Reading between the rings: Climatic and biotic controls of shrub growth and expansion in the tundra biome

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Declaration

I declare that this thesis was composed by myself, and that the work contained herein is my own, except where explicitly stated at the beginning of each chapter. This work has not been submitted for any other degree or professional qualification.

Appendix I and Chapter 7 are published articles. My contribution and those of the other authors are explicitly indicated below. I have obtained the permission of all authors and publishers to reproduce the articles in my thesis.

- Appendix I has been published in Global Change Biology under the following title:

Ropars, P., **Angers-Blondin, S.**, Gagnon, M., Myers-Smith, I.H., Lévesque, E., Boudreau, S., 2017. Different parts, different stories: climate sensitivity of growth is stronger in root collars vs. stems in tundra shrubs. Global Change Biology 23, 3281–3291. https://doi.org/10.1111/gcb.13631

Pascale Ropars designed the study, carried out the sampling, and took the lead in writing the manuscript. I contributed to field sampling, conducted the statistical analyses, wrote the corresponding methodological section, and provided feedback on several drafts of the manuscript. Marianne Gagnon processed and measured the samples. All other authors provided feedback on various versions of the manuscript.

- Chapter 7 has been published in Polar Biology under the following title:

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I designed the study with inputs from my two supervisors Isla Myers-Smith and Stéphane Boudreau. I carried out the experiment, analysed the data, and wrote the manuscript with feedback from the co-authors.

Some run like a river and some wander like a stream

Some reveal their secrets like the rings within a tree

A tree that's rooted to the ground and refuses to fall down

Though it's deafened by the sound of wind and thunder

(Karine Polwart & Gordie Sampson)

Abstract

The tundra biome has undergone dramatic vegetation shifts in recent decades, which have been partly attributed to climate warming. Shrub species in particular are expanding widely throughout the Pan-Arctic region, and are involved in complex vegetation-atmosphere interactions that have important implications for the global energy balance and carbon budget. However, projections of vegetation change and associated feedbacks are complicated by the high variability in the sensitivity of shrub growth to temperature among sites and species. A mechanistic understanding of the individual-to-regional controls of climate sensitivity is therefore needed to accurately predict future vegetation change at the biome scale. This thesis quantifies the influence of environmental and ecological factors, and especially of plant-plant interactions, on the growth response of Arctic shrub communities to climate change.

Climate change in the Arctic has resulted in warmer, but also longer growing seasons in many locations due to earlier snowmelt. These two factors are often treated as one single control of plant growth, but with scarce records of green-up and senescence dates for the Arctic, few studies have measured the sensitivity of shrub growth to changes in growing season length. Using radial growth time series from over 300 shrubs collected at four sites of contrasting climatic regimes and greening trajectories in Northern Canada, I measured the sensitivity of shrub growth to summer temperature and satellite-derived growing season length. I found that growing season length and summer temperature were decoupled within sites and had inconsistent effects on growth across the four sites. My findings indicate that longer and warmer growing seasons do not necessarily act as combined drivers of vegetation change across the biome. My research also demonstrated that growth at the root collar of shrubs is more climate sensitive than stem growth, possibly indicating differential internal resource allocation strategies, and highlighting the importance of standardised protocols when comparing dendroecological data across multiple sites.

Individual and species traits are thought to play an important role in the response of tundra vegetation to climate change. Taller shrub species have been shown to be more climate-sensitive than dwarf shrubs, but whether this relationship holds at the individual level is unknown. I tested whether plant size, as a proxy for competitive ability, explained variation in the climate sensitivity of shrub growth using 1085 individual size and growth-ring records from 16 species at 18 sites across the tundra biome. I did not find evidence that taller shrubs were more climate sensitive, and found that height became a progressively poorer predictor of other growth dimensions at higher latitudes. This suggests that predictions of functional and structural change based on allometric equations from boreal or sub-Arctic populations may not be valid for the tundra biome as a whole.

Plant-plant interactions are a strong driver of community dynamics. With increasing shrub densities in the circumpolar region, competition could have an increasingly important influence on shrub growth, potentially limiting climate-driven expansion. I found that competition with trees might slow down shrub expansion in the boreal forest biome, as the climate sensitivity of shrub growth was much lower in a boreal forest in southwest Yukon compared to shrubs growing in the alpine tundra in the same region. However, my findings did not indicate a strong control of shrub-shrub competition on growth. A canopy removal experiment did not reveal any difference in the growth rate of shrubs having experienced a decrease in aboveground competition compared to shrubs growing in intact shrub patches. Additionally, shrubs experiencing more competition were generally as climate sensitive as those with fewer or more distant neighbours, as I demonstrated through spatial analysis at four sites across the Canadian Arctic. However, their spatial arrangement, with positive size-distance relationships between pairs of neighbours, suggested that competition does play a role in the life history of these shrubs, especially at more productive sites. Finally, I found evidence of physical and chemical interference of ground vegetation on the germination of deciduous shrub seeds, indicating that interactions with other plant functional groups may control rates of shrub expansion.

Shrub expansion at the plot to landscape scale has been heavily documented over multiple decades through several lines of evidence including long-term monitoring, remote sensing, and experimental studies. The increase in shrub biomass in the tundra has high certainty both in detection and in attribution to climate warming. However, my thesis highlights the complexity and variability of growth responses when using radial growth as an indicator of climate sensitivity. I detected this variability at multiple scales, from plant parts within an individual showing inconsistent climatic signals, to site-scale sensitivity responding to different facets of global change. I did not find strong or consistent influences of biotic and abiotic controls on the growth responses of tundra shrubs; however, these relationships may change over time as shrub densities continue to increase and exacerbate resource limitations. With 80%

of tundra biomass potentially located below ground, understanding whole-plant and community-level responses to climate will be critical to improve projections of tundra plant community responses to global change. Understanding the different drivers of primary and secondary growth will be key to using estimates of climate sensitivity derived from growth-ring records to project biomass change and associated feedbacks across the tundra biome.

Lay summary

The tundra biome is the part of the world that extends beyond the treeline, and is characterised by a cold climate, short growing season, and low-statured vegetation. The Arctic region is currently warming at twice the rate of the rest of the planet, causing shifts in plant communities. Notably, shrub species are growing faster, taller, and colonising new environments. Shrub expansion has been documented throughout the tundra biome, but the rate of change and the magnitude of the response vary greatly among sites and species. It is crucial to understand the environmental and ecological factors that can either limit or promote climate-driven shrub expansion if we are to predict accurately future vegetation change and its repercussions on the carbon balance, landscape structure, wildlife, and people of the Arctic.

This thesis aims to measure the climate sensitivity of shrub growth, i.e. how strongly annual growth in a plant is influenced by the temperatures or other growing conditions in that year. I then explain how sensitivity varies according to individual characteristics, environmental context, and competitive interactions with other shrubs. I used growth-ring measurements from some of the most common expanding tundra shrub species from four locations in Northern Canada to explore how Arctic shrub communities might change at sites with contrasting climatic conditions and environment types. I also used an experimental and a spatial approach to determine whether competition for resources may become a limitation to shrub expansion as plant densities increase in the circumpolar region.

With changing climatic conditions and rapid warming in the Arctic, it is often assumed that Arctic summers are getting both longer and warmer. I found that my four sites exhibited contrasting rather than consistent temporal changes, and that these two possible drivers of plant growth (summer temperature and duration) are not necessarily coupled. Shrubs did not respond very strongly to either driver, except at one mountain site where growth was highly temperature-sensitive. My research also demonstrated that growth at the root collar of shrubs (i.e. the main “trunk” of the shrub) tracks variations in climate better than stem growth, indicating complex resource allocation strategies within plants and highlighting the importance of standardised protocols when attempting to synthesise data from multiple sites and observers.

Taller shrub species have been shown to be more climate-sensitive than dwarf shrubs. At the individual level, plant size could reflect competitive ability and make some shrubs better able to capitalise on a warming climate, but this relationship has never been quantified. I tested this hypothesis using 1085 individual size and growth-ring records from 16 species at 18 sites across the tundra biome. I did not find evidence that taller shrubs were more climate sensitive, and found that height became a progressively poorer predictor of other growth dimensions at higher latitudes. This suggests that equations developed for boreal or sub-Arctic populations to predict biomass or other ecosystems processes from plant size may not be valid for the tundra biome as a whole.

With marked increases in vegetation cover around the Arctic region, competition between plants could have a growing influence on shrub communities, potentially limiting climate-driven expansion. I found that shrubs growing in boreal forests may not benefit from warmer climate because of competition with trees; in contrast, shrubs growing in the alpine tundra were much more responsive to warmer temperature. I also detected competitive interactions in the relative size and position of shrubs in the landscape, especially at sites with denser vegetation. However, I did not find that competition between shrubs species exerted a strong control of shrub growth, or on their ability to respond to climate change. Finally, I found evidence that the ground vegetation could interfere physically and chemically with the germination of shrub seeds, suggesting that potential climate-driven expansion of shrub species beyond their current distribution limit might be slowed down by plant-plant interactions.

This thesis highlights the great variability in the responses of shrub growth to climate at multiple scales, from plant parts within an individual showing inconsistent climatic signals, to site-scale sensitivity responding to different facets of global change. Competition did not determine the ability of shrubs to respond to warmer temperatures, but may become a more important constraint over time as shrub densities continue to increase and exacerbate resource limitations. With 80% of tundra biomass potentially located below ground, understanding whole-plant and community-level responses to climate will be critical to improve projections of tundra plant community responses to global change and associated feedbacks across the tundra biome.

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Chapter 1 Introduction

1.1 A greener Arctic: shrub expansion in the tundra

The tundra biome, which comprises areas above the treeline and is characterised by an Arctic climate and flora, covers approximately 5% of the Earth's land surface (Walker et al. 2005). Arctic regions are currently warming twice as fast as the rest of the planet, and warming is expected to accelerate by the end of the century (IPCC 2013). The northern circumpolar region of the planet contains approximately 50% of the global belowground organic carbon store (Tarnocai et al. 2009; Hugelius et al. 2013), and thus shifts in the structure and biophysical processes of tundra ecosystems are likely to have disproportionate consequences on the global carbon cycle and energy balance. Tundra vegetation is currently undergoing remarkably rapid and widespread directional change throughout the biome, with potential for many complex vegetation-atmosphere interactions. The most notable changes are an increase in woody shrubs (Myers-Smith et al. 2011, Elmendorf et al. 2012a), herbs, and graminoids (Elmendorf et al. 2012a; McManus et al. 2012), often associated with a decrease in bare ground (Elmendorf et al. 2012a, Myers-Smith et al. in press) and in cryptogam cover (Cornelissen et al. 2001; Fraser et al. 2014).

Shrub species, which are the focus of this thesis, are the tallest plants in treeless tundra environments, and in many ways act as ecosystem engineers. Their tall stature interacts with the abiotic environment, intercepting snow in winter (Sturm et al. 2001; Bonfils et al. 2012) and affecting energy balance through interception of solar radiation (Sturm et al. 2005a; Juszak et al. 2014). These physical properties affect in turn seasonal soil thermal regime (Bonfils et al. 2012; Myers-Smith and Hik 2013; Paradis et al. 2016), with knock-on effects on permafrost (Blok et al. 2010; Loranty et al. 2016) and soil microbial activity and nutrient cycling (Sturm et al. 2005b; DeMarco et al. 2011). They also provide habitat and food for wildlife (Rich et al. 2013; Boelman et al. 2015; Christie et al. 2015). Therefore, shrub expansion, colloquially termed "shrubification", will have complex and far-reaching impacts on the structure and functioning of tundra ecosystems, and likely affect regional to global climate and biogeochemical cycles. In recent decades, research priorities have involved the collection of evidence of shrub expansion from many taxa and locations, and the attribution of this expansion to global change drivers.

1.1.1 Observations of shrub expansion

Shrub expansion may be defined as increases in canopy height, increases in shrub cover (from either accelerated growth of established individuals or recruitment of new individuals), and colonisation of new sites (Myers-Smith et al. 2011). Over the last half-century, these changes have been documented and quantified across the tundra biome (reviewed in Myers-Smith et al. 2011) using historical ecology and repeat photography (Tape et al. 2006, Callaghan et al. 2011; Danby et al. 2011; Vellend et al. 2013; Steinbauer et al. 2018), remote sensing (Blok et al. 2011a; McManus et al. 2012; Guay et al. 2014; Ju and Masek 2016), demographic studies (Büntgen et al. 2015; Angers-Blondin and Boudreau 2017; Myers-Smith et al. 2017) and ecological monitoring (Rundqvist et al. 2011; Elmendorf et al. 2012a; Hobbie et al. 2017; Myers-Smith et al. in press). Overall, several lines of evidence point to a majority of shrub populations expanding rather than decreasing or remaining stable (Myers-Smith et al. 2011), suggesting that tundra vegetation is responding directionally to changes in a common, regional-scale driver.

1.1.2 Attribution of shrub expansion to warming

Tundra vegetation is limited by cold temperatures, short growing seasons, and harsh environmental conditions (Bliss 1971; Aerts et al. 2006), and can therefore be expected to change if and when these limitations are lifted. In fact, pollen records show that tundra vegetation has frequently shifted in abundance and composition in the past, tracking climatic changes (Anderson and Brubaker 1994; Overpeck et al. 1997). In the 1980's and 1990's, coordinated experiments such as the International Tundra Experiment (ITEX) were set up to identify the drivers of vegetation change (Walker et al. 2006; Elmendorf et al. 2012b). Experimental warming and fertilisation demonstrated that tundra shrubs are generally temperature- and nutrient-limited (Chapin et al. 1995; Dormann and Woodin 2002; Wahren et al. 2005; Walker et al. 2006). Therefore, Arctic warming is very likely to be the main driver of shrub expansion, through direct effects of temperature on plant physiology and, perhaps more importantly, through indirect effects on biogeochemical cycling (Chapin 1983). The attribution of shrub expansion to warming in the Arctic is thought to be the ecological response to climate change in which we have the highest degree of confidence (IPCC 2014).

1.1.3 Dendroecology as a tool for quantifying and predicting shrub responses to a changing climate

Some of the most conclusive evidence of shrubs responding to climate change comes from dendroecology, the study of annual growth increments in woody species. The development of dendrochronological techniques adapted to shrub species (Schweingruber and Poschlod 2005) opened the door to a new way of quantifying the climate sensitivity of tundra vegetation. Initial studies revealed strong, positive associations between warmer temperatures and increased annual growth of many shrub species (Johnstone and Henry, 1997; Bär et al., 2008; Forbes et al., 2010; Blok et al., 2011a; Jørgensen et al. 2015). But while there is no questioning that the tundra biome is undergoing large-scale, climate-driven increases in the abundance and growth of shrub species, a recent data synthesis using dendroecological data from 25 shrub species at 37 alpine and Arctic tundra sites highlighted the important variability in the climate sensitivity of shrub growth (Myers-Smith et al. 2015a). The causes of this heterogeneity are not very well understood but likely to be a combination of plant traits, site characteristics, and ecological interactions, all acting at different scales. Understanding these mechanisms will be critical to improving projections of vegetation-atmosphere interactions at high latitudes and their effects on the global energy and carbon budget.

1.2 Heterogeneity of shrub expansion

Most current projections of Arctic vegetation change and associated feedbacks assume a consistent, strong, positive response of shrub species to climatic drivers, and primarily to summer temperature, across the whole tundra biome (Pearson et al. 2013). However, these predictions could be greatly over-estimated if other factors constrained the climate response of shrubs. In a biome-scale analysis (Myers-Smith et al. 2015a), just under half (46%) of the populations had positive associations between climate and growth, with high variation in the magnitude of sensitivity across sites and species (**Figure 1-1**). Moreover, within populations, as few as 5% and as many as 97% of individuals had climate-sensitive growth. Therefore, the heterogeneity in the climate sensitivity of shrub growth appears to arise at multiple scales of biological organisation. Potential explanatory factors explaining this variability include local environmental context and plant-plant interactions. This section will cover the possible factors interfering with the climate response of shrubs and highlight the key unknowns that currently preclude the development of more accurate predictions of vegetation trajectories in the tundra biome.

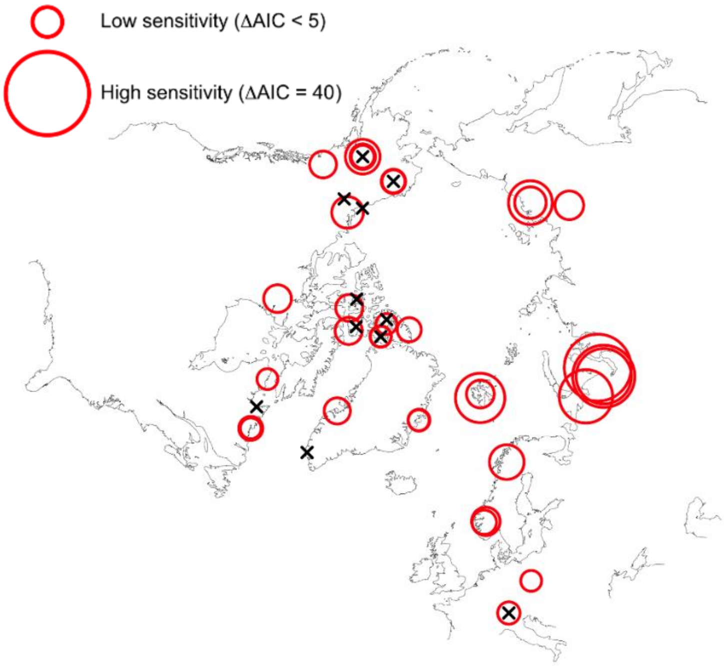


Figure 1-1 *Climate sensitivity of shrub growth to summer temperature is highly heterogeneous across the tundra biome. The size of the circles indicates the magnitude of the sensitivity measured from linear mixed-effects models (for more details, see Myers-Smith et al. 2015a). Figure prepared by Isla Myers-Smith.*

1.2.1 Intra-individual responses of plant organs

Shrubs are woody plants with a multi-stemmed morphology and complex architecture. Overall, very little is known about internal resource allocation to growth modules within shrub plants. Branching patterns and resource allocation to different architectural components are partly genetically determined, and partly plastic responses to environmental conditions (Charles-Dominique et al. 2015). Moreover, Arctic shrub canopies can be vertically structured to maximise light interception at low solar angles (Paradis et al 2016; Magney et al. 2016). This plasticity in canopy organisation and resource allocation likely benefits the plant as whole, but as a result, different modules may be experiencing sub-optimal conditions. For instance, self-shading within a plant or shrub patch (Street et al. 2007; Fletcher et al. 2012) may lead to differential performance of stems. Thus, growth within a stem may not be representative of the whole individual life history – especially considering localised effects of disturbances like herbivory. Furthermore, as shrubs get older, growth may cease in the oldest parts (Wilmking et al. 2012; Buchwal et al. 2013), and old stems die and get replaced. Clonal growth with stem dieback can mean that genetic individuals may persist over timescales from centuries to over a thousand years, but with live parts rarely exceeding 200 years old (de Witte et al. 2012). Stem demographics and resource allocation within shrubs may therefore have methodological implications for the quantification of climate sensitivity (Myers-Smith et al. 2015b) if different parts do not respond coherently to environmental drivers (Buchwal et al. 2013).

1.2.2 Inter-individual differences in climate sensitivity

At the site-to-regional scale, growth within plant communities is broadly controlled by abiotic variables, but fine-tuned by a range of factors including genetic differences between populations, site topography, ecological interactions, and disturbances, which this section will briefly review. If shrub growth is limited by these multiple drivers, it is perhaps not surprising to find high variability in the climate response of growth (Myers-Smith et al. 2015a). Understanding the relative importance of these controls on shrub growth are current research priorities to refine estimates of shrub expansion rates.

Local topography, moisture and resource availability

Tundra ecosystems are spatially heterogeneous, resulting in a mosaic of expanding and stable shrub patches (Tape et al. 2012). Shrub performance and expansion rates may be controlled by meso-scale topographic features such as aspect, slope, and elevation (Ropars and Boudreau 2012; Myers-Smith and Hik 2017; Lemay et al. 2018). Disturbances from degrading permafrost may create additional landscape heterogeneity and open new sites to rapid colonisation and succession (Lantz et al. 2010). Other abiotic factors such as soil temperature, moisture, chemistry, and nutrient content (Gough et al. 2000; Moulton and Gough 2011; Tape et al. 2012), as well as snow accumulation patterns (Wipf and Rixen 2010; Suding et al. 2015), can all influence growth and reproduction of shrub species. As these factors may vary over short (metre scale) distances at some tundra sites (Graae et al. 2018), microtopography could therefore drive individualistic responses in shrubs within a population.

Plant-plant interactions

Vegetation can also mediate the abiotic factors mentioned above through feedbacks on soil temperature, wind exposure, nutrient cycling, etc., as well as having direct effects on plant performance. The presence of positive and negative plant-plant interactions could explain part of the variability in the climate sensitivity of tundra shrubs. On one hand, facilitative interactions can help plants to establish under sub-optimal abiotic conditions (Choler et al. 2001; Batllori et al. 2009; Ballantyne and Pickering 2015) and therefore could promote faster expansion or range shifts of species. On the other hand, negative interactions, and especially competition, might induce growth limitations (Choler et al. 2001; Dormann et al. 2004; Pellissier et al. 2010), thereby preventing plants from capitalising on longer or warmer growing seasons.

Competitive interactions are often overlooked in dynamic global vegetation models. When they are incorporated, they are modelled a) between, not within, plant functional groups, and b) for areas below the boreal treeline only (Arora and Boer 2006). The shrub species that currently drive much of the shrub expansion patterns in the tundra biome are competitive plants with plastic growth and fast nutrient acquisition strategies (Bret-Harte et al. 2002; Myers-Smith et al. 2011; Elmendorf et al. 2012b; Morrissette-Boileau et al. 2018). As shrub cover increases in tundra ecosystems, competitive interactions between these tall deciduous shrubs are likely to intensify, and could eventually lead to a deceleration of shrub expansion if local resources become more limiting than temperature.

Other processes

Many other factors which are not the focus of this thesis are likely to play an important role in determining the climate sensitivity and future responses of tundra vegetation. Genetic differences among individuals and populations and their degree of plasticity to climate change have implications for the rate at which plants may adapt to climate change or migrate to new locations (Bjorkman et al. 2017; Graae et al. 2018). Herbivory and disturbances such as extreme climatic events can exert strong controls over plant dynamics resulting in community shifts different from predictions based solely on climate change (Olofsson et al. 2009; Aerts 2010; Speed et al. 2013; Kaarlejärvi and Olofsson 2014; Bokhorst et al. 2012a).

1.2.3 Biogeographic trends in sensitivity

Identifying broad-scale patterns in the responses of plant growth to climate change in the Arctic is a current research priority that will allow more realistic estimates of future vegetation change in the tundra biome. Biome-wide syntheses have allowed to generalise a few key findings. First, vegetation responses to temperature seem stronger at sites that were already warmer to begin with (Elmendorf et al., 2012b), and at wetter versus drier sites (Myers-Smith et al. 2011; Elmendorf et al. 2012a; Ackerman et al. 2017). Furthermore, shrubs are more climate sensitive near their northern or upper distribution limit (Myers-Smith et al. 2015a). Species with taller maximum canopy height also tend to have greater sensitivity (Myers-Smith et al. 2015a). Together, these findings suggest that the greater shifts in vegetation may initially occur at low to mid-latitudes of the tundra biome, where climatic conditions are not too severe and tall deciduous shrubs already dominate the landscape.

1.3 Objectives and research questions

The expansion of shrub species in the tundra biome is a well-documented response to climate change with compelling evidence (IPCC 2014). However, the heterogeneity of growth responses to warming complicates predictions of future vegetation change in the Arctic and its associated feedbacks. The objectives of this thesis are:

1- to identify the climatic factors controlling the radial growth of tundra shrubs;

2- to quantify the variation in the strength of these signals;

3- to attribute this variation to morphological, ecological or biogeographic factors.

Variation in the strength of the climate signal detected in growth rings may be caused by different factors acting on different scales, from morphological differences among parts of a plant to plot-level ecological constraints and all the way up to biogeographic patterns in sensitivity (**Figure 1-2**). I asked the following principal research questions:

1- Do longer and warmer summers have additive effects on shrub growth?

Arctic summers are getting longer and warmer (IPCC 2013). Growing season length and temperature are often referred to interchangeably as drivers of shrub growth, but few tests have quantified their relative importance in controlling shrub expansion. Given the heterogeneity in warming trends and snowmelt timing across the tundra biome (Ernakovitch et al. 2014), it is crucial to understand the respective influence of rising temperatures versus longer growing seasons on current and future future vegetation change. **Chapter 3** compared the sensitivity of radial growth to summer temperatures and growing season length, using 324 shrubs from four sites across Northern Canada. I hypothesised that a greater part of variation in shrub growth would be explained by temperature than by growing season length.

Because climate sensitivity measured from dendroecological data is obtained from different protocols in different studies (Myers-Smith et al. 2015a, b), it may not be directly comparable across sites and species given complex internal resource allocation patterns (Buchwal et al. 2013). I collaborated with colleagues from Université Laval to quantify the strength of intra-individual climatic signals within different plant parts (Ropars et al. 2017). We found that root collars in *Betula glandulosa* from different landscape types in Northern Québec had stronger climatic sensitivity than stems from the same individuals (**Appendix I**). These results informed the rest of my doctoral work and my sampling protocols.

2- How does plant size influence the climate sensitivity of shrub growth?

Plant height is an important structural trait that affects physical processes in tundra ecosystems. Shrub species with taller canopy heights appear to be more climate sensitive (Myers-Smith et al. 2015a), although whether this reflect wider functional group strategies or relate mechanistically to individual performance is unknown. **Chapter 4** tested the influence of plant size on the climate sensitivity of 551 shrubs belonging to 15 species across 16 sites around the circumpolar region. I also tested the same question on a smaller (306 shrubs) but more homogenous and better-replicated dataset that I collected in Northern Canada. I hypothesised that taller plants would show a stronger climate signal than smaller shrubs because they are more competitive (thus less limited by local resource availability) and their canopies are less vulnerable to ground-level microclimatic effects.

3 – How does the biotic context influence the climate sensitivity of shrub growth?

Shrub expansion has been documented across the tundra biome (Myers-Smith et al. 2011; Naito and Cairns 2011; Elmendorf et al. 2012a), in boreal forests (Frost and Epstein 2014; Grabowski 2015) and in alpine environments (Danby et al. 2011; Formica et al. 2014; Venn et al. 2014; Dial et al. 2016), but it is not clear whether the climate sensitivity varies across forest-tundra transitions where the competitive environment differs. **Chapter 5** explored local variations in the climate sensitivity of dominant tall shrub species from the Kluane region of the Yukon Territory in Canada. Shrub expansion has been documented in the area, both in boreal forests and in alpine environments, but it is not clear whether these vegetation trajectories will continue as shrub densities increase and competition with trees (boreal) and among shrubs (boreal and alpine) intensify. I compared growth rates and climate sensitivity of willow shrubs from the alpine and boreal zones to test the hypothesis that the growth and climate response of shrubs in boreal forests are suppressed by competition from trees. I also took advantage of a past canopy removal experiment to test how sensitive shrub growth was to competition with other shrubs in alpine communities. I hypothesised that a release from competition after canopy removal would trigger higher growth rates in neighbouring shrubs.

4- Does competition influence the climate sensitivity of shrub growth, and do competition intensity and importance vary along an environmental severity gradient?

Climate-driven shrub expansion in the tundra may not continue indefinitely if competition among shrubs intensifies to the point where resources become more limiting to growth than temperature. The relative importance of competition in driving plant community dynamics is thought to be more important in productive sites, and less so in sites with harsh environmental conditions (Bertness and Callaway 1994; Maestre et al. 2009). Therefore, shrub growth could be more limited by competition at lower latitudes of the tundra biome, with major implications for current Earth-System models which assume strong and uniform positive growth responses of shrubs to warming (Pearson et al. 2013). **Chapter 6** used a spatial approach to explicitly test the influence of the competitive environment on the radial growth and climate sensitivity of tundra shrubs. The location and contrasting environmental conditions of the four field sites across Northern Canada allows to place the results in a broader competition theory ecological framework. I hypothesised that:

a. Individuals that experience more competition, from closer or larger neighbours, show decreased climate sensitivity of radial growth compared to shrubs growing in lower densities

b. According to the stress-gradient hypothesis, the two northern sites will show greater climate sensitivity overall than the two southern sites, where competition is expected to be more important.

Finally, because plant-plant interactions in a changing Arctic will not only impact the growth of tundra shrubs, but will also likely play a role in controlling species distribution (Gilman et al. 2010; Hellmann et al. 2012; HilleRisLambers et al. 2013), **Chapter 7** (Angers-Blondin et al. 2018) tests whether the vegetation already in place may interfere with seed germination, a key aspect of shrub expansion in expected climate-driven range shifts.

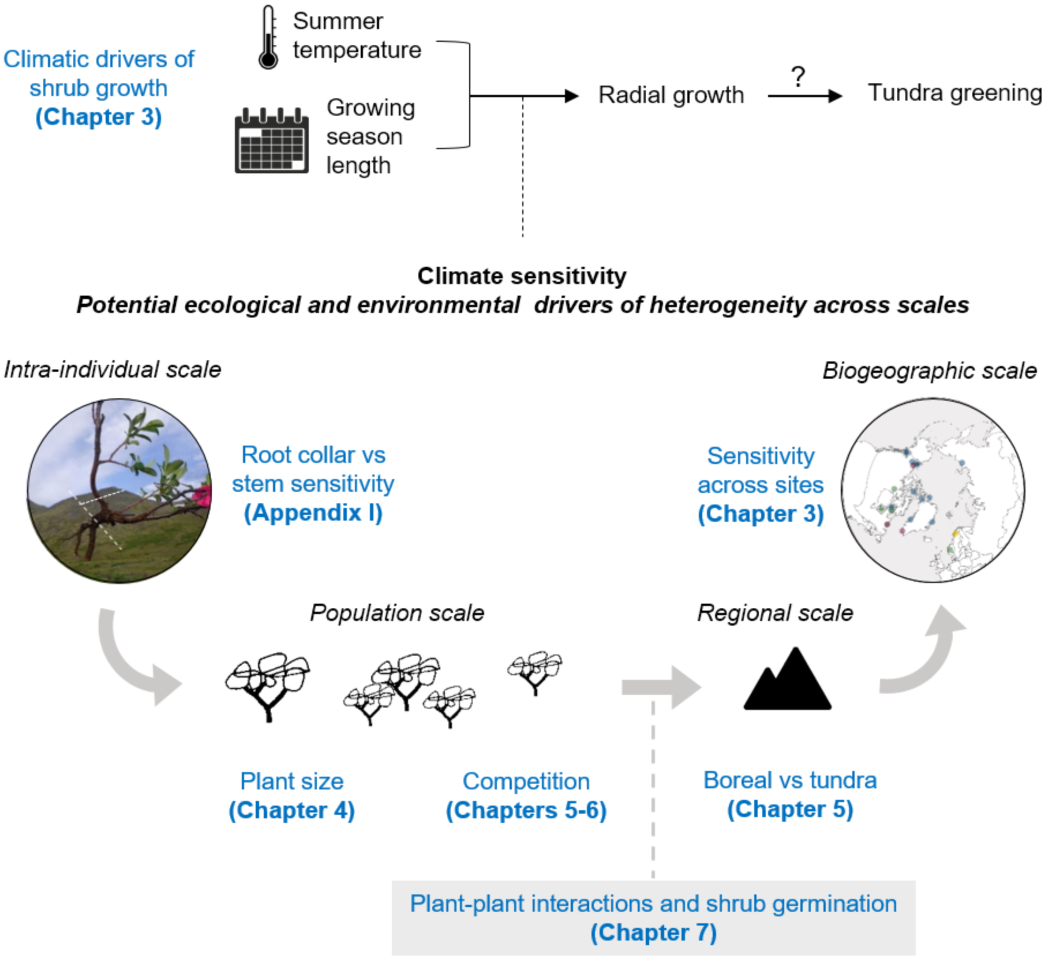


Figure 1-2 *Conceptual diagram of the key potential factors explaining the climate sensitivity of growth tested in this thesis*

Chapter 2 Methodology

The four main data chapters of this thesis rely on annual growth ring measurements to identify biotic and abiotic controls of shrub growth and quantify their climate sensitivity. I sampled shrub populations at four sites across Northern Canada, and these data are used in various subsets or in combination with other dendroecological data to answer the objectives of my thesis. To avoid undue repetition of site descriptions and sampling protocols, the main methods and detailed information on the dataset are presented here. Other data sources and detailed statistical analyses are presented where relevant in each chapter.

2.1 The role of dendroecology in quantifying shrub sensitivity to environmental change

Shrub dendroecology is now an established and growing field that greatly contributes to our understanding of tundra vegetation change (**Chapter 1**). The adaptation of traditional tree-ring techniques for plant species with secondary growth such as shrubs and perennial herbs (Schweingruber and Poschlod 2005) provides a powerful tool for ecological studies in extreme, treeless environments where long-term ecological records are scarce. Annually-resolved growth records in tundra shrubs have not only demonstrated their potential for climatic reconstructions (Rayback and Henry 2005; Schmidt et al. 2006; Bär et al. 2008; Hantemirov et al. 2011), but can also be useful in land-use (Rixen et al. 2004; Zverev et al. 2008), geomorphological (Owczarek 2010; Buras et al. 2012), and ecological (Schweingruber et al. 2013; Büntgen et al. 2015; Grabowski 2015; Morrissette-Boileau et al. 2018) studies. Nevertheless, the study of multi-stemmed plants with complex morphology and internal resource allocation strategies, combined with environmentally induced growth eccentricities and missing rings (Wilmking et al. 2012; Buchwal et al. 2013), poses technical challenges (**Figure 2-1**) and uncertainty in biological interpretation.

Sampling strategies in dendroecology tend to follow a different philosophy than most other areas of ecology. Sampling is usually highly selective rather than random, and biased towards dominant individuals that are expected to be chiefly limited by a variable of interest, often climatic (Kuivinen and Lawson 1982; Liang and Eckstein 2009; Hantemirov et al. 2011). For studies aimed at reconstructing past climate from shrub-ring records where a strong, consistent climatic signal is needed, selecting individuals more likely to be limited by regional climate rather than local-scale factors is understandable and desirable (Pilcher and Gray 1982; Mäkinen and Vanninen 1999). However, such selective sampling will inevitably lead to an inflated measure of climate sensitivity (**Figure 2-2**) and may lead to over-estimating future responses of tundra vegetation to warming (Pearson et al. 2013). Random, indiscriminate sampling incorporating ecological factors such as competition (Rollinson et al. 2016) are more likely to yield a representative estimate of population-level climate sensitivity.

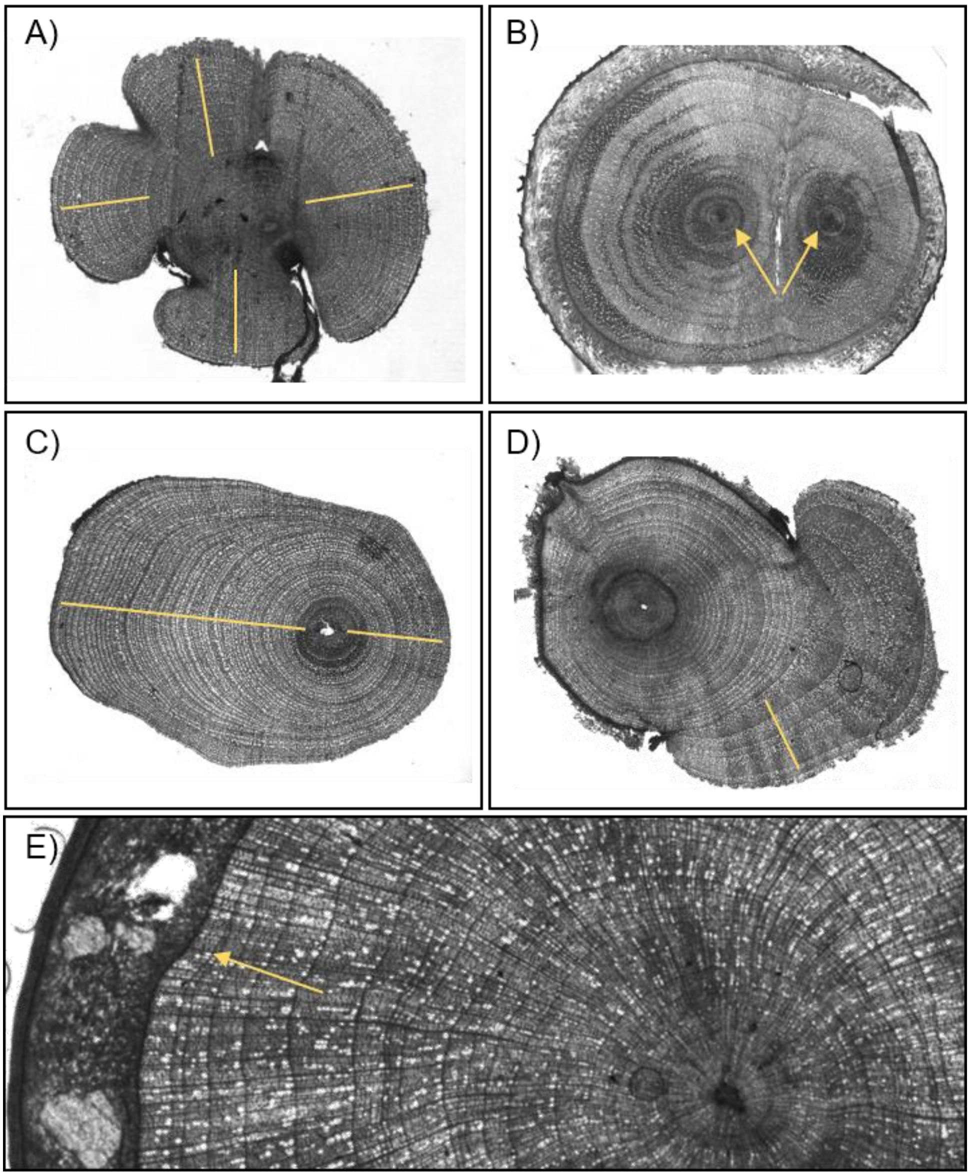


Figure 2-1 *Anatomical complexity of root collars in tundra shrubs. Root collars often exhibit heavy lobing (A), and roots and stems grow so close together that it can be difficult to obtain a cross section that does not comprise multiple piths (B). Growth is often eccentric (C-D), with wedging rings that appear only one one side of the stem (E).*

Recent efforts to standardise sampling, processing and analysis of shrub growth-ring data across sites and observers (Myers-Smith et al. 2015b) will facilitate biome-wide data syntheses and enable comparisons of the drivers of vegetation change in the tundra. However, there is currently still a great deal of variability in protocols, from site selection and sample design to the anatomical part of the shrub that is sampled. A project on which I collaborated during my PhD sought to quantify the strength of the climate signal within different parts (stem versus root collar) of the shrub *Betula glandulosa* (**Appendix I**; Ropars et al. 2017). We found that root collars show higher climate sensitivity than the largest stem, possibly because the root collar integrates growth from the whole plant, whereas stems can experience different growth rates depending on their respective aspect, presence of herbivory, or shading from other branches. Dendroecological sampling must therefore be conducted with all these physiological and ecological considerations in mind.

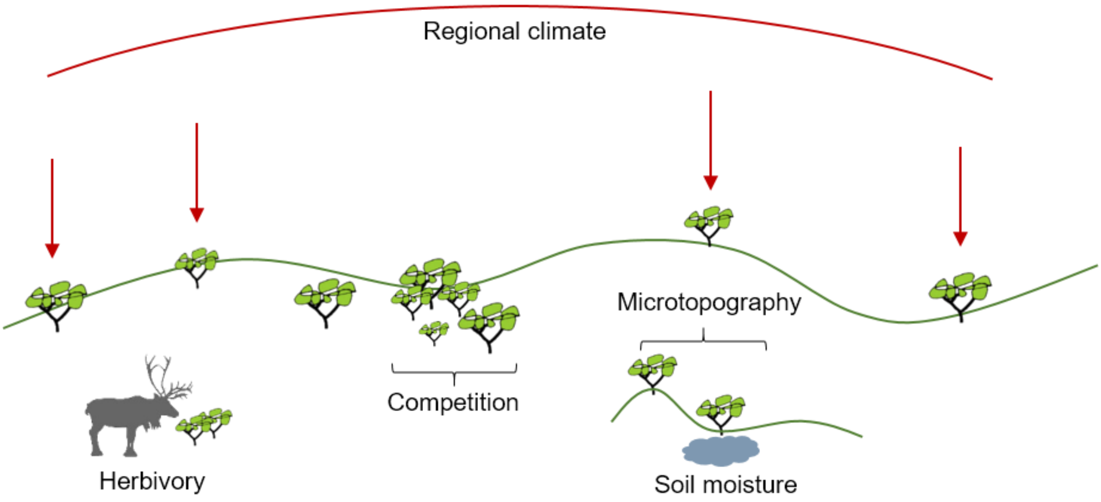


Figure 2-2 *Selective rather than random sampling may lead to inflated estimates of climate sensitivity for shrub populations. Here, if only individuals indicated with red arrows are sampled, the effects of site-specific ecological factors interfering with the climate response of many shrubs are not taken into account.*

2.2 Site description

Sampling took place between June and August 2015 at four locations across Northern Canada (**Figure 2-3**). Qikiqtaruk-Herschel Island and Kluane in the Yukon Territory are separated by ca. 1000 km along a north-south gradient; Salluit and Umiujaq in Northern Québec are separated by ca. 600 km.

2.2.1 Kluane

The Kluane region in southwest Yukon is characterised by boreal coniferous forest and mountainous terrain. Beyond the treeline, the vegetation shifts to tall shrub tundra, with the shrubline of canopy-forming species lying at around 1600-1700 meters of elevation (Myers-Smith 2011). Summits harbour Arctic-alpine tundra vegetation. My sampling locations in Pika Valley (plots "P") and on the Kluane Plateau (plots "K") were characterised by alpine tall shrub tundra dominated by different willow species: *Salix richardsonii* Hook., *Salix pulchra* Cham., and *Salix glauca* L. Hook. The ground layer is composed of dwarf shrubs *Dryas octopetala* L. and *Salix reticulata* L., and of various graminoids, forbs, mosses and lichens (Myers-Smith and Hik, 2013). Given the high elevations of these sites, climatic conditions in the summer are relatively similar to those that prevail ca. 1000 km north on Qikiqtaruk, although Kluane is warmer in the winter and shoulder seasons (**Figure 2-4**).

2.2.2 Qikiqtaruk-Herschel Island

Qikiqtaruk-Herschel Island is a Yukon Territorial Park in the Beaufort Sea. The island measures around 100 km^2. It experiences an Arctic climate and the vegetation is characterised by erect dwarf-shrub tundra (Walker et al. 2005). It is the driest and coldest of the four sites, except during the summer (**Figure 2-4**). The island is underlain by ice-rich permafrost that is degrading rapidly, with large retrogressive thaw slumps eroding as fast as 15 meters per year (Burn 2017). Different vegetation types exist on the island (Smith et al. 1989). My plots were characterised by the following vegetation types:

- Herschel type: moist acidic tussock tundra, dominated by *Eriophorum vaginatum*
- Komakuk type: dwarf shrub and forb tundra characterised by disturbance from freeze-thaw processes exposing bare ground; dominance of *Dryas integrifolia* Vahl. and *Salix arctica* Pall.; occasionally canopy-forming willows such as *Salix glauca* L.
- Orca type: coastal floodplain dominated by canopy-forming willows such as *Salix richardsonii* Hook.

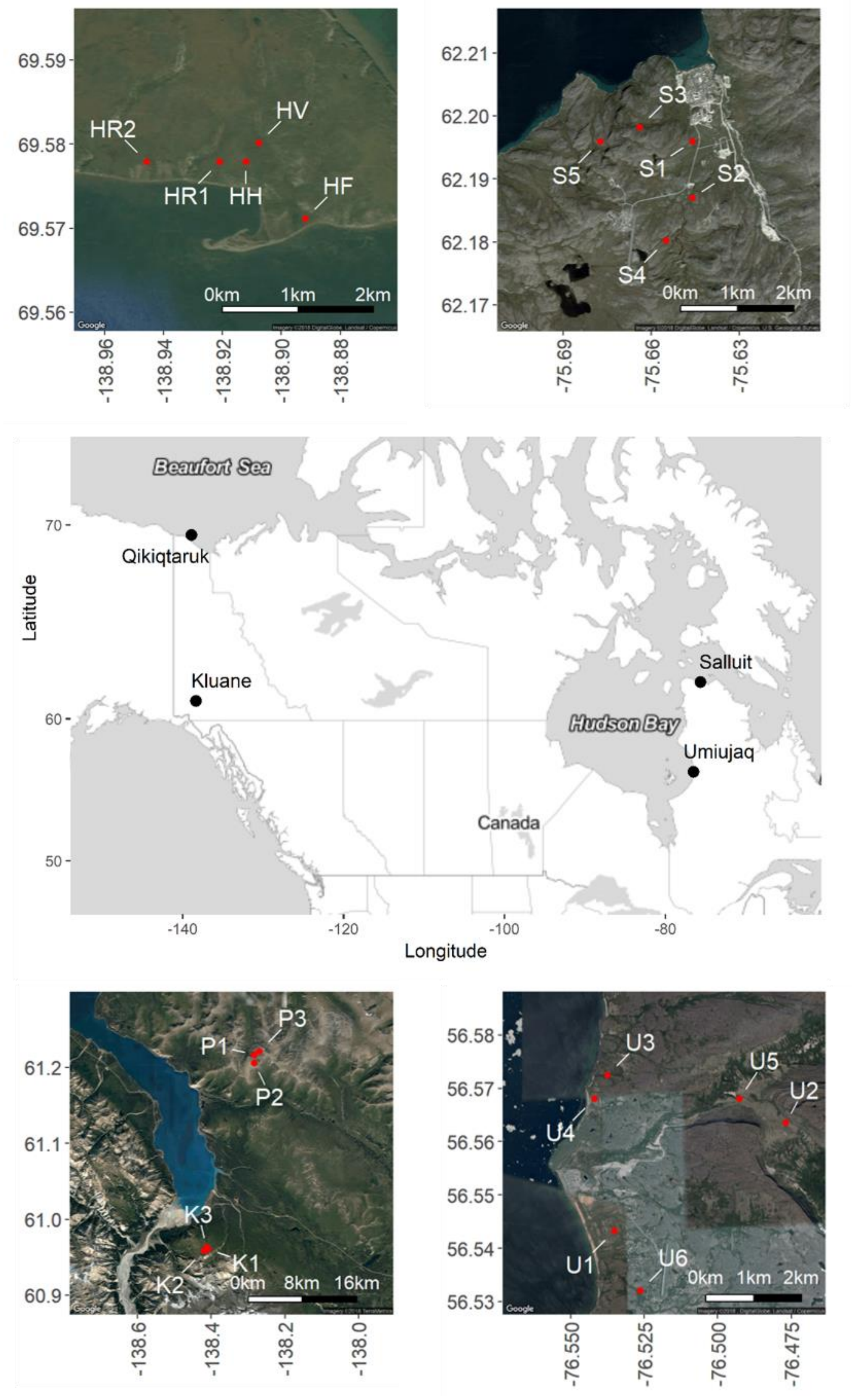


Figure 2-3 *Map of the four field sites in Northern Canada (center panel) and location of the study plots (red dots) within sites (top and bottom panels).*

2.2.3 Umiujaq

Umiujaq is an Inuit settlement of Nunavik (Northern Québec) located at the Arctic treeline on the eastern coast of Hudson Bay. It experiences a sub-Arctic climate with summer temperatures above 10°C (**Figure 2-4**), and the vegetation consists of sparse spruce forests in the lowlands, coastal tundra near the shore, and tall shrub tundra (almost exclusively *Betula glandulosa*) encroaching on lichen plateaux on higher ground (Provencher-Nolet et al. 2014). The region is characterised by gently rolling hills (Caccianiga and Payette 2006) and underlain by the Canadian Precambrian Shield. It belongs to the discontinuous permafrost zone, with permafrost occurring primarily in the bedrock and under palsas (Allard and Séguin 1987). Northern Québec warmed strongly during the 1990’s (Bhiry et al. 2011), but warming trends have slowed down recently (see Chapter 3).

2.2.4 Salluit

Salluit is an Inuit settlement of Nunavik located on the Hudson strait. It lies over 500 km beyond the Arctic treeline and is, in summer, the coldest of the four sites (**Figure 2-4**). The landscape is characterised by gently rolling hills. The vegetation consists mainly of herbaceous tundra with very scarce shrub cover, except along creeks and rivers where taller shrubs are found. Willows dominate the shrub layer, although the dwarf birch *Betula glandulosa* is also found. The area is underlain by continuous permafrost (Allard and Séguin 1987). Salluit is located on the margin of the Rivière-aux-Feuilles caribou herd summer range (Le Corre et al. 2016). Caribou densities are low around the hills near the village where my study plots are located, but herbivory is likely to be an important constraint to shrub expansion in this part of the biome (Morrissette-Boileau et al. 2018).

2.3 Study species

I sampled a total of seven tall shrub species across the four sites. All the species sampled in the Yukon Territory (Kluane and Qikiqtaruk-Herschel Island) were willows: *Salix pulchra*, *Salix richardsonii*, *Salix niphoclada*, *Salix glauca*, and *Salix barrattiana*. The first three species account for over 95% of my sampling effort in the Western Arctic. Canopy-forming tundra willows are deciduous shrubs characterised by fast growth rates (Bret-Harte et al. 2002) and produce small, wind-dispersed seeds in great quantities, which allow rapid colonisation of sites after disturbances (Brinkman 1974; Forbes et al. 2001).

In Northern Québec, shrub expansion is mostly driven by *Betula glandulosa*, the dwarf birch (Ropars and Boudreau 2012). This was the only tall shrub species present in the plots in Umiujaq. At my other Nunavik site, Salluit, the tall shrub community mostly consists of willows, and *Salix planifolia* was the most common species (78% of sampling), with rarer occurrences of Salix glauca (13%) and of *B. glandulosa* (9%). *Betula glandulosa* can hybridise with the closely related and widespread *Betula nana*. Dwarf birch has high plasticity of growth (Bret-Harte et al. 2002) and forms mycorrhizal associations allowing carbon transfer among individuals (Deslippe et al. 2011).

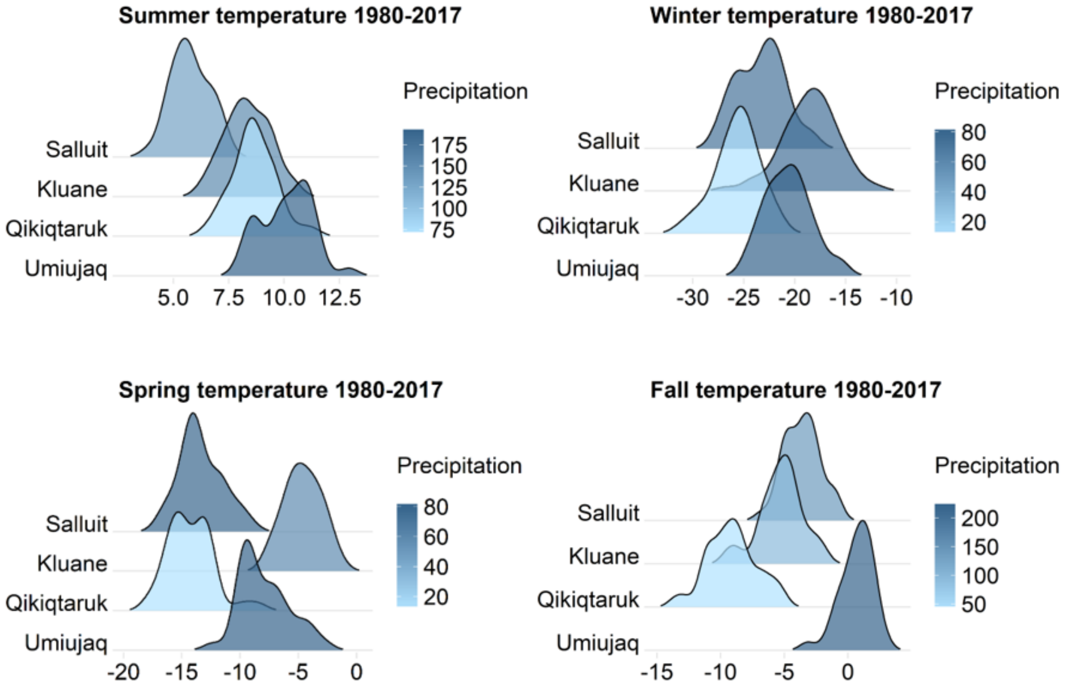


Figure 2-4 *Quarterly climatic summaries for the four sites, obtained from CRU 3.24.01 gridded climate data. The density histograms represent the distribution of temperatures for the period 1980-2017; the colour of the curve represents the corresponding mean precipitation sums for this quarter.*

2.4 Sampling

At each of the four sites, I set up five to six square sampling plots ranging from 25 m^2 to 100 m^2. The size of the plots was determined by shrub density, with a target number of ca. 30 shrubs per plot (median = 32, range = 19 – 54). To capture the landscape heterogeneity and avoid spatial autocorrelation, plots within a site were located at least 300 meters apart, with a median distance to the closest neighbouring plot of 1.9 km (range = 0.304 – 30.4 km).

Within each plot, every canopy-forming shrub taller than 10 cm was identified to species level. I measured canopy height, canopy width along two perpendicular diameters, and the diameter of the largest stem. Shrubs on the edges of the plot were considered if more than half of the canopy was found inside the plot.

I mapped the position of each individual within the plot using a laser rangefinder mounted on a tripod with an attached protractor (**Figure 2-5**). The tripod was systematically set up in one corner of the plot, with a horizontal plane parallel to the slope of the terrain. I chose plots with minimal spatial heterogeneity, i.e. avoiding deep depressions or tall hummocks of vegetation. By measuring the distance of each shrub (using the canopy centre) from the tripod and the angle from a reference point, I could calculate Cartesian coordinates for each shrub. To validate my mapping method, I compared distances between selected pairs of individuals that were measured in the field with distances calculated from my digital mapping. I found that the rangefinder mapping had an error margin of less than 10 cm, which is acceptable given the uncertainty in locating the exact center of a shrub canopy, and considering that the biotic interactions which are the focus of this thesis occur over several meters.

2.5 Dendroecological methods

2.5.1 Processing and measuring

Every individual shrub within the study plots was sampled at the root collar, i.e. the oldest part of a shrub at the root-shoot interface. If the root collar was damaged or rotten, I also sampled the largest stem as close as possible to the root collar. Woody sections were air-dried and brought back to the laboratory, and processed according to standard dendroecological protocols for shrub species (Myers-Smith et al. 2015). This included softening the wood by soaking the samples in water for a few days, then cutting the samples into thin cross-sections (ca. 20 µm) with a sledge microtome (Reichart-Jung). The thin sections were mounted on glass slides and photographed under a microscope (Leica Application Suite image capture software) for further analysis. I measured growth rings along two to four radii on each sample using the ObjectJ plugin (https://sils.fnwi.uva.nl/bcb/objectj/index.html) for the ImageJ software (Schindelin et al. 2012).

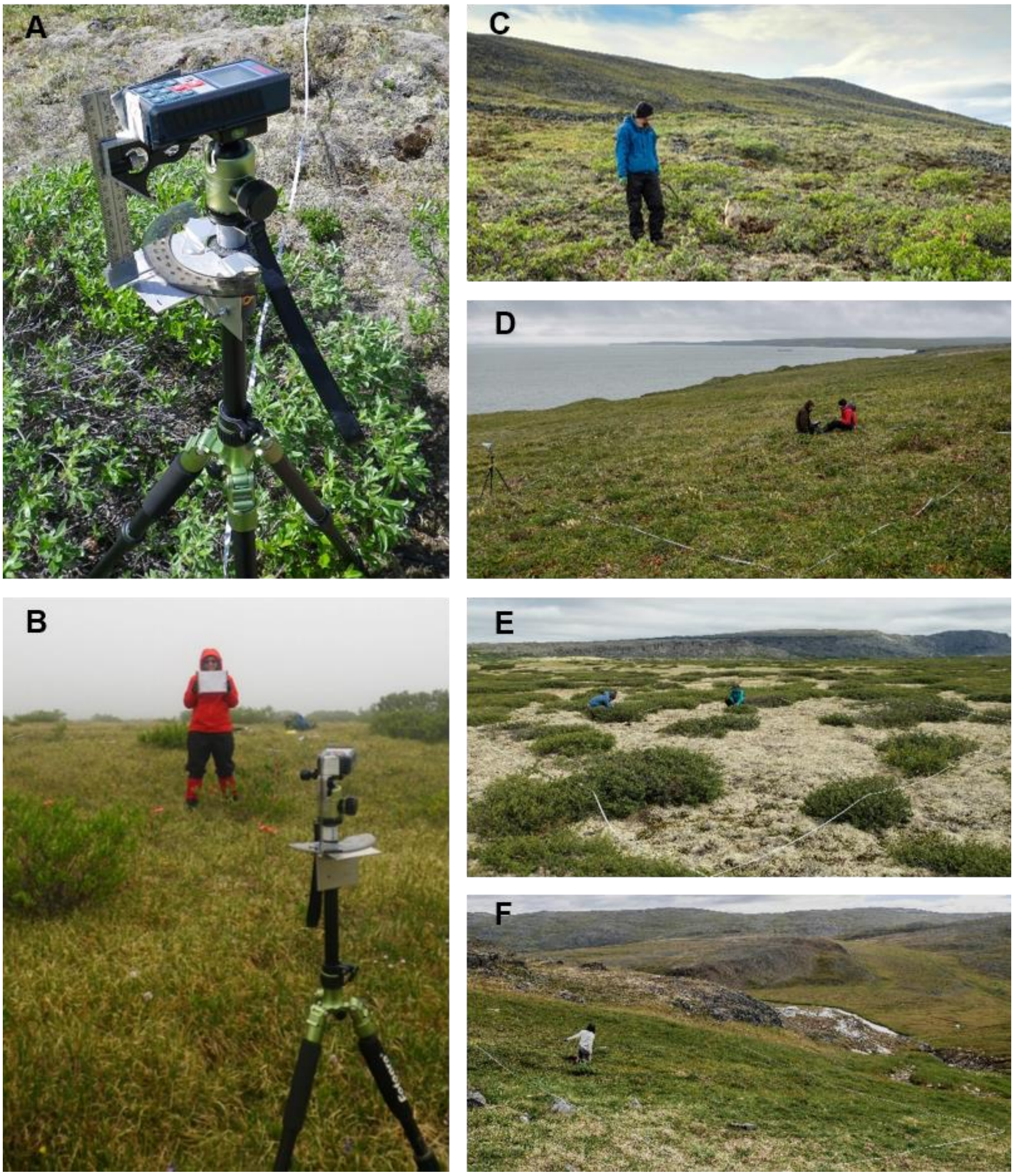


***Figure 2-5** Plots were mapped using a digital rangefinder mounted on a tripod and rotating around a protractor (A). The distance to the target (B) and the angle from a reference point allow to calculate coordinates for each shrub. Photographs on the right-hand side show representative plots for Kluane (C), Qikiqtaruk (D), Umiujaq (E) and Salluit (F).*

2.5.2 Data quality

Ring-width measurements were restricted to the period 1990-2014. Most individuals were older than this, in which case the rings were counted but not measured to get an approximate age for each sample (**Table 2-1**). We did not extend the measurement period beyond 1990 for two reasons. First, most of the climatic or ecological variables used in the different chapters either have short time series (e.g. land surface greenness satellite data), or represent a snapshot of the environment at the time of sampling (e.g. number of neighbours within a given radius), which becomes less relevant going further back in time. Second, the longer the time series, the higher the risk of introducing dating errors by missing a year. A time span of 25 years was therefore considered optimal to quantify relationships with environmental variables with enough statistical power and biological relevance while minimising measurement error. Additionally, for young individuals, I removed rings that represented the first five years of growth as young growth patterns are often irregular (Myers-Smith et al. 2015a), and discarded individual time series that were shorter than five years.

I calculated the correlation among radii within each sample (**Table 2-1**). General overall agreement was ca. 75% (Pearson’s correlation). Tundra shrubs experience harsh growing conditions that cause growth anomalies (**Figure 2-1**), which could explain why ca. 10% of the individuals in the dataset had low mean radii intercorrelation (< 0.50). After verifying that these individuals did not have different climate sensitivity than the rest of the dataset, I did not eliminate them. For all subsequent analyses, radii were averaged so that each individual had a single corresponding time series.

Individual time series were correlated to all other individuals with a plot. Average correlations showed variable agreement across plots and sites (**Table 2-1**). Visual or statistical crossdating (Myers-Smith et al. 2015b) are procedures that increase dating accuracy by ensuring that time series show a common signal, usually in response to regional climate. This is valid for studies seeking to use chronologies to reconstruct environmental drivers, when sampling is conducted to enhance the climatic signal (e.g. tall trees without competitors or deformities). To suit the aims of this thesis, I sampled the plots exhaustively rather than selectively to capture the demographics of the population and a wide variety of growth rates (Schweingruber et al. 2013; Büntgen et al. 2015). Therefore, I chose not to exclude individuals with lower correlations. The lack of agreement among individual growth patterns may be caused by biotic interactions and other local factors interfering with the climate response of growth (Mäkinen and Vanninen 1999), which are of particular interest to this thesis.

2.6 Climate data

Arctic weather station data are often patchy, inconsistent, and not available for long periods. To ensure consistency in climate sensitivity analyses of shrub growth among my four different sites in Northern Canada, I used gridded climate data from the Climate Research Unit (CRU monthly temperatures, version TS 3.24.01, 0.5° resolution).

Precipitation data from gridded datasets are not as reliable as temperature data, given that precipitation is more spatially heterogeneous and therefore more challenging to interpolate (Karger et al. 2017). Growth correlations to precipitation should thus be treated with caution. For most chapters, I preferred the use of temperature data only for climate-growth relationships, given the abundant evidence of summer temperature being the main control of shrub growth (Dormann and Woodin 2002; Walker et al. 2006; Forbes et al., 2010; Myers-Smith et al. 2015a). Nevertheless, I explored correlations to other climatic variables such as precipitation when summer temperatures did not seem to exert a strong influence on growth (Chapter 3).

Table 2-1 *Summary of dendroecological sampling across four sites in Northern Canada. Mean radii intercorrelation within individuals (Radii R) and the range of pairwise individual correlations within plots (Plot R) are presented along with information on the sample size and population age and size structure.*

Site	**Plots** n	**Shrubs** n	**Radii R** (mean ± SD)	**Plot R** (min-max)	**Age (y)** (mean ± SD)	**Canopy height (m)** Median (max)
Qikiqtaruk	3	70	0.76 ± 0.16	0.03 – 0.46	28 ± 15	0.20 (0.65)
Kluane	3	73	0.76 ± 0.18	0.21 – 0.70	36 ± 12	0.32 (1.92)
Umiujaq	5	91	0.82 ± 0.16	0.02 – 0.32	27 ± 11	0.18 (0.60)
Salluit	3	90	0.66 ± 0.25	0.26 – 0.34	17 ± 8	0.18 (0.51)

2.7 Statistical analysis

Specific details of statistical analyses are described where appropriate in the data chapters. However, most sensitivity analyses in this thesis follow the same two-steps framework (**Figure 2-6**): first, (standardised) ring width is modelled as a function of a climatic variable (often summer temperature) through linear regression. The slope of this relationship then becomes a metric of climate sensitivity (Myers-Smith et al. 2015a). Mixed-effects models are then used to explain the variation in climate sensitivity as a function of ecological or environmental variables of interest while taking into account the hierarchical nature of the sampling (Harrison et al. 2018).

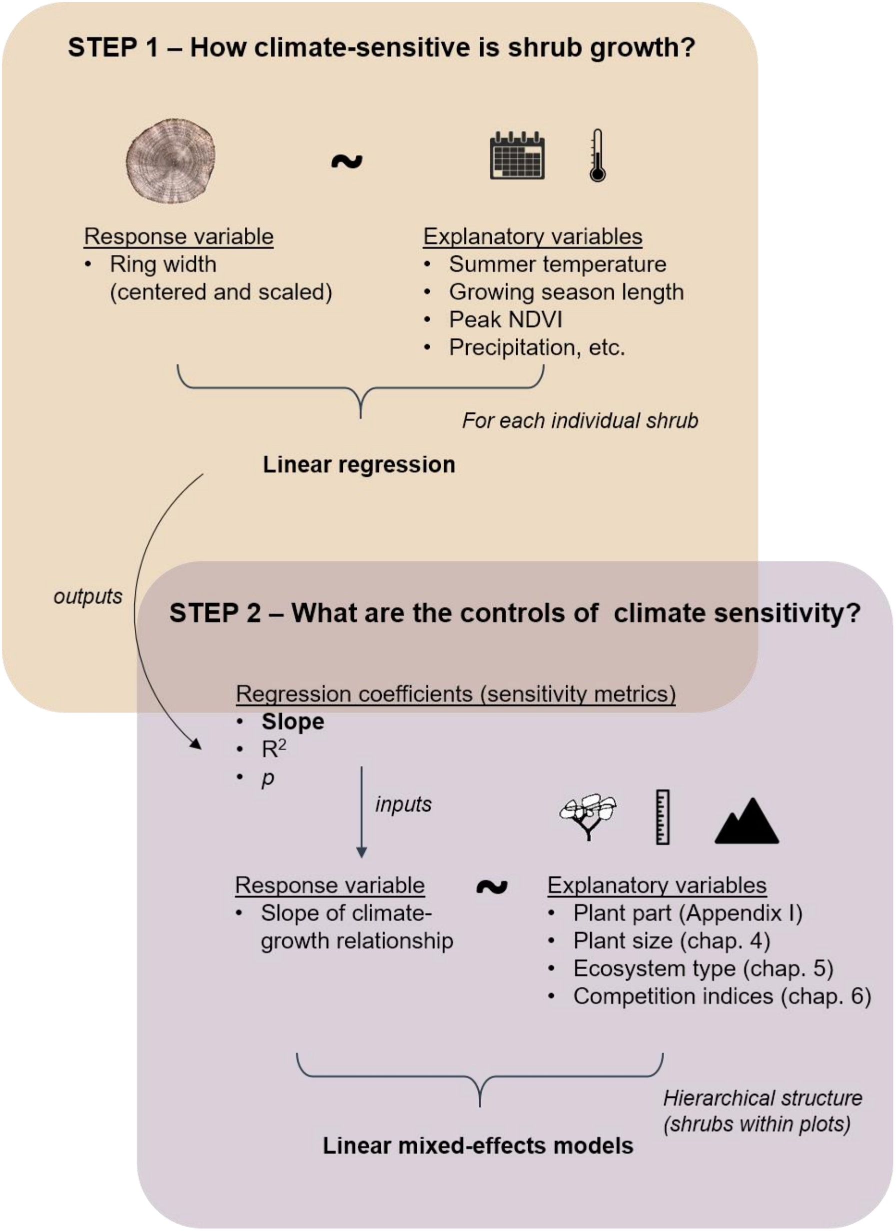


Figure 2-6 *General sensitivity analysis framework used throughout this thesis to explain variation in the climate sensitivity of shrub growth.*

Chapter 3 A study in green: The non-synergetic effects of warming and increasing growing season length on shrub growth

Abstract

Climate change in the Arctic is causing not only warmer, but also often longer growing seasons due to earlier snowmelt. The respective effects of longer versus warmer growing seasons on vegetation change, and notably on the expansion of woody species, are not well quantified but often assumed to work in combination. Recent advances in remote sensing, with higher-resolution satellite imagery, allow to estimate the length of the growing season from greenness indices across the tundra biome, with time series just now long enough to test for correspondence between growing season length and vegetation dynamics. In this chapter, I measured the sensitivity of annual growth to summer temperature and growing season length in 324 tundra shrubs from four sites across Northern Canada for the period overlapping MODIS 6 (Moderate Resolution Imaging Spectroradiometer) satellite observations (2000-2014). I hypothesised that shrub growth would be positively influenced by both factors, but more strongly by temperature. I also hypothesised that individuals would be consistent in the direction and magnitude of their responses to both factors. Finally, I tested the hypothesis that temporal variations in surface greenness (NDVI, the Normalised Difference Vegetation Index) are tracked in the radial growth of tundra shrubs. I found that overall climate sensitivity was weak, and the relative importance of temperature versus growing season length was variable across sites. Individuals were not consistent in their response to both factors. Furthermore, variations in greenness were not mirrored in the radial growth of shrubs. The de-coupling of growth sensitivity to two major global change drivers, growing season length and temperature, could affect rates of shrub expansion in parts of the Arctic with contrasting climatic regimes.

Author contributions

I designed the study and analysis framework with input from Isla Myers-Smith. I carried out the data collection and all statistical analyses. Jakob Assmann kindly extracted MODIS data from the Google Earth Engine and made recommendations on key remote sensing and phenology literature. Isla Myers-Smith wrote the Phenex code for deriving growing season length from MODIS data. I am thankful to Santeri

Lehtonen, Joe Boyle, Haydn Thomas, Jakob Assmann, Clara Morrissette-Boileau, Marc-André Lemay and Marianne Caouette for assistance in the field.

3.1 Introduction

3.1.1 Shrub expansion may be concurrently driven by several climatic factors

Arctic summers are not only getting warmer, but also longer (Tucker et al. 2001; Piao et al. 2007; Ernakovitch et al. 2014; Park et al. 2016) at many sites around the circumpolar region. The currently ongoing biome-wide expansion of shrub species (Tape et al. 2006; Myers-Smith et al. 2011) has conclusively been attributed to Arctic warming through many lines of evidence (see Chapter 1). But while temperature is undoubtedly a major control of plant growth in cold environments (Chapin et al. 1995; Elmendorf et al. 2012b), it is difficult to tease apart the multiple environmental drivers that can be acting concurrently on woody encroachment in the tundra. A challenging question that remains to be answered is the extent to which the length of the growing season, rather than its temperature, plays a role in enhancing Arctic plant productivity.

Phenology, i.e. the timing of life events, is especially sensitive to warming at higher latitudes (Root et al. 2003; Prevéy et al. 2017; Post et al. 2018). Northern plant communities have shown advanced green-up in the spring by ca. 1.7 to 4.7 days per decade (Zeng et al. 2001; Park et al. 2016). Snow manipulation experiments have revealed a strong control of snowmelt timing on plant development, growth, and reproductive success (Wipf and Rixen 2010; Cooper et al. 2011; Bjorkman et al. 2015). However, the environmental cues that dictate plant green-up and senescence are not fully understood (Richardson et al. 2013; Rumpf et al. 2014; Khorsand Rosa et al. 2015). In a shrub expansion context, the timing and length of the photosynthetically active period may be of paramount importance for tundra carbon stocks (Piao et al. 2007). Deciduous shrubs have fast green-up rates, and a 10-day lengthening of the peak productivity period is projected to increase carbon uptake by up to 84% (Sweet et al. 2015); however, an extension of the snow-free period could amplify warming feedbacks in the Arctic (Chapin et al. 2005).

3.1.2 The greening of the tundra

Plant productivity can be quantified over large geographic areas through satellite products such as the Normalised Difference Vegetation Index (NDVI), an index of land surface greenness (Glenn et al. 2008). Despite the difficulty of linking coarse-scale, remotely sensed data to plot-level vegetation measurements, NDVI data for the Arctic region seems to be a reliable predictor of plant biomass (Raynolds et al. 2012). Around the circumpolar region, since the 1980s, satellites have detected a greening trend suggesting an increase in plant biomass and photosynthetic activity (Myneni et al. 1997; Jia et al. 2009; Eastman et al. 2013; Ju and Masek 2016; but see Bhatt et al. 2013; Phoenix and Bjerke 2016 for “browning” trends), especially at higher latitudes in shrub- or graminoid-tundra (Goetz et al. 2005; Verbyla 2008; McManus et al. 2012).

Several regional studies have reported increases in NDVI concurrent with on-the-ground vegetation change and shrub encroachment (Blok et al. 2011a; McManus et al. 2012; Ropars et al. 2015), suggesting that shrub expansion is directly responsible for satellite-derived increases in greenness. Moreover, positive correlations between maximum NDVI and shrub growth have been documented for regions of Siberia (Forbes et al. 2010; Blok et al. 2011a; Macias-Fauria et al. 2012) and North America (Blok et al. 2011a; Ropars et al. 2015; Weijers et al. 2018). Until recently, the coarse spatio-temporal resolution of satellite data precluded explicit, mechanistic attribution of greening to shrub growth rates and cover change. Recent advances have led to the development of higher-resolution (sub-km) NDVI time series. Only now, with nearly two decades of these finer-scale observations, can we attempt to quantitatively establish relationships between tundra plant growth and satellite-derived greenness and growing season length.

3.1.3 Objectives and hypotheses

Here, I used radial growth time-series from 324 tundra shrubs across four sites of contrasting growing season characteristics to compare the influence of growing season length and temperature on shrub growth, and to test whether large-scale temporal trends in tundra greenness are reflected in the interannual variability of secondary growth. My hypotheses were:

1- Shrub growth is sensitive to both growing season length and temperature, but temperature better explains interannual variation in growth rings. I therefore expected to see stronger positive relationships between ring width and temperature.

2- Individual shrubs are consistent in their sensitivity to growing season length and temperature. I predicted that shrubs with higher temperature sensitivity would show a correlated magnitude and direction of sensitivity to growing season length.

3- Inter-annual variations in tundra greenness can be detected in the radial growth of shrubs. I expected to find a positive relationship between ring width and NDVI.

3.2 Methods

3.2.1 Study sites and sampling

I sampled canopy-forming, deciduous shrubs at four sites in northern Canada (Chapter 2). These sites vary in their climatic regime and in the magnitude and direction of recent warming and greening trends (**Figure 3-1**; Table S3-1). This present study uses 324 shrubs from three to five plots per site. Thin sections were obtained from the root collar, and growth rings were measured along two to four radii on each section (Chapter 2) for the period 2000 – 2014.

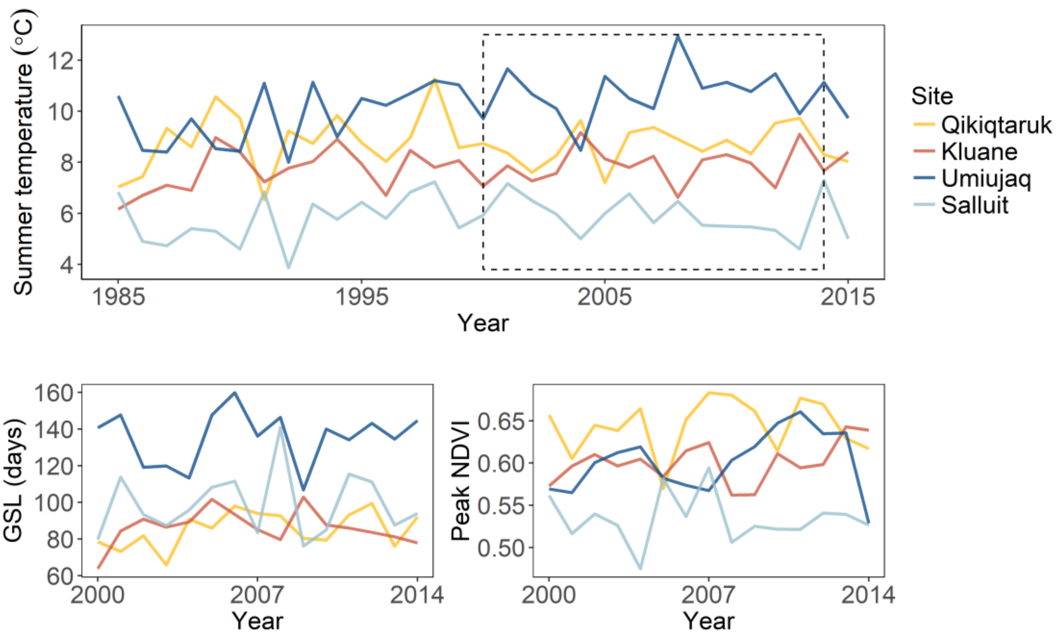


Figure 3-1 *Temporal trends in a) mean June-July-August temperature, b) mean growing season length derived from MODIS6 data, and c) maximum greenness at the four study sites. Longer temporal trends are presented for temperature but time series were constrained to the period common to all datasets (dashed window).*

3.2.2 Gridded datasets

I obtained monthly gridded temperature data (0.5° resolution) from the Climate Research Unit (TS 3.24.01) for each site. An average summer temperature calculated from June-July-August temperatures was used as it best represents the growing season for all sites. Land surface greenness data (NDVI) was obtained from the MODIS 6 (MOD13Q1 V6 16 days) dataset for each grid cell (250 m resolution) in which a sampling plot was present were extracted using the Google Earth Engine (http://earthengine.google.com/). The pixel values corresponding to two coastal plots (one on Qikiqtaruk, one in Umiujaq) were replaced with values from the nearest plot (Qikiqtaruk: 1.2 km; Umiujaq: 0.6 km) because the proximity to the ocean gave erroneous NDVI values. I used maximum (peak) NDVI as a measure of greenness or productivity. I derived growing season length from interpolated and smoothed curves obtained with the Phenex library in R. To achieve this, logistic curves are fitted through available NDVI data, and green-up and senescence dates are calculated as a threshold of relative peak greenness (Figure S3-1). I used a threshold of 5% of peak greenness: this metric does not necessarily represent the realised growing season, but may be indicative of the snow-free period, with or without earlier plant activity (Liu et al. 2016). Growing season length values presented here should therefore be interpreted as the potential duration in which photosynthetic activity might occur. I also present values for the more photosynthetically active period in which 50% of peak greenness is attained (**Figure 3-2**; Figure S3-2).

3.2.3 Statistical analyses

To measure the sensitivity of shrub growth to growing season length versus temperature (Hypothesis 1), I ran mixed-effect models for each site separately. I used ring width as the response variable, and mean June-July-August temperature and growing season length as fixed effects. To account for the hierarchical nature of the data, plot was specified as a random effect. Year was also added as a random effect to account for the fact that all individuals experience similar environmental conditions in a given year (Harrison et al. 2018). Species could not be incorporated as a random effect given that only one species was present at Umiujaq – however, species within a site had generally similar growth correlations to the environmental drivers used in this study (Figure S3-3). Analyses were constrained to the same time period, 2000-2014, which is the maximum length for which all environmental variables and growth ring measurements overlap.

The same model structure was used to test whether NDVI trends were reflected in radial growth (Hypothesis 3). To ensure that effect sizes of drivers with different units could be compared, all variables were mean-centered and variance-scaled: ring width at the individual level, growing season length and NDVI at the plot level, and temperature at the site level.

To test Hypothesis 2, I calculated individual Spearman correlations between ring width and both growing season length and temperature. I then used linear regression to test whether there was a significant association between these correlations. I chose Spearman correlations because they allow for non-linear relationships between variables; a test with Pearson correlations did not change the interpretation of the results.

All analyses were conducted in R version 3.3.2.

3.3 Results

The four sites experience markedly different summer regimes in terms of mean temperature, growing season length, and peak season greenness. The eastern sites have longer growing seasons than the western sites, but Salluit is much colder than Umiujaq, and shows the least productive peak season (**Figure 3-2**). Moreover, interannual variations in growing season temperature and length are not strongly correlated, i.e. a warmer summer is not necessarily longer (median correlation for all plots = 0.03, standard deviation = 0.20, min-max = -0.43 – 0.33).

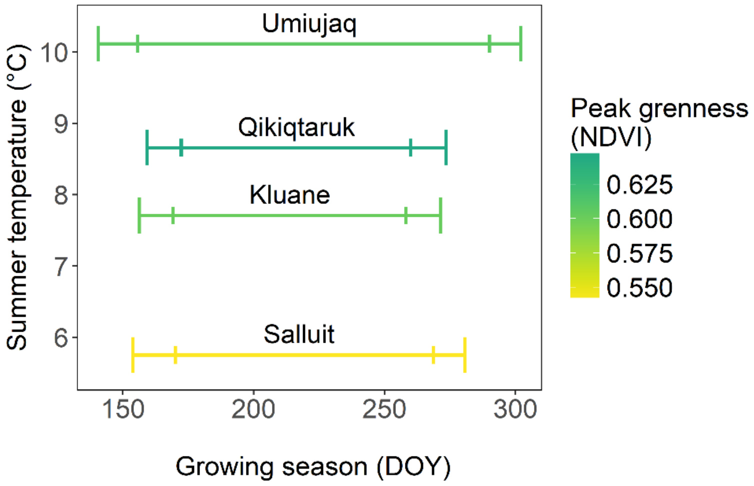
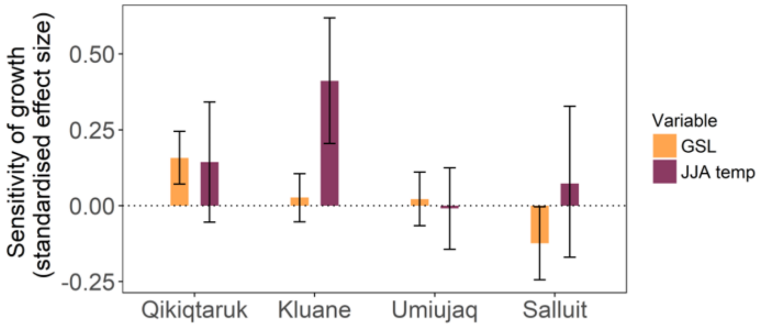


Figure 3-2 *Different summer temperature and growing season regimes at the four study sites across Northern Canada. The colour of the bar indicates mean NDVI values at the peak of the growing season. The longer growing season (wider ticks) represents the period during which NDVI values are above 5% of maximum NDVI; the shorter period (smaller ticks) is the more productive period during which NDVI values are at least 50% of peak NDVI.*

3.3.1 Heterogeneity in growth responses to growing season length and temperature

Shrub growth responded heterogeneously to the two drivers across the four sites (**Figure 3-3A**). Temperature had the strongest influence on growth at Kluane, and growing season length was the primary control on Qikiqtaruk. Shrub growth at Umiujaq was not explained by either variable, and growth at Salluit was slightly negatively associated with longer growing seasons (Table S3-2). Further exploration of climate-growth relationships for Salluit revealed a positive association with summer precipitation that was not present for the other sites (**Figure 3-3B**).

A) Growth responses to growing season length and temperature



B) Growth correlations to summer precipitation

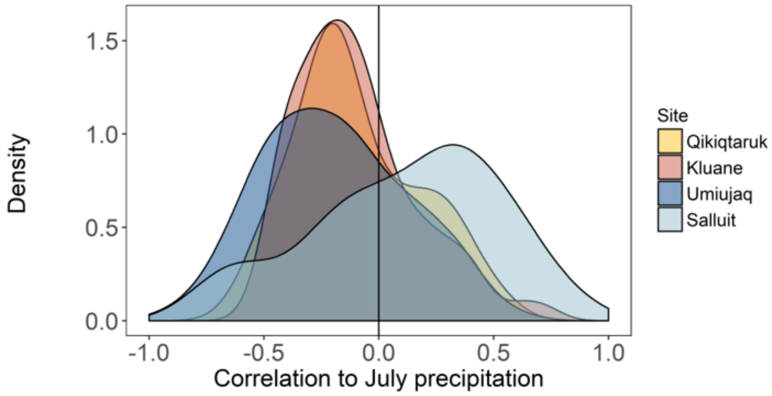


Figure 3-3 *Shrub growth was not consistently explained by either summer temperature or growing season length at the four sites (A). Effect sizes are standardised so are directly comparable (GSL = growing season length; JJA temp: mean June-July-August temperature). Error bars represent 95% confidence intervals. B) Density curves of individual correlations between annual growth and July precipitation. Salluit was the only site where shrubs had positive associations to summer precipitation.*

3.3.2 Inconsistency of shrub-level response

Individual shrubs were not consistent in the magnitude and direction of their sensitivity to growing season length and temperature, especially in Kluane and Salluit (**Figure 3-4**). The growth of shrubs that were strongly temperature-sensitive could be positively, negatively, or not at all correlated to growing season length, and vice-versa.

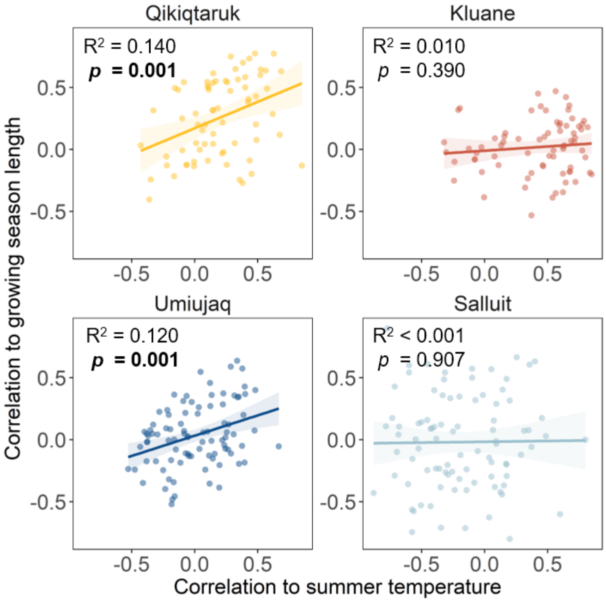


Figure 3-4 *Individual shrubs do not have consistent growth correlations to growing season length and to summer temperature, especially at Kluane and Salluit. Pearson's correlations were calculated for the period 2000-2014 between ring width and either June-July-August temperature or growing season length derived from MODIS NDVI data.*

3.3.3 Radial growth not related to greenness

Inter-annual variations in peak tundra greenness (NDVI) were not tracked by the radial growth of shrubs (**Figure 3-5**). Only Qikiqtaruk showed weak positive correspondence between shrub growth and NDVI (**Figure 3-5**; Table S3-3).

3.4 Discussion

In this study, I found that there is not one consistent driver of shrub growth at four tundra sites in Northern Canada. Rather, the relative importance of growing season length versus temperature varied across sites, with low overall sensitivity of shrub growth. The alpine tundra site in Kluane exhibited the strongest temperature sensitivity, while other sites suggested different underpinning controls such as moisture limitation. Individuals responded inconsistently to the two drivers. Furthermore, I found variable and weak correspondence between annual growth and temporal variation in remotely sensed tundra greenness. These results demonstrate that the warming and lengthening of Arctic summers are not necessarily happening concurrently, nor acting synergistically on shrub growth, and that annual variations in shrub growth may only partly contribute to remotely sensed estimates of tundra productivity.

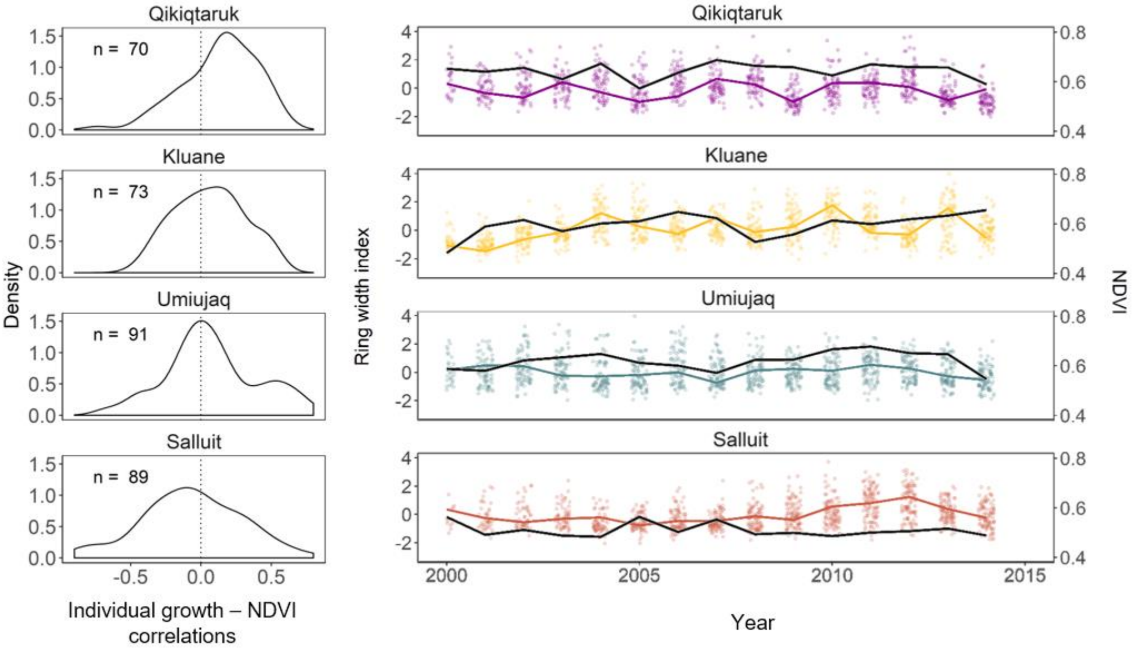


Figure 3-5 *Interannual variations in NDVI are not reflected in the radial growth of tundra shrubs. The left panel shows the distribution of individual correlations between growth and NDVI (2000-2014). The right panel shows time series of average growth (coloured lines) and greenness (black lines) at each site.*

3.4.1 Heterogeneity across sites in response to growing season length and temperature

Temperature sensitivity of growth

The four sites exhibited markedly different sensitivity of shrub growth to growing season length and temperature, highlighting the importance of examining several aspects of global change. The low temperature sensitivity of shrub growth on Qikiqtaruk-Herschel Island and the high temperature sensitivity of shrubs in Kluane align with previous findings from independent datasets at these sites (Myers-Smith et al. 2015a) and generally high variability and low inter-site agreement of ring-width series across southwest Yukon for trees and shrubs (Brehaut and Danby 2018). The difference in climate sensitivity along this north-south gradient might be indicative of genetic differentiation between populations, with the northern population locally adapted to colder temperatures and less plastic with respect to growth responses (Bjorkman et al. 2017). The complete lack of temperature sensitivity at Umiujaq may indicate that temperature is not a strongly limiting factor: Umiujaq is the warmest site in this study, with average summer temperatures above 10 °C. Salluit was the coldest site, and yet growth was not associated to warmer temperatures, and negatively associated to longer growing seasons. This seems indicative of a soil moisture deficit (Wilmking et al. 2004), with additional evidence from positive correlations to summer precipitations. Shifts in soil moisture regimes under a warming climate and increased water demand from denser vegetation may become a critical limitation on the productivity of northern ecosystems (Berner et al. 2013; Cahoon et al. 2016; Ackerman et al. 2017).

Season length sensitivity of growth

Qikiqtaruk was the only site where growing season length had a positive effect on growth. Qikiqtaruk has experienced advances in plant phenology, as evidenced from long-term monitoring of the common tundra species *Dryas integrifolia*, *Eriophorum vaginatum* and *Salix arctica* (Myers-Smith et al. in press). For *S. arctica*, leaf-out time has been advancing by ca. eight days per decade, with little change in the timing of senescence, resulting in a lengthening of the growing season by 12 days per decade for this shrub species. At the other sites, I did not find patterns of increased growth with longer potential growing seasons for tundra willows and *Betula glandulosa*, suggesting that a longer period of photosynthetic activity may not result in increased wood formation. Similarly, the dwarf shrub *Cassiope tetragona* showed phenological responses to snowmelt timing without associated changes in growth rates measured from shoot elongation (Johnstone 1995). Several other studies have shown that phenological advances may (Arft et al. 1999; Wipf 2010) or may not (Starr et al. 2000; Post et al. 2008; Wipf 2010; Khorsand Rosa et al 2015) result in a longer or more productive period of plant growth. In some tundra species, growth is periodic, stopping once a threshold has been attained (Starr et al. 2000; Rumpf et al. 2014). Moreover, the timing of plant life cycles responds to multiple environmental cues apart from temperature (Wahren et al 2005; Ernakovitch et al. 2014; Bjorkman et al. 2015), so that plants may not be able to capitalise on an early start to accumulate resources over a longer period if senescence is triggered deterministically (Parker et al. 2017).

3.4.2 Inconsistency of shrub-level response

I expected that shrubs with a greater sensitivity for one driver would also be sensitive to the other in a similar order of magnitude, according to individual plasticity in growth responses. However, I found that there was no correlation in the degree to which shrub growth is associated to temperature and growing season length. The highly individualistic nature of shrub responses to climatic drivers may therefore explain the overall low site-level sensitivity, as different magnitudes and directions of effects may cancel each other out. This dichotomy has been observed in boreal forests of Alaska, where trees cluster as “positive responders” to spring temperature, suggesting a positive influence of earlier snowmelt and longer season, or “negative responders” to previous summer temperatures, indicative of drought stress (Wilmking et al. 2004). The proportion of trees in these categories was consistent across the landscape and unrelated to topographical features but seemingly dependent on stem density, with negatively responding trees more frequent in more productive sites (Wilmking et al. 2004). This suggest that competition may affect the way tree- and shrub-tundra ecotones respond to a warming climate, and is of particular interest in the context of Chapter 5 and Chapter 6.

3.4.3 Radial growth not related to greenness

Contrarily to my hypothesis, annual shrub growth was decoupled from year-to-year variations in NDVI. This finding is surprising given that previous studies have found that tundra greenness was strongly associated with shrub biomass (reviewed in Epstein et al. 2013; also see Raynolds et al. 2012; Berner et al. 2018) and sometimes correlates with variation in annual growth over large geographic areas (Forbes et al. 2010; Berner et al. 2013). However, my results align with recent findings of variable, non-directional trends in shrub growth across southwest Yukon, where one of my study sites belongs, despite increases in greenness since the 1990’s (Brehaut and Danby 2018). In Northern Québec, NDVI values were correlated to radial growth during a period of rapid warming and shrub expansion (Ropars et al. 2015). However, it appears that once the shrub cover is well established, interannual variation in NDVI values become decoupled from radial growth (Ropars et al. 2015) and can saturate or be influenced by other vegetation features than shrub dominance (Lemay et al. 2018). Because primary and secondary growth do not necessarily correlate strongly (Chapter 4) or respond in a similar way to global change drivers (Bret-Harte et al. 2002; Campioli et al. 2012a-b), radial growth and investments in the woody structure may not be the most likely growth response to be picked up by satellite sensors, which are more sensitive to leaf cover and biomass (Pettorelli et al. 2005; Raynolds et al. 2006).

3.4.4 Limitations and future research

This study used remote sensing products to derive growing season length at the study sites. MODIS NDVI is only one of several data products available to quantify vegetation change. NDVI trends derived from different satellite platforms do not always correspond (Guay et al. 2014), and some uncertainty exists as to what pixel greenness represents across different temporal and spatial scales (Frost et al. 2014; Raynolds and Walker 2016). Ground-based observations would allow a more direct, mechanistic test of sensitivity of plant growth, but few long-term phenological records encompassing both leaf emergence and senescence exist in the tundra biome (Prevéy et al. 2017). A challenge is to establish long-term monitoring of multiple aspects of vegetation and environmental change, a goal that we have been working towards on the Qikiqtaruk monitoring programme (Myers-Smith et al. in press).

Growing season length measured from above-ground vegetation (either through surveying or remote sensing) may not be an accurate representation of the growing conditions experienced at the root collar, where the shrubs in this study were sampled. Growth patterns can differ among plant parts due to physiology or climatic gradients (Buchwal et al. 2013; Ropars et al. 2017 (Appendix I); Shetti et al. 2018). The below-ground growing season for roots can be 50% longer than above-ground (Blume-Werry et al 2016), and therefore shrub growth at the root collar (root-shoot interface) might be more closely coupled to the duration of root activity than to leaf senescence. Root dynamics and whole-plant phenology are poorly understood and deserve more attention, given that below-ground biomass makes up to 80% of total tundra biomass (Iversen et al. 2015).

3.5 Conclusion

Growing season length and temperature are often assumed to be two sides of the same coin when it comes to controlling tundra vegetation. This study demonstrates that sites across Northern Canada experience a wide range of growing season conditions, and that plants do not respond predictably and consistently to longer and warmer summers. Changes in radial growth may only track greenness during active shrub expansion phases, as this study found no strong association between peak NDVI and growth-ring time series. Tundra plant phenology is more sensitive to temperature at higher latitudes of the tundra biome (Prevéy et al. 2017; Post et al. 2018), but whether this will translate to increased plant growth rates and strong greening in the northern portion of the biome is uncertain. Spatial heterogeneity in temperature and precipitation patterns, genetic differentiation along latitudinal gradients, and local factors like soil moisture and ecological interactions may interact to drive contrasting vegetation trajectories across the tundra biome.

Chapter 4 Size and Sensitivity: Plant size does not explain the heterogeneity in the climate sensitivity of shrub growth across the tundra biome

Abstract

Shrub species are expanding rapidly across the tundra biome, with great heterogeneity in the climate sensitivity of shrub growth both within and among sites. Species with taller maximum canopy heights tend to have higher climate sensitivity, but whether this represent a mechanistic relationship at the individual level remains to be tested. Additionally, plant size is an important structural trait, and understanding how primary and secondary growth scale with one another across the biome would allow for more accurate projections of changes in above-ground plant productivity. I used dendroecological and plant size measurements from a circumpolar dataset (551 shrubs, 16 sites) and from a smaller but homogeneously sampled dataset (306 shrubs, four sites) to test the hypothesis that taller plants have stronger climate-growth relationships due to better competitive ability and lower vulnerability to ground-level microclimate. I also explored relationships between canopy growth dimensions (height and diameter) and between measures of primary (canopy size) and secondary (radial growth) growth in relation to latitude and distance from treeline. I hypothesised that allometric relationships are less reliable at higher latitudes of the biome where growth is suppressed by severe environmental conditions. I found that canopy dimensions did not explain the climate sensitivity of shrub growth. The association between canopy height and diameter became weaker at higher latitudes. Primary and secondary growth were not strongly associated, hinting at different controls and responses to environmental drivers. Plant size, while being an important structural trait of tundra ecosystems, appears to be a poor predictor of the climate sensitivity and future growth responses of tundra shrubs.

Author Contributions

I designed the analysis framework for this study with Isla Myers-Smith. One dataset was assembled by myself; the Shrub Hub dataset was compiled by Isla Myers-Smith (http://shrubhub.biology.ualberta.ca/) and the following people have contributed data to this study: Isla Myers-Smith, David Hik, Noémie Boulanger-Lapointe, Esther Lévesque, Martin Hallinger, Martin Wilmking, Andrew Trant, Laura Siegwart Collier, Luise Hermanutz, James D. M. Speed, Trevor Lantz, Rasmus H. Jørgensen, and

Daan Blok. These contributors have also provided helpful comments on earlier versions of this manuscript. I presented a previous version of this analysis at the Perth III: Mountains of our Future Earth in 2015.

4.1 Introduction

4.1.1 Widespread but heterogeneous responses of tundra vegetation to climate change

The tundra biome is undergoing large-scale, widespread increases in the abundance and growth of woody shrubs (Tape et al. 2006; Myers-Smith et al. 2011; Naito and Cairns 2011; Elmendorf et al. 2012; Martin et al. 2017). Shrub expansion is expected to have major implications for the structure and functioning of Arctic ecosystems due to complex interacting effects of shrub canopies on soil temperature regime and permafrost (Anisimov and Reneva 2006; Blok et al. 2010; Bonfils et al. 2012; Paradis et al. 2016), snow accumulation patterns (Sturm et al. 2001; Myers-Smith and Hik 2013; Busseau et al. 2017), nutrient cycling (Hobbie 1996; Buckeridge and Grogan 2010; McLaren et al. 2017; Christiansen et al. 2018), and wildlife (Rich et al. 2013; Boelman et al. 2015; Christie et al. 2015; Zamin et al. 2017), with potential knock-on effects on regional-to-global biogeochemical cycles (Shaver et al. 2000; Callaghan et al. 2004; Sturm et al. 2005b; Lafleur and Humphreys 2018) and climate (Chapin et al. 2005; Sturm et al. 2005a; Pearson et al. 2013).

Climate warming has been identified as a major circumpolar driver of shrub expansion (Walker et al. 2006; Myers-Smith et al. 2011; Elmendorf et al. 2012b), but the climate sensitivity of shrub growth is highly heterogeneous across the tundra biome (Myers-Smith et al. 2015a). This variability suggests that local-scale controls like topography (Tape et al. 2012; Ropars and Boudreau 2012), soil moisture (Walker et al. 2006; Ackerman et al. 2017), and herbivory (Olofsson et al. 2009; Speed et al. 2013; Morrissette-Boileau et al. 2018), as well as species functional traits and growth strategies (Bret-Harte et al. 2002; Heskel et al. 2013), can modify the response of shrub communities to regional-scale climate change. At the site level, Myers-Smith et al. (2015a) found that between 5% to 97% of individuals displayed climate-sensitive growth. It is therefore critical to identify what are the other constraints acting upon plant growth if we are to better predict vegetation change under warming.

4.1.2 Plant size as a determinant of climate sensitivity

The biome-scale observation that shrub species with a taller potential maximum canopy height have more climate-sensitive growth (Myers-Smith et al. 2015a) might lead to the assumption that larger shrubs are more climate-sensitive than smaller ones at the population scale (Ackerman et al. 2018). This assumption has not been tested for individual shrubs. As a functional group, deciduous canopy-forming shrubs have been shown to be generally very responsive to warming (Walker et al. 2006; Elmendorf et al. 2012b). However, Myers-Smith's et al. (2015a) observations relating to canopy height were based on species-level trait data of potential maximum size, not site-level measurements, and therefore do not test the mechanistic, ecological role of plant size on individual climate sensitivity. If present, this influence could contribute to explain the high variation in individual growth responses to temperature among shrubs within a site.

Plant size could affect the climate sensitivity of shrubs within a population for two main reasons. First, plant competition studies suggest that compared to smaller conspecifics, bigger plants have higher growth rates due to their competitive advantage when it comes to resource acquisition (Weiner and Damgaard 2006; Coomes and Allen 2007). Reciprocally, monoculture field experiments (Purves and Law 2002) and forestry studies (Simard and Sachs 2004) reported that the growth of target plants was negatively affected by the size of nearby competitors. Competition for resources at the local scale may thus diminish the ability of plants to respond to regional-scale drivers like warming (Ettinger et al. 2011). However, it is unclear whether those relationships hold in extreme environments like the tundra, where facilitative interactions may obscure the presence or outweigh the importance of competition (Dormann and Brooker 2002). Second, the size of a plant has implications regarding the way it interacts with its physical environment. The growth of smaller shrubs is more likely to be controlled by microtopographical features (snow depth, temperature at ground level, etc.) compared to taller shrubs (Buras and Wilmking, 2014). Taller plants experience more heat exchange with the free atmosphere, and therefore their growth is more strongly coupled with air temperature (Körner 2012).

4.1.3 Understanding relationships between growth dimensions

The scaling of metabolic or functional plant traits according to plant size is of relevance to shrub expansion ecology, because of its implications for the structure and functioning of individuals to whole ecosystems (Enquist 2002). The development of allometric equations has regained interest as a way of predicting biomass in high-latitude ecosystems using simple measurements (Berner et al. 2015; Ackerman et al. 2018), and conversely, of validating remotely sensed biomass estimates (Chen et al. 2009). However, most of these equations were developed for the low to mid-latitudes of the tundra biome, and site-specific scalings of growth dimensions (Au and Tardif 2007; Berner et al. 2015) may not be representative of the biome as a whole, especially at higher latitudes where the abiotic environment severely limits growth (Arsenault and Payette 1992). Moreover, relationships between primary and secondary growth have received surprisingly little attention. Secondary growth, i.e. the thickening of stems by accumulation of woody biomass, plays a major role in the carbon balance of the tundra, contributing one third to half of above-ground net primary production for some species (Shaver 1986). It is therefore important to understand the linkages and potential trade-offs between dimensions relating to primary and secondary growth, especially considering that experiments have highlighted differential responses to global change drivers (Bret-Harte et al. 2002; Campioli et al. 2012a).

4.1.4 Objectives and hypotheses

Tall deciduous shrubs are one of the plant functional groups changing most rapidly over time (Myers-Smith et al. 2011; Elmendorf et al. 2012a). If attaining taller canopy heights does enhance the ability of individuals to respond to variations in climate, there might be a positive feedback leading to an acceleration of shrub expansion with warming. It is therefore critical to quantify the role of plant size in explaining the high individual variation in climate sensitivity of shrub growth in the tundra. Predicting climate sensitivity of growth from plant size and understanding how aboveground primary and secondary growth dimensions scale with one another across the biome would allow for more accurate projections of changes in future above-ground biomass and carbon storage in tundra ecosystems. I tested the following hypotheses using both a large, global-scale dataset of shrub growth comprising 551 individuals from 16 sites and belonging to 14 species around the circumpolar region, and a smaller but more highly replicated and homogeneously sampled dataset of four sites in Northern Canada:

1. Larger shrubs have more climate-sensitive growth. If variation in plant size within a population translates to smaller individuals being more resource-limited from size-asymmetric competition, and taller individuals being more climate-limited through a tighter canopy-air temperature coupling, then radial growth should be more closely associated with summer temperature in larger and taller shrubs within a site and genus.

2. The relationship between canopy dimensions is not consistent across the biome, given that vertical growth is more subjected to abiotic constraints than lateral growth.

I predicted that there would be a saturating relationship between canopy height and diameter, and this relationship would become weaker with increasingly severe environmental conditions.

3. Radial growth scales positively and predictably with canopy area across sites. I predicted that mean annual ring width and total stem width would be larger for older individuals with taller and/or wider canopies.

4.2 Methods

4.2.1 Study sites and species

I used a large collaborative dataset assembled by the Shrub Hub network (http://shrubhub.biology.ualberta.ca/). The dataset contains radial growth time series and associated size measurements for over 1800 shrubs from 37 species at 25 sites across the biome (for more detail, see Myers-Smith et al. 2015a). I filtered the dataset to keep only those sites and shrubs which had associated individual canopy height and/or diameter measurements, and kept only the genus-by-site combinations that had more than eight individual shrubs. One site (Kluane) was subsetted down to two subsites to obtain a balanced dataset, because the sample size was initially tenfold the average sample size of other sites. This left 551 shrubs from 14 species (four genera) distributed across 16 sites (***Figure 4-1***; **Table 4-1A**).

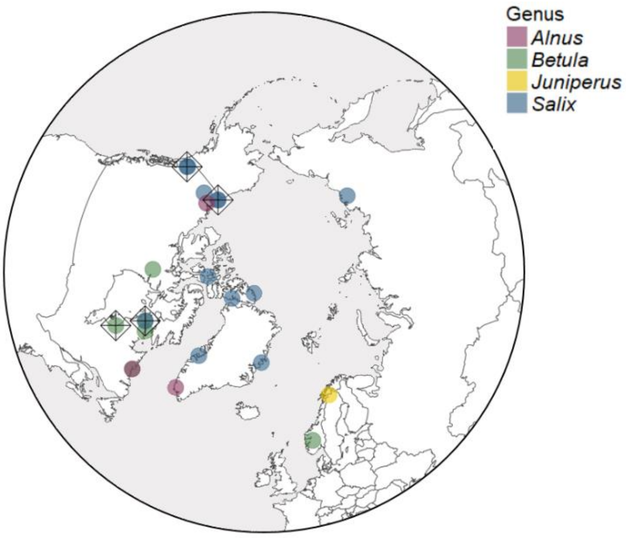


Figure 4-1 *Location of the 18 study sites across the circumpolar region. The colour of the circles represents the genus sampled. The four sites from a different dataset are indicated with diamonds.*

Table 4-1 *Description of study sites and samples used in this chapter. References to published literature can be found in Appendix III*

A. SHRUB HUB DATASET

Country	Site	Latitude	Longitude	Genus	Shrub *n*	Timespan	Contributor (Reference)
CANADA	Qikiqtaruk	69.58	-138.94	*Salix*	58	1983 - 2008	I. Myers-Smith, D. Hik (1,2)
	Kluane	61.11	-138.66	*Salix*	54	1981 - 2008	I. Myers-Smith, D. Hik (1,2)
	Demptser	66.84	-136.25	*Salix*	39	1983 - 2008	I. Myers-Smith, D. Hik (1,2)
	Nowell Lake	68.54	-133.64	*Alnus*	40	1980 - 2006	T. Lantz (3)
	Baker Lake	64.37	-95.88	*Betula*	50	1985 - 2009	E. Lévesque
	Resolute	74.71	-94.88	*Salix*	31	1983 - 2008	N. Boulanger-Lapointe, E.L. (4)
	Alexandra Fiord	78.86	-75.90	*Salix*	29	1984 - 2008	N. Boulanger-Lapointe, E.L. (4)
	Ellesmere Island	83.00	-75.38	*Salix*	19	1984 - 2008	N. Boulanger-Lapointe, E.L. (4)
	Kangiqsujuaq	61.63	-71.94	*Betula*	19	1985 - 2009	E. Lévesque
	Nain	56.54	-61.72	*Alnus, Betula*	22, 21	1985 - 2009	A. Trant, L.S.C., L.H.
GREENLAND	Kangerlussuaq	68.45	-52.03	*Salix*	30	1982 - 2009	M. Hallinger, M.W.
	Arsuk Fjord	61.27	-48.01	*Alnus*	26	1985 - 2009	R. Jørgensen (5, 6)
	Zackenberg	74.51	-20.47	*Salix*	31	1984 - 2008	N. Boulanger-Lapointe (4)
NORWAY	Minnestølen	60.70	7.94	*Betula*	40	1985 - 2009	J. D. Speed (7)
SWEDEN	Abisko	68.35	18.82	*Juniperus*	33	1982 - 2006	M. Hallinger, M.W. (8, 9)
RUSSIA	Kytalyk	70.82	147.47	*Salix*	9	1984 - 2008	D. Blok (10)

B. NEW DATASET

CANADA	Qikiqtaruk	69.58	-138.94	*Salix*	67	1990 - 2014	S. Angers-Blondin
	Kluane	61.11	-138.66	*Salix*	71	1990 - 2014	S. Angers-Blondin
	Umiujaq	56.56	-76.53	*Betula*	75	1990 - 2014	S. Angers-Blondin
	Salluit	62.20	-75.65	*Salix, Betula*	83, 10	1990 - 2014	S. Angers-Blondin

I repeated the analyses on a different dataset of 306 shrubs belonging to seven species at four sites (**Table 4-1B**) where all samples were collected in 2015 (Chapter 2). Two sites (Kluane and Qikiqtaruk, Yukon Territory) overlapped with ShrubHub locations. At each of these four sites, all canopy-forming shrubs within study plots ranging from 5 x 5 m to 10 x 10 m were cut at the root collar. I also measured the canopy height, canopy width along two perpendicular diameters, and the diameter of the largest stem of each shrub. Woody sections were cut in thin sections (20 µm) with a sledge microtome and photographed under the microscope for further analysis (Chapter 2; Myers-Smith et al. 2015b). Growth rings were measured along two to four radii on each sample for the period 1990-2014, and radii were averaged for each individual.

4.2.2 Climate sensitivity

I define climate sensitivity as the strength (slope) of the linear regression between radial growth and June-July temperature for a given shrub individual (Myers-Smith et al. 2015a). Mean June-July temperature was chosen as a climate variable because growing season temperature has consistently been identified as the strongest climatic driver of plant growth in the Arctic (Johnstone and Henry 1997; Bär et al. 2008; Blok et al. 2011b; Myers-Smith et al. 2015; Ackerman et al. 2018; Weijers et al. 2018), and this variable encompasses peak growing season for all sites in the study (some plants having already senesced in August at high-latitude sites). Sensitivity to other correlated growing season variables such as July or June-July-August temperature was similar (Table S4-1). Ring-width series were constrained to 25 years for all individuals to facilitate comparisons among sites. Ring-width measurements were mean-centred and variance-scaled at the individual level. I used absolute slope values for the analyses as this study focuses on the magnitude, not the direction of climate-growth relationships. The majority of sites exhibited positive or non-directional sensitivity to summer temperature (**Figure 4-2**). Monthly climate data for each site was obtained from the CRU 3.24.01 gridded dataset.

4.2.3 Effect of plant size on climate sensitivity

To test the hypothesis that larger plants are more climate-sensitive throughout the tundra biome, I ran mixed-effects models using climate sensitivity (slopes of individual climate-growth relationships) as the response variable, and plant height or canopy diameter as explanatory variables. For the Shrub Hub analysis, I used the genus-by-site combination as a random effect (Myers-Smith et al. 2015a) to account for the hierarchical nature of the data. I allowed random slopes and random intercepts to account for taxonomic differences in potential magnitude and direction of the relationship. I ran the two models (canopy height vs diameter) separately because not all size variables were measured at all sites.

I used a similar model structure to repeat the analysis with my four field sites. There was only one genus present at each site except at Salluit, where 10 *Betula* individuals were sampled in addition to many *Salix* shrubs. Given the low *Betula* sample size and the similar climate sensitivity of *Betula* and *Salix* shrubs at this site (**Figure 4-2**), I used site rather than genus-by-site combination as a random effect. The rest of the model was specified as described above. All analyses were conducted in R v. 3.3.2. Mixed effects models were fitted with the package lme4.

4.2.4 Allometric relationships

To explore the potential or deriving canopy height, an important structural trait, from canopy area, I explored relationships between canopy height and diameter for all sites where both measurements were available (seven ShrubHub sites and my four sites). I present linear equations for each genus-by-site combination with a sample size of at least 15 individual shrubs. To investigate resource allocation to primary and secondary growth dimensions, I modelled the width of the largest stem and mean ring width as a function of either canopy height (11 + 4 sites) or diameter (11 + 4 sites). I then tested whether the goodness of fit of the genus-by-site relationships could be explained as a function of latitude using linear regression.

Globally, there is a decrease in plant size with latitude (Moles et al. 2009). However, within the tundra biome, latitude is not the best indicator of environmental sensitivity due to transitions between continental versus oceanic climate. Therefore, I measured the distance between each site and the Arctic treeline using the Circumpolar Arctic Coastline and Treeline Map (http://www.arcticatlas.org/maps/themes/cp/cpcoast) and modelled maximum plant height within a site as a nonlinear negative asymptotic function (nls function from “stats” package in R) of the distance to treeline.

For each genus-by-site combination, I correlated all growth dimensions to the minimum age of individuals, as provided by data contributors from growth-ring counting on the sampled disks. This is a minimum age as most samples were taken at the base of the largest stem rather than at the root collar.

4.3 Results

The climate sensitivity of shrub growth was heterogeneous both within and among sites (**Figure 4-2**). A more detailed study of the among-site variability has been published (Myers-Smith et al. 2015a), but the within-site heterogeneity in individual response with respect to plant size has not been quantified before.

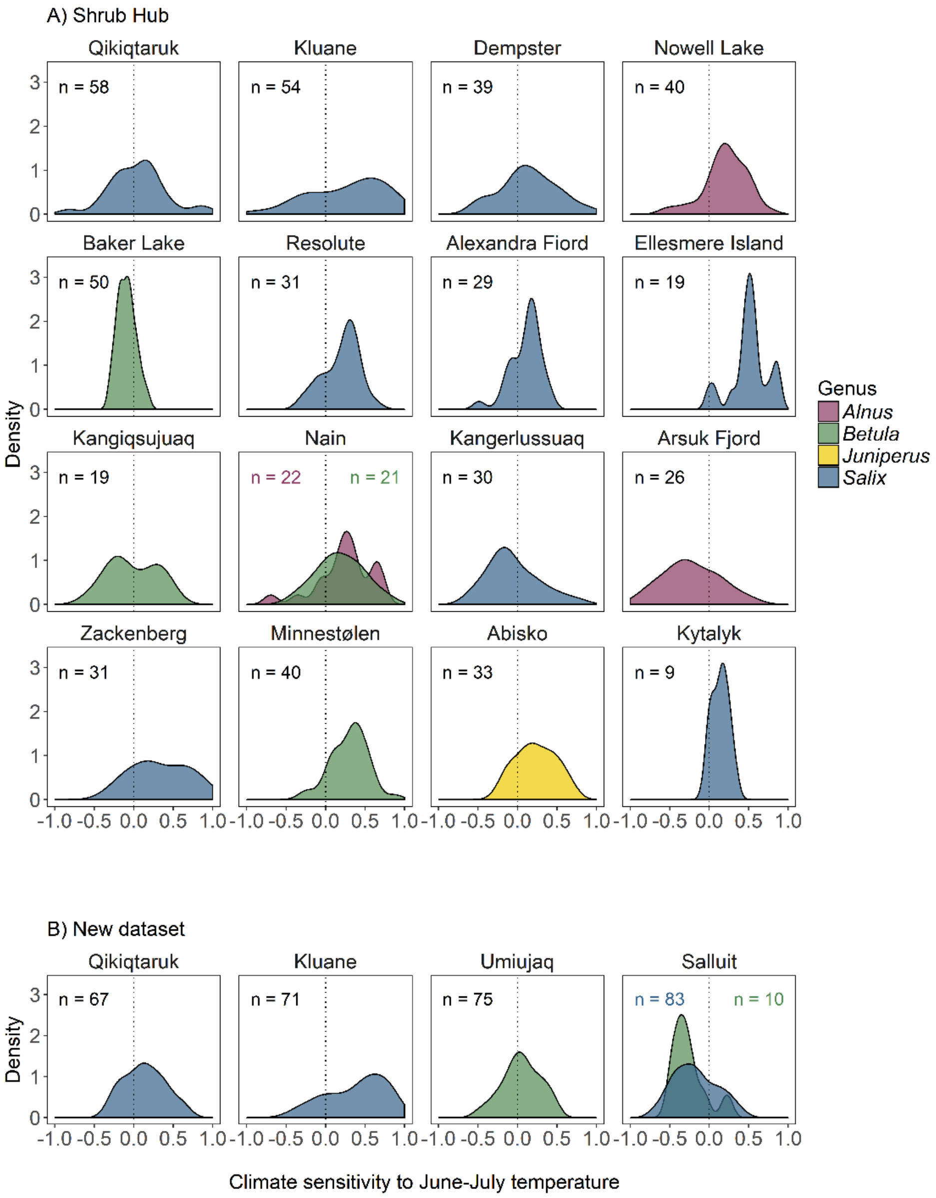


***Figure 4-2** Most sites across the tundra biome exhibit low and variable, but generally positive sensitivity of growth to summer (June-July) temperature. Curves represent the density of climate-growth relationship slopes for each genus-by-site combination, obtained by fitting linear models between radial growth and temperature for each individual (sample size indicated on each panel).*

4.3.1 Plant size is not a predictor of climate sensitivity

Neither shrub height nor canopy diameter explained variation in the climate sensitivity of radial growth consistently across the tundra biome. Random slopes for the different genus-by-site combinations did not show any consistent pattern linked to canopy height, with only two out of 13 genus-by-site combinations not overlapping zero, and the overall model estimate very close to zero (**Figure 4-3A**, Table S4-2). Canopy diameter had an overall slightly negative but very low effect size, and as many positive as negative random slopes.

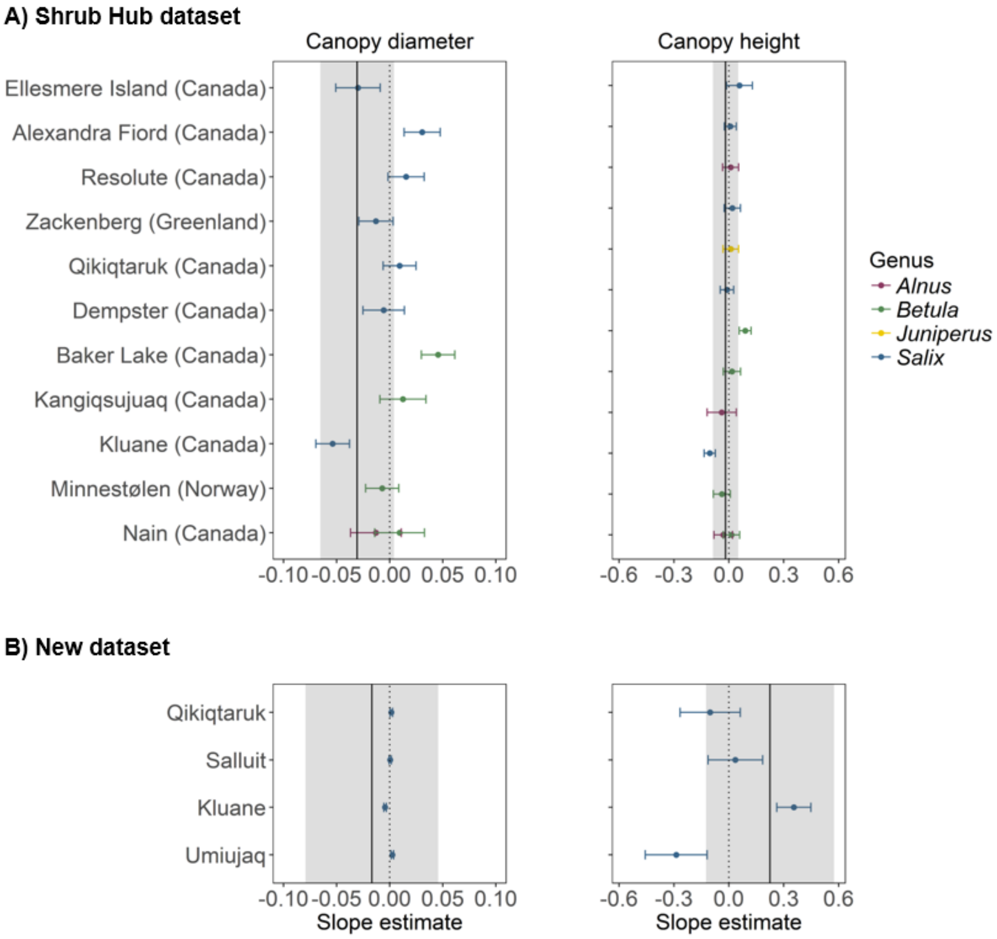


Figure 4-3 *There is no overall effect of canopy diameter (left panels) or height (right panels) on the climate sensitivity of radial growth to June-July temperature for shrubs across the tundra biome. Dots are random slope estimates for each genus-by-site combination (top panels) or for each site (bottom panels). Error bars represent a 95% confidence interval. The solid line and shaded area represent the overall model effect size (slope estimate and 95% confidence interval). The site Salluit (bottom row) contains a small number (n = 10) of Betula shrubs in addition to Salix spp.*

A more detailed exploration of four sites with homogenously collected and highly replicated data supported the biome-wide finding that plant size alone cannot explain the strength of the relationship between radial shrub growth and summer temperature (**Figure 4-3B**). Effect sizes for both canopy height and diameter were undistinguishable from zero (Table S4-2).

4.3.2 Relationships between canopy dimensions

Associations between canopy dimensions were also heterogeneous across the biome. Canopy diameter explained as little as 2 % and as much as 66 % (median: 28 %) of the variation in canopy height (**Table 4-2**). The strength of these relationships did not vary randomly: sites at the southern edge of the biome showed stronger relationships between canopy dimensions than shrubs at northernmost sites (**Figure 4-4A**), with latitude explaining 38% of the variation in the goodness of fit of allometric equations ($n = 11$; $F_{1,10} = 6.0$; $p = 0.034$). Across sites, there was a general decrease ($n = 14$; lrc = -7.54; $p < 0.001$) in maximum canopy height with increasing distance beyond the Arctic treeline (**Figure 4-4B**). Variation in canopy dimensions was not strongly related to plant age (**Figure 4-5**).

Table 4-2 *Model fits for linear allometric equations of shrub height (H) as a function of canopy width (W), using only sites with > 15 observations. The sites marked (SAB) are the four sites sampled for the new dataset.*

Site	Genus	Equation	R^2	F	n	*p*
Qikiqtaruk	*Salix*	$H = 0.044\,W + 0.234$	0.06	2.84	67	0.099
Qikiqtaruk (SAB)	*Salix*	$H = 0.102\,W + 0.174$	0.06	3.07	45	0.086
Demptser	*Salix*	$H = 0.132\,W + 0.225$	0.25	12.37	39	**0.001**
Baker Lake	*Betula*	$H = 0.124\,W + 0.244$	0.13	7.09	50	**0.011**
Salluit (SAB)	*Salix*	$H = 0.209\,W + 0.129$	0.20	4.50	82	**< 0.001**
Kangiqsujuaq	*Betula*	$H = 0.052\,W + 0.262$	0.02	0.39	19	0.542
Kluane	*Salix*	$H = 0.090\,W + 0.255$	0.07	20.37	54	**< 0.001**
Kluane (SAB)	*Salix*	$H = 0.401\,W + 0.119$	0.52	8.67	70	**< 0.001**
Minnestølen	*Betula*	$H = 0.980\,W + 0.310$	0.66	140.13	33	**< 0.001**
Umiujaq (SAB)	*Betula*	$H = 0.162\,W + 0.087$	0.66	74.14	75	**< 0.001**
Nain	*Alnus*	$H = 0.347\,W + 0.115$	0.36	10.63	26	**0.004**
Nain	*Betula*	$H = 0.146\,W + 0.086$	0.44	15.66	27	**0.001**

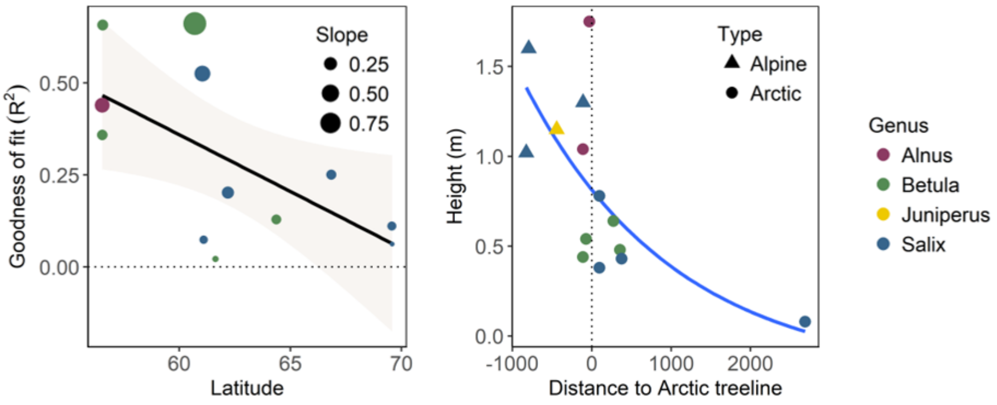


Figure 4-4 *A) Allometric relationships between canopy dimensions (height and diameter) lose explanatory power at higher latitudes. The size of the dot indicates the slope of the equation. B) Higher constraints on plant size in more stressful sites, as shown by a decrease in maximum canopy height with increasing distance beyond the Arctic treeline. (NB: The point with the lower height at the farthest distance represents the northernmost extent of woody shrubs, which do not grow taller than 10 cm, and was added to constrain the relationship.)*

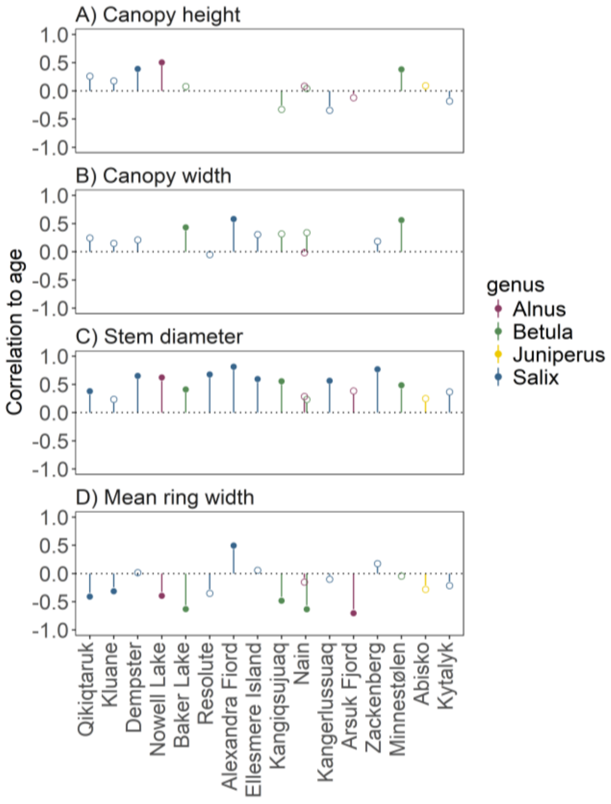


Figure 4-5 *Canopy dimensions (A, B) were not strongly correlated to plant age, but older individuals tended to have larger stems (C) and narrower growth rings (D). Correlations are Pearson's coefficients for correlations between growth dimensions and minimum stem age within a site and genus. Filled circles indicate statistically significant correlations ($p < 0.05$).*

Table 4-3 *Summary of relationships between size variables linked to primary (canopy height, canopy diameter) and secondary (mean ring width, stem diameter) growth. For each combination of variables, the median goodness of fit is presented (minimum and maximum in brackets), along with the proportion of genus-by-site combinations (n) that had a statistically significant relationship ($p < 0.05$).*

	Mean ring width	**Stem diameter**
Canopy height	R^2 = 0.08 (0.00 – 0.50) n = 7/16	R^2 = 0.22 (0.00 – 0.65) n = 12/16
Canopy diameter	R^2 = 0.08 (0.01 – 0.32) n =8/16	R^2 = 0.20 (0.00 – 0.72) n = 10/16

4.3.3 Primary-secondary growth relationships

Size dimensions linked to primary growth, i.e. canopy height and diameter, were only weakly to moderately linked to stem dimensions (**Table 4-3**). Stem diameter was better predicted than mean ring width by canopy size (similarly by height or diameter). Mean ring width and stem diameter were correlated at some but not all sites (median Pearson coefficient: 0.56; min – max: 0.16 – 0.87). The explanatory power of these relationships did not vary with latitude ($R^2 < 0.03$ and $p > 0.50$ for relationships between stem width and canopy height or diameter), but age was a good predictor of stem diameter at the majority of the sites (**Figure 4-5**).

4.4 Discussion

In this study, I demonstrate that the climate sensitivity of tundra shrubs cannot be predicted by individual plant size. Climate-growth relationships were highly heterogeneous both within and across sites, and canopy height and diameter were poor predictors of individual variation in climate sensitivity. I obtained the same results using both a highly-replicated, rigorously homogenous dataset focusing on a small number of sites and species, and a more heterogeneous but very large dataset covering most of the circumpolar region and comprising tall shrub species that are involved in ongoing, biome-wide vegetation shifts. I found stronger correlations between canopy dimensions (height and diameter) within the southern part of the biome, but these relationships did not hold at higher latitudes where environmental controls on canopy height become more severe. Canopy dimensions were only moderately associated with stem size and were more dependent on plant age than environmental conditions. I conclude that plant size, while being an important determinant of tundra plant community structure across broad geographic gradients, has limited use in predicting growth responses to climate change and future vegetation changes in the Arctic.

4.4.1 Plant size does not influence the climate sensitivity of growth

Taller maximum canopy heights have been linked to higher climate sensitivity in cross-species studies (Myers-Smith et al 2015a). This observation may reflect a functional group response where tall deciduous shrubs are generally more responsive to climate change than dwarf shrubs, especially if warming is coupled with increased nutrient availability (Chapin et al. 1995; Wahren et al. 2005; Walker et al. 2006; Epstein et al. 2013; but see Dormann and Woodin 2002; Zamin et al. 2014). According to plant strategy theory, tall, deciduous shrubs are usually on the fast end of the nutrient cycling and leaf economics spectrum and can respond to improved conditions quickly, while (evergreen) dwarf shrubs usually exhibit more conservative growth strategies (Westoby et al. 2002).

My findings across different intensities and extents of sampling indicate that the assumed relationship between shrub size and climate sensitivity at the individual level is not as strong as previously assumed (Ackerman et al. 2018). These findings were also consistent across taxa of varying life-history strategies: most of the individuals sampled belonged to *Salix* and *Betula* genera, but the dataset also comprised nitrogen-fixing *Alnus* and coniferous *Juniperus* shrubs. I thus could not verify my hypotheses that size-asymmetric competition or microtopographic constraints limited the climate sensitivity of tundra plants at the site or biome scale.

The apparent unimportance of microtopographic effects on the climate sensitivity of smaller plants is in line with a consistent regional climatic signal detected in the dwarf shrub *Empetrum hermaphroditum* in Norway across contrasting environment types (Bär et al. 2008). Size-asymmetric competition is most apparent in plants competing for light (Weiner 1990; Newton and Joliffe 1998; Falster and Westoby 2003), but it is unclear whether competition for belowground resources is also size-asymmetric (Weiner 1990). Considering that up to 80-90 % of tundra plant biomass is found belowground (Iversen et al. 2015), tundra shrubs are more likely to be limited by nutrient availability (Chapin et al. 1989; Dormann and Woodin 2002; Hobbie et al. 2002) rather than by light (Chapin et al. 1995). Therefore, it is possible that the competitive ability of tundra shrubs is not strongly dependent on size. The heterogeneity of sampling methods in the larger dataset may have prevented the detection of competitive interactions, as some protocols selectively sampled dominant or isolated plants, and I did not have access to plot-level shrub density. Spatially explicit, unbiased sampling will be required to quantify the impact of competition on shrub growth and climate sensitivity (Chapter 6).

4.4.2 Relationships of canopy dimensions across an environmental severity gradient

In agreement with theory and empirical observations (Moles et al. 2009), there was a decrease in maximum plant height with increasing distance from the Arctic treeline. The finding of weaker associations between the height of a shrub and its canopy diameter at higher latitudes is in line with our understanding of constraints on growth in tundra environments, where height is limited by harsh winter conditions to approximately the height of the snowpack (Arsenault and Payette 1992). The stronger allometric relationships at lower latitudes may also indicate that the lateral spread of plants is limited by space and competition in more densely populated tundra communities, and shrubs grow mainly vertically to escape light competition (Walker et al. 2006). On the contrary, at high Arctic sites with sparse shrub cover, plants experience stronger constraints on canopy height but have more room to spread laterally (van der Wal and Stien 2014). Finally, local adaptation to varying conditions across a species range (Bjorkman et al. 2017) could mean that vertical growth rates of shrub canopies in response to warmer conditions will not increase greatly at higher latitude sites.

4.4.3 Heterogeneity in the strength of shrub primary and secondary growth relationships

My results indicate substantial heterogeneity in the relationships between size dimensions across sites. I found that overall, only ca. 20% of the variation in stem width was explained by shrub canopy size. This may be indicative of trade-offs in resource allocation: taller shrubs need to maintain their vertical structure (Shaver 1986). As a result, they may be investing more in secondary growth than in the elongation of stems that influence canopy dimensions, weakening correlations between total plant size and stem diameter. Previous studies have nevertheless found strong links between plant height and woody biomass (Paradis et al. 2016) or basal area (Berner et al. 2015), but at boreal and sub-Arctic sites where conditions are not representative of the tundra biome as whole.

Whereas canopy height decreased predictably with environmental severity and became less correlated with canopy diameter, relationships between stem and canopy dimensions did not follow a biome-wide pattern. Site-level growth associations are possibly controlled by factors like nutrient status, soil moisture (Ackerman et al. 2018), microtopography and aspect (Au and Tardif 2007). My findings and other shrub allometry studies highlight the need to identify the physiological and environmental factors underpinning relationships of plant growth dimensions and, in the meantime, warn against using equations developed for one site to predict growth at another (Au et Tardif 2007), especially from boreal to tundra systems (Berner et al. 2015).

4.5 Conclusion

Plant height and lateral extent are plastic traits that readily respond to warming, as demonstrated both through long-term monitoring (Elmendorf et al. 2012a; Myers-Smith et al. in press) and experimental studies (Walker et al. 2006; Hudson and Henry 2010; Elmendorf et al. 2012b). Canopy structure affects many key ecosystem functions in tundra ecosystems through interactions with snow cover, solar radiation, and community diversity (Sturm et al. 2001; Thompson et al. 2004; Wookey et al. 2009; Bonfils et al. 2012; Bråthen and Lortie 2016). Therefore, understanding how growth dimensions will respond to global change drivers is key to predicting future changes in biomass and associated feedbacks.

Shrubs are expected to get taller with climate warming, but this may not translate in a predictable way to an acceleration in shrub growth across the tundra biome. My results highlight the complexity in mechanistically linking plant size to secondary growth and climate sensitivity. If size alone cannot explain inter-individual variations in climate sensitivity, more work is needed to test possible causes of this heterogeneity. Neighbour removal experiments (Chapter 5) and spatial analyses (Chapter 6) could provide a test of the hypothesis that competition among rapidly expanding shrubs will eventually limit their growth responses to climate.

A pattern of shorter canopy heights under more severe abiotic conditions means that allometric relationships became weaker for more northern tundra sites, precluding the use of allometric equations developed for boreal or sub-Arctic populations. The inconsistent scaling of growth dimensions complicates the improvement of remotely sensed estimates of biomass, which would benefit from including estimates of canopy height (Chen et a. 2009). Emerging technologies such as structure-from-motion photogrammetry (Cunliffe et al. 2016) may help to improve biomass estimates by providing finer-scale, 3D information on canopy structures.

In conclusion, plant size does not appear to be a predictor of future vegetation trajectories in the tundra biome. However, it remains crucial to understand the environmental constraints and internal resource allocation strategies acting upon various growth dimensions, as well as their possible interactions and relative importance across the biome, as they will ultimately drive changes in canopy structure, with feedback on ecological processes.

Chapter 5 A tale of two biomes: different limitations to growth in boreal versus alpine shrubs

Abstract

Northern environments are warming rapidly, driving widespread changes in vegetation communities. In the boreal forest and alpine tundra of the Kluane region in southwest Yukon, shrub species are increasing in abundance. Shrubs tend to displace smaller and less competitive species, but the magnitude of shrub-shrub or tree-shrub interactions is not very well quantified. Competition between canopy-forming shrubs in the tundra, and with trees in boreal forests, could potentially limit the growth and the climate sensitivity of shrubs, thereby slowing their expansion. I compared radial growth rates and the sensitivity of shrub growth to summer temperature between 40 shrubs from boreal forest plots and 101 shrubs from alpine plots. I hypothesised that competition from trees would reduce the climate sensitivity of shrub growth in the boreal forest compared to alpine tundra shrubs. I also took advantage of a past canopy removal experiment in the alpine tundra, predicting that shrubs that had experienced a decrease in surrounding aboveground shrub biomass would be released from competition and have wider annual growth rings post-removal. I found that shrubs in the boreal forest had growth rings nearly twice as wide as shrubs in the alpine tundra, but also exhibited much lower climate sensitivity (by ca. 75%). Shrubs around the canopy removal plots had the same growth rates as shrubs in undisturbed dense patches. My findings indicate that competition among shrubs in the tundra may not be a strong control on growth compared to climate. On the contrary, the growth of shrubs in boreal forests may not be tracking variations in temperature because of competitive effects of trees. Future shrub expansion could therefore occur faster in alpine environments.

Author contributions

I designed the study with input from Isla Myers-Smith. The canopy removal experiment was initially set up by Isla Myers-Smith and David Hik (Myers-Smith and Hik 2013). I collected data at the alpine sites. I am thankful to Meagan Grabowski for collecting and sharing dendroecological data on boreal shrubs. I performed all statistical analyses.

5.1 Introduction

5.1.1 Intensification of plant-plant interactions in northern ecosystems

Recent warming in northern ecosystems has triggered an increase in plant productivity through direct and indirect impacts on growth rates and regeneration success (Chapin 1983; De Long et al. 2015; Chapter 1). On the ground, this translates to an increase in most plant functional types (Myers-Smith et al. 2011; Elmendorf et al. 2012a; McManus et al. 2012), and to some range expansion of tree (Kullman 2001; Harsch et al. 2009; Dufour Tremblay et al. 2012a; Tremblay et al. 2012; Danby and Hik 2007a) and shrub (Hallinger et al. 2010; Dial et al. 2016; Myers-Smith and Hik 2017) species towards higher latitudes or elevations. There is however strong heterogeneity in the climate sensitivity of growth and the speed of climate responses across sites and species (Tape et al. 2012; Myers-Smith et al. 2015a). Higher vegetation density and woody encroachment in the tundra biome are likely to result in more frequent and intense plant-plant interactions like competition (Mekonnen et al. 2018), which could locally constrain the expected climate-driven expansion of shrubs in northern ecosystems. Measuring climate sensitivity across biotic gradients and testing the effects of competition with canopy removal experiments can allow us to quantify the influence of the competitive environment on shrub growth.

Tall deciduous shrubs are particularly successful at increasing their canopy height (Walker et al. 2006; Hobbie et al. 2017), infilling their populations through growth and recruitment (Tape et al. 2006; Myers-Smith et al. 2011; Tremblay et al. 2012; Formica et al. 2014), and, occasionally, expanding their ranges (Hallinger et al. 2010; Dial et al. 2016; Myers-Smith and Hik 2017). This responsiveness of tall, deciduous shrubs to climate change (Myers-Smith et al. 2015) may arise in part from plasticity in growth (Bret-Harte et al. 2002, Campioli et al. 2012a-b) and fast nutrient uptake strategies (Chapin et al. 1995) Combined with their tall stature, these traits make shrubs fierce competitors that tend to displace less competitive organisms like lichens and mosses (Elmendorf et al. 2012b; Fraser et al. 2014). Shrublands are expected to increase by as much as 52% by 2100 (Pearson et al. 2013). While the increasing dominance of shrubs at the expense of other functional groups is relatively well documented, there is a comparatively poor understanding of whether competition among shrubs, or between shrubs and trees at the forest-tundra ecotone (but see Boudreau and Villeneuve-Simard 2012), is a current limiting factor that could interfere with the expected climate-driven expansion of shrub species.

5.1.2 Tree and shrub expansion in southwest Yukon

The Kluane region in southwest Yukon (Chapter 2 **Figure 2-3**) lies within the boreal part of the Yukon Territory. The mountainous terrain results in sharp bioclimatic gradients with vegetation transitioning from boreal forests dominated by white spruce, *Picea glauca* Moench (Voss), to alpine tundra summits, with a transitional zone of tall shrub tundra gradually decreasing in density and canopy height. Upslope advances of treelines (Danby and Hik 2007a; Conway and Danby 2014) and shrublines (Danby and Hik 2007b; Myers-Smith and Hik 2017) have occurred in the region over the last century. These range shits are consistent with warming trends for southwest Yukon (Danby et al. 2011; Myers-Smith et al. 2017), but can be controlled by topographic features like aspect, slope and presence of permafrost (Danby and Hik 2007b).

Current projections of vegetation trajectories assume high and uniform climate sensitivity of shrub species across the tundra biome (Pearson et al. 2013). This may result in an overestimation of shrub expansion if competitive interactions buffer climate-driven increases in growth (Dormann et al. 2004). The performance of shrub species may become density-dependent under increased competitive interactions from expanding trees and shrubs, with individuals surrounded by more neighbours competing for limited resources including light, nutrients and water. This plant-plant competition might be especially strong at the southern, more productive end of the biome (Bertness and Callaway 1994; Maestre et al. 2009; Pellissier et al. 2010). These potential interactions are largely unquantified but are critical for predicting the future extent and rates of shrub expansion across the tundra biome.

5.1.3 Objectives and hypotheses

To compare the regional climate sensitivity of shrubs across two biomes, I used dendroecological data from willow species (*Salix* spp.) coming from two boreal forest locations (Grabowski 2015) and two alpine shrub tundra sites in the Kluane region (Chapter 2). I hypothesised that the climate sensitivity of shrubs at the boreal site would be lower than at the alpine site, in accordance with the stress-gradient hypothesis. The stress-gradient hypothesis states that interactions between plants shift from negative to positive along a gradient of increasing environmental severity, so that the growth of plants is thought to be mainly temperature-limited in harsh environments, and competition-limited in productive environments (Bertness and Callaway 1994; Brooker and Callaghan 1998; Maestre et al. 2009).

To quantify competition among canopy-forming deciduous shrubs, I took advantage of a canopy removal experiment carried out in 2007-2009 in the alpine tundra of the Ruby Range mountains (Myers-Smith and Hik 2013). I hypothesised that annual radial growth would have increased in the post-removal period for shrubs on the margin of the removal plots, having experienced a release from competition compared to shrubs in undisturbed patches.

5.2 Methods

5.2.1 Study sites

The boreal forest and alpine tundra sites were located within the Kluane region in southwest Yukon, Canada (**Figure 5-1**). The boreal sites consisted of forest dominated by white spruce (*Picea glauca*), with a canopy cover of ca. 45-60% (Grabowski 2015). Grey willow (*Salix glauca*), dwarf birch (*Betula glandulosa*) and soapberry (*Sheperdia canadensis*) are the main understory shrub species. The growth of the willow shrubs in this dataset was compared to the growth of shrubs that I sampled from alpine plots in the Ruby Range mountains and on the Kluane Plateau (see Chapter 2).

The canopy removal experiment was conducted in the Ruby Range mountains (61.22°N, 138.28°W; **Figure 5-1** Pika). The environment is an alpine tall shrub tundra dominated by the willows *Salix richardsonii* Hook., *Salix pulchra* Cham., and *Salix glauca* L. Hook. The ground layer is composed of dwarf shrubs *Dryas octopetala* L. and *Salix reticulata* L., and of various graminoids, forbs, mosses and lichens (Myers-Smith and Hik, 2013). The tall shrubline lies at ca. 1600-1700 meters of elevation in the region (Myers-Smith 2011).

5.2.2 Experimental design

In 2007, six pairs of circular plots (six meters in diameter) were established at the study site to investigate the effects of shrub canopies on snow cover (Myers-Smith and Hik, 2013). Plots were established in shrub patches of the dominant species of willows (Myers-Smith and Hik, 2013). One plot in each pair had all aboveground vegetation clipped to the ground, and this treatment was repeated in 2008 and 2009 to eliminate regrowth (Myers-Smith and Hik, 2013). The other plot in the pair was used as a control and left undisturbed.

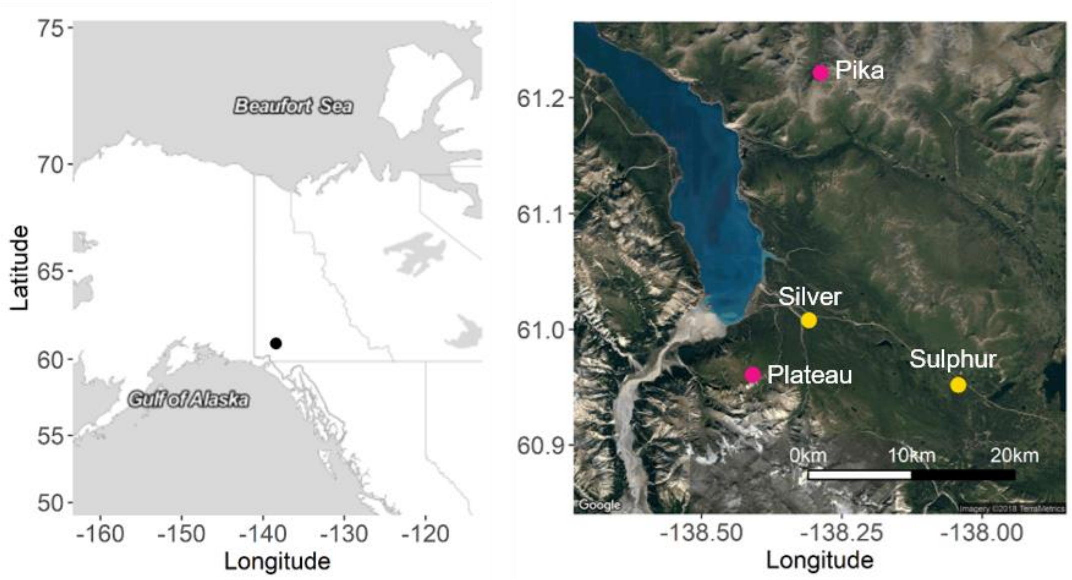


Figure 5-1 *Kluane region within southwest Yukon (left) and location of the two alpine (pink) and boreal (yellow) sampling plots within the Kluane region (right). The canopy removal experiment was set up at Pika.*

I revisited the plots in 2015. In a 1.5-metre margin around the experimental plots, I collected the main stem of up to ten willow shrubs per plot, and an equal number in the paired control plot. Because one of the control plots had very little shrub cover, two sets of plots were pooled together for analysis. As these plots were less than 50 m apart, I do not expect markedly different growth between plots. Stems were cut at the base in sections of 3-5 cm and kept dry until processing.

5.2.3 Dendroecological processing

For the alpine sites (including the canopy removal experiment), I cut thin sections (ca. 20 µm) from the stem samples using a sledge microtome, following standard dendrochronological procedures for shrub species (Myers-Smith et al., 2015b; Chapter 2). The thin sections were photographed under a microscope, and the growth rings were measured using the ObjectJ plug-in for ImageJ software as described in Chapter 2. For the canopy removal study, I restricted the measurements to the period 1999-2014 to have pre- and post-removal periods of equal length, ensuring a balanced design. For the other alpine plots, ring width was measured for the period 1990-2014.

Shrubs at the boreal sites were sampled by Meagan Grabowski in 2014 in two 1km^2-plots, Silver and Sulphur. Within each plot, *Salix glauca* individuals were selected randomly but were located at least 30 m apart (Silver: 16 shrubs, Sulphur: 24 shrubs). The largest stem was sampled and rings were counted and measured following the same procedures (see Grabowski 2015 for more details).

5.2.4 Statistical analyses

Climate sensitivity analysis

For the comparison between alpine and boreal shrubs, individual growth series were restricted to a common period (1990-2013). Climate sensitivity was calculated as the slope of the linear regression between ring width and summer (June-July-August) temperature for each individual shrub. Climate data was extracted from the CRU gridded dataset (v. 3.24.01) for the Kluane Plateau area and standardised (mean-centred and scaled) to retain only the interannual variability in climate rather than the actual values. Because temperature patterns are strongly autocorrelated over large spatial areas, these data are representative of the year-to-year broad fluctuations experienced by shrubs at all sites.

Canopy removal experiment

I compared mean annual growth for the pre- (1999-2006) and post- (2007-2014) removal period, in control and experimental plots. Because of the hierarchical sampling design (shrubs within plots within blocks), I used a linear mixed model with this nested random effect structure. I also added year as a crossed random effect to account for the fact that all individuals are experiencing year-to-year variations in the environment (Harrison et al. 2018). The fixed effects were treatment (control or removal) and period (pre- or post- removal), and I allowed an interaction between the two as I expected a change in growth rates in the post-removal period for the experimental, but not for the control treatment. All statistical analyses were carried out in R (v. 3.3.2) with the package lme4 for mixed model analyses.

5.3 Results

5.3.1 Climate sensitivity of shrub growth at boreal versus alpine sites

Willow shrubs from the alpine sites (control shrubs from the canopy removal experiment and other plots in the Pika Valley and Kluane Plateau) had higher temperature sensitivity of growth compared to boreal willows (**Figure 5-2**). However, boreal shrubs had growth rings on average twice as large as alpine shrubs (**Figure 5-2**). Statistical information is presented in Table S5-1 (Appendix IV).

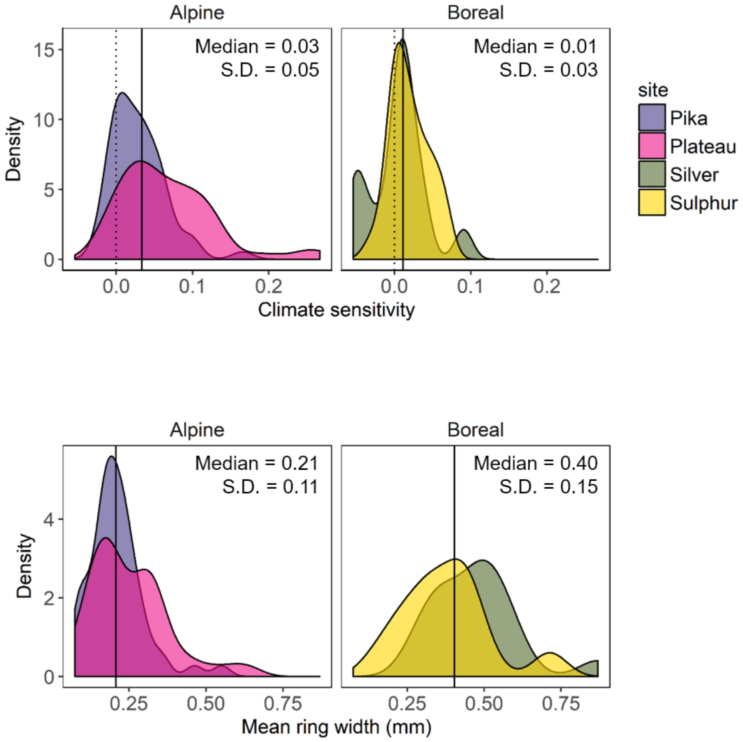


Figure 5-2 *Alpine willows have higher climate sensitivity (top left) but narrower growth rings bottom left) than their boreal counterparts (right-hand panels). Solid vertical lines indicate the median of observations; dotted lines in the top row represent a complete lack of climate sensitivity. Sample size: Pika = 53; Plateau = 48; Silver = 16; Sulphur = 24.*

5.3.2 Canopy removal effects on growth

In Pika Valley, radial growth varied inter-annually, but the shrubs in the experimental plots did not show any increases in growth after the removal of competitors (**Figure 5-3**). Growth rates did not significantly differ between treatment and control shrubs, neither before nor after the onset of the experiment (**Table 2-1**).

Table 5-1 *Radial growth of tundra willows did not vary between treatments nor over time. The fixed effects did not explain any of the variance in growth (marginal R^2 = 0.01), while the whole model (fixed and random effects) explained 63% of the variance (conditional R^2), with most of the variance at the individual level.*

Fixed effect	Estimate	Standard error	t value
Intercept (control, pre-removal)	221.42	47.51	4.66
Period (post)	7.05	25.21	0.28
Treatment (removal)	-31.14	62.45	-0.50
Interaction (post*removal)	13.42	11.35	1.18

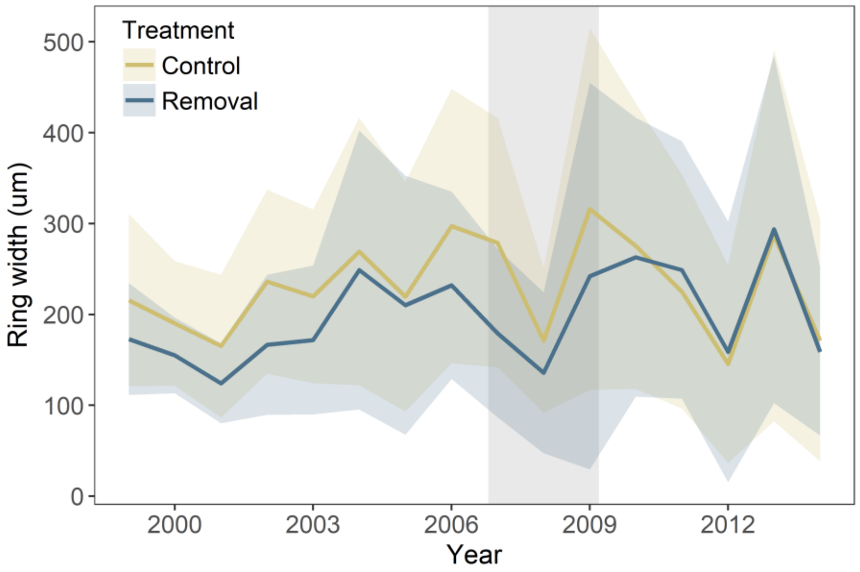


Figure 5-3 *Radial growth did not increase after the removal treatment (blue chronology) and growth was not different from control plots (yellow chronology). The shaded area indicates the duration of the removal experiment.*

5.4 Discussion

In this study, I found that willow shrubs in a boreal forest of southwest Yukon had higher absolute growth rates but lower climate sensitivity than willows growing above the treeline in the alpine tundra. I also demonstrated that a manipulated decrease in shrub density, and therefore a potential reduction in competition intensity, did not affect rates of radial growth in tundra shrubs. My results suggest that above-ground competition is not a strong limitation to shrub growth at this alpine tundra location, and that the climate-driven expansion of tall shrub species could be expected to continue, with tundra shrubs reaching higher densities in tundra locations (Myers-Smith et al. 2017). However, my results also suggest that shrub growth is less strongly controlled by climate under tree canopies in the boreal forest, and therefore the observed shrub expansion at lower elevations (Grabowski 2015) may be limited by competition.

5.4.1 Low climate sensitivity of shrub growth in boreal forests

Tall shrubs are responsive to increased summer temperatures, with evidence coming from warming experiments (Chapin et al. 1995; Henry and Molau 1997; Elmendorf et al. 2012b), long-term or repeat monitoring (Callaghan et al. 2011; Elmendorf et al. 2012a; Hobbie et al. 2017), and dendroecology (Blok et al. 2011b; Myers-Smith et al. 2015a; Ropars et al. 2015). As seen is this thesis (Chapter 3, Chapter 4) and elsewhere (Myers-Smith et al. 2015a), the strength of this response is spatially heterogeneous across northern regions and may depend on individual resource allocation (Ropars et al. 2017; Appendix I) and genetic differences (Bjorkman et al. 2017), as well as on local limiting ecological factors like herbivory (Olofsson et al. 2009; Speed et al. 2013; Christie et al. 2015), topography (Danby et al. 2007; Ropars and Boudreau 2012; Tape et al. 2012), soil moisture (Myers-Smith et al. 2015a; Ackerman et al. 2017), and competition (Boudreau and Villeneuve-Simard 2012).

In a boreal forest environment, shrubs are part of the understory and therefore experience reduced light availability because of interception from tree canopies. I found very weak climate sensitivity in boreal compared to alpine willows, which supports the idea that tree competition may restrict shrub expansion in the boreal biome (Grabowski 2015). While my data did not allow to test specifically for competitive effects of trees on shrubs, the growth of *Salix glauca* in the boreal forest was significantly but not strongly associated to canopy openness ($p = 0.01$, $R^2 = 0.03$; see Grabowski 2015). Above-ground competition may therefore not be very intense in this system, but can still act as a limiting factor to shrub growth. For instance, in a canopy removal experiment at the forest-tundra ecotone in Northern Québec, the growth of understory shrubs increased and became more strongly correlated to temperature after tree clearing (Boudreau and Villeneuve-Simard 2012). Such a removal experiment at the boreal site in Kluane would allow for better comparison with the alpine site.

Alternative and non-mutually exclusive explanations for lower climate sensitivity in the forest environment include potential moisture limitations (Berner et al. 2013) and different microclimatic conditions not detected by gridded temperature datasets. For instance, forests typically experience lower day-night variations in temperature than open areas (Chen et al. 1999). Correlations with local weather station data would allow to test for growth responses to micro-, rather than macro-climate.

5.4.2 No evidence of competition among shrubs

The removal of above-ground shrub biomass over a period of three years did not seem to enhance the growth of tundra shrubs around the cleared patches. Alpine shrubs in this study had strong temperature sensitivity, suggesting that climate is a more important control of growth than competition in this shrub tundra ecosystem, and likely the key driver of shrub expansion and range shifts in the area (Myers-Smith et al. 2017). At current densities, shrub growth may not be strongly affected by competition with conspecifics, or at least, its impact is masked by the stronger limitation of temperature. Given the many constraints that may be acting at once upon plant growth, alternative growth limitations should not be dismissed (Rollinson et al. 2016), especially as they may become important once the chief limitation is lifted. For instance, shrub growth may become increasingly controlled by soil moisture under warmer conditions (Berner et al. 2013; Ackerman et al. 2017). Similarly, an increasing demand on resources from climate-driven increases in vegetation could mean that competition will play a more important role in structuring tundra ecosystems in the future.

It is also possible that the removal experiment, which was initially designed to investigate snow cover dynamics rather than competition, did not have the expected effect on the target individuals. The removal of above-ground vegetation would have increased light availability, but this is probably not the most strongly limiting factor for the dominant canopy-forming plants in a high-latitude system with long daylight hours (Chapin et al. 1989). In tundra ecosystems, up to 80% of the plant biomass is stored below ground (Iversen et al. 2015), and therefore it is likely that the majority of plant-plant interactions occur where they are most difficult to detect. When we revisited the plots, six years after the removal experiment was discontinued, we had difficulty locating the removal plots because so much vegetation had resprouted from the clipped stems (Angers-Blondin and Myers-Smith, personal obs.). This means that the belowground parts were still probably highly active during the removal experiment, and therefore the intensity of competition might not have been decreased sufficiently to observe a measurable effect on target shrubs.

Removal experiments in the tundra often reveal mixed effects on target plants that depend on species associations and interacting warming and fertilisation treatments (Shevtsova et al. 1997; Gerdol et al. 2000; Bret-Harte et al. 2004; Rixen and Mulder 2009). These contrasting responses may arise from the environmental disturbance these experiments cause (Dormann and Brooker 2002) and the elimination of concurrent facilitative interactions in addition to the alleviation of competition (Dormann et al. 2004). Spatial point-pattern and nearest neighbour analyses are other ways to explore competitive interactions without disrupting the study system, although they offer correlative rather than mechanistic evidence (Dullinger et al. 2007; Pellissier et al. 2010; Kunstler et al. 2011; Lara-Romero et al. 2016). Relating measures of shrub growth and performance explicitly to the competitive environment of tundra shrubs (Chapter 6) would be a complementary way to test for the influence of competition in driving community organisation and current and future vegetation responses to climate change.

5.5 Conclusion

My findings indicate that shrubs in the alpine tundra of the Kluane region are more climate- than competition-limited, leading to lower annual growth rates but higher climate sensitivity than shrubs growing in the boreal forest. In the boreal forest, abiotic conditions are not as severe, but competition with trees and potential microclimatic effects of the forest cover may lead to the observed decoupling of growth and summer temperature. It could therefore be predicted that shrub expansion will occur at a faster rate in shrub tundra environments where current shrub densities do not seem to exert strong competitive effects on the growth of canopy-forming shrubs. Despite the benefits of an experimental approach allowing to mechanistically test for competition among shrubs, this study only considered aboveground competition, which may not provide a full picture considering that biotic interactions are more likely to be happening below ground where most of tundra biomass is found. A spatially explicit approach is required to quantify the effects of crowding on whole-plant growth and to understand the potential of plant-plant competition to restrict the climate responses of shrub growth (Chapter 6).

Chapter 6 Midnight sun duels: Competition structures tundra shrub communities but does not reduce the climate sensitivity of growth

Abstract

Competition is a strong driver of plant community dynamics, but is thought to be less important at higher latitudes where severe abiotic conditions control plant growth. With increasing shrub densities in the tundra biome, it is possible that local resource limitations arising from competition may limit the expected climate-driven expansion of shrub species. The impact of shrub competition on the climate sensitivity of shrub growth has not yet been quantified in the tundra biome. Here, I used a spatially explicit approach to directly link the competitive environment of a shrub to its growth and ability to respond to climate change. Using four sites of contrasting climate regimes and productivity across Northern Canada, I found that in general, competition did not have consistently directional effects on shrub growth and climate sensitivity. However, increasingly positive size-distance relationships between pairs of neighbours at more productive sites suggested that competition may control some aspects of shrub community dynamics, especially at warmer, more vegetated sites. The varying direction and magnitude of plant-plant interactions across tundra sites could lead to contrasting future vegetation trajectories under warming.

Author contributions

I designed the study with input from Isla Myers-Smith and Stéphane Boudreau. I collected the data and carried out the statistical analyses with help from Isla Myers-Smith. I am thankful to Santeri Lehtonen, Joe Boyle, Haydn Thomas, Jakob Assmann, Clara Morrissette-Boileau, Marc-André Lemay and Marianne Caouette for assistance in the field.

6.1 Introduction

6.1.1 Overview

The controls and limits to shrub expansion in tundra ecosystems need to be understood if we want to predict vegetation change and resulting feedbacks to the global climate. Plant competition is generally thought to be relatively unimportant in shaping community dynamics in northern environments, but the tundra biome comprises a strong gradient of plant productivity, and competitive interactions have yet to be measured across this gradient. Current dynamic vegetation models do not explicitly account for plant-plant interactions; however, if competition among rapidly increasing shrubs reduces their ability to respond to future warming, models might overestimate the extent and speed of shrub expansion. Spatially explicit analyses of climate sensitivity taking into account plant density may help to test for competition-driven buffering effects to shrub expansion.

6.1.2 Intensity versus importance of competition: some definitions

Competition is a major driver of plant community assembly and population dynamics, and can act as a limitation to growth, reproduction and survival of individual plants. Quantifying the magnitude of these effects and the degree to which they impact ecosystem processes and structure is a keystone of ecological theory (Whittaker 1965; Grime 1977; Tilman 1987; Silvertown 2004). However, there are many ways to measure competition, leading to substantial debate and lack of clarity in the literature when the definitions of competition intensity versus relative importance are not defined rigorously (Grace 1995; Brooker et al. 2005). Before discussing competition in the tundra, I therefore define the terms used in this study.

In this chapter, I follow the terminology of Welden and Slauson (1986), where the *intensity* of competition is the absolute decrease in growth (or survival, or other aspects of plant performance) experienced by a plant as a direct result of competition from another plant. The *importance* of competition is the relative impact it has on individual performance compared to the impact of other environmental stressors (Welden and Slauson 1986). These two measures are not necessarily correlated (Welden and Slauson 1986), so that plants could experience either a strong (high intensity) or a weak (low intensity) absolute decrease in growth in the presence of a competitor, and the presence of this competitor could either be the main factor reducing growth in that plant (high importance), or one of many other factors that reduce growth (low importance).

6.1.3 How much competition in the tundra? The stress-gradient hypothesis

The importance and intensity of plant-plant competition vary across bioclimatic gradients: it is thought to be strongest in highly productive environments, but weaker in low-productivity ecosystems with harsh abiotic conditions, like the tundra (Campbell and Grime 1992; Maestre et al. 2009; but see Theodose and Bowman 1997; Pellissier et al. 2010). This is formalised by the stress-gradient hypothesis, which states that along a gradient of increasingly environmental severity, positive interactions (facilitation) become increasingly common while negative interactions like competition become less frequent (Bertness and Callaway 1994; Maestre et al. 2009). The stress-gradient hypothesis has received some support over regional gradients in arctic-alpine regions where established plants create a more favourable microclimate for growth (Choler et al. 2001) or provide physical protection that facilitate recruitment (Batllori et al. 2009).

However, the prevalence of positive interactions does not mean that competition is absent from harsh environments. In fact, several studies have detected facilitative and competitive effects acting together in boreal, Arctic and alpine systems (Dormann and Brooker 2002; Klanderud and Totland 2005, Montgomery et al. 2010); a common example is when a plant facilitates the establishment of another but reduces its growth subsequently (Grau et al. 2012; Cranston and Hermanutz 2013). It has been suggested that for plants living in stressful environments with limited resources, even a slight pull on these resources by a competitor could have an intense effect on plant performance (Dormann et al. 2004).

Furthermore, important gradients of productivity occur in tundra ecosystems: from barren polar semi-deserts to the dense, almost continuous tall shrub tundra at the southern edge of the biome, there is a hundred-fold increase in total phytomass (Raynolds et al. 2012). It is therefore possible that tundra vegetation is controlled to some degree by competition (Chapin et al. 1989; Pelissier et al. 2010), especially at the low- to mid-Arctic latitudes where tall shrubs are dominant and expanding rapidly (Elmendorf et al. 2012a; Myers-Smith et al. 2015a).

6.1.4 Competition as a regulator of shrub expansion?

Canopy-forming deciduous shrubs can be fast-growing, opportunistic species when the resources are available, which explains why some of these species are increasing the most rapidly in tundra ecosystems (Bret-Harte et al. 2002; Walker et al. 2006; Myers-Smith et al. 2011; Elmendorf et al. 2012a). As shrub expansion continues, decreased light availability from shading and an increased belowground demand for nutrients and water could exacerbate competitive interactions and eventually limit the ability of shrubs to respond to improved climatic conditions. Trees growing in closed-canopy forests were shown to be less sensitive to climate than trees growing at the treeline (Ettinger et al. 2011); however, it is unknown whether similar patterns can arise from shrub-shrub competitive interactions in the tundra.

Syntheses of plot-based changes (Elmendorf et al., 2012a) and of dendroecological data (Myers-Smith et al. 2015) suggest that shrub species become more climate-sensitive towards their northern or upslope range limit. This could be indicative of a shift from more important competition at lower latitudes and elevations towards higher importance of abiotic controls at colder sites, in accordance with the stress-gradient hypothesis (Bertness and Callaway 1994, Maestre et al. 2009). However, few studies have quantified the link between competitive environment and performance at the individual level in northern ecosystems (Doležal et al. 2006; Kunstler et al. 2011; Wang et al. 2016), and none in the tundra for rapidly expanding shrub species.

6.1.5 Testing for competition

Plant-plant interactions can be quantified using experiments such as neighbour removal (Chapter 5; Campbell et al. 1991; Shevtsova et al. 1997; Bret-Harte et al. 2004; Rixen and Mulder 2009). They have the benefit of testing mechanistically for competition, although in tundra systems may also have unexpected effects on other biotic interactions and environmental conditions (Dormann and Brooker 2002). Alternatively, spatial analyses (Goulard et al. 1995; Perry et al. 2006) can be used to infer interactions between plants and their influence on performance (Kunstler et al. 2011; Wang et al. 2016). For instance, density-dependent growth, resource acquisition and mortality within a population should result in a clear relationship between the spacing and the combined size of two neighbours (Pielou 1962; Briones et al. 1996). Possibly because of the assumption that competition is not an important control of plant growth at high latitudes with low plant densities and severe abiotic conditions (Grime 1977; Bertness and Callaway 1994), spatially explicit analyses are rare in northern ecosystems (but see Doležal et al. 2006; Boudreau et al. 2010). Quantifying the degree to which competition may impact future shrub community dynamics in a warming and greening Arctic could be a critical step towards constraining Earth-system models to predict vegetation change more realistically (Miller and Smith 2012; Pearson et al. 2013).

6.1.6 Research questions and hypotheses

In this chapter, I examine the growth and the climate sensitivity of tundra shrubs in a spatially explicit context and across a range of sites of contrasting environmental severity to quantify the intensity and importance of competition among tall deciduous shrubs. My research questions were: Does competition affect the distribution, growth, and climate sensitivity of growth in tundra shrubs? And does the magnitude of competitive effects vary predictably across sites along a plant productivity gradient? I hypothesised that:

1. Competition between tundra shrubs impacts their overall growth and performance. I predicted that pairs of shrubs that are closer together would have a smaller combined canopy area than two neighbours that are located further apart.

2. Competitive interactions with neighbours reduce both the absolute growth and the climate sensitivity of growth. I predicted that shrubs with closer neighbours or a denser shrub cover within their neighbourhood would show lower growth rates (narrower growth rings) and weaker ring-width correlations to summer temperature compared to shrubs that are more isolated.

3. The intensity and importance of competition increase along a productivity gradient according to the stress-gradient hypothesis. I predicted that the effect size (a measure of intensity) and goodness of fit (a measure of importance) of size-distance relationships and of crowding-radial growth relationships would be stronger in plots with denser shrub cover.

6.2 Methods

6.2.1 Study sites and species

Tall deciduous shrub species were mapped and sampled in five to six square plots across four sites in Northern Canada (Chapter 2 **Figure 2-3**). Mapped representations of the plots are presented in Appendix V (Figure S6-1). The spatial analysis uses all the shrubs within the plots (n = 755). Because not all wood samples were measured, the dendroecological analysis is restricted to 339 shrubs, but competition indices described below were still computed with the full spatial dataset (i.e. a shrub whose rings were not measured still counts as a neighbour for another measured shrub), so that the full competitive environment is represented for any given shrub.

6.2.2 Size-distance relationships

Within each plot, I calculated pairwise distances between all shrubs and retained the nearest neighbour (shortest distance) for each shrub. I computed their combined canopy area as the sum of two ellipses calculated from two perpendicular diameters, and regressed this total size against the distance between them. I used a linear mixed-effects model with size as the response variable, distance as the fixed effect, and plot nested within site to account for the hierarchical sampling design. I allowed random slopes and intercepts at the plot level given the heterogeneity in the spatial structure and shrub cover across plots (Figure S6-1).

6.2.3 Indices of competition

The competitive environment of plants can be quantified through a wide suite of competition indices relating to the size, abundance, proximity and identity of nearby competitors (Weigelt and Joliffe 2003). I chose two indices that are easy to interpret, complement each other in the type of information they provide, and are not strongly autocorrelated. The first is the distance to the nearest neighbour, a frequent indicator of immediate competition (Pielou 1962; Perry et al. 2006). The second is the shrub cover within the “zone of influence”. The zone of influence of a shrub is defined as the area in which the plant interacts with its immediate environment to acquire light, water, and nutrients. Shrub cover within this zone will result in competition over shared resources and is therefore a measure of crowding, similar to indices derived from basal area in forestry studies (Green and Hawkins 2005; Doležal et al. 2006; Kunstler et al. 2011). Because the zone of influence depends on plant size, I computed a circular zone based on a custom diameter for each shrub, equal to four times the canopy diameter. Given that up to 80% of tundra biomass is found below ground (Iversen et al. 2015) and that shrub root networks can extend laterally for several metres beyond the canopy range (**Figure 6-1**), this arbitrary range for interactions is probably conservative.

Figure 6-1 *Shrub roots can run for several meters under the soil surface: here, they extend for more than 5 m beyond the ca. 1-m diameter of this shrub canopy. Location: Pika Valley, Kluane, Yukon Territory.*

6.2.4 Growth and climate sensitivity

I calculated the average raw ring width for each individual shrub as a measure of growth. I measured the climate sensitivity of individual shrubs as the slope of the linear regression between standardised growth-ring measurements (restricted to the period 1990-2014; see Chapter 2 for details on dendroecological methods) and summer (June-July-August) temperature, obtained from CRU 3.24.01 gridded dataset. Young individuals with fewer than eight years measured were excluded (n = 23, or 7%).

I used indices of growth and of climate sensitivity as the response variables in mixed-effects models to test my hypothesis that more competition reduces the growth (smaller rings) and the climate sensitivity of growth (weaker climate-growth slope). The fixed effects, i.e., the distance to the nearest neighbour and the shrub cover within the zone of influence, were centred and scaled. I used plot nested within site as random effects. The growth model included random slopes and an intercept for each plot. In the sensitivity model, I used random intercepts only because the added complexity of using random slopes led to model convergence issues.

6.2.5 Intensity and importance of competition along a productivity gradient

Given that the intensity of competition is the absolute effect of competition on plant performance (Welden and Slauson 1986), it can be quantified as the slope (effect size) of a competition-growth relationship such as a size-distance relationship

(Briones et al. 1996). Similarly, because the importance of competition is relative to all the other factors that may influence performance (climate, herbivory, pathogens, etc.), the goodness of fit of a competition-growth relationship is indicative of the part competition plays in explaining the variation in performance; the lower the fit, the least important competition is relative to other factors (Welden et al. 1988; Briones et al. 1996). I chose to use these indices to test the stress-gradient hypothesis because they are intuitive to interpret, easy to obtain from linear regressions, and commonly accepted and understood in the competition literature (Weigelt and Joliffe 2003).

To test whether the stress-gradient hypothesis holds across the four study sites of contrasting climatic regimes (Chapter 2, Chapter 3), I calculated a measure of plot productivity: the total shrub cover within each plot, obtained by summing the canopy area of all mapped shrubs. Because study plots varied in size, shrub density is reported in square metres of shrub cover per hectare. I then used a linear regression to determine whether the intensity (slope) or importance (coefficient of determination) of competitive relationships could be explained as a function of productivity. I used the outputs of the size-distance relationships and of the growth-crowding relationships as response variables. All analyses were run in R 3.3.2. Mixed-effects models were run with the package lme4.

6.3 Results

6.3.1 Size-distance relationships

Size-distance relationships were variable across plots but generally positive, with an overall positive slope (**Figure 6-2**; **Table 6-1**). Pairs of closest neighbours tended to reach larger cumulative sizes when they were further apart, and to be smaller when they were closer together.

6.3.2 Effect of competition on growth and climate sensitivity

The distance to the nearest neighbour and the shrub cover within the zone of influence of a given shrub are two useful indices of competition that are not highly autocorrelated (Pearson’s R = 0.15). However, the mean ring width of shrubs was not strongly associated to either measure of competition, with very high heterogeneity in plot-level responses (**Figure 6-3**). The two competition indices did not explain variation in annual growth (**Table 6-2**).

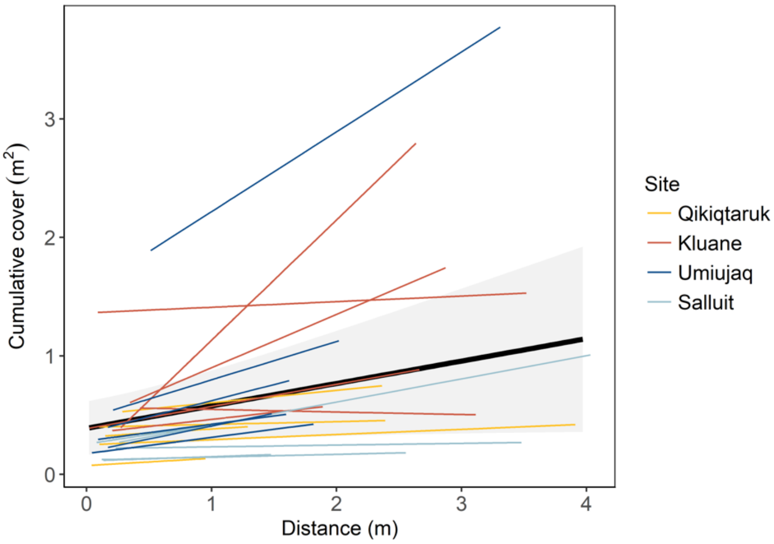


***Figure 6-2** Pairs of nearest neighbours have higher cumulative canopy area when they are more distant to each other. The bold black lines indicate the slope of the overall mixed-effects model (shaded area: 95% confidence interval). The coloured lines are the plot-level predictions obtained from random slopes and intercepts in the model.*

Climate sensitivity was similarly heterogeneous and was not explained by the competition indices (**Figure 6-3**). Some plots in Kluane seemed to follow the expected relationship of higher growth and climate sensitivity with less crowding, while most plots in Umiujaq showed the reverse trend (**Figure 6-3**).

***Table 6-1** Weak positive relationship between the combined canopy area of two shrub neighbours and the distance between them. The values are estimates from mixed-effects models using plot within site as nested random effects.*

	Combined cover
Fixed effect	
Distance between neighbours (SE)	0.19 (0.10)
Random effects	
Plot:Site random slope (SD)	0.08 (0.29)
Plot:Site intercept (SD)	0.16 (0.40)
Site random slope (SD)	0.01 (0.11)
Site intercept (SD)	0.01 (0.12)
Residual	0.41 (0.64)
Observations	675
Marginal R^2	0.02
Conditional R^2	0.42

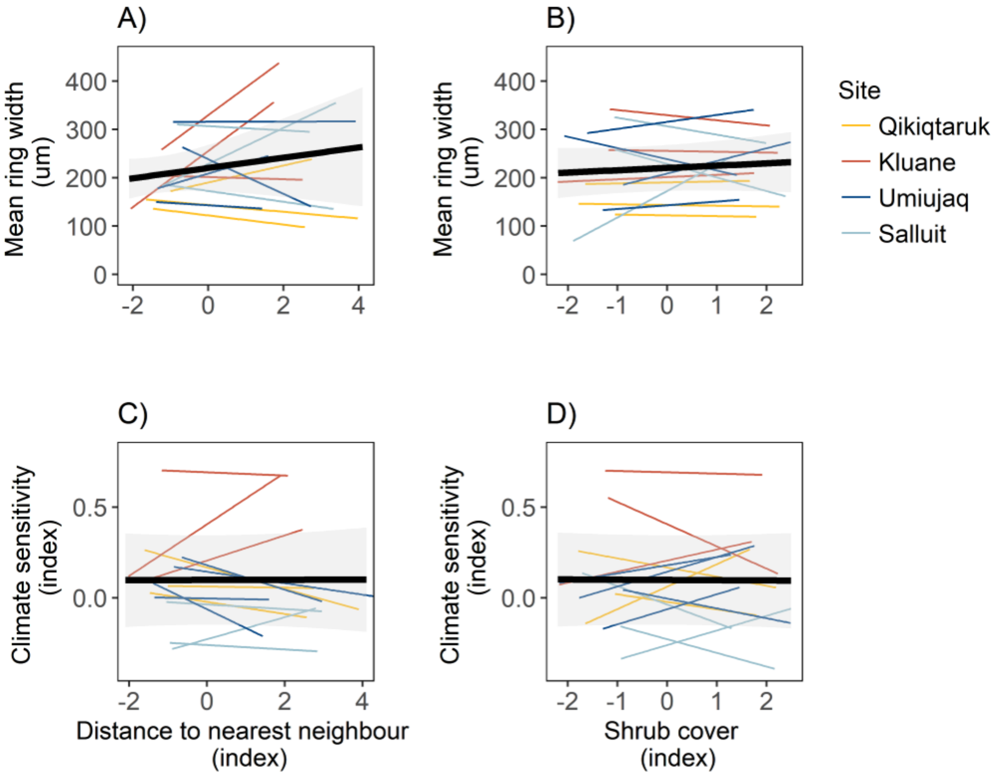


Figure 6-3 *Mean annual growth rates (A-B) and climate sensitivity of growth (C-D) of tundra shrubs were not explained by two competition indices in most plots. Coloured lines are plot-level relationships; the bold line and shaded area represent the overall model slope and 95% confidence interval.*

6.3.3 Stress-gradient hypothesis

The intensity, but not the importance of competition, as measured from the size-distance relationships of the 23 shrub plots across Northern Canada, varied as a function of shrub cover: more productive plots showed more intense competition (**Figure 6-4**). However, the relationships between competition and radial growth did not follow the same expected pattern (Figure S6-2).

6.4 Discussion

In this study, I found that the spatial distribution of tundra shrubs at four sites across Northern Canada is overall indicative of competitive interactions. The intensity (but not the importance) of these competitive interactions varied across a productivity gradient, in line with the stress-gradient hypothesis. However, my findings suggest that competition is not acting strongly on radial growth, as shrubs showed highly heterogeneous responses of growth rates and climate sensitivity to crowding indices within plots. The variability in the magnitude and direction of these relationships was not explained by the productivity gradient. Overall, this study highlights a discrepancy between the responses of radial growth and general performance of tundra shrubs to competition. Current rates of radial growth may not be representative of the whole life-history of a shrub, and effects of competition may be felt at earlier stages such as establishment. Combined experimental tests of the effects of warming and competition on shrub growth, reproduction and survival will be necessary to identify potential vegetation density thresholds at which competition between shrubs may become more limiting to their growth than temperature.

6.4.1 Spatial patterns of tundra shrubs

I found that shrubs that grew closer together tended to have smaller canopy sizes, a pattern likely arising from density-dependent growth and usually associated to competition (Pielou 1962; Briones et al. 1996). Few comparable studies exist for high-latitude plant communities, and therefore my results provide a new line of evidence that competition may have a structuring role in plant communities even in environments where abiotic controls are thought to prevail (Billings 1987; Bertness and Callaway 1994). This finding adds to evidence from correlative (Pellissier et al. 2010) and experimental (Choler et al. 2001; Bret-Harte et al. 2004) studies that have reported competitive effects among tundra plants.

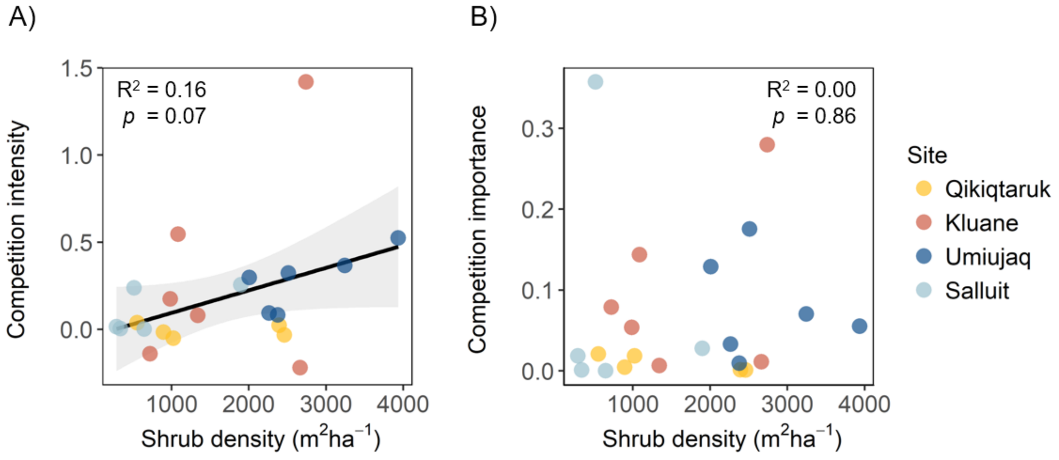
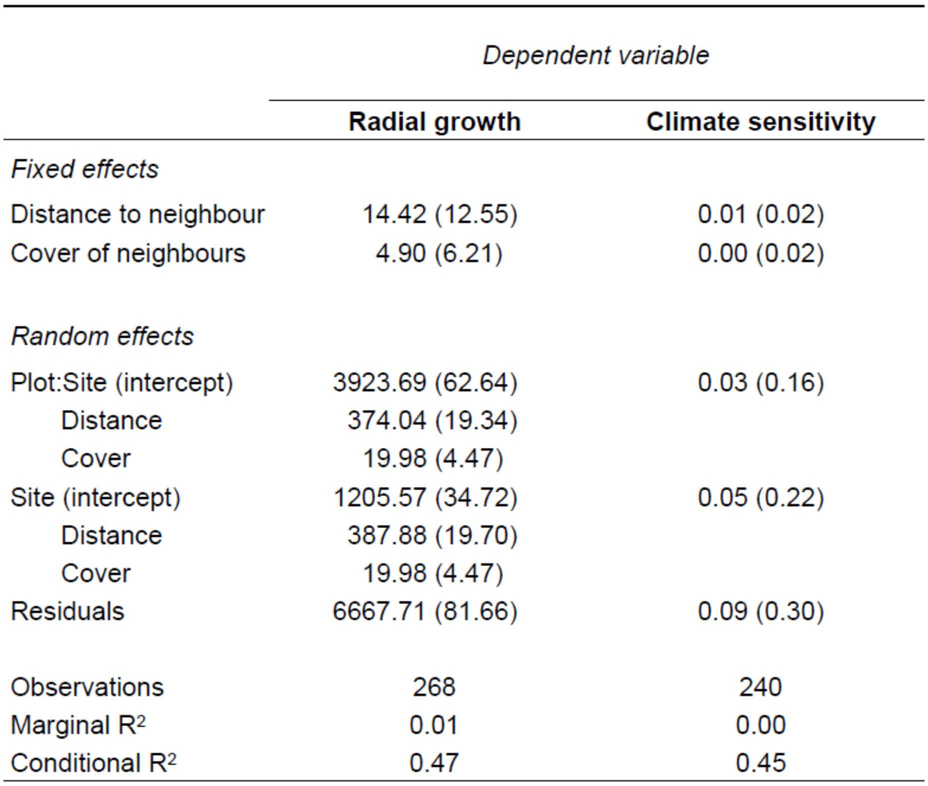


Figure 6-4 *Competition intensity (A), measured as the slope of size-distance relationships within plots, increases along a productivity gradient, measured as shrub density within plots (n = 22). Competition importance (B), measured as the goodness of fit of the same relationship, does not show any pattern related to shrub cover.*

Table 6-2 *Effects of crowding indices on the growth and climate sensitivity of tundra shrubs at four sites across Northern Canada, as assessed through linear mixed-effects models. Competition does not have an overall directional effect on either growth or sensitivity.*



	Dependent variable	
	Radial growth	**Climate sensitivity**
Fixed effects		
Distance to neighbour	14.42 (12.55)	0.01 (0.02)
Cover of neighbours	4.90 (6.21)	0.00 (0.02)
Random effects		
Plot:Site (intercept)	3923.69 (62.64)	0.03 (0.16)
Distance	374.04 (19.34)	
Cover	19.98 (4.47)	
Site (intercept)	1205.57 (34.72)	0.05 (0.22)
Distance	387.88 (19.70)	
Cover	19.98 (4.47)	
Residuals	6667.71 (81.66)	0.09 (0.30)
Observations	268	240
Marginal R^2	0.01	0.00
Conditional R^2	0.47	0.45

It is of particular interest that in the current study, size-distance relationships suggested competitive effects between shrubs, while their growth and climate sensitivity seemed largely unaffected. Primary and secondary growth are not always strongly coupled in tundra shrubs (Chapter 4; Bret-Harte et al. 2002; Campioli et al. 2012a-b), and plant-plant interactions may act differently upon these growth dimensions, or else affect only certain life stages (Callaway and Walker 1997). Therefore, it is possible that competitive interactions were detected for some aspects of plant performance without necessarily being reflected in contemporary growth rates. In that respect, spatial patterns of plant populations may be more broadly encompassing of whole plant life histories, increasing the detection of past and current competitive interactions.

6.4.2 Neighbour interactions effects on growth and climate sensitivity

The high inter-individual variability in the climate sensitivity of shrub growth highlighted earlier in this thesis (Chapter 3, Chapter 4) was not explained by the competitive environment of these shrubs for most plots, nor were absolute individual growth rates. However, a few directional trends suggest that plant-plant interactions may play a role in controlling shrub growth under some site- and species-specific circumstances.

Two out of three plots in Kluane showed the expected trend of higher growth with more distant neighbours. This alpine tundra site is also the most climate sensitive (Chapter 3) and has the widest range of plant sizes (Chapter 2 **Table 2-1**). It is possible that competitive interactions are more easily detected over such a range: more competition studies across a steeper gradient of shrub cover would help to quantify the density threshold at which competition becomes important.

Shrubs at Umiujaq tended to show the reverse associations, i.e. higher growth rates at higher shrub densities or with closer neighbours. Umiujaq is the only site in this study dominated by the dwarf birch, *Betula glandulosa*, rather than by willows. Dwarf birch forms mycorrhizal associations which enables carbon transfer within conspecific shrubs (Deslippe and Simard 2011). In this case, proximity can be an asset, with closer shrubs benefitting from shared resources. More work is needed to confirm this facilitative mechanism, but the ability to transfer resources within shrubs at a site may explain the high plasticity (Bret-Harte et al. 2002) and near mono-dominance (Deslippe and Simard 2011) of *Betula glandulosa* in Northern Québec (Tremblay et al. 2012) and other tundra locations (Tape et al. 2006; Cahoon et al. 2016).

In this study, I tested whether competition had a predictable and consistent effect on shrub growth across Northern Canada. Given the heterogeneity of plot-level responses within a site, further studies should examine competitive relationships in combination with landscape heterogeneity (soil moisture, nutrient availability, etc.) to unpick the causes for divergent plant-plant interactions at regional scales.

6.4.3 Stress-gradient hypothesis and competition in a shrubbier biome

In this study, I found that the importance of competition, measured as the effect size of size-distance relationships (Briones et al. 1996), increased along a productivity gradient. These findings are in line with predictions from the stress-gradient hypothesis (Bertness and Callaway 1994; Brooker and Callaghan 1998) and align with some empirical observations along tundra ecotones (Choler et al. 2001; Pellissier et al. 2010; Michalet et al. 2014). If competition is a control of community dynamics at the most productive tundra sites, shrub expansion may be regulated through a negative feedback and be slower than expected: it is therefore critical to consider plant competition in vegetation models (Brooker et al. 2007; HilleRisLambers 2013; Welk et al. 2014).

Future rates of shrub expansion will likely be determined by the balance between increasing intensity of competition and the acceleration of biogeochemical cycles. Warming enhances plant growth, but also enhances nutrient availability, by promoting microbial activity and nitrogen mineralisation (Aerts et al. 2006; Wookey et al. 2009). Higher shrub densities may introduce “priming” effects on the soil through positive feedbacks to these processes (Hartley et al. 2012). All in all, if resource availability increases in proportion to increasing shrub expansion, tundra ecosystems might reach a new equilibrium with faster turnover under higher shrub densities. If and when resource levels fail to keep pace with shrub encroachment, then competition may become a constraint to vegetation change.

6.4.4 Conclusion

Plant competition in the tundra biome, although traditionally considered negligible, may play an increasingly important role under Arctic warming and the observed widespread increases in vegetation cover. This study found evidence for a structuring effect of competition on spatial patterns of tundra shrubs, and this effect was stronger at more productive sites. Competitive interactions likely structure community interactions in tundra ecosystems; yet, radial growth and climate sensitivity do not seem to be strongly controlled by plant competition. Therefore, we cannot use these growth indices alone to understand how plant-plant competition might influence rates of future vegetation change in the tundra. Studying competitive interactions across a wider range of shrub densities and monitoring more aspects of plant performance would improve our knowledge of the role of competition in shaping tundra ecosystems. Conversely, facilitative interactions such as mycorrhizal networks deserve more attention. The balance between positive and negative plant-plant interactions may play a strong role in determining community composition and dominance under climate warming.

Chapter 7 Plant-plant interactions could limit recruitment and range expansion of tall shrubs into alpine and Arctic tundra

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Author contributions

I designed the study and carried out the field experiments with help from Isla Myers-Smith. I analysed the data and wrote the manuscript with inputs from Isla Myers-Smith and Stéphane Boudreau.

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ORIGINAL PAPER

Plant–plant interactions could limit recruitment and range expansion of tall shrubs into alpine and Arctic tundra

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Abstract

Species in cold-limited biomes are expected to expand their distribution ranges in response to climate warming. For plants, range shifts can only occur via successful recruitment beyond their current distribution limit. However, many environmental and ecological filters can act upon recruitment and establishment, thereby potentially limiting the expected climate-driven shifts. In this study, we investigate potential mechanical and chemical constraints that vegetation above the tall shrubline in alpine and Arctic tundra could impose upon the successful establishment of willow species in the Canadian Western Arctic. We collected willow seeds from an alpine and an Arctic shrubline and conducted germination trials to test (1) for seedbed preferences among three natural and one experimentally scarified seedbeds, and (2) for vulnerability to allelopathic chemicals produced by ericaceous dwarf shrub species. We found that germination was almost four times higher on manually exposed bare ground than on intact, herbaceous vegetation. Seeds of two willow species, *Salix arctica* and *Salix pulchra*, were not affected by leaf extracts from dwarf shrubs, *Cassiope tetragona* and *Vaccinium uliginosum*, but the germination of *Salix richardsonii* was reduced by as much as 24% in the presence of chemicals from *C. tetragona*. Our results suggest that biotic interactions could limit the predicted expansion of tall shrubs in the tundra by interfering with germination. Seemingly species-specific responses highlight the need for replicated studies across a wider range of species combinations. Potential range shifts may not occur as a uniform translocation of the shrubline, but could change the composition of the plant community by filtering out certain species.

Keywords Allelopathy · Seedbed · Germination · Seedlings · Shrubline · Tundra

Introduction

Ecosystem boundaries are in part controlled by temperature, and have shifted with past variations in climate as species migrated to track their climatic optimum (Davis and Shaw 2001). Under the current rapid rates of warming at the global scale (IPCC 2013), latitudinal or elevational advances in distribution limits have recently been observed in most taxa including invertebrates, plants, birds, and mammals (Chen et al. 2011). In tundra ecosystems, tall shrub species are projected to expand their range up mountain slopes and northward to higher latitudes (Post et al. 2009; Myers-Smith et al. 2011).

In sessile species such as plants, range shifts occur via the recruitment and establishment of new individuals beyond the current distribution limit. Because of the multiple environmental and ecological filters acting on regeneration (Fig. 1), these shifts are spatially heterogeneous and often lag changes in climate (Corlett and Westcott 2013; Ash et al. 2016). For instance, treelines have only advanced in around half of the sites studied in a global meta-analysis (Harsch et al. 2009). Similarly, although tundra shrubs have been expanding in the circumpolar region over the last half-century (Myers-Smith et al. 2011), most of the observed increases in growth and reproduction have only led to population infilling, and range shifts remain mostly anecdotal (but see Myers-Smith and Hik 2017). Some of the non-climatic limitations interfering with range expansion may include species traits like dispersal ability (Brooker et al. 2007; Kambo and Danby

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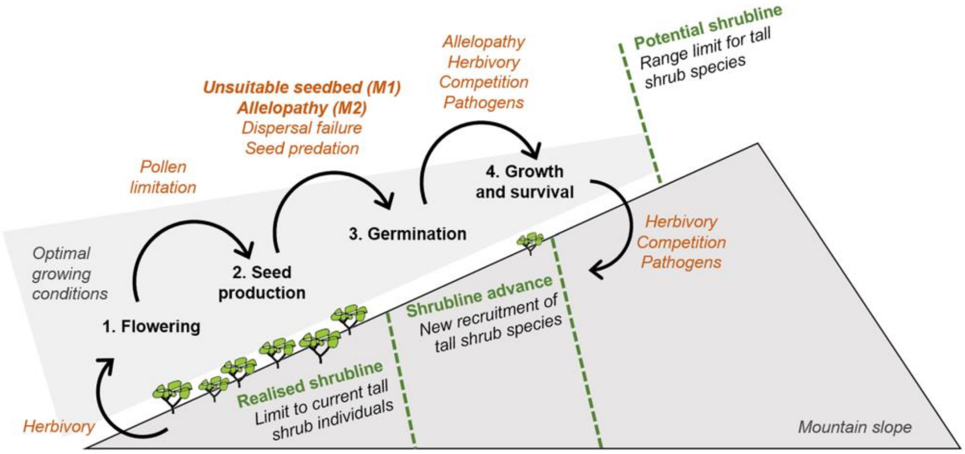


Fig. 1 Biological constraints (orange) potentially acting as ecological filters on the process of regeneration (green) above the shrubline with the mechanisms of seedbeds (mechanism 1) and allelopathy (mechanism 2) highlighted in bold, the foci of this study. (Color figure online)

2017), and a wide range of biotic interactions (reviewed in HilleRisLambers et al. 2013).

Species interactions are affected by climate change, and in turn control community assembly in environments where new species could meet their temperature requirements (Tylianakis et al. 2008; Gilman et al. 2010; Van der Putten et al. 2010). In plant communities, interactions with herbivores (Olofsson et al. 2009; Munier et al. 2010; Christie et al. 2015), soil biota (Van Grunsven et al. 2007), pathogens (Olofsson et al. 2011) and other plants (Grau et al. 2012; Liang et al. 2016) may all promote or constrain range shifts. It is therefore critical to better understand biotic interactions and incorporate them in species distribution models (Brooker et al. 2007; Hellmann et al. 2012; Meier et al. 2012).

In addition to direct competition for resources, several other types of plant–plant interactions can interfere with the establishment of a species beyond its current range. The vegetation already in place can prevent seeds from reaching a suitable seedbed. For instance, conifers at the treeline have been shown to become preferentially established after disturbance exposing the bare ground (Dufour Tremblay and Boudreau 2011). In addition, vegetation may chemically interfere with seed germination when allelopathic species are present. Allelopathy is the production of toxic compounds by some plants; when leached into the ground, these chemicals can affect the germination, growth, and survival of other species (Wardle et al. 1998). For example, some conifer seeds and seedlings are vulnerable to chemicals released by ericaceous dwarf shrubs (Nilsson and Zackrisson 1992; Dufour Tremblay et al. 2012). It is currently unknown whether these biotic controls of treeline dynamics act similarly upon shrublines at higher latitudes and elevations.

To investigate whether plant–plant interactions have the potential to limit range shifts of tall shrubs into the tundra, we carried out germination experiments using seeds of widespread and rapidly expanding willow species (*Salix* spp.) collected from an Arctic and an alpine shrubline in the Yukon Territory. Our research question was the following: Does vegetation above the tall shrubline affect the germination of shrub seeds? We experimentally tested two potential mechanisms of interference: (1) vegetation acts as a physical barrier preventing shrub seeds from reaching a suitable seedbed (M1 in Fig. 1); and (2) chemicals released by ericaceous dwarf shrubs inhibit germination (M2 in Fig. 1). Correspondingly, we predicted (1) that seeds of the tall willow shrub, *Salix pulchra* Cham. would germinate to a higher extent on bare ground than on vegetated ground, and (2) that seeds of the tall willows *S. pulchra* and *Salix richardsonii* Hooker and of the dwarf willow *Salix arctica* Pall., would germinate to a lesser extent when exposed to potentially allelopathic leachates from the ericaceous dwarf shrubs, *Vaccinium uliginosum* L. And *Cassiope tetragona* (L.) D. Don.

Materials and methods

Study sites

We conducted two germination experiments (scarification and allelopathy) on Qikiqtaruk-Herschel Island (69.568°N, 138.918°W), a Yukon territorial park in Northern Canada.

The allelopathy experiment was replicated in the Kluane region of the Southwest Yukon Territory (61.027°N, 138.411°W, Fig. 2). These two sites are 1000 km apart and represent both Arctic and alpine tundra ecosystems where tall shrubs are thought to be expanding their ranges.

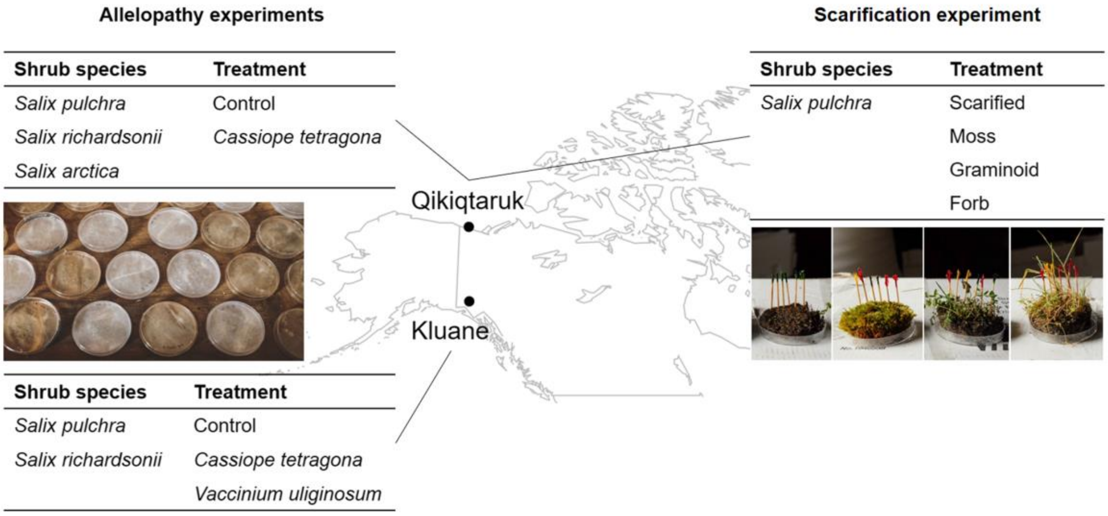
Qikiqtaruk is underlain by ice-rich permafrost (Burn and Zhang 2009) and harbours several types of tundra vegetation (described by Smith et al. 1989), including the Herschel type characterised by moist acidic tussock tundra, and the Komakuk type comprising herbaceous tundra disturbed by freeze–thaw processes. Alpine habitats of the Kluane Region are underlain by bedrock containing permafrost. The alpine zone is characterised by willow-dominated tall shrub tundra transitioning to dwarf shrub and herbaceous tundra at around 1600-1900 m elevation (Myers-Smith 2011).

On Qikiqtaruk, both experiments were set up in front of a window in an unheated warehouse. The average daily minimum, mean and maximum temperatures during the 10 days spanning both experiments were 7.4/12.0/18.0 °C, respectively, measured by iButton Thermochron data loggers (± 1 °C, model DS1921G-F5, Dallas Semiconductor Corporation, Dallas, TX, USA) with hourly recording. In Kluane, the allelopathy experiment was set up in a laboratory (average daily minimum, mean and maximum temperatures were 18.9/21.0/24.1 °C, respectively, measured as above over 9 days). A scarification experiment was initially also set up in Kluane, but coincided with a week of unusually high temperatures. The laboratory not being climate controlled, this resulted in the seedlings drying out and dying within 48 h after emerging, and the experiment was discontinued.

Study species

Salix pulchra and *Salix richardsonii* are willow species with an erect growth form. They are widespread in the Western Arctic and dominant species at our study sites; on Qikiqtaruk, they approximately reach their northern distribution limit (Argus 2007). *Salix arctica* is a dwarf willow widely distributed in the circumpolar region all the way up to the High Arctic, over 80°N (Argus 2007). It is a dominant species on Qikiqtaruk and could therefore greatly contribute to woody plant encroachment there. However, germination of this species is highly variable both spatially and temporally, and thus expansion could be limited by regeneration failures (Boulanger-Lapointe et al. 2016). This is why we included this species in the experiment despite it being far from its leading range edge. Willows are capable of spreading clonally, but while this certainly contributes to the infilling of existing populations (Myers-Smith et al. 2011), colonisation of new sites in a range shift context requires establishment from seed. Willows tend to be early-successional plants characterised by fast growth rates (Bret-Harte et al. 2002) and the production of great numbers of small, wind-dispersed seeds that can recolonize sites rapidly after disturbances (Brinkman 1974; Forbes et al. 2001).

Vaccinium uliginosum, a blueberry, is an ericaceous deciduous dwarf shrub known to have allelopathic effects on conifer seeds (Dufour Tremblay et al. 2012). *Cassiope tetragona* is an ericaceous evergreen dwarf shrub for which no allelopathic effects have yet been reported; however, it has been shown to interfere with the growth of Arctic



Allelopathy experiments

Shrub species	Treatment
Salix pulchra	Control
Salix richardsonii	*Cassiope tetragona*
Salix arctica	

Shrub species	Treatment
Salix pulchra	Control
Salix richardsonii	*Cassiope tetragona*
	Vaccinium uliginosum

Scarification experiment

Shrub species	Treatment
Salix pulchra	Scarified
	Moss
	Graminoid
	Forb

Fig. 2 Location of the two field sites in the Western Canadian Arctic and details of the experiments carried out at each research station using seeds from local shrubline tundra sites

graminoids (Michelsen et al. 2012). These dwarf shrubs typically come in later during succession (Lambert 1972) and have higher investments in reproduction and defences.

Scarification experiment

Our first objective was to test whether seedbed type influenced willow germination. The four seedbeds tested were (1) moss-dominated; (2) grass-dominated; (3) forb-dominated; and (4) scarified. For each treatment, we collected four discs (10 cm diameter, ca. 3 cm deep) of undisturbed tundra vegetation on Qikiqtaruk. Cover of the target vegetation type for the moss, grass and forb treatments was over 90% on each disc. For the scarified discs, we randomly collected discs with a mixed cover of grasses and forbs and carefully stripped them of all above-ground vegetation to expose the organic soil. Samples were collected in a ca. 50-m-by-50-m plot on a south-facing ridge belonging to the Komakuk vegetation type (Smith et al. 1989) and brought back to the warehouse.

Catkins of *Salix pulchra* were collected at a nearby site. Only ripe catkins were collected, and no more than 10 catkins per individual shrub were harvested to reduce genetic bias. Seeds were all pooled together before sowing on the discs.

On all discs, 36 seeds were sown in a six-by-six arrangement, with a toothpick marking the emplacement of each row to facilitate monitoring. The discs were misted twice daily with a spray-bottle containing distilled water to prevent seeds from drying. Emergence was monitored daily until no further germination occurred.

Allelopathy experiment

Our second objective was to test whether willow seeds were vulnerable to potentially toxic compounds leached from the leaves of two ericaceous dwarf shrubs. Allelopathy experiments were run at both field sites (Fig. 2). In the alpine shrub tundra of Printer's Pass (Ruby Range mountains, Kluane), we collected ca. 200 ripe catkins of *S. pulchra* and *S. richardsonii* following the sampling protocol described in the previous section. Around 100 g of fresh leaves of *Vaccinium uliginosum* and *Cassiope tetragona* were collected in the same area. Leachates were prepared by soaking 75 g of leaves in 500 mL of distilled water for 24 h to obtain a 15% solution (Dufour Tremblay et al. 2012).

On Qikiqtaruk, around 150 catkins were collected for *S. pulchra*, *S. richardsonii* and *S. arctica*. As *V. uliginosum* is not locally abundant, we only used a leachate of *C. tetragona* in this experiment. The leaf extract was prepared as described above.

Seeds were sown on filter paper in 9-mm Petri dishes (25 seeds per dish in Kluane; 50 seeds per dish on Herschel Island). At the start of the experiment, 3 mL of either leaf extract (*C. tetragona* or *V. uliginosum*) or distilled water (control treatment) were put in every dish. We added 2 mL of the same treatments the following day, then kept all dishes moist as needed with distilled water for the duration of the experiment. In Kluane, we set up eight replicate dishes of the factorial design (all combinations of species and treatments). On Qikiqtaruk, we set up four replicate dishes. The dishes were spatially randomised and rotated daily to avoid spatial effects. We monitored emergence daily until no further germination occurred.

Statistical analyses

Analyses were conducted using generalised linear models with a binomial distribution (logit link function) to account for germination rates being constrained between 0 and 1. Germination rates were not zero-inflated. For the scarification experiment, which was conducted with a single species, we used seedbed as the explanatory variable. For the allelopathy experiments, we ran separate models for the two study locations, using treatment (control, *V. uliginosum* extract, *C. tetragona* extract) and willow species as interacting explanatory variables. When means differed significantly among treatments, we conducted Tukey's post hoc tests using the "lsmeans" package. All analyses were conducted in R v. 3.3.2 (R Core Team 2016).

Results

Scarification experiment

Emergence of *Salix pulchra* was significantly higher on scarified ground than on forb- or grass-dominated ground, and intermediate on moss-covered ground (Fig. 3; Table 1A). Germination started within 24 h of sowing and ceased after 4 days.

Allelopathy experiment

On Qikiqtaruk (Fig. 4a; Table 1B), *S. pulchra* and *S. richardsonii* had high and similar germination rates, but the germination of *S. richardsonii* was reduced in the presence of *C. tetragona* leaf extract, while that of *S. pulchra* was not. *Salix arctica* experienced much lower germination that was not affected by the allelopathic treatment.

In Kluane (Fig. 4b; Table 1C), the germination of *S. richardsonii* was slightly lower than that of *S. pulchra,* and like on Qikiqtaruk, was reduced in the presence of *C. tetragona* leaf extract compared to the control. Extract of *V. uliginosum* had no effect on either *S. richardsonii* or *S. pulchra*.

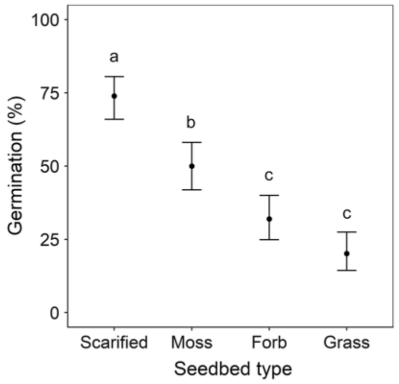


Fig. 3 Germination of *Salix pulchra* presenting higher on scarified ground than on forb- or grass-covered ground, and intermediate on moss. Dots represent binomial model estimates (error bars are 95% confidence intervals), and letters indicate significant differences between treatments, as identified by Tukey's post hoc test

Discussion

In this study, we demonstrated that willow seeds preferentially germinated on bare ground. Moreover, our experiments revealed a potential vulnerability of some shrub species to chemical interference from ericaceous dwarf shrubs. Together, these findings have implications for expected range shifts and community composition changes under climate warming. Our results suggest that the community already in place above the shrubline may physically or chemically impede shrub recruitment. Biotic interactions are likely to shape future vegetation trajectories in the tundra, and it is critical to gain a better understanding of the mechanisms involved to predict more accurately future range expansion of shrub species.

Scarification experiment

Willows are pioneer species in boreal and tundra succession, producing a large number of small seeds that can be wind-dispersed over long distances and rapidly colonise disturbed sites (Walker et al. 1986). Our dedicated germination study found that emergence of willow seedlings was higher on bare ground than on ground covered by herbaceous vegetation, supporting succession theory. These results also agree with observations of higher abundance and performance of shrubs on ground disturbed by thermokarst processes (Lantz et al. 2009). More widely, our results align with treeline studies that have shown increased conifer recruitment on exposed mineral soil (Dufour Tremblay and Boudreau 2011). Few similar experiments have been conducted with shrub species, but our results are in accordance with those of Graae et al.

Table 1 Model outputs from binomial logistic regressions to explain germination of tundra willows as a function of (A) ground layer composition and (B–C) allelopathic effects of ericaceous dwarf shrubs at two field sites

	Estimate	SE	*z* value	*p*
(A) Scarification—Qikiqtaruk				
Scarified (intercept)	1.04	0.19	5.37	< 0.0001
Moss	−1.04	0.26	−4.07	< 0.0001
Forb	−1.80	0.26	−6.82	< 0.0001
Grass	−2.42	0.28	−8.51	< 0.0001
Contrasts			*z ratio*	
Scarified—moss	1.04	0.26	4.07	**0.0003**
Scarified—forb	1.80	0.26	6.82	< **0.0001**
Scarified—grass	2.42	0.28	8.51	< **0.0001**
Moss—forb	0.76	0.24	3.10	**0.0106**
Moss—grass	1.38	0.27	5.17	< **0.0001**
Forb—grass	0.62	0.27	2.27	0.1058
Sample size: 16				
Null deviance: 156.15 on 15 df				
Residual deviance: 58.21 on 12 df				
(B) Allelopathy—Qikiqtaruk				
Intercept	0.87	0.16	5.62	< 0.0001
TreatmentCAS	0.31	0.23	1.36	0.1747
SpeciesSR	−0.02	0.22	−0.11	0.9130
SpeciesSA	−2.23	0.23	−9.52	< 0.0001
TreatmentCAS:SpeciesSR	−0.94	0.31	−3.02	0.0025
TreatmentCAS:SpeciesSA	−0.16	0.33	−0.49	0.6263
Contrasts			*z ratio*	
SP: C– CAS	−0.31	0.23	−1.36	0.1747
SR: C–CAS	0.62	0.21	2.98	**0.0028**
SA: C–CAS	−0.15	0.24	−0.61	0.5447
Sample size: 24				
Null deviance: 298.185 on 23 df				
Residual deviance: 36.565 on 18 df				
(C) Allelopathy—Kluane				
Intercept	0.10	0.16	6.25	< 0.0001
TreatmentCAS	−0.26	0.22	−1.20	0.2294
TreatmentVAC	−0.46	0.21	−2.14	0.0326
SpeciesSR	−0.85	0.21	−4.01	< 0.0001
TreatmentCAS:SpeciesS R	−0.24	0.30	−0.81	0.4200
TreatmentVAC:SpeciesSR	0.12	0.30	0.41	0.6806
Contrasts			*z ratio*	
SP: C–CAS	0.50	0.22	1.20	0.4521
SP: C–VAC	0.46	0.22	2.14	0.0825
SP: CAS–VAS	−0.16	0.21	0.95	0.6120
SR: C–CAS	0.50	0.20	2.50	**0.0335**
SR: C–VAC	0.34	0.20	1.70	0.2059
SR: CAS–VAC	−0.16	0.20	−0.81	0.6982
Sample size: 48				
Null deviance: 110.254 on 47 df				
Residual deviance: 42.834 on 42 df				

Species codes are *SP Salix pulchra*, SR: *Salix richardsonii*, *SA Salix arctica*. Allelopathic treatments are coded *C* for control, *CAS* for *Cassiope tetragona* leachate, and *VAC* for *Vaccinium uliginosum* leachate. For each model, pairwise post hoc contrasts are presented using Tukey's post hoc test, and significant contrasts are bolded

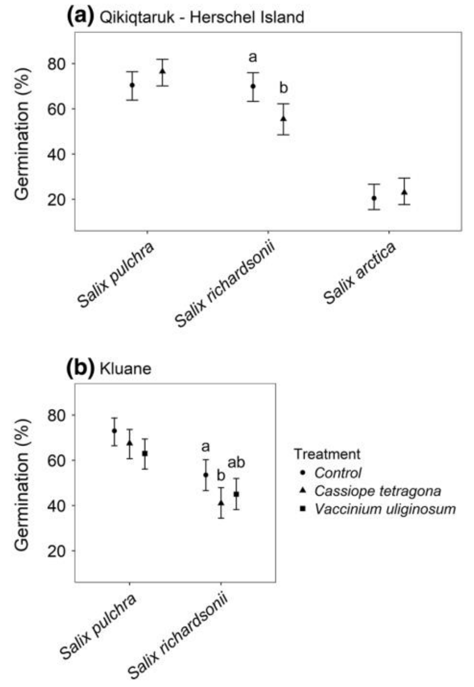


Fig. 4 Effect of leaf extracts from *Cassiope tetragona* and *Vaccinium uliginosum* on seed germination of three willow species from **a** Qikiqtaruk and **b** Kluane. Dots represent binomial model estimates (error bars are confidence intervals), and letters indicate significant differences between treatments, as identified by Tukey's post hoc test

(2011), who found consistently higher germination of tundra species on bare ground.

Willows typically produce short-lived seeds that must germinate within a few days of ripening (Bliss 1958; Brinkman 1974). It therefore seems likely that when seeds are dispersed on dense, tall vegetation, they cannot always reach the ground and meet their moisture requirement for germinating, and rapidly lose viability. On the contrary, seeds that fall onto bare ground can germinate within a day, as we observed during this study. We found that the moss seedbed had intermediate rates of germination, which could be due to high water retention capacity compared to herbaceous vegetation. In stressful environments, mosses can facilitate recruitment by sheltering seedlings from herbivores and temperature extremes (Wheeler et al. 2011; Lett et al. 2017).

We cannot generalise our observations to all tundra shrub species, as it is likely that species-specific traits like seed longevity play an important role in these interactions. Nonetheless, our results suggest that vegetation above the shrubline might act as a physical barrier for establishment of some dominant tundra shrub species. In a context of vegetation encroachment and decrease in bare ground at our field site (Myers-Smith et al. in review), and in the tundra biome in general (Elmendorf et al. 2012), there might be limited opportunities for shrubline advance. This could lead to an increasing reliance on disturbance for regeneration (Lantz et al. 2010; Frost et al. 2013) as optimal recruitment microsites become sparser.

Allelopathy experiment

At both sites, the germination of *Salix richardsonii* was reduced when seeds were exposed to *C. tetragona* leaf extracts. In addition to producing allelopathic compounds, ericaceous species can change soil nutrient status and chemical properties (Bloom and Mallik 2006). Previously, negative effects of *C. tetragona* on the growth of graminoids have been explained by the labile carbon in the extracts promoting nutrient uptake by soil biota, thereby depleting resources for plants (Michelsen et al. 1995). As our seeds were placed directly on sterile filter paper without the possibility of third-party interactions, our results suggest that the leaves of *C. tetragona* may contain allelopathic compounds affecting the germination of some species. Alternatively, other chemical properties of the solution, such as reduced pH, could have affected germination. Edaphic factors are important in controlling shrub distribution: for instance, *Salix pulchra* is more tolerant to acidic soils than *S. richardsonii* (Swanson 2015). More work will be needed to validate our findings and identify the precise mechanism of interference. The very low germination of *Salix arctica* is unsurprising: unlike the other two species, it is a late disperser with conditionally dormant seeds (Densmore and Zasada 1983).

All three of our focal research species are found at the shrubline in the Kluane region (Myers-Smith and Hik 2017) and are widely distributed on Qikiqtaruk (Smith et al. 1989), yet they each have different habitat preferences. Interestingly, *Salix richardsonii* is spatially segregated from *C. tetragona* on Qikiqtaruk, the former being typically associated with other canopy-forming willows, and the latter mostly found with other evergreen shrubs and *Betula nana* in the Komakuk vegetation type characterised by soil disturbance from freeze–thaw processes (Smith et al. 1989). These habitat preferences likely reflect the different tolerance and plasticity of willow species to soil characteristics and other environmental and succession-related characteristics: throughout the Yukon Territory, *Salix richardsonii* is most commonly found on alluvial sites or floodplains, while *Salix pulchra* has a wider range of habitats (Cody 1996). The higher environmental plasticity of *S. pulchra* might be partially linked to the apparent absence of vulnerability to chemical interference from common ericaceous dwarf shrubs, although further studies will be required to test this specifically.

The fact that only one out of three willow species seemed vulnerable to allelopathy raises the issue of replication in this study and the question of the specificity of biotic interactions. Species-specific allelopathic responses have been reported at the treeline, with for instance black spruce, but not larch, being affected by ericaceous species (Dufour Tremblay et al. 2012). However, the scarcity of similar studies and low sample sizes make it difficult to rule out experimental artefacts and identify general patterns. To validate our findings and make them more generally applicable to the tundra biome, we call for more tests of allelopathic effects with these and other species in the Arctic region.

Biotic filters for shrubline expansion

While shrub encroachment in the tundra biome has received considerable attention, shrublines are understudied, with only six studies focusing specifically on range shifts (reviewed in Myers-Smith and Hik 2017). A study of 14 elevational shrublines in the Kluane region, one of our field sites, consistently found younger willows at higher elevations, a pattern suggestive of climate-driven range expansion (Myers-Smith and Hik 2017). However, we still have a poor understanding of the local factors that may mitigate the speed of shrubline advances. Our results and the lack of comparable studies highlight the need to better understand plant–plant interactions within tundra communities. Standardised replication of our experiments at more sites and with a more diverse range of tundra species could help determine whether biotic interactions are likely to be a major constraint to shrub expansion above the shrubline.

The biotic interactions investigated in this study, i.e. interaction with ground cover and allelopathy, are only a subset of all the possible interactions that may affect seedling establishment above the shrubline. Notably, below-ground interactions in the tundra are still poorly understood, and it is unclear whether some positive associations, like those arising from mycorrhizal symbionts and other interactions with soil microbiota (Grau et al. 2010; Pellissier et al. 2013; Sedlacek et al. 2014), may balance out negative interactions like allelopathy. The growth and survival of seedlings could be positively or negatively affected by the presence of taller plants through nurse effects or competition, respectively: the direction and importance of these interactions can even vary across life-stages (e.g. seed–seedling conflicts; Cranston and Hermanutz, 2013).

Overall, the realised extent of range shifts depends not only on climate suitability but also on biotic interactions within the new community (HilleRisLambers et al. 2013). Therefore, range shifts of Arctic and alpine shrublines will almost certainly be slower than predicted by climate envelope models. The species-specific nature of biotic interactions may act as an ecological filter where the advance of some species may be limited or prevented by the presence of competitors, allelopathic plants, or selective herbivores. Thus, it is unlikely that tundra shrubline range shifts will occur as intact plant communities moving to higher elevations or latitudes; instead, filtering will occur, with biotic interactions leading to different species assemblages forming beyond the current range limit.

Conclusion

Climate change is altering ecosystem boundaries, and a growing research focus is to achieve the integration of biotic interactions into predictive models of climate-driven range shifts. While treelines have received extensive attention and the effects of a wider range of plant–plant interactions on recruitment are starting to be better understood, it is unclear whether those mechanisms have the same importance at high-elevation and high-latitude shrublines. Our two simple experiments showed that the effects of two types of plant–plant interactions, namely seedbed type and allelopathy, are also relevant processes partly limiting germination at and above Arctic and alpine shrublines. Acknowledging the high spatio-temporal variability in seed production and viability in northern environments, we call for replication of these types of studies to gain a better understanding of the constraints acting upon regeneration in the tundra biome.

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Author Contributions S.A.B. designed the study with inputs from all authors. S.A.B. and I.M.S. conducted the experiments. S.A.B. analysed the data. S.A.B. wrote the manuscript with inputs from all authors.

Compliance with Ethical Standards

Conflict of interest The authors declare that they have no conflict of interest.

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Chapter 8 Discussion

8.1 Summary of main findings

The aims of this thesis were to quantify the variation in the climate sensitivity of shrub growth, and to attribute this variation to environmental and ecological factors. My findings reveal the complexity and heterogeneity of shrub growth responses to climate change at sites across the Canadian Arctic. This thesis both proposes mechanistic relationships and raises further questions about which factors best explain the high variability in the climate sensitivity of shrub growth across a range of spatial and biological scales. My main findings were:

1. Temperature versus growing season length differ as controls of shrub growth across sites with contrasting climate regimes and greening trajectories. The sensitivity of shrub growth to these drivers is often low and decoupled within individuals (**Chapter 3**). Tundra plant communities may therefore follow divergent trajectories depending on the main bioclimatic controls prevailing at each site and how they change over time.
2. Radial growth data collected at the root collar of tundra shrubs shows greater climate sensitivity than above-ground stem growth (**Appendix I**). This has implications for future sampling protocols to facilitate comparisons among studies.
3. Plant size does not explain the high inter-individual variability in climate sensitivity among tundra shrubs, challenging the assumption that taller shrubs are more responsive to warming. Allometric relationships between canopy height and diameter are stronger around the southern edge of the tundra biome but lose explanatory power at higher latitudes (**Chapter 4**). Allometric equations developed from boreal or low-Arctic shrubs should therefore not be used to predict changes in biomass and canopy structure across the whole biome.
4. Shrubs in boreal forests experience higher growth rates, but are less sensitive to summer temperatures compared to alpine shrubs (**Chapter 5**). The expansion of shrub species will likely be much slower in boreal ecosystems than in alpine or Arctic tundra because of competition with tree species.
5. Radial growth of alpine tundra shrubs was not influenced by a decrease in aboveground competition when compared to intact shrub patches (**Chapter 5**).

6. Shrubs with nearer or larger neighbours do not differ systematically in their growth rates or climate sensitivity compared to more isolated shrubs (**Chapter 6**). Together with the previous finding, this suggests that shrub expansion in tundra ecosystems is not currently strongly limited by competition among canopy-forming shrubs.
7. Spatial patterns of shrub distribution reveal a more important structuring effect of competition at more productive sites (**Chapter 6**). The absence of a direct effect of competition on the climate sensitivity of shrub growth does not mean that competition is absent from tundra ecosystems.
8. Plant-plant interactions beyond competition can limit the germination of canopy-forming willow species, including potential allelopathic effects of evergreen dwarf shrubs (**Chapter 7**). This may restrict or slow down climate-driven range shifts of tall shrubs into dwarf-shrub tundra.

These findings demonstrate the importance and interplay of physiological, ecological and environmental factors in determining the climate sensitivity of shrub growth (**Figure 8-1**). The strongest patterns were found at the intra-individual scale, where the root collar of shrubs displays a stronger climatic signal than stems (**Appendix I**), and at the regional scale, where shrubs beyond the treeline are far more sensitive to temperature than boreal shrubs (**Chapter 5**). My methodological approach, using indiscriminate sampling, highlighted the great variability in individual climate sensitivity within plots. This heterogeneity in growth responses was not conclusively linked to plant size or competitive environment. Shrub life histories and individual determinants of growth responses will need to be better understood if we are to estimate population-level climate sensitivity more accurately.

In the following section, I discuss the contributions of this thesis in the wider ecological context of vegetation change in a warming Arctic. I then highlight challenges in measuring and attributing the climate sensitivity of shrub growth to ecological factors, make recommendations for dendroecological practices, and highlight some research priorities to improve future projections of vegetation change in the tundra biome.

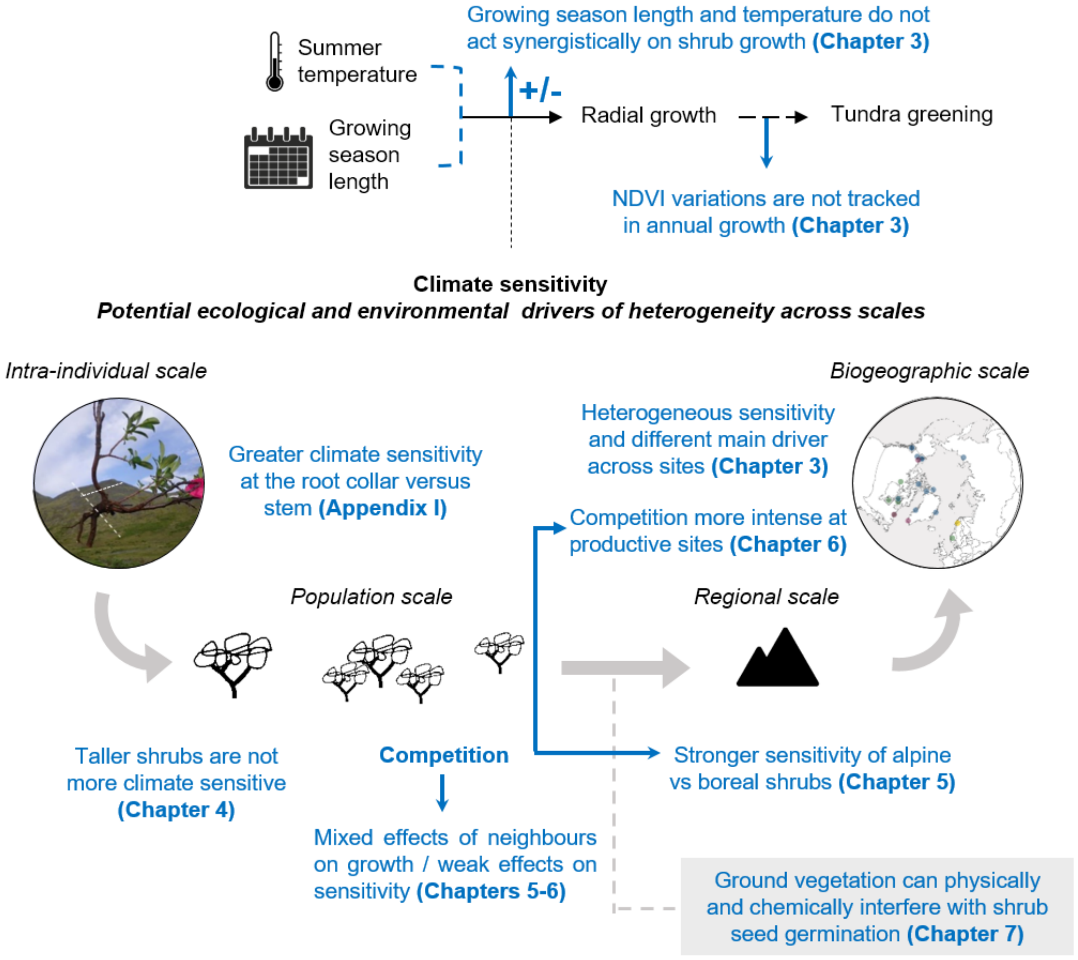

Figure 8-1 *Main findings of this thesis in the context of the initial framework for investigating determinants of the variation in shrub responses to climate change.*

8.2 Synthesis

8.2.1 Longer, warmer, greener?

My finding that shrub growth at different sites across Northern Canada responds to growing season length and temperature in variable, and sometimes opposite ways (**Chapter 3**) demonstrates the need for caution when making assumptions about future growth responses under warming. The western Arctic sites were more sensitive to longer (Qikiqtaruk) and warmer (Kluane) growing seasons than the eastern sites. Site-specific characteristics like soil moisture (Berner et al. 2013; Ackerman et al. 2011), genetic differences and local adaptation in populations (Bjorkman et al. 2017), and the traits of the dominant vegetation may all dictate to some degree how vegetation will respond to new conditions.

8.2.2 Bigger is not better

Chapter 4 demonstrated that the broad pattern of greater climate sensitivity for species with taller maximum canopy heights (Myers-Smith et al. 2015a) does not hold at the individual level, and cannot explain the different responses of shrubs to temperature within a site, despite previous assumptions (Ackerman et al. 2018). This highlights the need to identify at which scale ecological and environmental factors operate if we want to accurately predict biome-wide changes in the tundra biome while accounting for site- and species-specific responses.

Allometric equations are empirical relationships between plant dimensions that allow estimations of biomass or other ecological processes at the site level. These relationships are often site- and species-specific (Au et Tardif 2007; Berner et al. 2015), and **Chapter 4** suggests that they become weak and unreliable at high latitudes of the tundra biome. This is further complicated by the fact that various growth dimensions, such as primary and secondary growth, do not necessarily respond in the same way to global change drivers (Bret-Harte et al. 2002), and, perhaps as a result, do not scale predictably with one another (**Chapter 4**). The secondary growth of woody shrubs contributes considerably to tundra primary production (Shaver 1986) and, given the longevity of Arctic shrub species (typically 50 – 200 years), has important implications for carbon balance at high latitudes. Understanding the ecological controls of primary and secondary growth and potential trade-offs between them will be key to modelling future tundra carbon balance and productivity.

8.2.3 Competition with trees, but not with shrubs, reduces the climate sensitivity of shrub growth

Shrub expansion is occurring throughout the circumpolar region, including boreal, alpine and Arctic environments (Danby et al. 2011; Myers-Smith et al. 2011; Naito and Cairns 2011; Elmendorf et al. 2012a; Formica et al. 2014; Frost and Epstein 2014; Grabowski 2015; Dial et al. 2016). **Chapter 5** demonstrated that shrubs growing in boreal forests of the Yukon Territory have higher absolute growth rates but a climate sensitivity three times lower than shrubs growing on adjacent mountain slopes. Climate-driven shrub expansion may therefore occur at a slower pace in the boreal biome due to competitive interactions with trees.

In the tundra, where tall deciduous shrubs are the canopy-forming species, competition did not seem to have a strong effect on climate sensitivity. However, my findings did indicate an effect of competition on overall performance – as measured by size-distance relationships (Pielou 1962, Briones et al. 1996) – which was stronger in more productive environments. This discrepancy between overall plant size and growth-ring data highlights once more the necessity of better understanding how primary and secondary growth scale with one another (**Figure 8-1**; Bret-Harte et al. 2002).

With continued shrub expansion across the tundra biome, competition – and other types of plant-plant interactions – might be amplified in the future, especially in the mid-latitudes of the Arctic where tall shrubs are most sensitive to warming (Myers-Smith et al. 2015a). A combination of correlative and experimental tests for a range of plant-plant interactions across environment types and species would be a useful step towards explain population-level variations in climate sensitivity and predicting future community structure under novel conditions.

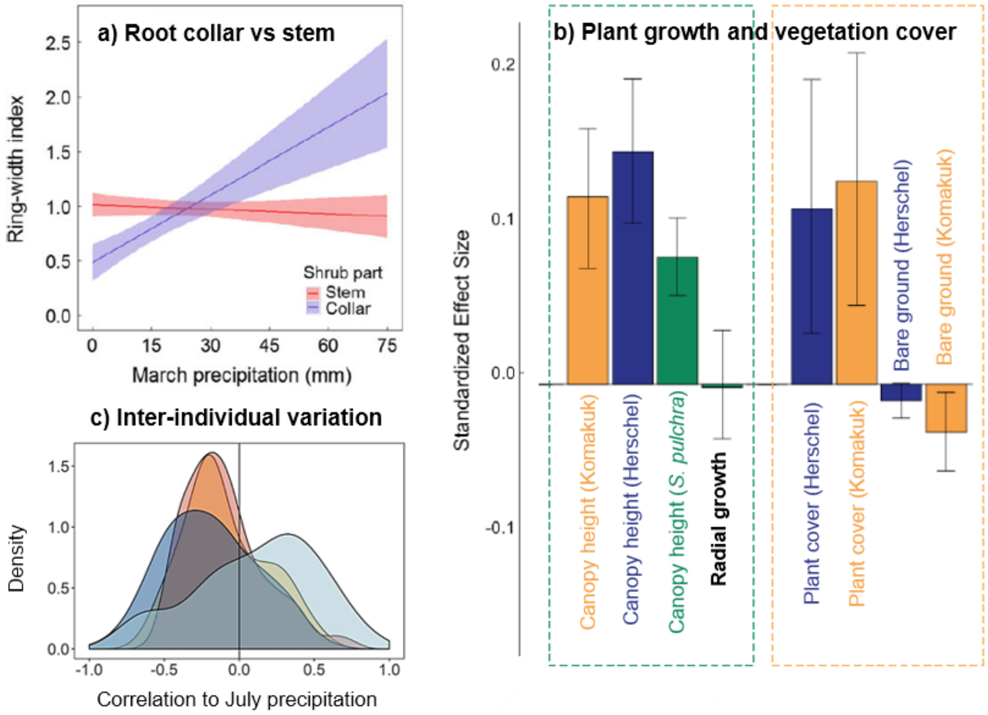

Figure 8-2 *Heterogeneity of the climate sensitivity of shrub growth (a) when measured from different plant parts (Appendix I); (b) compared to other temporal trends of vegetation change at a long-term monitoring field site (Myers-Smith et al. in press); (c) among individuals (spread of the distributions) within sites and among sites (different density curves; Chapter 3).*

8.3 Reconciling different indicators of vegetation change: challenges and limitations

This thesis, like the wider literature, relies predominantly on plot-scale data from a number of sites to make predictions about pan-Arctic environmental change. Various lines of evidence, accumulating over time and space, provide valuable insights into how tundra ecosystems have changed in the last half-century (**Chapter 1**). However, measures of vegetation change all have their respective spatio-temporal limitations, and reflect different underlying processes that do not necessarily align with each other (**Figure 8-2**).

8.3.1 Spatial limitations

The dendroecological data at the heart of this thesis were collected within small plots at four sites representing different growing conditions in the tundra biome. They highlighted the strong variability of growth trajectories among individuals of a same population, an important consideration for future sampling methods. But the strong differences in average climate sensitivity across sites also point at the need of understanding controls of climate sensitivity across large geographic areas, which in the case of dendrochronological data may be difficult to achieve given the time-consuming nature of sample processing and data acquisition.

Remote sensing products, such as the NDVI data used in **Chapter 3**, have gained in popularity as they capture vegetation patterns over large areas, but linking these to specific site-level changes in the tundra remains a challenge (Raynolds et al. 2013; Frost et al. 2014). The rise of new technologies such as drones now allows to capture imagery at the landscape scale, which may in time help to resolve inconsistencies between plot-scale observations and pixel values covering hundreds or thousands of square meters (Anderson and Gaston 2013; Assmann et al. 2018).

8.3.2 Temporal limitations

Most vegetation change observations or experiments at the plot scale are only made over a short period of time, long-term protocols being rarer and confined to a few well-established research stations (e.g. Hobbie et al. 2017; Myers-Smith et al. in press). Dendroecology is a useful source of historical data, as woody plants may record decades or even centuries of environmental conditions in their growth rings, with an annual resolution. The drawback of this remarkable feature is that growth series need to be rigorously cross-dated, i.e. years of growth need to be assigned to calendar years with high certainty, for any analysis to be valid. This is a time-consuming process, complicated by the low and irregular growth of tundra shrubs (**Chapter 2**). This therefore creates a very strong data quality versus quantity dilemma: it is nearly impossible logistically to collect dendroecological data with enough replication to cover large geographic areas, all the while conducting rigorous cross-dating on the resulting series.

Additionally, there is also an important seasonal bias in our understanding of vegetation change, which relies mostly on measures made in the summer season when field sites are easily accessible. However, a growing number of studies point to the importance of winter (Bokhorst et al. 2012b) and shoulder seasons (Ernakovitch et al. 2014; Gallinat et al. 2015) in driving patterns of vegetation change and associated feedbacks, as well as the existence of “teleconnections” between seemingly remote elements of the Arctic system such as sea ice and terrestrial production (Macias-Fauria et al. 2012).

8.3.3 Representation of biological processes

The results of **Chapter 3** challenged the assumption that higher growth rates in tundra shrubs are associated to landscape-scale greenness. The mismatch between annual NDVI and growth ring measurements both points to a potential caveat of using dendroecology as a measure of productivity, and reinforces the need to bridge the gap between satellite-acquired data and ground-based observations. Even recent remote sensing advances, which allow sub-kilometre estimates of vegetation trajectories, do not necessarily match on-the-ground variations in shrub growth as they are sensitive to non-vegetation related factors such as soil moisture (Raynolds and Walker 2016). On the other hand, once shrub canopies are in place, radial growth is not necessarily representative of canopy growth and leaf production (Ropars et al. 2015). This thesis and related work (**Appendix I**; Myers-Smith et al. in press) show that dendroecological data are sensitive to sampling methods and do not necessarily vary concurrently with other facets of vegetation change (**Figure 8-2**). This does not mean that either dendroecological or remote sensing observations are “wrong”, but highlights a critical gap in our mechanistic understanding of how physiological effects of temperature on shrub growth translate and scale up to landscape-level changes in vegetation cover.

8.4 Recommendations and future research priorities

8.4.1 Shifting practices in dendroecology

Dendroecology is a powerful tool for measuring growth responses to a variety of environmental and ecological factors (Schweingruber et al. 2013; Büntgen et al. 2015; Grabowski 2015; Myers-Smith et al. 2015a, Morrissette-Boileau et al. 2018) and has provided some of the most convincing evidence base for shrub expansion in the tundra (IPCC 2014). However, as established above, there is an increasing realisation that annual wood formation does not necessarily correlate to growth dimensions (**Chapter 4**; Myers-Smith et al. in press) or remotely sensed observations of vegetation (**Chapter 3**, Ropars et al. 2015). The development of high-quality, well-replicated chronologies is further complicated by the complex morphology of shrub growth (**Appendix I**; Ropars et al. 2017; Shetti et al. 2018) and the strong landscape heterogeneity across tundra environments, and therefore care is needed when collecting and interpreting dendroecological data.

Sampling populations indiscriminately, rather than selecting isolated individuals, unsurprisingly yields low inter-individual agreement in growth patterns within a site (**Chapter 2**) compared to traditional dendrochronological methods seeking to maximise the signal-to-noise ratio (Pilcher and Gray 1982). This heterogeneity in growth patterns testifies to the varied life histories of plants within a site and, arguably, better represents the potential of a population to respond to climate change in the presence of multiple other constraints (Avanzi et al. 2019). Dendroecological sampling should always be designed with clear research questions in mind; for predicting climate-driven shrub expansion, selective sampling might lead to overestimations. Given that whole-plot or random sampling introduce much variability in the magnitude and direction of climate-growth relationships measured at a site (**Figure 8-1**), clustering approaches separating “positive responders” and “negative responders” before modelling climate sensitivity as a function of environmental or ecological factors may provide a fuller picture of the different mechanisms controlling shrub responses to climate (Wilmking et al. 2004).

A new, promising approach to understanding population dynamics under a changing climate is to forego cross-dating entirely, and instead use data aggregation techniques to look at responses over coarser time periods. This approach is of course ill-suited to studies requiring precise annual resolution (e.g. climatic reconstructions), but can be justified and beneficial for ecological studies (Büntgen 2019). First, dispensing with cross-dating (while still conducting careful ring-counting) allows to develop a much greater number of time series, enabling higher spatial replication at a lower processing time and cost (Büntgen et al. 2015, Myers-Smith et al. 2015b). Second, many biological responses to climate change, such as range shifts or increases in reproductive success, exhibit time lags or occur over several years (Danby and Hik 2007b; Ash et al. 2016). To measure the climate sensitivity of these processes, it may appropriate, and even desirable, to bin observations into classes of a few years up to a decade. The use of low-pass filters has successfully allowed the reconstruction of population dynamics and recruitment pulses at decadal scales in relation to periods of warming (Büntgen et al. 2015, 2018).

In short, research questions and the processes they are concerned with should always govern dendroecological sampling. Relaxing some of the traditional principles for series development (i.e. not only sampling isolated, “ideal” specimens, and not applying cross-dating techniques over large numbers of difficult samples) may overcome some of the limitations currently associated with dendroecology and lead to new advances in the field.

8.4.2 Plant-plant interactions in a warming tundra

This thesis examined mainly the effect of competition within one plant functional type (**Chapter 5**; **Chapter 6**), and the potential physical and chemical interference of ground vegetation with shrub germination (**Chapter 7**). There are many more biotic interactions at play within tundra ecosystems, and the balance between positive and negative interactions is difficult to quantify. Species interactions have the power to either constrain or promote climate-driven vegetation change (Gilman et al. 2010; Hellmann et al. 2012; HilleRisLambers et al. 2013), and in turn will be affected by the consequences of warming on biotic and abiotic conditions, including changes in nutrient availability and new species invading the community (Heegaard and Vandvik 2004; Klanderud 2005; Tylianakis et al. 2008). Given the capacity of biotic interactions to shape ecosystem structure and processes beyond what can be solely expected from climate (Brooker et al. 2007; Hellmann et al. 2012; Mod et al. 2014), it is crucial to understand the underlying mechanisms, not only in isolation, but considering their interactions with a changing environment.

Research on negative interactions such as allelopathy (Nilsson 1994, Dufour Tremblay et al. 2012b; Angers-Blondin et al. 2018) and on positive interactions such as mycorrhizal associations (Deslippe et al. 2011; Hewitt et al. 2016) has revealed highly species-specific associations. A better quantification of the extent and importance of these processes for whole-community dynamics would involve distributed experiments across a range of species and environmental types. Some of these less-documented interactions involve soil chemistry, microbial communities and below-ground root networks, all of which can be challenging to measure. Yet, the below-ground component of plant-plant interactions is critical to understanding community structure and processes (Montgomery et al. 2010). This introduces the last, and perhaps the most important research priority to improve our understanding of vegetation responses to climate change.

8.4.3 Towards a whole-plant perspective of vegetation change

With up to 80% of tundra biomass located below-ground (Iversen et al. 2015), identifying and quantifying the drivers of below-ground growth is crucial to predicting carbon stocks and vegetation climate feedbacks (Norby and Jackson 2000; Smithwick et al. 2014). Determinants of above- and below-ground growth can be decoupled and asynchronous: for instance, the growing seasons for roots in Arctic soils can be 50% longer than the above-ground growing season (Blume-Werry et al. 2016). Therefore, to quantify whole-plant growth responses to climate, dendroecological studies should aim to collect data at the root collar when possible (**Appendix I**; Ropars et al. 2017), as root collar growth integrates signals from stems and roots. Understanding resource allocations to above- versus below-ground components and to primary versus secondary growth (**Chapter 4**) would be a first step towards predicting biomass changes in response to warming. However, dedicated rhizotron experiments would provide a better mechanistic test of the effects of global change drivers on root productivity (Norby and Jackson 2000; Blume-Werry et al. 2016). Below-ground dynamics are all the more important in the context of rapidly thawing permafrost across the tundra biome (Anisimov and Reneva 2006; Burn and Zhang 2009; Schuur et al. 2015), which may release an hitherto untapped nutrient supply promoting further shrub expansion (Keuper et al. 2012).

8.5 Conclusion

With projected warming of up to 11°C by 2100 (IPCC 2013), Arctic ecosystems are being rapidly pushed beyond the conditions they have experienced for the last two millennia (Kaufman et al. 2009). Widespread vegetation changes such as shrub expansion (Myers-Smith et al. 2011) testify to the plasticity and adaptability of plants to respond to a warming climate (Franks et al. 2014). However, future rates and magnitude of change will depend on the potential for adaptation and rapid evolution (Davis and Shaw 2001), species' capacity to track their climatic optimum (Brooker et al. 2007; Chen et al. 2011), and the balance and outcomes of biotic interactions, which can either accelerate or impede climate-driven vegetation shifts (Hellmann et al. 2012; HilleRisLambers et al. 2013; Tylianakis et al. 2008). My thesis explored the variation in the climate sensitivity of tundra shrubs at multiple scales to understand how some of these factors interact with climate to generate shifts in Arctic vegetation.

This thesis has demonstrated that the growth of tundra shrubs is under the control of different and not necessarily synchronised global change drivers (Chapter 3), and that the sensitivity of shrub growth to these drivers is highly heterogeneous not only among sites (Chapters 3-4) but also, significantly, within populations. In this set of studies, neither plant traits such as height (Chapter 4) nor competitive interactions with neighbours (Chapters 5-6) explained to a great extent the climate sensitivity of individual shrubs within a site. This does not mean that these factors are not important in shaping other aspects of plant community structure and dynamics (Dormann et al. 2004; Gilman et al. 2010; Bonfils et al. 2012; Bråthen and Lortie 2016), or will not play a more preponderant role in the future. With increasing vegetation cover around the circumpolar region under a warming climate, the potential for competition and other plant-plant interactions to dictate patterns of community assembly will also increase: this may especially be the case at the lower to mid-latitudes of the tundra biome where tall deciduous shrubs dominate (Myers-Smith et al. 2015a). Experimental tests of a portfolio of biotic interactions across bioclimatic gradients would be helpful in assessing to which degree interactions like mycorrhizal associations, allelopathic effects (Chapter 7), facilitation, and competition are likely to promote or limit the persistence and dominance of species under changing conditions.

In addition to the substantial inter-individual heterogeneity in the climate sensitivity of tundra shrubs, even different parts of a single plant may have different growth responses to climatic factors (Appendix I; Ropars et al. 2017; Shetti et al. 2018). These contrasting responses hint at complex resource allocation strategies and emphasise the need for standardised dendroecological protocols when comparing climate responses from multiple sites. Crucially, a better understanding of resource allocation to above- and below-ground biomass and to primary and secondary growth is needed to better quantify climate sensitivity. These components are controlled by different climate drivers (Blume-Werry et al. 2016) and feed back to ecosystem processes in many complex ways (Wookey et al. 2009; De Marco et al. 2014). Therefore, a whole-plant perspective will be necessary to predict the fate of Arctic carbon stocks (Parker et al. 2015) and potential feedbacks of vegetation to global climate and to biogeochemical cycles (Chapin et al. 2005; Sturm et al. 2005a-b).

The titles of my four main results chapters were inspired by works of literature. Like the characters in these novels, tundra shrubs are full of life, with varied life histories and distinct, sometimes temperamental personalities. The shrubs in this thesis bear witness to a half-century of rapid changes at the top of the world. Without words, but with their combined growth rings representing 13 078 shrub-years of life in the tundra, they tell a story of complex vegetation responses and uncertain future for Arctic ecosystems.

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Appendix I

Different parts, different stories: climate sensitivity of growth is stronger in root collars vs stems in tundra shrubs

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Author contributions

I participated in fieldwork for this study, analysed the data, prepared the figures and drafted the corresponding methods and results sections. I gave feedback on various versions of the manuscript and contributed to the revisions. Pascale Ropars designed the study and led the writing of the paper, Marianne Gagnon processed the samples and conducted preliminary analyses, and Esther Lévesque and Stéphane Boudreau provided comments on the manuscript.

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Different parts, different stories: climate sensitivity of growth is stronger in root collars vs. stems in tundra shrubs

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Abstract

Shrub densification has been widely reported across the circumpolar arctic and subarctic biomes in recent years. Long-term analyses based on dendrochronological techniques applied to shrubs have linked this phenomenon to climate change. However, the multi-stemmed structure of shrubs makes them difficult to sample and therefore leads to non-uniform sampling protocols among shrub ecologists, who will favor either root collars or stems to conduct dendrochronological analyses. Through a comparative study of the use of root collars and stems of *Betula glandulosa*, a common North American shrub species, we evaluated the relative sensitivity of each plant part to climate variables and assessed whether this sensitivity is consistent across three different types of environments in northwestern Québec, Canada (terrace, hilltop and snowbed). We found that root collars had greater sensitivity to climate than stems and that these differences were maintained across the three types of environments. Growth at the root collar was best explained by spring precipitation and summer temperature, whereas stem growth showed weak and inconsistent responses to climate variables. Moreover, sensitivity to climate was not consistent among plant parts, as individuals having climate-sensitive root collars did not tend to have climate-sensitive stems. These differences in sensitivity of shrub parts to climate highlight the complexity of resource allocation in multi-stemmed plants. Whereas stem initiation and growth are driven by microenvironmental variables such as light availability and competition, root collars integrate the growth of all plant parts instead, rendering them less affected by mechanisms such as competition and more responsive to signals of global change. Although further investigations are required to determine the degree to which these findings are generalizable across the tundra biome, our results indicate that consistency and caution in the choice of plant parts are a key consideration for the success of future dendroclimatological studies on shrubs.

Keywords: *Betula glandulosa*, climate sensitivity, dendrochronology, dwarf birch, shrub densification, subarctic, tundra

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Introduction

Shrubs are one of the most responsive plant functional groups to recent climate change (Elmendorf *et al.*, 2012), and their increase in abundance in tundra ecosystems has been cited as a driver of the satellite-observed greening of the Arctic (Raynolds *et al.*, 2006; Tape *et al.*, 2006; McManus *et al.*, 2012). The increase in shrub cover and abundance is widespread across northern circumpolar regions and has been recorded at both high-latitude and high-altitude sites in North America (Sturm *et al.*, 2001a; Tape *et al.*, 2006; Myers-Smith *et al.*, 2011a; Ropars & Boudreau, 2012), northern Europe (Bär *et al.*, 2008; Hallinger *et al.*, 2010) and Russia (Forbes *et al.*, 2010). Shrubs either have expanded in patch size (Sturm *et al.*, 2001a; Tape *et al.*, 2006; Ropars & Boudreau, 2012; Tremblay *et al.*, 2012), recruited in areas where they were less abundant in the past (Sturm *et al.*, 2001a; Frost *et al.*, 2013; Frost & Epstein, 2014; Büntgen *et al.*, 2015) or have increased in height (Myers-Smith *et al.*, 2011b; Paradis *et al.*, 2016). Though this increase in tundra shrubs has been attributed to recent warming in tundra ecosystems (Elmendorf *et al.*, 2012; Ropars *et al.*, 2015), the climate sensitivity of shrub growth has been demonstrated to be variable across the tundra biome (Myers-Smith *et al.*, 2015a).

Understanding how shrub growth is controlled by climate is key to predicting vegetation change and its associated impacts on ecosystem function in a warming tundra biome. In treeless ecosystems, erect shrubs

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provide structure for both plant and animal communities (Tape *et al.*, 2016) and modify important ecological processes and physical characteristics of the environment (Cushman *et al.*, 2010). In tundra regions, shrubs are expected to have complex and sometimes seasonally contrasting or species-specific effects on permafrost dynamics or soil temperature regime (Sturm *et al.*, 2001b; Blok *et al.*, 2011; Myers-Smith & Hik, 2013; Paradis *et al.*, 2016) and absorption of solar radiation (Chapin *et al.*, 2005; Williamson *et al.*, 2016). Shrubs provide important habitat and food sources for moose, caribou, ptarmigan, hare and other wildlife species (Tape *et al.*, 2010, 2016; Boelman *et al.*, 2015; Christie *et al.*, 2015), but might also reduce lichen availability in caribou winter ranges (Joly *et al.*, 2007). Since erect shrub species have a significant impact on the dynamics and physical properties of arctic and subarctic ecosystems, it is essential to better understand the factors driving their growth and rapid expansion.

Dendrochronological approaches have successfully been applied to shrub species to analyze temporal and spatial processes in fast-changing tundra ecosystems (e.g., Bär *et al.*, 2008; Forbes *et al.*, 2010; Blok *et al.*, 2011; Myers-Smith *et al.*, 2015a; Ropars *et al.*, 2015). Like trees, shrubs form annual growth rings that can be related to climate variables (e.g., Myers-Smith *et al.*, 2015a) or disturbances in ecosystem processes such as landslides (e.g., Gers *et al.*, 2001) and permafrost degradation (e.g., Gaertner-Roer *et al.*, 2013). However, the multi-stemmed growth form of shrubs has several ecological and physiological implications that may influence climate sensitivity among their different parts. For example, shrubs have the potential to allocate resources to different stems and roots depending on environmental conditions (Pajunen, 2009) and competition for light and nutrients in dense shrub patches could lead to differential stem growth within an individual (Hallinger *et al.*, 2010; Myers-Smith *et al.*, 2015b). Moreover, there is still very little known about how stems are initiated and replaced within a shrub individual (but see Charles-Dominique, 2011). All of these complex interactions could result in different radial growth patterns between the stems of a single individual. Despite these considerations, stems and root collars (i.e., the oldest part of a shrub, found at the junction between roots and stems) are often used without distinction both across (Myers-Smith *et al.*, 2011a) and within studies (Dumais *et al.*, 2014).

A review of shrub dendrochronological studies reveals that stems are more frequently used than root collars (44/69 studies compared to 15/69; Fig. 1 and Table S1). The strong preference toward stems likely arises from some of the following reasons: Root collars are hard to access in certain environments and in areas of continuous shrub cover, their sampling is destructive and their identification can be difficult, especially when shrub individuals display complex morphologies such as adventitious roots and buried stems (Myers-Smith *et al.*, 2015b). As a consequence, it is often easier to sample the largest and/or longest stems of an individual, even if it does not track the entire shrub growth record (De Witte *et al.*, 2012). However, comparing the climate sensitivity of shrubs across different sites or regions could be potentially problematic if different shrub parts exhibit different growth trends that are influenced not only by climate but also by within-individual competition and resource allocation.

The growing number of studies dealing with the sensitivity of shrub growth to climate change highlights the need to converge toward standardized methods in dendroecology applied to shrubs, especially in the fast-changing tundra biome. Here, we present a comparative study of the use of root collars and stems in dendroclimatology analyses. Specifically, we aim (i) to evaluate the relative sensitivity of stems and root collars to climate and (ii) to evaluate whether this relative sensitivity is consistent across different types of environments. We hypothesize that climate sensitivity will be higher for root collars, given that they integrate growth from the whole individual, and that this difference will be maintained across the landscape.

Materials and methods

Study area and climatic trends

The study area is located around the Boniface River research station (Centre d'études nordiques, http://www.cen.ulaval.ca/page.aspx?lien=stationboniface; 57°45′N, 76°20′W), about 10 km south of the Arctic treeline in subarctic Québec (Canada). The area lies within the discontinuous permafrost zone (Payette, 2001) and belongs to the shrub subzone of the forest–tundra ecotone (Payette, 1983). At the landscape scale, shrub tundra covers *ca.* 70% of the well-drained sites (Payette *et al.*, 2008). Wetlands, which include palsas and snowbeds, cover 7% of the terrestrial area. *Betula glandulosa* Michx. (hereafter referred to as dwarf birch), a multi-stemmed species widely distributed in North America, is the most abundant shrub species and is responsible for most of the shrub expansion observed in the study area (Ropars & Boudreau, 2012). According to Ju & Masek (2016), this is the Canadian region where satellite-observed greening has been the most extensive in the last three decades. Large herbivores (caribou: *Rangifer tarandus* L.) are present in the area, but browsing is mostly restricted to *Salix* species.

The closest meteorological station (Inukjuak Meteorological Station, Environment Canada; 58°28′N, 78°05′W; 130 km northwest of the study site) recorded an annual mean temperature of −7 °C for the 1971–2000 period, with the highest and

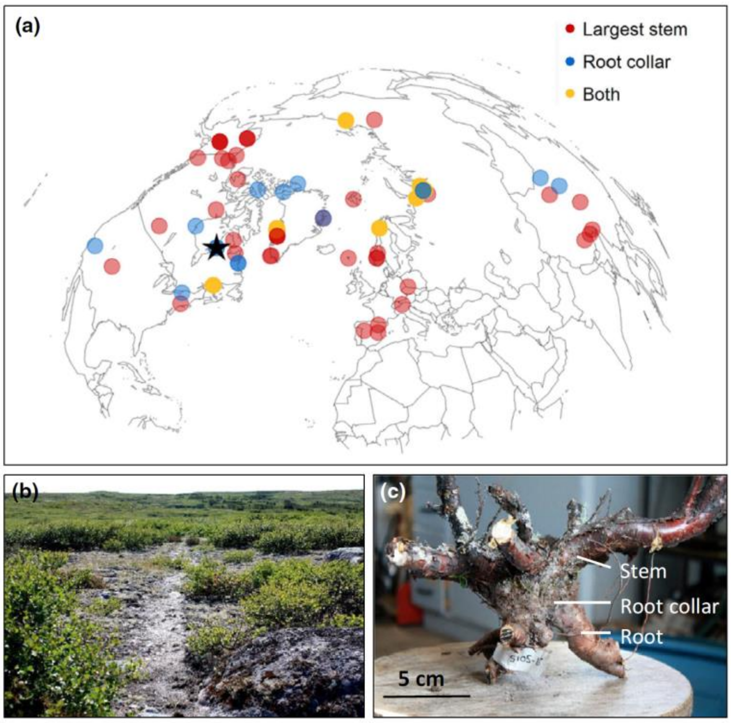

Fig. 1 (a) Map of shrub sampling methods for dendroclimatological analyses in Northern Hemisphere. The black star represents our study area near the Boniface River research station, Nunavik, Québec, Canada; darker dots represent regions for which more than one study took place. (b) General landscape around the Boniface River research station, with extensive *Betula glandulosa* thickets. (c) An uprooted *B. glandulosa* individual with large proportion of its stems and roots removed. The location of the root collar, roots and stems is shown.

lowest mean monthly temperatures recorded in July (9.4 °C) and February (−25.8 °C), respectively (Canadian Climate Normal; Environment Canada, 2016). Annual precipitation averaged 460 mm, of which 42% fell as snow (Canadian Climate Normal; Environment Canada, 2016). Between 2000 and 2009, mean annual temperature has reached −5.5 °C, with July and February temperatures averaging 11.7 °C and −24.8 °C. Like many regions in northern Québec, Inukjuak is experiencing a warming trend that began in the early 1990s (Chouinard *et al*., 2007; Bhiry *et al*., 2011).

Site selection and field sampling

The root collar and the two main stems of dwarf birch were sampled in three different environments to assess potential site-driven differences in climate sensitivity: sandy terraces (hereafter referred to as terraces), low-altitude hilltops (hereafter referred to as hilltops) and snowbeds. The terraces are well-drained, low-elevation sites located on the banks of the Boniface River. They are characterized by lichens, graminoids and large patches of shrub species, mainly dwarf birch, although willows and alders can be found close to the river. The hilltops are characterized by the presence of arctic–alpine species and exposed mineral soil. Snowbeds are periglacial environments where snow accumulates preferentially during winter and melts later in the growing season, sometimes as late as mid-July. Consequently, they are characterized by plant species well adapted to winter conditions and to an excess of moisture in the first half of the growing season (Payette & Lajeunesse, 1980; Filion & Payette, 1982; Morin & Payette, 1986). One site in each environment type was randomly selected from a pool of 147 identified sites (50 terraces, 50 hilltops and 47 snowbeds; see Ropars *et al*., 2015 for more details on site selection).

In summer 2010, we selected and uprooted 20 dwarf birch individuals at each site. We prioritized large and relatively isolated individuals with a circular form, as they were thought to be older individuals grown from seed. When such individuals were not available, particular attention was taken to discard individuals for which the root collar could not be easily identified. Dwarf birch individuals grown from seeds usually display a short (<3 cm) but well-defined root collar, located between the root and stem systems (Fig. 1c). From the three to six main stems directly emerging just above the root collar, we selected the two largest ones and cut them as close as possible to the root collar and the soil surface. The two stem samples and the root collar of each dwarf birch individual were collected, carefully cleaned and left to fully dry at room temperature.

Radial growth measurement

Dwarf birch root collars were sliced (*ca.* 25 μm) using a rotary microtome after being boiled for at least 3 hours. Thin sections were then stained with safranin (1% solution, Safranin O, Fisher Science Education), dried and permanently mounted with a 66% toluene solution (SHUR/mount^{TM} liquid cover glass, Triangle biomedical sciences). Digital photographs of each sample were taken using a binocular-mounted camera (Olympus SZ61 with a SC100 camera; Olympus Imaging America, Center Valley, PA, USA). Root collars were discarded if they could not be sliced perpendicularly (stems and roots were too intermingled), or if they were rotten. Of the 60 root collars processed for the three sites, 46 were kept for further analyses (terrace: 15, hilltop: 16, snowbed: 15). The two largest stems of each of these 46 individuals (92 stems) were processed following the above procedures.

Using digital photographs, we aged each root collar and stem sample with the IMAGEJ freeware (v. 1.40 g; Research Services Branch of the National Institute of Mental Health, Bethesda, MD, USA), while ring widths were measured using the dendrochronological software LIGNOVISION (v. 1.36, Rinntech, Heidelberg, Germany). If possible, ring widths were measured along two opposite radii and averaged for each sample. Growth measurements were visually examined and statistically verified with COFECHA, a widely used statistical crossdating program (Holmes, 1983). We used the mean detrending method for every root collar and stem ring-width series to allow comparison between individuals. Incomplete rings were frequently encountered, but easily detectable. Unlike other willow and birch species growing at their altitudinal limit (Wilmking *et al.*, 2012), no missing rings were identified in the root collar samples.

Measuring climate sensitivity

The climate sensitivity of root collars and stems was measured using mixed-effects models. We used ring-width data for the period 1947–2009, for which monthly temperature and precipitation data were available from the Inukjuak Meteorological Station. We ran a series of linear mixed-effects models using standardized (mean centered) ring width as a response variable, monthly temperature and/or precipitation variables (singly or in combination; see Table S2 for the full list of models) and the sample type (root collar vs. stem) as interacting predictors, and with year as a random effect. We also ran a null model, i.e., a model with the same random-effect structure that does not include any climate variables as fixed effects to serve as baseline for the climate sensitivity analysis (Ettinger *et al.*, 2011; Myers-Smith *et al.*, 2015a). We allowed for interactions between fixed effects because we were specifically interested in the potentially different climate responses of shrub root collars and stems. We ran a separate series of models for each site, as the added complexity of including a site level in the model structure while allowing for random slopes caused convergence issues. We ran the analyses with the LME4 package (Bates *et al.*, 2015) of the R software (version 3.2.2, http://cran.rproject.org), using the maximum likelihood estimation for model selection and the restricted maximum likelihood estimation to estimate slopes.

As our interaction models (sample type * climate) were driven mostly by the stronger response of the root collars, we also ran separate models for stems vs. root collars at each site to check whether stems might be more responsive to a different climate variable. We additionally ran the same model structure with the NLME package to compare model results to models with a temporal autocorrelation structure, and using raw (non-standardized) ring-width data and a subset of the data restricted to the common period covered by both stem and root collar chronologies (1960–2009). These complementary analyses yielded the same results and thus are not presented in the main text (see Table S3 for results obtained with raw data, the 1960–2009 subset and using the NLME package).

We used model selection analysis to identify the best climate model(s), i.e., the variables that best explain variations in radial growth. We ranked the models according to the Akaike information criterion (AIC) and calculated the difference between each model and the null model, which we denoted by ΔAIC_{null}. ΔAIC_{null} is used as a measure of the sensitivity of radial growth to specific climate variables (Myers-Smith *et al.*, 2015a). As the AIC only assesses the relative quality of competing models, but not the absolute goodness of fit, we also calculated the marginal and conditional R^2 of each model with the r.squaredGLMM function of the MUMIN package (R version 3.2.2). The conditional R^2 represents the amount of variance explained by all the fixed and random effects in the model, while the marginal R^2 is the amount of variance explained by the fixed effects only (Nakagawa & Schielzeth, 2012).

Linear models

To investigate whether sensitivity of stem and root collar was correlated or decoupled within an individual, we ran a linear model with ring width as a function of the two best climate variables (July temperature and March precipitation) identified through the model selection described above for each individual. We then compared whether the slopes differed between plant parts for each individual. We also used these slope values to test whether there was a significant relationship between climate sensitivity of root collars and their stem counterparts. To do so, we ran a linear model with the slope values obtained for stems as a function of the ones obtained for root collars. We applied a square root transformation to the slope values to attain normality (Legendre & Legendre, 1998). A constant was added to the slope values prior to transformation to cope with negative numbers.

Results

Sensitivity of stems and root collars to climate

We found greater sensitivity of *Betula glandulosa* root collars vs. stems across our sampling sites (Fig. 2).

Climate sensitivity of stems was generally weak, the null model ranking between the fourth and seventh best model (Table S1). Moreover, the proportion of the variance in growth explained by climate variables (i.e., marginal R^2) for root collars was at least twice as high as for stems in the snowbed and hilltop sites, and there was a similar, but weaker trend, for the terrace site.

Climate variables best explaining growth

We found that March precipitation and July temperature best explained shrub growth, but with a strong interaction with sample type. Root collars showed a consistent positive response to these two climate variables, but not stems (Fig. 2). Moreover, when stems and root collars were analyzed separately, the latter showed greater climate sensitivity than stems to most climate variables (monthly mean temperature and total precipitation; Fig. 3). The difference in AIC score between the null model and the best climate model was systematically higher for root collars than for stems in each type of environment (Table 1). March precipitation and July temperature best explained the growth at the root collar, and this relationship was maintained across the landscape. On the other hand, stems showed weak and inconsistent responses among the three environments; August, May and April temperature best explained stem growth in snowbed, hilltop and terrace, respectively.

Climate sensitivity of individuals among shrub parts

Individual-level climate sensitivity did not show a consistent trend among root collar and stems (Fig. 4). Individuals having a climate-sensitive root collar did not tend to have climate-sensitive stems, as only five climate-sensitive root collars out of 42 had one or two of their stem counterparts sensitive to climate as well. Of the 11 climate-sensitive stems, seven were associated with climate-sensitive root collars. Moreover, root collar and stems from the same individual showed opposite significant relation with July temperature in one

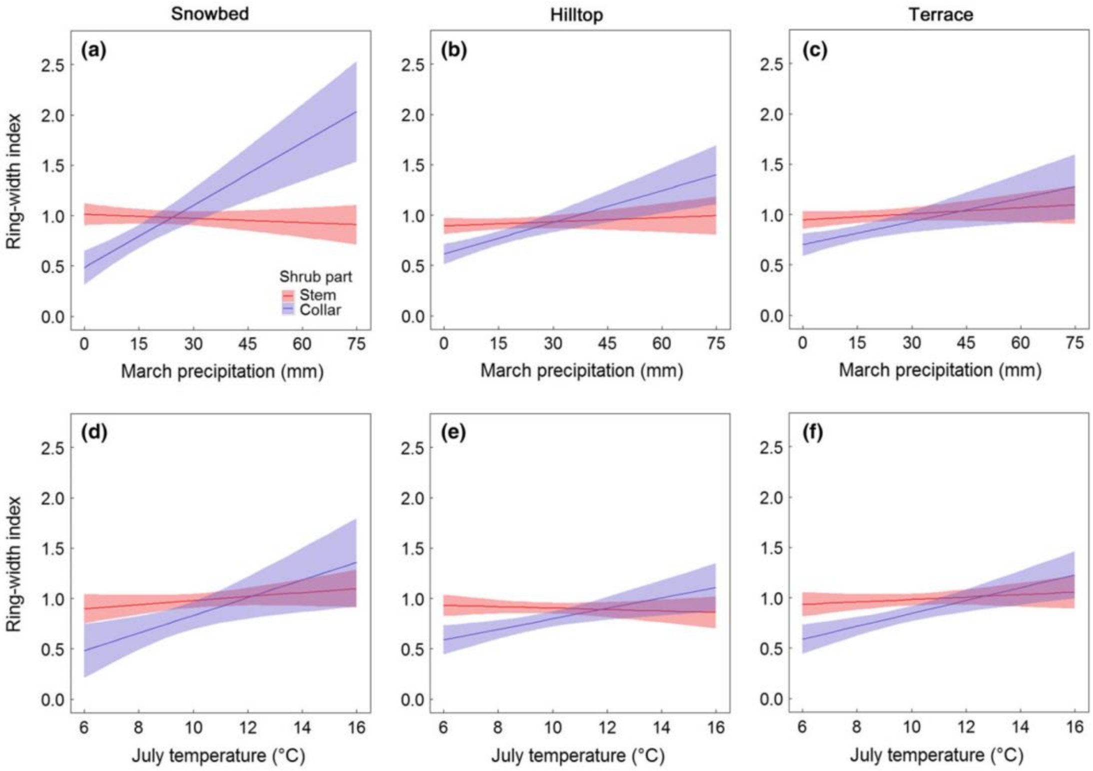

Fig. 2 Differences in climate sensitivity of growth for March precipitation (a–c) and July temperature (d–f), the two best climate models, between stems (red) and collars (blue). Solid lines and shaded areas indicate the slope estimates and 95% confidence interval for the mixed model analyses.

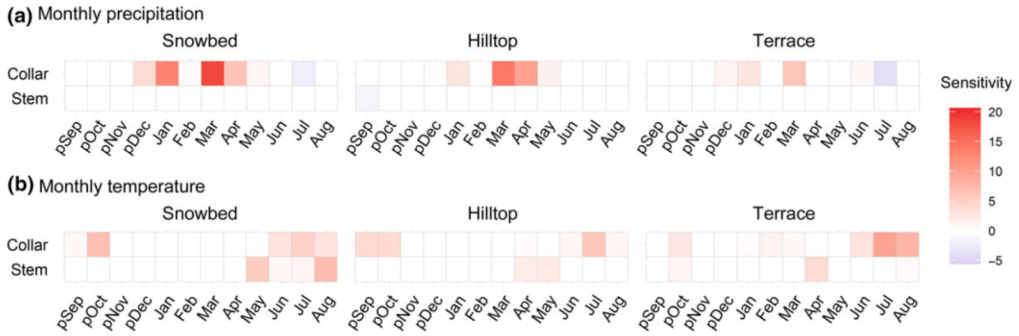

Fig. 3 Sensitivity of collar and stem growth to monthly (a) precipitation and (b) temperature, as expressed by the difference between the AIC of each linear models and the AIC of the null model. The metric 'sensitivity' was obtained by multiplying the ΔAIC_{null} by +1 or −1 depending on the sign of the slope of the regression to represent positive and negative growth responses, respectively. 'P' preceding a month stands for previous year.

Table 1 Results from the model selection using Akaike information criterion. The sensitivity (i.e., difference between the best and the null model, in terms of ΔAIC), the marginal R^2 (i.e., the amount of variance explained by fixed effects) and the conditional R^2 (i.e., the amount of variance explained by both fixed and random effects) are shown only for the more plausible model(s) for stem and collar in each type of environment. T and P stand for temperature and precipitation, respectively

Site	Shrub part	Best climate model	Sensitivity (ΔAIC_{null})	Marginal R^2	Conditional R^2
Snowbed	Root collar	July T + March P	19.0	0.29	0.53
	Stem	August T	7.1	0.15	0.31
Hilltop	Root collar	July T + March P	16.2	0.13	0.24
	Stem	May T	2.2	0.02	0.09
Terrace	Root collar	July and August T	12.2	0.07	0.13
		July T + March P	11.8	0.06	0.12
	Stem	April T	3.8	0.04	0.15

particular case (individual S27, Fig. 4). The climate sensitivity of stems to both July temperature (linear model, $F_{1,90} = 2.927$, $P = 0.091$) and March precipitation (linear model, $F_{1,88} = 1.624$, $P = 0.206$) was not explained by the climate sensitivity of their root collar counterparts.

Root collar and stem sample characteristics

We found that root collar ages were greater than stem ages and that ages varied across the different environments sampled. Root collar samples averaged 41 years of age, but ranged between 10 and 96 (Table 2). The oldest root collar was from an individual growing on a hilltop, whereas the youngest were found in the snowbed environment. There was no difference in root collar samples age between the three types of environments ($F_{1,3} = 1.02$, $P = 0.369$). Stem samples averaged 23 years of age, but some reached over 60 years in the hilltop environment. The stems of dwarf birch individuals growing in the snowbed site were younger (18 years old compared to 27 and 25 for hilltop and terrace; Tukey multiple comparison, $P < 0.01$) and longer (from the root collar to the tip of the stem) than those of individuals growing on the hilltop and terrace sites (Table 2; 133 cm compared to 92 cm and 102 cm for hilltop and terrace, Tukey multiple comparison, $P < 0.01$).

Discussion

In this study, we demonstrated that different parts of an important tundra shrub species in North America, *Betula glandulosa*, have contrasting responses to climate, with root collars exhibiting far greater sensitivity than stems. Growth at the root collar was best explained by spring precipitation and summer temperature, and this relationship was maintained across the landscape. Stems, on the other hand, showed weak and inconsistent responses. These results highlight the complexity of resource allocation in multi-stemmed shrubs and call for caution in sampling when aiming to assess the climate sensitivity of shrub growth.

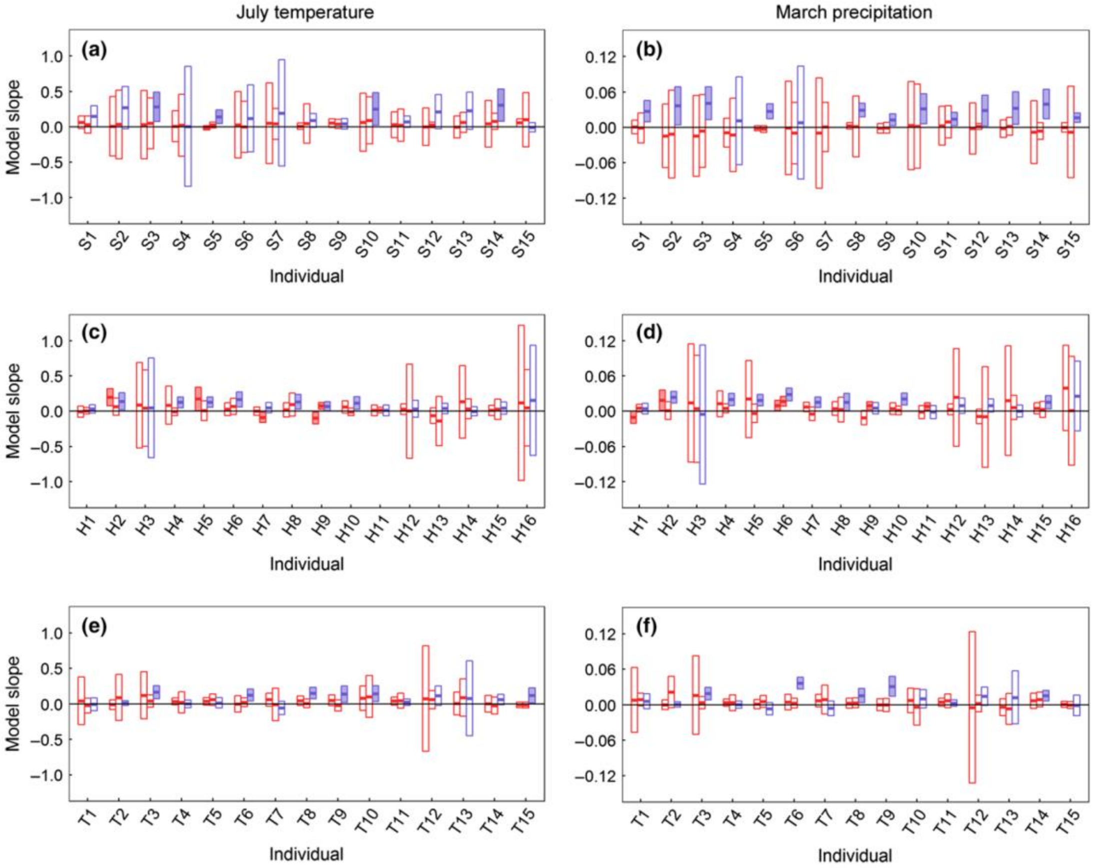

Fig. 4 Climate sensitivity of stems (red) and root collars (blue) to July temperature (a, c, e) and March precipitation (b, d, f) are shown for individuals growing on snowbed (a, b), hilltop (c, d) and terrace (e, f). Bars are the slope and standard error (linear models). Filled bars indicate regression slopes that are significantly different from 0 ($P < 0.05$).

What explains the difference in sensitivity of root collars vs. stems?

The multi-stemmed structure of shrubs results in complex resource allocation patterns among plant parts that could dampen the influence of climate on stems growth. In their review of intra-plant competition, Sadras & Denison (2009) concluded that plant individuals might use competition-like mechanisms to allocate resources such as nutrients, but only if it increases overall individual fitness. Competition within plant individuals is known to lead to trade-offs between size and number of plant units (Sadras, 1995; Chikov, 2008; Sadras & Denison, 2009) as well as between vegetative and reproductive structures (e.g., Liu *et al.*, 2007; Quilot & Genard, 2008). The vertical growth of shrubs can also be limited by the abrasive effect of windblown ice particles (Sonesson & Callaghan, 1991), resulting in differential growth patterns among stems. Moreover, the drivers of stem initiation at the root collar are poorly understood. Light availability promotes stem initiation of *Rhamnus cathartica* L., a deciduous shrub growing in southern Québec (Charles-Dominique *et al.*, 2012), and an increased herbivory pressure is known to alter the vertical structure of *Salix* and *Betula* species in northern Alaska (Tape *et al.*, 2010; Christie *et al.*, 2014). The growth of each stem is therefore affected not only by climatic and other environmental conditions, but also by differential resources allocation among plant parts that enhances the individual's global fitness. On the other hand, root collars integrate the growth of each plant part. Thus, they might be less affected by competition-like mechanisms and more responsive to climate.

Table 2 Information on individual root collar and stem samples in three different types of environments in the Boniface River region, Nunavik, Québec, Canada. The stem length refers to the measure (in cm) from the root collar to the tip of the stem. The numbers in brackets (second column) represent the sample size

		Age		Length	
		Mean value (years)	SD	Mean value (cm)	SD
Root collar	Snowbed (15)	35.3	17.5	-	-
	Hilltop (16)	45.2	20.7	-	-
	Terrace (15)	43.5	21.1	-	-
	Mean value	41.4	20.5	-	-
Stem	Snowbed (30)	17.9	9.5	146.8	31.1
	Hilltop (32)	26.9	14.5	92.4	16.4
	Terrace (30)	25.3	12.2	101.8	21.3
	Mean value	23.4	13.0	109.1	28.9

Root collars showed consistent responses to climate variables across the landscape, with both July temperature and March precipitation promoting enhanced radial growth. Warmer temperatures during the short growing season have been identified as key factors for promoting shrub growth in different Arctic regions (e.g., Bär *et al.*, 2008; Forbes *et al.*, 2010; Hallinger *et al.*, 2010; Myers-Smith *et al.*, 2015a). Higher precipitation in March could reduce the risk of frost damage following early leaf-out, and protect buds and stems from the abrasive effect of drifting ice particles (Sonesson & Callaghan, 1991). Among other possible explanations, an increase in snow precipitation could also promote a better radial growth by increasing water discharge and thus water availability in early summer. Greater snow accumulation may also lead to greater insulation, higher soil temperature and increased microbial activity, which in turn could lead to higher nutrient availability (Chapin *et al.*, 2005).

To our knowledge, the present study is the first to compare climate sensitivity among different parts of shrub individuals. The harsh climatic conditions of arctic and alpine regions can result in intra-plant growth irregularities that could influence climate sensitivity, such as missing or incomplete rings (Hallinger *et al.*, 2010; Buchwal *et al.*, 2013). The distribution of these growth irregularities has been shown to be heterogeneous among shrub parts (Hallinger *et al.*, 2010). For *Salix polaris* Wahlenb for instance, the growth at the root collar and in the belowground system was consistently greater than the growth in stems (Buchwal *et al.*, 2013). While serial sectioning (Kolishchuk, 1990), a technique consisting in repeated tree ring-width measurements along shrub stems, allows for the accurate dating of properly date woody plant individuals (Hallinger *et al.*, 2010; Wilmking *et al.*, 2012; Buchwal *et al.*, 2013; Hollesen *et al.*, 2015), as well as emphasizing the growth heterogeneity among plant parts. For different northern pine and spruce species, differences in growth–climate relationships have been observed among plant parts, breast height and upper stem samples being more sensitive to previous and current season temperatures and moisture, respectively (Kozlowski *et al.*, 1991; Chhin & Wang, 2008; Chhin *et al.*, 2008, 2010). Our findings suggest that complex controls are also at play in determining the growth of shorter-statured but multi-stemmed plants.

Implication of the study

Increased shrub cover will play an important ecological role in Arctic regions with warming, emphasizing the need to better understand and predict the drivers and magnitude of this tundra vegetation change. Large-scale meta-analyses focusing on many taxa are useful to address these questions (see Myers-Smith *et al.*, 2015a), but their conclusions could be challenged by a lack of consistency in sampling methods across studies. Our results show that root collars are consistently more climate sensitive than stems for a widely distributed shrub species, *B. glandulosa*, one of the most commonly reported shrub species to be expanding in tundra ecosystems (Tape *et al.*, 2006; Myers-Smith *et al.*, 2011a; Ropars & Boudreau, 2012; Tremblay *et al.*, 2012). Moreover, a climate-sensitive root collar was not necessarily associated with climate-sensitive stems (Fig. 4). In their recent meta-analysis, Myers-Smith *et al.*, 2011a found greater climate sensitivity in northwest Russia compared to North America. Based on our literature review (Fig. 1 and Table S1), these differences could be partly explained by the differential use of stems and root collars across studies. Indeed, most Russian studies have used root collars (eight out of 11 studies, 73%), whereas only a third of North American ones did (10 out of 30 studies, 33%; Table S1). The sensitivity of North American shrubs could therefore have been underestimated and could overlook the potential increase in shrub abundance and canopy height. While the differences between shrub parts have been overlooked in the past, our study highlights the importance of establishing consistent sampling protocols for shrub dendrochronological analysis.

How do we move forward with future dendroecological analyses?

While this study clearly demonstrates that different plant parts show different climate sensitivity, further investigations are required to understand how generalizable our findings are across the tundra biome. In our study, we focused on one shrub species, *Betula glandulosa*, growing in a specific subarctic area of North America. Shrub species having similar growth forms and branching architecture (like alders and willows) could potentially also show similar differences in climate sensitivity among plant parts, but a multi-species comparison would be needed to confirm this hypothesis. Architectural studies of shrubs are arising in the scientific literature and could bring us a step further in our comprehension of energy allocation among plant parts (Charles-Dominique, 2011). We therefore propose that architectural and comparative dendrochronological studies be combined to account for potential differences in growth patterns among shrub parts. If dissimilarities between plant parts are also observed in other sites and species, we urge for the establishment of a standardized sampling methodology for future studies. Based on the fact that root collars were more climate sensitive than stems, we propose that future studies systematically sample shrub individuals as close as possible to the root collar.

Understanding the dynamic of shrub populations and the drivers of their growth is key to assess and predict global ecosystem processes under climate change, especially in Arctic regions where they structure plant communities. Our study clearly demonstrates that root collars provide a better integration of the climate sensitivity of shrub individuals for a widely distributed species in North America, *Betula glandulosa*. Root collars were more climate sensitive than stems and showed consistent sensitivity to July temperature and March precipitation across three different types of environments in the Boniface River region. Finally, we found no consistency between shrub parts, individuals having a climate-sensitive root collar did not necessarily have a climate-sensitive stem. While different shrub parts have been sampled for dendrochronological analyses in the past, this study urges for a standardized sampling methods. To reveal reliable climate sensitivity of tundra shrub species and, more importantly, to conduct multi-sites and multi-species analysis, we propose to systematically sample at root collar.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1 List of dendroclimatological studies on shrubs in high latitude or altitudinal sites.
Table S2 Results of the model selection using Akaike's information criterion (AIC) explaining the radial growth of *Betula glandulosa* root collars and stems (separate suites of models for each plant part) growing on (a) snowbed, (b) hilltop and (c) terrace in the Boniface River region, Nunavik, Québec, Canada.
Table S3 Results from the model selection using Akaike information criterion (a) with the raw (non-standardized) ring-width data, (b) with a subset of the data restricted to the common period covered by both stem and root collar chronologies (1960–2009), and (c) when the models were run with a temporal autocorrelation term (1-year lag; package NLME).

Appendix II – Supplementary material for Chapter 3

Table S3-1 *Changes over time in mean summer temperature, growing season length (JSL), and peak greenness (MODIS NDVI) at the four field sites in Northern Canada. For summer temperature, trends over a longer period are presented. For growing season length, both the season during which 5% and 50% of peak greenness are maintained are presented. Significant trends are indicated in bold.*

	Site															
	Qikiqtaruk				Kluane				Umiujaq				Salluit			
	Estimate	SE	p	R^2	Estimate	SE	p	R^2	Estimate	SE	p	R^2	Estimate	SE	p	R^2
JJA temperature (°C)*																
1980-2014	0.2	0.2	0.31	0.03	0.3	0.1	**0.02**	0.15	0.6	0.2	**0.001**	0.30	0.2	0.1	0.29	0.03
2000-2014	0.3	0.4	0.47	0.04	0.4	0.4	0.37	0.06	0.2	0.6	0.68	0.01	-0.6	0.4	0.16	0.13
GSL (days)*																
5% max greening	17.0	8.1	**0.05**	0.23	11.0	7.3	0.15	0.13	6.9	7.9	0.40	0.05	11.2	11.0	0.91	0.00
50% max greening	14.3	4.8	**0.01**	0.37	9.5	5.3	0.09	0.17	5.1	6.9	0.47	0.04	3.9	8.1	0.64	0.01
Peak NDVI	0.01	0.02	0.52	0.03	0.01	0.01	0.38	0.05	0.02	0.02	0.26	0.08	0.00	0.01	0.78	0.01

* Estimate and standard error presented in units per decade

Table S3-2 *The growth of tundra shrubs was best explained by summer temperature at Kluane, and by growing season length at Qikiqtaruk and Salluit. Slope estimates for standardised variables are presented with their standard error (SE) or standard deviation (SD). Coefficients are bolded when the confidence interval does not overlap zero. ΔAIC$_{null}$ is the difference between the Aikaike's Information Criterion for the model compared to a null model with the same random effect structure.*

	Qikiqtaruk	**Kluane**	**Umiujaq**	**Salluit**
Fixed effects				
Summer temperature (SE)	0.144 (0.101)	**0.411** (0.106)	-0.009 (0.070)	0.073 (0.126)
Growing season length (SE)	**0.157** (0.044)	0.027 (0.040)	0.022 (0.046)	**-0.124** (0.062)
Random effects				
Plot variance (SD)	0.010 (0.102)	0.001 (0.036)	0.000 (0.000)	0.006 (0.076)
Year variance (SD)	0.147 (0.283)	0.157 (0.386)	0.059 (0.243)	0.198 (0.445)
Residual variance (SD)	0.781 (0.884)	0.797 (0.893)	0.955 (0.977)	0.739 (0.860)
Observations	865	1019	1229	863
ΔAIC$_{null}$	10.8	8.4	--	--

Note: The absence of a ΔAIC$_{null}$ indicates that the corresponding model did not perform better than a null model with the same random effect structure but without any fixed effects.

Table S3-3 *The growth of tundra shrubs was not associated with peak greenness at any of the sites. Slope estimates are presented with their standard error (SE) or standard deviation (SD). ΔAIC$_{null}$ is the difference between the Aikaike's Information Criterion for the model compared to a null model with the same random effect structure – none of the models reached the threshold of two AIC points to be considered a better model.*

	Qikiqtaruk	**Kluane**	**Umiujaq**	**Salluit**
Fixed effects				
NDVI (SE)	-0.013 (0.035)	-0.023 (0.035)	-0.018 (0.042)	-0.051 (0.055)
Random effects				
Plot variance (SD)	0.010 (0.099)	0.001 (0.037)	0.000 (0.000)	0.182 (0.426)
Year variance (SD)	0.186 (0.431)	0.329 (0.574)	0.057 (0.238)	0.007 (0.085)
Residual variance (SD)	0.791 (0.889)	0.797 (0.893)	0.954 (0.977)	0.742 (0.861)
Observations	865	1 019	1 229	863
ΔAIC$_{null}$	--	--	--	--

Note: The absence of a ΔAIC$_{null}$ indicates that the corresponding model did not perform better than a null model with the same random effect structure but without any fixed effects.

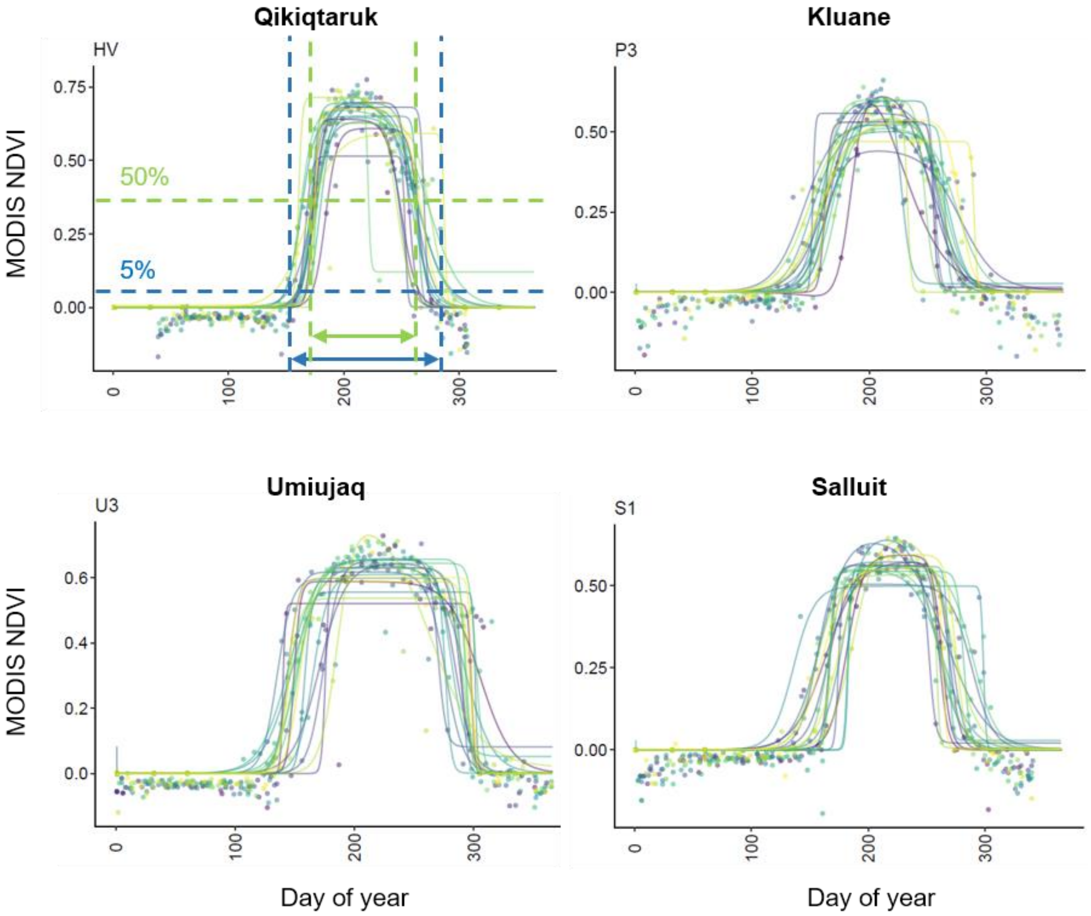


Figure S3-1 *Example of the calculation of growing season length with smoothed interpolated curves from the Phenex library in R. Available MODIS6 NDVI data in a given year (each coloured curve represents a year) for each plot are plotted and a smoothing function is applied. Winter days are given a zero value. The highest y-value of this function is the peak greenness from which threshold values are calculated. Chapter 3 uses a 5% threshold value to calculate growing season length (blue line on top left panel) to capture the snow-free period. Other studies use a threshold of 50% to represent the photosynthetically active period (green line).*

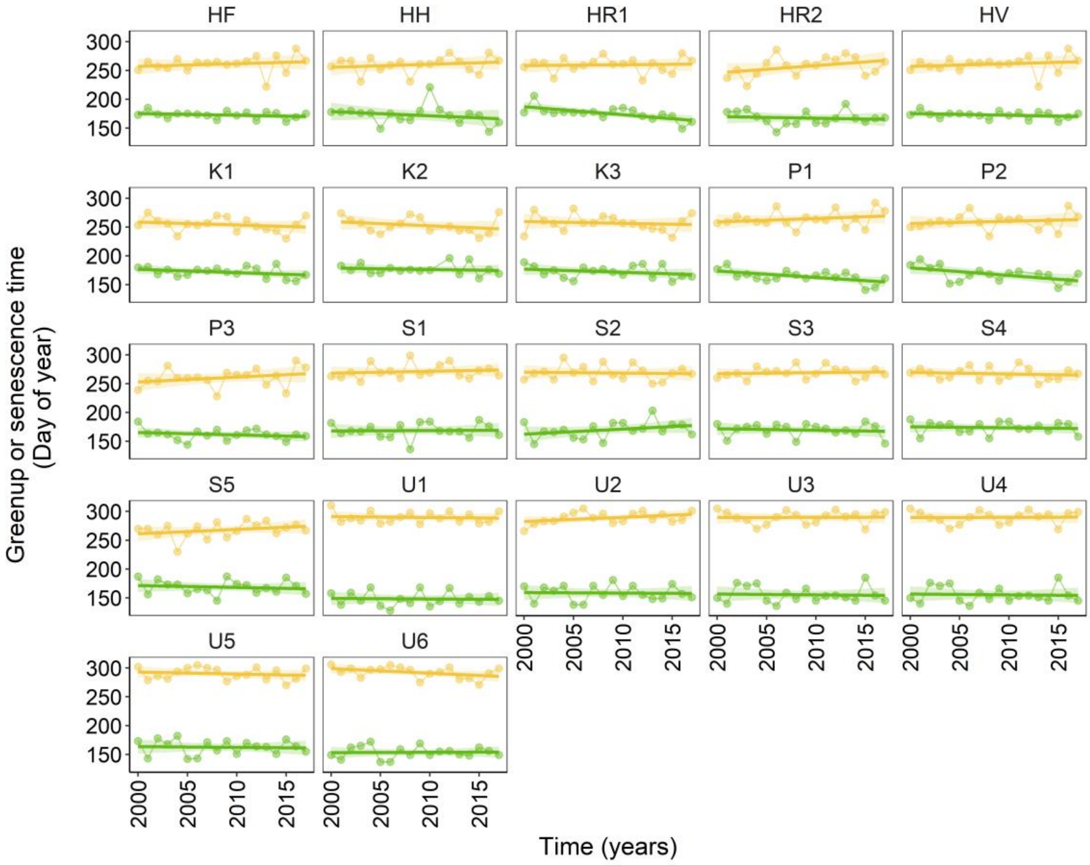


Figure S3-2 *Temporal trends in the timing of plant green-up (green) and senescence (yellow) for each plot. (H plots: Qikiqtaruk / K and P plots: Kluane / U plots: Umiujaq / S plots: Salluit) as identified from smoothed interpolated curves of MODIS6 NDVI data (see Figure S3-1).*

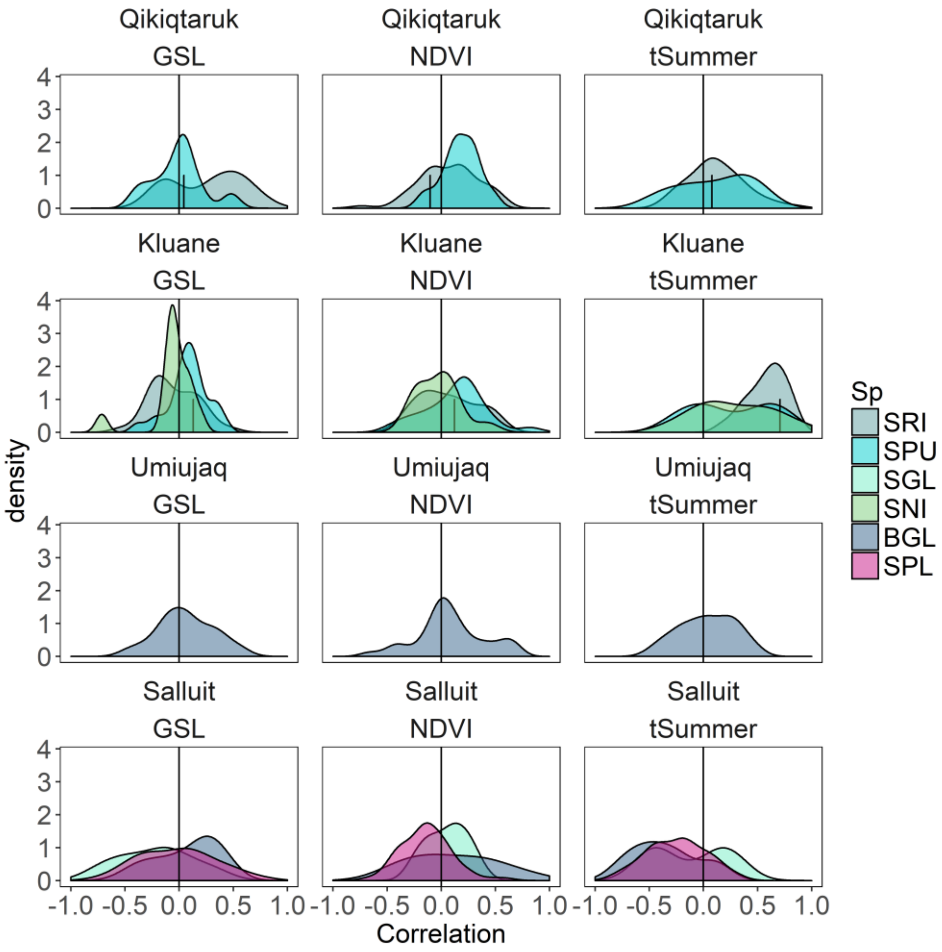
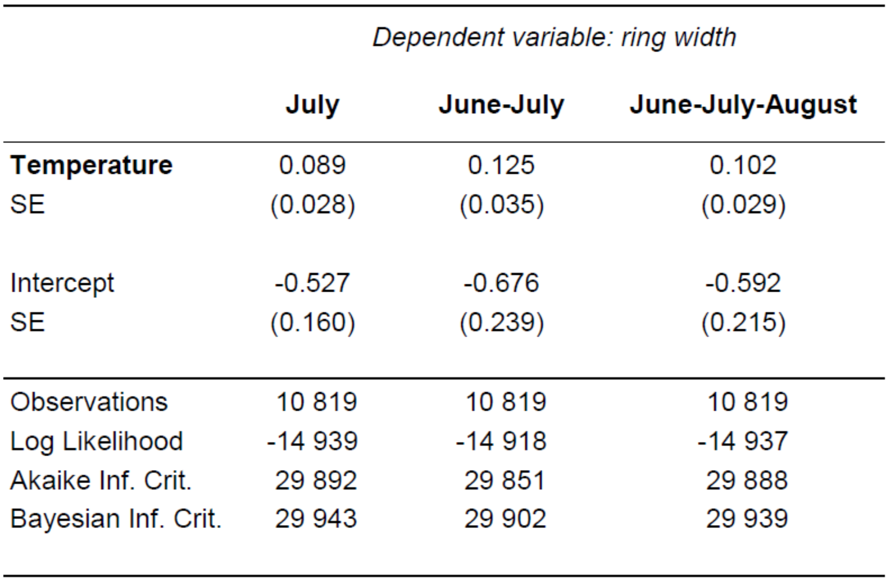


Figure S3-3 *Correlations between ring width and the variables used in this study (GSL: growing season length; NDVI: peak greenness; tSummer: mean June-July-August temperature), broken down by species. Sensitivity is generally similar among species within a site.*

SRI: Salix richardsonii
SPU: Salix pulchra
SGL: Salix glauca
SNI: Salix niphoclada
SPL: Salix planifolia
BGL: Betula glandulosa

Appendix III – Supplementary material for Chapter 4

Table S4-1 *The sensitivity of shrub growth to July, June-July or June-July-August temperatures was similar in terms of effect sizes. I chose to use June-July temperature in the main analysis because it has the lowest AIC score and represents best the overall growing season across all sites, given that plants senesce in early August at the higher latitude sites.*



	Dependent variable: ring width		
	July	**June-July**	**June-July-August**
Temperature	0.089	0.125	0.102
SE	(0.028)	(0.035)	(0.029)
Intercept	-0.527	-0.676	-0.592
SE	(0.160)	(0.239)	(0.215)
Observations	10 819	10 819	10 819
Log Likelihood	-14 939	-14 918	-14 937
Akaike Inf. Crit.	29 892	29 851	29 888
Bayesian Inf. Crit.	29 943	29 902	29 939

Table S4-2 *The sensitivity of shrub growth to June-July temperature could not be explain as a function of either individual shrub height or canopy diameter. The outputs are from mixed-effects model for A) the Shrub Hub dataset and B) the dataset collected for this thesis. See main text for details on model structure.*

	Dependent variable: climate sensitivity	
	Canopy height	**Canopy diameter**
A. Shrub Hub dataset		
Estimate	-0.018	-0.031
Standard error	0.035	0.018
Random effects		
Genus-by-site variance (SD)	0.015 (0.120)	0.021 (0.146)
random slope variance (SD)	0.003 (0.054)	0.001 (0.028)
Residual variance (SD)	0.055 (0.235)	0.056 (0.237)
Observations	428	413
ΔAIC_{null}	--	--
B. New dataset		
Estimate	0.225	-0.017
Standard error	0.178	0.032
Random effects		
Site variance (SD)	< 0.001 (0.010)	0.014 (0.120)
random slope variance (SD)	0.080 (0.283)	< 0.001 (0.003)
Residual variance (SD)	0.035 (0.188)	0.038 (0.195)
Observations	306	306
ΔAIC_{null}	2.5	3.7

Note: The absence of a ΔAIC_{null} indicates that the corresponding model did not perform better than a null model.

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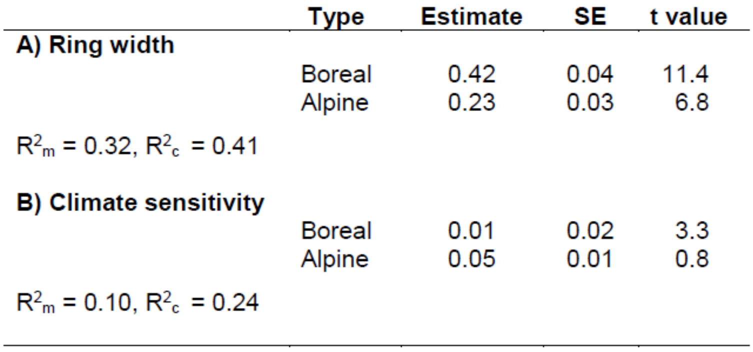
Appendix IV – Supplementary material for Chapter 5

Table S5-1 *Differences in A) mean annual growth and B) climate sensitivity of growth between boreal and alpine shrubs (n = 40, 101) in the Kluane region. Estimates are from hierarchical mixed-effects models with sampling plot as a random effect. Indicators of goodness of fit are provided in the form of marginal* R^2 *(*R^2_m*) assessing the explanatory power of fixed effects only, and of conditional* R^2 *(*R^2_c*) assessing the fit of the full model.*



	Type	Estimate	SE	t value
A) Ring width				
	Boreal	0.42	0.04	11.4
	Alpine	0.23	0.03	6.8
R^2_m = 0.32, R^2_c = 0.41				
B) Climate sensitivity				
	Boreal	0.01	0.02	3.3
	Alpine	0.05	0.01	0.8
R^2_m = 0.10, R^2_c = 0.24				

Appendix V– Supplementary material for Chapter 6

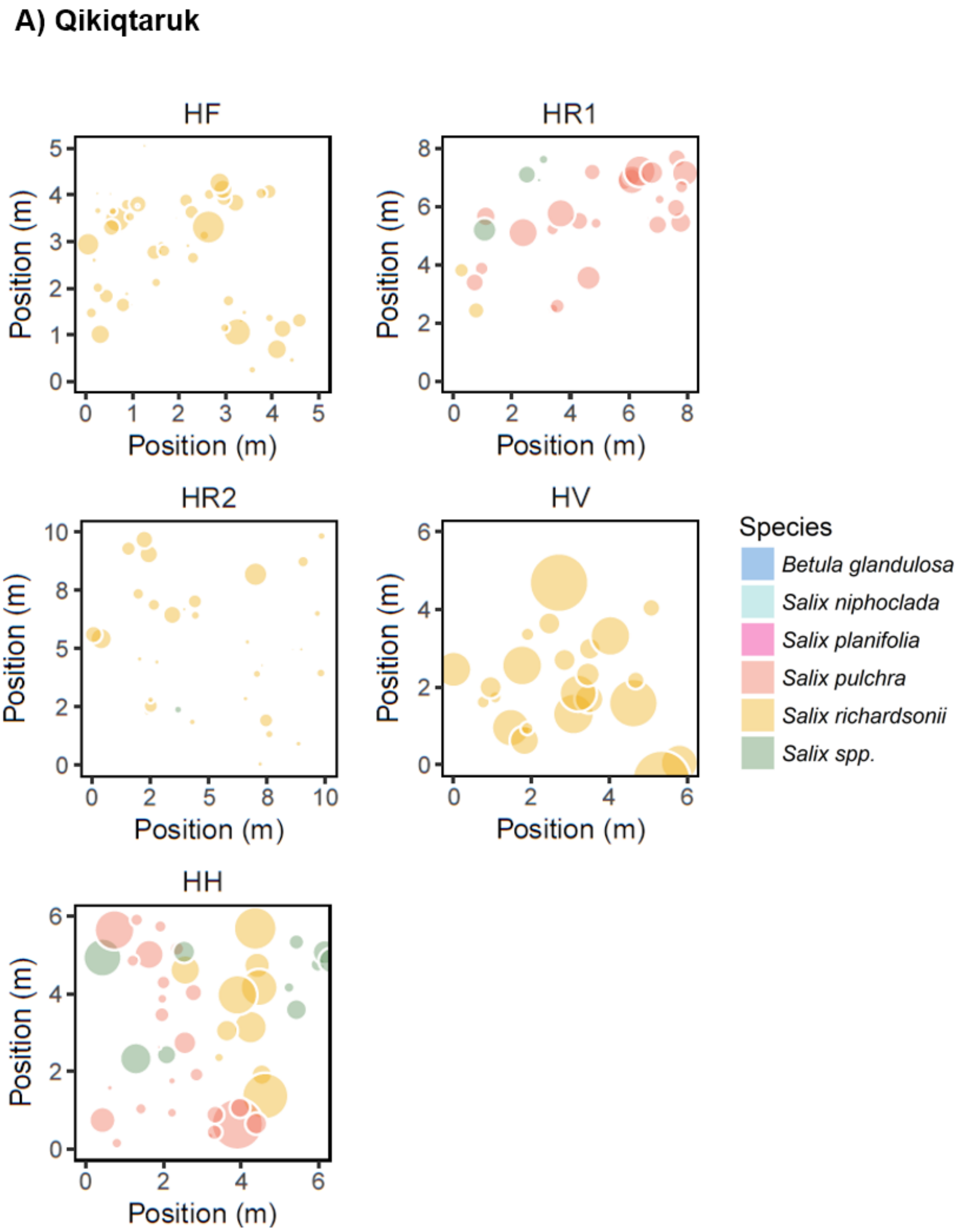


Figure S6-1 *Representation of the mapped plots at A) Qikiqtaruk, B) Kluane, C) Umiujaq and D) Salluit, showing the position and species identity of the individuals, with the diameter of the circles representing the largest canopy diameter. See Chapter 2 for details on mapping. (Continued on following pages)*

B) Kluane

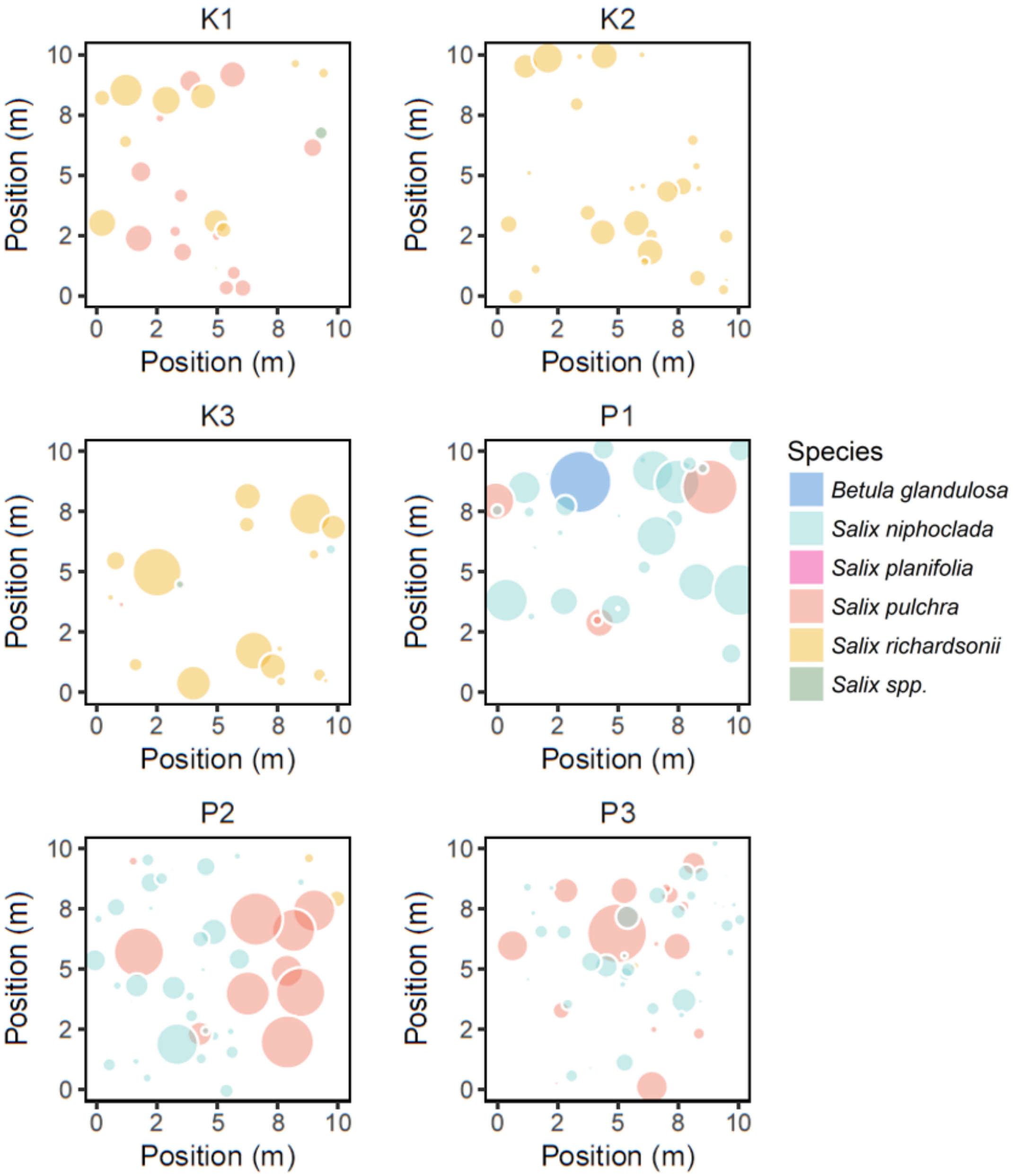


Figure S6-1 *(continued)*

C) Umiujaq

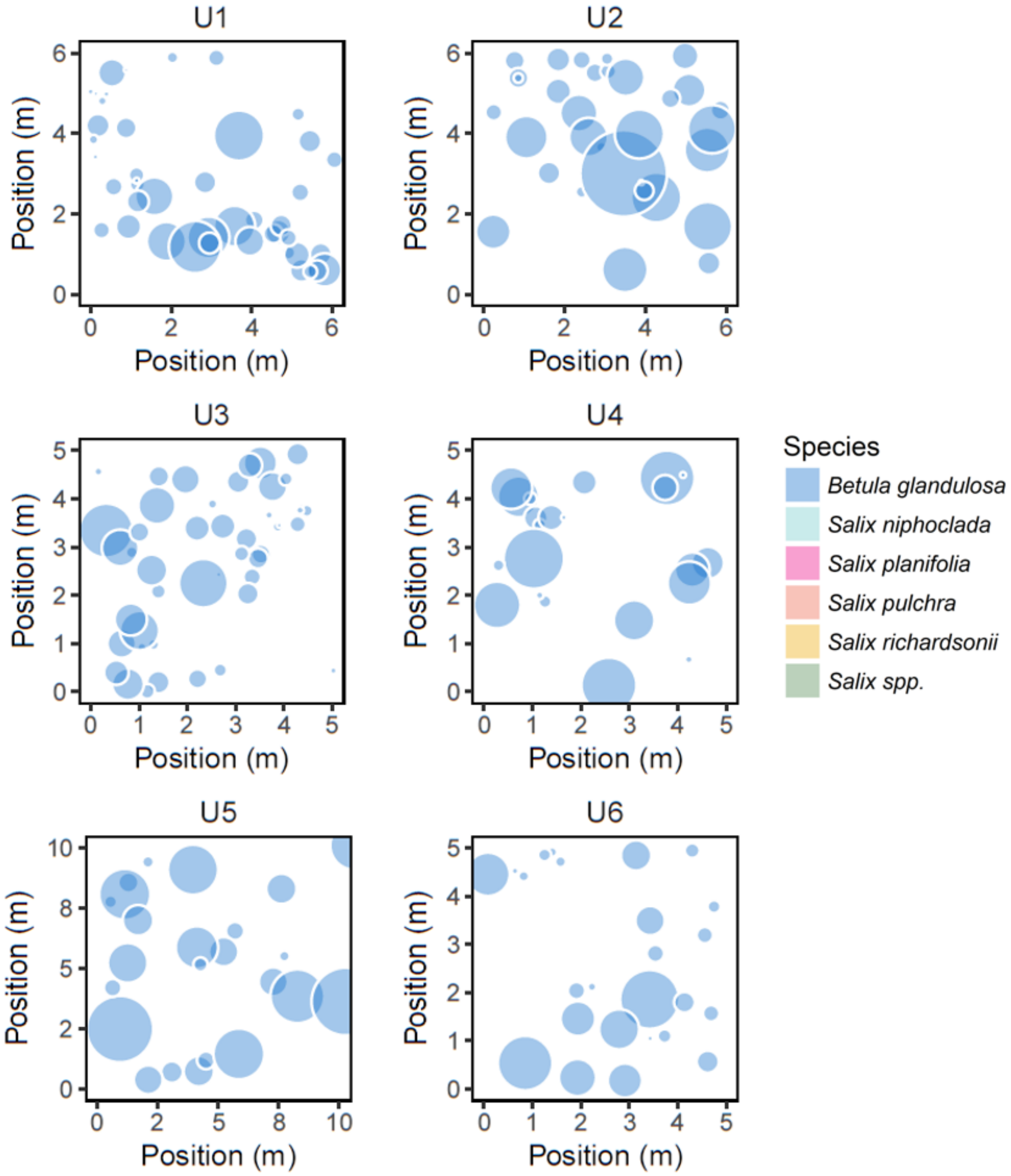


Figure S6-1 *(continued)*

D) Salluit

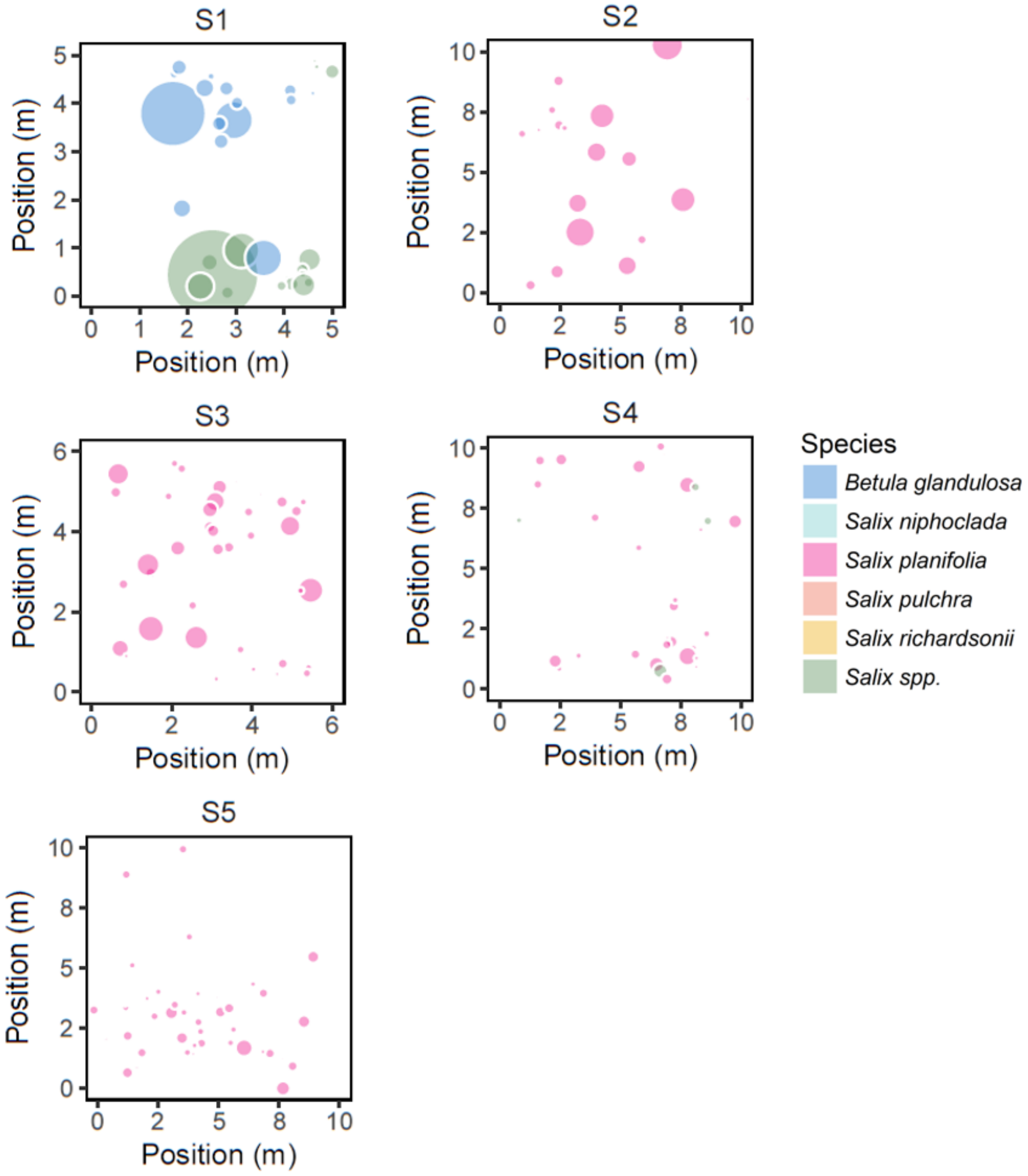


Figure S6-1 *(continued)*

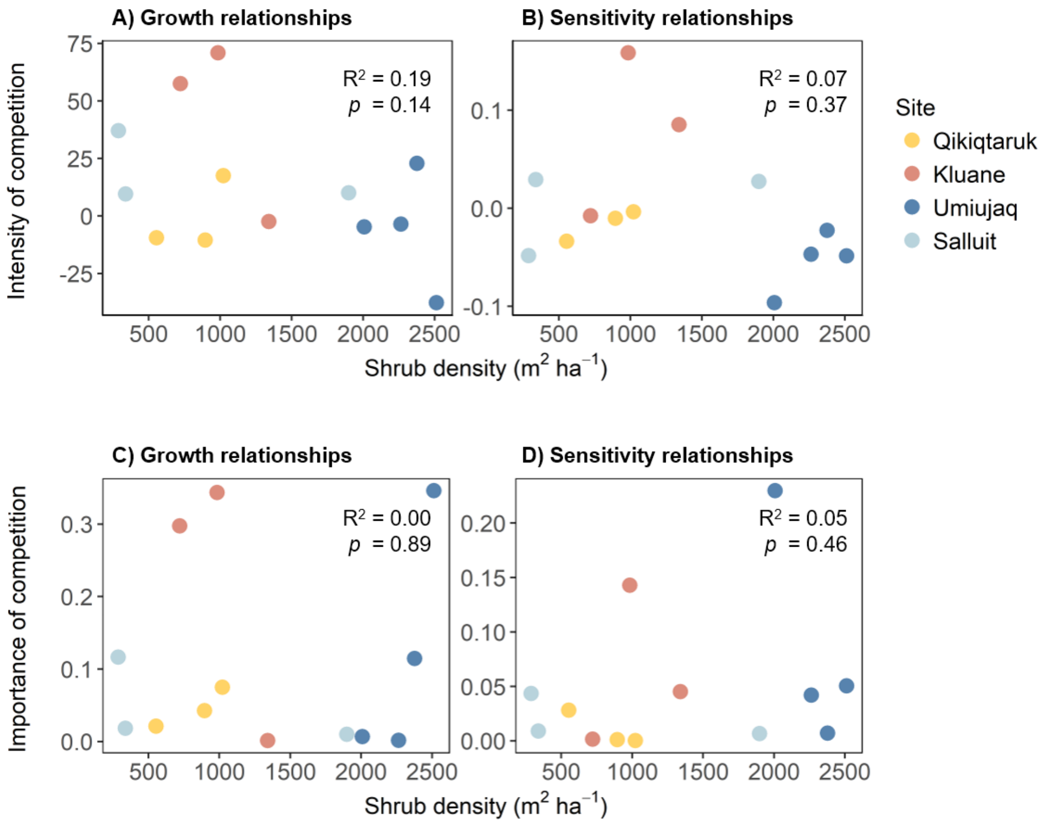


Figure S6-2 *Neither the intensity (A-B) nor the importance (C-D) of competitive effects on shrub radial growth (A-C) or sensitivity of growth to summer temperature (B-D) varied according to shrub density within a plot. Within a plot, intensity was defined as the slope of the linear regression between individual growth variables and the distance to the nearest neighbour; importance was defined as the coefficient of determination of these linear regressions (Welden and Slauson 1986).*