Climate change as a driver of Arctic tundra shrub expansion

CONFIRMATION REPORT

Haydn Thomas University of Edinburgh 27th March 2015

TABLE OF CONTENTS

<u>1.0</u>	INTRODUCTION	1
1.1	OVERVIEW	1
1.2	SUPERVISORY ARRANGEMENTS	2
<u>2.0</u>	LITERATURE REVIEW	3
2.1	ARCTIC CHANGE	3
2.2	OBSERVED SHRUB EXPANSION	3
2.3	CAUSES OF CHANGE	4
2.3.1	Summer Temperatures	4
	Growing Season Length	5
2.3.3		5
	Nutrients	5
2.3.5		6
	VARIATION IN SHRUB RESPONSE	6
2.4.1	Habitat Availability	6
2.4.2	Community response	6
2.4.3	· ·	7
2.5	CONSEQUENCES OF SHRUB EXPANSION	7
2.5.1	Biodiversity	7
2.5.2	Surface energy and soil temperature	7
2.5.3	Decomposition rates	8
2.5.4	Carbon Cycling	9
2.6	CONCLUSION AND RESEARCH NEEDS	9
3.0	RESEARCH QUESTIONS	10
3.1	ARE LONGER GROWING SEASONS THE PRIMARY DRIVER OF SHRUB EXPANSION IN	
	ORA ECOSYSTEMS?	10
	Background	10
	Aims	10
	Hypothesis	10
	Methods	10
	Initial findings	12
3.2	WILL LOCAL ADAPTATION INFLUENCE SHRUB RESPONSE TO CHANGE ACROSS	
SPEC	IES RANGES?	14
3.2.1	Background	14
3.2.2	Aim	14
3.2.3	Hypothesis	14
3.2.4	Methods	14
3.2.5	Anticipated findings	15
3.3	$How \ will \ shrub \ expansion \ affect \ tundra \ litter \ decomposition \ rates?$	16
3.3.1	Background	16
3.3.2	Aim	16
3.3.3	71	16
3.3.4		16
3.3.5	Initial Results	17
4.0	TIME SCHEDULE	19
4.1	PROPOSED SCHEDULE OF WORK	19

4.2	DESCRIPTION OF KEY ACTIVITIES	19	
4.3	COMPLETED ACTIVITIES	20	
<u>5.0</u>	PROJECT RESOURCES	22	
5.1	DATA	22	
5.2	SKILLS	22	
5.3	COMPUTING	22	
5.4	FIELD WORK	22	
5.5	FINANCE	23	
5.5.1	1 Funding Requirements	23	
5.5.2	2 Fieldwork Costs	23	
5.5.3	3 Available Funding	24	
<u>6.0</u>	DATA MANAGEMENT	25	
6.1	DATA PRODUCTION AND STORAGE	25	
6.2	DATA SHARING	25	
6.3	LONG-TERM ARCHIVING AND MANAGEMENT	26	
6.4	AUTHORSHIP	26	
<u>7.0</u>	REFERENCES	27	
APPENDIX I: FIELD SITES			
APF	PENDIX II: FIELDWORK SCHEDULE	37	
<u>AP</u> F	PENDIX III: STUNDRA DATA POLICY	38	

1.0 INTRODUCTION

1.1 Overview

The Arctic is currently experiencing a period of rapid change. Annual mean temperatures have increased by 2.06°C since 1978, approximately twice the global average (Callaghan et al., 2011b; Elmendorf et al., 2012b). This has been accompanied by increases in growing season length, thawing of permafrost, and melting of sea ice (Hinzman et al., 2013). These environmental changes have coincided with an increase in the growth and abundance of shrubs, observable from the satellite records (Raynolds et al., 2008), repeat photography (Sturm et al., 2001b), plot measurements (Elmendorf et al., 2012b), dendro-ecological analysis (Hallinger et al., 2010) and indigenous knowledge (Thorpe, 2002). While highly likely that these two processes are linked, the drivers of change, and their relative importance are still not fully understood. This greatly constrains our ability to predict and model future changes to Arctic ecosystems in response to climate change.

In addition, vegetation communities across the Arctic display highly differential responses to environmental change (Myers-Smith et al., 2011a, 2015a; Elmendorf et al., 2012b), which can result in alterations to microclimate, community composition, phenotypic trait variation, or genetic adaptations (Hudson and Henry, 2010; Elmendorf et al., 2012b). In particular, local adaptation can be a critical determinant of species response to change at physiological limits such as range margins (Aitken et al., 2008; Gonzalo-Turpin and Hazard, 2009; Hoffmann and Sgrò, 2011). Local adaptation in tundra shrubs may therefore be highly influential in determining patterns and consequences of shrub expansion (Frost et al., 2014). However, to date there has been little study of genetic variation in shrub species across the tundra biome.

Finally, shrub expansion in tundra environments has highly significant consequences. As the largest vegetation type in the Arctic, shrubs have important interactions with atmospheric, soil, carbon, nutrient and biotic dynamics (Myers-Smith et al., 2011a). Changes in shrub growth and abundance influences species diversity, surface albedo and carbon storage in tundra ecosystems, which could enhance positive feedbacks to climate change (Pearson et al., 2013). Impacts upon ecosystem carbon cycling are of particular concern, since it is not known whether changes in community composition will enhance or retard decomposition rates. This is a major unknown is assessing the future carbon balance of the Arctic (Cornelissen et al., 2007).

This research will investigate the causes and consequences of the observed trend towards shrubs expansion in the Arctic. It specifically aims to address three questions:

- 1) Are longer growing seasons the primary determinant of shrub expansion in tundra ecosystems?
- 2) Will local adaptation influence shrub response to change across species ranges?
- 3) How will shrub expansion affect tundra litter decomposition rates?

1.2 Supervisory Arrangements

This research will be supervised by Dr. Isla Myers-Smith (primary supervisor) and Prof. Mathew Williams (secondary supervisor).

Dr. Isla Myers-Smith

Role: Dr. Myers-Smith will be the primary point of contact for research

concerns and guidance, and will offer direct support at the preparation and planning stage of research. This will transition to a more advisory role over time. In particular, assistance with existing data and field experiments will be required at an early stage, since these pre-date this research. Fieldwork will also be supervised by Dr. Myers-Smith.

Expertise: Arctic shrub expansion, shrub-albedo feedbacks, decomposition and

permafrost thaw, Arctic fieldwork.

Contact: Contact will take the form of weekly progress emails, fortnightly one-

to-one meetings, lab meetings and discussion groups, and ad-hoc support. This will increase during important periods such as field-trip

preparation.

Prof. Mathew Williams

Role: Prof. Williams will provide additional support as required, offer

guidance on the overall progress of the research, and help identify

potential implications for wider ecological research.

Expertise: Ecological modelling, plant traits, decomposition, Arctic research.

Contact: Contact will take the form of one-to-one meetings every three months,

regular lab meetings and ad-hoc support.

Additional support may be provided by 'Team Shrub', who will assist with statistical analysis and wider disciplinary insight, and by Dr. Marc Metzger who will hold the position of PhD advisor for this research.

1.1 Funding

Research is funded by the UK National Environment Research Council (NERC) as part of the University of Edinburgh Doctoral Training Programme (DTP), and as additional funds to support field research.

Research will take place over 3.5 years and is based at the University of Edinburgh, with fieldwork in two locations in the Canadian Arctic (see Appendix I).

2.0 LITERATURE REVIEW

2.1 Arctic Change

Climate change in the Arctic has been rapid and profound. Temperatures are increasing at a rate of approximately 0.07° C per year, while there have also been dramatic declines in summer sea ice (Stroeve et al., 2007) and permafrost (Lawrence and Slater, 2005). The Arctic arguably has the greatest concentration of critical positive feedbacks, or tipping points, that combined may induce rapid climate change both for the region and globe (Duarte et al., 2012). These may be contributing to 'Arctic amplification' of change, though it is likely that other factors such as atmospheric circulation are also important (Serreze and Barry, 2011; Pithan and Mauritsen, 2014).

Arctic warming is also associated with a number of important ecological changes (Post et al., 2009; Pearson et al., 2013). Vegetation is severely temperature limited in Arctic and tundra environments, while terrestrial temperature increase is correlated with the lengthening of the snow-free season and growing season by 9.1 and 4.7 days per decade respectively (Chapin et al., 2005; Zeng et al., 2011). This has likely contributed to widespread change, notably an increase in the growth and abundance of shrubs (Settele et al., 2014).

2.2 Observed shrub expansion

There is now widespread evidence for an expansion of shrubs in the tundra biome over the last 30-40 years (Myers-Smith et al., 2011a). First identified by Sturm et al. in 2001, this comprises an increase in shrub abundance, growth and extent in Arctic and alpine regions. Evidence is primarily derived from satellite data (Bunn and Goetz, 2006; Raynolds et al., 2008; Fraser et al., 2011; McManus et al., 2012), repeat photography (Myers-Smith et al., 2011b; Tape et al., 2012; Tremblay et al., 2012) and long-term ecological plots (Elmendorf et al., 2012b), though other sources include dendro-ecological analysis (Myers-Smith et al., 2015b) and indigenous observations (Thorpe, 2002). All lines of evidence point to a strong trend towards 'shrubification' of the tundra biome, though significant variation exists within this (Myers-Smith et al., 2011a).

Satellite-derived measurements of the Normalized Difference Vegetation Index (NDVI) reveal significant 'greening' of tundra areas over the satellite period (Bhatt et al., 2010; Frost et al., 2014). Since NDVI correlates well with above-ground biomass in tundra ecosystems, this provides good evidence that vegetation productivity is increasing (Forbes et al., 2010). Mean NDVI for the Arctic increased by approximately 0.14% per year over the 1980s and 1990s (Bunn et al., 2007). The majority of this change has occurred in the southernmost tundra zones, accounting for 20-26% of the observed increase (Epstein et al., 2012). However, greening is not ubiquitous; there is a high degree of heterogeneity across regions, floristic provinces and vegetation types (Bunn et al., 2007; Bhatt et al., 2010; Epstein et al., 2013). Furthermore, greening of tundra environments does not necessarily imply shrub expansion since trends could result from greening of other tundra species or a

conversion from non-vegetated to vegetated tundra (Beck and Goetz, 2011). Finally, NDVI is sensitive to a number confounding, non-ecological factors, including atmospheric changes and satellite drift, and may also saturate above certain levels of production (Gamon et al., 2013; Guay et al., 2014).

Shrub expansion has also been identified through repeat photography, allowing the comparison of historical and current landscapes. This reveals increases in shrub patch size, height and extent throughout the Arctic, though greatest change is commonly associated with disturbed or fluvial environments (Sturm et al., 2001b; Tape et al., 2006; Myers-Smith et al., 2011a; Naito and Cairns, 2011, 2015; Tremblay et al., 2012; Frost and Epstein, 2014). Such observations are also supported by plot-based measurements, which reveal increases in both deciduous and evergreen shrubs since the 1980s (Elmendorf et al., 2012b). This has been accompanied by increases in canopy height, maximum plant height and litter abundance (ibid; Walker et al., 2006), and decreases in bare ground (Beck and Goetz, 2011). Finally, annual ring growth has been used to demonstrate an increase in photosynthetic activity since the 1980s, with correlations between growing season temperature, ring width and shoot length (Forbes et al., 2010; Myers-Smith et al., 2011b, 2015b).

2.3 Causes of change

It is likely that climate change is the main driver of shrub expansion in the Arctic. This is supported by paleoenvironmental research, which indicates that shrubs were more abundant during warmer periods in the Holocene (Bigelow, 2003; Klemm et al., 2013). However, the relationship between climate and vegetation is not simple; climate change pertains a range of direct and indirect impacts, which occur in addition to wider ecosystem changes, inter-species interactions, and multiple feedbacks.

2.3.1 Summer Temperatures

Shrub expansion in tundra environments is most commonly linked to summer temperatures (Myers-Smith et al., 2011a; Elmendorf et al., 2012a, 2012b; Macias-Fauria et al., 2012) Walker et al. (2012) demonstrate a linear relationship between aboveground biomass and summer warmth over continental-scale latitudinal gradients in both remote sensing and field data. There is also significant spatial correlation between the Summer Warmth Index (the sum of mean monthly temperatures above 0°C) and NDVI (Blok et al., 2011; Raynolds et al., 2008, 2006). Furthermore, long-term experimental warming plots indicate increased shrub abundance, canopy height, biomass, shoot growth and fruit production with summer temperature (Buizer et al., 2012; Elmendorf et al., 2012b).

However, shrub response varies by climatic zone, moisture regime and the presence of permafrost, among other factors (Myers-Smith et al., 2015a). Elmendorf et al. (2012a) find that shrub abundance shows highest increases in sites that are already warm and moist, while initial increases in growth in cold, dry sites are not sustained. Some experiments also display notable resilience to change (Hudson and Henry, 2010). Furthermore, Blok et al. (2011) find no inter-annual variation between maximum NDVI and summer warmth over a ten year period, suggesting that vegetation does not respond linearly to temperature change.

2.3.2 Growing Season Length

Pan-Arctic greening trends correspond with with increases in growing season length (Goetz et al., 2005; Bunn and Goetz, 2006; Bonfils et al., 2012). For example, Jia et al. (2006) found that variances in growing season length in Alaska corresponded closely to variances in time-indexed NDVI between 1991-2000. This is influenced particularly by snow-melt and the length of the snow-free season (Post et al., 2009). Weijers et al. (2013) also found that growing degree days were the best predictor of shoot length in *Cassiope tetragona*. The influence of growing season was stronger where temperature or moisture was less limiting (Hallinger et al., 2010), though other factors such as herbivory or competition could suppress this signal (Speed et al., 2010; Ettinger et al., 2011; Boudreau and Villeneuve-Simard, 2012). However, while acknowledged as a likely influence (for example, see Rundqvist et al., 2011), few studies have explicitly examined the role of growing season length as a driver of shrub expansion. There is therefore significant potential to increase understanding of this potential driver of change.

2.3.3 Moisture

Moisture is also a significant limiting factor for shrub growth in much of the tundra. Soil moisture has been found to modify shrub relationships to climate, with wetter sites typically showing greater sensitivity to change (Elmendorf et al., 2012b; Myers-Smith et al., 2015a). A significant positive correlation has been found between summer precipitation and both growth and leaf area index of *Betula nana* in the following year (Blok, 2010; Blok et al., 2011). Similarly, expansion of both *Alnus* and *Larix* in the Siberian tundra correlate better with mean annual precipitation than with summer temperature (Frost and Epstein, 2014). There is also evidence that evergreen species are more responsive to changes in moisture than temperature (Elmendorf et al., 2012a). However, high vapour pressure deficits in warm periods further place hydraulic limitations on photosynthesis (Beck et al., 2011), while there is evidence that expanding shrub patches tend to be drier than surrounding areas, though it is unclear whether this is a cause or consequence of growth (Tape et al., 2012).

2.3.4 Nutrients

While temperature has a direct impact on stimulating plant growth, it can also influence nutrient availability by stimulating higher decomposition rates (Weintraub and Schimel, 2003, 2005). This may better explain observed changes in shrub abundance (DeMarco et al., 2014a). Deciduous shrubs tend to respond rapidly to nutrient addition, showing increases in foliar nitrogen, biomass and photosynthetic rate (Baddeley et al., 1994). Some deciduous shrubs are also strong competitors for soil nutrients and increasingly dominate fertilised plots in long-term experiments (Deslippe and Simard, 2011; Sistla et al., 2013; DeMarco et al., 2014a). However, in the majority of cases the greatest change arises from a combination of warming and nutrient addition rather than either in isolation (DeMarco et al., 2014a). CO₂ enrichment has also been proposed as a mechanism for observed shrub expansion in tropical and dry savannah environments, though there is currently insufficient evidence to assess its influence in tundra environments (Beck et al., 2011).

2.3.5 Herbivory

In some regions changes in herbivore abundance may better explain observed shrub expansion than climate trends (Jørgensen et al., 2015). Browsing by reindeer, moose, hare, rodents and ptarmigan strongly reduces growth and increases mortality (den Herder et al., 2008; Tape et al., 2010; Ehrich et al., 2012; Plante et al., 2014; Ravolainen et al., 2014). Herbivore exclusion experiments indicate that grazing inhibits shrub expansion, decoupling the relationship between temperature and growth (Post and Pedersen, 2008; Olofsson et al., 2009; Speed et al., 2010, 2011). Grazing can also influence community traits such as composition and canopy height by altering the relative abundance and growth form of shrub species. For example, moose browsing tends to favour late-successional species such as Alnus tenuifolia and Populus balsamifera, while unpalatable evergreen shrubs may benefit as competitors are selectively browsed (Butler and Kielland, 2008; Yu et al., 2011). However, high density herbivore populations may also promote shrub growth, either through the creation of new seed beds as mineral soil is exposed by trampling (Ropars and Boudreau, 2012), or through high fecal inputs of carbon and nitrogen, which can be five and eight times higher respectively than ungrazed areas (Butler and Kielland, 2008).

2.4 Variation in Shrub Response

It is clear that both shrub sensitivity to change, and resulting patterns of shrub expansion, are highly variable across the tundra biome (Myers-Smith et al., 2011a, 2015a; Naito and Cairns, 2011; Elmendorf et al., 2012b). This is to be expected as climatic drivers will be mediated by both local environmental conditions and species-specific traits (Danby and Hik, 2007).

2.4.1 Habitat Availability

Rates and patterns of shrub response will be dependent upon the availability of suitable habitats for colonisation, the impact of changing disturbance regimes, and the dispersal ability of individual species (Beck et al., 2011; Caviezel et al., 2014). There is evidence that increasing disturbance in Arctic environments, for example through fire (Racine et al., 2004), fluvial action (Frost and Epstein, 2014), permafrost (Frost et al., 2013) or thermokarst features (Lloyd et al., 2003) may facilitate shrub establishment through the creation of suitable habitat for colonisation or expansion. For example, Frost et al. (2013) observe that almost all new shrub stands are located in bare microsites in cryogenic patterned-ground landscapes, likely due to the provision of seedbed availability. Pre-existing conditions may therefore limit shrub expansion even in climatically suitable regions (Tape et al., 2012).

2.4.2 Community response

There is evidence that some vegetation communities display remarkable resistance to environmental change (Hudson and Henry, 2010), while the limited response of shrubs in High Arctic sites to experimental warming may indicate resistance to shrub expansion in the short term (Elmendorf et al., 2012a). This is likely due to the absence

of responsive species or genotypes. As such, change in the longer term may occur due to migration or gene flow, though understanding of this is currently limited. There is therefore substantial potential to both investigate the extent to which local adaptation occurs within tundra shrub species, and to explore the impact this may have on shrub response to environmental change.

2.4.3 Local adaptation

Plant traits, including nutrient ratios, seed mass, plant height and specific leaf area, show distinct trends with latitude (De Frenne et al., 2013). While environmental constraints in tundra ecosystems will likely exert strong influence over traits, studies of interspecific variation in tundra environments are scarce. Furthermore, the extent to which local genetic adaptation influences plant traits and growth forms in tundra species is relatively unknown. In alpine environments, evidence from transplant and common-garden experiments suggest local adaptation in *Poa hiernata* (Byars et al., 2007), Festuca eskia (Gonzalo-Turpin and Hazard, 2009) and Salix herbacea (Sedlacek et al., 2014) along altitudinal gradients. This is expressed as differences in fitness-related traits and growth-form, with selection for survival at higher altitudes and for reproduction at lower altitudes (Gonzalo-Turpin and Hazard, 2009). However, Cortés et al. (2014) find no evidence for genetic variation between microclimates for Salix herbacea. In tundra environments, there has been some study of variation at the forest-tundra ecotone, though this has largely focused on intra-species competition (Grau et al., 2012). As yet only one study has examined local adaptation over latitudinal gradients for tundra shrub species (Bjorkman, 2015).

2.5 Consequences of shrub expansion

2.5.1 Biodiversity

Shrub expansion may result in a decline in species richness as a result of competition and heavy modification of the light, moisture and nutrient environment (Brantley and Young, 2007; Pajunen et al., 2011). This is exacerbated by increased litter fall, particularly in young thickets, which can smother low-lying plants such as forbs and lichens (Brantley and Young, 2008). Net species loss has been observed in a number of sites due to the shift towards dwarf-shrubs (Callaghan et al., 2011a), though Elmendorf et al. (2012a) only observed decreases in vascular plant diversity in moist sites. Decreases in diversity have also been observed in warming and nutrient addition plots, most notably for lichens (Walker et al., 2006; Lang et al., 2012; DeMarco et al., 2014a). However, species richness has remained stable or increased in some locations, with no clear overall trend in alpha diversity for the tundra as a whole (Anthelme et al., 2003; Danby et al., 2011; Vellend et al., 2013).

2.5.2 Surface energy and soil temperature

Shrubs generally have a lower albedo than surrounding tundra and as such shrub expansion may contribute to local warming (Bonfils et al., 2012). Albedo impacts are particularly pertinent during snowmelt, as protruding stems induce rapid warming

compared to shrub-free areas (Sturm et al., 2001a; Chapin et al., 2005; Sturm, 2005; Pomeroy et al., 2006; Myers-Smith et al., 2011a). However, there is some evidence that this may not be ubiquitous, with shrub tundra showing higher albedo than wet or barren tundra (Blok et al., 2011). Shrubs also trap snow in winter, insulating the soil (Sturm et al., 2001). As such, winter soil temperatures are 3-10°C warmer under shrubs that in shrub-free areas (Chapin et al., 2005). Combined, these factors can result in increased atmospheric and soil temperatures where shrubs are present, which in turn can encourage permafrost thaw.

Conversely, shrubs may contribute to the protection of permafrost due to canopy shading in the summer (Myers-Smith et al., 2013). Shrub cover was found to be negatively correlated with active layer depth in experimentally warmed plots in Siberia (Blok, 2010). Similarly, Blok et al. (2010) found that removal of *Betula nana* increased active layer depth by an average of 9% in the late growing season. This is due to differences in ground heat flux following the loss of canopy shading, which has been shown to result in rapid permafrost collapse in Siberian tundra (Nauta et al., 2014).

2.5.3 Decomposition rates

Decomposition rates are dependent upon the physical properties of the environment, such as temperature and precipitation, the quantity and quality of litter inputs, and the characteristics of the soil biological community (Aerts, 2006). Shrub expansion will therefore influence decomposition rates through both changes to soil temperatures and modification of litter inputs (Mack et al., 2004). However, Cornwell et al. (2008) found that difference in litter inputs produced three times more variation in decomposition rate than difference in environmental factors, while Myers-Smith and Hik (2013) found that artificial shrub canopies did not increase decomposition rates, despite inducing changes in local soil temperatures. As such, litter quality appears to be the predominant driver of decomposition rates in tundra environments (Shaw and Harte, 2001; Dorrepaal et al., 2005; Cornwell et al., 2008).

Decomposition rates vary according to the volume and the physical and chemical properties of litter inputs (Cornelissen, 1996; Aerts et al., 2012). Litterfall is generally found to be higher following shrub expansion (Brantley and Young, 2008), while litter quantity and quality has been found to increase in long-term warming and nutrient addition experiments (DeMarco et al., 2014a; Paradis et al., 2014). However, litter quality may vary substantially by species or functional group (Buckeridge et al., 2009), and over space (Cahoon et al., 2012). In contrast, recalcitrant woody tissue in stems and root systems may retard decomposition rates (Cornelissen et al., 2007). For example, *Betula nana* allocates 79% of above ground biomass to stems, which decompose three times slower than leaves and up to eight times slower than graminoids and sedges (DeMarco et al., 2014b). As such, changes in plant traits arising from community composition change are likely to be a major control on decomposition rates, and subsequently carbon and nutrient cycling, in tundra ecosystems (Wookey et al., 2009).

2.5.4 Carbon Cycling

It is still unclear how the cycling and storage of carbon in tundra environments will respond to climate change and the expansion of shrubs. This will be highly dependent upon both energy dynamics (2.5.2) and decomposition rates (2.5.3). Soil carbon is predicted to remain constant, though with a restructuring of the mineral layer following 'biotic awakening' at depth, higher litter inputs and increased cryoturbation (Sistla et al., 2013). In contrast, carbon storage in living biomass will likely increase (Weintraub and Schimel, 2005; Sistla et al., 2013). As such, it is estimated that total ecosystem carbon storage will increase in the short term, though this will vary substantially over space and may be highly vulnerable to loss following disturbance (Thompson et al., 2006; Epstein et al., 2012; DeMarco et al., 2014b).

2.6 Conclusion and Research Needs

Understanding the trends, causes, variation and consequences of shrub expansion in tundra environments is a highly pertinent area of research. Shrub expansion represents a rapid ecosystem-wide response to anthropogenic climate change that could have profound feedbacks on earth system processes. However, predicting the future of the tundra remains highly challenging, since there are still a large number of unknowns in relation to shrub response to change. Firstly, the relative importance of the drivers of change is still unclear. Notably, while the impact of growing season is often acknowledged, there has been little quantification of its influence on vegetation change. Secondly, it is unclear whether genetic variation within species groups will mitigate or modify shrub response. Thirdly, the contribution of community changes to litter decomposition rates remains unknown, despite clear consequences for ecosystem carbon cycling. These three research needs form the basis of this PhD, and are outlined in detail in Section 3.0.

3.0 RESEARCH QUESTIONS

3.1 Are longer growing seasons the primary driver of shrub expansion in tundra ecosystems?

3.1.1 Background

It is highly likely that observed shrub expansion is the result of climate change (Settele et al., 2014). Shrub growth is strongly associated with summer warmth and as such this is often considered the primary driver of patterns of vegetation change (Elmendorf et al., 2012b). However, shrub sensitivity to climate shows widespread variability, and it is therefore likely that other factors may play an important role (Myers-Smith et al., 2015a). In particular, longer growing seasons may drive shrub expansion by increasing the duration of growth each year (Myneni et al., 1997; Jia et al., 2006). While associated with summer temperature, it is possible that growing season length better explains variation in shrub response. Few studies have focused on this since availability of growing season length data is limited compared to temperature data. Relationships are also complicated by other factors including nutrient availability (Zamin and Grogan, 2012), herbivory (Olofsson et al., 2009), disturbance (Racine et al., 2004), and changing biotic interactions (Deslippe et al., 2011). Understanding the relative importance of these factors is vital to predicting future rates and patterns of shrub expansion in tundra ecosystems.

3.1.2 Aims

I aim to examine the relationship between growing season length and vegetation change in the Arctic tundra on Herschel Island, Canada. I will make use of existing long-term monitoring of plant composition and phenology, which I will extend during the research period.

3.1.3 Hypothesis

Increases in growing season length will better explain trends in vegetation change than increases in summer temperature.

3.1.4 Methods

I will make use of existing data sources to compare changes in plant traits and community composition over time with climate data. These sources are as follows:

i) Long-term plot-based monitoring on Herschel Island, covering three vegetation types (Herschel, Komakuk, Orca). Data exists for five sampled years (1999, 2004, 2009, 2013 and 2014), providing a 15-year dataset. I will initially focus on changes in community composition, canopy height, specific leaf area, and stem density. This will comprise both existing long-term records and additional data collected though fieldwork on Herschel Island. There is also potential to include other changes in plant traits, such as leaf carbon and nitrogen, though long-term records are limited for these variables.

- ii) Long-term ecological data from the sTUNDRA dataset, covering approximately 100 sites across the Arctic (see Figure 3.1). This provides a larger spatial coverage than the Herschel Island data, though also represents a wider range of environmental conditions and species. As such, it may be harder to determine relevant comparisons between sites. Sites also vary in the time scale and type of data collected. However, I will aim to identify broad trends within the dataset as a whole, while a smaller number of sites may be directly comparable with Herschel Island. Colleagues within the sTUNDRA working group will update this dataset during the course of the research.
- iii) Plant traits from the TRY trait database, which will expand the available number of traits and sites available for analysis.
- iv) Climate data from the CRU gridded climate dataset. This has been made available as part of the sTUNDRA dataset and will be updated during the course of the research.

I will use a hierarchical model to assess the influence of summer temperature and growing season length upon multiple changes in vegetation composition and growth. I will initially focus upon vegetation change on Herschel Island, taking into account variation across species, sub-sites and plots. However, I aim to expand analysis to include variation between Herschel Island and other Arctic sites. Model comparison analysis will then be used to assess the relative importance of each driver, according to the Akaike information criterion (AIC). Analysis will primarily be performed using the 'R' statistical software package.

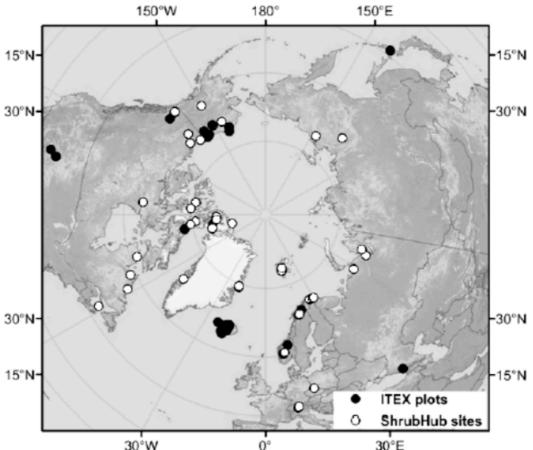


Figure 3.1: Location of sites covered by the sTUNDRA dataset

3.1.5 Initial findings

I have not yet begun data analysis for this chapter, but initial data exploration indicates significant change in both climate and vegetation variables over the data period (Figures 3.2 & 3.3).

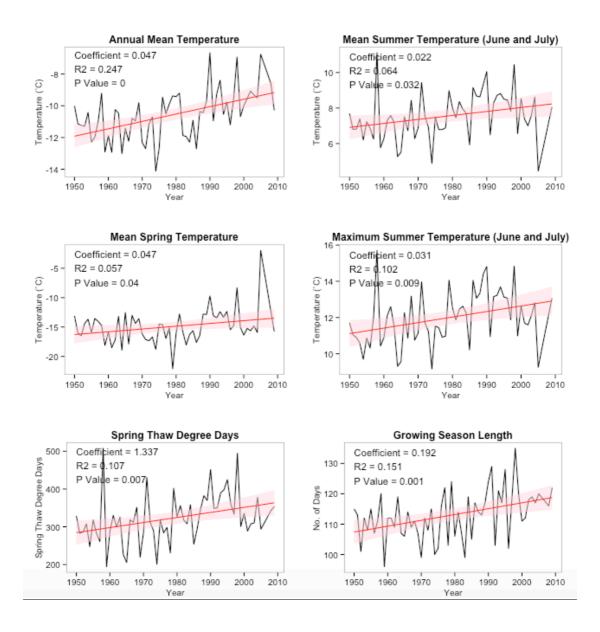


Figure 3.2: Trends in selected climate variables for Herschel Island, 1950-2010. There has been a significant increase in all selected climate variables on Herschel Island since 1950. Mean annual and summer temperatures have increased by approximately 2°C and 1°C respectively since 1950, while growing season has extended by approximately 10 days. However, there is large interannual variability in these trends, which will be used to explore patterns of vegetation change since 1999 on the island.

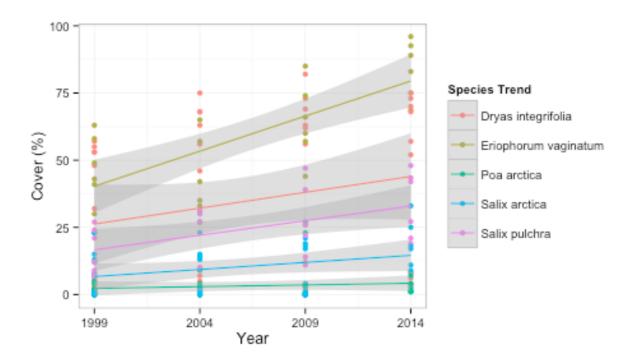


Figure 3.3: Change in cover for five most abundant species on Herschel Island, 1999 – 2014. The graminoid species *Eriophorum vaginatum* shows the greatest change, though two deciduous shrubs (*Salix arctica*, *Salix pulchra*) and one evergreen shrub (*Dryas integrifolia*) are also increasing in abundance. Relationships between cover change and potential climatic drivers will be explored further, both for this site and for sites across the tundra biome.

3.2 Will local adaptation influence shrub response to change across species ranges?

3.2.1 Background

Both patterns of shrub expansion and their impact on tundra ecosystems are dependent upon the extent to which vegetation responds to environmental change. Tundra vegetation is often assumed to be uniform, notably in global vegetation models (Chapin et al., 2000; Pearson et al., 2013). However, there is growing evidence that variation in vegetation and traits over space can result in very different responses to environmental change (Hudson and Henry, 2010). While there has been some focus on variation at the level of the species or functional group, the extent of within-species genetic variation, for example over latitudinal gradients, is unknown. Should responsive genotypes be absent from certain communities, changes may be dramatically different from those predicted, at least in the short term (Elmendorf et al., 2012b).

Genetic variation can be investigated through common garden experiments, which bring together individuals from different environments to assess adaptive differences between species, rather than plastic responses to the environment (De Frenne et al., 2013). While widely used in ecological research (e.g. see Alberto et al., 2013), common gardens have been little applied to tundra environments.

3.2.2 Aim

I aim to investigate the role of local adaptation across a latitudinal gradient in determining growth responses to climate change. Two willow species (*Salix pulchra*, *Salix richardsonii*) from two sites along a 1,000km latitudinal gradient will be compared in a common garden experiment to explore differential growth response.

3.2.3 Hypothesis

Southern species will have faster rates of growth than northern species.

3.2.4 Methods

Cuttings of *Salix pulchra* and *Salix richardsonii* were planted in a common garden, established in 2013. Cuttings were taken from two field sites, Herschel Island (70°N) and Kluane National Park (61°N), which span a 1,000km latitudinal gradient.

I will monitor survival and growth of the willows over at least two field seasons, with the potential to either delegate data collection or conduct a shorter field season in the third year of the PhD. The final dataset will therefore represent five years of growth (2013-2017). I will explore differences between species and sites of origin using a mixed-model approach, particularly focusing on whether there is any significant difference in growth (canopy height, leaf traits) between sites of origin.

3.2.5 Anticipated findings

This research question is heavily reliant upon data collection from the common garden experiment throughout the course of the PhD. Although some initial data is available for the first two years of growth, I have not yet performed any analysis for this research question. However, example outputs that illustrate the potential results of the research are outlined in Figures 3.4 and 3.5.

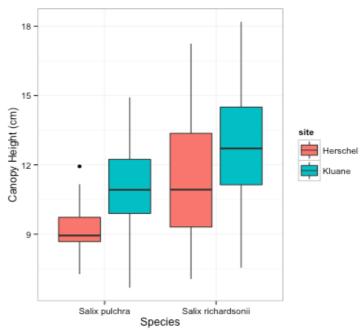


Figure 3.4: Example output, indicating differences in five year canopy height of *Salix richardsonii* and *Salix pulchra* between northern (Herschel) and southern (Kluane) populations.

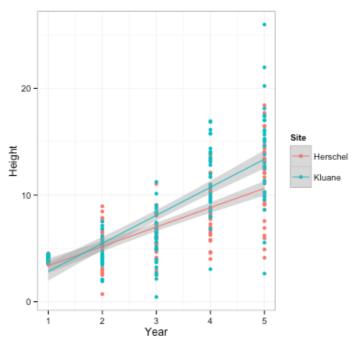


Figure 3.5: Example output, indicating divergence in canopy height over time in *Salix richardsonii* between northern and southern populations. This would be evidence for local adaptation of growth form across the 1000km latitudinal gradient.

3.3 How will shrub expansion affect tundra litter decomposition rates?

3.3.1 Background

Vegetation change in tundra ecosystems is expected to be both rapid and dramatic. More than 50% of areas are predicted to experience a switch in vegetation class by 2050, with a 52% increase in woody cover (Pearson et al., 2013). This will have dramatic consequences for Arctic ecosystems, and indeed could impact earth system processes as a whole through strong positive climate feedbacks (Chapin et al., 2005). At the regional scale, an increase in shrubs alters litter quantity and quality (Cornelissen et al., 2007) energy flux and partitioning (Liston and Mcfadden, 2002), snow distribution and extent (Sturm, 2005), and soil temperatures (Myers-Smith et al., 2013). At the global scale, shrub expansion may determine whether tundra ecosystems become a sink or source of carbon, either through their impact upon rates of decomposition and permafrost thaw (Lawrence and Swenson, 2011), or through the storage of carbon in biomass and litter (Cornwell et al., 2008). The direction and magnitude of these changes are poorly understood and represent a large unknown in the quantification of the carbon cycle (Cornelissen et al., 2007).

3.3.2 Aim

I aim to predict changes in decomposition rates and carbon storage as a result of vegetation and community response to warming. To do this I will combine the results of a litter decomposition experiment with long-term composition and plant trait data to examine how changes to a) individual plant traits and b) community-weighted mean traits are linked to tundra ecosystem decomposition over time.

3.3.3 Hypothesis

Community shift towards shrubs and graminoids will enhance decomposition rates.

3.3.4 Methods

I will combine data from the previously published 'Meeting of Litters' (MOL) experiment (Cornelissen et al., 2007) with long-term composition (ITEX plots) and plant trait data (TRY database) from around the Arctic. These datasets may be expanded throughout the course of the research with additional input from colleagues in the sTUNDRA network, and through an additional decomposition experiment. I will explore relationships between decomposition rate and functional traits among species, accounting for both litter chemistry (nitrogen and carbon) and physical traits (specific leaf area, lignin content). I aim to build a Bayesian model to expand these relationships with the wider TRY database of plant traits. Since decomposition has been shown to be consistently controlled by the same traits across species and functional groups, this will enable me to estimate decomposability for a wider range of tundra species (Freschet et al., 2012). I will use this to estimate changes in community-level decomposability over time, taking into account intraspecific trait variation and changes to individual plant traits. This will indicate the net effect of vegetation change on decomposition rates and carbon storage in response to climate warming.

3.3.5 Initial Results

Initial results indicate that cold environments are experiencing a shift towards more recalcitrant vegetation types, notably due to an expansion of shrub species (Figures 3.6). However, changes in leaf traits such as community-weighted specific leaf area over time could enhance decomposability of litter inputs to the soil. Initial analysis of the relationship between leaf traits and decomposability suggests that leaf carbon content is significantly related to decomposition rate (Figure 3.7), though this is only based on the MOL dataset and does not take into account the additional TRY traits.

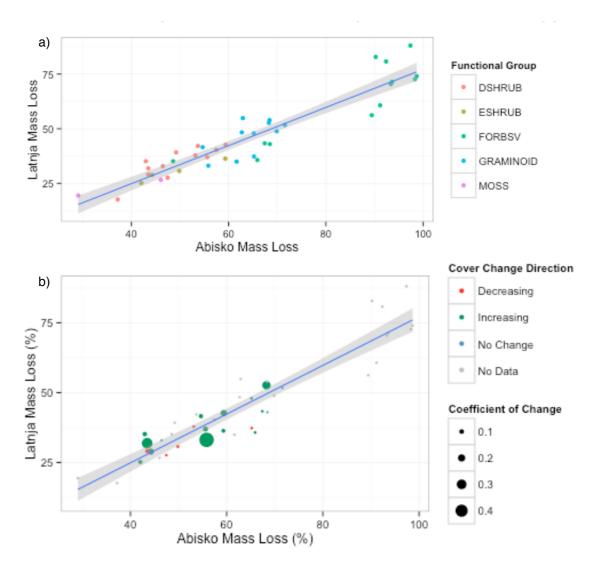


Figure 3.6: Decomposition rates display substantial variation between species, but are clustered according to functional group (a). Mass loss is closely correlated for each decomposition site (p=<0.001, $R^2=0.87$). There is no clear relationship between decomposition rate and direction of cover change (b), though cover data is absent for most forb species.

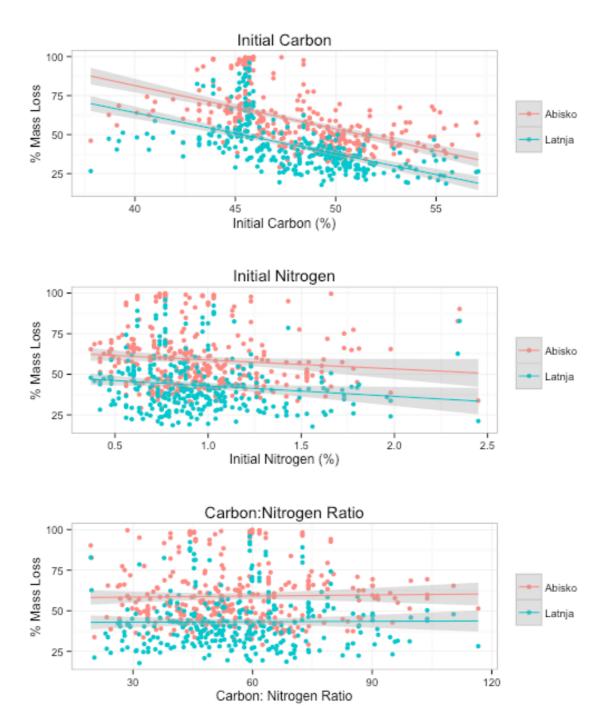


Figure 3.7: Relationship between mass loss and litter chemistry for samples in the Meeting of Litters experiment. Only initial carbon is significant for both sites (Abisko: p=<0.001, R²=0.27; Latnja: p=0.001, R²=0.30). The relationship between chemistry and mass loss does not vary between decomposition sites. Functional group (Figure 3.6a) appears to have a stronger relationship with decomposition rate than litter chemistry (following Dorrepaal et al., 2005; Aerts et al., 2012; Freschet et al., 2012), though this finding will be explored in more detail.

4.0 TIME SCHEDULE

4.1 Proposed schedule of work

The proposed work schedule is outlined in Figure 4.1, which presents the key workstreams and expected duration. It is worth noting that timescales beyond 18 months into the PhD are estimates at this time, but will be revised every six months.

4.2 Description of key activities

Data analysis: Statistical data analysis will form the most substantial

component of this PhD. I am currently working on analysis for Research Question 3 with the aim of presenting this work at the sTUNDRA workshop in May and Perth Mountain Conference in October. I aim to have completed this chapter by the end of 2015. Work on Research Question 1 is also on-going, and I expect this to take up the majority of time in my second year of the PhD. Analysis for Research Question 2 will take place towards the end of the PhD due to the limitations on available

data from the common garden experiment.

Fieldwork: Fieldwork is based in the Yukon Territory, northern Canada,

across two field sites (see Appendix I). Fieldwork will take place over two months (mid-June to mid-August) in 2015 and 2016, with the potential for a third season in 2017 if necessary.

Since field sites are in isolated locations, with extreme conditions, extensive preparation will be essential. This is currently underway, including acquiring a research permit, preparing a risk assessments, undertaking necessary training, booking transport, and booking shipping, equipment, transport and field assistance. A detailed fieldwork schedule for 2015 is

outlined in Appendix II.

Literature Review: A good literature review is an essential aspect of a PhD thesis,

and as such this has comprised a significant proportion of my time in the early stages of this PhD. While I now have reviewed

a large volume of material, and started work on a draft literature review, I consider this activity to be on-going to account for new paper releases. I also hope to publish one review paper as a result of this PhD, with possible topics including a synthesis of common garden experiments, with particular reference to Arctic research, and the impact of shrubs

upon soil temperature and decomposition rates.

Conferences: Planned upcoming workshops and conferences are the

Postgraduate Research Conference (April 2015), the

sTUNDRA workshop in Germany (May 2015), the "Mountains of Our Future Earth" conference in Perth (Oct 2015) and the British Ecological Survey conference in Edinburgh (Dec 2015).

4.3 Completed Activities

R' Training: The statistical software package 'R' is the primary tool of

analysis for this research. Prior to starting this PhD I had no experience in using R, so have undertaken a number of training courses to increase my skills with the software. I now consider myself to be competent using R and am confortable using it for

analysis.

Laboratory Analysis: I have measured specific leaf area for all Herschel Island

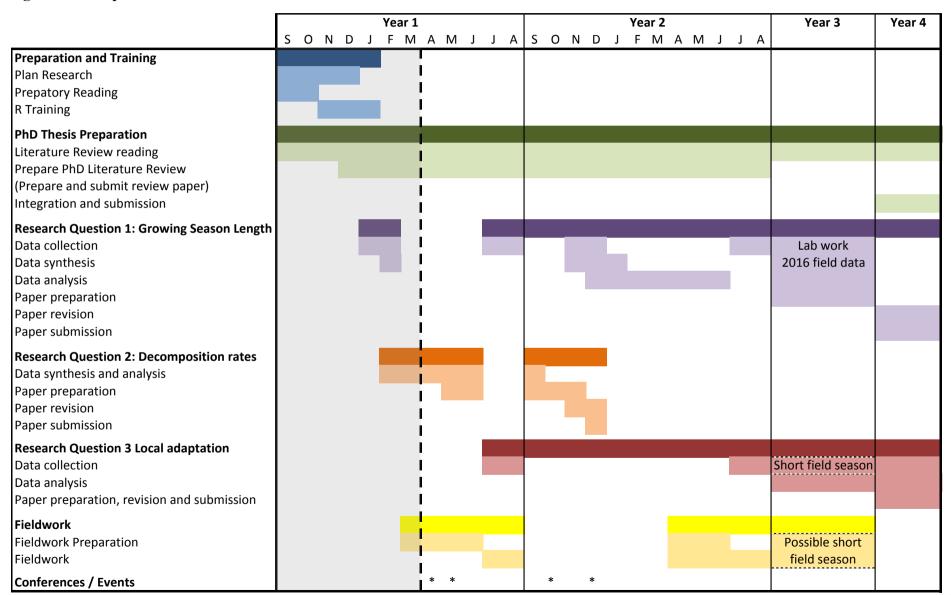
samples and additional Abisko samples from the 2014 field

season.

Data Entry: I have uploaded data from 2014 field books into electronic

form to be used in future analysis. I will store future raw data in field books in the same manner (see data management below).

Figure 4.1: Proposed work schedule



5.0 PROJECT RESOURCES

5.1 Data

This research is dependent upon the availability of a range of previously collected data. These are as follows:

- sTUNDRA database of plant traits, community composition and CRU climate data
- 'Meeting of Litters' Experiment plant trait, community composition and litter decomposition rates
- TRY database plant traits

Access to these data sources has already been secured. For more information, see Section 6.0.

5.2 Skills

The main skills required for this research are:

- Individual research skills; the ability to read, understand and competently write scientific literature, to organise time and to collaborate with other organisations and researchers
- Quantitative and statistical analysis skills, including the use of 'R' and Bayesian modelling techniques.
- Field work skills, notably the ability to conduct ecological field work in remote Arctic locations

These skills will be supported by training courses provided by the DTP and other organisations.

5.3 Computing

The principle computing resources required for this research are as follows:

- Availability of 'R' software package
- Access to GitHub online database
- 500GB storage, provided by the University of Edinburgh

5.4 Field Work

The fieldwork component of this research will require:

- Research permits for field sites, currently under application
- Suitable research supplies, field gear and safety equipment (inc. firearms)
- Training in first aid, bear awareness and fire arm safety
- Field assistance, provided by undergraduate members of 'Team Shrub'

5.5 Finance

5.5.1 Funding Requirements

This research is heavily dependent upon financial resources. It will require fieldwork in remote Arctic locations, travel to international meetings and conferences, and laboratory analysis. An overall budget is outlined in Table 5.1.

Table 5.1: Research Budget

Name	Description	Cost
Laboratory Analysis	Plant trait analysis, including specific leaf area and stem density	£1,000
Meetings and Conferences	National and international meetings, including the Perth Mountain Conference (Scotland) and British Ecological Survey (Scotland)	£1,200
Fieldwork	Travel to Arctic field sites, accommodation and food for two months, shipping of equipment and samples, insurance (see 5.5.2).	£16,110
Total		£18,310

5.5.2 Fieldwork Costs

The principle costs associated with this research are for fieldwork since travel to the Canadian Arctic is both logistically difficult and expensive. Costs will be minimised through collaboration with the Alfred Wegener Institute Helmholtz Centre for Polar and Marine research in Potsdam, Germany, Yukon Territorial Parks and other partners. An estimated annual fieldwork budget is outlined in Table 5.2. Note that estimates are based on three field seasons in case this should be necessary.

Table 5.2: Annual Fieldwork Budget

Name	Description	Annual Cost
Flights	Including the cost of flights from Edinburgh to Canada (£1,200), flights within Canada (£700) and chartered flight to research sites (£1,300).	£3,200
Accommodation	Provided by two field stations, which will include basic field accommodation, field logistical support, technical support and safety coordination.	£930
Food	Food must be purchased and prepared by the research team for the month in the Herschel Island field site.	£900
Shipping	Shipping of equipment and samples.	£500
Insurance	Additional insurance will be required due to the remote nature of research.	£200
Vehicle Rental	Vehicle rental will be necessary to travel within field sites.	£100
Total		£5,370
Total (three years	£16,110	

5.5.3 Available Funding

Funding will be primarily provided by NERC as part of the DTP at the University of Edinburgh. Additional NERC funds have also been made available to assist with fieldwork costs, both through the DTP and directly to Dr. Myers-Smith to fund her research programme.

Table 5.3: Sources of Finance

Name	Description	Value	Status
NERC DTP	Funding provided for research as part of the DTP.	£3,450	Secured
Additional NERC Funding (DTP)	Additional funding to support fieldwork costs.	£4,000	Secured
Additional NERC funding (Research Team)	Additional funding to support 'Team Shrub' research, including fieldwork costs.	£10,680	Secured
Total		£18.310	

6.0 DATA MANAGEMENT

6.1 Data Production and Storage

This project will use a variety of data sources. Existing data sources include:

- Plant trait and community composition information from ~100 sites from around the Arctic. Data is stored in the sTUNDRA database in a data and code repository in GitHub. Access rights have already been secured, and a specific data policy applies to the use of this data (Appendix III).
- Climate data from the CRU gridded climate dataset. This is included as part of the sTUNDRA dataset and follows the same conditions for access.
- Decomposition rates from the 'Meeting of Litters' experiment (Cornelissen et al., 2007). Information will be shared through the ShrubHub GitHub account. Permission has already been granted to use this data and any further requirements in terms of access or authorship rights will be secured in writing at an early stage in the research.

In addition, a number of further data sources will be produced throughout the course of the project:

- Expansion of the sTUNDRA dataset through field study and laboratory analysis. Key variables of measurement will be community composition, canopy height, specific leaf area, wood density and leaf carbon and nitrogen content.
- Potential expansion of decomposition data from field experiments.
- Growth rate and plant trait data from the common garden experiment.

Field data will be carefully recorded and backed up to reduce the risk of loss during and after collection. Field notebooks will be scanned during data collection and these digital copies will be backed up at the end of the season. Data will be entered during and after each field season and will also be backed up to university servers. The School of GeoSciences at University of Edinburgh will provide server space and computing resources to maintain databases and facilitate data sharing among collaborators.

Data will primarily be in the form of ecological variables (community composition, growth rates, plant traits), which will be stored both locally and in the GitHub cloud server. In addition, statistical code (in R) will be backed up to the GitHub repository.

6.2 Data Sharing

Much of the data used in this research is currently publically available, including the ITEX and CRU datasets. Other major datasets will become publically available over the course of the project following publication. Ecological data and R code is also shared across the ShrubHub community.

Where possible, all datasets, metadata and code from database manipulation and statistical analyses will be translated into publically available files using NERC approved protocols. My data will be made public at the time of publication using an online data repository such as the Polar Data Catalogue (https://www.polardata.ca/).

6.3 Long-term archiving and management

This project forms a part of long-running ecological monitoring of the Arctic environment, and exists within the ShrubHub community. As such, all relevant data will be entered into the sTUNDRA database and the Polar Data Catalogue to enable it to inform future research.

6.4 Authorship

Haydn Thomas will be the lead author on all papers produced as a direct result of this research. Any other researchers who have made intellectual contributions to publishable work will be offered authorship.

sTUNDRA protocols require authors contributing 5% or more to data sources to be offered authorship (Appendix III). This will be followed in this project, though important additional contributions will also be noted.

7.0 REFERENCES

- Aerts, R., 2006. The freezer defrosting: global warming and litter decomposition rates in cold biomes. Journal of Ecology 94, 713–724.
- Aerts, R., van Bodegom, P.M., Cornelissen, J.H.C., 2012. Litter stoichiometric traits of plant species of high-latitude ecosystems show high responsiveness to global change without causing strong variation in litter decomposition. New Phytologist 196, 181–188.
- Aitken, S.N., Yeaman, S., Holliday, J. a., Wang, T., Curtis-McLane, S., 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. Evolutionary Applications 1, 95–111.
- Alberto, F.J., Aitken, S.N., Alía, R., González-Martínez, S.C., Hänninen, H., Kremer, A., Lefèvre, F., Lenormand, T., Yeaman, S., Whetten, R., Savolainen, O., 2013. Potential for evolutionary responses to climate change evidence from tree populations. Global change biology 19, 1645–61
- Anthelme, F., Michalet, R., Barbaro, L., Brun, J.-J., 2003. Environmental and Spatial Influences of Shrub Cover (Alnus viridis DC.) on Vegetation Diversity at the Upper Treeline in the Inner Western Alps. Arctic, Antarctic, and Alpine Research 35, 48–55.
- Baddeley, J., Woodin, S., Alexander, I., 1994. Effects of increased nitrogen and phosphorus availability on the photosynthesis and nutrient relations of three arctic dwarf shrubs from Svalbard. Functional Ecology 8, 676–685.
- Beck, P., Goetz, S., 2011. Satellite observations of high northern latitude vegetation productivity changes between 1982 and 2008: ecological variability and regional differences. Environmental Research Letters 7, 029501.
- Beck, P., Juday, G., Alix, C., 2011. Changes in forest productivity across Alaska consistent with biome shift. Ecology ... 14, 373–9.
- Bhatt, U.S., Walker, D. a., Raynolds, M.K., Comiso, J.C., Epstein, H.E., Jia, G., Gens, R., Pinzon, J.E., Tucker, C.J., Tweedie, C.E., Webber, P.J., 2010. Circumpolar Arctic Tundra Vegetation Change Is Linked to Sea Ice Decline. Earth Interactions 14, 1–20.
- Bigelow, N.H., 2003. Climate change and Arctic ecosystems: 1. Vegetation changes north of 55°N between the last glacial maximum, mid-Holocene, and present. Journal of Geophysical Research 108, 8170.
- Bjorkman, A.D., 2015. Ecological and Evolutionary Consequences of Experimental Warming in a High Arctic Tundra Ecosystem. PhD Thesis, The University of British Columbia.
- Blok, D., 2010. Climate change effects on vegetation in Northeastern Siberian tundra-How does shrub growth relate to local climate and what are potential effects of shrub expansion. EGU General ... 12, 11086.
- Blok, D., Heijmans, M.M.P.D., Schaepman-Strub, G., Kononov, a. V., Maximov, T.C., Berendse, F., 2010. Shrub expansion may reduce summer permafrost thaw in Siberian tundra. Global Change Biology 16, 1296–1305.

- Blok, D., Sass-Klaassen, U., Schaepman-Strub, G., Heijmans, M.M.P.D., Sauren, P., Berendse, F., 2011. What are the main climate drivers for shrub growth in Northeastern Siberian tundra? Biogeosciences Discussions 8, 771–799.
- Blok, D., Schaepman-Strub, G., Bartholomeus, H., Heijmans, M.M.P.D., Maximov, T.C., Berendse, F., 2011. The response of Arctic vegetation to the summer climate: relation between shrub cover, NDVI, surface albedo and temperature. Environmental ... 6, 035502.
- Bonfils, C.J.W., Phillips, T.J., Lawrence, D.M., Cameron-Smith, P., Riley, W.J., Subin, Z.M., 2012. On the influence of shrub height and expansion on northern high latitude climate. Environmental Research Letters 7, 015503.
- Boudreau, S., Villeneuve-Simard, M.-P., 2012. Dendrochronological evidence of shrub growth suppression by trees in a subarctic lichen woodland. Botany 90, 151–156.
- Brantley, S.T., Young, D.R., 2007. Leaf-area index and light attenuation in rapidly expanding shrub thickets. Ecology 88, 524–530.
- Brantley, S.T., Young, D.R., 2008. Shifts in litterfall and dominant nitrogen sources after expansion of shrub thickets. Oecologia 155, 337–45.
- Buckeridge, K.M., Zufelt, E., Chu, H., Grogan, P., 2009. Soil nitrogen cycling rates in low arctic shrub tundra are enhanced by litter feedbacks. Plant and Soil 330, 407–421.
- Buizer, B., Weijers, S., van Bodegom, P.M., Alsos, I.G., Eidesen, P.B., van Breda, J., de Korte, M., van Rijckevorsel, J., Rozema, J., 2012. Range shifts and global warming: ecological responses of Empetrum nigrum L. to experimental warming at its northern (high Arctic) and southern (Atlantic) geographical range margin. Environmental Research Letters 7, 025501.
- Bunn, A.G., Goetz, S.J., 2006. Trends in Satellite-Observed Circumpolar Photosynthetic Activity from 1982 to 2003: The Influence of Seasonality, Cover Type, and Vegetation Density. Earth Interactions 10, 1–19.
- Bunn, A.G., Goetz, S.J., Kimball, J.S., Zhang, K., 2007. Northern high-latitude ecosystems respond to climate change. Eos, Transactions American Geophysical Union 88, 333–335.
- Butler, L.G., Kielland, K., 2008. Acceleration of vegetation turnover and element cycling by mammalian herbivory in riparian ecosystems 136–144.
- Byars, S.G., Papst, W., Hoffmann, A. a., 2007. Local adaptation and cogradient selection in the alpine plant, Poa hiemata, along a narrow altitudinal gradient. Evolution 61, 2925–2941.
- Cahoon, S., Sullivan, P., Shaver, G., Welker, J., Post, E., 2012. Interactions among shrub cover and the soil microclimate may determine future Arctic carbon budgets. Ecology ... 15, 1415–22.
- Callaghan, T. V., Christensen, T.R., Jantze, E.J., 2011a. Plant and Vegetation Dynamics on Disko Island, West Greenland: Snapshots Separated by Over 40 Years. Ambio 40, 624–637.
- Callaghan, T. V., Tweedie, C.E., Åkerman, J., Andrews, C., Bergstedt, J., Butler, M.G., Christensen, T.R., Cooley, D., Dahlberg, U., Danby, R.K., Daniëls, F.J. a., de Molenaar, J.G., Dick, J., Mortensen, C.E., Ebert-May, D., Emanuelsson, U., Eriksson, H., Hedenås, H., Henry, G.H.R., Hik, D.S., Hobbie, J.E., Jantze, E.J., Jaspers, C., Johansson, C., Johansson, M., Johnson, D.R., Johnstone, J.F., Jonasson, C., Kennedy, C., Kenney, A.J., Keuper, F., Koh, S., Krebs, C.J., Lantuit, H., Lara, M.J., Lin, D., Lougheed, V.L., Madsen, J., Matveyeva, N., McEwen, D.C., Myers-Smith, I.H., Narozhniy, Y.K., Olsson, H., Pohjola, V. a., Price, L.W., Rigét, F., Rundqvist, S., Sandström, A., Tamstorf, M., Van Bogaert, R., Villarreal, S., Webber, P.J., Zemtsov, V. a., 2011b. Multi-Decadal Changes in Tundra Environments and Ecosystems:

- Synthesis of the International Polar Year-Back to the Future Project (IPY-BTF). Ambio 40, 705–716.
- Caviezel, C., Hunziker, M., Zoller, O., Wüthrich, C., Kuhn, N.J., 2014. Soil development as limiting factor for shrub expansion in southwestern Greenland 16, 20120479.
- Chapin, F., Eugster, W., McFadden, J., Lynch, A., Walker, D., 2000. Summer differences among arctic ecosystems in regional climate forcing. Journal of ... 2002–2010.
- Chapin, F.S., Sturm, M., Serreze, M.C., McFadden, J.P., Key, J.R., Lloyd, a H., McGuire, a D., Rupp, T.S., Lynch, a H., Schimel, J.P., Beringer, J., Chapman, W.L., Epstein, H.E., Euskirchen, E.S., Hinzman, L.D., Jia, G., Ping, C.-L., Tape, K.D., Thompson, C.D.C., Walker, D. a, Welker, J.M., 2005. Role of land-surface changes in arctic summer warming. Science (New York, N.Y.) 310, 657–60.
- Cornelissen, J.H.C., 1996. An Experimental Comparison of Leaf Decomposition Rates in a Wide Range of Temperate Plant Species and Types. The Journal of Ecology 84, 573.
- Cornelissen, J.H.C., van Bodegom, P.M., Aerts, R., Callaghan, T. V, van Logtestijn, R.S.P., Alatalo, J., Chapin, F.S., Gerdol, R., Gudmundsson, J., Gwynn-Jones, D., Hartley, A.E., Hik, D.S., Hofgaard, A., Jónsdóttir, I.S., Karlsson, S., Klein, J. a, Laundre, J., Magnusson, B., Michelsen, A., Molau, U., Onipchenko, V.G., Quested, H.M., Sandvik, S.M., Schmidt, I.K., Shaver, G.R., Solheim, B., Soudzilovskaia, N. a, Stenström, A., Tolvanen, A., Totland, Ø., Wada, N., Welker, J.M., Zhao, X., 2007. Global negative vegetation feedback to climate warming responses of leaf litter decomposition rates in cold biomes. Ecology letters 10, 619–27.
- Cornwell, W.K., Cornelissen, J.H.C., Amatangelo, K., Dorrepaal, E., Eviner, V.T., Godoy, O., Hobbie, S.E., Hoorens, B., Kurokawa, H., Pérez-Harguindeguy, N., Quested, H.M., Santiago, L.S., Wardle, D. a, Wright, I.J., Aerts, R., Allison, S.D., van Bodegom, P., Brovkin, V., Chatain, A., Callaghan, T. V, Díaz, S., Garnier, E., Gurvich, D.E., Kazakou, E., Klein, J. a, Read, J., Reich, P.B., Soudzilovskaia, N. a, Vaieretti, M.V., Westoby, M., 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. Ecology letters 11, 1065–71.
- Cortés, a J., Waeber, S., Lexer, C., Sedlacek, J., Wheeler, J. a, van Kleunen, M., Bossdorf, O., Hoch, G., Rixen, C., Wipf, S., Karrenberg, S., 2014. Small-scale patterns in snowmelt timing affect gene flow and the distribution of genetic diversity in the alpine dwarf shrub Salix herbacea. Heredity 233–239.
- Danby, R.K., Hik, D.S., 2007. Variability, contingency and rapid change in recent subarctic alpine tree line dynamics. Journal of Ecology 95, 352–363.
- Danby, R.K., Koh, S., Hik, D.S., Price, L.W., 2011. Four Decades of Plant Community Change in the Alpine Tundra of Southwest Yukon, Canada. Ambio 40, 660–671.
- De Frenne, P., Graae, B.J., Rodríguez-Sánchez, F., Kolb, A., Chabrerie, O., Decocq, G., De Kort, H., De Schrijver, A., Diekmann, M., Eriksson, O., Gruwez, R., Hermy, M., Lenoir, J., Plue, J., Coomes, D. a., Verheyen, K., 2013. Latitudinal gradients as natural laboratories to infer species' responses to temperature. Journal of Ecology 101, 784–795.
- DeMarco, J., Mack, M., Bret-Harte, M., 2014a. Long-term experimental warming and nutrient additions increase productivity in tall deciduous shrub tundra. Ecosphere 5, 1–22.
- DeMarco, J., Mack, M., Bret-Harte, M., 2014b. Effects of arctic shrub expansion on biophysical versus biogeochemical drivers of litter decomposition. Ecology 95, 1861–1875.

- Den Herder, M., Virtanen, R., Roininen, H., 2008. Reindeer herbivory reduces willow growth and grouse forage in a forest-tundra ecotone. Basic and Applied Ecology 9, 324–331.
- Deslippe, J.R., Hartmann, M., Mohn, W.W., Simard, S.W., 2011. Long-term experimental manipulation of climate alters the ectomycorrhizal community of Betula nana in Arctic tundra. Global Change Biology 17, 1625–1636.
- Deslippe, J.R., Simard, S.W., 2011. Below-ground carbon transfer among Betula nana may increase with warming in Arctic tundra. The New phytologist 192, 689–98.
- Dorrepaal, E., Cornelissen, J.H.C., Aerts, R., Wallén, B., Van Logtestijn, R.S.P., 2005. Are growth forms consistent predictors of leaf litter quality and decomposability across peatlands along a latitudinal gradient? Journal of Ecology 93, 817–828.
- Duarte, C.M., Lenton, T.M., Wadhams, P., Wassmann, P., 2012. Abrupt climate change in the Arctic. Nature Climate Change 2, 60–62.
- Ehrich, D., Henden, J.-A., Ims, R.A., Doronina, L.O., Killengren, S.T., Lecomte, N., Pokrovsky, I.G., Skogstad, G., Sokolov, A. a, Sokolov, V. a, Yoccoz, N.G., 2012. The importance of willow thickets for ptarmigan and hares in shrub tundra: the more the better? Oecologia 168, 141–51.
- Elmendorf, S., Henry, G.H.R., Hollister, R.D., Björk, R.G., Bjorkman, A.D., Callaghan, T. V, Collier, L.S., Cooper, E.J., Cornelissen, J.H.C., Day, T. a, Fosaa, A.M., Gould, W. a, Grétarsdóttir, J., Harte, J., Hermanutz, L., Hik, D.S., Hofgaard, A., Jarrad, F., Jónsdóttir, I.S., Keuper, F., Klanderud, K., Klein, J. a, Koh, S., Kudo, G., Lang, S.I., Loewen, V., May, J.L., Mercado, J., Michelsen, A., Molau, U., Myers-Smith, I.H., Oberbauer, S.F., Pieper, S., Post, E., Rixen, C., Robinson, C.H., Schmidt, N.M., Shaver, G.R., Stenström, A., Tolvanen, A., Totland, Ø., Troxler, T., Wahren, C.H., Webber, P.J., Welker, J.M., Wookey, P. a, 2012a. Global assessment of experimental climate warming on tundra vegetation: Heterogeneity over space and time. Ecology Letters.
- Elmendorf, S., Henry, G.H.R., Hollister, R.D., Björk, R.G., Boulanger-Lapointe, N., Cooper, E.J., Cornelissen, J.H.C., Day, T. a., Dorrepaal, E., Elumeeva, T.G., Gill, M., Gould, W. a., Harte, J., Hik, D.S., Hofgaard, A., Johnson, D.R., Johnstone, J.F., Jónsdóttir, I.S., Jorgenson, J.C., Klanderud, K., Klein, J. a., Koh, S., Kudo, G., Lara, M., Lévesque, E., Magnússon, B., May, J.L., Mercado-Dr'az, J. a., Michelsen, A., Molau, U., Myers-Smith, I.H., Oberbauer, S.F., Onipchenko, V.G., Rixen, C., Martin Schmidt, N., Shaver, G.R., Spasojevic, M.J., Þórhallsdóttir, Þ.E., Tolvanen, A., Troxler, T., Tweedie, C.E., Villareal, S., Wahren, C.-H., Walker, X., Webber, P.J., Welker, J.M., Wipf, S., 2012b. Plot-scale evidence of tundra vegetation change and links to recent summer warming. Nature Climate Change.
- Epstein, H.E., Myers-Smith, I., Walker, D. a, 2013. Recent dynamics of arctic and sub-arctic vegetation. Environmental Research Letters 8, 015040.
- Epstein, H.E., Raynolds, M.K., Walker, D. a, Bhatt, U.S., Tucker, C.J., Pinzon, J.E., 2012. Dynamics of aboveground phytomass of the circumpolar Arctic tundra during the past three decades. Environmental Research Letters 7, 015506.
- Ettinger, a. K., Ford, K.R., Hillerislambers, J., 2011. Climate determines upper, but not lower, altitudinal range limits of Pacific Northwest conifers. Ecology 92, 1323–1331.
- Forbes, B.C., Fauria, M.M., Zetterberg, P., 2010. Russian Arctic warming and "greening" are closely tracked by tundra shrub willows. Global Change Biology 16, 1542–1554.
- Fraser, R.H., Olthof, I., Carrière, M., Deschamps, a, Pouliot, D., 2011. Detecting long-term changes to vegetation in northern Canada using the Landsat satellite image archive. Environmental Research Letters 6, 045502.

- Freschet, G.T., Aerts, R., Cornelissen, J.H.C., 2012. A plant economics spectrum of litter decomposability. Functional Ecology 26, 56–65.
- Frost, G. V, Epstein, H.E., 2014. Tall shrub and tree expansion in Siberian tundra ecotones since the 1960s. Global change biology 20, 1264–77.
- Frost, G. V, Epstein, H.E., Walker, D. a, 2014. Regional and landscape-scale variability of Landsatobserved vegetation dynamics in northwest Siberian tundra. Environmental Research Letters 9, 025004.
- Frost, G. V, Epstein, H.E., Walker, D. a, Matyshak, G., Ermokhina, K., 2013. Patterned-ground facilitates shrub expansion in Low Arctic tundra. Environmental Research Letters 8, 015035.
- Gamon, J. a., Huemmrich, K.F., Stone, R.S., Tweedie, C.E., 2013. Spatial and temporal variation in primary productivity (NDVI) of coastal Alaskan tundra: Decreased vegetation growth following earlier snowmelt. Remote Sensing of Environment 129, 144–153.
- Goetz, S.J., Bunn, A.G., Fiske, G.J., Houghton, R. a, 2005. Satellite-observed photosynthetic trends across boreal North America associated with climate and fire disturbance. Proceedings of the National Academy of Sciences of the United States of America 102, 13521–5.
- Gonzalo-Turpin, H., Hazard, L., 2009. Local adaptation occurs along altitudinal gradient despite the existence of gene flow in the alpine plant species Festuca eskia. Journal of Ecology 97, 742–751.
- Grau, O., Ninot, J.M., Blanco-Moreno, J.M., van Logtestijn, R.S.P., Cornelissen, J.H.C., Callaghan, T. V., 2012. Shrub-tree interactions and environmental changes drive treeline dynamics in the Subarctic. Oikos 121, 1680–1690.
- Guay, K.C., Beck, P.S. a, Berner, L.T., Goetz, S.J., Baccini, A., Buermann, W., 2014. Vegetation productivity patterns at high northern latitudes: A multi-sensor satellite data assessment. Global Change Biology 3147–3158.
- Hallinger, M., Manthey, M., Wilmking, M., 2010. Establishing a missing link: warm summers and winter snow cover promote shrub expansion into alpine tundra in Scandinavia. The New phytologist 186, 890–9.
- Hinzman, L.D., Deal, C.J., Mcguire, A.D., Mernild, S.H., Polyakov, I. V., Walsh, J.E., 2013. Trajectory of the Arctic as an integrated system. Ecological Applications 23, 1837–1868.
- Hoffmann, A.A., Sgrò, C.M., 2011. Climate change and evolutionary adaptation. Nature 470, 479–485.
- Hudson, J.M.G., Henry, G.H.R., 2010. High Arctic plant community resists 15 years of experimental warming. Journal of Ecology 98, 1035–1041.
- Jia, G.J., Epstein, H.E., Walker, D. a., 2006. Spatial heterogeneity of tundra vegetation response to recent temperature changes. Global Change Biology 12, 42–55.
- Jørgensen, R.H., Hallinger, M., Ahlgrimm, S., Friemel, J., Kollmann, J., Meilby, H., 2015. Growth response to climatic change over 120 years for Alnus viridis and Salix glauca in West Greenland. Journal of Vegetation Science 26, 155–165.
- Klemm, J., Herzschuh, U., Pisaric, M.F.J., Telford, R.J., Heim, B., Pestryakova, L. a., 2013. A pollenclimate transfer function from the tundra and taiga vegetation in Arctic Siberia and its applicability to a Holocene record. Palaeogeography, Palaeoclimatology, Palaeoecology 386, 702–713.

- Lang, S.I., Cornelissen, J.H.C., Shaver, G.R., Ahrens, M., Callaghan, T. V., Molau, U., Ter Braak, C.J.F., Hölzer, A., Aerts, R., 2012. Arctic warming on two continents has consistent negative effects on lichen diversity and mixed effects on bryophyte diversity. Global Change Biology 18, 1096–1107.
- Lawrence, D.M., Slater, A.G., 2005. A projection of severe near-surface permafrost degradation during the 21st century. Geophysical Research Letters 32, L24401.
- Lawrence, D.M., Swenson, S.C., 2011. Permafrost response to increasing Arctic shrub abundance depends on the relative influence of shrubs on local soil cooling versus large-scale climate warming. Environmental Research Letters 6, 045504.
- Liston, G., Mcfadden, J., 2002. Modelled changes in arctic tundra snow, energy and moisture fluxes due to increased shrubs. Global Change
- Lloyd, A.H., Yoshikawa, K., Fastie, C.L., Hinzman, L., Fraver, M., 2003. Effects of permafrost degradation on woody vegetation at arctic treeline on the Seward Peninsula, Alaska. Permafrost and Periglacial Processes 14, 93–101.
- Macias-Fauria, M., Forbes, B.C., Zetterberg, P., Kumpula, T., 2012. Eurasian Arctic greening reveals teleconnections and the potential for structurally novel ecosystems. Nature Climate Change 2, 613–618.
- Mack, M.C., Schuur, E.A.G., Bret-harte, M.S., 2004. Ecosystem carbon storage in arctic tundra reduced by long-term nutrient fertilization 431, 658–661.
- McManus, K.M., Morton, D.C., Masek, J.G., Wang, D., Sexton, J.O., Nagol, J.R., Ropars, P., Boudreau, S., 2012. Satellite-based evidence for shrub and graminoid tundra expansion in northern Quebec from 1986 to 2010. Global Change Biology 18, 2313–2323.
- Myers-Smith, I., Lévesque, E., Grogan, P., Lantz, T., 2013. The influence of shrub canopies on soil temperatures across northern Canada. Geophysical Research Letters 15, 2013.
- Myers-Smith, I.H., Elmendorf, S., Beck, P., Wilmking, M., Hallinger, M., Blok, D., Tape, K., Rayback, S., Macias-Fauria, M., Speed, J., Boulanger-Lapointe, N., Rixen, C., Lévesque, E., Schmidt, N., Baittinger, C., Trant, A., Hermanutz, L., Collier, L.S., Dawes, M., Lantz, T., Weijers, S., Jørgensen, R.H., Buchwal, A., Buras, A., Naito, A., Ravolainen, V., Schaepman-Strub, G., J Wheeler, S., Wipf, K., Guay, D., Hik, S., Vellend., M., 2015a. Climate sensitivity of shrub expansion across the tundra biome. Accepted to Nature Climate Change.
- Myers-Smith, I.H., Forbes, B.C., Wilmking, M., Hallinger, M., Lantz, T., Blok, D., Tape, K.D., Macias-Fauria, M., Sass-Klaassen, U., Lévesque, E., Boudreau, S., Ropars, P., Hermanutz, L., Trant, A., Collier, L.S., Weijers, S., Rozema, J., Rayback, S. a, Schmidt, N.M., Schaepman-Strub, G., Wipf, S., Rixen, C., Ménard, C.B., Venn, S., Goetz, S., Andreu-Hayles, L., Elmendorf, S., Ravolainen, V., Welker, J., Grogan, P., Epstein, H.E., Hik, D.S., 2011a. Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. Environmental Research Letters 6, 045509.
- Myers-Smith, I.H., Hallinger, M., Blok, D., Sass-Klaassen, U., Rayback, S. a., Weijers, S., J. Trant, A., Tape, K.D., Naito, A.T., Wipf, S., Rixen, C., Dawes, M. a., A. Wheeler, J., Buchwal, A., Baittinger, C., Macias-Fauria, M., Forbes, B.C., Lévesque, E., Boulanger-Lapointe, N., Beil, I., Ravolainen, V., Wilmking, M., 2015b. Methods for measuring arctic and alpine shrub growth: A review. Earth-Science Reviews 140, 1–13.
- Myers-Smith, I.H., Hik, D., Kennedy, C., Dorothy, C., Johnstone, J., Kenney, A., Krebs, C., 2011b. Expansion of canopy-forming willows over the twentieth century on Herschel Island, Yukon Territory, Canada. Ambio 40, 610–623.

- Myers-Smith, I.H., Hik, D.S., 2013. Shrub canopies influence soil temperatures but not nutrient dynamics: An experimental test of tundra snow-shrub interactions. Ecology and evolution 3, 3683–700.
- Myneni, R., Keeling, C., Tucker, C., 1997. Increased plant growth in the northern high latitudes from 1981 to 1991. Nature.
- Naito, A.T., Cairns, D.M., 2011. Relationships between Arctic shrub dynamics and topographically derived hydrologic characteristics. Environmental Research Letters 6, 045506.
- Naito, A.T., Cairns, D.M., 2015. Patterns of shrub expansion in Alaskan arctic river corridors suggest phase transition. Ecology and Evolution 5, 87–101.
- Nauta, A.L., Heijmans, M.M.P.D., Blok, D., Limpens, J., Elberling, B., Gallagher, A., Li, B., Petrov, R.E., Maximov, T.C., van Huissteden, J., Berendse, F., 2014. Permafrost collapse after shrub removal shifts tundra ecosystem to a methane source. Nature Climate Change 5, 67–70.
- Olofsson, J., Oksanen, L., Callaghan, T., Hulme, P.E., Oksanen, T., Suominen, O., 2009. Herbivores inhibit climate-driven shrub expansion on the tundra. Global Change Biology 15, 2681–2693.
- Pajunen, a. M., Oksanen, J., Virtanen, R., 2011. Impact of shrub canopies on understorey vegetation in western Eurasian tundra. Journal of Vegetation Science 22, 837–846.
- Paradis, M., Mercier, C., Boudreau, S., 2014. Response of Betula glandulosa seedlings to simulated increases in nutrient availability, temperature and precipitation in a lichen woodland at the forest-tundra ecotone. Plant Ecology 1–10.
- Pearson, R.G., Phillips, S.J., Loranty, M.M., Beck, P.S. a., Damoulas, T., Knight, S.J., Goetz, S.J., 2013. Shifts in Arctic vegetation and associated feedbacks under climate change. Nature Climate Change 3, 673–677.
- Pithan, F., Mauritsen, T., 2014. Arctic amplification dominated by temperature feedbacks in contemporary climate models. Nature Geoscience 7, 181–184.
- Plante, S., Champagne, E., Ropars, P., Boudreau, S., Lévesque, E., Tremblay, B., Tremblay, J.P., 2014. Shrub cover in northern Nunavik: Can herbivores limit shrub expansion? Polar Biology 37, 611–619.
- Pomeroy, J.W., Bewley, D.S., Essery, R.L.H., Hedstrom, N.R., Link, T., Granger, R.J., Sicart, J.E., Ellis, C.R., Janowicz, J.R., 2006. Shrub tundra snowmelt. Hydrological Processes 20, 923–941.
- Post, E., Forchhammer, M.C., Bret-Harte, M.S., Callaghan, T. V, Christensen, T.R., Elberling, B., Fox, A.D., Gilg, O., Hik, D.S., Høye, T.T., Ims, R. a, Jeppesen, E., Klein, D.R., Madsen, J., McGuire, a D., Rysgaard, S., Schindler, D.E., Stirling, I., Tamstorf, M.P., Tyler, N.J.C., van der Wal, R., Welker, J., Wookey, P. a, Schmidt, N.M., Aastrup, P., 2009. Ecological dynamics across the Arctic associated with recent climate change. Science (New York, N.Y.) 325, 1355–8.
- Post, E., Pedersen, C., 2008. Opposing plant community responses to warming with and without herbivores. Proceedings of the National Academy of Sciences of the United States of America 105, 12353–8.
- Racine, C., Jandt, R., Meyers, C., Dennis, J., 2004. Tundra fire and vegetation change along a hillslope on the Seward Peninsula, Alaska, USA. Arctic, Antarctic, and Alpine ... 36, 1–10.
- Ravolainen, V.T., Bråthen, K.A., Yoccoz, N.G., Nguyen, J.K., Ims, R. a., 2014. Complementary impacts of small rodents and semi-domesticated ungulates limit tall shrub expansion in the tundra. Journal of Applied Ecology 51, 234–241.

- Raynolds, M., Comiso, J., Walker, D., Verbyla, D., 2008. Relationship between satellite-derived land surface temperatures, arctic vegetation types, and NDVI. Remote Sensing of Environment 112, 1884–1894.
- Raynolds, M.K., Walker, D. a., Maier, H. a., 2006. NDVI patterns and phytomass distribution in the circumpolar Arctic. Remote Sensing of Environment 102, 271–281.
- Ropars, P., Boudreau, S., 2012. Shrub expansion at the forest–tundra ecotone: spatial heterogeneity linked to local topography. Environmental Research Letters 7, 015501.
- Rundqvist, S., Hedenås, H., Sandström, A., Emanuelsson, U., Eriksson, H., Jonasson, C., Callaghan, T. V., 2011. Tree and Shrub Expansion Over the Past 34 Years at the Tree-Line Near Abisko, Sweden. Ambio 40, 683–692.
- Sedlacek, J.F., Bossdorf, O., Cortés, A.J., Wheeler, J. a., van Kleunen, M., 2014. What role do plant-soil interactions play in the habitat suitability and potential range expansion of the alpine dwarf shrub Salix herbacea? Basic and Applied Ecology 15, 305–315.
- Serreze, M.C., Barry, R.G., 2011. Processes and impacts of Arctic amplification: A research synthesis. Global and Planetary Change 77, 85–96.
- Settele, J., Scholes, R., Betts, R., Bunn, S., Leadley, P., Nepstad, D., Overpeck, J., Taboada, M., 2014.
 Terrestrial and inland water systems, in: Field, C.B., Barros, V.R., Dokken, D.J., K.J. Mach, M.D., Mastrandrea, Bilir, T.E., Chatterjee, M., Ebi, K.L., Estrada, Y.O., Genova, R.C., Girma, B., Kissel, E.S., A.N. Levy, S., MacCracken, Mastrandrea, P.R., White, L.L. (Eds.), Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects.
 Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 271–359.
- Shaw, M.R., Harte, J., 2001. Control of Litter Decomposition in a Subalpine Meadow-Sagebrush Steppe Ecotone under Climate Change. Ecological Applications 11, 1206–1223.
- Sistla, S. a, Moore, J.C., Simpson, R.T., Gough, L., Shaver, G.R., Schimel, J.P., 2013. Long-term warming restructures Arctic tundra without changing net soil carbon storage. Nature 497, 615–8.
- Speed, J., Austrheim, G., Hester, A.J., Mysterud, A., 2010. Experimental evidence for herbivore limitation of the treeline. Ecology 91, 3414–3420.
- Speed, J.D.M., Austrheim, G., Hester, A.J., Mysterud, A., 2011. Browsing interacts with climate to determine tree-ring increment. Functional Ecology 25, 1018–1023.
- Stroeve, J., Holland, M.M., Meier, W., Scambos, T., Serreze, M., 2007. Arctic sea ice decline: Faster than forecast. Geophysical Research Letters 34, n/a–n/a.
- Sturm, M., 2005. Changing snow and shrub conditions affect albedo with global implications. Journal of Geophysical Research 110, G01004.
- Sturm, M., McFadden, J., Liston, G., Chapin, S., Racine, C., Holmgren, J., 2001a. Snow-shrub interactions in Arctic tundra: a hypothesis with climatic implications. Journal of ... 336–344.
- Sturm, M., Racine, C., Tape, K., Cronin, T.W., Caldwell, R.L., Marshall, J., 2001b. Increasing shrub abundance in the Arctic. Nature 411, 2001–2002.
- Tape, K., Sturm, M., Racine, C., 2006. The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. Global Change Biology 12, 686–702.

- Tape, K.D., Hallinger, M., Welker, J.M., Ruess, R.W., 2012. Landscape Heterogeneity of Shrub Expansion in Arctic Alaska. Ecosystems 15, 711–724.
- Tape, K.D., Lord, R., Marshall, H.-P., Ruess, R.W., 2010. Snow-Mediated Ptarmigan Browsing and Shrub Expansion in Arctic Alaska. Ecoscience 17, 186–193.
- Thompson, C.C., McGuire, a. D., Clein, J.S., Chapin, F.S., Beringer, J., 2006. Net Carbon Exchange Across the Arctic Tundra-Boreal Forest Transition in Alaska 1981–2000. Mitigation and Adaptation Strategies for Global Change 11, 805–827.
- Thorpe, N., 2002. Nowadays it is not the same: Inuit Quajimajatuqangit, climate and caribou in the Kitikmeot Region of Nunavut, Canada, in: The Earth Is
- Tremblay, B., Lévesque, E., Boudreau, S., 2012. Recent expansion of erect shrubs in the Low Arctic: evidence from Eastern Nunavik. Environmental Research Letters 7, 035501.
- Vellend, M., Baeten, L., Myers-smith, I.H., Elmendorf, S., Beauséjour, R., Brown, C.D., 2013. Global meta-analysis reveals no net change in local-scale plant biodiversity over time. Proceedings of the National Academy of Sciences of the United States of America 110.
- Walker, D. a, Epstein, H.E., Raynolds, M.K., Kuss, P., Kopecky, M. a, Frost, G. V, Daniëls, F.J. a, Leibman, M.O., Moskalenko, N.G., Matyshak, G. V, Khitun, O. V, Khomutov, a V, Forbes, B.C., Bhatt, U.S., Kade, a N., Vonlanthen, C.M., Tichý, L., 2012. Environment, vegetation and greenness (NDVI) along the North America and Eurasia Arctic transects. Environmental Research Letters 7, 015504.
- Walker, M.D., Wahren, C.H., Hollister, R.D., Henry, G.H.R., Ahlquist, L.E., Alatalo, J.M., Bret-harte, M.S., Calef, M.P., Callaghan, T. V, Carroll, A.B., Epstein, H.E., Jo, S., Robinson, C.H., Shaver, G.R., Suding, K.N., Thompson, C.C., Tolvanen, A., Totland, Ø., Turner, P.L., Tweedie, C.E., Webber, P.J., Wookey, P.A., 2006. Plant community responses to experimental warming across the tundra biome 103.
- Weijers, S., Wagner-Cremer, F., Sass-Klaassen, U., Broekman, R., Rozema, J., 2013. Reconstructing High Arctic growing season intensity from shoot length growth of a dwarf shrub. The Holocene 23, 721–731.
- Weintraub, M.N., Schimel, J.P., 2003. Interactions between Carbon and Nitrogen Mineralization and Soil Organic Matter Chemistry in Arctic Tundra Soils. Ecosystems 6, 129–143.
- Weintraub, M.N., Schimel, J.P., 2005. Nitrogen Cycling and the Spread of Shrubs Control Changes in the Carbon Balance of Arctic Tundra Ecosystems. BioScience 55, 408.
- Wookey, P. a., Aerts, R., Bardgett, R.D., Baptist, F., Bråthen, K.A., Cornelissen, J.H.C., Gough, L., Hartley, I.P., Hopkins, D.W., Lavorel, S., Shaver, G.R., 2009. Ecosystem feedbacks and cascade processes: understanding their role in the responses of Arctic and alpine ecosystems to environmental change. Global Change Biology 15, 1153–1172.
- Yu, Q., Epstein, H., Walker, D., 2011. Modeling dynamics of tundra plant communities on the Yamal Peninsula, Russia, in response to climate change and grazing pressure. Environmental ... 6, 045505.
- Zamin, T.J., Grogan, P., 2012. Birch shrub growth in the low Arctic: the relative importance of experimental warming, enhanced nutrient availability, snow depth and caribou exclusion. Environmental Research Letters 7, 034027.
- Zeng, H., Jia, G., Epstein, H., 2011. Recent changes in phenology over the northern high latitudes detected from multi-satellite data. Environmental Research Letters 6, 045508.

APPENDIX I: FIELD SITES

Research will take place at two field sites (Figure I.1, Table I.1)

- i) Herschel Island, Yukon Territory (70°N), located on the Arctic coast of the Yukon at the northern extent of tall shrubs and in a zone of ice rich permafrost.
- ii) Kluane, Yukon Territory (61°N), located 1000km south of the Arctic coast of the Yukon with elevational gradients from boreal forest, through tall shrubs to alpine tundra. The common garden experiments will be conducted at the two supporting research stations the Kluane Lake Research Station and the Aurora Research Institute.

Figure I.1: Map and photographs of the field sites in this study, showing Kluane (left) and Herschel Island (right).

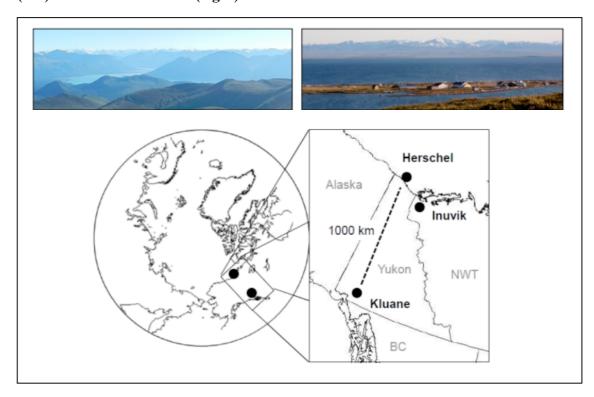


Table I.1: Study locations, climate and ecological data

Site	Lat.	Lon.	Ele. (m)	Mean Summer Temperatures	Growing Season	Canopy Cover	Max. Canopy Height
Herschel Island	69.6	-139.9	28	12.5°C	56 days	5 – 50%	15 – 50 cm
Alpine Kluane	61.1	-138.7	1693	8.1°C	77 days	20 - 70%	30 - 75 cm
Inuvik	68.4	-133.7	694	12.8°C	63 days	Boreal	~ 300 cm
Kluane Lake	61.0	-138.4	781	15.1°C	84 days	Boreal	~ 300 cm

Appendix II: Fieldwork Schedule

Date	Day	Transport	Key tasks	
Week 0: 8th June - 1	3th June	Whitehorse		
08-Jun-15	Monday	Arrive in Whitehorse	Driver for Aaron Thierry	
13-Jun-15	Saturday	Return to Whitehorse		
Week 1: 14th June - 20th June		Whitehorse/Kluane		
14-Jun-15	Sunday	Arrive in Whitehorse		
15-Jun-15	Monday	To Kluane	Common garden maintenance	
			Set up decomp experiment	
			Collect plant trait data	
Week 2: 21st June - 2	27th June	Kluane/Pika Camp		
26-Jun-15		Trip to Pika Camp	As above	
Week 3: 28th June -	4th July	Kluane/Pika Camp		
01-Jul-15	Wednesday	Return to Kluane	As above	
Week 4: 5th July - 11	th July	Kluane/Whitehorse/In	nuvik	
06-Jul-15	Monday	To Whitehorse		
07-Jul-15	Tuesday	To Inuvik	Pack for Herschel	
Week 5: 12th July - 1	<u> </u>	Herschel		
12-Jul-15	Sunday	To Herschel	Monitor vegetation plots	
			Collect NDVI data	
			Conduct herbivory survey	
			Ground truth NDVI data	
			Set up experiments	
			Work on vegetation protocol	
Week 6: 19th July - 2	-	Herschel		
19-Jul-15			Collect plant trait data	
Week 7: 26th July - 1		Herschel		
26-Jul-15	•		As above	
Week 8: 2nd August		Herschel		
02-Aug-15	•		As above	
Week 9: 9th August - 15th August		Herschel/Inuvik/Whitehorse		
	Wednesday	To Inuvik		
15-Aug-15		To Whitehorse		
Week 10: 16th August - 22nd August		Kluane/Whitehorse		
16-Aug-15	Sunday	To Kluane	Common garden experiment	
			Complete experiments	
22-Aug-15	Saturday	Depart Whitehorse		

Appendix III: sTUNDRA Data Policy

Data use and authorship policy agreement

We are requesting that you give us your explicit agreement to follow this data use and authorship policy before we incorporate your data into this database. In order for you to give us your consent, please read through the policy and then write us an email saying that you accept and agree with the sTUNDRA data use and authorship policy. If you don't agree with the policy just let us know and we will delete any data that you have given us and it will not be incorporated into the database.

Due to the time-consuming nature of database compilations such as this, we will not be able to include any data from data contributors who do not agree with the policy. It's just too complicated to try to keep the submissions of those who don't want their data made available separate from the rest. Thanks for your understanding on this.

Data contributors and PIs

It will be the responsibility of the data contributor (the person who sends us the data) to inform us of all data PIs (all people with academic ownership over the data). All data contributors and PIs will be asked to agree to the data use and authorship policy and will be invited to be authors on the first manuscript that will use this database (see below). The names of data contributors and PIs will be entered into the data and the contact information for the data contributors listed in the dataset, so that future data users know both the ownership of the data and can contact the data contributors.

Data policy - Data will be made public at time of first publication

In accordance with our belief that it is the responsibility of scientists to publically archive their data for the future, after publication of the first manuscript we will submit all the compiled trait data to one or more public data repositories (most likely the TRY trait database, https://www.try-db.org and/or the Polar Data Catalogue, https://www.polardata.ca/). At that time it will be in the public domain and available for future research with out restriction. At the same time, we will also make the tundra trait database available to anyone who contributed data, in the hopes that many of the contributors will also find it useful. The data will also be completely citable with a DOI number, once made public, and thus all contributors will be data authors and can list the database as an academic contribution on their CV.

The Trait Biogeography Manuscript

Our first publication will be a trait biogeography manuscript currently with the working title: "Biogeographic patterns in functional traits across the tundra biome". In this manuscript we will test the questions:

- 1. What are the patterns of plant traits across climate gradients in the tundra biome?
- 2. How do canopy, leaf, wood and seed traits vary within and among species?
- 3. Do patterns of plant traits across climate gradients correspond with patterns of community weighted plant trait change over time?

The authorship policy

Our authorship and data use policy is as follows: Everyone who contributes trait data that end up being used in the final analyses will be offered participation and authorship on the first publication of the data: the tundra trait biogeography manuscript that we are currently working on. In addition to submitting trait data, every author will be requested to participate in the manuscript finalization. If someone does

not read and approve the final version of the manuscript, we will not be able to include them as an author, as per journal guidelines.

Of course, if anyone would prefer to submit data for use and doesn't want to join in the analysis/writing effort (i.e., not be an author), that's absolutely fine too - in that case the person will be thanked profusely in the acknowledgements. It will also be up to each person who submits data to tell us who else should be invited to be an author on the final manuscript (i.e., who the "data authors" are for the data that were submitted) – see "Data contributors and PIs" section.

The 5% rule

Any future manuscripts published from these data will be encouraged to follow the 5% rule for authorship - in other words, anyone who contributed 5% or more of the data used in the final versions of analyses in any future papers will be extended the opportunity of authorship on that paper. Other data contributors whose contributions amount to less than 5% could be extended authorship or thanked in the acknowledgements as deemed appropriate by the lead author of the paper. The database should always be cited in all manuscripts using the data following database the citation guidelines of TRY, DRYAD and other online data repositories (http://wiki.datadryad.org/Citing_Data). Since the data will be in the public domain, we can only ask that future authors follow these guidelines, we cannot guarantee that they will. This is the policy that we will follow strictly with any future papers that we are leading as a part of the sTUNDRA collaboration.

Examples of the 5% rule

Example 1: In an analysis of intra-specific variation in Specific Leaf Area data for a variety of tundra plant species across tundra sites – if you contributed 10 records for each of 10 species (100 records total) or more to an overall database of 2000 records – this would constitute 5% of the database – and you would be eligible for authorship under the 5% rule.

Example 2: In an analysis of community weighted means over time for one study site – if you contributed 10 records for 10 species (100 records total) to the sTUNDRA database; however, only data for two species were used in the final analysis of this example manuscript (10 records for each of 2 species – 20 records total) that were added to a trait database with a total of 1000 other records of trait data that were then used to calculate the community weighted means from a database of 100 point-frame-points at 10 plots over three different time points (3000 data points). Your data (20 data points) would constitute only 0.005% of the overall database (4000 data points total) – and thus you would not be eligible for authorship based on data contribution alone under the 5% rule and your data contribution would just be acknowledged as appropriate in the acknowledgements section.

We hope that this data use and authorship policy is clear to you all. If you have any questions, don't hesitate to contact us.

For more information on the sTUNDRA project see http://www.idiv-biodiversity.de/sdiv/workshops/workshops-2014/stundra

For more information on the ITEX-ShrubHub Tundra Protocols see https://imyerssmith.wordpress.com/tundra-protocols/

For more information on the TRY database see https://www.try-db.org/TryWeb/Home.php