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Plant Responses to Experimental Warming of a Dry Heath
Tundra at Barrow, Alaska

presented by
Lisa Jeanne Walker

has been accepted towards fulfillment
of the requirements for

Masters degree in Botany and Plant Pathology

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**PLANT RESPONSES TO EXPERIMENTAL WARMING OF A DRY HEATH
TUNDRA AT BARROW, ALASKA**

By

Lisa Jeanne Walker

A THESIS

**Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of**

MASTER OF SCIENCE

Department of Botany and Plant Pathology

1997

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ABSTRACT

PLANT RESPONSES TO EXPERIMENTAL WARMING OF A DRY HEATH TUNDRA AT BARROW, ALASKA

By

Lisa Jeanne Walker

The International Tundra Experiment (ITEX) was created to examine effects of increased temperature, as predicted by current Global Climate Models, on vegetation in the Arctic. This region is predicted to be the most strongly effected by temperature change. In ITEX the seasonal development, and growth patterns of plant species are examined throughout the Arctic. This report is focused on responses of dry heath vegetation at Barrow, Alaska to experimental warming. Small fiberglass chambers are used to induce warming over the tundra. Phenophases were examined according to Julian date of occurrence, number of days since snow melt, and accumulated growing degree days. Measurements were made to determine the effects of increased temperature on the total height of reproductive and vegetative growth and in 1996 stature was monitored to determine differences in growth rates. Plant responses to warming were not consistently significant during the years of this study, or between species, showing that plants respond individualistically.

ACKNOWLEDGMENTS

I would like to thank Dr. Patrick Webber for introducing me to ITEX and allowing me the opportunity to work on this exciting project. The ITEX community and meetings are an excellent opportunity to learn about other countries and the work that is being done around the circumpolar Arctic. I would also like to thank Bob Hollister for his help with the abiotic data, and Lisa Koch and Ian Ramjohn for assistance in the field. I am greatly indebted to Dr. Christian Bay, who initiated the Barrow ITEX site in 1994, and taught me about the Arctic and its plants during the 1995 field season. Partial funding for this research came from the National Science Foundation grant to Dr. Kaye R. Everett at The Ohio State University, and Dr. Fritz E. Nelson at the State University of New York at Albany. I would like to thank my committee members, Dr. Stuart Gage, and Dr. Frank Telewski, as well as Dr. Kelly McConnaughay, my family, and my friends for all their help and support.

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Chapter 1

ITEX - THE INTERNATIONAL TUNDRA EXPERIMENT

Introduction

As the amount of greenhouse gases continue to increase in the atmosphere, the likelihood that there will be a significant change in the climate within our lifetimes also increases (MacCracken, 1995; Cohen, 1990). Global Climate Change Models (GCMs) are the usual basis for these predictions. A change such as this is expected to take place in the form of global warming, being most pronounced at polar latitudes (Maxwell, 1992). There is evidence of warming in some parts of the Arctic, especially the Western Arctic including Alaska (Chapman and Walsh, 1993). Arctic ecosystems are likely to be the most affected by future global warming (Maxwell and Barrie, 1989), which makes arctic tundra the ideal location to study possible effects of warming on vegetation. The arctic regions are also most likely to be the location of the largest impact on climate from anthropogenic pollution, as demonstrated by the trend of an earlier snowmelt (since 1945) at Barrow, Alaska, suggesting a longer growing season (Foster, 1989). Arctic plants have adapted to living in conditions that are limited by

low temperature, short growing season, low light intensity, and low nutrient availability (Chapin, 1987), and arctic ecosystems are characterized as having a low amount of annual net primary productivity (Haag, 1974). Temperature is seen as being the most important limiting factor to plant growth in tundra vegetation (Bliss, 1962), which suggests that arctic vegetation is likely to show a response to warming. Most tundra plants fall into a height range of 6-8 cm, often forming a dense mat layer, with most of the aboveground growth of the plants being in the part of the microenvironment of the tundra that has a warmer temperature, which is important since relatively small changes in temperature become highly significant to plant metabolic processes (Bliss, 1962). The small stature of many arctic plants also means that the canopy temperature is more closely related to soil surface temperature, than to the ambient air temperature, which should be more responsive to climate change than air temperature (Foster, 1989). Therefore, tundra plants should show a response to the warming of (1 - 4°C) predicted by most GCMs.

Many climate models have been introduced as a tool in predicting possible future climate changes. Currently three dimensional models that couple a general circulation model of the atmosphere to that of ocean patterns, are used to predict possible future scenarios of climate change (MacCracken et al., 1991; Manabe 1997). There are two general types of GCMs (General Circulation Models, or Global Climate Change Models) used to study the effects of the increasing amount of greenhouse gases found in the atmosphere. The first type of GCM has the amount of gas concentration

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(usually CO₂) doubled and the model is run until a new equilibrium is reached. In the other type of GCM, the gas concentration is increased slowly with time (the rate at which the gas concentration is increased changes with different models, usually based on past concentration increases, or predicted future changes) and includes oceanic behavior, which must be accurately represented. Although results differ from model to model (using these two general types of models), most agree that with the continuing increase in greenhouse gas concentrations there will be a global average surface air temperature warming in the next century assuming that other forces affecting the climate do not counteract this effect (MacCracken et al. 1991). The sensitivity of these global scale models is being tested on regional levels, to address environmentally important issues (Grotch, 1991). The models are also being coupled with biological models that simulate surface (vegetation) changes, so that exchange processes will be included within the final output of the larger GCMs (Fennessy and Xue, 1997).

The International Tundra Experiment (ITEX) is a project designed to examine the effects of experimental warming at the plant canopy level (Henry and Molau, 1997). ITEX began at a meeting at the Kellogg Biological Station of Michigan State University on 2 - 5 December, 1990 (Molau and Molgaard, 1996). ITEX examines the responses of vascular plants to experimental warming at 26 sites in 11 different countries. Climate and geophysical features are monitored. Developmental stages, as well as quantitative growth data are collected each growing season in control and experimental plots from

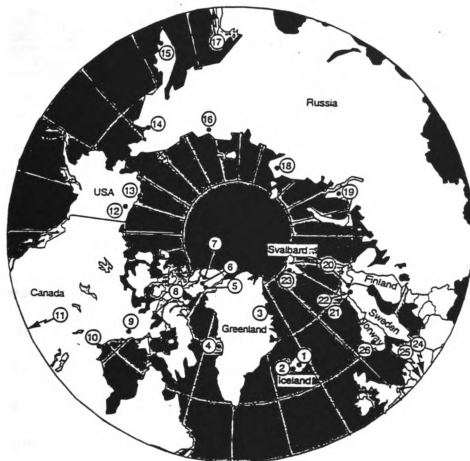
each of the sites. By comparing these individual plant responses at each site to those at different sites, it is anticipated that a better ecological understanding of how warming effects the tundra, or high latitude systems will result. As the effects of increasing the ambient growing temperature on the reproductive cycles of arctic plants are relatively unknown (Moore, 1995), the ITEX community is examining these responses on a circumpolar level, by comparing phenological and growth data from similar species at each site. Tundra plants appear to have sufficient genetic variability and plasticity to confer some resistance to climate change (McGraw and Fetcher, 1992). Temperature influence on plant growth is seen as one of the most important feedback mechanisms at the global level, which also makes it an important part of present and future modeling (van Minnen et al., 1995). One of the major constraints in developing higher resolution regional models is the lack of information on a smaller scale (Cohen, 1990). In the future, ITEX response data could possibly fill this need. The ITEX project does not examine all aspects of global warming or global change, but instead focuses on the effects of growing season temperature on plant performance. The study described here is from one of two sites at Barrow, a dry heath ridge. The other site is a wet sedge meadow.

At each ITEX site the standard basic experiment consists of a series of small fiber-glass chambers that trap energy and cause plant canopy warming. The construction and effectiveness of the chambers will be discussed later. Each of these sites has 20 or more replicates of chambers and control plots. A

large number of replicates is needed to monitor this extremely variable system. The standard basic experiment requires that air temperature, plant phenology and growth be monitored. It is also desirable for other variables such as relative humidity, incoming solar radiation, and soil temperature to be measured at each of the ITEX sites. Of the species that are monitored, each site is expected to target at least one of the species or genus that is on the ITEX circumpolar list (Molau and Molgaard, 1996) which ranks the important species to monitor at each site. This will contribute to the circumarctic goal of ITEX to understand plant responses to warming. Figure 1 depicts the locations of the established ITEX sites around the circumarctic, including both arctic and alpine sites.

Barrow, Alaska is one of three existing sites in the United States (the others are at Niwot Ridge, Colorado, and Toolik Lake, Alaska; see Figure 1 for locations). Another site near Barrow has been partially established for future monitoring at Atqasuk, Alaska (not shown in Figure 1). Barrow is located at 71 °19'N, 156°37'W, in the northernmost portion of the United States, on the North Slope of Alaska (Table 1). Barrow is within the Arctic Coastal Zone, which is characterized by cool summers, and relatively warm winters, due to the buffering effect of the Arctic ocean, and also has a low amount of precipitation of which more than 50% falls as snow (Zhang et al., 1996). Both sites at Barrow (dry heath and wet sedge) are an important part of ITEX, as they represent two very different aspects of Arctic seacoast tundra. Table 1 lists the conditions and components of the dry heath site at Barrow.

Circumpolar Arctic ITEX Map



- | | |
|-----------------------------|----------------------------|
| 1 Hveravellir, Iceland | 14 Anadyr, Russia |
| 2 Mt. Sidiataf, Iceland | 15 Petropavlovsk, Russia |
| 3 Zachenberg, Greenland | 16 Lower Kolyma, Russia |
| 4 Disko Island, Greenland | 17 Taietsu Mts., Japan |
| 5 Alexandra Fjord, Canada | 18 Taimyr, Russia |
| 6 Sverdrup Pass, Canada | 19 Yamal, Russia |
| 7 Hot Weather Creek, Canada | 20 Kipisjärvi, Finland |
| 8 Truslove Lowland, Canada | 21 Abisko, Sweden |
| 9 Baker Lake, Canada | 22 Lathajauru, Sweden |
| 10 Churchill, Canada | 23 Ny-Ålesund, Svalbard |
| 11 Niwot Ridge, USA | 24 Val Berola, Switzerland |
| 12 Toolik Lake, USA | 25 Furka Pass, Switzerland |
| 13 Barrow, USA | 26 Finse, Norway |

(from Marion et al., 1993)

Figure 1. ITEX map showing the locations of established sites.

Table 1. Characteristics of the dry heath ridge, at Barrow, Alaska.

July mean temperature (°C)	3.7
Length of thaw season (days)	91
Number of thaw degree days	251
Elevation (msm)	4.5 - 5.0
Slope	0.5 °W
Landform	Raised beach ridge
Substrate	Fine silts, sands, and gravels
Soil	Pergelic Cryaquept
Characteristic Bryophytes	<i>Dicranum elongatum</i> <i>Racomitrium lanuginosum</i>
Characteristic Lichens	<i>Alectoria nigricans</i> <i>Thamnolia vermicularis</i>

Hypotheses

The underlying hypotheses of this project are as follows: 1) the dry heath tundra vegetation will show an acceleration of phenophases as a response to artificially induced warming inside the chambers; 2) the dry heath plants will exhibit an increase in stature in response to warming; 3) the dry heath plants will exhibit an increase in growth rate in response to elevated ambient temperature, and; 4) the species on the dry heath tundra will respond in an individualistic manner to the increase in temperature within the chambers. Although tundra plants are seen as having a large amount of genetic variability and plasticity, the specific species should respond on a microhabitat level to an increase in temperature, even if the ecosystem as a whole is somewhat resistant to change.

Table 2. List of all vascular species found within plots on the dry heath ridge.

Vascular species Family	Genus and Species
Graminae	<i>Alopecurus alpinus</i> Sm ssp. <i>alpinus</i>
Graminae	<i>Arctagrostis latifolia</i> (R.Br.) Griseb var. <i>latifolia</i> *
Cyperaceae	<i>Carex stans</i> Wahlenb. ssp. <i>stans</i> (Drej.) Hult.
Ericaceae	<i>Cassiope tetragona</i> (L.) D. Don ssp. <i>tetragona</i>
Cruciferae	<i>Draba lactea</i> Adams
Cruciferae	<i>Draba micropetela</i> Hook.
Juncaceae	<i>Juncus biglumis</i> L.
Juncaceae	<i>Luzula arctica</i> Blytt
Juncaceae	<i>Luzula confusa</i> Lindeb.
Polygonaceae	<i>Oxyria digyna</i> (L.) Hill
Papaveraceae	<i>Papaver hultenii</i> Knaben
Papaveraceae	<i>Papaver lapponicum</i>
Scrophulariaceae	<i>Pedicularis kanei</i> Durand ssp. <i>kanei</i>
Graminae	<i>Poa arctica</i> R. Br. ssp. <i>arctica</i>
Rosaceae	<i>Potentilla hyparctica</i> Malte
Ranunculaceae	<i>Ranunculus nivalis</i> L.
Salicaceae	<i>Salix rotundifolia</i> Trautv.
Saxifragaceae	<i>Saxifraga caespitosa</i> L.
Saxifragaceae	<i>Saxifraga cernua</i> L.
Saxifragaceae	<i>Saxifraga foliolosa</i> R. Br. var. <i>foliolosa</i>
Saxifragaceae	<i>Saxifraga flagellaris</i>
Saxifragaceae	<i>Saxifraga nivalis</i> L.
Saxifragaceae	<i>Saxifraga punctata</i> L. ssp. <i>nelsoniana</i> (D.Don) Hult.
Compositae	<i>Senecio atropurpureus</i> (Ledeb.) Fedtsch. ssp. <i>frigidus</i> (Richards) Hult.
Caryophyllaceae	<i>Stellaria laeta</i> Richards.
Ericaceae	<i>Vaccinium vitis-idaea</i> L. ssp. <i>minus</i> (Lodd.) Hult.

* Bolded species are those analyzed in this thesis
(Nomenclature according to Hulten, 1968)

Table 3. All Phenological stages measured for each of the species.

Barrow Dry Heath		
Phenophases		
Species	Phenological stages	Growth Measures
<i>Alopecurus alpinus</i>	P1; P2; P5; P8; P18; P19	Q1
<i>Arctagrostis latifolia</i> *	P1; P2; P10; P11	Q1
<i>Carex stans</i>	P1; P2; P5; P8; P11	Q1
<i>Cassiope tetragona</i>	P3; P4; P6; P12	Q3; Q4; Q5; Q12
<i>Draba lactea</i>	P1; P3; P4; P9	
<i>Draba micropetala</i>	P1; P3; P4; P9	
<i>Juncus biglumis</i>	P1; P3; P4; P9; P11	Q1
<i>Luzula arctica</i>	P1; P2; P5; P11	Q1; Q2
<i>Luzula confusa</i>	P1; P2; P5; P11	Q1; Q2
<i>Oxyria digyna</i>	P1	
<i>Papaver hultenii</i>	P1; P3; P4; P7	Q1
<i>Papaver lapponicum</i>	P1; P3; P4; P7	Q1
<i>Pedicularis kanei</i>	P1; P2; P3; P4; P7	
<i>Poa arctica</i>	P1; P2; P7; P10; P11	Q1; Q2
<i>Potentilla hyparctica</i>	P1; P3; P4; P6	
<i>Ranunculus nivalis</i>	P1	
<i>Salix rotundifolia</i>	P1; P5; P13; P14; P15; P16	Q2; Q5; Q6; Q7; Q8; Q9; Q10; Q11;
<i>Saxifraga caespitosa</i>	P2; P3; P4; P7	Q1
<i>Saxifraga foliolosa</i>	P1; P2; P3; P4; P6; P7	Q1
<i>Saxifraga flagellaris</i>	P1	
<i>Saxifraga punctata</i>	P1; P3; P4; P6; P7	Q1
<i>Saxifraga nivalis</i>	P1; P5	Q1
<i>Senecio atropurpureus</i>	P1	
<i>Stellaria laeta</i>	P1; P3; P4; P7	
<i>Vaccinium vitis-idaea</i>	P1	

P1: Emergence of first green leaf

P2: Inflorescence visible

P3: First flower bud visible

P4: First flower open/visible

P5: First stigma visible

P6: Elongation of peduncel

P7: First flower withering

P8: Stigma withering

P9: In fruit

P10: Inflorescence expanding

P11: Inflorescence open

P12: Corolla drop

P13: Onset of seed dispersal

P14: First pollen shed

P15: All pollen shed

P16: First yellowing of leaves

P17: Emergence of stem

P18: First anther visible

P19: Anther withering

P 20: First petal drop

Q1: Length of flowering shoot

Q2: Length of longest leaf

Q3: Total number of flowers

Q4: Total number of fruits

Q5: Fruit/flower ratio

Q6: Total number of flowering catkins

Q7: Number of flowers in each catkin

Q8: Total number of mature catkins

Q9: Number of capsules in each catkin

Q10: Weight of largest leaf

Q11: Mature catkin/flowering ratio

Q12: Annual growth increment

* **Bolded species are those analyzed in this thesis**

Species:

Twenty-six species are found within the dry heath plots (Table 2) for which phenological stages were recorded (Table 3). The phenological stages listed are the standard visible vegetative and reproductive stages for each of the individual species that could be measured. From this data set it was determined that the following species had sufficient numbers to be examined: *Arctagrostis latifolia*, *Cassiope tetragona*, *Luzula arctica*, *Luzula confusa*, *Papaver hultenii*, *Salix rotundifolia*, and *Saxifraga punctata*.. The following is a discussion of the characteristics and distribution of these seven tundra species of focus and a listing of the species specific measurements. All seven species are among the ten most common species within the site.

Arctagrostis latifolia

Family: Gramineae. It is a tall, purple grass, often found in wet meadows, along rivers and on tundra and has a wide, circumpolar distribution. In Barrow, it occurs most frequently on dry sites and on high center polygons, well drained banks, and former beach ridges. The phenophases that were measured include: first green leaf emerged, first inflorescence visible, first inflorescence expanding, and in 1996 first glume open(P1, P2, P10, P11). The height of the first individual to emerge in each plot was monitored throughout the growing season by measuring from the base of the plant to the tip of the longest leaf. At the end of the season the height of the three largest individuals was measured in the same way, as well

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as measuring the three largest reproductive shoots, from the base of the plant to the end of the inflorescence.

Cassiope tetragona

Family: Ericaceae. This is an arctic bell heather species, that is an evergreen woody dwarf shrub. It is found on dry heaths and rocks on tundra, or in the mountains throughout the circumpolar arctic. At Barrow it is quite rare, of only small stature, and restricted to a few beach ridges. It is more abundant and robust to the south of Barrow. Phenophases recorded were: first buds visible, first elongation of buds, first flower open, and first corolla drop (P3, P4, P6, P12). The annual growth increment was measured at the end of the growing season.

Luzula arctica

Family: Juncaceae. This is a short rush with flat leaves, found on tundra, mountain tundra, and moist slopes in central and northern Alaska, as well as around the circumpolar Arctic. *Luzula arctica* is common at Barrow and occurs in several habitats. It is most abundant on dry sites, but is a common component of most tundras. The phenophases that were measured are: first green leaf emerged, first inflorescence visible, and first inflorescence open (P1, P2, P5, P11). The height of the first individual to emerge in each plot was monitored throughout the growing season by measuring from the base of the plant to the tip of the longest leaf. At the end of the season the height of the three largest individuals and the three largest

reproductive shoots were measured from the base of the plant to the end of the tallest leaf or inflorescence.

Luzula confusa

Family: Juncaceae. This is a rush with narrow leaves, slightly larger than *L. arctica*. It is found on dry heaths in mountains and tundra throughout Alaska, and the circumpolar arctic. Like *L. arctica* it is common at Barrow in moist to dry habitats. It is most abundant on the driest sites. The phenophases that were measured are: first green leaf to emerge, first inflorescence visible, and first inflorescence open (P1, P2, P5, P11). The height of the first individual to emerge in each plot was monitored throughout the growing season by measuring from the base of the plant to the tip of the longest leaf. At the end of the season the height of the three largest individuals was measured in the same way, as well as measuring the three largest reproductive shoots, from the base of the plant to the end of the inflorescence.

Papaver hultenii

Family: Papaveraceae. This is an arctic poppy that has yellow flowers and silver gray leaves. It is found on sandy and gravelly soil and is restricted to the northernmost part of Alaska. It is closely related to the *Papaver radicum* complex which is measured at several other ITEX sites.

Phenophases measured were: first green leaf to emerge, first bud to emerge,

first peduncle to elongate, first flower to open, and first flower to wither (P1, P3, P4, P6, P7). Throughout the growing season the length of the longest peduncle was monitored from the base of the plant to the tip of the bud, or flower. At the end of the growing season the length of the three longest peduncles were measured.

Saxifraga punctata subspecies *Nelsoniana*

Family: Saxifragaceae. This robust saxifrage has small white flowers, dark green leaves and is found in alpine meadows, tundra hummocks, and along creeks throughout Alaska and parts of Siberia. At Barrow it is a wide ranging plant which reaches its greatest abundance on dry sites. Phenophases measured were: first green leaf to emerge, first bud to emerge, first peduncle to elongate, first flower to open, and first flower to wither (P1, P3, P4, P6, P7). Throughout the growing season the length of the longest peduncle was monitored from the base of the plant to the tip of the bud, or flower. At the end of the growing season the height of the three longest peduncles were measured.

Salix rotundifolia

Family: Salicaceae. This dwarf, prostrate shrub willow, with thin small annual shoots and roundish leaves, has separate male and female catkins, and is found on arctic and alpine tundra, as well as on rocky places throughout southern and northern Alaska, and parts of Siberia. Phenophases

measured were: Emergence of first green leaf, first stigma visible, first pollen shed, all pollen shed, first seed dispersal, and first color change (P1, P5, P13, P14, P15, P16). At the end of the season the length of the longest leaf was recorded.

Chapter 2

EXPERIMENTAL WARMING IN OPEN TOP CHAMBERS

Control and Experimental plot descriptions

The standard basic ITEX project uses small open top chambers (OTCs) to induce warming on target tundra plant communities at the plant canopy level. Chambers at Barrow, Alaska are 1.5 m² hexagonal structures, made from Sun-Lite HP™ (Solar Components Corp., Manchester, NH) fiberglass. These sheets are 1mm thick and have the following optical properties: high solar transmittance in the visible wavelengths (86%), and a low transmittance in the infra-red range (<5%) (Molau and Molgaard, 1996). Figure 2 depicts the sloping sides of the OTCs.

Experimental plots are all permanently marked with a numbered identification stake, and by small metal stakes placed at each of the chamber corners, so that exact locations of the chambers can be determined each year as the snow melt occurs. Monitoring of OTCs and control plots begins after snow melt (end of May/ beginning of June) and continues until mid-August.



Figure 2. Open top chamber at Barrow, Alaska.

Control plots are 1 m² in size with permanent stakes at each corner. These stakes are placed deep into the soil so that they will remain in the same location from year to year. Control plots are not manipulated in any way, and are only used as a base-line comparison to responses observed in OTC experimental plots.

The dry heath site was established in 1994 by Dr. Christian Bay. Areas of the beach ridge with important ITEX target species and a uniform species composition were located. Experimental and control plots were randomly placed within these areas. Figure 3 shows the locations of each control and OTC plot along the beach ridge. These areas were co-dominated by *Cassiope tetragona* and *Salix rotundifolia*.

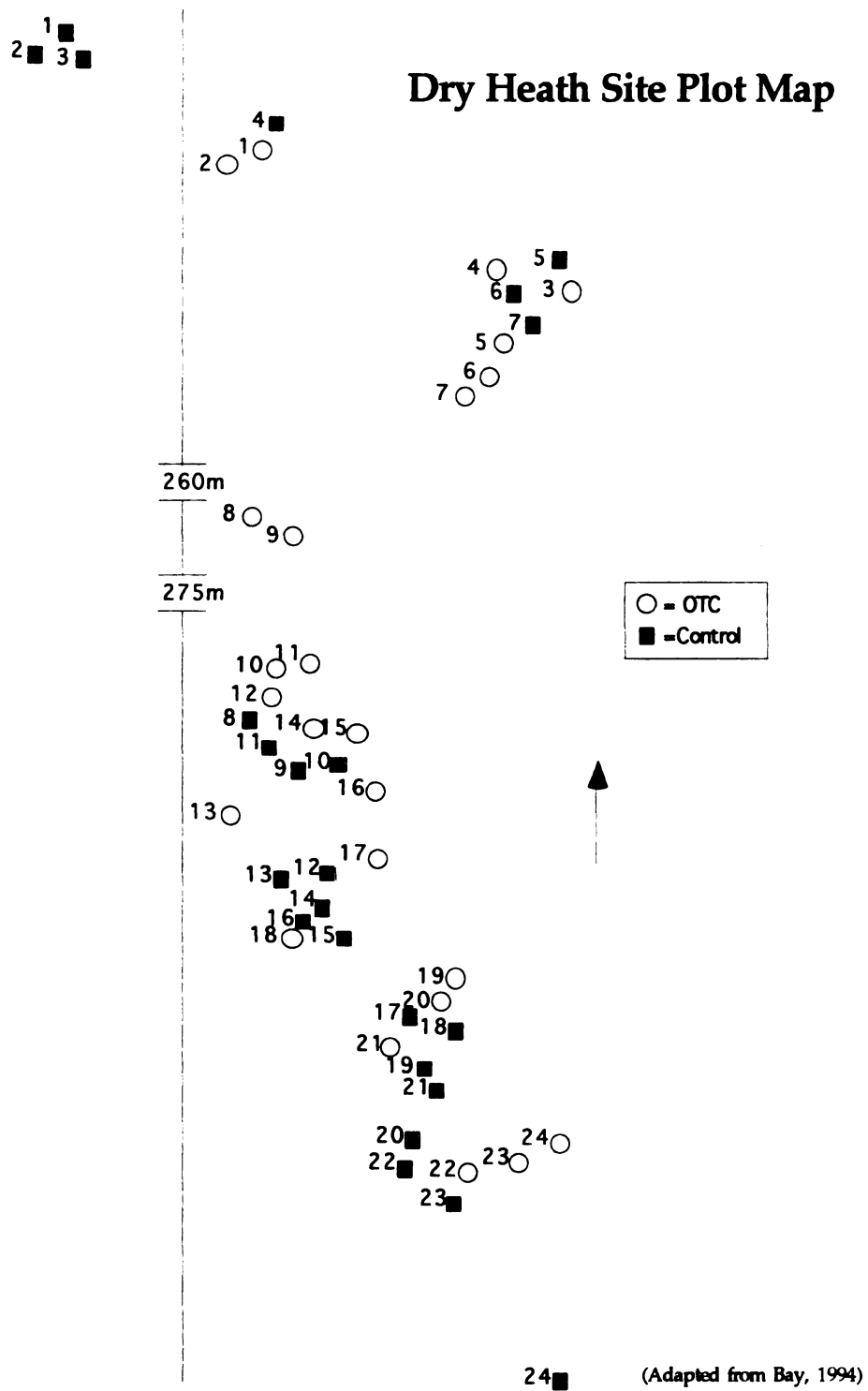


Figure 3. Location map of OTC and control plots along the beach ridge.

Chamber effectiveness:

ITEX hexagonal chambers are designed to warm the plant canopy. Each side of the hexagonal chamber is at an incline of 60°. This causes the chamber to act like a greenhouse and trap heat, and also makes the chambers more favorable to incoming radiation, since the optimal transmittance is at a 90° to the surface of the fiberglass (ITEX Manual, 1996). Chamber performance has been field tested at other locations (Marion et al., 1993). Although the validity of using greenhouse chambers as a means of examining possible responses to warming, has been criticized on the basis of possible complex and poorly understood modifications of climate (Kennedy, 1995), the open top chambers used in this project have been intensely examined (Marion et al., 1993, Marion et al., 1997) and have been determined to raise the ambient temperature in a manner consistent with the predicted global warming. Although light levels within the chambers are slightly altered, no etiolation was readily visible, and the relative humidity within the chambers tracks the temperature as it rises and cools, much as in a natural environment (Figures 4 and 5).

Hobo™ and Stowaway™ dataloggers and thermistors (Onset Computer Corp., MA) were used in both OTCs and control plots to record temperature, and relative humidity. Both of these dataloggers employ small thermistors at the end of a short cord, which allows the thermistor to be placed at a different

location than that of the datalogger. The dataloggers are computer activated to read for a programmed time, which dictates the frequency of the readings which are then stored in the dataloggers memory for downloading at a later

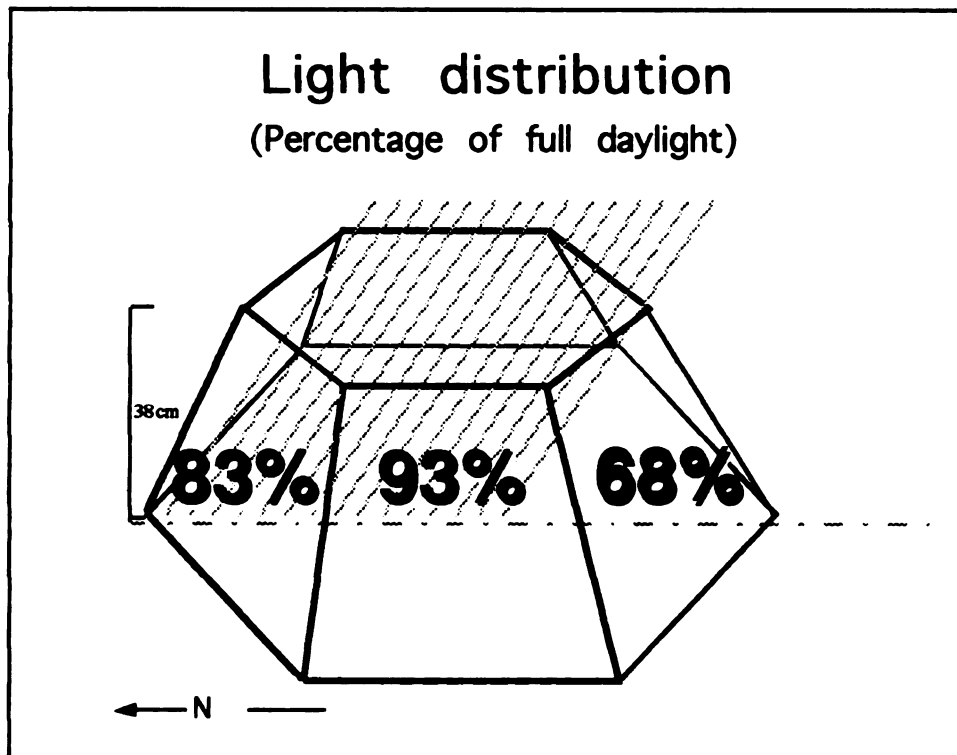


Figure 4. Light distribution within an OTC.

date. Figure 6 shows the horizontal and vertical variations of temperature measurements within and outside of the chamber. The highest temperature occurs at 16 cm above the soil level. This essentially coincides with the height at which temperatures are measured in both the OTCs and the control plots. Relative humidity sensors are also made by Onset Computer Corp., MA, and

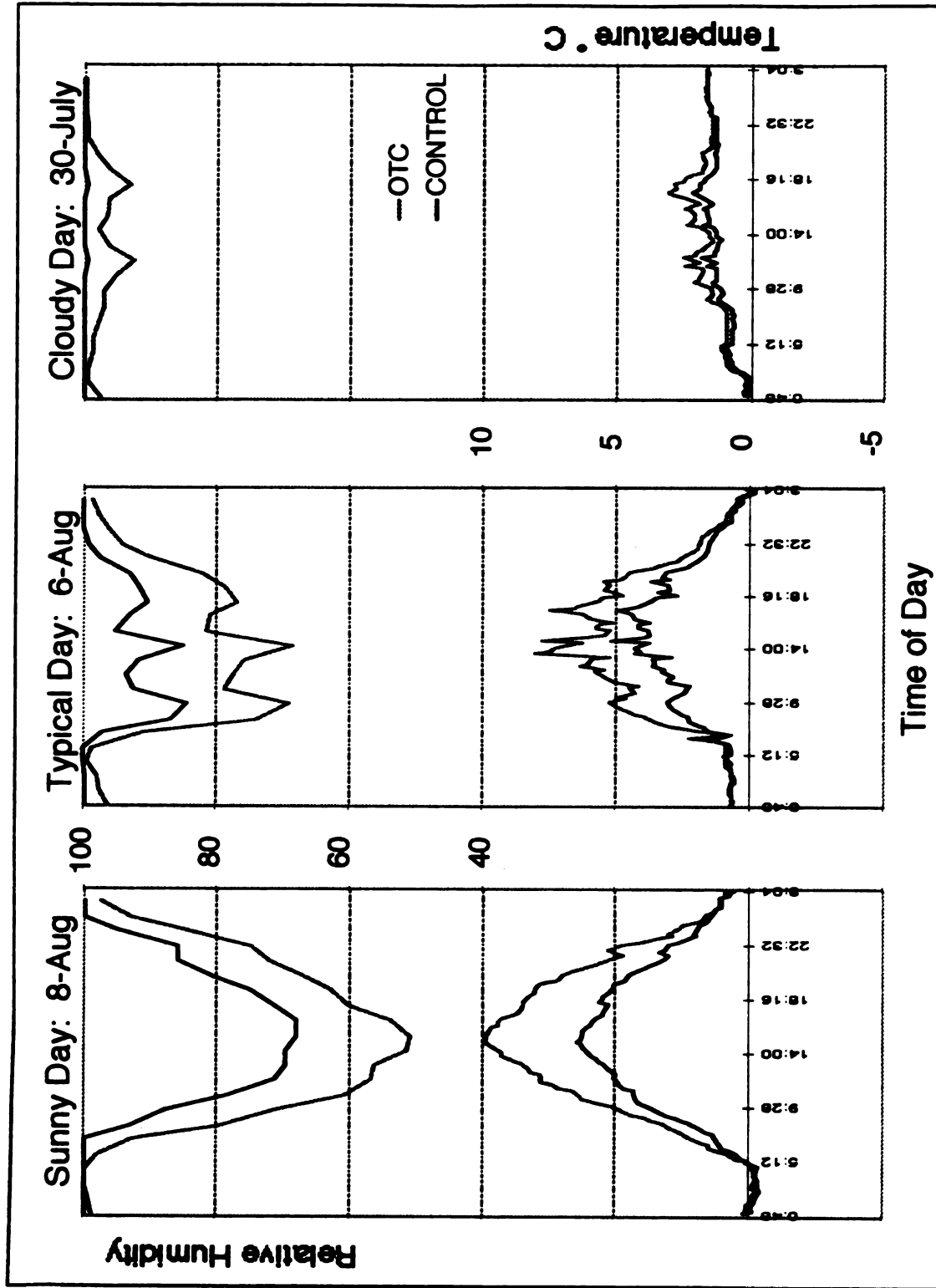


Figure 5. Typical temperature and relative humidity records for 1995.

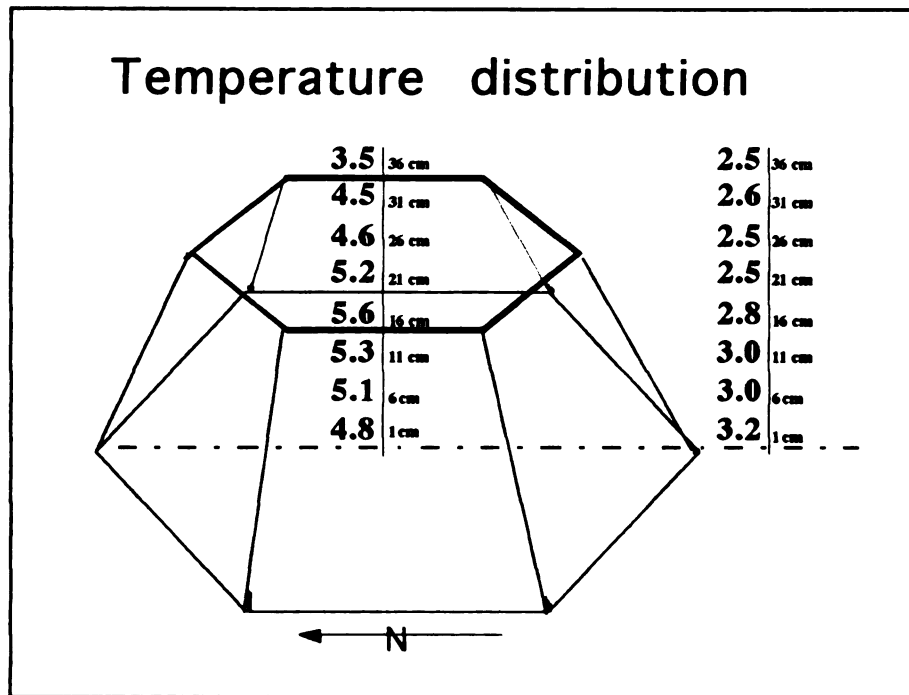


Figure 6. Spatial variation of temperature within a chamber

work in a similar fashion, although the sensor is contained within the datalogger. Temperature thermistors, and relative humidity sensors rest inside Gill six-plate containers at 15 cm above the ground, so that they are screened from both solar and ground radiation. The Gill six-plates also allow ventilation around the sensors. The sensors, for both relative humidity and temperature, were set to monitor continuously (every 12 - 16 minutes) throughout the growing season (approximately 1 June - 20 August) each year.

Table 4 compares ITEX temperature readings at the level of the vegetation canopy to that of a NOAA (United States National Oceanic and Atmospheric Administration) meteorological screen, located to the North of

the site. This chart illustrates the difference between standardized NOAA data and ITEX air temperature data, as well as emphasizing the need for the continuous measurements made at the plant canopy level in both the chambers and the controls. The importance of obtaining temperature data at the plant canopy level is demonstrated in Table 4, as the NOAA temperature data is extremely different than the ITEX data. The average increase in ambient air temperature within the chambers throughout each growing season was on the order of 1.5 and 1.7°C for each of the three years. This is consistent with the predictions of the GCMs (Chapman and Walsh, 1993).

Table 4. A comparison of ITEX and NOAA temperature readings.

Location	Height	Number of measurements	Temperature °C
NOAA shelter	2m screen	1/hour	4.9
Δ Control - Shelter	15 cm Gill 6 plate	at least every 16 min.	0.6
Δ OTC - Control	15 cm Gill 6 plate	at least every 16 min	1.5

Growing degree days were calculated in the following manner: from the continuous seasonal measurements the above 0°C temperatures were averaged for each day. These daily averages were summed consecutively to obtain the accumulated growing degree days. This yields an index of how much energy was accumulated in both the control plots and OTCs for each

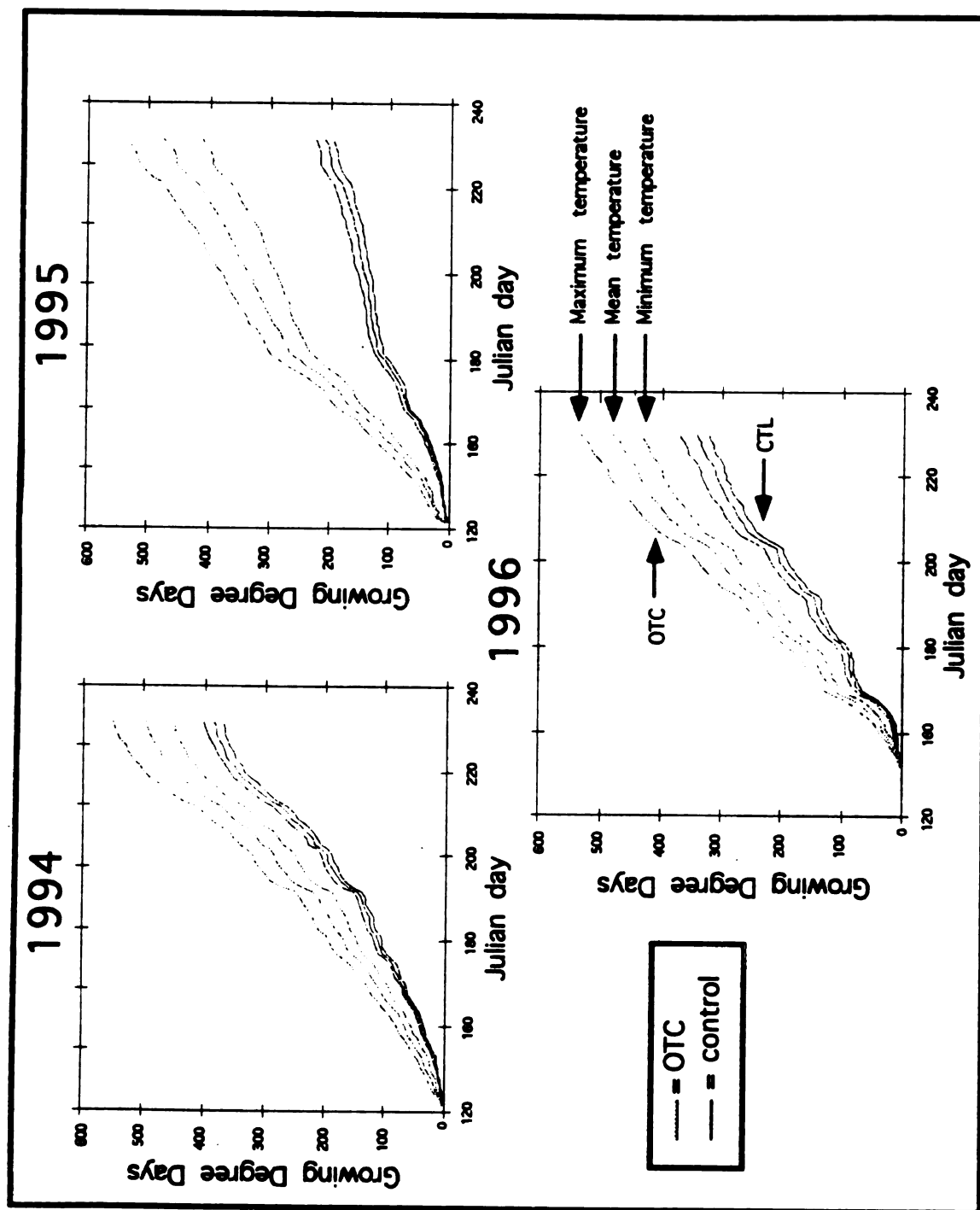


Figure 7. Accumulated growing degree days in OTCs and control plots.

monitored growing season (Figure 7). In Figure 7, the center line in each set of three represents the mean, with upper line being the maximum, and the lower line the minimum. In all three years the course of the lines show that the OTC degree days are separate from the degree days in the control plots. This indicates that the chambers accumulated more energy than the control plots. Figure 8 represents the total amount of degree days accumulated in the OTCs and control plots for each of the three growing seasons.

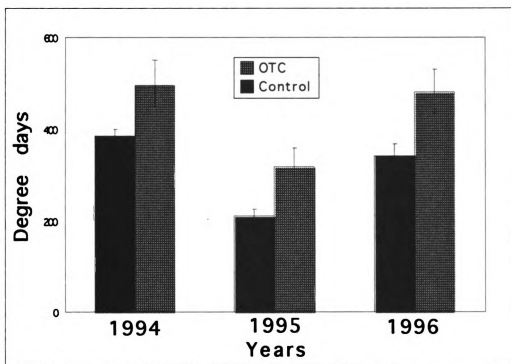


Figure 8. OTC and control plot degree day accumulations during the growing seasons of 1994, 1995, and 1996

The total degree days accumulated for 1994, and 1996 were approximately the same, while 1995 was an comparatively cold summer, as seen by the fewer

number of degree days accumulated. Each summer the OTCs accumulate more degree days than the control plots (Figure 7).

Belowground temperatures were also measured for a portion of the summer in 1996. Thermistors were inserted into grooves on a wooden dowel, at 1cm, 5cm, 10cm, 15cm, and 30cm below the soil surface. The dowel was inserted into the ground, beneath a chamber and beneath a control plot. This provides a profile of soil temperature for both OTCs and control plots. Measurements were made from 12 July, 1996 and until 18 August, 1996. The data (Table 5) demonstrate little difference between average soil temperatures between chambers and control plots. Using an ANOVA method of analyses (With a Box-Cox transformation of square root, see chapter three for a more detailed description of analyses) this difference was determined to not be significant. The absence of significant soil warming in the OTCs may be

Table 5. Average soil temperature (°C) at different depths (cm)

Depth of thermistor	OTC plots	Control plots
1	6.56	5.98
5	4.79	4.97
10	3.65	3.49
15	2.24	2.35
30	0.63	0.36

because of the large heat sink properties of the surrounding tundra. Larger chambers might create such an effect although Hollister (personal

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communication) recorded a warming in a wet meadow site with identical chambers, at Barrow. Therefore, it is likely that the fine silts, sand, and gravel soils of the dry heath site do not store heat, but instead it may be conducted to the large surrounding heat sink. Active later measurements confirm the observation that the OTCs do not warm the soil underneath the chambers (Figure 9). The active layer (the zone of the soil that melts each growing

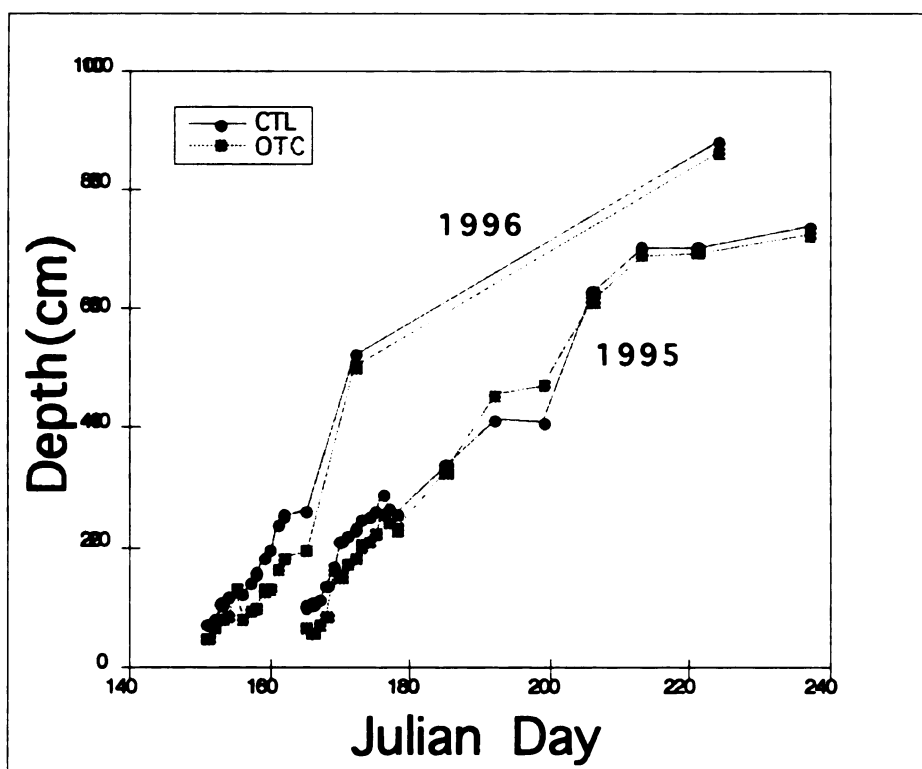


Figure 9. Average thaw depth for 1995 and 1996.

season and in which the roots and microflora are active) was measured every day for the first two weeks after snow melt. The active layer was

measured by forcing a small metal rod (1cm diameter) into the soil until the rod reached the permafrost. The thaw depths measured throughout the season show that the thawing of the active layer is not significantly deeper in the OTCs. The fact that the overall thawing was greater in a warmer year (1996) compared to a colder year (1995) supports the idea that the OTCs are not large enough to overcome the massive heat sink of the ground. Active layer development was greatest in 1996 and thaw began earlier.

Community composition

In the summer of 1995 the community composition of each of the plots was determined using the point-frame analysis method (ITEX Manual, 1996). This method utilizes a 75cm by 75cm frame that has a grid with cross-wires at each 7.5cm interval. This creates a 100 point grid, which at each point, the name of the plants and the height at which they were sighted was recorded, down to the ground level. This allows for percentage cover and frequency of each species to be calculated which permits a comparison of the control and experimental plots. This data also serves as a baseline measurement for future studies of community change.

Table 6 contains the average percentage cover, and frequency for the ten most common vascular plants for each of the plots. A percentage similarity test indicated that although there are differences between the percentage cover of species between the OTCs and the control plots, that this difference (86% similar) is within the limits (80% similarity) acceptable to

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Summary

phytosociologists (P.J. Webber, personal communication). The OTC plots have 8.95% cover of moss, 24.5% cover of lichens, and 1.67% bare ground. Control plots have 10.50 % cover of mosses, 21.86% cover of lichens, and 1.03% bare ground. The ITTEX experiment is designed to minimize the effects of this natural variation by having a large number of replicates. The dry heath ridge at Barrow consists of 24 OTCs and 24 control plots.

Table 6. Average percentage cover of common vascular plants.

	% cover OTC	± S.E. OTC	% cover Control	+ S.E. Control	Frequency of occurrence OTC	Frequency of occurrence Control
<i>Cassiope tetragona</i>	23.1	1.9	16.0	1.1	100	100
<i>Salix rotundifolia</i>	18.4	1.7	20.6	1.5	100	100
<i>Luzula confusa</i>	3.4	0.7	3.6	0.5	91	100
<i>Stellaria laeta</i>	2.4	0.5	2.4	0.4	100	100
<i>Arctagrostis latifolia</i>	2.0	1.0	2.1	0.7	62	62
<i>Potentilla hyparctica</i>	2.2	0.4	6.0	4.1	96	100
<i>Poa arctica</i>	1.2	0.2	1.0	0.2	92	83
<i>Luzula arctica</i>	1.0	0.2	0.8	0.2	75	71
<i>Carex stans</i>	1.1	0.7	0.2	0.1	12	12
<i>Saxifraga punctata</i>	0.9	0.2	0.7	0.1	83	92

Summary:

The Dry Heath ridge ITEX site was established at Barrow, Alaska in the summer of 1994. 24 OTCs and 24 control plots were randomly assigned across this heath tundra. Plots are permanently marked with stakes and corner markers. The chambers are constructed of a light weight fiberglass , Sun-Lite HP™ , in a hexagonal shape. Point-frame analysis was performed on all plots to determine the percentage cover and frequency of species. *Cassiope tetragona* and *Salix rotundifolia* are the co-dominant species. The plant composition within the chambers and controls were determined to be the same (86% similarity) with some natural variation.

Chambers were shown to be effective in increasing the air temperature during the growing season by 1.5 - 1.7°C. Degree day accumulation in the OTCs was separate and more evident in the OTCs than in the controls throughout the growing season. Total accumulation was larger in the OTCs. Chambers were determined to not have an effect on the soil temperature at different depths, and the active layer depth in both OTCs and controls was similar throughout the season. Active layer development was greatest in 1996 and thaw began earlier, possibly because 1996 was warmer than 1995, and snow melt occurred earlier. Each year had a greater growing degree day accumulation in the chambers than in control plots, with a similar pattern of accumulation.

Chapter 3

PLANT RESPONSES TO EXPERIMENTAL WARMING

Experimental design summary

The ITEX site on the dry heath at Barrow, consists of 24 OTCs and 24 control plots, in which plant developmental stages and growth are monitored visually throughout each growing season. Due to a large amount of variability inherent in tundra ecosystems, a large number of replicates are needed. Each plot is treated as a separate replicate, with the earliest occurrence of phenophases for each of the species recorded as a data point. Chambers increase the ambient air temperature 1.5 - 1.7 °C (see discussion in chapter 2). Effects of this induced warming are analyzed using an ANOVA, with a conservative significance level of 0.01, to try and compensate for the large amount of variability within the data (see pp. 32-33, this chapter)

Effects on phenophases

Phenology is the study of the seasonal timing of plant development. Each phenophase is a specific stage in this development. Phenophases for species found both in OTCs and control plots were monitored daily.

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Phenology was monitored for all species contained within plots. In 1994 plots were monitored from 15 June - 18 August, in 1995 from 12 June - 23 August, and in 1996 from 28 May - 14 August. Average monitored growing season length for 1994, 1995, and 1996 was 72 days. Phenophases were monitored daily by examining each plot visually to determine if any of the contained species had reached the next phenophase. The Julian date was recorded for the first plant within a plot to undergo each of the monitored stages, with each plot being treated as a separate replicate throughout the project. This method of visually monitoring each plot is also described in the ITEX handbook, which in addition states that each OTC plot has a parallel control plot, so that pseudo-replication is avoided (ITEX Manual, 1996). The design of the experiment allows for examination of the data by Analysis of Variation (ANOVA).

Phenophase data were examined in three ways: first, the Julian date of occurrence of a phenophase determines the actual date of occurrence of a developmental stage of the plant; second, the number of days that the plot has been snow free before a developmental stage was reached; and third, each of the Julian dates of occurrence of phenophases were replaced with the average number of growing degree days that had accumulated up to the time that the phenophase occurred. These three methods of analyses allow a comparison of calendar date, days since snow melt, and cumulative temperature to determine significant differences between development in OTCs to that in the control plots.

Data Desk 5.0.1 software (Data description Inc., 1995) was used to analyze all data. Data was examined for normality and equality of variance, and was transformed using a dynamic method. It was determined that because there was not an *a priori* reason for transforming the data, the Box-Cox method was necessary to transform the data. This method utilizes a log-likelihood function to determine the best transformation, which was -0.5 for all Julian date of occurrence of phenophases; 0.0 for all growing degree day accumulations for each of the phenophases; and 0.0, or -0.5 for days since snow free occurrence of phenophases and growth measurements, (which allowed for \approx normal distribution, and \approx variances). A three-way ANOVA was used to determine significance between category variables of species, year, and treatment for all response variables, except for phenophases undergone by *Salix* and *Cassiope* that did not have corresponding phenophases in other species, for which a two way ANOVA was performed. All interactions were examined as well, with Post-Hoc Sheffe tests as a conservative method of determining all possible contrasts, and partitioning of the variance (Sokal and Rohlf, 1995). Julian date of occurrence data was analyzed by separating woody from herbaceous data, so that the assumptions of normality and equality of variances could be met for the two separate ANOVAs that were performed. The distributions and variances of the number of days since snow free, and the accumulated growing degree days allowed for all species to be analyzed together. Responses were considered to be significantly different in the OTCs

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and control plots, either positive or negative responses, if the p value was less than 0.01, so that a 99% confidence level was established.

For all phenophases measured the main effects of species, year, and treatment (OTC or control) were all significant for Julian date of occurrence. These main effects were also significant for days since snow free, except for the main effect of treatment (OTC or control) for elongation of peduncles. The main effects of species, and year were all significant for the number of growing degree days accumulated, while the main effect of plot type was not significantly different. These main effects indicate responses across species, plot type (either OTC or control), and year, regardless of the other effects. Appendix A (Tables 8-10) contains all ANOVA tables for all dependent variables tested. Appendix B (Tables 11-13) contains all significance levels of Post - Hoc Scheffe tests.

Emergence of first green leaf, emergence of first inflorescence, and inflorescence open (first stigmas visible, or glume open) were monitored for the graminoid species of *Arctagrostis latifolia*, *Luzula confusa*, and *Luzula arctica*. The phenophases of emergence of first green leaf, and first inflorescence visible were not significant at the $p < 0.01$ level for the species of *Arctagrostis latifolia*, *Luzula arctica*, and *Luzula confusa* for all three years, regardless of whether Julian date of response, or days since snow free of the response, were being examined. The Julian date of first inflorescence open was significant ($p < 0.01$) for *Luzula confusa* in 1996 ($p < 0.001$), as well as the days since snow free (Box-Cox transformation 0.0) in 1996 ($p < 0.001$). Table 7

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records the total number of responses for each of the species, indicating the trend of the species in response to experimental warming. Figures 10 and 11 show the trends for the occurrence of phenophases in both sets of data to occur earlier in OTCs, although these differences were not significant. Figure 12 represents the average amount of degree days that were accumulated before *Arctagrostis latifolia*, *Luzula arctica*, and *Luzula confusa* underwent the next developmental stage. There is a general trend that the amount of energy accumulated in the OTCs is approximately the same as, or larger than the amount accumulated in the corresponding control plots. In 1996, a significantly larger amount of growing degree days were accumulated in the OTCs for *Luzula arctica* to have the first inflorescence visible ($p < 0.01$). Figure 12 demonstrates that although Figures 10 and 11 show trends of phenophases occurring earlier within the chambers, it is not always due to the effects of increased temperature. Although the trend is for the phenophase to occur earlier in the OTCs, there is an additional energy requirement to do this, demonstrated by the trend for OTCs to accumulate more growing degree days than the control plots. This trend also suggests that some factor or condition that is not, or less, temperature dependent needs to be met to reach the next phenophase.

Table 7. Number of responses to warming as a determination of trends in plant responses.

Species	Type of analysis	# of earlier (+) responses	# of later (-) responses	# of significant + responses ($p < 0.01$)	# of equal responses	trend
<i>Arcagrostis latifolia</i>	Julian Date	4	0	0	3	equal or earlier
	Days snow free	3	0	0	4	equal or earlier
<i>Cassiope tetragona</i>	GDD	2	0	0	5	equal
	Julian Date	11	0	8	0	earlier
	Days snow free	11	0	3	0	earlier
<i>Lucula arctica</i>	GDD	7	2	1	2	earlier
	Julian Date	6	0	0	3	equal or earlier
	Days snow free	5	2	0	2	equal or earlier
<i>Lucula confusa</i>	GDD	6	0	2	3	more
	Julian Date	3	1	2	4	equal or earlier
	Days snow free	5	0	0	4	equal or earlier
<i>Papaver hultenii</i>	GDD	5	0	0	4	equal or more
	Julian Date	12	0	1	1	earlier
	Days snow free	11	1	0	2	earlier
<i>Salix rotundifolia</i>	GDD	9	5	0	0	variable
	Julian Date	13	0	10	5	earlier
	Days snow free	12	0	4	6	earlier
<i>Saxifraga punctata</i>	GDD	9	0	8	9	equal or earlier
	Julian Date	11	1	1	1	earlier
	Days snow free	12	1	0	1	earlier
	GDD	14	0	1	0	more

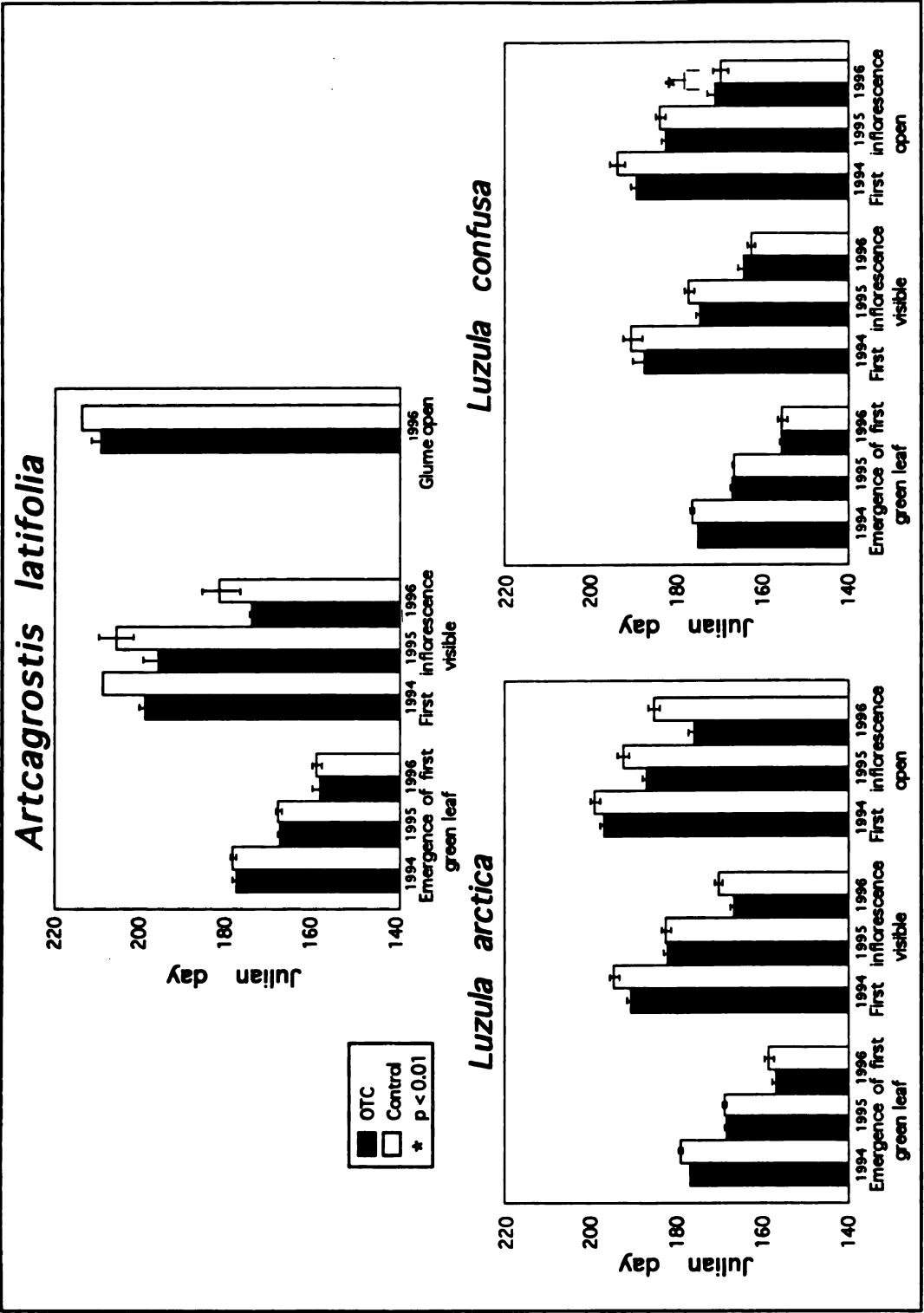


Figure 10. Julian date of phenophase occurrence for three graminoid species

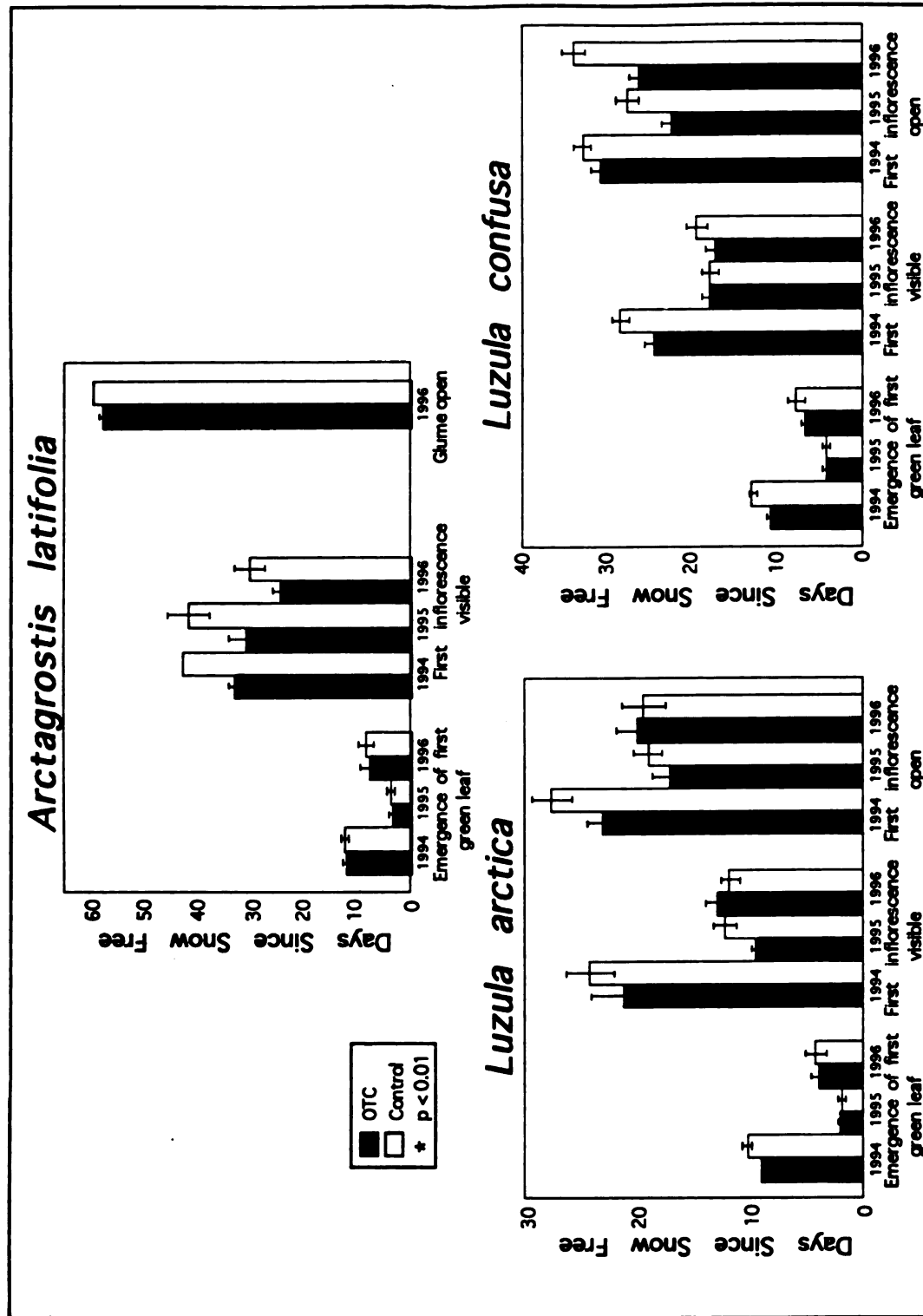


Figure 11. Number of snow free days prior to the onset of phenophases for three graminoid species

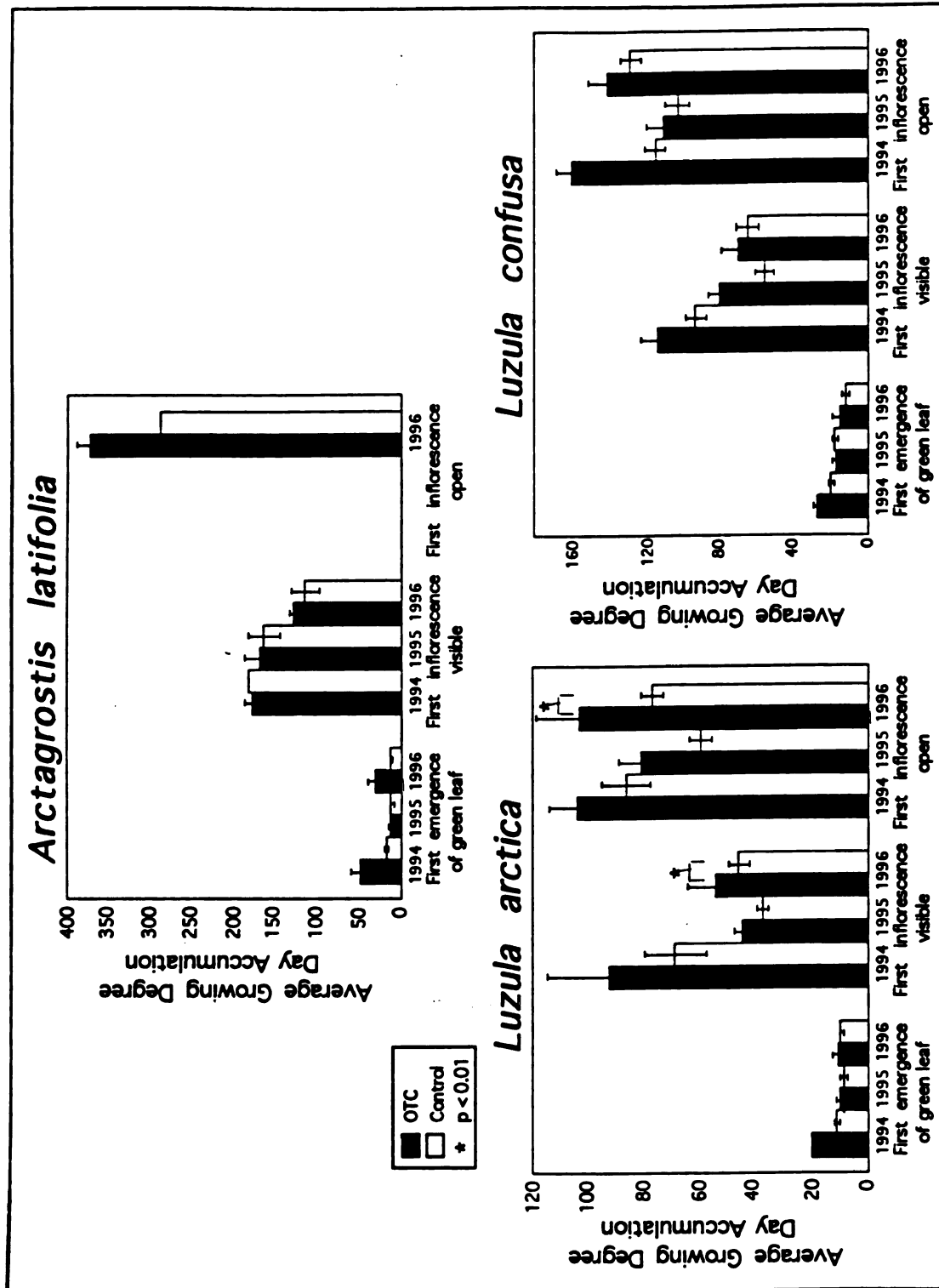


Figure 12. Growing Degree Day accumulations prior to the occurrence of phenophases in three graminoid species.

Emergence of first green leaf, emergence of first inflorescence, elongation of peduncles, opening of first flower, and withering of first flower were monitored for *Papaver hultenii* and *Saxifraga punctata*, two erect forb species. The phenophase emergence of first green leaf did not occur significantly earlier in the OTCs, in any of the three monitored growing seasons. In 1994 the emergence of first inflorescence occurred significantly earlier in the OTC for *Papaver hultenii* ($p < 0.001$) when examining Julian date of occurrence, and in 1995 for date since snow free ($p < 0.01$). The phenophase of first bud elongation occurred earlier in OTCs in 1996 for Julian date of occurrence for the species of *Saxifraga punctata*. OTCs did not have a significant effect for the phenophase of first flower open. In 1996, the Julian date of occurrence of the first withering of a *Papaver* flower occurred earlier in the OTCs ($p < 0.001$). Figures 13 and 14 represent the Julian date of occurrence, and the days since the plot was snow free at which time the phenophases happened for both of these species. Again there was a general trend for most phenophases to occur earlier in the OTCs, although most of these results were not significant ($p < 0.01$). Although Figure 13 shows a trend for there to be more degree days accumulated in the OTCs before undergoing phenophases, most of these differences were not significant. The only phenophase for *Papaver hultenii* to require a significantly larger amount of accumulated growing days was the stage of the first withering of the flowers.

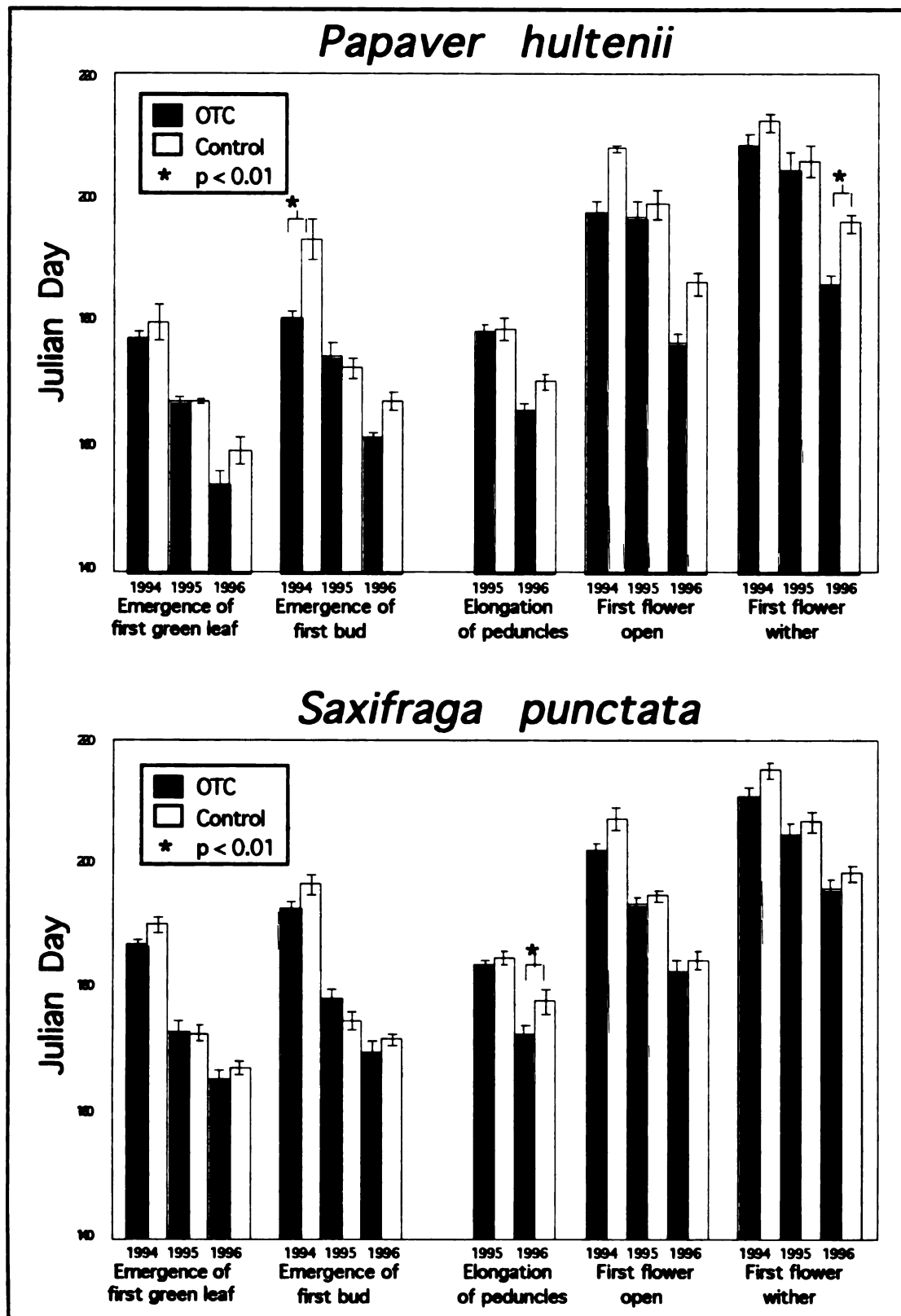


Figure 13. Effects of OTC warming on Julian Date of occurrence of forb phenophases.

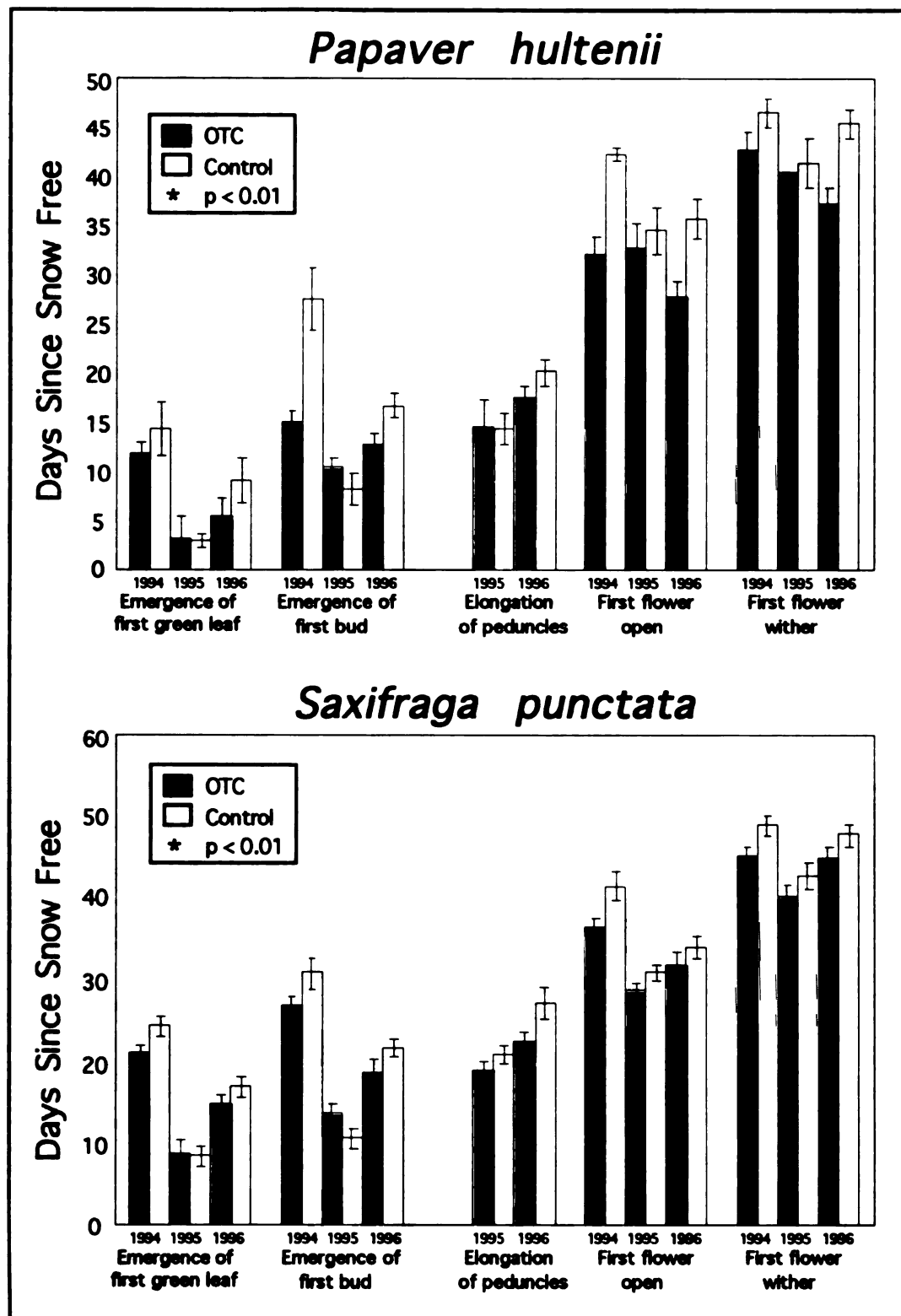


Figure 14. Number of days snow free prior to the occurrence of forb phenophases.

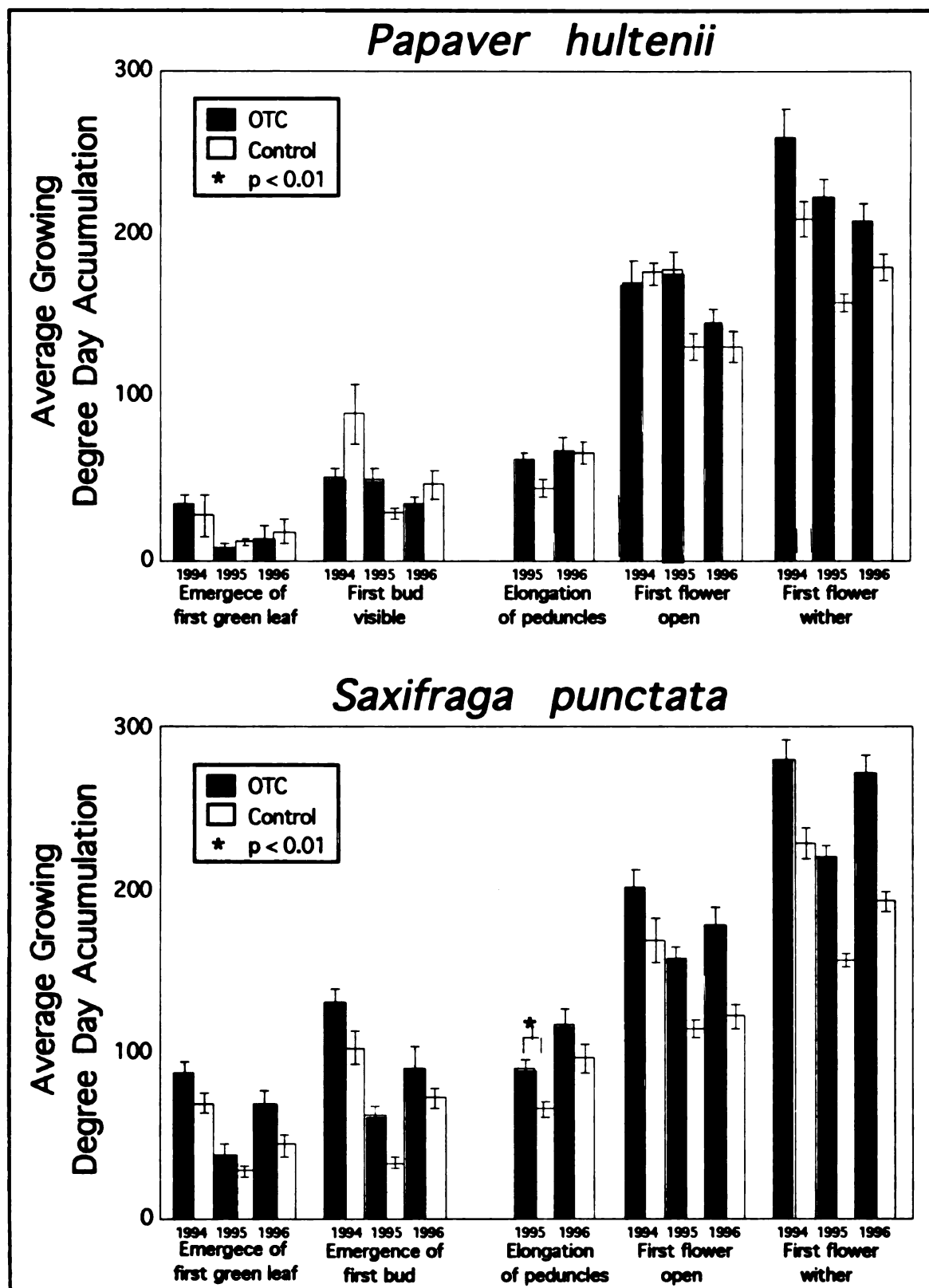


Figure 15. Number of accumulated Growing degree days prior to the occurrence of forb phenophases.

Many *Saxifraga punctata* phenophases seemed to need significantly larger amounts of growing degree days within the OTCs. In 1995 the phenophase of first elongation of peduncles required a significantly larger amount of Growing degree days ($p = 0.01$). The phenophase of first withering of a flower required significantly more growing degree days within the chambers in all three years ($p < 0.01$, $p < 0.000001$, $p < 0.000001$). Both forb species also show a general trend of equal or larger amounts of growing degree days within the OTCs to undergo phenophases, although most phenophases show a trend of occurring earlier within the chambers.

For *Salix rotundifolia* emergence of first green leaf, first stigma visible, first pollen shed, all pollen shed, first seed dispersal, and first color change were monitored. In 1994 small wires were placed within the plots to mark off small areas of *Salix* that were determined to have male or female catkins. These became the monitored areas for the proceeding growing seasons, and only stages that occurred within these units were monitored (also stated in ITEX Manual, 1996).

In 1994, and 1996 for *Salix rotundifolia* the Julian date of occurrence of first green leaf visible took place significantly earlier in the OTCs. The Julian date of occurrence for the phenophase of first stigma visible occurred earlier in the OTCs in 1994, and 1995 ($p < 0.00001$; $p < 0.01$). The male stage of first pollen shed took place significantly earlier in the OTCs in 1994, 1995, and 1996 for the Julian date of occurrence ($p = 0.01$; $p < 0.01$; $p < 0.01$), and for the days

since the plots were snow free in 1994 and 1995 ($p < 0.01$; $p < 0.01$). The next male phenophase, all pollen shed, took place significantly earlier in OTCs in 1994, and 1995 for Julian date of occurrence ($p < 0.01$; $p < 0.01$), and in 1995, and 1996 for days since snow free ($p < 0.01$; $p < 0.01$). The OTCs did not have a significant effect for the next female stage of onset of first seed dispersal. In 1996 the vegetative stage of first color change had a significantly earlier Julian date of occurrence, and fewer days since the snow melted off the plots ($p = 0.001$; $p < 0.01$). Figures 16 and 17 again show the general trend of phenophases occurring earlier in OTCs than in controls. These trends agree with those found on other *Salix* species (as well as *S. rotundifolia*) within the ITEX community (Jones et al. 1997).

Salix had several phenophases that consistently appeared to need significantly more energy in the OTCs than in the control plots. Significantly more energy accumulated within the OTCs in all three years ($p < 0.01$; $p < 0.000001$; $p < 0.00001$) before the male phenophase of all pollen shed was reached, even though the phenophase occurred earlier. Significantly more energy amassed within the chambers in 1995, and 1996, before the female phenophase of first seed dispersal was reached, even though the phenophase did not occur significantly earlier.

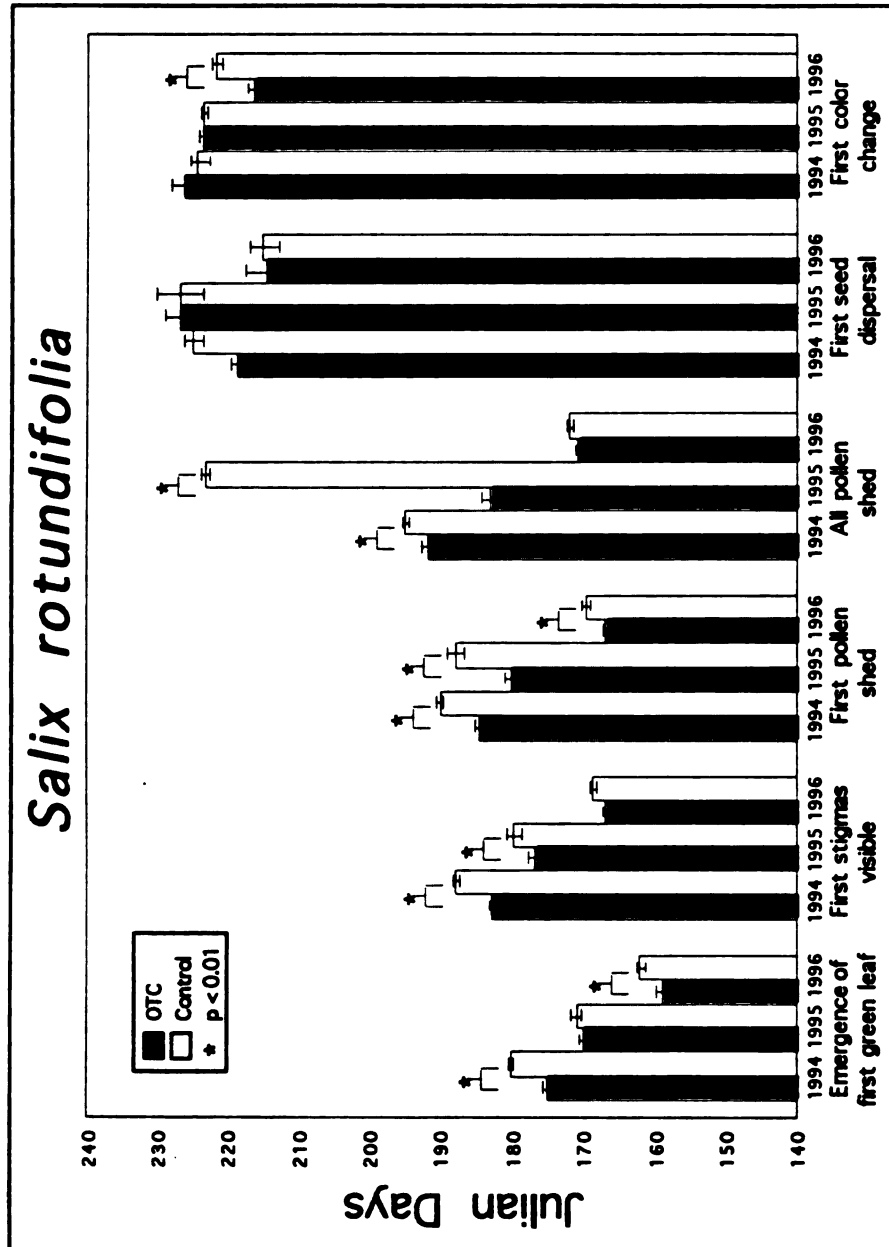


Figure 16. Julian Date of occurrence of *Salix rotundifolia* phenophases.

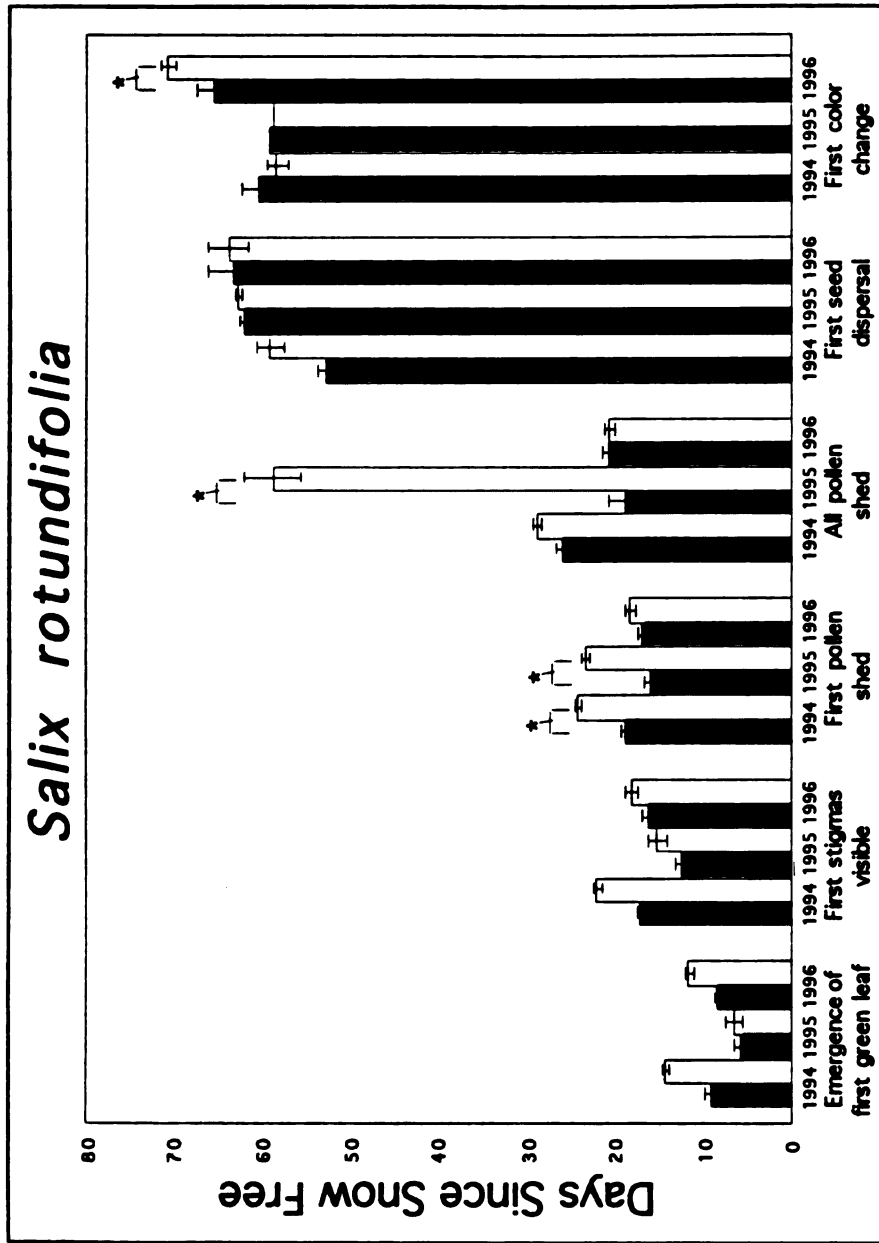


Figure 17. Number of days the plot has been snow free before a phenophase occurred.

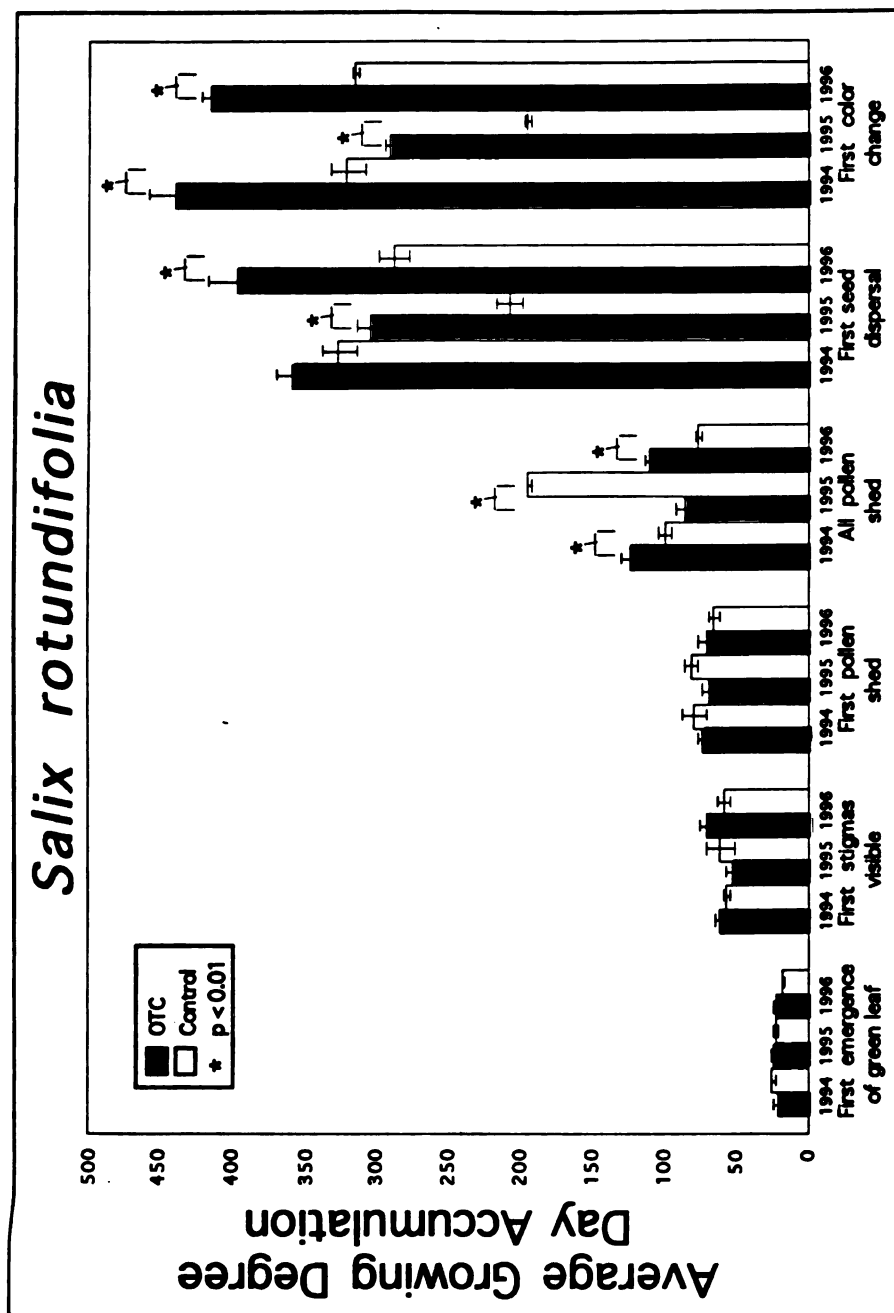


Figure 18. Accumulated Growing Degree Days prior to *Salix rotundifolia* phenophases.

These results show that the earlier phenophases are perhaps more dependent upon the date of occurrence, or time since snow free, while the latter phenophases are less dependent on temperature, since the OTCs accumulated more energy, although for the most part the phenophases did not occur earlier

In *Cassiope tetragona* the phenophases of first bud visible, first elongation of peduncles, first flower open, and first corolla drop were monitored on a specific marked ramet for the growing seasons of 1994, and 1995, and the stage of first bud visible in 1996. Because in the 1996 growing season there were not any marked ramets that had buds emerge, the entire plot (control or OTC) then became the monitored unit, and any stages that any of the *Cassiope* within the plot underwent were then recorded.

The first phenophase of bud emergence was significantly earlier in the OTCs in 1995, than it was in the control plots for the Julian day (Figure 19) at which it occurred ($p < 0.01$), and earlier in the OTCs than in the control plots for the days since snow free (Figure 20, $p < 0.01$). The next stage of first elongation of buds was significantly earlier in the OTCs in 1994, and 1995 for the Julian date at which they elongated ($p < 0.01$) and in 1995, for the days from which the plot had been snow free at which they elongated ($p = 0.01$). In 1994, 1995, and 1996 flowers opened significantly earlier in the OTCs for the

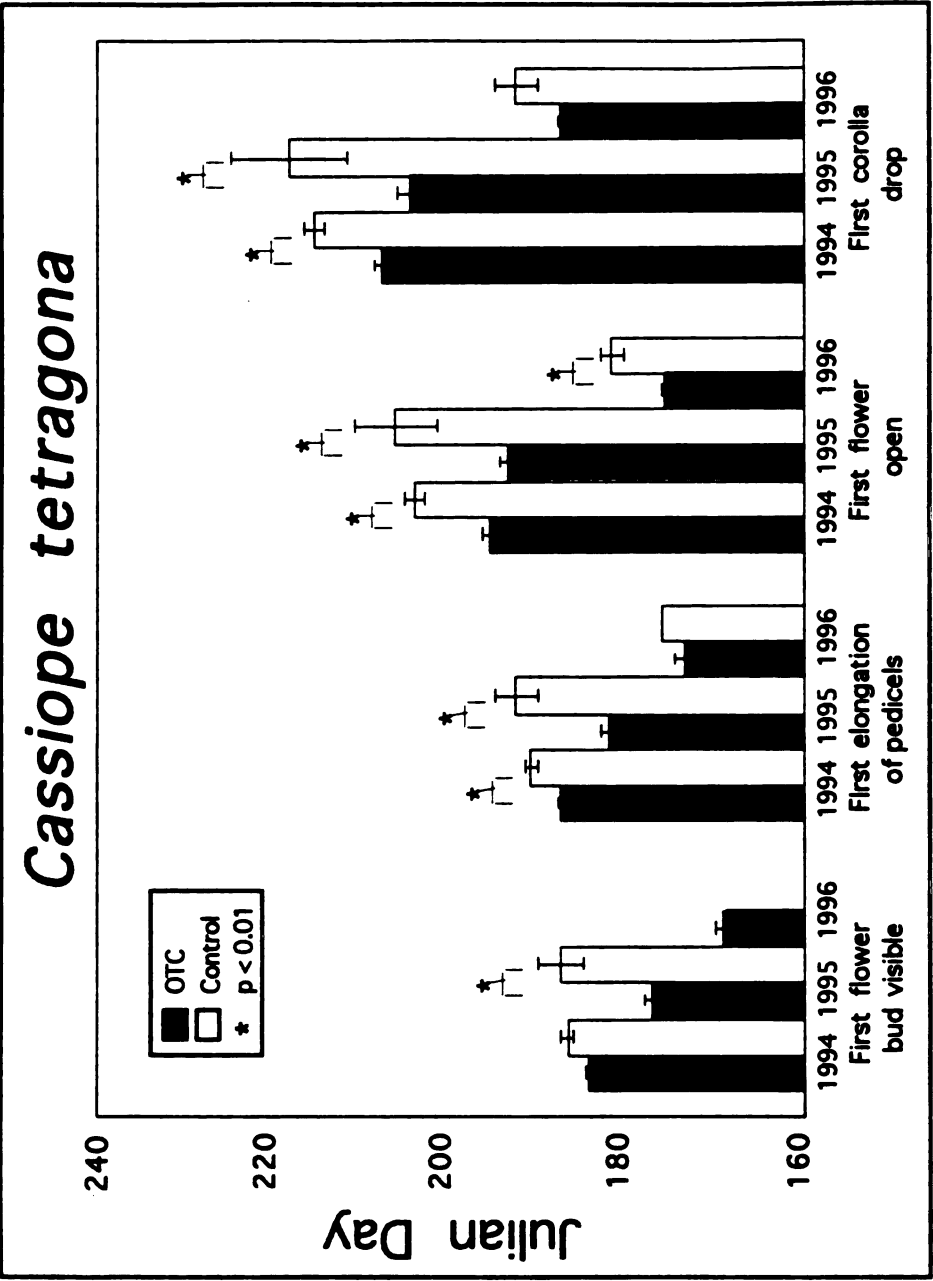


Figure 19. Julian date of occurrence of phenophases for *Cassiope tetragona*.

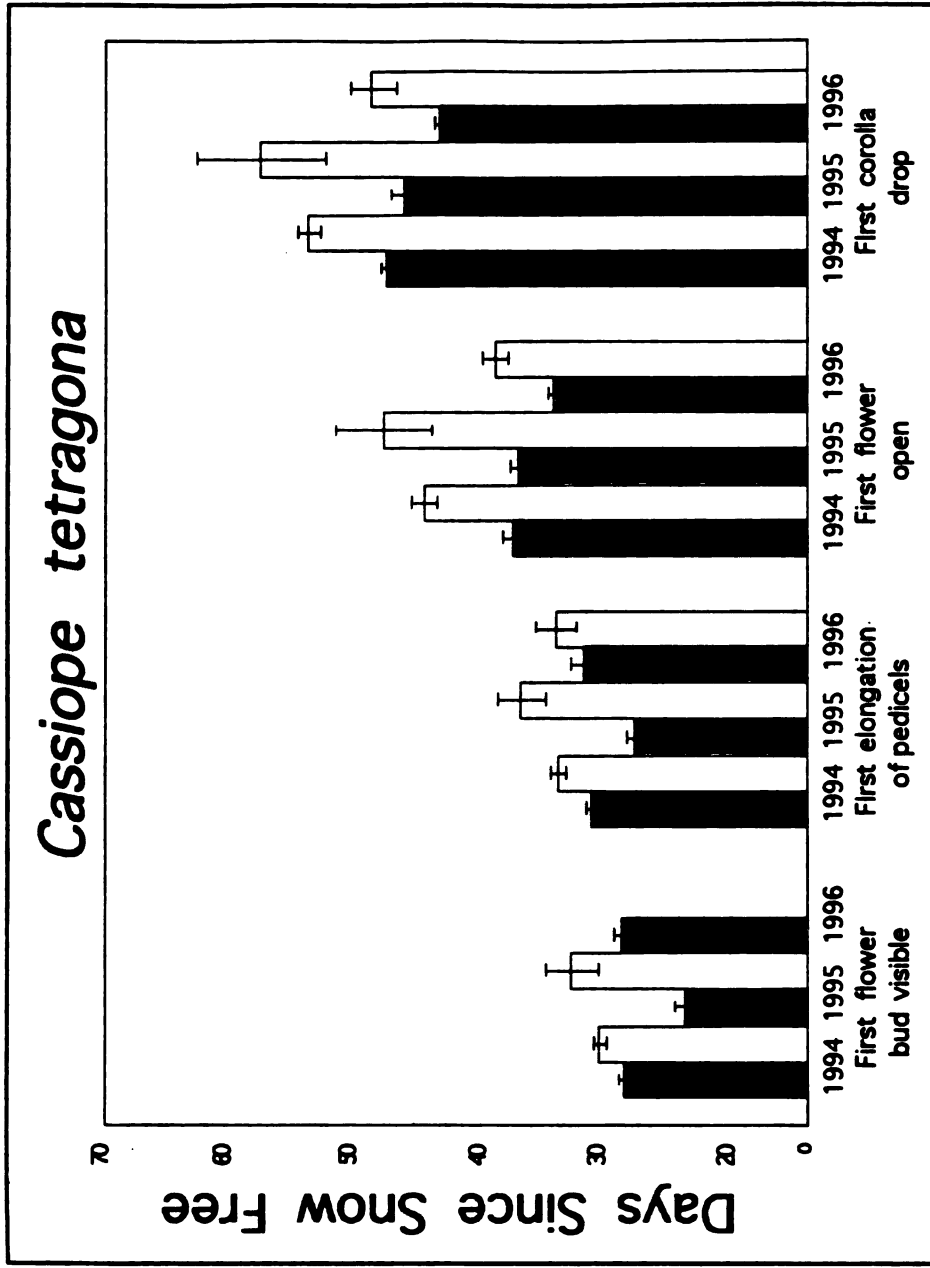


Figure 20. The number of days that the plot was snow free before *Cassiope* reached a particular phenophase.

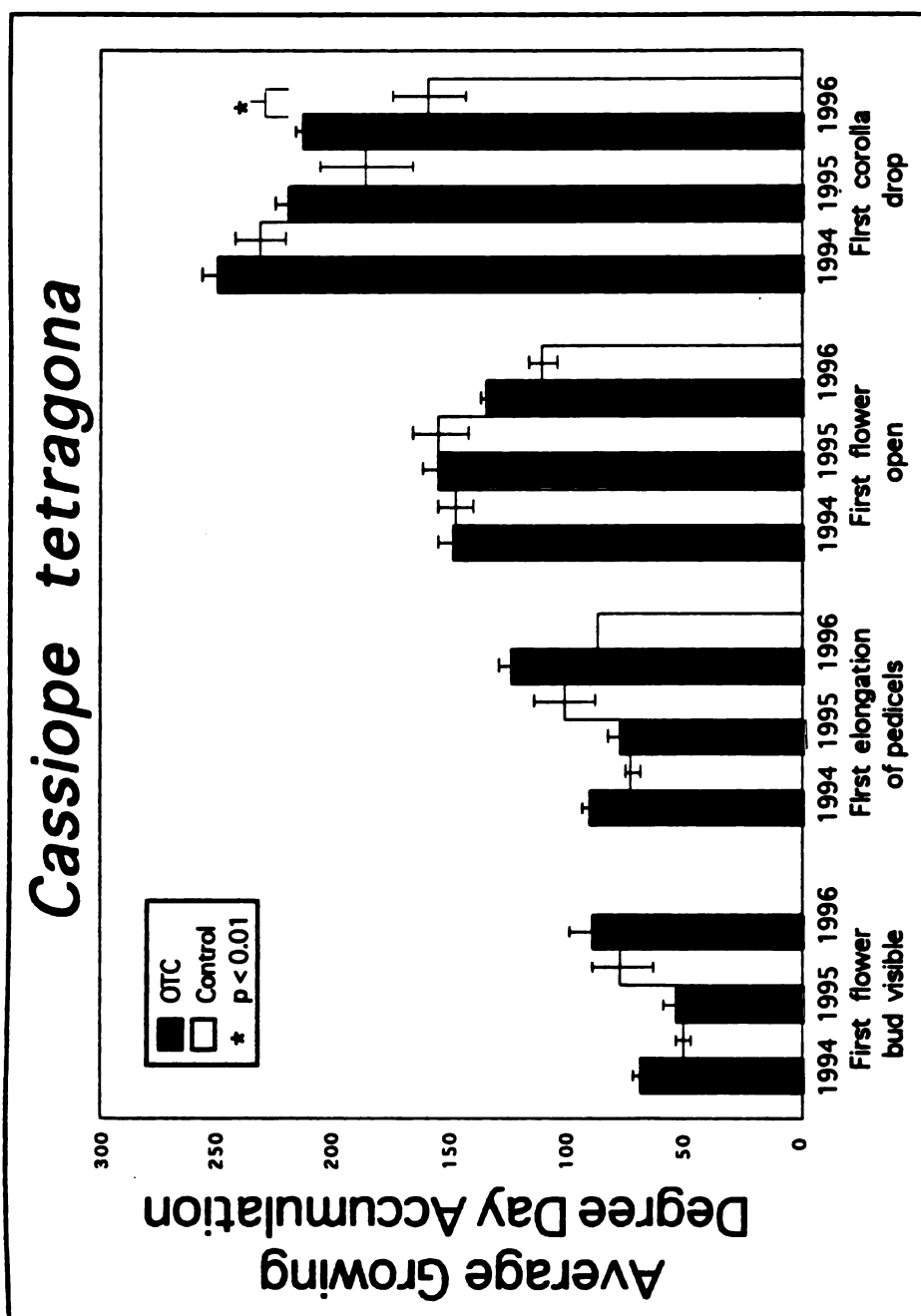


Figure 21. The average amount of Growing Degrees for *Cassiope* to undergo a phenophase.

Julian date at which the phenophase occurred ($p = 0.000001$; $p = 0.00001$; $p = 0.001$). In 1994 flowers opened significantly fewer days after the plots had been snow free in the OTCs than in the controls ($p = 0.01$). The last phenophase of corolla drop occurred earlier in the chambers in 1994 and 1995 for the Julian date at which the flowers dropped their corollas ($p < 0.001$; $p = 0.001$). Corollas dropped significantly fewer days since the plot had been snow free, from the flowers in the chambers, than in the control plots for all three years ($p < 0.001$; $p < 0.0001$; $p = 0.01$). Figures 19 and 20 show the responses of *Cassiope* plants to warming at the canopy level. This species also shows the general trend of phenophases occurring earlier in the OTCs, but again many of these differences between chambers and control plots are not significant. Significantly more growing degree days accumulated in 1996 before the developmental stage of first corolla drop occurred ($p < 0.01$). Except for this one phenophase in 1996, all other phenophases show a trend of similar amounts of accumulated energy within years.

Figures 10 - 21 and Table 7 all show trends of the phenophases occurring earlier in the OTCs, however, because of the variability of the system these trends were not found to be significant for most species phenophases. Measurement of the Julian day at which a particular stage occurred for a plant, or the days the plot has been snow free before a stage takes place both determine that the woody species, *Cassiope tetragona*, and *Salix rotundifolia* are more responsive to the effects of warming (Appendix 1

and 2). Table 7 contains a summary of the significant responses to warming that occurred during the three monitored growing seasons. The total number of significant responses per year indicate that regardless of the year's environmental conditions the chambers had the same effect (Table 7). Julian date of occurrence of phenophase graphs indicate a trend for phenophases to occur at earlier Julian dates each year, but since the control plots are also undergoing phenophases at earlier dates, this indicates that it is not a cumulative effect from the chambers that is being observed, and is likely an effect of time of snow melt. Comparing Julian date of occurrence to number of days the plot is snow free before emergence of green leaf occurs indicates that this stage is dependent upon when the plots melt out. All species undergo this stage at a later date in 1995, than in 1996, but the number of days since snow free until the first leaf emerges determines that 1995 takes the least amount of snow free days until a leaf emerges. This indicates that it is a complex series of processes by which the first green leaf emerges, since 1995 was the coldest year, with the least amount of heat accumulation. Also, since each of the species utilized a significantly different amount of energy each year, emergence of the leaf is not likely to be dependent upon the amount of heat that is accumulated.

Graphs 12, 15, 18, and 21 show the total amount of energy that is accumulated before a phenophase occurs. These graphs determine that it is not temperature alone that is the determining factor of a species

development. If the hypothesis that it was only temperature that was causing the accelerated phenology, the total amount of energy for the different phenophases would be expected to be similar regardless of year, Julian date of occurrence, or the time period since snow free. However, some of the examined species show that some phenophases, although they do occur earlier within the chambers, seem to use significantly larger amounts of energy than the corresponding control response. This suggests that there is a more complex reason than just increased temperature as to why the phenophase is occurring earlier. The amount of growing degree days accumulated before a phenophase is induced, is also very dependent upon the species. Some species are more responsive to temperature treatments, and therefore, similar amounts of energy are accrued in the OTCs and in the control plots.

Both species of *Luzula* show a trend that suggests that a step-wise pattern in the Julian date of occurrence of a phenophase for both reproductive stages measured, with 1994 having inflorescence visible, and open at the latest date, and 1996 with the earliest date (Figure 10). However, the number of days since the plot was snow free indicates that the plants must be snow free for a similar (or minimum) length of time before an inflorescence can emerge, or open (Figure 11). In *Luzula confusa* the emergence of an inflorescence and the opening of that inflorescence may also be dependent upon the amount of heat accumulated within the plot, since more time has elapsed in the control

plots than in the chamber plots. However, this relationship becomes more complex (Figure 12) as the chambers in 1994 accrue a significantly larger amount of energy before the inflorescence can open. Lindskog and Jonsdottir (1997) found in their study of the graminoid sedge *Carex bigelowii* that the vegetative efforts of plants within the chambers and in control plants are similar, although reproductive efforts within the chambers are accelerated. This trend is similar to that of the graminoid phenology on the dry heath, although the differences between OTCs and controls in Barrow are not significant. The examination of the amount of accumulated growing days shows that this trend of the phenophases occurring earlier in the OTCs requires even more energy than the plants in the controls, which suggests a trade off between occurring earlier, and needing more accumulated energy to undergo a developmental stage.

The two forb plants, *Papaver hultenii* and *Saxifraga punctata*, also show this decreasing step pattern of the Julian date of occurrence of when phenophases occurred. Again, the number of days that the plot has been snow free reverses this pattern, and instead indicates that for at least the first three phenophases, fewer days occurred in 1995 before phenophases developed than in 1994, or 1996. In 1996 the average number of days before flowers opened and flowers withered in *Papaver hultenii* within control plots was similar to the number of days in 1995 that produced the same phenophases. This suggests that it is not the specific date (or corresponding

environmental conditions such as light intensity) that triggers the plants to open their flowers. However, significantly different amounts of energy each year are used to produce the phenophases of these species. It is likely that other environmental conditions are playing a role in allowing these species to develop. Molgaard and Christensen (1997), and Alatalo and Totland (1997) found in studies of *Papaver radicum* (which is related to *Papaver hultenii*), and *Silene acaulis* (a forb), that both had an earlier onset of flowering in response to increased warming. *Papaver hultenii*, and *Saxifraga punctata* follow this trend, although the differences between the OTCs and control are not large enough to be significant.

The two most responsive species, of those that were examined, were the woody species, *Cassiope tetragona*, and *Salix rotundifolia*. In 1994 and 1995 all reproductive stages for Julian date occurred significantly earlier in OTCs than in control plots, except for the phenophase of the first bud visible. The number of days since the plot was snow free, displayed a similar result except for the first bud visible, and the first bud elongating, which did not occur significantly earlier in the controls. In 1994 and 1995 the Julian date at which *Salix rotundifolia* underwent reproductive phenophases all occurred earlier in the chambers than in the controls. The stage of first pollen shed, and all pollen shed in 1995, and the stage of first pollen shed in 1994, took place a significantly fewer number of days from the plots being snow free in the OTCs, than did the control plots of *Salix*. Unlike the trends shown in the

graminoid and forb plants, the patterns of response in *Cassiope* do not change when examining the Julian date at which a phenophase occurred, or the number of days since the plot had been snow free that the stages took place. Also, all stages of *Cassiope* development, except for corolla drop in 1996, accumulate similar amounts of energy to undergo phenophases, which suggests that *Cassiope* is sensitive to changes in temperature. This contradicts what was found in a similar study in the Swedish Lapland site of Latnjajaure (Molau, 1997). However, because Barrow and Latnjajaure represent two different areas within the species distribution, the findings of Wookey et al. (1993) support that species found in the High Arctic respond more to an increase temperature. The latter phenophases that *Salix* undergoes show very little difference between treatment, or the way in which they were analyzed, which suggests that a possible “catch up” effect is taking place as reported for alpine species by Bock, 1976 and Webber et al., 1976. This means that at the end of the season plants within the control plots have reached the developmental advancement level of the plants in the chambers. However, Figure 18 shows that the amount of energy trapped during the time at which these latter phenophases is significantly larger, which suggests that perhaps a different factor than that of temperature, is responsible for the occurrence of these phenophases.

Effects on growth and stature:

Two different types of growth measurements were recorded to determine a quantitative response of the tundra plants to the experimental warming. At the end of each of the three monitored growing seasons the stature of each species was ascertained. In 1994, 1995, and 1996 the length of the reproductive shoots (graminoid inflorescence, or forb peduncles) were measured. In each of these three growing seasons, the tallest three individuals of a species were measured for each of the plots that contained the species. In 1996 the stature of vegetative shoots (for graminoids) were also measured following this same procedure. *Cassiope tetragona* was measured for annual growth increment, by measuring the amount of growth that had been produced at the end of each growing season. The length of the longest *Salix* leaf within a marked unit was also measured for each of the three years. Data was again transformed using a dynamic Box-Cox method. All growth data was transformed to 0.0 level, except for *Cassiope*, which was transformed to the -0.5 level. All end of the season stature and growth measurements were analyzed using a three-way ANOVA with the main effects of species, year, and plot type (OTC or control plot), and Scheffe Post-Hoc tests to look at specific non-orthogonal contrasts for each of the interactions. Again, the data was examined at a significance level of 99% ($p \leq 0.01$).

In 1994 and 1995, two species, *Luzula confusa*, and *Saxifraga punctata*, had a significantly larger length of reproductive shoots inside the OTCs, than plants in the control plots (Figures 22 and 23 , $p < 0.01$, $p < 0.01$, $p < 0.01$, $p < 0.01$ respectively by species, and year). Figure 24 shows that *Cassiope* did not have a significant increase in annual growth increment. This lack of significant differences in yearly growth is also supported by Molau (1997), who suggests that because *Cassiope* and other cushion and dwarf evergreen plants show a similar lack of response to increased temperature that they could be a possible grouping of plants for further analyses. In 1996 the only species to produce taller reproductive shoots within the chambers, as compared to those within the control plots was *Luzula arctica*. Further studies are needed to determine the possible cause of this observed increase in growth. In 1996, *Luzula confusa* and *Luzula arctica* had significantly larger vegetative shoots inside the chambers ($p < 0.01$). However, since increased length is a common response among graminoids to shelter (Lindskog and Jonsdottir, 1997), it is impossible to determine if these increases in growth are in response to the increase in temperature.

In 1996 growth measurements were also made throughout the season to track the differences between plants of each species within the chambers, to plants within the control plots. This was accomplished by placing a small wire circlet around the first emerging individual of each species, in each plot. This allowed for the same marked plant to be measured every other day for

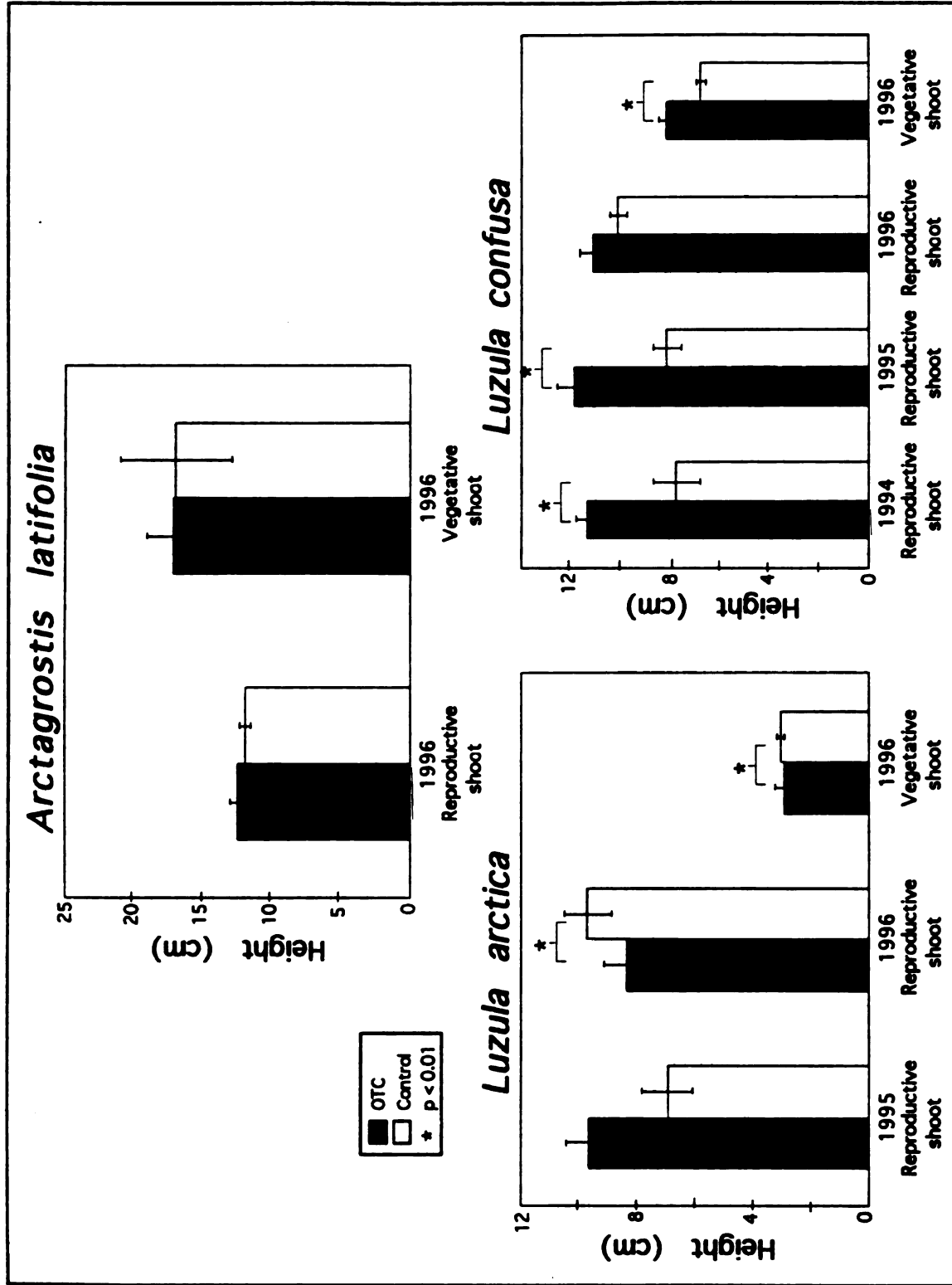


Figure 22. Growth responses of *Luzula arctica*, *Luzula confusa*, and *Arctagrostis latifolia* to increased warming.

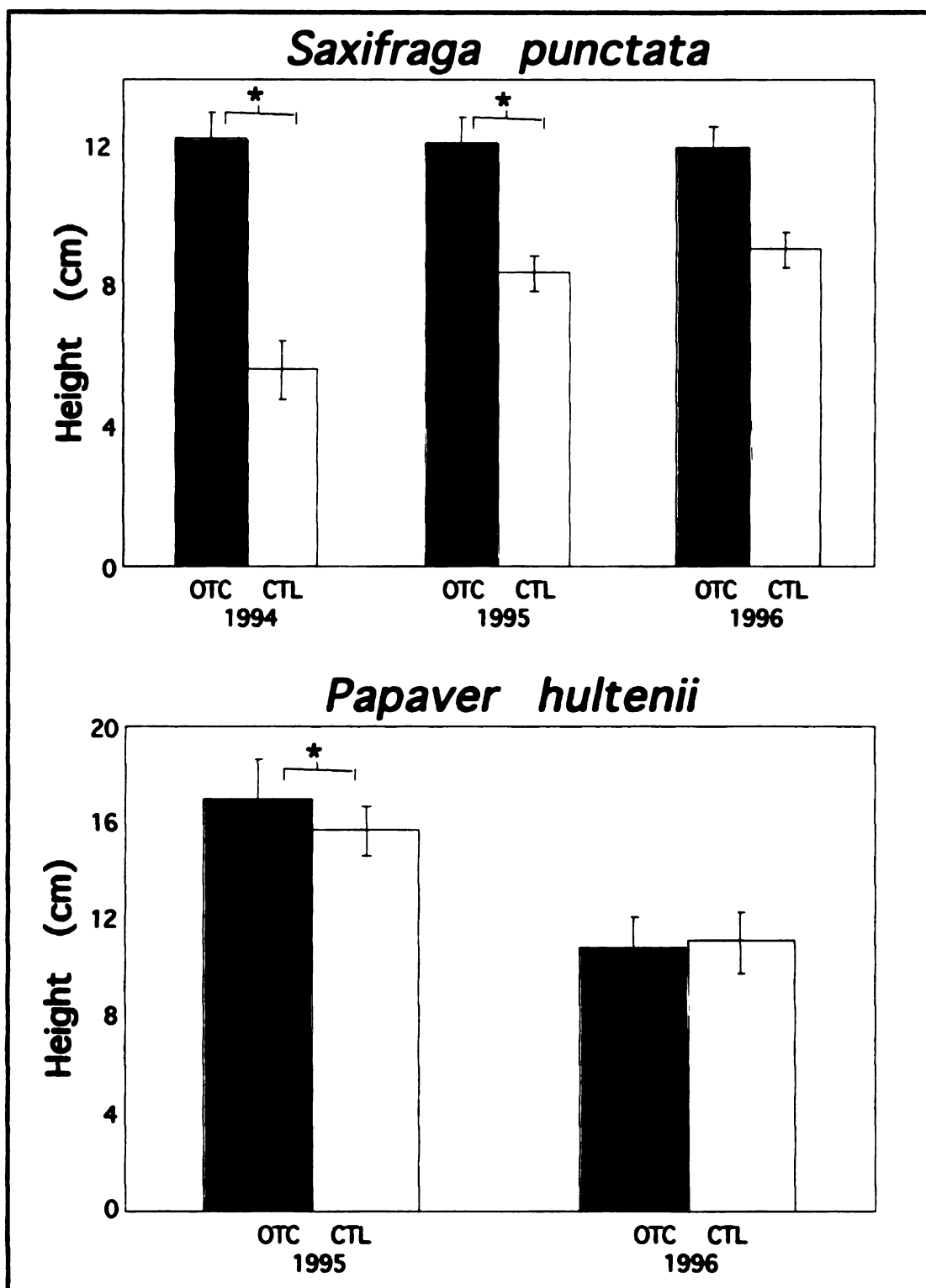


Figure 23. Growth responses of *Papaver* and *Saxifraga* to increased warming.

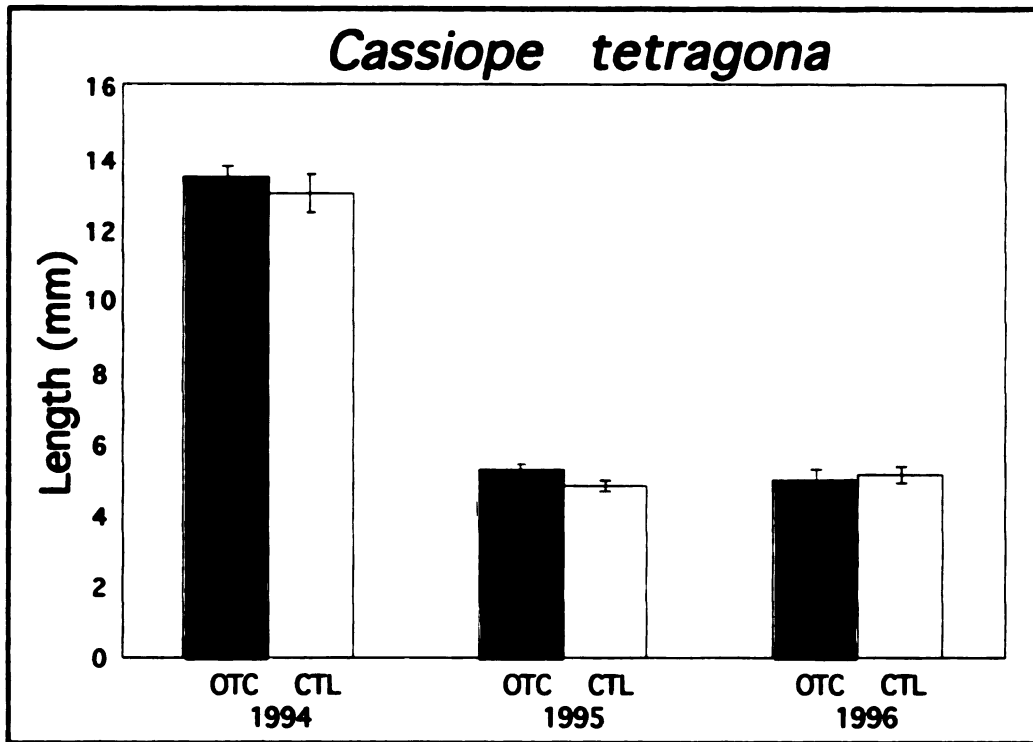


Figure 24. Annual growth increment of *Cassiope tetragona*.

the entire growing season. The largest leaf of the marked plants of *Arctagrostis latifolia*, *Luzula arctica*, and *Luzula confusa* plants were monitored throughout the entire season. Data was plotted using a scatter plot, at which time a true-ess smoothing curve (Data Desk, 1988) was fit to the data, so that the approximate line model that the data fit could be determined. A second order polynomial curve was determined to have the best fit for all scatterplots. A comparison of curves test (Potvin et al., 1990) allowed the differences of the growth patterns of plants in the OTCs to be compared to the patterns of plants grown in control plots. The comparison of

curves test uses an F-test to determine if the fitted-curves of each of the different treatments (OTC and control plants) are significantly different from a curve of the same model that includes both of the treatments together.

Second order best-fit polynomial lines fit to the *Arctagrostis latifolia* scatter plots (Figure 25) indicated that the plants in the OTCs were always larger throughout the entire season, and at no time did the height of plants in control plots equal that of plants in experimental plots, although the curving slope of the line suggests that the actual growth rates were similar. The comparison of curves test determined that the lines were significantly different ($F_{4,565} 20.99$; $p < 0.001$).

Second order polynomial lines fit to *Luzula arctica* and *Luzula confusa* scatterplots (Figures 26, and 27). *Luzula arctica* lines are extremely different for the OTC and the control. The first half of the growing season, the rates and the amount of growth are approximately equal. However, during the rest of the season, the plants in the chambers seem to have a growth rate that reaches a critical level and then levels off. The *Luzula arctic* control plants seemed to have a growth rate that continued to increase, forming an almost straight line. The scatter of the points for the graph also differ. Plants within the OTCs have a much smaller range than that of the plants within the control plots. The comparison of curves test indicates that the lines are significantly different ($F_{4,804} 21.35$; $p < 0.001$). The best fit second order polynomial curves that are fit to the *Luzula confusa* data show that the

experimental and control plants are almost identical. This measurement of growth rate indicates that an increase in warming does not cause an increase of height for this species, with the comparison of curves test indicating that the lines were not significantly different ($F_{4,929} 1.057$; $p < 0.01$). The monitoring of the growth patterns of these co-genors indicates that the plants vegetative growth patterns do not respond similarly.

The differences that are seen in the results from measuring the three largest plants at the end of the season, and monitoring plants throughout the season can be explained by the fact that the number of points on the scatter plot indicates that there were many measurements taken in order to reach that point. The points reflect the data from many chambers. Within a plot, there is only one plant being measured per species, and the monitored plant was selected based on emergence, and not on size. These graphs also demonstrate the need to monitor the growth of the plants throughout the entire season and not just at the end, as important trends could be missed. The end of the season height measurements yield data that suggest that it is reproductive growth that is most responsive to experimental warming. This trend is also supported by the phenological data. In the phenology data, only one species in two years (and only for the Julian date of occurrence) happened significantly earlier in the chambers. The rest of the species demonstrated little response in the vegetative stage of first green leaf. Throughout the growing season there were however significantly earlier occurrences of

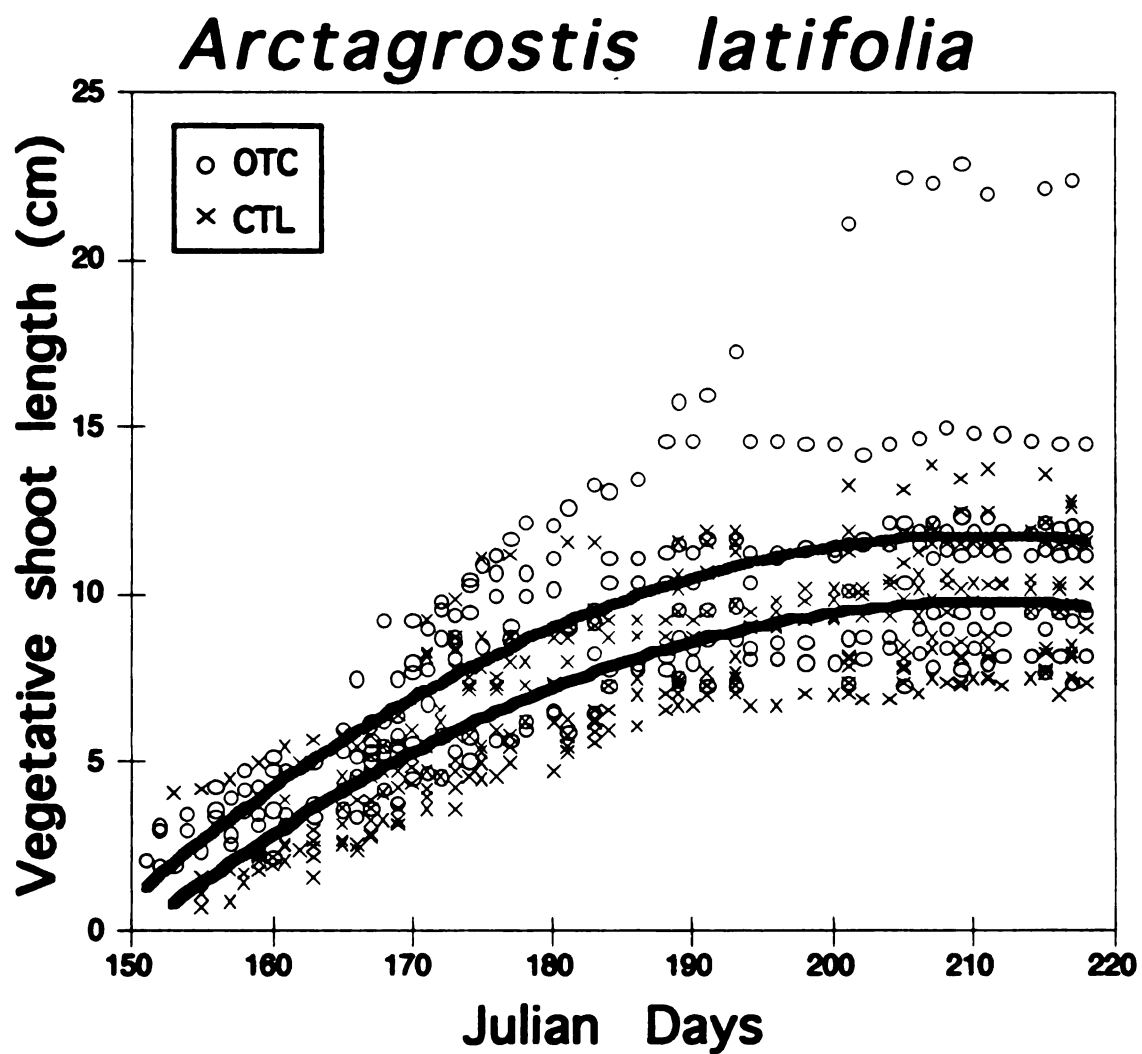


Figure 25. The effects of warming on *Arctagrostis latifolia* stature during 1996.

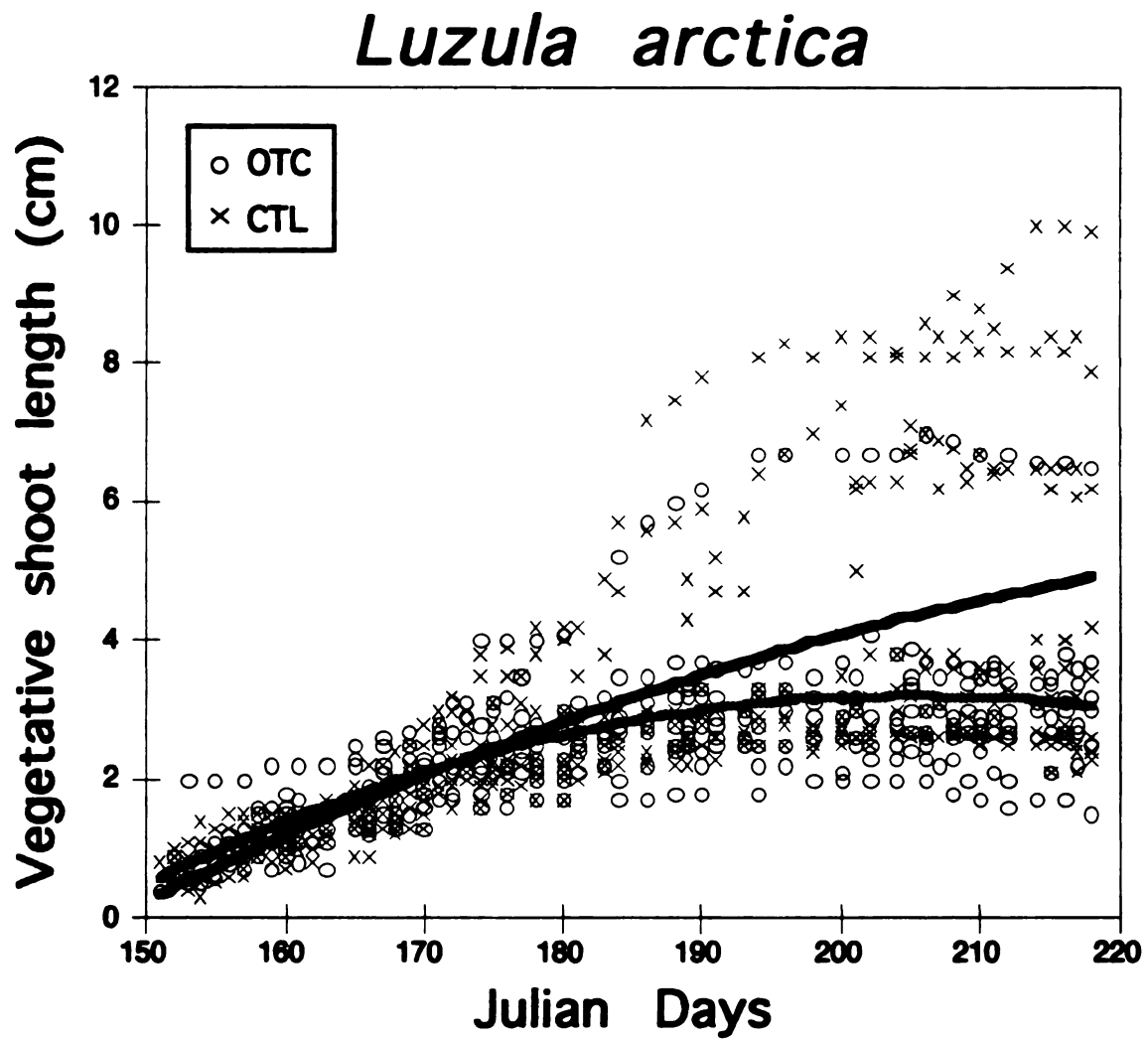


Figure 26. The effects of warming on *Luzula arctica* stature during 1996.

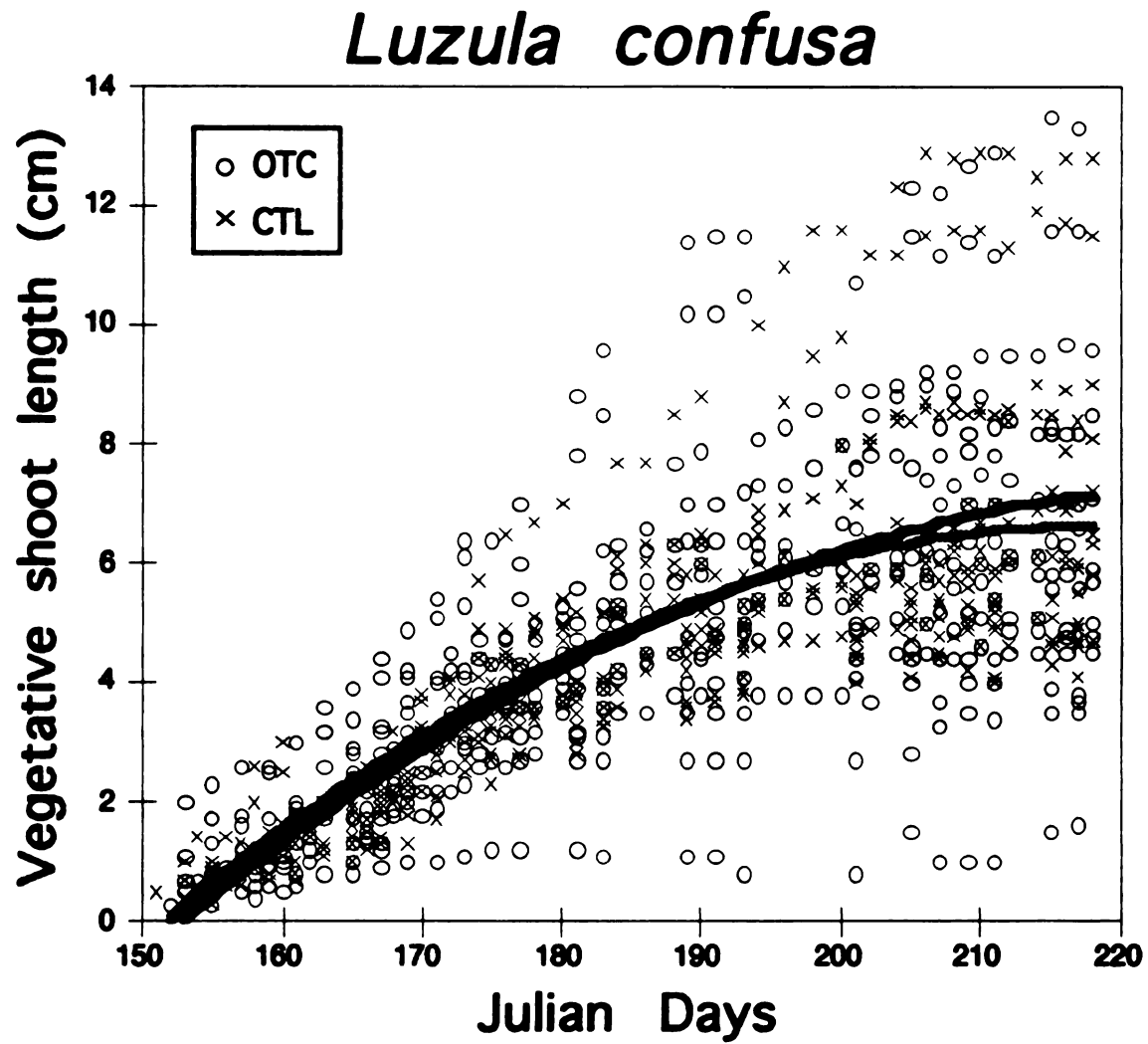


Figure 27. The effects of warming on *Luzula confusa* stature during 1996.

reproductive phenophases, most notable in *Cassiope* and *Salix*.. These response patterns could be an important tool in examining how these species will react to a possible global warming. Sexual reproduction could become more important in this established perennial community that has little seedling recruitment under present conditions.

Final discussion

Fossil records show that vegetation responses have lagged behind climatic changes (Davis, 1989). Nevertheless, the present arctic ecosystem is more limited by physical stresses, than by competition, and therefore these ecosystems are sensitive to environmental changes (Roots, 1989). This project was designed to examine responses to an increase in temperature that is within the predicted magnitude of global change. To date, only short-term responses of one environmental factor (i.e. temperature change) have been examined at the Barrow site. Long-term studies of impacts of environmental change upon vegetation have shown that short-term responses are relatively poor predictors of plant responses after a longer time period (Chapin et al. 1995). However, this study lays the ground work for continued monitoring of plant responses to increased warming.

A number of authors (for example: Webber, 1978; Shaver and Kummerow, 1992) have shown that tundra species behave individualistically

to, and have unique requirements and responses to environmental variation. This study shows that the seven species examined at the dry heath site at Barrow exhibit very differing responses to the experimental warming. Among all of the herbaceous species none have consistent significant responses to the increased warming, either between species, or between years. However, the trends (Table 7) indicate in the data that most responses tend to occur earlier within the OTCs, however these differences are not, for the most part statistically significant. Most species undergo phenophases equal or earlier in terms of Julian Days, and days since snow free, and use more accumulated GDD within the chambers before undergoing a phenophase. *Papaver* is the exception to using more accumulated energy, since the trends for this species indicate that the control plots accumulate more energy than the OTCs before some phenophases can occur. Growth responses are also not consistent within species or within years.

Although the current year may have no effect on flower buds, as many arctic species pre-form buds in previous years, the success of these buds is dependent upon the conditions of the current year (Shaver and Kummerow, 1992). The two woody species that were studied were both the most responsive in terms of the number of significantly earlier occurrences of phenophases. More stability in the occurrence of a significant response is evident in *Cassiope*. In 1995 all phenophases occurred earlier within the chambers, and since the total amount of accumulated energy is not

significantly different within the chambers and controls, this suggests that *Cassiope* is dependent on temperature. *Salix* consistently utilizes more energy that has accumulated within the chambers to undergo phenological development, even though the phenophases are mostly occurring at the same time (Julian date, or days since snow free) in both the control and OTC plots. This suggests that the process by which *Salix* undergoes its latter phenophases is an extremely complex process, that is likely not dependent on temperature.

Although temperature is an important factor in any arctic ecosystem, the plants on the dry heath tundra showed few consistent year to year responses to an increase in temperature. Most species show some response in phenophase occurrence, even though these responses between the OTCs and the control plots are not consistently significant. Most of the phenophases that occur significantly earlier within the chambers are reproductive stages, which suggest that increased temperature could provide some evolutionary advantage in seed production and set, or perhaps a shift from predominantly vegetative growth that dominates the arctic to a more sexually dominated life cycle. However, the nature of the phenophase monitoring is biased towards recording more reproductive stages than vegetative, which means that the trend for reproductive phenophases to be more likely to occur earlier within chambers could be biased. A continuation of monitoring in the same detailed fashion is necessary to determine the long-term effects of increased warming,

so that this information could be potentially useful to global change modelers that would like to include vegetation responses, as a part of their predictions.

APPENDICES

APPENDIX A

APPENDIX A

Raw data and metadata for all species are stored on floppy disk at Michigan State University (in care of Dr. Patrick J. Webber). Data are in the ITEX recommended format used for compiling all of the circumpolar data for the NCEAS (National Center for Ecology and Synthesis) conference in December of 1996.

Key

The following key applies to Tables 8 - 13 (Appendices A and B), for ANOVA and Post-Hoc results. ANOVA tables are set up in standard format.

Const = Constant term

Spc = Species

yr = year

Spc*yr = interaction between species and year

pt = plot type (OTC or control)

Spc*pt = interaction between species and plot type

yr*pt = interaction between year and plot type

Spc*yr*pt = interaction between species, year and plot type

Error = the error term for the ANOVA

Total = the total amount of degrees of freedom and sums of squares that are accounted for

Prob = probability

APPENDIX A

Table 8. Analysis of Variance result tables - **Julian Date of Occurrence.**

Dependent variable: Emergence of First Green Leaf (-0.50 transformed)					
Source	df	Sums of Squares	Mean Square	F-ratio	Prob
Const	1	1595.27	1595.27	510860417	≤ 0.0001
Spc	4	0.001209	0.000302	96.820	≤ 0.0001
yr	2	0.006424	0.003212	1028.6	≤ 0.0001
Spc*yr	8	0.000111	0.000014	4.4280	≤ 0.0001
pt	1	0.000039	0.000039	12.432	0.0005
Spc*pt	4	0.000013	0.000003	1.0355	0.3884
yr*pt	2	0.000018	0.000009	2.8664	0.0580
Spc*yr*pt	8	0.000016	0.000002	0.64149	0.7428
Error	438	0.001368	0.000003		
Total	467	0.009792			

Dependent variable: First Inflorescence Visible (-0.50 transformed)					
Source	df	Sums of Squares	Mean Square	F-ratio	Prob
Const	1	1007.33	1007.33	245818824	≤ 0.0001
Spc	4	0.000939	0.000235	57.268	≤ 0.0001
yr	2	0.003023	0.001512	368.88	≤ 0.0001
Spc*yr	8	0.000210	0.000026	6.4086	≤ 0.0001
pt	1	0.000113	0.000113	27.497	≤ 0.0001
Spc*pt	4	0.000059	0.000015	3.5785	0.0073
yr*pt	2	0.000038	0.000019	4.6080	0.0108
Spc*yr*pt	8	0.000062	0.000008	1.8998	0.0603
Error	264	0.001082	0.000004		
Total	293	0.006963			

APPENDIX A

Table 8 (Cont'd)

Dependent variable: First Inflorescence Visible (-0.50 transformed)					
Source	df	Sums of Squares	Mean Square	F-ratio	Prob
Const	1	359.315	359.315	77603367	≤ 0.0001
Spc	1	0.000153	0.000153	33.053	≤ 0.0001
yr	1	0.000416	0.000416	89.947	≤ 0.0001
Spc*yr	1	0.000004	0.000004	0.79534	0.3747
pt	1	0.000032	0.000032	7.0021	0.0095
Spc*pt	1	0.000001	0.000001	0.13359	0.7155
yr*pt	1	0.000020	0.000020	4.2867	0.0411
Spc*yr*pt	1	0.000000	0.000000	0.03344	0.8553
Error	97	0.000449	0.000005		
Total	104	0.001134			

Dependent variable: First Elongation of Pedicels (-0.50 transformed)					
Source	df	Sums of Squares	Mean Square	F-ratio	Prob
Const	1	359.315	359.315	77603367	≤ 0.0001
Spc	1	0.000153	0.000153	33.053	≤ 0.0001
yr	1	0.000416	0.000416	89.947	≤ 0.0001
Spc*yr	1	0.000004	0.000004	0.79534	0.3747
pt	1	0.000032	0.000032	7.0021	0.0095
Spc*pt	1	0.000001	0.000001	0.13359	0.7155
yr*pt	1	0.000020	0.000020	4.2867	0.0411
Spc*yr*pt	1	0.000000	0.000000	0.03344	0.8553
Error	97	0.000449	0.000005		
Total	104	0.001134			

APPENDIX A

Table 8 (Cont'd)

Dependent variable: First Inflorescence Open (-0.50 transformed)					
Source	df	Sums of Squares	Mean Square	F-ratio	Prob
Const	1	1159.59	1159.59	250029400	≤ 0.0001
Spc	4	0.001220	0.000305	65.761	≤ 0.0001
yr	2	0.000917	0.000459	98.915	≤ 0.0001
Spc*yr	6	0.000072	0.000012	2.5988	0.0180
pt	1	0.000034	0.000034	7.3401	0.0071
Spc*pt	4	0.000055	0.000014	2.9615	0.0200
yr*pt	2	0.000006	0.000003	0.61779	0.5398
Spc*yr*pt	6	0.000072	0.000012	2.5906	0.0183
Error	311	0.001442	0.000005		
Total	336	0.005671			

Dependent variable: First Flower Wither (-0.50 transformed)					
Source	df	Sums of Squares	Mean Square	F-ratio	Prob
Const	1	515.355	515.355	122594098	≤ 0.0001
Spc	1	0.000034	0.000034	8.1459	0.0050
yr	2	0.000821	0.000410	97.625	≤ 0.0001
Spc*yr	2	0.000027	0.000013	3.1979	0.0439
pt	1	0.000064	0.000064	15.243	0.0001
Spc*pt	1	0.000006	0.000006	1.3955	0.2395
yr*pt	2	0.000019	0.000009	2.2043	0.1142
Spc*yr*pt	2	0.000016	0.000008	1.9144	0.1514
Error	137	0.000576	0.000004		
Total	148	0.001565			

APPENDIX A

Table 8 (Cont'd)

Dependent variable: First Green Leaf (<i>Salix rotundifolia</i> , -0.50 transformed)					
Source	df	Sums of Squares	Mean Square	F-ratio	Prob
Const	1	477.314	477.314	205882044	≤ 0.0001
yr	2	0.001411	0.000706	304.35	≤ 0.0001
pt	1	0.000069	0.000069	29.874	≤ 0.0001
yr*pt	2	0.000020	0.000010	4.3536	0.0147
Error	134	0.000311	0.000002		
Total	139	0.001827			

Dependent variable: First Inflorescence visible (-0.50 transformed)					
Source	df	Sums of Squares	Mean Square	F-ratio	Prob
Const	1	668.011	668.011	322450333	≤ 0.0001
Spc	1	0.000016	0.000016	7.5098	0.0067
yr	2	0.000497	0.000249	119.99	≤ 0.0001
Spc*yr	2	0.000018	0.000009	4.3357	0.0145
pt	1	0.000095	0.000095	45.965	≤ 0.0001
Spc*pt	1	0.000008	0.000008	3.8480	0.0513
yr*pt	2	0.000016	0.000008	3.8774	0.0224
Spc*yr*pt	1	0.000032	0.000032	15.601	0.0001
Error	184	0.000381	0.000002		
Total	194	0.001997			

Dependent variable: First Elongation of buds (<i>Cassiope tetragona</i> , -0.50 transformed)					
Source	df	Sums of Squares	Mean Square	F-ratio	Prob
Const	1	281.631	281.631	159526344	≤ 0.0001
yr	2	0.000185	0.000093	52.425	≤ 0.0001
pt	1	0.000043	0.000043	24.502	≤ 0.0001
yr*pt	2	0.000025	0.000012	6.9554	0.0017
Error	76	0.000134	0.000002		
Total	81	0.000511			

APPENDIX A

Table 8 (Cont'd)

Dependent variable: First Flower Open(<i>Cassiope tetragona</i> , -0.50 transformed)					
Source	df	Sums of Squares	Mean Square	F-ratio	Prob
Const	1	361.298	361.298	122149789	≤ 0.0001
yr	2	0.001403	0.000702	237.22	≤ 0.0001
pt	1	0.000217	0.000217	73.295	≤ 0.0001
yr*pt	2	0.000012	0.000006	2.0116	0.1392
Error	99	0.000293	0.000003		
Total	104	0.001947			

Dependent variable: First Corolla Drop (-0.50 transformed)					
Source	df	Sums of Squares	Mean Square	F-ratio	Prob
Const	1	311.034	311.034	100909295	≤ 0.0001
yr	2	0.000880	0.000440	142.70	≤ 0.0001
pt	1	0.000116	0.000116	37.672	≤ 0.0001
yr*pt	2	0.000011	0.000005	1.7534	0.1795
Error	84	0.000259	0.000003		
Total	89	0.001451			

Dependent variable: First Pollen Shed (<i>Salix rotundifolia</i> , -0.50 transformed)					
Source	df	Sums of Squares	Mean Square	F-ratio	Prob
Const	1	397.488	397.488	226227454	≤ 0.0001
yr	2	0.001402	0.000701	398.97	≤ 0.0001
pt	1	0.000142	0.000142	80.612	≤ 0.0001
yr*pt	2	0.000013	0.000006	3.6201	0.0300
Error	110	0.000193	0.000002		
Total	115	0.001761			

APPENDIX A

Table 8 (Cont'd)

Dependent variable: All Pollen Shed (<i>Salix rotundifolia</i> , -0.50 transformed)					
Source	df	Sums of Squares	Mean Square	F-ratio	Prob
Const	1	395.600	395.600	290920245	≤ 0.0001
yr	2	0.002689	0.001345	988.91	≤ 0.0001
pt	1	0.000772	0.000772	567.89	≤ 0.0001
yr*pt	2	0.001077	0.000538	395.95	≤ 0.0001
Error	109	0.000148	0.000001		
Total	114	0.004876			

Dependent variable: First Seed Dispersal (<i>Salix rotundifolia</i> , -0.50 transformed)					
Source	df	Sums of Squares	Mean Square	F-ratio	Prob
Const	1	264.414	264.414	42205448	≤ 0.0001
yr	2	0.000153	0.000077	12.211	≤ 0.0001
pt	1	0.000010	0.000010	1.5642	0.2152
yr*pt	2	0.000013	0.000006	1.0235	0.3647
Error	70	0.000439	0.000006		
Total	75	0.000622			

Dependent variable: First Color Change (<i>Salix rotundifolia</i> , -0.50 transformed)					
Source	df	Sums of Squares	Mean Square	F-ratio	Prob
Const	1	299.424	299.424	207002150	≤ 0.0001
yr	2	0.000057	0.000028	19.610	≤ 0.0001
pt	1	0.000003	0.000003	1.7488	0.1898
yr*pt	2	0.000020	0.000010	6.9672	0.0016
Error	80	0.000116	0.000001		
Total	85	0.000186			

APPENDIX A

Table 9. Analysis of Variance result tables - Days since snowfree.

Dependent variable: Emergence of First Green Leaf (0.0 transformed)					
Source	df	Sums of Squares	Mean Square	F-ratio	Prob
Const	1	2323.53	2323.53	10068	≤ 0.0001
Spc	5	75.8993	15.1799	65.775	≤ 0.0001
yr	2	132.616	66.3078	287.31	≤ 0.0001
Spc*yr	10	11.2257	1.12257	4.8641	≤ 0.0001
pt	1	3.30157	3.30157	14.306	0.0002
Spc*pt	5	2.11399	0.422799	1.8320	0.1047
yr*pt	2	0.708412	0.354206	1.5348	0.2164
Spc*yr*pt	10	1.36011	0.136011	0.58934	0.8232
Error	566	130.625	0.230786		
Total	601	360.977			

Dependent variable: First Inflorescence Visible (0.0 transformed)					
Source	df	Sums of Squares	Mean Square	F-ratio	Prob
Const	1	3914.22	3914.22	49781	≤ 0.0001
Spc	6	15.6660	2.61100	33.206	≤ 0.0001
yr	2	15.7228	7.86139	99.980	≤ 0.0001
Spc*yr	12	8.81384	0.734487	9.3411	≤ 0.0001
pt	1	1.52972	1.52972	19.455	≤ 0.0001
Spc*pt	6	1.24067	0.206779	2.6298	0.0162
yr*pt	2	0.594247	0.297124	3.7788	0.0236
Spc*yr*pt	11	4.87514	0.443194	5.6365	≤ 0.0001
Error	446	35.0688	0.078630		
Total	486	95.7982			

APPENDIX A

Table 9 (Cont'd)

Dependent variable: First Elongation of Pedicels					
Source	df	Sums of Squares	Mean Square	F-ratio	Prob
Const	1	462.043	462.043	212009	≤ 0.0001
Spc	3	0.124892	0.041631	19.102	≤ 0.0001
yr	2	0.035307	0.017653	8.1003	0.0004
Spc*yr	2	0.007697	0.003849	1.7660	0.1741
pt	1	0.011998	0.011998	5.5054	0.0201
Spc*pt	3	0.000972	0.000324	0.14865	0.9304
yr*pt	2	0.003614	0.001807	0.82906	0.4382
Spc*yr*pt	2	0.012925	0.006462	2.9653	0.0541
Error	175	0.381388	0.002179		
Total	190	0.854681			

Dependent variable: First Inflorescence Open					
Source	df	Sums of Squares	Mean Square	F-ratio	Prob
Const	1	4931.47	4931.47	136199	≤ 0.0001
Spc	4	10.6812	2.67029	73.749	≤ 0.0001
yr	2	2.66137	1.33068	36.751	≤ 0.0001
Spc*yr	8	1.64143	0.205179	5.6667	≤ 0.0001
pt	1	2.62776	2.62776	72.574	≤ 0.0001
Spc*pt	4	0.484602	0.121150	3.3460	0.0103
yr*pt	2	0.018973	0.009486	0.26200	0.7696
Spc*yr*pt	8	0.502602	0.062825	1.7351	0.0885
Error	408	14.7728	0.036208		
Total	437	33.9431			

APPENDIX A

Table 9 (Cont'd)

Dependent variable: First Withering of Flowers					
Source	df	Sums of Squares	Mean Square	F-ratio	Prob
Const	1	2109.36	2109.36	113649	≤ 0.0001
Spc	1	0.115308	0.115308	6.2126	0.0139
yr	2	0.290888	0.145444	7.8363	0.0006
Spc*yr	2	0.060030	0.030015	1.6172	0.2022
pt	1	0.255712	0.255712	13.777	0.0003
Spc*pt	1	0.009330	0.009330	0.50270	0.4795
yr*pt	2	0.042290	0.021145	1.1392	0.3231
Spc*yr*pt	2	0.049070	0.024535	1.3219	0.2700
Error	137	2.54276	0.018560		
Total	148	3.41369			

Dependent variable: First Pollen Shed (<i>Salix rotundifolia</i>)					
Source	df	Sums of Squares	Mean Square	F-ratio	Prob
Const	1	275.947	275.947	139984	≤ 0.0001
yr	2	0.041731	0.020865	10.585	≤ 0.0001
pt	1	0.095309	0.095309	48.349	≤ 0.0001
yr*pt	2	0.020850	0.010425	5.2884	0.0064
Error	110	0.216840	0.001971		
Total	115	0.375407			

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Table 9 (Cont'd)

Dependent variable: All Pollen Shed (<i>Salix rotundifolia</i>)					
Source	df	Sums of Squares	Mean Square	F-ratio	Prob
Const	1	297.164	297.164	268635	≤ 0.0001
yr	2	0.111522	0.055761	50.408	≤ 0.0001
pt	1	0.174663	0.174663	157.89	≤ 0.0001
yr*pt	2	0.244697	0.122348	110.60	≤ 0.0001
Error	109	0.120576	0.001106		
Total	114	0.668153			
Dependent variable: First Seed Dispersal (<i>Salix rotundifolia</i> , 0.0 transformed)					
Source	df	Sums of Squares	Mean Square	F-ratio	Prob
Const	1	1297.27	1297.27	67930	≤ 0.0001
yr	2	0.227015	0.113508	5.9437	0.0041
pt	1	0.041475	0.041475	2.1718	0.1450
yr*pt	2	0.042975	0.021488	1.1252	0.3304
Error	70	1.33679	0.019097		
Total	75	1.75185			
Dependent variable: First Color Change (<i>Salix rotundifolia</i>)					
Source	df	Sums of Squares	Mean Square	F-ratio	Prob
Const	1	1470.04	1470.04	277542	≤ 0.0001
yr	2	0.374763	0.187382	35.378	≤ 0.0001
pt	1	0.004423	0.004423	0.83506	0.3636
yr*pt	2	0.050612	0.025306	4.7778	0.0110
Error	80	0.423730	0.005297		
Total	85	0.923840			

APPENDIX A

Table 9 (Cont'd)

Dependent variable: First Corolla Drop (<i>Cassiope tetragona</i> , 0.0 transformed)					
Source	df	Sums of Squares	Mean Square	F-ratio	Prob
Const	1	1242.47	1242.47	99092	≤ 0.0001
yr	2	0.298055	0.149027	11.886	≤ 0.0001
pt	1	0.586721	0.586721	46.794	≤ 0.0001
yr*pt	2	0.042869	0.021434	1.7095	0.1872
Error	84	1.05323	0.012539		
Total	89	2.00540			

APPENDIX A

Table 10. Analysis of Variance result tables - **Growing Degree Day Accumulation.**

Dependent variable: Emergence of First Green Leaf (-0.50 transformed)					
Source	df	Sums of Squares	Mean Square	F-ratio	Prob
Const	1	4801.53	4801.53	8232.5	≤ 0.0001
Spc	5	149.761	29.9522	51.355	≤ 0.0001
yr	2	46.6995	23.3498	40.035	≤ 0.0001
Spc*yr	10	31.3325	3.13325	5.3721	≤ 0.0001
pt	1	1.65198	1.65198	2.8324	0.0929
Spc*pt	5	9.63210	1.92642	3.3030	0.0060
yr*pt	2	3.08044	1.54022	2.6408	0.0722
Spc*yr*pt	10	12.3037	1.23037	2.1095	0.0221
Error	571	333.030	0.583240		
Total	606	584.662			

Dependent variable: First Inflorescence Visible (-0.50 transformed)					
Source	df	Sums of Squares	Mean Square	F-ratio	Prob
Const	1	8225.00	8225.00	59684	≤ 0.0001
Spc	6	31.9460	5.32434	38.636	≤ 0.0001
yr	2	9.60967	4.80484	34.866	≤ 0.0001
Spc*yr	12	16.0710	1.33925	9.7182	≤ 0.0001
pt	1	0.023532	0.023532	0.17076	0.6796
Spc*pt	6	4.16240	0.693734	5.0340	≤ 0.0001
yr*pt	2	0.364041	0.182020	1.3208	0.2680
Spc*yr*pt	11	6.80214	0.618377	4.4872	≤ 0.0001
Error	447	61.6006	0.137809		
Total	487	139.687			

APPENDIX A

Table 10. (Cont'd)

Dependent variable: First Elongation of Buds (-0.50 transformed)					
Source	df	Sums of Squares	Mean Square	F-ratio	Prob
Const	1	3524.37	3524.37	40306	≤ 0.0001
Spc	2	3.18156	1.59078	18.193	≤ 0.0001
yr	2	1.46594	0.732971	8.3824	0.0003
Spc*yr	2	0.109237	0.054619	0.62463	0.5367
pt	1	0.037717	0.037717	0.43134	0.5122
Spc*pt	2	0.174781	0.087391	0.99942	0.3702
yr*pt	2	0.268396	0.134198	1.5347	0.2185
Spc*yr*pt	2	0.725790	0.362895	4.1502	0.0174
Error	172	15.0399	0.087441		
Total	185	25.4887			

Dependent variable: First Inflorescence Visible (-0.50 transformed)					
Source	df	Sums of Squares	Mean Square	F-ratio	Prob
Const	1	10373.6	10373.6	160130	≤ 0.0001
Spc	5	22.5999	4.51997	69.771	≤ 0.0001
yr	2	1.48834	0.744171	11.487	≤ 0.0001
Spc*yr	8	2.31858	0.289823	4.4738	≤ 0.0001
pt	1	0.279891	0.279891	4.3205	0.0383
Spc*pt	5	1.04958	0.209917	3.2403	0.0070
yr*pt	2	0.143326	0.071663	1.1062	0.3318
Spc*yr*pt	8	1.29295	0.161619	2.4948	0.0118
Error	410	26.5609	0.064783		
Total	441	65.3455			

APPENDIX A

Table 10. (Cont'd)

Dependent variable: First Flower Withers (-0.50 transformed)					
Source	df	Sums of Squares	Mean Square	F-ratio	Prob
Const	1	4253.21	4253.21	182786	≤ 0.0001
Spc	1	0.211919	0.211919	9.1074	0.0030
yr	2	1.33697	0.668487	28.729	≤ 0.0001
Spc*yr	2	0.191190	0.095595	4.1083	0.0185
pt	1	2.15048	2.15048	92.419	≤ 0.0001
Spc*pt	1	0.030154	0.030154	1.2959	0.2570
yr*pt	2	0.114832	0.057416	2.4675	0.0886
Spc*yr*pt	2	0.081973	0.040986	1.7614	0.1757
Error	136	3.16455	0.023269		
Total	147	8.27370			

Dependent variable: First Corolla Drop (<i>Cassiope tetragona</i> , -0.50 transformed)					
Source	df	Sums of Squares	Mean Square	F-ratio	Prob
Const	1	2609.64	2609.64	139240	≤ 0.0001
yr	2	0.997671	0.498836	26.616	≤ 0.0001
pt	1	0.455112	0.455112	24.283	≤ 0.0001
yr*pt	2	0.184111	0.092055	4.9117	0.0096
Error	84	1.57433	0.018742		
Total	89	2.99423			

Dependent variable: First Pollen Shed (<i>Salix rotundifolia</i> , 0.50 transformed)					
Source	df	Sums of Squares	Mean Square	F-ratio	Prob
Const	1	2109.37	2109.37	21246	≤ 0.0001
yr	2	0.279019	0.139510	1.4052	0.2497
pt	1	0.098303	0.098303	0.99012	0.3219
yr*pt	2	0.234307	0.117154	1.1800	0.3111
Error	110	10.9212	0.099283		
Total	115	11.5582			

APPENDIX A

Table 10. (Cont'd)

Dependent variable: All Pollen Shed (<i>Salix rotundifolia</i> , 0.50 transformed)					
Source	df	Sums of Squares	Mean Square	F-ratio	Prob
Const	1	2109.37	2109.37	21246	≤ 0.0001
yr	2	0.279019	0.139510	1.4052	0.2497
pt	1	0.098303	0.098303	0.99012	0.3219
yr*pt	2	0.234307	0.117154	1.1800	0.3111
Error	110	10.9212	0.099283		
Total	115	11.5582			

Dependent variable: All Pollen Shed (<i>Salix rotundifolia</i> , 0.50 transformed)					
Source	df	Sums of Squares	Mean Square	F-ratio	Prob
Const	1	2536.56	2536.56	59720	≤ 0.0001
yr	2	1.89356	0.946779	22.291	≤ 0.0001
pt	1	0.275728	0.275728	6.4917	0.0122
yr*pt	2	8.28525	4.14263	97.533	≤ 0.0001
Error	109	4.62968	0.042474		
Total	114	15.7699			

Dependent variable: First Seed Dispersal (<i>Salix rotundifolia</i> , 0.50 transformed)					
Source	df	Sums of Squares	Mean Square	F-ratio	Prob
Const	1	2530.68	2530.68	104653	≤ 0.0001
yr	2	1.22447	0.612234	25.318	≤ 0.0001
pt	1	1.14007	1.14007	47.146	≤ 0.0001
yr*pt	2	0.271101	0.135550	5.6055	0.0055
Error	70	1.69271	0.024182		
Total	75	3.98836			

APPENDIX A

Table 10. (Cont'd)

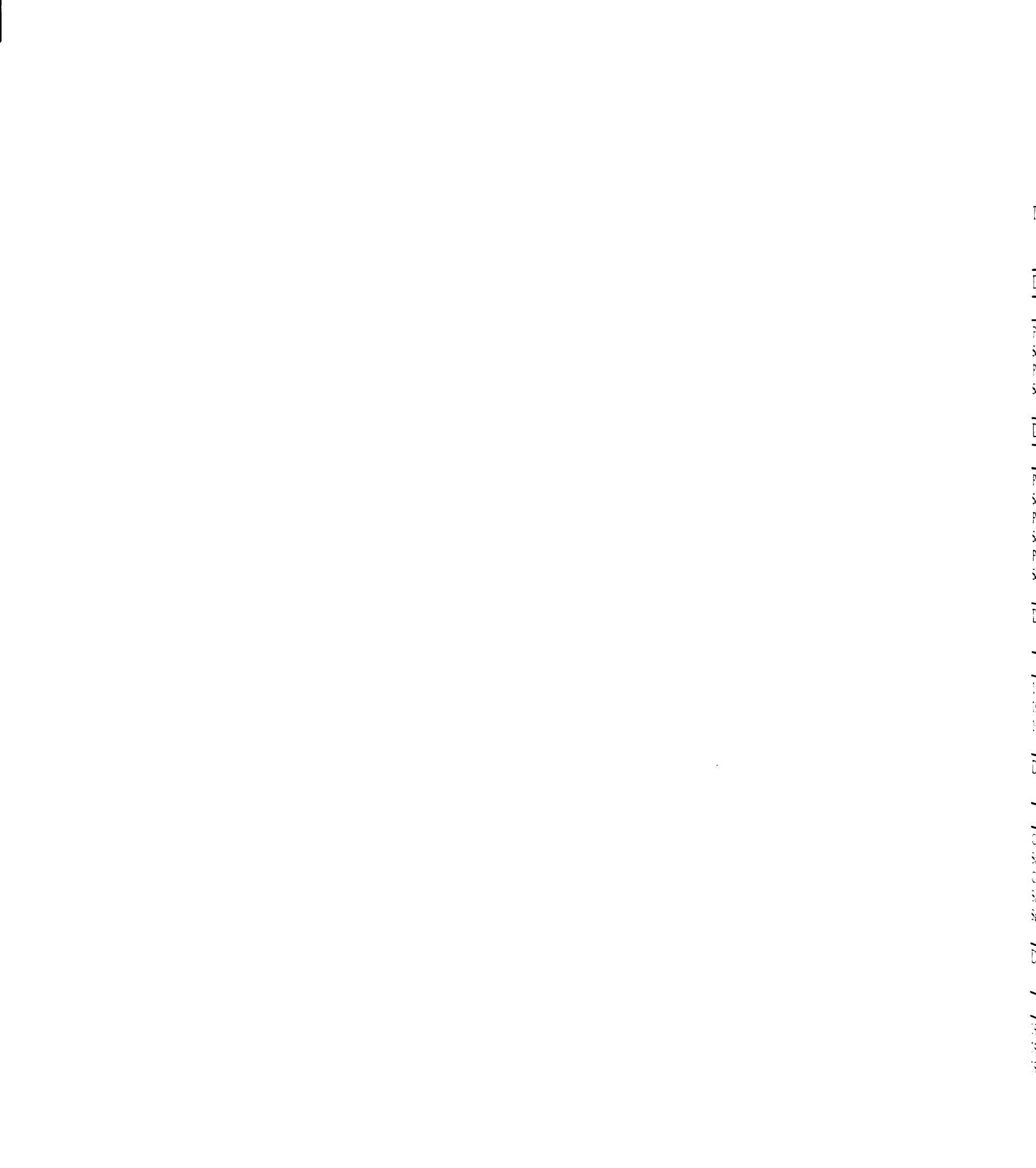
Dependent variable: First Color Change (<i>Salix rotundifolia</i> , 0.50 transformed)					
Source	df	Sums of Squares	Mean Square	F-ratio	Prob
Const	1	2841.24	2841.24	372984	≤ 0.0001
yr	2	3.44215	1.72108	225.93	≤ 0.0001
pt	1	2.25344	2.25344	295.82	≤ 0.0001
yr*pt	2	0.057176	0.028588	3.7529	0.0277
Error	80	0.609408	0.007618		
Total	85	6.01709			

APPENDIX B

Table 11. Scheffe Post Hoc test results - Julian Date of Occurrence

Dependent variable: Emergence of First Green Leaf (-0.5 transformed)				
		Difference	std. err.	Prob
Arclat,1994,OTC	- Arclat,1994,CTL	-0.000222	0.0007	1.00000
Luzarc,1994,OTC	- Luzarc,1994,CTL	-0.000533	0.0006	0.999507
Luzcon,1994,OTC	- Luzcon,1994,CTL	-0.000931	0.0005	0.926870
Paphul,1994,OTC	- Paphul,1994,CTL	-0.001002	0.0008	0.992737
Saxpun,1994,OTC	- Saxpun,1994,CTL	-0.001292	0.0006	0.749999
Arclat,1995,OTC	- Arclat,1995,CTL	-0.000141	0.0007	1.00000
Luzarc,1995,OTC	- Luzarc,1995,CTL	0.000057	0.0006	1.00000
Luzcon,1995,OTC	- Luzcon,1995,CTL	-0.000162	0.0005	1.00000
Paphul,1995,OTC	- Paphul,1995,CTL	-0.000075	0.0008	1.00000
Saxpun,1995,OTC	- Saxpun,1995,CTL	0.000159	0.0006	1.00000
Arclat,1996,OTC	- Arclat,1996,CTL	-0.000458	0.0007	0.999892
Luzarc,1996,OTC	- Luzarc,1996,CTL	-0.000014	0.0006	1.00000
Luzcon,1996,OTC	- Luzcon,1996,CTL	-0.000852	0.0006	0.973636
Paphul,1996,OTC	- Paphul,1996,CTL	-0.002701	0.0008	0.201658
Saxpun,1996,OTC	- Saxpun,1996,CTL	-0.000834	0.0006	0.985747

Dependent variable: First Inflorescence Visible (-0.5 transformed)				
		Difference	std. err.	Prob
Arclat,1994,OTC	- Arclat,1994,CTL	-0.003320	0.0018	0.918038
Luzarc,1994,OTC	- Luzarc,1994,CTL	-0.001132	0.0012	0.998926
Luzcon,1994,OTC	- Luzcon,1994,CTL	-0.001492	0.0008	0.894657
Paphul,1994,OTC	- Paphul,1994,CTL	-0.004885	0.0010	0.004497
Saxpun,1994,OTC	- Saxpun,1994,CTL	-0.001397	0.0007	0.856332
Arclat,1995,OTC	- Arclat,1995,CTL	-0.003412	0.0013	0.557513
Luzarc,1995,OTC	- Luzarc,1995,CTL	-0.000955	0.0008	0.995678
Luzcon,1995,OTC	- Luzcon,1995,CTL	-0.000097	0.0007	1.00000
Paphul,1995,OTC	- Paphul,1995,CTL	0.000733	0.0009	0.999628
Saxpun,1995,OTC	- Saxpun,1995,CTL	0.001512	0.0007	0.825675
Arclat,1996,OTC	- Arclat,1996,CTL	-0.003026	0.0017	0.909199
Luzarc,1996,OTC	- Luzarc,1996,CTL	0.000795	0.0011	0.999828
Luzcon,1996,OTC	- Luzcon,1996,CTL	-0.001701	0.0009	0.895485
Paphul,1996,OTC	- Paphul,1996,CTL	-0.002763	0.0010	0.446759
Saxpun,1996,OTC	- Saxpun,1996,CTL	-0.000982	0.0009	0.996770



APPENDIX B

Table 11. (Cont'd)

Dependent variable: First Elongation of Pedicels (-0.5 transformed)				
		Difference	std. err.	Prob
Paphul,1995,OTC	- Paphul,1995,CTL	-0.000012	0.0010	0.990822
Saxpun,1995,OTC	- Saxpun,1995,CTL	-0.000496	0.0007	0.497458
Paphul,1996,OTC	- Paphul,1996,CTL	-0.001999	0.0010	0.040404
Saxpun,1996,OTC	- Saxpun,1996,CTL	-0.002160	0.0007	0.004863
Dependent variable: First Flower Wither (-0.5 transformed)				
		Difference	std. err.	Prob
Paphul,1994,OTC	- Paphul,1994,CTL	-0.001265	0.0011	0.531564
Saxpun,1994,OTC	- Saxpun,1994,CTL	-0.001288	0.0008	0.277899
Paphul,1995,OTC	- Paphul,1995,CTL	-0.000502	0.0009	0.862207
Saxpun,1995,OTC	- Saxpun,1995,CTL	-0.000702	0.0007	0.612467
Paphul,1996,OTC	- Paphul,1996,CTL	-0.003727	0.0009	0.000606
Saxpun,1996,OTC	- Saxpun,1996,CTL	-0.000951	0.0007	0.426382
Dependent variable: First Emergence of Green Leaf (<i>Salix Rotundifolia</i> , -0.5 transformed)				
		Difference	std. err.	Prob
1994,OTC	- 1994,CTL	-0.002194	0.0004	0.000011
1995,OTC	- 1995,CTL	-0.000399	0.0004	0.663670
1996,OTC	- 1996,CTL	-0.001633	0.0005	0.002398
Dependent variable: First Stigma Visible (<i>Salix Rotundifolia</i> , -0.5 transformed)				
		Difference	std. err.	Prob
Castet,1994,OTC	- Castet,1994,CTL	-0.000968	0.0004	0.020855
Salrot,1994,OTC	- Salrot,1994,CTL	-0.002000	0.0004	0.000003
Castet,1995,OTC	- Castet,1995,CTL	-0.004320	0.0007	0.000000
Salrot,1995,OTC	- Salrot,1995,CTL	-0.001251	0.0005	0.008945
Salrot,1996,OTC	- Salrot,1996,CTL	-0.000822	0.0005	0.118488
Dependent variable: First Pollen Shed (<i>Salix Rotundifolia</i> , -0.5 transformed)				
		Difference	std. err.	Prob
1994,OTC	- 1994,CTL	-0.002167	0.0004	0.000002
1995,OTC	- 1995,CTL	-0.003091	0.0004	0.000000
1996,OTC	- 1996,CTL	-0.001411	0.0004	0.008694

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Table 11. (Cont'd)

Dependent variable: All Pollen Shed (<i>Salix Rotundifolia</i> , -0.5 transformed)				
		Difference	std. err.	Prob
1994,OTC	- 1994,CTL	-0.001108	0.0004	0.008633
1995,OTC	- 1995,CTL	-0.014013	0.0004	0
1996,OTC	- 1996,CTL	-0.000575	0.0004	0.363890
Dependent variable: First Seed Dispersal (<i>Salix Rotundifolia</i> , -0.5 transformed)				
		Difference	std. err.	Prob
1994,OTC	- 1994,CTL	-0.001938	0.0010	0.148047
1995,OTC	- 1995,CTL	-0.000110	0.0012	0.995532
1996,OTC	- 1996,CTL	-0.000220	0.0010	0.975845
Dependent variable: First Color Change (<i>Salix Rotundifolia</i> , -0.5 transformed)				
		Difference	std. err.	Prob
1994,OTC	- 1994,CTL	0.000608	0.0005	0.458801
1995,OTC	- 1995,CTL	0.000017	0.0005	0.999290
1996,OTC	- 1996,CTL	-0.001670	0.0004	0.000951
Dependent variable: First Corolla Drop (<i>Cassiope tetragona</i> , -0.5 transformed)				
		Difference	std. err.	Prob
1994,OTC	- 1994,CTL	-0.002502	0.0006	0.000958
1995,OTC	- 1995,CTL	-0.004401	0.0011	0.000516
1996,OTC	- 1996,CTL	-0.001993	0.0007	0.025710

APPENDIX B

Table 12. Scheffe Post Hoc test results - Days since snow free

Dependent variable: Emergence of First Green Leaf (0.0 transformed)				
		Difference	std. err.	Prob
Arclat,1994,OTC	- Arclat,1994,CTL	-0.052225	0.1861	1.00000
Luzarc,1994,OTC	- Luzarc,1994,CTL	-0.120219	0.1754	0.999995
Luzcon,1994,OTC	- Luzcon,1994,CTL	-0.189213	0.1435	0.997937
Paphul,1994,OTC	- Paphul,1994,CTL	-0.146854	0.2232	0.999997
Salrot,1994,OTC	- Salrot,1994,CTL	-0.512537	0.1387	0.192432
Saxpun,1994,OTC	- Saxpun,1994,CTL	-0.146696	0.1561	0.999900
Arclat,1995,OTC	- Arclat,1995,CTL	-0.080048	0.1907	1.00000
Luzarc,1995,OTC	- Luzarc,1995,CTL	0.029746	0.1727	1.00000
Luzcon,1995,OTC	- Luzcon,1995,CTL	0.015813	0.1454	1.00000
Paphul,1995,OTC	- Paphul,1995,CTL	-0.176166	0.2232	0.999981
Salrot,1995,OTC	- Salrot,1995,CTL	-0.095661	0.1387	0.999995
Saxpun,1995,OTC	- Saxpun,1995,CTL	-0.019492	0.1674	1.00000
Arclat,1996,OTC	- Arclat,1996,CTL	-0.276404	0.1820	0.993283
Luzarc,1996,OTC	- Luzarc,1996,CTL	0.128292	0.1727	0.999989
Luzcon,1996,OTC	- Luzcon,1996,CTL	-0.069016	0.1559	1.00000
Paphul,1996,OTC	- Paphul,1996,CTL	-0.544687	0.2207	0.806831
Salrot,1996,OTC	- Salrot,1996,CTL	-0.364036	0.1450	0.788341
Saxpun,1996,OTC	- Saxpun,1996,CTL	-0.183145	0.1679	0.999611

Dependent variable: First Inflorescence Visible (0.0 transformed)				
		Difference	std. err.	Prob
Arclat,1994,OTC	- Arclat,1994,CTL	-0.256529	0.2560	0.999946
Castet,1994,OTC	- Castet,1994,CTL	-0.124256	0.0809	0.996692
Luzarc,1994,OTC	- Luzarc,1994,CTL	-0.127600	0.1685	0.999997
Luzcon,1994,OTC	- Luzcon,1994,CTL	-0.152944	0.1098	0.998650
Paphul,1994,OTC	- Paphul,1994,CTL	-0.610419	0.1413	0.071448
Salrot,1994,OTC	- Salrot,1994,CTL	-0.266548	0.0809	0.458397
Saxpun,1994,OTC	- Saxpun,1994,CTL	-0.125509	0.0969	0.999317
Arclat,1995,OTC	- Arclat,1995,CTL	-0.234993	0.1983	0.999713
Castet,1995,OTC	- Castet,1995,CTL	-0.723047	0.1389	0.005351
Luzarc,1995,OTC	- Luzarc,1995,CTL	-0.239890	0.1170	0.962942
Luzcon,1995,OTC	- Luzcon,1995,CTL	0.010624	0.0910	1.00000
Paphul,1995,OTC	- Paphul,1995,CTL	0.501546	0.1288	0.180141
Salrot,1995,OTC	- Saxpun,1995,CTL	0.226453	0.0980	0.912613
Saxpun,1995,OTC	- Saxpun,1995,CTL	0.287960	0.1008	0.697822
Arclat,1996,OTC	- Arclat,1996,CTL	-0.196584	0.2290	0.999989
Luzarc,1996,OTC	- Luzarc,1996,CTL	0.067268	0.1514	1.00000
Luzcon,1996,OTC	- Luzcon,1996,CTL	-0.118521	0.1254	0.999970
Paphul,1996,OTC	- Paphul,1996,CTL	-0.261137	0.1363	0.978008
Salrot,1996,OTC	- Salrot,1996,CTL	-0.110523	0.1021	0.999882
Saxpun,1996,OTC	- Saxpun,1996,CTL	-0.179509	0.1254	0.998254

APPENDIX B

Table 12 (Cont'd)

Dependent variable: First Elongation of Pedicels (-0.50 transformed)				
		Difference	std. err.	Prob
Castet,1994,OTC	- Castet,1994,CTL	-0.029945	0.0136	0.092230
Castet,1995,OTC	- Castet,1995,CTL	-0.110873	0.0231	0.000020
Paphul,1995,OTC	- Paphul,1995,CTL	0.012542	0.0227	0.858374
Saxpun,1995,OTC	- Saxpun,1995,CTL	-0.024656	0.0158	0.297910
Castet,1996,OTC	- Castet,1996,CTL	-0.024660	0.0381	0.811371
Paphul,1996,OTC	- Paphul,1996,CTL	-0.031926	0.0209	0.313011
Saxpun,1996,OTC	- Saxpun,1996,CTL	-0.038563	0.0163	0.062795

Dependent variable: First Inflorescence Open (-0.50 transformed)				
		Difference	std. err.	Prob
Castet,1994,OTC	- Castet,1994,CTL	-0.268993	0.0603	0.012140
Luzarc,1994,OTC	- Luzarc,1994,CTL	-0.175415	0.0777	0.746348
Luzcon,1994,OTC	- Luzcon,1994,CTL	-0.073164	0.0581	0.990978
Paphul,1994,OTC	- Paphul,1994,CTL	-0.288628	0.0983	0.377106
Saxpun,1994,OTC	- Saxpun,1994,CTL	-0.137724	0.0721	0.886423
Castet,1995,OTC	- Castet,1995,CTL	-0.373487	0.0943	0.049890
Luzarc,1995,OTC	- Luzarc,1995,CTL	-0.114915	0.0733	0.963159
Luzcon,1995,OTC	- Luzcon,1995,CTL	-0.197354	0.0595	0.204391
Paphul,1995,OTC	- Paphul,1995,CTL	-0.063842	0.0855	0.999794
Saxpun,1995,OTC	- Saxpun,1995,CTL	-0.076419	0.0654	0.994609
Castet,1996,OTC	- Castet,1996,CTL	-0.204770	0.0645	0.263017
Luzarc,1996,OTC	- Luzarc,1996,CTL	0.024675	0.1059	1.00000
Luzcon,1996,OTC	- Luzcon,1996,CTL	-0.265722	0.0653	0.037422
Paphul,1996,OTC	- Paphul,1996,CTL	-0.252317	0.0874	0.404232
Saxpun,1996,OTC	- Saxpun,1996,CTL	-0.074485	0.0673	0.996305

Dependent variable: First Flower Wither (0.0 transformed)				
		Difference	std. err.	Prob
Paphul,1994,OTC	- Paphul,1994,CTL	-0.090277	0.0746	0.482895
Saxpun,1994,OTC	- Saxpun,1994,CTL	-0.087887	0.0532	0.259261
Paphul,1995,OTC	- Paphul,1995,CTL	-0.028469	0.0612	0.897633
Saxpun,1995,OTC	- Saxpun,1995,CTL	-0.065509	0.0471	0.382025
Paphul,1996,OTC	- Paphul,1996,CTL	-0.198600	0.0626	0.007776
Saxpun,1996,OTC	- Saxpun,1996,CTL	-0.062157	0.0483	0.438501

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Table 12. (cont'd)

Dependent variable: First Pollen Shed (0.0 transformed)				
		Difference	std. err.	Prob
1994,OTC	- 1994,CTL	-0.058702	0.0134	0.000142
1995,OTC	- 1995,CTL	-0.091268	0.0146	0.000000
1996,OTC	- 1996,CTL	-0.023055	0.0150	0.311521
Dependent variable: All Pollen Shed (0.0 transformed)				
		Difference	std. err.	Prob
1994,OTC	- 1994,CTL	-0.022106	0.0100	0.092812
1995,OTC	- 1995,CTL	-0.211159	0.0110	0.000000
1996,OTC	- 1996,CTL	-0.002792	0.0115	0.970906
Dependent variable: First Seed Dispersal (0.0 transformed)				
		Difference	std. err.	Prob
1994,OTC - 1994,CTL	-0.117653	0.0540	0.100521	
1995,OTC - 1995,CTL	-0.008719	0.0640	0.990756	
1996,OTC - 1996,CTL	-0.021118	0.0549	0.928651	
Dependent variable: First Color Change (0.0 transformed)				
		Difference	std. err.	Prob
1994,OTC	- 1994,CTL	0.033647	0.0293	0.520495
1995,OTC	- 1995,CTL	0.003377	0.0275	0.992492
1996,OTC	- 1996,CTL	-0.080742	0.0259	0.010289
Dependent variable: First Corolla Drop (0.0 transformed)				
		Difference	std. err.	Prob
1994,OTC	- 1994,CTL	0.033647	0.0293	0.520495
1995,OTC	- 1995,CTL	0.003377	0.0275	0.992492
1996,OTC	- 1996,CTL	-0.080742	0.0259	0.010289

APPENDIX B

Table 13 Scheffe Post Hoc test results - Growing Degree Day Accumulation

Dependent variable: Emergence of First Green Leaf (0.0 transformed)		Difference	std. err.	Prob
Arclat,1994,OTC	- Arclat,1994,CTL	0.845230	0.2958	0.612740
Luzarc,1994,OTC	- Luzarc,1994,CTL	0.655101	0.2745	0.839170
Luzcon,1994,OTC	- Luzcon,1994,CTL	0.398307	0.2282	0.979984
Paphul,1994,OTC	- Paphul,1994,CTL	0.507094	0.3549	0.995921
Salrot,1994,OTC	- Salrot,1994,CTL	-0.824181	0.2205	0.177419
Saxpun,1994,OTC	- Saxpun,1994,CTL	0.256815	0.2481	0.999758
Arclat,1995,OTC	- Arclat,1995,CTL	-0.040042	0.3032	1.00000
Luzarc,1995,OTC	- Luzarc,1995,CTL	0.049951	0.2660	1.00000
Luzcon,1995,OTC	- Luzcon,1995,CTL	-0.095525	0.2312	1.00000
Paphul,1995,OTC	- Paphul,1995,CTL	-0.320149	0.3433	0.999907
Salrot,1995,OTC	- Salrot,1995,CTL	-0.064091	0.2205	1.00000
Saxpun,1995,OTC	- Salrot,1995,CTL	0.359836	0.2568	0.996541
Arclat,1996,OTC	- Arclat,1996,CTL	0.336902	0.2887	0.999286
Luzarc,1996,OTC	- Luzarc,1996,CTL	0.227634	0.2660	0.999958
Luzcon,1996,OTC	- Luzcon,1996,CTL	-0.005543	0.2478	1.00000
Paphul,1996,OTC	- Paphul,1996,CTL	-0.527410	0.3509	0.993816
Salrot,1996,OTC	- Salrot,1996,CTL	-0.007040	0.2305	1.00000
Saxpun,1996,OTC	- Saxpun,1996,CTL	0.423662	0.2705	0.991387

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Table 13. (Cont'd)

Dependent variable: First Inflorescence Visible (0.0 transformed)				
		Difference	std. err.	Prob
Arclat,1994,OTC	- Arclat,1994,CTL	-0.029097	0.3389	1.00000
Castet,1994,OTC	- Castet,1994,CTL	0.326364	0.1072	0.596798
Luzarc,1994,OTC	- Luzarc,1994,CTL	0.311655	0.2231	0.998608
Luzcon,1994,OTC	- Luzcon,1994,CTL	0.201328	0.1454	0.998720
Paphul,1994,OTC	- Paphul,1994,CTL	-0.551135	0.1871	0.651236
Salrot,1994,OTC	- Salrot,1994,CTL	0.060365	0.1072	1.00000
Saxpun,1994,OTC	- Saxpun,1994,CTL	0.241750	0.1298	0.982518
Arclat,1995,OTC	- Arclat,1995,CTL	0.013698	0.2396	1.00000
Castet,1995,OTC	- Castet,1995,CTL	-0.415099	0.1839	0.925420
Luzarc,1995,OTC	- Luzarc,1995,CTL	0.182417	0.1550	0.999731
Luzcon,1995,OTC	- Luzcon,1995,CTL	0.378417	0.1204	0.542834
Paphul,1995,OTC	- Paphul,1995,CTL	0.417033	0.1669	0.855043
Salrot,1995,OTC	- Salrot,1995,CTL	-0.061266	0.1221	1.00000
Saxpun,1995,OTC	- Saxpun,1995,CTL	0.599497	0.1334	0.046096
Arclat,1996,OTC	- Arclat,1996,CTL	0.143215	0.3031	1.00000
Castet,1996,OTC	- Luzarc,1996,CTL	1.63254	0.2396	0.000006
Luzarc,1996,OTC	- Luzarc,1996,CTL	1.02097	0.2005	0.007800
Luzcon,1996,OTC	- Luzcon,1996,CTL	0.044553	0.1660	1.00000
Paphul,1996,OTC	- Paphul,1996,CTL	-0.190433	0.1804	0.999909
Salrot,1996,OTC	- Salrot,1996,CTL	0.204737	0.1351	0.997059
Saxpun,1996,OTC	- Saxpun,1996,CTL	0.153435	0.1660	0.999976
Dependent variable: First Elongation of Pedicels (0.0 transformed)				
		Difference	std. err.	Prob
Castet,1994,OTC	- Castet,1994,CTL	0.226862	0.0863	0.033752
Castet,1995,OTC	-Castet,1995,CTL	-0.275205	0.1465	0.174377
Paphul,1995,OTC	- Paphul,1995,CTL	0.351718	0.1437	0.052607
Saxpun,1995,OTC	- Saxpun,1995,CTL	0.300671	0.1000	0.012219
Castet,1996,OTC	- Castet,1996,CTL	0.353280	0.2414	0.345113
Paphul,1996,OTC	- Paphul,1996,CTL	0.001388	0.1322	0.999945
Saxpun,1996,OTC	- Saxpun,1996,CTL	0.176913	0.1045	0.241727

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Table 13. (Cont'd)

Dependent variable: First Inflorescence Open (0.0 transformed)				
		Difference	std. err.	Prob
Castet,1994,OTC	- Castet,1994,CTL	0.000143	0.0807	1
Luzarc,1994,OTC	- Luzarc,1994,CTL	0.193271	0.1039	0.901489
Luzcon,1994,OTC	- Luzcon,1994,CTL	0.325912	0.0777	0.026443
Paphul,1994,OTC	- Paphul,1994,CTL	-0.058009	0.1314	0.999996
Saxpun,1994,OTC	- Saxpun,1994,CTL	0.173059	0.0964	0.918998
Castet,1995,OTC	- Castet,1995,CTL	-0.015125	0.1261	1.00000
Luzarc,1995,OTC	- Luzarc,1995,CTL	0.285998	0.0980	0.387567
Luzcon,1995,OTC	- Luzcon,1995,CTL	0.071566	0.0795	0.999169
Paphul,1995,OTC	- Paphul,1995,CTL	0.272516	0.1144	0.683391
Saxpun,1995,OTC	- Saxpun,1995,CTL	0.293068	0.0875	0.192798
Arclat,1996,OTC	- Arclat,1996,CTL	0.259540	0.2939	0.999277
Castet,1996,OTC	- Castet,1996,CTL	0.220600	0.0863	0.587734
Luzarc,1996,OTC	- Luzarc,1996,CTL	0.614507	0.1416	0.017483
Luzcon,1996,OTC	- Luzcon,1996,CTL	0.076792	0.0873	0.999297
Paphul,1996,OTC	- Paphul,1996,CTL	0.092996	0.1169	0.999668
Saxpun,1996,OTC	- Saxpun,1996,CTL	0.368338	0.0900	0.035266

Dependent variable: First Flower Wither (0.0 transformed)				
		Difference	std. err.	Prob
Paphul,1994,OTC	- Paphul,1994,CTL	0.200403	0.0836	0.059759
Saxpun,1994,OTC	- Saxpun,1994,CTL	0.190384	0.0596	0.007296
Paphul,1995,OTC	- Paphul,1995,CTL	0.340917	0.0686	0.000012
Saxpun,1995,OTC	- Saxpun,1995,CTL	0.334159	0.0527	0.000000
Saxpun,1996,OTC	- Saxpun,1996,CTL	0.341499	0.0551	0.000000

Dependent variable: First Pollen Shed (<i>Salix rotundifolia</i> , 0.0 transformed)				
		Difference	std. err.	Prob
1994,OTC	- 1994,CTL	-0.056329	0.0950	0.839044
1995,OTC	- 1995,CTL	-0.173976	0.1039	0.250782
1996,OTC	- 1996,CTL	0.054583	0.1066	0.877197

Dependent variable: All Pollen Shed (<i>Salix rotundifolia</i> , 0.0 transformed)				
		Difference	std. err.	Prob
1994,OTC	- 1994,CTL	0.216223	0.0621	0.003212
1995,OTC	- 1995,CTL	-0.869398	0.0680	0.000000
1996,OTC	- 1996,CTL	0.356585	0.0712	0.000012

APPENDIX B

Table 13. (Cont'd)

Dependent variable: First Seed Dispersal (<i>Salix rotundifolia</i> , 0.0 transformed)		Difference	std. err.	Prob
1994,OTC	- 1994,CTL	0.087510	0.0608	0.359749
1995,OTC	- 1995,CTL	0.380260	0.0720	0.000008
1996,OTC	- 1996,CTL	0.305509	0.0617	0.000027
Dependent variable: First Color Change (<i>Salix rotundifolia</i> , 0.0 transformed)		Difference	std. err.	Prob
1994,OTC	-1994,CTL	0.314583	0.0352	0.000000
1995,OTC	-1995,CTL	0.397439	0.0330	0.000000
1996,OTC	-1996,CTL	0.274766	0.0311	0.000000

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