**University of Alberta**

# Shrub encroachment in arctic and alpine tundra: Patterns of expansion and ecosystem impacts.

by

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A thesis submitted to the Faculty of Graduate Studies and Research
in partial fulfillment of the requirements for the degree of

Doctor of Philosophy
in
Ecology

Department of Biological Sciences

Fall 2011
Edmonton, Alberta

# Dedication

To George Argus, and the other Alaska ecological pioneers including my former neighbour Ginny Woods for inspiring my love of the north and the less charismatic flora such as the willows that grow there…

…and to my parents Judy Myers and Jamie Smith who were my first ecological mentors and from day one set me on a path of scientific inquiry.

## Abstract

With a warming climate, northern ecosystems will face significant ecological changes such as permafrost thaw, increased frequency of forest fires, and shifting ecosystem boundaries including the spread of canopy-forming shrubs into tundra communities. A growing number of observations show increases in canopy-forming shrubs at sites around the circumpolar Arctic, which could cause major modifications to the diversity and functioning of tundra ecosystems. In this study of changes in willow (*Salix* spp.) cover and abundance in tundra ecosystems of the Yukon Territory, I found evidence that canopy-forming willow patches have expanded and canopy heights have increased on Herschel Island and that willows have advanced upslope to extend their altitudinal ranges in the Kluane Region. The growth of these willows is temperature sensitive, with early growing season temperatures explaining approximately half of the variation in annual growth rings. I conducted an experimental manipulation of shrub canopy cover that demonstrated that canopies significantly influenced soil temperatures. Snow trapping by shrub canopies insulated soils in winter, and shading by canopies in summer kept soils cool under shrub cover. The experimental manipulations of artificial canopies and canopy removals functioned similarly to the unmanipulated treatments, indicating that the shrub canopy is the dominant control of soil temperatures in this system. I did not, however, observe many significant differences in the nutrient cycling parameters that I measured, and this indicates that the direct effects of shrub canopies on soil temperatures are weak controls over the carbon and nitrogen fluxes at this study site. Understanding both the rate of change in canopy forming woody shrubs and the impacts of this change on ecosystem function will improve projections of future carbon storage, permafrost integrity and wildlife habitat in tundra ecosystems.

## Acknowledgements

Thank you to my advisor David Hik and my PhD thesis committee Janice Cook, JC Cahill, and Peter Kershaw. Thank you also to Judith Myers, Trevor Lantz, Sierra McLane, Sonja Wipf, Jill Johnstone, Charley Krebs, Roger Ruess, and Chris Burn for reading and providing very helpful comments on the draft chapters of this thesis.

I would like to give recognition to Trevor Lantz, Martin Wilmking, Martin Hallinger, Ken Tape, Daan Blok and the other shrub researchers who laid the groundwork for this study. And I would like to thank the Shrub Hub Research Network for sharing ideas and for supporting data synthesis efforts.

Much credit for the completion of the field and laboratory research goes to Team Shrub who gave their all to carry out the four years of this study.
Team Shrub is:
2007: Jodie Pongracz, Mark Wong, Hillary Quinn, Catherine Henry, Eric Vezeau
2008: Catherine Henry, Christina McDonald, Meagan Saunders, Krystal Reaume
2009: Meagan Grabowski, Tammy Elliot, Amber Briggs, Natalie Stafl, Annika Trimble
2010: Meagan Grabowski, Véronique Demers, Andrew Shaw, Kristen Peck

Thanks also to members of the Hik Lab and Martin Labs including Helen Wheeler and the other Members of Team Squirrel for putting up with us folks on Team Shrub, to Ryan Danby, Kieran O'Donovan, Sarah Trefry, James Hudson, Françoise Cardou, Vijay Patil, Mark Wong, Alana Clason, John Allsopp, Oliver Moore, Clair Edwards, Jolene Swain, Charlotte Adamson, Hannah Horn, Jessie Zgurski, Shawn Morrison, Saewan Koh, Scott Williams and other Pika Campers for the good times in the field and lab, to Scott Williamson for assistance with spatial data, to Amanda Edworthy for help with statistics and for keeping me fit with some intense squash matches, to Sarah Elmendorf, Jamie Lethem, Kris Metzger and other members of the Martin, Henry Labs and Ecology and

Evolution group at UBC for assistance and encouragement along the way, to the UBC forestry band know either as the Outliers or Residuals for all the jams, and to my housemate Erin Cameron for her support during the writing process.

Thank you to Andy Williams, Lance Goodwin, Sian Williams, and the staff of the Kluane Lake Research Station for field logistical support and training in how to drive off road in a 4 x 4 truck, sling with a helicopter, and other essential northern skills. Thank you to Don Reid, Scott Gilbert, Val Loewen, and the Aurora Research Institute for field logistical support for the Herschel Island field work. Thank you also to Qikiqtaruk – Herschel Island Territorial Park wardens and park management, in particular Lee John Meyook and Richard Gordon, the 2008 and 2009 ArcticWOLVES Herschel Island field crews, and to Frank Doyle, David Neufeld, Alice Kennedy and Liz Hoffer for collecting data or contributing photographs.

Funding for my thesis research was provided by Canon National Parks Science Scholars Program, W. Garfield Weston Foundation, Alberta Ingenuity Program, the Government of Canada International Polar Year Program, NSERC, Arctic Institute of North America, Northern Research Institute at Yukon College, Northern Scientific Training Program INAC, and C-BAR Grant Program, Canadian Circumpolar Institute, Polar Continental Shelf Program, Canada Foundation for Innovation, and Air North (flight discounts).

Finally, I would like to thank the Kluane First Nation and the Inuvialuit people for the opportunity to conduct research on their traditional lands.

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# Chapter 1. Introduction

## Part 1. Evidence of shrub increase

Climate change is altering tundra ecosystems. A growing number of studies report ecological changes such as permafrost thaw (Hinzman et al. 2005, Jorgenson et al. 2006, Lawrence et al. 2008, Åkerman and Johansson 2008), tundra fires (Kasischke and Turetsky 2006, Jones et al. 2009, Mack et al. 2011). In addition, climate warming is projected to lead to changes in ecosystem boundaries including the spread of canopy-forming shrubs into tundra communities (Post et al. 2009). Changes in the density or extent of shrub cover in tundra ecosystems could modify snow distributions, nutrient inputs, carbon stores, surface albedo and associated energy fluxes, potentially creating positive feedbacks to climate change (Chapin et al. 2005). Ongoing efforts to summarize climate impacts in the Arctic have highlighted the need to better monitor these rapidly changing ecosystems (ACIA 2005).

In the last 50 years, increases in shrub abundance have been documented in arctic and subarctic tundra ecosystems in northern Alaska (Sturm et al. 2001b, Tape et al. 2006), the Northwest Territories (Lantz et al. 2009, 2010, Mackay and Burn 2011), Northern Quebec (*pers. comm.* B. Tremblay, E. Lévesque and S. Boudreau), and Siberia (Forbes et al. 2010). In addition, studies of population structures of woody shrub and tree species indicate the advancement of shrubs up slopes in alpine tundra ecosystems in subarctic Sweden (Hallinger et al. 2010) and sites in Norway (Hofgaard et al. 2009). Local indigenous Nenets people in the Western Russian Arctic report increasing willow and alder shrubs (Forbes et al. 2009, 2010) and similar observations of vegetation change by Inuit have been reported in arctic Canada (Thorpe et al. 2002).

### *Warming and greening*

Growing season temperatures are warming in Alaska and western Canada (Chapin et al. 2005, ACIA 2005), and concurrent with this trend, satellite imagery shows a greening of the arctic tundra (Jia et al. 2003, Stow 2004, Jia et al. 2009, Bhatt et al. 2010). A growing number of studies have made the link between the recent warming trend at high latitudes and increases in woody shrub species (Sturm et al. 2001b, Tape et al. 2006, Jia et al. 2009, Forbes et al. 2010). Ground-based studies in tundra ecosystems have measured increased plant growth over time (Hudson and Henry 2009) and dieback from extreme weather events (Bokhorst et al. 2009). However, further research is necessary to determine the impacts of climate change on shrub proliferation in tundra ecosystems.

### *Paleoecological evidence of increasing shrubs*

Willows are well adapted to invading ecosystems when conditions change. Pollen records indicate that willows were wide spread in arctic ecosystems during warmer and wetter periods after the last glacial maximum (Brubaker et al. 1983, Anderson and Brubaker 1994, Bigelow et al. 2003, Higuera et al. 2008, Naito and Cairns 2011). This evidence of historic high shrub abundance and the current observations of shrub increases suggest that, if growing conditions continue to improve, shrub species will again increase in tundra ecosystems. Therefore, we need to better understand the factors that influence the rate of increasing cover and range expansion of willows and other canopy-forming shrub species in tundra ecosystems.

### *“Shrubification” – increases in woody species in tundra ecosystems*

At high elevations (Klanderud 2005) or latitudes (Doak and Morris 2010) plants can suffer from resource or climate limited growth. The growing season is shorter, nutrients can be limited and growing conditions can be harsher, with periodic snow and colder summer temperatures than at lower elevations and latitudes. Canopy-forming shrub species differ from other tundra plants in that they can grow vertically. Certain shrub species such as *Betula nana* can take advantage of better growing conditions by rapidly elongating “short shoots” (Bret-Harte et al. 2001, 2002, Wookey et al. 2009). In warming and fertilization experiments woody shrubs can rapidly increase in canopy cover and height to dominate experimental plots (Mack et al. 2004). The formation of a closed canopy drastically alters the structure and function of tundra ecosystems, and this change in the dominance of woody species has been colloquially termed “shrubification”.

There are three ways we can classify changes in the abundance of shrub species:

1) “Filling in” (Fig. 1-1a) is the expansion of currently existing patches, or the establishment of new individuals in areas where shrub species are already growing, which results in an increase in the overall shrub cover. This represents the most common identified shrub increase from repeat photography studies (e.g., Sturm et al. 2001b, Tape et al. 2006).
2) Change in growth form (Fig. 1-1b), such as an increase in canopy height, can occur when climate, nutrients or some other growth-limiting factor(s) has changed. Increases in canopy height have been observed in greenhouse warming and fertilization experiments such as the long-term warming and nutrient addition showing dramatic increases in *Betula nana* at Toolik Lake, Alaska (Mack et al. 2004).
3) An advancing shrubline (Fig. 1-1c) is the new recruitment of individuals where canopy-forming shrub species were not previously growing, and represents the elevational or latitudinal shift in the range of woody shrub species. This third type of shrub expansion is the hardest to identify and monitor over time, and only a few studies have addressed advancing shrublines explicitly (Hofgaard et al. 2009, Hallinger et al. 2010).

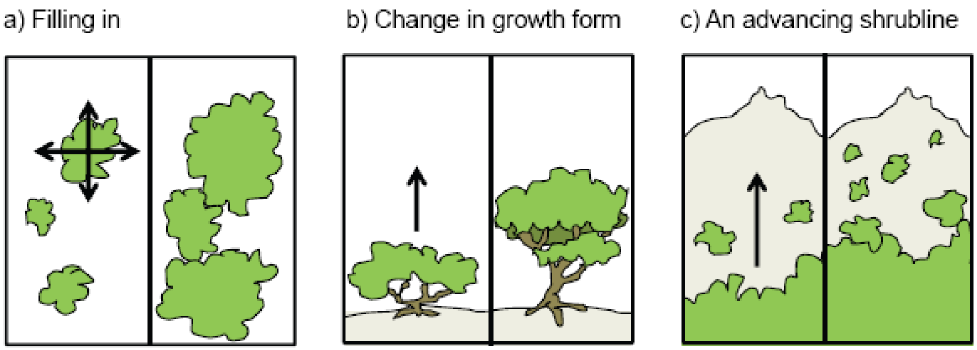

Figure 1-1. The three general categories of shrub increase including a) filling in, b) change in growth form and c) advancing shrublines.

*Growth of woody species*

All woody species growing in temperate or polar ecosystems respond to early summer temperatures by increasing wood formation (Ainsworth et al. 2001). The wood formed early in the growing season when temperature and photoperiod are favourable for active growth is known as early wood. As cambial cell division and expansion declines in the late summer or autumn, late wood is formed. Since physiological studies indicate that most wood is formed in the early growing season, this is likely the period of the year when changing conditions will influence the growth of woody species.

Although warm temperatures are likely to promote shrub growth when other factors are not limiting, the mechanisms driving shrub increase are probably more complex (Fig. 1-2). A combination of changes in nutrient mineralization, snow depth, microclimate (Sturm et al. 2001a, 2005), disturbance (Lantz et al. 2009), and species interactions, particularly factors that influence the germination and establishment of new shrub individuals are most likely all contributing factors explaining shrub expansion patterns on the landscape (Fig. 1-2).

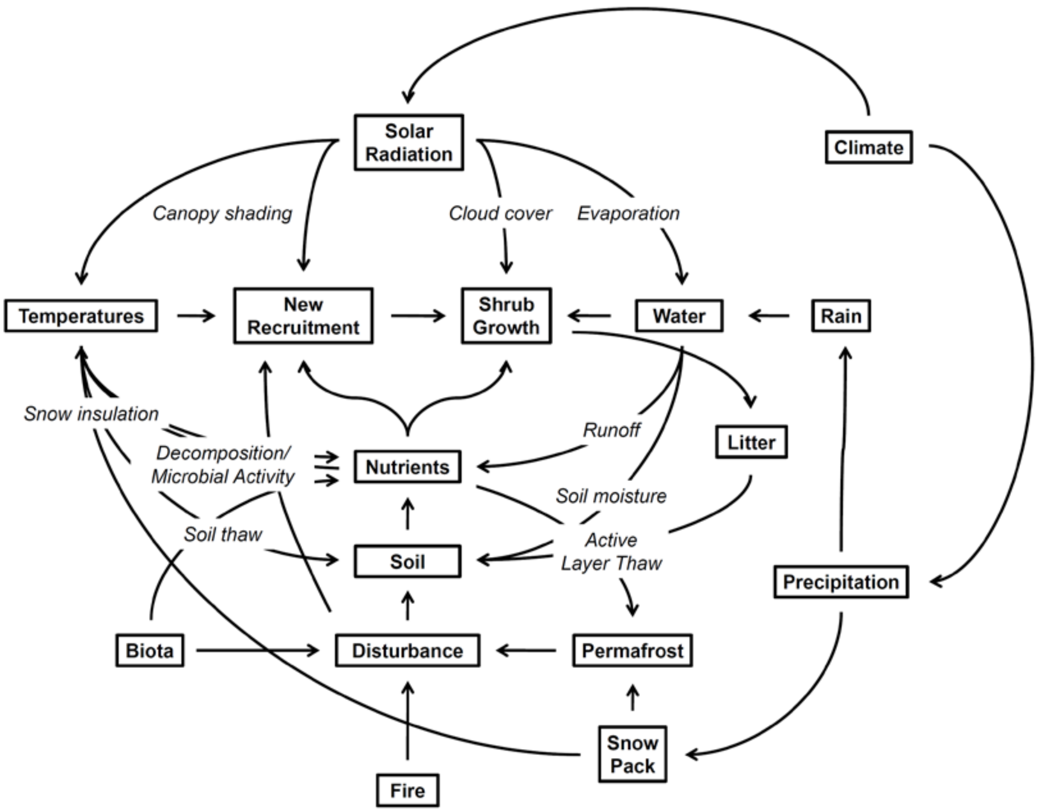

Figure 1-2. Some of the many factors influencing the growth and recruitment of tundra shrub species. The climate, microclimate, sunlight, water and nutrient availability, snow melt, growing season length and disturbance all interact in complex ways making it difficult to establish what specific factors control the growth and recruitment of shrub species. This figure does not take into account many of the biotic interactions such as those with other competing tundra plants (Chapin et al. 1989), herbivores (Olofsson et al. 2009) or soil mycorrhizae (Deslippe et al. 2011), which add even greater complexity.

### *Landscape-level disturbance*

Landscape-level disturbances such as fire, permafrost degradation, runoff channels, or animal burrows can create micro sites appropriate for the establishment of woody shrubs. Disturbance has been identified as a key factor determining recruitment of woody species in tundra systems (Munier et al. 2010, Lantz et al. 2010). Fire (Lantz et al. 2010) and permafrost degradation (Lantz et al. 2009) have been positively associated with recruitment and growth in alder (*Alnus viridis* subsp. *fruticosa*). Disturbances such as fire (Kasischke and Turetsky 2006, Mack et al. 2011) and permafrost (Jorgenson et al. 2006, Lawrence et al. 2008, Åkerman and Johansson 2008) degradation are increasing in tundra ecosystems. When examining changes in shrub abundance, disturbances rather than climate warming could be the most important factor determining recruitment of new individuals. And interactions among the disturbance regime, nutrient availability, herbivory, disease and weather conditions could all interact to influence the establishment and growth of woody tundra species (Fig. 1-2).

### *Herbivory*

Herbivory controls new recruitment of shrub species and can limit or reduce shrub patch expansion on the landscape. Shrub encroachment in tundra ecosystems has been shown to be reduced or inhibited by herbivores in exclosure experiments (Post and Pedersen 2008, Olofsson et al. 2009). Herbivory by sheep and reindeer is thought to be the primary factor determining the height of the shrubby treeline ecotone at sites in northern Scandinavia (Hofgaard et al. 2010, Speed et al. 2010, 2011). The influence of herbivory on the increase in cover or advance of shrubline in tundra ecosystems can vary with the prevalence of herbivores and with the palatability of the shrub species; therefore, the importance of herbivory in limiting shrub expansion can vary between regions.

## Part 2. Impacts of shrub expansion

Shrub expansion is a major structural change in arctic systems with implications for altering microclimates, biogeochemical cycles and ecological habitats. Greenhouse and nutrient addition experiments have been used to project impacts of expanding shrub tundra (Arft et al. 1999, Walker et al. 2006); however, the specific ecosystem and community-level impacts of increasing shrubs are still poorly understood. Interactions between shrubs, microclimate, litter inputs and carbon storage, nutrient cycling, decomposition, albedo and disturbance have been hypothesized to create positive and negative feedbacks to climate warming and further shrub expansion (Fig. 1-3, after Chapin et al. 2005).

### *Snow trapping and soil shading*

Tundra shrubs can significantly modify the distribution and physical characteristics of snow, influencing the exchanges of energy and moisture between terrestrial ecosystems and the atmosphere (Liston et al. 2002, Pomeroy et al. 2006, Marsh et al. 2010). In the winter snow trapping can insulate soils by trapping heat, and has been proposed as a positive feedback mechanism for promoting the expansion of shrubs in the Arctic (Fig. 1-3, Sturm et al. 2001a, Grogan and Jonasson 2006). During spring, shrubs that extend above the snow alter the albedo and accelerate local snow melt (Sturm et al. 2001a, Pomeroy et al. 2006, Loranty et al. 2011). In summer, shading decreases soil temperatures under shrub canopies (Pomeroy et al. 2006).

### *Nutrient cycling*

Interactions between the abiotic and biotic influences of a shrub canopy could alter tundra nutrient cycling (Fig. 1-3). Fertilization experiments show that vascular plant productivity is nitrogen limited in tundra ecosystems (Shaver and Chapin 1980, Mack et al. 2004), and fertilization experiments in tundra ecosystems have resulted in an increase in the biomass of shrubs in plots where shrubs species are present (Dormann and Woodin 2002). Increases in canopy cover and height of shrub species can alter litter inputs to soils (Cornelissen et al.

2007) and increase the amount of carbon stored in above and belowground biomass (Mack et al. 2004). In addition, experimental manipulations have demonstrated that deeper snow depth and warmer winter soils under shrub canopies can increase litter decomposition (Baptist et al. 2009) and nitrogen cycling (Schimel et al. 2004, Nobrega and Grogan 2007, Buckeridge and Grogan 2010). However, quantifying the exact influences of changes in the abundance of shrub species on tundra ecosystem functions across variation in shrub cover, canopy height and density is an ongoing challenge.

### *Biodiversity*

Increases in shrub abundance could have negative effects on tundra species richness, through the loss of shade-intolerant species under shrub canopies (Pajunen et al. 2011). Loss of tundra biodiversity could alter species interactions and ecosystem functions. At tundra sites in northwestern Fennoscandia and the Yamal Peninsula in Russia, the species richness of vegetation declined with increasing shrub height and cover (Pajunen et al. 2011). Lichens have been shown to decline with increases in shrub cover in arctic Alaska (Joly et al. 2009). As an important forage species, the declines of lichens could negatively impact caribou and reindeer populations, and thus influence hunting or herding activities.

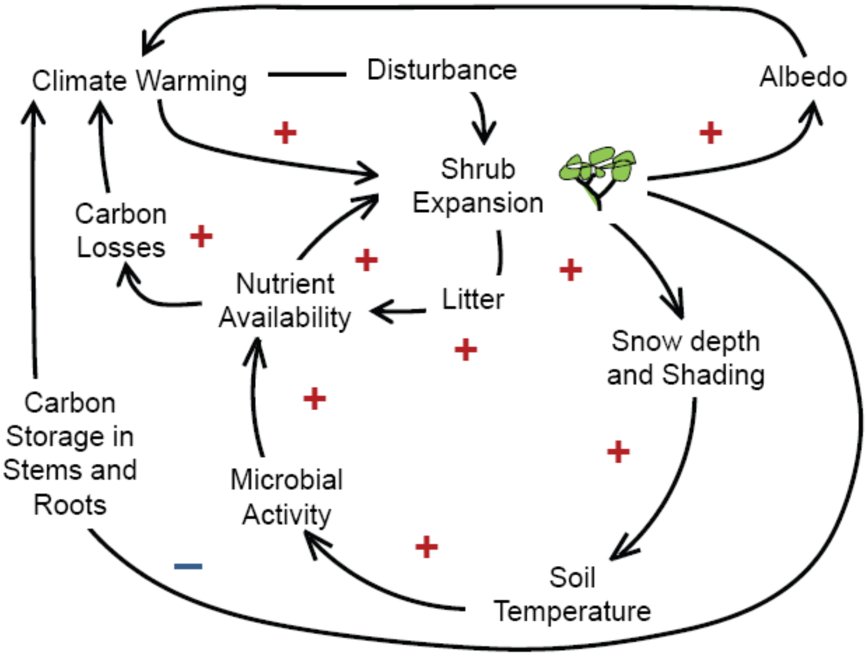

Figure 1-3. The positive and negative feedbacks to shrub expansion and climate warming proposed in the literature (after Chapin et al. 2005).

## Part 3. The willows

Willows are one of the main shrub taxa undergoing a change in abundance in tundra ecosystems (Forbes et al. 2010, Tape et al. 2006). The *Salix* genus is very diverse with 34 species present in the Yukon Territory (Cody 2000). I recorded 10 different alpine willow species in the Kluane Region (Chapter 3, six of the most common species are described in Table 1-1 and illustrated in Fig. 1-4). Many of these species have wide geographic distributions in arctic and alpine ecosystems in the northern regions of Canada, USA and Eurasia (Argus et al. 1999). The elevational range limits of all these species in the Kluane Region are found between 1600 – 2000 m and they grow in decreasing density, patch size, canopy height and age with increasing elevation in this region (Fig. 1-5). On Herschel Island, seven common willow species grow (*S. pulchra*, *S. richardsonii*, *S. glauca*, *S. niphoclada*, *S. arctica*, *S. polaris*, *S. phlebophyla*). All of these species, with the exception of the species *S. phlebophyla*, are present in the Kluane Region.

When surveying the abundance of species in the alpine tundra of the Kluane Region (Chapter 3), I observed no clear segregation of elevational ranges between species, though species diversity was higher at lower elevations. The three most common species at shrubline were *S. niphoclada*, *S. pulchra*, and *S. richardsonii*, which made up ~ 80 % of all individuals surveyed (Chapter 3). The species differ in their reproductive phenology with *S. pulchra* and *S. richardsonii* producing catkins before their leaves and seeding in July, and *S. glauca* and *S. niphoclada* producing catkins later in the growing season and seeding in late August or September (Argus et al. 1999, Fig. 1-6). Willows are dioecious, having both male and female plants. These species also have a uniformly female biased sex ratio of approximately 2:1 in the Kluane Region (Myers-Smith and Hik, unpublished data). The differing reproductive phenologies, uniform female-biased sex ratio and observed poor reproductive output at high elevations (Myers-Smith, Saunders and Hik, unpublished data) are factors that are likely to interact to determine new recruitment and expansion upslope of these species.

Table 1-1. Distribution, phenology, chromosome, ploidy and evidence of hybridization (from Argus et al. 1999) for the six most common species sampled in this study and the sample size for each of the different species at sites for which sex could be determined for greater than 50% of individuals.

| Canopy-forming Willows | Timing of Pollination | Chromosome Number | Ploidy lLvels Rcorded | Documented Hybridization | Geographic Range |
|---|---|---|---|---|---|
| *Salix alaxensis* (Andersson) *Cov. var. alaxensis* | before leaves | 2*n* = 38 | 2x | none | Canada (Alta., B.C., Man., Que., Yukon, N.W.T., Nunavut), United States (Alaska), Eurasia (northern and eastern Siberia). |
| *Salix barrattiana* Hook. | before leaves | unknown | unknown | yes | Canada (B.C., Yukon, N.W.T., Nunavut), United States (Alaska, Montana, Colorado), Eurasia (northern and eastern Siberia). |
| *Salix glauca L. var. acutifolia* (Hook.) C. Schneider | with leaves | 2*n* = 76, 95, and 114 | 4, 5, and 6x | yes | Canada (B.C., Yukon, N.W.T., Nunavut), United States (Alaska), Eurasia (eastern Russia). |
| *Salix niphoclada* Rydb. | with leaves | 2*n* = 38 | 2x | yes | Canada (B.C., Yukon, N.W.T., Nunavut), United States (Alaska), Eurasia (Siberia). |
| *Salix pulchra* Cham. | before leaves | 2*n* = 76 | 4x | none | Canada (B.C., N.W.T.), United States (Alaska), Eurasia (Russia). |
| *Salix richardsonii* Hook. | before leaves | 2*n* = 38 | 2x | yes | Canada (B.C., Man., Yukon, N.W.T., Nunavut), United States (Alaska), Eurasia (Russia). |

*Salix alaxensis* *Salix glauca* *Salix pulchra*

*Salix barratiana* *Salix niphoclada* *Salix richardsonii*

Figure 1-4. Panel of the six most common canopy-forming willow species growing above 1600 m in the Kluane Region.

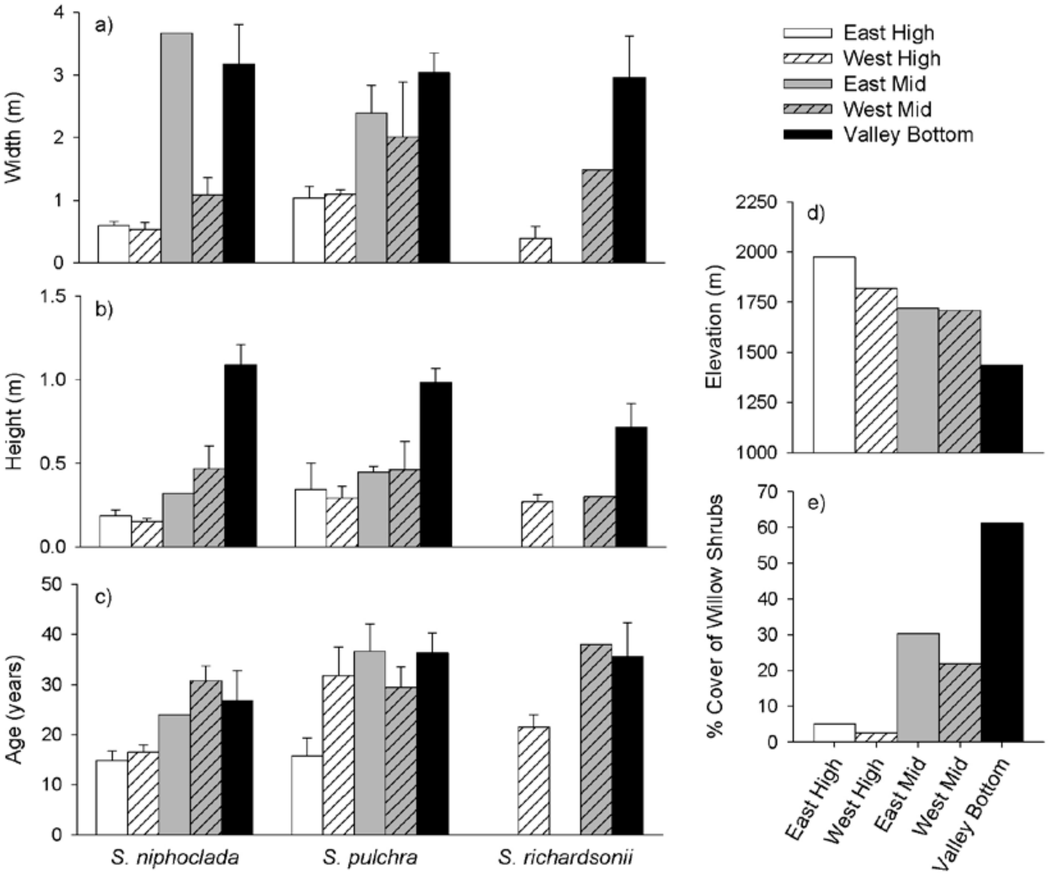

Figure 1-5. Mean ± SE for a) patch width, b) patch height, and c) largest stem age of individuals of the three most common willow species growing in Pika Valley in the Kluane Region: *S. niphoclada,* S. *pulchra,* and *S. richardsonii* (Chapter 3, Myers-Smith, Saunders and Hik, unpublished data). The d) elevation and e) % cover are presented for all canopy-forming willows growing at each of the sample transects in the valley. White bars indicate the high site on the east (solid) and west (hatched) slopes, the grey bars indicate the site located on the mid slope of the east (solid) and west (hatched) slopes, and the black bars indicate the site at the valley bottom.

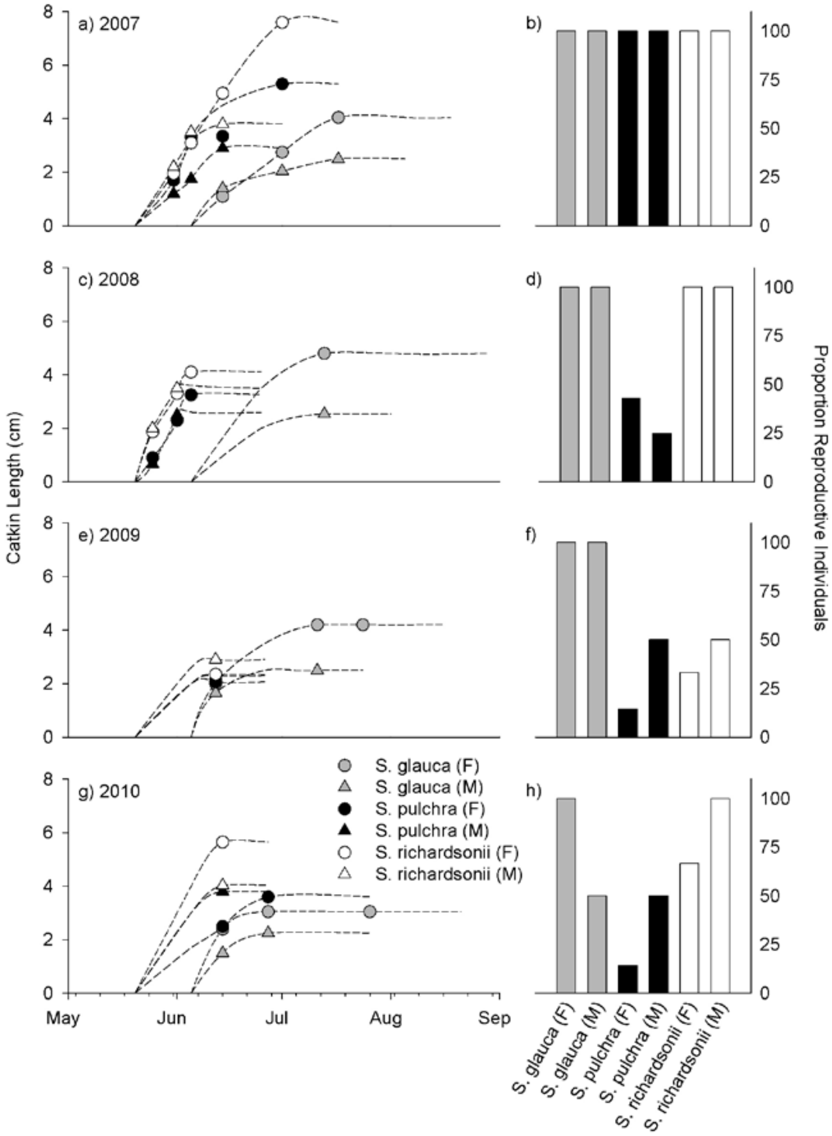

Figure 1-6. Variation in catkin phenology between years for 2007 to 2010 in Pika Valley in the Kluane Region (Myers-Smith, Saunders and Hik, unpublished data). Plots a, c, e, and g indicate the change in catkin length (cm) over each growing season. Plots b, d, f and h indicate the proportion of reproductive individuals out of the 20 monitored across the growing season (*S. glauca*: 2 female, 2 male; *S. pulchra*: 7 female, 4 male; *S. richardsonii*: 3 female, 2 male). Grey symbols and bars indicate *S. glauca*, black symbols and bars indicate *S. pulchra*, and white symbols and bars indicate *S. richardsonii*. Circles indicate female individuals and triangles indicate males.

## Part 4. Study objectives and methodology

Increased shrubiness is a major structural change in arctic systems with implications for altering microclimates, biogeochemical cycles and ecological habitats (Chapin et al. 2005, Post et al. 2009). By combining historical ecological data, annual growth ring analysis, and an experimental canopy manipulation, I have tested the following hypotheses:

$H_1$: Canopy-forming willows are increasing in cover and elevational range extent in arctic and alpine tundra of the Yukon Territory.

$H_2$: Growth of willow species is temperature sensitive, with greater growth of willows occurring in summers with warm early growing seasons.

$H_3$: Canopies will alter ecosystem function in tundra ecosystems to promote continued shrub expansion.

In my thesis dissertation, I address the subject of the encroachment of canopy-forming willows in tundra ecosystems by investigating the following topics at sites across the Yukon Territory (Fig. 1-7):

*Chapter 2: Historical changes in the cover of canopy –forming willows*

To investigate historic changes in cover of canopy-forming willows on Herschel Island off the arctic coast of the Yukon Territory, I utilized repeat photography, long-term monitoring data from the International Tundra Experiment, and annual growth ring analysis.

*Chapter 3: Advance of shrubline in the Kluane Region*

To examine changes in the shrubline and growth of willows over the past half century, I surveyed 379 willows from 10 species growing in 12 alpine valleys at the elevation range limit of canopy-forming willows of the Kluane Region.

*Chapter 4: Temperature sensitivity of willow growth*

To test the temperature sensitivity of growth, I compared annual growth ring data of the same willow species surveyed in the Kluane Region to those growing in the Northern Yukon along the Dempster Highway and on Herschel Island off the Yukon arctic Coast.

*Chapter 5: Influence of willow canopies on tundra soil temperatures*

I established an experimental manipulation to examine the influence of willow canopies on tundra soil temperatures. By comparing adjacent natural tundra and shrub patches, canopy removals and artificial canopies over tundra without canopy-forming shrubs, I was able to isolate the influence of a canopy structure from the biotic components of willow shrubs.

*Chapter 6: Influence of willow canopies on tundra nutrient cycling*

I used the same canopy experiment presented in Chapter 5 to investigate the influence of willow canopies on tundra nutrient cycling. I analyzed carbon dioxide, ammonia and nitrate fluxes, and litter decomposition.

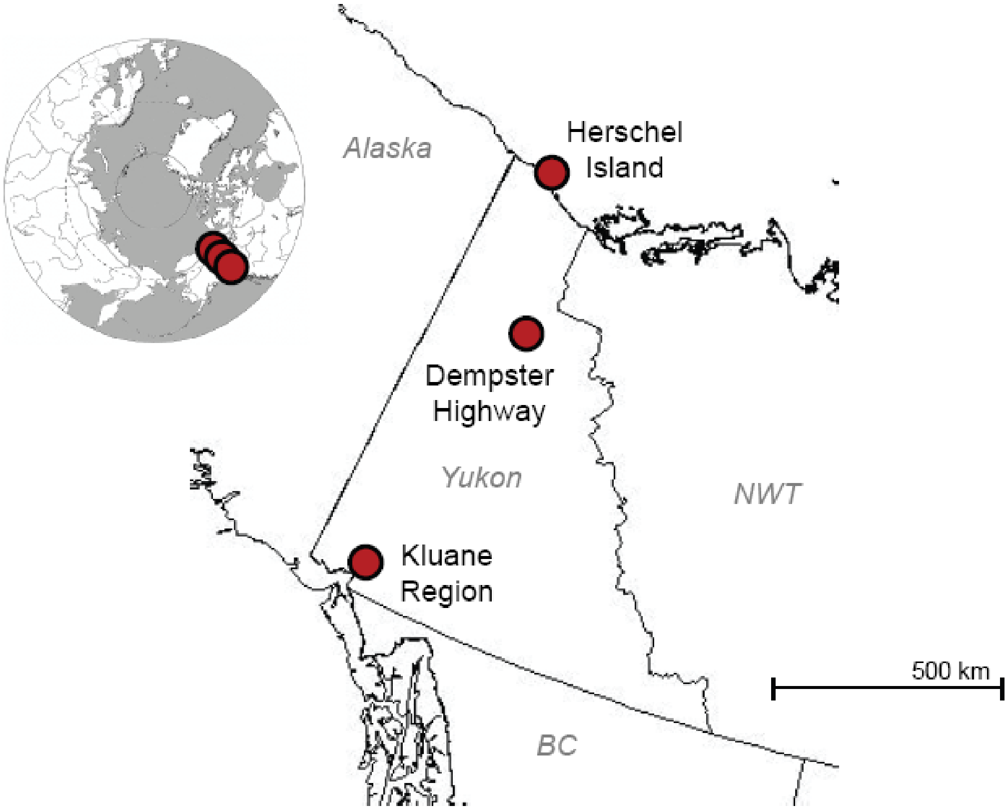

Figure 1-7. Dissertation field sites located across the Yukon Territory: Herschel Island on off the arctic coast of the Yukon, the Dempster Highway in the Northern Yukon and the Kluane Region of the Southwest Yukon.

These different chapter subjects all fit within the primary research areas under investigation by those working on shrub encroachment in tundra ecosystems (Fig. 1-8). My study is unique in that it combines studies of the patterns of shrub increase with investigations of the ecosystem-level impacts of a change in canopy cover in tundra ecosystems. This is the first time that elevational shrubline advance has been investigated in willow species on such a large geographic scale, and the first time that a fully factorial canopy manipulation experiment with artificial canopies has been conducted in a tundra ecosystem.

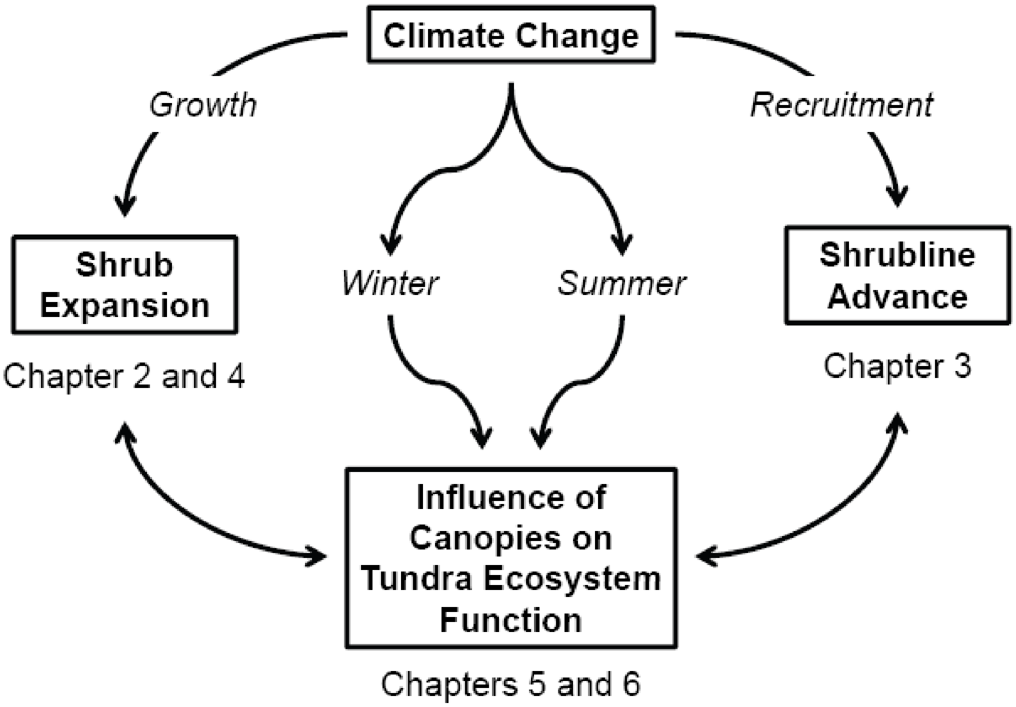

Figure 1-8. The connections between climate change shrub expansion, shrubline advance and the impacts of increasing canopy cover on tundra ecosystem function. The diagram outlines the links between the different chapters of this dissertation.

The results present in this dissertation will contribute to our understanding of vegetation changes in northern alpine ecosystems. I describe both the elevational advance of canopy-forming willow species in mountainous valleys of the southwest Yukon, and changes in canopy height and patch cover near the latitudinal range limit of canopy-forming willows species on Herschel Island off the Yukon arctic coast (Fig. 1-7). This dissertation presents data that will contribute to a synthetic examination of shrub expansion at sites around the circumpolar Arctic and provide better estimates of the strength of climate forcing mechanisms and feedbacks to future shrub encroachment.

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# Chapter 2. Expansion of canopy-forming willows over the 20th century on Herschel Island, Yukon Territory*

*****A version of this chapter has been published. Myers-Smith, Myers-Smith, I. H., D. S. Hik, C. Kennedy, D. Cooley, J. F. Johnstone, A. J. Kenney, and C. J. Krebs. 2011. Expansion of canopy-forming willows over the twentieth century on Herschel Island, Yukon Territory, Canada. Ambio 40:610-623.

## Introduction

Recent evidence indicates an expansion of canopy-forming shrubs in tundra ecosystems including on the North Slope of Alaska (Sturm et al. 2001, Tape et al. 2006), on the coast of the Northwest Territories (Lantz et al. 2009), in Northern Quebec (*pers. comm.* B. Tremblay, E. Lévesque and S. Boudreau) and in northern Russia (Forbes et al. 2010). In arctic Alaska, canopy cover of alder shrubs has increased by 14 - 20 % on average within the last 40 years, with increases of up to 80% in some areas (Tape et al. 2006). Local indigenous Nenets people in the western Russian Arctic report increasing willow shrubs (Forbes et al. 2009) and similar observations of vegetation change by Inuit have been reported in arctic Canada (Thorpe et al. 2002). Ecological disturbances such as fire and permafrost degradation (Lantz et al. 2009, 2010) or human disturbances (Johnstone and Kokelj 2008, Kemper and Macdonald 2009) are responsible for some observations of increasing shrub species; however, reports also show widespread changes in shrub cover in the absence of localized disturbances (Sturm et al. 2001, Tape et al. 2006).

In addition to observations of changing shrub cover, modeling and experimental studies forecast future increases in shrub species in arctic tundra. Ecological models project increases in shrub functional groups (Euskirchen et al. 2009), and experiments have shown that deciduous shrub species respond positively to warming and fertilization treatments (Chapin et al. 1995, Dormann and Woodin 2002, van Wijk et al. 2004, Hollister et al. 2005, Wahren et al. 2005, Walker et al.

2006). However, to extend our understanding of future shrub change we need to look back as well as forward, and make use of historic data sets, photographs and local knowledge of tundra ecosystems. Unconventional sources of ecological data could fill in gaps in our understanding of how tundra ecosystems have responded to previous changes in climate.

In this study, I applied repeat photography, vegetation surveys, and annual growth ring analysis to quantify changes in canopy-forming shrub species on Herschel Island in the western Canadian Arctic. We tested the hypothesis that willow cover and canopy height have increased on Herschel Island. This site has a long human history, from Inuvialuit inhabitants, to a whaling settlement established in 1890, a mission established in 1897, police detachment in 1903, and the foundation of a Yukon Territorial Park in 1987 (Yukon Territorial Government, Heritage Branch 2001). The historic record over the past 100 years provides a unique source of data on vegetation changes on the island. The western arctic coastlands were amongst the first parts of the Canadian Arctic to be documented by photographs, and these historic photographs can be used to study environmental and ecological change (Mackay and Burn 2011). Previous work at sites along the Yukon Coast has documented an increase of 1% to 5% cover for the graminoid species *Arctagrostis latifolia* on disturbed substrates between 1986 and 1999 (Kennedy et al. 2001). For willows (*Salix* spp.), changes over an even longer period can be examined by using multiple lines of evidence. My study identifies multi-decadal past changes in the structure and function of tundra ecosystems and establishing a baseline from which to assess future change.

## Methods

### *Study site*

Herschel Island (69.57 N 138.91 W) covers approximately 100 km$^2$ and reaches maximum height of 183 m above sea level. The soils are composed of glacial and marine deposits, underlain by ice-rich permafrost (Burn and Zhang 2009). Prominent geomorphic features include numerous retrogressive thaw slumps, most of which were activated by coastal erosion of ice-rich permafrost (Lantuit and Pollard 2008, Burn and Zhang 2009).

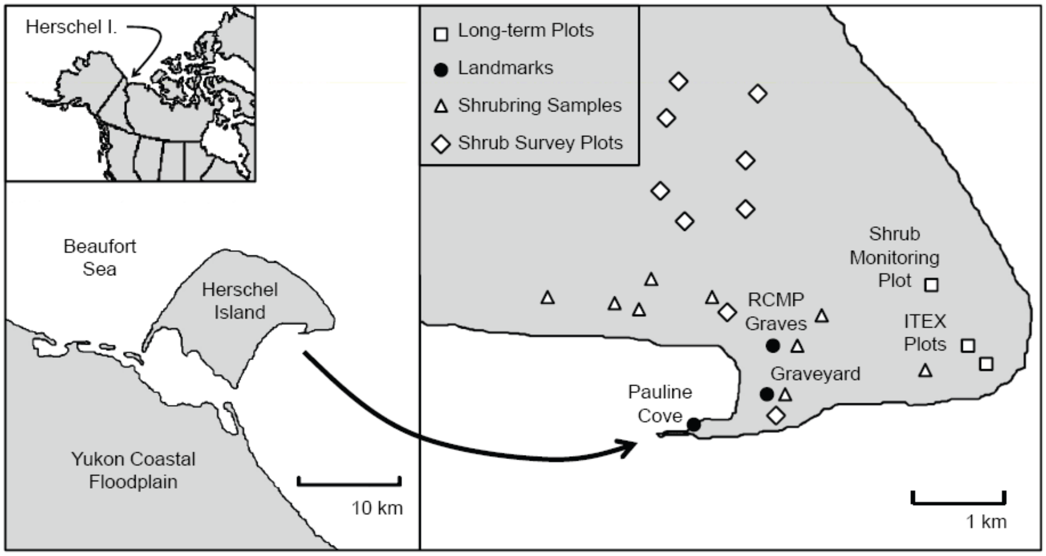

Figure 2-1. The study site, Herschel Island, on the arctic coast of the Yukon Territory

The flora of Herschel Island is lowland tundra composed of various vegetation types which were described in the vegetation survey conducted during the establishment of Qikiqtaruk Territorial Park (Smith et al. 1989). The “Herschel” vegetation type consists primarily of tussocks of *Eriophorum vaginatum* L. with varying cover of the potentially canopy-forming willow species *Salix pulchra* Cham. The “Komakuk” vegetation type is made up of previously disturbed terrain where the ground cover is dominated by *Dryas integrifolia* Vahl., various forb species such as *Lupinus arcticus* S. Wats., *Oxytropis* spp., *Pedicularis* spp., grasses and mosses and the prostrate willow *Salix arctica* Pall. The canopy-forming willow *Salix glauca* L. is found on south-facing ridges. The “Orca” vegetation type is found on the alluvial floodplain near the Pauline Cove settlement (Fig. 2-1) and is dominated by the canopy-forming willow *Salix richardsonii* Hook. and various sedge and moss species. In this study, I visited sites in each of these three vegetation types that were within walking distance of the Pauline Cove.

There are a variety of herbivore species on Herschel Island including musk oxen (*Ovibos moschatus* Zimm.), caribou (*Rangifer tarandus* L.), collared lemmings (*Dicrostonyx groenlandicus* Tr.), brown lemmings (*Lemmus sibiricus* Kerr.), tundra voles (*Microtus oeconomus* Pall.), and rock ptarmigan in winter (*Lagopus muta* Montin). All these species could feed on willows, particularly if their preferred forage species are in low abundance or not available.

### *Repeat photographs*

I used repeat photography to quantify visual changes in canopy cover of shrubs. From the over 100 photographs that I located, 55 of which contained views of the tundra vegetation, I was able to locate and retake five photographs showing change in cover of canopy-forming willow species. The photographs included 11 historic photographs from 1898-1920 taken during the whalers occupation of Herschel Island, 22 from 1953-1956 taken by William McFarland and Jim Hickling when the RCMP were stationed on Herschel Island, and 22 from 1978-1987 taken during vegetation, soils and cultural surveys conducted prior to the establishment of the Territorial Park. I identified the locations of the original photographs and retook the photographs at approximately the same angles using landscape features to compare between images. I visually identified willow patches on the photographs by outlining the canopy-forming willow cover. Exact photo retakes could not be achieved because landmarks had moved over time. Permafrost-underlain soils have slumped, snow melt has eroded the creek banks, or graves have fallen down, been re-erected or rebuilt. An image of the police graves located near Pauline Cove from the 1950s was not retaken because willows were removed in 2009, but a survey of the intact shrub patch was made before shrub removal and stem samples were taken from willows after removal for age analysis (see annual growth ring methods below).

### *Long-term plots*

The International Tundra Experiment (ITEX) is a scientific network of warming experiments focusing on the impact of climate change on plant species composition in tundra vegetation (Walker et al. 2006). To track changes in vegetation composition, long-term monitoring plots were established 10 years ago using the ITEX protocols (Molau and Mølgaard 1996). In 1999, twelve 1-$m^2$ plots were established in two sets of six plots in two areas representing the “Herschel” and “Komakuk” vegetation types near Collison Head, Herschel Island. In 1999, 2004 and 2009, plant cover and height in the plots was surveyed using a grid of 100 point-intercepts within a fixed frame (for detailed methods see Molau and Mølgaard 1996). I used these data to compare changes in canopy height and cover of *S. pulchra*. In 1999 and 2004, height was recorded for only the tallest species growing at each of the 100 points in the sampling grid in each plot. In 2009, I additionally recorded the maximum height for *S. pulchra* when it was growing below the tundra canopy at each point in the sampling grid.

### *Vegetation surveys*

I conducted vegetation surveys to quantify the canopy height of the three dominant canopy-forming willow species. On 20 April 2008, a transect of willow canopy height and snow depth was measured on the “Orca” alluvial fan near Pauline Cove (Fig. 2-1). At 28 locations, located 20 m apart, the canopy height of the *S. richardsonii* shrubs were measured and a visual estimate of the percent cover of willow canopy in circular plots of one and three m radii around each transect point were conducted. On 13-15 August 2009, I conducted surveys of willow canopy height for *S. pulchra* (50 x 50 m plot, sample points every 10 m for a total of 36 points), *S. richardsonii* and *S. glauca* (90 m transects, sample points every 10 m for a total of 10 points, Fig. 2-1). At each of these survey points, I also measured the stem increment length of the current year’s new growth on five arbitrarily chosen branchlets on stems growing within a 1m radius of each sample point.

To compare previously-collected data to the current willow extent on Herschel Island, I repeated vegetation surveys and measured canopy height in areas visited during the establishment of the Territorial Park. In 1985, 125 plots were sampled for vegetation classification across Herschel Island. These plots were circular and approximately 20 m in diameter (Smith et al. 1989). In 2008, I resurveyed the two vegetation classes with canopy-forming willows (the “Herschel” and “Orca” vegetation types) within walking distance of Pauline Cove. I surveyed 11 plots in the same general areas as 13 plots from the 1985 survey (Fig. 2-1). I made a visual estimate of the percent cover of each willow species following the protocol used in 1985 (Smith et al. 1989); however in 2008, I had two observers walk the plot area and make independent estimates to account for potential observer bias.

### *Annual growth rings*

I conducted annual growth ring analysis to age willow stems of each of the dominant canopy-forming willow species. In 2008 and 2009, I sampled the largest stem from six individual shrubs located 10 or more meters apart at each of nine plots (Fig. 2-1). I recorded the species, sex, width, height and diameter of the largest stem for a total of 14 individuals of *S. richardsonii*, 9 individuals of *S. glauca*, and 13 individuals of *S. pulchra* (Table 2-1). To prepare samples for counting rings, I made thin sections of the willow stems, mounted the sections on glass slides, and took digital images. I counted and measured annual growth rings along four radii at 0°, 90°, 180°, 270°, unless the placement of radii had to be moved or omitted due to growth deformities or rotten wood. Rings were counted and measured at a resolution of 0.0001 mm using digital treering analysis software (WinDendro, Québec, Canada). Stems and radii were visually cross dated to determine final stem age estimates. Partial rings were observed in ~60% of willows samples when cross dating the four measured radii. Missing rings were identified in five out of the 14 *S. richardsonii* and one of the 13 *S. pulchra* individuals sampled. The partial and missing rings were accounted for in the visual cross-dating of the ring counts.

*Willow patch establishment*

Canopy-forming willows form discrete patches in most of the habitats on Herschel Island. I was able to follow shallow root systems between stems, and therefore assume that each of the patches surveyed represented one establishment event. I measured the width and height of each of the individual patches surveyed, and was able to estimate the annual stem growth increment for each individual (see above). I calculated the maximum patch radius ($R_{max}$) by dividing the maximum patch width by two. I also sampled the largest stem of each of these individuals for annual growth ring analysis, and was able to estimate the patch age (see above). Using these data (Table 2-1), I created two simple models to estimate establishment dates for the willow patches surveyed in this study (Eq. 1 and 2). The models assume that growth is radial and constant over the life of the individual, although is a simplification of the growth of these species, I do not have data to parameterize a more complex growth model with multiple age classes or variable growth.

$PA_{mean}$ = Patch age estimate based on the mean measured annual stem elongation (years before 2008)

$$PA_{mean} = \frac{R_{max}}{\sqrt{\left(\frac{H_{max}}{S_{age}}\right)^2 + {G_{mean}}^2}} \qquad \text{(Equation 1)}$$

$PA_{min}$ = Patch age estimate based on the maximum measured annual stem elongation (years before 2008)

$$PA_{min} = \frac{R_{max}}{\sqrt{\left(\frac{H_{max}}{S_{age}}\right)^2 + {G_{max}}^2}} \qquad \text{(Equation 2)}$$

$G_{mean}$ = mean measured annual growth (cm/year)

$G_{max}$ = maximum measured annual growth (cm/year)

$R_{max}$ = maximum patch radius (cm)

$S_{age}$ = age of the largest stem (years)
$H_{max}$ = maximum patch height (cm)

The models make two different estimates: an older patch age estimate ($PA_{mean}$, Eq. 1) using the mean measured annual growth ($G_{mean}$), and the minimum patch age ($PA_{min}$, Eq. 2) using the maximum measured annual growth ($G_{max}$). The models estimate the patch age by dividing the maximum patch radius ($R_{max}$) by the estimated annual lateral growth. I used the Pythagorean Theorem to estimate annual lateral growth from an estimate of the vertical annual growth based on the age of the largest stem in the patch ($S_{age}$) and the measured maximum patch height ($H_{max}$) and the measured stem elongation ($G_{mean}$ or $G_{max)}$. Since I collected measurements of the maximum patch diameter only, I feel that using the measured minimum annual growth rate, I would overestimate the patch age, so I have not included this permutation of the model.

### *Statistical analysis*

Statistical analyses were conducted with the software R (version 2.10.1, R Development Core Team, Vienna). I used analysis of variance (ANOVA) and Tukey’s tests to assess whether cover (point-frame hits) and height of *S. pulchra* had increased over time. I compared the variables patch width, canopy height, mean annual growth ring width, and stem age between species using multivariate analysis of variance (MANOVA) and Pillai’s trace statistic to determine significance of the MANOVA as each of these variables were collected from the same individuals. I then used ANOVA on each of the significant variables and Tukey’s tests to make pairwise comparisons to test for differences between species. To compare annual stem elongation between species, I used analysis of variance (ANOVA) and Tukey’s tests as these data were collected from different individuals than in the previous comparison. The variables shrub width, canopy height and patch size were log transformed to meet the assumptions of normality and homoscedasticity.

## Results

### *Repeat photographs*

Repeat photographs showed expansion of individual willow patches in the shrubby habitats dominated by the species *S. richardsonii* at sites on the alluvial peninsula at Pauline Cove (Fig. 2-2). Patches have increased in size and height (Fig. 2-2a, b, c, d) and cover has transitioned from discrete patches to nearly continuous cover (Fig. 2-3). Establishment of new patches is also suggested in some of these photograph comparisons (Fig. 2-2d).

### *Repeat vegetation surveys*

Point-intercept sampling indicated increases in canopy height for the canopy-forming willow *S. pulchra* in the six long-term plots located in the "Herschel" vegetation type (ANOVA, $F_{2,15} =$ 6.21, $P$ = 0.02, n = 6; Fig. 2-4). Even when using the plot mean height for canopy and below canopy measurements of *S. pulchra* in 2009, I found that this species was significantly taller than the canopy-only height measurements taken in 1999 (ANOVA, $F_{2,12}$ = 4.44, $P$ = 0.03, n = 6; Fig. 2-4).

I found no significant difference in abundance of *S. pulchra* over the 10 years of monitoring of the six ITEX plots located in the "Herschel" vegetation type (ANOVA, $F_{2,15}$ = 1.43, $P$ = 0.27, n = 6; Fig. 2-4); however, abundance data were variable. Higher abundance of *S. pulchra* was recorded in four of the six plots in 2009, when compared with the first two sampling years (Fig. 2-4). In contrast to the directional change in *S. pulchra*, I observed no significant change in abundance or height for the prostrate willow species present in the long-term monitoring plots (*S. arctica*, *S. reticulata*, and *S. phlebophylla*, n = 6).

*S. pulchra* plants were often shorter in stature than the other willow species, with a mean canopy height of 13.3 ± 0.7 cm measured in the vegetation survey (n = 36) and 7.3 ± 0.9 cm in the 2009 monitoring of the ITEX plots (n = 6, Fig. 2-4). Canopy cover and height of current patches of *S. richardsonii* were larger than *S. pulchra* patches in the individuals sampled for growth ring analysis (ANOVA,

$F_{2,33} = 4.95$, $P = 0.01$, $n_{richardsonii} = 14$, $n_{pulchra} = 13$; Fig. 2-5a and b). During this sampling, I encountered some taller-statured *S. pulchra* individuals including one individual growing 76 cm tall, and as a result there was no significant difference in canopy height in the comparison of these data (Fig. 2-5a).

Repeat vegetation surveys indicated an increase in the cover of *S. pulchra* between the mid 1980s and 2008 (ANOVA, $F_{1,15} = 12.17$, $P < 0.01$; Fig. 2-6e); however, the difference in cover between sample years was not significant for *S. richardsonii* (ANOVA, $F_{1,4} =$ 0. 04, $P = 0.84$; Fig. 2-6a).

### *Willow species growth characteristics*

Canopy cover and height of current patches of *S. richardsonii* were larger than *S. pulchra* patches in the individuals sampled for growth ring analysis (ANOVA, $F_{2,33} = 4.95$, $P = 0.01$, $n_{richardsonii} = 14$, $n_{pulchra} = 13$; Fig. 2-5a and b). During this sampling, I encountered some taller-statured *S. pulchra* individuals including one individual growing 76 cm tall, and as a result there was no significant difference in canopy height in the comparison of that data (Fig. 2-5a). However, in general *S. pulchra* plants were shorter in stature than the other willow species, with a mean canopy height of $13.3 \pm 0.7$ cm measured in the vegetation survey (n = 36) and $7.3 \pm 0.9$ cm in the 2009 monitoring of the ITEX plots (n = 6, Fig. 2-4). *S. pulchra* had shorter annual stem elongation than the other two species (ANOVA, $F_{2,53} = 13.3$, $p < 0.01$, $n_{richardsonii} = 10$, $n_{glauca} = 10$, $n_{pulchra} = 36$; Fig. 2-4c). *S. pulchra* ring widths were narrower than either *S. richardsonii* or *S. glauca* annual growth rings (ANOVA, $F_{2,33} = 6.10$, $p < 0.01$, $n_{richardsonii} = 14$, $n_{glauca} = 9$, $n_{pulchra} = 13$; Fig. 2-4d). Mean stem age for the largest stems of willows sampled in the different vegetation zones was 20 to 30 years old ($n_{richardsonii} = 14$, $n_{glauca} = 9$, $n_{pulchra} = 13$; Fig. 2-4e).

### *Willow patch establishment*

Modeled shrub patch expansion, based on measurements of annual stem elongation for each of the dominant canopy-forming willow species (Table 2-1), indicated that shrub patches were initiated between 1910 and 1960, and that current large diameter stems began growing in the late 1970s and early 1980s (Fig. 2-6). If maximum growth rates are used in the model, shrub patches are estimated to have been established as late as 1974 – 1981, approximately the same time as the stem establishment dates.

Table 2-1. Parameters for the shrub patch growth model: measured mean growth in 2009 for each species, estimated vertical growth per year and projected lateral growth, and shrub patch growth model projections. Values indicate the mean ± SE for measured values.

| Species | Growth Ring Sample Size | Mean Height (cm) | Mean Age (years) | Mean Growth (mm) | Annual Growth Sample Size | EstimatedVertical Growth (mm) | Estimated Lateral Growth (mm) |
|---|---|---|---|---|---|---|---|
| *S. richardsonii* | 14 | 34 ± 4 | 25 ± 16 | 25 ± 3 | 10 | 14 | 21 |
| *S. glauca* | 9 | 43 ± 3 | 27 ± 12 | 25 ± 5 | 10 | 16 | 18 |
| *S. pulchra* | 13 | 32 ± 7 | 31 ± 9 | 13 ± 1 | 36 | 11 | 7 |

Table 2-2. Model estimates of patch and stem establishment dates. Dates are mean estimates for all patches of each species ± SE.

| Species | Sample Size | Mean Age $PA_{mean}$ Eq. 1 | Minimum Age $PA_{min}$ Eq. 2 | Stem Age $\frac{H_{max}}{S_{age}}$ |
|---|---|---|---|---|
| *S. richardsonii* | 14 | 1951 ± 8 | 1975 ± 5 | 1976 ± 2 |
| *S. glauca* | 9 | 1956 ± 9 | 1981 ± 5 | 1982 ± 5 |
| *S. pulchra* | 13 | 1913 ± 23 | 1974 ± 8 | 1980 ± 3 |

a) Upper Ice Creek

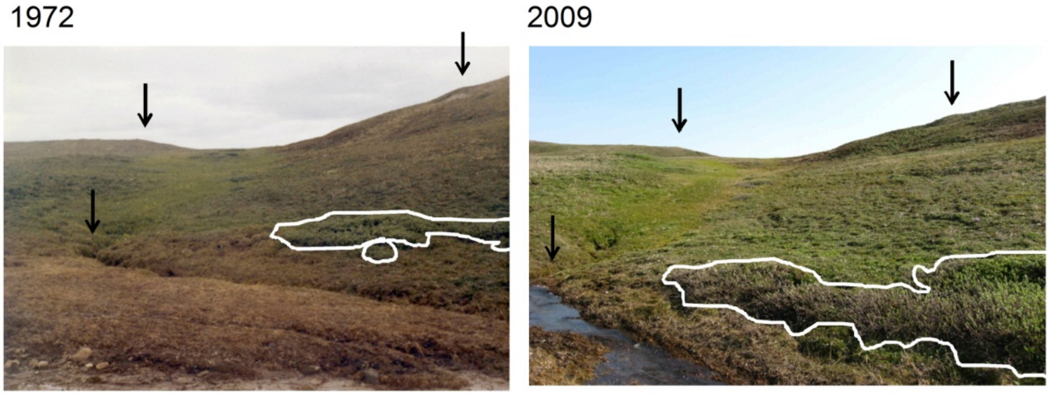

Photo credit: Inter-Disciplinary Systems Ltd.,1972

b) Lower Ice Creek

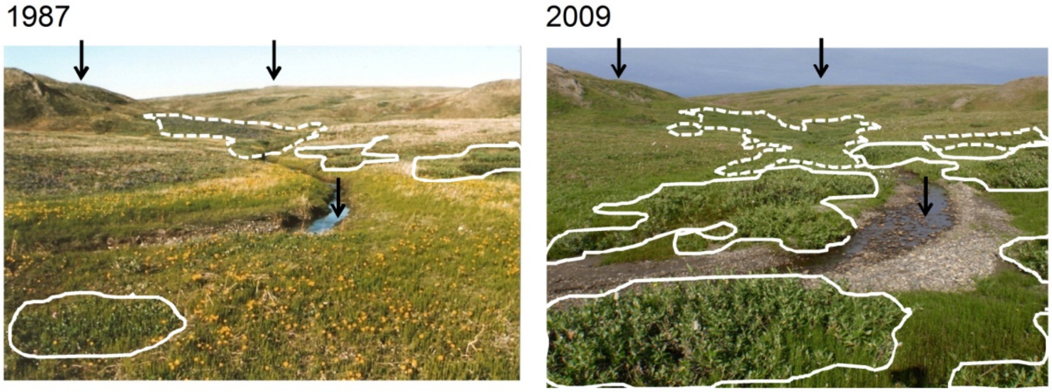

Photo credit: unknown

Figure 2-2. Repeat photographs of *S. richardsonii* patch expansion and new recruitment (photo credit: Inter-Disciplinary Systems Ltd 1972). White lines indicate the boundaries of the patches, dotted white lines indicate areas of variable willow cover where patches cannot be determined from the photographs, and black arrows indicate features present between photographs. Due to the low resolution of the early black and white photographs, I cannot conclusively determine if willow patches are absent.

a) Graveyard

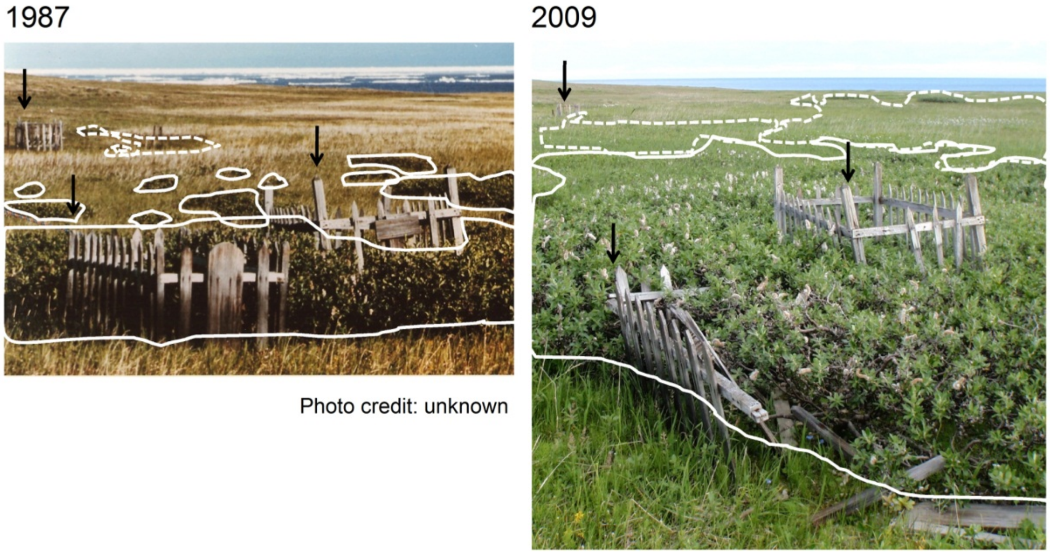

Photo credit: unknown

b) Ice Houses

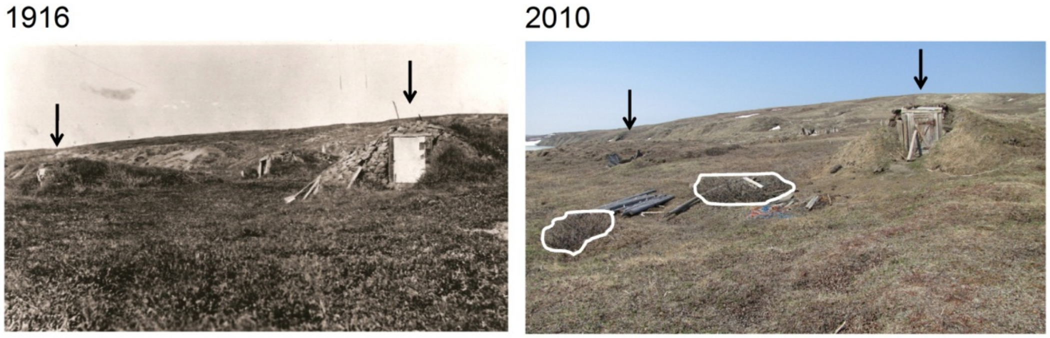

Photo credit: unknown

Figure 2-3 continued. Repeat photographs of *S. richardsonii* patch expansion and new recruitment (photo credit: Inter-Disciplinary Systems Ltd 1972). White lines indicate the boundaries of the patches, dotted white lines indicate areas of variable willow cover where patches cannot be determined from the photographs, and black arrows indicate features present between photographs. Due to the low resolution of the early black and white photographs, I cannot conclusively determine if willow patches are absent.

a) Whalers graves looking eastward

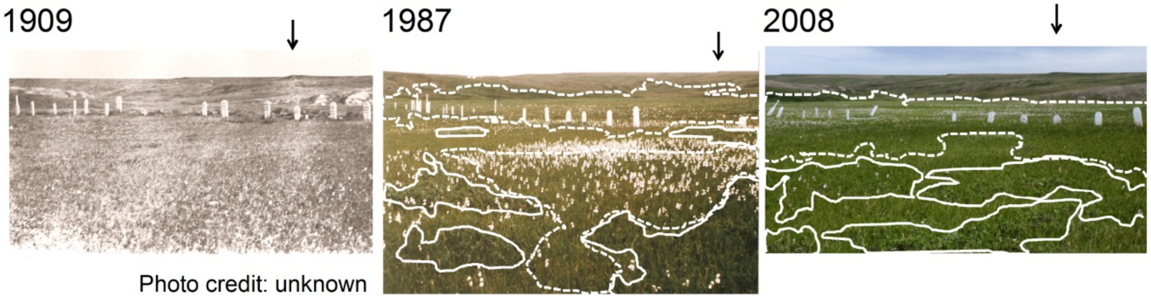

Photo credit: unknown

Photo credit: unknown

b) Whaler's graves looking northward

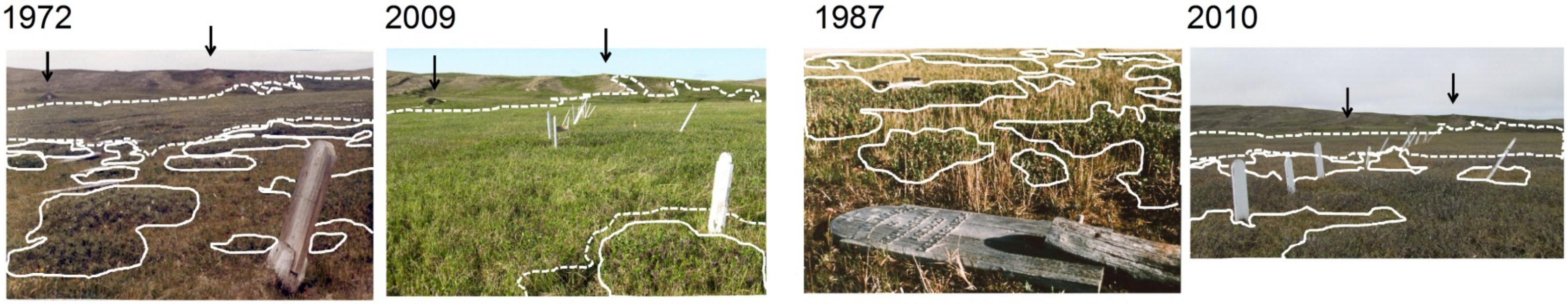

Photo credit: Inter-Disciplinary
Systems Ltd.,1972

Photo credit: unknown

Figure 2-4. Photographs illustrating filling in of *S. richardsonii* patches in the graveyard area of the alluvial fan near Pauline Cove. White lines indicate the boundaries of the patches, dotted white lines indicate areas of variable willow cover where patches cannot be determined from the photographs, and black arrows indicate features present between photographs. The photographs of the whaler’s graves looking northward (b) show photographs taken close to the locations of the grave markers and show a change from discrete patches to more continuous cover of *S. richardsonii* in this area. Due to the low resolution of the early black and white photographs, I cannot conclusively determine if willow patches are absent.

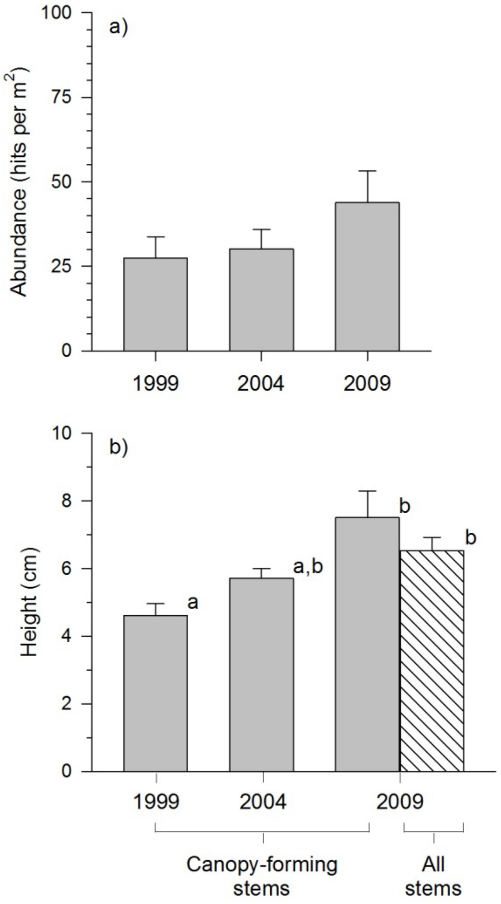

Figure 2-5. Mean abundance (a), and canopy height (b) of the potentially canopy-forming willow species *S. pulchra* recorded in ITEX control plots from 1999 to 2009. Abundance was measured as the sum of all live leaf and stem interceptions recorded across 100 grid points within each of the six 100 cm x 100 cm plots. In panel b, grey bars indicate the mean height of canopy-forming *S. pulchra* individuals at each grid point. The hatched bar is the mean canopy height for all *S. pulchra* stems at each grid point in 2009. Error bars indicate SE and letters indicate significant differences between monitoring years.

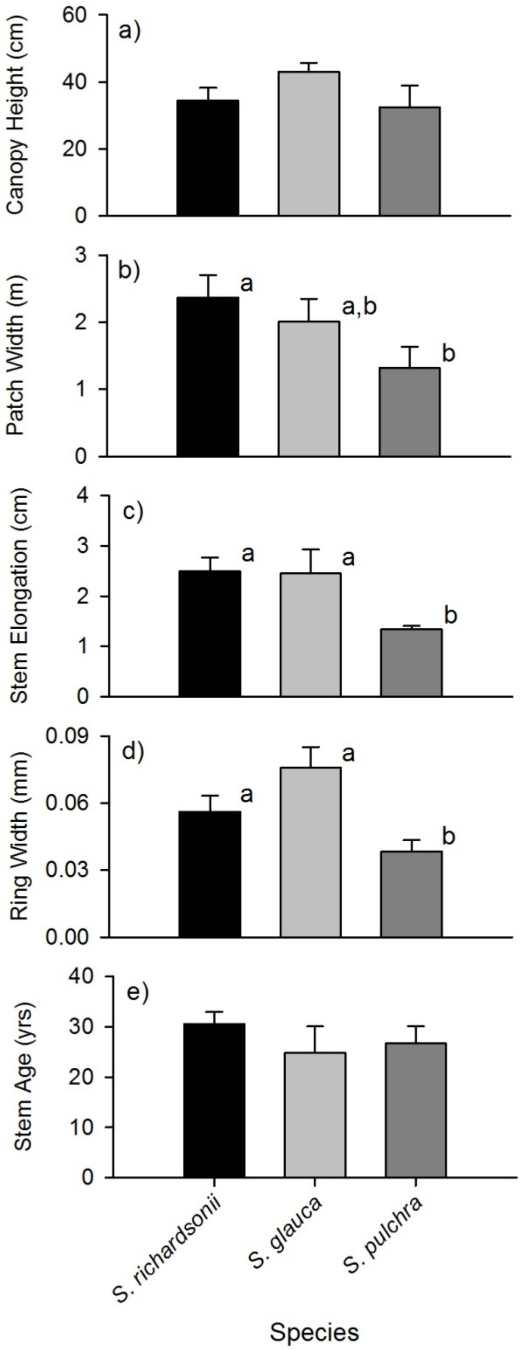

Figure 2-6. Mean a) canopy height, b) patch width, c) annual stem elongation, d) ring width, and e) stem age for the three dominant canopy-forming willow species sampled in 2008. Error bars indicate SE and letters indicate significant differences between species (MANOVA, Pillai's trace = 0.46, $F_{2,33} = 2.31$, $P = 0.03$).

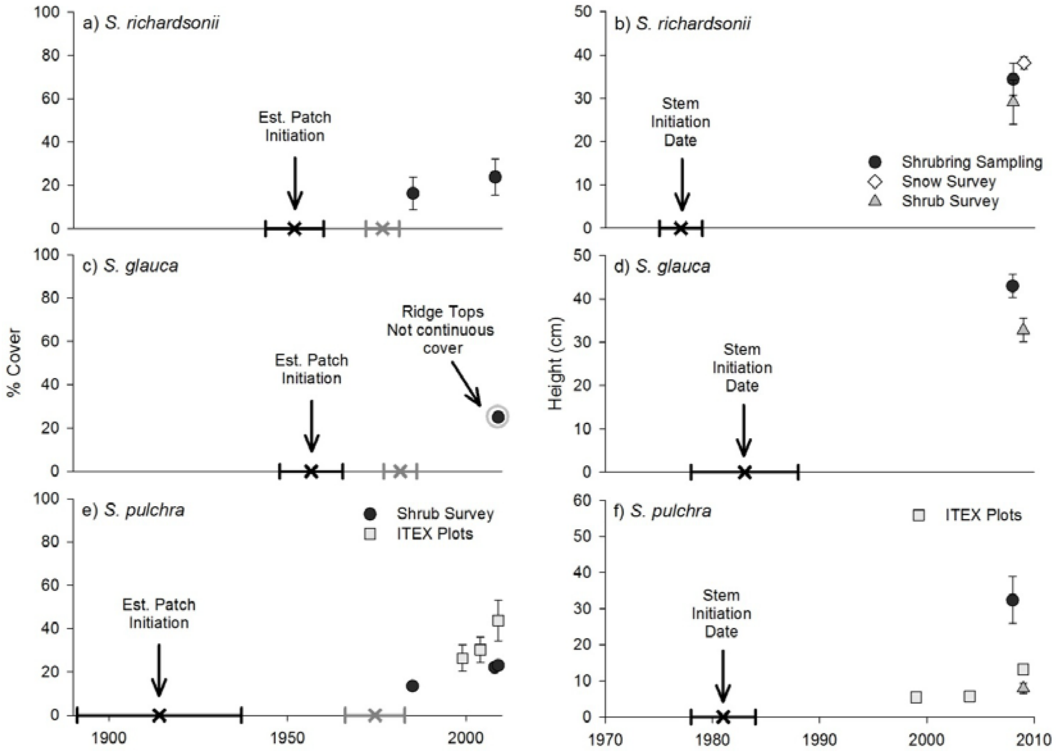

Figure 2-7. Mean canopy cover and projected shrub initiation dates for percent cover of willow patches (a, c and e) and mean canopy height and stem initiation dates (b, d and f) for each of the three dominant canopy-forming willow species. Black crosses indicate the mean patch age estimated using the measured mean annual growth rate ($PA_{mean}$, Eq. 1) and gray crosses indicate the mean patch age estimated using the maximum measured annual growth ($PA_{min}$, Eq. 2). Vertical and horizontal error bars indicate SE.

## Discussion

Multiple lines of evidence indicate increases in canopy cover and height of willows on Herschel Island. Repeat photographs show an increase in the canopy cover of the willow *S. richardsonii*. The repeat vegetation surveys suggest greater cover of both *S. richardsonii* and *S. pulchra*. The long-term vegetation monitoring plots show increases in cover and height of *S. pulchra*. *S. glauca* stems growing near the police grave sites first established in shrub-free tundra in the 1950s. Annual growth ring analysis of these stems show them to be 25 ± 1 years old (mean ± SE), suggesting that these approximately 80 cm-tall willows have grown established and grown to this height over the past three decades. When repeating past vegetation surveys using different observers, there could be significant measurement error; however, the use of multiple lines of evidence including repeat photographs, vegetation surveys and annual growth ring analysis, increases the confidence I have in these findings.

### *Growth of woody shrubs*

Both shrub and graminoid species have been found to increase in cover and height in warming experiments (Chapin et al. 1995, Dormann and Woodin 2002, van Wijk et al. 2004, Hollister et al. 2005, Wahren et al. 2005, Walker et al. 2006). Herbaceous species have been shown to have stronger and more consistent vegetative growth responses than woody species (Arft et al. 1999). However, these two groups should respond in different ways to improved growing conditions. In years with harsher growing conditions, the aboveground biomass of herbaceous species will reach lower canopy heights and cover than in warm years with long growing seasons. Regardless of growing conditions, stems of woody species will elongate incrementally unless reduced by herbivory, disease or dieback from exposure to extreme conditions, though the annual growth increments will be larger in warmer growing seasons.

Recent studies have used annual growth ring analysis of shrub species growing in tundra ecosystems to link increased secondary growth of woody shrub species to growing season temperatures (Forbes et al. 2010, Hallinger et al. 2010, Blok et al. 2011). I found that on Herschel Island, although willow growth is sensitive to temperature change, not all individuals have strong positive responses to warm growing season conditions (Chapter 4). In the absence of significant observed mortality, herbivory or dieback, it is not surprising to observe increases in cover of these species. Recent synthesis of data from the International Tundra Experiment show that changes in cover and height of certain tundra functional groups and species are not correlated with warming growing season temperatures for many arctic sites (*pers. comm.* S. Elmendorf). Therefore, the observed changes in willow species might not relate directly to the observed increases in mean annual temperatures on Herschel Island (Burn and Zhang 2009) or to potentially improved growing season conditions in the western Canadian Arctic.

### *Herbivory and mortality*

Herbivory controls new recruitment of shrub species and could limit or reduce shrub patch expansion on the landscape. Shrub encroachment in tundra ecosystems has been shown to be reduced or inhibited by herbivores in exclosure experiments (Post and Pedersen 2008, Olofsson et al. 2009). And herbivory by sheep and reindeer is thought to be the primary factor determining the height of the shrubby treeline ecotone at sites in northern Scandinavia (Hofgaard et al. 2010, Speed et al. 2010, 2011).

I observed little die back, mortality or herbivory in the 2008 and 2009 willow surveys and sampling. In three of the 46 willow individuals sampled for ageing (two *S. richardsonii* and one *S. glauca*), I observed some evidence of scarring in the stem cross sections initiated between 1999 and 2003. Scarring could indicate past herbivory, as was observed in sections of willows from a site experiencing periodic lemming herbivory on the Kent Peninsula, Northwest Territories, Canada (Predavec and Danell 2001). The low occurrence of scarring does not indicate high levels of stem herbivory in recent decades on Herschel Island. I observed caribou and muskox feces and shed qiviuq (muskox wool) in and around the

ITEX long-term monitoring plots; however, I did not observe any evidence of willow herbivory while surveying the plots in 2009.

There is no evidence of recent declines in herbivore populations on Herschel Island; instead, large herbivore presence has increased in the past 50 years (*pers. comm.* D. Reid). Caribou populations were likely decimated by the whalers at the turn of the 20th century, and their activity on Herschel has increased since the 1970s. Musk oxen were reintroduced to the Arctic National Wildlife Refuge in 1969-70 and spread to Herschel Island during the following decades. Taken together, these data suggest that willow herbivory has historically been low on Herschel Island and might not be a significant factor determining rates of expansion of willow patches over the past century.

### *The role of disturbance*

Disturbance has been identified as a key factor determining recruitment of woody species in tundra systems (Munier et al. 2010, Lantz et al. 2010), and both fire (Lantz et al. 2010) and permafrost degradation (Lantz et al. 2009) have been positively associated with recruitment and growth in alder (*Alnus viridis* subsp. *fruticosa*). When examining changes in shrub abundance in tundra ecosystems, disturbances rather than climate warming might be the most important factor determining recruitment of new individuals. And interactions among the disturbance regime, nutrient availability, herbivory, disease and weather conditions could all influence the establishment and growth of woody tundra species.

A deeper active layer and more active permafrost degradation have been observed on Herschel Island over the last century (Lantuit and Pollard 2008, Burn and Zhang 2009). Greater disturbance of the surface terrain could provide microsites appropriate for establishment of new willow patches. Alder (*Alnus viridis* subsp. *fruticosa*) shrub encroachment has been previously observed in retrogressive thaw slumps in the Mackenzie Delta region of the Northwest Territories (Lantz et al.

2009). The previously observed increase in the graminoid species, *Arctagrostis latifolia* (R.Br.) Griseb, on disturbed terrain on Herschel Island was likely a result of vegetation succession (Kennedy et al. 2001). It could be that changes in the disturbance regime rather that growing season conditions are primarily responsible for the observed willow change on Herschel Island. The alluvial floodplain habitat, where *S. richardsonii* is dominant, experiences annual flooding during thaw, and the ridges where *S. glauca* is found show evidence of erosion. However, the "Herschel" vegetation type, the *Eriophorum* sedge tussock habitat where *S. pulchra* is found, is less disturbed. If *S. pulchra* is increasing in height and cover in this habitat, this change is unlikely to have been induced by large-scale disturbance as is possible in the other habitats.

### *Recruitment of willows*

Clonal species can have extremely long lifespans and do not necessarily experience senescence over time (de Witte and Stöcklin 2010); therefore, willow patches, once established could continue to increase in size into the future for an undetermined length of time. I assume that willow patches on Herschel Island have established from seed. I observed few dead stems, and little dieback or dead portions of willow patches indicating mature willow stands, as is common at sites farther south in the Yukon Territory. Adjacent to the coastline, dead *S. richardsonii* patches did occur, likely due to salt water inundation. In some higher elevation habitats, I observed dead tips of stems, potentially indicating winter dieback and exposure to cold temperatures and wind abrasion above the snowpack. However, the majority of canopy-forming willows growing on Herschel Island appear to be healthy and in good condition.

My results suggest that the majority of the current patches of canopy-forming willow species found on Herschel Island today established between the 1920s and 1980s, and that these willow individuals have expanded incrementally over time. Because annual incremental growth of branches and stems were smaller for the species *S. pulchra*, this species is projected to have initiated earlier than the faster growing *S. richardsonii* and *S. glauca*. My models do not take into account changes in growing conditions over time. If growing conditions have been more favorable in recent years, I could be overestimating mean annual stem elongation in our model.

My data do not definitively indicate when initial recruitment of these willow species occurred on Herschel Island. Reports of canopy-forming willows (likely *S. richardsonii*) on the alluvial floodplain adjacent to Pauline Cove exist from the 1970s (Hardy Associates Ltd. 1979), and photographs taken by Jim Hickling of the Royal Canadian Mounted Police show evidence of *S. pulchra* and *S. richardsonii* from two unknown locations on Herschel Island in the 1950s. This evidence of willow cover from over 30 years ago, suggests these canopy-forming shrubs species were prevalent before the middle of the 20th century. However, the repeat photography and survey data that I present here indicate substantial increases in cover of all three species. In particular, *S. richardsonii* growing on the alluvial flood plain and *S. glauca* growing on the south-facing ridges around Pauline Cove appear to have increased in cover and stature in the last half century.

On the North Slope of Alaska, Tape et al. (2006) suggested that the initial recruitment resulting in the observed expansion of alder patches could have occurred coincident with the end of the Little Ice Age cool period in approximately 1850. This historic shift in climate could also be responsible for an expansion of willow cover on Herschel Island and the adjacent arctic coast of the Yukon. In addition to climate-driven shrub recruitment, disturbance can facilitate the establishment of new individuals. In the Northwest Territories fire (Lantz et al. 2010) and permafrost thaw (Lantz et al. 2009) have been associated with recruitment and expansion of alder shrubs. On Herschel Island, disturbance regime could interact with climate to create recruitment pulses, and patch expansion and increases in canopy height can proceed in the intervening years between these pulses.

Herschel Island is located near the northern extent of canopy-forming willow species (Argus et al. 1999). As individuals from the canopy-forming species *S. richardsonii*, *S. glauca* and *S. pulchra* increase in size, they will likely increase in reproductive output. Increases in the production of viable seed could have implications for future recruitment at this site and the advance northwards of these species.

## Conclusion

In this study, I report evidence of increases in canopy cover and height of canopy-forming willows on Herschel Island in the western Canadian Arctic. The long-term photographic, plot-based and growth ring data reported in this study, provide multiple lines of evidence of shrub increase at this site. Continued monitoring of long-term vegetation plots, will improve our estimates of shrub change and rates of patch expansion. However, to better understand this changing tundra ecotone, the focus of future research should move beyond whether canopy-forming shrub patches are expanding clonally, to the identification of factors that are responsible for the recruitment of new individuals and the quantification of the impact of this canopy-cover change to the functioning of tundra ecosystems.

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# Chapter 3. Shrubline advance in alpine tundra of the Kluane Region, southwest Yukon

## Introduction

Temperature has been suggested to be the primary factor determining species range limits in northern ecosystems (Doak and Morris 2010). Experimental studies indicate that warming will increase the dominance of woody species (Arft et al. 1999, Walker et al. 2006), and the link between warming and increasing shrub species in tundra ecosystems has been made in a variety of studies (Sturm et al. 2001, Post et al. 2009). Annual growth ring-climate relationships have been used to illustrate climate limitation (Forbes et al. 2010, Hallinger et al. 2010, Blok et al. 2011); however, recruitment, in addition to growth, has the potential to determine the advance of woody shrub species beyond current range limits. Patterns of population age structure along elevational gradients can be examined to begin to address whether shrub species are currently advancing in tundra ecosystems.

Paleoecological records indicate that shrub species were much more abundant during past warm periods (Higuera et al. 2008). It is thought that future climate warming in tundra ecosystems could lead to the development of a largely deciduous tree or shrub dominated tundra ecosystem (Swann et al. 2010). Growing evidence from a variety of studies confirms an increase in the cover of shrub species at sites around the Arctic (Sturm et al. 2001, Tape et al. 2006, Lantz et al. 2009, Forbes et al. 2010, Mackay and Burn 2011, *pers. comm.* B. Tremblay, E. Lévesque and S. Boudreau, Chapter 2). But, whether these tundra ecosystems are currently in transition towards a dense shrubland remains to be determined.

Shrub expansion in the Arctic has been documented using repeat aerial photography (Sturm et al. 2001, Tape et al. 2006), satellite imagery (Forbes et al. 2010) and ground observations (Lantz et al. 2009, Forbes et al. 2010, Lantz et al. 2010b, Mackay and Burn 2011, Chapter 2). In addition, the increase in cover of woody shrub species has been linked to the remotely sensed greening of tundra ecosystems (Sturm et al. 2001, Jia et al. 2003, Stow 2004, Tape et al. 2006, Jia et al. 2009, Forbes et al. 2010). However, caution has been recommended when attributing a greening NDVI signal to increases in shrub species alone since increases in soil moisture can also have an influence on these signals (Huemmrich et al. 2010). Repeat image analysis can identify changes in vegetation cover; however, ground-based surveys are necessary for investigations of expansion of shrub species upslope or north of current range limits in arctic or alpine tundra.

Treeline advance has been studied in more detail than changes in the elevational limit of canopy-forming woody shrub species, referred to here as shrubline. A global meta-analysis of 166 treelines found that over half had advanced in elevation since 1900, while just under half remained unchanged over the same period (Harsch et al. 2009). Shrubline advancement in northern alpine tundra has been reported in only a few studies of prostrate junipers (*Juniperus nana*) in subarctic Sweden (Hallinger et al. 2010), and mountain birch (*Betula pubescens* ssp. *tortuosa*) in alpine ecosystems in Norway (Tømmervik et al. 2009, Speed et al. 2010, 2011) and Sweden (Kullman 2002, Sundqvist et al. 2008). Climate is often invoked as the cause of tree or shrubline advance (Truong et al. 2007, Harsch et al. 2009, Hallinger et al. 2010). However, confirming the relationship between new recruitment and warmer temperatures is a greater challenge than demonstrating that shrub growth is sensitive to warming climates.

Factors other than temperature, such as precipitation, cold-induced photoinhibition, disturbance or plant–plant interactions, could also influence elevational treeline advance (Harsch et al. 2009) and shrubline expansion. In addition, herbivory can play an important role in structuring shrubline ecotones. Shrub encroachment in tundra ecosystems has been shown to be reduced or inhibited by herbivores in exclosure experiments (Post and Pedersen 2008, Olofsson et al. 2009). In mountain birch, herbivory negatively influenced growth of established individuals (Speed et al. 2011) and caused mortality of seedlings

(Speed et al. 2010). The influence of herbivory on the increase in cover or advance of shrubline in tundra ecosystems is likely to vary with the prevalence of herbivory on the shrub species in question.

Treeline advance has been observed on south-facing slopes in the Kluane Region (Danby and Hik 2007). In this same study, willow age structures near treeline had high abundances of younger stems suggesting potential recent increases in willow densities in the later part of the 20th century. To investigate advance of the altitudinal range limit of shrub species, I surveyed canopy-forming willows (*Salix* spp.) in alpine tundra of the Yukon Territory. Using age distributions derived from age estimates based on annual growth ring analysis, I tested the following hypotheses that: 1) willow shrubs have expanded to higher elevations in the Kluane region in the past 50 years, and 2) shrubline advance is greater in sites with warmer microclimates.

## Methods

### *Field surveys*

I surveyed willows in 12 valleys in the Kluane Region of the Yukon Territory (Fig. 3-1). The six most abundant species were *Salix pulchra* Cham. (diamond-leaf willow), *Salix niphoclada* Rydb. (barren-ground willow), *Salix* glauca L. Hook. (gray-leaf willow), *Salix richardsonii* Hook. (Richardson's willow), *Salix barrattiana* Hook. (Barratt's willow), and *Salix alaxensis* Andersson (felt-leaf willow).

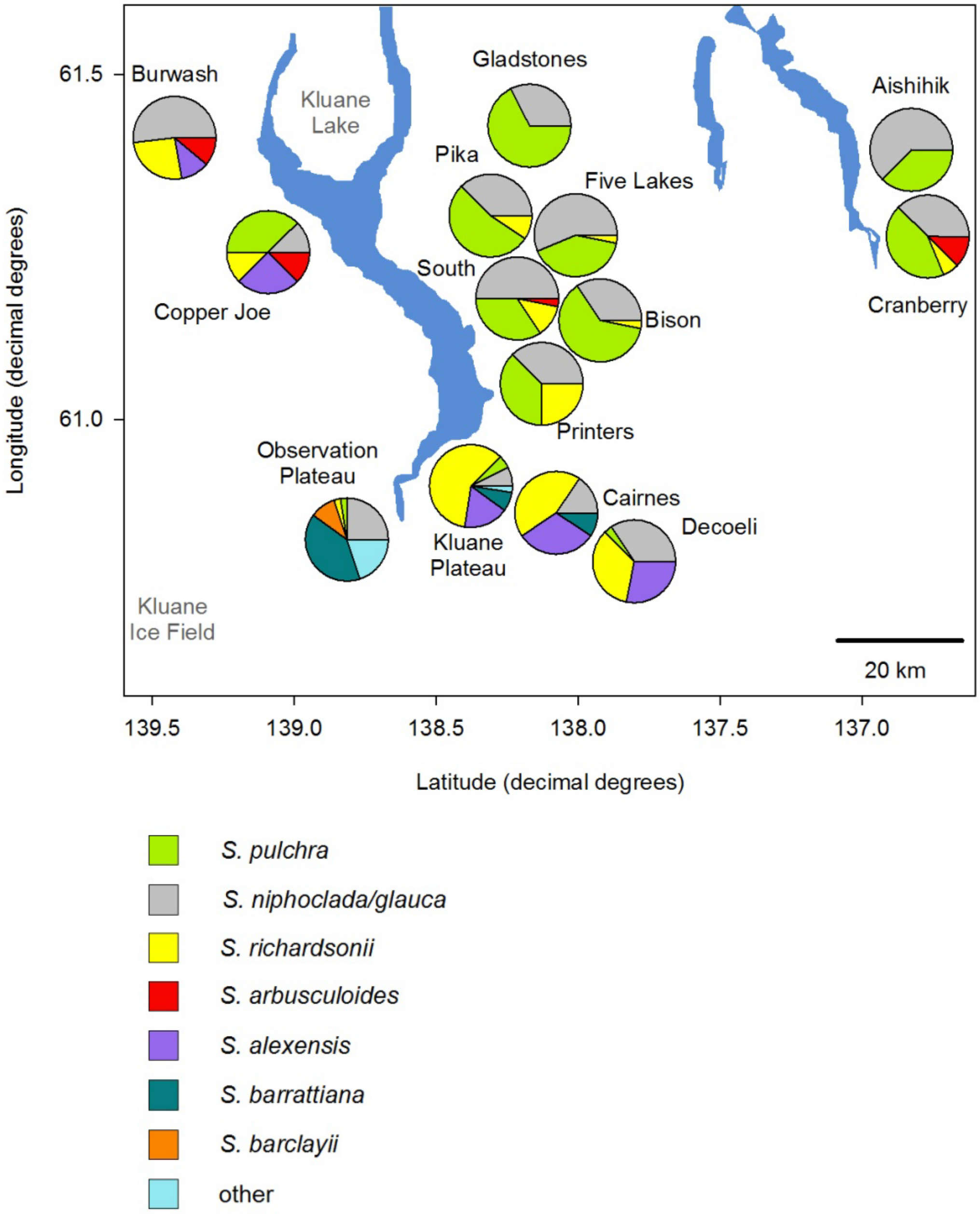

Figure 3-1. Map of species composition across Kluane Region. Pie charts are slightly displaced from actual geographic locations to prevent overlap.

At each site, I hiked to shrubline, the maximum elevation at which canopy-forming willows grow, and established a sampling transect parallel to the valley slope. A search was conducted for the highest canopy-forming willow plant along the slope. The individual found growing at the highest elevation became the first transect point and shrub surveyed in the shrubline transect. I identified each willow individual for each different species found within 3 m of a transect point located every 10 m along the slope from the first shrub sampled, until I had sampled 8 individuals. If no willows were present at a given transect point, I walked further along or slightly down towards the shrubline transition until I came to the next willow. When I had completed sampling at shrubline, I walked down the slope until I came to an arbitrarily determined area in which approximately 50% of the cover of tundra was occupied by canopy-forming willow shrubs. At two sites, Burwash and Bison, cover was closer to 25% as the topography of the valley did not permit sampling on the same aspect at a lower elevation. At all sites except Bison and Copper Joe, I repeated this sampling on the opposite aspect of the valley. At two sites, Gladstones and Observation Plateau, I sampled again at a lower elevation where shrub cover was approximately 75%. On the Kluane Plateau, I found a section of shrubline further along a slope at a higher elevation and I also sampled this. I restricted my sampling to less than continuous shrub cover and higher elevations as here, willow patch sizes were less than 10 m in diametre, and therefore, I was likely sampling only distinct genetic individuals.

I identified the species of each willow and where possible the sex if the individual had visible catkins. I was not always able to distinguish between the species *S. niphoclada* and *S. glauca* during field surveys, and so have combined these individuals into one taxonomic category; however, I believe that most individuals sampled in this group belong to the species *S. niphoclada*. Species identifications were confirmed by George Argus (Emeritus, National Herbarium of Canada). The location, elevation, slope, and aspect were also recorded as well as the largest diameter of the shrub patch and the maximum height. I estimated patch size by calculating the approximate volume ($m^3$) of each patch by multiplying the height by the square of the width. I used this simplified cubic estimate, rather than a more complex shape, as I only wished to calculate a relative measure of size between shrub patches. I took a 3-5 cm sample of the largest stem of the individual for growth ring analysis.

### *Age estimates*

Rings were counted from thin sections of the shrub stems and mounted on glass slides. Digital images were made with a microscope mounted camera. Annual increments were measured for each shrub section along four radii (each at 90° from the other unless the placement of radii had to be moved to avoid growth deformities or rotten wood) with a resolution of 1/1000 mm (WinDendro, Québec, Canada or ImageJ, Research Services Branch, National Institute of Mental Health, Maryland, USA). I repeated the count for the first radii after the other three radii were complete. A statistic of the repeatability of the measurement was calculated by correlating the ring width measurements between these two radii. A repeatability of greater than 80% correlation was found for 96% of samples. The radii for each stem sample were averaged. A statistic of uniformity between the four radii was calculated for each sample by averaging the correlation for each radii with the mean of all four radii. Correlations between each of the sample radii were greater than 80% for 88% of the samples.

The age of shrub stems was estimated as the maximum number of rings measured between the four radii for each shrub sample. I compared two stem segments for a subset of the total sample to account for missing rings. I was able to identify missing rings in 19% of samples of these repeated measurements. Because the first rings in the pith of the stem were sometimes rotten and the largest stem or basal stem section might not represent the oldest part of the willow shrub, my stem ages are only estimates. I compared age estimates between the first and second largest stems on 18 different shrub individuals, and found that the stem age varied by an average of 6 ± 2 (SE) years between these stems.

*Statistical analysis*

Statistics were conducted with the software R (version 2.10.1, R Development Core Team, Vienna). I used linear mixed models to test for differences of shrubline elevations between sites, with site as a random effect. I compared the age of shrub individuals between sites using the Friedman rank sum test, as age distributions at high elevations were right skewed and could not be normalized. To compare the patch size of shrubs between sites, I used mixed models with site as a random effect, testing for a difference in patch width and height using the cbind function. To test for variation in age and patch size among sites and species, I used ANOVA. To meet criteria for normality and homogeneity of variance, the variables were log transformed.

## Results

*Species diversity*

Canopy-forming willow diversity was variable across the Kluane Region with different willow species growing at the shrubline ecotone (Fig. 3-1). However, three species, *S. niphoclada*, *S. pulchra*, and *S. richardsonii*, were most abundant making up ~ 80% of all the individuals sampled. Only one shrub in my survey of 379 individuals was dead. When travelling between sites, three other dead shrubs were recorded, with evidence of stem girdling present in each case.

*Shrubline*

The elevation of shrubline (Fig. 3-2) varied across the Kluane Region. This elevation was not explained by slope ($t_{1,8} = -0.48$, $P = 0.64$) or aspect ($t_{1,8} = -0.48$, $P = 0.16$). Willows were smaller at shrubline relative to lower elevations (Fig. 3-4; MANOVA, $F_{2,308} = 41.37$, $P < 0.01$), and the sizes of willows varied significantly among sites at shrubline (ANOVA, $F_{10,52} = 8.494$, $P < 0.01$).

*Age*

Overall, there were differences among willow species for age (ANOVA, sex/species: $F_{17,313} = 4.41$, $P < 0.01$) and size of patches (ANOVA, sex/species:

$F_{17,313} = 7.76$, $P < 0.01$). The variation in patch size, width and height was consistent with species descriptions. *S. alaxensis* individuals grew taller, and *S. barratiana* individuals were generally shorter in stature that the other species. The three most common species groups, *S. niphoclada*/*S. glauca*, *S. pulchra*, and *S. richardsonii* , did not differ in age or size (Tukey's Test pair-wise comparisons, ns, Fig. 3-3). Since most comparisons of height and age between species were not different, I lumped all species for further analysis of age distributions.

Willows were smaller (Fig. 3-4) and younger at shrubline transects than in the zone of 50% shrub cover (Fig. 3-5; Friedman rank sum test = 14.22, $F_{2,144} = 64$, $P_{\chi 2} < 0.01$, $P_F < 0.01$). Ages at shrubline did not vary significantly between sites (Fig. 3-2; ANOVA, $F_{10,52} = 0.97$, $P = 0.56$). Four of the 19 slopes did not differ in median age and all had stable population structures. On 15 of the 19 slopes shrublines appear to be advancing, with a mean difference in median population age of approximately 10 years over 100 m increase in elevation (Fig. 3-6).

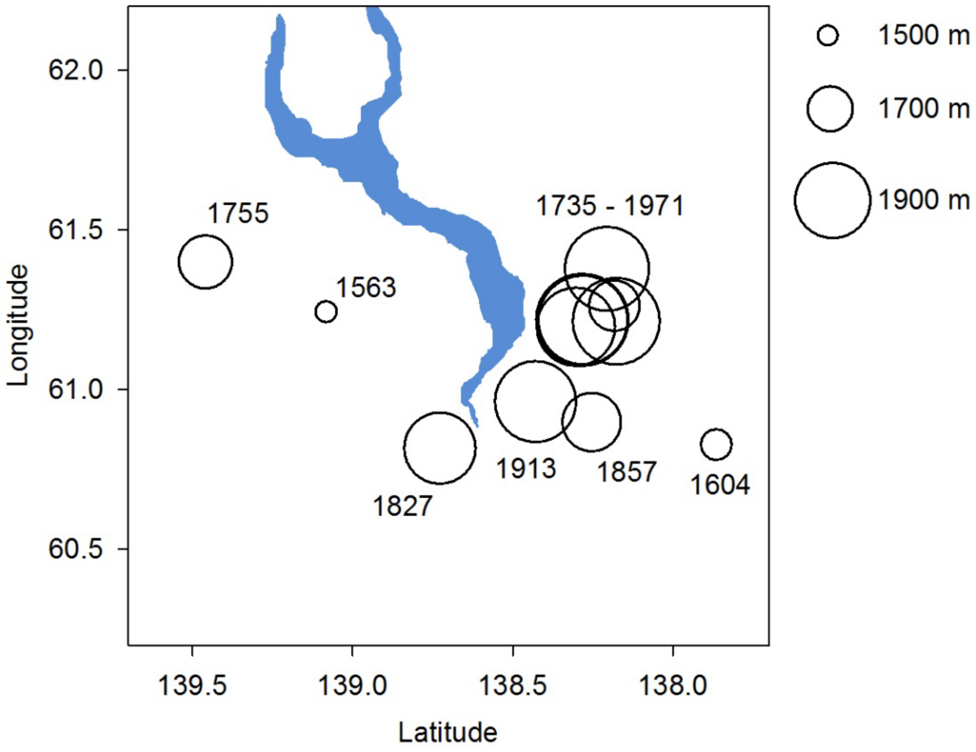

Figure 3-2. Shrubline elevation across the landscape. The size of the circles and the values next to the circles indicate the average elevation of shrubline at each of the sites.

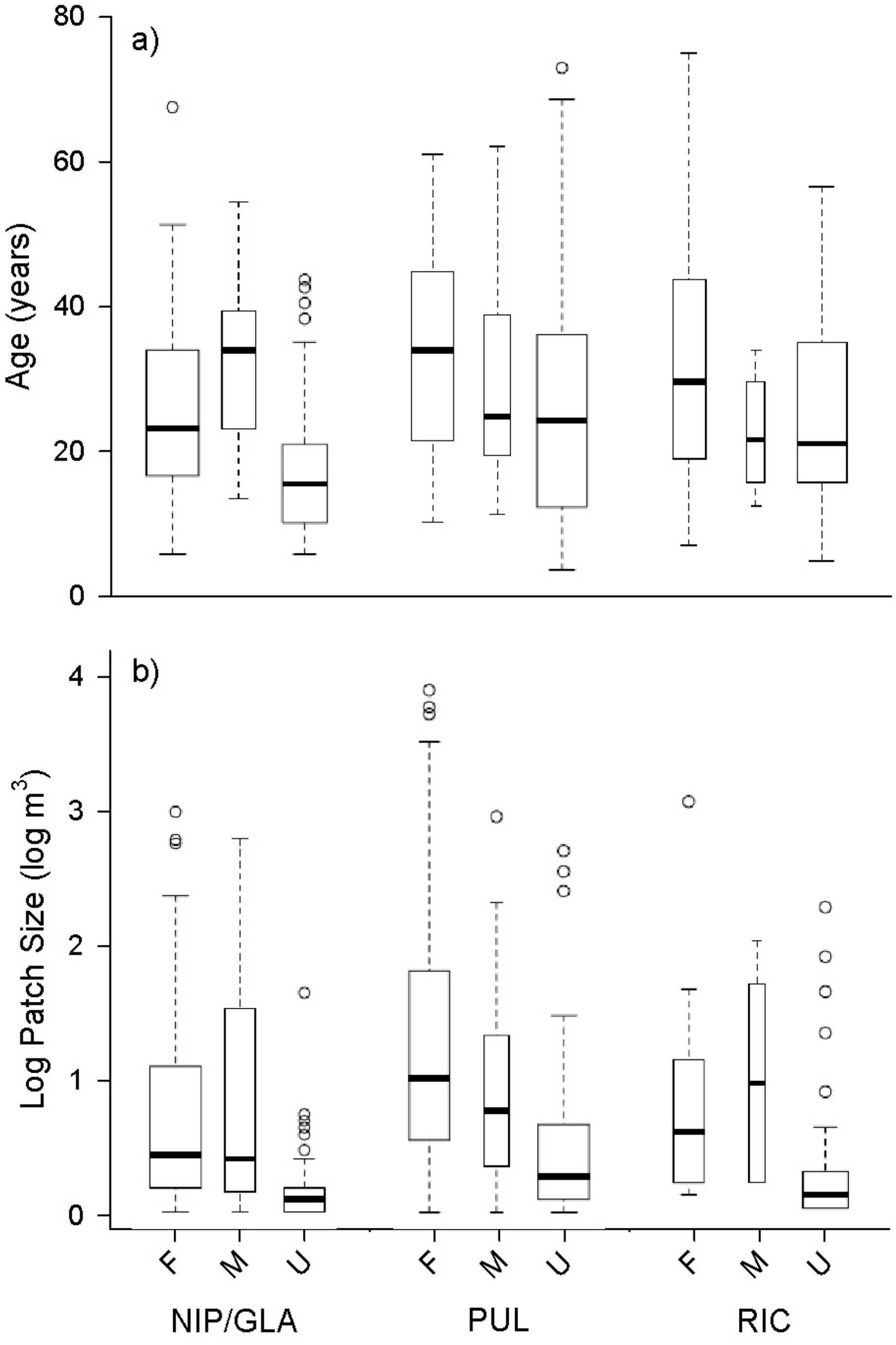

Figure 3-3. Box plots of differences in a) age and b) log patch size among females (F), males (M) and those individuals for which I could not identify sex (U) for the three willow species categories: *S. niphoclada*/*S. glauca* (NIP/GLA), *S. pulchra* (PUL) and *S. richardsonii* (RIC). The width of the box is relative to the sample size for each category.

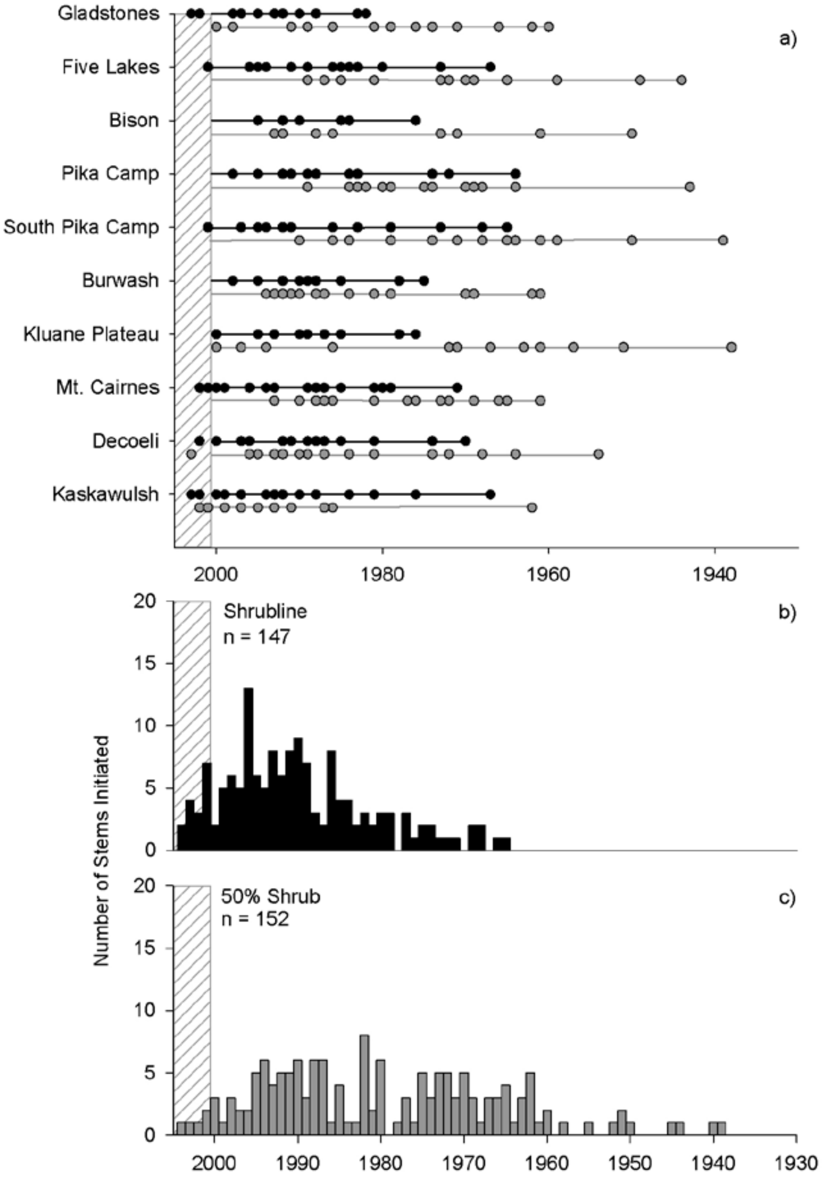

Figure 3-4. Age distributions of willows at and below shrubline for a) each site and b and c) pooled amongst all sites. Grey dots and bars indicate ages of willows in the 50% shrub cover zone and black dots and bars indicate the ages of willows at shrubline. The distribution of willows at shrubline is right skewed (Shapiro-Wilk normality test, W = 0.94, *P* < 0.01). Hatched area in b and c indicates the period since 2000 when young willows many have be under represented in the sample.

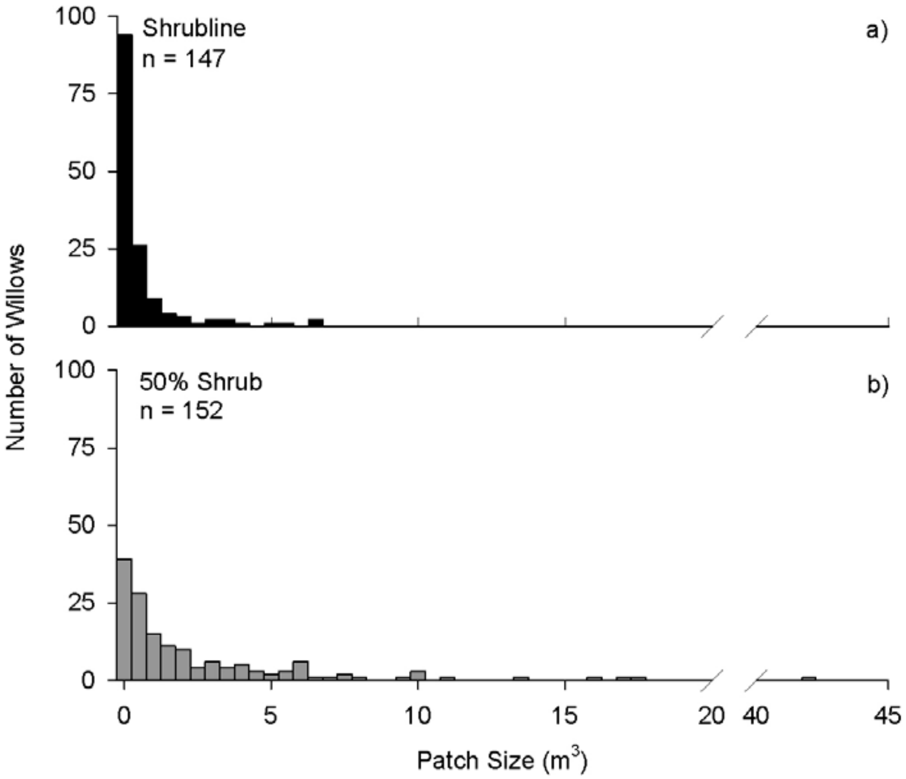

Figure 3-5. Patch size distributions for all sites pooled together of willows a) at and b) below shrubline. Grey bars indicate ages of willows in the 50% shrub cover zone and black bars indicate the ages of willows at shrubline. There is a break in the x axis from 20 to 40 m$^3$.

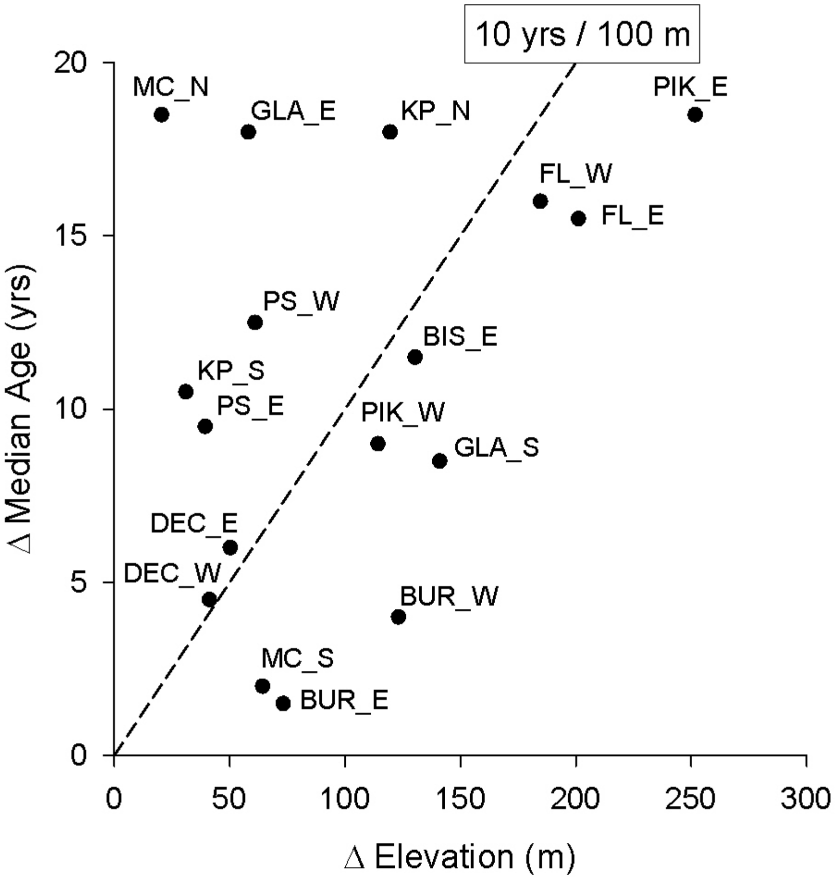

Figure 3-6. Difference between shrubline and the 50% shrub zone regressed against the median age difference between populations growing at shrubline and the 50% shrub zone. The dashed line indicates the mean difference in median population age of approximately 10 years over 100 m increase in elevation.

## Discussion

Willow surveys across a 2500 km$^2$ region indicate that populations were younger at the shrubline ecotone than within the zone of 50% shrub cover. These data support my first hypothesis that willow shrubs have expanded to higher elevations in the Kluane region. The age of willow stems was surprisingly uniform among sites and between species (Fig. 3-1), with a median shrubline age of 17 years, despite variation shrubline elevation (Fig. 3-2). I observed stem ages of over 75 years; therefore, a median age of 17 years indicates many young individuals in the population. My second hypothesis that shrubline advance is greater in sites with warmer microclimates was not supported by my data. I observed no variation in age or height of shrubline with valley aspect (Fig. 3-2), indicating that, unlike with treeline advance (Danby and Hik 2007), differences in microclimate might not be as important in determining the rate of shrubline advance in this region. The maximum recruitment of shrubs at shrubline occurred between 1989 and 1996, and began earlier, between 1980 – 1985, in the 50% shrub cover zone (Fig. 3-4). I observed almost no dead individuals, and saw little evidence of dieback or dead stems in my field surveys indicating that willow mortality is very low in recent years. Taken together, these data provide compelling evidence for recent shrubline advance in the Kluane Region. This is the first demographic study to illustrate advance of woody shrub species in alpine tundra over such a large geographic region.

### *Canopy-forming willow species composition*

I identified ten species during my survey of 379 individuals. These species vary in flowering phenology, chromosome number, ploidy level, and evidence of hybridization. It is surprising that no particular species was found to be the dominant shrubline species, and that there was no significant variation in age or patch size between the three most common species groups, *S. niphoclada*/*S. glauca*, *S. pulchra*, and *S. richardsonii*. These willow species grow together and show no particular evidence of spatial sex or species segregation within a site (Myers-Smith and Hik, unpublished data). All these willow species can form dense canopies over tundra soils when growing at lower elevations, and likely provide a similar functional role in this alpine tundra ecosystem.

### *What controls willow recruitment?*

Substantial proportions of the populations of willows were composed of young individuals, which suggest significant recruitment over the past few decades in the Kluane region. At shrubline, 61% of individuals became established after 1990, compared to only 31% at the 50% shrub cover zone. In two scarified plots cleared in 2000, I observed germination of five different species of willow seedlings at a density of approximately four seedlings per $m^2$. My data on age distributions do not indicate specific pulses of recruitment, but could indicate that conditions for recruitment have improved over the past half century. Willow seeds have low germination rates (Shevtsova et al. 2009, Graae et al. 2010), and therefore studying the factors promoting recruitment in these species is logistically difficult. It is likely that summer conditions, disturbance, and nutrient availability, seed quality, seed production or other reproductive factors could all interact to determine the new recruitment of willow species observed in this study.

### *Climate and recruitment*

Climate has been identified as a significant factor influencing the establishment of woody species in northern alpine ecosystems (Van Bogaert et al. 2010). Summer temperatures could either negatively influence (Shevtsova et al. 2009) or promote (Graae et al. 2008, Milbau et al. 2009) seedling establishment, and winter temperatures and cold stratification can influence fungal infection and germination rates (Graae et al. 2008). Aspen (*Populus tremula*) establishment was highest in years following a year with a high June–July temperature in subarctic Sweden (Van Bogaert et al. 2010). I attribute the increased recruitment in the Kluane Region in the latter half of the 20th century to improved conditions for establishment. Summer temperatures have increased in this region (linear regression of June-July daily maximum temperatures versus year, $R^2 = 0.32$, $P < 0.01$ , unpublished data, Burwash Weather Station, Environment Canada).

Warmer growing season temperatures, earlier snow melt and a longer growing season, increased soil disturbance due to thaw or drainage, or other factors related to changing climate conditions could have improved germination rates, or decreased seedling mortality.

### *Disturbance and recruitment*

Disturbance has been identified as a critical factor necessary for recruitment of woody species in tundra systems (Munier et al. 2010, Lantz et al. 2010a). Fire (Lantz et al. 2010a) and permafrost degradation (Lantz et al. 2009) have been positively associated with recruitment and growth in alder (*Alnus viridis* subsp. *fruticosa*). Herbivory can limit the establishment of new seedlings (Speed et al. 2010), and physical disturbances and herbivory can interact to influence the recruitment of shrub and tree species. Both microsite disturbances and herbivory exclosures had positive influences on recruitment of black spruce (*Picea mariana*) in alpine tundra of the Mealy Mountains, Labrador, Canada (Munier et al. 2010). In the Kluane Region, disturbance, herbivory and climate likely all interact to determine new recruitment of willows.

### *Herbivory*

Herbivory can limit the advance of woody species up slope in northern mountainous regions, as has been observed at sites in Scandinavia (Cairns and Moen 2004, Hofgaard et al. 2009, Olofsson et al. 2009, Van Bogaert et al. 2010, Speed et al. 2010, 2011). Various animal species feed on willow shrubs from large herbivores such as reindeer (Olofsson et al. 2009, Forbes et al. 2010), bird species such as ptarmigan (Tape et al. 2010), small mammals such as voles and lemmings (Predavec and Danell 2001, Olofsson et al. 2009), and insect herbivores (Olofsson and Strengbom 2000, Den Herder et al. 2004). Herbivory could both influence the establishment of new recruits and decrease the survival of adults; however, the impacts of herbivory on recruitment, will likely have a larger influence on the population age structure (Speed et al. 2010). At my field sites in the Kluane region, herbivore damage that resulted in plant mortality was only observed once in surveys of hundreds of willow individuals. Because seedlings are small and difficult to observe, I likely under-sampled willows younger than ~10 years old in my surveys, and therefore I might not have properly accounted for seedling damage or mortality.

### *Clonal growth form*

The arctic and alpine willow species surveyed in this study exhibit clonal growth. When surveying at these high elevations with my sampling design, I am confident that I am sampling distinct genetic individuals. However, at lower elevations at and below treeline the willow patches are large and likely to be older, and what appear to be distinct patches today could in fact be a part of the same genet. Clonal species can have extremely long lifespans and might not experience any senescence over time (de Witte and Stöcklin 2010); therefore, willow patches, once established could continue to increase into the future. I observed almost no dead shrubs in my surveys indicating a high survival rate of adult individuals in recent years. In these cold tundra environments woody material decomposes slowly (Hobbie 1996) and could be preserved for decades. The lack of observed dead stems indicates that the younger populations at higher elevations are indeed evidence of an advancing shrubline over the past half century.

### *Limits to shrubline advance*

Currently active disturbance is one of the factors limiting shrubline advance at the sites that I observed to have low shrublines. Many slopes with talus, scree or exposed rock are not sufficiently stable at higher elevations to support further elevational willow range expansion. On many of the slopes with high shrublines, canopy-forming willows are already growing close to the tops of ridges. These plants are small in stature and do not make up a significant proportion of the overall shrub cover; however, they have established and are persisting at these high elevation sites. I observed low reproductive effort and potential pollen or resource limitation in these individuals (Myers-Smith, Saunders and Hik, unpublished data). Inadequate successful reproduction is one of the common demographic explanations for range limits (Gaston 2009). Willows growing at the highest elevations in Kluane might not currently be reproductive and many currently established seedlings at the shrubline ecotone could come from seed sources located further down the slope. Reproduction in these high elevation individuals could improve with age allowing greater recruitment of individuals from seeds produced at high elevations in the future.

## Conclusions

I found younger populations of willows at higher elevations and observed almost no mortality of willow shrubs in the Kluane Region. Taken together, these findings suggest recent shrubline advance in the region. A significant change in canopy cover and elevational range extent in this region will begin to alter soil temperatures, tundra ecosystem function, and habitat availability for tundra-dwelling animals. Herbivory, climate die-back, drought and disease do not result in mortality of established plants, I predict that these species will continue to expand clonally over the coming decades.

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# Chapter 4. Temperature sensitive growth in tundra willows of the Yukon Territory

## Introduction

Temperatures are warming in the Arctic (Arctic Climate Impact Assessment 2004, Trenberth and Josey 2007), sea ice cover is declining (Comiso et al. 2008) and growing seasons are becoming longer (Chapin et al. 2005). These warming trends are particularly strong in the western Canadian Arctic and Alaska (Chapin et al. 2005, ACIA 2005, Bhatt et al. 2010), and could be associated with the observed increase in woody shrub biomass in the region (Sturm et al. 2001, Tape et al. 2006).

Increases of shrub species have been observed in tundra ecosystems around the circumpolar north: in Northern Alaska (Sturm et al. 2001, Tape et al. 2006), in the western Canadian Arctic (Lantz et al. 2009, Mackay and Burn 2011, Chapter 2), in Northern Quebec (*pers. comm.* B. Tremblay, E. Lévesque and S. Boudreau), and in Siberia (Forbes et al. 2010). While many studies have linked warming and the remotely-sensed greening of tundra ecosystems to an increase in shrub growth (Sturm et al. 2001, Jia et al. 2003, Stow 2004, Tape et al. 2006, Jia et al. 2009, Forbes et al. 2010), caution is necessary when interpreting the greening signal as being due to a change in shrub biomass alone (Huemmrich et al. 2010). It is only with plant-based measurements of shrub growth parameters, such as annual growth ring analysis (Forbes et al. 2010, Hallinger et al. 2010, Blok et al. 2011), that weather conditions can be linked to shrub expansion. Dendroecological data can be used to determine how climate warming alters woody shrubs in tundra ecosystems and to quantify the strength of the relationship between warming, greening and shrub growth.

The discrete annual growth rings (Ainsworth et al. 2001) or stem elongation marks (Rozema et al. 2009, Weijers et al. 2010) of woody plants growing in temperate and polar ecosystems can be used to track variation in growth over time. Recently several studies have been done using annual growth rings to examine temperature-growth relationships in woody shrubs in tundra ecosystems (Forbes et al. 2010, Hallinger et al. 2010). Tree ring data have been used at sites around the world to understand changes at the elevational and latitudinal treeline (Harsch et al. 2009), and likewise annual growth rings in woody shrub species can help to quantify changes in shrub abundance and biomass in tundra ecosystems.

Woody species grow incrementally each year (Ainsworth et al. 2001) and therefore assuming there is little herbivory or dieback, even if climate conditions are not changing, the biomass of shrub species will increase over time. With recent observed warming in tundra ecosystems however, individual growth rates can also be increasing in woody shrub species and the growth form of some shrub species could be changing. Greenhouse experiments indicate increases in growth with passive warming (Arft et al. 1999, Walker et al. 2006); however, temperature is not the only limit to plants growing in tundra ecosystems (Chapin 1983), nutrients, water or light availability could also be important, and growth rates will vary with the size and age of the plant. However, if willow growth is currently primarily temperature limited, an increase in growing season temperatures should result in an increase in annual growth. To determine how willow growth will respond to warming temperatures, I address the following hypotheses that: 1) willows have temperature sensitive growth, with wider annual growth rings in warmer growing seasons, and 2) ring widths are smaller and temperature-growth correlations stronger at the elevational range limit of tundra willow species.

## Methods

I surveyed willows in 11 valleys around the Kluane Region. See Chapter 3 for further description of the sampling procedure.

### *Ring counting*

To process samples for counting rings, I made thin sections of the shrub stems, mounted the sections on glass slides, and took digital images with a microscope mounted digital camera. Each shrub section was measured along four radii (each at 90° from the other unless the placement of radii had to be moved to avoid growth deformities or rotten wood, which occurred in approximately 10% of samples) for annual increment with a resolution of 1/1000 mm (WinDendro, Québec, Canada or ImageJ, Research Services Branch, National Institute of Mental Health, Maryland, USA). I repeated the count for the first radii after the other three radii were complete.

### *Uniformity of growth*

Willow stem sections varied in the ease at which rings could be counted and the information that these rings contained. A statistic of the repeatability of the measurement was calculated by correlating the ring width measurements between these two radii. A repeatability correlation of greater than 80% correlation was found for 96% of samples. The radii for each stem sample were averaged. A statistic of uniformity between the four radii was calculated for each sample by averaging the correlation for each radii with the mean of all four radii. Correlations between each of the sample radii were greater than 80% for 88% of the samples. I was able to identify missing rings in 19% of samples of these repeated measurements, and these missing rings were accounted for during the visual cross dating I conducted on the raw ring width measurements. Stem sections with uniform or irregular growth did not contain as much information as those samples that had variable ring widths between years (Fig. 4-1). To estimate the correlation among willow samples used to build site chronologies, I calculated the correlation between ring widths for each willow sample and the mean of all ring widths for the site, here after referred to as the site correlation.

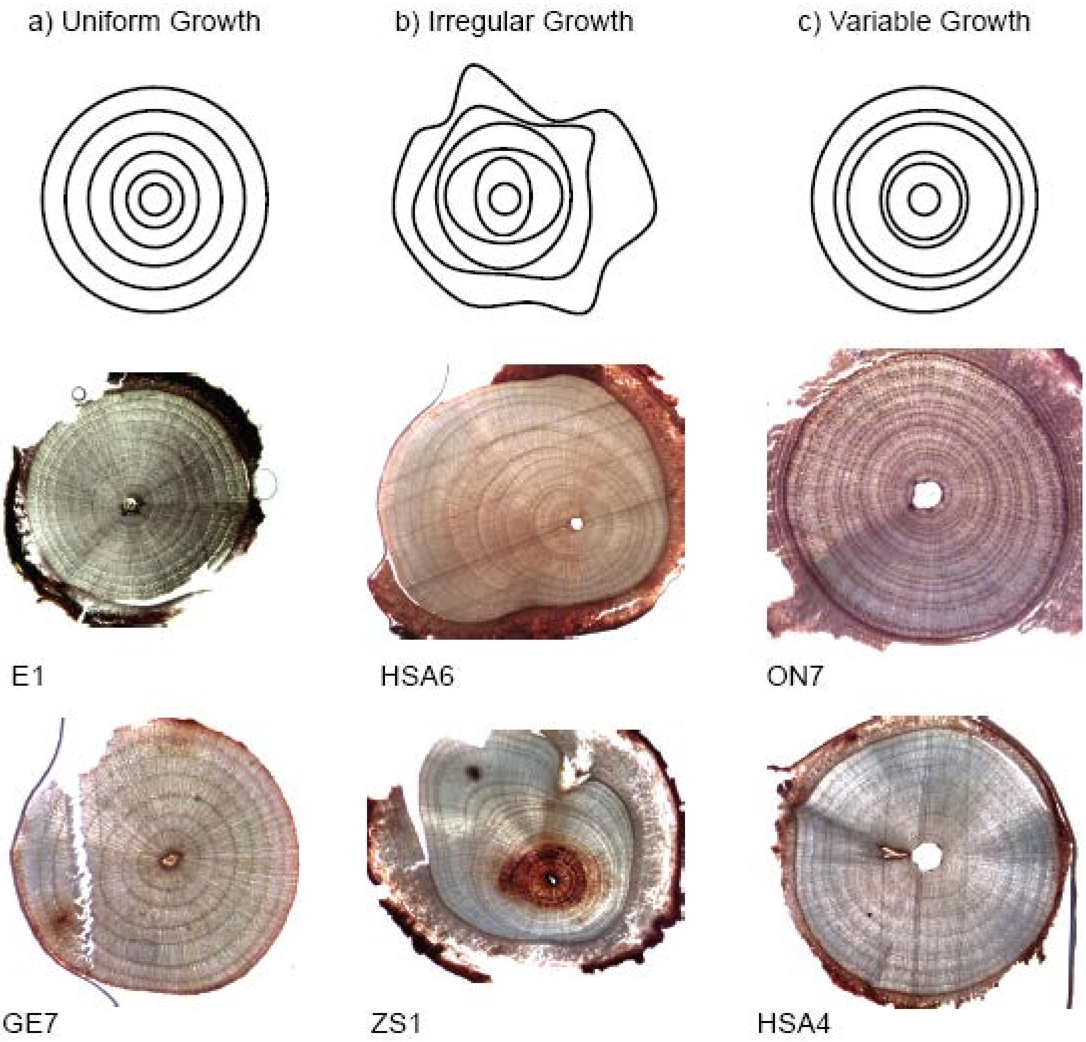

Figure 4-1. Annual growth rings patterns can differ between individual shrub stem samples. Rings can have a) uniform, b) irregular, or c) variable growth. It is samples with variable growth that best exhibit growth-climate sensitivity.

*Climate data*

Climate data were obtained from the Burwash weather station (Environment Canada), the Climate Western North America data set (Hamann and Wang 2005, Wang et al. 2006) and from a composite of Herschel Island and other Environment Canada weather stations along the Yukon coast (Burn and Zhang 2009). Favourable growing conditions during the early part of the growing season promote the production of early wood, creating wider growth rings (Ainsworth et al. 2001). Several recent studies have documented significant positive correlations between ring widths or shoot lengths and early and mid-growing season temperatures for tundra shrub species (Forbes et al. 2010, Hallinger et al. 2010, Blok et al. 2011). I hypothesized that warm early growing season temperatures would also be influential at my study sites; therefore, I focused my analyses on the mean of the June and July maximum daily temperatures (here after referred to as JJ Tmax) to test for temperature sensitive growth. To treat all samples similarly, I used the regional JJ Tmax to perform temperature-growth correlations on the raw ring widths for each willow stem sample. When comparing JJ Tmax to site ring width chronologies, I extracted temperature and precipitation data from the Climate Western North America data set for each of my study site locations. The Climate Western North America data set is modelled data based on weather station records and adjusted for factors such as elevation and aspect, which influence microclimate in mountainous areas. I correlated the following variables with the site chronologies (Table 4-2): mean June daily maximum temperature (June Tmax), mean July daily maximum temperature (July Tmax), mean June and July daily maximum temperature (JJ Tmax), total June precipitation (June PPT), total July precipitation (July PPT), total June and July precipitation (JJ ppt), mean summer daily maximum temperature (Sum. Tmax), mean summer daily temperature (Sum. Tave), degree days greater than 5 (DD > 5), degree days less than 0 (DD < 0).

### *Statistical analysis*

Statistical analyses were conducted with the software R (version 2.10.1, R Development Core Team, Vienna). I conducted correlations in Excel (Microsoft 2007) using the correl() function between the raw ring widths for each willow stem sample and the regional JJ Tmax and between site chronologies and a suit of site specific climate variables extracted from the Climate Western North America data set (Table 4-2). I used linear mixed models and the nlme package to test for differences in age, mean ring width and temperature-growth correlation between individual willows sampled. I treated site as a random effect in these models. To meet criteria for normality and homogeneity of variance, variables were log transformed.

*Chronologies*

I used ring width measurements from 1997 to 2006 to build site chronologies. Many willows were young, and populations at the shrubline ecotone were younger than those growing further down the slope (Chapter 3); therefore, I chose the last ten years of rings to build chronologies to maximize the sample sizes. Only samples with the full ten years of data were included when building chronologies. Radii were standardized and site chronologies were built using the dendrochronology program library in R (dplR, Bunn 2008). I did not de-trend ring widths prior to building the chronologies as these willow species did not have a uniform age related growth trend (see results), and I wanted all individuals to be treated in the same manner statistically.

## Results

### Growing season warming

Temperature data from the Climate Western North America data set confirm more frequent warm June and July months in recent decades, which results in a positive trend in JJ Tmax in the Kluane and Dempster Regions of the Yukon Territory (Fig. 4-2). However, data from Herschel Island did not have this same trend (Fig. 4-2).

*Variation among species and sexes*

Ring widths (ANOVA $F_{2,221} = 4.1$, $P = 0.02$) and temperature correlations (ANOVA $F_{2,221} = 5.6$, $P < 0.01$) differed among willow species (Fig. 4-3). Of the three most common species groups, *S. niphoclada*/*S. glauca*, *S. pulchra*, and *S. richardsonii*, female and male *S. richardsonii* had larger rings and female and male *S. niphoclada*/*S. glauca* had lower temperature correlations between individual raw ring widths and the regional JJ Tmax (Fig. 4-3).

### *Variation with elevation, age and patch size*

Ring widths were smaller in older and larger willows; however, in an analysis of ring widths and growth-temperature correlations for all individuals sampled, these variables did not significantly differ with elevation (Table 4-1). When I compared willows growing at the shrubline ecotone, which occurs at different elevations in different valleys (Chapter 3), to those growing at the zone of approximately 50% shrub cover, I found that shrubline willows exhibited more temperature sensitive growth and had on average more positive growth-temperature correlations (Table 4-1).

### *Growth trends*

In addition to younger individuals more frequently having wider rings, 46% of shrub samples had a negative growth trend ($r < -0.3$), with an increasing number of relatively narrower rings over time. However, 18% of willows had a positive growth trend ($r > 0.3$), and 37% had no growth trend ($r = -0.3 – 0.3$). At most sites, older individuals have more frequent large growth rings in recent years (Fig. 4-4).

### *Temperature sensitive growth*

At all but one site, willows in the Northern Yukon and the Kluane Region exhibited temperature sensitive growth as shown by positive correlations of growth ring widths with JJ Tmax (linear mixed effect model, $t_{197}= 7.2$, $P < 0.01$, Table 4-2, Fig. 4-5, Fig. 4-6). A strong negative correlation also existed between ring widths and June and July precipitation (linear mixed effect model, $t_{197}= -5.5$, $P < 0.01$, Table 4-2). Because precipitation and JJ Tmax were strongly inversely related (linear mixed effect model, $t_{197}= 8.3$, $P < 0.01$), further analyses considered only the relationships with early-summer maximum temperatures.

The shrubs from the Observation Plateau site were the only ones for which the ring width chronology and JJ Tmax were not correlated (Fig. 4-6). This site was also unique in that the correlations of ring widths among individuals were weak (Fig. 4-6c).

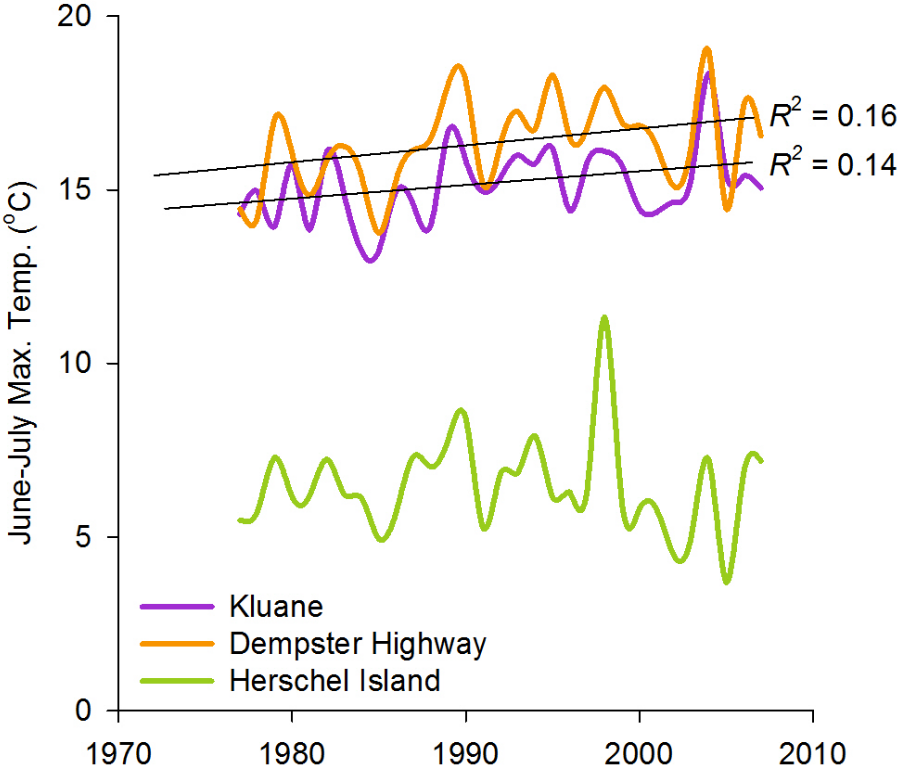

Figure 4-2. Change in June – July maximum daily temperatures from weather station data from the Kluane Region at 1600 m, Dempster highway at 1000 m (Climate Western North America data set, Hamann and T. L. Wang 2005, T. Wang et al. 2006) and Herschel Island at sea level (Burn and Zhang 2009). There is a significant trend in JJ Tmax over time for Kluane (Linear Regression, $R^2$ = 0.14, $F_{1,29}$ = 4.6, $P$ = 0.04) and the Dempster highway (Linear Regression, $R^2$ = 0.16, $F_{1,29}$ = 5.5, $P$ = 0.03).

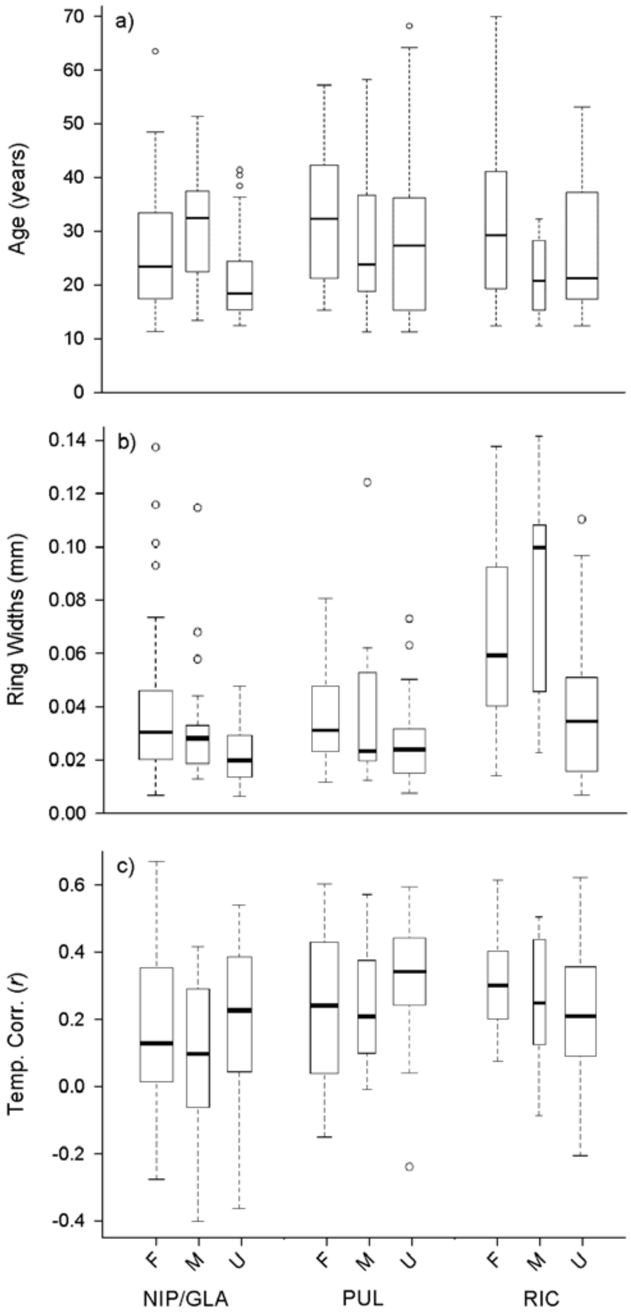

Figure 4-3. Box plots of differences in a) age, b) ring widths and c) the correlation between the JJ Tmax among females (F), males (M) and those individuals for which I could not identify sex (U) for the three willow species categories: *S. niphoclada/S. glauca* (NIP/GLA), *S. pulchra* (PUL) and *S. richardsonii* (RIC). The width of the box is relative to the sample size for each category.

Table 4-1. Linear mixed model results of the influence of elevation, age, patch width, and patch height and ANOVA results comparing shrubline and the 50% shrub cover zone for variation in ring widths and the correlation between the JJ Tmax for all willow samples. I included site as a random effect in these models.

| | | Ring Width | | Temp Corr. | |
|---|---|---|---|---|---|
| | *DF* | *t* value | *P* value | *t* value | *P* value |
| Elevation | 272 | -0.5 | 0.2 | 1.2 | 0.2 |
| Age | 272 | -6.9 | <0.01 | -1.3 | 0.2 |
| Patch Width | 272 | 2.7 | <0.01 | -1.2 | 0.2 |
| Patch Height | 272 | 6.0 | <0.01 | 0.8 | 0.4 |

| ANOVA | *DF* | *F* value | *P* value | *F* value | *P* value |
|---|---|---|---|---|---|
| Shrubline Ecotone | 274 | 2.26 | 0.13 | 5.2 | 0.02 |

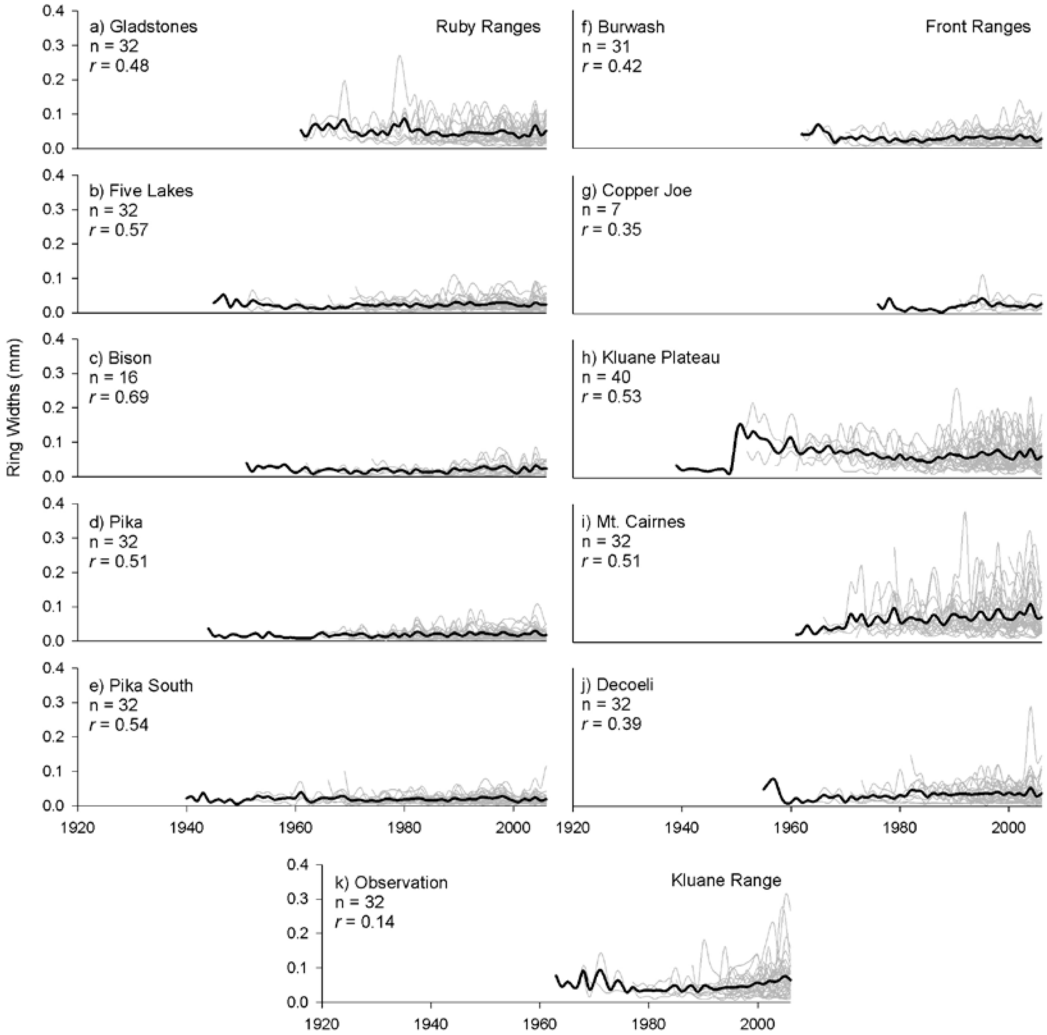

Figure 4-4. Raw ring widths for each shrub sampled at the shrubline and 50% shrub zones for each site. The panels to the left indicated the sites located in the Ruby Range (a – e), the panels to the right indicate the sites located in the Front Range (f – j) and the bottom panel is the site closer to the ice fields in the Kluane Range (k). The grey lines indicate the raw ring widths (mm) for each sample and the black line indicates the mean ring with for all samples over time. The sample size (n) and the correlation between all samples and the site mean (*r*) are also indicated in the top left of each panel.

Table 4-2. Correlations between weather variables and site chronologies. Bold and shaded numbers indicate correlation coefficients of greater than 0.5 or less than -0.5.Two separate chronologies were built and correlations conducted for each aspect of each valley (with the exception of Bison and Copper Joe where only one aspect was sampled) and then the two aspects were averaged together. I chose the variables mean June daily maximum temperature (June Tmax), mean July daily maximum temperature (July Tmax), mean June and July daily maximum temperature (JJ Tmax), total June precipitation (June PPT), total July precipitation (July PPT), total June and July precipitation (JJ ppt), mean summer daily maximum temperature (Sum. Tmax), mean summer daily temperature (Sum. Tave), degree days greater than 5 (DD > 5), degree days less than 0 (DD < 0), as previous work indicate that these variables are most correlated with growth of shrub species (Forbes et al. 2010, Hallinger et al. 2010). Site specific snow depth data were not available.

| Sites | June Tmax | July Tmax | JJ Tmax | June PPT | July PPT | JJ ppt | Sum. Tmax | Sum. Tave | DD > 5 | DD < 0 |
|---|---|---|---|---|---|---|---|---|---|---|
| Bison | **0.5** | 0.3 | **0.5** | -0.3 | **-0.6** | **-0.6** | 0.4 | 0.3 | 0.3 | 0.1 |
| Copper Joe | 0.4 | 0.3 | 0.4 | **-0.5** | -0.4 | **-0.6** | 0.2 | 0.1 | 0.1 | 0.4 |
| Decoeli | **0.6** | 0.2 | **0.5** | **-0.5** | -0.2 | -0.4 | 0.3 | 0.2 | 0.2 | 0.2 |
| Five Lakes | **0.7** | 0.3 | **0.6** | -0.4 | -0.3 | **-0.5** | 0.4 | 0.3 | 0.3 | 0.3 |
| Observation | -0.4 | -0.1 | -0.3 | 0.4 | 0 | 0.3 | -0.4 | **-0.5** | **-0.5** | 0.1 |
| Burwash | 0.2 | 0.4 | 0.3 | -0.3 | **-0.5** | **-0.5** | 0.1 | 0 | 0 | 0.3 |
| Kluane Plateau | **0.5** | 0.4 | **0.5** | -0.3 | **-0.5** | **-0.5** | 0.3 | 0.2 | 0.2 | 0.2 |
| Pika | **0.6** | **0.5** | **0.7** | -0.4 | **-0.6** | **-0.6** | **0.5** | 0.4 | 0.4 | 0.2 |
| Pika South | 0.4 | **0.6** | **0.6** | -0.4 | **-0.7** | **-0.7** | 0.4 | 0.3 | 0.3 | 0.4 |
| Mt. Cairnes | 0.4 | **0.5** | **0.5** | **-0.5** | **-0.6** | **-0.7** | 0.3 | 0.3 | 0.3 | 0.3 |
| Gladstones | **0.7** | 0.4 | **0.7** | **-0.5** | -0.3 | **-0.5** | **0.5** | 0.4 | 0.4 | 0.2 |

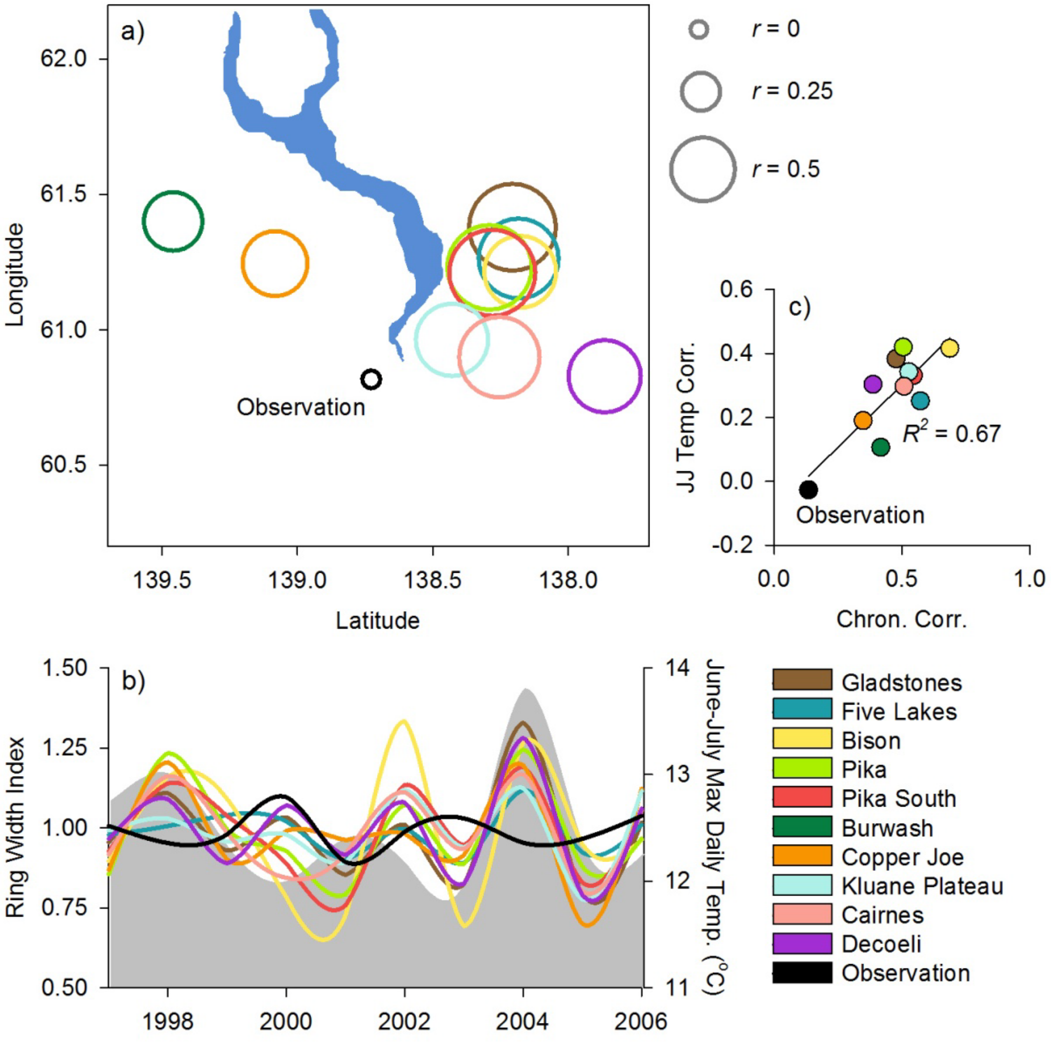

Figure 4-5. Temperature correlations of ring width chronologies for each site in the Kluane Region. The top panel (a) indicates the correlation between the mean JJ Tmax and the ring width chronology for each site. Sites are indicated by the coloured circles. The bottom panel (b) illustrates the ring width chronologies over time (ring width index, coloured lines) and the mean JJ Tmax (°C, grey filled area). The plot to the right (c) shows the relationship between the chronology correlation and the correlation with the JJ Tmax for each of the site chronologies (c, Linear Regression, $R^2 = 0.67$, $F_{1,9} = 17.9$, $P < 0.01$). Sites with low correlation between individual shrub samples also have weak correlations with summer temperatures.

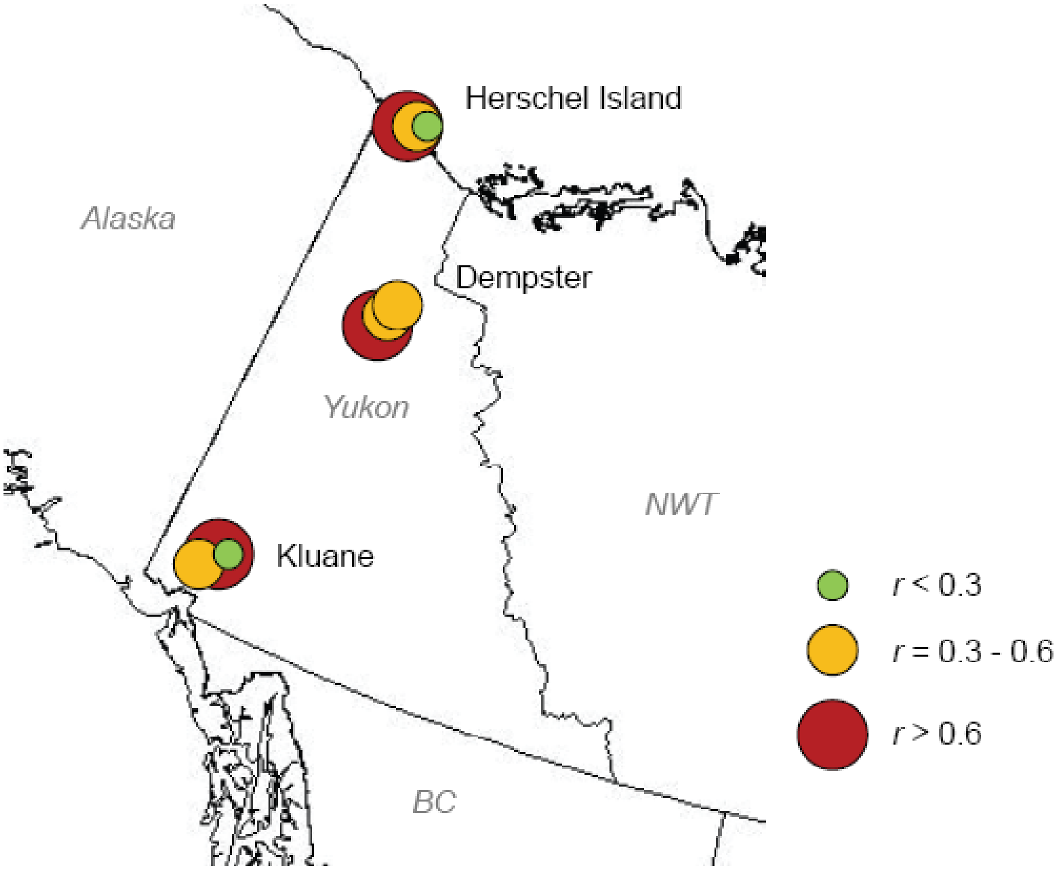

Figure 4-6. Correlation between the mean JJ Tmax and the ring width chronology for sites across the Yukon Territory (in the Kluane Region, along the Dempster Highway and on Herschel Island). The coloured circles indicate the strength of the correlations between growth rings and JJ Tmax. Overlapping circles indicate multiple sites in the same study region. The 11 sites in the Kluane Region (Fig. 4-5) are illustrated with three representative circles. The three sites along the Dempster highway are indicated with three circles, and the three species chronologies sampled on Herschel Island (*S. richardsonii*, *S. pulchra* and *S. glauca*) are also indicated by three circles.

## Discussion

My results indicate that tundra willows grew more in years with warm and dry early summers and approximately half of the variation in annual growth rings was explained by early growing season temperatures or potentially by correlates of these with precipitation, direct sun light, or snow cover. Wide growth rings were more frequent in recent years in many individuals, with the abnormally warm growing season of 2004 being a particularly good year for growth. With an increased frequency of warm growing season conditions in the Yukon Territory, I project that the growth rates of canopy-forming willow shrubs will continue to increase.

### *Temperature and growth*

Temperature has been reputed to be the primary factor determining the elevational or latitudinal range extent of trees (Harsch et al. 2009). If the location of the current elevational or latitudinal range extent of canopy-forming willows is determined by climate, I would expect willows growing at their range limits to exhibit more temperature-sensitive growth. I observed no relationship between temperature-sensitive growth and elevation of individuals across all sites; however, the elevational range limit of canopy forming willows, varied between valleys (Chapter 3). When I compared willows growing at shrubline to those growing in the approximately 50% cover zone, I found that willows growing at shrubline did indeed exhibit more climate sensitive growth. This confirms the assumption that the growth of willows at the shrubline is temperature limited; however, I saw no evidence of narrower ring widths at shrubline. The uniform radial growth observed between willows growing at different elevations, indicate that willows growing at higher elevations are able to grow at rates similar to that of willows growing farther down slope. This corroborates the findings of chapter 3 that variation in microclimate does not explain the variation in willow growth or age across the landscape.

Temperature-growth correlations were strong for the majority of sites, similar to those reported for willow species growing in arctic Siberia (Forbes et al. 2010, Blok et al. 2011). However, some sites exhibited weaker temperature-growth correlations (Figs. 4 and 5). At the Observation Plateau site, I did not observe positive temperature-growth correlations and correlations among shrub ring widths from the sampled individuals at the site were poor. This field site is close to the Kluane ice fields, and has a very different species composition compared to the other sites, with the dominant species being *S. barrattiana*, a less common species at the other sites and the species *S. barclayii* being present which was completely absent at all other sites (Chapter 3). Moisture stress, different localized climate or other factors could explain why willows growing at this site showed no climate-growth relationship. Sites along the Dempster Highway and on Herschel Island also had lower temperature-growth correlations. The Dempster Highway sites had very shallow soils, and the Herschel Island site has much cooler growing season temperatures and fewer sunny days. These factors could weaken the correlations between growing season temperatures and willow growth.

### *Other factors influencing growth*

Temperature is not the only factor determining plant growth in tundra ecosystems (Chapin and Shaver 1985). Growing season length, the depth of the snowpack in the spring, the amount of solar radiation, and extreme winter and summer weather events could also influence variation in growth in canopy forming willows. In addition to factors promoting willow growth, extreme weather events can also cause “browning”, the damage to or death of shrub species. Frost damage from winter warming and loss of the snowpack has been observed for prostrate shrub species growing in subarctic Scandinavia (Bokhorst et al. 2008). I observed little evidence of mortality or frost damage to willows growing at my field sites. Tundra willows are well adapted to tolerate winter conditions, they can bend under the weight of snow, maintain a more prostrate growth form to remain below the snowpack, and have high freeze tolerance (Marsh et al. 2010, *pers. comm.* Syndonia Bret-Harte). As early successional and disturbance-loving plants, willows could be well adapted both to deal with adverse conditions and take advantage of favourable growing season conditions.

## Conclusions

My results indicate that with increases in warm summers in the Yukon Territory, the growth of individual willows should increase. Evidence of advancing shrublines in the Kluane region (Chapter 3), patch expansion on Herschel Island (Chapter 2) and reports of increased shrub abundance in the western Arctic (Sturm et al. 2001, Tape et al. 2006, Lantz et al. 2009, Mackay and Burn 2011), indicate that warmer summers coupled with disturbances and conditions appropriate for new recruitment, are resulting in increased shrub cover and abundance in addition to growth of individuals. Quantifying growth-climate relationships using dendroecological methods will help to establish under what conditions and where the greatest increases in shrub abundance can occur. Though I project continued increases in shrub growth rates under conditions similar to now, as water stress or nutrient availability become limiting the relationship between increased growth and growing season temperatures cannot hold in the future. It is only with experimental manipulations and continued monitoring, that growth trajectories can be determined under future climate scenarios.

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# Chapter 5. An experimental test of canopy shading and snow trapping on soil temperatures in alpine tundra

## Introduction

Tundra soils store large quantities of carbon which are important components of global carbon budgets (McGuire et al. 2009). These carbon stores are currently protected by cold soil temperatures and permafrost, which slow down microbial decomposition and release of carbon into the atmosphere. However, with climate warming and permafrost thaw, this stored carbon will become vulnerable to decomposition (Mack et al. 2004, Schuur et al. 2009). Great uncertainty still exists about the temperature sensitivity of soil carbon decomposition and potential feedbacks to climate warming (Davidson and Janssens 2006). Therefore, to predict and model the impacts of future climate on tundra ecosystem function requires an in depth understanding of plant-soil-climate feedbacks (Euskirchen et al. 2009, Chapin et al. 2009).

Growing evidence indicates increases in woody shrubs in tundra ecosystems. Repeat photographs indicate expansion of shrub species in northern Alaska (Sturm et al. 2001b, Tape et al. 2006), in the western Canadian Arctic (Lantz et al. 2009, Mackay and Burn 2011, Chapter 2), and in northern Quebec (*pers. comm.* B. Tremblay, E. Lévesque and S. Boudreau). Population age distributions indicate advance of shrub species up slopes in subArctic Sweden (Hallinger et al. 2010) and the Yukon Territory (Chapter 2). And satellite imagery suggests the same pattern in northern Russia (Forbes et al. 2010). These increases in woody shrub species around the circumpolar north will alter ecosystem structure and could feedback to influence abiotic and biotic ecosystem processes.

Abiotic ecosystem functions potentially influenced by increasing shrub canopies include light penetration, soil moisture, and fire frequency in surrounding ecosystems (Knapp et al. 2008). In arctic and alpine ecosystems, shrub canopies could also alter snow distribution, snow melt and permafrost thaw (Sturm et al.

2001a, Pomeroy et al. 2006, Marsh et al. 2010). In the winter, shrub canopies influence the distribution and physical characteristics of snow, and alter the exchanges of energy and moisture between the terrestrial ecosystem and the atmosphere (Liston et al. 2002, Marsh et al. 2010). Shrub canopies can trap snow (Marsh et al. 2010), potentially insulating soils and boosting microbial mineralization and nutrient availability (Sturm et al. 2005). During spring, shrub stems that extend above the snowpack alter the albedo and accelerate local snow melt (Sturm et al. 2001a, Pomeroy et al. 2006, Loranty et al. 2011). Current literature suggests that interactions between shrubs, snow and soil warming could act as a positive feedback to shrub expansion (Sturm 2005, Grogan and Jonasson 2006).

Biotic ecosystem functions will also be influenced by increases in canopy cover and height of tundra shrub species. Shrub biomass will store carbon in above and belowground biomass; however, changes to soil temperatures can influence decomposition of belowground soil carbon (Mack et al. 2004, Schuur et al. 2009). Deciduous shrub species produce more litter than other tundra species; however, this litter is more recalcitrant than herbaceous litter. Woody plants allocate more carbon to recalcitrant forms such as lignin, and can produce more polyphenols and tannins which can retard decomposition (De Deyn et al. 2008). As a result of having more recalcitrant litter, shrub increases in tundra ecosystems are predicted to reduce soil decomposition rates potentially creating a negative feedback to climate warming (Cornelissen et al. 2007). Influences of canopies on soil temperatures could enhance winter nitrogen cycling and lead to the release of larger pulses of nitrogen in spring (Weintraub and Schimel 2003, 2005, Buckeridge et al. 2010a, 2010b, Buckeridge and Grogan 2010). However, the balance between potential enhanced decomposition and nutrient cycling from warmer temperatures under shrubs in wintertime and decreased decomposition due to greater inputs of more recalcitrant litter from increasing shrub species remains unknown (Wookey et al. 2009).

In this study, I set out to test experimentally the influence of shrub canopies on tundra soil temperatures. I established a fully-factorial manipulative experiment by removing natural shrub canopies and creating artificial canopies over previously shrub-free tundra soils, to isolate the abiotic influences of shrub canopies from the biotic. Using this approach, I can test the influence of canopy in isolation from soil conditions or plant biomass, which differ between shrub and shrub-free tundra, and independently of potential microclimatic differences that might have played a role in the shrub establishment and distribution of the shrub patches. Artificial canopies have been used in desert ecosystems to test the influence of shading and water availability on understory species (Holzapfel and Mahall 1999), but have yet to be employed in tundra ecosystems. My results allow me to experimentally test the relative importance of the 'snow trapping' and 'soil shading' hypotheses (Sturm et al. 2001a, Liston et al. 2002, Sturm et al. 2005, Pomeroy et al. 2006). These hypotheses predict that winter soil temperatures will be warmer under shrub canopies due to insulation, while summer temperatures will be cooler as a result of shading.

## Methods

### *Study site*

I conducted my experimental manipulation in alpine tundra with a landscape mosaic of approximately 50% cover of shrub patches with canopy heights of 30 - 100 cm. I define canopy-forming shrubs as those with an upright growth form with leaves and branches that shade understory plants and the soil surface. My experimental site (61.22 N, 138.28 W, at 1450 m asl) was located on either side of a stream that bisected a valley with east- (18° slope) and west- (23° slope) facing slopes in the Ruby Range, southwest Yukon Territory, Canada (Fig. 5-1a and b). The dominant canopy-forming shrubs in this region are the willow species *Salix pulchra* Cham., *Salix glauca* L. Hook. and *Salix richardsonii* Hook. Common understory species include *Salix reticulata* L., *Dryas octopetala* L., *Polygonum bistorta* L. ssp. *plumosum* (Small) Hultén, *Festuca* spp., and *Carex* spp. Soils are

5 – 50 cm deep organic cryosols (Canadian System of Soil Classification) and are underlain by bedrock or buried talus, with permafrost located in the bedrock.

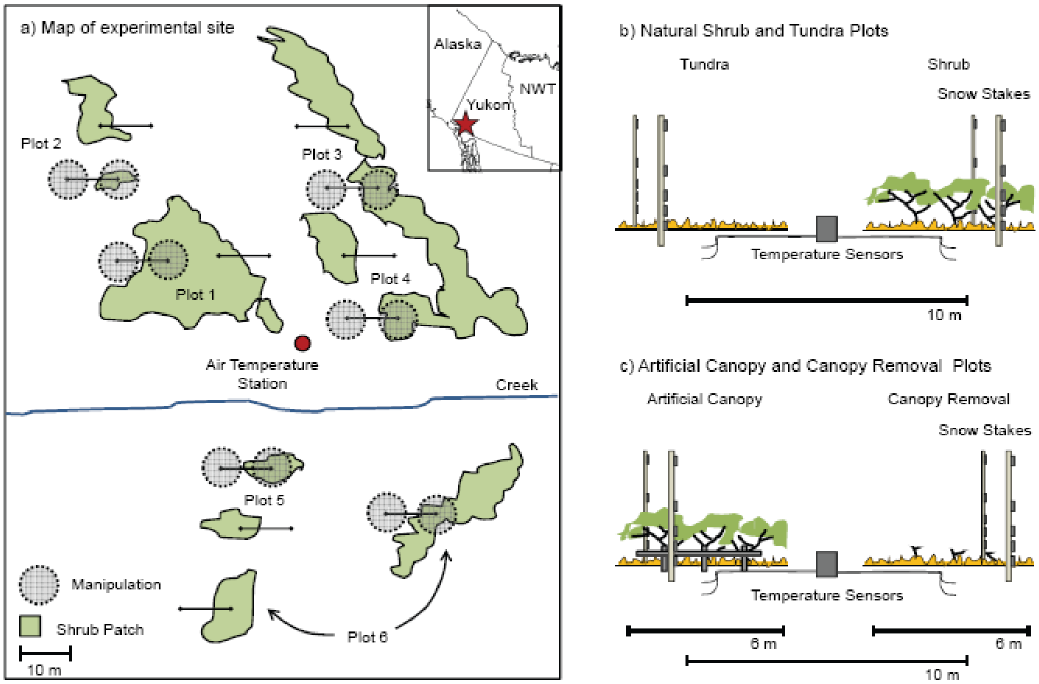

Figure 5-1. The a) location of experimental plots and b and c) design of the canopy manipulation. The inset indicates the general location of the study site in the Yukon Territory. The dashed grey circles represent the manipulated artificial-canopy and canopy-removal treatments and the dark green polygons are shrub patches. Plot b shows the shrub and tundra plots and plot c shows the manipulated artificial-canopy and canopy-removal treatments.

*Experimental manipulation*

To examine the influence of snow-capture by shrubs, I measured year-round soil temperatures over three years in six plots of each of the four treatments: 1) intact shrubs, 2) artificial canopies, 3) canopy removals, and 4) adjacent tundra (Fig. 5-1). In September 2007, I constructed artificial-canopy plots and canopy-removal plots of 6 m in diameter, similar in size to many shrub patches in the study area (Figure 1), by cutting shrubs at the stem base and affixing them to wooden stakes in the soil in tundra without shrub cover. Since artificial canopies lacked foliage, these plots were covered by 60% knitted green shade cloth to mimic natural canopy shading for approximately two months each year. The shade cloth treatment was implemented from July 1 2008 – September 7 2008 and July 1 2009 – September 5 2009.

To establish whether shade cloth mimicked the shading of natural shrub canopies, I recorded light penetration through each of the natural and artificial canopies using a multi-sensor quantum light meter measuring photosynthetically active radiation (Spectrum Technologies, Plainfield, Illinois, USA). Measurements were taken 12:30 to 13:30 during peak radiation (1000 – 1400 $\mu$mol $m^2$ $s^{-1}$) on July 4 and August 14 2009, both cloud-free days. I found no difference in light penetration between natural and artificial treatments (ANOVA, $F_{1,10} = 0.08$, $P = 0.78$), the though spectral properties of this light will likely differ.

Artificial-canopy and canopy-removal treatments were circular in shape, and approximately 6 m in diameter if located in large shrub patches (Fig. 5-1, plots 1, 3, 4, 6) or the size of the removed shrub patch (Fig. 5-1, plots 2, 5). The density of artificial shrub patches was constructed to mimic the structure of the shrub canopies removed from the adjacent canopy-removal treatment. I was not able to exactly duplicate natural shrub canopies and the artificial canopies had lower canopy height, slightly different stem spacing and reduced stem flexibility. The measured mean shrub height for all plots was 65 ± 4 cm in 2008 and 76 ± 4 cm in 2009 for the natural shrub treatment, and 47 ± 4 cm in 2008 and 60 ± 7 cm in

2009 for the artificial-canopy treatment. Over each growing season, I clipped new growth from the canopy-removal plots and maintained the artificial canopies. I measured the distances to surrounding shrub canopies from soil temperature and snow depth sensors at each plot. Because the natural and artificial-canopy treatments were not continuous in cover, and the natural tundra controls were not completely shrub free, distances to the nearest shrub canopy differs for all plots.

### *Biomass*

To quantify the biomass of shrub and understory species, I conducted above-ground biomass harvests in August 2007. Two 50 × 50 cm subplots were harvested 1 m up- and down- slope of the centre of each the 24 treatment plots. I sorted samples into eight functional groups (graminoids, forbs, prostrate shrubs, canopy-forming shrubs, green moss, lichen, brown moss and litter) and oven-dried them at 60°C prior to weighing. In September 2007, I dug soil pits 1 m up- and down- slope of the centre of each treatment plot, and I measured the organic matter depth and the total soil depth to bedrock.

### *Soil temperatures*

To measure soil temperatures, I installed Hobo Micro Station 12-bit temperature sensors (± 0.1°C, HOBO, Onset Computer Corp., Massachusetts, USA) at 2 and 5 cm below the soil surface in the centre of each plot. To measure snow depth, I attached iButton Thermochron temperature loggers (± 1°C, Model DS1921G, Dallas Semiconductor Corporation, Dallas, Texas, USA) to stakes at 2, 5, 25, 50, and 100 cm above the soil surface in the artificial-canopy, canopy-removal, control shrub and control tundra plots. Wooden stakes were used for the snow stakes during the 2007 – 2008 winter; however, some stakes broke during installation and removal so during the winter of 2008 – 2009, I switched to metal stakes with each iButton sensor insulated from the metal stake using 1 cm-thick closed-pore sealing foam. Snow stakes were installed 1.5 m up and down slope of the soil temperature sensors at the centre of each of the treatment plots (Fig. 5-1). Hobo and iButton temperature loggers were also installed 1.5 m above the soil surface in a radiation shield in the centre of the experimental site to measure air temperature (Fig. 5-1). Hobo Microstation temperature measurements were logged every 5 min, and iButton temperature measurments were logged every 6 hours.

During the course of the experiment, wires between sensors and data loggers at four plots were chewed by animals or damaged during maintenance of the shrub removal treatment. I repaired all damaged wires within two weeks, except for the sensor at 2 cm depth at the tundra plot 2a that could not be fixed and stopped logging measurements on 27 July 2008. To calculate monthly means and annual projections, I interpolated missing data by projecting temperatures from regressions between soil temperature data measured at the same location but a different depth or the closest plot with the same treatment and same depth. Regression relationships used to fill the data gaps had $R^2$ of greater than 0.80.

*Snow depth*

Snow depth was determined by comparing the daily mean temperature difference between iButtons at each height on the snow stake and air temperature (Danby and Hik 2007). For the calculation of snow depth, a temperature difference of greater than 3°C was considered to indicate that the iButton sensor was in the snowpack if 1) the sensor was reading a temperature below freezing and 2) if all sensors located below also met the same criteria. Snow depths were first measured as intervals (less than 2, 2 – 5, 5 – 25, 25 – 50, 50 – 100, greater than 100 cm) with the median temperature of the two replicate stakes used for further analysis. During the course of each winter, some of the 240 iButtons failed or fell off their stakes (33 iButtons in 2007 – 2008 and 10 in 2008 – 2009 and 36 in 2009 – 2010). In these instances, I used the data from the iButton placed at the same height on the replicate stake, or if these data were also missing, increased the snow-depth interval to account for lack of measurement at the height of the missing sensor. As the snow-depth data are not continuous, I presented central tendency using medians.

### *Soil moisture*

I conducted soil moisture measurements in the top 10 cm of the soil profile using a HydroSense® system (Campbell Scientific, Hyde Park, NSW, Australia). Measurements were taken at intervals of approximately two to three weeks throughout the growing season including eight days in 2007 (May 22, 31, June 6, July 4, 18, August 18, September 11, 26), three days in 2008 (June 6, July 15, September 8) and seven days in 2009 (June 15, 21, July 4, 13, 25, August 16, September 4).

### *Statistical analysis*

Statistical analyses were conducted using the software R (version 2.10.1, R Development Core Team, Vienna). I used Analysis of Variance (ANOVA) to test for differences in mean July and January temperature between the experimental treatments (Table 5-1). To test for differences in January snow depth between the experimental treatments, I used the Friedman rank sum test as these data were not continuous (Table 5-2). I chose four explanatory variables that were independent and might influence soil temperatures (distance to nearest shrub, soil moisture, moss biomass and organic layer depth) and used forward and backward stepwise model selection by Akaike information criterion (AIC), a measure of the relative goodness of fit of a statistical model, to identify variables that best explained mean July and January soil temperatures (Table 5-3). The variables moss biomass and soil moisture were log transformed and the variable distance to shrub was square root transformed to meet criteria for normality and homogeneity of variance.

## Results

### *Conditions prior to manipulation*

Soils in shrub plots were significantly cooler than tundra plots in July 2007 prior to the experimental manipulation (ANOVA, $F_{1,22} = 4.90$, $P = 0.04$), and during this time there was no significant difference between mean July soil temperatures of the plots retained as controls and those that underwent the experimental manipulation (ANOVA, $F_{1,22} = 0.01$, $P = 0.90$).

### *Snow depth*

After experimental manipulation, natural and artificial canopies trapped more snow than tundra and canopy-removal plots. Snow depth was greater in canopy plots in all years, but the difference between treatments was only significant in 2009 (Table 5-2 and 3, Fig. 5-2).

### *Soil temperatures*

Over the three years of this study, mean January soil temperatures were warmer in shrub versus tundra plots, and artificial-canopy plots versus canopy-removal plots (Tables 1 and 2, Fig. 5-3). There was a significant interaction between canopy and manipulation for mean January temperatures at 5 cm depth, indicating a difference between the natural and artificial treatments; however, there was no significant interaction at 2 cm depth (Table 5-1). Mean July soil temperatures were cooler in shrub compared with tundra plots, and artificial-canopy compared with canopy-removal plots when the shade cloth treatment was in effect (Tables 1 and 2, Fig. 5-3). Tundra plots had both greater thawing and freezing degree days than shrub plots (Table 5-1, Fig. 5-3).

A plot-level analysis of shrub cover, soil, and moss biomass data indicates that the distance to the shrub canopy is a major explanatory variable describing soil temperatures (Table 5-3, Fig. 5-4). The minimum distance to shrub canopy from the snow stakes was negatively correlated and snow depth was positively correlated with mean January soil temperatures at 2 cm depth (Fig. 5-4). Moss biomass was also a significant predictor of mean July soil temperatures (Table 5-3), though it did not significantly differ between canopy, tundra, canopy-removal or artificial-canopy treatments (ANOVA, $F_{1,22} = 0.42$, $P = 0.74$).

Table 5-1. Comparisons of soil temperature, thaw degree days (TDD) and freezing degree days (FDD, ANOVA) and snow depth (Friedman rank sum test) between canopy and canopy-free treatments (canopy) and manipulated and natural canopies (manipulation) and the interaction between canopy and manipulation treatments with year as a repeat measure.

| Soil Temperatures: ANOVA | | | | | | |
|---|---|---|---|---|---|---|
| Variable | Depth | *DF* | *F* Value | *P* value canopy | *P* value manipulation | *P* value canopy*manipulation |
| Mean July | 2 cm | 1,43 | 20.7 | <0.01 | 0.36 | 0.53 |
| | 5 cm | | 11.6 | <0.01 | 0.39 | 0.35 |
| Mean January | 2 cm | 1,66 | 32.3 | <0.01 | 0.29 | 0.10 |
| | 5 cm | | 27.2 | <0.01 | 0.56 | 0.02 |
| TDD | 2 cm | 1, 21 | 6.6 | 0.02 | *Not calculated for manip. plots* | |
| | 5 cm | | 4.7 | 0.04 | | |
| FDD | 2 cm | 1,43 | 12.8 | <0.01 | 0.43 | 0.36 |
| | 5 cm | | 11.8 | <0.01 | 0.55 | 0.10 |

| Snow Depth: Friedman rank sum test | | | | | | |
|---|---|---|---|---|---|---|
| Variable | *DF* | *F* Value | *P* value $\chi^2$ | *P* value F | Treatment | Sum of Ranks |
| Day with maximum temperature difference | 18 | 20.5 | 0.04 | <0.01 | Shrub | 11 |
| | | | | | Art. Canopy | 10 |
| | | | | | Canopy Removal | 6 |
| | | | | | Tundra | 3 |

Table 5-2. Maximum difference in mean daily soil temperatures and accumulated soil temperatures between shrub and tundra plots and artificial canopies and canopy removal treatments in summer and winter. Underlined values indicate differences in treatment plots prior to the experimental manipulation.

| | | | ∆ Shrub and Tundra plots | | ∆ Artificial canopies and Canopy removals | |
|---|---|---|---|---|---|---|
| | Date | Year | 2 cm | 5 cm | 2 cm | 5 cm |
| Max. ∆ in Soil Temp. (°C) | 22 July | 2007 | -2.8 | -1.4 | 1.9 | 2.0 |
| | 14 July | 2008 | -3.3 | -3.1 | -0.7 | -0.1 |
| | 29 July | 2009 | -1.6 | -1.5 | -3.6 | -2.2 |
| | 8 Feb. | 2008 | 8.7 | 8.7 | 5.9 | 3.6 |
| | 7 Jan. | 2009 | 6.7 | 6.5 | 5.1 | 3.6 |
| | 2 Jan. | 2010 | 5.1 | 4.9 | 3.9 | 2.3 |
| Accumulated Soil Temp.(°C) | Summer (1 June – 31 Aug.) | 2007 | 90 | 51 | 91 | 100 |
| | | 2008 | 98 | 88 | 40 | 32 |
| | | 2009 | 94 | 87 | 128 | 87 |
| | Winter (1 Oct. – 30 Apr.) | 2008 | 463 | 462 | 219 | 90 |
| | | 2009 | 435 | 435 | 239 | 202 |
| | | 2010 | 364 | 355 | 182 | 90 |
| Max. ∆ in Snow Depth (cm) | 8 Feb. | 2008 | 14 | | 9 | |
| | 7 Jan. | 2009 | 33 | | 4 | |
| | 2 Jan. | 2010 | 26 | | 6 | |

Table 5-3. Stepwise linear regression using the variables distance to shrub, mean July soil moisture, moss biomass and organic layer depth for mean July and January soil temperatures at 2 cm depth.

| | Year | Initial Model | Final Model | Slope ± SE | *DF* | *F* Value | *P* value canopy | $R^2$ |
|---|---|---|---|---|---|---|---|---|
| Mean July | 2008 | Distance<br>+ Moisture<br>+ Moss<br>+ Organic | Moss** | -0.7 ± 0.2 | 1,22 | 11.9 | <0.01 | 0.32 |
| | 2009 | | Distance<br>+ Moss* | 0.1 ± 0.1<br>-0.6 ± 0.3 | 2,21 | 3.6 | 0.05 | 0.18 |
| Mean Jan. | 2008 | Distance<br>+ Moisture<br>+ Moss<br>+ Organic | Distance* | -0.3 ± 0.1 | 1,22 | 7.9 | 0.01 | 0.23 |
| | 2009 | | Distance<br>+ Moisture** | -0.3 ± 0.1<br>0.9 ± 0.7 | 2,21 | 7.2 | <0.01 | 0.35 |
| | 2010 | | Distance* | -0.2 ± 0.1 | 1,22 | 7.0 | 0.02 | 0.21 |

Signif. codes: **<0.01 *0.01-0.05

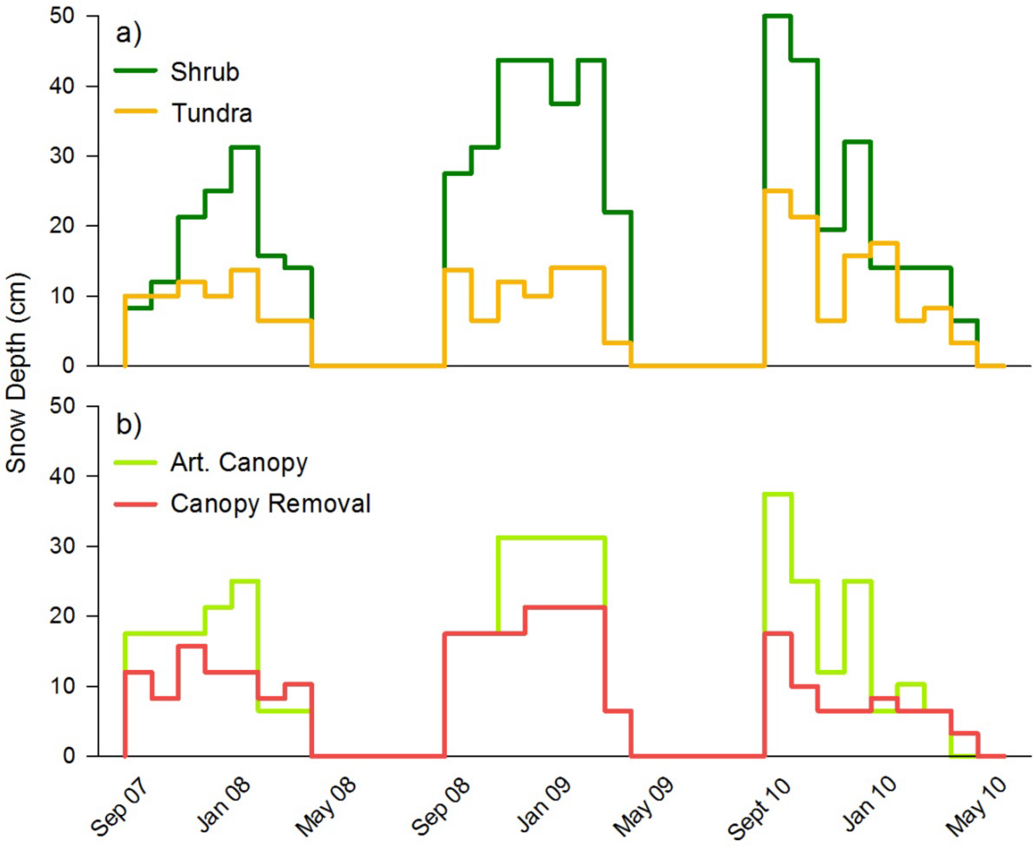

Figure 5-2. The median of snow depth at a) shrub and tundra plots and b) manipulated treatments for the day with the maximum difference in soil temperatures over the 2007 – 2008 and 2008 – 2009 winters (8 Feb. 2008, 7 Jan. 2009, 2 Jan. 2010).

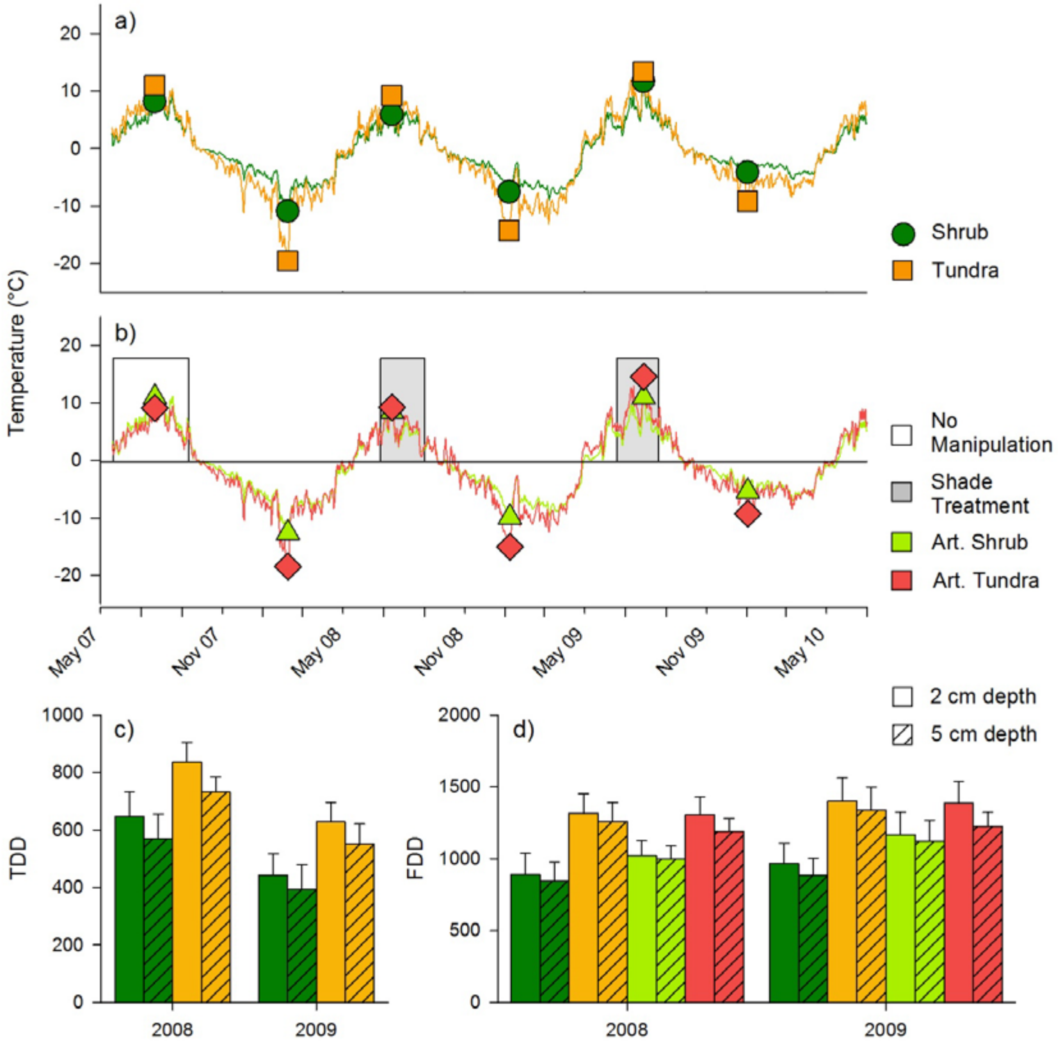

Figure 5-3. Soil temperature profiles between a) shrub and tundra plots and b) manipulated treatments and c) mean ± SE of thawing degree days (TDD) and d) freezing degree days (FDD). In plot b, the white box indicates the period prior to the manipulation, where the ‘canopy removal’ line is the temperature under an intact shrub canopy and the ‘artificial canopy’ line is the temperature in unmanipulated tundra. The grey boxes show the period of the manipulation when shade cloth covered the artificial canopy. In plots c and d, the solid bars indicate degree days at 2 cm depth and hatched bars indicate degree days at 5 cm depth.

## Discussion

My study provides experimental evidence that encroachment of woody shrubs will influence soil temperatures. Several studies highlight the importance of snow-shrub interactions on winter biological processes such as enhanced microbial activity under shrub canopies (eg. Sturm et al. 2001a, 2005); however, shrub canopies also influence summer soil temperatures (this study, Blok et al. 2009). Therefore, year-round temperature-sensitive, biological processes such as decomposition and nitrogen cycling in winter (Nobrega and Grogan 2007), summer (Buckeridge et al. 2010b) and shoulder seasons (Buckeridge et al. 2010a) could be altered by the presence of shrub canopies.

### Winter warming and summer cooling

Multiple factors will interact to alter the effects of shrubs on understory vegetation and soil temperatures. Summer shading is controlled by the height and density of the canopy (Pomeroy et al. 2006, Brantley and Young 2010) and winter insulation by, canopy structure and snow-loading capacity in addition to snow-pack development, wind and landscape topography (Sturm et al. 2001a, Liston et al. 2002, Sturm et al. 2005, Marsh et al. 2010). My data allow for a comparison of the relative importance of the ‘snow trapping’ and ‘soil shading’ influences of shrub canopies in a heterogeneous tundra environment. My experiment supports the hypothesis that shrubs trap snow in areas where snow is redistributed by wind and that this additional snow insulates soils (Sturm et al. 2005). However, my data also indicated 2°C cooler soils under shrub canopies in summer. This amount of cooling during the most biologically active time of year is significant when compared to the 4-5°C warming observed during the coldest part of the winter.

Canopy-forming shrub tundra can have deeper snow and warmer mean annual soil temperatures relative to shrub-free or prostrate shrub tundra. Warmer winter soils can lead to greater winter soil $CO_2$ respiration (Nobrega and Grogan 2007), faster nitrogen cycling (Buckeridge et al. 2010b), increased nutrient availability in spring (Schimel et al. 2004, Buckeridge et al. 2010a), and thaw of permafrost resulting in the decomposition of old carbon (Schuur et al. 2009). However, the influence of canopy shading on summer soil temperatures, annual carbon budgets and nutrient cycling can be also be quite large. Over the long term, if canopy-forming shrubs begin to dominate tundra ecosystems, cooler soils can reduce active layer depths, potentially restoring permafrost (Lantz 2008, Blok et al. 2009). Understanding the relative importance of the winter-warming and summer-cooling effects of a shrub canopy will be critical when modeling the influence of shrub canopies on tundra ecosystem functions such as soil carbon storage, nitrogen cycling or permafrost degradation.

### *Experimental treatments versus control plots*

Though artificial-canopy treatments functioned similar to natural shrub canopies, the strength of the soil cooling in summer and soil insulation in winter was weaker for artificial canopies. These canopies were formed with dead stems fastened to the surface, rather than being rooted in the soil, and by spring, some stems had fallen over. The artificial canopies were therefore lower, less dense and likely had reduced strength to trap and hold snow during winter, and therefore these factors could explain the lower snow depths and cooler winter soil temperatures observed in the artificial canopy treatment. Alternatively, the artificial canopy plots might have been located in sites that had lower snow depths due to localized topography. Likewise, though light penetration was similar between natural and artificial-canopy treatments (Fig. 5-4), shade cloth did not completely replicate leaves and this could explain the slightly warmer soils in the artificial-canopy versus shrub plots. As moss biomass was also a significant predictor of mean July soil temperatures (Table 5-3), greater moss biomass and soil insulation in artificial-canopy treatments could have decreased the strength of the canopy cooling in these plots.

Summer soil temperatures in the canopy removal treatment were warmer than those in any other treatment (Fig. 5-3). Removal of the canopy exposed mostly litter and bare soil, as understory species cover was reduced under dense shrub canopies. Due to the lower surface albedo, these plots warmed substantially during the summer relative to the other treatments (Table 5-2). My study was conducted over three years, but if the experiment was maintained over a longer period, plants would likely colonize the canopy removal plots. Over a longer-term experiment, the influence of the canopy on soil temperatures might change as both the canopy-removal and artificial-canopy treatments adjusted to the manipulated conditions.

### *Weather conditions*

The influence of shrub canopies on snow trapping and snow melt rates is moderated by weather conditions in a given year (Pomeroy et al. 2006). In my experiment, the influence of canopies on soil temperatures varied between years with different weather conditions. Differences in snow depth between treatments were larger in the high snowfall winters of 2008 – 2009 and 2009 - 2010 (Table 5-2, Environment Canada, Burwash Weather Station). Differences in summer cooling between natural and artificial canopies and tundra and canopy-removal treatments were greater in 2009 (Table 5-2), one of the warmest summers in recent years (Environment Canada, Burwash Weather Station). The influence of shrub canopies on soil temperatures could vary both temporally and spatially across a gradient in weather conditions. Further investigations of shrub canopies and soil temperatures could be conducted at a variety of different locations around the Arctic experiencing both continental and coastal climates.

### *Shrub densities*

When extrapolating my results across different extents of shrub cover, one would expect the relative influence of winter warming and summer cooling to vary (Fig. 5-4, Grogan and Jonasson 2006). In areas of dense shrub cover, shrub-induced summer cooling will likely dominate winter warming, as snow redistribution should be minimal (Lantz 2008). My study indicates that where shrubs occupy about half of the ground surface, winter warming will be balanced to some extent by summer cooling. In zones of sparse canopy-forming shrub cover, both shading and snow trapping will likely be minimal. In addition, the spatial arrangement of shrub cover will influence the distribution of snow and resulting soil insulation (Lantz 2008). Therefore, further investigations of the influence of shrubs on soil temperatures should be conducted using shrubs of varying densities and canopy heights.

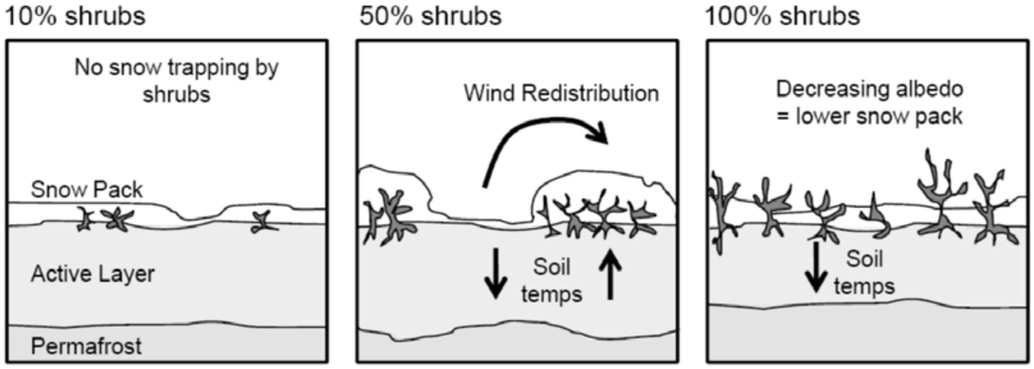

Figure 5-4. Influence of the ‘snow trapping’ hypothesis in 10%, 50% and 100% shrubs (modified after Grogan and Jonasson 2006, Lantz 2008).

## Conclusion

My experimental manipulations quantified the impact of shrub canopies on the ground thermal regime. Soil temperatures were cooler in summer and warmer in winter under shrubs and artificial canopies. The manipulated treatments functioned similarly to unmanipulated treatments, indicating that the shrub canopy was a dominant factor influencing soil temperatures. Tundra ecosystems are an important component of global carbon budgets (McGuire et al. 2009) and efforts to model the influence of future climate on tundra ecosystem function needs to include vegetation change (Euskirchen et al. 2009). Both influences of shrub canopies, the insulation provided by snow trapping in winter and soil shading in summer, must be added to ecosystem models projecting albedo, carbon cycling and permafrost integrity. Further experimental research is required to quantify the ecological impacts of increasing shrubs in tundra ecosystems.

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# Chapter 6. The influence of shrub canopies on carbon and nitrogen pools and fluxes in alpine tundra

## Introduction

Growing evidence indicates that canopy-forming shrubs are becoming more prevalent in tundra ecosystems (Forbes *et al.* 2010, Lantz *et al.* 2009, Sturm *et al.* 2001a, Tape *et al.* 2006). Increases in woody shrubs will likely alter abiotic components of tundra ecosystems including reflectance (Chapin et al. 2005, Loranty et al. 2011) snow melt (Pomeroy et al. 2006, Marsh et al. 2010) and soil temperatures (Sturm et al. 2001, 2005). In addition, increases in canopy cover and height of shrub species are predicted to alter tundra biotic ecosystem functions such as litter inputs to soils (Cornelissen et al. 2007) and nutrient cycling (Weintraub and Schimel 2003, 2005, Wookey et al. 2009, Buckeridge et al. 2010b). In addition, higher evapotranspiration from greater shrub biomass could dry soils, reducing methane emissions and increasing carbon dioxide fluxes (Merbold et al. 2009). However, few studies have quantified the influence of shrub canopies on ecosystem functions such as decomposition or nitrogen cycling in isolation from the biotic factors that are altered by shrub encroachment including litter inputs, woody roots and species composition of the understory.

Shrub canopies have been shown to influence the distribution of snow (Marsh et al. 2010), which results in warmer winter soil temperatures under shrub canopies (Chapter 5). During spring, shrubs that extend above the snow alter the albedo and accelerate local snow melt, and in summer, shading reduces soil temperatures under shrub canopies (Chapter 5, Pomeroy et al. 2006). Experimental manipulations have demonstrated that deeper snow depth and warmer winter soils can increase litter decomposition (Baptist et al. 2009) and nutrient cycling (Schimel et al. 2004, Nobrega and Grogan 2007, Buckeridge and Grogan 2010). Building from these experiments, snow-shrub interactions have been hypothesized to create a positive feedback to shrub growth and expansion by increasing nutrient availability in soils under shrub canopies (Sturm et al. 2001, Weintraub and

Schimel 2005, Sturm et al. 2005, Grogan and Jonasson 2006, Buckeridge et al. 2010b).

Fertilization experiments show that vascular plant productivity is nitrogen limited in tundra ecosystems (Shaver and Chapin 1980, Mack et al. 2004), and both nitrogen fertilization experiments and warming experiments in tundra ecosystems increase biomass of shrub species (Dormann and Woodin 2002). Tying together the influence of shrub canopies on decomposition and nutrient cycling in tundra ecosystems is still an emerging field of study. Buckeridge et al. (2010) investigated nitrogen cycling in a shrub tundra ecosystem with canopy-forming and prostrate birch canopies and reported that larger inputs of higher quality litter promoted rapid soil nitrogen cycling and enhanced shrub growth in canopy-forming birch tundra. Increases in shrubs are predicted to alter tundra nutrient cycling through snow-shrub interactions (Sturm et al. 2001), but it remains unclear whether the changes in nutrient cycling will be due to direct effects of canopy cover or indirect effects of changes to plant composition, litter inputs and altered soil biogeochemistry.

I investigated carbon and nitrogen dynamics in shrub and adjacent shrub-free tundra and using a manipulative experiment with canopy removals and artificial canopies. I compared the direct impacts of canopy cover and resulting soil temperature changes, to the indirect effects of willows on soils that develop over decades. I investigated soil carbon and nitrogen, decomposition, plant-available nitrogen and $CO_2$ efflux rates using in situ and laboratory incubations to test the following hypotheses: 1) that decomposition is lower under shrub canopies due to cooler soil temperatures, 2) that plant available nitrogen is lower under shrub canopies due to greater nutrient uptake from shrub plants, and 3) that the rate of $CO_2$ efflux is higher under the shrub canopy during the growing season due to enhanced decomposition and higher autotrophic respiration.

## Methods

My experimental site was located in the Ruby Range, southwest Yukon Territory, Canada (61°N, 138°W, ele. 1450 m). Here, I measured nutrient pools and fluxes in alpine tundra with approximately 50% cover of canopy-forming shrub patches that were 30 -100 cm tall. The dominant canopy-forming shrubs in this region are willow species (*Salix pulchra* Cham., *Salix glauca* L. Hook. and *Salix richardsonii* Hook.), common understory species include *Salix reticulata* L., *Dryas octopetala* L., *Polygonum bistorta* L. ssp. *plumosum* (Small) Hultén, *Festuca* spp., and *Carex* spp. For a more detailed description of the field site see Chapter 5.

My study was established in 12 paired tundra and shrub plots, and in September 2007, I experimentally manipulated 6 tundra and shrub plots resulting in four treatments: 1) intact shrubs, 2) canopy removals, 3) artificial canopies, and 4) adjacent tundra. The six artificial-canopy plots and six canopy-removal plots were constructed by cutting shrubs at the stem base and affixing them to wooden stakes in the soil in tundra without shrub cover. Since artificial canopies lacked foliage, these plots were covered by shade cloth to mimic natural canopy shading for approximately two months of the summer. For a more detailed description of the experimental treatments see Chapter 5. To measure soil temperatures, I installed Hobo Micro Station 12-bit temperature sensors (± 0.1°C, HOBO, Onset Computer Corp., Massachusetts, USA) at 2 and 5 cm below the soil surface in the centre of each plot. To measure snow depth I used iButton Thermochron temperature loggers (± 1°C, Model DS1921G, Dallas Semiconductor Corporation, Dallas, Texas, USA) attached to stakes (see Chapter 5 for further descriptions).

### *Biomass*

In August of 2007, I destructively harvested paired 50 × 50 cm plots 1 m up- and 1 m down- slope and 1 m adjacent to the centre of each of the 24 treatment plots. Biomass samples were sorted into the following plant functional group categories: canopy-forming shrubs (*Salix* and *Betula* species with a canopy height greater than 10cm), prostrate shrubs (shrub species growing less than 10 cm tall), graminoids (live and dead), *Dryas* (live and dead), *Cassiope*, green moss and liverworts, lichens, fungus, forbs, brown moss and decomposed litter, dried at 65°C and then weighed.

### *Soils*

On 21 September 2007, I dug and described soil pits and measured the depth of each soil layer according to the Canadian Soil Classification System in the same plots harvested for biomass samples. At the same time I harvested 5 × 5 × 5 cm cubes of the top 5 cm of the soil surface, immediately below the moss layer. These samples were collected, transported to the laboratory and stored frozen. The soil samples were divided into sub samples. One set of the subsamples (2 × 5 × 5 cm cubes) were dried at 65°C, weighed for the calculation of bulk density and then ground for nutrient analysis, the other subsamples (3 × 5 × 5 cm cubes) were used for laboratory $CO_2$ incubations.

### *Soil incubations*

I conducted soil $CO_2$ incubations on 5 × 5 × 3 cm frozen blocks of surface soils from each of my treatment plots. Samples were weighed prior to the start of the experiment. Samples were incubated in an environmentally controlled chamber (University of Alberta Department of Biological Sciences Biotron facility) for 20 hours of full light, a humidity of 50% and a temperature of 20°C. On 8 July 2008, I placed 54 mason jars (900mL) with the frozen blocks of soil placed on top of a sponge (approx. 5 × 4 × 4 cm) wetted with 30ml of distilled water in the growth chamber. Into each of the mason jars I placed a small, unsealed vial of 10ml 1M NaOH that rested on the bottom of the mason jar beside the sponge and soil block. Six randomly chosen jars were designated control jars and contained a wetted sponge, vial of 1M NaOH, but no soil. After seven days of incubation on 15 July 2008, the reacted vials of 1M NaOH were removed and replaced by vials containing unreacted 1M NaOH. I performed two replicate titrations using phenolphthalein as an indicator and 1M HCl on each of the vials of 1M NaOH as they were removed from the incubation jars. Incubations were repeated after 14 and 25 days on 22 July and 25 August 2008. After the final titration, the blocks of soil were dried at 65°C and ground for carbon and nitrogen analysis. Soil carbon respiration was determined by subtracting the final volume after titration by half the initial volume of 1M NaOH, resulting in the volume of reacted 1M NaOH. I then converted this volume to respiration in $\mu$g $CO_2$ $m^{-3}$ $s^{-1}$.

### *Decomposition*

I used litter bags to measure rates of decomposition between treatment plots. I stapled 10 × 10 cm bags made out of 1 × 1 mm mesh divided into two pouches. In each side of the litter bags I inserted 0.5 g of cellulose filter paper (75 mm Whatman qualitative) or homogenized and air dried *Betula glandulosa* litter from a common site adjacent to the experimental plots. Litter bag contents were weighed to 0.01g before installation. Litter bags were incubated for one year from 21 September 2007 to 26 September 2008. I placed paired litter bags on the ground surface and horizontally in the soil at 5 cm depth. Litter bags were installed 1 m up and down slope of the centre of the shrub and tundra treatments. After removal, paper and litter samples from the litter bags were dried at 65°C and weighed to an accuracy of 0.01g. Litter samples were then ground for carbon and nitrogen analysis using a mortar and pestle.

### *Nitrogen*

To measure ammonium and nitrate bioavailability, I installed anion and cation exchange resin probes (Plant Root Simulator™ probes, Western Ag Innovation Inc., Saskatoon, Saskatchewan, Canada). Nitrogen availability was measured as $NO_3$-N and $NH_4$-N accumulation onto PRS™ ion exchange probes that were charged with $HCO_3^-$ and $H^+$, respectively. The probes were incubated for 2 months from 1 July to 20 August in 2007 and 1 July to 31 August in 2008 in the surface soils of each treatment plot. When removed, probes were cleaned with de-ionized water, inserted into clear plastic bags, and shipped on ice to the Western Ag Innovations laboratory for analysis.

### *Soil respiration and soil moisture*

I conducted soil $CO_2$ efflux measurements using a LI6400 infrared gas analyzer (*LI-COR Environmental*, Lincoln, Nebraska, USA) throughout the growing season during the 3 years of the experiment. Efflux measurements were made using an LI-6400-09 Soil $CO_2$ Flux Chamber placed on top of three replicate PVC collars installed permanently at each treatment plot into the top 3 cm of the soil. Three repeat efflux measurements were conducted at each of the three collar locations at each treatment plot, during daylight hours between 9 am and 9 pm. The LI6400 was calibrated using soda lime $CO_2$ scrub and a 397 ppm $CO_2$ reference gas before each measurement campaign. I conducted measurements at intervals of approximately two to three weeks across the growing season on 8 days in 2007 (May 22, 31, June 6, July 4, 18, August 18, September 11, 26), 3 days in 2008 (June 6, July 15, September 8) and 7 days in 2009 (June 15, 21, July 4, 13, 25, August 16, September 4). For some of the dates at the beginning and end of the growing season, when efflux measurements were slower, I was only able to complete a subset of the plots. Soil moisture measurements were conducted at the same time as soil $CO_2$ efflux measurements using a HydroSense® system (Campbell Scientific, Hyde Park, NSW, Australia).

### *Carbon and nitrogen*

I ground soil samples, subsamples of biomass from the dominant plant functional groups, and litter from the decomposition experiment. Samples were homogenized by hand and ground with a ball mill or coffee grinder. I analyzed 2-3 μg of each soil, plant or litter sample for of total carbon and nitrogen analysis using a Control Equipment Corporation Model 440 Elemental Analyzer (Chelmsford, MA, USA).

### *Statistical analysis*

Statistical analyses were conducted using the software R (version 2.10.1, R Development Core Team, Vienna). I used Analysis of Variance (ANOVA) and

Multivariate Analysis of Variance (MANOVA) to test for differences between treatments prior to and after experimental manipulation. I chose explanatory variables that were independent and used forward and backward stepwise model selection by AIC to identify variables. To meet criteria for normality and homogeneity of variance, variables were log transformed when appropriate.

## Results

### *Initial conditions*

Shrub plots had 2.4 times more live biomass, three times the nitrogen and 2.4 times the carbon in the live plant biomass relative to tundra plots. The greatest difference in live biomass was between the canopy-forming shrub functional group, which was nearly absent in tundra plots (Fig. 6-1). Litter mass and organic layer depths were similar between treatments (Table 6-1, Fig. 6-1). I observed no significant differences between soil parameters, percent soil carbon or nitrogen, total understory biomass, or carbon respired from soil samples between the tundra and shrub plots at the establishment of the experiment (Table 6-2).

### *Litter bag decomposition*

I observed no significant difference in decomposition of litter or filter paper at either the soil surface or 5 cm depth, with the exception of the paper substrate at 5 cm depth (Table 6-3). The percent carbon and percent nitrogen in the litter substrate after decomposition, was the same with the exception of percent carbon in the litter bags deployed on the soil surface, which was lower in shrub versus artificial canopy and canopy removal plots (Table 6-3, Fig. 6-2c). I observed higher decomposition in the shrub plots at 5 cm depth when compared to the other treatments (Fig. 6-2). The only significant model for the decomposition data showed that soil bulk density and soil percent nitrogen explained 42% of the variation in decomposition among plots for the paper substrate at 5 cm depth (Table 6-4).

### *Nitrogen incubations*

I observed no significant relationship between shrub canopy treatments and total nitrogen, $NH_4$ or $NO_3$ in either 2007 or 2008 (Table 6-2 and 3), with the exception of total nitrogen in 2008 (Table 6-3). Absorbed nitrogen was higher in the canopy removal treatment in 2008 when compared to the 2007 data from prior to the establishment of the experimental treatments (Fig. 6-3). The only significant model explaining nitrogen incubation data showed that mean July soil temperature at 2 cm depth explained 19% of the variation in absorbed nitrogen across all plots (Table 6-4).

### *Incubations, soil efflux, soil moisture*

I observed no significant difference in field and laboratory measurements of respired $CO_2$ between treatments (Table 6-2, Fig. 6-4, repeated-measures ANOVA, $F_{1,25} = 0.52$, $P = 0.67$). Field measurements of $CO_2$ soil efflux were weakly associated with the variables soil percent carbon, and mean July soil temperature at 2 cm depth (Table 6-4). Field measurements of soil moisture were significantly different between treatments, with lower soil moisture observed in the shrub plots in 2007 prior to the experimental manipulation, no difference in 2008 between treatments and lower soil moisture in the canopy removal and shrub plots in 2009 (Repeated Measures ANOVA, , $F_{3,267} = 4.14$, $P = 0.01$, Fig. 6-2).

Table 6-1. Biomass, %C, %N and carbon and nitrogen in biomass for shrub and tundra plots prior to the establishment of canopy removal and artificial canopy treatment plots.

| | Treatment | Litter | Green Moss | Lichen | Graminoids | Deciduous Shrub |
|---|---|---|---|---|---|---|
| Biomass g m$^{-2}$ | Shrub | 790 ± 59 | 201 ± 58 | 31 ± 8 | 65 ± 12 | 55 ± 27 |
| | Tundra | 720 ± 48 | 163 ± 43 | 56 ± 9 | 81 ± 12 | 220 ± 50 |
| % N | Shrub | 1.7 ± 0.1 | 1.2 ± 0.1 | 1.5 ± 0.2 | 1.3 ± 0.1 | 1.4 ± 0.1 |
| | Tundra | 1.3 ± 0.1 | 1.0 ± 0.1 | 0.9 ± 0.1 | 1.1 ± 0.1 | 1.3 ± 0.04 |
| % C | Shrub | 41 ± 3 | 42 ± 0 | 31 ± 5 | 38 ± 3 | 43 ± 5 |
| | Tundra | 40 ± 3 | 42 ± 0 | 23 ± 6 | 36 ± 4 | 42 ± 5 |
| g N m$^{-2}$ | Shrub | 13.4 ± 1.0 | 2.5 ± 0.7 | 0.5 ± 0.1 | 0.9 ± 0.2 | 0.8 ± 0.4 |
| | Tundra | 9.6 ± 0.6 | 1.6 ± 0.4 | 0.5 ± 0.1 | 0.9 ± 0.1 | 2.9 ± 0.7 |
| g C m$^{-2}$ | Shrub | 323 ± 24 | 85 ± 24 | 10 ± 3 | 25 ± 5 | 23 ± 11 |
| | Tundra | 289 ± 19 | 69 ± 18 | 13 ± 2 | 29 ± 4 | 92 ± 21 |

| Table 6-1 continued: | *Dryas* | Forbs | *Cassiope* | Canopy-forming Shrub | Total |
|---|---|---|---|---|---|
| Biomass g m$^{-2}$ | 5 ± 3 | 1 ± 1 | 33 ± 22 | 1074 ± 247 | 1464 ± 377 |
| | 86 ± 21 | ~0 | 16 ± 9 | ~0 | 622 ± 145 |
| % N | 1.5 ± 0.2 | 2.0 ± 0.4 | 1.3 ± 0.1 | 1.5 ± 0.1 | |
| | 1.2 ± 0.0 | 1.6 ± 0.2 | 1.5 ± 0.2 | 1 | |
| % C | 47 ± 1 | 26 ± 21 | 52 ± 1 | 42 ± 5 | |
| | 47 ± 0 | 44 ± 0 | 52 ± 0 | 45 | |
| g N m$^{-2}$ | 0.1 ± 0.04 | ~0 | 0.4 ± 0.3 | 16.2 ± 3.7 | 21 ± 5 |
| | 1.1 ± 0.3 | ~0 | 0.2 ± 0.1 | ~0 | 7 ± 2 |
| g C m$^{-2}$ | 2 ± 1 | ~0 | 17 ± 12 | 456 ± 105 | 618 ± 161 |
| | 40 ± 10 | ~0 | 9 ± 5 | ~0 | 252 ± 60 |

Table 6-2. Comparison of soil conditions between shrub and tundra plots prior to shrub canopy manipulations (tundra vs shrub, n = 12).

| Category | Variables | *DF* | *F* value | *P* value ANOVA | *P* value MANOVA |
|---|---|---|---|---|---|
| Soils | Soil depth | | ns | | ns |
| | Soil mass | | ns | | |
| | Organic layer depth | | ns | | |
| Soil CN | % carbon | | ns | | Pillai = 0.27<br>F = 3.91<br>P = 0.04 |
| | % nitrogen | | ns | | |
| Biomass | Total Biomass | 1, 22 | 14.81 | <0.01 | Pillai = 0.70<br>F = 15.61<br>P = 0.01 |
| | Understory | | ns | | |
| | Moss | | ns | | |
| Incubations | Day 0 | | ns | | ns |
| | Day 7 | | ns | | |
| | Day 14 | | ns | | |
| Nitrogen 2007 | Total | | ns | | ns |
| | $NO_3$ | | ns | | |
| | $NH_4$ | | ns | | |

Table 6-3. Comparison of nutrient variables after manipulation between tundra, shrub, canopy removal, artificial canopy treatments (n = 6).

| Category | Variables | *DF* | *F* value | *P* value ANOVA | *P* value MANOVA |
|---|---|---|---|---|---|
| Decomposition | Litter (0 cm) | | ns | | ns |
| | Paper (0 cm) | | ns | | |
| | Litter (5 cm) | | ns | | |
| | Paper (5 cm) | 3,20 | 4.02 | 0.02 | |
| Decomp. CN | %N (0 cm) | | ns | | Pillai = 0.96<br>F = 2.24<br>P = 0.02 |
| | %C (0 cm) | 3, 20 | 4.91 | 0.01 | |
| | %N (5 cm) | | ns | | |
| | %C (5 cm) | | ns | | |
| N Probes 2008 | Total | 3,20 | 4.64 | 0.01 | ns |
| | $NO_3$ | | ns | | |
| | $NH_4$ | | ns | | |

Table 6-4. Stepwise multiple linear regression describing variation in soil $CO_2$ respired during incubations, nitrogen accumulated on PRS probes, decomposition of litter bag treatments, and measured $CO_2$ and soil moisture for all plots.

| Data Set | Dependent Variable | Initial Model | Final Model | Slope ± SE | *DF* | Adj. $R^2$ | *F* value | *P* value |
|---|---|---|---|---|---|---|---|---|
| Incubations | Day 7 | mass<br>+ %C<br>+ biomass<br>+ July temp | ns | | | | | |
| | Day 14 | | ns | | | | | |
| | Day 25 | | ns | | | | | |
| N Probes 2007 | Total | OM<br>+ %N<br>+ moss<br>+ July temp<br>+ moisture | ns | | | | | |
| | $NO_3$ | | ns | | | | | |
| | $NH_4$ | | ns | | | | | |
| N Probes 2008 | Total | | July temp** | 0.08 ± 0.03 | 1,22 | 0.18 | 6.20 | 0.02 |
| | $NO_3$ | | ns | | | | | |
| | $NH_4$ | | ns | | | | | |
| Litter Bags | Litter 0 cm | mass<br>+ %N<br>+ biomass<br>+ Jan temp | ns | | | | | |
| | Paper 0 cm | | ns | | | | | |
| | Litter 5 cm | | ns | | | | | |
| | Paper 5 cm | | Mass*<br>+ %N**<br>+ Jan temp | -0.16 ± 0.06<br>10.89 ± 2.96<br>0.80 ± 0.42 | 3,20 | 0.48 | 8.18 | <0.01 |
| $CO_2$ Flux | | OM<br>+ %C<br>+ biomass<br>+ July temp<br>+ moisture | %C<br>+ July temp. | 0.02 ± 0.01<br>0.09 ± 0.05 | 2,21 | 0.20 | 3.80 | 0.04 |
| Soil Moisture | | mass<br>+ moss<br>+ July temp | ns | | | | | |

Signif. codes: **<0.01 *0.01-0.05

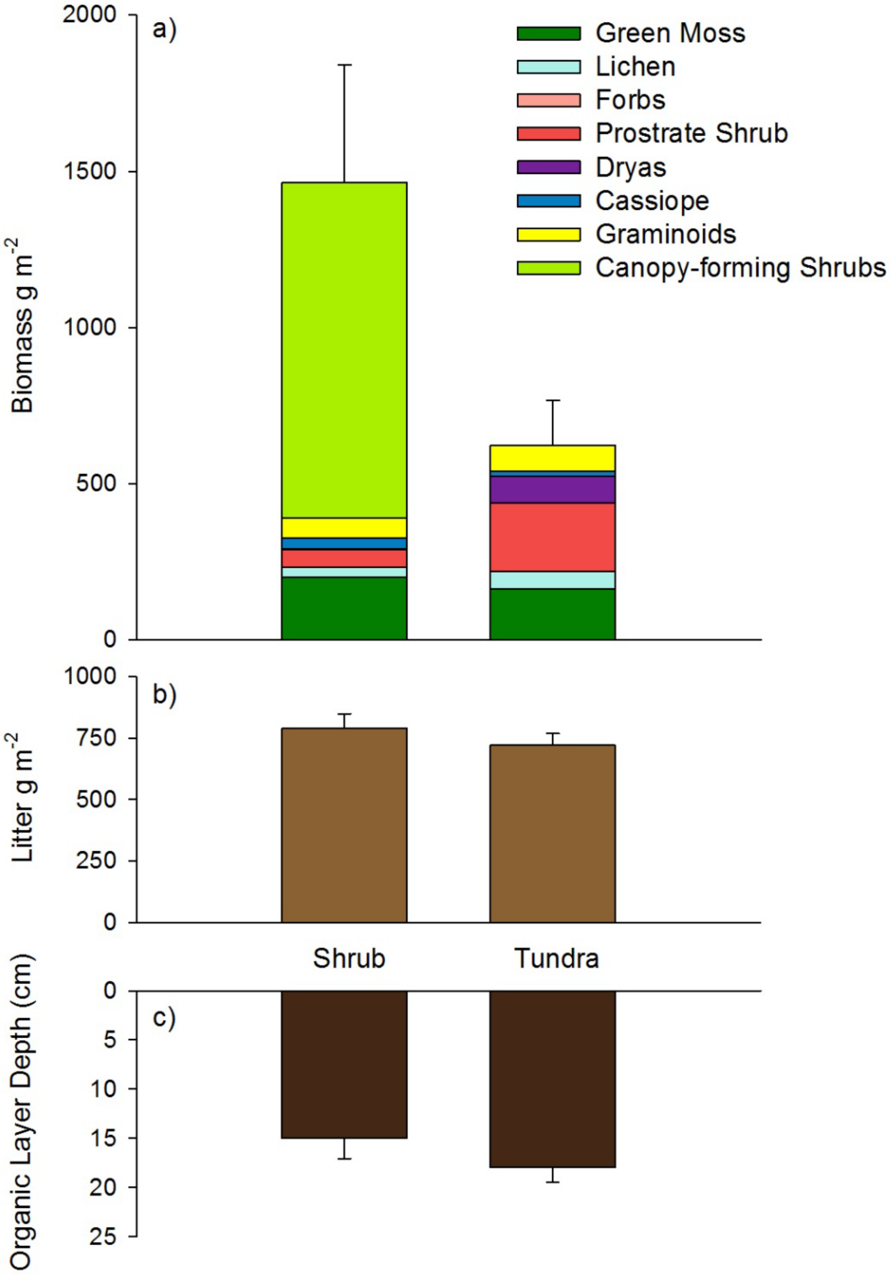

Figure 6-1. Biomass and percent carbon in biomass of plant functional groups (a), and soil layer depths and percent carbon in soils in shrub and shrub-free tundra plots.

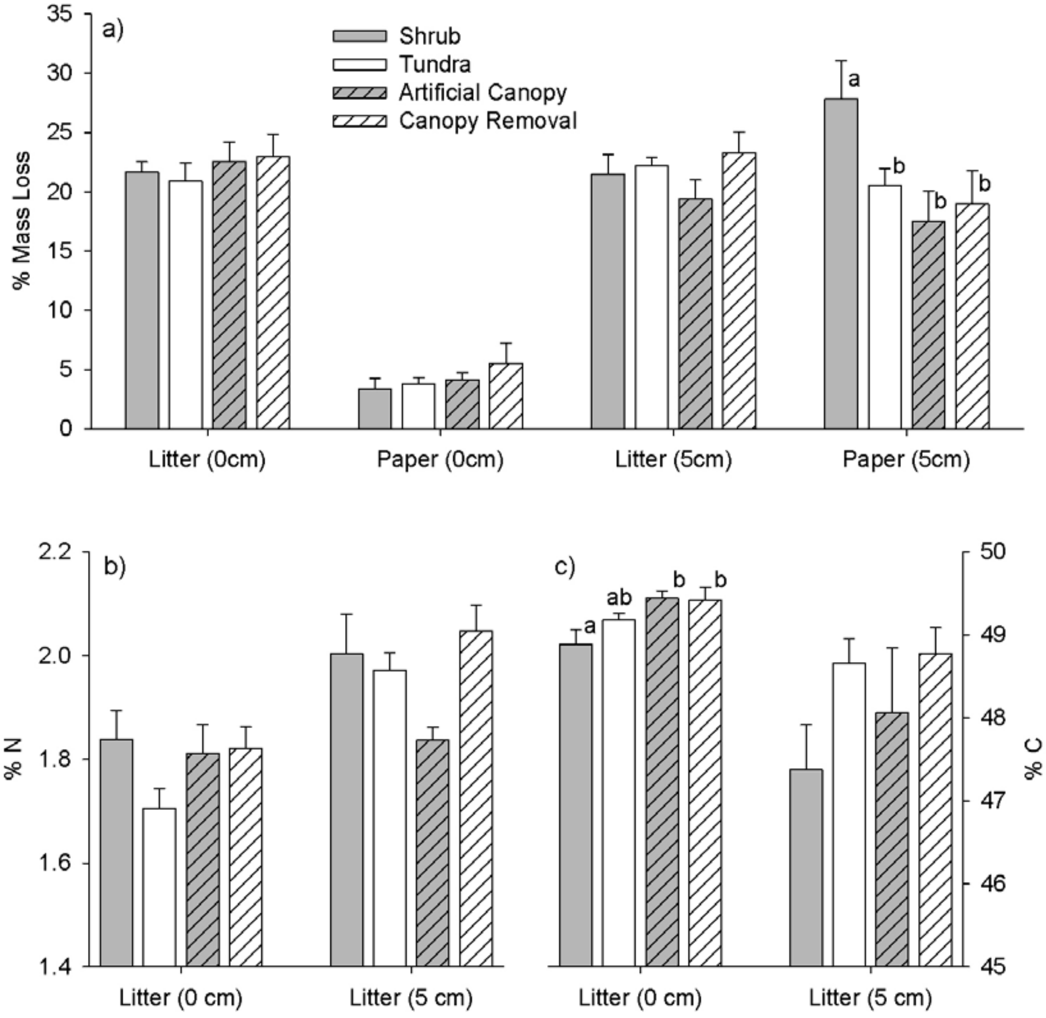

Figure 6-2. Percent mass loss between the litter and paper substrates over one year from 21 September 2007 to 26 September 2008, on a) the surface and at 5 cm depth in the soil profile for experimental treatments, b) percent nitrogen in leaf litter after incubation, and c) percent carbon in leaf litter after incubation. Significant differences between treatments for litter mass loss at 5 cm depth and percent carbon in incubated litter at the soil surface are indicated by letters (Table 6-3).

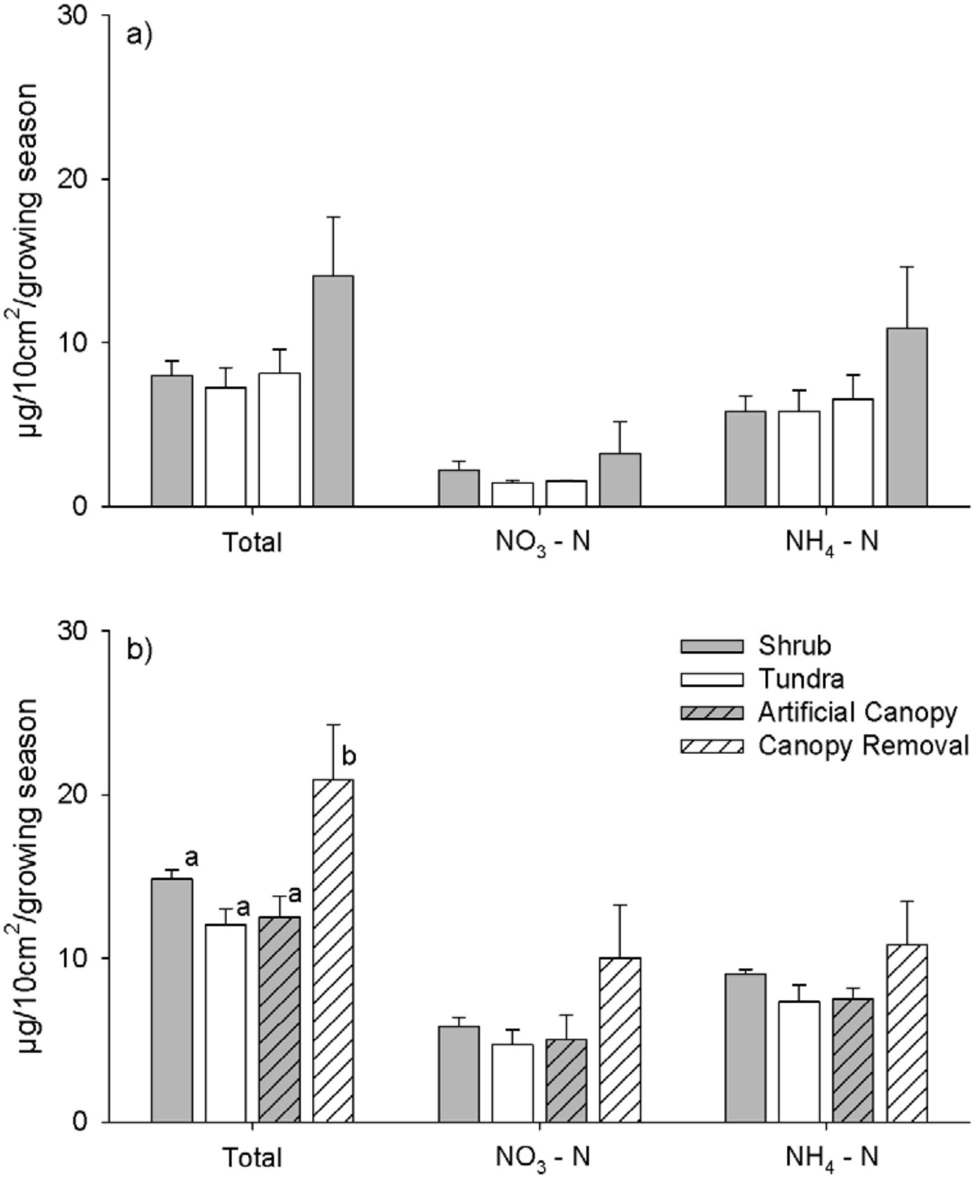

Figure 6-3. Accumulation of nitrate and ammonium on the membrane of PRS™ probes in each of the treatment plots across the growing seasons of a) 2007 and b) 2008. In 2007, incubations were conducted prior to the establishment of the experimental treatments; therefore, in plot a, I present bars for the control shrub and tundra plots and the shrub and tundra plots that were assigned to the experimental treatments. A significant difference in total accumulation (nitrate plus ammonia) was observed between treatments in 2008 as indicated by the letters (Table 6-3).

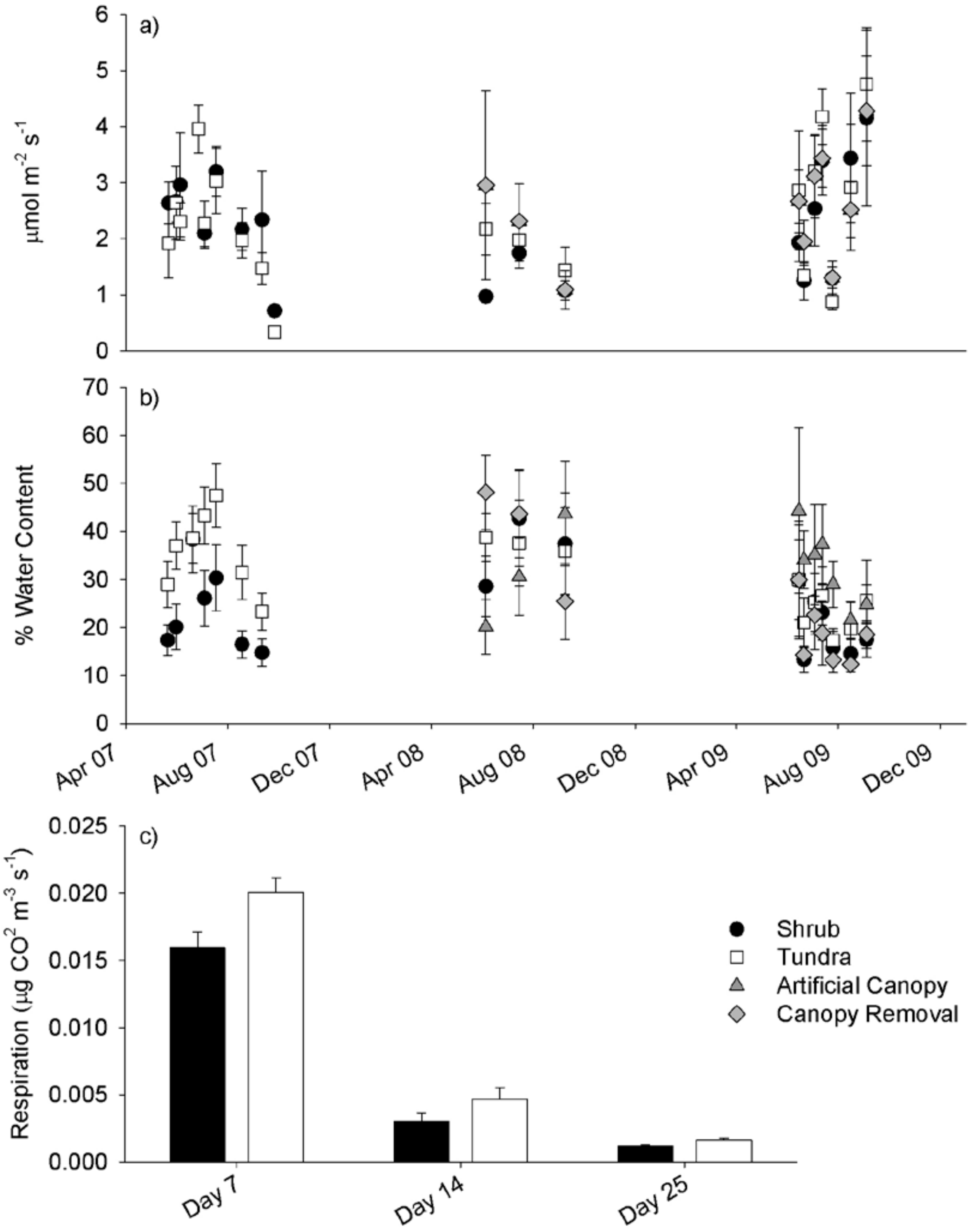

Figure 6-4. Field measurements of a) soil $CO_2$ respiration and b) soil moisture for 2007, 2008 and 2009 for each of the experimental treatments, and c) laboratory measurements of soil $CO_2$ respiration from 25-day incubations at 20°C.

## Discussion

Though other studies have shown compelling evidence of differences in nutrient cycling between canopy-forming shrub and prostrate tundra plots (Weintraub and Schimel 2005, Buckeridge et al. 2010b), I did not find strong evidence of an influence of shrub canopies on nutrient parameters using a manipulative experiment. My data suggest that shrub canopies can influence nutrient cycling, but that the direct effects of shrub canopies on soil temperatures as a result of snow trapping and shading are weak controls on the variables and time period investigated in this study (Fig. 6-5). Shrub canopies undoubtedly influence shrub canopies over the long term by altering litter inputs, course woody debris, and soil biota (De Deyn et al. 2008); however, without clear directional influences of shrub canopies on soil nutrient dynamics over shorter time periods, the proposed feedbacks to climate warming and further shrub expansion (Chapter 1, Figure 1-5) might not be as strong as currently suggested in the literature.

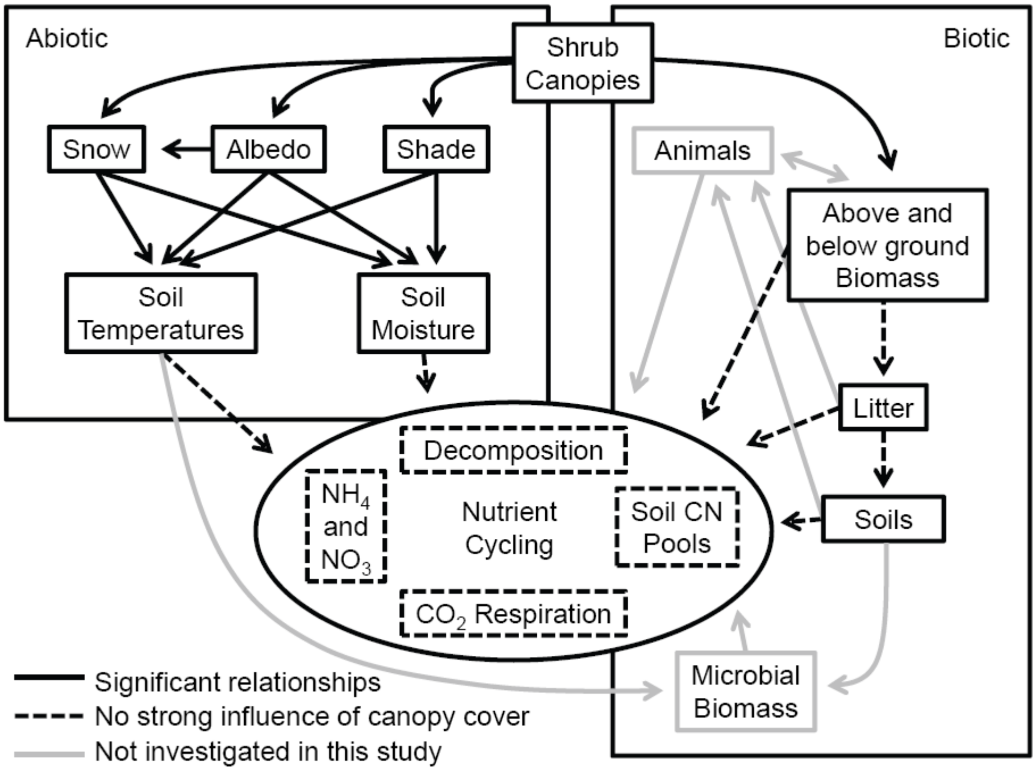

Figure 6-6. Conceptual diagram of abiotic and biotic variables predicted to influence nutrient cycling that can differ between shrub canopies. Solid black lines indicate variables that were significantly different, dashed lines indicate variables that did not have strong or consistent differences between plots with and without canopies, and grey lines indicate variables that were not investigated in this study.

### *Decomposition*

Snow fence and reciprocal litter transplants have shown that snow depth and winter soil temperatures influence decomposition rates in tundra ecosystems (Baptist et al. 2009); however, experimental investigations of winter warming events and reduced snowpack do not find evidence of changes in litter decomposition (Bokhorst et al. 2010). My data also do not show strong evidence that shrub canopies, and resulting soil insulation due to snow trapping, determine decomposition rate, although I observed greater paper decomposition at 5 cm depth in shrub plots (Fig. 6-2). The shrub plots experienced cooler soils in summer and warmer soils in winter and had deeper snow depths (Chapter 5); however, mean January soil temperature was only one of the four explanatory variables that best described the variation in paper decomposition. I did not observe greater paper decomposition at 5 cm depth in artificial shrub plots which also trapped snow and had warmer soil temperatures over winter. Deciduous shrub litter is more recalcitrant than litter from other plant functional groups (Hobbie 1996, Cornelissen et al. 2007, Baptist et al. 2009), and this could explain why I did not observe significant differences in litter decomposition between treatments.

### *Nutrient cycling*

I observed significantly greater total nitrogen accumulation (ammonia plus nitrate) in the canopy removal treatments in 2008 (Fig. 6-3), which could be related to warmer temperatures experienced during summer in those plots (Table 6-4, Chapter 5) or to the disturbance caused by the canopy removal. Shrub canopy removals exposed an understory of primarily litter and bare soil in many of the plots. These plots had a lower surface albedo and therefore, warmed substantially during the summer relative to the other experimental treatments (Chapter 5); however, high nitrogen accumulation was also observed in these experimental plots prior to manipulation (Fig. 6-3a). I did not observe significant differences in nitrogen accumulation between other canopy treatments (Fig. 6-3), even though these plots had significantly different soil temperatures in both summer and winter seasons (Chapter 5). In addition, I did not observe significant differences in percent soil nitrogen, $NO_3$-N or $NH_4$-N accumulation between canopy treatments across the growing season.

In winter, shrub canopies that trap more snow can function similarly to snow fence experiments. In a snow fence experiment at Daring Lake, NWT, nutrient flux was higher in plots with greater snow depth during thaw (Buckeridge et al. 2010a), and under birch shrub canopies, winter nitrogen cycling was higher (Buckeridge et al. 2010b). In contrast, at Toolik Lake Alaska, snow addition was found to increase summer, but not winter, N-mineralization rates (DeMarco et al. 2011). I was not able to measure winter or spring fluxes of nitrogen in this experiment as the field site was not accessible.

### *Annual carbon release*

I did not observe significant differences in soil $CO_2$ efflux between canopy treatments (Fig. 6-4), even though mean July soil temperatures differed (Chapter 5). Litter from deciduous shrub species has been demonstrated to be more recalcitrant (Cornelissen et al. 2007), and therefore plots with greater willow litter inputs could have lower rates of heterotrophic respiration. Due to a greater root biomass, autotrophic respiration should be greater under willow canopies, and perhaps lower rates of heterotrophic respiration in shrub plots are being offset by greater autotrophic respiration.

In a snow fence experiment at Daring Lake, NWT, ~60 cm experimentally deeper snow resulted in a ~40% increase in total winter $CO_2$ efflux (Nobrega and Grogan 2007). If the influence of increased snow in canopy addition plots functioned similarly at my site, and not taking into account the differences in litter quality and soils between plots, I would expect the increased snow trapping of approximately 15 – 30 cm additional snow would result in increases of ~20% total winter $CO_2$ efflux. Given the ~350 gC $m^{-2}$ additional carbon stored in annual above ground biomass observed in shrub plots and the assumed greater belowground storage by woody roots of the shrub species, this increase in winter time carbon loss would likely be less than the increased carbon storage provide by the willow biomass, suggesting that increased cover of canopy-forming willows should increase the strength of the carbon sink in this tundra ecosystem. Unfortunately, due to the fact that I did not make winter efflux measurements and I found weak temperature efflux relationships for the summer months, I was unable to build an annual carbon budget to compare sink and source dynamics between the tundra and shrub plots in this study.

### *Implications for permafrost*

My experimental manipulation demonstrates that shrub canopies shade soils in summer and trap snow in winter, thereby altering soil temperatures. Over the long term, if my experimental manipulations were maintained these temperature differences might begin to influence deeper soil temperatures. In Siberian tundra, experimental canopy removal has been demonstrated to reduce the summer active layer thaw (Blok et al. 2009). At Toolik Lake, Alaska, plots with experimentally deeper snow and deeper active layers respire older carbon than control plots (Nowinski et al. 2010). My study site in the Ruby Range Mountains, YT, is underlain by bedrock, and therefore will not be influenced by permafrost thaw as dramatically as shrub-tundra sites underlain by ice-rich permafrost. Future experimental manipulations of shrub canopies could be conducted in areas of ice-rich permafrost so that the impacts of shrub canopies on active layer depth and nutrient cycling can be assessed.

## Conclusions

Increasing shrub cover will lead to greater aboveground carbon storage (Mack et al. 2004) and potentially enhanced nitrogen cycling (Weintraub and Schimel 2005, Buckeridge et al. 2010b); however, more recalcitrant shrub litter inputs (Cornelissen et al. 2007) and shading (Pomeroy et al. 2006) appear to reduce heterotrophic decomposition. My findings suggest that the direct and short-term effects of canopy cover are weak controls on nutrient cycling, relative to the indirect effects of changes in plant composition and altered soil biogeochemistry from shrub encroachment.

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# Chapter 7. Conclusions

*Dissertation summary*

Research on the impacts of global warming has led to a body of work that examines causal linkages between observed increases in the abundance of woody shrub species, remote-sensed ‘greening’ in arctic and alpine ecosystems. Collectively, these observations are interpreted to indicate increases in the abundance and cover of shrub species, changes in growth form, or advance of the shrubline ecotone (Sturm et al. 2001, Tape et al. 2006, Lantz et al. 2009, 2010, Forbes et al. 2010, Hallinger et al. 2010). Other studies are also investigating the ecological impacts of this increasing shrub cover (Blok et al. 2011, Buckeridge et al. 2010a, 2010b, Buckeridge and Grogan 2010, Marsh et al. 2010). In my work, I investigated both evidence for willow shrub expansion in the Kluane region of the Yukon Territory and the influence of increasing shrub cover on tundra ecosystem function by testing three specific hypotheses:

$H_1$: Canopy-forming willows are increasing in cover and elevational range in arctic and alpine tundra of the Yukon Territory.
In Chapters 2 and 3, I presented supporting evidence for this hypothesis. Willow patches have expanded and canopy heights have increased on Herschel Island, and canopy-forming willows have advanced upslope to extend their altitudinal ranges in the Kluane Region.

$H_2$: Growth of willow species is temperature sensitive, with greater growth of willows occurring in summers with warm early growing seasons.
Data supporting this hypothesis are presented in Chapter 4 where I demonstrated that willow growth is temperature sensitive, with early growing season temperatures explaining approximately half of the variation in annual growth rings.

$H_3$: Increases in canopy-forming willows will alter physiological functions in tundra ecosystems by creating temperature and nutrient feedbacks to further increase shrub expansion.

My results presented in Chapters 5 and 6 suggest that this hypothesis is not strongly supported. Even though, experimental manipulations of shrub canopy significantly influenced soil temperatures, the impact of canopies on nutrient cycling was weak.

The connections between each of the major findings of my thesis chapters are illustrated in the following diagram:

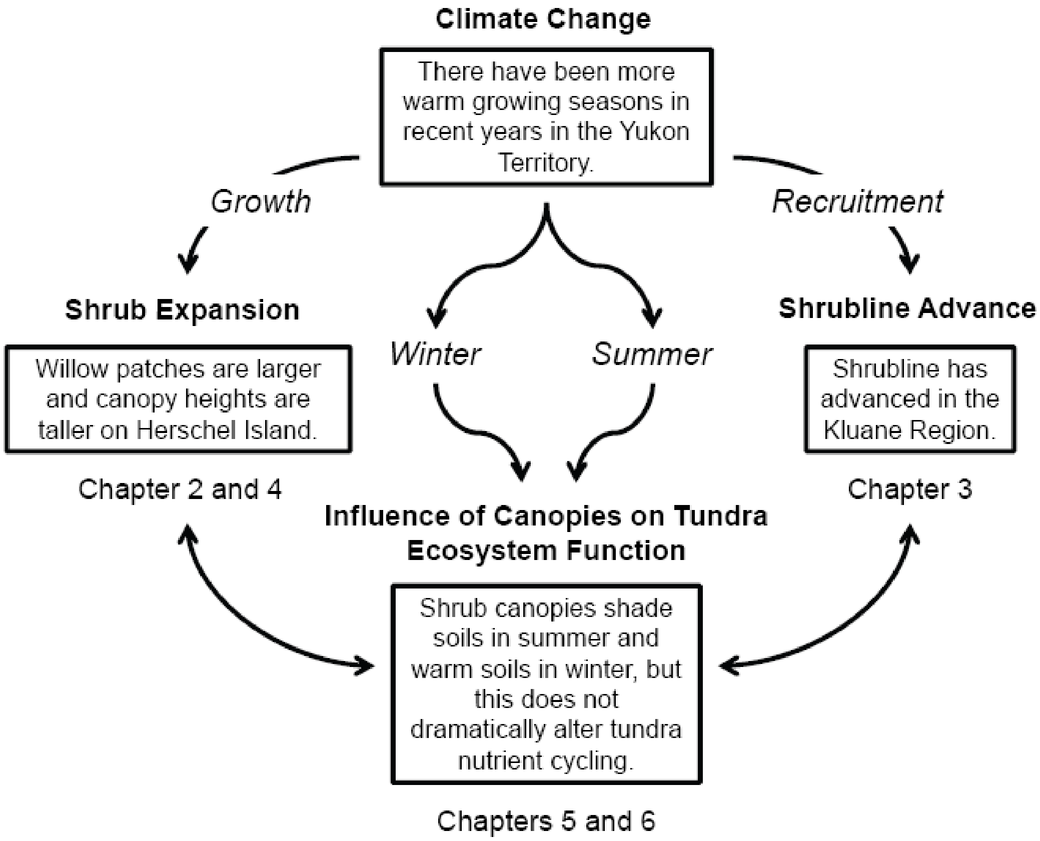


Figure 7-1. A diagram illustrating the connections between the different results presented in this dissertation.

*Chapter 2: Historical changes in the cover of canopy–forming willows*

Canopy-forming shrubs are reported to be increasing at sites around the circumpolar Arctic. My results indicate expansion in canopy cover and height of willows on Herschel Island located at 70° north on the western arctic coast of the Yukon Territory. I examined historic photographs, repeated vegetation surveys and conducted monitoring of long-term plots and found evidence of increases of each of the dominant canopy-forming willow species (*S. richardsonii*, *S. glauca* and *S. pulchra*), during the 20th century. A simple model of patch initiation indicates that the majority of willow patches for each of these species became established between 1910 and 1960, with stem ages and maximum growth rates indicating that some patches could have established as late as the 1980s. Collectively, these results suggest that willow species are increasing in canopy cover and height on Herschel Island. I did not find evidence that expansion of willow patches is currently limited by herbivory, disease, or growing conditions.

*Chapter 3: Advance of shrubline in the Kluane Region*

With climate warming, woody shrub species are projected to expand their range limits and increase in cover in arctic and alpine tundra ecosystems. To quantify and describe the pattern of shrub advancement in the northern alpine tundra of the Kluane Region of the Yukon Territory, I surveyed and aged 379 individual willows from ten species growing in 12 valleys at and below the elevational range of canopy-forming patches. Species composition varies across the Kluane Region with several species of canopy-forming willows growing at 1600 – 2000 m elevations. Many young willows became established after 1990 at these high elevation sites. At shrubline, the maximum elevation at which these canopy-forming shrub species grow, ~ 60% of individuals were recruited after 1990, compared with ~ 30% at the 50% shrub cover zone at lower elevations. Shrub survival was high and I observed only one instance of mortality during my survey. These data indicate elevational range expansion and infilling of canopy-forming willows in the Kluane Region over the last half century. If future growing conditions remain as suitable as current conditions, shrubline expansion is likely to continue.

### *Chapter 4: Temperature sensitivity of willow growth*

The climate is warming and a growing number of large scale observations show the expansion of woody shrub species in tundra ecosystems. My data on the growth of willow shrubs from arctic and alpine sites across the Yukon Territory indicate that half of the variation in annual growth rings is explained by early growing season temperatures. The widths of annual growth rings varied among species and ages of willow individuals; however, growing season temperature correlations with ring widths did not vary with age of the individual, patch size or elevation of the shrubs sampled. Willows growing at the elevational range limit of canopy-forming shrubs, an ecotone located at different elevations at each site, showed stronger growth correlations than did willows growing further down slope. These data provide strong evidence that growth is temperature limited at these sites, although precipitation, direct sun light, or snow cover, all of which covary with early growing season temperatures, could also influence shrub growth. If growing season conditions in the Yukon Territory continue to warm in the future, I project that the growth rates of canopy-forming willow shrubs will continue to increase, until other factors influencing growth become limiting.

### *Chapter 5: Influence of willow canopies on tundra soil temperatures*

Modifications to the diversity and functioning of tundra ecosystems are projected to occur as a result of the expansion of canopy-forming shrubs. By trapping snow, shrub canopies could warm winter soils, and increase the rates of nutrient turnover and carbon cycling to create positive feedbacks and promote further shrub expansion. However, to quantify the strength of these feedbacks, the abiotic and biotic influences of shrub canopies on tundra ecosystem functioning must be measured in isolation. I conducted a unique factorial experiment on the interacting influence of shrub canopies and soil parameters on year-round soil temperatures. I removed 0.5 m high willow shrubs (*Salix* spp.) and created artificial shrub canopies with dead branches, and compared their soil temperatures to nearby natural tundra and shrub patches. Shrub canopies increased soil temperatures in January by 4-5 ºC, but cooled soils in July by an average of 2 ºC at 2 cm depth. Shrub plots had 14 - 33 cm more snow in January than adjacent shrub-free plots. Artificial canopies and canopy removals functioned similarly to the respective unmanipulated plots, indicating that the shrub canopy was a dominant factor influencing the soil thermal regime. My findings indicate that increasing shrub cover influences the thermal regime of tundra soils, but that summer cooling could offset the effects of winter warming on ecosystem processes.

### *Chapter 6: Influence of willow canopies on tundra nutrient cycling*

Changes in canopy cover have the potential to alter nutrient cycling and tundra ecosystem functions. I used a manipulative experiment to investigate the influence of shrub canopies on litter decomposition, and carbon and nitrogen pools and fluxes in alpine tundra of the Yukon Territory, Canada. I predicted that these nutrient fluxes would differ as shrub cover has been shown in these same plots to increase snow depth and temperatures over the winter and to reduce soil temperatures in the summer. Shrub plots had over two times more live biomass, nitrogen and carbon in live plant biomass relative to tundra plots; however organic matter depths and litter mass were similar between shrub and tundra plots. Total N accumulation, paper decomposition at 5 cm depth, and percent carbon in surface litter differed significantly between shrub and tundra plots; however, surface decomposition, carbon fluxes, and nitrate or ammonia accumulation were the same between plots with shrub, tundra, artificial canopies, or canopy removals. This suggests that the direct effects of shrub canopies on soil temperatures as a result of snow trapping and shading are weak controls over the carbon and nitrogen fluxes at this study site.

### *Future research questions*

My dissertation research greatly improves our understanding of changes in the growth and abundance of canopy-forming willow species and the ecological impacts of this structural change in tundra ecosystems of the Yukon Territory. This research has also stimulated more questions which deserve future investigation:

1. *What controls new recruitment of shrub species in tundra ecosystems?*

Much of the current research on shrub expansion focuses on what factors control growth. Dendroecological studies (Forbes et al. 2010, Hallinger et al. 2010) and greenhouse experiments (Arft et al. 1999, Bret-Harte et al. 2001, Walker et al. 2006, Hudson and Henry 2010) focus on the change to pre-existing individuals when growing conditions warm, but perhaps more important when considering dramatic shifts in canopy-forming shrub abundance are controls on new recruitment (Lantz et al. 2009, 2010). Lantz et al. (2009, 2010) have examined the influence of fire and permafrost degradation on recruitment of alder (*Alnus viridis* subsp. *fruticosa*); but, this type of study has yet to be conducted with willow species in tundra ecosystems. There is a clear need to identify both what conditions allow for pulses of recruitment and what factors lead to seedling mortality such as herbivory which has been suggested to limit shrub expansion in some tundra ecosystems (Post and Pedersen 2008, Olofsson et al. 2009). Connecting together the factors that promote new recruitment and those that result in mortality of seedlings will allow better estimation of future conditions that could result in shrub expansion.

2. *How do shrub encroachment rates and the temperature sensitivity of growth vary between shrub species and tundra ecosystems?*

Several studies report increases in canopy forming shrub species: including alder in northern Alaska (Sturm et al. 2001b, Tape et al. 2006), willow in the Yukon Territory (Chapter 2), and birch in Northern Quebec (*pers. comm.* B. Tremblay, E. Lévesque and S. Boudreau). Dendroecological studies indicate temperature sensitive growth of canopy-forming willow species growing in Siberia (Forbes et al. 2010) and the Yukon Territory (Chapter 4) and juniper growing in subarctic

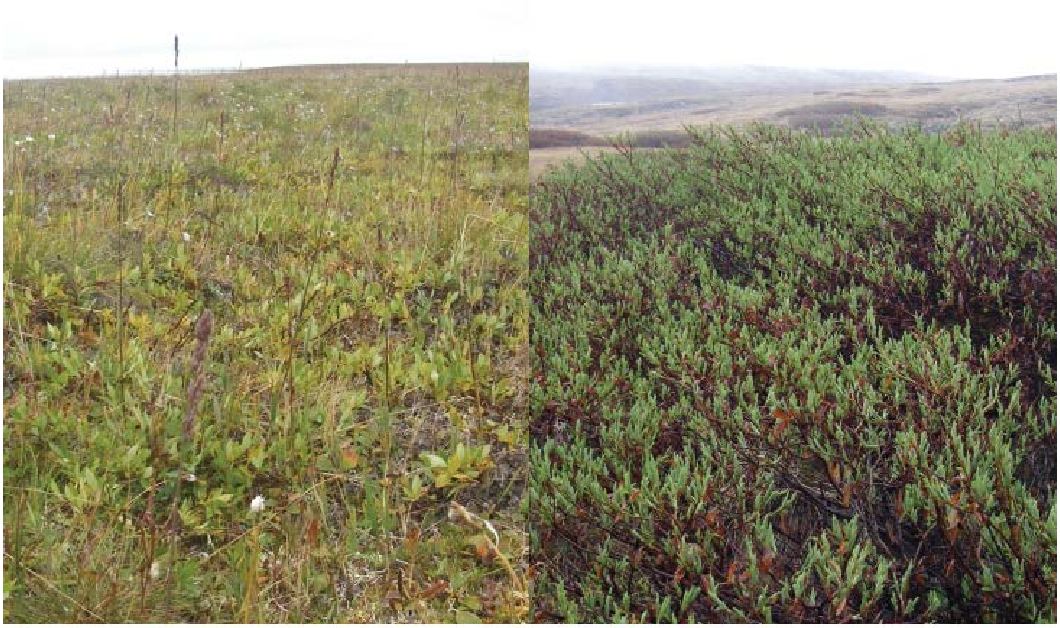
Sweden (Hallinger et al. 2010). Each of these studies was conducted in a different region of the Arctic.

My dissertation results indicate that variation exists in the temperatures sensitivity of canopy-forming willow growth between sites (Chapter 4). Likely, the variation that I observed in the Yukon Territory also occurs between more disparate arctic regions. Herbivory, which has been found to be an important control of alpine tree and shrub abundance in Scandinavia and Greenland (Olofsson et al. 2009, Hofgaard et al. 2010, Speed et al. 2010), might not be such an important factor limiting rates of shrub expansion in the Western Canadian and the Alaskan Arctic where there is little livestock grazing or reindeer herding (Chapter 2).

In addition, to variation in shrub growth and recruitment between sites, each of these shrub species can differ in their potential to invade tundra ecosystems. Some shrub species could have more temperature sensitive growth, be better able to out-compete other tundra plants, or could be less palatable to herbivores. A collaborative data synthesis will help to further our understanding of how circumpolar shrub encroachment can vary among species and sites.

3. *Do shrubs at latitudinal range limits have the genetic potential to form dense canopies?*

Much of the current evidence for increasing shrub species comes from low arctic sites such as north of the Brooks Range on the North Slope of Alaska (Bret-Harte et al. 2001, Sturm et al. 2001b, Tape et al. 2006). To understand if canopy-forming shrub species will increase in cover and height in more northern areas such as the Canadian arctic coastline and archipelago, we must determine if the shrubs individuals growing there have the genetic potential to form canopies. For example, the canopy-forming willow species *S. pulchra* grows in both the Kluane Region and on Herschel Island (Fig. 2). In the Kluane Region this willow can have a canopy height of up to 2 m (Chapter 3), on Herschel Island this species is growing throughout much of the tussock tundra habitat, but only reaches a canopy height of 10 – 50 cm tall (Chapter 2). If growing conditions improve on Herschel Island, will the *S. pulchra* individuals growing there be able to form a closed canopy shrubland as occurs further south?



*Salix pulchra*
Arctic: Herschel Island, 70° North
Canopy Height: 10 – 50 cm

*Salix pulchra*
Subarctic: Kluane, 61 ° North
Canopy Height: 30 – 200 cm

Figure 7-2. *S. pulchra* growing on Herschel Island and in the Kluane Region. Canopy height and density is much lower on Herschel Island. Do the willows growing here have the genetic potential to form closed canopies such as can occur in the Kluane Region?

There are multiple ways to address the genetic potential of shrubs to increase in canopy height and cover in high-altitude tundra ecosystems. Warming experiments such as the international tundra experiment (Arft et al. 1999, Walker et al. 2006) can be used to examine rates of plant growth between warmed and control plots, and common garden experiments (Jump et al. 2009) can test how individuals from different sites at different latitudes grow under the same conditions.

Understanding whether willow species growing at the current latitudinal extend of canopy-forming shrubs in arctic tundra have the same genetic potential to form canopies as individuals from the same species growing further south, will help us project how shrub encroachment will progress over the coming decades. If the currently low-in-stature *S. pulchra* growing on Herschel Island has the genetic potential to form dense and tall canopies, a major structural change could already be underway at that site.

4. *What is the balance between positive and negative feedbacks to shrub encroachment, how does this vary across different densities and canopy heights of shrub cover?*

Winter biological processes have been hypothesized to create a positive feedback to shrub encroachment (Sturm et al. 2001a, 2005, Chapin et al. 2005). My experimental results indicate that shrub canopies do trap snow and insulate soils in the winter, but that the shading and resulting cooling of soils in the summer is an equally important influence of shrub canopies (Chapter 5). In addition, my experimental results indicated weak influences of shrub canopies on nutrient cycling parameters, suggesting that the hypothesized positive feedbacks to shrub encroachment might not be as strong as hypothesized. My experiment was conducted in a zone of approximately 50% canopy-forming shrub tundra, where canopy-forming shrubs occupied about half of the total land surface. We would expect that the influence of shrub canopies on tundra soil temperatures and ecosystem functions will vary with the cover, height, density and structure of shrub canopies (Grogan and Jonasson 2006, Lantz 2008).

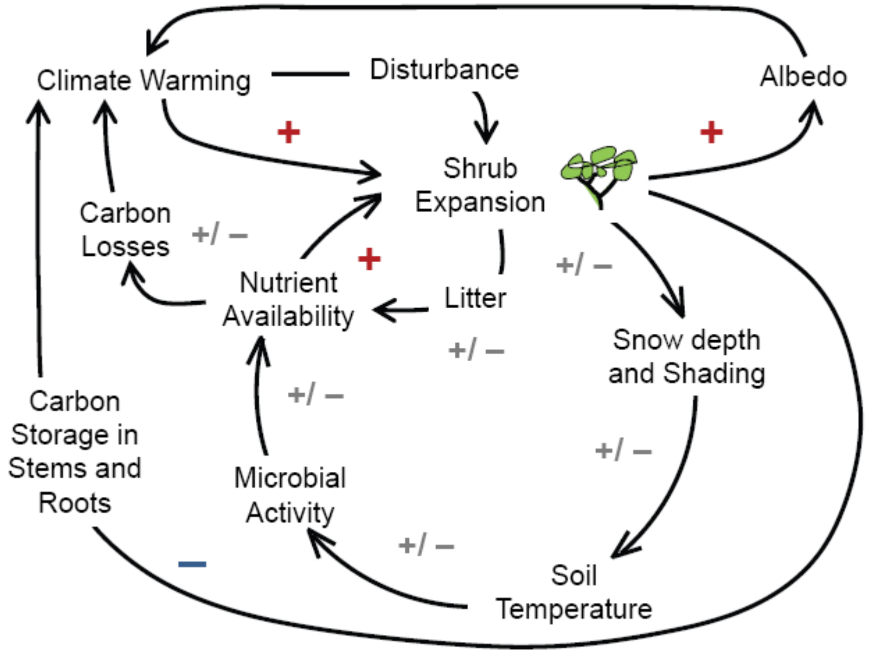


Figure 7-3. Diagram illustrating the uncertainty potentially associated with positive and negative feedbacks to shrub expansion and climate warming (after Chapin et al. 2005).

To better project future shrub encroachment and ecosystem functions, we need to understand how factors influencing shrub growth and tundra ecosystem functions interact. We also need to understand how the strength of these positive and negative feedback mechanisms vary across the landscape. Future experimental work using artificial canopies and canopy removals in addition to the monitoring of intact shrub and shrub-free tundra will improve models of tundra ecosystems undergoing shrub encroachment. However, it will be an ongoing challenge to figure out methods of collecting year-round $CO_2$ and nutrient flux measurements. Building winter accessible field sites with more infrastructure such as flux towers, meterological stations and the development of consistent monitoring protocols that can be used between sites will improve our abilities to estimate annual nutrient budgets. Greater spatial and temporal coverage of monitoring and experimental work will allow us to better project the future structure and function of northern tundra ecosystems.

### 5. *How does the influence of increasing shrubs on ecosystem function vary between ecosystems?*

Shrub species are increasing in a variety of ecosystems throughout the world including temperate grasslands, deserts, savannahs and tundra ecosystems (Knapp et al. 2008, Naito and Cairns 2011). Some of the same factors influencing shrub proliferation in tundra ecosystems are also acting in these other ecosystems, such as for example, increased soil carbon storage after shrub invasion (De Deyn et al. 2008). Some studies report reductions in plant species richness under shrub canopies in temperate grasslands due to the loss of shade-intolerant species (Lett and Knapp 2005, Price and Morgan 2008), as has been observed in high-latitude ecosystems (Pajunen et al. 2011). Conversely, grassland shrub encroachment has also been shown to increase vascular plant richness (Maestre et al. 2009). Shrub encroachment in arid ecosystems has been suggested to either advance or reverse desertification depending on the influence of shrub canopies on ecosystem function (Maestre et al. 2009). With uncertain future precipitation projections for the Arctic (ACIA 2005), comparing and contrasting the impacts of shrub encroachment between ecosystems could provide useful insights for future projections of shrub increases.

### *Conclusions*

My research provides:

1) A ground-based estimate of shrub change in the Yukon Territory.
2) Evidence of a positive relationship between warm summers and growth in willow shrubs in arctic and alpine tundra.
3) Quantitative measurements of the impacts of shrub expansion on ecosystem functions such as carbon storage, nitrogen cycling and soil insulation.

My dissertation findings will help to improve model projections of future shrub expansion in Northern Canada. Understanding both the rate of change in canopy forming woody shrubs and the impacts of this change on ecosystem function will improve circumpolar estimates of future carbon storage, wildlife habitat and permafrost integrity of the tundra. Northern peoples are observing vegetation changes in their traditional lands (Thorpe et al. 2002, Forbes et al. 2010, 2009) and have concerns about the impact of this change on hunting, travel and other traditional activities. My research will also help resource managers and local peoples to understand the dynamics of tundra vegetation change to project what these ecosystems will be like in the future. During my PhD research, I conducted outreach with local peoples, in schools both in the North and in Edmonton to share my findings with the public. Making sure research, and in particular northern research, comes full circle and is presented to the peoples who live closest to the changes being observed is a critical part of the scientific process that strove to accomplish during my doctoral studies.

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