

School of Geosciences

Confirmation report

Climatic and biotic controls of shrub growth and expansion in the Arctic

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THESIS SUMMARY

Climate is warming rapidly in the Arctic, causing important changes to tundra ecosystems. Plants, and especially shrubs, are increasing in abundance, and their expansion is likely to promote further warming due to complex vegetation-atmosphere interactions. However, it is difficult to predict the strength of these feedbacks, because non-climatic factors can constrain vegetation dynamics locally. For instance, competitive interactions between shrubs could alter responses to climate by inducing resource limitations. The objective of my PhD is to quantify the relative influence of climate and plant interactions on shrub growth and expansion in the Arctic. I will address the following questions:

1) Does competition between shrubs alter the climate sensitivity of shrub growth? I will take advantage of a past canopy removal experiment to look for differences in the climate sensitivity of willow shrubs whose neighbours have been removed. I hypothesise that competition alleviation has triggered a growth release (wider growth rings) and a more consistent response to climate (higher correlations between ring width and summer temperature) in the post-removal period.

2) Does the relative importance of climatic versus biotic controls of shrub growth vary in relation to environmental severity? This study will be conducted at four sites of contrasting temperatures and productivity in subarctic and arctic Canada. At each site, I will map different types of shrub communities and collect wood samples from dominant shrub species to perform growth-ring analyses. I hypothesise that shrub growth is more limited by competition than by climate at the warmer, more productive sites, leading to weak climate-growth relationships. Conversely, if climate is the main determinant of growth at harsher sites, ring width should be positively correlated to summer temperatures. At the local scale, I expect that individuals with more or bigger neighbours will display lower climate sensitivity than isolated shrubs.

3) Is size a determinant of climate sensitivity? I hypothesise that taller shrubs respond more strongly to climate because of their superior resource acquisition abilities. I will analyse a large dataset comprising ring-width and plant size data for over 1000 individuals belonging to 16 shrub species across the circumpolar region (24 sites), using linear mixed models to determine whether greater individual size is associated with stronger climate-growth relationships.

4) Are there biotic constraints limiting tall shrub establishment above the shrubline? I hypothesise that biotic factors other than direct competition, such as allelopathy and seedbed availability, may prevent a range shift of tall shrubs even under a more favourable climate. I will set up a factorial sowing experiment to test for seedbed preferences (mineral soil, organic soil, moss, lichen) of two dominant willow species (*Salix richardsonii* and *S. pulchra*) under ambient and elevated temperatures. I expect seeds to germinate better on exposed mineral soil than in undisturbed vegetation, especially under warming. I will also run germination trials in growth chambers, exposing willow seeds to toxic solutions prepared from the leaves of dwarf

shrubs (*Empetrum nigrum*, *Vaccinium uliginosum*). I expect that seeds subjected to allelopathy will germinate to a lesser extent than control seeds.

Under a warming climate, shifting biotic interactions could alter the structure and composition of tundra communities. A better understanding of the nature and intensity of interactions between shrubs will help identify potential “winners” and “losers” in a warming context. Assessing the extent to which competitive interactions mitigate the climate response of shrub communities is critical to improve the accuracy of vegetation change projections across the tundra biome.

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Climate warming and vegetation change in the Arctic

High latitudes are expected to be disproportionately affected by current climate change (IPCC 2013). Arctic regions are already warming at a rate of +0.4°C to +1.1°C per decade (Comiso, 2003) and have experienced since 1950 four of the five warmest decades of the last two millennia (Kaufman et al., 2009). This rate of warming is projected to accelerate in the future (IPCC 2013).

This warming of the circumpolar region drives changes in Arctic plant communities, which are highly controlled by temperature (Bliss, 1971; Aerts et al., 2006). Longer, warmer summers can promote growth, advance phenology, and enhance reproductive effort and success (Arft et al., 1999; Henry et al., 2012). This increased performance at the individual level is the first step towards transformations of ecological communities at the landscape scale, such as densification of existing populations and altitudinal or latitudinal range shifts of ecosystem boundaries (Harsch et al., 2009; Myers-Smith et al., 2011a).

Shrubs have been identified as important actors in these current, tundra biome-wide vegetation changes. Over the last half-century, arctic and alpine sites all over the world have undergone shrub expansion (see Myers-Smith et al., 2011a for a comprehensive review). These observations are based on multiple lines of evidence including remote sensing (Verbyla, 2008; Beck and Goetz, 2011; McManus et al., 2012), repeat photographs (Tape et al., 2006; Myers-Smith et al., 2011b; Ropars and Boudreau, 2012; Formica et al., 2014) and plot-based surveys (Danby et al., 2011; Rundqvist et al., 2011; Elmendorf et al., 2012a). Furthermore, dendrochronological analyses (Johnstone and Henry, 1997; Bär et al., 2008; Forbes et al., 2010; Blok et al., 2011a) and warming experiments (Wookey et al., 1993; Chapin et al., 1995; Walker et al., 2006; Elmendorf et al., 2012b) have confirmed the positive effects of increased temperatures on the growth and reproduction of many shrub species. These widespread changes in shrub communities have the potential to dramatically alter arctic ecosystems and their processes.

Impacts of shrub expansion on ecosystem structure and function

In treeless environments, shrubs are usually the tallest and most long-lived growth forms, and they act as ecosystem engineers due to the many ways in which they interact with their biotic and abiotic environment (Cushman et al., 2010). It can thus be expected that changes in the structure and composition of shrub communities will also alter ecosystem functioning (Callaghan et al., 2004). In fact, shrubs are involved in a number of complex feedbacks to the atmosphere, some of which could accelerate global warming. For instance, shrub vegetation generally absorbs a higher fraction of the solar radiation than bare or lichen-covered ground (but see Blok et al., 2011b), which could lead to an increase in regional temperatures that would in turn promote further shrub expansion (Chapin et al., 2005).

Another potential positive feedback involves the trapping of snow by shrubs, which could increase soil temperature in winter, accelerating decomposition and making more nutrients available to plants (Sturm et al., 2005). The positive effects of snow trapping by shrubs on winter soil temperatures have been experimentally confirmed (Myers-Smith and Hik, 2013), but the evidence of associated changes in microbial processes or nutrient cycling is mixed (Myers-Smith and Hik, 2013; DeMarco et al., 2014; Vankoughnett and Grogan, 2014). However, biotic processes associated with shrub presence (e.g. litter deposition, microbial community composition, etc.), rather than physical properties, could still play an important role in driving soil dynamics (Myers-Smith and Hik, 2013).

Changes in shrub abundance could have many more effects on various biotic and abiotic ecosystem components. For instance, ground shading from shrub canopies in the summer can have a cooling effect on soil temperatures and reduce permafrost thaw (Blok et al., 2010). Shrubs are also important for wildlife, being a major food resource for large and small mammals (Ravolainen et al., 2014), birds (Tape et al., 2010) and insects (Rich et al., 2013). For instance, an increase in the population size of the Porcupine caribou herd (Alaska and Yukon) has also been tentatively linked to an increase in plant productivity over its range (Henry et al., 2012). Shrubs also provide shelter to some animals. For example, due to breeding preferences, an increase in tall shrubs could expand the habitat range of a species of migratory songbird, but reduce that of another (Boelman et al., 2014).

Because shrub expansion has so many potential implications over a wide range of ecosystem components and processes, vegetation-climate interactions need to be incorporated into Earth system models if we are to better project future Arctic change (Miller and Smith, 2012; Pearson et al., 2013).

Heterogeneity of shrub response

A major shortcoming of most current projections of vegetation change and its associated feedbacks is that they assume a uniform response of all shrub species across the tundra biome. In reality, an increasing number of studies highlight the important variability in shrub expansion between sites and species.

Spatial heterogeneity is the first aspect of this variability: although many sites are undergoing shrub expansion, other shrub populations – sometimes very close to expanding ones – have remained stable or experienced declines (Myers-Smith et al., 2011a; Callaghan et al., 2013). This variability is mainly attributable to local topography and its effects on soil thermal regime and moisture, snow accumulation patterns, nutrient cycling, etc. (Walker et al., 2006; Elmendorf et al., 2012a; Tape et al., 2012). Moreover, a synthesis of warming experiments has shown that expansion was more important in sites that were already warm to begin with (Elmendorf et al., 2012b), so that subarctic regions may experience greater vegetation change in the short term. Fire regime, herbivory and other disturbances can also lead to contrasting responses between sites (Callaghan et al., 2013).

Species-specific morphological, physiological and ecological characteristics add even more variability, rendering some species (or groups of species) more capable of responding to increased temperatures. For instance, tall shrubs have been identified as particularly responsive (Elmendorf et al., 2012a; Myers-Smith et al., in press.). This has been linked to their photosynthetic efficiency, high nutrient uptake and cycling rates, and energy allocation strategies (Bret-Harte et al., 2002; Heskell et al., 2013). Dwarf birch (*Betula nana*), for example, is opportunistic in its growth pattern, transforming short shoots into long, structural shoots when resources allow (Bret-Harte et al., 2002). Understanding species-specific differences in climate sensitivity has been identified as one of the main research priorities in shrub expansion research (Myers-Smith et al., 2011a).

Species possessing traits that allow rapid responses to change could benefit disproportionately from current arctic warming not only directly, but also through shifts in the outcome of biotic interactions. Differential growth responses to climate could lead to increased dominance of a few species that become more competitive as their performance is enhanced by warmer temperatures (Heegaard and Vandvik 2004). These changes in plant-plant interactions are of great importance as they could unbalance community composition and decrease diversity, affecting in turn ecosystem carbon balance, energy exchange and nutrient cycling (Callaghan et al., 2004; Aerts et al., 2006).

Plant-plant interactions

Plant competition theory and the stress gradient hypothesis (Bertness and Callaway, 1994) provide a useful framework for exploring the influence of biotic interactions on the response of tundra plant communities to climate change. On one hand, negative plant-plant interactions such as competition for light, water and nutrients are a key driver of plant population dynamics, influencing individual performance as well as community succession, composition, and diversity (Connell and Slatyer, 1977; Grime, 1977; Virtanen et al., 2013). On the other hand, competition is thought to decrease in importance along gradients of increasing severity of the growing environment, and even to switch to facilitation in highly stressful environments (Bertness and Callaway, 1994; Brooker and Callaghan, 1998). This change in the direction and magnitude of biotic interactions in relation to environmental severity is referred to as “the stress gradient hypothesis”.

In northern environments, plant-plant interactions affect vegetation dynamics in complex and sometimes opposing ways. For instance, tree seedlings often benefit from the presence of a “nurse” neighbour when they first emerge, but suffer from competition later on, which creates ecological conflicts between life stages (Grau et al., 2012; Cranston and Hermanutz, 2013). Studies on alpine plant communities (mostly herbs and forbs) have either supported the stress gradient hypothesis (Choler et al., 2001) or found no strong evidence of it (Dullinger et al., 2007). Few studies have investigated shrub-shrub interactions within this framework, although shrub growth seems to comply

broadly with the stress gradient hypothesis in subalpine heaths (Gerdol et al., 2000). However, a missing link remains to be investigated: are the effects of shrub-shrub interactions on individual performance reflected in the climate response of shrub communities? Trees growing at the treeline have been shown to be more climate-sensitive than trees experiencing competition in denser stands (Ettinger et al., 2011), and I propose that similar controls may be at work in shrub communities.

Research aims

My general objective is to determine how the climate response of Arctic shrub communities may be affected by plant-plant interactions. The four chapters detailed in the next section address specific questions that I will test during my PhD (Figure 1). This research will provide a better understanding of the determinants of shrub sensitivity to climate change in order to improve predictions of vegetation trajectories and their associated feedbacks in the Arctic.

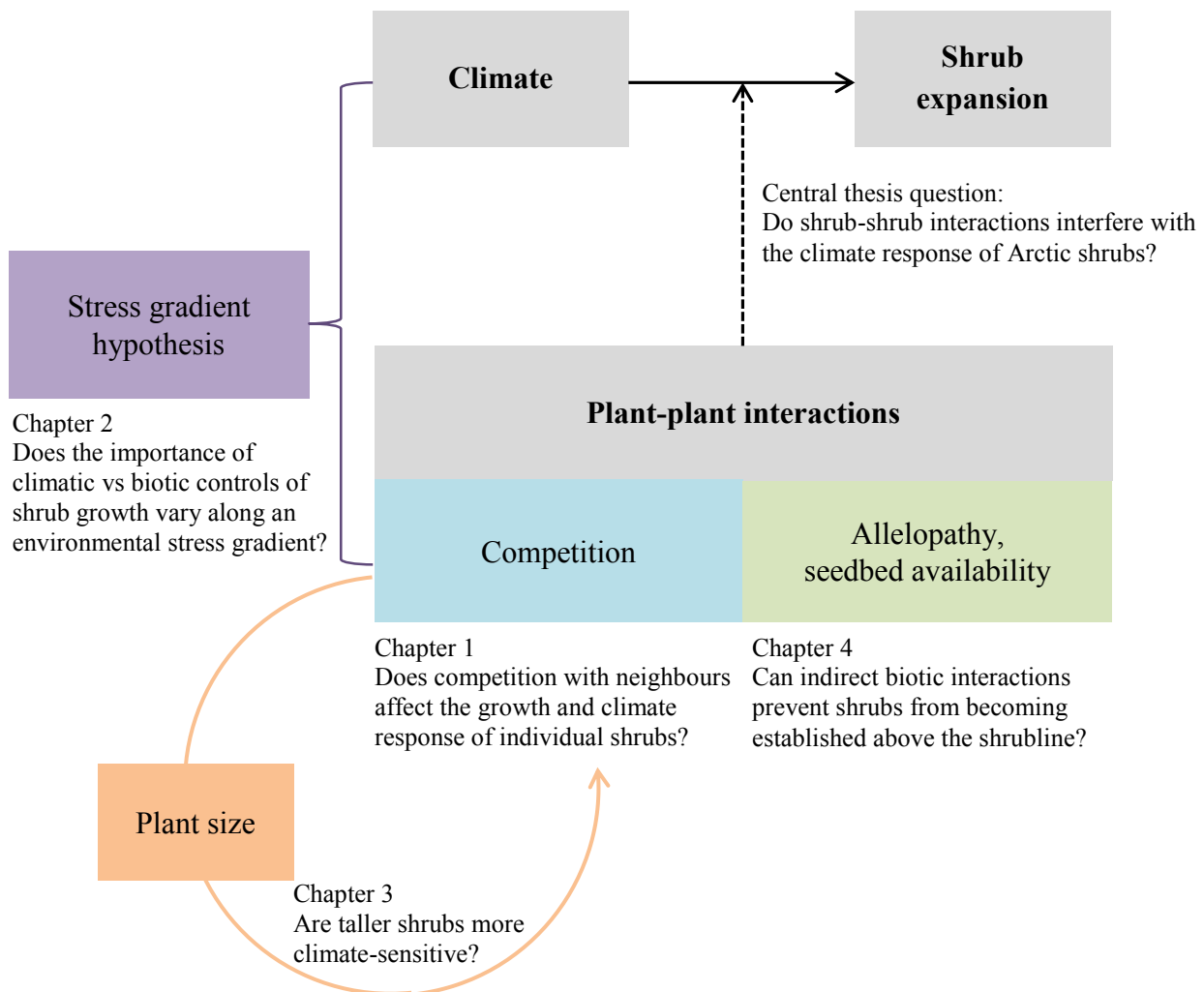


Figure 1. Conceptual plan of my PhD research.

Chapter 1 – Effects of competition alleviation on the climate sensitivity of sub-arctic shrubs

Background

Ecologists commonly use neighbour removal experiments to study plant-plant interactions (Brooker and Callaghan, 1998; Choler et al., 2008; Schöb et al., 2012). If target individuals experience a decrease in performance after the removal of a neighbour, the interaction can be said to have been facilitative, whereas enhanced performance after removal would suggest a release from competition. Such experiments have highlighted both types of interactions in Arctic shrubs, using shoot elongation or biomass as indicators of performance (Shevtsova et al., 1997; Gerdol et al., 2000).

However, very few studies have investigated the potential effect of competition alleviation on climate sensitivity. One study from a subarctic woodland in Northern Québec showed a suppression of dwarf birch (*Betula glandulosa*) radial growth by tree cover (Boudreau and Villeneuve-Simard, 2012). Once trees were removed, not only did *B. glandulosa* experience a growth release, but interannual radial growth patterns became better synchronised with growing season temperatures (Boudreau and Villeneuve-Simard, 2012). This study suggests that biotic interactions can interfere with growth-climate relationships. It is therefore likely that shrub-shrub competition in tundra ecosystems could have a similar effect, but this hypothesis has never been explicitly tested.

Objective and hypothesis

This chapter takes advantage of a past canopy removal experiment to explore changes in the climate sensitivity of willows (*Salix* spp.) following a decrease in competition intensity.

H1: Willows near the cleared plots have experienced higher climate sensitivity since the removal of their neighbours.

Henceforth, the term “climate sensitivity” should be understood to mean “correspondence between annual growth (here, ring width) and climatic variables (e.g. summer temperatures) over time” (cf. Myers-Smith et al., in prep.).

Methodology overview

The removal experiment was set up in 2007 in the Ruby Range Mountains of the Kluane region (Yukon Territory, Canada). All shrub canopy vegetation was clipped to the ground in six circular plots of 6 m diameter, while vegetation was left intact in six control plots of the same size. The experiment was maintained in 2008-09 (Appendix I; see Myers-Smith and Hik, 2013 for full details).

I will revisit this site in June 2015 and collect wood samples in the vicinity of each of the 12 plots (control and removal) for growth-ring analyses. Whenever possible, the samples will be taken at the root collar (root-shoot interface, i.e. the oldest part of the individual). Target species are *Salix richardsonii*, *S. pulchra* and *S. glauca* (and possibly *Betula glandulosa*). I will harvest all root collars (up to 30 per plot) in a 1-m-wide corridor circling each plot.

Wood samples will be shipped back to Edinburgh, where I will process them using shrub-adapted dendrochronological techniques (Schweingruber and Poschlod, 2005; Myers-Smith et al., 2015) involving thin sections that will be stained and mounted on microscope slides. Ring width will be measured on four radii per section from high-resolution photographs.

Data analysis

I will process and explore dendrochronological data using dedicated R packages such as *dplR* for crossdating and *BootRes* for correlation and response functions with climate data.

For each individual, I will compute several indicators of climate sensitivity (Annex I) separately for pre- (1999-2006) and post-removal (2007-2014) periods (even if the shrub is older, the pre-removal period will be constrained to the length of the second period to achieve a balanced design). I will then perform repeated measures ANOVAs to look for differences in growth (raw ring width) and in climate sensitivity before and after the removal and for control (no removal) versus experimental (removal) shrubs.

Anticipated results

I expect mean ring width to be significantly higher in the post-removal period for shrubs that have experienced a decrease in competition. If competition was indeed masking the climate signal (H1), the correlation between ring width and climate data in the pre-removal period can be expected to be weak or non-significant. This should shift to a significant, positive correlation after the removal. I do not expect control shrubs to display significant temporal changes in climate sensitivity.

Chapter 2 – Effects of plant-plant interactions on the climate sensitivity of Arctic shrub communities

Background

Meta-analyses of plot-based changes (Elmendorf et al., 2012a) and of dendroecological data (Myers-Smith et al. in prep.) suggest that shrub species become more climate-sensitive towards their northern or upslope range limit. These findings fall in line with the stress gradient hypothesis. Moreover, Myers-Smith et al. (in press.) have observed high inter-individual variability in climate sensitivity across sites, with 5-97% of individuals showing significant correlations with summer temperatures. Part of this variability might be explained by the intensity of plant-plant interactions prevailing at different sites, and the absence of a common signal between individuals could be due to competition overriding the influence of climate. In this study, I will use spatial and dendroecological analyses to separate and quantify the roles of climate and biotic interactions as determinants of shrub growth.

Objectives and hypotheses

The objectives of this chapter are: (1) to compare the climate sensitivity of shrub communities along severity gradients and (2) to assess the effects of plant-plant interactions on individual climate sensitivity within these communities. I hypothesise that:

H1: As a corollary to the stress gradient hypothesis (Bertness and Callaway, 1994), the climate sensitivity of shrubs is higher at harsher, less productive sites because biotic interactions do not constrain growth as much as in warmer, more benign sites.

H2: Competition with neighbours negatively affects the climate sensitivity of individual shrubs.

Methodology overview

The study will take place at four sites in Northern Canada: Kluane and Herschel Island in the Yukon Territory and Umiujaq and Salluit in Northern Québec (Figure 2). The Kluane and Umiujaq sites belong to the subarctic climate zone, while Herschel Island and Salluit experience an Arctic climate (Appendix II).

I will sample three types of shrub communities at each of the four sites: birch-dominated, willow-dominated and dwarf shrub-dominated communities (Figure 3). For each community type, I will set up two plots (ca. 20 m x 20 m; exact size to be determined on the field) in which shrubs of the three most abundant species will be mapped, measured (height and crown area) and sampled. I will collect 15 wood samples per species per plot. Mapping will be done *a posteriori* using photographs of the plot and image processing software (ImageJ).



Figure 2. Location of the four study sites in Northern Canada.

To capture enough variability in the intensity of inter-shrub competition, the 15 samples will be harvested on 5 individuals with a neighbour (i.e. a shrub more than 10 cm tall or 20 cm wide) less than 2 m away, 5 individuals with a neighbour 2-5 m away, and 5 individuals without any neighbour in a 5-m radius.

In Kluane, I will also sample willow-dominated communities across an elevational gradient (2 plots at each of three different altitudes). Sampling will be carried in the same way as described above, and this subset will be used to provide a local-scale test of the stress-gradient hypothesis.

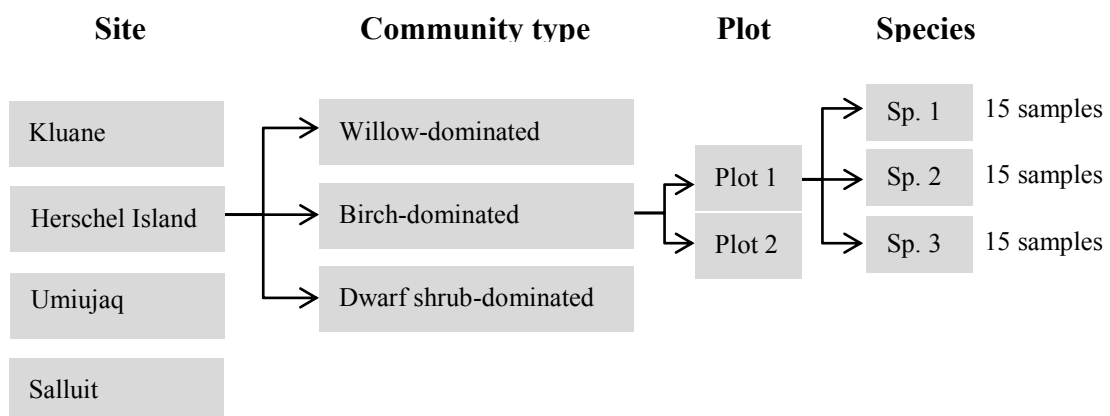


Figure 3. Sampling hierarchy for Chapter 2: each site will have the same nested sampling design as shown here for Herschel Island, for a total of 1080 wood samples. Additional sampling will be carried out at Kluane (3 willow-dominated communities; not shown).

Data analysis

I will process wood samples and calculate climate sensitivity as described previously (Chapter 1, Appendix I). Climate data for all sites are freely available from the Government of Canada's website (http://climate.weather.gc.ca/index_e.html) and the Climate Research Unit of the University of East Anglia (<http://www.cru.uea.ac.uk/>).

I will also calculate several indicators of environmental severity for each site, resulting in a series of stress gradients. These indicators will include mean and minimum summer and winter temperatures, growing season length, growing season thermal sum (degree-days) and mean percentage cover of vascular species within a plot (inspired from Dullinger et al., 2007). The four sites will not necessarily rank in the same order for all variables.

I will then use linear mixed models to try and relate climate sensitivity to environmental stress (see Appendix II for model terms). I will conduct these analyses at the local scale (Kluane elevation gradient) and at the pan-Canadian scale (all four sites).

To address the second objective and evaluate the importance of plant-plant interactions at the individual scale, I will combine ring-width data and spatial analysis. Using the community maps, I will run nearest neighbour analyses (e.g. R packages "spatial", "spatstat" and "spdep") and extract, for every individual, the distance to, and the size and identity (species) of, its nearest neighbour. I will then use these variables as fixed effects in a linear mixed model to investigate their impact on the climate sensitivity of individuals (Appendix II).

Anticipated results

If climate sensitivity increases along a severity gradient (H1), shrub communities should respond to climate more strongly at sites that are colder or have short growing seasons (e.g. Salluit, Herschel Island). Correlations between annual growth and summer temperatures are expected to be high at these sites, while weaker or non-significant relationships are anticipated for the warmer subarctic sites (Kluane, Umiujaq).

If competition negatively affects the climate response of shrubs (H2), there should be a significant negative relationship between the climate sensitivity and the number, size and/or proximity of neighbours of an individual.

Chapter 3 – Size as a determinant of climate sensitivity

Background

The size of a plant has implications regarding the way it interacts with its biotic and abiotic environment. The growth and phenology of smaller shrubs is more likely to be dependent on microtopography (snow depth, temperature at ground level, etc.) compared to taller shrubs (Buras and Wilmking, 2014). Moreover, small growth forms are more susceptible to be outcompeted by taller plants for resources such as light, water and nutrients (Grime, 2001). Better competitive ability might therefore explain in part why tall shrubs seem more responsive to climate change than dwarf shrubs (Elmendorf et al., 2012a; Myers-Smith et al., in press.).

Objective and hypothesis

The objective of this chapter is to determine the importance of size as a determinant of climate sensitivity.

H1: Larger shrubs are more climate-sensitive because they are less limited by local factors such as resource availability and microtopography.

Methods

I will analyse a subset of an extensive dataset collected by members of the Shrub Hub (<http://shrubhub.biology.ualberta.ca/>). About a third of this dataset contains associated plant height and/or patch width data (1019 individuals from 21 species and 24 sites; Appendix III) that can be used to test for individual-level differences in climate sensitivity in relation to plant size.

Data analysis

At the moment, I have only conducted exploratory analyses comparing the climate sensitivity of one species across sites, or of various species within a site. I will next work on integrating all data within linear mixed models (package nlme in R) using shrub height and width as fixed effects and year, individual, species and site as random effects. Indicators of climate sensitivity will again be the response variables (Chapter 1, Appendix I).

Anticipated results

Assuming that taller shrubs are more efficient at capturing resources and therefore less limited by site-specific factors (H1), I should find a significant and positive relationship between the size of an individual and its climate sensitivity.

Chapter 4 – Biotic limitations to tall shrub invasion in the dwarf shrub tundra

Background

The tall shrub/dwarf shrub tundra ecotone is likely to be very responsive to climate change (Myers-Smith et al., in press.), but range shifts can only occur if tall shrubs succeed in becoming established above their current distribution limit. Warmer temperatures could promote regeneration by increasing the production of viable seeds (Meunier et al., 2007), enhancing germination (Thompson and Naeem, 1996; Milbau et al., 2009) and improving seedling growth and survival (Weih and Karlsson, 1999; Grau et al., 2012).

However, even if climate improves, many other barriers must be overcome before successful regeneration can occur. Treeline studies have shown that recruitment is often much higher on exposed mineral soil than in undisturbed vegetation (Munier et al., 2010; Dufour Tremblay and Boudreau, 2011). Observations of important recruitment of green alder (*Alnus viridis* subsp. *fruticosa*) in burned sites (Lantz et al., 2010) and on thaw slumps (Lantz et al., 2009) suggest that the same could apply to shrubs, but this remains to be more widely tested.

Other treeline studies have demonstrated the negative impacts of allelopathic compounds produced by dwarf shrubs (especially ericaceous species) on tree seeds and seedlings (Nilsson and Zackrisson, 1992; Dufour Tremblay et al., 2012). To our knowledge, this potential bottleneck has never been investigated at the tall shrub/dwarf shrub boundary despite the obvious parallels between treeline and shrubline ecology.

Objective and hypotheses

The objective of this chapter is to determine whether two types of biotic constraints, seedbed availability and allelopathy, could offset the benefits of increased temperatures for willow recruitment above the tall shrubline.

H1: In the absence of biotic constraints, higher temperatures promote germination of willow seeds.

H2: Availability of suitable seedbeds limits the establishment of tall willows (*Salix richardsonii* and *S. pulchra*) above their distribution range.

H3: Allelopathy from dwarf shrub species (*Empetrum nigrum*, *Vaccinium uliginosum*) inhibits the germination of willow seeds.

Methodology overview

To investigate the seedbed preferences of willows, I will set up a factorial sowing experiment. I will collect *Salix richardsonii* and *S. pulchra* seeds and sow them in four different seedbed types: exposed mineral soil, moss, lichen, and organic soil. Half of the plots will furthermore be subjected to increased temperatures using small open-top plastic greenhouses (Danby and Hik, 2007). So far, very few studies have examined

biotic interactions in a warming context (HilleRisLambers et al., 2013). The experiment will be conducted simultaneously in Kluane (altitudinal tall shrubline) and Herschel Island (approximate latitudinal range margin of tall shrub species). It will be set up in July 2015 and monitored and repeated in July 2016.

I will also record the availability (percent cover) of these seedbeds in the natural environment in 50 plots (1 m x 1 m) in the dwarf shrub tundra at each site. If seedlings are present, I will count them and record the type of seedbed in which they occur.

To test the allelopathy hypothesis, I will subject *Salix* seeds (*S. richardsonii* and *S. pulchra*) to leaf leachates from two dwarf shrub species: *Empetrum hermaphroditum* and *Vaccinium uliginosum*. Leaves and seeds will be collected in Kluane and Herschel during the summer 2015 and brought back to Edinburgh. This experiment will be replicated with seeds of *Betula glandulosa* by my co-supervisor's team in Québec.

Allelopathic solutions will be prepared by soaking fresh leaves in distilled water (Nilsson and Zackrisson, 1992; Appendix IV). The experiment will be run in two growth chambers (Biological Sciences, King's Buildings) experiencing different climate regimes (warm and cool). I will use five replicates of 20 seeds for each of the 40 combinations of site/species/allelopathic treatment/temperature (Appendix IV).

Data analysis

For both experiments, I will compare final germination (%) between treatments using analysis of variance (ANOVA). For the seedling and seedbed survey, I will compare seedbed preference (proportion of seedlings found in each seedbed type) and availability (percent cover of each type) using a chi-square test.

Anticipated results

Little is known about the establishment preferences of willows, and the combination of this sowing experiment and a survey of naturally occurring seedbeds above the shrubline should help us predict if, and to what extent, potential range shifts could occur. If exposed mineral soil is the preferred seedbed of *Salix* spp. – as suggested by Lantz et al. (2009, 2010) – final germination of sown seeds should be higher on this substrate than on any other seedbed type. Likewise, naturally established seedlings, if any, should be found in higher proportion on mineral soil than on other seedbed types. If germination is promoted by warm temperatures (H1), emergence should be greater for the greenhouse treatments.

The sensitivity of shrub species to allelopathic compounds has never been investigated. If willow seeds are vulnerable to these chemical compounds (H3), the final germination of seeds subjected to leaf leachates should be significantly lower than that of control seeds.

PROJECT RESOURCES

Material resources

Most of this project is based on field-collected data and samples. Planning for my first fieldwork season (mid-June to mid-August 2015) started in March 2015 with the rest of the research team. In Kluane, I will be based at the Kluane Lake Research station (managed by the Arctic Institute of North America). Accommodation on Herschel Island is facilitated by Herschel Island-Qikiqtaruk Territorial Park. In Northern Québec, I will stay at the Umiujaq and Salluit research stations, which are administered by the Centre for Northern Studies (Université Laval, Québec). I aim to spend around two weeks at each site.

Bookings for air travel and accommodation will be made in April 2015. Other considerations such as research permits, authorisations from national parks and import/export paperwork for biological material are currently being addressed. Any equipment needed and not already available on the stations will be purchased in April.

I will need to process my wood samples (Chap. 1 and 2) in a dendroecology laboratory. These analyses require access to basic lab equipment (hotplates, microscope slides, etc.), a microtome, staining solutions, and a dissecting microscope fitted with a digital camera. I am currently working with Isla Myers-Smith and Mathew Williams to put together a list of potential equipment that could be purchased to extend the dendroecological facilities available in the Crew Labs of the School of Geosciences. If this proposal is unsuccessful, I will enquire at the Royal Botanic Garden Edinburgh and the School of Biological Sciences, University of Edinburgh.

I will need to use growth cabinets to conduct my germination trials (Chap. 4). Facilities are available on-campus in the School of Biological Sciences and will be booked in April 2015 (to start in February 2016).

Funding

The estimated cost of my contribution to the 2015 fieldwork season is around £6300 (Table 1). Most of my Research Training and Support Grant (£1000/y x 3 y) will go towards this (saving around £800 for conference travel, training courses, etc.). I will receive additional contributions from my supervisor Isla Myers-Smith for fieldwork in the Yukon, and support from my external co-supervisor Stéphane Boudreau for fieldwork in Québec. I will keep on seeking further funding opportunities over the course of my PhD. For instance, I have recently applied for the Canadian Centennial Scholarship Fund (£1000-£5000). If I am successful, this grant would contribute to a second field season, allowing me to expand the scope of my first chapter by adding more sites.

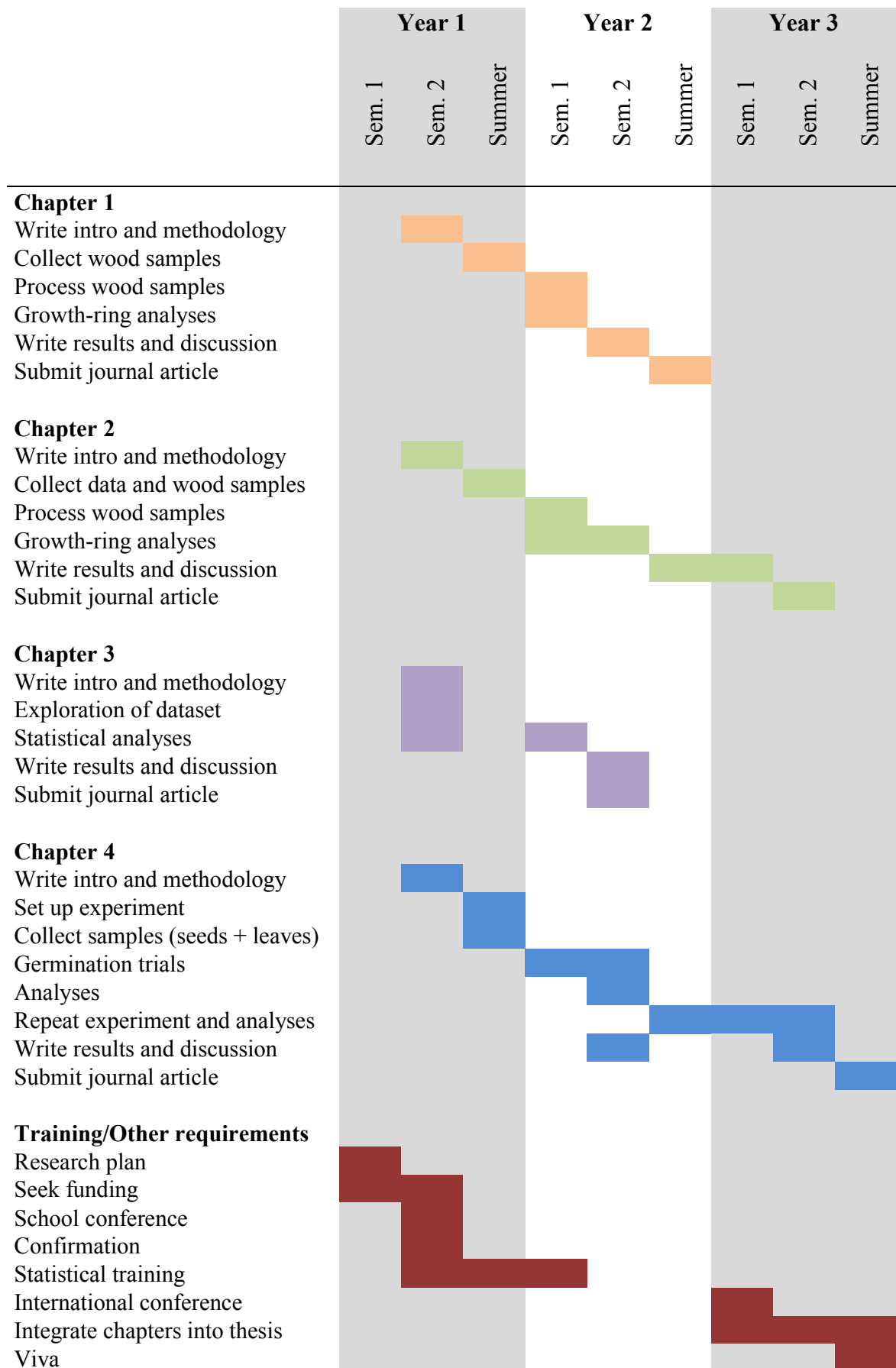
Table 1. Budget for the 2015 fieldwork season and for other PhD activities.

Activity	£
FIELDWORK	
Travel	
Commercial flights to, from and within Canada	2 500
Contribution to chartered airplane (Herschel Island)	700
Car hire (Kluane)	100
Road travel in Northern Quebec	500
Accommodation and food	
Kluane Lake Research Station (2 w.)	500
Inuvik/Herschel (2 w.)	600
Kuujjuarapik (2 w.)	400
Salluit (2 w.)	400
Equipment	200
Travel insurance	200
Shipping of samples/equipment	200
LAB WORK AND ANALYSES	
Access to growth chambers	ca. 300
Access to Crew Labs	100
OTHER EXPENSES	
Conference travel	500
Statistical training course (?)	tbd
TOTAL	7 200

TIME PLAN

The next six months will be dedicated to planning, undertaking and completing fieldwork for most of my thesis chapters. I have started exploring the dataset of plant size and radial growth (Chapter 3) and intend to design and run most of the analyses before leaving for fieldwork in June. When I get back from Canada, I will process my wood samples (fall 2015), take ring-width measurements and analyse the data (winter 2016). At the same time (winter 2016), I will run my germination trials. I will stage my writing over the whole span of my PhD and format the manuscripts into chapters during my third year (Table 2).

Table 2. Thesis completion timeline.



SUPERVISORY ARRANGEMENTS

My main supervisor is Dr Isla Myers-Smith, Chancellor's Fellow in the Global Change Research Group. My project fits in directly with her work on shrub expansion around the Arctic, and she will be able to provide guidance and support at all stages of my project. We are at present meeting as needed, in a rather informal but frequent manner approximately every two to three weeks. Our research team meets every other week for discussion/training sessions.

My second supervisor within the School of Geosciences is Dr Mathew Williams, who specialises in modelling the carbon cycle. He is interested in the sensitivity of Arctic ecosystems to warming and could therefore bring interesting ideas and scope to my project. He also has some expertise in dendroecology and ecophysiology, which will be relevant for my proposed research. I will contact him as needed, and we will hold one committee meeting every semester.

Dr Stéphane Boudreau (Université Laval, Québec City) will be my external co-supervisor. He also works on shrub expansion in the Arctic and will provide complementary advice as to the direction of the project. Most of his research is based in Northern Québec, so I will benefit from the infrastructures of the Centre for Northern Studies, to which he belongs, while working there.

My advisor is Dr Kyle Dexter, lecturer in Terrestrial Vegetation Ecology.

DATA MANAGEMENT

Data for chapters 1, 2, and 4 will be generated through my fieldwork and sample processing. They will consist of dendrochronological data (chap. 1, 2), spatial data (chap. 2) and experimental results (chap. 4).

Climate data from weather stations near my fieldwork sites will be needed to perform climate-growth analyses. These can be downloaded for free from the Government of Canada website (<http://climate.weather.gc.ca/>).

To investigate the effect of size on climate sensitivity (chap. 3), I will use a large dataset assembled by the sTUNDRA working group (<http://www.idiv-biodiversity.de/sdiv/workshops/workshops-2014/stundra>). Use of this dataset will comply with the Data Use and Authorship Policy of the group (Appendix V).

Data will be stored primarily on my backed-up desktop space in the School of Geosciences, with frequent backups to an external drive, to my personal laptop and to the UoE research Data Store. Digital backups (photos) of notebooks will be made each night on the field. The data and R code for all my statistical analyses will be stored with version control in a private GitHub online repository maintained by the sTUNDRA research group and Dr Isla Myers-Smith. My data will be made public at the time of publication through the Polar Data Catalogue (<https://www.polardata.ca/>).

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Study site

Ruby Range Mountains, Yukon Territory, Canada (61.22°N, 138.28°W)

Canopy removal experiment

In 2007, six circular plots (diameter = 6 m) were cleared of all vegetation as part of an experiment on snow-shrub interactions (Fig. A1.1; Myers-Smith and Hik, 2013). The canopy removal was maintained in 2008- 2009 by clipping all regrowth to the ground.

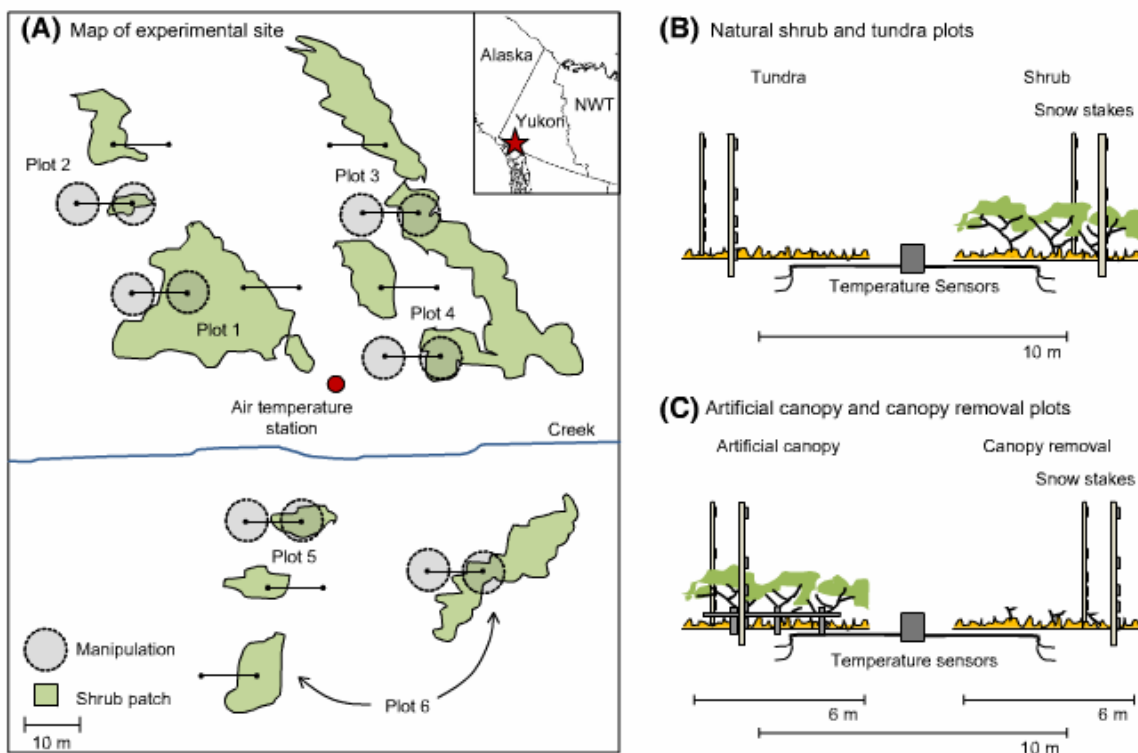


Figure A1.1. The location of experimental plots (A) and the design of the canopy manipulation (B and C). The inset indicates the general location of the study site in the Yukon Territory. The dashed gray circles represent the manipulated artificial canopy and canopy removal treatments and the green polygons are shrub patches. *Image and caption adapted from Myers-Smith and Hik, 2013.*

Calculation of climate sensitivity

The following indicators of climate sensitivity will be generated by mixed models using monthly temperature and precipitation data as fixed effects, year within individual as random nested effects and ring-width as the response variable, as described by Myers-Smith et al. (in press):

- ΔAIC between the best climate model and a null model
- R^2 of the best climate model
- Slope of the best climate model
- Percentage of individuals responding significantly to the best climate variable

Study sites

The study sites are Kluane and Herschel Island in the Yukon Territory and Umiujaq and Salluit in Northern Québec (Table A2.1).

Table A2.1. Description of the four study sites in Northern Canada.

Site	Latitude	Longitude	July temp.	Feb. temp.
Umiujaq ¹	56.6	-76.5	12.2 °C	-22.4°C
Salluit ¹	62.2	-75.6	9.6°C	-23.1°C
Kluane ¹	61.1	-138.7	13.0°C	-18.0°C
Herschel ²	69.6	-139.9	8.7°C	-26.3°C

1. Source: INTERAC network: <http://www.eu-interact.org/field-sites/canada-9/>

2. Source: Burn and Zhang, 2009.

Data analysis

I will address my research questions through linear mixed-effects models, which can appropriately handle the spatial structure and temporal replication of my data (Table A2.2).

Table A2.2. Model terms for mixed model analyses linking climate sensitivity of shrubs to A) environmental severity and B) competition with neighbours.

A. Does climate sensitivity of shrubs vary according to environmental stress?		
Response variables	Fixed effects	Random effects
ΔAIC	Mean summer temperature	Individual
R ²	Min. summer temperature	Plot
Slope	Mean winter temperature	
% indiv. signif.	Min. winter temperature	
	Growing season length	
	Sum of growing degree-days	
	% cover of vascular species	
B. Do neighbours affect the climate sensitivity of an individual?		
Response variables	Fixed effects	Random effects
ΔAIC	Distance to nearest neighbour	Individual
R ²	Identity of nearest neighbour	Plot
Slope	Height of nearest neighbour	
% indiv. signif.	Width of nearest neighbour	

APPENDIX III. SUPPLEMENTARY INFORMATION FOR CHAPTER 3

The dataset used for this chapter comprises ring width and plant size (height and/or width) data for over 1000 individuals from many sites (Table A3.1) and species (Table A3.2).

Table A3.1. Structure of the plant size dataset.

Country	Site	N species	N individuals	Height data	Width data
Canada	Nain	2	43	x	x
	Nowell Lake	1	40	x	
	Wakeham Bay	1	19	x	x
	Alexandra Fjord	1	29		x
	Baker Lake	1	50	x	x
	Ellesmere Island	1	19		x
	Resolute Bay	1	31		x
	Dempster	6	41	x	x
	Herschel Island	5	46	x	x
	Kluane	10	297	x	x
Greenland	Arsuk Fjord	1	26	x	
	Disco island	1	30	x	
	Zackenbergl-fell-field	1	31		x
Norway	Endalen	1	32	x	
	Spitsbergen	1	10	x	
	Finse	2	20	x	x
	Minnestølen	1	40	x	x
Russia	AFYL	1	24	x	
	SLYL	1	29	x	
	SLVR	1	39	x	
	SLYR	1	27	x	
	Kytalyk	2	38	x	
Sweden	Abisko	1	33	x	
U.S.A.	Denali	4	25	x	

Table A3.2. List of the species for which height and/or width data is available.

Genus	Species
<i>Alnus</i>	<i>viridis</i> ssp. <i>crispa</i> ; ssp. <i>fruticosa</i>
<i>Betula</i>	<i>glandulosa</i> ; <i>nana</i> ; <i>pubescens</i>
<i>Cassiope</i>	<i>tetragona</i>
<i>Juniperus</i>	<i>nana</i>
<i>Salix</i>	<i>alaxensis</i> ; <i>arbusculoides</i> ; <i>arctica</i> ; <i>barclayi</i> ; <i>barrattiana</i> ; <i>lapponum</i> ; <i>glauc</i> ; <i>lanata</i> ; <i>myrtillifolia</i> ; <i>niphoclada</i> ; <i>polaris</i> ; <i>pulchra</i> ; <i>richardsonii</i> ; <i>setchelliana</i>

Seedbed preferences

Sites: Kluane, Herschel Island

Seedling survey:

At each site, I will position 5 x 50-m-long linear transects set apart by 25 m. Every 5 m along the transects, I will record the percent cover of seedbed types (mineral soil, organic soil, moss, lichen, litter) in a 1 m x 1 m quadrat. If seedlings are present, I will record the type of substrate on which they occur. It might not be possible to identify young seedlings to the species, but shrubs should be distinguishable from other plant groups.

Sowing experiment:

At each site, I will set up ten blocks of 8 plots with the following factorial treatments:

- Seedbed type: mineral soil, organic soil, moss, lichen
- Temperature: warm vs control

Plots will be 40 cm x 40 cm in size. At the center of each plot, 25 seeds from both *Salix richardsonii* and *S. pulchra* will be sown in a 5 x 5 arrangement, leaving 1 cm between each seed and 10 cm between the sowing locations of the two species (Figure A4.1). Ripe seeds will be collected from neighbouring willows (min. 30 individuals to avoid genetic bias). Emergence will be recorded at the end of the summer (2015) and again the following summer (2016) as seeds are likely to require a cold stratification period before germinating. The experiment will be repeated in 2016.

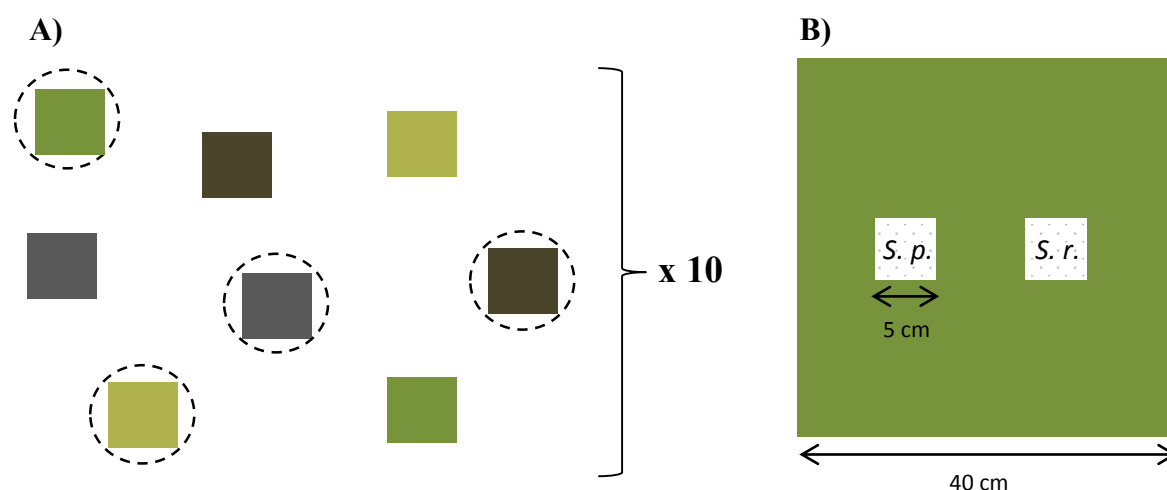


Figure A4.1. Experimental set-up for the seedbed experiment. A) An experimental block with four seedbed types (mineral soil, organic soil, moss, lichen) and two temperature treatments (increased T. using greenhouses (circles), and ambient T). B) Detail of a single plot: two subplots in the center will receive 25 seeds of *Salix pulchra* (S. p.) and *S. richardsonii* (S. r.).

The elevated temperature treatment will be achieved by surrounding the plots with small greenhouses made of flexible plastic sheet bolted on wooden stakes (Figure A4.2; Danby and Hik, 2007). Actual dimensions will be ca. 60 cm wide at the base, 40 cm wide at the top and 30 cm in height.

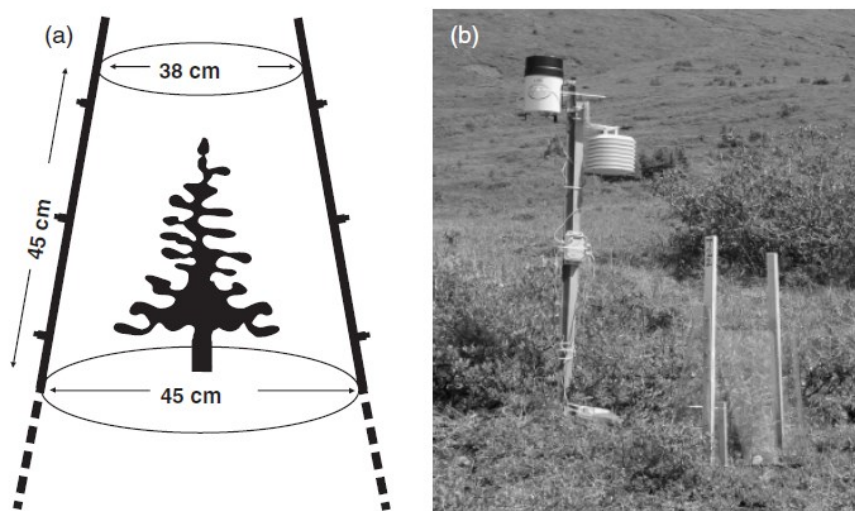


Figure A4.2. Open-top chamber made of a polycarbonate panel bolted to wooden stakes. A) Design of the open-top chamber, B) open-top chamber in the field. Figure from Danby and Hik, 2007.

Allelopathy experiment

On the field:

Seeds from *Salix richardsonii* and *S. pulchra* will be collected in Kluane and Herschel Island during the summer 2015. Catkins containing seeds will be collected on at least 40 randomly selected individuals of each species to avoid genetic bias, and then pooled together for the germination trials.

I will collect ca. 250 g of leaves from several individuals (ca. 15) of the dwarf shrub species *Vaccinium uliginosum* and *Empetrum nigrum*. Fresh leaves will be frozen until leachates can be prepared.

In the lab:

Since allelopathic compounds are naturally released by rain, the solutions will be prepared by soaking the leaves in distilled water for 48 hours (Nilsson and Zackrisson, 1992; Dufour Tremblay et al, 2012). Two concentrations will be used following Dufour Tremblay et al. (2012): a 15% solution obtained by soaking 150 g of leaves in 1000 mL of water, and a 7.5% solution obtained by diluting the first solution by half.

Allelopathic solutions will be added to Petri dishes containing 20 seeds of either *Salix richardsonii* or *S. pulchra* from both sites on a filter paper. Treatment levels are as follow:

Species:

- *Salix richardsonii*
- *Salix pulchra*

Site:

- Kluane
- Herschel Island

Allelopathy:

- Control (2 mL distilled water)
- Emni 15% (2 mL *E. nigrum* 15% solution)
- Emni 7.5% (2 mL *E. nigrum* 7.5% solution)
- Vacc 15% (2 mL *V. uliginosum* 15% solution)
- Vacc 7.5% (2 mL *V. uliginosum* 7.5% solution)

Temperature:

- Cool (growth chamber set at 15°/5°C day/night, photoperiod = 24 h)
- Warm (growth chamber set at 25°/15°C day/night, photoperiod = 24 h)

One block containing every combination will therefore require 40 Petri dishes, and the whole experiment will be replicated five times.

All seeds will have been cold-stratified at 4°C for three months before experimentation. As little information is available about the germination requirements of these two species, cold stratification and germination under constant light will ensure we lift temperature- or light-induced dormancy of the seeds, if any.

I will monitor germination every other day and add distilled water as needed to keep the filter papers moist.

APPENDIX V. DATA USE AND AUTHORSHIP POLICY FOR THE sTUNDRA WORKING GROUP

Please do not share access, distribute or publish data in the ShrubHub repository ***without*** first getting the consent of the sTUNDRA leaders (Isla, Sarah, Pieter and Anne). We will point you to the appropriate data contributors to check in with if you would like to use the data for projects other than those outlined above, and let you know if we are aware of someone already working on the project describe in order to avoid redundant effort. Not all of the data in the repository are public and the repository is hosted privately for this reason.

Data restrictions – All data that is not already public will be the property of the individual data contributors even when a part of the combined data set. Only participants who have contributed to the working group will have access to the data repository until such time as data in the repository are made public. A precondition for data use of non-public data is written permission from each data contributor. All data contributors will be listed in the supplementary materials and potentially included as authors (following the current TRY data protocols for multi-data contribution papers), though intellectual contribution to any papers will likely be the main criteria for authorship. There are probably around 150 data contributors to the repository including the growth, composition and trait data. We only have access to these data in the context of this working group and many contributors are entrusting us with these data, so we need to use best practices with these data.

Authorship agreement – Intellectual contributions to research approach, analysis, and writing are all criteria for inclusion as authors in subsequent papers arising from the data synthesis. Author order will be determined by intellectual contributions, order between authors providing similar contributions will be determined alphabetically. For any publications resulting from subprojects, authorship should be extended to all data contributors that have contributed greater than ~10% of the data in the subproject. All data contributors (any data contribution large or small, public or otherwise) will be listed in a data contributor list in the supplementary materials or included as authors as appropriate.

The intent of this policy is NOT to discourage additional analyses – there are a lot more analyses than could be done with these data than we have people or brains to do, and we encourage you all to think creatively about potential projects you and/or your students would like to take on. That being said, we need to respect the agreements by which data were supplied.