($P < 0.05$), leaf production ($P < 0.05$) and flower bud development ($P < 0.01$) (Table 2.16).

During the months of June, July and August in the open-top chamber treatment, the correlation coefficients between summer temperatures and the two growth and number of flower bud variables changed sign twice (Table 2.16). No correlations were significantly different from zero, however ($n = 6$ for the months of January-July; $n = 7$ for months August-December; $P > 0.05$). The correlations between annual flower peduncle production and surface temperatures were negative throughout the summer. Annual leaf production appeared to be the only variable which was positively influenced by extended warmth into September in the open-top chamber treatment.

Table 2.17. Pearson's correlation coefficients relating biweekly thermocouple average surface temperature for the previous year (year C-1) and current year (year C) to control and the open-top chamber (OTC) master chronologies for annual growth increment (AGI), number of leaves, number of flower buds and number of flower peduncles for the treatment period of 1992-1998.

OTC 1992-1998									
Control 1992-1998					Average Thermocouple Surface Temperature				
Year	Biweekly Period	Average Thermocouple Surface Temperature			Biweekly Period	Average Thermocouple Surface Temperature			Number of Peduncles
		Annual Growth Increment	Number of Leaves	Number of Buds		Annual Growth Increment	Number of Leaves	Number of Buds	
(year C)	May Day 1-15	0.103	0.339	-0.072	-0.186	May Day 1-15	0.490	0.787	-0.033
	May Day 16-30	0.751	0.772	0.450	0.949 *	May Day 16-30	0.733	-0.429	0.352
	June Day 1-15	0.871 *	0.576	0.931 **	0.631	June Day 1-15	0.373	-0.466	-0.180
	June Day 16-30	0.677	0.288	0.557	0.759	June Day 16-30	-0.316	-0.363	-0.761
	July Day 1-15	-0.583	-0.658	-0.739	-0.261	July Day 1-15	-0.141	0.486	0.541
	July Day 16-31	-0.076	-0.390	0.101	-0.357	July Day 16-31	-0.100	0.005	-0.402
	Aug Day 1-15	0.037	0.040	0.407	-0.556	Aug Day 1-15	0.519	-0.024	-0.255
	Aug Day 16-31	-0.010	-0.315	0.312	-0.191	Aug Day 16-31	-0.077	-0.600	-0.006
	Sept Day 1-15	0.700	0.534	0.712	0.729	Sept Day 1-15	-0.002	-0.595	0.676
	Sept Day 11-31	0.873 *	0.816 *	0.977 **	0.450	Sept Day 11-31	0.352	-0.558	0.184

* = $P < 0.05$, ** = $P < 0.01$.

Note, because thermocouples were not put into place in the open-top chambers and control plots before late July 1992, there were no temperature measurements to compare with growth and reproduction for the period May-July 1992 in this analysis. Thus, for the months May, June and July, $n = 6$, and for the months August and September, $n = 7$. In addition, as the number of flower peduncles chronology is one year shorter for the treatment period (1992-1997) than the other growth and reproduction chronologies, $n = 5$ for the months of May, June and July and, $n = 6$ for the months August and September.

2.3.6.2. Coastal Climate Station Air Temperature and Thawing Degree Days, 1986-1998

In the open-top chamber treatment during the pre-treatment period (1986-1991), the annual production of leaves was positively and significantly correlated ($P < 0.05$) with average air temperature in May (Table 2.18a). During the same period, the annual production of flower peduncles in the open-top chambers was negatively and significantly correlated ($P < 0.05$) with average air temperature in the previous November (year C-1). No other correlation coefficients were significantly different from zero in the control or open-top chamber treatment during the pre-treatment period ($P > 0.05$).

During the treatment period (1992-1998), annual production of leaves in the control plots were negatively and significantly correlated with July average air temperature ($P < 0.05$) (Table 2.18b). In the open-top chamber treatment during the treatment period, annual stem elongation was negatively and significantly correlated ($P < 0.05$) with average air temperature in October of the previous year (year C-1). No other correlation coefficients were significantly different from zero for the treatment period ($P > 0.05$). However, a comparison of annual stem elongation across the pre-treatment and treatment periods revealed a moderately consistent growth relationship with average air temperature over time in the control and open-top chamber treatment (Tables 2.18 a and b). The association between flower peduncles in the control and open-top chambers with average air temperature across the pre-treatment and treatment periods was also moderately stable through time.

No relationships between the growth and reproductive variables and thawing degree days during the pre-treatment period across the control and open-top chambers, were significantly different from zero ($P > 0.05$) (Table 2.19 a). However, the signs of the correlation coefficients relating annual stem elongation to thawing degree days during the pre-treatment period, in both the control and open-top chamber treatment, were similar. During the treatment period, only the annual production of leaves in the control plots was significantly and negatively correlated ($-P < 0.05$) with July thawing degree days (Table 2.19 b). In addition, a comparison of annual production of leaves during the treatment period showed a consistent growth relationship to thawing degree days in both the control and open-top chamber treatment.

Table 2.18 a. Pearson's correlation coefficients relating monthly average air temperature recorded at the Coastal station, Alexandra Fiord for the previous (year C-1) and current (year C) year to control and open-top chamber (OTC) master chronologies for annual growth increment (AGI), number of leaves, number of flower buds and number of flower peduncles for the pre-treatment period of 1986-1991. $n = 6$ for all chronologies in both the control and open-top chamber (OTC) treatment.

OTC 1986-1991											
Average Air Temperature											
Year	Month	Annual Growth Increment	Number of Leaves	Number of Buds	Number of Peduncles	Month	Annual Growth Increment	Number of Leaves	Number of Buds	Number of Peduncles	
(year C-1)	October	0.143	-0.286	0.250	0.169	October	-0.546	-0.604	-0.372	0.148	
	November	-0.558	-0.641	0.115	-0.222	November	-0.119	0.099	-0.408	-0.816 *	
	December	0.216	-0.084	0.511	0.354	December	0.806	-0.314	-0.023	-0.334	
(year C)	January	-0.075	0.258	0.177	0.083	January	0.522	0.521	0.196	-0.297	
	February	-0.193	-0.317	-0.139	-0.446	February	-0.316	-0.060	0.376	0.561	
	March	0.283	0.756	-0.229	0.271	March	-0.505	0.366	-0.115	0.267	
	April	-0.372	-0.295	0.104	-0.263	April	-0.798	0.222	-0.102	0.077	
	May	-0.807	-0.326	-0.332	-0.724	May	-0.452	0.865 *	0.221	-0.194	
	June	0.241	0.601	0.031	0.434	June	-0.481	0.263	-0.403	-0.110	
	July	-0.335	0.048	-0.759	-0.279	July	-0.777	0.352	-0.450	-0.341	
	August	-0.385	0.140	-0.024	-0.186	August	-0.365	0.781	0.027	-0.204	
	September	-0.378	0.204	-0.419	-0.321	September	-0.632	0.748	-0.001	-0.038	

* = $P < 0.05$.

Note, because the Coastal station data set covered the period, 1980-1998, data for the months of October, November and December of 1985 were included in the correlation analysis, and thus, $n = 6$ for all correlation coefficients.

Table 2.18 b. Pearson's correlation coefficients relating monthly average air temperature recorded at the Coastal station, Alexandra Fiord for the previous (C-1) and current (year C) year to control and open-top chamber (OTC) master chronologies for annual growth increment (AGI), number of leaves, number of flower buds and number of flower peduncles for the treatment period of 1992-1998. n = 7 for the two growth and number of flower buds chronologies. n = 6 for the number of flower peduncles chronology. The treatment period for number of flower peduncles is shortened by one year, 1992-1997.

Control 1992-1998												OTC 1992-1998											
Average Air Temperature						Average Air Temperatures																	
Year	Month	Annual Growth Increment	Number of Leaves	Number of Buds	Number of Peduncles	Month	Annual Growth Increment	Number of Leaves	Number of Buds	Number of Peduncles		Year	Month	Annual Growth Increment	Number of Leaves	Number of Buds	Number of Peduncles						
(year C-1)	October	0.416	0.528	0.255	0.609	October	-0.804 *	0.409	-0.580	-0.193		(year C)	January	0.131	-0.089	0.071	0.187						
	November	-0.336	-0.164	-0.210	-0.383	November	0.464	-0.102	0.635	0.130			February	-0.439	0.258	-0.241	0.050						
	December	0.284	0.133	-0.172	0.609	December	-0.158	-0.424	0.068	-0.584			March	0.422	-0.257	0.420	0.025						
(year C)	January	-0.431	-0.460	-0.705	0.116	January	0.131	-0.089	0.071	0.187		April	-0.089	-0.002	0.377	-0.517							
	February	-0.060	0.069	-0.343	0.347	February	-0.439	0.258	-0.241	0.050		May	-0.383	0.243	0.139	-0.590							
	March	-0.005	-0.012	-0.177	0.098	March	0.422	-0.257	0.420	0.025		June	0.066	-0.316	-0.011	-0.565							
	April	-0.316	-0.301	-0.550	-0.220	April	-0.089	-0.002	0.377	-0.517		July	-0.031	-0.712	0.002	-0.391							
	May	0.102	0.127	-0.477	0.232	May	-0.383	0.243	0.139	-0.590		August	-0.095	0.091	-0.256	-0.130							
	June	0.291	-0.029	-0.094	0.386	June	0.066	-0.316	-0.011	-0.565		September	0.351	-0.277	0.038	0.186							
	July	-0.622	-0.811 *	-0.626	0.124	July	-0.031	-0.712	0.002	-0.391													
	August	0.130	-0.046	0.095	-0.032	August	-0.095	0.091	-0.256	-0.130													
	September	-0.500	-0.676	-0.245	-0.528	September	0.351	-0.277	0.038	0.186													

* = P<0.05; ** = P<0.01.

Note, because the Coastal station data set covered the period, 1980-1998, data for the months of October, November and December of 1991 were included in the correlation analysis, and thus, n = 7 for the two growth and flower bud chronologies and n = 6 for the number of flower peduncles chronology.

Table 2.19 a. Pearson's correlation coefficients relating average monthly thawing degree days recorded at the Coastal station, Alexandra Fiord for the previous (year C-1) and current (year C) year to control and open-top chamber (OTC) master chronologies for annual growth increments (AGI), number of leaves, number of flower buds and number of flower peduncles for the pre-treatment period 1986-1991. $n = 6$ for all chronologies in both the control and open-top chamber (OTC) treatment.

Control 1986-1991										OTC 1986-1991									
Monthly Thermal Degree Days										Monthly Thermal Degree Days									
Year	Month	Annual Growth Increment	Number of Leaves	Number of Buds	Number of Peduncles	Year	Month	Annual Growth Increment	Number of Leaves	Number of Buds	Number of Peduncles	Year	Month	Annual Growth Increment	Number of Leaves	Number of Buds	Number of Peduncles		
(year C)	May	0.300	0.714	-0.117	0.051	(year C)	May	0.043	0.429	0.565	0.739								
	June	0.166	0.525	0.260	0.404		June	-0.221	0.378	-0.217	-0.138								
	July	-0.434	0.046	-0.792	-0.396		July	-0.639	0.534	-0.278	-0.334								
	August	-0.538	-0.068	-0.224	-0.320		August	-0.562	0.703	-0.166	-0.384								
	September	0.288	0.227	-0.058	0.398		September	0.588	-0.226	-0.326	-0.521								

* = $P < 0.05$; ** = $P < 0.01$.

Table 2.19 b. Pearson's correlation coefficients relating average monthly thawing degree days recorded at the Coastal station, Alexandra Fiord for the previous (year C-1) and current (year C) year to control and open-top chamber (OTC) master chronologies for annual growth increments (AGI), number of leaves, number of flower buds and number of flower peduncles for the treatment period 1992-1998. $n = 7$ for the two growth and number of flower buds chronologies. $n = 6$ for the number of flower peduncles chronology. The treatment period for number of flower peduncles is shortened by one year, 1992-1997.

Control 1992-1998										OTC 1992-1998									
Monthly Thermal Degree Days										Monthly Thermal Degree Days									
Year		Month	Annual Growth Increment	Number of Leaves	Number of Buds	Number of Peduncles	Year	Month	Annual Growth Increment	Number of Leaves	Number of Buds	Number of Peduncles							
(year C)		May	-0.191	-0.361	-0.164	-0.277	(year C)		May	0.053	-0.208	0.125	-0.430						
		June	0.158	-0.119	-0.292	0.337			June	0.147	-0.335	0.163	-0.586						
		July	-0.622	-0.811 *	-0.626	0.124			July	-0.031	-0.712	0.002	-0.391						
		August	0.286	0.108	0.080	0.060			August	-0.085	0.141	-0.151	-0.263						
		September	0.000	0.000	0.000	0.000			September	0.000	0.000	0.000	0.000						

* = $P < 0.05$; ** = $P < 0.01$.

2.4. Discussion

2.4.1 Critique of Methods

2.4.1.1. *Cassiope tetragona* Chronologies

The results from this study reaffirmed the use of dendrochronological techniques, specifically the measurements of internode length patterns to cross-date annual growth increments and create master chronologies for the growth and reproductive variables of *C. tetragona*. The 16 chronologies developed for this study covered the time period, 1986-1998. While the lengths of the chronologies were much shorter than those reported by other studies (Callaghan *et al.* 1989; Havström *et al.* 1995; Johnstone and Henry 1997), they did cover a six year pre-treatment period (1986-1991) and the seven year treatment period (1992-1998) of the warming experiment at Alexandra Fiord.

The retrospective analysis technique allowed the use of a modified Before-After-Control-Paired-Impact-Comparison (BACIP) (Osenberg *et al.* 1994; Underwood 1994) approach to analyze the effect of the warming treatment. The responses of annual growth and reproduction variables to natural climatic variation were measured and precisely dated for the pre-treatment period. Measurements and the results of the repeated measures analyses of variance effectively established benchmarks for comparison with the same measured variables during the treatment period. Retrospective analysis also allowed for the investigation of the growth and reproductive responses over the treatment period, removing the need to conduct annual measurements each field season. Despite the success of developing chronologies for the control and open-top chamber treatments at the *Dryas* ITEX site at Alexandra Fiord, several problems and difficulties with the sampling and measurement methodology need to be addressed before the results are discussed.

The *C. tetragona* plants selected in 1992 for destructive sampling at the *Dryas* ITEX site were small in stature and the stem lengths were short when compared with *C. tetragona* plants in other populations. Hence, the short stem lengths precluded the construction of site chronologies prior to 1986 and made it impractical to use the cross-dating software COFECHA, commonly used in dendrochronological studies (Holmes 1983; Holmes *et al.* 1986; Grissino-

Mayer *et al.* 1992; Holmes 1994; Grissino-Mayer 2001). Despite these problems, cross-dating was accomplished using the visual method of skeleton-plotting. The technique of skeleton-plotting facilitated the generation of growth and reproductive chronologies, albeit slowly when compared to the construction of tree-ring chronologies. High intra- and inter-plant variability present in the chronologies contributed to the difficulties in cross-dating *C. tetragona*, as well. Johnstone and Henry (1997) encountered the same variability problem in their retrospective study of *C. tetragona* plants. High amounts of variance within-plants and between-plants reduce the strength of the signal-to-noise-ratio and can necessitate an increase in the sample size in order to estimate population variables within desired limits (Fritts 1976; Cook and Briffa 1990). However, at least some of the variability within the chronologies was likely a product of community dynamics. The short length of the chronologies also tempered interpretation of perceived trends and variability beyond the inter-annual time scale in the reproduction and growth of *C. tetragona* prior to or during the warming treatment. Finally, the time period ($n = 6$, 1986-1991; $n = 7$, 1992-1998) covered in this study was short, and the number of plants and stems per plant was low. Thus, the power of the given statistical tests was low. Therefore, it should be emphasized that while the results of the study are interesting, they should be interpreted with caution and treated as an initial retrospective assessment of *C. tetragona*'s growth and reproductive response to natural and experimental climate variation.

2.4.2. Experimental Temperature Manipulation

Temperature enhancing experiments in the field have the potential for unwanted ecological effects including temperature extremes and increased range of temperatures, modified moisture and gas concentrations, decreased light and wind, anthropogenic site disturbance, and alterations to animal and insect access to plants (Marion *et al.* 1997). In addition, recent field greenhouse experiments have been critiqued by Kennedy (1995), who pointed out that by altering other environmental factors within temperature enhancement experiments, it is difficult to examine the effect of temperature alone. Despite the potential drawbacks and criticism of the open-top chamber design, the greenhouses were found to simulate the predictions of General Circulation Models of increases in modern average surface temperature for the Arctic, while maintaining ambient levels of light, moisture and gases (Marion *et al.* 1997).

In this study, the average monthly surface temperatures in the open-top chambers were warmer in July, August and September than in the control plots. However, the magnitude of the temperature response to the open-top treatment was not statistically significant for most of the growing season ($P > 0.05$). The absence of a treatment effect was expected as changes in monthly surface temperatures were small when compared to among-year variation in temperature. Interestingly, the treatment did impact the magnitude of temperature response at the end of the summer (September, $P < 0.05$), suggesting that increased temperature throughout the growing season leads to drying of the ground surface in the open-top chambers at the *Cassiope* ITEX site. The among-year variation in surface temperature at the *Cassiope* ITEX site was significant for all months but one (July, $P > 0.05$), during the summer growing season. The impact of among-year climatic variability on arctic plant growth and reproduction, particularly extreme climatic events, is substantial (Robinson *et al.* 1998; Molau 2001). Havström *et al.* (1993) noted no predictions of change in variability of temperature have been made for the effects of global change in the Arctic. Extremes of temperature may have an important influence on some plant species which respond opportunistically to more favorable climate conditions, but for other species the impact of greater variability may result in growth and reproduction limitations (Chapin and Shaver 1985; Molau 2001), damage to plant parts, or death of the plant.

Published daily temperature measurements for a 68-day period in 1993 at the *Cassiope* ITEX site also supported the use of open-top chambers to simulate the General Circulation Models' predicted increases in average arctic temperature (Marion *et al.* 1997). They showed the mean daily near surface temperature warmed by an average of 1.3°C during the growing season. The warming effects within the open-top chambers varied diurnally, with the greatest differences between the open-top chambers and controls in the early afternoon followed by minimum differences at night (Marion *et al.* 1997). Much of the temperature enhancement in the open-top chambers was due to increased daily maximum temperatures, with the greatest effect on clear days with light to moderate winds (Marion *et al.* 1997). Thus, within the open-top chambers, daytime temperatures were warmer than ambient temperatures and the overall range of temperatures increased. An increased range of temperature is a common byproduct of passive greenhouse designs (Debevec and MacLean 1992). Finally, published snowpack depth measurements taken in January 1993 and 1994 showed that snow depths were somewhat deeper inside the open-top chambers at Alexandra Fiord (Marion *et al.* 1997). However, the date of

complete snowmelt in June within the open-top chambers and the control plots did not differ (Marion *et al.* 1997). Overall, the unwanted ecological and secondary effects of the open-top chambers were generally less than those produced by methods used in previous studies to enhance near-surface temperatures.

Despite the difficulties presented above, examination of the results from the control and open-top chamber treatments yielded some interesting effects and interpretations. Furthermore, the results of this study compare well with those of previous work on *C. tetragona* (e.g., Bliss *et al.* 1977; Nams 1982; Callaghan *et al.* 1989; Havström *et al.* 1993; 1995; Johnstone 1995; Johnstone and Henry 1997).

2.4.3. Relationship of Climate to *Cassiope tetragona* Growth and Reproduction

2.4.3.1. Control and OTC Treatment – Pre-treatment Period (1986-1991)

It was expected that *C. tetragona* plants in the control and open-top chamber populations would respond similarly to local climate conditions during the pre-treatment period (1986-1991). Indeed, the relationships between the vegetative growth variables and average monthly air temperature were similar. However, the relationships between the reproductive variables and average monthly air temperature exhibited much less similarity between the two populations. High intra- and inter-plant variability, in particular the species sensitivity to inter-annual growing season conditions, may have contributed to the lack of similarity. Observations of reproductive effort in *C. tetragona* showed that under naturally or artificially ameliorated growing season conditions, the species increased flower bud and flower peduncle production in one summer (Bliss *et al.* 1977; Nams and Freedman 1987b; Johnstone 1995).

The lack of similarity in the response of the reproductive variables to temperature in the control and open-top chamber treatment, and the small number of significant correlations across all variables during the pre-treatment period, made interpretation of the climate-growth and climate-reproduction relationships problematic. As a further complicating factor, evidence from previous studies has indicated that the measurement of temperature at the ground surface (0 cm) is a more accurate assessment of the microenvironment influencing the growth and reproduction

of arctic plants (Savile 1964; Svoboda 1977; Nams 1982). At Alexandra Fiord, average temperature at the ground surface may be 3°C or warmer than air temperature at 1.5 metres. Despite these difficulties, repeated measures analyses of variance showed the growth and reproductive variables from the two populations exhibited a consistent response to annual variation in the environment during the pre-treatment period. The consistent responses of the variables prior to 1992 provided support for a stable, similar base-line response of the plants from 1986-1991. These results indicated that differences between the two populations were not substantial enough to alter the interpretation of the effect of the warming treatment on *C. tetragona*, and supported the use of the Before-After-Control-Impact-Paired-Comparison (BACIP) methodological approach. Given this base-line understanding of the relationship of *C. tetragona* to pre-treatment conditions, greater attention was paid to understanding the meaning of the correlations for the treatment period by examining the relationship of the plants to ground surface (0 cm) temperatures.

2.4.3.2. Control – Treatment Period (1992-1998)

The relationships between the mean growth and reproduction indices of the control plants to monthly and biweekly temperature measurements during the treatment period (1992-1998) were complex. However, the correlation coefficients pointed towards a general and biologically logical response of the control *C. tetragona* chronologies to previous (year C-1) and current year (year C) monthly, and current year (year C) biweekly surface temperature. In addition, these were the first correlations reported between *C. tetragona* growth and reproductive variables and average surface temperatures for winter months. Few studies have been carried out on the effects of winter temperature on growth and reproduction of arctic plants.

Correlation coefficients between the growth and reproduction variables of *C. tetragona* and winter surface temperatures in the control plots were negative. However, not all the correlations were significantly different from zero ($P > 0.05$). From October (year C-1) to April (year C), growth and reproduction, particularly annual flower bud production, were negatively impacted by cold winter temperatures. Possibly, *C. tetragona* responded negatively in the control plots to both severe winter surface temperatures, which can reach a daily minimum of

-26 °C at Alexandra Fiord, as well as a shallower snow pack. During the winter months, snowpack is generally thinner above the control plots than above the open-top chamber plots. However, snowpack depth does vary over the course of the winter due to drifting and blowing snow at Alexandra Fiord.

Beginning in early summer, control growth and reproduction of *C. tetragona* were positively correlated with May and June surface temperatures. In late May and early June, global solar radiation and accompanying temperatures increase causing snow pack to melt and exposing arctic plants to temperatures high enough to begin photosynthesis (Chapin 1983; Shaver and Kummerow 1992). Typically, the Alexandra Fiord lowland is snow-free by mid-June (Freedman *et al.* 1994; Bean 2002). Evergreen species, like *C. tetragona*, have the ability to resume photosynthetic activity within a few days of snow melt. Temperatures in the first two weeks of June were positively and significantly associated with stem elongation and flower bud formation. Vegetative bud break in *C. tetragona* usually does not occur until late June or early July at Alexandra Fiord, depending on the date of complete snowmelt (Nams 1982; Johnstone 1995). However, *C. tetragona* plants may have already taken advantage of available moisture and nutrients in the rapidly thawing soil of early summer as well as drawing upon nutrient reserves stored up from the previous year (Chapin 1983; Shaver and Kummerow 1992).

Cassiope tetragona, like many other arctic plants, is traditionally thought to employ a conservative growth strategy of holding nutrients in perennial plant tissues for use early on in summer (Haag 1974; Berendse and Jonasson 1992; Shaver and Kummerow 1992). In fact, Nams (1982) found the highest concentrations of nitrogen, phosphorus and potassium in leaf buds and flower buds during the time period directly preceding rapid shoot elongation and flower bud expansion in early July. Accumulation of these elements often occurs in actively differentiating tissues (Larcher 1980; Nams 1982). Flower buds are generally visible and swollen in the leaf axils by late June to mid-July, depending on date of complete snowmelt (Nams 1982; Johnstone 1995). In many arctic plants, flower bud development typically takes place during the first four to six weeks of the summer in the high arctic (Shaver and Kummerow 1992). Flower peduncle development also appears to be strongly influenced by increasing early summer temperature, particularly during the last two weeks of May. The warming temperatures possibly initiate the elongation of the flower peduncles and the subsequent formation of the flowers early in the season. By the first two weeks in July, flower peduncles are usually visible, but the corolla remains undeveloped (Johnstone 1995). Evidence for the positive effect of early

summer temperature on *C. tetragona* growth and reproduction, whether direct or indirect, has been reported in other studies (Nams and Freedman 1987b; Callaghan *et al.* 1989; Johnstone and Henry 1997).

Beginning in July, the signs of the correlations between surface temperature and growth and reproduction variables in the control plots changed from positive to negative correlations. The negative correlations are a departure from previous studies which found significant positive correlations between July temperatures and vegetative growth in *C. tetragona* (Johnstone and Henry 1997). Potential explanations for these negative July correlations include moisture stress and/or within-plant resource depletion after a period of high production. As mentioned previously, snowmelt is completed generally by mid-June at Alexandra Fiord (Freedman *et al.* 1994; Johnstone 1995; Bean 2002). In the early summer, soils are saturated following snowmelt, but soil moisture decreases steadily as the season progresses as a result of thinner snow pack, low summer precipitation, poor water retention, and exposed soils (Nams 1982; Oberbauer and Dawson 1992; Johnstone 1995). If the early summer months are particularly warm, the combination of low humidity and high leaf temperatures may produce substantial water vapor gradients between the air and leaves. Evapotranspiration may increase resulting in a situation where plants may be moisture stressed by mid-summer. For the period 1992-1998, June and July average temperature departures relative to the 1980-1998 mean from the Coastal weather station at Alexandra Fiord, were greater than average during five and four of the seven years, respectively. Further support for possible moisture-stress in *C. tetragona* by mid-summer is provided by Welker *et al.* (1995) who showed that the primary source of water for *C. tetragona* was from snowmelt and not summer precipitation. Thus, when snowmelt has evaporated or percolated beyond the root zone of the *C. tetragona* plants, moisture stress becomes a growth-limiting factor.

An interesting counterpoint to the moisture-stress hypothesis was noted by Nams (1982) who found an inverse correlation between *C. tetragona* production and soil moisture along a topographically controlled snow melt gradient. The greatest production in *C. tetragona* plants was measured at a site in the lowland at Alexandra Fiord with relatively well-drained, warm, mesic soils (Nams 1982). Tikhomirov *et al.* (1969) and Porsild (1920) also made similar observations of *C. tetragona* plant communities found in Russia and Greenland, respectively,

reporting that the plants grew best on sunny exposures with well drained soils and, a reliable source of moisture during the growing season.

From August to September, the correlations between surface temperature and flower bud production were positive once again. At Alexandra Fiord, flower buds continued to develop throughout August, even after vegetative growth has slowed or ceased (Nams and Freedman 1987b; Johnstone 1995). Successful reproductive organ development in the current year in *C. tetragona* is dependent in part upon the length of the growing season. Continued warmth throughout the month of August into September potentially enables flower buds to over-winter at a more highly developed stage, increasing the odds of successful seed maturation the following summer. *Cassiope tetragona*, like several other arctic species, pre-forms flower buds at least one year prior to actual flowering (Sørensen 1941). By end of summer, nitrogen and phosphorus are most highly concentrated in the flower buds compared to the rest of above-ground biomass tissue acting as a source of nutrients for the following year's flower production (Nams and Freedman 1987b).

Temperatures in September were significantly and positively correlated with *C. tetragona* growth and reproduction variables, specifically annual stem elongation, leaf and flower bud production. While vegetative growth has ceased by late summer, gradual reduction in temperature or fluctuations around 0°C may facilitate winter hardening. However, prior studies of *C. tetragona* have found no evidence of nutrient movement out of current-year tissues and into specialized storage organs at the end of the growing season (Nams 1982). Instead, arctic evergreen shrubs retain nutrients and photosynthates in their stems and leaves (Chapin *et al.* 1980). The aboveground storage allows for more rapid access to these elements the following growing season as soon as snowmelt occurs, but when soil nutrients may still be locked up in frozen soil. Johnstone and Henry (1997) also found positive correlations between growth and September temperatures. In addition, the prolonged warmer temperatures may allow the further development of flower buds. The length of the growing season may determine both the number of flower buds produced annually, and also the stage at which a flower bud over-winters (Sørensen 1941; Nams 1982). Qualitative observations of the size of pre-formed flower buds which failed to flower the following summer (not presented here) showed particularly tiny buds for years during which average temperatures in August and September were below normal (e.g., 1996 and 1997).

2.4.3.3. Open-Top Chamber Treatment – Treatment Period (1992-1998)

The correlations between the average growth and reproductive chronologies from the open-top chambers and monthly and biweekly surface temperature during the treatment period (1992-1998) were more moderate and variable than in the control plots. Correlation coefficients for annual stem elongation, flower bud, and flower peduncle production in the open-top chamber treatment were mostly positive. Annual leaf production was negatively correlated, however. Evidence suggests that the open-top chambers at the *Cassiope* ITEX site tended to capture snow within the confines of the greenhouse walls. The additive effect of snow capture within the open-top chambers during the winter months may have better insulated the plants from cold temperatures. On average, surface temperatures within the open-top chambers throughout the winter months were warmer than in the control plots. In addition to providing insulation, a thicker snowpack protects plants from physical damage due to abrasion by wind-blown snow crystals and mineral particles and physiological damage due to freezing and desiccation (Sørensen 1941; Billings and Mooney 1968; Bliss 1988; Parsons *et al.* 1994). Despite the thicker snowpack, there was little difference in the dates of complete snowmelt in June of 1993 and 1994 between the open-top chambers and control plots (Johnstone 1995; Marion *et al.* 1997), or through the rest of the treatment period (Henry *et al.*, in prep.).

The responses of *C. tetragona* growth and reproduction variables to summer monthly surface temperatures over seven years of experimental warming were variable. The month-by-month (May-September) responses of the two growth variables to manipulated summer temperatures were of opposite signs. Correlation coefficients between annual leaf production and monthly summer temperatures were almost identical to that of the control plants. Annual leaf production responded positively to elevated temperatures in the early and late summer. As soon as summer temperatures are warm enough, photosynthesis begins within the leaves. The positive correlations between leaf production and summer temperatures continued into late summer, indicating a positive association between gradual temperature decrease and winter hardening. As in the control treatment, the correlation coefficient between the annual production of leaves and July monthly temperature was negative, although not significantly different from zero ($P > 0.05$). In a similar temperature enhancement study, Michelsen *et al.* (1996) suggested that warming may reduce water use efficiency in *C. tetragona* by increasing stomatal conductance relative to carbon assimilation. Reduced water use efficiency is thus

likely to be harmful to the plants, particularly in communities where soil moisture content is reduced and where there may be competition for water (Michelsen *et al.* 1996).

The correlation coefficients between annual stem elongation and summer temperature were of opposite sign when compared with the control plots. One plausible explanation for the change in correlation signs between the two populations may center on the shift in the timing of shoot elongation when exposed to enhanced temperatures. Evidence from prior studies showed that the effect of enhanced temperatures tended to shift the start of the growing season forward, resulting in earlier growth initiation or vegetative bud break in *C. tetragona* plants (Nams 1982; Johnstone 1995). In addition, the annual shoot elongation rates tended to be more rapid in temperature manipulation plots early in the growing season while later in the season, shoot elongation rates accelerated in the control plots (Johnstone 1995). Earlier and more rapid stem elongation in the open-top chamber treatment over an extended period of temperature enhancement could potentially place a strain on the stored carbon and nutrient reserves of the plant so early in the growing season. *Cassiope tetragona* stores the majority of its reserve nutrients in its stems and leaves over the winter. The reserves are critical resources in the early summer, when growth requirements cannot be met by current uptake of nutrients (Berendse and Jonasson 1992; Shaver and Kummerow 1992). Thus, shorter-term, earlier vegetative growth under the conditions of temperature enhancement may occur at the expense of stored plant reserves. The longer-term cost would be a decline in growth if the plants cannot recover and restore reserves (Arft *et al.* 1999). A combination of repeatedly warmer early growing season temperatures which facilitate early growth initiation and a concurrent potential nutrient deficit may result in the negative correlations of annual growth and surface temperature in May and June. However, no decline in annual stem elongation was detected in the open-top chambers in this study.

Interestingly, in July, annual stem elongation and surface temperature were positively correlated, potentially indicating a mid-summer surplus of nutrients for shoot growth in the open-top chambers. It is possible that the increased soil temperatures within the open-top chambers facilitated an increase in soil carbon and nutrient pools by increasing decomposition, mineralization and perhaps nitrogen fixation in soil-dwelling microbes and algae (Billings 1987; Oberbauer and Dawson 1992; Rolph 2003). Wookey *et al.* (1995) suggested that, for arctic species such as *Dryas octopetala*, low nutrient availability can be compensated for by high

“absorption potential” when nutrients are made available. Also, in a 5-year study at a high-montane fellfield site in Swedish Lapland, Michelsen *et al.* (1996) found that an increase in green biomass in artificially warmed *C. tetragona* plants did not lead to a proportional dilution of shoot nitrogen concentration. They argued that *C. tetragona* has the ability to adjust its nutrient uptake to match increased growth (Michelsen *et al.* 1996). However, in a similar study at Alexandra Fiord, Tolvanen and Henry (2001) found that C:N ratios in biomass of both *C. tetragona* and *Dryas integrifolia* increased in response to experimental warming. They concluded that the evergreen shrubs were unable to match their nutrient uptake to increased growth in the open-top chambers, unlike the graminoid and forb species.

Prior studies have shown that, while the timing of the vegetative phenophases shift in response to changes in growing season conditions, the total period of actual growth in *C. tetragona* remains relatively stable (Svoboda 1977; Nams and Freedman 1987b; Johnstone 1995). In this study, temperature enhancement did not appear to affect the total annual stem elongation when compared to the control treatment. In addition, temperature enhancement did not affect annual production of leaves during the treatment period, but leaf production did respond to year-to-year changes in climate. The year-specific responses in the annual production of leaves may reflect the growth response to inter-annual variation in temperature as well as precipitation and nutrient supply (Robinson *et al.* 1998). Observations made by Johnstone (1995) and Molau (1997; 2001) of annual stem elongation in *C. tetragona* under ambient and enhanced temperature conditions showed little vegetative growth response as well. The rather conservative response of annual stem elongation and leaf production to short-term variations in growing season climate, and the plant’s inflexible use of the extended growing season may serve to stabilize annual variability in productivity of this species (Sørensen 1941; Shaver and Kummerow 1992).

The results of this study at Alexandra Fiord contrast with those found in a 3-year study of *C. tetragona* by Havström *et al.* (1993) at Ny-Ålesund, Svalbard, a high arctic site, and at Abisko, Swedish Lapland, a subarctic site. In addition, the results from a 5-year study of *C. tetragona* at the same site at Abisko also showed increased biomass with temperature enhancement (Michelsen *et al.* 1996). However, the absence of a significant vegetative growth response to temperature enhancement in this study parallels the observations of other similar short-term studies of high arctic plants including, *C. tetragona* (Molau 1997; 2001), *D.*

octopetala (Welker *et al.* 1993; 1997), *Polygonum viviparum* L. (Wookey *et al.* 1994), *Saxifraga oppositifolia* (Stenström *et al.* 1997; Desrosiers 1991) and *Diapensia lapponica* L. (Molau 1996). In a recent meta-analysis of the ITEX data, the influence of short-term warming (4 years) on vegetative growth across all species in the high arctic, and more specifically woody species, showed only small-to-moderate effects (Arft *et al.* 1999). Examination of the more narrow functional groups showed evergreen shrubs experienced a small, but non-significant positive effect during the first three treatment years; however, the effect was diminished in the fourth year (Arft *et al.* 1999).

The reproductive response of *C. tetragona* to summer monthly surface temperatures over seven years of experimental warming was neither straight-forward, nor was interpretation simple due to the lack of significant correlation coefficients. In general, the correlation coefficients were not significantly different from zero ($P > 0.05$). Indeed, the small number of significant correlation coefficients may be related to the number of annual growth increments measured ($n = 6$, 1986-1991; $n = 7$, 1992-1998) in this study; hence, the power of the given statistical tests was low.

Annual production of flower buds was positively correlated with surface temperatures in the open-top chambers during the months of May and July. Annual production of flower peduncles was positively correlated with temperature in the month of May, as well as during the first two weeks of July and September. Repeated measures analyses of variance showed that the reproductive variables were strongly affected by the experimental warming. The mean annual production of flower buds was especially high in 1994, 1995, 1996, and 1998. The effect of the warming experiment on the production of flower buds in 1996 was particularly notable, as the growing season (June-August) was the second coldest on record at Alexandra Fiord. During the summers of 1994, 1995, and 1998 at Alexandra Fiord, the open-top chambers appeared to enhance already warm growing season temperatures, resulting in a higher mean number of flower buds produced. The mean number of flower peduncles produced in the summers of 1992, 1994, 1995 and 1996 was also high. The strong positive effect of the warming experiment on mean number of flower peduncles was clearly evident in 1992, the first year of treatment. Interestingly, the growing season of 1992 was cool at Alexandra Fiord. The immediate response to the warming experiment further emphasizes the rapid response of *C. tetragona* reproduction to warmer temperatures as observed in other studies (Nams and

Freedman 1987b; Johnstone 1995). Similarly, mean flower peduncle production was high in 1996. The open-top chambers enhanced growing season temperatures enough to off-set the effects of a cold growing season. Notably, both mean production of flower buds and peduncles decrease in 1997 in the open-top chambers, the second coldest growing season during the treatment period. Possibly, the high level of reproduction in the treatment population could not be sustained through two cold summers.

Johnstone (1995) also found a significant positive treatment effect on the percentage of tagged shoots that developed mature flowers. In the same study, she found that the number of flower buds produced per mature shoot showed a strong positive response to temperature enhancement. Observations of *C. tetragona* reproduction following years of naturally favorable growing season conditions also showed increased flower production (Bliss *et al.* 1977; Nams and Freedman 1987b). From evidence provided in studies done at Alexandra Fiord and elsewhere, the strong reproductive response of *C. tetragona* to enhanced surface temperatures suggests that this evergreen species has adapted to take advantage of increased temperature during the growing season.

Whether the extra investment in reproduction by *C. tetragona* at Alexandra Fiord is a positive and cost-effective population strategy remains questionable. In an open, polar semi-desert community, investment in reproduction during warm summers could lead to the colonization of open ground by the plants and an increase in distribution (Wookey *et al.* 1993). However, the lowland at Alexandra Fiord is dominated by closed-cover vegetation. Intra and interspecific competition for nutrients, water, light, and space may leave few available suitable microsites for *C. tetragona* seed germination and development, thus resulting in a poor investment of resources (Callaghan and Emanuelsson 1985; Carlsson and Callaghan 1990; Karlsson *et al.* 1990; Callaghan *et al.* 1992; Eriksson and Ehrlén 1992; Wookey *et al.* 1993;). Seedlings of *C. tetragona* have rarely been found at Alexandra Fiord (Freedman *et al.* 1981; Johnstone 1995; personal observation). However, continued investment in reproduction ensures that viable seeds will be dispersed after each favorable growing season, thus increasing the chances of beneficial genetic recombination and potentially improved survival capabilities in a changing environment (Bloom *et al.* 1985; Philipp *et al.* 1990; Crawford *et al.* 1993; Wookey *et al.* 1995).

Interestingly, there was no detectable effect on *C. tetragona* flower frequency due to short-term greenhouse warming at either a subarctic subalpine heath or at a high altitude fellfield site at Abisko, Swedish Lapland (Havström *et al.* 1993). On the other hand, other short-term experimental warming studies of other arctic species have found striking effects of increased temperature on reproduction: these studies include observations on *C. tetragona* (Molau 1997; 2001), *D. octopetala* (Welker *et al.* 1993; 1997; Wookey *et al.* 1993; 1995), *Polygonum viviparum* (Wookey *et al.* 1994), *Saxifraga oppositifolia* (Stenström *et al.* 1997), *Salix arctica* Pall. (Jones *et al.* 1997), *Silene acaulis* L. (Alatalo and Totland 1997), *Eriophorum vaginatum* L. (Molau and Shaver 1997), *Carex bigelowii* Torr. (Stenström and Jónsdóttir 1997) and *Papaver radicum* (Mølgaard and Christensen 1997). Meta-analysis of ITEX data on short-term response of reproductive effort to enhanced temperatures showed a positive effect (Arft *et al.* 1999). The magnitude of the effect increased over the four years of the study indicating a trend towards greater reproductive effort in the warmed plots (Arft *et al.* 1999). In addition, analysis of the high arctic data showed a greater response than that from the low arctic, particularly for the second and third years of treatment which were significantly different from the controls (Arft *et al.* 1999). When examining the results for the functional groups, the mean effect size for reproductive effort in woody plants was positive, with most of the response contributed by evergreen shrubs (Arft *et al.* 1999). Finally, Arft *et al.* (1999) also reported high levels of inter-annual variability in reproductive effort for both evergreen and deciduous shrubs.

2.4.4. Chronology Characteristics

2.4.4.1. A Comparison of *Cassiope tetragona* Populations

The estimates for mean annual growth and reproduction of *C. tetragona* presented in this study were similar to those found in comparable temperature enhancement studies (Table 2.20). Measurements of annual shoot elongation in the control and open-top chamber treatment during the pre-treatment and treatment periods were similar to those made by Nams (1982) and Johnstone (1995) at Alexandra Fiord. However, measurements of annual stem growth were slightly smaller than those reported by Havström *et al.* (1993) for Ny-Ålesund, Svalbard (control plots only), and substantially shorter when compared with values from the ITEX site at

Table 2.20. Comparative data on the mean growth (annual growth increments (AGI), annual production of leaves) and reproduction (annual production of flower buds and peduncles) of *Cassiope tetragona* from temperature enhancement studies in the Arctic. CON = control plots. OTC = open-top chamber treatment. Buds = flower buds. Peds = flower peduncles. SD = standard deviation of the mean. SE = standard error of the mean. nd = no data.

Study	Site and Date	Mean± SD/SE	CON AGI	OTC AGI	CON Leaf	OTC Leaf	CON Buds	OTC Buds	CON Peds	OTC Peds
Rayback, Chapter 2 Alexandra Fiord Ellesmere Island	Dryas ITEX site 1986-1991	mean	3.69	3.76	10.28	10.44	0.16	0.15	0.16	0.23
		SD	1.69	1.69	2.88	3.12	0.37	0.41	0.37	0.53
	Dryas ITEX site 1992-1998	mean	3.51	3.53	9.02	10.70	0.14	0.25	0.21	0.43
		SD	1.69	1.70	2.90	3.28	0.35	0.51	0.45	0.70
Johnstone 1995 Alexandra Fiord Ellesmere Island	Dryas ITEX site 1992	mean	2.87	3.24	nd	nd	nd	nd	nd	nd
		SD	0.25	0.39	nd	nd	nd	nd	nd	nd
	Dryas ITEX site 1993	mean	4.06	3.68	nd	nd	nd	nd	0.55*	0.21
		SD	0.32	0.32	nd	nd	nd	nd	0.67	0.22
	Cassiope ITEX site 1992	mean	3.03	3.70	nd	nd	nd	nd	nd	nd
		SD	0.15	0.21	nd	nd	nd	nd	nd	nd
	Cassiope ITEX site 1993	mean	3.17	3.48	nd	nd	nd	nd	0.49	0.14
		SD	0.15	0.15	nd	nd	nd	nd	0.18	0.11
Nams 1982** Alexandra Fiord Ellesmere Island	Central Plain 1981	mean	3.40	4.00	nd	nd	1.8***	4.20	nd	nd
		SE	0.10	0.30	nd	nd	0.50	1.10	nd	nd
Havstrom et al. 1993 Abisko, Sweden	Tree-line heath 1989-1991	mean	8.29	nd	19.48	nd	nd	nd	nd	nd
		SE	0.22	nd	0.39	nd	nd	nd	nd	nd
	Summit fellfield 1989-1991	mean	6.25	nd	13.29	nd	nd	nd	nd	nd
		SE	0.25	nd	0.36	nd	nd	nd	nd	nd
Ny-Ålesund Svalbard, Norway	Beach ridge heath 1990-1991	mean	5.21	nd	10.78	nd	nd	nd	nd	nd
		SE	0.22	nd	0.35	nd	nd	nd	nd	nd
Molau 2001 Latnjajaura, Sweden	ITEX site 1993-1997	mean	9.12	9.14	nd	nd	nd	nd	nd	nd
		SE	0.32	0.29	nd	nd	nd	nd	nd	nd

* Mean numbers of flowers per live shoot measured in 1993 (Johnstone 1995).

** Greenhouse design was a closed-top chamber (Nams 1982).

*** Mean number of flower buds per shoot on tagged shoots (Nams 1982).

Latnjajaure, Sweden (Molau 2001). Measurements of mean annual leaf production in this study were similar to those for a population at Ny-Ålesund, Svalbard (control plots only), but much smaller than those reported for two populations at Abisko, Sweden (Havström *et al.* 1993).

Differences between the mean growth estimates reported in this study and others are, in some cases, a product of the latitudinal location of the study sites. Havström *et al.* (1993) suggested *C. tetragona* stem elongation and leaf production decreases with latitude and specifically, *C. tetragona* plants found at high latitudes would invest resources into strengthening and protecting fewer leaves on a shorter stem to prevent desiccation damage. Regarding annual shoot length, there was also the possibility that the stems collected in this study could have been juvenile stems, and therefore, would have exhibited shorter annual growth. Callaghan *et al.* (1989) discovered a similar developmental trend in leaf length on *C. tetragona* plants, specifically; smaller leaves were produced in the first years of growth of a juvenile shoot.

Apart from the one-season (1981) experimental warming study done by Nams (1982) at Alexandra Fiord, there were no comparable, long-term data for annual production of flower buds in *C. tetragona*. The values presented by Nams (1982) represent the mean number of flower buds per shoot, and were notably higher in both the control and greenhouse plots in comparison to estimates presented in this study. However, in the experiment conducted by Nams (1982), greenhouse temperature were raised on average 1-3 °C more than in the ITEX open-top chambers at Alexandra Fiord. In addition, it is not known if flower buds were counted on two or four sides of the stem for each annual increment. Finally, estimates of mean annual production of flower peduncles were slightly smaller in the control plots and slightly larger in the open-top chamber plots, than values estimated by Johnstone (1995).

2.4.4.2. Intra- and Inter-Plant Variability in *Cassiope tetragona*

High intra- and inter-plant variability in *C. tetragona* was apparent through visual comparison of individual plants and correlation analysis of the chronologies in this study. Qualitative observations of the inter-annual growth and reproductive responses of individual

plants to environmental variables revealed asynchronous patterns in both populations from 1986-1998. However, during summers with lower or higher average temperature, individual plants tended to respond in unison. For example, the growth variables in both populations responded negatively to environmental conditions in 1996, the second coldest summer on record at Alexandra Fiord.

Interpretation of the correlations between the master growth chronologies during the pre- and treatment periods was difficult. It was expected that a contemporaneous suite of environmental conditions for the same time period (pre-treatment, 1986-1991) would produce comparable correlations between the control and open-top chamber treatment. Similarly, it was expected that the control master chronologies would exhibit consistent responses across the pre-treatment and treatment time periods. Instead, it appears that the high degree of intra- and inter-plant variability resulted in few correlation coefficients of the same sign.

High intra-plant variation is not surprising in a plant with a complicated, multi-branching structural architecture as was noted by Johnstone (1995). The position of individual stems within a densely branching plant may influence the amount of solar radiation each plant part receives, as well as surface temperature. Strong temperature gradients exist in tundra ecosystems between the ground surface (0 cm) and 10 cm above the ground. While *C. tetragona* plants rarely reach a height above 15 cm tall, the difference in temperature is often several degrees between those stems near the ground surface and those at a height of 15 cm (Savile 1964; Svoboda 1977; Nams 1982). Surface temperatures (0 cm) in the control plots were approximately 2.0°C higher than air temperature (10 cm) in July from 1995-1998. In addition, temperatures measured at various points on and within high arctic tundra cushion plants and rosettes have recorded values as high as 28°C (Warren Wilson 1957; Kjellberg *et al.* 1982; Mølgaard 1982; Philipp *et al.* 1990; Wookey *et al.* 1993; G. Henry, personal communication).

Resource partitioning among stems may also be an important factor affecting individual stem growth and reproduction in *C. tetragona* (Johnstone 1995). Because of apical dominance and rapid growth, certain stems within a plant may be sinks for a disproportionate amount of nutrients and water, despite all stems being attached to a central root system. Havström *et al.* (1993) suggested that differences in response between individual mature and juvenile stem

growth to simulated environmental change may be caused by internal resource partitioning. As a further complication to cross-dating and assessing the climate signal, apical dominance likely changes throughout the lifetime of the plant due to the natural senescence of the dominant stems, or to damage and death by wind desiccation and freezing temperatures.

Intra- and inter-plant variability linked to resource partitioning and possible intra- and inter-species dynamics may have dampened the response of the plant to larger-scale climate factors. At present, there is a limited amount of research available on intra-species and inter-species competition in arctic tundra ecosystems, particularly high arctic ecosystems (Bliss and Peterson 1992). Although untested at Alexandra Fiord, it is possible that *C. tetragona* plants may compete to a limited degree for available light, heat, nutrients and water, particularly in densely occupied communities like that of the lowland at Alexandra Fiord and other high arctic oases. Plant competition theory suggests that low levels of competition occur in tundra communities as vascular plant species are limited more by stressful environmental conditions than by competitive interactions (Grime 1977). In a study by Hobbie *et al.* (1999), the results suggested that the direct limitation of environmental conditions was more important than the limitations by species interactions in low arctic, Alaskan tussock tundra. It is unclear at this point, what role competition plays in this high arctic ecosystem and how it influences *C. tetragona* growth and reproduction.

Finally, our lack of understanding of high arctic plant and community interactions presents a problem when selecting sampling sites. In dendrochronology, site selection is driven by the goal to enhance the effect of a given set of growth-limiting factors and to reduce the influence of local endogenous and community exogenous disturbance factors (Fritts 1976; Cook and Briffa 1990; Pilcher *et al.* 1990). While the selection of the Alexandra Fiord lowland meets site selection criteria as an appropriate region where the species is at its climatic distribution limit, and where climatic factors greatly affect annual growth and reproductive variability, it cannot be said with certainty that community-dynamics do not influence the strength of the chronology signal (Pilcher *et al.* 1990).

2. 4. 5. Principal Findings

Despite some of the difficulties inherent in the analysis of the warming experiment, examination of the results from the control and open-top chambers yielded some interesting findings. *Cassiope tetragona* growth and reproductive chronologies were reconstructed successfully for the control and open-top chamber treatment at Alexandra Fiord. However, high intra- and inter-plant variability, most likely linked to resource partitioning and species dynamics, characterized the chronologies. Despite the high levels of variability, the chronologies provided a baseline estimate of growth and reproduction prior to (1986-1991) and during (1992-1998) the warming experiment.

The study's results showed that *C. tetragona* plants did respond to local climate conditions and to the warming experiment during the treatment period. Repeated measures analysis of variance provided evidence for a strong reproductive and weak vegetative growth response to increased temperature. The two reproductive variables were significantly affected by the warming treatment, but the two growth variables were not.

Correlation analyses revealed that thicker snowpack in the open-top chambers may have better insulated *C. tetragona* plants from cold temperatures, as well as provided protection from physical and physiological damage during the winter months. Correlation analysis also suggested increasing temperatures early in the summer may have shifted the start of the growing season forward and resulted in earlier growth initiation in the open-top chambers. Earlier and accelerated shoot elongation rates may have placed a strain on the plants' stored carbon and nutrient reserves so early in the growing season. However, by mid-summer, a potential surplus of soil nutrients for shoot growth resulted in a positive relationship with annual stem elongation and July temperatures. In addition, the reproductive variables were positively influenced by early summer temperatures in warming experiment.

Correlation analysis also showed growth and reproduction in the control plots responded positively to increasing temperatures early in the summer which facilitated the initiation of photosynthesis and the formation of flowers and flower buds. However by mid-summer, moisture stress and/or within-plant resource depletion may have stressed plant growth, resulting in negative correlations. By the end of the growing season, gradually decreasing temperatures

likely facilitated winter hardening within the control plants, while at the same time enabled flower buds to develop more fully.

These results compare well and support previous studies which characterize *C. tetragona* as a slow-growing, long-lived, conservative plant, similar in its life history to other northern evergreen species, including conifers and other ericaceous shrubs. However, further studies of *C. tetragona*'s growth and reproductive responses to longer-term ambient and enhanced temperatures are needed at both Alexandra Fiord and from other sites across the Arctic.

3. The reconstruction of past climate for Alexandra Fiord, Ellesmere Island, Canada

3.1. Introduction

3.1.1. The Need for Proxy Climate Data in the Canadian Arctic

In order to understand modern climate and past climate change in the Canadian Arctic, a high resolution paleoclimatic record documenting temporal and spatial patterns of natural climatic variability over a long time period is crucial (Bradley 1985; Smol 1988; Bradley and Jones 1993; Hardy and Bradley 1997; Mann *et al.* 1998; 1999). Multiproxy studies of climate during the Late Holocene have shown that, within the last two hundred years, the Arctic has experienced the coldest and warmest temperatures within the last millennium (Overpeck *et al.* 1997). The need for long and high resolution proxy records from arctic sites is particularly pressing in light of the present discussion of the origins and mechanisms for current global climate change. The results of General Circulation Models (GCMs) predict a warmer global climate (+1.4 - 5.8 °C) by 2100 (IPCC 2001). The greatest temperature increase is forecasted for the high northern latitudes, ranging from 4.0 – 7.5 °C in summer to 2.5 - 14.0 °C in winter (IPCC 2001). While the predicted future warming in the circumpolar north will vary both spatially and temporally, the direct and indirect impacts on the biophysical environment in the Arctic will be substantial (Maxwell 1992; IPCC 2001). To understand the current and future impact of climate change in the Arctic on these systems, it is important to develop proxy records to obtain an empirical description of past climate variability including its modes of behavior, its extremes and the duration of trends and cycles. With proxy climate records, a more confident estimation can be made of the roles of different external forcing factors and internal sources of variability on past and recent climate.

3.1.2. Instrumental Records in the Canadian Arctic

While high quality instrumental data exist for the Canadian Arctic, they cannot be used to assess regional climatic patterns in space and time (Hardy and Bradley 1997). The major difficulties encountered when using these data in the examination of climatic patterns and the

development of proxy data for high arctic locations are: (1) the brevity of the meteorological record, and (2) the location and number of long-term, year-round climate stations (Hardy and Bradley 1997). In the Queen Elizabeth Islands, five High Arctic Weather Stations (H.A.W.S.) are in operation, all of which began collecting weather data in the 1940s. The H.A.W.S. at Mould Bay, Prince Patrick Island and Isachsen, Ellef Ringnes Island closed in 1997 and 2002, respectively. The situation is similar for the mid- and low arctic, with only four weather stations in operation before 1940. The remaining 31 stations began collecting weather data in the 1940s or later (Chapman and Walsh 1993; Hardy and Bradley 1997). As climatic variability operates at many time scales, from years to decades to centuries (Mitchell 1976), the length of the H.A.W.S. instrumental record precludes most investigations of climatic variability over time intervals equal to or longer than the meteorological record (Hardy and Bradley 1997). Moreover, the brevity of the instrumental record at the H.A.W.S. makes calibration and verification of reconstructions difficult and their results tenuous.

The second constraint of the instrumental record involves the location and number of the H.A.W.S. All five climate stations in the Canadian High Arctic are situated at coastal locations at less than 100 m a.s.l. In the low and mid arctic, the majority of climate stations are also located on the coast. However, five high elevation sites (100-640 m a.s.l.) exist on Baffin Island (Maxwell 1981; Hardy and Bradley 1997). Although the coastal plain topography of the western half of the Canadian Arctic is similar to that of the climate station sites, the plateaus, mountains and fiords of the eastern Arctic are in direct contrast. Thus, climatic conditions at the coastal H.A.W.S. may not be directly representative of all locations around the Canadian Arctic (Hardy and Bradley 1997). Given the constraints and limitations of the instrumental record and the pressing need to examine climatic variability over time periods longer than the recorded data, the development of proxy climate data sets is necessary.

3.1.3. Current State of Proxy Climate Data for the Canadian Arctic

While significant advances have been achieved in recent years in the reconstruction of the arctic proxy climate record, our knowledge of past climate conditions in the Canadian Arctic remains incomplete. In particular, there are very few data sets from sites within the large region of Nunavut and the Northwest Territories, Canada, documenting the spatial and temporal

variability of climate. Available proxy climate data sets and other evidence of paleoclimatic change from Canadian Arctic sites include: ice cores, laminated lake sediments, fresh water diatoms, pollen and tree-rings, as well as glacial and glacio-isostatic evidence and radiocarbon dates of organic matter (Bradley 1990). Many of these proxy data sets are spatially and temporally limited, which can present certain problems when climatic information is derived from a limited region and extrapolated to much larger areas (Jones and Kelly 1983). Currently only ice cores, laminated lake sediments, and tree-rings offer long duration, high resolution proxy records. Ice core and tree-ring sampling sites are limited geographically to glaciers in the high arctic and south of tree-line in the low arctic, respectively. To address the problems of better spatial coverage in the Arctic and highly resolved data sets, a recently developed proxy technique to reconstruct climate using the circumpolar evergreen, dwarf shrub, *Cassiope tetragona* is used in this study.

3.1.4. Reconstructing Climate Using *Cassiope tetragona*

The retrospective analysis technique used in this study is based upon the principles of dendrochronology, the study of the patterns of annual tree-ring widths (Fritts 1976). The retrospective analysis technique was first introduced in Chapter 2. Dendrochronological studies have been successfully carried out on several tree species in the low arctic (e.g., Kay 1978; Cropper and Fritts 1981; Jacoby and Cook 1981; Cropper 1982; Kuivinen and Lawson 1982; Jacoby *et al.* 1985; Briffa *et al.* 1988; Jacoby and D'Arrigo 1989; Briffa *et al.* 1990; 1995; D'Arrigo *et al.* 1992; 1993; 1999; Jacoby *et al.* 2000), but studies on shrub species north of treeline have proven more problematic (Beschel and Webb 1962; Warren Wilson 1964; Walker 1987; Kolishchuk 1992).

The retrospective analysis technique developed by Johnstone and Henry (1997) is used in this research to investigate the vegetative growth and reproductive response of *C. tetragona* to climate and to reconstruct proxy climate data for a high arctic site. It is a long-lived species found throughout the circumpolar north (Hultén 1971; Bliss and Matveyeva 1992). A more detailed description of the plant and its habitat can be found in Chapter 2.

Previous studies (Havström *et al.* 1995; Johnstone and Henry 1997) strongly support the use of retrospective analysis of *C. tetragona* to develop proxy data sets of high resolution and moderate duration. If chronologies of one hundred years or longer can be generated using *C. tetragona* plants from multiple sites, a better understanding of the temporal variability of climate over the last century or more might be achieved. Previous studies reported chronologies of 20 to 35 years (Callaghan *et al.* 1989; Johnstone and Henry 1997), but more recent field observations suggest chronologies of 100 years or more may be generated (personal observation). The development of *C. tetragona* chronologies, which cover the late 19th and entire twentieth century, is of particular interest given the range of environmental conditions the Arctic has experienced since the end of the Little Ice Age (c.1850).

Furthermore, as *C. tetragona* is a circumpolar species and can be found as a dominant or co-dominant plant in multiple arctic tundra ecosystems, it may be used to generate proxy climate data from a network of high latitude terrestrial sites. The potential for increasing the available number of proxy data sets for Arctic Canada through the retrospective analysis of *C. tetragona* would contribute greatly to our understanding of the spatial and temporal variability of northern climate, and hence, would improve our understanding of the arctic climate system. Multiproxy networks appear to provide the best opportunity for larger-scale paleoclimatic reconstruction and climate signal detection (Mann *et al.* 1998).

3.1.5. Research Objectives

In this chapter, the four research objectives are: (1) to construct two vegetative and two reproductive chronologies at each of the three sites which follow an elevational gradient (30 m a.s.l. to 500 m a.s.l.) at Alexandra Fiord, Ellesmere Island; (2) to reconstruct summer climate conditions at Alexandra Fiord from the late 1800s to the present; (3) to investigate high- and medium-frequency variability in the climatic reconstruction; and (4) to relate the climatic reconstruction based on *C. tetragona* to the results of other single and multi-proxy studies and to instrumental data from the Canadian Arctic.

3.2. Methods

3.2.1. Species Characteristics

The long-lived, ericaceous, dwarf shrub *Cassiope tetragona* (L.) D. Don, has a circumarctic distribution and is a major component of low shrub, dwarf shrub and mixed heath communities (Böcher 1954; 1959; 1963; Gjaerevoll and Bringer 1965; Igoshina 1969; Rønning 1969; Beschel 1970; Chepurko 1972; Thompson 1980; Nams and Freedman 1987a; Bliss and Matveyeva 1992). A full description of the species' characteristics and the associated retrospective analysis technique based on the species morphology is given in Chapter 2.

3.2.2. Study Area and Sampling Sites

Field work was conducted at Alexandra Fiord, Ellesmere Island, Canada (78° 53' N, 75° 55' W) in the summer of 1998. A description of the study area is provided in Chapter 2. Plants were collected at three sites at Alexandra Fiord along an elevational gradient. The three sampling sites are referred to in the text as Lowland, Bench and Dome, in order of their position from the bottom to the top of the elevational gradient (Figure 3.1).

The Lowland sampling site is located at 30 m above sea level (a.s.l.) within the central plain zone (Nams and Freedman 1987b) of the Alexandra Fiord lowland (Figure 3.2). The central plain zone has the greatest annual net production of all vegetation communities at Alexandra Fiord, characterized by the warmest temperatures, relatively early snowmelt, and the deepest soil thaw (Nams and Freedman 1987b). *Cassiope tetragona* plants were sampled in early July 1998 within 50-250 metres west to northwest of the *Cassiope* ITEX site (Chapter 2). The vegetation community of the Lowland site is dominated by *C. tetragona*, but also includes *Dryas integrifolia* M. Vahl, *Salix arctica* Pall., *Luzula nivalis* Spreng., *Saxifraga oppositifolia* L. and *Papaver radicum* Rottb. (Muc 1989). Longer-stemmed *C. tetragona* plants were found growing within frost cracks and depressions, as well as alongside broken granitic outcroppings on the gently sloping outwash plain (Figure 3.3). The protection from the wind, as well as increased warmth provided by the darker rocks, and a prolonged source of water from late-melting snow trapped within the cracks most likely contributed to the increased stem lengths

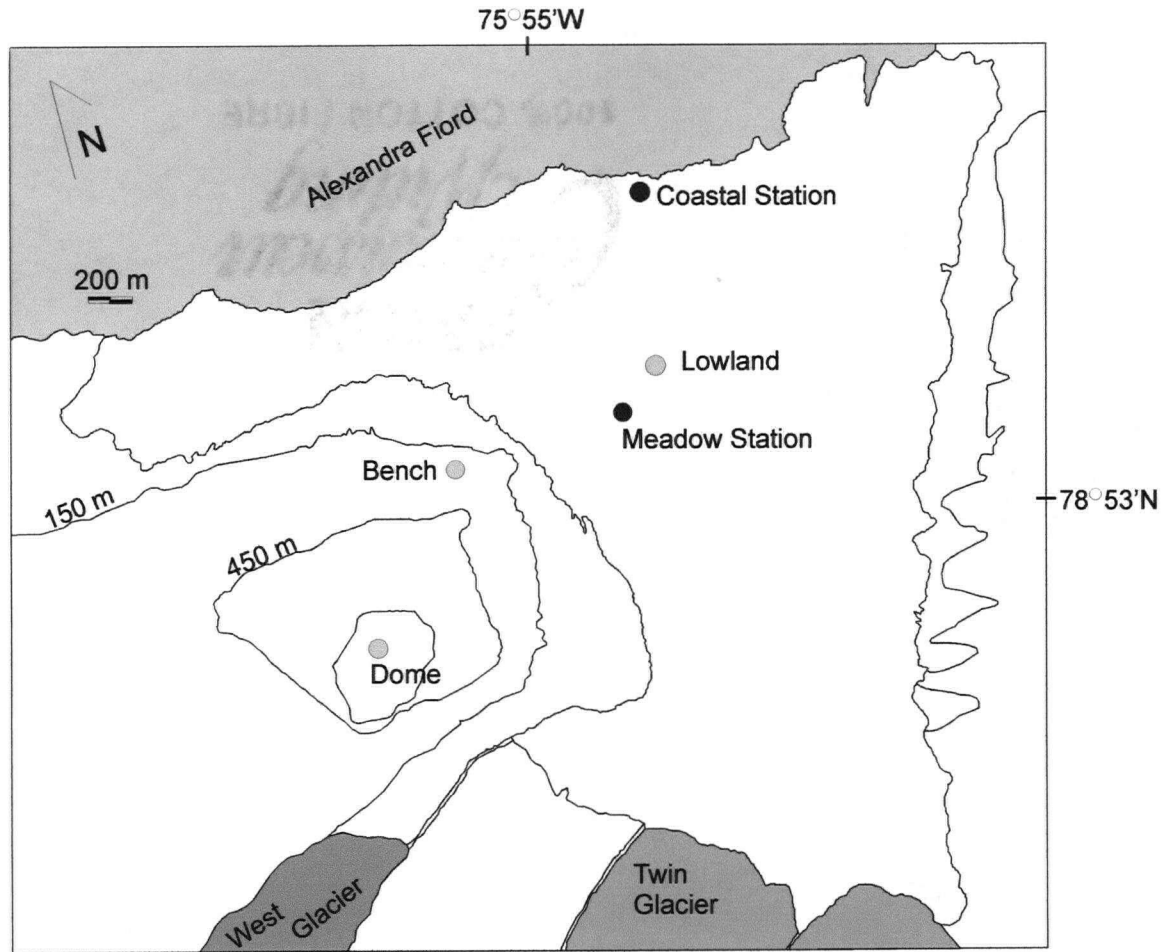


Figure 3.1. Map showing the locations of the Lowland (30 m a.s.l.), Bench (150 m a.s.l.) and Dome (500 m a.s.l.) sampling sites, and the Coastal and Meadow automated weather stations at Alexandra Fiord, Ellesmere Island.

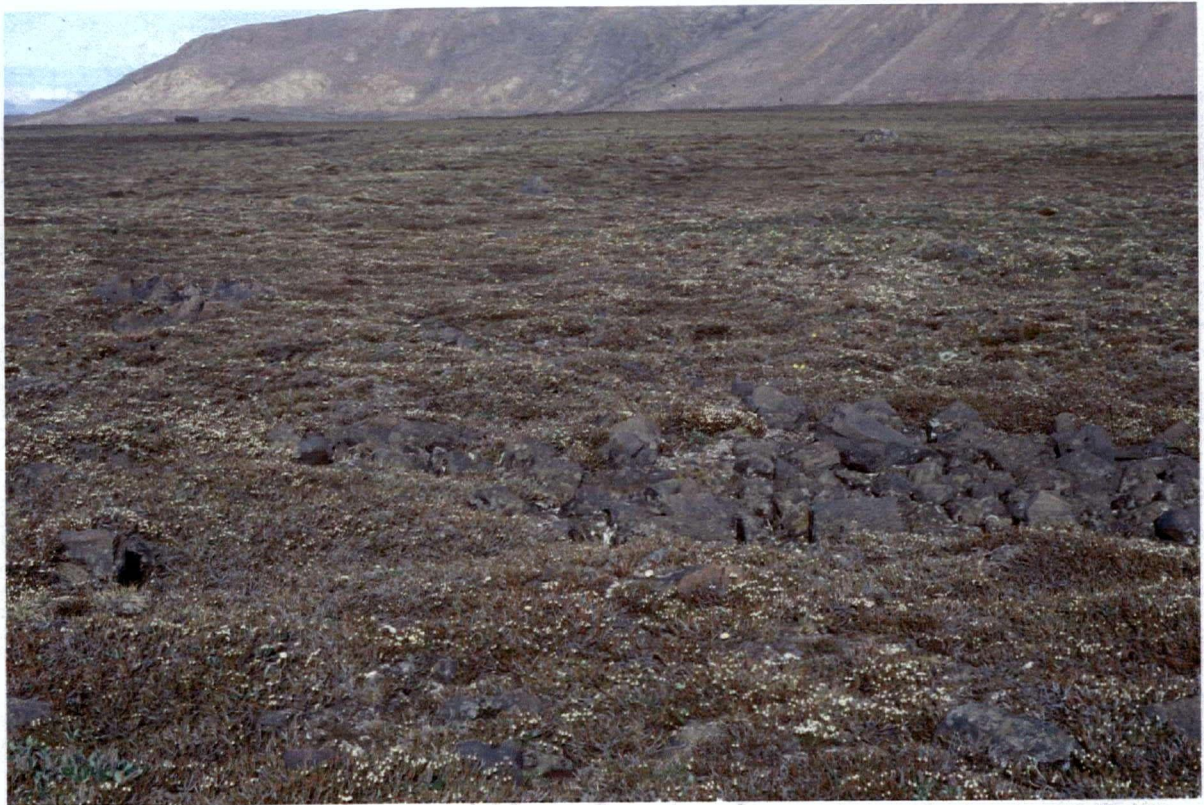


Figure 3.2. The Lowland sampling site (30 m a.s.l.) at Alexandra Fiord, Ellesmere Island, Canada. In the foreground, *Cassiope tetragona* plants are located around the rock outcrops and are in bloom.



Figure 3.3. *Cassiope tetragona* plant growing around a rock outcrop at the Lowland site, Alexandra Fiord, Ellesmere Island, Canada. Note the unusually long stems of the plant growing around the rock.

(Bruggemann and Calder 1953; Callaghan *et al.* 1989; Carlsson and Callaghan 1991). Many plant stems were found to extend along the length of the protected cracks. However, no evidence of etioliation was present in these stems. Shorter-stemmed and much smaller *C. tetragona* plants were present on the raised ground between frost cracks and on top of hummocks within the sampling area.

The Bench site is located at approximately 150 m a.s.l. on a northeast-facing slope, on the west side of the Alexandra Fiord lowland (Figure 3.4). The site is dominated by large granitic outcrops and boulders. In early July 1998, small patches of snow were found in deeply shaded cracks around the rocks. Meltwater from snowbeds upslope of the sampling site was present at the soil surface. *Cassiope tetragona* dominated the site's vegetation community, but *D. integrifolia*, *S. oppositifolia*, and *Luzula confusa* Lindeberg were also found. Similar to the Lowland site, the longest *C. tetragona* stems were found growing either in the protected space at the base of boulders and rock outcrops, or hanging down into the openings between the rocks from clumps of bryophyte-covered soil (Figure 3.5).

The third site along the elevation gradient, the Dome, is located at 500 m a.s.l. on the Western Plateau (Figure 3.6). It is believed that the present ice-free uplands of the Canadian High Arctic, including the Western Plateau at Alexandra Fiord may have been covered by glaciers, ice crusts and persistent snowbeds as recently as 100-150 years ago (Svoboda 1982; Svoboda and Henry 1987; Batten and Svoboda 1994). The western arm of Twin Glacier has retreated approximately 1.5 km from the Dome site exposing a bare upland. The upland is strongly marked by the geologic unconformity of a roughly circular, Paleozoic outlier of non-metamorphosed and undeformed sedimentary rock underlain and surrounded by Arcane gneisses. (Sternberg and Stone 1992). The recent deglaciation and the underlying geological substrate have influenced the vegetation community type and patterning within the plant communities at the Dome site (Batten and Svoboda 1994; Bliss *et al.* 1994). The vegetation communities are most influenced by the soil-moisture content of the Dome site. The absence of a well developed soil profile and drier conditions of the uplands result in lower species richness compared to elsewhere at Alexandra Fiord (37 species vs. 92 species). The granitic acidic soils with a pH between 5.0 and 7.0, host a rich vascular flora including *C. tetragona*, *S. arctica*, *D. integrifolia*, *Pedicularis hirsute* L., *Festuca hyperborea* Holmen ex. Frederiksen, *Oxyria digyna*



Figure 3.4. In the foreground, the Bench sampling site (150 m a.s.l.) at Alexandra Fiord, Ellesmere Island, Canada. The *Cassiope tetragona* plants were located in the protected spaces at the base of the boulders and rock outcrops.



Figure 3.5. *Cassiope tetragona* plants growing down into the spaces between small boulders at the Bench site, Alexandra Fiord, Ellesmere Island. Note the unusually long and green tipped stems of the plant.



Figure 3.6. (Top) Photo of the Dome site taken from the Eastern Plateau on the eastern side of Alexandra Fiord; (bottom) the Dome sampling site (500 m a.s.l.) (Photo courtesy of S. Rolph, 2001). Note the dolomitic substrate on the left hand side of the photo, and the granitic substrate on the right hand side. *Cassiope tetragona* plants were collected from surface cracks on the granitic side of the Dome site. The Dome ITEX open-top chambers and the Dome automated weather station are visible in the background, as well as Twin Glacier.

(L.) Hill, *Saxafraga caespitosa* L., *S. oppositifolia*, *S. cernua* L., and *S. nivalis* L. (Batten and Svoboda 1992). *Cassiope tetragona*, like many of the other plants at this site, congregates in the frost cracks in search of protection from the wind (Bruggemann and Calder 1953; Callaghan *et al.* 1989). Very few *C. tetragona* plants were found outside of these protective depressions at the Dome site.

3.2.3. Climate Measurements at Alexandra Fiord and Eureka, Ellesmere Island

The instrumental climate records from two sites on Ellesmere Island, Alexandra Fiord and Eureka, were used in this study to investigate the relationship between *C. tetragona* growth and reproduction and local and regional climate, and to reconstruct past climate for Alexandra Fiord. As summarized in Chapter 2 and in Labine (1994), the influence of the synoptic conditions on the climate of eastern Ellesmere Island, and the impact of the unique topographic configuration of the lowland on local climate at Alexandra Fiord are discussed.

Instrumental climate data have been collected at Alexandra Fiord since the summer of 1980 through the use of automated meteorological stations (Labine 1994). Climate data used in this study were recorded by two autostations at Alexandra Fiord, the Coastal station at 10 m a.s.l. (1980-1998) (Labine 1994; C. Labine, unpublished) and the Meadow station at 30 m a.s.l. (1989-1998) located 1 km inland (Henry *et al.* in prep) (Figure 3.1). Detailed descriptions of the Coastal and Meadow autostations and the climate data sets are provide in the Methods section of Chapter 2. The autostations measured all or several of the following variables: air, surface and soil temperatures, relative humidity, incoming global solar radiation, and wind speed and direction.

As the Coastal station record was the longest and most continuous data set at Alexandra Fiord, it was selected for use in this study. Any data gaps from 1989 to 1996 in the Coastal Station set were estimated using the Meadow station data set via linear regression analyses. Air temperature data used in this study were measured at 1.5 m above the ground surface at both the Coastal station and Eureka H.A.W.S. While surface temperatures (0 cm) and soil temperatures (-10 cm) do exist for Alexandra Fiord and are a useful indicator of the plant's microenvironment, these data were not available for the Eureka H.A.W.S. In addition, despite

the fact the Coastal station record was the best local dataset for retrospective modeling of climate at Alexandra Fiord, its length (1980-1996) was too short to verify any reconstruction. Hence, the longer data set from the Eureka H.A.W.S. (1948-1996) was chosen for response and transfer function analysis to estimate climate at Alexandra Fiord.

Eureka, Ellesmere Island (79° 59'N, 85° 59'W), is one of two weather stations located on Ellesmere Island and one of only five in the Canadian High Arctic. It is located on the coast of western Ellesmere Island on the Fosheim Peninsula at 10 m a.s.l. The station has collected hourly and daily meteorological data continuously since May 1947, including temperature and precipitation data (Meteorological Service of Canada, National Archive and Data Management Division, Environment Canada, 2002; <http://www.msc-smc.ec.gc.ca>). Eureka is approximately 250 km from Alexandra Fiord, separated by the Saw-Tooth Mountains and the Prince of Wales Ice Field. While Eureka and Alexandra Fiord were not classified into the same climate region (Maxwell 1981), climate variables recorded during the growing season correlated more strongly between Alexandra Fiord and Eureka than with the H.A.W.S. at Alert, Ellesmere Island (85° N) (Labine 1994). Eureka has the warmest summer climate conditions of any of the H.A.W.S., thus making it a good counterpart to the thermal oasis of Alexandra Fiord (Maxwell 1981; Labine 1994). The relationship between the climate conditions of Alexandra Fiord and Eureka for the period 1980-1988 was discussed in Labine (1994). Labine (1994) found that the annual air temperature at Alexandra Fiord was 5-6 °C higher than at Eureka for 1980-1988, but much of this difference was due to milder temperatures at Alexandra Fiord during the winter months (January to May; September to December). Labine's (1994) observations are supported by comparisons of annual air temperatures for the period 1980-1996 (Table 3.1). Paired comparisons t-tests were used to compare average monthly air temperature for 1980-1996 at the Coastal station, Alexandra Fiord with average monthly temperature at Eureka, H.A.W.S. (Table 3.2).

Unfortunately, there are no long-term climate data recorded at the Bench or Dome sites at Alexandra Fiord. Recently, however, as part of a long-term warming experiment at Alexandra Fiord, continuous temperature measurements have been made using thermocouples at the Dome site since 1993 in the control and open-top chamber treatment plots. In addition, measurements of air temperature at 1.5 m above the ground surface have been made. As the

Table 3.1: Comparison of average annual air temperature at the Coastal station, Alexandra Fiord, Ellesmere Island and Eureka H.A.W.S., Ellesmere Island for the period 1980-1996.

Year	Eureka Annual Air Temperature °C	Coastal Station Annual Air Temperature °C
1980	-19.9	-15.3
1981	-17.6	-14.1
1982	-20.4	-15.4
1983	-19.3	-15.1
1984	-21.2	-16.5
1985	-20.0	-15.4
1986	-20.8	-16.4
1987	-21.2	-16.6
1988	-17.5	-14.6
1989	-20.6	-15.7
1990	-19.4	-15.4
1991	-18.5	-14.9
1992	-20.5	-15.9
1993	-18.8	-15.2
1994	-18.0	-14.4
1995	-18.2	-14.0
1996	-18.7	-14.0
Average	-19.4	-15.2

Table 3.2. Comparison of average monthly air temperature at the Coastal station, Alexandra Fiord, Ellesmere Island with Eureka, H.A.W.S., Ellesmere Island for the period 1980-1996 using a paired comparisons t-test. n = 17.

Month	Eureka Monthly Air Temperature °C	Coastal station Monthly Air Temperature °C	paired t-test
January	-36.9	-29.2	**
February	-37.7	-29.8	**
March	-37.5	-30.2	**
April	-27.5	-21.8	**
May	-10.5	-8.0	**
June	2.5	2.2	ns
July	5.7	4.8	**
August	2.7	2.7	ns
September	-7.2	-5.7	**
October	-21.6	-16.5	**
November	-31.0	-24.1	**
December	-34.3	-27.3	**

**P < 0.01; ns = not significant.

data set increases in length, it could be used in future retrospective studies of *C. tetragona* plants from the Dome site.

3.2.4. Plant Sampling and Measurement

In July 1998, *C. tetragona* plants were collected at the Lowland, Bench and Dome sampling sites. Fifteen to twenty plants were collected from a visually homogenous area at each site. Every attempt was made to collect plants that could be considered genetic individuals. However, this could not be ascertained in this study, since *C. tetragona* shoots are known to trail and produce adventitious roots (Havström 1995). When the genets disintegrate, the individual plants may be physically separated, but are genetically identical (Havström 1995). The plants were selected for the longest stems possible as the goal of the study was to reconstruct climate for the longest period possible. Plants were collected from frost cracks and depressions around gneiss outcroppings at the Lowland site, from the base of and in between granite boulders and outcrops at the Bench site, and from frost cracks on the gneissic side of the unconformity on the Dome site. Following harvest, the collections were air-dried for seven days and then stored in paper bags.

In the laboratory, five to nine stems per plant were selected for measurement. Stems were selected for length and, when possible, for live green leaves and leaf buds at the tips of the shoots. Bends in the shoots, whether natural or from storage, were removed by placing the stems in a lukewarm bath for five to ten minutes. Stems were inserted into 1 cm diameter glass tubes and allowed to dry overnight. When dry, two adjacent rows of leaves on the stem were removed by hand. Any flower buds or flower peduncles found on the shoot were left in place. A complete description of laboratory procedures was given in Chapter 2.

Measurement of the internode distances between leaf scars along the length of the stem was carried out under a dissecting microscope (10X to 30X magnification) using a manually operated caliper system (designed by J. Svoboda, University of Toronto, 1992). The internode lengths were measured from the base to the tip of the shoot, while taking care to record the number and location of flower buds and peduncles. Data were recorded in a spreadsheet program.

3.2.5. Retrospective Growth and Reproduction Analysis

Two variables of growth (annual stem elongation, annual production of leaves) and two of reproduction (annual production of flower buds and flower peduncles) for the sampled *C. tetragona* plants were measured and recorded. A complete description of retrospective growth and reproduction analysis is given in Chapter 2. Annual growth increments were determined by the wave-like patterns in internode lengths, with the terminus of annual growth delimited by the shortest internode length at the end of each wave-series (Johnstone 1995). Each year is referred to as an annual growth increment (AGI). The annual production of leaves, flower buds, and flower peduncles were counted and recorded for each annual growth increment.

3.2.5.1. Cross-Dating: Skeleton Plots and COFECHA

The procedure of cross-dating ensures the proper placement in time of individual annual growth increments by matching common patterns of yearly growth (Fritts 1976). It is assumed in cross-dating that environmental factors (e.g., climate) affect annual growth and, thus, will produce observable synchronous variations in annual growth sequences over long time periods and across large number of individual plants over wide geographical areas. Skeleton plotting, a graphic technique of representing annual growth increment variations, aids the researcher in matching up synchronous growth patterns within- and between-plants to create site chronologies. Each site chronology is constructed from precisely dated time series of growth increments.

In this study, each stem was cross-dated using skeleton plots of annual growth increments (Stokes and Smiley 1968). Five to nine stems per plant were cross-dated and 10 to 15 plants were used to create site chronologies. The dendrochronological software program, COFECHA, available in the Dendrochronological Program Library (DPL), was used to verify further the visual cross-dating and to detect missed measurement and cross-dating errors in the measured series (Holmes *et al.* 1986; Grissino-Mayer 2002). Chronologies for annual production of leaves, flower buds, and flower peduncles were constructed as well, based on the number of variables per year as defined by the annual growth increment. These chronologies were not formally cross-dated.

3.2.5.2. Standardization

In this study, standard chronologies of average growth and reproduction for each of the three sites at Alexandra Fiord were constructed from a subset of all *C. tetragona* plant stems measured. The annual growth increment series selected for each study site were: (1) visually and statistically cross-dated to insure proper placement in time, (2) at least 20 years in length, and (3) positively inter-correlated with the master series (Daniels 2000). The chronologies were standardized using traditional dendrochronological methods (Fritts 1976; Cook *et al.* 1990).

In dendrochronology, the dual purpose of standardization is: (1) to remove non-climatic growth trends from the annual growth increment series, and (2) to allow the resultant standardized values of individual plants to be averaged together into a mean-value function by adjusting the series for differences in growth rates (Cook *et al.* 1990). Commonly, time series of annual growth increments contain a low frequency component resulting from uneven growth of the species over its lifetime (Bradley 1999). It is necessary to remove this juvenile growth function particular to the individual stem before annual increment variation between different stems can be compared (Bradley 1999). Otherwise, the record from one stem with larger than average growth for a given year will dominate other series of smaller than average annual growth when the series are combined into a mean chronology (Fritts 1976).

Inspection of individual series of *C. tetragona* revealed that smaller annual growth increments occurred during the first years of shoot elongation, whether on a main stem or a branching auxiliary stem. The juvenile growth trend in shoot growth is similar to what Callaghan *et al.* (1989) noted for leaf lengths in early stem growth. In order to avoid an age-related bias, the growth chronologies were standardized. In addition, it was hypothesized that reproduction in *C. tetragona* may be influenced by juvenile growth effects. However, as no one has been able to date a stem back to its first year of growth with certainty, it can only be estimated that a plant reproduces after 10 years of growth. To minimize the juvenile effect on reproduction: (1) all chronologies for annual production of flower buds and flower peduncles were truncated to begin at the first year of bud formation or flower production, and (2) were standardized. Johnstone and Henry (1997) also truncated and standardized the chronology for annual production of flower peduncles used in their study (J. Johnstone, personal communication, 2002). In addition, any stems found to have neither flower buds nor flower

peduncles were eliminated from the chronology building process. By eliminating these non-reproductive stems, the number of stems upon which the flower bud and flower peduncle chronologies were constructed is lower than the number of stems included in the growth chronologies.

Standard chronologies for the Lowland, Bench and Dome sites were produced using the dendrochronological software program ARSTAN (also in the DPL) (Cook 1985; Cook and Holmes 1986). The two growth and two reproductive chronologies per site were standardized using flexible cubic-splines. Flexible cubic splines are symmetrical, low-pass digital filters (Cook and Peters 1981). There is little theoretical basis behind the selection of the proper degree of curve flexibility or data smoothing when using digital filters, such as cubic splines, in dendrochronology (Cook and Briffa 1990). As the frequency-dependent properties of the noise (i.e. band limited spectral properties of the age trend and stochastic disturbance effects) are unknown *a priori* in most situations, it is hard to choose objectively and to justify a selected digital filter (Cook and Briffa 1990). However, when *a priori* information about the species, the site and the environmental conditions is known, a more objective selection of an optimal frequency response for a low-pass filter is possible (Cook and Briffa 1990). When considering cubic splines, one possible criterion for choosing the proper low-pass filter is the signal-to-noise-ratio (Wigley *et al.* 1984; Cook and Briffa 1990). The SNR is defined as:

$$SNR = \frac{N \bar{r}}{(1 - \bar{r})} \quad (3.1)$$

where \bar{r} is the average correlation between plants and N is the total number of plants included to construct the chronology. The SNR expresses the strength of the observed common signal among plants. The goal is to find the frequency response of the filter which best maximizes the SNR (Cook and Briffa 1990).

The maximum SNR criterion does have drawbacks because it assumes, in the derivation of the equation above, that the series being cross-correlated are random (Cook and Briffa 1990). The limitation of the SNR is that it measures the strength of the observed high-frequency signal in the growth and reproductive indices, but not the lower frequency signal often of interest in climate change research (Cook and Briffa 1990). Thus, the SNR criterion may select a digital

filter which removes more low frequency variance than intended or desired (Cook and Briffa 1990). With the bias of the SNR criterion in mind, it still provides a reasonable and objective benchmark for selecting the frequency response of the digital filter (Cook and Briffa 1990).

Using a SNR criterion, as well as *a priori* information regarding the plant growth characteristics, flexible cubic splines on the order of twenty years were selected for the annual growth increment and number of leaves chronologies. Cubic splines of 60 and 70 years were selected for the number of flower peduncle and flower bud chronologies, respectively. The flexible cubic splines were selected to smooth out the local fluctuations which constitute the high-frequency variation in growth and reproduction in order to produce a smoothed estimate of the actual series (Cook and Peters 1981). For the purposes of this study, a smoothing spline was needed that would maximize the inter-shoot correlation without losing the climate signal entirely. It was hypothesized that small changes within the *C. tetragona* plant's architecture (e.g., due to inter-shoot shading, resource partitioning, apical dominance) would likely have a greater effect on plant growth than climate over the lifetime of the plant. Thus, intra-plant effects must be filtered out as much as possible. In previous work, Johnstone and Henry (1997) effectively selected a 10 year weighted moving average to smooth chronology values and develop response and transfer functions for Alexandra Fiord. A weighted moving average is similar to a cubic spline. However, one drawback of the use of flexible cubic splines is their use essentially precludes the possibility of reconstructing climate trends that last multiple decades to centuries (Cook and Briffa 1990). Hence, the climate reconstruction in this study is one that focuses on higher-frequency climate variation.

The process of standardization results in a new time series of annual growth indices or annual reproduction indices. Each time series has a defined mean and a relatively constant common variance that is approximately the same throughout the entire length of the series (Fritts 1976; Cook *et al.* 1990). After each cross-dated stem is standardized, the annual growth indices from the multiple individual stems may be averaged year by year to produce a master chronology for the site, independent of growth function and differing sample age (Bradley 1999). The master chronology is often referred to as a mean value function in dendrochronology. In this study, the individual standardized stems were averaged together using a biweight robust mean to calculate the mean value function (Mosteller and Tukey 1977). The biweight robust mean for year t is computed by iteration as:

$$\bar{I}_t^* = \sum_{j=1}^m w_{tj} I_{tj} , \quad (3.2)$$

where

$$w_{tj} = \left[1 - \left\{ \frac{I_{tj} - \bar{I}_t^*}{cS_t^*} \right\}^2 \right]^2 , \quad (3.3)$$

when

$$\left\{ \frac{I_{tj} - \bar{I}_t^*}{cS_t^*} \right\}^2 < 1 , \quad (3.4)$$

otherwise 0. I_{tj} is the detrended index for each year, j is the number of stems or series, and m is the number of indices available in year t across all series. The weight function, w_{tj} , is symmetric, and, therefore, unbiased in its estimation of central tendency when the data are symmetrically distributed (Cook 1985; Cook *et al.* 1990). S_t^* is a robust measure of the standard deviation of the frequency distribution, which will be the median absolute deviation (MAD)

$$S_t^* = \text{median} \left\{ |I_{tj} - \bar{I}_t^*| \right\} , \quad (3.5)$$

and c is a constant, often taken as six or nine (Mosteller and Tukey 1977). The constant c determines the point at which a discordant value is given a weight of zero. When this is the case, the outlier is totally discounted in computing the mean and, thus, has no influence on the estimation of the mean index. To start the iteration for computing the final \bar{I}_t^* , the arithmetic mean or median can be used as an initial estimate. Ordinarily, only three to four iterations are

needed to converge on an estimate of \bar{I}_t^* that does not change by more than 10^{-3} (Cook *et al.* 1990).

The use of the biweight robust mean is recommended to discount the influence of possible outliers in the computation of the means, thus reducing the variance and bias caused by those outliers (Cook *et al.* 1990). Averaging the standardized indices also increases the signal (climatic) to noise ratio (Bradley 1999). The climatically related variance or signal is common to all time series and is not lost by averaging (Fritts 1976; Bradley 1999). However, non-climatic “noise”, varying from plant to plant, will be partially cancelled out in the averaging process (Bradley 1999). To increase the climate signal, it is important that a large number of stems be included in the master chronology in order to enhance the climatic signal common to all plants (Briffa and Jones 1990; Bradley 1999).

In order to maintain the low frequency signal in the three site chronologies, the standard chronologies were retained for analysis. Following the methodology outlined in Szeicz and MacDonald (1995), D'Arrigo and Jacoby (1992), and Jacoby and D'Arrigo's (1989) work on the reconstruction of temperature using arctic tree species, autoregressive modeling was not carried out. Autoregressive modeling or “prewhitening” removes the low-order autocorrelation or climatically-induced variance in a chronology. It was decided that prewhitening was not necessary given the use of flexible cubic splines and low autocorrelation values for the mean value functions.

3.2.6. Descriptive Statistics

Descriptive statistics were calculated for the growth and reproductive chronologies for each of the sites as outlined in Fritts (1976). Statistics included the mean, standard deviation, mean sensitivity and first-order autocorrelation. Mean sensitivity is defined as

$$ms_x = \frac{1}{n-1} \sum_{t=1}^{n-1} \left| \frac{2(x_{t+1} - x_t)}{x_{t+1} + x_t} \right|, \quad (3.6)$$

where x_t is the ordered annual growth increment such that time (indicated by the subscript t) varies sequentially from 1 (the calendar year of the earliest dated annual growth increment), to n (the last calendar year) (Fritts 1976). The denominator of the term scales the absolute values of the differences between adjacent annual growth increments, x_t and x_{t+1} , so that the differences are proportional to the average of the two widths (Fritts 1976). The values of mean sensitivity range from 0, where there is no difference, to 2, where a zero value occurs next to a non-zero one in the time sequence (Fritts 1976). Mean sensitivity is the mean percentage change from each measured annual growth increment to the next (Douglass 1936).

3.2.7. Mean Correlation Analysis

As described in Chapter 2, mean correlation analysis, an alternative approach to estimating the quantities obtained in the analysis of variance, provides a relative measure of variability in common within and between plants (Fritts 1976; Briffa and Jones 1990). Mean correlation analysis was carried out using the software program ARSTAN (Cook 1985; Cook and Holmes 1986). The program computes the correlation statistics using an optimum common interval. The optimum common interval is the maximum time span which is covered by the maximum number of index series (Cook and Holmes 1986). The correlation statistics calculated include the between-plant signal, \bar{r}_b , which is an estimate of the common signal in the *C. tetragona* chronologies, and the within-plant signal, $1 - \bar{r}_w$, which is an estimate of the within-plant noise.

3.2.8. General Linear Model

In order to determine whether a significant difference in annual growth, number of leaves, number of flower buds or number of flower peduncles among the three sites existed, general linear models were used to obtain repeated measures analyses (MGLH procedure, SYSTAT v. 5.0, 1990-1992). The number of plants sampled per site and the time period covered by all time series were not equal. Plant time series were calculated by averaging all stem time series for each plant. All time series were based on non-standardized data and

averaged using the arithmetic mean. In the general linear model, year was used as the continuous variable, site (Lowland, Bench and Dome) was used as the class variable, and year by site interaction was used as the independent variable. The variable, site, was considered a fixed effect while year was considered as a continuous variable (Neter *et al.* 1996). In this case, the variable, year, was not of intrinsic interest in itself, but constituted a sample from a larger population (Neter *et al.* 1996). The general linear model was calculated as a Type III multiple analysis of variance. The assumptions of parametric statistics were tested using visual examination of residual plots, the modified Levene's test, and the correlation test for normality (Neter *et al.* 1996).

3.2.9. Spearman's Rank Correlation Coefficients

To understand the relationships among the growth and reproductive chronologies both within each site and among the three sites, simple correlation coefficients were calculated. As not all of the mean standardized chronologies were normally distributed, the nonparametric Spearman's rank coefficient, r_s , was used (Conover 1971).

3.2.10. Response Function Analysis

In order to select an optimum season for climate reconstruction, correlation and response function analysis were carried out (Briffa *et al.* 1990). A response function is a statistical representation of the climate variables and prior growth (or reproduction) factors that control index growth (or reproduction) (Cropper 1985). In this study, the relationships between climate variables measured at Alexandra Fiord and the Eureka H.A.W.S. and *C. tetragona* growth and reproduction standard chronologies were investigated. Correlation and response function analyses were carried out using the software program PRECONK, Version 5.11 (Fritts 1996). First, PRECONK ran a correlation analysis, producing simple correlation coefficients between the growth or reproduction chronologies and monthly climate variables (e.g., average temperature, total monthly precipitation, and monthly thawing degree days). Next, PRECONK ran the response function analysis. In the response function analysis, the most important

eigenvectors of monthly temperature, total monthly precipitation (and/or other climate variables) and previous growth (or reproduction) were extracted from a correlation matrix of the climatic and prior growth variables. The normalized climatic and prior growth variables were multiplied by the eigenvectors to obtain the principal components. These principal components contain the same information that was in the original correlation matrix; however, they have been rotated so that they are uncorrelated or orthogonal with one another. Using the PVP criterion (Guiot 1985; 1991), the principal components that explained too little of the variance were excluded from the analysis. The PVP criterion is the point where the cumulative product of the eigenvalues falls just below one (Guiot 1985). Next, the principal components with significant eigenvectors were used as predictors in multiple regression analysis. Because the regression coefficients using the principal components as predictors cannot be interpreted easily, the coefficients were back-transformed into the original monthly climatic and prior growth variables. The back-transformation was accomplished by multiplying the regression weights by the eigenvectors which met the PVP criterion. The re-rotated set of regression coefficients are the coefficients of the response function. At this point in the analysis, however, the variables are no longer uncorrelated and the significance of the coefficients is overestimated (Cropper 1985). To address this problem, a bootstrap procedure is used (Guiot 1991). The bootstrap procedure estimates the errors in the results by replicating the calculations m times by randomly drawing n sets of data with replacement, simulating n years of data. At the end of the procedure, the pooled data are used to calculate the standard errors of each response function coefficient. All coefficients with absolute values exceeding two standard errors are marked as significant. While response function analysis cannot prove a cause-and-effect relationship between climate and growth, the statistical technique is a useful tool to infer which aspects of the climate-growth relationship are important. The sign of the response function weight for each monthly variable provides an indication of the direction of the growth or reproductive response to the climatic variable (Cropper and Fritts 1981).

Climate data, including average monthly air temperature and monthly thawing degree days from the Coastal station at Alexandra Fiord (1980-1996) were used to investigate the climate-growth and climate-reproduction relationships with the chronologies from the three sites at Alexandra Fiord. Air temperature was measured at a height of 1.5 m above the soil surface. Monthly thawing degree days were calculated as the sum of the average daily temperature across all days with an average daily temperature above zero degrees Celsius. No precipitation

data were available from the Coastal station site. Correlations and response functions were calculated for the twelve-month time period from September of the previous year (year C-1) to August of the current year (year C) using average monthly air temperature. In addition, one year of previous growth (or reproduction) was included in the response function models to account for lag effects. Due to limitations in the PRECONK software program, it was only possible to calculate correlation and response functions using monthly thawing degree days for the prior May, June, July and August and the current May, June, July and August (H.C. Fritts, personal communication, 2002). For the months of September-April, the total number of thawing degree days at Alexandra Fiord was zero. The zero values caused a computational error in the PRECONK software and thus, these months could not be included in the analysis. One year of prior growth (or reproduction) was included in the response function models.

Climate data from Eureka H.A.W.S. were also used to investigate climate-growth relationships with the Lowland, Bench and Dome chronologies. Correlation and response functions were calculated using average monthly air temperature and total monthly precipitation measurements for the common overlap period of 1948-1996. Air temperature was measured at 1.5 m above the ground surface. Total monthly precipitation, including rainfall and snowfall, was measured using the standard Canadian rain gauge, a cylindrical container 40 cm high and 11.3 cm in diameter and Nipher snow gauges. All measurements were carried out by the Meteorological Service of Canada. Correlations and response functions were calculated for the time period of May of the previous year (year C-1) to September of the current year (year C). Two years of previous growth were included in the response function models to account for lag effects. Once the potential for reconstructing temperature or precipitation for a particular month or season was established through response function analysis, the form of the regression model was explored using transfer function analysis.

3.2.11. Transfer Function Analysis

Transfer function models predicting climate from growth and reproduction of *C. tetragona* were calibrated using stepwise multiple linear regression analysis for the common overlap period between the chronologies from the Lowland and Bench sites and the climate records from the Coastal Station, and Eureka H.A.W.S. All stepwise multiple regression

analyses were carried out using the MGLH procedure in SYSTAT (v. 5.0, 1990-1992). The set of potential predictor variables included growth and reproductive variables from the Lowland and Bench sites at years t , $t + 1$, $t + 2$, and $t - 1$. Both positive and negative lags were included in the analyses in order to capture persistence effects in the growth-reproduction-climate relationship (Fritts 1976; Briffa *et al.* 1986; Jacoby and D'Arrigo 1989). Predictor variables lagged forward by one and two years were entered into the model as temperature in the previous year(s) has been shown to correlate significantly with current year *C. tetragona* growth and reproduction (Fritts 1976; Briffa *et al.* 1986; Callaghan *et al.* 1989; Johnstone and Henry 1997). In addition, a sampling site may lead or lag regional and hemispheric climate shifts (Jacoby and D'Arrigo 1989). Leading and lagging of predictor variables may enhance the low frequency variance modeled (Jacoby and D'Arrigo 1989). However, it may also smooth out high frequency variability as the individual site response to changing climate may not be in sync with greater regional changes (Jacoby and D'Arrigo 1989). The Dome site was not included in the transfer function analysis as the lengths of the Dome chronologies were considerably shorter than the chronologies from the other two sites. Non-significant candidate predictor variables were eliminated by the stepwise procedure ($\alpha = 0.05$) to develop a parsimonious model (SYSTAT v. 5.0 1990-1992).

Initial models predicting summer temperature at Alexandra Fiord were developed using stepwise multiple linear regression for single months of the growing season (June, July, August) and for combinations of summer months (e.g., July-August) calculated from the Coastal station data set. After the full model was selected, an examination of the residuals was carried out using visual examination of residual plots, the modified Levene's test and the correlation test for normality (Neter *et al.* 1996). Given the short overlap period between the Coastal station data set and the chronologies (1980-1996), it was impossible to verify the calibrated model as is recommended in dendrochronological protocols (Fritts 1976; Cook *et al.* 1990).

Preliminary models predicting summer temperature for single months of the growing season (May, June, July, August, September) and for combinations of summer months (e.g., May-September) for the full period of overlap between the Eureka H.A.W.S. climate data and Lowland and Bench chronologies (1948-1996) were calibrated. While total monthly precipitation was included as a climatic variable in the response function model, it was decided that precipitation is a more local phenomenon than temperature, and its reconstruction would be

difficult and the models possibly unstable. Moreover, precipitation at Alexandra Fiord is influenced by the mountain ranges which separate the two locations as well as ice fields, local glaciers, and the open water of the large North Water Polynya at the northern end of Baffin Bay. In addition, there can be different predominant synoptic systems which influence Alexandra Fiord. Once the model for predicting temperature was selected, cross-calibration and verification were performed to test the general form of the regression equation to be used in the reconstruction of climate. It is common practice within dendroclimatology for empirically derived equations which link growth and reproduction to climate time series to be verified (Briffa *et al.* 1988). The model was divided into two parts following the data-splitting method of Fritts (1976). The full data set was split into an "early" period (1948-1980) and a "late" period (1964-1996) and transfer functions calibrated for each period using stepwise regression on the same predictor variables as the full model (Case and MacDonald 1995). The calibration models developed for the early (1948-1980) and late periods (1964-1996) were then verified over the late (1981-1996) and early (1948-1963) verification periods. Verification statistics included the Pearson's product-moment correlation coefficient (r), reduction of error statistic (RE), coefficient of efficiency (CE) and the first difference sign test (Fritts 1976; Briffa 1988). The reduction of error statistic is defined as

$$RE = 1.0 - \frac{\sum_{i=1}^N (y_i - \hat{y}_i)^2}{\sum_{i=1}^N (y_i - \bar{y})^2} \quad (3.7)$$

where y_i are the measured temperatures in year i and \hat{y}_i are the estimated temperatures in year i , \bar{y} is the mean of the measured temperatures over the calibration period, and N is the number of years in the verification period (Briffa *et al.* 1988). The reduction of error statistic is commonly used in dendroclimatology to compare estimated data with values assumed to be equal to the calibration period mean (Briffa *et al.* 1988). The coefficient of efficiency (CE) differs from the RE in that the \bar{y} in equation (3.7) is replaced by the mean of the verification period. The coefficient of efficiency, used in hydrology (Nash and Sutcliffe, 1971), is a measure of the variance in common between the real and the estimated data over the verification period (Briffa *et al.* 1988). Any positive RE or CE value is generally accepted as indicative that

there is meaningful climatic information in the reconstruction (Fritts 1976; Briffa *et al.* 1988). Unfortunately, the level of significance of the RE and CE statistics cannot easily be tested (Briffa *et al.* 1988). In the nonparametric sign test of first differences, the number of agreements and disagreements between two series are counted and then their measure of association is tested using a sign test (Fritts 1976). The direction of change in the variable from one year to the next is recorded as either an increase (+) or a decrease (-) for each series. The two series are compared and the number of agreements in sign are totaled. If the number of similarities is significantly larger than the number of dissimilarities, then an association between the two series exists (Tate and Clelland 1957; Fritts 1976). When the verification statistics are examined together, they provide information on the quality of the reconstructions at high and medium frequencies (Briffa *et al.* 1988). Following successful calibration and verification, the model, calibrated over the full period of 1948-1996, was considered time stable and used to reconstruct climate prior to the period of instrumental data on Ellesmere Island.

3.3 Results

3.3.1. Chronology Characteristics for Lowland, Bench and Dome Sites

At the Lowland site, between 74 and 86 stems representing 15 plants were measured, cross-dated and standardized to develop two growth and two reproductive chronologies (Table 3.3). The Lowland chronologies for annual stem growth and annual production of leaves covered the 118 year time period of 1879-1996. The chronologies for annual production of flower buds and flower peduncles were shorter, extending from 1900 to 1996 (97 years) and 1917 to 1996 (80 years), respectively. As all *C. tetragona* plants were collected in early July of 1998 and annual stem elongation had yet to begin, the 1998 growth year was not included in the chronologies. This delay in stem elongation made measurement of the 1997 growth year difficult as well; thus, chronologies were truncated at 1996 to ensure proper measurement and dating.

Growth and reproductive chronologies developed for the Bench site were constructed with 59 to 79 stems from 13 plants (12 plants were used in the flower peduncle chronology) (Table 3.3). The chronologies for annual stem growth and production of leaves covered the 113

Table 3.3. Annual plant performance (from non-standardized data) of *Cassiope tetragona* from the Lowland, Bench and Dome sampling sites at Alexandra Fiord, Ellesmere Island. AGI = annual growth increment; Leaf = number of leaves; Bud = number of flower buds; Ped = number of flower peduncles.

	Lowland				Bench				Dome			
	AGI ¹ 1879-1996	Leaf ² 1879-1996	Bud ³ 1900-1996	Ped ³ 1917-1996	AGI ¹ 1884-1996	Leaf ² 1884-1996	Bud ³ 1894-1996	Ped ³ 1904-1996	AGI ¹ 1922-1996	Leaf ² 1922-1996	Bud ³ 1927-1996	Ped ³ 1931-1996
Chronology Length	1879-1996	1879-1996	1900-1996	1917-1996	1884-1996	1884-1996	1894-1996	1904-1996	1922-1996	1922-1996	1927-1996	1931-1996
# of Years	118	118	97	80	113	113	103	93	75	75	70	66
Sample Size (plants)	15	15	15	15	13	13	13	12	10	10	10	10
# of Stems Measured	86	86	85	74	79	79	74	59	69	69	60	58
# of Stems per Plant	2 to 8	2 to 8	2 to 8	2 to 8	4 to 9	4 to 9	4 to 9	4 to 9	5 to 9	5 to 9	5 to 9	5 to 9
Mean	4.76	10.16	0.42	0.35	3.95	8.78	0.48	0.25	3.73	9.82	0.65	0.41
Standard Deviation	2.06	2.86	0.65	0.60	1.45	2.26	0.66	0.51	1.71	3.04	0.85	0.68
Maximum	18.48	24.00	4.00	3.00	11.55	20.00	3.00	3.00	13.32	24.00	5.00	5.00
Minimum	1.07	4.00	0.00	0.00	1.05	4.00	0.00	0.00	1.18	4.00	0.00	0.00
Median	4.51	10.00	0.00	0.00	3.74	8.00	0.00	0.00	3.41	10.00	0.00	0.00

AGI¹ = annual growth increment estimates are measured in mm per year.

Leaf² = annual leaf production estimates are for four leaf rows on a stem.

Bud³ and Ped³ = estimates for annual production of flower buds and peduncles are for 2 of 4 leaf rows on a stem.

year time period of 1884-1996. The chronologies for annual production of flower buds and flower peduncles covered a shorter time period, 1894-1996 (103 years) and 1904 -1996 (93 years), respectively.

The Dome chronologies for growth and reproduction were developed from 58 to 69 stems representing 10 plants (Table 3.3). The chronologies for annual stem growth and production of leaves were the longest for the site, covering the period from 1922-1996 (75 years). The two shortest chronologies developed at Alexandra Fiord were the Dome's annual production of flower buds (1927-1996, 70 years) and flower peduncle chronologies (1931-1996, 66 years).

General linear models showed significant differences existed among the three sites for one growth and one reproductive variable (annual growth increment, $P < 0.01$; flower buds, $P < 0.001$) (Table 3.4). In addition, both annual growth increment ($P < 0.01$) and flower bud ($P < 0.001$) variables showed significant site-by-year interactions. Annual production of leaves only showed significant year-to-year differences ($P < 0.001$). No significant differences were detected for the annual production of flower peduncles variable ($P > 0.05$). Unfortunately, none of the models developed met all the assumptions of parametric statistics. The model which tested for differences in the annual growth increment variable among sites violated assumptions of normality. The models which tested for differences in the variables for annual production of leaves, flower buds and flower peduncles among sites violated assumptions of normality and nonconstancy of the error variance. Due to the problems with violations of parametric assumptions, the general linear model results are viewed with caution.

Investigation of the signal strength for the growth and reproductive chronologies showed that the common signal, \bar{r}_{bt} , is very weak across all three sites (Table 3.5). The estimate of the within-plant noise, $1 - \bar{r}_{wt}$, was much greater than the common signal across all variables and sites.

In dendrochronology, the strength of the observed common signal among plants within the sample data set is given in the signal-to-noise ratio (SNR) (Cook and Briffa 1990). The SNRs calculated for the growth and reproductive chronologies from each of the three sites were

Table 3.4. General linear model results showing the differences over time in annual stem growth (AGI), annual production of leaves, flower buds and flower peduncles among the three sites at Alexandra Fiord, Ellesmere Island, Canada. n = 2863 for annual growth increments, n = 2864 for number of leaves, n = 2583 for number of flower buds and n = 2200 for number of flower peduncles.

Annual Growth Increments

Source	Sum of Squares	df	Mean-Square	F
Year	49.974	1	49.974	31.047 ***
Site	16.133	2	8.066	5.01 **
Site*Year	17.685	2	8.843	5.494 **
Error	4598.77	2857	1.61	
Total	4682.562	2862		

Number of Leaves

Source	Sum of Squares	df	Mean-Square	F
Year	16.636	1	16.636	20.178 ***
Site	2.853	2	1.426	1.73 ns
Year*Site	3.148	2	1.574	1.909 ns
Error	2356.293	2858	0.824	
Total	2378.93	2863		

Number of Flower Buds

Source	Sum of Squares	df	Mean-Square	F
Year	0.509	1	0.509	2.344 ns
Site	2.95	2	1.475	6.797 ***
Year*Site	2.957	2	1.478	6.813 ***
Error	559.147	2577	0.217	
Total	565.563	2582		

Number of Flower Peduncles

Source	Sum of Squares	df	Mean-Square	F
Year	0.227	1	0.227	1.388 ns
Site	0.463	2	0.232	1.415 ns
Year*Site	0.421	2	0.211	1.286 ns
Error	359.217	2194	0.164	
Total	360.328	2199		

* P<0.05, ** P<0.01, *** P<0.001, ns = not significant (P>0.05)

Table 3.5. Mean correlation results from the three sampling sites at Alexandra Fiord, Ellesmere Island. The mean correlation technique (Briffa and Jones 1992) indicates the climate signal strength present in the growth and reproductive chronologies (see Chapter 2). Chronologies cover a common time interval selected by the software program ARSTAN to maximize the number of stems included in the calculations. The common intervals are shorter than those reported in Tables 3.3 and 3.6. AGI = annual growth increment; Leaf = number of leaves; Bud = number of flower buds; Ped = number of flower peduncles.

	Lowland				Bench				Dome			
	AGI	Leaf	Bud	Ped	AGI	Leaf	Bud	Ped	AGI	Leaf	Bud	Ped
Common interval	1952-1992	1952-1992	1960-1994	1966-1994	1957-1995	1957-1995	1957-1994	1971-1995	1965-1992	1965-1992	1967-1992	1964-1994
# of Plants	10	10	10	10	13	13	12	11	10	10	10	6
# of Stems	34	34	31	25	36	36	28	21	24	24	24	13
\bar{r}_{br}	0.01	0.01	0.01	0.03	0.05	0.03	0.01	0.02	0.05	0.03	0.01	0.02
$1 - \bar{r}_{wi}$	0.93	0.96	0.97	0.76	0.89	0.95	0.99	0.99	0.93	0.90	0.93	0.97

\bar{r}_{br} is the between plant signal. It is similar to the fractional variance component for between plants.

$1 - \bar{r}_{wi}$ is the within-plant noise. It is similar to the fractional variance component for within plants.

relatively weak when compared to tree-ring chronologies (Table 3.6). However, the SNR values were the largest for each of the master chronologies selected when compared with the other standardization methods attempted.

Mean sensitivity values and the standard deviation of the mean provide an estimate of the sensitivity of the measured growth or reproductive parameter to climatic conditions (Fritts 1976) (Table 3.6). In general, high mean sensitivity and standard deviation values and low first-order auto-correlation values are indicative of high inter-annual variability and sensitivity to yearly climate conditions (Case and MacDonald 1995; Fritts and Shatz 1975). Across the three sites, the chronologies for annual stem growth and annual production of leaves showed the lowest mean sensitivity and standard deviation values. In contrast, the chronologies for annual production of flower buds and flower peduncles had a mean sensitivity four to ten times greater than the growth chronologies at all sites. The first-order autocorrelation values were low across all sites and chronologies.

At the three sites at Alexandra Fiord, standard chronologies or mean value functions were constructed for each of the growth and vegetation chronologies (Figures 3.7., 3.8 and 3.9). A minimum sample depth of three stems was maintained for each chronology. At the Lowland and Bench sites, chronologies for annual growth increments and number of leaves showed high variability during the late nineteenth to early twentieth century, but this variability decreased throughout the rest of the twentieth century. The early variability in these chronologies may be an artifact of fewer stems extending backwards in time (Figure 3.10). In the standardized growth and reproduction chronologies, annual indices were based on a minimum of three stems. The chronologies for number of flower buds and number of flower peduncles from plants at the Lowland and Bench sites also showed high inter-annual variability, but for the entire length of the chronologies. The chronologies for annual growth increments and number of leaves from plants at the Dome site showed slightly more inter-annual variability throughout the twentieth century than either the Lowland or Bench chronologies. Similar to the Lowland and Bench reproductive chronologies, the chronologies for flower buds and number of flower peduncles at the Dome site were also highly variable in the twentieth century. It is difficult to make definitive statements regarding longer-term trends in any of the chronologies given the flexible cubic splines used to standardize them.

Table 3.6. Growth and reproductive standard chronology statistics (from standardized data) for *Cassiope tetragona* from the Lowland, Bench and Dome sampling sites at Alexandra Fjord, Ellesmere Island. AGI¹ = annual growth increment; Leaf² = number of leaves; Bud³ = number of flower buds; Ped³ = number of flower peduncles.

	Lowland				Bench				Dome			
	AGI ¹	Leaf ²	Bud ³	Ped ³	AGI ¹	Leaf ²	Bud ³	Ped ³	AGI ¹	Leaf ²	Bud ³	Ped ³
Chronology Length	1879-1996	1879-1996	1900-1996	1917-1996	1884-1996	1884-1996	1894-1996	1904-1996	1922-1996	1922-1996	1922-1996	1931-1996
Mean	0.978	0.988	0.753	0.816	0.986	0.988	0.604	0.559	0.975	0.986	0.902	0.590
Standard Deviation	0.107	0.079	0.390	0.414	0.090	0.061	0.673	0.582	0.117	0.083	2.858	1.077
Mean Sensitivity	0.123	0.084	0.565	0.632	0.093	0.065	0.798	0.806	0.145	0.101	0.809	1.178
1st-order Autocorrelation	-0.287	-0.280	0.268	0.020	-0.261	-0.177	0.390	0.215	-0.154	-0.038	0.061	-0.069
Signal to Noise Ratio	0.139	0.105	0.068	0.353	0.658	0.372	0.107	0.204	0.500	0.293	0.132	0.135

AGI¹ = annual growth increment estimates are measured in mm per year.

Leaf² = annual leaf production estimates are for four leaf rows on a stem.

Bud³ and Ped³ = estimates for annual production of flower buds and peduncles are for 2 of 4 leaf rows on a stem.

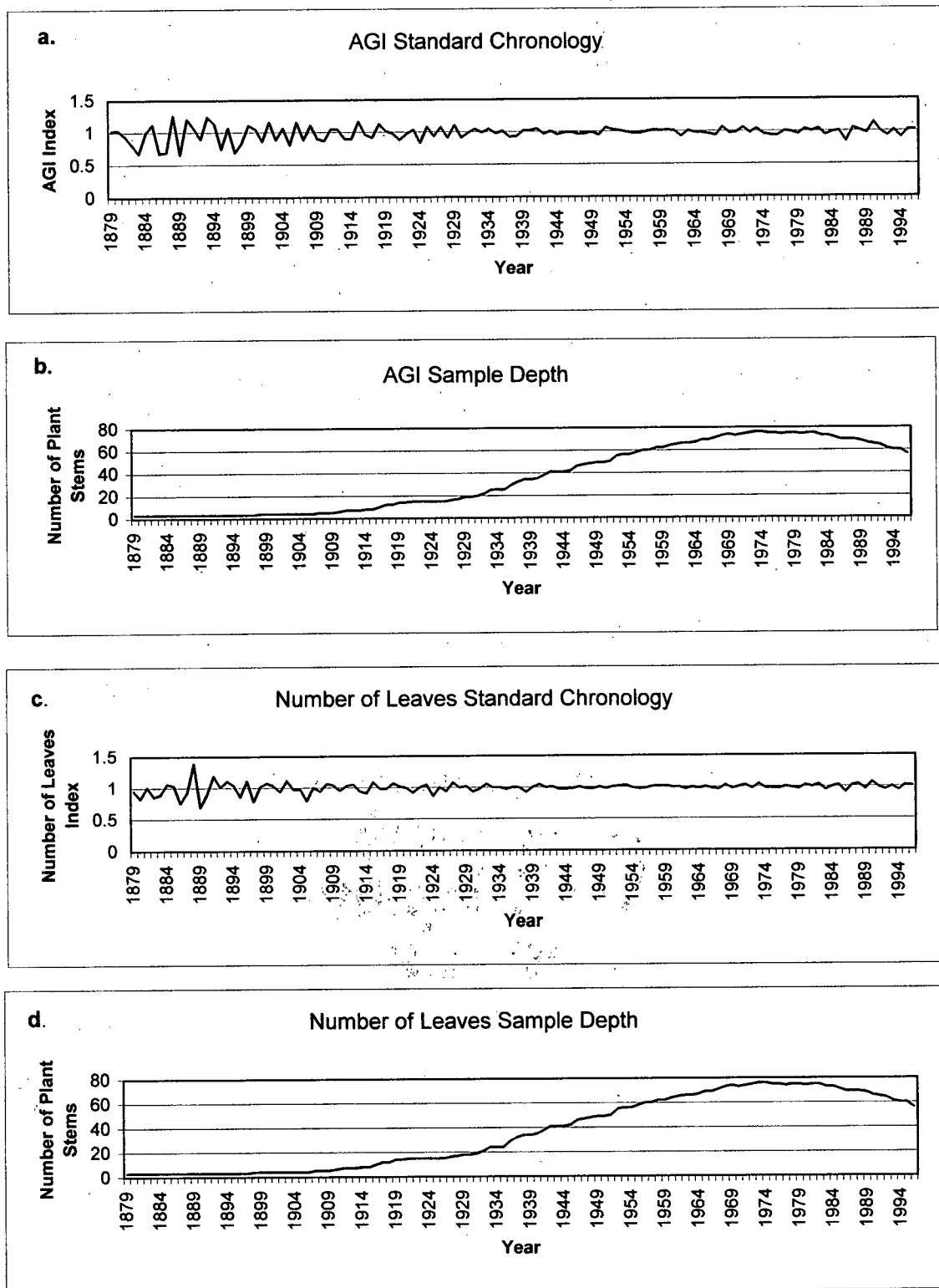


Figure 3.7 a. (a.) Standardized chronologies and (b.) sample depth for annual growth increment (AGI), and (c.) standardized chronologies and (d.) sample depth for annual production of leaves chronologies for the Lowland site, Alexandra Fiord, Ellesmere Island. Minimum number of stems measured was three.

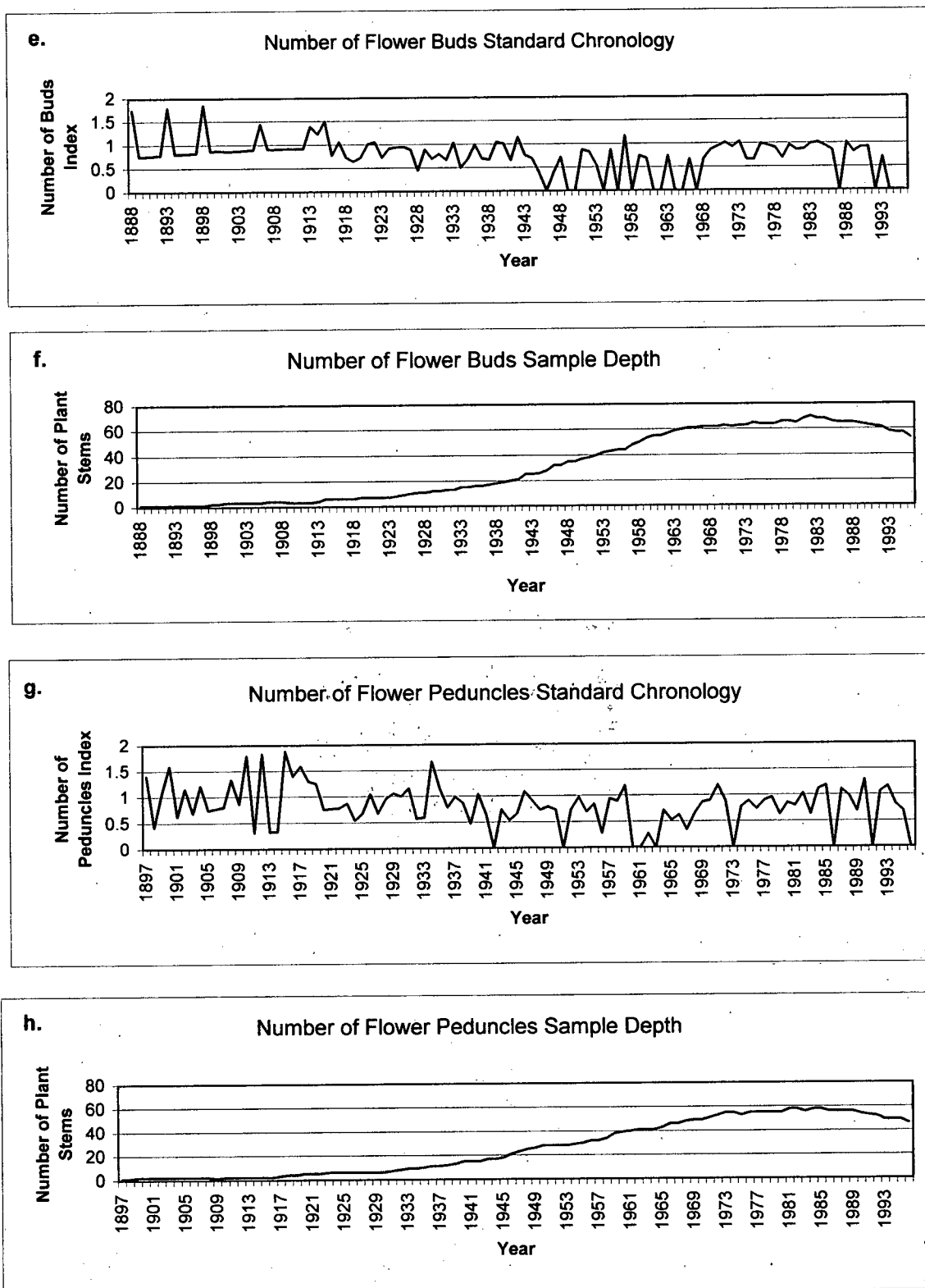


Figure 3.7 b. (e.) Standardized chronologies and (f.) sample depth for annual production of flower buds, and (g.) standardized chronologies and (h.) sample depth for annual production of flower peduncle chronologies for the Lowland site, Alexandra Fiord, Ellesmere Island. Minimum number of stems measured was three.

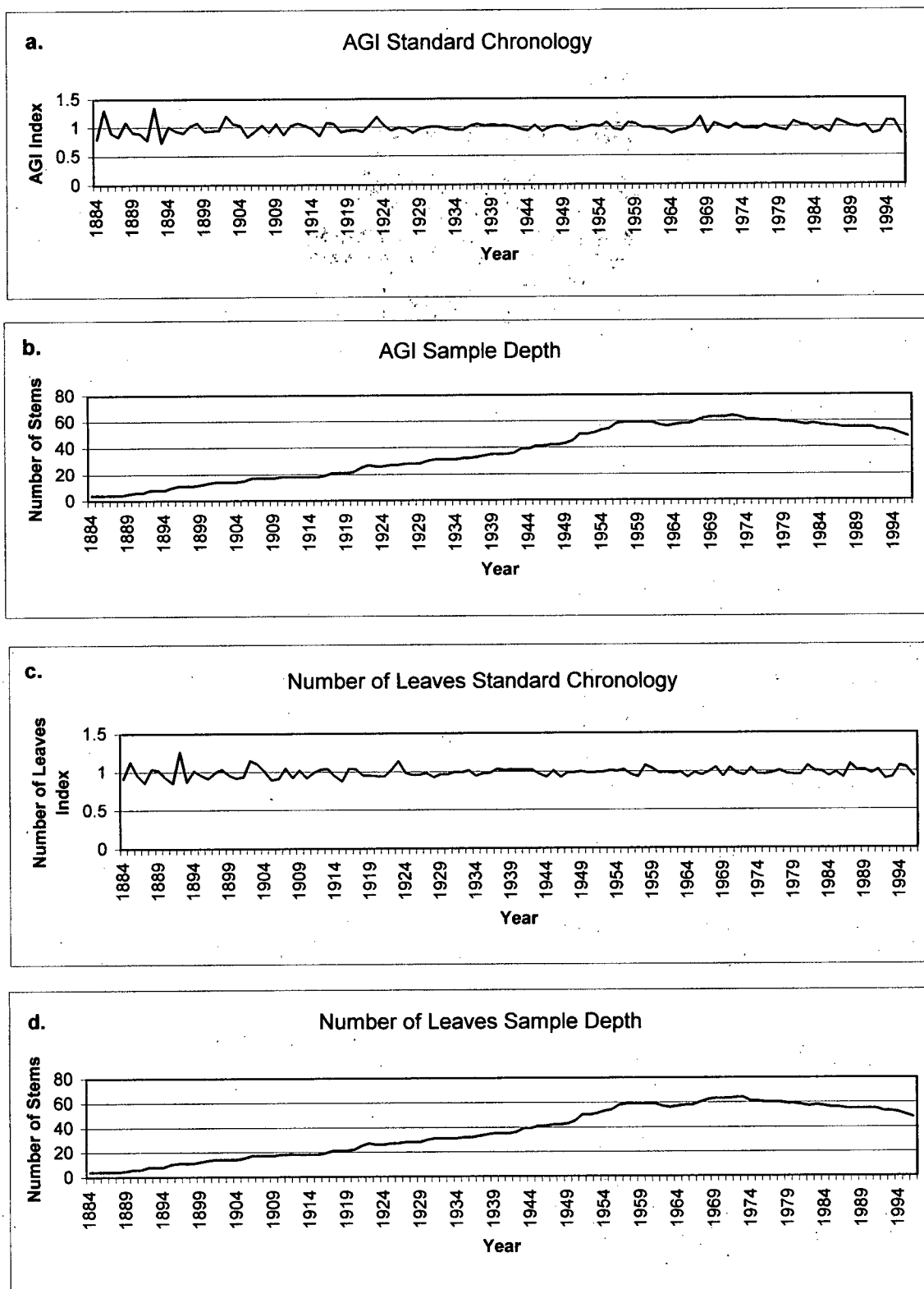


Figure 3.8 a. (a.) Standardized chronologies and (b.) sample depth for annual growth increment (AGI), and (c.) standardized chronologies and (d.) sample depth for annual production of leaves chronologies for the Bench site, Alexandra Fiord, Ellesmere Island. Minimum number of stems measured was three.

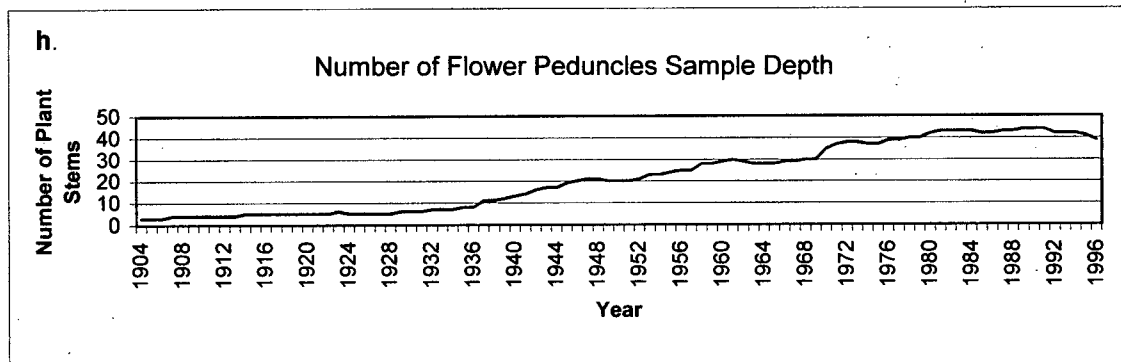
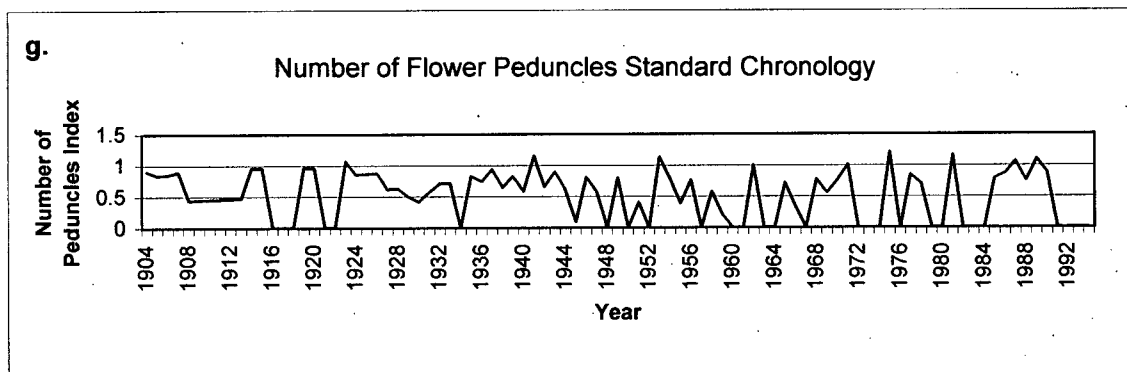
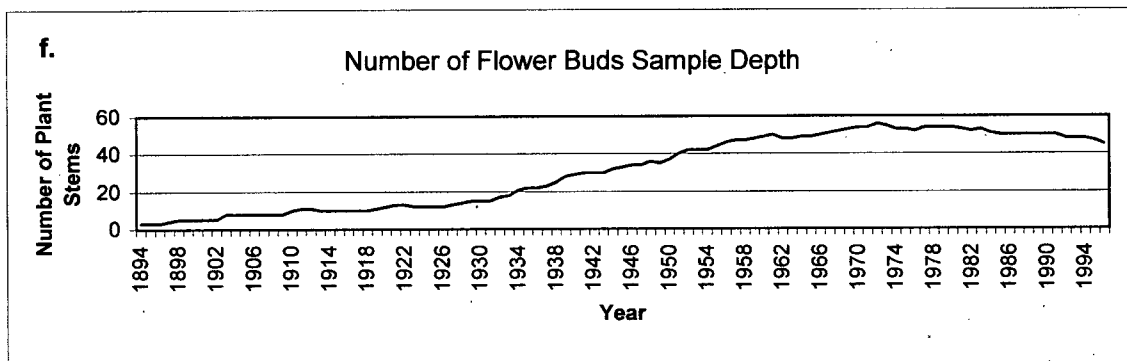
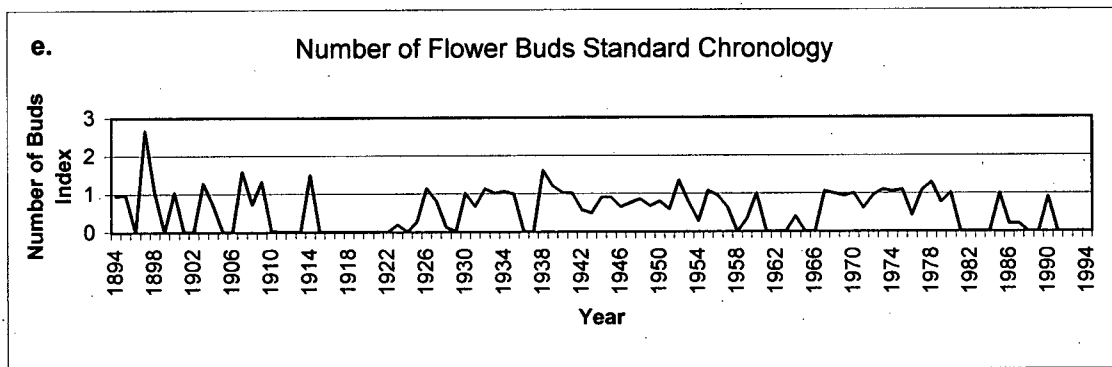


Figure 3.8 b. (e.) Standardized chronologies and (f.) sample depth for annual production of flower buds, and (g.) standardized chronologies and (h.) sample depth for annual production of flower peduncle chronologies for the Bench site, Alexandra Fiord, Ellesmere Island. Minimum number of stems measured was three.

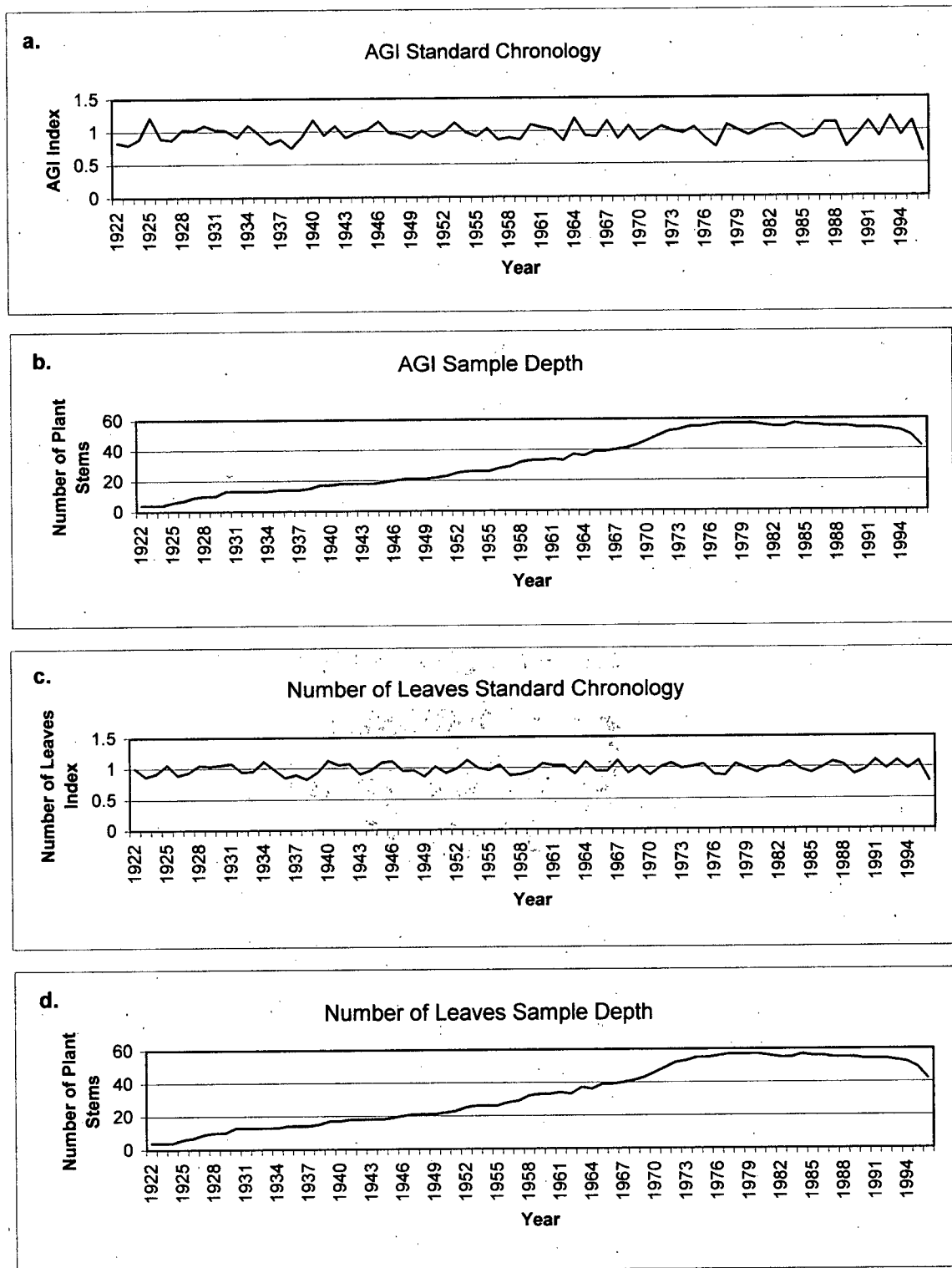


Figure 3.9 a. (a.) Standardized chronologies and (b.) sample depth for annual growth increment (AGI), and (c.) standardized chronologies and (d.) sample depth for annual production of leaves chronologies for the Dome site, Alexandra Fiord, Ellesmere Island. Minimum number of stems measured was three.

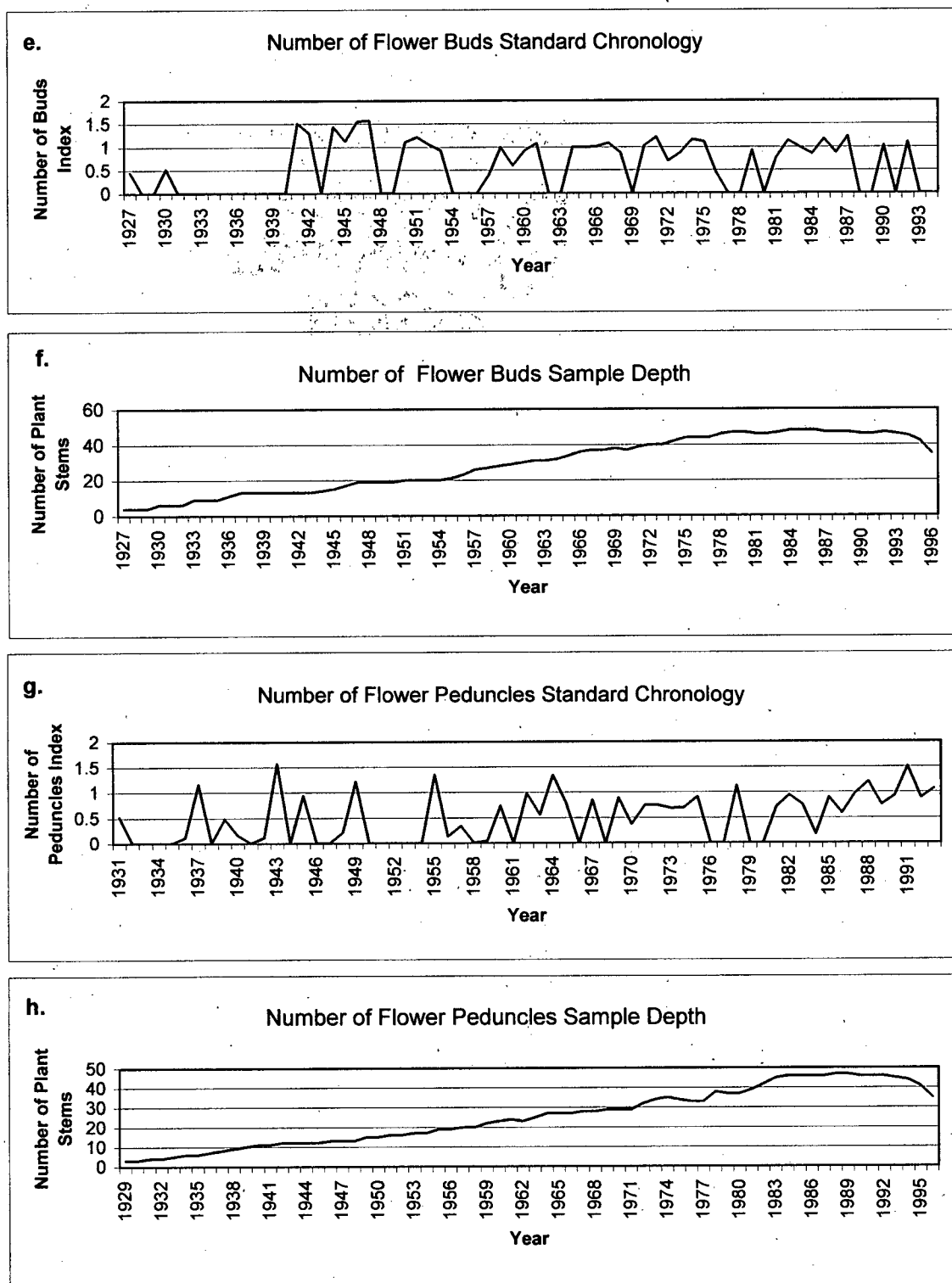


Figure 3.9 b. (e.) Standardized chronologies and (f.) sample depth for annual production of flower buds, and (g.) standardized chronologies and (h.) sample depth for annual production of flower peduncle chronologies for the Dome site, Alexandra Fiord, Ellesmere Island. Minimum number of stems measured was three.

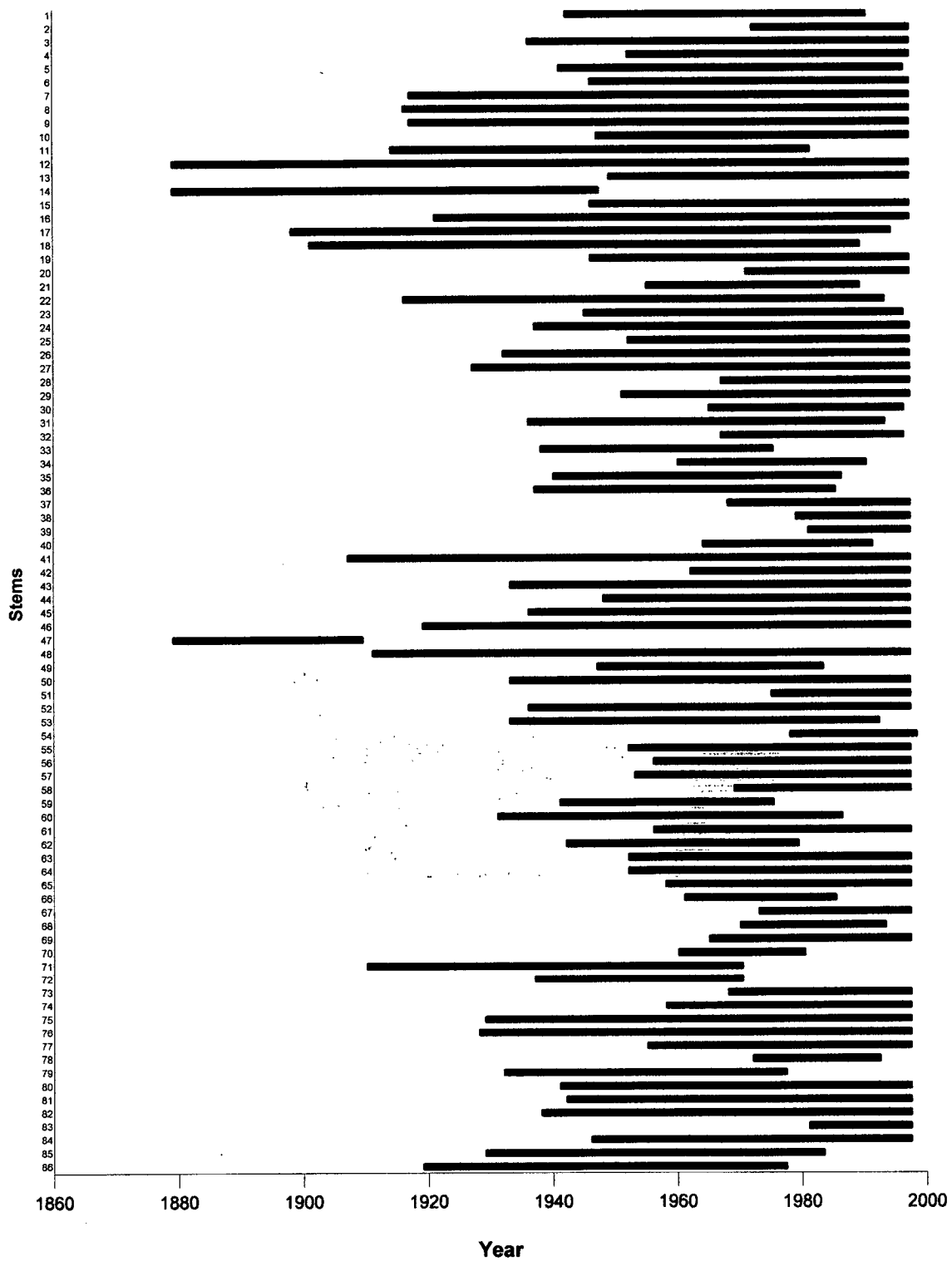


Figure 3.10. Example of stem depth from the Lowland site, Alexandra Fiord for the period, 1879-1996.

3.3.2. Correlation Analysis

At the Lowland, Bench and Dome sites, current year (year C) annual stem elongation was significantly and positively correlated with current year (year C) production of leaves ($P < 0.01$) (Table 3.7). In addition, current year (year C) stem elongation and production of leaves were positively correlated with current year (year C) production of flower buds and flower peduncles at the three sites. The annual production of flower peduncles for the current year (year C) was positively correlated with annual production of flower buds from the previous summer (year C-1). Finally, the annual production of flower buds in the previous year (year C-1) was positively correlated with current year flower bud production (year C). However, not all the correlations were significantly different from zero ($P > 0.05$).

Correlations between standardized growth and reproductive chronologies revealed little similarity among the three sites (Table 3.8). A significant and positive correlation was detected between the annual growth increment chronologies of the Lowland and Bench ($P < 0.05$). In addition, a significant and positive correlation was present between the Lowland and Bench annual production of leaves chronologies ($P < 0.01$). There were no correlations between the reproductive chronologies among the three sites that were significantly different from zero ($P > 0.05$). However, comparisons of the three sites' chronologies for number of peduncles were positive.

3.3.3. Response Functions: Response of *Cassiope tetragona* to Climate

3.3.3.1. Coastal Station and Alexandra Fiord Chronologies, 1980-1996

Examination of the response function coefficients revealed a significant relationship between the chronology for the number of leaves at the Lowland site and July thawing degree days ($P < 0.05$). However, there were no other relationships between the two growth variables and air temperature (Figures 3.11, 3.12, and 3.13), and thawing degree days (Figures 3.14, 3.15, and 3.16) at the three sites that were significantly different from zero ($P > 0.05$). Only the response function coefficients will be discussed in this study. The results of the correlation analysis are found in Appendices II and III. Despite the low number of significant coefficients,

Table 3.7. Spearman's rank correlation coefficients showing relations between values of the current (year C) and previous year (year C-1) of two growth and two reproductive chronologies from the Lowland, Bench and Dome sites. $n = 79$ years for the Lowland, $n = 92$ years for the Bench, and $n = 65$ years for the Dome. $n = 78$, $n = 91$, and $n = 64$ for the Lowland, Bench and Dome, respectively, when a variable from the previous year (year C-1) is included in the correlation.

Lowland	Annual Growth Increment		Number of Leaves		Number of Flower Buds		Number of Flower Peduncles	
	year C	year C-1	year C	year C-1	year C	year C-1	year C	year C-1
AGI (year C)	1.00							
Leaf (year C)	0.84 **		1.00					
Bud (year C)	0.14		0.16		1.00			
Peduncle (year C)	0.15		0.21		0.07		1.00	
AGI (year C-1)	-0.31 *	1.00	-0.22 *		-0.06		-0.04	
Leaf (year C-1)	-0.29 **	0.84 **	-0.28 **	1.00	-0.10		-0.03	
Bud (year C-1)	0.09	0.12	0.02	0.17	0.20	1.00	0.22 *	
Peduncle (year C-1)	0.00	0.13	-0.04	0.21 *	0.11	0.08	0.12	1.00

Bench	Annual Growth Increment		Number of Leaves		Number of Flower Buds		Number of Flower Peduncles	
	year C	year C-1	year C	year C-1	year C	year C-1	year C	year C-1
AGI (year C)	1.00							
Leaf (year C)	0.93 **		1.00					
Bud (year C)	0.09		0.06		1.00			
Peduncle (year C)	0.11		0.07		0.11		1.00	
AGI (year C-1)	0.01	1.00	-0.02		0.02		0.02	
Leaf (year C-1)	-0.02	0.93 **	-0.06	1.00	0.07		-0.01	
Bud (year C-1)	-0.10	0.08	-0.08	0.05	0.41 *	1.00	0.15	
Peduncle (year C-1)	-0.06	0.10	-0.11	0.06	0.03	0.09	0.13	1.00

Dome	Annual Growth Increment		Number of Leaves		Number of Flower Buds		Number of Flower Peduncles	
	year C	year C-1	year C	year C-1	year C	year C-1	year C	year C-1
AGI (year C)	1.00							
Leaf (year C)	0.93 **		1.00					
Bud (year C)	0.17		0.24 *		1.00			
Peduncle (year C)	0.25 *		0.23		-0.09		1.00	
AGI (year C-1)	-0.20	1.00	-0.18		0.03		-0.22	
Leaf (year C-1)	-0.05	0.93 **	-0.06	1.00	0.07		-0.18	
Bud (year C-1)	0.25 *	0.13	0.26 *	0.20	0.33 **	1.00	0.09	
Peduncle (year C-1)	-0.07	0.23	-0.09	0.21	0.13	-0.11	0.01	1.00

* = $p < 0.05$, ** = $p < 0.01$.

Table 3.8. Spearman's rank correlation coefficients showing relations of the growth and reproductive variables between sites. $n = 75$ years for the annual growth increment, $n = 75$ years for number of leaves, $n = 70$ years for number of flower buds, and $n = 66$ years for number of flower peduncles.

Annual Growth Increment	Lowland AGI year C	Bench AGI year C	Dome AGI year C
Lowland AGI	1.00		
Bench AGI	0.19 *	1.00	
Dome AGI	0.07	-0.15	1.00

Number of Leaves	Lowland Leaves year C	Bench Leaves year C	Dome Leaves year C
Lowland Leaves	1.00		
Bench Leaves	0.29 **	1.00	
Dome Leaves	-0.04	-0.14	1.00

Number of Flower Buds	Lowland Buds year C	Bench Buds year C	Dome Buds year C
Lowland Buds	1.00		
Bench Buds	0.17	1.00	
Dome Buds	-0.13	0.05	1.00

Number of Flower Peduncles	Lowland Peds year C	Bench Peds year C	Dome Peds year C
Lowland Peduncles	1.00		
Bench Peduncles	0.17	1.00	
Dome Peduncles	0.14	0.10	1.00

* = $p < 0.10$, ** = $p < 0.05$.

Year C denotes current year values of the chronologies.

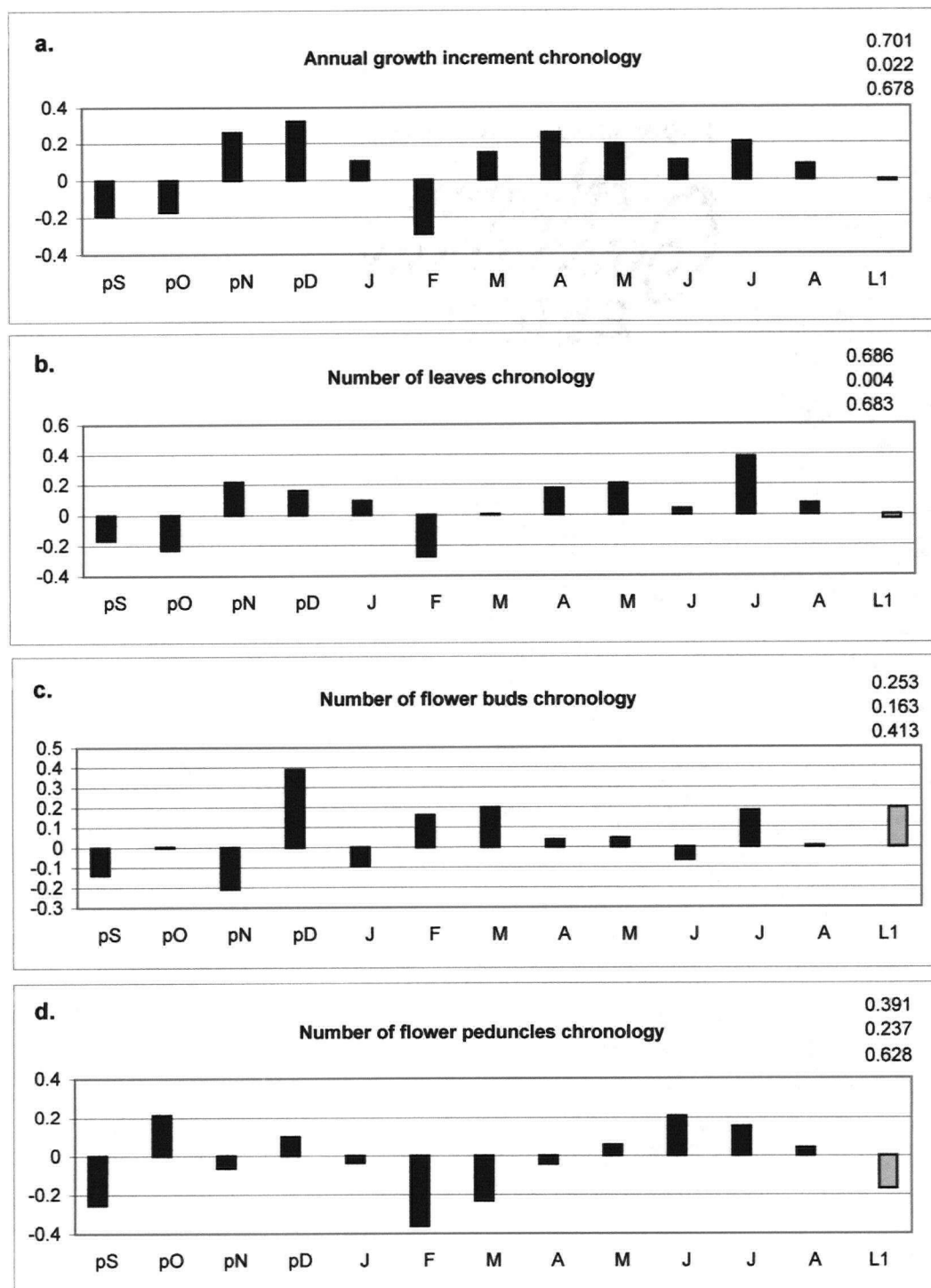


Figure 3.11: Response function coefficients relating growth and reproduction chronologies from the Lowland site to average monthly air temperature from the Coastal station, Alexandra Fiord from 1980-1996. The time period covered begins in the previous September (pS) and continues to the current August (A). L1 is the one year lag effect, denoted by the gray bar on the far right of the graphs. In the upper right hand corner of each graph three percentage of variance explained are given: amount of variance explained by climate alone (top), by previous growth or reproduction alone (middle), and by climate and previous growth or reproduction together (bottom). Temperature = white bars. Precipitation = black bars. Annual growth increment, number of leaves, number of flower buds and flower peduncles, $n = 17$. * $P < 0.05$.

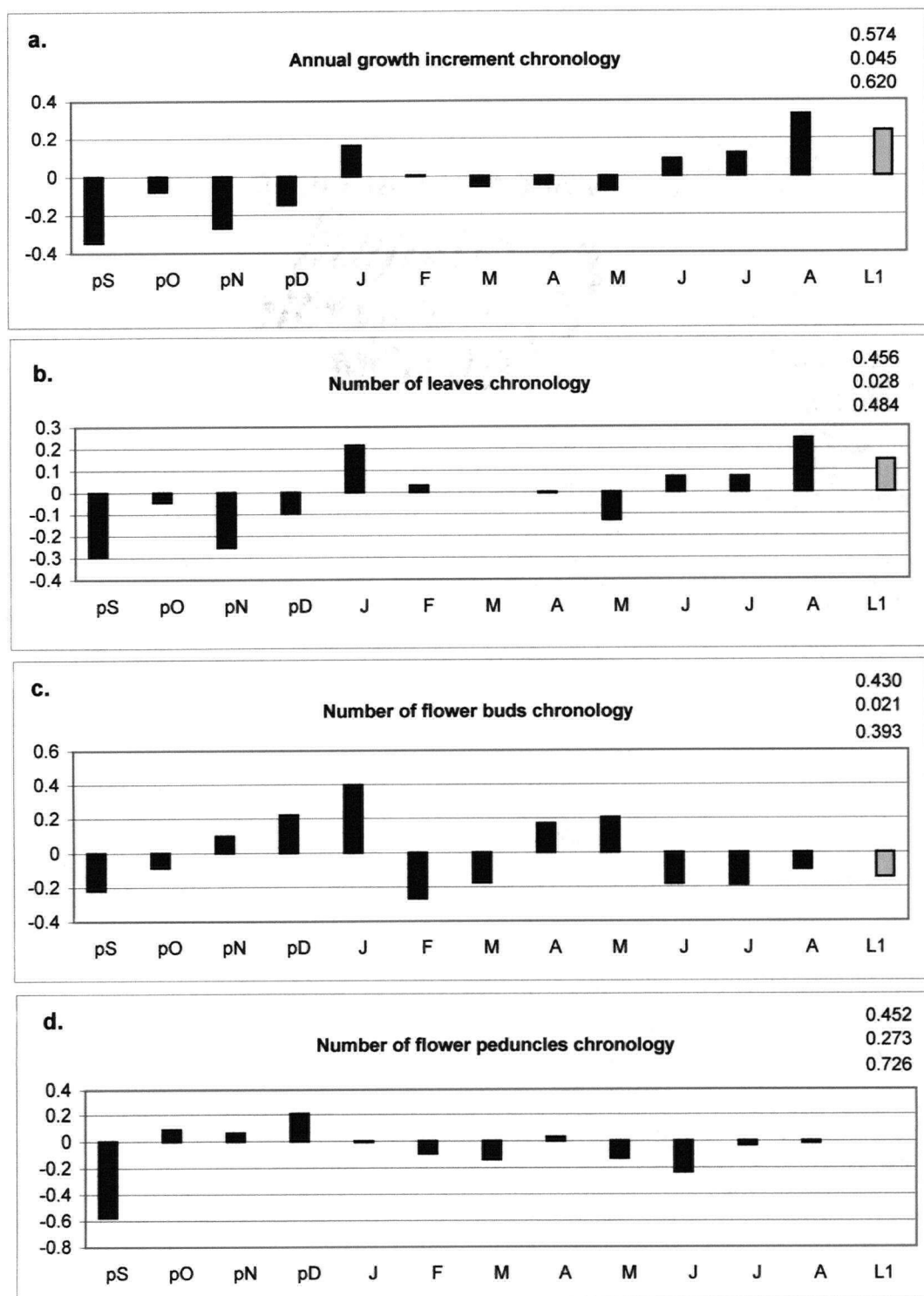


Figure 3.12. Response function coefficients relating growth and reproduction chronologies from the Bench site to average monthly air temperature from the Coastal station, Alexandra Fiord from 1980-1996. The time period covered begins in the previous September (pS) and continues to the current August (A). L1 is the one year lag effect, denoted by the gray bar on the far right of the graphs. In the upper right hand corner of each graph three percentage of variance explained are given: amount of variance explained by climate alone (top), by previous growth or reproduction alone (middle), and by climate and previous growth or reproduction together (bottom). Temperature = white bars. Precipitation = black bars. Annual growth increment, number of leaves, number of flower buds and flower peduncles, $n = 17$. * $P < 0.05$.

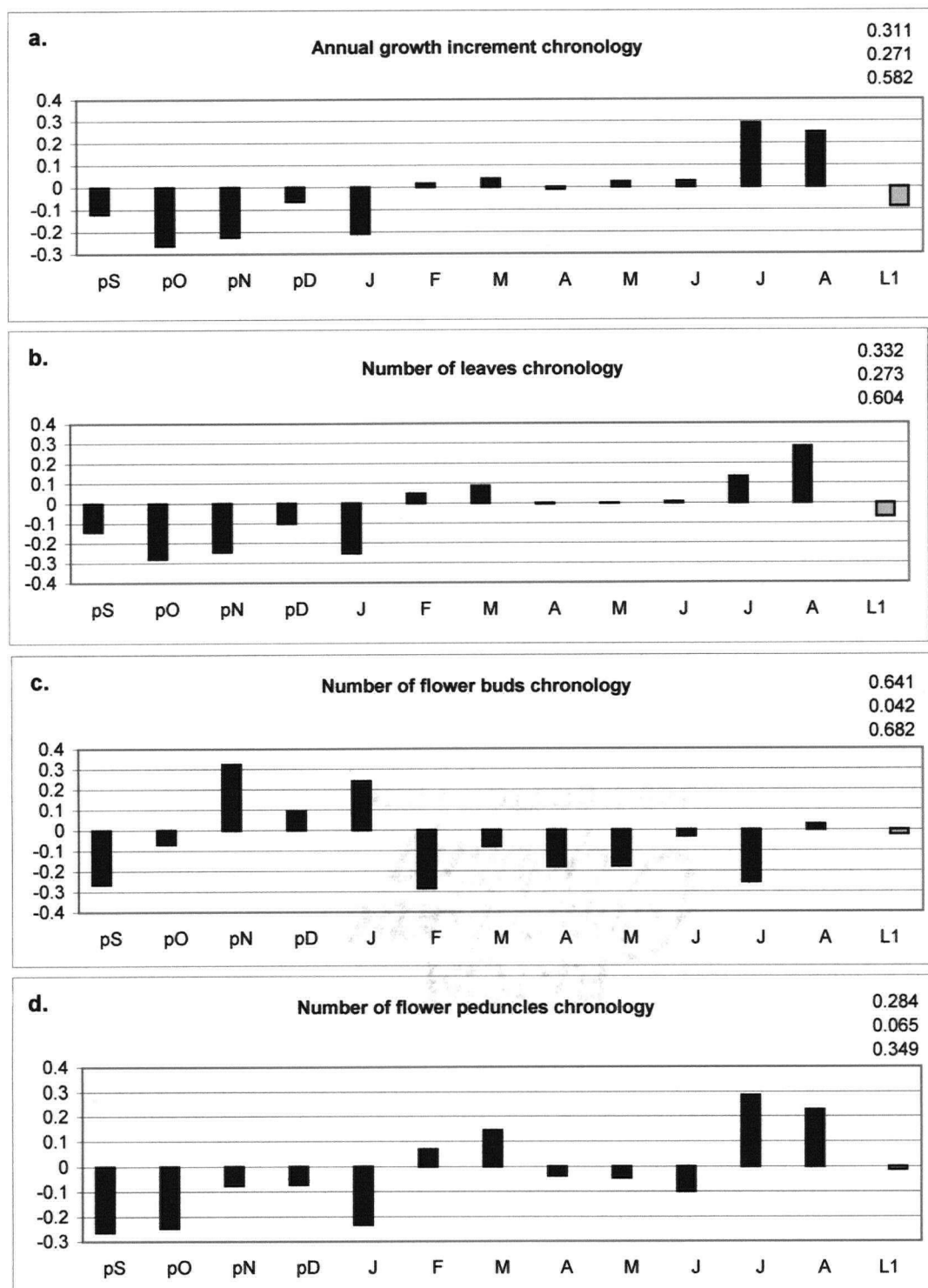


Figure 3.13. Response function coefficients relating growth and reproduction chronologies from the Dome site to average monthly air temperature from the Coastal station, Alexandra Fiord from 1980-1996. The time period covered begins in the previous September (pS) and continues to the current August (A). L1 is the one year lag effect, denoted by the gray bar on the far right of the graphs. In the upper right hand corner of each graph three percentage of variance explained are given: amount of variance explained by climate alone (top), by previous growth or reproduction alone (middle), and by climate and previous growth or reproduction together (bottom). Temperature = white bars. Precipitation = black bars. Annual growth increment, number of leaves, number of flower buds and flower peduncles, $n = 17$. * $P < 0.05$.

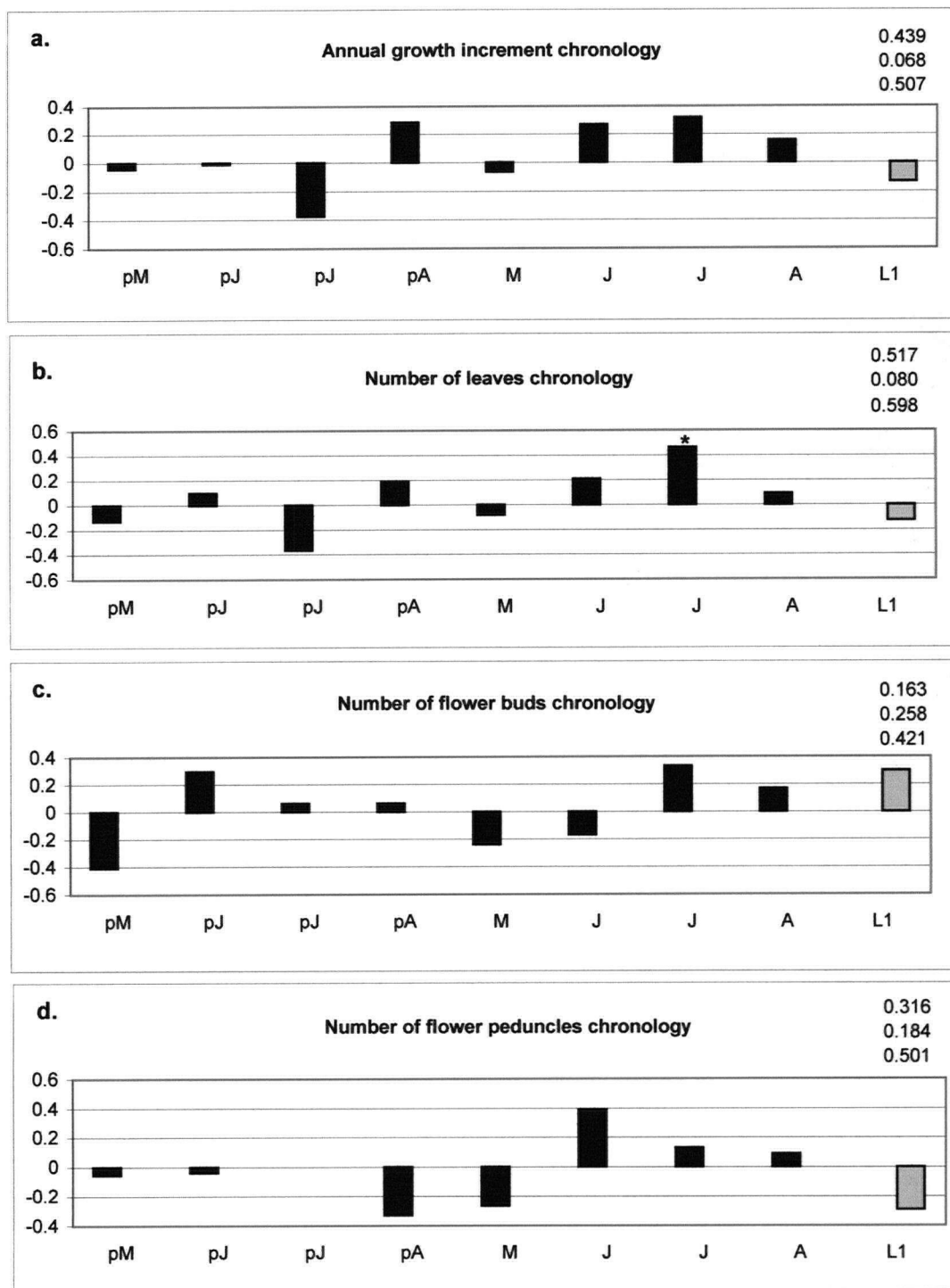


Figure 3.14. Response function coefficients relating growth and reproductive chronologies from the Lowland site to average monthly thawing degree days from the Coastal station, Alexandra Fiord from 1980-1996. The time period covers previous May (pM) to previous August (pA) and current May (M) to current August (A). L1 is the one year lag effect, denoted by the gray bar on the far right of the graphs. In the upper right hand corner of each graph three percentage of variance explained are given: amount of variance explained by climate alone (top), by previous growth or reproduction alone (middle), and by climate and previous growth or reproduction together (bottom). Temperature = white bars. Precipitation = black bars. Annual growth increment, number of leaves, number of flower buds and flower peduncles, $n = 17$. * $P < 0.05$.

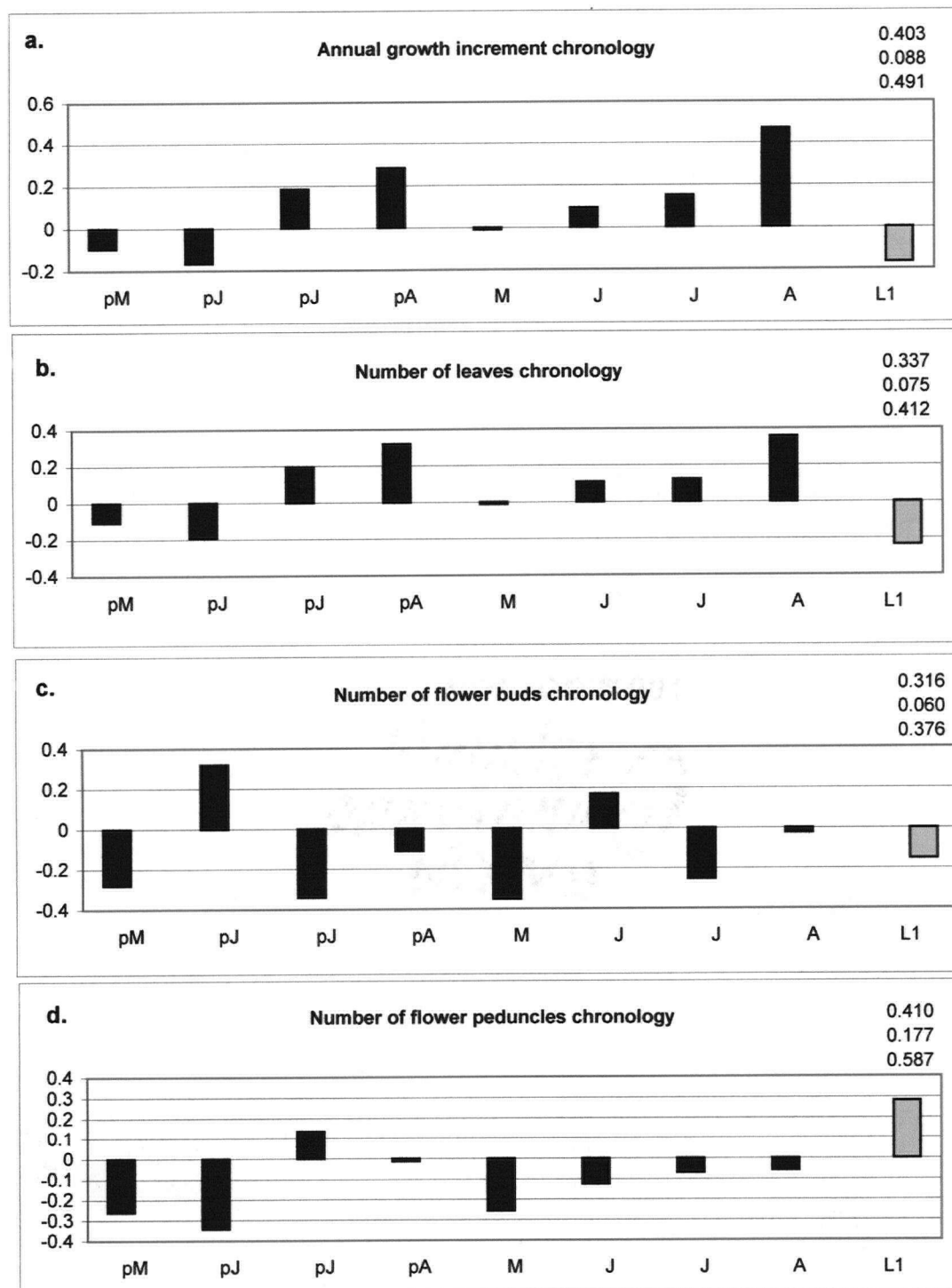


Figure 3.15. Response function coefficients relating growth and reproductive chronologies from the Bench site to average monthly thawing degree days from the Coastal station, Alexandra Fiord from 1980-1996. The time period covers previous May (pM) to previous August (pA) and current May (M) to current August (A). L1 is the one year lag effect, denoted by the gray bar on the far right of the graphs. In the upper right hand corner of each graph three percentage of variance explained are given: amount of variance explained by climate alone (top), by previous growth or reproduction alone (middle), and by climate and previous growth or reproduction together (bottom). Temperature = white bars. Precipitation = black bars. Annual growth increment, number of leaves, number of flower buds and flower peduncles, $n = 17$. * $P < 0.05$.

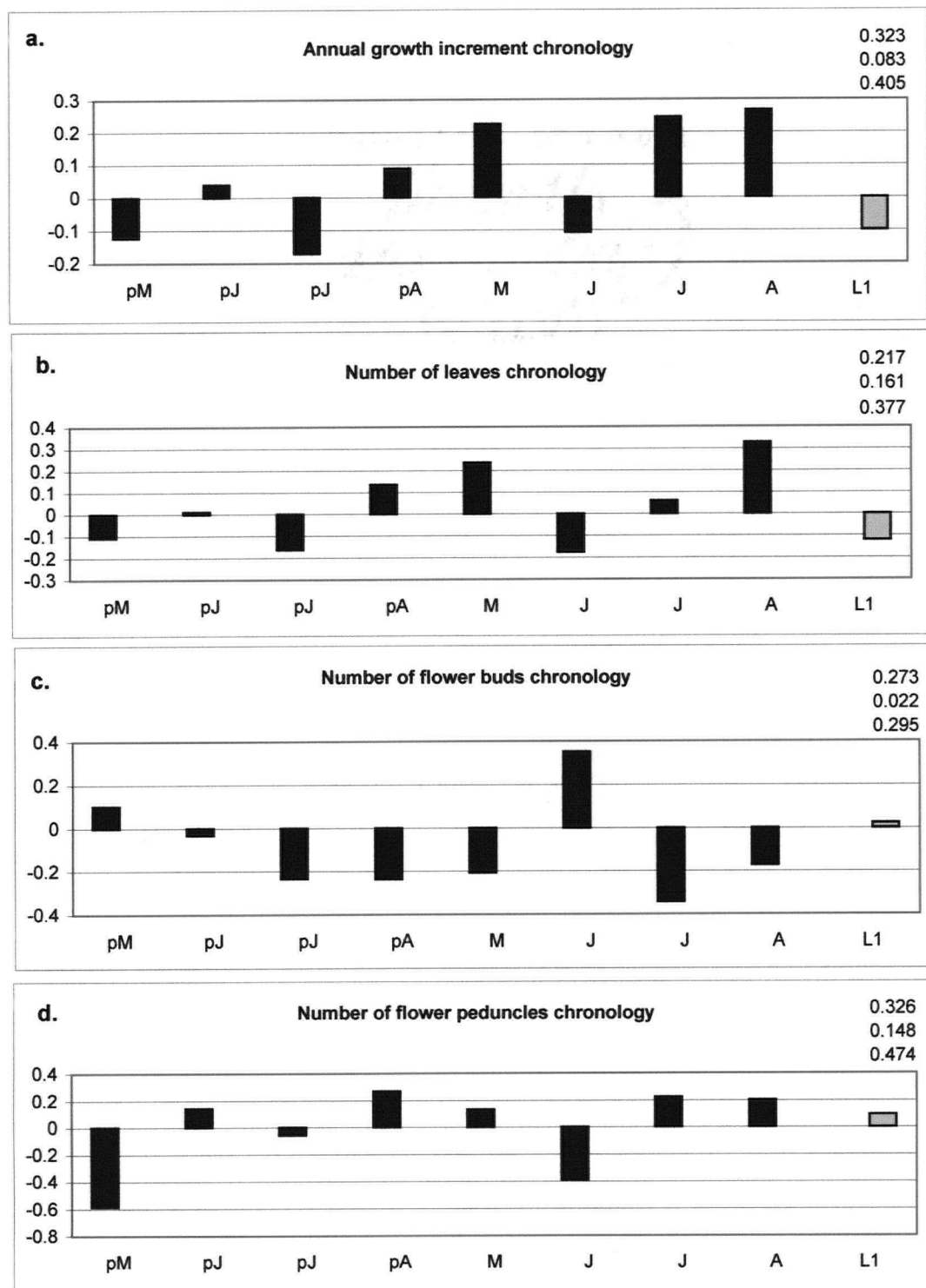


Figure 3.16. Response function coefficients relating growth and reproductive chronologies from the Dome site to average monthly thawing degree days from the Coastal station, Alexandra Fiord from 1980-1996. The time period covers previous May (pM) to previous August (pA) and current May (M) to current August (A). L1 is the one year lag effect, denoted by the gray bar on the far right of the graphs. In the upper right hand corner of each graph three percentage of variance explained are given: amount of variance explained by climate alone (top), by previous growth or reproduction alone (middle), and by climate and previous growth or reproduction together (bottom). Temperature = white bars. Precipitation = black bars. Annual growth increment, number of leaves, number of flower buds and flower peduncles, $n = 17$. * $P < 0.05$.

the relationships between the growth chronologies at the three sites with average air temperature and monthly thawing degree days (mtdd) during the months of June, July and August were positive. Only the relationships between the Dome site's two growth chronologies and June thawing degree days were negative. In addition, one year of prior growth (or reproduction) was included in each model, but none of the coefficients were significant ($P > 0.05$). Average air temperature and monthly thawing degree days, plus prior growth, accounted for a moderate to moderately-high amount of variance in the annual stem growth (58-68% with air temperature; 40-51% with mtdd) and leaf production (48-68% with air temperature; 38-60% with mtdd) of *C. tetragona* at Alexandra Fiord for the period 1980-1996.

Response function models relating the two reproductive variables (annual production of flower buds and flower peduncles) with average air temperature (Figures 3.11, 3.12, and 3.13) and monthly thawing degree days (Figures 3.14, 3.15, and 3.16) revealed no coefficients at the three sites that were significantly different from zero ($P > 0.05$). The relationships between annual flower bud production and average summer air temperature and monthly thawing degree days at the three sites were not uniform. The response function coefficients relating the flower bud chronologies from the Bench and Dome sites with average air temperature in June, July and August were mostly negative. The relationships between the Lowland flower bud chronology and average air temperature during the same months were mixed. However, the relationships between the Lowland annual flower peduncle chronology and average air temperature and thawing degree days during the summer months were positive. Interestingly, the relationships were reversed for the Bench site chronology, just 250 metres upslope. At the Dome site, the chronology for flower peduncles exhibited a negative relationship with average air temperature and with monthly thawing degree days in early summer (June), but switched to a positive relationship in July and August. In addition to the climate variables, one year of previous growth (or reproduction) were included in all models, but they were found to be not significantly different from zero ($P > 0.05$). The amount of variance explained by the two climatic variables and previous growth in the flower bud production models (39-68% with air temperature; 30-42% with mtdd) and the flower peduncle production models (35-73% with air temperatures; 47-59% with mtdd) ranged from low to moderately high for the period 1980-1996.

3.3.3.3. Eureka H.A.W.S. and Alexandra Fiord Chronologies, 1948-1996

Examination of the response function coefficients for the Lowland site's two growth chronologies revealed significant and positive relationships with June and July (June only for leaf chronology) average air temperature and with January and April total precipitation ($P < 0.05$) (Figures 3.17, 3.18, and 3.19). At the Bench site, the two growth chronologies were positively and significantly related to current September and previous May average air temperatures ($P < 0.05$). The same growth chronologies were also positively related to January precipitation ($P < 0.05$). Although the relationships of the Dome site's two growth chronologies to temperature and precipitation were similar, no monthly coefficients were significantly different from zero ($P > 0.05$). Moderately high levels of variance were accounted for by temperature and precipitation variables, plus previous growth (or reproduction), in the Lowland and Bench annual growth increment (73-75%) and number of leaves (70-72%) chronologies. Less variance was accounted for by the climate variables and previous growth in the Dome annual growth increment (51%) and annual production of leaves (48%) chronologies.

At the Lowland site, annual flower peduncle production was negatively and significantly related to April average air temperature, and positively and significantly related to June total precipitation ($P < 0.05$). The relationships between the Lowland site's two reproductive chronologies and summer temperature were weakly positive for three out of five summer months (May-September). At the Bench site, annual production of flower buds was negatively and significantly related to previous August, and positively and significantly related to current April precipitation ($P < 0.05$). However, the Bench site's two reproductive chronologies were not significantly related to average air temperature during the summer months ($P > 0.05$). Finally, the Dome site's flower bud chronology was negatively and significantly related to air temperature in February and April ($P < 0.05$). The chronology was also significantly and negatively related to June precipitation ($P < 0.05$). Moderate to moderately high amounts of variance were accounted for by the climate variables and previous growth for the flower buds (52-74%) and flower peduncle (38-70%) chronologies. The results from the response function analyses using the Coastal station and Eureka H.A.W.S. data were used as a guide in the development of transfer functions to reconstruct past climate.

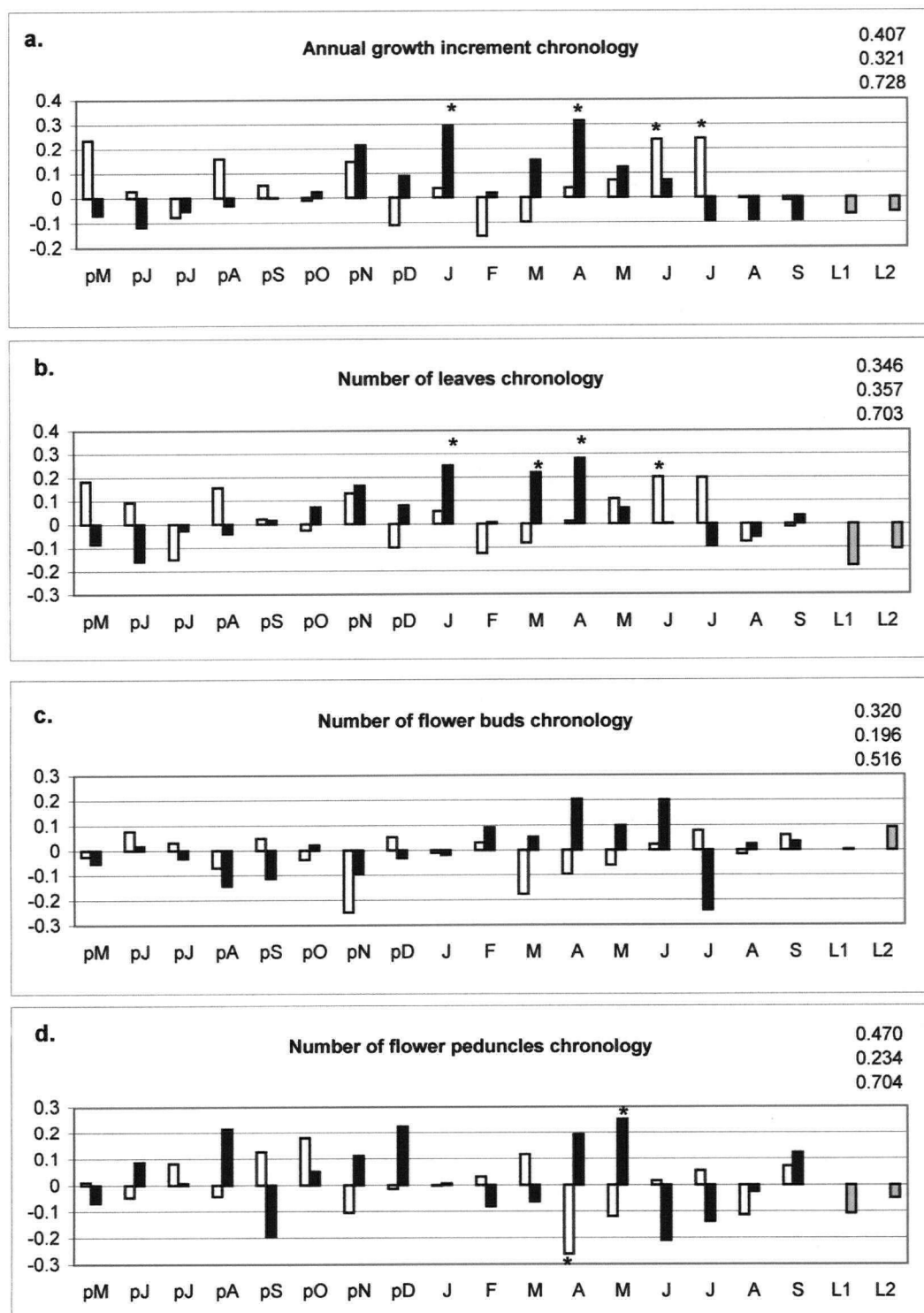


Figure 3.17. Response function coefficients relating growth and reproduction chronologies from the Lowland site to average monthly air temperature and total precipitation from Eureka H.A.W.S. from 1948-1996. The time period covered begins in the previous May (pM) and continues to the current September (S). L1 and L2 are the one and two year lag effects, denoted by the gray bars on the far right of the graphs. In the upper right hand corner of each graph three percentage of variance explained are given: amount of variance explained by climate alone (top), by previous growth or reproduction alone (middle), and by climate and previous growth or reproduction together (bottom). Temperature = white bars; Precipitation = black bars. $n = 49$. * $P < 0.05$.

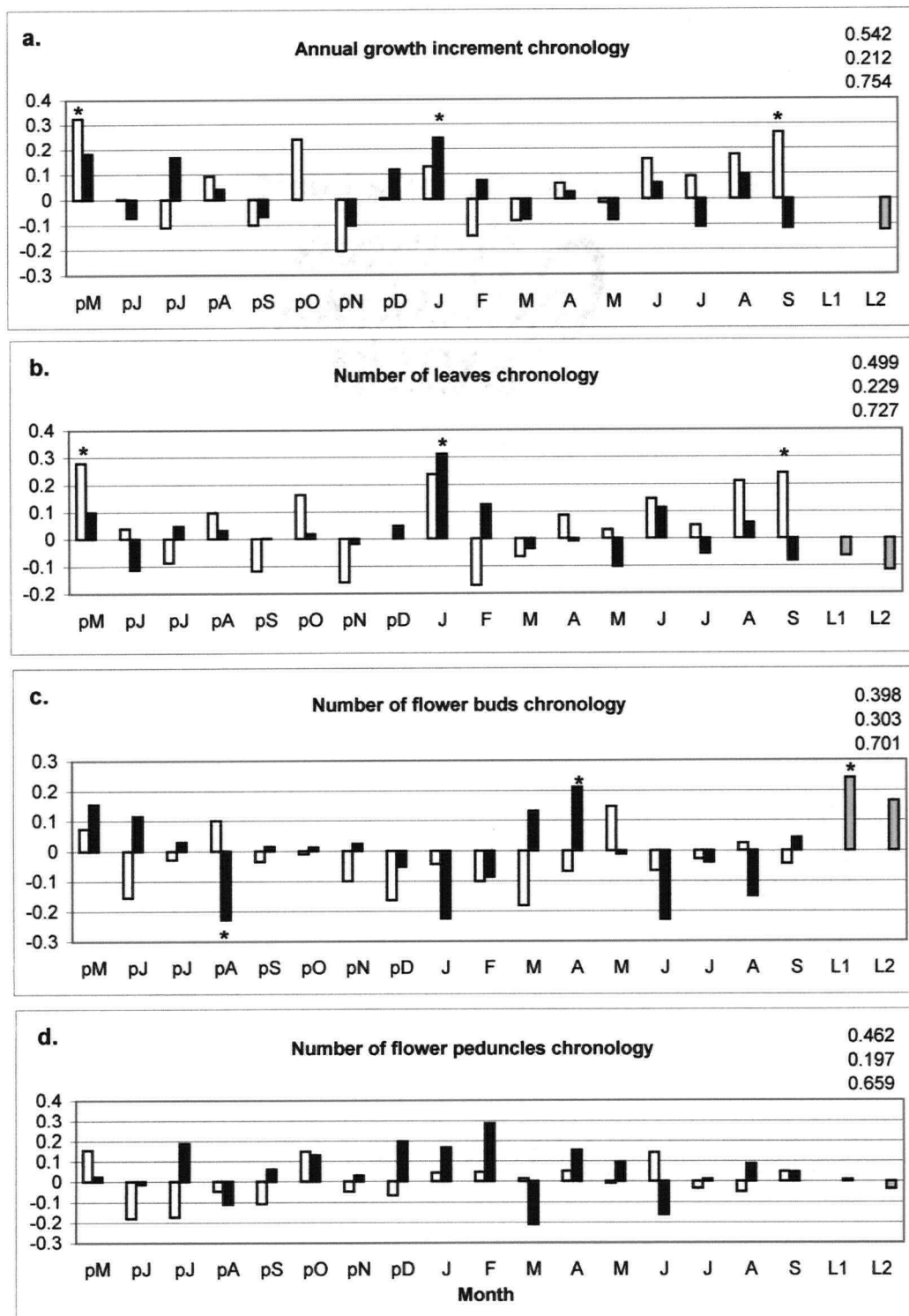


Figure 3.18. Response function coefficients relating growth and reproduction chronologies from the Bench site to average monthly air temperature and total precipitation from Eureka H.A.W.S. from 1948-1996. The time period covered begins in the previous May (pM) and continues to the current September (S). L1 and L2 are the one and two year lag effects, denoted by the gray bars on the far right of the graphs. In the upper right hand corner of each graph three percentage of variance explained are given: amount of variance explained by climate alone (top), by previous growth or reproduction alone (middle), and by climate and previous growth or reproduction together (bottom). Temperature = white bars. Precipitation = black bars. $n = 49$. * $P < 0.05$.

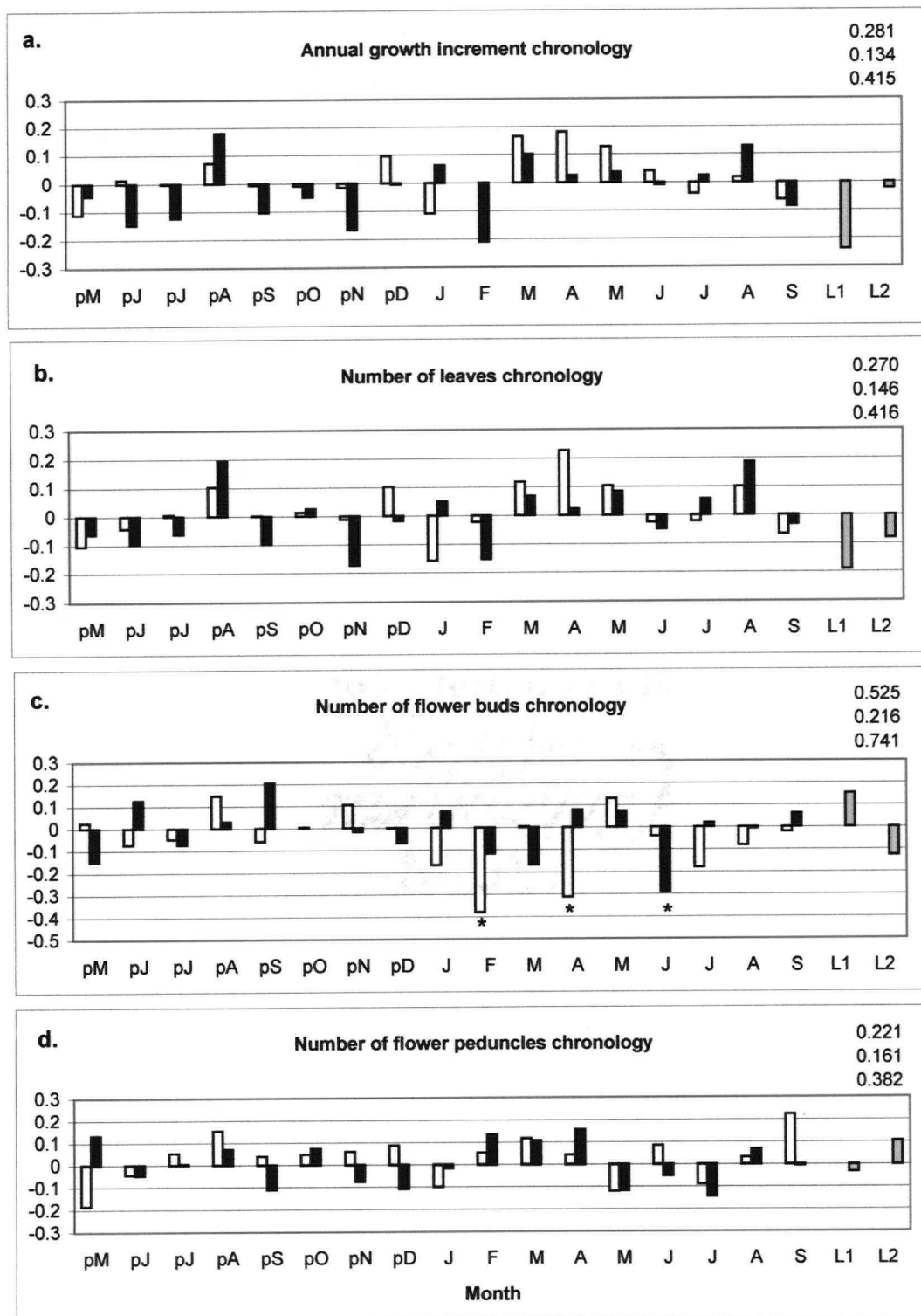


Figure 3.19. Response function coefficients relating growth and reproduction chronologies from the Dome site to average monthly air temperature and total precipitation from Eureka H.A.W.S. from 1948-1996. The time period covered begins in the previous May (pM) and continues to the current September (S). L1 and L2 are the one and two year lag effects, denoted by the gray bars on the far right of the graphs. In the upper right hand corner of each graph three percentage of variance explained are given: amount of variance explained by climate alone (top), by previous growth or reproduction alone (middle), and by climate and previous growth or reproduction together (bottom). Temperature = white bars. Precipitation = black bars. $n = 49$. $*P < 0.05$.

3.3.4. Transfer Functions – Reconstruction of Summer Temperature

3.3.4.1. Transfer Function and Coastal Station Data, 1980-1996

Standardized chronologies from the Lowland and Bench sites were used to produce reconstructions of summer temperature for Alexandra Fiord, Ellesmere Island. After examination of the response function coefficients using the Coastal station climate data to model growth and reproduction at Alexandra Fiord, it was decided to reconstruct average summer air temperature. Exploratory stepwise multiple regression analysis investigating single summer months (May, June, July, August), seasonal periods (May-August) and combinations of summer months (e.g., May-September) indicated that the estimation of average July-August temperature provided the best model based on the coefficient of determination, adjusted for loss of degrees of freedom (R^2_{adj}). Although many of the coefficients for the summer months in the response function analysis were not significantly different from zero ($P > 0.05$), it was decided the possibility of the inclusion of all growth and reproductive variables in the final climate reconstruction model was biologically possible. Furthermore, evidence of their utility in other transfer function models (Havström *et al.* 1995; Johnstone and Henry 1997) supported this decision. Using the standard techniques of Fritts (1976), a dendroclimatic reconstruction was carried out yielding a transfer function for July-August average air temperature (Table 3.9). This model of July-August average temperature explained 78% of the variance (adjusted for loss of degrees of freedom) for the period 1980-1996. Examination of the residuals showed assumptions regarding normality, independence and homogeneity of variance were not violated. As stated previously, cross-calibration and verification statistics were not carried out on this model due to the short duration of the climate record at the Coastal station (16 years). Verification of the transfer function would have required additional climate data from Alexandra Fiord which were not available. Johnstone and Henry (1997) also encountered this problem in their study. A comparison of the reconstructed and observed July-August average air temperature values showed that this model captured the annual variation in summer temperature for this short time period well (Figure 3.20).

Table 3.9. Climate transfer function for July-August average air temperature at Alexandra Fiord, Ellesmere Island based on growth and reproduction chronologies of *Cassiope tetragona* from the Lowland and Bench sites. Transfer function was developed for the time period, 1980-1995. $n = 16$.

Predictor Variables	Estimated Regression Coefficients	Standard Error	p-value	Multiple R	Multiple R ²	Adjusted Multiple R ²
Constant	-6.634	3.531	0.090	0.923	0.853	0.779
LowAGI1	13.636	3.647	0.004			
LowLeaf	9.905	2.009	0.001			
LowLeaf1	-16.851	5.675	0.014			
BenLeaf	4.169	1.556	0.023			
BenPed	-0.807	0.173	0.001			

*Low = Lowland site, Ben = Bench site, AGI = annual growth increment for year C, AGI1 = annual growth increment for year C+1, Leaf = number of leaves for year C, Leaf1 = number of leaves for year C+1, Ped = number of flower peduncles for year C.

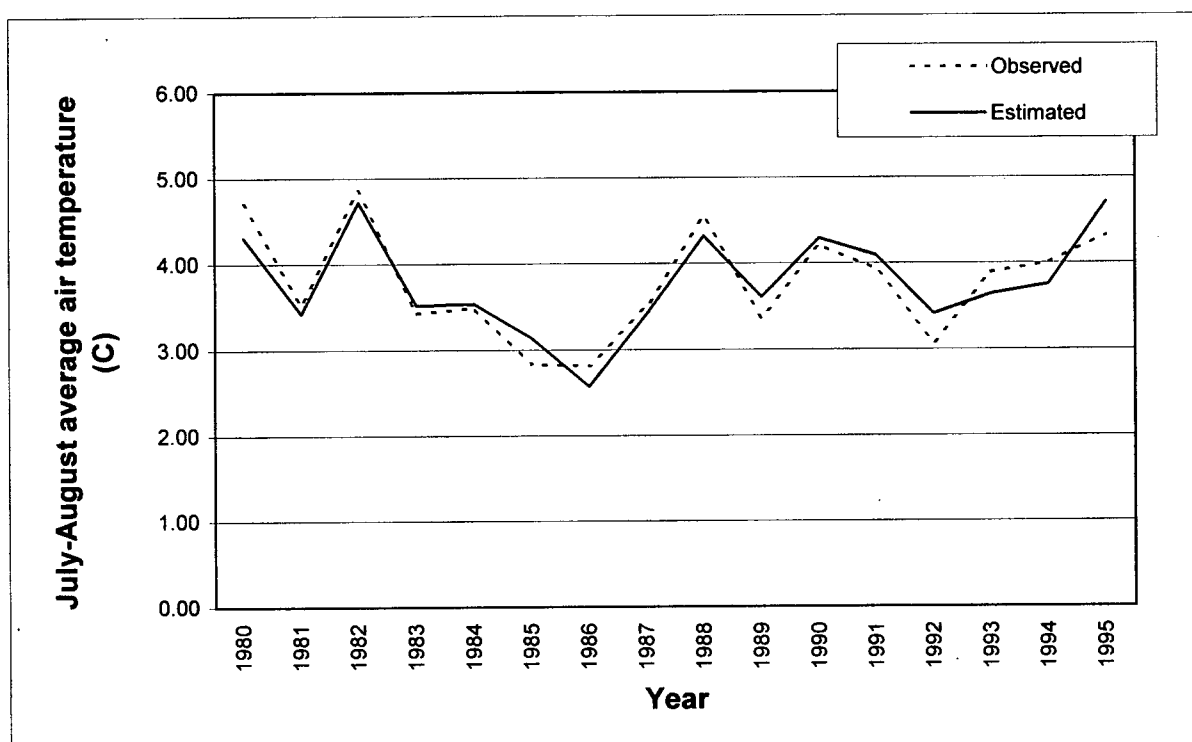


Figure 3.20. Comparison of observed and estimated July-August average air temperature at Alexandra Fiord, Ellesmere Island for the 1980-1995 calibration period.

3.3.4.2. Transfer Function and Eureka H.A.W.S. Data, 1948-1996

Following investigation of the response function coefficients using the Eureka H.A.W.S. climate data to model growth and reproduction at Alexandra Fiord, it was also decided to reconstruct average summer air temperature. Preliminary models predicting average air temperature for single summer months (May, June, July, August, September) and for combinations of summer months (e.g., June-August) for the period 1948-1996 were calibrated using stepwise multiple regression analysis (Figure 3.21). *Cassiope tetragona* was most highly correlated with average air temperature during August-September ($R^2_{adj} = 0.51$) for the period 1948-1996 (Table 3.10). Examination of the residuals showed that all assumptions of parametric statistics were met by the full model. Early and late calibration models accounted for 45% and 60% of the variance (adjusted for loss of degrees of freedom) in the temperature record, respectively (Table 3.11). The CE values (0.320; 0.280) while positive, indicated that only a small proportion of the variance in the observations was reduced by the model. The RE statistics (0.110; 0.340) were also positive, a sign that the model was better than using the average of the calibration period. However, the CE and RE values were not high when compared with tree-ring studies. The Pearson' product-moment correlation coefficients ($r = 0.70$; $r = 0.54$) were significant showing that the model adequately estimated the temporal patterns in the observations. Despite some low values, overall, the verification statistics indicated there was evidence of meaningful climatic information in the reconstruction (Fritts 1976; Fritts *et al.* 1979). Only the sign tests for the verification periods were not significant. Given that the early and late periods passed three out of four of the verification tests, the sub-period transfer function estimates of August-September average air temperature were considered relatively time stable. The model calibrated over the full 1948-1996 period was therefore also considered to be time stable and could be used to reconstruct summer air temperature prior to the time of instrumental data collection.

The reconstructed August-September air temperature model for 1948-1994 underestimated the instrumentally recorded data in particularly warm or cold August-September periods (Figure 3.22). In addition, there were several periods (i.e. 1958-1960, 1971-1974, 1988-1991) in the comparison when the estimated model smoothed over short periods of moderate inter-annual variability. Generally, the model followed the observed data from the Eureka H.A.W. S.

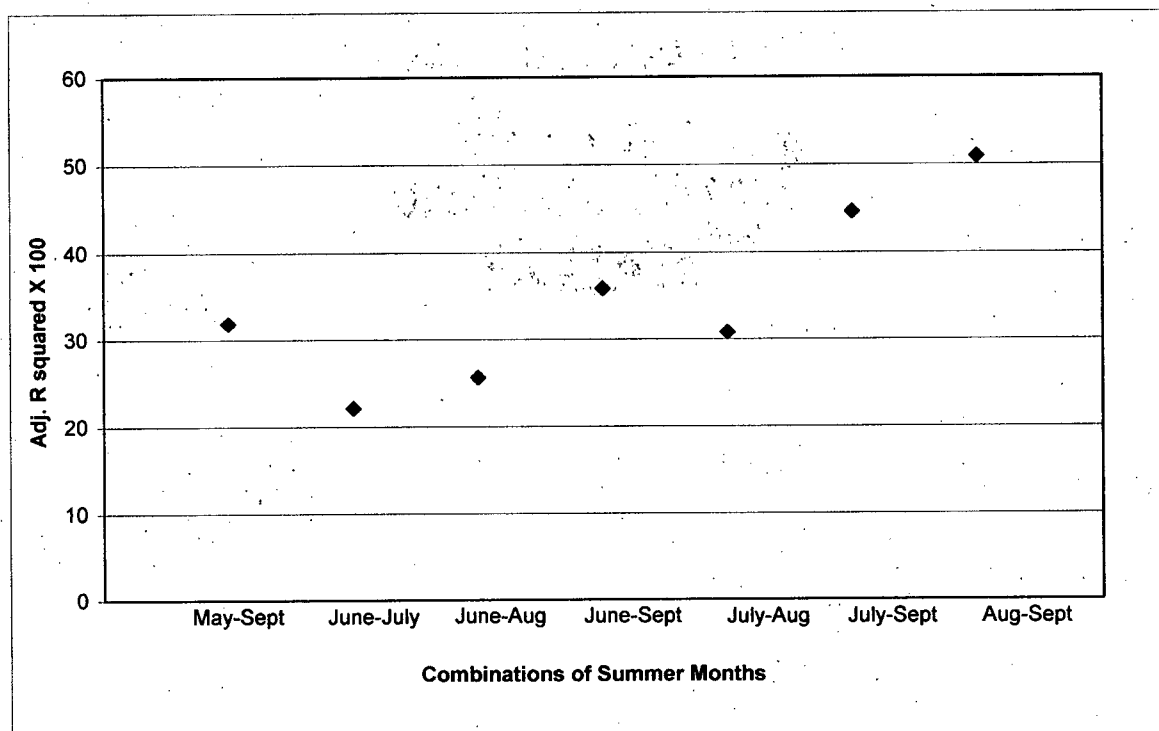


Figure 3.21. The adjusted coefficients of determination X 100 produced from growth and reproduction chronologies of *Cassiope tetragona* from the Lowland and Bench sites at Alexandra Fiord, Ellesmere Island. The potential models are based upon different combinations of average monthly summer air temperature from 1948-1996 from the Eureka H.A.W.S. on western Ellesmere Island. The R^2 adjusted was greatest for August-September average air temperature (51%). $n = 49$. Aug = August. Sept = September.

Table 3.10. Climate transfer function for August-September average air temperature at Alexandra Fiord, Ellesmere Island based on growth and reproduction chronologies of *Cassiope tetragona* from the Lowland and Bench sites. Transfer function was developed for the time period, 1948-1994. n = 47.

Predictor Variables	Estimated Regression Coefficients	Standard Error	p-value	Multiple R	Multiple R ²	Adjusted Multiple R ²
Constant	-37.921	7.581	0.000	0.771	0.594	0.509
LowAGI	8.742	3.406	0.014			
LowAGI3	-14.911	7.696	0.060			
LowLeaf3	37.210	12.191	0.004			
LowBud1	-0.653	0.364	0.081			
LowBud2	-1.004	0.400	0.016			
BenAGI	5.889	2.46	0.022			
BenBud2	1.064	0.337	0.003			
BenBud3	-1.168	0.351	0.002			

*Low = Lowland site, Ben = Bench site, AGI = annual growth increment for year C, AGI3 = annual growth increment for year C-1, Leaf3 = number of leaves for year C-1, Bud1 = number of flower buds for year C+1, Bud2 = number of flower buds for year C+2, Bud3 = number of flower buds for year C-1.

Table 3.11. Calibration and verification statistics for predicting August-September average air temperature from growth and reproduction chronologies of *Cassiope tetragona* from the Lowland and Bench sites at Alexandra Fiord, Ellesmere Island, Canada.

Model	Calibration Period	n	X	x	R	R ²	R ² adj
Early	1948-1980	33	24	7	0.755	0.571	0.450
Late	1964-1994	31	24	6	0.824	0.679	0.599
Full	1948-1994	47	24	8	0.771	0.594	0.509

Model	Verification Period	n	r	r ²	RE	CE	sign test (hit/miss)
Early	1981-1994	14	0.700**	0.490	0.110	0.320	9/4 ns
Late	1948-1963	16	0.540*	0.290	0.340	0.280	8/7 ns

* = $P < 0.05$, ** = $P < 0.01$, ns = not significant.

Note: n = sample size; X, initial number of candidate predictor variables in backward stepwise multiple regression; x, final number of predictor variables after elimination for insignificant variables by backward stepwise regression; R, multiple correlation coefficient; R², multiple coefficient of determination; R²adj, multiple coefficient of determination adjusted for loss of degrees of freedom; r, correlation coefficient; r², coefficient of determination; RE, reduction of error statistic; CE, coefficient of efficiency.

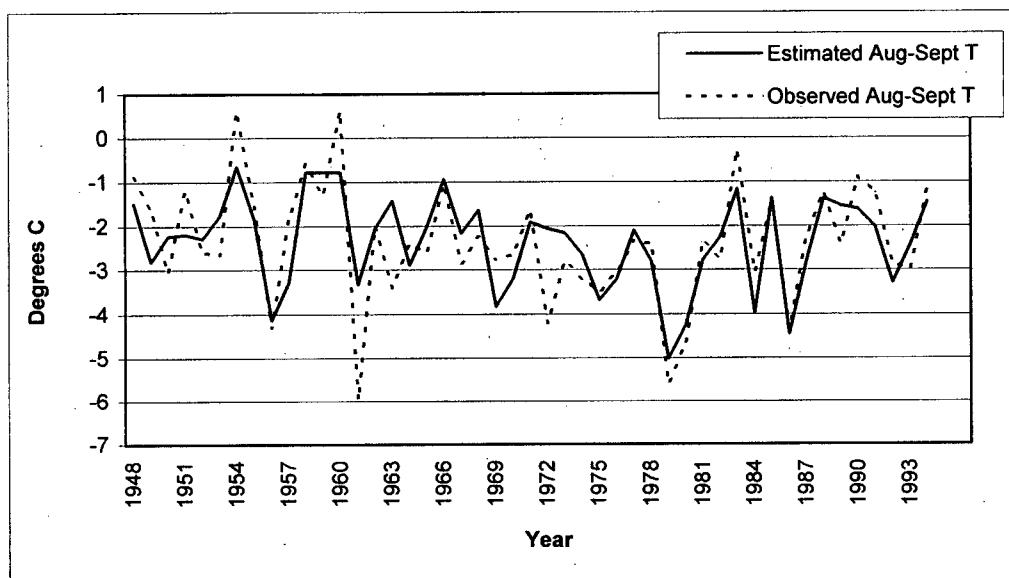


Figure 3.22. A comparison of observed (Eureka H.A.W.S.) and estimated average August-September air temperature for Alexandra Fiord, Ellesmere Island for the period 1948-1994.

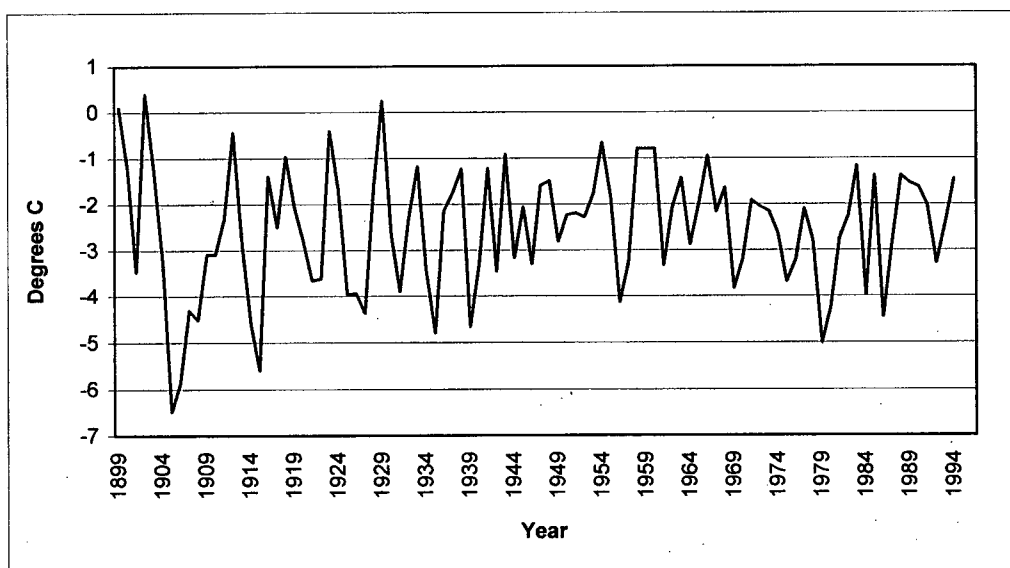


Figure 3.23. Reconstruction of annual August-September average air temperature from 1899-1994 for Alexandra Fiord, Ellesmere Island, Canada.

The reconstruction of August-September average air temperature for the period 1899 to 1994 was the longest proxy (95 years) yet developed for the Arctic using *C. tetragona* chronologies (Figure 3.23). However, the record was shortened by the shortest predictor chronology, the number of flower buds at the Lowland site (1899-1996). The final reconstruction was also necessarily shortened by lags and leads included in the reconstruction. Additional predictive power was gained by lagging behind or by leading ahead by one to two years of the climate data.

In the August-September average air temperature reconstruction, there were strong indications of high frequency variance, specifically rapidly alternating periods of warmth and cold at Alexandra Fiord in the early twentieth century (Figure 3.24). The five highest and six of the ten lowest single year temperature anomalies occurred within the first 30 years of the reconstructed temperature record (Table 3.12). Support for periods of colder conditions at Alexandra Fiord in the early part of the century was found in the 10-year (1905-1914; 1919-1928), 20-year (1903-1922) and 30-year (1905-1934) negative departure means (Table 3.12; Figure 3.24). Interspersed between the periods of cooler conditions in the early twentieth century were short warm spells. The brief warm periods were evident in the 10-year (1916-1925; 1929-1938) and 20-year (1916-1935) temperature anomalies (Table 3.12; Figure 3.24). The early twentieth century variability in summer air temperature was evident in the 5-year non-overlapping means in Figure 3.25 a. The 5-year and 10-year non-overlapping means calculated from the reconstructed August-September temperature departures were provided as an aid in recognition of directional tendencies in the data (Graybill and Shiyatov 1989). Emerging from the early twentieth century variability, a prolonged warm period began in the 1920s and lasted into the 1960s (Figure 3.25). Six of the warmest, reconstructed years occurred during this period (1929, 1943, 1954, 1958, 1959, 1960), as well as the warmest 30-year mean (1943-1972), 20-year mean (1947-1996) and 10-year mean (1958-1967 and 1946-1955) (Table 3.12; Figure 3.24; Figure 3.25 b). Influential inter-annual variability during the 1930s included colder summer temperatures in 1935 and 1939, as well as a low 10-year mean from 1931-1940 (Table 3.12). The impact of this variability was evident in the 5-year and 10-year non-overlapping means (Figure 3.25).

At the decadal scale, the warm period lasted until the early 1960s after which summers were colder (Figure 3.25). Colder summer temperatures in the 1960s and 1970s were supported

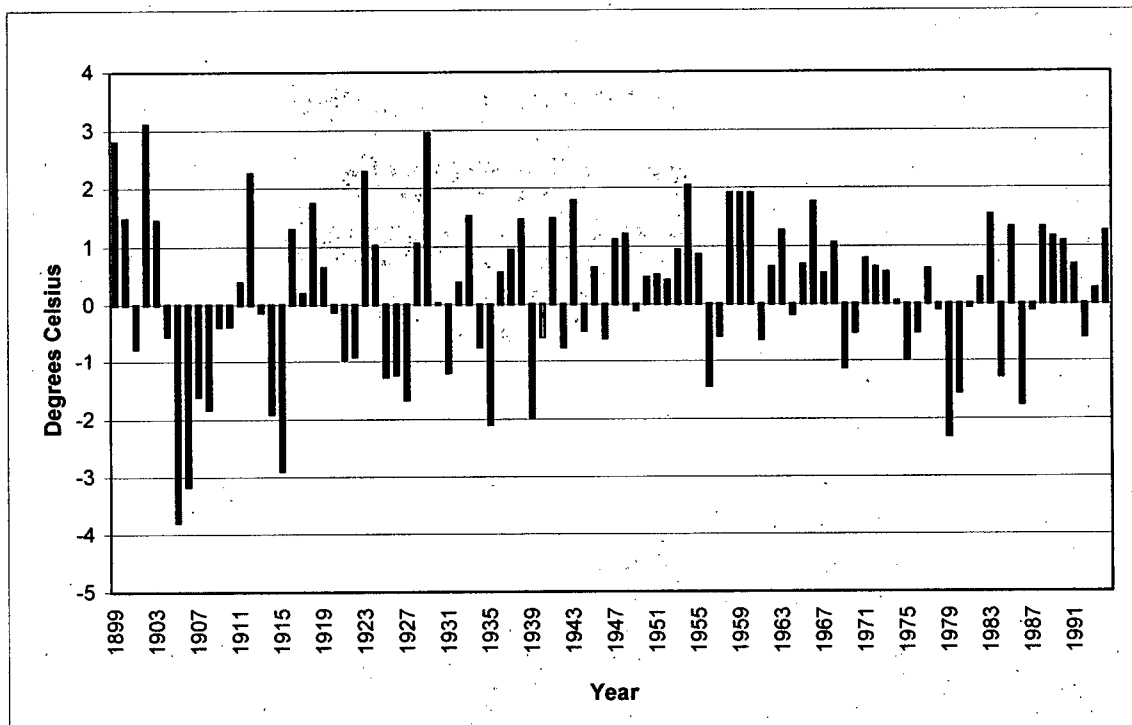


Figure 3.24. The reconstruction of August-September average air temperature departures for Alexandra Fiord, Ellesmere Island relative to the 1961-1990 mean from Eureka, H.A.W.S. on western Ellesmere Island.

Table 3.12. Largest temperature anomalies and trends for individual years, and for extreme mean values from among all 10-year, 20-year and 30-year non-overlapping periods. The temperatures are shown as anomalies with respect to the 1961-1990 mean calculated from the Eureka H.A.W.S. data set.

Individual Summers

Lowest		Highest	
Year	Anomaly (°C)	Year	Anomaly (°C)
1905	-3.80	1902	3.10
1906	-3.17	1929	2.95
1915	-2.89	1899	2.80
1979	-2.31	1912	2.26
1935	-2.10	1923	2.29
1939	-1.96	1954	2.04
1914	-1.91	1958	1.91
1908	-1.82	1959	1.91
1986	-1.75	1960	1.91
1927	-1.67	1943	1.79

10-year Mean Periods

Lowest		Highest	
Years	Anomaly (°C)	Years	Anomaly (°C)
1905-1914	-1.06	1958-1967	0.98
1975-1984	-0.40	1946-1955	0.68
1931-1940	-0.18	1985-1994	0.46
1919-1928	-0.12	1916-1925	0.39
		1929-1938	0.38

20 year Mean Periods

Lowest		Highest	
Years	Anomaly (°C)	Years	Anomaly (°C)
1903-1922	-0.54	1947-1966	0.73
1968-1987	-0.17	1916-1935	0.14

30-year Mean Periods

Lowest		Highest	
Years	Anomaly (°C)	Years	Anomaly (°C)
1905-1934	-0.28	1943-1972	0.58

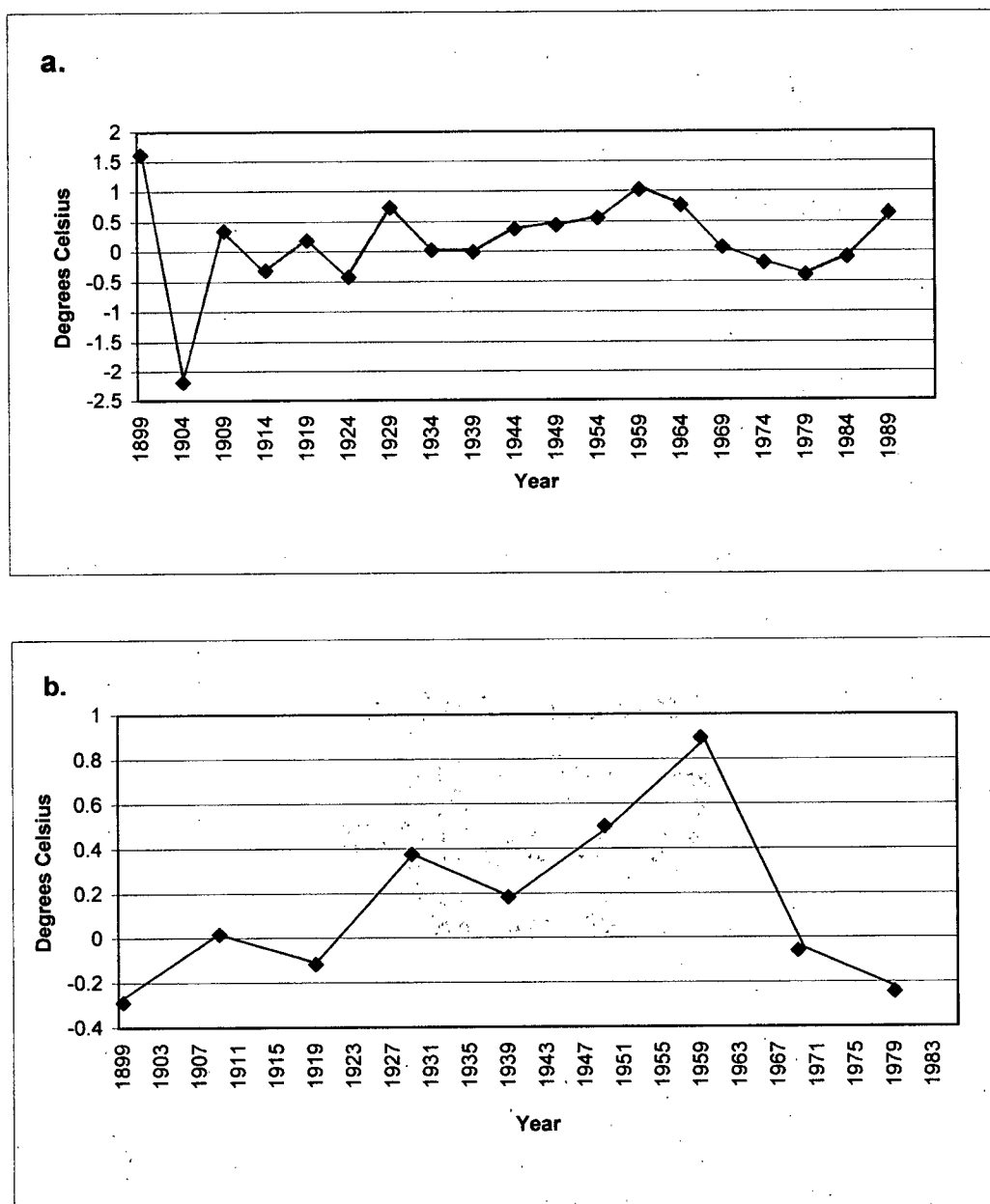


Figure 3.25. (a.) 5-year and (b.) 10-year non-overlapping means calculated from the reconstructed August-September average air temperature departures.

by the 10-year and 20-year means for the periods 1975-1984 and 1968-1987, respectively, as well as the single cold summer of 1979 (Table 3.12; Figure 3.24). Beginning in the 1980s, summer temperatures began to increase again at Alexandra Fiord (Figure 3.25 a). The mean of the 10-year departure from 1985-1994 signaled this increase. The period of warm temperatures was further supported by recent instrumental data from the Coastal and Meadow automated weather stations at Alexandra Fiord and Eureka, H.A.W.S. (Table 3.12; Figure 3.25). Of note, the reconstruction of August-September summer air temperatures for the most recent warm period did detect the single year temperature anomaly for 1986, the coldest summer on record at Alexandra Fiord. While the brevity of the climate reconstruction using *C. tetragona* precluded discussion of lower frequency variability, the proxy record did exhibit interesting high frequency variability over the last century, comparable with instrumental data and other proxy data sources.

3.4. Discussion

3.4.1. Critique of Methodology

3.4.1.1. Building *Cassiope tetragona* Chronologies

In this study, the longest reconstruction (1899-1994) of summer temperature for the Arctic using *Cassiope tetragona* as a proxy indicator was achieved through the use of traditional dendrochronological techniques. The results of this study provided further support for the measurement of internode length patterns to delimit annual growth increments in *C. tetragona*. The growth and reproductive chronologies developed for the Lowland, Bench and Dome sites were the longest for the Alexandra Fiord site and the Arctic as a whole. The chronologies in this study ranged from 30 to 82 years longer than the chronologies developed by Johnstone and Henry (1997) at Alexandra Fiord. The Lowland, Bench and Dome chronologies were 40 to almost 100 years longer than those constructed in studies by Callaghan *et al.* (1989) and Havström *et al.* (1995) in which the patterns of leaf-lengths were used to date annual growth. However, when compared to the lengths of tree-ring chronologies at or near the North American boreal forest-tundra ecotone, the *C. tetragona* chronologies were much shorter (e.g., Cropper

and Fritts 1981; Cropper 1982; Edwards and Dunwiddie 1985; Jacoby *et al.* 1985; Jacoby and D'Arrigo 1989; D'Arrigo and Jacoby 1993; Szeicz and MacDonald 1995; 1996).

The expansion of glacial ice, ice crusts and persistent snowbeds at Alexandra Fiord during the Little Ice Age, may have limited the lifespan of the *C. tetragona* plants at the site. In particular, it is hypothesized that the length of the chronologies at the highest site (Dome) were shortened significantly due to the recent glaciation of the site. Air photos from 1959 revealed Twin Glacier's western arm had retreated approximately 1.0 km south of the Dome sampling site. For the period 1959-1981, Bergsma *et al.* (1984) determined a glacial front retreat rate of 4.0 m/yr using air photo interpretation. Using the establishment dates of *Salix arctica*, Jones and Henry (2003) determined glacial retreat to be 6.9 m/yr for the same period. Increased rates of glacial retreat, between 7.6 to 11.2 m/yr, were recorded by Jones and Henry (2003) for the period 1986-1995. The delay between glacial retreat from the Dome and the establishment of *C. tetragona* plants may be attributed to colder conditions associated with the proximity of the glacial lobe and the elevation of the Dome, as well as the generally harsher environmental conditions of the site. Young, acidic soils, limited in development, as well as drier soil moisture conditions distinguish this upland site from the lowland of Alexandra Fiord (Batten and Svoboda 1994; Muc *et al.* 1994; Nams and Freedman 1987b).

3.4.1.2. Measurement and Cross-Dating

Overall, the measurement of the internode lengths, the counting of leaves and the identification and counting of in-place or missing buds and flower peduncles was accomplished without difficulty. Some questions remained as to the accuracy of some internode measurements due to unavoidable bends and curves in the stems. Another measurement problem included the use of branching stems to construct chronologies. While every effort was made to select stems which did not branch, often branching stems had to be included in the chronology building process in order to extend the chronologies sufficiently backward in time. The primary difficulty lay in measuring the distances between the internodes accurately as they transitioned from the main to the auxiliary stem. When the accuracy of the measurements was in doubt, measurement was terminated. Finally, due to the time-consuming nature of the measurement process, the stems were only re-measured when problems were detected (Fritts

1976). Despite these difficulties, it was easy to distinguish leaf scars along the entire length of most stems. When there was doubt as to whether scars were actually leaf scars or adventitious roots which had broken off, measurement was discontinued.

Cross-dating of *C. tetragona* stems proved to be time-consuming and tediously difficult when compared with the process of cross-dating tree-rings from many tree species. Skeleton-plotting was relied upon heavily to cross-date all stems and later, to verify the results of COFECHA. In this study, multiple stems with green leaves and leaf buds at their tips were found to have stopped growing one to two years prior to sampling. Johnstone (1995) also encountered this problem in her study. Thus when cross-dating supposedly "live" stems, it could not be assumed that the last annual increment measured corresponded to the last growing season. Johnstone and Henry (1997) also mentioned the possibility of dormancy in *C. tetragona* stem growth. In this study, no periods of arrested growth were detected through skeleton plotting in any mid-stem measurements. Whether these dating problems are characteristic of other populations of *C. tetragona* in the Arctic remains a question. However, it does emphasize the importance of cross-dating when developing chronologies for retrospective analysis as opposed to the common mistake of just "counting rings." A further problem which plagued the cross-dating process was the abundance of short stems of 30 years or less. It was necessary to include some of these short stems because, only the short stems cross-dated with the live plant chronologies in many cases.

In addition to using the skeleton-plot technique to cross-date *C. tetragona* stems, the software program COFECHA was used to verify the visual cross-dating and to detect errors (Holmes *et al.* 1986). COFECHA was designed to detect stand and regional scale variability that is common to many samples influenced by similar broad-scale climate factors. However, its use in this study was limited by the high levels of within- and among-plant variation in the stems. The dates of stems which were flagged as erroneous by the software program were checked carefully using skeleton plots, but the majority was found to be related to intra-plant noise rather than inaccurate dating. In the end, the skeleton-plot technique was the final determinant in cross-dating all stems.

3.4.2. Chronology Variability

High levels of intra-plant variability, or within-plant noise ($1 - \bar{r}_{wt}$), were evident in the Alexandra Fiord chronologies. In dendrochronology, it is inferred that when high amounts of annual growth variability coincide across all stems, plants and groups at the stand to landscape scale, a large-scale factor such as climate has varied annually and influenced growth in the same way within the plant and across all plants and groups (Fritts 1976). On the other hand, if there are large differences in stem and plant chronologies so that the chronology summed for all plants and groups has low variance, as in this study, then it is inferred that multiple factors have limited growth and thus, have diminished the effect of climate (Fritts 1976). Johnstone and Henry (1997) also found high levels of intra-plant variability when constructing *C. tetragona* chronologies. The high amounts of within-plant variability detected in this study may be the product of the plant architecture and the associated microenvironmental conditions, as well as within-plant resource partitioning (Havström *et al.* 1993; Johnstone and Henry 1997; Chapter 2). Resource partitioning among stems within the individual plant may influence the constancy of annual growth and reproduction and thus, modify the plant's response to regional climate conditions. Inter-plant variability may be the product of community dynamics, such as competition or differences in the micro-environment. *Cassiope tetragona* could conceivably compete at a low level for light, water, nutrients and space in a closed-vegetation communities like the Lowland and Bench sites; however, this may be less likely at the Dome site.

The lack of quantitative evidence concerning the mechanisms for intra- and inter-plant variability in *C. tetragona* presents a problem when selecting sampling sites. Careful site selection seeks to enhance the signal of a selected growth-limiting factor, such as climate, and to reduce local endogenous and community exogenous disturbance factors (Fritts 1976; Cook and Briffa 1990; Pilcher *et al.* 1990). However, with little empirical evidence of the influence of community dynamics on the growth and reproduction of *C. tetragona* at Alexandra Fiord, it is impossible to assess their impact.

The selection of flexible cubic splines to standardize the growth and reproductive chronologies at the three sampling sites may have also increased the level of variability present within the chronologies. By utilizing the signal-to-noise-ratio (SNR) criterion to select a cubic

spline filter, more of the low frequency signal may have been removed than intended. Traditionally, it is the low frequency signal that is of interest in dendroclimatological studies (Cook and Briffa 1990). Thus, by using the SNR, the strength of the observed high-frequency signal may have been emphasized.

3.4.3. Chronology Characteristics

The mean and standard deviation values for annual growth and production of leaves reported for the Lowland, Bench and Domes sites are similar to those reported for other high arctic populations including ones at Alexandra Fiord (Nams 1982; Havström *et al.* 1995; Johnstone and Henry 1997) and two on Svalbard, Norway (Callaghan *et al.* 1989; Havström *et al.* 1993) (Table 3.13). However, growth measurements in one high arctic *C. tetragona* population on Svalbard (Callaghan *et al.* 1989) and in four subarctic populations near Abisko, Swedish Lapland were slightly larger than those reported in this study (Callaghan *et al.* 1989; Havström *et al.* 1993; Molau 2001). The larger mean values for *C. tetragona* growth reported for the Swedish Lapland populations are due to the more southerly latitudinal position of these study sites. Moreover the mean values reported in this study support the hypothesis that *C. tetragona* stem elongation and leaf production decrease with latitude (Havström *et al.* 1993), as well as with elevation. Havström *et al.* (1993) suggested high latitude populations of *C. tetragona* plants invest resources into strengthening and protecting fewer leaves on a shorter stem to prevent desiccation damage.

In this study, the mean number of flower peduncles produced annually was smaller than the mean values reported by Havström *et al.* (1995) and Johnstone and Henry (1997) for Alexandra Fiord (Table 3.13). Interestingly, the mean number of flower peduncles produced around the sixteenth and seventeenth centuries reported by Havström *et al.* (1995) is similar to the mean values reported in this study. Reduced mean flower production in this study was likely influenced in the early part of the chronologies by the rapidly changing climate in the Canadian High Arctic following the Little Ice Age. It is hypothesized that potentially variable environmental conditions at Alexandra Fiord in the early twentieth century may have suppressed flower bud development and flower production in mature plants and delayed it in

Table 3.13. Comparative data on the mean growth (annual growth increments (AGI), annual production of leaves) and reproduction (annual production of flower buds and flower peduncles) of *Cassiope tetragona* from retrospective analysis and temperature enhancement studies (control plots only) in the Arctic. Buds = flower buds. Peds = flower peduncles. LIA = Little Ice Age. SD = standard deviation of the mean. SE = standard error of the mean. nd = no data available.

Study	Site and Date	Mean± SD/SE	AGI	Leaves	Buds	Peduncles
Rayback, Chapter 3 Alexandra Fiord Ellesmere Island, Canada	Lowland 1879-1996	mean	4.76	10.16	0.42	0.35
		SD	2.06	2.86	0.65	0.6
	Bench 1884-1996	mean	3.95	8.78	0.48	0.25
		SD	1.45	2.26	0.66	0.51
	Dome 1922-1996	mean	3.73	9.82	0.65	0.41
		SD	1.71	3.04	0.85	0.68
Johnstone & Henry 1997 Alexandra Fiord Ellesmere Island, Canada	Lowland 1957-1992	mean	4.78	10.4	nd	1.9
		SD	1.32	2.5	nd	0.96
Havström et al. 1995 Alexandra Fiord Ellesmere Island, Canada	Glacier Foreland 1965-1991	mean	nd	11.37	nd	1.3
		SD	nd	2.93	nd	nd
	Glacier, LIA ~1425 and 1665	mean	nd	9.72	nd	0.68
		SD	nd	2.28	nd	nd
Nams 1982* Alexandra Fiord Ellesmere Island, Canada	Central Plain 1981	mean	3.40	nd	1.8**	nd
		SE	0.10	nd	0.50	nd
Callaghan et al. 1989 Adventdalen, Svalbard	Svalbard-winter 1967-1986	mean	nd	10.25	nd	nd
		SE	nd	0.084	nd	nd
Adventdalen, Svalbard	Svalbard- summer 1967-1986	mean	nd	12.62	nd	nd
		SE	nd	0.196	nd	nd
Mt. Slättatjåkka, Sweden	Swedish Lapland 1967-1986	mean	nd	12.23	nd	nd
		SE	nd	0.18	nd	nd
Havström et al. 1993* Absiko, Sweden	tree-line heath 1985-1991	mean	8.29	19.48	nd	nd
		SE	0.22	0.39	nd	nd
Abisko, Sweden	summit fellfield 1985-1991	mean	6.25	13.29	nd	nd
		SE	0.25	0.36	nd	nd
Ny-Ålesund, Svalbard	Beach ridge heath 1985-1991	mean	5.21	10.78	nd	nd
		SE	0.22	0.35	nd	nd
Molau 2001* Latnjajaura, Sweden	ITEX control 1993-1997	mean	9.12	nd	nd	nd
		SE	0.32	nd	nd	nd

* Mean values are from control plots in temperature enhancement experiments.

** Mean number of flower buds per shoot on tagged shoots (Nams 1982).

juvenile ones. The mean annual flower bud production values reported in this study are the first observations of this variable recorded for a period of greater than one year (Nams 1982).

Statistics commonly used in dendrochronology such as mean sensitivity, standard deviation and first-order autocorrelation are used to gauge the sensitivity of chronologies to the climatic signal (Fritts 1976; Cook and Briffa 1990). The two growth variables across the three sites exhibited low mean sensitivity. *Cassiope tetragona* exhibits a rather conservative vegetative growth response to short-term variations in growing season climate. The conservative growth response was present in the standardized chronologies for the Lowland, Bench and Dome sites which exhibited low levels of high frequency variability throughout most of the twentieth century. The plant's low sensitivity to inter-annual climate variability may serve to stabilize the annual vegetative productivity of this species (Sørensen 1941; Shaver and Kummerow 1992). In addition, the two growth variables across the three sites exhibited low first-order autocorrelation values. Low autocorrelation values may indicate that the growth variables of *C. tetragona* are relatively uninfluenced by low-frequency climatic trends. The accumulated effect of past climate over several years does not appear to influence *C. tetragona* growth. However, the use of the flexible cubic splines in standardization process of the growth chronologies may have removed more of the low-frequency climatic fluctuations than intended. Furthermore, the short lengths of the *C. tetragona* chronologies compared with those of tree-ring chronologies preclude the observation of low frequency climatic trends.

The mean sensitivity and first-order autocorrelation values for growth were very similar to those in Johnstone and Henry (1997), the only other study to report these statistics for *C. tetragona*. The mean sensitivity values in this study were not unlike those reported for the radial growth of North American boreal tree species in northern Alaska and Canada (e.g., Kay 1978; Cropper and Fritts 1981; Cropper 1982; 1984; Edwards and Dunwiddie 1985; Szeicz and MacDonald 1995; 1996; Tardif *et al.* 2002). The first-order autocorrelation values reported in this study for growth variables are lower than those reported for northern tree-ring chronologies (e.g., Kay 1978; Cropper and Fritts 1981; Cropper 1982; 1984; Edwards and Dunwiddie 1985; Szeicz and MacDonald 1995; 1996). However, it should be noted that the generating processes of annual tree growth and annual *C. tetragona* growth are not identical.

In direct contrast to the growth variables, the mean sensitivity values for the reproductive variables were high across all three sites. Visual inspection of the standardized chronologies for the Lowland, Bench and Dome sites showed high frequency variability throughout the twentieth century. Data supporting the reproductive sensitivity of *C. tetragona* to inter-annual climate conditions were presented in Chapter 2 and in other studies (Nams and Freedman 1987b; Johnstone and Henry 1997). When the mean sensitivity values for the Lowland site were compared with those reported in Johnstone and Henry (1997), the values were almost identical. However, the mean sensitivity values were higher at the Bench and Dome sites. The Bench and Dome sites are 150 m and 500 m, respectively, higher in elevation than the Lowland site and, most likely experience harsher climatic conditions during the growing season. The *C. tetragona* plants at these two sites may be more sensitive to any amelioration in growing season conditions. The first-order autocorrelation values for reproduction variables were low across the three sites. In general, high mean sensitivity and low first-order autocorrelation values are indicative of high inter-annual variability and sensitivity to yearly climate conditions (Fritts and Shatz 1975; Case and MacDonald 1995). Thus, data from this study supports a growing body of evidence that reproductive development in plants at high arctic sites may be more sensitive to the thermal environment than vegetative growth (Arft *et al.* 1999; Chapter 2). Furthermore, evidence from simulated environmental change studies on evergreen and semi-evergreen shrubs supports the idea that growing season temperatures are critical in high arctic tundra ecosystems for successful reproduction (Welker *et al.* 1993; Wookey *et al.* 1993; 1995; Johnstone 1995; Molau 1997; 2001).

The general linear models showed significant differences in the annual stem elongation and production of flower buds across the three sites and among years at Alexandra Fiord. However, the models which tested for differences in the annual growth increment variable and the annual production of flower buds among sites violated assumptions of normality and nonconstancy of the error variance (flower buds only). An increase in elevation (30 m, 150 m, 500 m a.s.l.) across the three sites, with the associated changes in air temperature, moisture regime, soil development, snowpack depth, length of growing season, and recent glacial history most likely contributed to the apparent differences in these two variables at the Lowland, Bench and Dome sites. Significant among year variation may be linked to annual conditions at the Dome site. It is hypothesized that annual fluctuations in microclimate and associated environmental factors may have had a greater impact on *C. tetragona* plants at the Dome site

than at the other two sites. Environmental conditions at the Dome site are unique given the recent retreat of Twin Glacier. Year-to-year differences were also apparent for the annual production of leaves. These results appear to contradict the interpretation of the mean sensitivity values discussed previously. However, unlike the data used to calculate the mean sensitivity values, the data in the general linear models were not standardized. In addition, while the two growth variables displayed an overall lower level of annual variability than the reproductive variables, the changes in growth variability may have been greater and more anomalous than the changes in reproductive variability. Overall, variability was high for both reproductive variables, but was similarly high for all years.

Although there was not full agreement across the three sites, the correlations among the growth and reproductive variables within each population were generally positive. Consistent with observations from other studies, both *C. tetragona* growth and reproduction benefit from favorable growing season conditions during the same year (Johnstone and Henry 1997; Chapter 2). While growth in *C. tetragona* has been shown to respond conservatively to ameliorated conditions (Chapter 2), improved environmental conditions may lead to additional production of photosynthates which could go towards current year reproductive development. In addition, there may be enough photosynthates and nutrient reserves stored up from the previous favorable growing season to benefit the early development and growth of buds during the current summer. Thus, several consecutively warm summers might create a positive lag effect, benefiting both the current year and next year's reproduction. Positive correlations were also found between previous year's production of flower buds (year C-1) and current year (year C) flower peduncle production. Favorable growing season conditions in the previous summer often result in the high production of flower buds on *C. tetragona* stems (Nams 1982; Johnstone 1995). If favorable growing conditions continue the following summer as well, the larger number of buds will develop into more flowers and increase the chance of reproductive success. No evidence was found of a trade-off between growth and reproduction as suggested by Johnstone and Henry (1997).

Correlations of *C. tetragona* growth and reproduction between populations revealed two significant coefficients. The positive and significant correlations between the Lowland and Bench chronologies for annual stem elongation and for the annual production of leaves suggested that growth among years fluctuated in a similar manner across both populations.

However, few similarities existed between the two growth variables at the Dome and Lowland sites, and the Dome and Bench sites. These associations between populations suggested that year-to-year environmental conditions influencing plant growth at the Lowland and Bench were similar, while those at the Dome were not. The high elevation of the Dome site (500 m. a.s.l.), in addition to the colder temperatures, shorter growing season, exposure to high winds, and recently glaciated substrate are all factors which differentiate this site from the other two. The absence of positive and significant correlations between the reproductive variables also suggested that the three populations responded individually to local community dynamics and environmental conditions. Evidence from other studies showed *C. tetragona* reproduction is sensitive to warmer temperatures (Nams 1982; Johnstone and Henry 1997; Chapter 2). In addition, the lack of positive correlations may also reflect the high degree of intra- and inter-plant variability in each population.

3.4.4. Response of *Cassiope tetragona* to Climate Variables

3.4.4.1. Response Functions and Coastal Station Climate Data, 1980-1996

In general, the response function coefficients relating *C. tetragona* growth and reproduction at the Lowland, Bench and Dome sites to average air temperature and monthly thawing degree days measured at the Coastal station were not significantly different from zero. However, the vegetative variables from the three sites were positively related to June, July and August climate variables. The importance of summer growing season temperatures for *C. tetragona*, particularly in the first four to six weeks of summer, has been observed in other studies (Nams and Freedman 1987b; Callaghan *et al.* 1989; Shaver and Kummerow 1992; Havstöm *et al.* 1993; Johnstone and Henry 1997). The generally positive response of *C. tetragona* growth to summer monthly temperatures was observed in the ITEX control plots as well (Chapter 2). Overall, the growth variables at the Lowland site tended to respond earlier and with greater magnitude to June and July temperature and thawing degree days, while the Bench and the Dome sites responded to July and August climate variables. The response of the plants at the Lowland site was not unexpected as the Lowland is, generally, warmer earlier and for the duration of the growing season (Labine 1994). The negative association of the Dome plants to monthly thawing degree days in June was also not unexpected as the daily temperature

of the site does not rise above 0 °C until late June or early July, a profound reduction in the growing season length when compared to the Lowland site.

The reproductive response of *C. tetragona* at the three sites to climate variables was more variable. At the Lowland site, the reproductive variables tended to respond in the same manner as reported for the ITEX control plants in Chapter 2; flower bud production was positively related to temperature in July and August, and flower production to temperatures during the entire growing season. The reproductive response of the Lowland plants was also similar to observations reported by Havström *et al.* (1995) and Johnstone and Henry (1997). However, the relationship between the reproductive variables to climate variables at the Bench and Dome sites were much more variable. Given the slightly cooler and shorter growing seasons at these two higher elevation sites, the predominance of negative associations with monthly climate during the growing season may be the response of highly stressed plants with few reserves from either the previous or current year to meet the expensive demands of reproduction.

The variance explained by a combination of climate alone, by previous growth (or reproduction) alone, and by climate and previous growth (or reproduction) together across all three sites for both growth and reproductive variables ranged from moderate to high levels. The lower amounts of variance explained by some variables may have been due to factors other than climate, or a combination of factors with climate which were more limiting to growth and reproduction in some years. The non-climatic factors may have included branch structure and resource partitioning, as well as plant community dynamics at each site as previously discussed.

3.4.4.2. Response Functions and Eureka Climate Data, 1948-1996

In general, the growth variables at the Lowland, Bench and Dome sites were positively related to average air temperature during the late spring and summer months at Alexandra Fiord. The Lowland growth variables responded positively and significantly to June and July average air temperature. Similar observations on the relationship between *C. tetragona* growth and June and July air temperatures were made by Callaghan *et al.* (1989), Havström *et al.* (1995) and Johnstone and Henry (1997), as well as in Chapter 2. The positive influence of early growing

season temperatures on the growth of *C. tetragona* and other arctic plants is well acknowledged in the literature (Shaver and Kummerow 1992). In general, growth variables at the Bench and Dome sites were positively associated with August and September average air temperatures. Warmer temperatures at the end of the growing season may facilitate winter hardening in these plants. Johnstone and Henry (1997) also noted a positive association between *C. tetragona* growth and September temperatures.

The response of the reproductive parameters of *C. tetragona* at the three sites to climate variables was more variable. At the Lowland, Bench and Dome sites, the reproductive variables were strongly influenced by early summer average air temperatures. By late June to mid-July, flower buds are visible on *C. tetragona* plant stems (Nams 1982; Johnstone 1995). Warming temperatures also initiate the elongation of the flower peduncles and formation of the flowers early in the growing season. Usually flower peduncles are visible, but the corolla remains undeveloped by early July (Johnstone 1995). Support for the direct and indirect positive effects of early summer temperature on *C. tetragona* reproduction has been reported in other studies (Nams and Freedman 1987b; Callaghan *et al.* 1989; Johnstone and Henry 1997; Chapter 2). Late summer temperature in August and September also benefited reproduction in *C. tetragona* at the three sites. As flower buds continue to develop throughout the end of the growing season, continued warmth in the months of August and early September may allow further development of flower buds prior to over-wintering (Nams and Freedman 1987; Johnstone 1995). *Cassiope tetragona* pre-forms flower buds at least one year prior to actual flowering (Sørensen 1941).

A high amount of variance was explained by both the monthly climate variables and the two years of prior growth (or reproduction) at the Lowland and Bench sites. Prior growth (or reproduction) of one to two years may supply the necessary accumulated surplus of nutrients and photosynthates needed early in, and throughout the growing season, particularly in less than optimum years. However, when examining the lower amount of variance explained by climate alone, it is hypothesized that there may be other factors influencing growth, including within-plant and community dynamics. The amount of variance explained by the monthly climate variables and two years of previous reproduction at the Lowland and Bench sites was also moderately high. However, the amount of variance explained by climate alone is smaller. The extent to which climate influences reproduction in *C. tetragona* plants varies depending on

growing season length and temperatures. Similar results have been reported in previous studies (Nams and Freedman 1987b; Johnstone and Henry 1997).

While the amount of variance explained using Coastal station data may be dampened by the influence of intra- and inter-plant variability, the relationship between Eureka climate variables and the Alexandra Fiord chronologies may be more difficult to interpret. The distance from Alexandra Fiord to the Eureka H.A.W.S. is approximately 250 km. The difference in monthly conditions at Eureka and Alexandra Fiord may be great enough to weaken the link between the growth and reproductive indices and climate. The problem of distance between a sampling site and a climate station is one that many paleoclimatologists must face when designing studies and conducting sampling in remote northern locations. It should also be noted that while some of the total monthly precipitation coefficients were significant using the Eureka data, precipitation is a local phenomenon and is most likely not comparable between sites. The influence of the Saw-Tooth Mountains and the Prince of Wales Icecap on synoptic systems which originate over the Arctic Ocean and deposit precipitation at Alexandra Fiord is most likely considerable. In addition, autumn-spring precipitation comes from systems that originate off of northern Baffin Bay (Maxwell 1982). However, no long-term precipitation measurements have been made at Alexandra Fiord for comparison with Eureka; thus, the assumption of difference is hypothetical. Given these caveats, the positive and biologically logical associations between the Lowland and Bench growth and reproduction chronologies and the monthly average air temperature, as well as the high amount of variance explained by climate and previous growth (or reproduction) supported development of transfer functions to reconstruct past climate.

3.4.5. Reconstruction of Summer Temperature

3.4.5.1. Transfer Functions and Coastal Station Climate Data, 1980-1995

The two best models for reconstructing climate at Alexandra Fiord, Ellesmere Island estimated average summer air temperature. The closely linked relationship between *C. tetragona* growth and reproduction with summer growing season temperatures has already been shown in this study and in others (Nams and Freedman 1987b; Callaghan *et al.* 1989; Havström

et al. 1993; 1995; Johnstone and Henry 1997; Chapter 2). The first model explored in this study reconstructed July-August average air temperature. The model explained 78% of the variance and closely followed inter-annual variation for the period 1980-1995. In particular, the estimated model captured the coldest summer on record (1986) at Alexandra Fiord as well as the warmest summer (1982) for the period 1980-1995. The July-August temperature model reveals the strong association of the Alexandra Fiord chronologies with climate, affirmation of *C. tetragona*'s sensitivity to local environmental conditions. The selected variables, annual stem elongation and production of leaves and flowers, were positively correlated with temperature in July and August. Previous observations showed substantial growth and reproduction in *C. tetragona* occur during these months (Nams and Freedman 1987b; Havström *et al.* 1993; Johnstone 1995). It is interesting to note the inclusion of both vegetative growth variables from the Lowland and Bench sites in the model despite their low mean sensitivity values. Perhaps the vegetative variables, both for the current year and lagged by one year, contain a greater climate signal in combination than when examined singly. Similar combinations of predictor variables have been used successfully in transfer functions by Havström *et al.* (1995) and Johnstone and Henry (1997) to predict July thawing degree days and mean July temperature, respectively. Unfortunately in this study, the limited length of the climate record at Alexandra Fiord prevents calibration and verification of the July-August temperature model at this time. However, the potential success of this model warrants further investigation when more climate data becomes available at Alexandra Fiord.

3.4.5.2. Transfer Functions and Eureka Climate Data, 1948-1994

3.4.5.2.1. Reconstruction of August-September Temperature

The 95-year long reconstruction (1899-1994) of inter-annual August-September average air temperature is the longest proxy yet constructed for the high arctic using *C. tetragona*. The August-September full model explained 51% of the variance, a value which is within range of other dendroclimatological models based on tree-rings from sites in northern North America (e.g., Jacoby *et al.* 1985; 1988; Jacoby and D'Arrigo 1989; D'Arrigo and Jacoby 1993; Szeicz and MacDonald 1993; 1995). The moderately high level of variance explained in this model

supports the use of instrumental data from Eureka H.A.W.S. to reconstruct summer temperature at Alexandra Fiord, and suggests that similar climate patterns influenced both locations.

3.4.5.2.2. Limitations of Climate Reconstruction

Prior to the interpretation of the August-September average temperature model, it is important to examine the limitations of the reconstruction. The August-September temperature model does remain somewhat ambiguous as only half of the dependent temperature response was retrieved ($R^2_{adj} = 0.51$), and the verification periods were short. However, the amount of variance explained is comparable to tree-ring proxies, as mentioned previously. In addition, the brevity of climatic records and the paucity of climate stations across the Canadian High Arctic is a challenge any study in the Canadian North faces when attempting to calibrate proxy climate. Due to the use of flexible standardization splines in this study, long-term fluctuations in climate cannot be reproduced (Briffa *et al.* 1988). However, as the reconstruction is less than one hundred years long, it would be difficult to impossible to discern longer-term fluctuations on the order of centuries or longer. Finally, while it was assumed the variability in the early part of the reconstruction was partially related to natural climate fluctuations, there remains the possibility that the uncommon variance or noise increased with decreasing sample size (Fritts 1976; Cook and Briffa 1990). In dendrochronology, the mean chronology variance is composed of both the signal and residual noise. By averaging multiple series, the uncommon variance or noise will cancel in direct proportion to the number of series averaged, but the common variance remains unaffected (Cook and Briffa 1990). The difficulties associated with decreasing sample size in the early part of a reconstruction are well understood and acknowledged in dendrochronology (Fritts 1976; Cook and Briffa 1990). Acknowledging the above limitations of the model, it was felt that the directional tendencies and variability within the reconstruction for the twentieth century were useful and directly comparable to other proxy data from northern North America.

3.4.5.2.3. Interpretation of and Supporting Evidence for the Temperature Reconstruction

The reconstruction of summer temperature during the first 20 years of the twentieth century reveals high frequency, oscillating temperature patterns at Alexandra Fiord. The

variability is not surprising given that, at the turn of the twentieth century, the Canadian High Arctic was rapidly emerging from a general temperature deterioration which had begun roughly around 4500-4200 yr BP and lasted until the mid-1800s (Hardy and Bradley 1997). Multiproxy evidence from North America supports the hypothesis that the most recent neoglaciation episode, referred to as the 'Little Ice Age' (ca. ~1550-1850 in Arctic Canada) (Moss 1951; Porter and Denton 1967; Grove 1988) was one of the coldest, if not the coldest period during the entire Holocene (Bradley 1990; Hardy and Bradley 1997; Overpeck *et al.* 1997). Evidence in the form of ice core melt records taken from the Agassiz Ice Cap, Ellesmere Island reveals the coldest summers of the Holocene occurred only 150 years BP (Koerner and Fisher 1990). In addition, observations at multiple sites across Arctic Canada indicate the maximum late Holocene glacial advance occurred within the last few hundred years (Christie 1957; Dowdeswell 1984). During this time, the terminal positions of many glaciers moved to their most advanced positions ever occupied during the Holocene (Bradley 1990). It should be noted, however, that the terminal position of a glacier is often determined by local climatic and topographic conditions, and thus, it may not be linearly related to climate (Oerlemans 1989; Bradley and Jones 1993). In addition, Smith *et al.* (2001) noted the virtual absence of thick lake varves below the year 1867 from cores taken at Lake Tuborg, Ellesmere Island. The absence of warm summer temperatures resulted in low levels of summer melting of the Agassiz Ice Cap and, thus, low runoff and sediment flux into marginal lakes (Hardy *et al.* 1996; Smith *et al.* 2001). In further support of extremely cold temperatures during the Little Ice Age, radio-carbon dates on organic matter recently exposed by retreating glacier termini at Alexandra Fiord and Sverdrup Pass, Ellesmere Island provided evidence that the plants were buried by snow and ice as recently as 400 ± 140 and 150 ± 50 years BP, respectively (Blake 1981; Bergsma *et al.* 1984). It is hypothesized that during the early nineteenth century, in particular, frequent and large sulfur-producing volcanic eruptions may have precipitated the dramatic drop in arctic temperature by reducing incoming solar radiation (Zielinski *et al.* 1994; Zielinski 1995). High sulfate loading of the atmosphere from volcanic eruptions entrains positive ocean feedbacks which may prolong and exacerbate periods of arctic cooling (Overpeck *et al.* 1997). Related evidence from lake varve sediment records from Ellesmere Island also suggests an increase in major rainfall events accompanied by colder temperatures following major volcanic eruptions (Lamoureux *et al.* 2001).

Beginning in the mid-nineteenth century, proxy data and instrumental records from the North American Arctic indicate a dramatic and nearly ubiquitous transition from anomalously

cold conditions to the warmer conditions of the twentieth century, marking the end of the Little Ice Age in the polar north (e.g., Koerner 1977; Jacoby and D'Arrigo 1989; Koerner and Fisher 1990; D'Arrigo and Jacoby 1993; Szeicz and MacDonald 1995; Overpeck *et al.* 1997). Tree-ring proxies developed from sites at or near tree-line in northern North America show a gradual warming trend from the mid to late 1800s to the present (D'Arrigo and Jacoby 1993; Szeicz and MacDonald 1995). The rapid increase in arctic temperature from the mid-nineteenth to the early twentieth century is thought to be the result of the readjustment of external drivers as volcanic forcing weakened and solar irradiance increased (Overpeck *et al.* 1997). In association with reduced volcanic aerosols, lake varve sediment records from Ellesmere Island indicate rainfall frequency was at its lowest during the early 1900s (Lamoureux *et al.* 2001). The influence of increasing greenhouse gases such as CO₂ and CH₄ is believed to have only moderately affected temperature change in the Arctic at the turn of the century (Overpeck *et al.* 1997).

When considering the early part of this study's reconstruction within the larger context of transitioning arctic climate at the beginning of the twentieth century, high frequency variability is not anomalous or unexpected. It is hypothesized that the first 20 years of the Alexandra Fiord reconstruction were strongly influenced by a rapidly warming, but most likely unstable climatic regime that was emerging from the coldest period of the Holocene. The unstable climatic conditions may account partly for the frequency of temperature oscillations in the early portion of the climate reconstruction. In addition, the close proximity of Twin Glacier at Alexandra Fiord may also have influenced, directly and indirectly, the annual growth and reproduction response of the plants. It is possible that during some summers in the early part of the reconstruction, the already stressful growing season conditions were exacerbated by the proximity of the glacier and its associated microclimate conditions. Experimental evidence supports the strong influence of inter-annual climate conditions on the growth and reproduction of *C. tetragona* (e.g., Nams 1982; Callaghan *et al.* 1989; Havström *et al.* 1993; Johnstone 1995; Molau 1997; Chapter 2).

Further examination of the reconstruction reveals a general directional increase in summer temperature beginning approximately in the 1920s and continuing into the early 1960s (Figure 3.26a). Analysis of multiproxy data from numerous Canadian Arctic sites shows that summer temperatures since 1925 within the context of the Late Holocene were exceptionally high (Bradley 1990; Hardy and Bradley 1997). Evidence from ice core melt records from

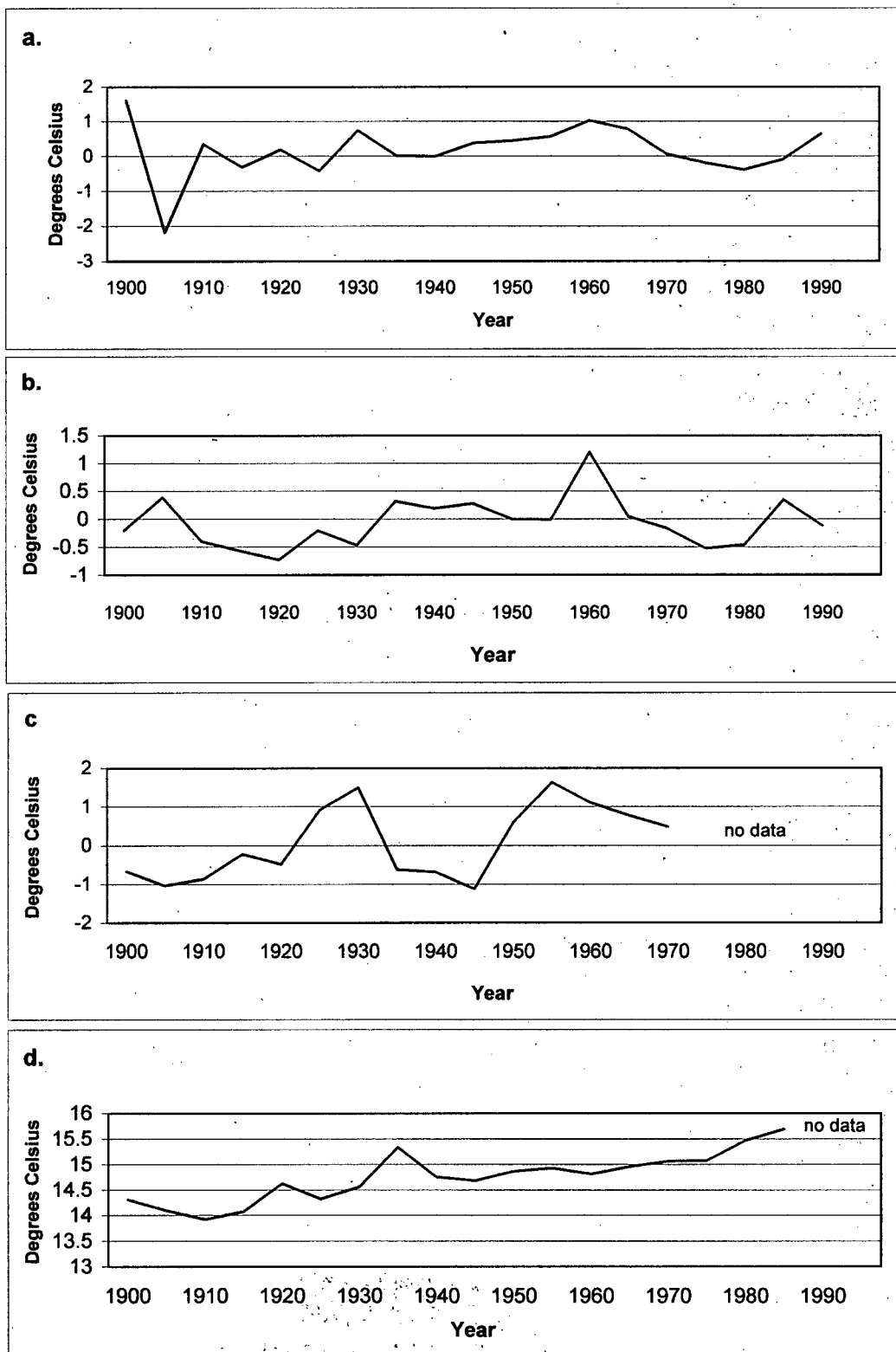


Figure 3.26: Comparison of standardized proxy temperature records for the North American Arctic from 1900 to 1995. (a.) *C. tetragona*-based reconstruction of August-September average air temperature for Alexandra Fiord; (b.) lake varve sediment-based reconstruction of surface air temperature for Lake C2, Ellesmere Island (Lamoureux & Bradley 1996); (c.) percent melt layers from ice cores taken from the Devon Island Ice Cap (Koerner 1977; Koerner & Fisher 1990); (d.) tree-ring based reconstruction of June-July temperature for northwestern Canada (Szeicz & MacDonald 1995). All series are presented as 5-year averages.

nearby Agassiz Ice Cap, Ellesmere Island, as well as the Devon Island and Axel Heiberg Island Ice Caps indicates that the warmest summers in the last 1000 years occurred in the last 100 years, reaching their maximums during the periods of the mid-1920s-1930s and the 1950s-1960s (Figure 3.26c) (Koerner 1977; Fisher and Koerner 1983; Koerner and Fisher 1990). The percentage of melt features in an ice core section is an indicator of summer temperatures (Smith *et al.* 2003). Lake varve sediment records from Lake C2 (Lamoureux and Bradley 1996) and Lake Tuborg (Smith *et al.*, 2003), Ellesmere Island also support warmer mid-century temperatures in the Canadian Arctic (Figure 3.26b). It is hypothesized that, since 1920, anomalously high solar radiation and lower volcanic aerosol loading, along with exponentially increasing atmospheric trace gases, have influenced the warming trend across the Arctic (Bradley and Jones 1992; Lean *et al.* 1995; Robock and Free 1995; Overpeck *et al.* 1997; Mann *et al.* 1998; Free and Robock 1999; Lean and Rind 1999). The August-September average air temperature model provides further evidence from a new high arctic site supporting a summer temperature increase during the middle of the century in Arctic Canada.

This reconstruction also shows a decrease in summer temperatures beginning in the early 1960s and lasting throughout the 1970s (Figure 3.26a). The cooling trend is evident in the melt records from the Agassiz Ice Cap ice cores, as well as in the sedimentary record from Lake C2 and Lake Tuborg, Ellesmere Island (Lamoureux and Bradley 1996; Smith *et al.* 2003). Varve thickness in the Lake Tuborg proxy decreased sharply after 1962 to levels similar to those recorded in the late nineteenth and early twentieth centuries (Smith *et al.* 2003). These three proxies, as well as instrumental climate data show a marked decline in temperature after 1962-1963. A combination of factors may have influenced the mid-century cooling in the high arctic. The change in climate after 1962 may be attributable to changes in atmospheric circulation at high northern latitudes (Bradley and England 1978; Kahl *et al.* 1993). During the summer of 1963, the lowering of summer freezing levels in the atmosphere was linked to the presence of anomalously warm ocean temperatures in the central northern Pacific Ocean, which in turn, altered pressure patterns in the Northern Hemisphere and resulted in the onset of this new climatic regime (Bradley 1973; Dronia 1974; Smith *et al.* 2003). The decline in temperature may also have been influenced by an increase in arctic tropospheric aerosols caused by increased volcanism after 1950 (Bradley and Miller 1972; Kulka *et al.* 1977; Jones *et al.* 1982; Overpeck *et al.* 1997). Lake varve sediment records from Nicolay Lake, Cornwall Island show a marked increase in rainfall after 1962, coinciding with this known period of cooler summers,

as well as with the 1963 eruption of Mount Agung (Lamoureaux *et al.* 2000). In addition, the leveling off of solar irradiance in the mid-twentieth century may also have influenced climate in the Arctic (Lean *et al.* 1995; Mann *et al.* 1998). In the Northern Hemisphere, the cooling trend from 1940 to 1970 is also apparent (Jones and Briffa 1992).

The recent temperature increase detected in arctic instrumental records since the early 1980s (Jones *et al.* 1982) is also present in the reconstruction (Figure 3.26a). The decade of the 1990s and the summer of 1998 were the warmest on record for the Canadian High Arctic (Meteorological Service of Canada 2002). Evidence from sub-arctic North American tree-ring records showed that trees began to recover from the mid-century cooling by the early 1980s as well (D'Arrigo and Jacoby 1993). In another dendroclimatological study near tree-line in northwestern Canada (Yukon and Northwest Territories), the tree-ring proxy indicated a steady increase in temperature throughout the last 150 years, culminating in the 1980s with the warmest temperatures for the entire record (1638-1988) (Figure 3.26d) (Szeicz and MacDonald 1995). It is postulated that the most recent temperature increase in the Arctic may be due to a combination of anthropogenic (increased greenhouse gases, sulfate aerosols, decreased stratospheric ozone) and natural (variation in solar irradiance and volcanic aerosols) forcing factors, as well as climate feedback mechanisms (Bradley and Jones 1993; Mann *et al.* 1998; Lean and Rind 1999; Moritz *et al.* 2002). It is also believed that the current increase in arctic temperature is linked with the Arctic Oscillation.

3.4.5.2.4. Arctic Oscillation

The Arctic Oscillation (Thompson and Wallace 1998; 2000; Thompson *et al.* 2000) has been described as the "master switch" for climate over high northern latitudes (Kerr 1999). A natural annular mode of climate in the Northern Hemisphere, the Arctic Oscillation (AO) exhibits a synchronous seesaw pattern in which atmospheric pressures in the polar region and the middle latitudes rise and fall, and in turn, the pressure differences cause winds to oscillate in strength (Thompson and Wallace 1998; 2000). The North Atlantic Oscillation (NAO) (Hurrell 1995) is viewed as a highly correlated, regional manifestation or signature of the Arctic Oscillation (Thompson and Wallace 1998; Kerr 1999; Baldwin and Dunkerton 2001; Overland and Adams 2001). In the negative phase, the AO is characterized by higher than normal

atmospheric pressure over the Arctic (north of 20° N) and lower than normal atmospheric pressure around 55° N. During a negative phase, the counterclockwise spinning of the air mass above the polar regions decelerates and is easily disturbed, resulting in the spillage of cold air into the middle latitudes. When the AO is in its positive phase, lower than normal atmospheric pressure predominates over the polar region, while higher than normal atmospheric pressure predominates around 55° N. During the positive phase, the counterclockwise spinning of the air mass above the Arctic accelerates, containing the cold arctic air within the polar region. When the AO changes phases, the change begins in the stratosphere and progresses downward to the troposphere, strengthening or weakening the circulation in the polar region. In the past 30 years, the stratosphere has cooled, causing the counterclockwise circulation around the North Pole to strengthen, particularly during the winter (Thompson and Wallace 1998).

The strengthening of the polar vortex over the past three decades may be behind the dramatic Arctic and Northern Hemisphere warming trend in the late twentieth century. Many of the recent changes in arctic climate and environmental variables, including changes in surface air temperature (SAT) and sea level pressure (SLP), have been related to the strong positive phase of the AO during the last 30 years (Walsh *et al.* 1996; Thompson and Wallace 1998; Dickson 1999; Jones *et al.* 1999; Shindell *et al.* 1999; Hartmann *et al.* 2000; Morison *et al.* 2000; Polyakov and Johnson 2000; Serreze *et al.* 2000; Overland and Adams 2001; Moritz *et al.* 2002). In association with the increase in the AO index, the amplitude of the interdecadal oscillations has increased during the late twentieth century as well (compared with 1900-1970) (Thompson *et al.* 2000). Arctic SAT for the period 1979-1997 have increased during the winter and spring (Rigor *et al.* 2000). In fact, the AO index explained over half of the wintertime temperature increase observed over the eastern Arctic Ocean, and less than half of the temperature increase over the western Arctic Ocean (Rigor *et al.* 2000; Thompson *et al.* 2000). Notably, both warming and cooling have characterized the western Arctic in the past several decades (Rigor *et al.* 2000). In comparison to the period prior to the 1980s, atmospheric sea level pressure (SLP) has decreased, while the cyclonic vorticity of winds has increased in the late 1980s and early 1990s, (Walsh *et al.* 1996; Polyakov and Johnson 2000). These changes are believed to be linked to the greater number of open breaks in the Arctic Ocean ice, as well as decreased sea-ice thickness in the central Arctic in the 1990s (Rothrock *et al.* 1999). Furthermore, springtime polar ozone losses in the 1990s have been related to the high AO index (Hartmann *et al.* 2000).

Possible connections between surface warming due to anthropogenic and natural climate change and atmospheric circulation, as manifested in the recent positive trend in the AO, have recently been suggested (Slonosky and Yiou 2001). There is support for the hypothesis that the recent positive trend in the AO is a consequence of anthropogenic radiative forcing (Fyfe *et al.* 1999; Shindell *et al.* 1999; Hoerling *et al.* 2001). Increased anthropogenic greenhouse gases and decreased stratospheric ozone are thought to cool the lower stratosphere at high latitudes and, thus, have the potential to increase the AO index (IPCC 2001). Evidence from historical instrumental data, as discussed above, and paleoclimatic reconstructions support the hypothesis that external forcing and internal dynamics have contributed to the recently observed temporal and spatial variations of arctic climate (Moritz *et al.* 2002). Paleoclimatic reconstructions have shown that the twentieth century was anomalously warm in the Arctic relative to the previous three centuries, and temperature increases have been greater in the Arctic than at lower latitudes (Overpeck *et al.* 1997; Mann *et al.* 1998; 1999). However, no paleoclimatic work on the AO has been published, so recent trends and variability of the AO relative to pre-industrial climate are ambiguous (Moritz *et al.* 2002).

Lastly, climate models (e.g., General Circulation Models) have been used to determine whether trends associated with internal modes of variability are anthropogenically forced, or temporary and coincidental to the trend in increasing greenhouse gases (Shindell *et al.* 1999). Results of recent models demonstrated that sea-level pressure trends can be simulated by realistic increases in greenhouse gas concentrations (Shindell *et al.* 1999). The models also suggested that, although temperature increases are a result of naturally occurring modes of atmospheric variability, they may be anthropogenically induced and could continue to increase (Shindell *et al.* 1999). Additional research using instrumental data, paleoclimatic reconstruction and modeling will clarify the importance of the driving factors including, anthropogenic greenhouse gas concentrations, radiative forcing and free variability (Moritz *et al.* 2002).

3.4.5.2.5. Supporting Arctic Paleoclimatic Data

Finally, in support of the results of this reconstruction, instrumental climate data from the Canadian Arctic, and data from other proxy studies of the past and present Arctic geosphere, biosphere, and cryosphere indicate that climate is changing. In the North American Arctic,

changes in permafrost conditions over the past 500 years have been detected through borehole temperature studies (e.g., Lachenbruch and Marshall 1986; Jessop *et al.* 1991; Beltrami and Taylor 1995; Majoriwicz and Skinner 1997; Pollack *et al.* 1998; Osterkamp and Romanovsky 1999; Huang *et al.* 2000). For example, multi-decadal increases in permafrost temperature have been observed in northern and central Alaska (Lachenbruch and Marshall 1986; Osterkamp and Romanovsky 1999), in northwestern Canada (Majoriwicz and Skinner 1997), and in central-eastern Canada (Jessop *et al.* 1991) over the past century. The geothermal data from borehole measurements offered an independent confirmation of multiproxy studies which have highlighted the unusual warming of the twentieth century (Pollack *et al.* 1998). Limnological evidence from Canadian arctic lakes also indicate dramatic changes in taxonomic diversification, increased diatom biomass and recent diatom recolonization over the last 150 to 200 years (Douglas *et al.* 1994; Overpeck *et al.* 1997). Studies of sediments from shallow lakes and ponds on eastern (Douglas *et al.* 1994), western (Wolfe and Perren 2001), and northern (Douglas *et al.* 1996) Ellesmere Island, northern Devon Island (Gajewski *et al.* 1997) and southern Baffin Island (Wolfe 1991; Wolfe and Perren 2001; Wolfe 2003) revealed strong shifts in diatom communities over the past 200 years with the establishment of diatom populations that previously were too light limited by perennial ice to survive (Overpeck *et al.* 1997). The changes in diatom communities are believed to be much greater than during any other time period of climatic variability during the Holocene, suggesting the rate and amplitude of recent warming is unprecedented for the Holocene (Overpeck *et al.* 1997; Wolfe and Perren 2001). Finally, the widespread retreat of low-lying glaciers, ice caps and the disappearance of permanent snowbeds throughout Arctic Canada during the last century provided further evidence of recent climate change. Just prior to the twentieth century, melting of polar ice caps was negligible. However, during the twentieth century, melting increased to a rate exceeded only twice in the last 4000 years (Bradley 2000). Long-term records show glaciers in the Canadian Arctic have experienced an overall negative mass balance for the last ca. 30 years (Bradley and Serreze 1987; Koerner and Lundgaard 1995; Cogley *et al.* 1996; Dowdeswell *et al.* 1997; Adams *et al.* 1998; Braun *et al.* 2001). The results of these proxy studies support the increase in arctic temperature during the twentieth century. Thus, the conclusion of this study, in comparison with, and in support of, other proxy records and instrumental climate data suggests that the rate of temperature change and the level of natural climatic variability at high latitudes during the last 100-150 years are unique and unprecedented for at least 400 years and possibly for several millennia (Koerner and Fisher 1990; Overpeck *et al.* 1997; Bradley 2000).

3. 4. 6. Principal Findings

The results from this study provide strong evidence that past arctic temperatures for the twentieth century can be reconstructed using *C. tetragona* as a proxy indicator. Two models of average summer air temperature were successfully developed using modified dendroclimatological techniques. In the first model, July-August average air temperature was reconstructed for Alexandra Fiord for the period 1980-1996 based on the chronologies from the Lowland and Bench sites. The model was calibrated using transfer function analysis and climate data from the Coastal station (1980-1996) at Alexandra Fiord. The model explained 78% of the dependent climatic variance. However, due to the short overlap period between the chronologies and climate data set, the model could not be cross-calibrated or verified.

In the second model, the longest reconstruction (1899-1994) of summer temperature for the Arctic was achieved after calibrating transfer functions using instrumental data from the High Arctic Weather Station at Eureka (79° 59'N, 85° 59'W). The 95-year long reconstruction of August-September average air temperature for Alexandra Fiord explained 51% of the dependent climatic variance. The reconstruction revealed high inter-annual variability during the first 20 years of the model. The variability may be due to increasing uncommon variance (noise) with decreasing sample size, to unstable local and regional climatic conditions, or both. From the 1920s to the 1960s, a directional increase in temperature was evident in the model. However, for the period of the 1960s to the 1970s, average air temperature decreased before increasing again in the 1980s and the 1990s. The August-September average air temperature reconstruction supports and is supported by proxy evidence (e.g., ice core melt records, lake varve sediments, tree-rings) from other North American Arctic sites, as well as research on anthropogenic and natural forcing mechanisms driving climate change.

4. The reconstruction of past climate for central Ellesmere Island, Canada

4.1. Introduction

4.1.1. Proxy Climate Data and Ellesmere Island, Canada

To understand current and future arctic climate change, it is important to understand how and why climate has varied in the past (Bradley and Jones 1993). Paleoclimatic research and the resulting proxies provide the needed perspective in order to understand climate system variability and its links to forcing factors and feedbacks (Bradley 2000; Briffa 2000). Long proxy records extend the time period available for analysis and can be used to evaluate how climate during the recent past compares to prior centuries (D'Arrigo *et al.* 1999).

Previous studies have established the key role that high northern latitudes play in the global temperature regime (Kelly *et al.* 1982; Jones and Kelly 1983; Lachenbruch and Marshall 1986; Walsh and Chapman 1990; D'Arrigo and Jacoby 1993). Thus, a thorough understanding of temperature fluctuations in the north is important to understanding larger-scale climatic trends (Kelly *et al.* 1982; Jones and Kelly 1983). However, a better understanding of climatic variability over space and time in the Canadian High Arctic cannot be gained by only examining instrumental data (Hardy and Bradley 1997). While the meteorological data in the Canadian Arctic is of high quality, the records are brief (1940s-present). The length of the instrumental record limits most investigations of climatic variability over time spans equal to or longer than the meteorological record (Hardy and Bradley 1997). In addition, High Arctic Weather Stations (H.A.W.S.) are few and widely scattered across Nunavut and the Northwest Territories. On Ellesmere Island, there are two H.A.W.S.: one at Eureka (79° 59'N, 85° 59' W) and the other at Alert (82° 30'N, 62° 20'W). Both stations are at or near sea level (Eureka, 10 m a.s.l.; Alert, 62 m a.s.l.). Given that the topography of Ellesmere Island is characterized by high mountain ranges, large ice sheets, glaciers and fiords, the climate conditions of the H.A.W.S. are not representative of all sites on the island. Thus, it is only through longer proxy climate records that we can extend the rather myopic perspective provided by instrumental data (Bradley 2000), particularly for Arctic Canada.

The number and type of available proxy climate data sets from Ellesmere Island, Canada is higher and more varied than for most arctic locations. A sample list of the proxy climate data available from Ellesmere Island includes: ice core melt records (Hattersley-Smith 1963; Fisher and Koerner 1983; Koerner and Fisher 1989; 1990; Fisher and Koerner 1994), fresh water diatoms (Smol 1983; 1988; Wolfe 1991; Douglas *et al.* 1994; 1996; Ludlam *et al.* 1996; Gajewski *et al.* 1997; Wolfe and Perren 2001; Wolfe 2003), laminated lake sediments (Blake 1981a; 1987a; Retelle 1986; Hardy *et al.* 1996; Lamoureux and Bradley 1996; Lasca 1997; Overpeck *et al.* 1997; Braun *et al.* 2000; Lamoureux *et al.* 2002; Smith *et al.* 2003) and pollen data (Hyvärinen 1985; Bourgeois 1986). At present, only ice cores and laminated lake sediments provide long-duration and high resolution proxy records for the Canadian High Arctic. However, a recently developed proxy technique using the circumpolar, evergreen dwarf shrub, *Cassiope tetragona*, may be used to reconstruct past climate on an annual basis and for multiple locations throughout the Canadian Arctic. Detailed information on *C. tetragona* and the technique for reconstructing past climate is presented in Chapters 2 and 3. Retrospective analysis of *C. tetragona* will be used in this study to reconstruct climate for central Ellesmere Island.

4.1.2. Reconstructing Climate on Ellesmere Island Using *Cassiope tetragona*

Previous studies have shown a strong link between growing season temperature and the growth and reproduction of *C. tetragona* in arctic tundra ecosystems (Callaghan *et al.* 1989; Havström *et al.* 1993; 1995; Johnstone and Henry 1997; Chapters 2 and 3). Using modified dendroclimatological techniques (Fritts 1976), past summer growing season climate can be reconstructed using *C. tetragona* growth and reproduction chronologies. In Chapter 3, past August-September average air temperature was reconstructed for the period 1899-1994 for Alexandra Fiord, Ellesmere Island from three site chronologies located along an elevation gradient. Using the Alexandra Fiord reconstruction as a starting point, the accuracy of climatic reconstruction can only be expected to improve with the inclusion of a greater number of sites (Fritts 1976). In general, by using a greater number of sites which cover a wider geographic area, more information can be extracted from the data on past climate (Fritts 1976). In this study, two sites, Alexandra Fiord and Hot Weather Creek, are included in the climate reconstruction for central Ellesmere Island. If *C. tetragona* chronologies from Hot Weather

Creek can be generated for 100 years or longer and combined with those from Alexandra Fiord to reconstruct past summer climate, a better understanding of the temporal variability of climate on Ellesmere Island over the last century will be achieved. In addition, if this study's reconstruction can be compared with other climate proxies from multiple locations on Ellesmere Island, a spatio-temporal understanding of climate variability will be gained. The study of recent climate change in the Canadian Arctic, since the end of the Little Ice Age to the present, is of great interest when one considers that the rate of temperature change in these marginal environments is unprecedented for at least several millennia (Bradley 2000).

Additionally, a recent study (Aanes *et al.* 2002) investigated the short-term response (12 years) of *C. tetragona* growth and reproduction to changes in the Arctic Oscillation (AO), a recently described spatial pattern of sea-level pressure centered over the Arctic (Thompson and Wallace 1998; 2001). Aanes *et al.* (2002) reported that high values in the AO index were related to reduced *C. tetragona* plant growth on Svalbard. In this study, chronologies from the Lowland site at Alexandra Fiord and the Hot Weather Creek site on the Fosheim Peninsula are related to the summer Arctic Oscillation (AOS) index. The goal is to determine if a similar long-term (50 years) response is detected in the two *C. tetragona* populations on Ellesmere Island.

4.1.3. Research Objectives

The research objectives for this study are: (1) to develop two growth and two reproductive chronologies for Hot Weather Creek, Ellesmere Island; (2) to reconstruct summer climatic conditions for central Ellesmere Island using chronologies from Hot Weather Creek and Alexandra Fiord; (3) to examine the high- and medium-frequency variability in the climate reconstruction; (4) to compare and contrast this study's summer climate reconstruction with that of Alexandra Fiord given in Chapter 3; (5) to relate the results of this study to other single and multi-proxy studies from Ellesmere Island and northern North America; and (6) to investigate the relationship between the growth and reproduction chronologies from Hot Weather Creek and Alexandra Fiord with the summer Arctic Oscillation index.

4.2. Methods

4.2.1. Species Characteristics

Cassiope tetragona (L.) D. Don is an evergreen dwarf shrub with a circumpolar distribution (Hultén 1971). A complete description of the species characteristics and the arctic tundra ecosystems in which it is found is given in Chapter 2.

4.2.2. Study Area

Field work was conducted in the Hot Weather Creek basin, Ellesmere Island, Canada (79° 58' N, 84° 28' W) in August of 1998 (Figure 4.1). Hot Weather Creek is located on the Fosheim Peninsula on the central western coast of Ellesmere Island. The Fosheim Peninsula, one of the largest lowlands in the high arctic, is surrounded by Greely and Cañon Fiords to the north and northeast and Eureka Sound to the west and south. The Saw-Tooth Mountains, rising to greater than 500 m a.s.l., form the eastern boundary of the Peninsula. The study area is 16 km from any major water body or mountain range. The silty soils in the Hot Weather Creek lowland are relatively uniform and weakly alkaline to neutral (Edlund *et al.* 1989; Woo *et al.* 1990). The broad, rolling lowland is dissected by networks of high-centre, frost-fissure polygons which are within fields of densely packed hummocks 10-50 cm high (Edlund *et al.* 1989; Woo *et al.* 1990; Young *et al.* 1997). Small local tributaries funnel spring meltwater into Hot Weather Creek which forms a 15 km long tributary of the Slidre River (Edlund *et al.* 1989). The hydrological budget of Hot Weather Creek is dominated by late spring and early summer snowmelt and later in the summer, by ground ice melt (Edlund *et al.* 1989).

There are approximately 130 vascular plant species on the Fosheim Peninsula and 144 found on northern and central Ellesmere Island (Bruggemann and Calder 1953; Brassard and Beschel 1968; Brassard and Longton 1970). Hot Weather Creek, like much of the Fosheim Peninsula, supports relatively dense, vegetated tundra communities. On average, vascular plant cover is greater than 50%, but does decrease upslope (Woo *et al.* 1990). The well-vegetated lowland is dominated by a prostrate *Salix arctica* Pall.-*Dryas integrifolia* M. Vahl. shrub community on the moderately to well drained, neutral to moderately alkaline, stable, silty soils of

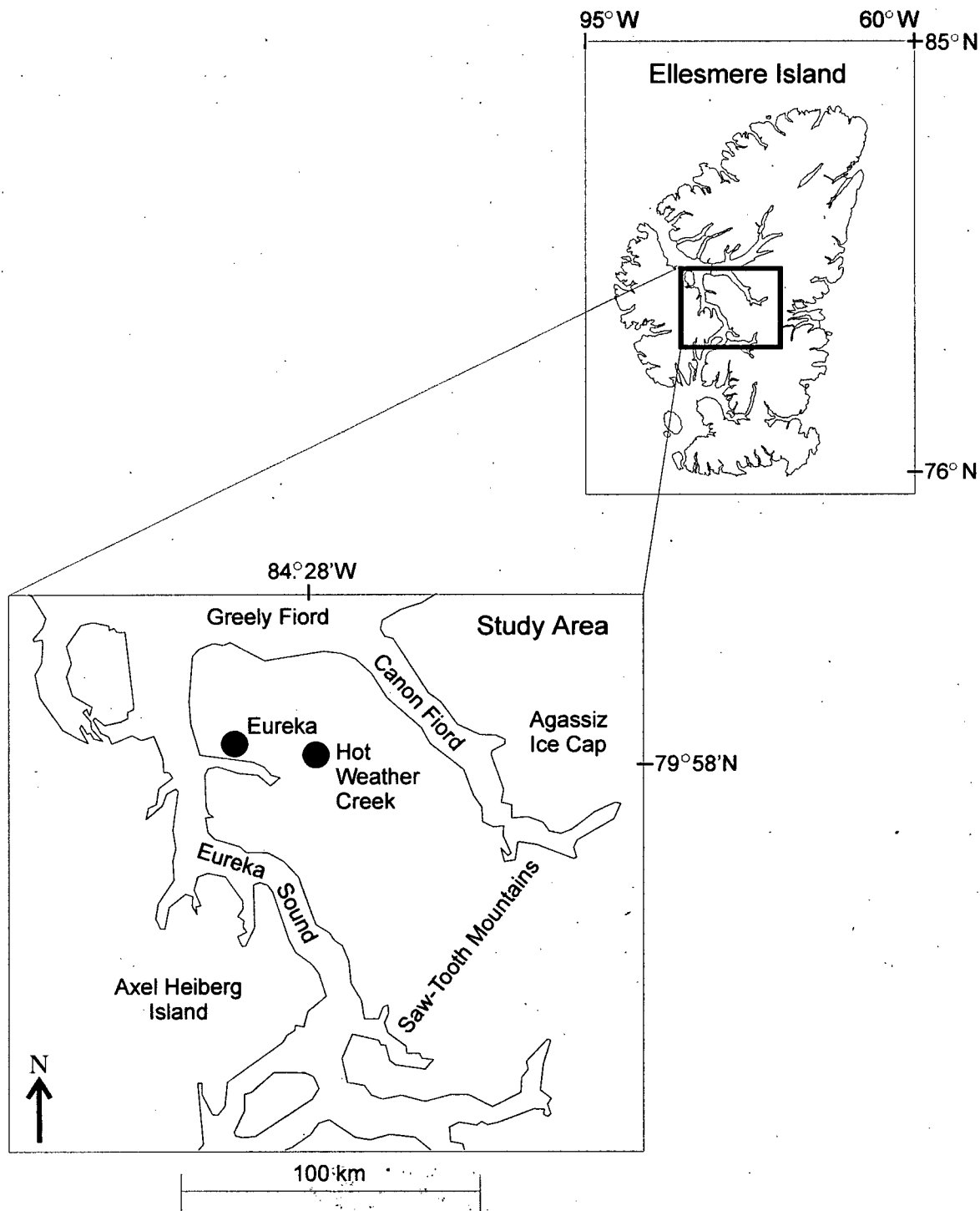


Figure 4.1. Map showing the location of Hot Weather Creek on the Fosheim Peninsula, Ellesmere Island, Nunuvut, Canada.

the plain (Edlund *et al.* 1989; Edlund and Alt 1989). Where rare acidic soils ($\text{pH} < 6.8$) are present, tundra communities are dominated by *S. arctica* and *C. tetragona*. *Cassiope tetragona* is found locally on weakly alkaline deposits, particularly at the bottom of steep slopes and associated with late-lying snowbeds (Edlund *et al.* 1989; Woo *et al.* 1990).

4.2.3. Climate Conditions

Both Hot Weather Creek and Alexandra Fiord lie within the Northern climate region (Maxwell 1981). Specifically, Hot Weather Creek is located within the sub-region of Nansen Sound and Adjacent Lowlands (Maxwell 1981) along with the Eureka High Arctic Weather Station (H.A.W.S.). The interior lowlands of the region are protected by the surrounding mountains of Ellesmere and Axel Heiberg Island from cyclonic activity along the Baffin Bay storm track and from the western Parry Channel (Maxwell 1981). The mountain ranges block the import of cold, moist air and associated low-level clouds from the central Arctic Ocean (Edlund and Alt 1989; Young *et al.* 1997). The predominance of clear conditions and subsequent higher radiation input warms the air and ground resulting in mean July temperatures of $> 5^{\circ}\text{C}$ (Young *et al.* 1997). The region experiences the greatest mean annual temperature range in the Queen Elizabeth Islands (up to 43°C at Eureka H.A.W.S.) (Maxwell 1981). In addition, the rainshadow effect results in the region receiving the least mean annual precipitation in Canada, approximately 64 mm at the Eureka H.A.W.S. (Maxwell 1981; Meteorological Service of Canada 2002).

4.2.4. Study Site

In August 1998, *C. tetragona* plants were collected at the Hot Weather Creek site from tundra plant communities on north- and south-facing slopes (Figure 4.2). The slopes are characterized by hummocky topography and late-lying snowbeds. Intensive studies of the local topography, soils, hydrology, climate and vegetation of Hot Weather Creek (Edlund *et al.* 1989; Woo *et al.* 1990; Young *et al.* 1997) indicate the north-facing slope receives the greatest amount of snowfall in winter and rainfall in summer. In the summer, rainfall is associated with the prevalence of southerly winds at Hot Weather Creek (Woo *et al.* 1990). In addition, the local



Figure 4.2. High Arctic mesic tundra near the Hot Weather Creek sampling site, Ellesmere Island, Canada.

topography causes a drop in wind speed encouraging local rainfall and snowfall deposition and redistribution on the north-facing slopes (Young and Lewkowicz 1990). The prolonged early summer snowmelt on northwest slopes is due to the greater snow accumulation when compared to that of other locations at Hot Weather Creek (Young *et al.* 1997). The soils of the sampled community ranged from predominantly silty (lower slopes) to silty-sand (middle and upper slopes) (Woo *et al.* 1990). The south-facing slopes received the second largest amount of rain and snowfall and the highest energy receipt (Woo *et al.* 1990; Young *et al.* 1997).

Similar to the plant populations sampled at Alexandra Fiord, the growth and reproduction of *C. tetragona* plants from Hot Weather Creek respond to the abiotic and biotic factors of the site and region. In this study, the response of the Hot Weather Creek *C. tetragona* to climate measured at the Eureka H.A.W.S. was examined.

4.2.5. Climate Measurements at Eureka, Ellesmere Island

In this study, the instrumental records from Eureka H.A.W.S. (1948-1997) were used to investigate the climate-*C. tetragona* growth and reproduction relationship, and to reconstruct past climate for central Ellesmere Island. Eureka H.A.W.S. is located 25 km west of Hot Weather Creek. A full description of the Eureka, H.A.W.S. (79° 59'N, 85° 59' W) instrumental data set was provided in Chapter 3.

Pearson's product moment correlation coefficients were calculated between Eureka H.A.W.S. average air temperature and total monthly precipitation for individual summer months (June–September) and for combinations of summer months (e.g., June–August) for the period 1948-1996. In addition, Pearson's product moment correlation coefficients were calculated between Eureka H.A.W.S. average air temperature and the summer Arctic Oscillation (AOS) index, and between Eureka H.A.W.S. total monthly precipitation and the AOS. As described previously in the Discussion section of Chapter 3, the Arctic Oscillation (AO) is a natural mode of Northern Hemisphere circulation (Thompson and Wallace 1998; 2001). The AO is characterized by the seesawing of average sea level pressure above the polar and the mid-latitude regions of the Northern Hemisphere (Thompson and Wallace 1998). Although the AO has been evaluated and modeled during the winter months (January–March) (Shindell *et al.* 1999;

Hartmann *et al.* 2000), recent research has indicated the existence of similar atmospheric pressure reductions during the summer months (Serreze *et al.* 1997; 2000). In this study, the AOS index was calculated based on data from the NCEP/NCAR Reanalysis Project (<http://tao.atmos.washington.edu/data/ao>). The AOS index values were calculated for each year (1948-1996) by averaging the monthly indices for June, July, August and September.

An automated weather station was installed at Hot Weather Creek by the Atmospheric Environmental Service (now Meteorological Service of Canada), Environment Canada in 1988 to monitor air, surface and ground temperatures, solar radiation, wind speed and direction and relative humidity (Headley 1990; Alt *et al.* 1992; Labine *et al.* 1994; Young *et al.* 1997). Year-round instrumental data from Hot Weather Creek is available from 1988 to 1996. The data set ends in 1996 because of destructive chewing of power cables by arctic foxes (*Alopex lagopus*). However, the station was revived in 1999. The data set from this auto-station was not used in this study due to its short duration (9 years).

4.2.6 Plant Sampling and Measurement

In August 1998, 11 *C. tetragona* plants were collected by G.H.R. Henry and M. Svoboda at the Hot Weather Creek site (~90 m. a.s.l.). Plants were collected from visually homogenous communities where *C. tetragona* was dominant. Other species present in the sampled community included *S. arctica*, *D. integrifolia*, *Kobresia myosuroides* (Vill.) Fiori & Paol. and *Pedicularis capitata* Adams. Sampled plants were taken from both the tops and sides of the hummocks and from the hollows. Hummocks were approximately 30-50 cm in diameter and 20-30 cm high. The plants were selected for the longest stems possible with the goal of developing chronologies for the site from which to reconstruct past climate. After harvesting, the individual plants were placed in paper bags, packed in boxes for transport to the laboratory at University of British Columbia, air dried for a week in the lab and then stored in paper bags. The measurement protocol followed in this study was outlined in Chapter 3.

4.2.7. Retrospective Growth and Reproduction Analysis

For the *C. tetragona* population sampled at Hot Weather Creek, two variables of growth (annual stem elongation and leaf production) and two variables of reproduction (annual production of flower buds and flower peduncles) were measured and recorded. A full description of the retrospective growth and reproduction analysis was given in Chapters 2 and 3.

4.2.7.1. Cross-dating: Skeleton Plots and COFECHA

Following standard dendrochronological methods, each stem was cross-dated by hand using skeleton plots of annual growth increments (Fritts 1976; Stokes and Smiley 1968). The software program, COFECHA, available in the Dendrochronological Program Library (DPL), was used to verify further the visual cross-dating and to detect missed measurements and cross-dating errors in the measured series (Holmes *et al.* 1986; Grissino-Mayer 2002). Two to nine stems per plant were cross-dated and eleven plants were used to create the Hot Weather Creek site chronology. The cross-dating protocol followed in this study was provided in Chapter 3.

4.2.7.2. Standardization

In this study, standard chronologies of growth and reproduction for the Hot Weather Creek site were constructed from a subset of all *C. tetragona* plant stems measured. For individual stems to be included in the master site chronologies, each time series needed to be, (1) visually and statistically cross-dated to insure proper placement in time, (2) at least 20 years in length, and (3) positively inter-correlated with the master series (Daniels 2000).

The chronologies were standardized using traditional dendrochronological methods as outlined in Chapter 3 (Fritts 1976; Cook *et al.* 1990). Using the signal-to-noise-ratio (SNR) criterion, flexible cubic splines on the order of 60 years were selected for the chronologies of annual stem elongation, annual production of leaves and flower peduncles. A cubic spline of 40 years was selected for the chronology of annual flower bud production. The biweight robust mean was used to average together the standardized series to calculate the master chronology

(mean value function) for each of the growth and reproductive variables. An explanation of this statistic and its formula was given in Chapter 3. Finally, the standard chronologies were selected for further analysis in order to retain what remained of the low frequency signal. This study followed the same reasoning as described in Chapter 3 for selecting a low-pass digital filter and for using standard chronologies in further analysis.

4.2.8. Descriptive Statistics

Descriptive statistics were calculated for the Hot Weather Creek growth and reproduction chronologies as described in Fritts (1976). The mean, standard deviation, mean sensitivity and first-order autocorrelation were calculated for each standardized chronology. An explanation of these statistics and their formulas was given in Chapter 3.

4.2.9. Mean Correlation Analysis

Mean correlation analysis was carried out using the software program, ARSTAN (available in the DPL) (Cook 1985; Cook and Holmes 1986). Based upon an optimum common interval, the software program computed the amount of variability between-plants, \bar{r}_{bt} , and within-plants, $1 - \bar{r}_{wt}$. This analysis is an alternative approach to a traditional analysis of variance (Briffa and Jones 1990). Further explanation of mean correlation analysis, its purpose and the statistical formulas are found in Chapter 2.

4.2.10. Correlation Analysis

Simple correlation coefficients were calculated to understand the relationship among the growth and reproductive chronologies for the current (year C) and previous year (year C-1) within the Hot Weather Creek site. In addition, correlation coefficients were calculated to examine the relationship of the growth and reproductive chronologies across sites by comparing Hot Weather Creek to the three sites (Lowland, Bench, Dome) at Alexandra Fiord. Not all

chronologies at the Hot Weather Creek and Alexandra Fiord sites were normally distributed, thus the nonparametric Spearman's rank coefficient, r_s was used (Conover 1971).

4.2.11. Response Function Analysis

The relationship between climate variables measured at Eureka H.A.W.S. and *C. tetragona* growth and reproduction chronologies from the Hot Weather Creek site were examined using correlation and response function analysis. A complete description of the correlation and response function analysis was given in Chapter 3.

Climate data from Eureka H.A.W.S., including average monthly air temperature and total monthly precipitation, were used to calculate simple correlation coefficients and response function coefficients for the common overlap period of 1948-1997. A description of the climatic measurements, including monthly average air temperature and total monthly precipitation, from Eureka H.A.W.S. was given in Chapter 3. Correlation and response function coefficients were calculated using the software program PRECONK (Fritts 1996) for the time period of May of the previous year (year C-1) to September of the current year (year C). Two years of previous growth (or reproduction) were included in the response function models to account for lag effects. Through the use of response function analysis, a month, a series of months, a season, or a longer period of time may be identified, and later used to reconstruct climate through transfer function analysis.

In addition to the correlation analysis carried out in PRECONK, Pearson's product moment correlation coefficients were calculated between Eureka H.A.W.S. average air temperature and total monthly precipitation and the growth and reproduction chronologies from Hot Weather Creek and the Lowland site at Alexandra Fiord. These correlations involved Eureka H.A.W.S. climate variables that had been averaged over periods of several summer months (e.g., June-August). The growth and reproductive variables from these two sites were also correlated with the AOS index. Correlations between the climate variables and the AOS index with the growth and reproductive variables from the Bench and Dome sites at Alexandra Fiord were also investigated, but will not be discussed.

4.2.12. Transfer Function Analysis

To calibrate transfer function models, stepwise multiple linear regression analysis was used to predict climate from the Hot Weather Creek and Alexandra Fiord growth and reproduction chronologies. In Chapter 3, a full description of transfer function analysis was provided. The period of common overlap among the Eureka H.A.W.S. climate and the chronology data sets was 1948-1996. The stepwise multiple linear regression analyses were performed using the MGLM procedure in SYSTAT (v. 5.0, 1990-1992). The set of potential predictor variables included growth and reproductive variables from the Hot Weather Creek site and from the Lowland and Bench sites at Alexandra Fiord at years t , $t + 1$, $t + 2$, and $t - 1$. Positive and negative lags were included in the analyses to capture persistence effects in the growth-reproduction-climate relationship (Fritts 1976; Briffa *et al.* 1986; Jacoby and D'Arrigo 1989). In order to develop a parsimonious model, non-significant candidate predictor variables were eliminated by the stepwise procedure ($\alpha = 0.05$) (SYSTAT v. 5.0 1990-1992).

Initial models predicting summer temperature for central Ellesmere Island were calibrated for single months of the growing season (June, July, August, September), for combinations of summer months (e.g., July-August) and for twelve-month periods (e.g., June-May) for the full period of overlap (1948-1996) between the Eureka H.A.W.S. climate data and the Hot Weather Creek and Alexandra Fiord chronologies. Following selection of the full model, investigation of the residuals was carried out using visual examination of residual plots, the modified Levene's test and the correlation test for normality (Neter *et al.* 1996). Next, cross-calibration and verification were carried out to test the general form of the full model before it was used in climate reconstruction. In order to verify the selected model, the full model was divided into two parts following the data-splitting method of Fritts (1976). The data set was split into an "early" period (1948-1978) and a "late" period (1965-1996) and transfer functions were calibrated for each period using stepwise regression on the same predictor variables as the full model (Case and MacDonald 1995). The calibration models developed for the early (1948-1978) and late periods (1965-1996) were then verified over the late (1979-1996) and early (1948-1964) verification periods. Statistics including Pearson's product-moment correlation coefficient (r), reduction of error (RE), coefficient of efficiency (CE) and the first difference sign test were calculated for both verification periods (Fritts 1976; Briffa 1998). An explanation of the formulas for the verification statistics were given in Chapter 3. Once the selected model was

successfully calibrated and verification statistics and tests of parametric assumptions were carried out, the full model was considered time stable and was used to reconstruct climate for the period prior to instrumental data on central Ellesmere Island.

4.3. Results

4.3.1. Chronology Characteristics for Hot Weather Creek

Between 49 and 56 stems representing 11 plants were used to create two growth and two reproductive chronologies for the Hot Weather Creek site (Table 4.1). The annual growth increment and annual production of leaves chronologies covered a 53 year time period from 1945-1997 and were the longest chronologies for the site. Because the plants were collected in early August, there still existed the possibility of vegetative growth and formation of reproductive structures by the plants in the late summer, thus measurements for 1998 were not included in the chronologies.

Examination of the \bar{r}_{br} values for the growth and reproduction chronologies at the Hot Weather Creek site revealed a weak common signal in the chronologies (Table 4.2). As expected, the within-plant noise, $1 - \bar{r}_{wt}$, was high for both growth and reproductive chronologies.

Investigation of the mean sensitivity and standard deviation values at Hot Weather Creek revealed the values for vegetative growth were much lower than those for reproduction (Table 4.3). Mean sensitivity was particularly high for the chronology for annual production of flower buds. The first-order autocorrelation values were extremely low across all vegetative growth and reproduction chronologies. In general, high mean sensitivity and standard deviation values and low first-order autocorrelation values are an indication that the chronology is sensitive to yearly climate conditions (Fritts and Shatz 1975), such as the reproductive variables in this study.

The signal-to-noise ratios (SNR) for the Hot Weather Creek chronologies were low, an indication of the high amount of noise present in the chronologies (Cook and Briffa 1990).

Table 4.1. Annual plant performance (non-standardized data) of *Cassiope tetragona* from Hot Weather Creek, Ellesmere Island, Canada. AGI = Annual Growth Increment; Leaf = annual production of leaves; Bud = annual production of flower buds; Peduncle = annual production of flower peduncles.

	AGI ¹	Leaf ²	Bud ³	Peduncle ³
Chronology Length	1945-1997	1945-1997	1949-1997	1952-1997
# of Years	53	53	49	46
Sample size (plants)	11	11	11	11
# of Stems Measured	56	54	51	49
# of Stems per Plant	2 to 9	2 to 9	2 to 9	2 to 9
Mean	6.05	11.94	0.36	0.26
Standard Deviation	3.12	2.03	0.63	0.53
Maximum	25.99	32.00	4.00	3.00
Minimum	1.26	6.00	0.00	0.00
Median	5.49	12.00	0.00	0.00

AGI¹ = annual growth increment estimates are measured in mm per year.

Leaf² = annual leaf production estimates are for four leaf rows on a stem.

Bud³ and Ped³ = estimates for annual production of flower buds and peduncles are for 2 of 4 leaf rows on a stem.

Table 4.2. Mean correlation results from the Hot Weather Creek sampling site. The mean correlation technique (Briffa and Jones 1990) indicates the climate signal strength present in the growth and reproductive chronologies (see Chapter 2). Chronologies cover a common time interval selected by the software program ARSTAN to maximize the number of stems included in the calculations. The common intervals are shorter than those reported in Table 4.1. AGI = Annual Growth Increment; Leaf = annual production of leaves; Bud = annual production of flower buds; Peduncle = annual production of flower peduncles.

	AGI	Leaf	Bud	Peduncle
Common Interval	1967-1997	1969-1997	1974-1997	1973-1997
# of Plants	11	11	11	11
# of Stems	25	26	24	20
\bar{r}_{bt}	0.07	0.04	0.02	0.02
$1 - \bar{r}_{wt}$	0.90	0.92	0.98	0.92

\bar{r}_{bt} is the between-plant signal. It is similar to the fractional variance component for between plants.

$1 - \bar{r}_{wt}$ is the within-plant noise. It is similar to the fractional variance component for within plants.

Table 4.3. Growth and reproductive standard chronology statistics (from standardized data) for *Cassiope tetragona* from the Hot Weather Creek site. AGI = Annual Growth Increment; Leaf = annual production of leaves; Bud = annual production of flower buds; Peduncle = annual production of flower peduncles.

	AGI ¹	Leaf ²	Bud ³	Ped ³
Chronology Length	1945-1997	1945-1997	1949-1997	1952-1997
n	53	53	49	46
Mean	0.98	0.98	0.42	0.39
Standard Deviation	0.11	0.07	0.62	1.34
Mean Sensitivity	0.12	0.08	1.12	0.45
1st-order Autocorrelation	-0.02	-0.01	0.07	0.05
Signal to Noise Ratio	0.63	0.41	0.20	0.12

AGI¹ = annual growth increment estimates are measured in mm per year.

Leaf² = annual leaf production estimates are for four leaf rows on a stem.

Bud³ and Ped³ = estimates for annual production of flower buds and peduncles are for 2 of 4 leaf rows on a stem.

However, as was the case in Chapter 3, the SNR values were the largest for each master chronology constructed when compared with other standardization methods attempted.

Standard chronologies (mean value functions) were constructed for each of the growth and reproductive variables for the Hot Weather Creek site (Figure 4.3 a - h). A minimum sample depth of three stems was maintained for each chronology. The chronologies for annual stem elongation and production of leaves showed moderate variability throughout their entire lengths. The chronology for annual production of flower buds showed higher inter-annual variability throughout the entire chronology. In contrast, the chronology for annual production of flower peduncles exhibited low variability, punctuated by infrequent excursions away from the mean. Definitive statements regarding any long-term trends in the mean value functions are impossible given the standardization methods used and the lengths of the chronologies.

4.3.2. Correlation Analysis

At the Hot Weather Creek site, correlations between the current year (year C) and previous year (year C-1) chronologies for annual stem elongation with current year (year C) and previous year (year C-1) chronologies for annual production of leaves and flower buds were positive and significantly different from zero ($P < 0.01$) (Table 4.4). The correlations between current year (year C) and previous year (year C-1) chronologies for annual production of leaves with the current year (year C) and previous year (year C-1) chronologies for annual production of flower buds were also positive and significantly different from zero ($P < 0.01$).

Investigation of the correlations between the Hot Weather Creek and Alexandra Fiord vegetative growth and reproduction chronologies revealed no significant coefficients (Table 4.5). The correlation coefficients for growth and reproduction were not significantly different from zero ($P > 0.05$).

Correlations between Eureka H.A.W.S. average air temperature and total monthly precipitation were negative and significantly different from zero for the months of July ($P < 0.05$) and August ($P < 0.01$), and for the periods June-August ($P < 0.05$), and July-August ($P < 0.01$) (Table 4.6). Correlation coefficients were negative and significantly different from zero for the

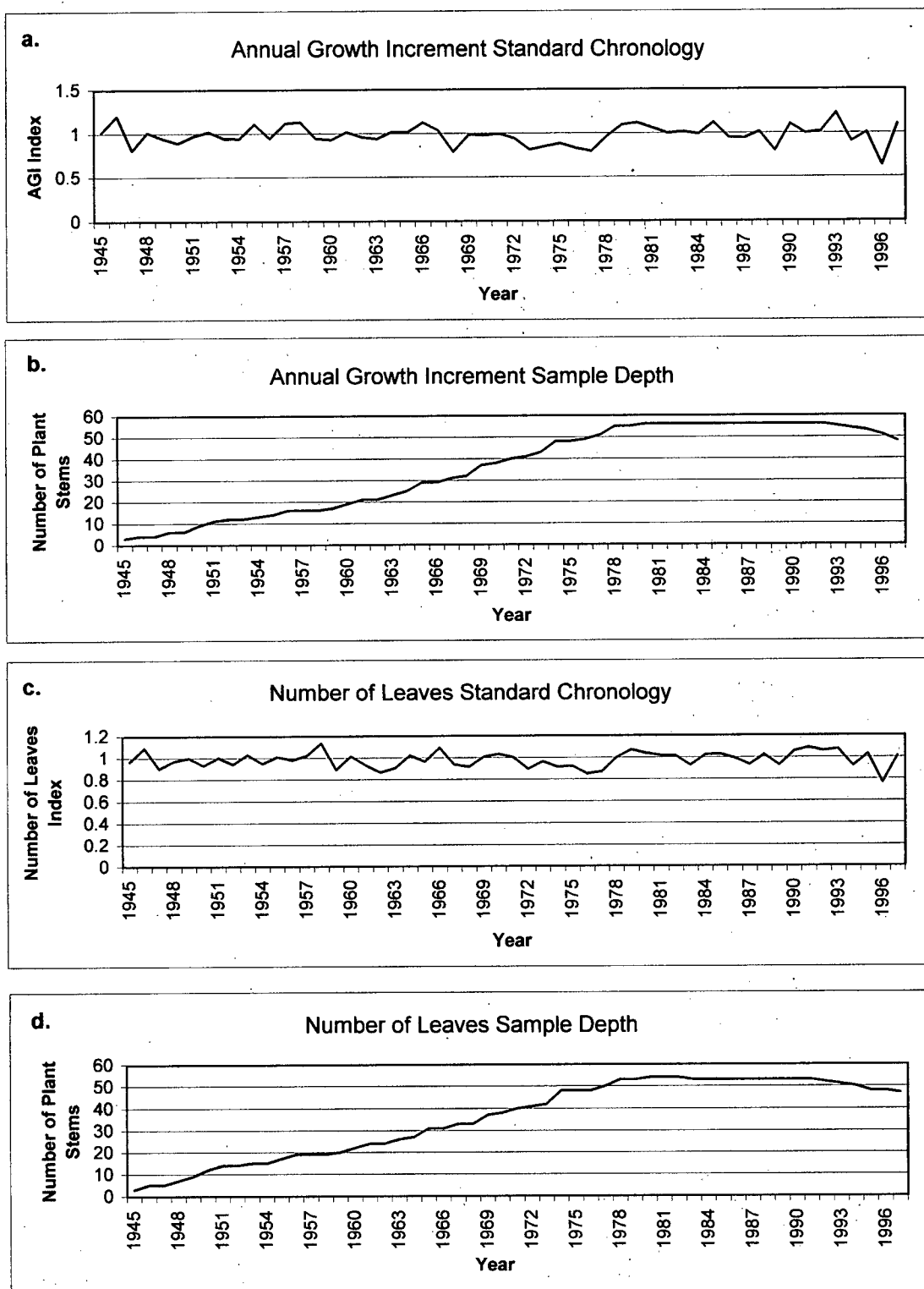


Figure 4.3. (a.) Standardized chronologies and (b.) sample depth for annual growth increment (AGI), and (c.) standardized chronologies and (d.) sample depth for annual production of leaves chronologies for Hot Weather Creek, Ellesmere Island. Minimum number of stems measured was three.

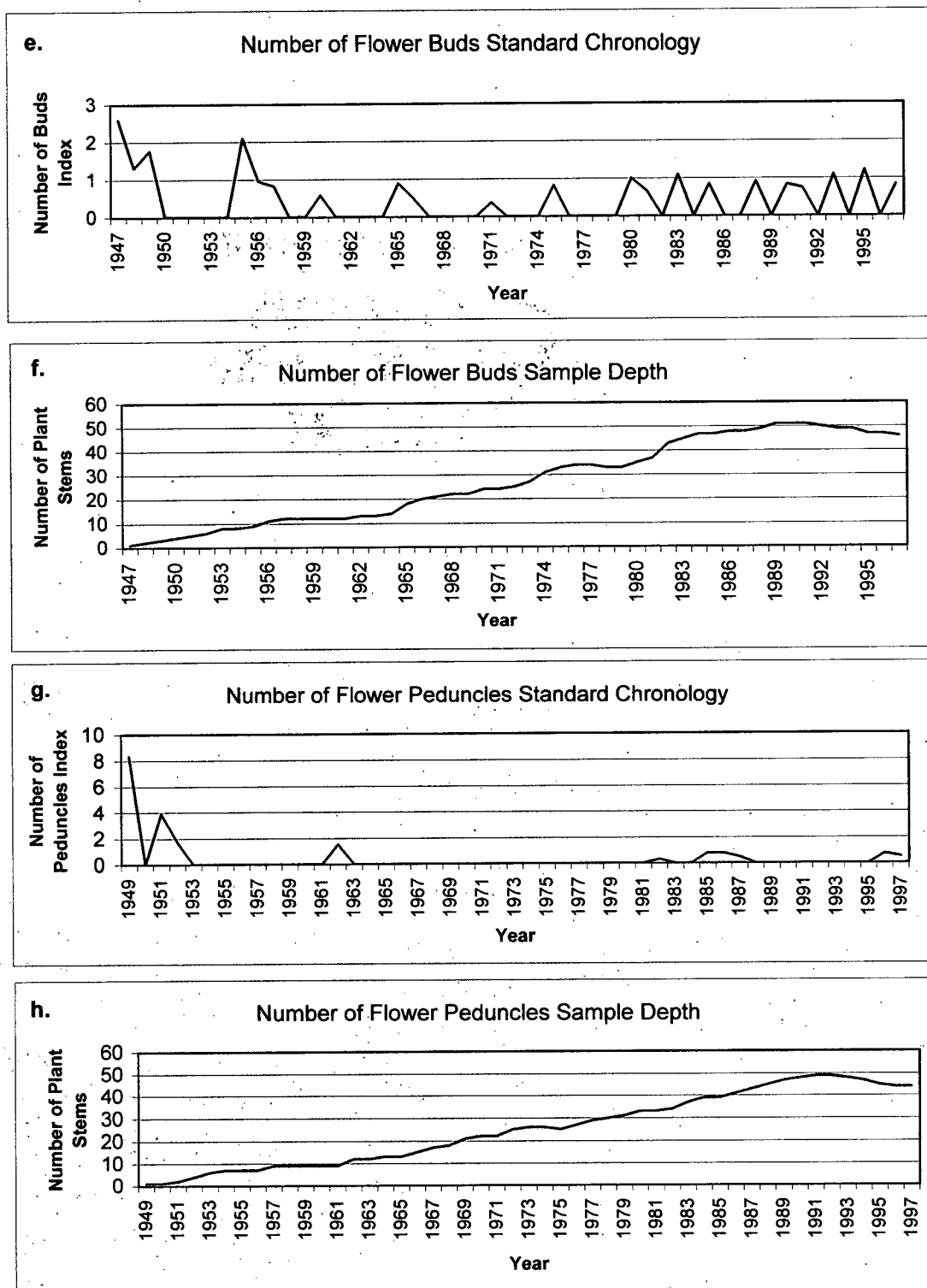


Figure 4.3. (e.) Standardized chronologies and (f.) sample depth for annual production of flower buds, and (g.) standardized chronologies and (h.) sample depth for annual production of flower peduncle chronologies for Hot Weather Creek, Ellesmere Island. Minimum number of stems measured was three.

Table 4.4. Spearman's rank correlation coefficients showing relations between values of the current year (year C) and previous year (year C-1) of two growth and two reproductive chronologies from Hot Weather Creek. AGI = Annual Growth Increment; Leaf = annual production of leaves; Bud = annual production of flower buds; Peduncle = annual production of flower peduncles. $n = 46$ for correlations between current year (year C) variables. $n = 45$ when previous year (year C-1) variables are included in the correlation.

	Annual Growth Increment		Number of Leaves		Number of Flower Buds		Number of Flower Peduncles	
	year C	year C-1	year C	year C-1	year C	year C-1	year C	year C-1
AGI (year C)	1.00							
Leaf (year C)	0.76 **		1.00					
Bud (year C)	0.52 **		0.39 **		1.00			
Peduncle (year C)	-0.02		-0.16		-0.09		1.00	
AGI (year C-1)	0.08	1.00	0.07		-0.07		0.08	
Leaf (year C-1)	0.23	0.75 **	0.11	1.00	0.03		0.04	
Bud (year C-1)	-0.02	0.48 **	0.00	0.40 **	-0.16	1.00	0.05	
Peduncle (year C-1)	-0.05	-0.03	-0.06	-0.19	0.03	-0.19	0.31 *	1.00

* = $P < 0.05$; ** = $P < 0.01$.

Table 4.5. Inter-site comparisons of the growth and reproductive chronologies from Hot Weather Creek and Alexandra Fiord (Lowland, Bench, Dome sites) using Spearman's rank correlation. None of the correlations were significantly different from zero ($* = P < 0.05$). AGI = Annual Growth Increment; Leaf = annual production of leaves; Bud = annual production of flower buds; Ped = annual production of flower peduncles.

	Alexandra Fiord		
	Lowland AGI	Bench AGI	Dome AGI
Hot Weather Creek AGI n = 53	0.09	-0.15	0.24
	Lowland Leaf	Bench Leaf	Dome Leaf
Hot Weather Creek Leaf n = 53	0.25	-0.14	0.15
	Lowland Bud	Bench Bud	Dome Bud
Hot Weather Creek Bud n = 49	0.16	-0.04	-0.27
	Lowland Ped	Bench Ped	Dome Ped
Hot Weather Creek Ped n = 46	-0.05	0.13	0.09

Table 4.6. Pearson's correlation coefficients showing the relationship between Eureka H.A.W. S. average air temperature (T) and total precipitation (P) for individual summer months, and combinations of summer months for the period, 1948-1996. $n = 49$.

Temperature & Precipitation	r
June T & P	-0.131
July T & P	-0.347 *
August T & P	-0.423 **
September T & P	0.187
June-July T & P	-0.219
June-August T & P	-0.281 *
June-September T & P	-0.026
July-August T & P	-0.410 **
July-September T & P	-0.028
August-September T & P	0.107

* $P < 0.05$, ** $P < 0.01$.

AOS index and July ($P < 0.01$), June-July ($P < 0.05$), June-August ($P < 0.05$), and July-August ($P < 0.05$) average air temperature (Table 4.7). In addition, correlation coefficients were positive and significantly different from zero for the AOS index and July ($P < 0.05$), August ($P < 0.05$), June-July ($P < 0.01$), June-August ($P < 0.01$), June-September ($P < 0.01$), July-August ($P < 0.01$), and July-September ($P < 0.05$) total monthly precipitation (Table 4.7).

4.3.3. Response Functions

4.3.3.1. Response of Hot Weather Creek *Cassiope tetragona* to Eureka H.A.W.S. Climate

To understand the relationships among the Hot Weather Creek growth and reproduction chronologies and the climate variables recorded at Eureka H.A.W.S., including average monthly air temperature and total monthly precipitation, response function analysis was used. While a cause-and-effect relationship cannot be determined by response function analysis, the technique provides useful information on which aspects of the climate-growth or climate-reproduction relationship are important. Both the sign and magnitude of the response function coefficients are clues to understanding the plant-climate relationship.

The response function model relating annual stem elongation and number of leaves to average air temperature and total monthly precipitation showed no significant coefficients (except for number of leaves and previous May precipitation) (Figure 4.4). The response function coefficients for growth were not significantly different from zero ($P > 0.05$). However, the two growth chronologies were positively related to average air temperature in the current May and September. In addition, annual stem elongation was positively related to previous July, August and September average air temperature, while the annual production of leaves was positively related to previous June, July, August and September average air temperature. The amount of variance explained by the two climatic parameters and previous growth was moderate, only 46-49%.

The chronology for annual production of flower buds was negatively associated with previous September total monthly precipitation and positively associated with current February average air temperature. Both coefficients were significantly different from zero ($P < 0.05$)

Table 4.7. Pearson's correlation coefficients showing the relationship between Eureka H.A.W.S. average air temperature (T) and total precipitation (P) with the summer Arctic Oscillation index (AOS) for the period 1948-1996. $n = 49$.

	AOS
June T	-0.159
July T	-0.386 **
August T	-0.187
September T	-0.009
June-July T	-0.287 *
June-August T	-0.310 *
June-September T	-0.197
July-August T	-0.360 *
July-September T	-0.189
August-September T	-0.087
June P	0.272
July P	0.344 *
August P	0.288 *
September P	-0.056
June-July P	0.429 **
June-August P	0.474 **
June-September P	0.416 **
July-August P	0.411 **
July-September P	0.353 *
August-September P	0.205

* $P < 0.05$, ** $P < 0.01$.

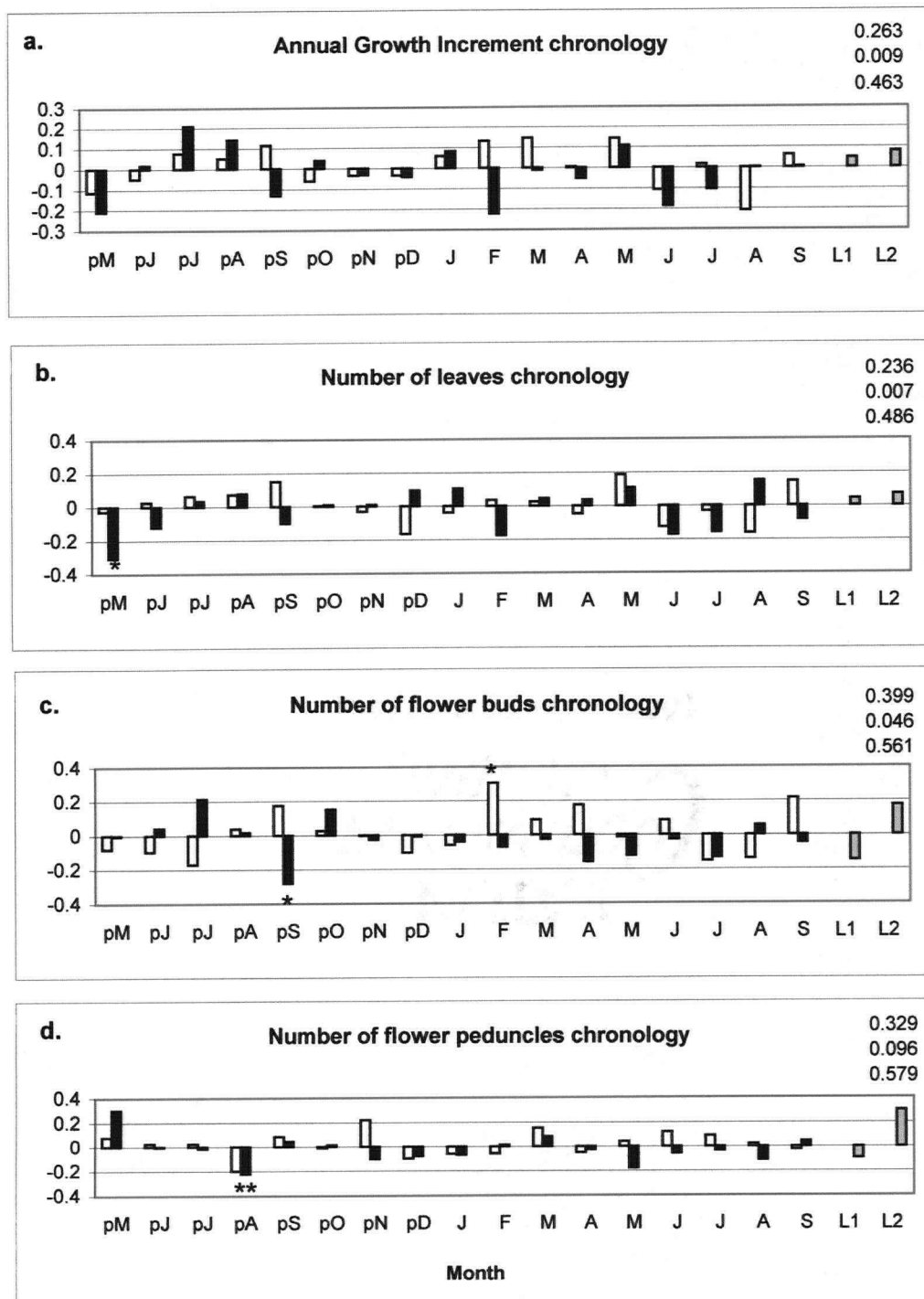


Figure 4.4. Response function coefficients relating Hot Weather Creek growth and reproduction chronologies to average monthly air temperature and total precipitation from the Eureka H.A.W.S. from 1948-1997. The time period covered begins in the previous May (pM) and continues to the current September (S). L1 and L2 are the one and two year lag effects, denoted by gray bars on the far right of the graphs. In the upper right hand corner of each graph three percentage of variance explained are given: amount of variance explained by climate alone (top), by previous growth or reproduction alone (middle), and by climate and previous growth or reproduction together (bottom). Temperature = white bars. Precipitation = black bars. Annual growth increment and number of leaves, $n = 50$; number of flower buds, $n = 49$; number of flower peduncles, $n = 46$. * $P < 0.05$.

(Figure 4.4). The flower bud chronology was also positively related to current June and September and previous August and September average air temperature, but the coefficients were not significantly different from zero. The flower peduncle chronology and previous August average air temperature and total monthly precipitation were positive and significantly different from zero ($P < 0.05$). In addition, the flower peduncle chronology and average air temperature in the current May, June, July and August, as well as the previous May, June, July and September were positive, but not significantly different from zero ($P > 0.05$). The amount of explained variance by the two climatic variables and previous reproduction was moderately high (56-58%). Using the results from the response function analysis of the Hot Weather Creek chronologies as a guide, transfer function models to reconstruct past climate for central Ellesmere Island were developed.

4.3.3.2. Correlation Analysis of Hot Weather Creek and Lowland *Cassiope tetragona* Chronologies with the Summer Arctic Oscillation Index and Eureka H.A.W.S. Climate

Correlation analysis was used to understand the relationships among the Hot Weather Creek and Lowland growth and reproduction chronologies with the AOS index, as well as, the Eureka H.A.W.S. climate variables. At the Lowland site, annual stem elongation and production of leaves were positively correlated with June ($P < 0.05$), June-July ($P < 0.05$), June-August ($P < 0.05$), and June-September ($P < 0.05$) average air temperature and the coefficients were significantly different from zero (Table 4.8; Appendix III). The correlation between annual production of leaves and July ($P < 0.05$) average air temperature was also positive and significantly different from zero. Correlations between the Lowland growth variables and total monthly precipitation were not significantly different from zero ($P > 0.05$), but the correlation coefficients were consistently negative (Table 4.8; Appendix III). Correlations between Lowland annual production of flower buds and flower peduncles with July ($P < 0.05$) and June-July ($P < 0.05$) total monthly precipitation, respectively, were negative. The coefficients were significantly different from zero ($P < 0.05$).

At the Hot Weather Creek site, correlations between the two growth variables and average air temperature were not significantly different from zero ($P > 0.05$), but all correlations were positive (Table 4.9; Appendix IV). In general, the correlations between the two growth

Table 4.8. Pearson's correlation coefficients showing the relationship between Eureka H.A.W.S. average air temperature (T) and total precipitation (P) and Lowland, Alexandra Fiord growth and reproduction chronologies for the period, 1948-1996. $n = 49$. AGI = annual growth increment, Leaf = number of leaves, Buds = number of flower buds, and Peduncles = number of flower peduncles.

	Lowland AGI	Lowland Leaf	Lowland Buds	Lowland Peduncles
June T	0.355 **	0.340 *	-0.025	0.172
July T	0.263	0.294 *	0.141	0.223
August T	0.080	0.024	-0.101	-0.110
September T	0.228	0.206	0.073	0.274
June-July T	0.374 **	0.377 *	0.044	0.223
June-August T	0.335 *	0.314 *	-0.006	0.133
June-September T	0.322 *	0.298 *	0.033	0.220
July-August T	0.212	0.191	0.013	0.055
July-September T	0.263	0.238	0.056	0.215
August-September T	0.220	0.178	0.017	0.177
June P	-0.035	-0.083	0.116	-0.258
July P	-0.116	-0.149	-0.329 *	-0.193
August P	-0.089	-0.048	0.167	0.068
September P	-0.066	0.071	0.071	0.123
June-July P	-0.177	-0.169	-0.225	-0.294 *
June-August P	-0.135	-0.147	-0.060	-0.167
June-September P	-0.147	-0.110	-0.030	-0.111
July-August P	-0.133	-0.128	-0.109	-0.083
July-September P	-0.145	-0.090	-0.072	-0.030
August-September P	-0.106	-0.002	0.172	0.119

* $P < 0.05$, ** $P < 0.01$.

Table 4.9. Pearson's correlation coefficients showing the relationship between Eureka H.A.W.S. average air temperature (T) and total precipitation (P) and Hot Weather Creek (HWC) growth and reproduction chronologies for the period, 1948-1996. $n = 49$. AGI = annual growth increment, Leaf = number of leaves, Buds = number of flower buds, and Peduncles = number of flower peduncles.

	HWC AGI	HWC Leaf	HWC Buds	HWC Peduncles
June T	0.049	0.044	0.233	0.184
July T	0.216	0.122	0.183	0.109
August T	0.010	0.007	0.097	0.037
September T	0.156	0.262	0.302 *	0.110
June-July T	0.131	0.086	0.250	0.182
June-August T	0.110	0.073	0.243	0.162
June-September T	0.146	0.175	0.301 *	0.156
July-August T	0.135	0.077	0.177	0.090
July-September T	0.174	0.217	0.295 *	0.121
August-September T	0.132	0.216	0.288 *	0.105
June P	-0.268	-0.235	-0.087	0.015
July P	-0.251	-0.228	-0.234	-0.038
August P	-0.037	0.177	-0.105	-0.070
September P	-0.008	-0.137	0.015	0.042
June-July P	-0.348 *	-0.312	-0.244	-0.026
June-August P	-0.267	-0.115	-0.234	-0.060
June-September P	-0.249	-0.154	-0.210	-0.041
July-August P	-0.188	-0.036	-0.211	-0.070
July-September P	-0.174	-0.084	-0.195	-0.048
August-September P	-0.034	0.072	-0.077	-0.035

* $P < 0.05$, ** $P < 0.01$.

variables and total monthly precipitation were negative, but they were not significantly different from zero ($P>0.05$). However, the correlation between annual stem elongation and June-July total monthly precipitation was negative ($P<0.05$) and significantly different from zero. Correlations between annual production of flower buds with September ($P<0.05$), June-September ($P<0.05$), July-September ($P<0.05$) and August-September ($P<0.05$) average air temperature were positive and significantly different from zero. Correlations between the two climate variables and annual production of flower peduncles were not significantly different from zero ($P>0.05$).

Lastly, correlations coefficients between the AOS index and Lowland annual stem elongation were negative and significantly different from zero ($P<0.05$) (Table 4.10). The correlation between Hot Weather Creek annual stem elongation and AOS index was also negative, but not significantly different from zero ($P>0.05$). Similarly, the correlations between Lowland and Hot Weather Creek annual production of leaves and AOS index were negative, but not significantly different from zero ($P>0.05$). Correlations between Lowland and Hot Weather Creek reproduction variables and the AOS index were also not significantly different from zero ($P>0.05$).

4.3.4. Transfer Functions

4.3.4.1. Reconstruction of Summer Temperature for Central Ellesmere Island

Standard chronologies from Hot Weather Creek and the Lowland and Bench sites at Alexandra Fiord were used to reconstruct summer temperature for central Ellesmere Island. Following examination of the response function coefficients from Hot Weather Creek and Alexandra Fiord, and consideration of the results from Chapter 3 and previous research on the relationship of *C. tetragona* growth and reproduction to summer climate conditions (Callaghan *et al.* 1989; Havström *et al.* 1993; 1995; Johnstone and Henry 1997), it was decided to reconstruct average summer air temperature. For reasons similar to those outlined in Chapter 3, reconstruction of past precipitation was not considered in this study. In addition, it was decided not to pursue reconstruction of climate using only the Hot Weather Creek chronologies. Initial investigations using stepwise multiple linear regression analysis on the Hot Weather Creek

Table 4.10. Pearson's correlation coefficients relating Lowland and Hot Weather Creek (HWC) growth and reproduction chronologies to the summer Arctic Oscillation index (AOS) for the period 1948-1996. AGI = annual growth increment, Leaf = number of leaves, Buds = number of flower buds, Peduncles = number of flower peduncles. n = 49.

	Lowland AGI	Lowland Leaf	Lowland Buds	Lowland Peduncles
AOS	-0.320 *	-0.250	0.015	-0.067
	HWC AGI	HWC Leaf	HWC Buds	HWC Peduncles
AOS	-0.186	-0.131	0.024	-0.165

chronologies revealed that only a small amount of the climatic variance was explained ($R^2_{adj} < 0.30$, adjusted for loss of degrees of freedom).

Using stepwise multiple linear regression analysis to investigate single summer months (May, June, July, August, September), combinations of summer months (e.g., July-August) and twelve-month periods (e.g., June-May), the time period of August-September was selected as the best potential transfer function model based on the coefficient of determination, adjusted for loss of degrees of freedom (R^2_{adj}) (Figure 4.5). Although many of the response function coefficients for summer months were not significantly related to growth and reproduction variables from the Hot Weather Creek and Alexandra Fiord sites, the inclusion of these variables in the final transfer function model was thought to be biologically important. Furthermore, previous work in climate reconstruction using *C. tetragona* supported this decision (Havström *et al.* 1995; Johnstone and Henry 1997).

A dendroclimatological reconstruction of August-September average air temperature was accomplished using the transfer function techniques recommended by Fritts (1976) (Table 4.11). The full model covered the time period of 1948-1996 and explained 66% of the climatic variance (R^2_{adj} , adjusted for loss of degrees of freedom). Parametric assumptions regarding normality, independence and homogeneity of variance were not violated for the full model. In Table 4.12, the cross-calibration results showed the models accounted for 23% (early model) and 63% (late model) of the variance (R^2_{adj} , adjusted for loss of degrees of freedom) in the temperature record. The positive CE (0.140; 0.070) and RE (0.150; 0.140) values, in addition to the significant Pearson's product-moment correlation coefficients ($r = 0.680$; $r = 0.420$), indicated that there was evidence of meaningful climatic information in the August-September air temperature reconstruction (Fritts 1976; Fritts *et al.* 1979). The sign tests for the early and late verification periods were not significant. Examination of the residuals for each calibration period showed that they met all assumptions of parametric statistics. The sub-period transfer function estimates of August-September average air temperature passed three out of the four verification tests and thus, were considered time stable. Therefore, the model calculated over the full period (1948-1996) was also considered time stable and could be used to reconstruct average air temperature for the time period prior to instrumental data collection.

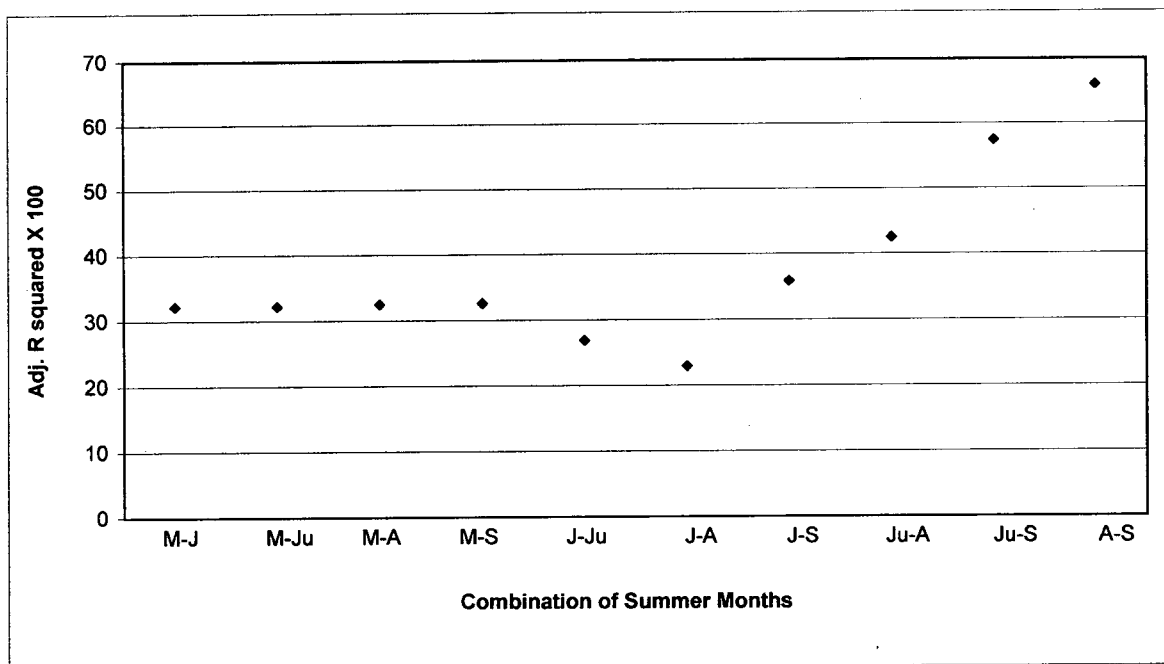


Figure 4.5. Graph of the adjusted coefficients of determination x 100 produced from *Cassiope tetragona* growth and reproduction chronologies from the Hot Weather Creek and Alexandra Fiord sites, Ellesmere Island. The potential models are based upon different combinations of average monthly summer air temperature from 1948-1996. The R^2 adj was greatest for August-September average air temperature (66%). $n = 49$. M = May, J = June, Ju = July, A = August, S = September.

Table 4.11. Climate transfer function for August-September average air temperature for central Ellesmere Island based on *Cassiope tetragona* growth and reproduction chronologies from Hot Weather Creek and the Lowland and Bench sites at Alexandra Fiord, Ellesmere Island. Transfer function was developed for time period, 1948-1996. n = 49.

Predictor Variables	Estimated Regression Coefficients	Standard Error	p-value	Multiple R	Multiple R ²	Adjusted Multiple R ²
Constant	-48.306	7.287	0.000	0.866	0.750	0.660
LowAGI	4.307	3.128	0.178			
LowAGI3	-16.423	6.739	0.020			
LowLEA3	43.926	10.396	0.000			
LowBUD2	-1.342	0.373	0.001			
BenAGI	8.866	2.238	0.000			
BenAGI1	4.771	2.116	0.031			
BenBUD2	1.055	0.302	0.001			
BenBUD3	-1.179	0.300	0.000			
HWCAGI1	2.984	1.569	0.066			
HWCLEA	4.692	2.362	0.055			
HWCLEA3	-6.138	2.219	0.009			
HWCBUD	0.612	0.252	0.021			

Low = Lowland site; Ben = Bench site; HWC = Hot Weather Creek site. AGI = Annual Growth Increment for year C; AGI1 = Annual Growth Increment for year C+1; AGI3 = Annual Growth Increment for year C-1; LEA = number of leaves for year C; LEA3 = number of leaves for year C-1; BUD = number of flower buds for year C; BUD2 = number of flower buds for year C+2; BUD3 = number of flower buds for year C-1.

Table 4.12. Calibration and verification statistics for predicting August-September average air temperature from *Cassiope tetragona* growth and reproduction chronologies from the Hot Weather Creek and Lowland and Bench sites at Alexandra Fiord, Ellesmere Island.

Model	Calibration Period	n	X	x	R	R ²	R ² adj
Early	1948-1978	31	44	3	0.556	0.309	0.232
Late	1965-1994	30	44	5	0.829	0.687	0.626
Full	1948-1994	47	44	12	0.866	0.750	0.660

Model	Verification Period	n	r	r ²	RE	CE	Sign Test (hit/miss)
Late	1979-1994	16	0.680**	0.460	0.150	0.140	12/5 ns
Early	1948-1964	17	0.420*	0.180	0.140	0.070	10/5 ns

Note: n = sample size; X, the initial number of candidate predictor variables in stepwise multiple regression analysis; x, the final number of predictor variables after elimination of insignificant variables by stepwise regression analysis; R, multiple correlation coefficient, R², multiple coefficient of determination; R²adj, multiple coefficient of determination adjusted for loss of degrees of freedom; r, correlation coefficient, r², coefficient of determination; RE, reduction of error statistic; CE, coefficient of efficiency.

* = P < 0.05; ** = P < 0.01; ns = not significant.

The model of reconstructed August-September average air temperature for central Ellesmere Island for the period 1949-1994 tended to follow most of the extreme peaks and troughs of the observed data (Figure 4.6). There appeared to be a tendency for the model to underestimate slightly the observed data in the first half of the common overlap period. In the second half of the common overlap period, the model tended to overestimate the observed data. Unfortunately, as the length of the August-September average air temperature reconstruction (1949-1994) was only as long as the Eureka H.A.W.S. instrumental data set (1948-1994), climate for the period prior to meteorological observations on Ellesmere Island could not be reconstructed. The August-September average air temperature model was shortened by the length of the shortest predictor chronology (Hot Weather Creek, number of flower buds, 1949-1997) and by lags and leads included in the reconstruction. Despite the shorter length of the model for August-September average air temperature for central Ellesmere Island, the reconstruction covered a period of 45 years and the amount of explained climatic variance was high ($R^2_{adj} = 0.66$).

While conclusions concerning low frequency variance would be tenuous given the length of the reconstruction and the type of standardization used, there appeared to be high frequency variance throughout the length of the reconstruction as shown in the departures from the 1961-1990 mean (Figure 4.7). A period of warmth characterized the first third of the reconstruction, from approximately 1951-1960 (Figures 4.7 and 4.8 a). The 5-year and 10-year non-overlapping means calculated from the reconstructed August-September temperature departures showed the directional tendencies of the reconstruction (Figure 4.8) (Graybill and Shiyatov 1989). The warmest 5-year (1954-1958) and 10-year (1951-1960) positive temperature departure means occurred during this time period. In addition, the first three single warmest summer positive temperature departures occurred during this period (Table 4.13). From approximately 1961-1980, the departures became more negative indicating cooler temperatures (Figures 4.7 and 4.8 a). The cooling spell was evident in the 5-year (1976-1980; 1971-1975; 1961-1965) and 10-year (1971-1980; 1961-1970) means, as well as in the departures for the summers of 1969, 1976 and 1979 (Table 4.13). The cold period was punctuated by the coldest individual summer temperature departure (1961), as well as the negative departures during the summers of 1964, 1975, 1976 and 1979 (Table 4.13). Finally, from the early 1980s into the early 1990s, the trend returned to warmer conditions, but the temperatures were slightly less pronounced than those from the early portion of the reconstruction (Figures 4.7 and 4.8 a). In Table 4.13, five of the

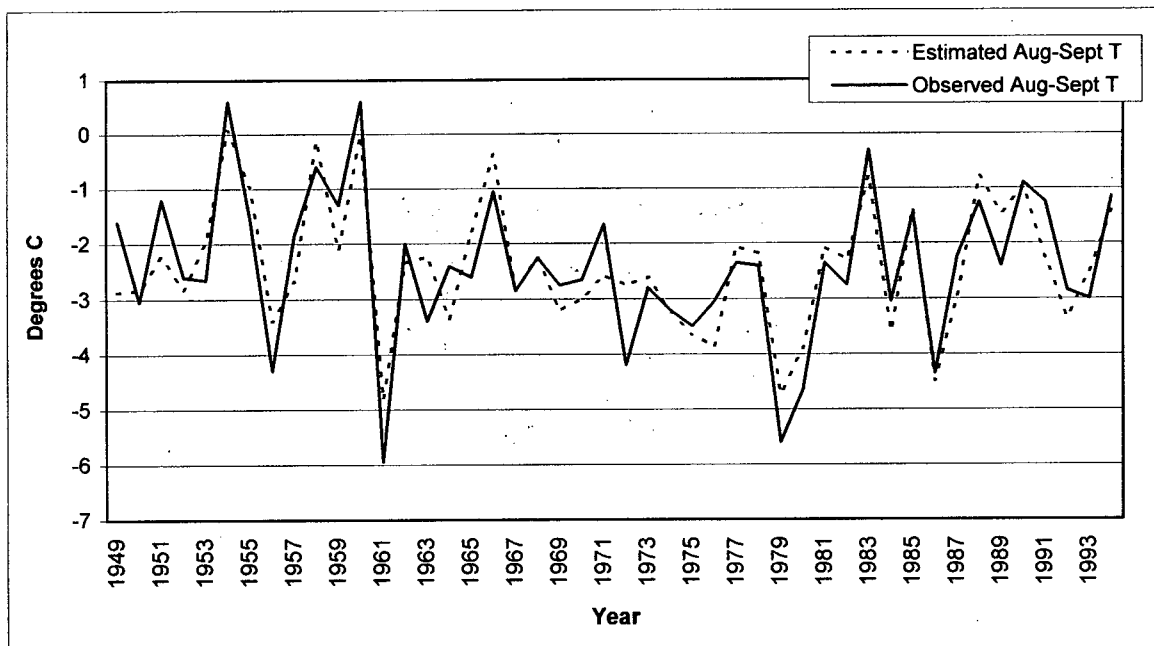


Figure 4.6. Observed and estimated average August-September air temperature for central Ellesmere Island, Canada from 1949-1994.

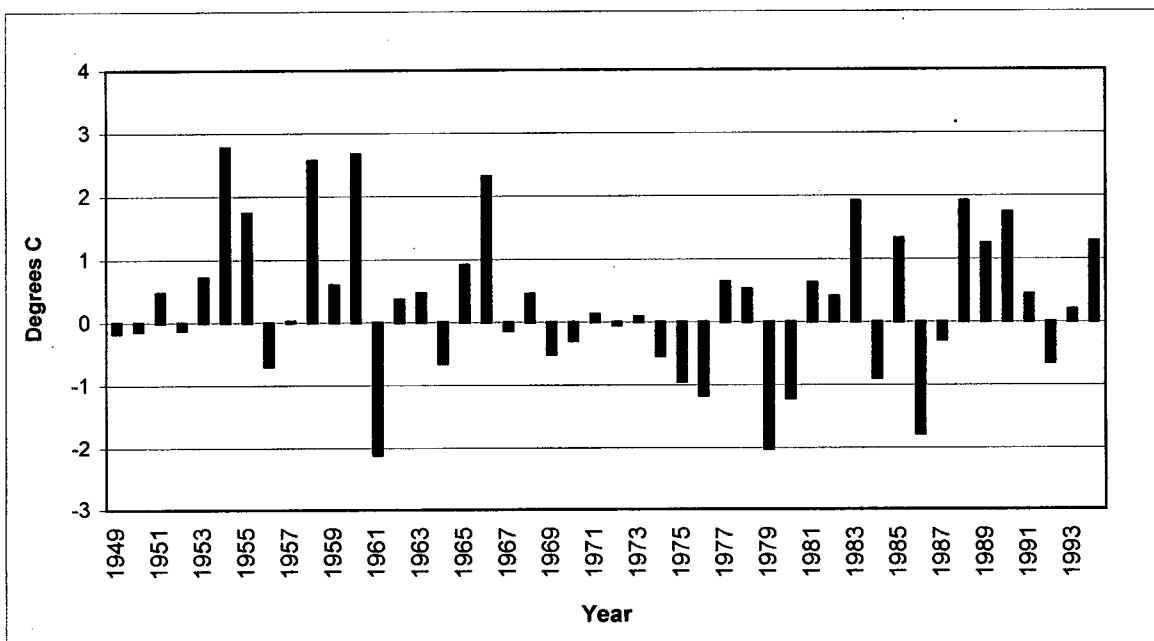


Figure 4.7. The reconstruction of August-September average air temperature departures for central Ellesmere Island relative to the 1961-1990 mean from Eureka H.A.W.S. on western Ellesmere Island.

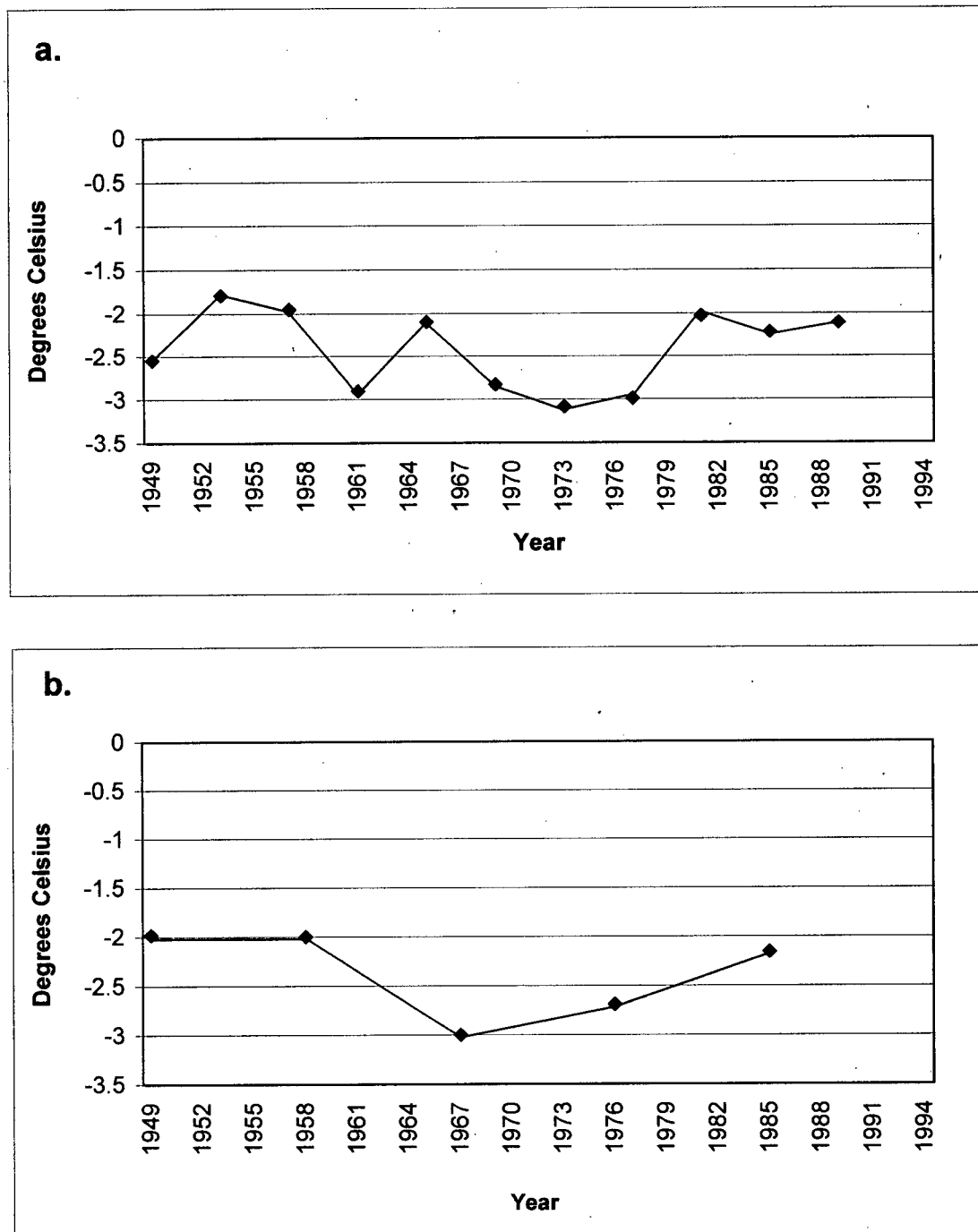


Figure 4.8: (a) 5-year and (b) 10-year non-overlapping means calculated from the estimated August-September average air temperature departures for central Ellesmere Island from the Eureka H.A.W.S. mean (1961-1990).

Table 4.13. Largest temperature anomalies and trends for individual years, and for extreme mean values from among all 5-year and 10-year non-overlapping periods. The temperatures are shown as anomalies with respect to the 1961-1990 Eureka H.A.W.S. mean.

Individual Summers

Lowest		Highest	
Year	Anomaly (°C)	Year	Anomaly (°C)
1961	-2.11	1954	2.77
1979	-2.02	1960	2.67
1986	-1.78	1958	2.57
1980	-1.21	1966	2.31
1976	-1.17	1988	1.91
1975	-0.95	1983	1.91
1984	-0.90	1955	1.73
1956	-0.69	1990	1.73
1964	-0.65	1985	1.32
1992	-0.65	1994	1.28

5-year Mean Periods

Lowest		Highest	
Years	Anomaly (°C)	Years	Anomaly (°C)
1976-1980	-3.35	1954-1958	-1.42
1971-1975	-2.97	1987-1991	-1.69
1961-1965	-2.90	1962-1966	-2.02
1983-1987	-2.65	1981-1985	-2.03

10-year Mean Periods

Lowest		Highest	
Years	Anomaly (°C)	Years	Anomaly (°C)
1971-1980	-3.16	1951-1960	-1.63
1961-1970	-2.62	1981-1990	-2.08

warmest individual summers fell within this recent period (1983, 1985, 1988, 1990, 1994), as well as the 5-year (1987-1991; 1981-1985) and 10-year (1981-1990) positive temperature departures. Interestingly, some of the coldest individual summers occurred during the 1980s and 1990s, including the summers of 1980, 1984, 1986 and 1992. As in the reconstruction of summer temperature for Alexandra Fiord (Chapter 3), the reconstruction of August-September air temperature in this study captured the cold summer of 1986. While the length of the transfer function model precluded any reconstruction of summer temperature prior to 1948 for central Ellesmere Island, the model showed interesting high frequency variability and compared well with the Alexandra Fiord reconstruction (Chapter 3), instrumental data from Eureka H.A.W.S., and other proxy data from the High Arctic.

4.4. Discussion

4.4.1. Critique of Methodology

4.4.1.1. Building *Cassiope tetragona* Chronologies for Hot Weather Creek

In this study, growth chronologies (annual growth increment and production of leaves) of 52 years and reproductive chronologies (annual production of flower buds and flower peduncles) of 40 and 45 years, respectively, were developed for Hot Weather Creek, Ellesmere Island. The four *C. tetragona* chronologies were the first proxy data set developed for this site. In addition, the Hot Weather Creek chronologies were the second longest set of *C. tetragona* growth and reproduction time series developed after those from the three sites at Alexandra Fiord (Chapter 3).

When first examined, the *C. tetragona* stems harvested from the Hot Weather Creek site were promisingly long. However, the annual stem elongation of the plants at Hot Weather Creek was greater than that of the plants at Alexandra Fiord, a mean of 6.05 mm/yr at Hot Weather Creek compared to a mean of 4.76 mm/yr at the Lowland site, Alexandra Fiord. It is hypothesized that the community at Hot Weather Creek from which the plants were collected was neither extremely temperature nor moisture-stressed during the growing season to the same extent that *C. tetragona* plants might be at other locations. Hot Weather Creek is characterized

by anomalously high summer temperatures ($\sim 5.4^{\circ}\text{C}$) for a latitude of almost 80°N (Edlund *et al.* 1989). In addition, the Hot Weather Creek sampling site was located in a late-lying snowbed which would have supplied the *C. tetragona* plants with supplemental moisture longer into the growing season. However, as discussed later, moisture-stress may limit *C. tetragona* growth and reproduction later in the growing season due to the higher temperatures and associated evapotranspiration at the site. Finally, the snowbed would also have protected the underlying plants and their vegetative buds from late spring freezing temperatures.

A second problem which prevented the generation of longer chronologies involved the shedding of the outer bark from the *C. tetragona* stems. The bark often retains the imprint of the leaf scars. However, when the bark falls off the stem through drying and old age, it becomes difficult to measure the inter-node distances accurately. The problem of flaking bark may necessitate that stems be measured as soon as possible after harvesting to avoid this difficulty and to reconstruct the longest chronologies possible for each site.

Measurement and cross-dating of the *C. tetragona* plants from Hot Weather Creek was carried out and similar problems addressed as described in Chapter 3 regarding accuracy of annual dating, length of chronologies and the use of the dendrochronological software program, COFECHA. The skeleton-plotting technique was relied upon in this study as the final determinant for cross-dating stems to create master chronologies.

4.4.2. Chronology Variability

High intra-plant variability characterized the Hot Weather Creek chronologies (also see the Alexandra Fiord chronologies in Chapter 3). When a chronology summed for all plants and groups exhibits low variance, it may be inferred that climate was not the primary factor limiting annual growth (Fritts 1976). The higher levels of intra-plant variability present in the Hot Weather Creek chronologies may be the result of within-plant resource partitioning, plant structure and microenvironmental conditions (Havström *et al.* 1993; Johnstone and Henry 1997: Chapters 2 and 3). Although not directly investigated in this study, inter-plant variability may be influenced by the vegetation community dynamics such as competition or variable micro-environments (Chapter 2).

Finally, the use of flexible cubic splines to standardize the growth and reproduction chronologies at the Hot Weather Creek site may have increased the level of intra-plant variability detected within the chronologies. The signal-to-noise-ratio (SNR) criterion selects a digital filter which emphasizes the observed higher-frequency signal as opposed to the lower frequency signal often associated with climate (Cook and Briffa 1990).

4.4.3. Chronology Characteristics

For the Hot Weather Creek site, the mean values for annual stem elongation and leaf production were larger than those recorded for the Lowland, Bench and Dome sites at Alexandra Fiord (Table 4.14). In addition, the Hot Weather Creek mean annual growth increment values were larger than those reported for other populations studied at Alexandra Fiord (Nams 1982; Johnstone and Henry 1997). However, mean values for annual production of leaves at the Hot Weather Creek site were similar to those reported for Alexandra Fiord by Johnstone and Henry (1997) and Havström *et al.* (1993). The slightly larger stem elongation values for the Hot Weather Creek site compared to the values from the Alexandra Fiord chronologies may have been partially due to warmer summer growing season temperatures at Hot Weather Creek, as well as the longer time period covered by the Lowland, Bench and Dome sites at Alexandra Fiord. The three site chronologies, in particular the Lowland and Bench chronologies, covered a time period (late nineteenth to early twentieth century) when the region was emerging from the Little Ice Age and may have experienced volatile growing season conditions (Chapter 3).

Observations of *C. tetragona* mean annual stem growth and leaf production at Hot Weather Creek were similar to those reported for three sites on Svalbard, Norway, as well as two sites in Swedish Lapland (Table 4.14) (Callaghan *et al.* 1989; Havström *et al.* 1993). The values may be attributable to the similar temperature regimes of the Hot Weather Creek and Scandinavian sites. The three sites on Svalbard, Norway and the site at Hot Weather Creek are located at 78° N and 79° N, respectively. While warm growing season conditions at Hot Weather Creek are a result of the surrounding mountains blocking cyclonic activity and the import of cold air from the Arctic Ocean, climate on Svalbard is ameliorated by the predominating influence of the Gulf Stream current. However, the similar values recorded at the

Table 4.14. Comparative data on the mean growth (annual growth increments (AGI), annual production of leaves) and reproduction (annual production of flower buds and flower peduncles) of *Cassiope tetragona* from retrospective analysis and temperature enhancement studies (control plots only) in the Arctic. Buds = flower buds. Peds = flower peduncles. SD = standard deviation of the mean. SE = standard error of the mean. nd = no data available.

Study	Site and Date	Mean± SD/SE	AGI	Leaves	Buds	Peduncles
Rayback, Chapter 4 Hot Weather Creek Ellesmere Island	Hot Weather Creek 1945-1998	mean SD	6.05 3.12	11.94 2.03	0.36 0.63	0.26 0.53
Rayback, Chapter 3 Alexandra Fiord Ellesmere Island, Canada	Lowland 1879-1996	mean SD	4.76 2.06	10.16 2.86	0.42 0.65	0.35 0.60
	Bench 1884-1996	mean SD	3.95 1.45	8.78 2.26	0.48 0.66	0.25 0.51
	Dome 1922-1996	mean SD	3.73 1.71	9.82 3.04	0.65 0.85	0.41 0.68
Johnstone & Henry 1997 Alexandra Fiord Ellesmere Island, Canada	Lowland 1957-1992	mean SD	4.78 1.32	10.40 2.50	nd nd	1.90 0.96
Nams 1982* Alexandra Fiord Ellesmere Island, Canada	Central Plain 1981	mean SE	3.40 0.10	nd nd	1.8** 0.50	nd nd
Havström et al. 1995 Alexandra Fiord Ellesmere Island, Canada	Glacier Foreland 1965-1991	mean SD	nd nd	11.37 2.93	nd nd	1.30 nd
Callaghan et al. 1989 Mt. Slättatjåkka, Sweden	Swedish Lapland 1967-1986	mean SE	nd nd	12.23 0.18	nd nd	nd nd
Adventdalen, Svalbard	Svalbard-winter 1967-1986	mean SE	nd nd	10.25 0.08	nd nd	nd nd
Adventdalen, Svalbard	Svalbard- summer 1967-1986	mean SE	nd nd	12.62 0.20	nd nd	nd nd
Havström et al. 1993* Abisko, Sweden	Summit Fellfield 1985-1991	mean SE	6.25 0.25	13.29 0.36	nd nd	nd nd
Ny-Ålesund, Svalbard	Beach Ridge Heath 1985-1991	mean SE	5.21 0.22	10.78 0.35	nd nd	nd nd

* Mean values are from control plots in temperature enhancement experiments.

** Mean number of flower buds per shoot on tagged shoots (Nams 1982).

high arctic Hot Weather Creek site and the sub-arctic Swedish Lapland sites were the most interesting. The growth values from the high arctic and sub-arctic sites suggest that climate conditions are similar, despite the ten degree difference in latitude. Using a simple linear regression model, Havström *et al.* (1995) showed that the number of leaves produced per year by *C. tetragona* at sites on Ellesmere Island, Devon Island, Svalbard and in Swedish Lapland was a function of average July temperature. Data from this study supports the model developed by Havström *et al.* (1995).

The mean annual production of flower peduncles at Hot Weather Creek was similar to values reported for the Lowland, Bench and Dome sites at Alexandra Fiord (Table 4.14), but much smaller than the means reported by Johnstone and Henry (1997) for a lowland community and by Havström *et al.* (1995) for a glacial foreland population at Alexandra Fiord. The mean annual flower bud production value reported in this study was slightly smaller than those reported for the Lowland, Bench and Dome sites at Alexandra Fiord.

At the Hot Weather Creek site, the mean sensitivity, standard deviation and first-order autocorrelation values were low for the chronologies for annual stem elongation and annual production of leaves. *Cassiope tetragona*'s growth response to short-term variation in growing season conditions is conservative, potentially serving to stabilize the species on a year-to-year basis to ensure regular vegetative growth and a consistent and adequate source of photosynthates (Sørensen 1941; Shaver and Kummerow 1992; Chapter 3). The standardized growth chronologies showed very low levels of inter-annual variability throughout their lengths. The low autocorrelation values indicated the vegetative growth of the plants from the Hot Weather Creek site was not strongly influenced by lower frequency climatic patterns.

In contrast, the mean sensitivity and standard deviation values were higher for the reproductive variables at Hot Weather Creek, but the first-order autocorrelation values were similar to those of the vegetative growth variables. High mean sensitivity and low first-order autocorrelation values are indicative of the species' reproductive sensitivity to yearly climate conditions. High frequency variability was also evident in the standardized reproductive chronologies, particularly the chronology for annual production of flower buds. These results support previous research which reported the positive reproductive response of *C. tetragona* to

experimentally enhanced and favorable ambient conditions (Nams 1982; Johnstone and Henry 1997; Chapters 2 and 3).

Similar mean sensitivity and first-order autocorrelation values were recorded for the Lowland, Bench and Dome sites at Alexandra Fiord (Chapter 3), as well as for a study done by Johnstone and Henry (1997). In addition, the mean sensitivity values for the growth chronologies were similar to those reported in tree-ring studies carried out at Low Arctic sites, but the first-order autocorrelation values reported in this study are much lower (e.g., Kay 1978; Cropper and Fritts 1981; Cropper 1982; 1984; Edwards and Dunwiddie 1985; Szeicz and MacDonald 1995; 1996). However, it should be noted that the annual growth processes of trees and *C. tetragona* are not identical. These results provide further support for the hypothesis that reproductive development in high arctic plants, particularly evergreen and semi-evergreen shrubs, may be more sensitive to and dependent on the thermal conditions of the surrounding environment than is vegetative growth (Arft *et al.* 1999).

Examination of the correlation coefficients between the growth and reproductive variables from the Hot Weather Creek site revealed significant positive relationships between the two growth chronologies and the chronology for annual production of flower buds ($P < 0.01$). However, the chronology for annual production of flower peduncles was neither significantly, nor positively, correlated with the chronologies for vegetative growth or flower bud production ($P > 0.05$). Vegetative growth and flower bud production at Hot Weather Creek responded synchronously to the prevailing environmental conditions during the same year. Despite the rather conservative growth response of *C. tetragona*, favorable environmental conditions may result in increased growth and the production of photosynthates, which in turn would benefit the current year production and growth of flower buds. The costly investment in the formation of flower buds would be realized the following growing season with the formation of flowers and seeds. If the following growing season is favorable (e.g., warmth, long duration), then the possibility for reproductive success increases for *C. tetragona*. While there were no significant correlations between chronologies from Hot Weather Creek to support this hypothesis ($P > 0.05$), there was support from the Lowland site which showed positive correlations between annual production of flower buds (year C-1) and annual production of flower peduncles (year C) (Chapter 2). There was also no evidence of a trade-off between vegetative growth and reproduction as was reported in an earlier study (Johnstone and Henry 1997).

Investigation of between-population correlations from the Hot Weather Creek and Alexandra Fiord sites revealed no coefficients significantly different from zero ($P>0.05$). However, the results of the between-population correlation analysis were not unlike those reported for Alexandra Fiord in Chapter 3. It is hypothesized that individual *C. tetragona* populations respond to local micro-environmental conditions and associated community dynamics, as well as climate. As well, intra-plant variability may obscure or dampen a population signal, as discussed in Chapters 2 and 3. Despite these difficulties, the chronologies from Hot Weather Creek did show promise for use as bio-indicators of past climate.

4.4.4. Response of *Cassiope tetragona* to the Summer Arctic Oscillation Index and Eureka H.A.W.S. Climate

4.4.4.1. Response of Hot Weather Creek and Lowland Chronologies to the Summer Arctic Oscillation Index

The Arctic Oscillation (AO), a large-scale mode of atmospheric circulation in the Northern Hemisphere (Thompson and Wallace 1998), and its associated regional climate variables, appear to have influenced the growth and reproduction of *C. tetragona* at the Lowland and Hot Weather Creek sites. Correlation analysis indicated that, in general, the Lowland and Hot Weather Creek chronologies for growth and reproduction were positively correlated with average air temperature and negatively correlated with total monthly precipitation. In addition, correlation analysis revealed that the same Lowland and Hot Weather Creek chronologies were negatively associated with the summer Arctic Oscillation (AOS) index for the period 1948-1996. However, only the correlation between the AOS index and the Lowland chronology for annual stem elongation was significantly different from zero ($P<0.05$). Furthermore, correlation analysis showed that high AOS index values were negatively associated with average air temperature and positively related with total precipitation during the growing season (June-September). High AOS index values appear to be associated with a small decrease in *C. tetragona* growth and reproduction from 1948-1996 (Figure 4.9). Thus, when the AOS index is in the positive phase (high index values), cooler and wetter conditions may predominate in the Arctic during the growing season (Aanes *et al.* 2002), which in turn, may lead to reduced growth in *C. tetragona*.

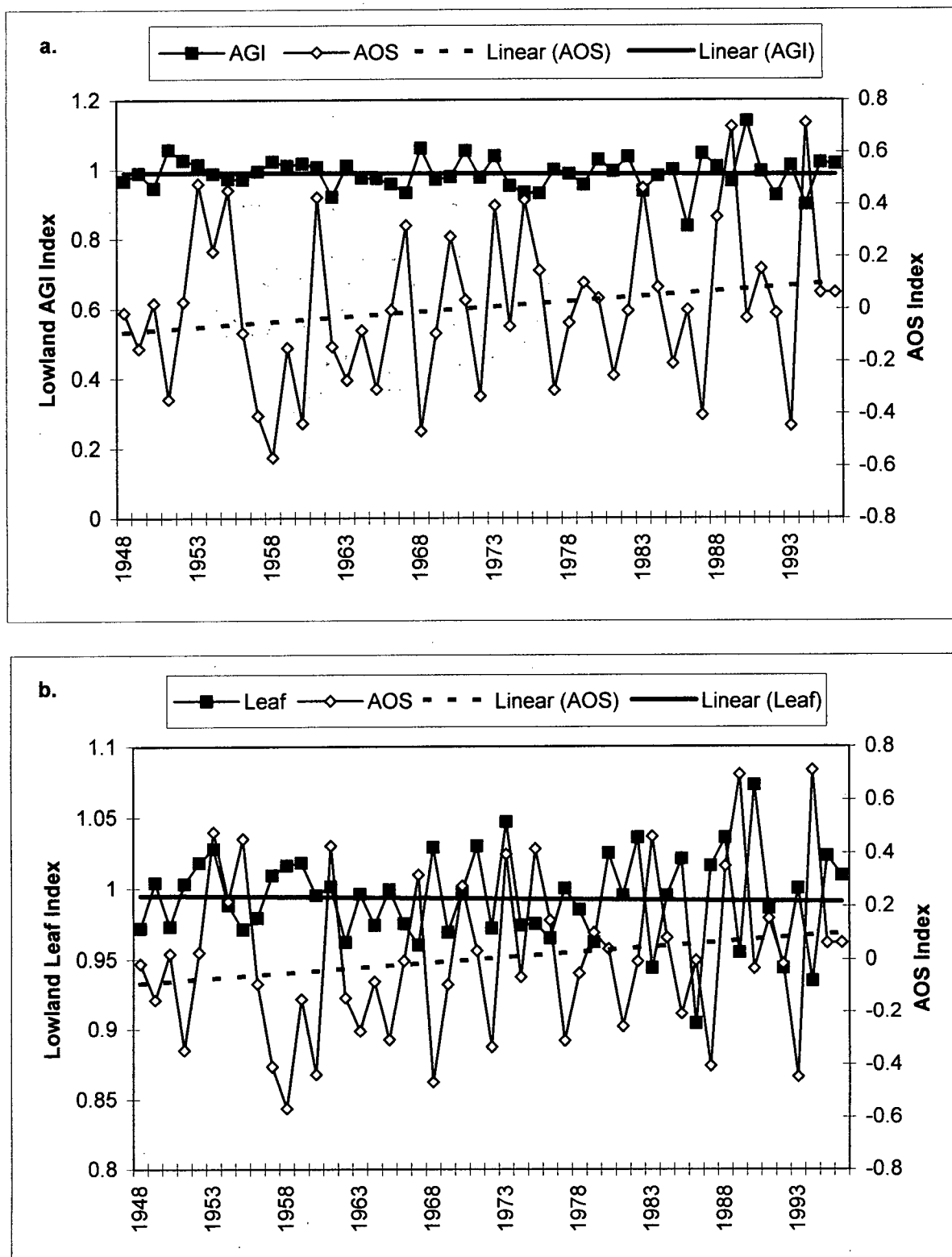


Figure 4.9. (a.) Comparison of the Lowland annual growth increment (AGI) and (b.) number of leaves (Leaf) chronologies with the summer Arctic Oscillation (AOS) index for the period 1948-1996. The solid (AGI and Leaf) and dashed (AOS) black lines show linear trends in the chronologies and the AOS index. $n = 49$.

When the AO is in the positive phase, low pressure is centered over the Arctic (Thompson and Wallace 1998). In the winter months, lower than average pressure is associated with an increase in winter temperatures and in the amount of precipitation (Thompson *et al.* 2000). However, during the summer months, low sea-level pressure is potentially associated with increased cyclonic activity and cloudier and wetter conditions (Serreze *et al.* 1997; Aanes *et al.* 2002). In fact, since 1948 at Eureka H.A.W.S., total June and September rainfall has increased (Meteorological Service of Canada, National Archive and Data Management Division, Environment Canada 2002). High AOS index values appear to be associated with unfavorable growing season conditions for *C. tetragona* on Ellesmere Island. In a study done at Brøggerhalvøya on Svalbard, Aanes *et al.* (2002) reported similar results for *C. tetragona*. In further support of these findings, the positive influence of mean daily global radiation influx on *C. tetragona* growth was reported by Molau (1997) for a site in Swedish Lapland. Other studies have also shown that *C. tetragona* responded strongly to summer climate variables, including thawing degree days and growing season average monthly air temperature (Callaghan *et al.* 1989; Havström *et al.* 1993; 1995; Johnstone 1995; Johnstone and Henry 1997; Chapter 2). While further investigation is needed, there appears to be a link between the growth and reproductive response of *C. tetragona* to local and regional-scale climate, which in turn, is linked to long-term changes in atmospheric modes of circulation like the AO (Hurrell 1995; Aanes *et al.* 2002).

4.4.4.2. Response of Hot Weather Creek Chronologies to Eureka H.A.W.S. Climate

Overall, response function coefficients relating *C. tetragona* growth to climate variables derived from the Eureka H.A.W.S. data were not significantly different from zero ($P > 0.05$). The conservative response of the growth variables to inter-annual climate variability was expected, as discussed in Chapter 3. However, the associations between the growth chronologies and current May and September average air temperatures were positive, although not significant ($P > 0.05$). In the early growing season, global solar radiation and increasing temperatures melt snowpack exposing *C. tetragona* plants to temperatures high enough to initiate photosynthesis (Chapin 1983; Shaver and Kummerow 1992). Observational studies at Hot Weather Creek report that snowmelt begins in mid to late May and is completed by early to mid-June (Woo *et al.* 1990;

Young *et al.* 1997). Evergreen species like *C. tetragona* have the ability to resume photosynthesis and apical growth within days of snowmelt (Molau 1997).

The negative relationship between vegetative growth and current year June, July and August average air temperature at Hot Weather Creek remains somewhat of a mystery. However, similar results were reported for the Alexandra Fiord ITEX control plants in Chapter 2. In other studies, vegetative growth was positively associated with average air temperature during most summer months (Nams and Freedman 1987b; Callaghan *et al.* 1989; Johnstone and Henry 1997; Chapter 3). The impact of moisture-stress may be the possible cause as the Hot Weather Creek region receives the least mean annual precipitation in Canada (Maxwell 1981). Furthermore, despite the lingering supply of snowmelt water from snowbeds where the *C. tetragona* plants are found on the Fosheim Peninsula, the anomalously warm temperatures of the site may increase growing season evapotranspiration, resulting in a moisture deficit within the plant. An alternative hypothesis for the negative correlations may be linked to within-plant resource depletion after a period of early summer increased production (Arft *et al.* 1999).

The average air temperatures for the previous summer months were also positively associated with vegetative growth at Hot Weather Creek. The positive relationship supports the hypothesis that favorable conditions in the previous summer do influence annual stem elongation and leaf production in the current year through accumulated photosynthates and the production of larger photosynthetic leaf area. Based on the sign and magnitude of the response function coefficients for the prior summer months, the argument can be made to include them as potential predictor variables in the transfer function models.

In general, the response function coefficients relating the reproductive indices of annual flower bud and flower peduncle production to Eureka H.A.W.S. climate variables were not significantly different from zero ($P > 0.05$). Annual flower bud production was positively related to current June and September average air temperature, while flower peduncle production was positively related to temperatures during the entire growing season (except September) ($P > 0.05$). Although *C. tetragona* flower buds are not usually visible on the plant stems until late June to mid-July (Nams 1982; Johnstone 1995), flower bud development typically takes place during the first four to six weeks of the growing season in the High Arctic (Shaver and Kummerow 1992). Warm June air temperature influences the availability of moisture and nutrients to the *C.*

tetragona plants in the rapidly thawing soil, potentially initiating new reproductive growth and increasing the odds that more fully developed flower buds will survive the winter. Like other arctic evergreen species such as, *Dryas octopetala*, *Cassiope tetragona* pre-forms flower buds at least one year prior to actual flowering. Flower peduncle production is also positively influenced by warm early growing season temperatures, facilitating earlier elongation of the peduncles and flower formation. The positive effect of early summer growing season temperatures on *C. tetragona* has been reported in other studies (Nams and Freedman 1987b; Callaghan *et al.* 1989; Johnstone and Henry 1997; Chapters 2 and 3).

In the late growing season (August, September), flower buds continue to develop beyond the point in time when vegetative growth has slowed or stopped (Nams and Freedman 1987b; Johnstone 1995). A prolonged summer growing season in the current year enables flower buds to develop more fully before overwintering (Nams 1982) and increases the chance of flower formation and successful seed production the following summer. Similarly, a warm, extended growing season allows for the full development of *C. tetragona* flowers, with the possibility of successful fruit formation and dehiscence at the end of the summer. Flower bud indices were positively associated with prior August and September average air temperature as well. However, the response function coefficients were not significantly different from zero ($P > 0.05$). In addition, a warm late summer growing season in the previous year may facilitate winter hardening within the plant. Finally, flower peduncle indices were positively related, but not significantly, to prior May, June, July and September average air temperature. The benefit of previous year summer growing season temperatures for flower peduncle production in the current year, is in fact, the result of the positive effect of warm summer temperatures on the number of flower buds produced in the year prior. It is hypothesized that the length of the growing season determines the number of flower buds produced annually and hence, the potential number of flowers in the following year (Nams 1982).

The variance explained by climate alone, and previous growth (or reproduction) alone, for the four variables was low. When climate and previous growth (or reproduction) were combined, the amount of variance explained was moderate. Examination of the two reproductive variables showed the combined amount of variance explained was slightly higher than for the vegetative growth variables; an indication of the stronger impact of climate on *C. tetragona* reproduction. The important effect of climate on *C. tetragona* reproduction has been

highlighted in other studies (Nams and Freedman 1987b; Johnstone and Henry 1997; Chapters 2 and 3). The moderate amount of variance explained for the growth and reproduction variables may be attributable to factors other than climate, or a combination of climate with other biotic and abiotic variables. As Hot Weather Creek is one of the warmest sites in the Canadian High Arctic during the summer months, temperature may not be as strongly limiting a factor as it is in other arctic locations. Non-climatic factors which may influence *C. tetragona* plant growth and reproduction include the impact of intra-plant architecture and resource partitioning, and inter-plant and community dynamics (Chapters 2 and 3).

As in dendroclimatological reconstructions of past climate, a goal of this study was to utilize multiple site chronologies to reconstruct climate for central Ellesmere Island. The results from the response function analyses of the Hot Weather Creek chronologies and of the Lowland and Bench site chronologies from Alexandra Fiord were compared in order to determine an optimal period of time and climate variable to reconstruct. Despite the low number of response function coefficients that were significantly different from zero for the Lowland and Bench sites at Alexandra Fiord, the amount of variance explained by previous growth and reproduction and Eureka H.A.W.S. climate variables was moderately high, indicating that climate does influence *C. tetragona* growth and reproduction at Alexandra Fiord. Few response function coefficients were significant different from zero ($P > 0.05$) at Hot Weather Creek and the amount of variance explained was moderate. However, given results from previous work (Havström *et al.* 1995; Johnstone and Henry 1997) and the successful reconstruction of August-September average air temperature for Alexandra Fiord (Chapter 3), it was decided to reconstruct average summer air temperature for central Ellesmere Island using the chronologies from Hot Weather Creek, and the Lowland and Bench sites at Alexandra Fiord. Total monthly precipitation was not reconstructed given the potential problems with the Alexandra Fiord chronologies, such as distance from Eureka H.A.W.S. and the influence of regional topography on synoptic systems (Chapter 3).

4.4.5. Reconstruction of Summer Temperature

4.4.5.1. Transfer Functions and Eureka H.A.W.S. Climate Data

The strongest model selected to reconstruct climate for central Ellesmere Island, Canada estimated average summer air temperature. The close relationship between *C. tetragona* growth and reproduction and summer temperature is well documented (Nams and Freedman 1987b; Callaghan *et al.* 1989; Havström *et al.* 1993; 1995; Johnstone and Henry 1997; Chapters 2 and 3). The model selected for this study reconstructed August-September average air temperature and explained 66% of the climatic variance (R^2_{adj} , adjusted for loss of degrees of freedom). The selected predictor variables, annual growth increment, number of leaves and number of flower buds, were derived from all three sites and, in general, the response function coefficients were positively associated with average August and/or September air temperature. The percent variance explained by this model was greater than the model developed for Alexandra Fiord (Chapter 3), and was similar to the amount of variance explained by dendroclimatological reconstructions of past climate in northern North America (e.g., Jacoby *et al.* 1985; 1988; Jacoby and D'Arrigo 1989; D'Arrigo and Jacoby 1993; Szeicz and MacDonald 1993; 1995). Unfortunately, due to the shorter length of the Hot Weather Creek chronologies included in the final model as predictor variables, it was not possible to reconstruct climate before 1948, the start of the instrumental record. However, it was possible to cross-calibrate the full model and to calculate the verification statistics needed to ensure the model was stable. The large amount of variance explained by the full model warrants further sampling of *C. tetragona* plants in the Hot Weather Creek region in order to extend the climate reconstruction beyond the starting date of the instrumental data at Eureka H.A.W.S.

4.4.5.2. Limitations of Climate Reconstruction

It is important to understand the limitations of the August-September temperature model before using it to reconstruct past climate in the Canadian Arctic. While the full model did explain 66% (R^2_{adj}) of the variance, a full third of the dependent temperature variance remained unexplained. Thus, definitive statements about climate change on Ellesmere Island based only on this reconstruction must be made with caution. However, when the reconstruction was

investigated in conjunction with other proxy climate data from the Canadian Arctic, its results were supported and interpretation of the proxy data was more tenable. Interpretation of the model was further limited by the use of flexible cubic splines to standardize the Hot Weather Creek, and the Lowland and the Bench chronologies. While this method of standardization does preclude reconstruction of longer-term climatic trends (Briffa *et al.* 1988), the length of the full model was too short (1948-1994, 47 years) to discern lower frequency climatic variation. Finally, while some of the reconstructed temperature variability in the early portion of the chronologies could be attributed to natural climatic fluctuations, there remains the possibility that the uncommon variance or noise increased with decreasing sample size (Fritts 1976; Cook and Briffa 1990). The mean chronology variance is composed of both the signal and residual noise. By averaging multiple series, the uncommon variance (noise) will cancel in direct proportion to the number of series averaged, but the common variance remains unaffected (Cook and Briffa 1990). The problems associated with decreasing sample size with time in proxy climate reconstruction are well acknowledged in dendrochronology (Fritts 1976; Cook and Briffa 1990). Hence, given the limitations of August-September temperature model, the reconstruction was noteworthy for: (1) the high amount of variance explained, (2) the fact that the model was the first temperature reconstruction using multiple *C. tetragona* site chronologies and, (3) its general agreement with the Alexandra Fiord model (Chapter 3) and other proxy climate data sets from Ellesmere Island and northern North America.

4.4.5.3. Interpretation of and Supporting Evidence for the Temperature Reconstruction

Examination of the first third of the August-September average air temperature reconstruction revealed a predominantly warm period over central Ellesmere Island from 1949-1960 (Figures 4.10 a). It is hypothesized that the period of warmth in the reconstruction was the tail end of a general warming trend in the Canadian Arctic which began in the 1920s and ended in the early 1960s. The reconstruction of August-September average air temperature for Alexandra Fiord (Chapter 3) (Figure 4.10 b) supported this assertion as did other proxy data sets (Koerner 1977; Fisher and Koerner 1983; Bradley 1990; Koerner and Fisher 1990; Lamoureux and Bradley 1996; Braun *et al.* 2000). Ice core melt records from Agassiz Ice Cap, Ellesmere Island and the Devon Island Ice Cap provide evidence that the warmest summers in the last 1000 years occurred during the period 1925-1960 (Koerner 1977; Fisher and Koerner 1983; Koerner

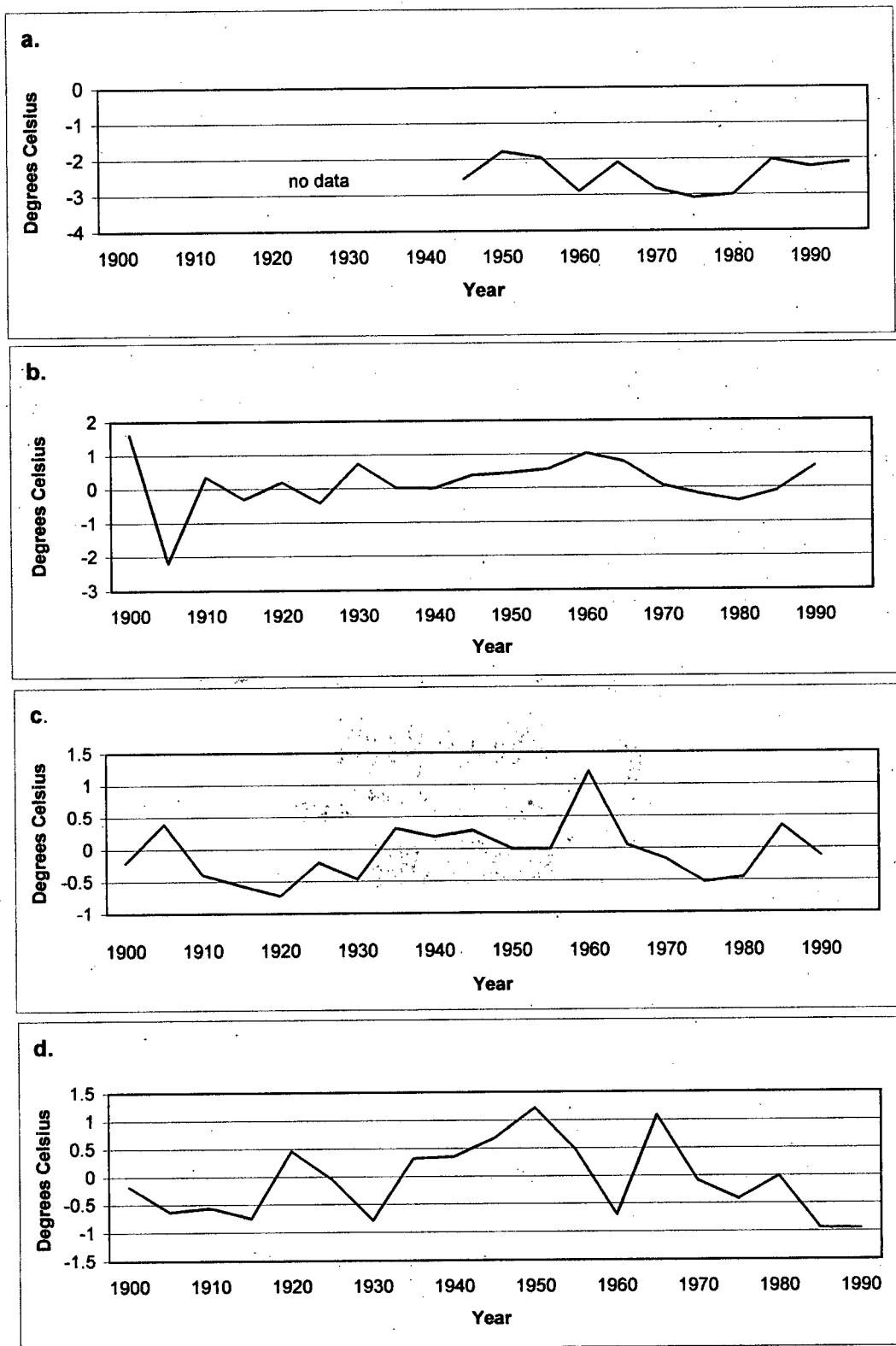


Figure 4.10. Comparison of standardized proxy temperature records from Ellesmere Island, Canada from 1900 to 1995. (a.) *C. tetragona*-based reconstruction of August-September average air temperature for central Ellesmere Island, and (b.) for Alexandra Fiord; (c.) lake varve sediment-based reconstruction of surface air temperature for Lake C2, and (d.) Lake C3, Ellesmere Island (Lamoreux and Bradley 1996; Lasca 1997). All series are presented as five-year averages.

and Fisher 1990). In addition, lake varve sediment records from northern Ellesmere Island support a period of increased warmth in the mid-twentieth century (Figure 4.10 c and d) (Lamoureux and Bradley 1996; Lasca 1997). It is hypothesized that the temperature increase from 1920-1960 in the Canadian Arctic was the result of natural (higher solar irradiance and lower volcanic aerosols) and anthropogenic forcing factors (increasing trace gases) (Lean *et al.* 1995; Robock and Free 1995; Overpeck *et al.* 1997; Mann *et al.* 1998; Free and Robock 1999; Lean and Rind 1999).

Beginning in the early 1960s, central Ellesmere Island experienced a two decade cooling period which lasted until the late 1970s-early 1980s. The August-September average air temperature model for Alexandra Fiord (Chapter 3) also supported a prolonged cooling trend in the middle of the twentieth century in the Canadian Arctic (Figure 4.10 b). Both reconstructions showed 1961, 1979 and 1980 were exceptionally cold summers, and 1966 as a particularly warm summer during this period. The cooling trend was also apparent in the melt record from the Agassiz Ice Cap ice cores and in lake varve sediment records from northern Ellesmere Island (Figure 4.10 c and d) (Koerner and Fisher 1990; Lamoureux and Bradley 1996; Lasca 1997). The decrease in temperature during the 1960s and 1970s is thought to have been caused by an increase in arctic tropospheric aerosols caused by increased volcanism after 1950, as well as the modulation of solar irradiance (Bradley and Miller 1972; Kulka *et al.* 1977; Jones *et al.* 1982; Lean *et al.* 1995; Overpeck *et al.* 1997; Mann *et al.* 1998; Free and Robock 1999; Lean and Rind 1999).

The recent increase in growing season temperature in the Canadian Arctic was evident in the reconstruction from approximately 1980s to the end of the proxy record. The temperature increase was also apparent in the instrumental climate records for the Canadian High Arctic; the 1990s were the warmest decade of the twentieth century in the Canadian Arctic (Meteorological Service of Canada 2002). The central Ellesmere Island reconstruction was supported further by the Alexandra Fiord reconstruction (Chapter 3) (Figure 4.10 b), including the exceptionally cold summer of 1986, as well as the warmer summers of 1983, 1985, 1988, 1989, 1990 and 1994. Dendrochronological reconstruction of low arctic climate in North America revealed tree-ring widths began to increase with increasing temperatures by the early 1980s after the mid-century cooling (D'Arrigo and Jacoby 1993). The warming trend of the 1980s and 1990s is thought to be the result of a combination of natural and anthropogenic forcing factors including, increased

solar radiation, lower volcanic aerosol loading of the atmosphere and the dramatic increase in greenhouse gases (Bradley and Jones 1993; Mann *et al.* 1998; Moritz *et al.* 2002).

Recent research suggests that the Arctic Oscillation (AO), a natural annual mode of Northern Hemisphere circulation, is directly linked with naturally and anthropogenically-caused climate variability (Thompson and Wallace 1998; 2001). A detailed explanation of the AO was given in the Discussion section of Chapter 3. Characterized by below normal sea level pressure above the polar region, strong sub-polar westerlies, and above normal surface air temperature, the positive phase of the AO has been dominant for the past 20 to 30 years in the Arctic (Walsh *et al.* 1996; Polyakov and Johnson 2000; Rigor *et al.* 2000; Thompson and Wallace 2001). For the period 1988-1997, there was a greater number of high index days than low index days, and sea level pressure has dropped 6-10 mb over the Arctic from 1968-1997 (Thompson and Wallace 2001). It is postulated that the recent positive phase of the AO is a consequence of anthropogenic radiative forcing (Thompson and Wallace 1998; Fyfe *et al.* 1999; Shindell *et al.* 1999; Hoerling *et al.* 2001). Increasing anthropogenically-produced greenhouse gases along with decreasing stratospheric ozone are thought to cool the lower stratosphere at high latitudes, resulting in an increase of the AO index (IPCC 2001). General Circulation Models, in which stratospheric dynamics are resolved, showed that the trends in the AO index and associated sea level pressure could be simulated under realistic increases in anthropogenically produced greenhouse gases (Shindell *et al.* 1999). A more thorough understanding of the role of the AO in arctic climate warming in the past 20 to 30 years is needed, as well as, a better understanding of arctic climate variability throughout the twentieth century.

4. 4. 6. Principal Findings

In this study, the accuracy of the summer temperature reconstruction for the twentieth century using *C. tetragona* as a proxy indicator was improved with the inclusion of chronologies from two sites on central Ellesmere Island. August-September average air temperature was reconstructed for central Ellesmere Island based upon chronologies from the Lowland and Bench sites at Alexandra Fiord and from a site at Hot Weather Creek on the Fosheim Peninsula. While the reconstruction was shorter (1949-1994) than the model presented in Chapter 3, the reconstruction explained 66% of the dependent climatic variance. The August-September

average air temperature reconstruction for central Ellesmere Island also showed the mid-century warming trend, followed by the decline in summer temperatures throughout the 1960s and 1970s, and the increase in temperatures in the 1980s and 1990s. The temperature trends in the August-September model are supported by proxy climate reconstructions from other sites on Ellesmere Island and in northern North America, as well as evidence for anthropogenic and natural forcing mechanisms.

Finally, correlation analysis revealed links between *C. tetragona* growth and reproduction, regional climate variables and the summer Arctic Oscillation index. It was shown that high summer Arctic Oscillation index values were associated with unfavorable growing season conditions (e.g., cooler, wetter, cloudier), resulting in reduced growth and reproduction in *C. tetragona* populations on central Ellesmere Island.

5. Summary and Conclusions

5.1. *Cassiope tetragona* and Experimental Warming

From data presented in this thesis, there is growing evidence that the reproductive development of *C. tetragona* at high arctic sites may be more sensitive to the thermal environment than is vegetative growth. The results from the repeated measures analyses of variance (Chapter 2) showed that the two reproductive variables were significantly affected by the warming treatment (1992-1998), but the two growth variables were not. Data from prior studies on evergreen and semi-evergreen plants (Welker *et al.* 1993; Wookey *et al.* 1993; 1995; Johnstone 1995; Molau 1997; 2001) provide strong experimental evidence that growing season temperatures are critical in high arctic tundra ecosystems for successful reproduction (Wookey *et al.* 1995). If differential investment in reproduction over vegetative growth during favorable growing seasons is cost-effective, there is the potential for increased colonization of open sites and an expansion or shift in plant distribution (Molau 1993; Wookey *et al.* 1993; Johnstone 1995). Johnstone (1995) observed a higher germination rate of *C. tetragona* seeds from warmed plots at Alexandra Fiord in 1993; however, very few *C. tetragona* seedlings have been found under ambient conditions at Alexandra Fiord (Freedman *et al.* 1982; Johnstone 1995; personal observation). Therefore, increased reproductive effort at Alexandra Fiord, an already closed-cover community, may not result in rapid expansion of *C. tetragona*. The effect of experimental warming on the growth and reproduction of *C. tetragona* may become more apparent over several more years. Longer-term data may better reflect the evergreen shrub's response to increased temperature over many years, as well as indicating more clearly how changes in this species might affect ecosystem-level processes.

In this thesis, vegetative growth and reproductive chronologies were reconstructed successfully for both the control and open-top chamber treatments at Alexandra Fiord, Ellesmere Island (Chapter 2). While the chronologies did cover the time period prior to the warming experiment and the entire treatment period, they were not long enough to provide evidence of longer-term temporal trends. However, the chronologies did establish baseline mean estimates of growth and reproduction prior to and after 1992, the year of treatment establishment.

High intra- and inter-plant variability in the *C. tetragona* growth and reproductive chronologies was apparent through visual comparison of individual plants and correlation analysis (Chapter 2). It is possible that intra- and inter-plant variability linked to resource partitioning and intra- and inter-species dynamics may have dampened the response of the plant to larger-scale climate factors. However, investigation of the relationships between vegetative growth and reproduction and ambient and artificially enhanced temperatures through correlation analysis revealed that *C. tetragona* does respond to local climate conditions (Chapter 2). Vegetative growth and reproduction were negatively correlated in the control plots and positively correlated in the open-top chamber plots with winter temperatures. Thicker snowpack in the open-top chambers during the winter months may have better insulated the *C. tetragona* plants from cold temperatures in addition to providing protection from physical and physiological damage (Sørensen 1941; Billings and Mooney 1968; Bliss 1988; Parsons *et al.* 1994). These results are of particular interest as few studies have investigated the effects of winter temperature on growth and reproduction of arctic plants.

In the early summer, growth and reproduction in the control plots responded positively to increasing temperatures as snowpack melted, exposing *C. tetragona* plants to temperatures high enough to begin photosynthesis and initiate the formation of flowers and buds (Chapin 1983; Shaver and Kummerow 1992; Molau 1997). Later in the growing season, moisture-stress and/or within-plant resource depletion may have stressed plant growth in the control plots, resulting in negative correlations with July temperatures. However, by September, growth and reproduction variables were positively correlated with temperature. While vegetative growth has ceased by early fall, an extended growing season may facilitate winter hardening. In addition, continued warmth throughout the months of August and September potentially enabled the flower buds to develop more fully, increasing the odds of reproductive success the following summer (Sørensen 1941; Nams 1982).

In the open-top chamber plots, annual leaf production responded to summer temperature similarly to that of the control plants. However, the relationship between annual stem elongation and summer temperature was opposite of that in the control plots. A possible forward shift in the timing of shoot elongation due to increased temperatures may have shifted the start of the growing season forward and resulted in earlier growth initiation in the treatment

plants (Nams 1982; Johnstone 1995). Shoot elongation rates may have also accelerated earlier in the summer (Johnstone 1995), placing a strain on the stored carbon and nutrient reserves of the plant early in the growing season. By mid-summer, annual stem elongation was positively correlated with July temperature, potentially indicating a mid-summer surplus of nutrients for shoot growth in the open-top chambers. Increased soil temperatures within the open-top chambers may have facilitated an increase in soil carbon and nutrient pools by increasing decomposition, mineralization and nitrogen fixation in soil-dwelling microbes and algae (Billings 1987; Oberbauer and Dawson 1992; Rolph 2003). While interpretation of the reproductive response to temperatures in the open-top chambers was difficult due to the small sample size and the resulting low power of the statistical tests, annual flower and bud production were positively correlated with temperature in May and July. In addition, repeated measures analyses of variance showed that the reproductive variables were strongly affected by the experimental warming treatment. The immediate response of the *C. tetragona* reproductive variables to the warming experiment supports other study results (Nams and Freedman 1987b; Johnstone 1995).

Finally, when examining the results of temperature enhancement experiments, in general, it is important to note that uniform changes in single environmental factors across large geographical regions are doubtful. There exists considerable spatial variability in recorded temperature change in the circumarctic since the beginning of the twentieth century, with some regions in the Arctic experiencing increasing temperatures while other regions are cooling (Jones and Briffa 1992; Chapman and Walsh 1993; Hardy and Bradley 1997). Spatial variability in temperature presumes some degree of spatial variability in the associated nutrient and hydrological regimes and, consequently, in their combined effect on and the responses of tundra ecosystems. As suggested by Press *et al.* (1998), it is important to continue to pursue comparative studies across arctic ecosystems and geographic locations to understand better the similarities and differences among arctic plant species and communities. It is also imperative to determine the applicability of results from the sites with the longest records (Chapin and Shaver 1985) to other locations in the circumpolar north.

Despite some of the difficulties inherent in the analysis of the warming experiment (Chapter 2), examination of the results from the control and open-top chamber treatments yielded some interesting results. Furthermore, the results compare well with those of previous

work on *C. tetragona* (e.g., Bliss *et al.* 1977; Nams 1982; Callaghan *et al.* 1989; Havström *et al.* 1993; 1995; Johnstone 1995; Johnstone and Henry 1997; Molau 1997;2001). However, simulated environmental change experiments cannot completely account for the complex interactions between environmental factors (e.g., nutrient availability, soil moisture) that limit the growth of tundra species (Chapin 1984; Henry *et al.* 1986; Maxwell 1992; Chapin *et al.* 1996; Henry and Molau 1997; Shaver *et al.* 1997; Robinson *et al.* 1998). Therefore, it should be emphasized that while the results of this thesis are interesting and informative, they should be interpreted with caution and viewed as a continuing investigation of *C. tetragona*'s response to natural and experimental climate variation.

5.2. *Cassiope tetragona* and the Reconstruction of Past Climate

In the second part of this thesis (Chapters 3 and 4), the relationship of *C. tetragona* growth and reproduction with past local and regional climate conditions was used to reconstruct climate for Alexandra Fiord and for central Ellesmere Island. In addition, the relationships between *C. tetragona* growth and reproduction, the Arctic Oscillation index, and regional climate variables were investigated. Through correlation analysis, it was shown that high summer Arctic Oscillation (AOS) index values appear to be associated with unfavorable growing season conditions (e.g., colder, wetter, cloudier), resulting in reduced growth and reproduction in *C. tetragona* populations on Ellesmere Island.

In Chapters 3 and 4, three models of past average summer air temperature were successfully developed using modified dendroclimatological methods. In the first model, July-August average air temperature was reconstructed for Alexandra Fiord for the period 1980-1996 based on the chronologies from the Lowland and Bench sites (Chapter 3). The model explained 78% (R^2_{adj} , adjusted for loss of degrees of freedom) of the climatic variance. It was impossible to calibrate or to verify this model, however, due to the short overlap period between the chronologies and the available climate data from the Coastal station at Alexandra Fiord. When additional climate data become available from the Coastal station, this model should be investigated further.

In the second model, August-September average air temperature was reconstructed for Alexandra Fiord using the climate data from Eureka H.A.W.S (Chapter 3). This time series was the longest (1899-1994) reconstruction developed for the circumpolar north using *C. tetragona* as a proxy climate indicator. The full model explained 51% (R^2_{adj} , adjusted for loss of degrees of freedom) of the climatic variance.

In the third model, August-September average air temperature was reconstructed for central Ellesmere Island, based upon chronologies from the Lowland and Bench sites at Alexandra Fiord and from a site at Hot Weather Creek on the Fosheim Peninsula (Chapter 4). While the reconstruction for central Ellesmere Island was shorter (1949-1994), the model explained 66% (R^2_{adj} , adjusted for loss of degrees of freedom) of the climatic variance. This model was within range of dendroclimatological reconstructions from northern North America (e.g., Jacoby and Cook 1981; Jacoby *et al.* 1985; 1988; Jacoby and D'Arrigo 1989; D'Arrigo and Jacoby 1993; Szeicz and MacDonald 1995; 1996), and the first to incorporate *C. tetragona* chronologies from multiple sites. The reconstruction was necessarily shortened by the inclusion of the Hot Weather Creek chronologies and, thus, average air temperature prior to the start of the instrumental record at Eureka H.A.W.S. (1948) cannot be described at this time. Further careful sampling at the Hot Weather Creek site may result in a longer climate reconstruction for central Ellesmere Island.

Examination of the August-September air temperature reconstruction for Alexandra Fiord (Chapter 3) revealed a period of high inter-annual variability during the first 20 years of the model. The variability may be due to increasing uncommon variance (noise) with decreasing sample size, to unstable local and regional climatic conditions, or both. Before any firm conclusions can be reached regarding the apparent swings in temperature, the number of samples covering the late nineteenth and early twentieth centuries must increase for the Alexandra Fiord site, or reconstructions from other sites covering the same time period are needed. Beginning in the 1920s, a directional increase in temperature was evident in the reconstruction, and the warming trend continued into the early 1960s. The August-September average air temperature reconstruction for central Ellesmere Island also supported the mid-century warming trend (Chapter 4). Both models exhibited a decline in summer temperatures throughout the 1960s and 1970s, as well as, the recent increase in temperatures beginning in the 1980s and continuing into the 1990s. Lastly, this study's reconstructions of average air

temperature supported, and were supported by, evidence presented in other proxy climate studies from Arctic Canada, including ice core melt records (e.g., Fisher and Koerner 1983; Koerner and Fisher 1990), tree-rings (e.g., Jacoby and D'Arrigo 1989; D'Arrigo and Jacoby 1993; Szeicz and MacDonald 1995) and lake varve sediment records (e.g., Lamoureux and Bradley 1996; Braun *et al.* 2000; Smith *et al.* 2003). In addition, the models followed the meteorological data from Eureka H.A.W.S. reasonably well for the period 1948-1994, in particular, capturing anomalously warm and cold summers. Research on anthropogenic and natural forcing mechanisms (e.g., solar irradiance, volcanic aerosols, Arctic Oscillation, greenhouse gases) and their links to past climate substantiate the conclusions of this study and other multiproxy interpretations (e.g., Bradley and Jones 1993; Overpeck *et al.* 1997; Mann *et al.* 1998; 1999).

The results reported in this thesis provided strong evidence that past arctic temperature can be reconstructed using *C. tetragona* as a proxy indicator. The chronologies from Alexandra Fiord, in particular, offered encouragement that longer records may be reconstructed for the High Arctic and for sites further south. While it is realized the *C. tetragona* time series are much shorter than other arctic proxies (e.g., ice core melt records, tree-rings, lake varve sediments), several points support their use, including: (1) *C. tetragona* proxies provide new data from previously unsampled terrestrial sites, (2) *C. tetragona* proxies may be reconstructed for multiple sites throughout the Arctic and, thus, are less geographically restricted than, for example, tree-ring proxies, (3) the length of the potential predictor chronologies (e.g., Lowland site, AGI chronology) can exceed the instrumental record by 70 years (more than doubling the length of the Eureka H.A.W.S. record), (4) the actual length of the reconstructed time series (e.g., August-September average air temperature for Alexandra Fiord) has already exceed the instrumental record by 50 years, and, (5) the length of the reconstructed time series covers a wide range of climatic variability during the early nineteenth and twentieth centuries. An increase in the length of the reconstructed time series would not necessarily cover a wider range of climatic variability. In addition, the reconstructions of August-September average air temperature for Alexandra Fiord and for central Ellesmere Island are useful and comparable contributions to the growing multiproxy data set for Ellesmere Island specifically, and for Arctic Canada as a whole. Most importantly, the time series' resolution and duration supply new information on the variability of summer temperature during the last century in the Canadian

High Arctic – a century which has witnessed a rate and magnitude of temperature change unprecedented for at least four hundred years.

5.3. *Cassiope tetragona* and Future Research

The successful reconstruction of past climate for Alexandra Fiord and central Ellesmere Island using *C. tetragona* as a proxy climate indicator has created multiple new research possibilities. In this thesis, chronologies were developed for only two sites, Alexandra Fiord and Hot Weather Creek, Ellesmere Island. *Cassiope tetragona* plant collections, sampled in the summers of 1998 and 1999, exist for an additional fourteen sites across the Canadian Arctic. The majority of the plant collections were sampled during the Swedish Royal Academy of Sciences Tundra Northwest 1999 scientific expedition. The sampling sites are located between 62° and 80° N and 66° and 139° W. In addition, *C. tetragona* plants were collected at multiple sites across Siberia during the Swedish Royal Academy of Sciences' Tundra Ecology 1994 scientific expedition, and there is the possibility that new collections will be made in Beringia in 2005 during a third expedition. Further Canadian samples will be collected on planned cruises of the new Canadian research icebreaker in 2005 and 2006. Together, these sampling sites will facilitate the reconstruction of climate during the late nineteenth, twentieth and twenty-first centuries across large latitudinal and longitudinal gradients in the circumpolar north. Comparison of the *C. tetragona*-based reconstructions of circumarctic climate with other climate proxies (e.g., ice-core melt records, tree-rings, lake varve sediments) will provide a more complete picture of climate variability in the north. A greater effort should be made to investigate the possibility of using retrospective analysis techniques on other arctic shrub species (e.g. *Salix* spp.) to generate proxy climate data. Multiproxy data networks sampled from a wide geographic area afford the best possibility for understanding the spatial and temporal details of climate change (Mann *et al.* 1998).

In addition to temperature reconstruction, other environmental signals may be reconstructed using *C. tetragona* as a proxy indicator. While reconstruction of past precipitation was not explored in this thesis, when plant collections are made in close proximity to arctic climate stations, the possibility for the reconstruction of precipitation should be investigated. In addition, the influence of other large-scale, hemispheric events, such as volcanic eruptions, on

C. tetragona growth and reproduction might also be explored. Other proxies such as lake varve sediments (Lamoureux *et al.* 2001) and tree-rings (e.g., Fillion *et al.* 1986; Yamaguchi *et al.* 1993; Szeicz 1996) have registered the indirect effects of volcanic eruptions. The circumarctic *C. tetragona* collections, discussed previously, may also be used to establish the presence and strength of the Arctic Oscillation (AO) signal, and to reconstruct the AO index on a regional-scale and for larger areas, such as Arctic Canada. While the AO is modeled and depicted as a primarily winter phenomenon, recent studies of atmospheric pressure reductions revealed a less vigorous, but still apparent AO pattern in summer months (Serreze *et al.* 1997; 2000). During the summer, the AO is important to and its effect has been recorded within the annual growth and reproduction of *C. tetragona* (Aanes *et al.* 2001; Chapter 4). The AO has also been shown to synchronize the timing of flowering across species and in multiple plant populations over large areas (Post 2003). Circumpolar collections of *C. tetragona* reproductive chronologies could be used to study population linkages with large-scale climate, like the AO (Post 2003). Furthermore, the circumarctic collections of *C. tetragona* may be used to reconstruct the long-term, annually-resolved patterns of oxygen and carbon isotopes ($\delta^{18}\text{O}$, δD , $\delta^{13}\text{C}$). In turn, these patterns can be used to investigate changes in precipitation regimes and modes of atmospheric circulation (e.g., AO) in the polar north.

The warming experiment results presented in this thesis also generated many unanswered questions and potential new research directions. Long-term, experimental studies must continue at arctic sites in order to assess the growth and reproductive responses of slow-growing, long-lived, conservative, evergreen shrubs, like *C. tetragona*, to ambient and artificially enhanced temperature. Longer pre-treatment chronologies would provide a better base-line estimate of *C. tetragona*'s response to ambient conditions, and longer treatment chronologies would clarify the stability and longevity of the evergreen shrub's response to increased temperature over the long-term. Retrospective analysis of *C. tetragona* plants sampled from the open-top chambers and control plots at the multiple ITEX sites could supply interesting comparative information on both the past climatic history of the sites, as well as, the growth and reproductive responses of *C. tetragona* to enhanced temperatures. In addition, retrospective analysis in association with new experiments which manipulate nutrients, water supply, and UV-B, for example, may help to elucidate the plant's response to long-term environmental changes associated with current global climate change.

A better understanding of *C. tetragona* plant autecology would also be helpful in understanding the processes which control the annual response of *C. tetragona* growth and reproduction to predominant climate signals. Growth and physiological studies of individual *C. tetragona* plants and populations subjected to experimental treatments could clarify these processes. Isotope analysis, in conjunction with retrospective analysis, could be used to investigate the past ecohydrology ($\delta^{18}\text{O}$, δD , $\delta^{13}\text{C}$), gas exchange ($\delta^{13}\text{C}$), mineral nutrition ($\delta^{15}\text{N}$) in *C. tetragona* plants under experimental and ambient conditions (Welker *et al.* 1995). In addition, studies of *C. tetragona* plant populations located along latitudinal, longitudinal and/or elevational gradients may elucidate geographic differences in populations' response to changing environmental conditions in association with changing climate.

Finally, the compatibility of different *C. tetragona* chronology construction methods should be revisited. The methods used in this thesis and by Johnstone and Henry (1997), and the methods used by Callaghan *et al.* (1989) and Havström *et al.* (1995) should be carefully investigated and compared to see which growth and reproductive variables are the most efficient for use in climate reconstruction. The two methods have never been compared directly. However, cross-dating and standardization of chronologies should be standard practice in all future *C. tetragona*-based climate reconstructions. Intensive, detailed work on the annual growth increments of individual plant stems may provide clues to past climate events during individual summer growing seasons. For example, Johnstone (1995) described a decrease in internode length following a summer snowstorm at Alexandra Fiord, and Molau (personal communication, 2003) noted brown, dried flowers on all, but the south sides of the *C. tetragona*-dominated tussocks during the 1999 growing season at Cape Hooper, Baffin Island. Interestingly, Molau found ripening fruits on the south side of the tussocks. He hypothesized that a snow storm with northerly winds impacted plant reproduction during peak flowering in late June or early July of 1999. Clearly, future retrospective analysis work on *C. tetragona* plants from sites across the circumpolar north holds great promise and offers many new research opportunities.

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7. Appendices

Appendix 1. Summary of two-factor repeated measures analysis of variance to test for year and treatment effect on average biweekly surface temperatures during the months of May to September at the Cassiope ITEX site.

Appendix Table 1.1. Effects of treatment and year on average biweekly May surface temperature measured in 7 open-top chambers and 7 control plots at the Cassiope ITEX site from 1993-1998. Effects were analyzed using a two-factor repeated measures analysis of variance. Year and treatment were considered fixed effects. $n = 6$

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, ns = not significant.

A. Weeks 1-2

1993-1998	Source of Variation	df	SS	MS	F	Probability
	Treatments	1	0.093	0.093	0.148	0.712 ns
	Error	7	4.405	0.629		
	Year	5	55.398	11.080	24.602	0.000 ***
	Year x Treatment	5	14.358	2.872	6.376	0.000 ***
	Error	35	15.763	0.45		
	Total	53	90.017			

B. Weeks 2-3

1993-1998	Source of Variation	df	SS	MS	F	Probability
	Treatments	1	6.861	6.861	3.428	0.101 ns
	Error	8	16.012	2.001		
	Year	5	166.063	33.213	17.601	0.000 ***
	Year x Treatment	5	59.467	11.893	6.303	0.000 ***
	Error	40	75.479	1.887		
	Total	59	323.882			

Appendix Table 1.2. Effects of treatment and year on biweekly average June surface temperature measured in 7 open-top chambers and 7 control plots at the Cassiope ITEX site from 1993-1998. Effects were analyzed using a two-factor repeated measures analysis of variance. Year and treatment were considered fixed effects. $n = 6$

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, ns = not significant.

A. Weeks 1-2

1993-1998	Source of Variation	df	SS	MS	F	Probability
	Treatments	1	0.817	0.871	0.118	0.742 ns
	Error	7	51.862	7.409		
	Year	5	465.040	93.008	39.051	0.000 ***
	Year x Treatment	5	86.118	17.224	7.232	0.000 ***
	Error	35	83.36	2.382		
	Total	53	687.197			

B. Weeks 3-4

1993-1998	Source of Variation	df	SS	MS	F	Probability
	Treatments	1	0.714	0.714	0.062	0.813 ns
	Error	5	57.525	11.505		
	Year	5	236.665	47.333	8.669	0.000 ***
	Year x Treatment	5	9.227	1.845	0.338	0.885 ns
	Error	25	136.5	5.46		
	Total	41	440.631			

Appendix Table 1.3. Effects of treatment and year on average biweekly July surface temperature measured in 7 open-top chambers and 7 control plots at the Cassiope ITEX site from 1993-1998. Effects were analyzed using a two-factor repeated measures analysis of variance. Year and treatment were considered fixed effects. $n = 6$
 * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, ns = not significant.

A. Weeks 1-2

1993-1998	Source of Variation	df	SS	MS	F	Probability
	Treatments	1	10.049	10.049	2.247	0.185 ns
	Error	6	26.837	4.473		
	Year	5	33.849	6.770	1.618	0.185 ns
	Year x Treatment	5	6.701	1.340	0.320	0.897 ns
	Error	30	125.491	4.183		
	Total	47	202.927			

B. Weeks 3-4

1993-1998	Source of Variation	df	SS	MS	F	Probability
	Treatments	1	11.630	11.630	3.383	0.125 ns
	Error	5	17.188	3.438		
	Year	5	90.906	18.181	5.142	0.002 **
	Year x Treatment	5	8.819	1.764	0.499	0.774 ns
	Error	25	88.389	3.536		
	Total	41	216.932			

Appendix Table 1.4. Effects of treatment and year on biweekly average August surface temperature measured in 7 open-top chambers and 7 control plots at the Cassiope ITEX site from 1992-1998. Effects were analyzed using a two-factor repeated measures analysis of variance. Year and treatment were considered fixed effects. $n = 7$
 * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, ns = not significant.

A. Weeks 1-2

1992-1998	Source of Variation	df	SS	MS	F	Probability
	Treatments	1	1.020	1.020	0.270	0.639 ns
	Error	3	11.349	3.783		
	Year	6	29.547	4.924	2.957	0.034 *
	Year x Treatment	6	2.578	0.430	0.258	0.949 ns
	Error	18	29.974	1.665		
	Total	34	74.468			

B. Weeks 3-4

1992-1998	Source of Variation	df	SS	MS	F	Probability
	Treatments	1	5.346	5.346	5.862	0.052 ns
	Error	6	5.472	0.912		
	Year	6	64.895	10.816	36.918	0.000 ***
	Year x Treatment	6	0.867	0.144	0.493	0.809 ns
	Error	36	10.547	0.293		
	Total	55	87.127			

Appendix Table 1.5. Effects of treatment and year on biweekly average September surface temperature measured in 7 open-top chambers and 7 control plots at the Cassiope ITEX site from 1992-1998. Effects were analyzed using a two-factor repeated measures analysis of variance. Year and treatment were considered fixed effects. $n = 7$
 * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, ns = not significant.

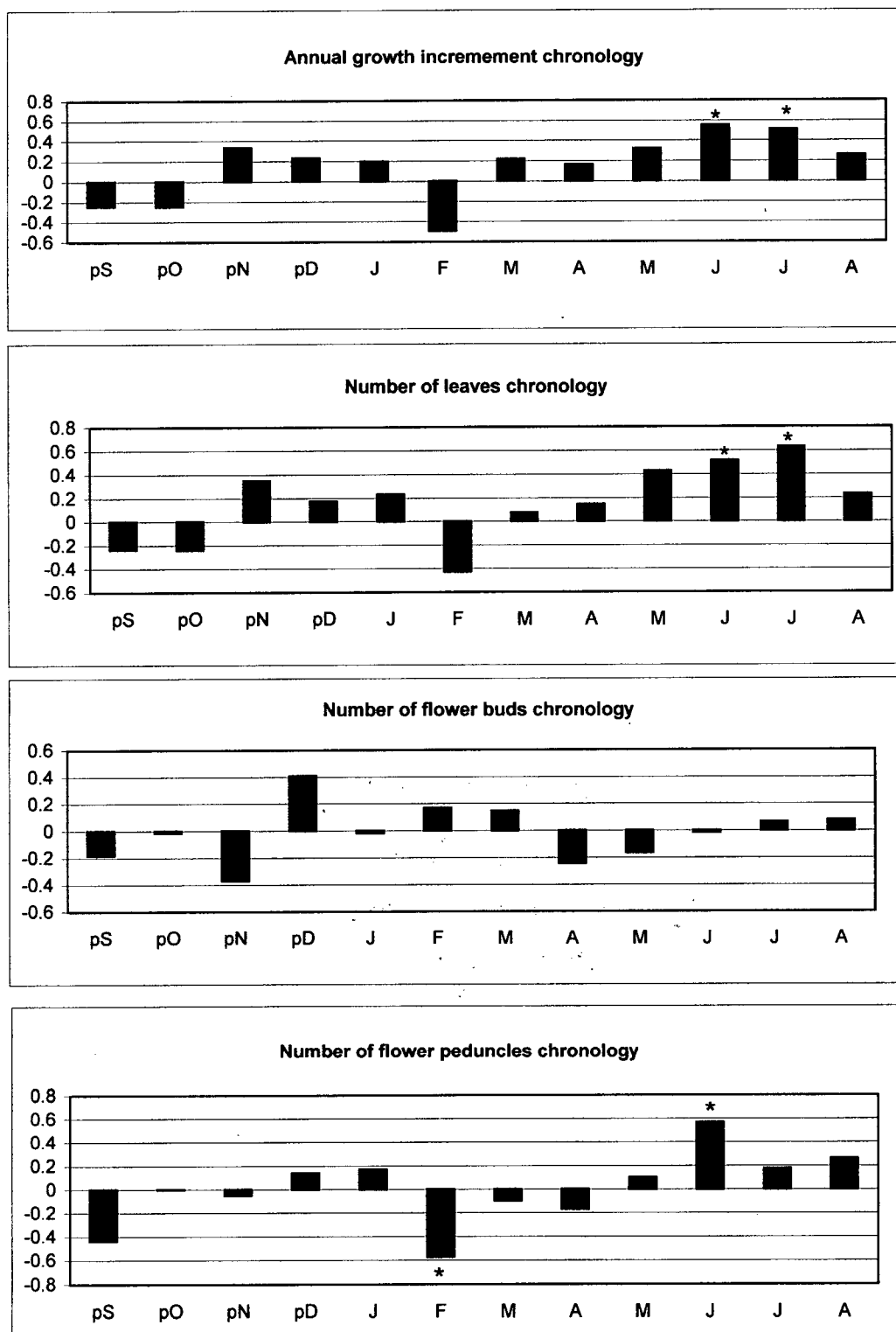
A. Weeks 1-2

1992-1998	Source of Variation	df	SS	MS	F	Probability
	Treatments	1	7.814	7.814	6.126	0.069 ns
	Error	4	5.102	1.276		
	Year	6	10.496	1.749	4.391	0.004 *
	Year x Treatment	6	4.610	0.768	1.929	0.117 ns
	Error	24	9.561	0.398		
	Total	41	37.583			

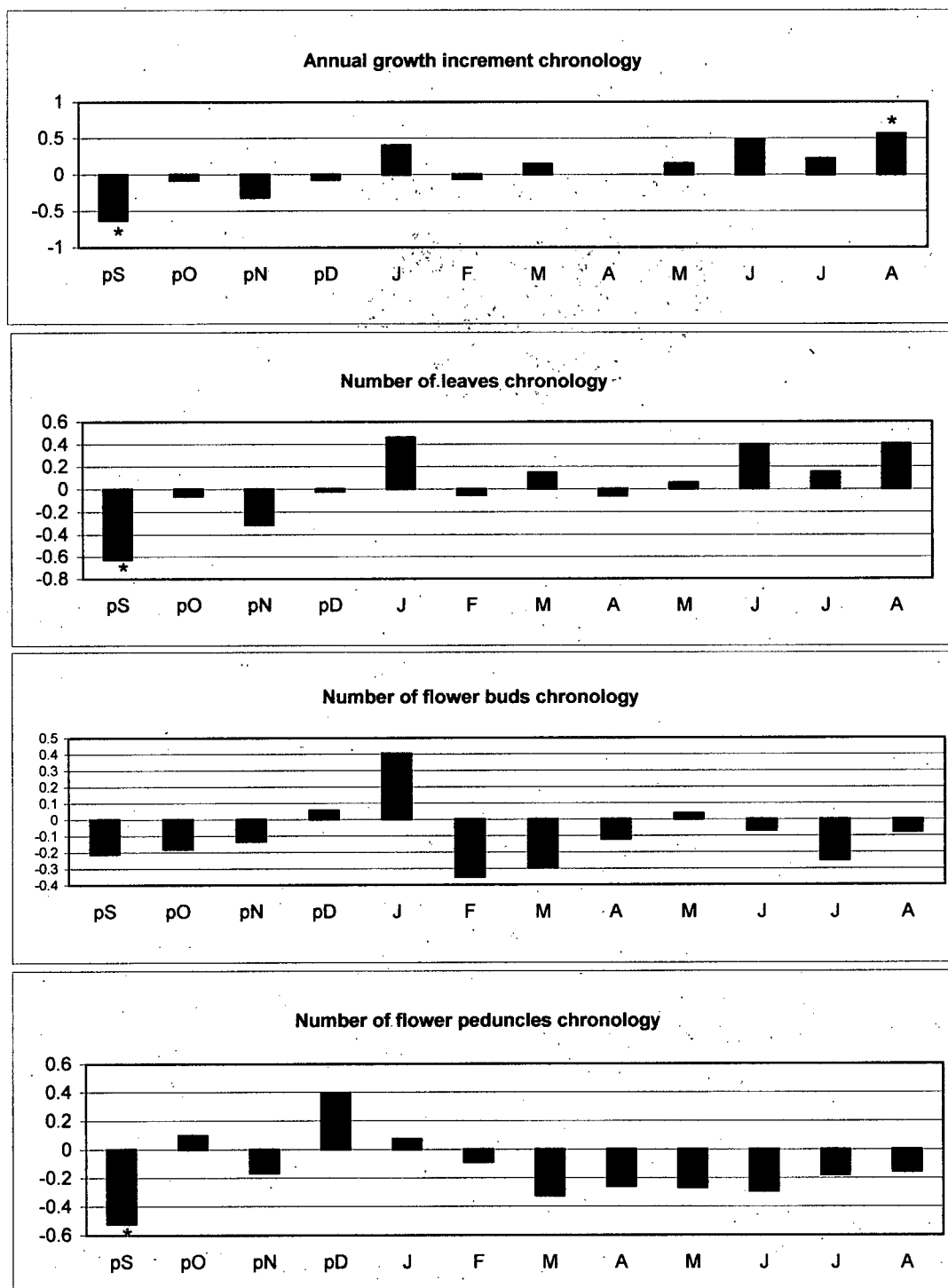
B. Weeks 3-4

1992-1998	Source of Variation	df	SS	MS	F	Probability
	Treatments	1	19.841	19.841	7.101	0.037 *
	Error	6	16.765	2.794		
	Year	6	124.705	20.784	29.667	0.000 ***
	Year x Treatment	6	7.621	1.270	1.813	0.124 ns
	Error	36	25.221	0.701		
	Total	55	194.153			

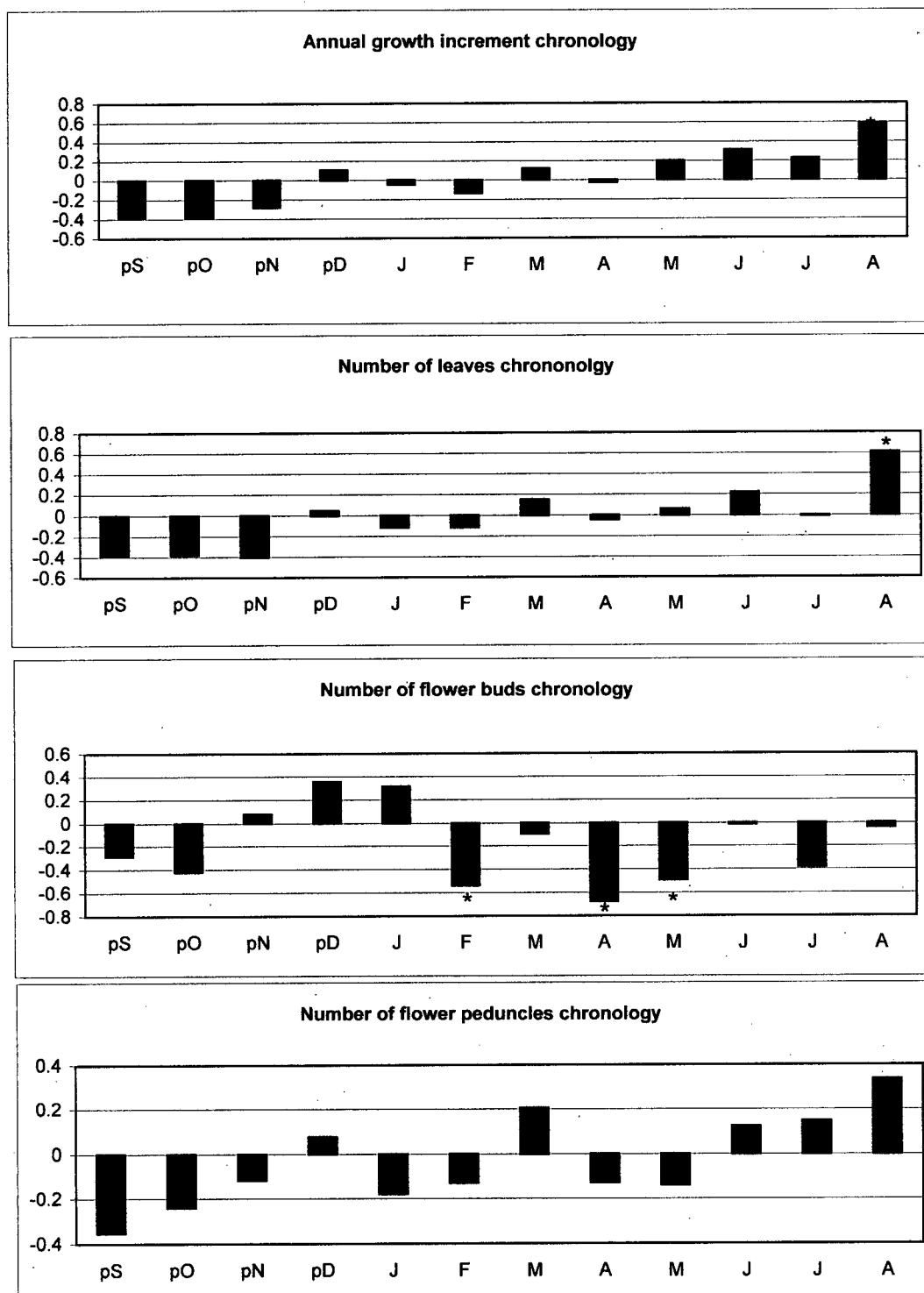
Appendix 2. Pearson's correlation analysis relating *Cassiope tetragona* growth and reproduction chronologies to average monthly air temperature and monthly thawing degree days (mtdd) from the Coastal station, Alexandra Fiord from 1980-1996.



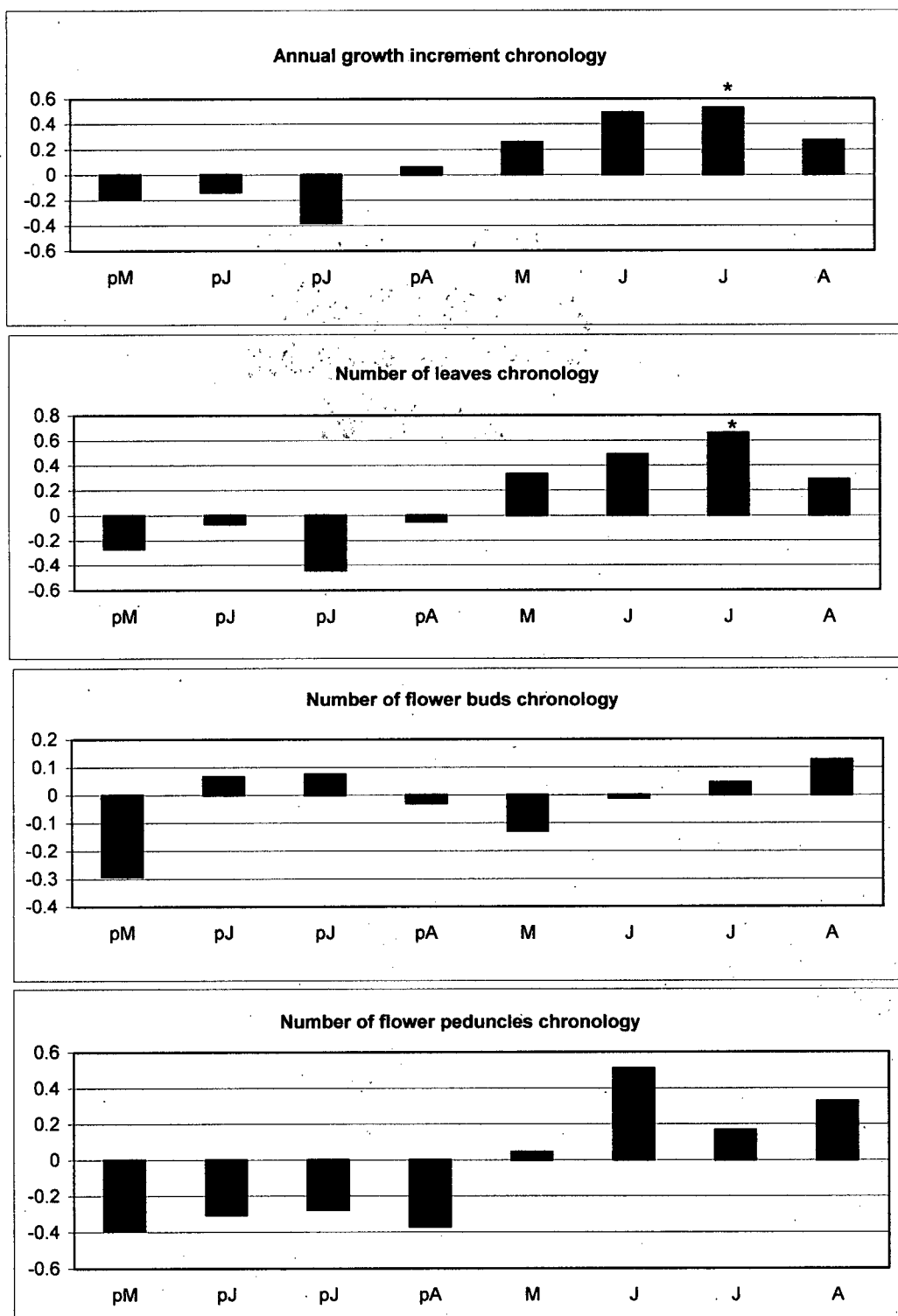
Appendix Figure 2.1. Correlation coefficients relating growth and reproduction chronologies from the Lowland site to average monthly air temperature from the Coastal station, Alexandra Fiord from 1980-1996. The time period covered begins in the previous September (pS) and continues to the current August (A). Annual growth increment, number of leaves, number of flower buds and flower peduncles, $n = 16$. * $P < 0.05$.



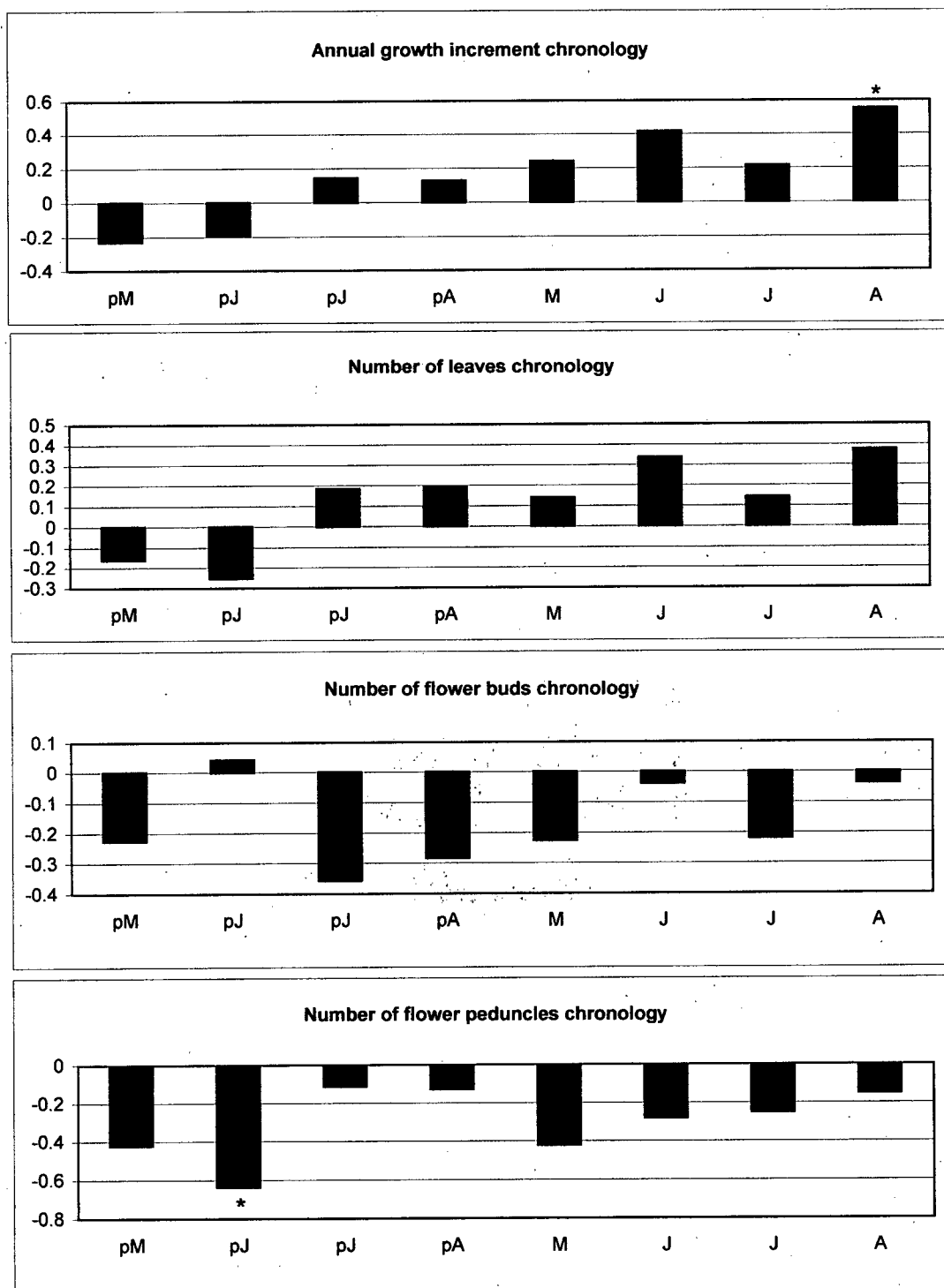
Appendix Figure 2.2. Correlation coefficients relating growth and reproduction chronologies from the Bench site to average monthly air temperature from the Coastal station, Alexandra Fiord from 1980-1996. The time period covered begins in the previous September (pS) and continues to the current August (A). Annual growth increment, number of leaves, number of flower buds and flower peduncles, $n = 16$. * $P < 0.05$.



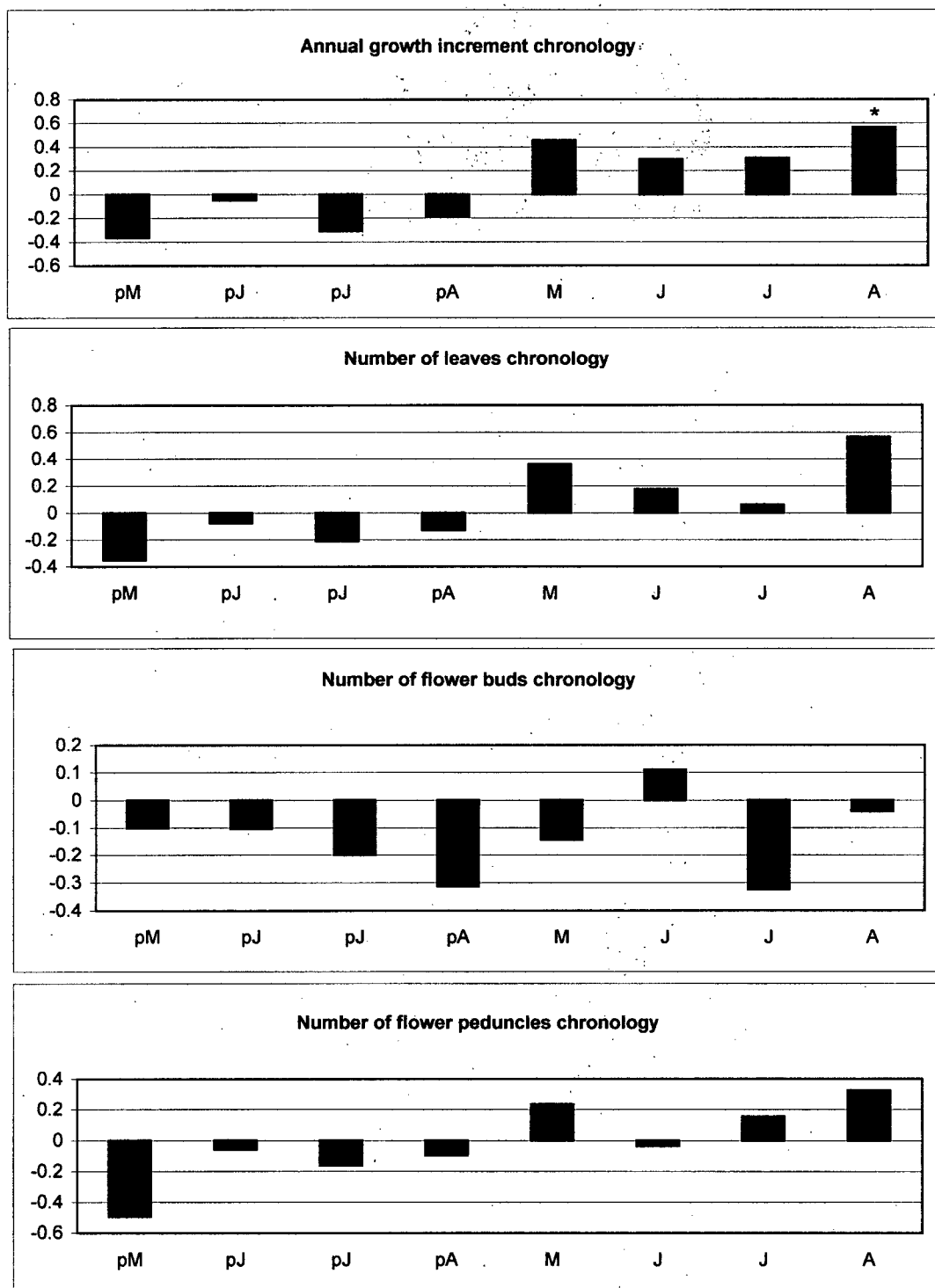
Appendix Figure 2.3. Correlation coefficients relating growth and reproduction chronologies from the Dome site to average monthly air temperature from the Coastal station, Alexandra Fiord from 1980-1996. The time period covered begins in the previous September (pS) and continues to the current August (A). Annual growth increment, number of leaves, number of flower buds and flower peduncles, $n = 16$. * $P < 0.05$.



Appendix Figure 2.4. Correlation coefficients relating growth and reproduction chronologies from the Lowland site to monthly thawing degree days (mtdd) from the Coastal station, Alexandra Fiord from 1980-1996. The time period covered begins in the previous September (pS) and continues to the current August (A). Annual growth increment, number of leaves, number of flower buds and flower peduncles, $n = 16$. * $P < 0.05$.

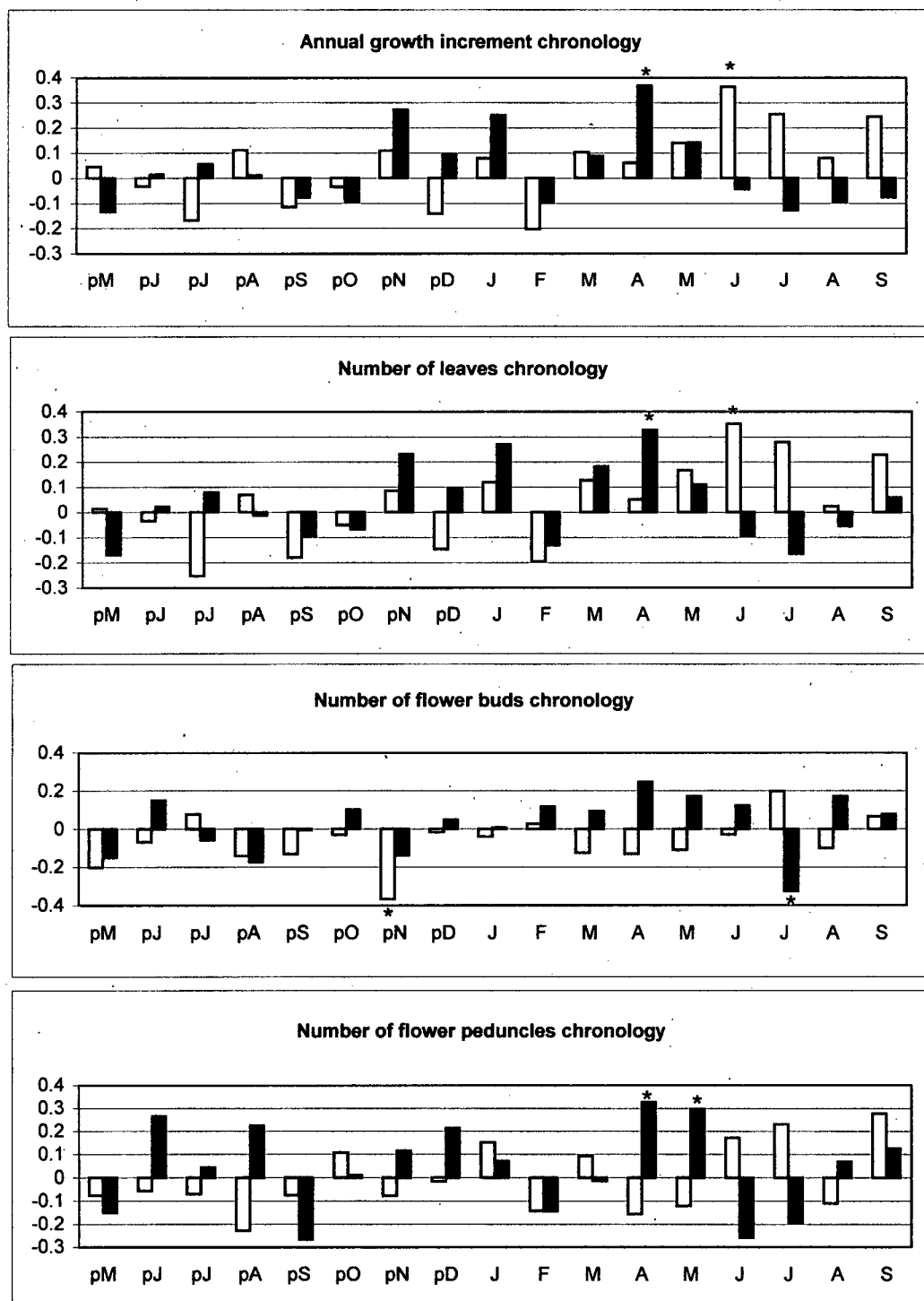


Appendix Figure 2.5. Correlation coefficients relating growth and reproduction chronologies from the Bench site to monthly thawing degree days (mtdd) from the Coastal station, Alexandra Fiord from 1980-1996. The time period covered begins in the previous September (pS) and continues to the current August (A). Annual growth increment, number of leaves, number of flower buds and flower peduncles, $n = 16$. * $P < 0.05$.

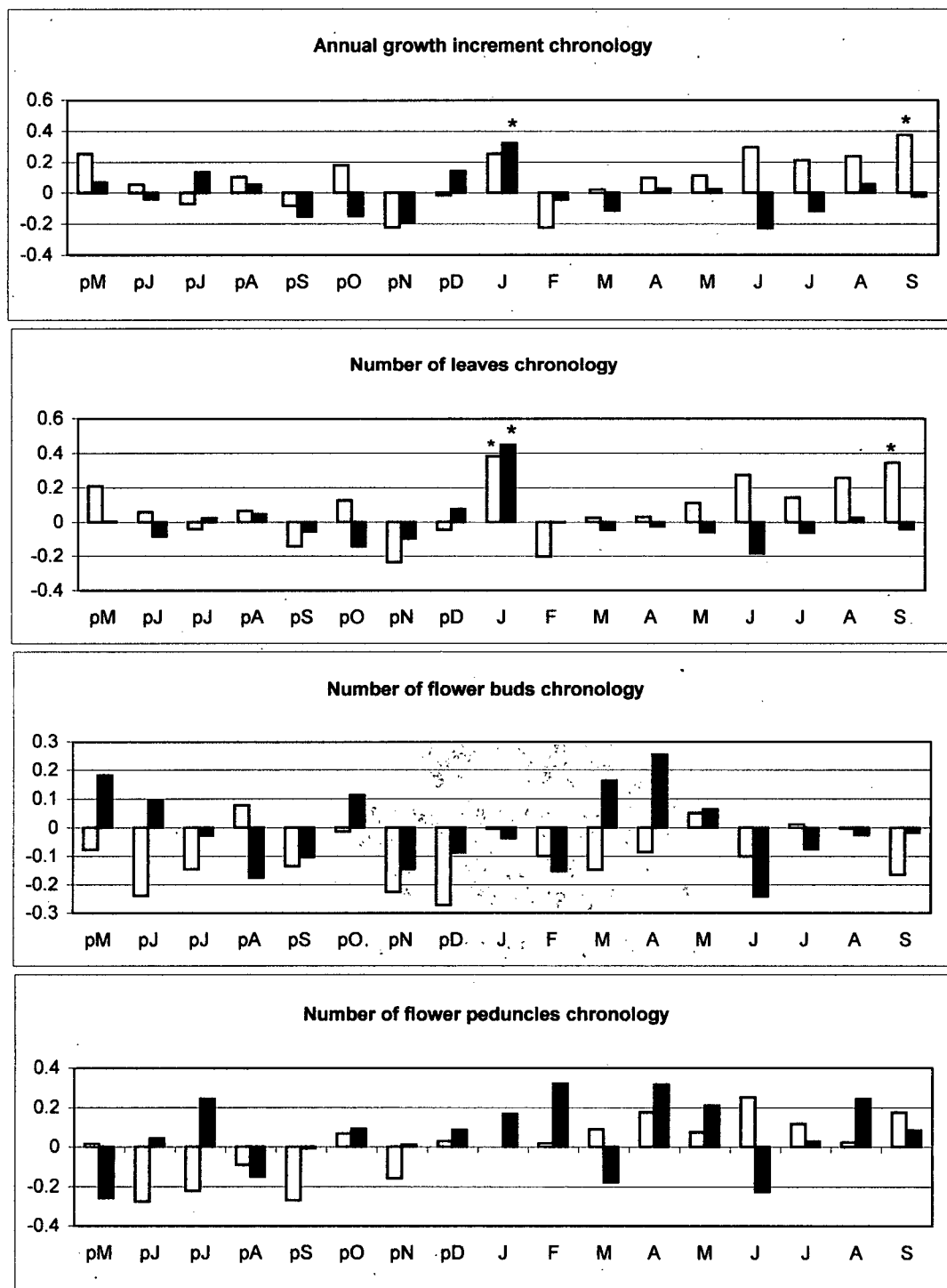


Appendix Figure 2.6. Correlation coefficients relating growth and reproduction chronologies from the Dome site to monthly thawing degree days (mtdd) from the Coastal station, Alexandra Fiord from 1980-1996. The time period covered begins in the previous September (pS) and continues to the current August (A). Annual growth increment, number of leaves, number of flower buds and flower peduncles, $n = 16$. * $P < 0.05$.

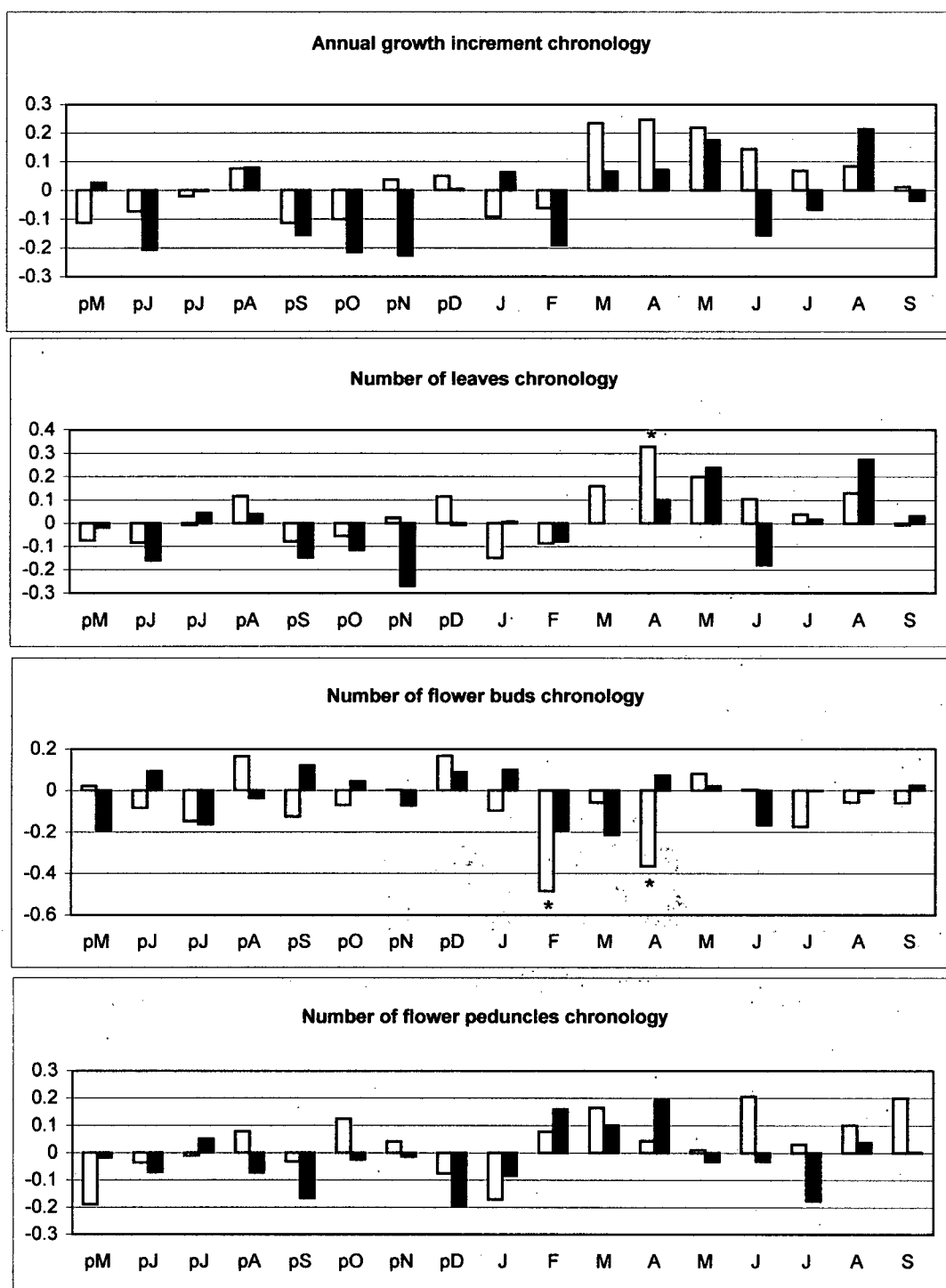
Appendix 3. Pearson's correlation analysis relating *Cassiope tetragona* growth and reproduction chronologies to average monthly air temperature and total monthly precipitation from Eureka H.A.W.S., Ellesmere Island from 1948-1996.



Appendix Figure 3.1. Correlation coefficients relating growth and reproduction chronologies from the Lowland site to average monthly air temperature and total monthly precipitation from the Eureka H.A.W.S. from 1948-1996. The time period covered begins in the previous May (pM) and continues to the current September (S). Temperature = white bars; Precipitation = black bars. $n = 49$. * $P < 0.05$.

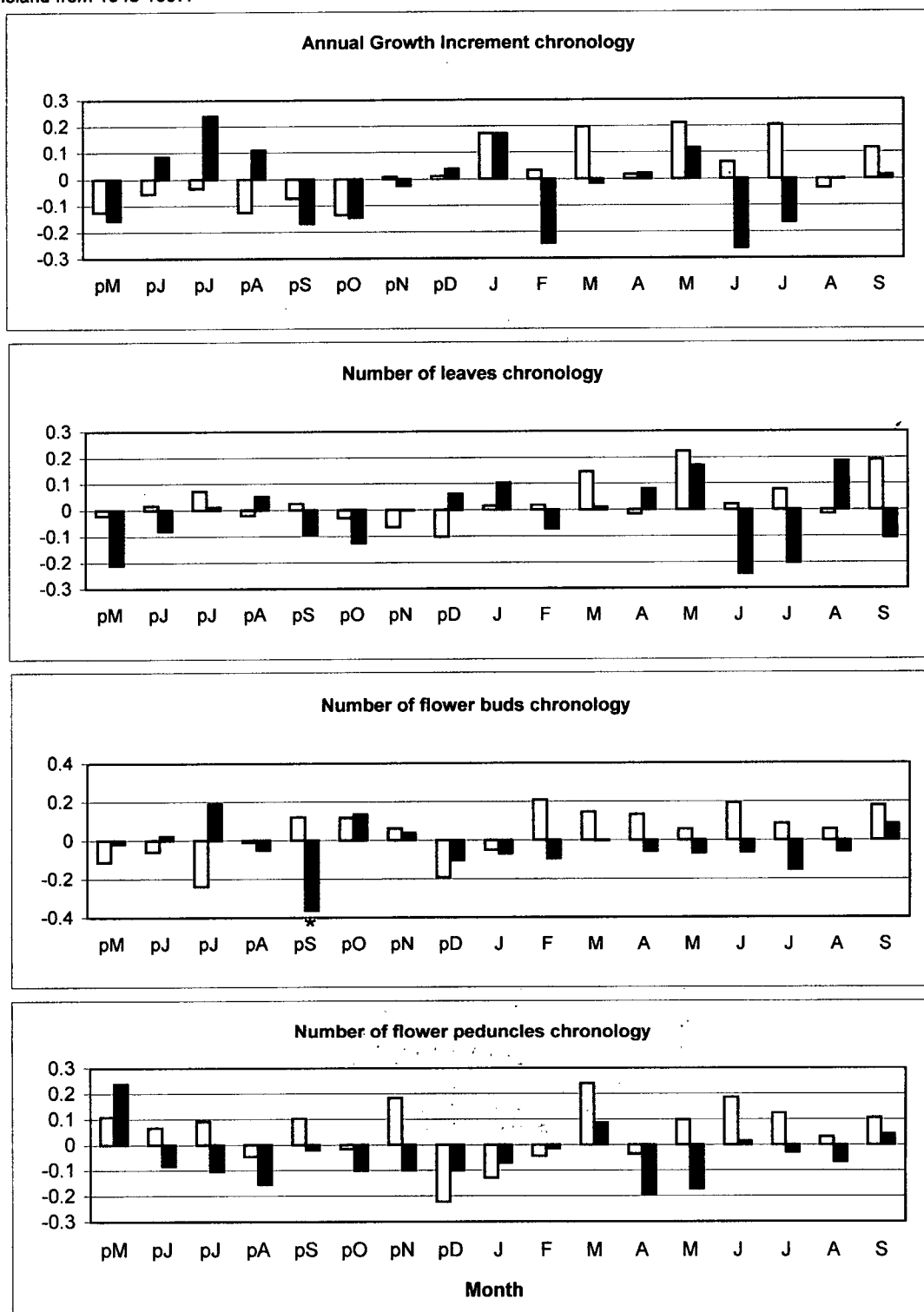


Appendix Figure 3.2. Correlation coefficients relating growth and reproduction chronologies from the Bench site to average monthly air temperature and total monthly precipitation from the Eureka H.A.W.S. from 1948-1996. The time period covered begins in the previous May (pM) and continues to the current September (S). Temperature = white bars; Precipitation = black bars. $n = 49$. * $P < 0.05$.



Appendix Figure 3.3. Correlation coefficients relating growth and reproduction chronologies from the Dome site to average monthly air temperature and total monthly precipitation from the Eureka H.A.W.S. from 1948-1996. The time period covered begins in the previous May (pM) and continues to the current September (S). Temperature = white bars; Precipitation = black bars. $n = 49$. * $P < 0.05$.

Appendix 4. Pearson's correlation analysis relating *Cassiope tetragona* growth and reproduction chronologies from Hot Weather Creek to average monthly air temperature and total monthly precipitation from Eureka H.A.W.S., Ellesmere Island from 1948-1997.



Appendix Figure 4.1. Correlation coefficients relating Hot Weather Creek growth and reproduction chronologies to average monthly air temperature and total monthly precipitation from the Eureka H.A.W.S. from 1948-1997. The time period covered begins in the previous May (pM) and continues to the current September (S). Temperature = white bars; Precipitation = black bars. $n = 50$. * $P < 0.05$.