ARCTIC VEGETATION RESPONSES TO GLOBAL CHANGE: REPRODUCTION, GROWTH, AND CONSEQUENCES FOR BIODIVERSITY

A Dissertation in
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by
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ABSTRACT

Understanding how biological systems respond to local and global environmental change is necessary to make useful and reliable predictions of future community dynamics. Multiple facets of environmental change, such as climatic shifts and increases or declines in large fauna, can interact to produce additive or counteracting effects on vegetation. Altered composition and dominance patterns in plant communities can, in turn, have consequences for ecosystem functioning through, for example, modification of biogeochemical processes or regional climate patterns. Global scale climate change has already strongly impacted the makeup and dynamics of ecological systems. The northern tundra biome is expected to undergo large changes, which previously have and likely will affect human wellbeing into the future. Thus, the tundra ecosystems of the Low Arctic provide the context within which my dissertation expands our understanding of ecological responses to environmental change.

Understanding how facets of global change, such as warming or human overexploitation of animal resources, affect plant communities in arctic tundra requires understanding responses across life history stages. In this dissertation, I have sought to address gaps in our knowledge related to the role of reproductive processes in contributing to the dynamical patterns that have become evident. In the chapters that follow, I identify the importance of accounting for individualistic species responses to change, and I further suggest that the similar patterns among arctic plant species within a functional group may be the consequence of different underlying processes.

I begin this dissertation by providing some background on global change and the ensuing shifts in the Arctic biome. I then discuss how a warming climate influences the niches of arctic plants and what the consequences of these changes are for biodiversity in tundra ecosystems. One key demographic parameter that can mediate species’ responses to change is the regeneration
niche. In Chapter 2, I addressed two of the earlier stages of the regeneration niche, the production of viable seed and germination, in an experimental context to bridge the gap between the effects of environmental change on established and establishing individuals. I hypothesized that the reproductive responses of arctic plant species to change would be species-specific and poorly predicted by plant functional type. I manipulated temperature and precipitation over three years in a factorial design and also sampled grazed and exclosed plots. The interannual variation in seed mass and germination appeared to reflect weather in those years for several species, and the effect sizes of this variation were similar to those of the warming, watering, and herbivore exclusion treatments. Grazing only affected graminoid species, but these effects were positive for some graminoids and negative for others. Both warming and watering as well as their interaction led to individualistic effects among species belonging to several different functional types, suggesting that some uses of these latter classifications are unlikely to result in reliable predictive generalities. Additionally, a few species demonstrated contrasting effects of warming and watering across years, suggesting these species are near thresholds for successful sexual reproduction. Such thresholds can occur when environmental conditions preclude plants or plant parts from attaining a minimum size required to complete reproduction.

The potential existence of such thresholds indicates that amelioration of abiotic stressors, such as temperature minima that can reduce survival or fecundity, as a result of warming in the Arctic may lead to increases in sexual reproduction and recruitment. In Chapter 3, I addressed the relative contributions of sexual recruitment and asexual spread in populations of *Salix glauca*, a deciduous shrub increasing in abundance in many tundra landscapes, distributed along an environmental gradient comprising a shift maritime to continental climates. I hypothesized that landscapes with warmer summers would have greater evidence of sexual recruitment. To test this, I located sites that appeared to have increased in shrub cover in recent decades and collected leaf samples from neighboring ramets (stems). I found evidence that sexual recruitment occurs
universally across this gradient, but the proportion of sexual recruits, inferred from the uniqueness of their genotypes, was greater in the inland landscapes that experience a continental climate, supporting my hypothesis. Additionally, I demonstrated that the probability of a ramet arising from clonal growth increases where neighbors are larger and vegetative cover is greater, suggesting light is a limiting factor for recruitment from seed.

The above results suggest that the responses of arctic plant communities to climatic change are shaped by the variable responses in growth and reproduction among species. This interspecific variation can lead to shifts in patterns of plant community diversity. While recent syntheses suggest species diversity at small spatial scales has not declined in a range of ecosystems in recent years, I documented the potential for notable declines in the diversity of local assemblages of mixed shrub-graminoid tundra. In Chapter 4, I demonstrate that warming increases the accumulation of biomass, resulting in eventual declines in taxonomic diversity approximately one decade after a disruptive caterpillar outbreak. In particular, shrub abundance was negatively associated with forb richness under warming, but only when large herbivores were experimentally excluded. Additionally, the nature of the relationship between biomass and taxonomic richness went from positive in grazed and unwarmed plots to unimodal in exclosed, warmed plots. Warming thus led to increased biomass, but this only resulted in decreased local diversity in the absence of ungulate herbivory.

The expansion of woody shrubs in the Arctic has become a particular focal point of research, but there remain many unknowns. In Chapter 5, I highlight the contributions of these studies to our current understanding and put them in the context of ongoing research on the causes and consequences plant community responses to global change. This dissertation adds to our understanding of the possible changes in tundra vegetation that may ensue in a warmer Arctic. It thus contributes to the broader body of knowledge on the ecology of clonal plants and the link between ecosystem function and biodiversity.
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Chapter 1

General overview

There are multiple facets to vegetation dynamical responses to climate change in the Arctic, and shrub expansion is one of the most conspicuous and widely documented (e.g. Myers-Smith et al. 2011 and references therein). Although tremendous effort has gone into understanding these responses, the mechanisms underlying this phenomenon and its consequences for plant community dynamics remain unresolved. In this dissertation, I address questions regarding the role of sexual reproduction in arctic shrub expansion by elucidating its importance relative to clonal spread in an increasing shrub across a climatic gradient. I also focus on the role of reproduction more generally among species at the community-level and how spatial patterns of shrub expansion that are similar in multiple species may result from different underlying processes. The insights deriving from these and other studies are then applied in addressing the consequences of global change for biodiversity in local assemblages of arctic tundra plants. Before presenting each of these studies as three separate chapters and an appendix, I will establish the context for my dissertation research by briefly reviewing recent climate change in the Arctic, the process of shrub expansion and other recent trends, tradeoffs between sexual reproduction and clonal growth, and the consequences for arctic plant community composition and dynamics.

Evidence for global change in the Arctic

Greenhouse gas emissions since the mid-18th century have resulted in an increase in atmospheric CO₂ by 40% over the pre-Industrial Revolution level of approximately 280 ppm to
about 400 ppm currently (IPCC 2013). This increase has resulted in globally averaged warming of about 0.89 °C since the turn of the 20th century (IPCC 2013). However, this warming is not evenly distributed across the globe (Figure 1.1). The temperature change resulting from increasing atmospheric greenhouse gases results in especially large changes at high latitudes, as Arrhenius (1896) postulated early on in the process of global industrialization. Now termed the Arctic amplification (Serreze and Francis 2006), it is generally thought to be a result of reduced albedo due to the loss of snow and ice cover throughout much of the year (Screen and Simmonds 2010). The magnitude of recent warming in the Arctic has been about twice that of the global average, but paleoclimate records indicate that global temperature change can be amplified three to four fold in the Arctic (Serreze and Barry 2011).

Warming in the Arctic is associated with both positive and negative feedbacks, including declines in the extent, timing, and duration of snow cover (Derksen and Brown 2012, Brutel-Vuilmet et al. 2013); declining extent and seasonal duration of sea ice (Comiso 2011, Stroeve et al. 2011); mass loss from ice sheets (Shepherd et al. 2012); and degradation of permafrost (Osterkamp 2007). This rapid change at high northern latitudes has led to pronounced localized and teleconnected changes (Macias-Fauria et al. 2012), and many of these changes differ among the various climates within the Arctic (Post et al. 2009). As an example of a trend expected to occur throughout the Arctic, precipitation is projected to increase due to the regional circulation of moisture evaporated from newly exposed surfaces no longer covered by sea ice (Bintanja and Selten 2014), but drier environments will not likely receive the same absolute increase in precipitation as wetter areas (Stendel et al. 2008). Nevertheless, regional warming in the Arctic, particularly because of the feedback with declining sea ice extent, can lead to pronounced effects on weather and climate at lower latitudes (Bhatt et al. 2014, Vihma 2014).

Large-scale changes in climate can influence the population dynamics of a range of vertebrates in the arctic and subarctic ecosystems (Hansen et al. 2013). This can include resident
herbivores critical to vegetation dynamics, such as different species separated by the Greenland ice sheet (Post and Forchhammer 2002) or different populations of the same species living on separate islands (Grenfell et al. 1998). In many parts of the Arctic, many disparate populations of *Rangifer tarandus* L. (caribou and reindeer), regarded as a flagship species in the region (Festa-Bianchet et al. 2011), are experiencing synchronous declines as a result of global change (Vors and Boyce 2009).

**Recent trends in arctic plant communities**

**Terrestrial biophysical changes**

The ways in which vegetation dynamics will be modified by global change are many and complex. Ecosystems are already experiencing transformations in the processes underlying the development and maintenance of permafrost (Osterkamp 2007, Rowland et al. 2010) as well as its interactions with vegetation (Lantz et al. 2009). For example, thermokarst developing from thawing permafrost in Alaska is associated with transitions from graminoid- to shrub-dominated tundra as well as increases in total canopy nitrogen (Schuur et al. 2007). Fire is also expected to become increasingly common in arctic tundra, leading to not only changes in short- and potentially longer term carbon cycling (Field et al. 2007), but perhaps also altering the trajectory of successional processes (Bret-Harte et al. 2013).

Perhaps the most substantial suite of biophysical changes in terrestrial arctic ecosystems is the widespread increase in the abundance of woody shrubs (Naito and Cairns 2011a). Repeat aerial photography has been a useful tool to detect changes in arctic landscapes. In some parts of northern Alaska, shrub-dominated tundra increased from about 10% to about 20% of the landscape over the course of 50 years (Sturm et al. 2001b). The species contributing most
strongly to this expansion is the nitrogen-fixing shrub *Alnus viridis* subsp. *crispa* (Dryl. *ex* Aiton) Turrill, so its increase is and will be of particular importance to these nutrient-limited ecosystems (Sturm et al. 2001b). Additionally, areas where shrubs were previously absent have accumulated shrubs in that time span, and existing shrubs have become taller (Tape et al. 2006). As mentioned above, this phenomenon is not unique to Alaska. For example, erect shrubs in the Low Arctic of Canada increased by nearly 30% between 1964 and 2003, and the sites experiencing the largest increase in continuous shrub cover were comparatively steep slopes (Tremblay et al. 2012).

Topography and landscape position are strong predictors of the occurrence of localized shrub expansion throughout the Arctic, and riparian zones are the main settings of woody shrub increase (Naito and Cairns 2011b, Ropars and Boudreau 2012, Tape et al. 2012).

To examine these trends at larger spatial extents, many have employed satellite imagery to document the proliferation of vegetation generally, though this usually comes at the cost of coarser spatial grain (Verbyla 2008, Epstein et al. 2012). The remotely sensed data are based on both maximum and time-integrated values of the normalized difference vegetation index (NDVI), a measure of plant ‘greenness’ based on reflectance values in the visible and near-infrared spectra that has been shown to be a reliable predictor of biomass for a variety of woody shrubs (Campioli et al. 2009, Boelman et al. 2011). It is also useful for assessing overall increases in plant biomass and can include biomass from non-vascular plants (Walker et al. 2003).

An assessment of arctic NDVI in a set of transects across bioclimatic subzones (CAVM) in the Arctic revealed aboveground biomass increased approximately 20% between 1982 and 2010 (Epstein et al. 2012). In a comparison of a maritime and a continental transect, Walker et al. (2012) demonstrated that, though physiognomy and summer temperature regimes were similar, the continental transect experienced a larger increase in NDVI. The higher soil pH and lower winter precipitation were the main factors differentiating the continental transect from the maritime (Walker et al. 2012). Increases in NDVI suggest relative increases of canopy leaf area
by 20-60% in mixed shrub tundra in northern Canada, with both shrubs and graminoids contributing the most to the increase in spite of considerable heterogeneity within and among functional groups (McManus et al. 2012). Shrub cover in tundra ecotones is increasing most in wetter areas (Frost and Epstein 2014), which corroborates the finer grain analyses conducted using repeat photography.

Disturbance can also play an important role in the magnitude and extent of shrub increase. Channelization in watersheds with sizeable floodplains reduces disturbances like flooding and scouring, thereby potentially promoting shrub establishment and reducing shrub mortality (Naito and Cairns 2011b, Frost and Epstein 2014). Conversely, cryogenic disturbances such as frost heaves can create patterned-ground landscapes in which shrub recruitment and establishment increase (Frost et al. 2013, Frost and Epstein 2014). Additionally, Bhatt et al. (2010) used NDVI data to demonstrate that rapid vegetation growth occurs in landscapes with habitats recently exposed by retreating glaciers. This overall trend in increasing vegetative biomass, and particularly the component ascribed to woody shrubs, has been linked with trends in warming and declining nearby sea ice (Jia et al. 2009, Bhatt et al. 2010).

Originally, shrub expansion and growth were expected to lead primarily to climate feedbacks through winter processes, such as the reduction in albedo during the cold season as branches protrude above snow (Sturm et al. 2001a, 2005a). Sites with erect shrubs tend to develop deeper winter snowpack than graminoid-dominated areas that are more open, shorter, and have less complex canopy architecture for trapping snow (Sturm et al. 2001a). Deeper snow layers in winter help insulates soils and keep soil temperatures from dropping well below freezing, thereby allowing microbial communities to maintain higher, or seasonally earlier, rates of activity (Euskirchen et al. 2012). The increasing dominance of woody shrubs in arctic plant communities mediates ecosystem carbon cycling through these changes in decomposition rates and thus nutrient availability (Weintraub and Schimel 2005).
A critical feedback loop may result from increasing shrub abundance to deeper snow, warmer soils, and consequently greater microbial activity that enhances plant-available nitrogen and favors shrub growth (Sturm et al. 2005b). However, the direction and magnitude of some of these relationships are currently unresolved (Myers-Smith et al. 2011). Shrub canopies can either increase or decrease the rate of snowmelt in the spring (Callaghan et al. 2011). Although greater shrub cover leads to higher winter temperatures, summer temperatures are cooler under shrub canopies, and as a result, rates of decomposition, nutrient adsorption, and net annual CO$_2$ flux may not differ between neighboring shrub dominated and shrub free sites (Myers-Smith and Hik 2013). Similarly, the depth of the thawed, active soil layer can be shallower under shrub canopies than in plots with shrubs removed (Blok et al. 2010). Regional differences in current climates are important for whether shrub-dominated sites are sinks or sources of carbon (Cahoon et al. 2012), so these feedbacks may not affect arctic tundra uniformly. Shrub expansion that promotes mineralization and thus nutrient resources under shrub canopies (Sturm et al. 2005b) may increase rates of seed germination and seedling establishment shrub species (Fenner and Thompson 2005). However, germination and establishment in many species are also sensitive to the light environment (Bliss 1958, Fenner and Thompson 2005), so taller and larger shrubs may suppress continued sexual recruitment under dense canopies.

**Niches of arctic plants**

It has been over a century since Johnson (1910) first used the word niche, a concept that has since generated multiple definitions (Grinnell 1917, Elton 1927, Hutchinson 1957, Grubb 1977) and continues to serve as a valuable way to generate new ideas and discussion (McInerny and Etienne 2012a, 2012b, 2012c). Grubb (1977) separated plant niches into four elements: the phenological niche, the life-form niche, the habitat niche, and the regeneration niche, with the
latter two identified by species’ physicochemical requirements for survival and reproduction. The regeneration niche is made up of a series of stages from viable seed production through dispersal, germination, establishment of individuals, and maturation (Grubb 1977).

Of these five stages of the regeneration niche, the latter four are comparatively well studied in the context of global change effects on plants. The near-term implications of warming include earlier onset of flower and fruit production, both increases as well as decreases in the total yield of seeds and other important reproductive structures, and shifts in species ranges, usually towards higher latitudes or elevations (Hedhly et al. 2009). Earlier flowering is generally thought to result in an elongation of the growing season and thus an increase in reproductive output, but in alpine and perhaps arctic regions, phenological advancement can lead to greater risk of frost damage and ultimately lead to declines in flowering and fruiting (Inouye 2000, 2008, Boggs and Inouye 2012). Additionally, temperature stress during gamete development can be costly to reproductive output in a wide range of plant species (Hedhly et al. 2009). Arctic plants, however, are nearly all clonal and thus able to increase via asexual spread (Jónsdóttir 2011), and there is often a tradeoff between reproductive effort and clonal growth (Moles and Westoby 2006, Herben et al. 2015).

Arctic plants display many adaptations for surviving in temperature-limited environments. For example, seeds of most *Salix* (willow) species germinate in the fall, but many arctic willows have some form of dormancy, usually physiological dormancy, necessitating cold stratification in the autumn and winter followed by dormancy breakage in the spring (Bliss 1958, Densmore and Zasada 1983). As well, longevity is a nearly universal trait in arctic plants, as evidenced by the almost complete absence of annual plants from Arctic floras (Bliss 1971, Gussarova et al. 2012), and individuals in some of these species can live for hundreds or even thousands of years (de Witte et al. 2012). This enables individuals to survive through unfavorable conditions and then reproduce and recruit new individuals when conditions improve (Büntgen et
al. 2014). Similarly, sexual reproduction and recruitment were considered both temporally rare and spatially limited early on in arctic plant research (Bliss 1958, 1971, Bell and Bliss 1980). This assumption was due in part to considerations of adaptations to interannual variation in air and soil temperatures, the seasonality and quantity of precipitation, wind, and other abiotic factors (Bliss 1971). Floral development and maturation is a multi-year process in many species with limited growing seasons (Wagner et al. 2012), though when germination and emergence occurs, seedling mortality may be high enough to limit recruitment in most species to favorable episodes (Philipp et al. 1990).

Recent studies have challenged the view that sexual reproduction is of limited demographic importance in arctic plant species. Although the availability of suitable microsites suggests that abiotic factors are critical for establishment from seed (Graae et al. 2011), species composition may also be limited by the availability of seeds (Dullinger and Hülber 2011). Many arctic seeds lack specific adaptations for dispersal (Baskin and Baskin book), so simply becoming taller (Hudson et al. 2011), especially in response to experimental fertilization, can lead to the capacity to dominate the community-level seed rain (Gough et al. 2015). However, germination may be a more limiting factor in arctic plant recruitment than seed dispersal (Cooper et al. 2004, Müller et al. 2011). Seed production in some species may be very high without necessarily resulting in increased recruitment (Moulton and Gough 2011). Even sites characterized by low productivity, with an abundance of open microsites, can be limited by both seed availability and microsite quality (Eskelinen and Virtanen 2005).

In the long-term, climate change might mediate adaptation by controlling the response of sexual reproduction, an important part of demographics in most species and thus a major contributor to fitness (Hedhly et al. 2009). The evolution of a life history strategy depends not only on variation in genes but also on the environment in which selection occurs (Lacey and Herr 2000). Walck et al. (2011) suggested that variation in the temperature ranges for cold
stratification, the period of time during which a seed experiences temperatures below some threshold that then allows for dormancy to be broken, will lead to individualistic responses of species to winter warming. This is particularly relevant in regions of the Arctic, such as Greenland, where winter and spring are projected to be the periods with the greatest relative increases in temperature (Stendel et al. 2008). Moreover, variation in conditions is an important determinant of the role of seed banks, whether existing over only one winter or multiple years, in the persistence of plant populations (Ooi 2012). The cues to which species respond also play an important role in determining how responsive they are to change. For example, species adapted to begin growth in response to snowmelt are more sensitive to the advance in the timing of snowmelt than those lacking adaptations to snowmelt as a reliable cue (Galen and Stanton 1995). Intraspecific variation in growth and reproduction phenologies resulting from differences in snowpack (Galen and Stanton 1991, 1993) means site-level factors mediate the effect of abiotic change on reproductive output. Over evolutionary time scales, species responsive to the timing of snowmelt may develop additional or alternative cues for emergence as advancing phenology becomes maladaptive (Inouye 2000).

The timing of germination may also be changing for spring emerging species (Walck et al. 2011). For example, climate warming may cause alpine spring emerging species to shift to autumn emergence as a result of changes in seed dormancy (Mondoni et al. 2012). Warming can also advance or accelerate the process of germination without necessarily increasing the overall proportion of germinants (Milbau et al. 2009). However, strong summertime experimental warming up to 8 °C reduced seedling emergence in two arctic forbs (Graae et al. 2009). Some evidence also indicates that the effect of experimental warming on germination and establishment is greater in early germinating than in later germinating species (Shevtsova et al. 2009). As for changes in mature established individuals, experimental warming has shortened the ripening period for one species in arctic tundra (Molau and Shaver 1997), but seed development was
independent of temperature in other arctic plants investigated in different regions with variable climates (Graae et al. 2008). Similarly, shortened growing seasons due to experimentally enhanced snowpack and thus delayed onset of the growing season led, in at least one study, to fewer flowers, fewer plots with dispersed seeds, and lower germination in several species (Cooper et al. 2011). Observational studies have also demonstrated that short growing seasons reduce flowering and seed production in a wide range of species (e.g. Kudo 1991). It is thus still unclear how climate impacts the aggregate duration and efficacy of seed development and maturation in arctic plants. There is more to climate change than increased temperatures, but regional differences include more variation than due climate alone. Furthermore, warming may lead to decreased germination from seed banks, but the effect of warming is mediated by disturbance (Hoyle et al. 2013). Disturbed sites, such as thaw slumps, are becoming increasingly common in arctic and subarctic regions, and can contribute to increased growth, reproductive output, and germination (Lantz et al. 2009). Those relationships that have been found in multiple species, either observationally or experimentally, are summarized in Figure 1.2.

The niches of established individuals of arctic plant species also appear to be changing in terms of occupied habitats and traits, particularly in shrub species that are increasing in abundance and responsive to experimental warming. As mentioned above, shrub expansion in recent decades has been greatest in wetter topographic and landscape positions that likely have greater resource inputs (Naito and Cairns 2011b, Ropars and Boudreau 2012, Tape et al. 2012). Long-term monitoring of small plots has contributed a great deal of evidence confirming this pattern. With up to thirty years of data from some locations, both low-statured and tall erect shrubs have generally increased in abundance across the Arctic in association with summer warming, although shrub growth is greatest in relatively warm regions and in mesic sites (Elmendorf et al. 2012b). However, our understanding of the drivers of variation among species and regions is limited, and patterns resulting from recent warming may not be indicative of future
changes under greater temperature increases (Elmendorf et al. 2012b). Experimental manipulations of key abiotic factors such as temperature, snow cover, and nutrient availability have corroborated the general pattern from long-term observations, as both graminoids and deciduous shrubs have increased in height and ground cover (Elmendorf et al. 2012a). Moreover, deciduous shrub growth responds to warming most strongly in habitats that are already comparatively warm, have high soil moisture and likely also greater soil nutrient content (Wahren et al. 2005, Elmendorf et al. 2012a, Vankoughnett and Grogan 2014). The spatial expansion and increasing dominance of woody shrubs in tundra ecosystems also has implications for species interactions. Plant species that can attain high local abundance, such as woody shrubs, can create negative and positive effects on the spatial distributions of other local competitors, though the latter are less common (le Roux et al. 2012).

Clonal life histories that allow for particularly long-lived individuals are quite common in the Arctic (de Witte et al. 2012, Gussarova et al. 2012). Their “persistence niche” gives many arctic species the capacity to resprout after a disturbance in addition to their capacity to spread via clonal growth (Bond and Midgley 2001). In low productivity habitats with infrequent disturbance like arctic tundra, it may still be adaptive to have the capacity to resprout because it promotes earlier occupancy of available space and thereby acquisition of limiting resources (Bellingham and Sparrow 2000). Climate warming is likely to alter the tradeoffs between clonal growth and sexual reproduction differently among species according to their life history strategies (Vallejo-Marín et al. 2010). In the deciduous shrub *Betula nana* L., experimental fertilization alters resource allocation patterns by increasing the number of branches and production of new meristems (Bret-Harte et al. 2001) as well as increasing secondary growth (Bret-Harte et al. 2002). Additionally, the direct and indirect effects of warming can increase meristem initiation and primary and secondary growth in existing apical stems in this same species, regardless of the presence or absence of herbivores (Zamin and Grogan 2012). Because *B. nana* focuses allocation
to clonal spread rather than sexual reproduction, it is capable of increasing in abundance
dramatically without recruiting from seed (Moulton and Gough 2011). As abiotic factors mediate
the relative importance of sexual reproduction based on species life history traits, responses are
likely to be individualistic and challenging to predict. A first step in such prediction should
include not only a determination of the proportional investment in reproduction and growth, but
also how allocation ‘rules’ are mediated by external forces such as climate, nutrient resource
availability, and disturbance regime (Winkler and Fischer 2002, Klimeš 2008).

The niches of arctic plants are not only structured by abiotic factors like climate and
nutrient deposition; biotic interactions from both neighboring plants and consumers play a key
role in the architecture of individual plants and thus mediate competitive and facilitative
interactions that also determine vegetation structure and composition. In low productivity
habitats, low level grazing can still allow for dominant species that can exclude some of their
local competitors within short time frames (Virtanen et al. 1997, Zamin and Grogan 2013).
Additionally, grazing in these habitats alters vegetation structure by maintaining open microsites
in which species can colonize and become established (Eskelinen and Virtanen 2005). Moreover,
herbivore diversity also influences the structure of tundra vegetation, and because different
herbivores will vary in their responses to abiotic change, the strength of plant-herbivore
interactions fluctuates through time (Olofsson et al. 2013). Herbivory mediates the habitat niche
of a range of species, including superior competitors capable of becoming locally dominant
(Pajunen et al. 2011, 2012), and thus local diversity can be maintained through species
differences in the regeneration niche.
**Consequences for biodiversity**

One of the major consequences of vegetation change in the Arctic is likely to be a decline in local diversity at small spatial grains (Walker et al. 2006). Although global biodiversity is well understood to be in decline, recent syntheses have suggested that there has been no net change in the number of species at local and regional scales (Vellend et al. 2013, Dornelas et al. 2014, but see Cardinale 2014), and the inclusion of human modified habitats in which the systems are recovering from severe disturbances did not weaken the overall conclusion (Vellend et al. 2013). This is due, in part, to replacement of taxa, rather than to a decrease in the number of taxa (Dornelas et al. 2014). One of the reasons this general conclusion may not apply to some Arctic regions is the importance of biogeographic barriers preventing colonization or invasion. Habitat specialists, such as species adapted to snowbeds, may yet undergo replacement by more widely distributed tundra species in response to warming, habitat loss, or an eventual combination of the two (Sandvik et al. 2004). Even some widespread taxa like lichens and bryophytes are expected to decline with warming, and current abundances are likely already in disequilibrium with current climate (Lang et al. 2012).

Vegetation change is not, however, a universal phenomenon in the Arctic. Over the four decades from 1968 to 2007, plant cover and community composition remained largely unchanged in sites near Tasiilaq in southeast Greenland (Daniëls et al. 2011). This may be somewhat related to the absence of oceanic warming in that part of the North Atlantic (see Figure 1.1). Mean summer (June/July/August) temperatures in Tasiilaq increased only slightly in that time span (0.2 °C per decade) compared with winter temperatures (0.7 °C per decade). Nonetheless, the flora did experience shifts towards more Low Arctic and subarctic species in a little over a century, and the greatest changes occurred in wetter sites, which may be drying due to decreasing winter snow (Daniëls and de Molenaar 2011).
One potential explanation for very gradual or nonexistent change in Tasiilaq’s plant community is the fine scale variation in temperatures can create microrefugia suitable for the maintenance of plant populations (Dobrowski 2011). Though much of the Arctic is quite flat, there remains the potential for fine spatial variability in temperature to buffer communities against recent and future warming (Lenoir et al. 2013). Microclimatic variation across aspects can reach over 8 °C, so migration distances of as little as a few meters may be sufficient for many arctic plant populations to persist in spite of climate warming (Scherrer and Körner 2010). Therefore, in order to understand whether the potential for microrefugia to provide resistance to warming can be realized in tundra communities, I have set out to address questions regarding sexual reproduction at the community-level, the importance of sexual reproduction relative to clonal spread across a climatic gradient in a deciduous shrub increasing in both cover and height, and what the consequences of climate change are for biodiversity in local assemblages.

**Organization of dissertation**

The Low Arctic region of West Greenland provides ideal plant communities in which to address vegetation dynamics in the context of climate change because the island’s flora is small and the competitive and trophic interactions are fewer than parts of the Low Arctic. Additionally, these landscapes contain biologically meaningful gradients over distances tractable for study that can nonetheless provide insight into changes anticipated over larger spatial scales. This dissertation comprises a series of case studies from this region in which I address a range of biological levels of organization, from individuals to communities, and from spatial scales ranging from small plots to landscapes across environmental gradients. In particular, I focus on how species’ different tradeoffs between growth and reproduction will play a major role in determining the future of arctic tundra. In Chapter 2, I use manipulations of the parental plants’
environments that potentially influence seed quality in species common in Low Arctic tundras to fill the gap in our understanding between the effects of climate change on growth and reproduction in established individuals and on seedling recruitment. In Chapter 3, I focus on *Salix glauca* L. (grayleaf willow), a deciduous shrub rapidly increasing in abundance in the Arctic. Here, I use this widely distributed species to explore the relative importance of sexual recruitment and clonal spread in sites with recent shrub expansion, and I do so across a maritime to continental climatic gradient. I explore the consequences of experimental warming and herbivore exclusion for local biodiversity in Chapter 4. In this study, I expand on our understanding of vegetation dynamics in the Arctic by placing the results in the context of theorized relationships between productivity and species richness. Finally, the Appendix consists of a collaborative study that enabled me to address how relationships between climate and secondary shrub growth differ among species and seemingly sites as well. The overarching goal of this dissertation is to synthesize the way in which species’ life history strategies dictate how their growth and reproduction might respond to current trends in climate and how their interactions will shape the structure and composition of tundra vegetation in coming decades.

**References**


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Figure 1.1. 1986-2015 temperature anomaly relative to the 1951-1980 climate normal. Map created using GISTEMP on the NASA Goddard Institute for Space Studies web-based tool (http://data.giss.nasa.gov/gistemp/).
Figure 1.2. Summary of how changes in or during the growing season affect seed germination (G) and seedling establishment (E). Increases in temperature (T+) can lead to advancement in the timing of G and E as well as declines in the cumulative total G and E. These changes occur primarily in early- rather than late-flowering species. Increased disturbance (D+) can result in increases in G and E. Shortened growing seasons (GS-, represented by dashed line) due to delayed snowmelt can lead to reduced G.
Chapter 2

Seed quality responses to drivers of global change vary widely across arctic plant species

Abstract

Arctic plant communities show diverse responses to climate change. Observational studies and experimental approaches have together established that most tundra landscapes are undergoing changes in the relative abundances of vascular and non-vascular plants. Established adults of many graminoid and woody shrub species in particular have increased in cover and height, and recruitment from seed is enhanced by warming and fertilization in some species. To address the gap between seeds and established individuals, I excluded large herbivores and simulated increases in temperature and precipitation in the parental environment of twelve forb, graminoid, and deciduous shrub species to investigate the responses of seed quality among species in the mixed shrub-graminoid tundra of Low Arctic West Greenland. Results for both seed mass and germination indicated that the effects of changes in temperature, precipitation, and ungulate herbivory are unique among species, including cases showing no evidence for climatic mediation of parental effects on seed quality. Warming and watering each led to increases in seed quality in some species and decreases in others. Both increases and decreases resulted from herbivore exclusion as well, but this treatment only significantly affected graminoid species. Interannual variation in weather contributed to the complexity of responses in species and suggests that at least some species are near potential thresholds of abiotic and biotic limitation of sexual reproduction. Additionally, the prevalence of fungal pathogens in the germination trials,

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and that fungal growth on seeds did not always prevent germination, suggests that further investigation into how these antagonistic interactions may shift under climate change is imperative. The aggregate insights from this study lend support to the hypothesis that tradeoffs between sexual reproduction and asexual spread in these facultatively clonal species mediate vegetation dynamics under environmental change.

**Introduction**

Prior research on plant responses to anticipated climate change has largely concentrated on how altered conditions affect either established individuals or the successful recruitment of new individuals into a population. In high latitude systems, experimentation has commonly focused on the effects of summer warming on, for example, leaf and reproductive phenology, leaf chemistry, physiology and functional traits, plant biomass and architecture, and carbon exchange (Arft et al. 1999, Bret-Harte et al. 2002, Walker et al. 2006). This approach has been validated by the fact that most plant growth responses are positively correlated with summer temperatures (Blok et al. 2011, Elmendorf et al. 2012). Demography is nonetheless central for the maintenance of arctic plant populations, and investment in sexual reproduction and germination and establishment of new individuals are key parameters. Though clonal spread has long been seen as playing the dominant role in arctic plant population dynamics due to the rarity of establishment from seed (Bliss 1958, 1971, Billings 1987, Welling et al. 2004), sexual reproduction is now understood to be commonplace and thus important in the demographics of some arctic plant species (Wookey et al. 1995, Gabrielsen and Brochmann 1998, Stamati et al. 2007, Steltzer et al. 2008, Klady et al. 2011).

Environmental conditions during the growing season can influence seed quality (Fenner and Thompson 2005), a key component of plant reproduction and regeneration (Grubb 1977). For
example, temperature is thought to affect germination in several ways. For example, some populations of a given species may occur in locations where temperature or length of the growing season remain below some threshold necessary for the production of germinable seeds (Alsos et al. 2003). Additionally, interannual variability in climate during the period of development influences the production and germination of arctic and alpine seeds (Laine et al. 1995). Some of this effect may be explained by variation in the timing of flowering (Post et al. 2001, Molau et al. 2005, Kudo and Hirao 2006, Menzel et al. 2006, Inouye 2008) and some measure of reproductive effort (Wookey et al. 1993, Molau and Shaver 1997, Arft et al. 1999, Kudo and Hirao 2006), both of which have consequences for fitness (Galen and Stanton 1991). For example, a meta-analysis revealed reproductive measures responded positively to nutrient fertilization as well as warming, but showed no response to CO₂ fertilization or watering (Dormann and Woodin 2002).

Temperature also directly affects entrance into and breakage of seed dormancy and subsequent germination (Baskin and Baskin 1998). Although temperature sensitivity is high for both alpine and arctic species, these latter processes have only been studied for select species (Wookey et al. 1995, Molau and Shaver 1997, Baskin et al. 2002, Graae et al. 2008, Wagner et al. 2012).

Precipitation can also exert direct and indirect effects on regeneration in arctic plants. Interannual variation in both the quantity and timing of precipitation can have substantial consequences for seedling survivorship. Some forb species show enhanced seedling emergence when seeds were transplanted to wetter environments (Meineri et al. 2013). Years in which there is no autumn snowfall or its onset is delayed by warmer temperatures are associated with the likelihood of plants experiencing cold temperatures, leaving seedlings vulnerable to mortality. This phenomenon has long been considered a primary constraint on population demographics in arctic plants (Wager 1938). The direct effects of increased precipitation may be weaker on seedling growth (Paradis et al. 2014) than adult growth (Blok et al. 2011), but increased adult
growth in years with greater precipitation may lead to increases in sexual reproduction via enhanced productivity resulting in greater resources that can be allocated to reproduction.

Dormancy and the development of seed banks provide ways for plants in stressful environments with temporal variability to hedge against the unpredictable occurrence of unfavorable conditions. Seed banks may be larger in more productive habitats (McGraw and Vavrek 1989, Cooper et al. 2004) but reduced in the presence of herbivores (Kuijper et al. 2006, Cooper 2006). A major factor underlying this control on seed production by herbivores is the timing of herbivory relative to the timing of plant reproduction (Briske and Noy-Meir 1998). The removal of reproductive tissue may have a greater direct impact on earlier flowering and fruiting species in tundra landscapes hosting herbivore populations present only during the growing season (Thing 1984). Herbivory on non-reproductive tissues outside of the growing season likely impacts not only the architecture of the vegetation but also the ability of plants to mobilize stored reserves of carbon (Gremer et al. 2010). Once seedlings emerge, grazing pressure on non-seedlings increases seedling survivorship and thus maintains higher species richness (Eskelinen and Virtanen 2005), possibly through removal of competitors. Thus, the effects of herbivory on regeneration are complex and still largely only understood in the context of damage to mature individuals and the subsequent effects on the number and movement of seeds.

Previously, experimentation has been conducted principally on seeds and seedlings rather than the mother plants (Hobbie and Chapin 1998, Graae et al. 2004, 2011, Milbau et al. 2009). Many studies have assessed the role of seed banks in population dynamics (e.g. McGraw and Vavrek 1989) because seed dormancy is adaptive in environments with temporal variation in the conditions necessary for establishment (Harper 1977). The direct or indirect effects of warming on seed quality in arctic plants have only been assessed in case studies (Wookey et al. 1995, Molau and Shaver 1997), but both temperature and soil moisture are important factors during seed development and maturation (Walck et al. 2011). Therefore, in a highly variable
environment like arctic tundra, in which species spread clonally as well as through sexual 
reproduction, changes in these basic abiotic factors might reveal phenotypic plasticity in the 
investment in seeds.

We lack crucial information linking the maternal environment to the likelihood of 
successfully recruiting offspring in most arctic plants. Relatively little work on seed quality has 
been done in arctic species, most of which are clonal perennials that are also capable of 
regenerating sexually. Consideration of only reproductive effort, i.e. number of flowers or seeds 
produced, without understanding maternal effects on seed quality, masks the complete set of 
responses to environmental changes (Germain and Gilbert 2014). Additionally, seeds rather than 
mother plants are usually the subjects of manipulative experiments in the Arctic (Graae et al. 
researched, it is often as case studies of one or a few species, precluding understanding of how 
the individualistic responses of species might shape the community as a whole. Here, I contribute 
to filling this gap in our knowledge by experimentally increasing growing season temperature and 
precipitation and manipulating the presence of ungulate herbivores to address the hypothesis that 
seed quality is mediated by both abiotic and biotic factors. I focused on seed quality, defined here 
as seed mass and germination, as an indicator of reproductive success because it is controlled 
primarily by weather during the growing season in which flowering occurs (Molau 1993). By 
contrast, reproductive effort (i.e. an organism’s investment in reproductive tissues like flowers) is 
integrative over multiple prior seasons because flower buds are pre-formed in prior years in most 
native plants. I anticipated that life history strategy would determine species-level 
responses to each of these factors. For example, I expected that deciduous shrubs, which have 
shown increased primary and secondary growth under warming, would invest more resources in 
reproduction and therefore have larger and more germinable seeds in the warming treatment 
compared with their conspecifics in the control. Additionally, I expected shrubs and graminoids
to show stronger responses to warming than forbs, as previously shown for reproductive effort and success (Klady et al. 2011). I predicted seed quality in graminoids would be positively associated with herbivory while forbs and deciduous shrubs would show positive responses to herbivore exclusion.

**Methods**

**West Greenland climate projections**

Results from recent projections for 2051-2080 using a regional climate model at 25 km horizontal resolution indicate that mean annual temperatures in West Greenland are expected to be 3-3.5 °C higher relative to the 1961-1990 mean (Stendel et al. 2008). However, this increase is not equitably distributed among the seasons. Summer temperatures are only expected to increase 1-2 °C, which is commensurate with how many researchers have been experimentally examining the effects of warming for the last two decades (Henry and Molau 1997). Moreover, winter and spring temperatures in West Greenland are projected to increase 6-8 °C. Conversely, autumn temperatures in much, but not all, of West Greenland are expected to undergo a slight cooling of about 0.5 °C (Stendel et al. 2008).

Concomitant with these projected increases in temperature are changes in patterns of precipitation because the hydrologic cycle is generally expected to intensify. Regional climate modeling projects a 45-55% increase in the total quantity of precipitation in West Greenland for the period 2051-2080 (Stendel et al. 2008). This increase is likely to occur over about 50% more precipitation days over the current annual mean of 39 days, roughly half of which occur during the growing season (Stendel et al. 2008). Furthermore, there is expected to be a greater proportion
of the area’s precipitation falling as rain rather than snow due to increased temperatures and an extended growing season, so winter snow depth is projected to decrease (Stendel et al. 2008).

**Study site and experimental design**

The study was conducted at a set of locations centered at 67.11 °N, 50.34 °W, approximately 18 km ENE of the town of Kangerlussuaq, Qeqqata Commune, in western Greenland. The mean annual temperature and precipitation were -5.7 C and 149 mm for the climate normal period of 1973-1999 (Cappelen 2013). These locations are at the margin of the summer calving grounds of the migratory Kangerlussuaq-Sisimiut herd of *Rangifer tarandus* ssp. *groenlandicus* L. (barren-ground caribou), and the area is also home to a resident population of *Ovibos moschatus* Zimmermann (muskoxen) that was reintroduced in the 1960s (Thing 1984, Pedersen and Aastrup 2000). The former are more abundant, and because they disperse from their calving grounds while fruit development and seed maturation is still occurring in some species (e.g. *Trisetum spicatum* (L.) K. Richt. and *Stellaria longipes* Goldie), only those species that reach the dispersal stage by mid-August were included in this study. The landscapes of West Greenland are characterized by noncarbonated mountain complexes creating a mosaic of habitat patches ranging from snowbeds and low lying wetlands to herb slopes and dry fellfields (Walker et al. 2005), so the dominant species in a given habitat can range from, for example, sedges to dwarf shrubs to cushion plants.

I established a total of 20 plots for both warmed and unwarmed watering treatments to add to the existing set of warmed and exclosed plots (see Post 2013). The composition of the plots used in this study is similar to the warmed and ambient point-frame plots discussed in further detail in Chapter 3 of this dissertation and Post (2013). Beginning in the summer of 2011, I established twelve 0.5 m radius circular plots, six near each of two exclosure sites described by
Post (2013), containing a mix of deciduous shrubs, graminoids, and forbs in such a manner as to capture representation by all common constituents listed above. These exclosures preclude access from ungulate herbivores, though arctic hares (*Lepus arcticus* Ross) and rock ptarmigan (*Lagopus muta* Montin) still have access to the exclosed vegetation. The plots were set up in pairs, each plot in a given pair having similar composition, slope, and aspect. The plots within each pair are < 3 m apart, while all pairs are > 5 m apart. One plot in each pair was randomly assigned the warming treatment, which consisted of a 0.5 m radius circular ITEX cone (Henry and Molau 1997) which increases near-surface air temperatures at this study site by 1-3 °C during the day (Post et al. 2008). In 2012, I then added four new pairs of plots to one of these exclosures, with the four warmed plots comprising ~0.75 m radius ITEX hexagons (Henry and Molau 1997). The warming treatment was implemented between mid-May and mid-August in all years.

On all of these plots, I simulated a 50% increase in mean monthly precipitation applied as a 50% increase in mean monthly precipitation days for May through August. For example, July currently has a mean monthly precipitation of 24 mm with 6 mean precipitation days (averaging 4 mm per day). I therefore augmented July precipitation with 4 mm of water on each of 3 days. The simulated precipitation additions occurred on cloudy days that had no or little (< 1 mm) measurable precipitation, and the water used was filtered through a Katadyn pleated glass fiber filter with a pore size of 0.2 μm (Katadyn NA, Inc., Minneapolis, MN, USA). The ambient/watered and warmed/watered treatments were randomly assigned to each plot pair, with the pre-existing point-frame plots representing the warmed/unwatered treatments. Samples for the ambient/unwatered treatments were selected haphazardly from individual plants within 5 m of either the ambient/watered or warmed/watered plots.

Several additional plots were included in this study to address the hypothesis that grazing reduces seed quality in forbs more than in graminoids. A total of twelve plots containing ITEX hexagones were set up at the same time each year as those mentioned above in three large
herbivore exclosures originally erected in 2002 (Post 2013). I collected seeds from each of the warmed/unwatered plots in these exclosures, as well as controls from nearby unwarmed individuals still within the exclosures. Sample sizes for the warmed/unwatered and ambient/unwatered treatments were further augmented by collecting seeds from the relevant species from sites whose plots were established for an otherwise unrelated experiment that did not include a watering treatment. Finally, because of the rarity of Potentilla hookeriana Lehm. on the plots mentioned above, I established several additional plots of the same size on dry, south-facing hillslopes covered only in biological soil crusts and P. hookeriana. These plots were randomly assigned to one of the watering treatments (watered or unwatered); there was no warming or herbivore exclusion.

In mid-August of each year from 2012 through 2014, I collected seeds from 1-3 individuals or ramets on each plot. Whenever multiple ramets from the same individual bore fruit, I sampled up to three ramets. I marked those individuals from which samples were collected in one year were marked so that samples would not be collected from those individuals in later years.

**Study species**

I sampled multiple species from each of three commonly used plant functional types (PFTs) (Chapin et al. 1996): forbs, graminoids, and deciduous shrubs. The forb species consisted of Bistorta vivipara (L.) Delarbre, Cerastium alpinum L., Draba breweri S. Wats., and P. hookeriana. The graminoid species included Carex supina Willd. ex Wahlenb., Festuca brachyphylla Schult ex Schult. & Schult. f., Kobresia myosuroides (Vill.) Fiori, Luzula confusa Lindeberg, Poa glauca Vahl, and Poa pratensis L. The two deciduous shrubs were Salix glauca L. and Betula nana L. With the exception of P. glauca, and P. pratensis, each species will
hereafter be referred to simply by its genus. Although *Bistorta* produces bulbils rather than true seeds, I treat them as such and hereafter refer to all diaspores as seeds for simplicity. The total number of individuals sampled ranged from 71 for *Kobresia* to 183 for *Salix* (see Table 2.1).

**Measuring seed quality**

Collected seeds were air dried in the field then put in cold storage upon return to the lab at Penn State, between one and two weeks after their collection. They were put in cold storage at approximately 4 °C for two weeks, then cold stratified at -20 °C for approximately 18 weeks (Klady et al. 2011). After stratification, seeds from each sample were separated from all other tissues and between 20 and 30 seeds from each sample were counted and weighed on either a Mettler AJ100 or Mettler M5 balance, depending on seed size (Mettler-Toledo International, Inc., Columbus, OH, USA). Note that seeds were weighed without having been oven-dried to a constant mass, so values of seed mass reflect fresh weight before imbibition rather than dry mass. *Potentilla* was collected only at the end of the 2012 growing season, and *Draba* seeds and *Salix* diaspores (seeds plus dispersal tissues such as pappi) collected in 2012 were not weighed. All seeds (including *Salix* seeds separated from pappi) collected in 2013 and 2014 were weighed. Additionally, the perigynia of *Carex* seeds from 2012 were not removed before the germination trial, but perigynia were removed from these species’ seeds collected in 2013 and 2014.

After all seeds were weighed, I then conducted the germination trials. Each sample of 20-30 seeds was placed on a 55 mm Grade 413 filter paper in an upside down lid of a 60 mm sterile, polystyrene petri dish with the inverted bottom of the dish serving as a lid. Approximately 2-3 ml of deionized water was added to each dish with a transfer pipet at the initiation of the germination trial, and filter papers were given near-constant access to moisture. I evaluated germination, defined as the radicle having emerged and elongated beyond 2 mm, every two to three days. I
removed germinated seeds from the petri dishes once they were discovered and recorded. The germination trials ran from 14 April to 18 May in 2013, 3 March to 23 April in 2014, and 11 February to 3 April in 2015. To provide suitable conditions for species with unknown light requirements for breaking dormancy, the lighting progressed from light/dark cycles of 14/10 h for the first week, 16/8 h for the second week, and then 24 h light until the end of each year’s germination trial. This protocol provided both diurnal and longer term variation in light environment as well as constant light to simulate conditions that satisfy common dormancy breakage requirements (Baskin and Baskin 1998, Fenner and Thompson 2005). In 2013 and 2014, temperatures for the entire duration of the germination trials ranged from daily minima near 10 °C to daily maxima near 20 °C. Because of a series of climate control system failures during the 2015 germination trial, the daily minima and maxima ranged from approximately 18 to 26 °C, and these values increased over the course of the trial by about 5 °C.

**Data analysis**

I performed separate analyses for each species because I had *a priori* hypotheses on the particular responses of species based on their life histories and functional groups. Furthermore, doing so enabled me to capture their differential responses to treatments across years. I conducted sequential analyses for seed mass and then germination for each species because these two responses to the treatments covary, and the association between the two differs among species. By deliberately separating these analyses, I can account for species-level differences in this relationship. Because mass was measured in cohorts of seeds, these data were divided by the number of seeds in each cohort to yield an estimate of the mean mass per seed. Seed mass values for *P. glauca* and *Salix* were normally distributed, but values for all other species were log-transformed to yield normally distributed residuals.
I began with a model for seed mass to address the hypotheses that the effects of increased temperature and precipitation and the absence of large herbivores would influence seed quality differently according to variation in life history strategies. For most species, relationships between warming, watering, and grazing factors and seed mass were assessed with linear mixed effects models of the form:

$$Y_{ij} = \beta_{0j} + (\beta_{1j} \text{Warming} \ast \beta_{2j} \text{Watering} + \beta_{3j} \text{Grazing})\beta_{4j} \text{Year} + e_{ij}$$

in which \(Y_{ij}\) is the estimate for mass per seed, \(\beta_{0j}\) is a random intercept for the seven \(j\) sites, \(\beta_{1j}, \beta_{2j}\), and \(\beta_{3j}\) are slopes for the warming, watering, and grazing fixed effects, respectively, \(\beta_{4j}\) is the slope for year, and \(e_{ij}\) is the residual error. I included the two-way interaction between warming and watering as well as all two-way interactions with year, but I did not include the three-way interaction between year, warming, and watering due to a lack of statistical power. The exceptions to this model structure were as follows: *Luzula* did not have a large enough sample size to permit assessing the effects of the removal of grazing but otherwise retained the remaining parameters from the full model, and *Potentilla* only included samples from the watering treatment in a single year and therefore only included a single fixed effect for watering and a random effect for site. Parameters for the fixed effects were derived from restricted maximum likelihood estimation.

Next, to assess the impact of these factors on germination, I fit generalized linear mixed effects models using only the non-significant fixed effects from the mass models of the form:

$$\frac{Y_{ij}^{\text{germ}}}{Y_{ij}^{\text{cohort}}} = \beta_{0j} + (\beta_{1j} \text{Warming} \ast \beta_{2j} \text{Watering} + \beta_{3j} \text{Grazing})\beta_{4j} \text{Year} + e_{ij}$$

in which the outcome is the proportion of the number of seeds that germinated, \(Y_{ij}^{\text{germ}}\), out of the total number of seeds in the cohort for each sample, \(Y_{ij}^{\text{cohort}}\). For example, the germination model for a given species for which grazing was a significant predictor of seed mass did not include the main effect for grazing. Note, however, that the interaction between grazing and year would have
been retained in the model for that species. The exceptions to the above framework for seed germination were the two sedges, Carex and Kobresia, because the germination trial in 2012 ended shortly after these seeds began to germinate. Because of the likelihood of continued germination in these species had the germination trial been continued, I excluded 2012 data from the germination analyses for these two species. Overdispersion was common for many species, so I used the NB2 negative binomial distribution to account for this overdispersion by fitting an additional parameter, $\theta$ (Hilbe 2011). In spite of the removal of significant predictors of mass from the germination analyses, the hypotheses for effects on seed mass and germination represent multiple comparisons for each species. I used the Holm-Bonferroni correction to control the familywise error rate at $\alpha = 0.05$ (Holm 1979). All analyses were conducted in R (R Core Team 2015) using the lme4 1.1-10 (Bates et al. 2015) and glmmADMB 0.8.0 (Fournier et al. 2012, Skaug et al. 2013) packages.

**Results**

**Warming and watering**

The effects of warming and watering on seed quality were highly variable between the twelve study species (Figures 2.1 and 2.2). Even species of similar life form, often ascribed to the same PFT, tended to show quite disparate responses. Using forbs as an example, watering resulted in decreased seed mass in Draba and increased seed mass in Bistorta (Figure 2.1), whereas the direct effect of watering on Cerastium was only apparent in seed germination (Figure 2.2). By contrast, Potentilla showed no response to watering in either measure of seed quality. None of the three forb species examined for the effects of warming exhibited any resulting changes in either seed mass or germination.
Graminoid species were similarly disparate in responses of seed quality to warming or watering. There was strong evidence that warming increased seed mass in *Festuca*, while there was moderate evidence of a small decrease in seed mass in *P. glauca* (Figure 2.1). Additionally, though the overall effect of warming on *Festuca* seed mass was positive, there were negative responses in the latter two years of this three year study. *Kobresia* showed no overall effect of warming but revealed a positive interaction between warming and watering as well as some limited evidence of a negative effect of watering in 2014 (Figure 2.1). The graminoids were largely similar in that neither warming nor watering impacted the proportion of germinating seeds. The two exceptions to this were the negative effect of watering on *Carex* germination and a negative effect of warming on *P. glauca* germination in 2014, but the evidence in support of these results is weak.

The two deciduous shrubs further illustrate the phenomenon of heterogeneity within PFTs with respect to how warming and watering affect seed quality. Warming resulted in a small but significant increase in *Salix* seed mass, whereas *Betula* seeds did not increase in mass (Figure 2.1). Warming led to both decreased and increased germination in *Betula*, depending on the year, and there was also some weak evidence that *Salix* seeds in the watering treatment were more likely to germinate (Figure 2.2).

**Grazing**

As anticipated, only graminoids were affected by grazing, though the effect differed in direction among these species. Moreover, in *Carex* and *P. glauca*, grazing led to overall increased seed mass and germination, respectively, but these outcomes significantly changed in 2014 for both species. In contrast with *P. glauca*, *P. pratensis* experienced a reduction in seed mass in response to grazing, further illustrating that changes in seed quality differ not only among species.
of the same PFT, but even among congeners. Finally, *Festuca* increased in both seed mass and germination in response to grazing, suggesting that there may be a positive causal association between seed size and germinability in this species.

**Interannual variation**

Each functional type consisted of species that clearly showed non-uniform outcomes after warming, watering, or both. However, in some instances, the effects of these abiotic factors on seed quality in species representing different functional types were remarkably similar. For example, the responses of *Festuca* seed mass to warming and *Cerastium* germination to watering, though contrasting in sign, present the same pattern. In each case, the overall effect was significant in one direction, but the effects in 2013 and 2014 were significant in the opposing direction (Figures 2.1 and 2.2). As mentioned above, the overall effect of warming on germination in *Betula* tended towards negative, but the warming treatment in 2013 led to the strongest positive response of any effect for any species in the three years investigated.

Interannual variation in both seed mass and germination not associated with any of the factors discussed above was also quite common. For example, *Kobresia* seed mass was significantly greater in 2014 than 2012 or 2013, while germination was markedly lower in 2013 than 2014 (recall that germination data from 2012 were not included in the germination model). Both seed mass and germination were lower in 2013 and 2014 than 2012 for *P. pratensis*, while only seed mass in 2013 showed a similar decline for *P. glauca* (Figure 2.2). Interestingly, all species for which germination in either 2013 or 2014 differed from the 2012 values representing the intercept showed declines in germination in one or both of these two later years.

Weather conditions also differed greatly between years (Figure 2.3). In 2012 through 2014, the growing degree days over a 5 °C baseline (GDD$_5$) from May 1 through August 18 were
454.4, 282.6, and 372.5. Not only did 2013 have fewer GDDs over the course of the growing season, but the temperatures during the period of fruit and seed maturation in that year were much lower than 2012 and 2014 (Figure 2.3). Ambient precipitation in 2012 through 2014 totaled 113.3, 54.6, and 37.1 mm, and the timing of precipitation also varied between years. In 2012 and 2014, the two years with warmer springs, approximately 36% and 39% of each respective growing season’s total precipitation fell during the first half of the period; this differs greatly from the less than 11% of the total precipitation falling in the first half of the 2013 growing season (Figure 2.3).

Discussion

Effects of simulated global change

As anticipated, grazing affected seed quality in multiple graminoid species; however, the differences in both sign and magnitude of responses among graminoid species were unexpected. The effects of grazing on seed quality were generally positive in species, such as P. glauca, Festuca, and Carex, that are generally caespitose, i.e. they form distinct bunches or clusters. As a result, the removal of biomass via grazing during the growing season means that the tissues lost from an individual might have been reproductive stems, meristems that could generate future reproductive tissues, or photosynthetic tissue assimilated resources to be contributed to reproduction at the scale of the whole clone. Any or all of these specific consequences of biomass removal can lead to reduced production of seeds (Briske and Noy-Meir 1998, Kuijper et al. 2006, Cooper 2006). The architecture of caespitose plants allows them to retain resources not in plant tissues but in the soil that accumulates beneath the cluster, including both nutrients and soil organic carbon (Briske and Derner 1998). This strategy allows for the monopolization of
resources and competitive advantages over neighboring vegetation, and the locations on the landscape where competition for soil resources is most intense, such as warm and dry south facing slopes, may also be where herbivory is most prevalent (Thing 1984). This experiment was designed to minimize differences among sites, which likely explains why there was little evidence for large site-specific responses (Table 2.2). Nevertheless, because exclosures were erected in only some sites, the responses of species to grazing or its exclusion may be more generalizable.

In this study, I focused on the quality of the seeds being produced rather than on the total quantity (number or mass) of seeds, in part because of the uncertainty with which any given species converts stored resources from one or more prior growing seasons into reproductive output (Molau and Shaver 1997, Gremer et al. 2010). Previous research on reproductive effort in tundra ecosystems has largely focused on the quantity of flowers, fruits, or seeds produced by individuals of a given size (Wookey et al. 1993, Kudo and Hirao 2006, Pedersen 2010). Experiments that have investigated the role of resource supply by altering light regime or the supply of water or nutrients demonstrate the commonality of the relationships between growth rate, particularly during particular reproductive phenophases, and the number of seeds produced (Sadras 2007). However, many of these relationships have been assessed in annual plants in which the tradeoff between growth and reproduction is more evident (Germain and Gilbert 2014), and the general decline in sexual reproduction with increasing clonality might indicate that variation among species in how reproduction responds to change might covary with overall reproductive effort that correlates with clonality (Herben et al. 2015). Looking across both short- and long-lived species, the absence of a relationship between seed mass and survival to seedlings (Moles and Westoby 2004a) still does not preclude the possibility of seed mass being positively associated with germination because mortality may occur predominantly after germination. By using a similar number of seeds and only those that appeared likely to be viable because the
embryo was fully developed, I standardized across species-level variation in the use of stored resources.

Seed size is widely thought to be under stabilizing selection in which the variation in seed size settles around a single central value for the trait (Harper 1977). In order for this to be the case, two of the vital conditions that must be met are that a species’ mean seed size is conserved under similar environmental conditions and that seed size is relevant for an organism’s fitness (Silvertown 1989). Species in which larger seeds are adaptive tend to occur in more stressful abiotic environments (Donohue and Schmitt 1998), so directional climate change might lead to increased fitness in species that are able to respond by increasing seed size.

In this study, 19 of the 22 changes in seed mass, positive or negative and resulting from any factor, occurred in graminoid species. By contrast, the effects of warming and watering on forbs and deciduous shrubs resulted largely in changes in the proportion of seeds that germinated. While other functional types might only experience a tradeoff between seed size and the number of seeds produced (Donohue and Schmitt 1998), graminoids may be have greater plasticity in their capacity to allocate resources to individual seeds. However, because I did not account for total reproductive output in this study, graminoids may not be any more sensitive to changes in abiotic conditions than other species. Additionally, I did not partition seed mass into embryo, endosperm, and seed coat, so if warming became an environmental stressor for any given species, the proportion of investment into tissues related to other processes than germination might have increased (Teller et al. 2014). Nevertheless, seed mass was positively associated with the probability of germination in the majority of species in this arctic plant community.
Plant functional type and species-specific responses

The contrasting responses of forb species to watering presents an interesting case study into their individualistic responses that likely reflect niche differences. The differences between the responses of *Bistorta* and *Draba* may reflect differences in allocation, the timing of seed development, or possibly an unrelated aspect of life history such as functional differences between bulbils and seeds. *Bistorta*, the species with the largest seeds in this study, showed no responses to any treatment. Considering the process of leaf bud formation and development into mature leaves is a multiyear duration process in this species (Diggle 1997), it is perhaps unsurprising that three years of manipulation during the growing season yielded no changes in either seed mass or germination. Interestingly, *Bistorta* was also the only species to exhibit a negative interaction between seed mass and watering in the relationship between seed mass and germination. Seed mass was positively associated with germination in unwatered samples, but negatively associated with germination in the watered samples.

Increases in the provisioning of resources to seeds makes them more vulnerable to predation (Donohue and Schmitt 1998), and this notion may also extend to pathogens, possibly through small conspecific density-dependence effects (Moles and Westoby 2004b, but see Beckman et al. 2013). However, increased seed mass does not necessarily mean enlargement of the endosperm, the likely target of most pathogens, and a more robust seed coat can actually protect seeds from pathogens (Lacey et al. 1997). Nonetheless, the increase in *Bistorta* seed mass may have been positively associated with the probability or intensity of fungal attack during the germination trial (pers. obs.), resulting in a negative relationship between seed mass and germination seemingly mediated by fungal pathogen(s). Alternatively, because the seed coat largely determines germination requirements, such as cold stratification or light regime (Donohue
and Schmitt 1998), changes in seed mass may have meant that the conditions of the germination trial were less likely to meet the requirements of *Bistorta* seeds for germination.

Species that vary in reproductive phenology may differentially experience the effects of increased precipitation. Currently, most precipitation falls late in the growing season, which is late in the fruit maturation process of early developing species like *Draba* and early in the fruit development process in later reproducing species like *S. longipes*, which was not included in this study precisely because seeds are not mature until early September in most years. If the anticipated increase in precipitation occurs within the current seasonal distribution in which approximately half the total annual precipitation falls during the growing season (Stendel et al. 2008, Cappelen et al. 2013), there may be opposing effects in early and late reproducing species. For example, early species may experience a decline in seed survivorship due to pathogens as dispersed seeds experience wetter conditions, while late species might undergo an increase in seed survivorship from increased nutrient resources resulting from an increase in the frequency of drying-rewetting events (Fierer and Schimel 2002), at least in habitats with comparatively well drained soils like those investigated here.

Interannual variation in climate exerts a clear influence on seed quality. The deciduous shrubs are an excellent example of the complexities arising from variation across years and within functional types. Both *Betula* and *Salix* are considered thermophilic species in the Low Arctic based on their habitat; they occur in comparatively sheltered sites, and their growth is positively associated summer temperature (e.g. Blok et al. 2011). In this study, I have demonstrated that, at least for the seed quality aspect of the regeneration niche, they are dissimilar in their responses to increases in temperature and simulated precipitation. *Salix* responded as expected, with a small but significant increase in seed mass due to warming and a stronger, marginally significant increase in germination due to watering. By contrast, *Betula* had no significant responses in seed mass, but warming appeared to reduce germination. Notably, though, the effect of warming was
negative in 2012 and 2014 but positive in 2013. Both the 2012 and 2014 growing seasons had temperatures well above the climate normal, while 2013 represented a much more historically normal year. I suggest that while Betula growth and recruitment likely increases in years with temperatures above the historical range, seed quality may in fact decline, particularly because seed mass may respond non-linearly to increasing temperatures (Sandvik 2001). Because large germinable seed banks routinely accumulate in arctic tundra and shrub heaths in particular (McGraw and Vavrek 1989, Cooper et al. 2004), pulses of Betula recruitment in warm years may be have originated from seeds that developed in cooler years. Although some responses, such as phenology, may be similar among constituents in a given PFT (Arft et al. 1999), there is not enough evidence to conclude that this is the case for seed quality. Dormann and Woodin (2002) found no effect of watering when aggregating by (PFT) but acknowledged that significant but opposing responses of different species within a PFT to experimental treatments could lead to non-detection of biologically important patterns. Here, I have shown significant species-level variation in responsiveness to a realistic increase in precipitation during the growing season, the consequences of which could be similarly important the effects on species distributions from increasing temperatures (Bykova et al. 2012).

Conclusions

Increased temperature and precipitation led to mixed responses in seed quality that varied individualistically among species, and much of this species-level variation in responses may be associated with traits such as growth form. In addition, grazing also both increased and decreased seed mass and germination, but these changes only occurred in graminoids. Interannual variation in seed quality was evident in many species, and it manifested as both main effects of year and interactions between particular years and treatments. Moreover, divergent responses among years
are in line with the view that thresholds of abiotic stress dictate the likelihood of sexual reproduction (Douhovnikoff et al. 2010). These findings do not support the hypothesis that those species that have shown the greatest vegetative growth under simulated climate change would also exhibit increased seed quality in warming and watering manipulations. They instead lend support to the idea that tradeoffs between vegetative growth and sexual reproduction will dictate species’ reproductive responses to climate change. Species like *Salix*, which increased in both seed mass and germination in response to warming and watering, respectively, are likely to benefit from climate change, in part because they are adapted for long distance dispersal and therefore likely colonizers of suitable microsites increasingly available following soil disturbances. Other species, such as *Betula*, may experience declines in seed quality as temperatures increase due to allocation to asexual growth over investment in reproduction (Moulton and Gough 2011). By examining seeds, the life stage between mature adults and establishing seedlings, I have contributed to our understanding of the demographic consequences of changes in climate and herbivory. I demonstrated that arctic plant responses to climate manipulations are species-specific across time and poorly characterized by functional groups.

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Figure 2.1. Parameter estimates for the effects of warming, watering, grazing and year on seed mass. A colon between factors indicates an interaction between two primary factors. Colors indicate species, while symbol represents plant functional type (circles are forbs, squares are deciduous shrubs, and triangles are graminoids). Symbols with black outlines indicate marginally significant effects after adjusting for familywise error rate ($0.05 < P < 0.1$).
Figure 2.2. Parameter estimates for the effects of warming, watering, grazing and year on the proportion of germinated seeds. A colon between factors indicates an interaction between two primary factors. Colors indicate species, while symbol represents plant functional type (circles are forbs, squares are deciduous shrubs, and triangles are graminoids). Symbols with black outlines indicate marginally significant effects after adjusting for familywise error rate (0.05 < $P$ < 0.1).
Figure 2.3. Environmental variables from a meteorological station measured throughout the growing season for each of 2012, 2013, and 2014. Black lines represent average daily air temperature (°C) measured at 2 m, and blue bars are total daily precipitation (mm). Green bars show dates and amounts (mm) of water added to plots in the watering treatment.
Table 2.1. Sample sizes for the twelve study species. Shown here are total sample sizes as well as sample sizes for each of the treatments split among the warming, watering, and grazing factors. Note that there was no watering treatment inside the exclosures. Because of their rarity, *Potentilla* was only sampled for the watering treatment, so dashes indicate zero samples for a treatment.

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<th>Species</th>
<th>Treatment</th>
<th>Total</th>
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<td>Warmed</td>
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<td></td>
<td>Unwatered</td>
<td>Watered</td>
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<td></td>
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<td>Exclosed</td>
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<tr>
<td>Potentilla</td>
<td>--</td>
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</tr>
<tr>
<td>Salix</td>
<td>25</td>
<td>15</td>
</tr>
</tbody>
</table>
Table 2.2. Estimates of the random effect for site, shown as the variance, and NB2 dispersion parameter, \( \theta \), for each of the twelve study species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Site (variance)</th>
<th>NB2 dispersion (( \theta ))</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Betula</em></td>
<td>6.26E-09</td>
<td>0.869</td>
</tr>
<tr>
<td><em>Bistorta</em></td>
<td>1.03E-08</td>
<td>2.255</td>
</tr>
<tr>
<td><em>Carex</em></td>
<td>2.10E-07</td>
<td>0.707</td>
</tr>
<tr>
<td><em>Cerastium</em></td>
<td>1.84E-08</td>
<td>8.082</td>
</tr>
<tr>
<td><em>Draba</em></td>
<td>2.79E-02</td>
<td>1.455</td>
</tr>
<tr>
<td><em>Festuca</em></td>
<td>1.01E-08</td>
<td>1.559</td>
</tr>
<tr>
<td><em>Kobresia</em></td>
<td>7.23E-08</td>
<td>10.007</td>
</tr>
<tr>
<td><em>Luzula</em></td>
<td>2.09E-09</td>
<td>1.066</td>
</tr>
<tr>
<td><em>P. glauca</em></td>
<td>1.94E-02</td>
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</tr>
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<td><em>P. pratensis</em></td>
<td>9.49E-02</td>
<td>1.399</td>
</tr>
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<td><em>Potentilla</em></td>
<td>3.00E-08</td>
<td>0.703</td>
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<td><em>Salix</em></td>
<td>5.86E-09</td>
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</table>
Chapter 3

The recruitment and spread of an arctic deciduous shrub: Sexual recruitment or clonal growth?²

Abstract

The recent expansion of deciduous shrubs in the Arctic has been well documented across a range of habitats, but the phenomenon is not universal. The spread of these shrubs is often associated with abiotic factors, such as increases in temperature, and the variation in this spread has been ascribed to variation in habitat wetness. Much less is known about the mechanisms by which these plants spread. Using molecular markers, I assessed the prevalence of two different modes of reproduction, asexual spread and sexual recruitment, across a maritime to continental climatic gradient in sites that experienced an increase in shrub abundance in the last several decades. The 400 samples collected across four sites comprised 310 genotypes. Though evidence of sexual recruitment was common across all sites, coastal sites contained both more and larger clonal genotypes. While I expected local soil conditions would influence clonality, defined here as the probability of a given genotype occurring in multiple neighboring samples, this was not the case. Instead, genet size, percent vascular plant cover, and to some degree litter depth were the best predictors of clonality. These factors suggest the light environment is of primary importance in driving recruitment patterns. Furthermore, in spite of the large distances between sites, there was no suggestion of genetic differentiation into distinct populations. These results indicate that climatic differences influence not only how much and where deciduous shrubs spread, but how they are likely to do so. I suggest that future research integrating how mode of increase is associated with the rate of spread will further our projections of change in arctic ecosystems.

² To be submitted to Journal of Ecology
Introduction

Climate change has been an important driver of trends in biodiversity in recent decades, especially at higher latitudes, and this trend will continue in the coming century (Millennium Ecosystem Assessment 2005). Temperatures in the Arctic are expected to increase at a rate of about twice the global average, and a major consequence of current warming has been the rapid increase in the abundance of woody shrubs over the previous half-century (Tape et al. 2006, Goetz et al. 2011, Frost and Epstein 2014). As a functional group, deciduous shrubs are expected to respond positively to direct warming over the next several decades (Chapin et al. 1996, Elmendorf et al. 2012a).

Three related forms of shrub expansion have previously been delineated for the Arctic region (Tape et al. 2006, Myers-Smith et al. 2011, Tremblay et al. 2012): 1) “new colonization,” i.e. areas that were previously essentially unoccupied now have some shrubs present; 2) “patch in-filling,” in which the interstitial spaces between shrubs have undergone increases in shrub cover; and, 3) “individuals getting larger” through the lateral spread of an individual shrub. These are processes that are inferred from visible spatial patterns, but there are underlying assumptions that have yet to be discussed, for instance, that it is possible to visually distinguish new sexual recruits from vegetative growth.

One key mechanism by which warming might cause increases in deciduous shrub abundance is through the release from abiotic stress that might otherwise hinder sexual reproduction and recruitment (Douhovnikoff et al. 2010). Contrary to the decades-old view that sexual recruitment in arctic plants is rare due to perceived low survivorship at early life stages (Bliss 1971, Billings 1987, Welling et al. 2004), more recent work suggests sexual recruitment is more common than expected in arctic plants (Gabrielsen and Brochmann 1998, Stamati et al. 2007, Steltzer et al. 2008). This mode of reproduction may therefore prove to be a key driver in
the spread of deciduous shrubs under climatic warming. Some arctic plants, particularly shrubs, experience increases in reproductive effort when environmental constraints are alleviated, such as through increases in temperature (Gartner et al. 1986) or resource availability (Bishop and Chapin 1989). Warming also increases the probability that viable seeds can germinate and establish because earlier and warmer springs create additional and more favorable microsites (Graae et al. 2011). Arctic shrubs may therefore be shifting from predominantly vegetative proliferation (Freedman et al. 1982, Hautala et al. 2001) to investing in both sexual reproduction and asexual spread.

The large spatial variation in warming, such as the panarctic temperature anomalies during the last interglacial maximum (Miller et al. 2010), suggests that any pattern in vegetation dynamics associated with warming will be similarly variable in space (Elmendorf et al. 2012a). Any increase in investment in sexual reproduction under warmer temperatures (Klady et al. 2011) will be of particular importance for predicting rates of spread within populations (Clark et al. 2003). Long distance dispersal is largely driven by sexual rather than vegetative propagules (Higgins et al. 2003). This is particularly true for organisms with wind dispersed seeds (Nathan et al. 2002), which includes all of the highly abundant genera of arctic deciduous shrubs. Meanwhile, infilling at the finer scales of individual patches is likely a result of clonal growth due to the importance of the potential for resource sharing within a genet through physiological integration (Caraco and Kelly 1991).

The role of increasing sexual reproduction and recruitment in contributing to the recent expansion of arctic shrubs remains largely unstudied, particularly in the context of spatial variation in climatic conditions like mean temperature and total precipitation (Douhovnikoff et al. 2010). Sexual recruitment may be the primary driver of increases in shrub abundance and range shifts (Myers-Smith et al. 2011). Though there is some support for a link between sexual recruitment and shrub expansion (Hallinger et al. 2010, Douhovnikoff et al. 2010), the empirical
evidence is sparse (Myers-Smith et al. 2011). Recruitment from dispersed propagules is the chief driver of new colonization, but the spread of shrub patches after the initial phase of colonization may not always be driven by continued sexual recruitment (e.g. Lian et al. 2003). Moreover, shrub abundance has shown the largest increases in mesic habitats like swales and floodplains (Naito and Cairns 2011b, Tape et al. 2012, Frost and Epstein 2014), and landscape-scale spatial heterogeneity is decreasing in these locations as ecotones become more uniform (Naito and Cairns 2015).

It remains unclear whether this rise in shrub abundance is driven by a particular mode of increase as well as whether the predominance of one mode over another varies with climate. Here I assessed the separate contributions of growth and recruitment to the latter two forms of shrub delineated by Myers-Smith et al. (2011) and discussed above. I addressed existing knowledge gaps by (1) evaluating the degree of sexual recruitment in a deciduous arctic shrub, (2) assessing variation in recruitment mode along a climatic gradient, and (3) evaluating how microsite variability influences the incidence of clonality. I predicted that sexual reproduction would be widespread as has been demonstrated elsewhere in the Arctic (Gabrielsen and Brochmann 1998, Steltzer et al. 2008, Boudreau et al. 2010). I also expected to find evidence of more frequent sexual recruitment in inland landscapes due to an increase in the suitable microenvironments beneficial to seed production and seedling establishment during the warmer growing seasons of continental climates (Bliss 1956, Graae et al. 2011). Conversely, if milder winters are more critical seedling survivorship than warmer summers are to their establishment, I would expect greater evidence of sexual reproduction in coastal landscapes. Similar proportions of each reproductive mode among sites would imply that a more universal change, such as fertilization from N deposition or increasing CO₂, may be a more important driver of reproductive mode in this deciduous shrub. I anticipated that soil moisture and electrical conductivity, the latter being a correlate of factors affecting productivity like soil texture and cation exchange capacity, would be
the best predictors of whether a particular ramet (i.e. stem) was the product of clonal growth or recruitment from seed.

Methods

Site selection

The study was conducted in western Greenland in a region exhibiting a climatic gradient over approximately 150 km (Figure 3.1) while simultaneously avoiding variation in other critical factors such as daylength. The inland landscapes of western Greenland are characterized by a drier continental climate with greater seasonal variability compared with landscapes near the coast, which are characterized by a wetter and more seasonally stable maritime climate (Figure 3.1). During the period of the Danish Meteorological Institute’s current climate normals, 1961-1990 for Sisimiut and 1973-1999 for Kangerlussuaq, the mean growing degree days above an ecologically relevant 5 °C baseline (Weijers et al. 2013) were approximately 150 and 497 at these locations, respectively. Moreover, these inland landscapes also experience less fog and generally have fewer clouds and thus more hours of sunshine (Cappelen 2013).

In order to select sampling locations that have increased in shrub abundance in recent decades, I qualitatively compared declassified CORONA satellite imagery from the late 1960s to contemporary satellite imagery from WorldView sensors. All images I compared were taken during the peak of the growing season between mid-July and early August. I selected sampling locations that underwent conspicuous increases in vegetation cover, the dark shade of which is strongly suggestive of shrubs (Frost et al. 2013). Furthermore, I only selected locations that appeared to be at an expanding front of vegetation rather than the result of the apparent novel colonization of a formerly open habitat.
The shrub species present in these sites include mainly *Salix glauca* L. and *Betula nana* L., with occasional individuals of *Vaccinium uliginosum* L., *Rhododendron lapponicum* (L.) Wahlenb., and *Empetrum nigrum* L. in some locations. The former two are deciduous shrubs that dominate these landscapes, and both genera have been major components in the recent substantial increases in vegetation cover in various parts of the Arctic (Blok et al. 2011a, 2011b, Naito and Cairns 2011a). Furthermore, because it is the largest of these species, *S. glauca* likely contributes the most to this signal (Boelman et al. 2011). Therefore, I selected *S. glauca* as the study organism.

**Study species**

*S. glauca* is a circumboreal-polar deciduous shrub (Elven et al. 2011), varying from 0.3 to over 2 m in height, that is highly polymorphic and, because of its complexity, has been described as a very widespread species or species group (Suda and Argus 1968). Although they do not form large colonies, sizeable clones can be formed through root shoots, rhizomes, layering, or branch fragmentation (Argus 2004). Individual ramets of congeners can live for over 70 years (Schmidt et al. 2006, Zalatan and Gajewski 2006, Forbes et al. 2010), and *S. glauca* ramets in the study area can also live for many decades (Young et al. 2016). Multiple ploidy levels have been reported (Suda and Argus 1968), even at the local scale (Suda and Argus 1969), ranging from tetra- to octoploid.

*S. glauca* is a useful species in which to assess clonal expansion for reasons beyond its abundance in West Greenland. The species is dioecious and has an approximately 2:1 female-biased sex ratio (Dudley and Galen 2007), so the sampling of only female individuals in each plot allowed estimates to be inherently more conservative than previous studies that included both males and females because individuals from different sexes inherently arise from distinct
genotypes. This design allowed for the sampling from individuals very near each grid intersection (see Sampling design below). Male *S. glauca* tend to dominate the most xeric sites, and females occur more commonly on mesic sites (Dudley 2006, but see Myers-Smith and Hik 2012). These wetter, more fertile sites are where the increase in shrub abundance has been greatest across a range of arctic ecosystems (Naito and Cairns 2011b, Tape et al. 2012, Frost and Epstein 2014).

A large number of nuclear microsatellite markers, tracts of DNA in which the number of repetitions of short motif sequences varies among genotypes, have been developed for a variety of *Salix* species (Lian et al. 2001, Hanley et al. 2002, Barker et al. 2003, Stamati et al. 2003, Kikuchi et al. 2005, Hoshikawa et al. 2009, Lauron-Moreau et al. 2013). These markers have enabled a range of population genetics questions to be addressed (Lian et al. 2003, Stamati et al. 2007, Reisch et al. 2007, Lin et al. 2009, King et al. 2010), including for congeneric species for which the markers were not developed but still showed successful amplification (Puschenreiter et al. 2010, Douhovnikoff et al. 2010, Budde et al. 2011).

**Sampling design**

I sampled clusters of *S. glauca* identified from satellite imagery, as described above, during July and August of 2013 and July 2014, from four main sites situated along a ~150 km long transect covering a maritime to continental climatic gradient (Figure 3.1). Using a modified version of a design previously determined to best represent the scale at which shrub expansion has occurred in the Arctic (Douhovnikoff et al. 2010), I established 6 x 6 m plots, each consisting of 16 sample points run along gridlines separated by 2 m, at each of these four sites (Figure 3.2). All plots were separated by a minimum of 25 m, and they varied in ecologically important factors such as slope, local productivity, and extent of interstitial space between apparent genets. Sites 1, 2, 3, and 4 contained seven, six, six, and six plots, respectively, for sample totals of 112, 96, 96,
and 96 ramets, respectively. I collected fresh tissue from healthy, undamaged leaves from the ramet with its base nearest to the intersection of the gridlines. I froze these samples shortly after collection, and they remained frozen at -20 °C until DNA isolation.

In addition to collecting leaves, I collected morphometric and ecological data for each ramet, the visually assessed genet of which it was a part, and each plot. At the ramet level, I recorded length, height, basal stem diameter above the root crown, current and previous year’s primary growth along the longest route from ground to shoot tip, litter depth, percent vascular plant cover and topographic curvature (flat, concave, convex) within a 15 cm radius, and electrical conductivity and soil moisture, by volumetric water content, in the top 5 cm of mineral soil. I calculated ramet size, \( S_R \), as

\[
S_R = \frac{3}{\sqrt{\pi}} \left( \frac{D_b}{2} \right)^2 \times L_R 
\]

[1]

where \( L_R \) and \( D_b \) are the ramet length and basal diameter, respectively. At the genet level, I calculated genet size, \( S_G \), as

\[
S_G = \frac{3}{\sqrt{\pi}} (L_G \times W_G \times H_G) 
\]

[2]

where \( L_G \), \( W_G \), and \( H_G \) are the genet’s longest dimension, the perpendicular width, and maximum height, respectively. At the plot level, I recorded slope and aspect in degrees.

**DNA isolation and PCR amplification**

I isolated genomic DNA from 40-45 mg of frozen leaf tissue following the protocol of the PowerPlant Pro DNA Isolation Kit (MO BIO Laboratories, Inc., Carlsbad, CA) and using the protocol’s recommended 40 μL of the Phenolic Separation Solution to maximize both yield and purity. I only departed from the specified protocol by extending the centrifugation times from 30 s to 2 min and 2 min to 5 min in order to improve yield. I tested an array of previously developed
microsatellite markers, or simple sequence repeats (SSR), for genomic loci for *S. glauca*, and these I ultimately distilled into a set of eight markers: SB24, SB196, SB199, SB201, SB233, and SB243 developed from *S. burjatica* (Barker et al. 2003), and Cha475 and Cha580 developed from *S. arbutifolia* (Hoshikawa et al. 2009). Each 10 μL single-plex reaction included 15-30 ng of template DNA and fluorescent M13-tail labeled primers (Schuelke 2000) in a master mix containing 3 mM MgCl2, 0.4 mM each dNTP, HotStart Taq polymerase, and proprietary stabilizers (AMRESCO, LLC, Solon, OH). Reaction conditions used were identical to those found in the original publications for loci and were performed in Mastercycler Gradient and Mastercycler Pro (Eppendorf AG, Hamburg, Germany) thermal cyclers. The amplification products to be used for fragment analysis were then co-loaded into separated by capillary electrophoresis in an Applied Biosystems 3730XL DNA analyzer (Thermo Fisher Scientific, Waltham, MA). Co-loaded plates included products labeled with the fluorophores HEX, 6-FAM, NED, and PET as well as the LIZ-500 size standard. Alleles were then sized and scored using Peak Scanner 2.0 (Thermo Fisher Scientific, Waltham, MA).

**Genotyping and ploidy estimation**

To assess the number of different genotypes, I used the resulting fragment size data. Because allele scoring errors, somatic mutations, and null alleles could all lead to the possibility that genetic distances between individuals of the same true genotype are slightly greater than zero (Narayan et al. 2015), I examined the distribution of pairwise genetic distances in GenoDive (Meirmans and Van Tienderen 2004). This program allows for polyploid samples (Arnaud-Haond et al. 2007), and its use aids in the identification of the similarity threshold needed to delineate multilocus genotypes (Douhovnikoff and Dodd 2003). I confirmed this selection threshold by comparing the distribution generated in GenoDive with those generated with the Bruvo and
Lynch distances (Figure 3.3) using the polysat package in R 3.2.2 (Clark and Jasieniuk 2011, R Core Team 2015). I also calculated the effective number of genotypes, $G_e$, as:

$$G_e = \frac{1}{\sum g_i^2}$$

where $g_i$ is the frequency of the $i$th genotype, which corresponds with the number of equally frequent genotypes needed to create the observed genetic diversity (Balloux et al. 2003). The proportion of distinguishable genotypes (PD) was calculated at the plot level by dividing the number of unique genotypes by 16, the number of samples in each plot (Ellstrand and Roose 1987). Values of PD closer to zero suggest a high degree of clonality, while values approaching one denote a low degree of clonality. A related measure of clonality is relative clone size (RCS) (Douhovnikoff and Hazelton 2014), which is calculated at the plot level as the number of samples in each genotype divided by 16, the number of samples in each plot. Although they are directly related, the relationship is a non-linear negative power function, so I have chosen to present both metrics of clonality.

Because of the structured sampling design, each of these measures of clonality reflect the degree of spatial extent rather than a measure of abundance such as biomass or the density of ramets. I tested for differences between means for the sites with a Kruskal-Wallis test followed by Wilcoxon exact tests for post-hoc comparisons. To investigate the possibility of population structure based on the potential clustering of samples from the same population, I conducted a principal coordinates analysis (PCoA) of the genetic distances using the polysat package in R 3.2.2 (Clark and Jasieniuk 2011, R Core Team 2015). I estimated ploidy level (sensu Suda et al. 2006) by counting the maximum number of alleles per microsatellite locus, an approach that is equally appropriate for autopolyploids and allopolyploids (Clark and Jasieniuk 2011). To assess spatial patterns in genome size, I then aggregated ramets into three levels of estimated ploidy:
tetraploids (4n), penta- and hexaploids (6n), and septa- and octoploids (8n). I tested for ploidy differences among sites with a chi-squared ($\chi^2$) test.

**Logistic regression**

Using the results from the identification of multilocus genotypes, I performed generalized linear mixed effects logistic regression, with the binary outcome defined as genotype uniqueness; i.e., whether a genotype was detected in only one sample or multiple samples. Fixed factors included litter depth, percent vascular plant cover, slope, aspect, genet size, ramet size, soil moisture, and electrical conductivity. Multicollinearity was not a concern because all factors exhibited variance inflation factors below two (Zuur et al. 2010), and, after confirming this, all fixed factors were standardized.

I included plot nested within site as random factors, which, although it precluded any understanding of spatial variation in these relationships, allowed me to aggregate all data for improved statistical power. Initially, I investigated the importance of these predictor variables in a Bayesian Markov Chain Monte Carlo (MCMC) framework to determine which factors correlated with clonality. I used parameter expanded priors for the standard deviation that were approximately flat because these priors improved the mixing properties of the chain (Hadfield 2010). I ran 1,300,000 iterations with a burn in of 300,000 and a thinning interval of 1,000. I also used a standard information theoretic framework to multimodel inference based on corrected Akaike Information Criteria (AICc) to assess the results from the MCMC method in a model averaging approach. To that end, I included models within two AICc units of the model with the lowest AICc in a final model. Finally, I calculated the average (across random factor groups) marginal probabilities for those fixed factors that were significant predictors of clonality. I conducted these analyses in R 3.2.2 using the lme4, MuMIn, and MCMCglmm packages, and
figures were generated with the plotMCMC and ggplot2 packages (Wickham 2009, Hadfield 2010, Magnusson and Stewart 2014, Bartoń 2015, Bates et al. 2015, R Core Team 2015).

Results

Genotyping and pairwise genetic distances

Using eight microsatellite markers, a grand total of 205 unique alleles were detected from 400 samples of *S. glauca* in West Greenland. Three of these loci (Cha580, SB196, and SB243) have similar allelic richness to the published values (Barker et al. 2003, Hoshikawa et al. 2009), while the other five loci yielded far greater allelic richness than anticipated (Table 1). This highly diverse set of alleles allowed me to identify 310 unique genotypes, with a threshold level of five in GenoDive, effectively separating the two distinct modes (Figure 3). At sites 1, 2, 3, and 4, the numbers of genotypes identified out of the number of samples at each site were 78/112, 61/96, 81/96, and 90/96, respectively, while the effective numbers of genotypes at these respective sites were 55.5, 22.6, 85.3, and 64.9. These differences among sites are highlighted by comparing the least and most clonal plots (Figure 3.2). No genotypes were detected in multiple plots.

The proportion distinguishable (PD) values for sites 1, 2, 3, and 4 were 0.696, 0.635, 0.938, and 0.844, respectively (Figure 3.4), while the PD values based on the effective number of genotypes for these respective sites were 0.496, 0.235, 0.889, and 0.676. Relative clone sizes (RCS) displayed a similar pattern to PD, with values of 0.093, 0.149, 0.067, and 0.074 for sites 1 through 4 (Figure 3.4). The Kruskal-Wallis test was marginally significant (Kruskal-Wallis $\chi^2 = 7.760, df = 3, P = 0.051$), suggesting that there were differences between the sites. Pairwise comparisons with Wilcoxon exact tests revealed that site 1 had a significantly greater degree of clonality, i.e. lower PD and higher RCS, than sites 3 (one-tailed $W = 0.5, P = 0.002$) and 4 (one-
tailed \( W = 8, P = 0.033 \), and site 3 had a significantly lower degree of clonality than site 4 (two-tailed \( W = 32, P = 0.035 \)). Additionally, both the largest clone sizes as well as the greatest variability among plots occurred at site 2 (Figure 3.4), the latter likely explaining the lack of significant pairwise comparisons involving this site. The two coastal sites contributed differently to these higher values of RCS, with site 1 having a notably greater number of multi-ramet clonal genotypes (Figure 3.5). Site 2 had a similar number of clonal genotypes to the two inland sites, but these multi-ramet clones were comparatively more spatially extensive (Figures 3.2 and 3.5).

The principal coordinates analysis (PCoA) revealed no detectable population structure (Figure 3.6). Moreover, the samples from each site exhibited approximately the same degree of spread, with the possible exception of site 2, which had slightly wider ranges along the first two principal coordinate axes, particularly axis one. This result may in part reflect the greater variability in PD and RCS among the plots at this site (Figure 3.4).

The estimation of ploidy based on allelic richness revealed that genome size varies widely, with ample representation of all ploidy levels aside from octoploids, of which there were only two. The \( \chi^2 \) test demonstrated that ploidy levels were not equally distributed in space. Low ploidy individuals were overrepresented at the most coastal site and underrepresented at the most inland site (Figure 3.7). Additionally, the highest ploidy individuals showed the opposite pattern, with the other coastal site having significantly fewer high ploidy individuals than expected, while the farthest inland site was highly overrepresented by these individuals (Figure 3.7). However, in spite of the spatial variation in both clonality and ploidy, there was no direct association between these two aspects of \( S. glauca \) in this study, even when accounting for site- and plot-level variation (\( \chi^2 = 0.663, \text{df} = 4, P = 0.412 \)).
Logistic regression and predicted probabilities

With the Bayesian Markov Chain Monte Carlo (MCMC) approach to logistic mixed effects regression, two of the predictor variables, genet size and percent cover of vascular plants, were significantly associated with clonality (Figure 3.8). Similarly, in the information theoretic based model averaging approach, the only two significant parameters in the full model were genet size and vascular plant cover (Table 2). Although the 95% credible interval included zero in the Bayesian approach, litter depth was significant in the conditional, though not the full, model in the multimodel inference approach. Ramet size is not shown here (Table 2) because it was not significant in any of the top models as ranked by AICc. The marginal and conditional $R^2$ values for the full model were 0.22 and 0.33, which represent, respectively, the variance explained by only the fixed factors and that explained by both fixed as well as random factors (Nakagawa and Schielzeth 2013). The two factors that were significantly associated with clonality, percent cover and genet size, had the most reliable predicted probabilities at the low end of their values (Figure 3.9). For both factors, maximal values suggest an even chance of a ramet being either the product of clonal growth or sexual recruitment, while the values at the low end of their respective ranges indicate that the probability of a ramet being clonal is markedly low.

Discussion

The general pattern demonstrated by previous research has revealed that increases in shrubs are prevalent throughout the Arctic (Naito and Cairns 2011a). These changes have been observed at multiple scales. The increase in shrub abundance has been unequal across habitats and positions within landscapes (Naito and Cairns 2011b, Tape et al. 2012, Frost et al. 2013). The rates and extents of ongoing changes at the regional-level may also be non-uniform (Beck and
Goetz 2011, Fraser et al. 2011, Frost and Epstein 2014). While these results do not address the spatial extent of the increase in shrubs in West Greenland, I have demonstrated that regional differences in climate, herbivory, or other latent factors influence recruitment patterns at the local scale.

It is likely that the environmental gradient between maritime and continental climates best explains the differences I detected in the proportion of sexual recruits across space. The importance of environmental conditions has been shown during both seed set (Bliss 1956) and recruitment from seed (Graae et al. 2011). Although seedling recruitment can be influenced by both the source climate as well as conditions during germination, the latter has a greater effect on overall emergence (Meineri et al. 2013). Warming over the entire growing season is expected to limit seedling recruitment to open microsites due to competition from increases in productivity (Shevtsova et al. 2009), while the onset of seedling development is projected to occur earlier with warming (Milbau et al. 2009). It is largely these early developmental stages that determine seedling emergence (Graae et al. 2011), and recruitment pulses have been associated with temperature in the High Arctic over the last century (Büntgen et al. 2014). Heat pulses can reduce recruitment from seed (Graae et al. 2009), and willow seeds are quite temperature sensitive (Densmore and Zasada 1983).

My data demonstrate that sexual recruitment of *S. glauca* individuals is more common in a continental climate with warmer summers. A warmer growing season allows for longer seed maturation because the timing of seed dispersal is not sensitive to minimum temperatures (Jones et al. 1997). The duration of the growing season is likely similar across the gradient used in this study, but there is a marked increase in growing degree days above 5 °C at the continental end. Winter mortality in arctic and alpine is greater in milder climates (Venn and Morgan 2009, Graae et al. 2011) and the difference in sexual recruitment along West Greenland’s climatic gradient may be partly due to greater mortality in coastal sites. My data indicate that sexual recruitment
likely occurs to some degree in most of these recently expanded or in-filled shrub patches, and to some extent, abiotic factors determine the likelihood of sexual recruitment from seed.

Alternative gradients that might explain the spatial patterns described here by my data include elevation and herbivory. The elevation of all samples increases from less than 50 m at the westernmost coastal site to over 250 m at the site nearest the ice sheet (Figure 3.1). Although elevation would certainly contribute to the climate experienced by these shrubs, this gradient may in fact operate in a fashion opposite that of these patterns in clonality in West Greenland. Because temperature decreases with increasing elevation, the low elevation coastal sites would have had warmer summers than any potential higher elevation coastal sites. If elevation had stayed the same across the latitudinal gradient, I may have found an even greater proportion of clonality at the coastal sites because summer temperatures would have been even lower.

There is also a gradient in herbivory from inland to coastal sites, as the population of muskoxen (*Ovibos moschatus*) in the region occurs almost entirely within the eastern, inland portion of the region. Additionally, the inland sites are near the calving ground of the Kangerlussuaq-Sisimiut population of caribou (*Rangifer tarandus groenlandicus*). As a result, this area houses much higher densities of caribou during the growing season (Tamstorf et al. 2005), and the migration away from coastal sites is early enough (Poole et al. 2013) that these locations do not likely experience herbivory on newly emergent seedlings. Damage from large herbivores alters the architecture of deciduous shrubs (Tolvanen et al. 2001, Christie et al. 2015), particularly in highly palatable species like willows (Christie et al. 2014). It is thus possible that the greater presence of herbivores decreases the abundance and stature of this species in the inland part of the region, thereby creating opportunities for establishment in microsites that are less light limited. The presence of large numbers of ungulate herbivores would lead to more disturbed microsites favorable to germination, even for woody species that are not considered early-successional (Suominen and Olofsson 2000). Additionally, there may not be a tradeoff
between the probabilities of flowering in successive years; growth and condition of an individual, which would be reduced by herbivory, are instead likely to be more strongly associated with flowering in *S. glauca* (Tolvanen et al. 2001). Thus, a greater density of herbivores near the inland sites would be expected to depress, rather than increase, the chances of these plants recruiting sexually.

The principal coordinates analysis revealed no separation or clustering based on site, suggesting that these samples were collected from a single panmictic population. Though at first unexpected given the extent of spatial separation between the four sites, this may be a reflection of the recentness with which these potential populations have progressed spatially as glaciers retreated over multiple millennia (Bennike and Björck 2002, Wagner and Bennike 2012). Moreover, it is not uncommon for plants to undergo long distance dispersal events that exceed 1 km (Cain et al. 2000, Kinlan and Gaines 2003), especially when, as in *Salix* spp., their seeds are dispersed by wind (Higgins et al. 2003). Gene flow in West Greenland may be sufficiently large as to have prevented demes from forming in the span of only a few thousand years, thus the region may only have a single spatially extended population (Freckleton and Watkinson 2002). Additionally, though each ramet may only live for several decades (Young et al. 2016), genets from severe environments are longer lived (Steinger et al. 1996). My detection of large clones suggests that unique genotypes can be long-lived, potentially to the degree that they might persist through unfavorable periods. Gene flow may then occur when local populations can coalesce and maintain regional dynamics during periods of favorable conditions (Eriksson 1996). Additionally, dispersal processes are critical in projecting species’ range shifts (Travis et al. 2013), and anticipated time lags in vegetation structure are related to limitations in dispersal as well as growth (Boulangeat et al. 2014).

Nonetheless, there does appear to be some spatial sorting of individuals based on my estimation of ploidy. Autopolyploidy might be a key source of differentiation and evolution in
plant genomes (Parisod et al. 2010). This again suggests that the younger environments of the inland landscapes might have offered greater opportunities for adaptation to individuals with larger genomes within which selective forces could operate as well as accelerate adaptive variation with increased genetic redundancy. Intraspecific variation in ploidy might predispose this species toward successful colonization of regions with pronounced habitat heterogeneity (te Beest et al. 2012), such as the topographically complex western Greenland. Moreover, given that polyploids, when compared with diploids, are over-represented in a number of plant families associated with invasiveness (te Beest et al. 2012), it is perhaps unsurprising that younger landscapes might be over-represented by high ploidy individuals. However, this spatial pattern in ploidy could also be the result of a more neutral process such as minority cytotype exclusion (Levin 1975), whereby the founding cytotype (level of ploidy) in novel habitats might preclude the establishment of other cytotypes. Changes in reproductive mode, such as becoming predominantly asexual or developing novel sexual reproduction in the introduced range, even in the same species (Castro et al. 2007, Costa et al. 2014), have been associated with polyploidy, but I found no evidence here linking clonality with ploidy level.

The importance of genet size, ground cover, and also to a small degree litter depth suggests that the infilling of new space by clonal expansion vs. sexual recruitment is largely driven by light limitation. Light limitation may drive intraspecific variation in the capacity for individuals to subsidize new clonal growth through, for example, resource sharing (Hutchings and Wijesinghe 1997). Physiological integration, the maintenance of connections between ramets that allow for the sharing of photosynthates or other resources, is thought to yield fitness benefits in resource-poor and spatiotemporally heterogeneous environments like the Arctic (Caraco and Kelly 1991, Callaghan et al. 1997, Jónsdóttir and Watson 1997). Physiological integration has also been negatively associated with light as well as associated more strongly with species’ clades than the degree of environmental stress (Klimeš 2008). Although I found that genotypes occupied
more space when light limited, I have no data that would allow me to assess if and when physiological integration ceased in these extensive genotypes.

At broader scales, topographic features on the landscape with high soil moisture are strongly associated with the increase in abundance of deciduous shrubs (Naito and Cairns 2011b, Tape et al. 2012). Because soil moisture is predictive of where shrub expansion occurs, I anticipated that soil moisture would also be associated with clonality. The Bayesian approach demonstrated that soil moisture, though not significantly different from zero, trended towards a positive association with clonality. One potential reason for this is that the scale at which I measured variation (meters) in soil moisture may not be representative of the previously documented patterns at the landscape scale (hundreds to thousands of meters). Another possible explanation for the absence of a significant relationship is that I measured soil moisture in the top five centimeters, while large stunted shrubs would have access to soil moisture at much greater depths (Schickhoff et al. 2002). Finally, it is also possible that greater soil moisture increases germination under warmer conditions (Jones et al. 1997); soil moisture may be positively associated with both clonal growth and sexual recruitment and thus the effect on one form may mask the other. Regardless of whether or not soil moisture and associated parameters are predictive of the origin of a given individual, future research should continue to account for these factors since shrub establishment and growth are closely linked to water availability at the scale of individuals (Boulanger-Lapointe et al. 2014).

The widespread pattern of increased shrub abundance at small scales is commonly associated with warming (Elmendorf et al. 2012a, 2012b). Experimental efforts have validated that increased temperatures directly led to shrubs becoming taller (Hudson and Henry 2010) as well as changing resource allocation patterns (Bret-Harte et al. 2001, 2002) and leading to longer shoots. Thus, there may be tradeoffs between individuals increasing in size and stature and any increase in microsite favorability. Warming, which can both enhance and reduce the production
of and establishment from seeds, also leads to larger individuals that trap more snow (Sturm et al. 2001), thereby sheltering nearby seeds and seedlings during the winter while simultaneously increasing shading during the growing season.

Conclusions

Clonal growth is an important mechanism by which *Salix* species can spread in new environments over decadal time scales as an alternative to increasing in abundance via sexual recruitment alone (Budde et al. 2011, Thomas et al. 2012). Though both modes of increase are evident for *Salix* species in tundra ecosystems (Reisch et al. 2007, Steltzer et al. 2008), their relative contribution to population dynamics over time are less clear. The dominance of sexual recruitment followed by increasing importance of asexual spread is better understood in sites undergoing primary succession (Barsoum 2001, Lian et al. 2003), and the relative importance of these two modes of increase may be determined in part by the pattern of disturbance in the system (Douhovnikoff et al. 2005). Further studies on the role of demographic processes in warming tundra ecosystems will enlighten projections of vegetation change (Normand et al. 2014). I have shown that a climatic gradient is associated with variation in the contribution of clonal growth in recently filled patches. Sites with warmer summers had greater proportions of small genotypes, indicating a greater role of sexual recruitment in these environments. Because individual-level variation in demographic parameters like dispersal can lead to large differences in the rate of range expansion (Dytham et al. 2014), the predominance of a given reproductive mode should be taken into account when projecting which landscapes and where within them arctic shrub expansion is most likely to occur.
References


Hoshikawa, T., S. Kikuchi, T. Nagamitsu, and N. Tomaru. 2009. Eighteen microsatellite loci in *Salix arbutifolia* (Salicaceae) and cross-species amplification in *Salix* and *Populus* species. Molecular Ecology Resources 9:1202–1205.


populations based on phenotypic characteristics and nuclear microsatellite (SSR) markers. Plant, Cell & Environment 33:1641–1655.


Figure 3.1. Climographs for the (A) Sisimiut and (B) Kangerlussuaq meteorological stations and topographic map of the West Greenland region and its location in Greenland (C). Numbers on the main map indicate the four site locations, and contour lines represent 100 m intervals. Climographs are based on climate normals for the periods 1961-1990 and 1973-1999 for Sisimiut and Kangerlussuaq, respectively; data are from the Danish Meteorological Institute (http://www.dmi.dk/groenland/arkiver/klimanormaler/).
Figure 3.2. Layout of the study’s sampling design. 16 samples per plot were collected at each of the intersections a 6x6 m grid. All plots at each of the four sampling sites, indicated by numbers, were at least 25 m apart. Shown here are the least (lower set) and most (upper set) clonal plots at each site.
Figure 3.3. Histograms of pairwise genetic distances among all sample pairs. Both Bruvo (A) and Lynch (B) distance metrics show bimodal distributions with distinguishable tails, indicating sample pairs belonging to the smaller mode represent the same genotype.
Figure 3.4. Indicators of clonality for each of the four sampling sites. Percent (or proportion) distinguishable (PD) and relative clone size (RCS) are shown on the left and right y-axes, respectively. PD and RCS are both calculated here at the plot level. Error bars represent one standard error of the mean; letters indicate results from post hoc pairwise comparisons of sites.
Figure 3.5. Relative clone sizes (RCS) for each of the four sampling sites. RCS here was calculated at the genotype level after excluding unique genotypes only represented by single sample, so only clonal genotypes are displayed here. Blue lines indicate coastal, maritime sites, and red lines indicate inland, continental sites. Lines have been slightly shifted in the y-dimension to preclude visual overlap.
Figure 3.6. Principal coordinate (PCo) axes from analyses of pairwise genetic distances across all four sampling sites. Shown here are the results based on the Bruvo (A) and Lynch (B) distance metrics, each of which reveals nearly complete overlap between all four sites. Blue symbols indicate coastal, maritime sites, and red symbols indicate inland, continental site.
Figure 3.7. Estimated ploidy level for each of the four sampling sites. The number of genotypes represents the difference between observed and expected for the three aggregated ploidy levels (see text for details). Asterisks indicate significant differences based on a chi-squared ($\chi^2$) test. Blue bars indicate coastal, maritime sites, and red bars indicate inland, continental sites.
Figure 3.8. Log-odds of the fixed effects predictors of clonality. Error bars represent 95% credible intervals from Bayesian logistic regression modeling. Only the credible intervals for genet size and percent cover do not overlap zero (red dashed line).
Figure 3.9. Predicted probabilities of clonality for percent cover and genet size, revealing declines in the probability of a given genotype being clonal as the predictors approached minimal values. Shaded curves denote 95% confidence intervals. See text for details on the calculation of genet size.
Table 3.1. Summaries of the eight microsatellite loci. Shown are the repeat motifs and number of alleles found in this study. The original reference sources contain the primer sequences and PCR conditions used here.

<table>
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<th>Locus</th>
<th>Repeat motif</th>
<th># of alleles</th>
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Table 3.2. Estimates of the fixed factors and model fits for the eight generalized mixed effects logistic models within 2 AICc units (sample size corrected Akaike Information Criterion) of the best model. Parameter estimates are standardized, and site and plot nested within site were random factors. Aspect and slope were measured at the level of the plot rather than the sample. Soil EC is electrical conductivity, and BIC is Bayesian Information Criterion.

<table>
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<th>Aspect (plot)</th>
<th>Percent cover</th>
<th>Genet size</th>
<th>Litter depth</th>
<th>Soil moisture</th>
<th>Soil EC</th>
<th>Slope (plot)</th>
<th>( R^2 )</th>
<th>df</th>
<th>( \Delta \text{AICc} )</th>
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Chapter 4

Relationship between plant community diversity and ecosystem function altered by warming and herbivore exclusion

Abstract

Multiple interacting drivers of global change can strongly influence the outcomes of a range of ecological processes, from interactions among competing individuals to biogeographic range shifts, and these drivers include both biotic and abiotic factors. Recent syntheses purport that local richness will increase in many ecosystems in response to combined global change drivers. Here, we demonstrate that the effects of two such drivers, warming and the exclusion of herbivores, appear to be additive, and together they negatively impact biodiversity in a low richness plant community assembled from a species-poor regional pool. In an eleven to thirteen year factorial warming and herbivore exclusion experiment in the mixed shrub-graminoid dominated tundra of Low Arctic Greenland, the treatments show different successional trajectories in response to a mass defoliation caused by a caterpillar outbreak early in the experiment. Warmed plots where herbivore grazing and browsing were absent showed the greatest increase in biomass. This increase was largely driven by deciduous shrubs and resulted in declines in the biodiversity of local assemblages, particularly in forb species. Though forbs may experience short-term increases in growth in response to a combination of warming and the mass defoliation reducing competitor abundance, longer-term data reveal that competitive exclusion of forbs by deciduous shrubs may already be under way. These results illustrate how multiple

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components of global change can interact to affect the relationship between biodiversity and biomass. Here, the shape of the relationship changed from positive to unimodal, but only under warming with large herbivores excluded. Although these data suggest that at least some aspects of ecosystem function, like carbon assimilation, may increase in the coming decades, there may be notable declines in biodiversity that could affect other aspects of ecosystem function. Even when aggregating many of these assemblages of competitors, the diversity of the herbivore exclusion treatments, irrespective of warming, did not return to the level of the grazed treatments.

**Introduction**

The theoretical relationships between biodiversity and ecosystem function have been hypothesized and described in detail for several decades (Grime 1973, Al-Mufti et al. 1977). Recent meta-analyses seeking generalizations in such relationships have concluded that there is tremendous variation in the nature of associations between biodiversity (often species or functional group richness) and ecosystem function (often a single function like productivity or an assumed proxy such as standing biomass), if any such association exists at all (Waide et al. 1999, Hooper et al. 2005, Gillman and Wright 2006). Consequently, plant community ecologists have yet to reach a consensus view on the generality of any particular pattern, such as positive or unimodal relationships (Grace et al. 2012). Nevertheless, there has been little investigation of how projected climate warming, which likely influences resource supply rates to some degree in all ecosystems, might affect the relationship between richness and productivity. The role of trophic interactions in shaping this relationship, and biodiversity-ecosystem functioning more generally, remains poorly understood (Hooper et al. 2005). Moreover, ecosystems in regions with small species pools, such as the Arctic, are rarely studied in this context, and any ability to detect
differences with so few species contributing to richness suggests that small changes in diversity may lead to disproportionately large changes in ecosystem function.

Arctic tundra plants exhibit low productivity as measured by aboveground biomass (Billings and Mooney 1968, Hobbie and Chapin 1998), so if there exists an underlying unimodal relationship between standing biomass and richness in these ecosystems, it may go undetected (Axmanová et al. 2013). Warming often leads to more rapid nutrient cycling, and where there are more nutrients, shrub growth is promoted relative to that of several other functional groups (Sturm et al. 2005). In contrast to patterns observed in other systems at lower latitudes, an increase in standing biomass may lead to a decrease in fine grain richness in arctic systems (at fine sampling grains) due to increasing competitive exclusion as competition for light supplants competition for belowground resources (Axmanová et al. 2013). This may be particularly true for species competing with comparatively tall shrubs that experience the greatest increases in height with warming (Elmendorf et al. 2012b).

Many of the experimental investigations of the relationship between biodiversity and ecosystem function in plants have been conducted in herbaceous communities (Tilman and Knops 1997, Spehn et al. 2005). In these studies, species richness has frequently been the experimental treatment imposed on plots that represent communities that have developed from sown seeds. Also common in such experiments is the manipulation of nutrients to modify productivity (Naeem et al. 2009). Each of these approaches differentially affects the relationship between richness and productivity (Schmid et al. 2009).

Herbivory and its interaction with resource supply also affect fine grain richness. Primary consumers often increase producer richness and evenness, broadly defined as a measure of the proportional equivalence of species abundances in a community, in terrestrial systems, while increased resource supply has tended to decrease producer richness and evenness (Hillebrand et al. 2007). Communities with greater productivity and higher dominance (lower evenness) are
more likely to experience positive effects of herbivory on richness and evenness (Hillebrand et al. 2007). Although only a minority of systems may exhibit a tradeoff between competitive ability and defense against consumers, this remains a plausible mechanism for maintaining diversity (Viola et al. 2010).

Throughout the Arctic, populations of woody shrubs are increasing in size as individuals are becoming larger and more numerous (Tape et al. 2006), largely in response to warmer temperatures (Walker et al. 2006, Elmendorf et al. 2012a, 2012b). However, bottom-up control from herbivores can inhibit the expansion of shrubs and create complexity in the plant community dynamics of tundra ecosystems (Olofsson et al. 2009, 2013, Kaarlejärvi et al. 2013). Previous work at a study site near Kangerlussuaq, Greenland, has shown that deciduous shrubs have increased in aboveground biomass with warming, especially in the absence of large herbivores (Post and Pedersen 2008), though this response may only be detectable with enough time after an outbreak of an irruptive invertebrate herbivore (Pedersen and Post 2008). Furthermore, species richness and community stability both declined as a result of large herbivore exclusion and warming, and these effects appear to be additive (Post 2013b).

My aim here is to expand upon previous investigations of plant community responses (Post and Pedersen 2008) and diversity-stability relationships (Post 2013b) in this experimental context by either corroborating or controverting previously documented trends in two ways: first, by characterizing differences in both richness and diversity among factorial warming and herbivore exclusion treatments; and second, by assessing whether changes in both diversity and productivity resulting from these treatments (or their interaction) have led to a change in the relationship between the two. Therefore, the objectives of this study were to 1) assess the taxonomic diversity after eleven to thirteen years of factorial warming and herbivore exclusion manipulations, respectively, and 2) determine how warming, herbivore exclusion, or both, alter the relationship between diversity and productivity in this low richness system. I anticipated that
there would be notably lower diversity in the exclosed compared with the grazed plots. Because I hypothesized that there is an important interaction between warming and exclusion, I also expected to find that any negative effect of warming on diversity would only be evident in the exclosed plots. For the second objective, I anticipated that a unimodal relationship would be most evident in the exclosed and warmed treatment due to the large increase in shrub canopy cover in these plots (Figure 4.1).

Methods

Study design

Between 2002 and 2004, a total of fifty 4.71 m\(^2\) circular plots were established inside and outside of three permanent circular fenced areas that excluded large herbivores from approximately 800 m\(^2\) of heterogeneous tundra, and baseline sampling was conducted prior to the construction of the fences (Post 2013b). These exclosures were situated in areas that represented the ecotone between shrub- and graminoid-dominated tundra, and each exclosure was associated with a similarly sized adjacent area to which large herbivores retained access for browsing and grazing. The pairwise distances for these three sites range from about 400 m to nearly 1 km. At each site, plots were established that contained each of the major functional groups of interest (deciduous shrubs, graminoids, forbs, mosses, and lichens), and these plots were situated away from the fencing to avoid edge effects. These plots were randomly assigned to receive an ambient control or warming treatment that consisted of open-topped chambers (OTCs) built in accordance with the International Tundra Experiment’s protocols (Henry and Molau 1997). Each OTC measured 0.4 m in height, a basal diameter of 1.5 m and a side angle of 60° leading to an opening diameter of 0.8 m. The warming treatment increased daytime temperatures above but near the soil
surface by 1.4-2.0 °C (Post et al. 2008). The warming treatment was initiated before the onset of
the growing season in 2003 at two of these sites, and this treatment was expanded to a third
enclosure site early in the following year, so in 2004 the number of plots was raised from seven,
seven, six, and six to 13, 13, 12, and 12 for the grazed + ambient (GA), grazed + warmed (GW),
enclosed + ambient (EA), and exclosed + warmed (EW) treatments, respectively.

Peak growing season sampling was conducted from 2003 until 2015 using the frame-
based point-intercept method to allow repeated, non-destructive measurements based on pin hits
that act as a reasonable surrogate for biomass for the three vascular plant functional groups
(Pedersen 2010). As in Post (2013b), I based my analyses on the raw number of pin hits, rather
than estimated biomass (Pedersen and Post 2008), to preclude the unnecessary inclusion of an
additional source of variation. Furthermore, I only included data from 2005 onwards in this study
because of the improvement in taxonomic resolution beginning in that year (Post 2013b). Hence,
in my analyses, I define plot-level richness as the total number of species of forbs and deciduous
shrubs plus the number of additional functional groups for graminoids, mosses, and lichens.

**Characterizing diversity**

Ecologists tend to conceive of diversity as consisting of two components, richness and
evenness (Tuomisto 2010), and there is a tendency to use richness to signify diversity, or,
similarly, an abundance-sensitive diversity index as a proxy for diversity in spite of these
concepts being unequal (Jost 2006). Richness is not strictly independent of evenness (Jost 2010,
Tuomisto 2012. Moreover, species richness, without consideration of relative abundances, has
been shown to be a weak proxy for true diversity (Wilsey et al. 2005). Until recently, researchers
have had to explicitly separate analyses of richness and the more generally defined diversity.
However, with the unified framework presented by Chao et al. (2014), it has now become
possible to assess richness specifically and diversity more broadly in a single analysis that accounts for the sensitivity of diversity to the intensity of sampling as well as the density of species or individuals in a given census.

One community can be said to be “intrinsically more diverse” than another by either having more species or more even abundances (Patil and Taillie 1982). In order to simultaneously account for both of these mechanisms that contribute to variation in diversity, I constructed diversity profiles to estimate diversity while accounting for sampling (Chao et al. 2014). All measures of diversity, including species richness, Simpson’s measures, Shannon’s entropy, and others, are monotonic functions that can be generalized to:

\[ D_q = \left( \sum_{i=1}^{S} p_i q \right)^{1/(1-q)} \]

where D is the diversity of the community where the relative abundance \( p_i \) for each taxon i to S, the total number of taxa, and q is a scaling parameter. D, commonly called Hill numbers, represents the effective number of species (Hill 1973). Rarefaction and extrapolation curves were created for the entire profile of diversity by varying the scaling parameter q in Equation 1 across the range of non-negative values (negative values lead to a higher effective number of species in a community than actually occur) (Tuomisto 2010). The value of the scaling parameter specifies how much weight is given to species’ abundances, with values of 0, 2, and infinity representing taxonomic richness, the inverse of the Simpson diversity index (Simpson 1949), and the Berger-Parker index of dominance (Berger and Parker 1970). Although Equation 1 is undefined when \( q = 1 \), the limit as \( q \) approaches 1 is the exponential of the Shannon diversity index (Shannon 1948).

Because Greenland’s flora, from which this community was assembled, is represented by so few vascular plant species, the dataset comprised only 14 taxa. Therefore, any differences made evident through rarefaction and extrapolation curves would suggest ecologically important changes resulting from the treatments, rather than any sampling effects (Cayuela et al. 2015). The
resulting curves allowed for the comparison of factor combinations (grazed/ambient, grazed/warmed, exclosed/ambient, and exclosed/warmed), because if any two or more curves crossed at any point at a single value of q or switch rank order across values of q, they were considered non-comparable. That is, one factor combination could not be said to be more diverse than any others whose curves it crossed. Conversely, if the curve from one factor combination was consistently higher than any other, it could be robustly concluded to have had greater diversity (Chao et al. 2014). Because this procedure is robust across a range of community sizes (Tóthmérész 1995), it is a useful and appropriate way to assess changes in community structure in local communities characterized by low richness.

Such procedures are most frequently used to make comparisons either among assemblages (Colwell et al. 2012) or along environmental gradients (Longino and Colwell 2011). In this case, I explicitly examined changes in the same assemblages, subject to different treatments, over time. After summing all pin hits for each treatment in a given year, I constructed these curves using the iNEXT package, version 2.0.3 (Hsieh et al. 2015) in R, version 3.2.2 (R Core Team 2015). Maximum extrapolation values for all treatments in a given year were 20% greater than the treatment with the most pin hits, and 95% confidence intervals were constructed by bootstrapping each curve 5000 times. I considered one treatment combination to have a higher level of diversity than another for a given year if their 95% confidence intervals were non-overlapping at any point along the rarefaction/extrapolation curve, especially at the lower values of pin hits because these reflect differences among treatments at the scale of only one or a few plots. For the sake of simplicity, I present here the results from the scaling parameter values \( q = 0, 1, \) and 2, as recommended by Chao et al. (2014), which equate to species richness, the Shannon entropy, and the Inverse Simpson entropy. Neither the inclusion of intermediate values nor values above two, i.e. approaching the Berker-Parker dominance index, qualitatively changed the patterns in any year.
Richness-biomass relationships

Because the temporal aspect of diversity was analyzed only implicitly with these sample-based rarefaction and extrapolation curves, I used generalized additive mixed models (GAMMs) to explicitly account for the temporal autocorrelation of the time series. Because GAMMs do not assume a defined mathematical relationship (e.g. linear, polynomial, or other) between all predictors and response variables, they allowed me to use non-parametric smoothing functions to reveal existing relationships in the data. Moreover, GAMMs offered improved goodness-of-fit over linear mixed effects models considering being predictive was not my goal. Instead, I sought to characterize how the shape of the relationship between biomass and richness varies among treatments to assess the evidence for competitive exclusion (Axmanová et al. 2013) or other underlying mechanisms (Michalet et al. 2006). These nonlinear relationships were also analyzed via linear mixed effects models to assess the importance of a quadratic term.

I first assessed the distributions that best described total taxonomic richness and forb species richness using the fitdistrplus package (Delignette-Muller and Dutang 2015) in R and found that, as expected, the Poisson distribution best matched the former, while the negative binomial distribution was a slightly better fit than the Poisson for the latter. I then constructed an initial GAMM with total taxonomic richness as the response assuming a Gaussian distribution. Site, exclusion, warming, and all of their two- and three-way interactions were included as fixed factors, and litter was included as a random factor. A thin plate regression spline for aboveground live biomass, measured as pin hits, was included as the smoothing function for each treatment, and a lag one-year (AR1) autoregressive term was included to account for first-order temporal autocorrelation. Secondarily, I assessed the particular influence of increasing shrub cover on forb richness via a GAMM using a negative binomial distribution. Other than the smoothing function being a thin plate regression spline of aboveground shrub pin hits, the fixed and random factors
and autoregressive structure were the same as above. All GAMMs were fit using the mgcv package, version 1.8-7 (Wood 2004, 2011).

To confirm the underlying function defining the relationships between biomass and taxonomic richness that emerged from the GAMMs, I fit simple linear mixed effects models for each treatment combination. Each of the four models consisted of taxonomic richness as the dependent variable and biomass, measured as pin hits, as the linear independent variable. I also included litter as a fixed factor because of its potential to act as an important mechanism underlying the general relationship between biomass and richness (Al-Mufti et al. 1977). Each model included a random effect for plot and an AR1 autoregressive covariance structure. I only considered a significant second-order polynomial term to be relevant if the fitted curve showed both the peak and the decline within the range of measured values of biomass (Axmanová et al. 2012). I calculated marginal and conditional $R^2$ goodness-of-fit statistics (Nakagawa and Schielzeth 2013) for models containing only the significant fixed effects using the piecewiseSEM package, version 1.0.3 (Lefcheck 2015).

**Results**

**Characterizing diversity**

The rarefaction and extrapolation curves revealed several patterns. The total abundance in the community increased over the 10 year period from 2005 to 2014. Aggregate biomass (pin hits summed across all plots) within a given treatment ranged from a minimum of 252 to a maximum value of 2063 in 2014, both for the EW plots. The year 2005 was the second, and peak, year in a two-year outbreak of the noctuid moth, *Eurois occulta* L., the larvae of which substantially reduced aboveground biomass of all functional groups at the site (Post and Pedersen 2008). In
2005, the summed plot-level aboveground biomass for a given treatment was at its minimum of 304.3 ± 23.0 pin hits (mean across all treatments ± 1 SE). Beginning in 2006, this value increased monotonically through 2014, the year with the greatest aboveground biomass (1690.8 ± 125.2 pin hits). The year 2015 was the only exception to this otherwise monotonic increase. Mean (± 1 SE) plot-level aboveground biomass across all years was 96.6 ± 2.9, 120.6 ± 4.3, 91.5 ± 3.0, and 96.6 ± 3.5 for the exclosed + ambient (EA), exclosed + warmed (EW), grazed + ambient (GA), and grazed + warmed (GW) treatments, respectively.

There was no monotonic trend in maximum (asymptotic) diversity over time. Although some of the rarefaction/extrapolation curves did not appear to be near an asymptote, the greatest value of $S_{\text{obs}}$, the number of taxa observed in the set of samples (the symbols in Figure 4.2), was 12, which occurred in 2013 in the GW treatment and in 2014 in the GA treatment. The lowest $S_{\text{obs}}$ value, six, occurred in the GW treatment in 2005, the year of the outbreak.

From 2005, the year of the major caterpillar outbreak, through 2008, there was no uniform rank order of treatments across the values of the abundance weighting parameter, $q$ (Figure 4.2). However, from 2009 through 2015, at low biomass values, both grazed treatments had greater diversity than the EW treatment for all values of $q$. For $q = 0$, the EA treatment tended to have greater values of diversity than the EW treatment across years, though only significantly so at any point in the curves in 2009 and 2013 (Figure 4.2). For $q = 1$ and 2, EW plots were never lower than EA plots in any year and higher in most years. In these latter years, there was no overlap between the 95% confidence intervals for the two exclosed treatments. This pattern was not mirrored in the two grazed treatments, i.e. in any given year, the GA treatment could have higher, lower, both higher and lower, or equivalent values of diversity compared with the GW treatment. These results differentiating the treatments over time also hold when making comparisons by sample coverage rather than pin hits accumulated across samples.
Richness-biomass relationships

The full generalized additive mixed model (GAMM) for total taxonomic richness indicated important differences among treatment combinations. The fixed effects for both site and herbivore exclusion significantly explained variation in the data, while the warming treatment was marginally significant (Tables 4.1 and S4.1). All two- and three-way interactions were significant, and the thin plate regression splines for aboveground live biomass were significant for all treatments except EA (Tables 4.1 and S4.1). The estimate for the autocorrelation parameter, $\phi$, was 0.362. Variance estimates for the litter random effects were 0.068 for the intercept and 0.594 for the residual variance.

The smoothing splines for the EW and GW treatments reveal nonlinear relationships between biomass and taxonomic richness, while the spline for the GA treatment suggests a positive linear relationship (Figure 3). At the upper end of the range of values for biomass in GA, the lower end of the 95% confidence interval occurs at a higher value of richness than for the same values of biomass in the EW treatment (Figure 3). Furthermore, because the splines for each treatment are centered on the mean for each treatment (3.76, 3.44, 4.08, and 4.06 for EA, EW, GA, and GW, respectively), this difference at higher values does not appear as large as it actually is.

The GAMM for forb richness as a function of shrub biomass also showed differences among treatments. Site, herbivore exclusion, and warming, as well as all two- and three-way interaction terms, were all significant fixed effects (Tables 4.1 and S4.1). The significant splines for the EA and EW treatments revealed nonlinear relationships between shrub biomass and forb species richness (Tables 4.1 and S4.1, Figure 4.4). The estimate for $\phi$ was 0.408, similar to the value for the total live biomass model. Variance estimates for the litter random effects were 0.274 for the intercept and 0.670 for the residual variance.
Linear mixed effects models further elucidated the underlying nature of the relationship, or lack thereof, between biomass and richness. For total live biomass, a negative second-order polynomial term was significant for only the EW treatment (Table 4.2). The inclusion of a negative term for litter biomass improved model fit in all but the GA treatment (Table 4.2). Overall, the models fit with only the significant fixed effects explained between 20 and 43 percent of the variation in richness, though in each case the greater proportion of variation explained was from the random effect (Table 4.3). Similarly, only for the exclosed treatments was a second-order polynomial term significant in the final models, and the addition of a term for litter improved the final EW model. Litter was a significant predictor of forb richness in all four treatments (Table 4.3). Finally, the trend of increasing biomass after the caterpillar outbreak in 2005 is clearly seen in all four treatments (Figure 2).

**Discussion**

This study revealed measurable differences in taxonomic diversity among factorial treatments in a warming and herbivore exclusion experiment within a decade of a major disturbance in a species-poor arctic ecosystem. Compared with the double control, diversity in the exclosed and warmed treatment recovered notably fewer taxa after the defoliating disturbance of a caterpillar outbreak early in the study. In some respects, these results are unsurprising. There can be rapid changes in how the plant community responds to increasing temperatures, especially in particular biogeographic and climatic contexts. For instance, the increase in deciduous shrub and litter layer cover, as well as graminoid and shrub canopy height, were all greatest in sites that were intermediate in moisture regime, and these responses were generally stronger at lower latitudes within the Arctic (Walker et al. 2006). Frequently such changes occur within just a few of years of warming treatments (Walker et al. 2006). More recent syntheses have further
illustrated that regions that have experienced the greatest increases in total shrub abundance have been those with the warmest summers of intermediate (Elmendorf et al. 2012a) and high moisture (Elmendorf et al. 2012b). The field site, though only approximately 5 km from the terminus of the Russell Glacier at the edge of the Greenland ice sheet, is nonetheless representative of those inland landscapes of West Greenland that experience warmer (often by over 5 °C) and more frequently sunny summers than coastal areas (Cappelen 2013).

The differences in diversity among treatments detected here likely do not reflect variation in factors that covary with temperature. For example, variation in the timing of snowmelt is likely unimportant here because, in most years, the warming treatments were initiated after the vast majority of the landscape was snow free. However, soil moisture in this low precipitation region does decline over the summer months, at least in the upper portion of the soil profile, in the same manner as in other dry regions of the Arctic (Oberbauer and Dawson 1992). Furthermore, primary consumers, like the large ungulate herbivores in the study site, can play a critical role in regulating primary producers in low productivity systems (Kaarlejärvi et al. 2013), especially in the absence of secondary consumers that could mediate plant community dynamics (Graham and Duda 2011).

The presence of herbivores is of particular importance to the trajectory of changing dominance hierarchies in arctic vegetation (Olsen and Klanderud 2014). In both low- and high-productivity habitats, arctic shrub removal led to an increase in the germination and emergence of seedlings, though the regrowth of vegetation over time did not translate into increases in the recruitment of seedlings into the adult population (Klanderud 2010). A mechanism similar to the recruitment limitation suggested by Klanderud (2010) could also be a factor here, with competitive interactions outweighing facilitative ones. Although microsite quality is of particular importance for establishment from seed (Graae et al. 2011), the increase in competitive effects like shading that result indirectly from warming may more than offset any direct benefits for
germination. Furthermore, species that were detected only intermittently across years may not have been truly absent from the plots. Rather, they may have simply been missed during point-intercept sampling, perhaps due to abundances below the threshold of detection. Despite the evolution of longevity in many arctic plants (de Witte and Stöcklin 2010), the forb species that declined under warming and herbivore exclusion in this study are generally closer to the phalanx (tightly packed ramets that preclude competitors) than the guerrilla (widely spaced ramets that intermingle with interspecific and conspecific individuals) end of the spectrum of clonal plant strategies (Lovett Doust 1981). Thus, the disappearance of a particular ramet likely reflects the loss of the entire genet from the plot, and the increase in shrub abundance may therefore be limiting the recruitment of new individuals through mechanisms like shading or propagule pressure (Gough et al. 2015).

The magnitude of complementarity effects that can arise through niche partitioning, including the increased probability of more speciose plots yielding greater biomass and leading to at least a monotonically positive relationship between diversity and productivity, tend to increase through time (Cardinale et al. 2007). However, the most productive plots in warmed treatments during the later years of the experiment had lower richness than plots in the ambient treatments (Figures 2 and 3). This suggests that the warming treatment, by increasing temperatures during the growing season, plays a fundamental role in changing the rate of resource supply, which is of particular importance in resource limited ecosystems like arctic tundra. For example, not all constituents in this tundra community respond similarly to neighbor removal, another form of increasing resource supply (Bret-Harte et al. 2004, 2008, Klanderud 2005). There can be direct effects of changing the rate of resource supply on standing biomass as well as indirect effects mediated through the production of new biomass as well as local richness (Kassen et al. 2000, Gross and Cardinale 2007). The former has been demonstrated through processes such as plasticity in plant architecture (Bret-Harte et al. 2001), but the elucidation of indirect effects has
only recently begun (Cardinale et al. 2009, Hillebrand et al. 2014). In my case, it is possible that warming directly stimulates growth through enabling greater rates of key physiological processes like photosynthesis (Cahoon et al. 2012b) as well as lengthening the growing season (Euskirchen et al. 2006, Reyes-Fox et al. 2014). I recognize that standing biomass is only a coarse surrogate for productivity (Gillman and Wright 2006), especially in the context of intense herbivory or other forms of tissue loss (terHorst and Munguia 2008). However, shrub abundance alone can explain nearly half the variation in net ecosystem exchange at this site (Cahoon et al. 2012a), suggesting that the intensity of herbivory is not so great as to decouple plant cover from productivity.

Biomass itself can be an important driver of ecosystem functioning (Lohbeck et al. 2015), particularly during succession. Successional processes are important drivers of the strength of the relationship between biodiversity and ecosystem function (Lasky et al. 2014), and therefore the shape of the relationship over the period of time during which succession occurs (Weis et al. 2007). Although studies on this phenomenon are few, most suggest that stronger positive relationships between biodiversity and ecosystem function occur early in succession (Balvanera et al. 2006, Weis et al. 2007, Lasky et al. 2014). However, Zhang et al. (2012) found that the magnitude of the effect of biodiversity on biomass increased with the age of forest stands. Contrary to the idea that successional processes can lead to increases in richness over time (Vellend et al. 2013), I have shown that the transition towards increasingly shrub-dominated tundra can reduce local-scale richness. Additionally, the rarefaction profiles revealed that both presence-based richness as well as any abundance-based measure of diversity showed declines on plots in the herbivore exclusion treatments relative to controls. Nonetheless, many of the previously reported increases are associated with recovery after disturbances (Vellend et al. 2013), and in this case the exclusion of large herbivores could be considered the cessation of an intermittent disturbance.
The importance of competitive interactions may only become clear after a long enough period of study within which differences in the relationships between biodiversity and productivity can be detected (Lasky et al. 2014). The time series in this study were from a period of recovery after a mass defoliation by caterpillars, so warming may alter biodiversity most strongly through indirect effects mediated by competitors. For instance, forb abundance has increased in association with trends in summer temperature in locations with near-surface permafrost (Elmendorf et al. 2012b), suggesting that declines in forbs are not necessarily directly driven by abiotic factors like warming. Rather, it may be that climate-mediated increases in shrub abundance are an important proximal driver of decreasing forb abundance (Figure 4). Similarly, the reduction in cryptogam abundance appears directly tied to the increase in vascular plants and the litter they produce (Cornelissen et al. 2001). Identity affects how litter inputs affect plant growth, and although forb litter may more strongly inhibit growth (Dorrepaal et al. 2006), the quantity of litter from deciduous shrubs likely makes this group a greater impediment to the growth of neighbors. Moreover, decomposition rates of deciduous shrubs vary widely depending on the intensity of herbivory and soil characteristics at a site (Olofsson and Oksanen 2002, Hobbie and Gough 2004). The recalcitrant litter of these shrub species may more greatly impact the growth of bryophytes and cryptogams in habitats where they do not dominate or even occur, ultimately leading to reduced diversity at scales larger than the plots measured in this study.

Environmental heterogeneity can be a key driver of the unimodal relationship between diversity and productivity (Kassen et al. 2000), as well as itself having a unimodal association with richness (Allouche et al. 2012). However, this latter relationship has also been shown to be positive in many circumstances, depending on the scale of the study, and quadratic relationships may also be a product of how heterogeneity is measured (Stein et al. 2014). Nevertheless, heterogeneity in the structure of vegetation can itself be a strong driver of richness (Stein et al. 2014), suggesting that it could be the structural simplification resulting from increased shrub
growth that limits species coexistence. The structural plasticity in at least one of the deciduous shrubs that can become dominant (Bret-Harte et al. 2001) might partially explain the reduction in diversity associated with increasing shrub abundance. Additionally, because all graminoid species have been aggregated, yielding a single taxonomic group, the true decline in diversity in shrub dominated plots over time may be even greater than demonstrated here.

Conclusions

The multiple abiotic effects of climate change can have cumulative and interactive effects on the trajectories of plant communities (Matesanz et al. 2009). Nonetheless, biotic interactions like competition and herbivory must be taken into account, as they can interact with abiotic factors as well as directly affect the structure and function of arctic ecosystems (Rundqvist et al. 2011, Post 2013a, Olofsson et al. 2013). Here, I show that the relationship between biodiversity and productivity can vary between positive linear, unimodal humped, and nonsignificant states. Species-poor local assemblages derived from a small regional species pool have undergone substantial changes after more than a decade of herbivore exclusion and a decade of warming. Warming led to increased standing biomass, but it is chiefly when warming occurred in the absence of large herbivores that diversity declined compared with grazed, unwarmed plots, and much of this change resulted from the loss of forbs as shrub biomass increased. With shifting species ranges, local richness is projected to increase as a result of global change drivers (Thuiller et al. 2014), but here I demonstrate that the opposite phenomenon may already be under way. Some species, such as shrubs, may be increasingly dominant over the coming few decades (Walker et al. 2006) at the expense of others, such as herbaceous species, that may only undergo growth increases in the short term (Arft et al. 1999). In an isolated location like Greenland, newly colonizing species may be unable to reach suitable habitats without human intervention,
intentional or otherwise (Normand et al. 2013). Considering that the loss of a single species represents a large portion of the locally interacting assemblages of this region, I anticipate there will be resulting declines in some aspects of ecosystem function, even as standing biomass accumulates.

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Figure 4.1. Hypothesized relationship between standing aboveground biomass and taxonomic richness. (A) A large disturbance, such as an outbreak of phytophagous insects, would reduce standing biomass to below the prior limit seen under historical climates (dashed bar). (B) Persistent herbivory may maintain the upper limit to standing biomass (dashed bar), so richness would appear to increase monotonically as the system approaches maximal biomass during the recovery from an outbreak. (C) Warming in combination with the loss of large herbivores may lead to reduced plant richness due to competitive exclusion as higher levels of standing biomass become attainable.
Figure 4.2. Rarefaction and extrapolation profiles for the four warming and herbivore exclusion treatments. Shown here are the individual years 2005 through 2015 (A through K). Note that the x-axes are scaled to be 1.2 times the total of the treatment with the maximal biomass for a given year. Taxonomic richness, the Shannon entropy, and the Inverse Simpson index represent values of the scaling parameter $q = 0, 1,$ and $2,$ respectively (see Equation 1 and associated text).
Figure 4.3. Generalized additive mixed model of total biomass and taxonomic richness. Smoothing splines are shown here separated by treatment: exclosed + ambient, exclosed + warmed, grazed + ambient, and grazed + warmed (A through D). Both warmed treatments as well as the grazed + ambient treatment contained significant smooths (see Table 4.1), though only the linear mixed effects model for the exclosed + warmed treatment had a significant second-order polynomial term for biomass (see Table 4.2).
Figure 4.4. Generalized additive mixed model of shrub biomass and forb richness. Smoothing splines are shown here separated by treatment: exclosed + ambient, exclosed + warmed, grazed + ambient, and grazed + warmed (A through D). Both exclosed treatments contained significant smooths (see Table 4.1), each of which was corroborated by the linear mixed effects models (see Table 4.2).
Table 4.1. Generalized additive mixed model fitted for taxonomic richness as a function of total aboveground live biomass and litter (A), and forb richness as a function of shrub biomass and litter (B). Shown are degrees of freedom (df), F-, and P-values for the fixed effects site, exclusion, warming, and all two- and three-way interactions, as well as estimated degrees of freedom (edf), F, and P-values for the smoothing splines for the exclosed + ambient (EA), exclosed + warmed (EW), grazed + ambient (GA), and grazed + warmed (GW) treatments. SEM is the standard error of the mean.

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<th>df/edf</th>
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<th>P</th>
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Table 4.2. Linear mixed effects models fitted for four herbivore exclusion and warming treatments (EA – exclosed + ambient; EW – exclosed + warmed; GA – grazed + ambient; GW – grazed + warmed) separating taxonomic richness as a function of total aboveground live biomass and litter (A), and forb richness as a function of shrub biomass and litter (B). Shown are parameter estimates, degrees of freedom (df), and $t$- and $P$-values. SEM is the standard error of the mean. Parameters for biomass included both first- and second-order polynomials, reported separately for aboveground live biomass (live and [live]$^2$) and shrub biomass (shrubs and [shrubs]$^2$).

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<tr>
<td>(B) Forbs</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>EA</td>
<td>Shrubs</td>
<td>0.317</td>
<td>1.073</td>
<td>117</td>
<td>0.296</td>
<td>0.768</td>
</tr>
<tr>
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<td>(Shrubs)$^2$</td>
<td>-2.205</td>
<td>0.897</td>
<td>117</td>
<td>-2.458</td>
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</tr>
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<td></td>
<td>Litter</td>
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<td>0.016</td>
<td>117</td>
<td>-2.361</td>
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<td>EW</td>
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<td>-0.456</td>
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<td>0.015</td>
<td>117</td>
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<tr>
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<td>Shrubs</td>
<td>3.013</td>
<td>1.329</td>
<td>127</td>
<td>2.267</td>
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</tr>
<tr>
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<tr>
<td>GW</td>
<td>Shrubs</td>
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<td>1.655</td>
<td>127</td>
<td>1.407</td>
<td>0.162</td>
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<tr>
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<td>Litter</td>
<td>-0.082</td>
<td>0.017</td>
<td>127</td>
<td>-4.893</td>
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Table 4.3. Linear mixed effects models fitted for taxonomic richness as a function of total aboveground live biomass and litter (A), and forb richness as a function of shrub biomass and litter (B) using significant parameters from Table 4.1. Separate models were fitted for the exclosed + ambient (EA), exclosed + warmed (EW), grazed + ambient (GA), and grazed + warmed (GW) treatments. Shown are variances explained by fixed factors only (marginal $R^2$) and fixed plus random factors (conditional $R^2$).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Parameters</th>
<th>Marginal $R^2$</th>
<th>Conditional $R^2$</th>
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<td><strong>(A) Total</strong></td>
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<td></td>
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</tr>
<tr>
<td>EA</td>
<td>Litter</td>
<td>0.033</td>
<td>0.195</td>
</tr>
<tr>
<td>EW</td>
<td>Live, (Live)$^2$, Litter</td>
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<td>0.405</td>
</tr>
<tr>
<td>GA</td>
<td>Live</td>
<td>0.036</td>
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</tr>
<tr>
<td>GW</td>
<td>Live, Litter</td>
<td>0.143</td>
<td>0.414</td>
</tr>
<tr>
<td><strong>(B) Forbs</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>EA</td>
<td>Shrubs, (Shrubs)$^2$, Litter</td>
<td>0.064</td>
<td>0.343</td>
</tr>
<tr>
<td>EW</td>
<td>Shrubs, (Shrubs)$^2$, Litter</td>
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<td>0.487</td>
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<tr>
<td>GA</td>
<td>Shrubs, Litter</td>
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<td>0.462</td>
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<tr>
<td>GW</td>
<td>Litter</td>
<td>0.155</td>
<td>0.325</td>
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</table>
Table S4.1. Generalized additive mixed model fitted for taxonomic richness as a function of total aboveground live biomass and litter (A), and forb richness as a function of shrub biomass and litter (B). Shown are parametric coefficients for the fixed effects site, exclusion, warming, and all two- and three-way interactions as well as t- and P-values. SEM is the standard error of the mean.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>SEM</th>
<th>t-value</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>(A) Total</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(Intercept)</td>
<td>1.184</td>
<td>0.061</td>
<td>19.270</td>
<td>0.000</td>
</tr>
<tr>
<td>Site 2</td>
<td>0.225</td>
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<td>2.729</td>
<td>0.007</td>
</tr>
<tr>
<td>Site 3</td>
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<td>0.072</td>
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<td>0.028</td>
</tr>
<tr>
<td>Grazed</td>
<td>0.260</td>
<td>0.085</td>
<td>3.066</td>
<td>0.002</td>
</tr>
<tr>
<td>Warmed</td>
<td>0.150</td>
<td>0.086</td>
<td>1.735</td>
<td>0.083</td>
</tr>
<tr>
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<td>0.116</td>
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</tr>
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</tr>
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</tr>
<tr>
<td>(B) Forbs</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>(Intercept)</td>
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</tr>
<tr>
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<td>0.240</td>
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</tr>
<tr>
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<td>0.295</td>
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</tr>
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<td>0.000</td>
</tr>
<tr>
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<td>0.991</td>
</tr>
<tr>
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<tr>
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<td>0.399</td>
<td>-4.051</td>
<td>0.000</td>
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<tr>
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<td>0.341</td>
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<tr>
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<td>0.559</td>
<td>3.949</td>
<td>0.000</td>
</tr>
<tr>
<td>Site 3<em>Grazed</em>Warmed</td>
<td>2.103</td>
<td>0.464</td>
<td>4.532</td>
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</table>
Chapter 5
Synthesis

Sexual reproduction in the Arctic

Sexual reproduction by plants in the Arctic is clearly receiving increasing attention in recent years. In part, this focus is a reflection of the changes arctic ecosystems are experiencing. It is likely the case that arctic ecologists examining ecosystems over half a century ago were correct in their assumption that successful sexual reproduction was negligible and thus relatively unimportant for the life histories of arctic plant species (e.g. Bliss 1956, 1958, 1962, 1971), at least at the temporal scale of most ecological questions. However, climate change may alter the dynamics of sexual recruitment away from the historical pattern of recurrent but unpredictable periods in which cohorts of arctic plants only survived to maturity during intermittent phases of favorable abiotic and biotic conditions.

Climate change may have positive or negative effects on abiotic and biotic limitations of sexual reproduction and recruitment. For example, warming can directly enhance reproductive effort and success (Kладy et al. 2011). Effects can also be bidirectional, as warming can reduce germination by drying soils while simultaneously increasing recruitment by reducing mortality to fungal pathogens in seed banks (Leishman et al. 2000). Here, the recent and future warming in the Arctic may have alleviated temperatures, the primary limiting abiotic stressor, and thus driven the probability of sexual reproduction and recruitment in arctic plants above some threshold below which only asexual vegetative growth occurs (Douhovnikoff et al. 2010, see Figure 5.1). In such a model, some species may now or soon be capable of consistently recruiting new individuals into the population by sexual means (Figure 5.1). The interannual variability in seed
quality evident in Chapter 2 suggests that many species are currently near such a potential threshold. For example, seed mass in *Poa pratensis* and germination in *Bistorta vivipara* were both lower in 2013 and 2014 compared with 2012, which was much warmer than the other two years (Figure 2.3). However, warming alone may not be sufficient to alleviate stressors in all species, and warming may reduce seed quality in some species, such as *Poa glauca* and *Betula nana*. This pattern may also be concurrent with warming enhancing establishment from seed, vegetative growth, and flower production (Suzuki and Kudo 2000, Graae et al. 2011, Elmendorf et al. 2012b).

Biotic interactions are also of critical importance for understanding sexual reproduction and recruitment in a warming Arctic. In Chapter 2, several species showed responses to watering (Figures 2.1 and 2.2), but these may have resulted from indirect effects mediated by fungi. For instance, watering increased seed mass in *Bistorta vivipara*, but there was no matching increase in germination. One possible explanation is the high incidence of fungal pathogen growth during the germination trials indicating the potential for top-down processes to mediate the effects of climate change. Seed mortality due to fungal pathogens can reduce seed banks in many, but not all, species (Leishman et al. 2000, Schafer and Kotanen 2004), thereby creating the potential for interactions to dictate the responses of plant demography to climate change. These effects are often species- and habitat-specific, and soil moisture plays a key role in determining the degree of fungal attack (Leishman et al. 2000, Schafer and Kotanen 2003). Antagonistic interactions from competitors can also influence reproduction. In Chapter 4, I demonstrated that warming and herbivore exclusion increase aboveground biomass, predominantly in woody shrubs. Shading from shrubs can reduce pollination and seed set in neighboring individuals (McKinney and Goodell 2010), so this indirect mechanism for competitive exclusion of shorter statured species may function in tandem with the direct effect of competition for light resources. The decline in
biodiversity in response to warming and herbivore exclusion illustrated in Chapter 4 may result from such direct and indirect mechanisms.

As pointed out by Myers-Smith et al. (2011), few have connected the increase in new sexual recruitment likely caused by warming to shrub increase in tundra landscapes. Although I did not directly increase temperatures, I took a comparative approach to this problem in Chapter 3. I assessed the relatedness of neighboring ramets at a spatial grain appropriate to the scale of shrub expansion to elucidate the relative importance of clonal growth and sexual recruitment in areas that appeared to have undergone an increase in shrub abundance in recent decades. I did so using a single focal species, *Salix glauca* (grayleaf willow). Evidence of at least some degree of sexual recruitment was universally present in all plots; however, there was clear spatial variation across the region. Of the two coastal sites, one contained more multi-ramet genotypes, and thus fewer genotypes overall. The other coastal site had similar numbers of multi-ramet genotypes to the two inland sites, but these clones tended to be much larger. The largest such multi-ramet genotype occupied nearly an entire plot (14 of the 16 samples in 36 m$^2$). So although sexual reproduction was essentially ubiquitous, it appears to play much more of a role in the process of shrub expansion in continental climates. I suggest that this is a consequence of a combination of warmer summers increasing the quality or quantity of microsites, which strongly limit establishment in arctic tundra (Graae et al. 2011).

Seed quality in *S. glauca* also increased in response to warming and watering. Warming caused a small but significant increase in seed mass (Figure 2.1), while watering increased germination (Figure 2.2). Interannual variation corroborated the influence of temperature on seed quality in this species because germination was lower in the coldest year, 2013 (Figure 2.2). Extrapolating these local manipulations to the climatic gradient, in which summer temperature is greater at the continental end but precipitation is greater at the maritime end, these results suggest two possibilities. First, either warming is of greater importance to seed quality since there is more
evidence of sexual reproduction in the continental end, or second, these effects cancel each other out in the presence of other limiting factors. For instance, logistic regression modeling revealed that, across all sites, sampling locations with greater plant cover and larger neighbors were much less likely to be occupied by unique genotypes, suggesting light competition favors spread by asexual means. The light environment may therefore be of greater importance to microsite quality than temperature or moisture.

Projections of the increase in flowering or establishment in response to warming and other aspects of global change are therefore not easily generalized either among or within plant functional groups, even in fairly species-poor and structurally simple ecosystems like arctic tundra. Moreover, understanding the likely species-level responses of flowers (phenology, abundance, degree of outcrossing, etc.) or seeds (total production, dispersal, availability limiting establishment, etc.) to abiotic factors does not necessarily allow for accurate predictions of vegetation dynamics due to the complexity of biotic interactions affecting plant reproduction (Elzinga et al. 2007). If climatic warming leads to variation in plant and pollinator phenologies, the resulting changes in already multifaceted biotic interactions between these communities and others with which they interact (e.g. pathogens, seed predators) will have important consequences for demography in all groups (Elzinga et al. 2007, Miller-Rushing et al. 2010).

It is clear that climate change will have direct effects on plant reproduction in the Arctic, as prior research has demonstrated warming in particular increases reproductive effort and success in many, but not all species (Molau and Shaver 1997, Klady et al. 2011), and recruitment from seed is also enhanced by warming and other abiotic factors (Shevtsova et al. 2009, Walck et al. 2011, Mondoni et al. 2012). In this dissertation, I have attempted to address a life cycle gap analogous to the “generation gap” identified by Price et al. (2008), in which the authors call for greater research across an organism’s ontogeny. Here, I have taken a manipulative approach to begin addressing a presumed knowledge gap between growth and reproductive output (i.e. flower
abundance and seed set) and post-dispersal recruitment and establishment in an arctic plant community projected to experience some of the largest absolute changes in climate in coming decades. Linking reproductive output and the quality of that output with the subsequent effects on establishment and eventually offspring fitness will be a challenging endeavor in arctic plants that are generally clonal and can be opportunistic in their reproduction (Kudo 1991), but it remains vital to understanding how community dynamics might unfold in arctic tundra ecosystems.

**Linking genomes to shrub expansion through life history**

*Salix glauca* appeared in West Greenland at around the end of Holocene Climatic Optimum (also known as Holocene Thermal Maximum), which ended between 4000 and 5000 years ago (Bennike 2000). Because this species likely arrived in Greenland from continental North America, the colonization of West Greenland’s landscapes likely progressed from west to east (Wagner and Bennike 2012). The climatic gradient from maritime coastal landscapes to continental inland landscapes predated the arrival of this species and was maintained throughout the Holocene (Wagner and Bennike 2012). In Chapter 3, I demonstrated that there is presently variation in the spatial distribution of estimated ploidy. Mechanisms that could potentially explain this spatial pattern in ploidy include both founder effects and natural selection. The former mechanism could act through chance colonization of inland areas by cytotypes of high ploidy that are incompatible with individuals of other ploidy levels derived from differing cytotypes (Dobeš et al. 2013). Polyploids tend to be associated with the generation of apomictic seeds compared with the seeds produced via sexual reproduction, usually involving outcrossing, from diploid or other lower ploidy conspecifics (Norrmann et al. 1989, Dobeš et al. 2013), and new polyploid cytotypes otherwise exhibit a propensity towards self-fertilization as a means for avoiding aneuploidy (Hörandl 2010). In each case, cytotypic incompatibility may arise and thus lead to
overrepresentation of high ploidy individuals in recently established populations by chance alone. By contrast, in Chapter 3, I showed that there is no evidence of a relationship between estimated ploidy and clonality, suggesting a similar lack of a relationship with sexual recruitment as well. In this study, inland landscapes feature greater proportions of both sexual recruits and high ploidy individuals.

Instead of or in addition to the above mechanisms that could cause founder effects, there could be selective pressure for high ploidy individuals colonizing the inland landscapes that are thousands of years younger than coastal landscapes (Bennike and Björck 2002). High ploidy is associated with invasion in a range of plant families (te Beest et al. 2012), so there may be an analogous process in which individuals with higher ploidy have greater fitness relative to their conspecifics in these inland landscapes that are characterized by much colder winters and less well developed soils compared with coastal West Greenland. For example, tetraploid Salix species not only exhibit greater growth than diploids, but also differ in associated traits like wood chemistry (Serapiglia et al. 2014). Because polyploidization occurs in response to biotic and abiotic stressors such as herbivory, wounding, water and nutrient stress, extreme temperatures, and more (Ramsey and Schemske 1998), polyploidy is likely an adaptive trait when selection arises from these conditions (Pandit et al. 2011). The significantly disproportionate number of high ploidy individuals in inland West Greenland found here may therefore represent local adaptation to these environments.

Betula nana is a similarly recent arrival to West Greenland, but it instead colonized the inland part of region first (Bennike 2000, Anderson et al. 2008). The seed source probably originates from southeast Greenland, and B. nana first appeared in inland West Greenland around 6500 years ago and does not make its first appearance in sediments from coastal lakes near the Davis Strait until approximately 2000 years later (Wagner and Bennike 2012). B. nana is only diploid, but there are two subspecies that are geographically distinct: B. nana ssp. exilis
(Sukaczew) Hultén occurs in northwestern North America and Siberia, while *B. nana ssp. nana* occurs in northwestern Europe and northeastern North America, including Greenland (Flora of North America Editorial Committee 1993+). Polyploidy thus plays no role in local adaptation in *B. nana ssp. nana* in West Greenland, though it declines in local abundance from east to west (Wagner and Bennike 2012). Therefore, the increase in abundance in response to warming is presumably driven by other mechanisms.

In the Appendix, my collaborators and I demonstrated that these two deciduous shrubs have contrasting responses of secondary growth to climate. Ramet-level secondary growth, i.e. the increase in girth in a given measured stem regardless of the growth or spread of other stems in the same genet, was positively associated with summer temperature in *S. glauca* but negatively associated with spring temperature in *B. nana*. We suggested that the consistent pattern of plot- and landscape-level increases in cover evident in both shrub species may be a result of divergent processes. In the south-facing slopes with greater angles of insolation, *S. glauca* growth was positively associated with summer temperature, but this was not the case in flatter terrain (Figure A.5). *B. nana* growth in the latter site also did not show a positive association with summer temperature; however, growth was negatively associated with spring temperature (Figure A.5). Although both species are increasing in abundance in these landscapes, the mechanisms behind these increases may differ among species as well as sites within landscapes (Drees and Daniëls 2009). For example, neither architecture nor allocation in *S. glauca* are altered by warming or fertilization. *B. nana* increases vegetative growth rather than sexual recruitment under fertilization (Moulton and Gough 2011), whereas *S. glauca* architecture is less plastic (Bret-Harte et al. 2001, 2002), suggesting greater allocation to reproduction than growth in the resource tradeoff (Herben et al. 2015).
Consequences for arctic communities

Arctic vegetation is in transition in response to warming climates, with lichens and bryophytes generally declining concurrent with increases in graminoids and erect woody shrubs in particular (Wahren et al. 2005, Walker et al. 2006, but see Virtanen et al. 1997). The individualistic responses of species, such as those I demonstrated in Chapter 2, are likely to lead to historically novel ecosystems. Though the assemblages themselves are unlikely to undergo drastic changes in terms of composition and more or less the same species will continue to exist in regional species pools, changes in the relative abundances of plant species in these local assemblages are already underway (Walker et al. 2006, Elmendorf et al. 2012a, 2012b). The effects of increasing shrub abundance on biophysical processes, as discussed in Chapter 1, may nonetheless lead to ecosystem-level transformations large enough to warrant these ecosystems being labelled novel in the context of arctic landscapes (Hobbs et al. 2014), regardless of the value, or lack thereof, of such a label (Aronson et al. 2014). Additionally, many biogeochemical changes not yet discussed are no less relevant. For example, the increasingly positive feedbacks between biosphere, pedosphere, and atmosphere may lead to large changes in carbon cycling that have implications for global climate (Field et al. 2007).

The capacity to provide accurate projections of arctic vegetation change in the coming decades is thus germane to regional as well as global societal interests. Many of the more commonly used models rely on coarser scales of information in order to provide tractability and generality. A discussion of the value of temporal or spatial grain and extent in modeling efforts is of value, but outside the domain of this body of work. The overriding goal in using functional types, also called life forms, plant strategies, etc. (Suding and Goldstein 2008) is capturing key variation in responses and effects of vegetation across spatial scales from ecosystems to biomes and even continents to classify functional responses for global models of the biosphere (Lavorel
et al. 2007). However, I have provided ample evidence in this dissertation that the coarse resolution of life history traits frequently used to frame studies on arctic plant community dynamics (Chapin et al. 1996) limits understanding and precludes accuracy in projections of future vegetation scenarios. Differences among species in responses to perturbations may override the expected similarity based on plant effect traits (Walker et al. 1999, Díaz and Cabido 2001), even in comparatively low diversity systems such as arctic tundra (Bret-Harte et al. 2008).

These aggregations can be useful in arctic ecosystems when applied to community-wide patterns in some functional traits and the consequences of shifts in these traits (Chapin et al. 1996). For instance, increases in the proportion of woody shrubs in tundra communities, either through increases in cover or height, can redistribute snow in arctic landscapes with low precipitation during cold months (Sturm et al. 2001). I similarly aggregated species into groups like deciduous shrubs and forbs and found a negative effect of the former on the latter under warming in the absence of large herbivores (Figure 4.4). Even response traits, like changes in seed quality (Chapter 2) or propensity toward either clonal growth or sexual reproduction under novel conditions (Chapter 3), may yet affect indirectly ecosystem function through changes in demography or community composition (Bret-Harte et al. 2008). Moreover, considerations of functional traits still often ignore many biotic interactions that mediate vegetation dynamics (Post and Pedersen 2008, Olofsson et al. 2009, Chapter 4).

As arctic plant communities become increasingly shrub dominated as a result of global change, these shifts influence communities at other trophic levels. The interactions between arctic plants and mammalian herbivores that result in strong feedbacks have been demonstrated throughout the Arctic (Olofsson et al. 2009, Christie et al. 2015) as well as in West Greenland (Post and Forchhammer 2008, Post and Pedersen 2008, Cahoon et al. 2012). Even with declining herd sizes, caribou are still capable of mediating the structure and function of arctic vegetation (Zamin and Grogan 2013). These feedbacks consequently affect more than the vegetation and
large herbivores. Landscape-level changes in shrub abundance and distribution can affect other mammalian (Ehrich et al. 2011, Christie et al. 2014b), avian (Tape et al. 2010, Ehrich et al. 2011, Christie et al. 2014a), and insect (Den Herder et al. 2004) herbivores. There are also important impacts at higher trophic levels, including on spider (Legault and Weis 2013, Rich et al. 2013) and songbird (Sokolov et al. 2012, Henden et al. 2013, Boelman et al. 2015) communities. For example, birch seeds are such a vital component of the diet of Acanthis spp. (redpolls) in both Finland and Alaska that the distribution of the shrub may largely determine the distribution of the birds (Brooks 1968).

Pollinators are also significantly affected by global change. Climatic variation contributes to long-term variation in flowering in plant communities in which species responses are unique (Tyler 2001), resulting in a mix of positive and negative effects of climatic warming on pollinator populations (Hegland et al. 2009). Dipterans are an important part of pollinator assemblages in the Arctic (Kevan 1972), and although many arctic species are not dependent on insects for reproduction by seed, a number of these species nonetheless experience increased outcrossing provided by insect pollinators (Bliss 1962). Two Dipteran families with many flower visiting species showed declines in abundance in recent years of decreasing community-wide flowering duration (Høye et al. 2013). Also, flowering can exhibit marked periodicity in woody species, particularly in tropical regions (Pallardy 2008), but this may not be the case for herbaceous species or those in colder climates as flowering in one year yields little ability to predict the probability of flowering in the next year (Tyler 2001). Floral resources may therefore increase without necessarily enlarging pollinator populations, because low floral abundance in colder periods (Hedhly et al. 2009) or a combination of frost (Inouye 2008) and strong phenological mismatch (Donnelly et al. 2011, Forrest 2015) in warm times could lead to declines or unpredictability in floral resources. Climate change may therefore cause shifts not only in arctic plant community dynamics, but also in the dynamics of communities at other trophic levels.
References


Figure 5.1. Conceptual model of the probability of successful sexual recruitment over time (e.g. decades to centuries) as abiotic stress varies. Historic abiotic stress is indicated by the solid black line, and a theoretical threshold above which sexual recruitment is possible because abiotic stress is sufficiently low. Gray areas represent periods in which sexual recruitment is possible. In historical climates, periods of conditions favorable for sexual recruitment were intermittent. With increasing temperatures in the Arctic in coming decades, abiotic stress limiting sexual recruitment may lessen, hypothetically enabling scenarios like A) sexual recruitment becomes increasingly likely with continued lessening of abiotic stress, or B) the probability of sexual recruitment stabilizes through time. Threshold values and future responses of reproduction would be species-specific. Modified from Douhovnikoff et al. (2010).
Appendix

Species and site differences influence climate-shrub growth responses in West Greenland

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**Abstract**

We examined the suitability of two deciduous arctic shrubs (*Salix glauca* L. and *Betula nana* L., hereafter *Salix* and *Betula*, respectively) for dendroclimatological analysis at two sites in West Greenland. Chronologies were successfully cross-dated, and the oldest covered the period 1954-2010 (Expressed Population Signal [EPS] >0.85, 1977-2010). Distinctive pointer years, also called micro-rings, including those from a known outbreak of the irruptive moth *Eurois occulta* L. (Lepidoptera: Noctuidae) that peaked in 2005, assisted in the dating process. Climate-growth analyses were performed in two ways: first, using correlation analysis between residual site-level chronologies and monthly and seasonal climate data, and second, using linear mixed effects models (LMM) with seasonal climate data and standardized chronologies for each individual. We used climate data for the current and previous years for a given growth ring for both analyses. Both analyses revealed differences in climate-growth response among species and among sites of contrasting topography. *Salix* ring widths from south facing slopes correlated positively with current year’s summer temperatures, while those on gentle slopes associated negatively with current year’s spring precipitation. *Betula* was only sampled at one site (flat), and displayed associations with temperature and precipitation in spring. Results from the LMM largely corroborated the correlations for *Betula* and *Salix* on south facing slopes. *Salix* at the flat site displayed significant associations with a large number of climate variables, most strongly previous year’s summer and autumn temperatures, though precipitation in multiple seasons of the current and prior year did a better job of accounting for the variation in the data. Many dendrochronological studies in the Arctic illustrate clear summer temperature responses, but the majority were conducted on a single topographic position. Due to the heterogeneity of West Greenland’s landscapes, it is important to examine individuals from varying topographies. We found that samples collected from south facing slopes do appear to respond positively to summer
temperatures, while those on shallow slopes respond to a wider array of seasonal temperature and precipitation parameters. Accounting for these species and topographic differences, when sampling, is imperative for improving our understanding of how plant communities in the Arctic will respond to ongoing and expected warming.

**Introduction**

Understanding how ecosystems have and will continue to respond to climate variability requires spatially explicit time series of temperature and precipitation data (Bradley, 2011). Time series of climate data from relatively dense networks of climate stations in more populated regions of the world have provided important insights into climatic variability and how the magnitude of recent climate change varies among regions (Hijmans et al., 2005). Recent temperature increases in the Arctic illustrate how the magnitude of warming varies regionally. Over the last several decades, the Arctic has warmed roughly twice as much as the global average (Trenberth et al., 2007), and this has led to pronounced localized changes in vegetation (Walker et al., 2006) that vary among Arctic climates (Post et al., 2009).

The Arctic as a whole has few spatially explicit time series of climate data compared to temperate regions (Hijmans et al., 2005). One approach for expanding knowledge of the spatial and temporal variation in historical climate in areas lacking highly-spatially resolved temperature data is to develop proxies to supplement the instrumental record (Mann et al., 1998). Past climatic variability has been reconstructed for parts of Greenland using climate proxies preserved in ice cores, which extend back to 100 ka (Andersen et al., 2004). The climate data preserved in ice cores has sub-annual (seasonal) resolution for some climate proxies and climate-associated parameters (e.g. snow accumulation, $\delta^{18}$O, CH$_4$, and NO$_2$ [Alley, 2000; Blunier et al., 2002;
Flückiger et al., 2004; Andersen et al., 2004]) and decadal to multidecadal resolution for others such as sea surface temperature and the Atlantic Multidecadal Oscillation (Dowdeswell and White, 1995; Chylek et al., 2012). However, the spatial resolution of ice core climate data is limited. Ice core-based climate data are derived from the Greenland ice sheet, often hundreds of kilometers from Greenland’s terrestrial ecosystems, and are therefore unlikely to represent climate variability in heterogeneous local environments.

Tree ring widths are sensitive to climatic variability, and tree rings are commonly used as a climate proxy. However, with the exception of Betula pubescens Ehrh. in sheltered valleys in southwest Greenland (western coast between 60-63 °N), trees are not present in most of ice-free Greenland (Böcher, 1979; Kuivinen and Lawson, 1982; Fredskild and Ødum, 1990). The most abundant woody plants in much of inland Greenland are deciduous shrubs. Many shrub species form annual rings, and have the potential to be used as climate proxies (Myers-Smith et al., 2015a). In spite of this, little research on shrub growth has been conducted in arctic ecosystems to evaluate their potential as climate proxies compared with the abundant research on tree growth in temperate regions. Shrub species in both temperate and arctic ecosystems are known to produce annual rings, and have been used to reconstruct past precipitation and temperatures (Schweingruber and Poschlod, 2005; Schweingruber et al., 2013). For example, arctic shrubs provide a record of past climate variability in Siberia (Blok et al., 2011), Canada (Rayback and Henry, 2006), Svalbard (Weijers et al., 2012), mainland Scandinavia (Bär et al., 2006, Meinardus et al., 2011, Weijers et al., 2012), and High-Arctic Greenland (Forchhammer et al., 2008).

Nonetheless, the Arctic remains understudied for dendrochronological climate reconstructions given the size of the region.

Greenland’s terrestrial ecosystem represents a particularly infrequently studied part of the Arctic. In Zackenberg, NE Greenland, an approximately 50-75 year long shrub ring width chronology has been developed for Salix arctica Pall. (Wilson, 1964; Schmidt et al., 2006;
Forchhammer et al., 2008; Schmidt et al., 2010). We are aware of only two studies, both recent, on secondary growth responses to climate in shrubs in the West Greenland region. Jørgensen et al. (2014) developed approximately 60 and 75 year long records of *Alnus viridis* (Chaix.) D.C. and *Salix glauca* L., respectively, and Hollesen et al. (2015) developed a nearly 90 year record of *Betula nana* L.; both studies demonstrate arctic shrub growth responses to maritime climates. *Betula nana* L. and *Salix glauca* L., hereafter *Betula* and *Salix*, are two of the dominant shrubs in the study area (Post and Pedersen, 2008). Both species have been successfully used for dendroecological and dendroclimatological investigations elsewhere (Blok et al., 2011; Meinardus et al., 2011; Buras et al., 2012).

The objectives of this study were to 1) determine if these two shrub species form annual growth rings that are amenable to reliable cross-dating in a continental climate in West Greenland and 2) conduct a climate-shrub growth analysis to determine how species and site differences mediate climate-shrub growth associations. We hypothesized that growth in both *Salix* and *Betula* would be associated with temperature and precipitation, especially on the well-drained sites on steep south-facing slopes.

**Materials and Methods**

**Study site**

The study area is located in West Greenland ca. 20 km northeast of Kangerlussuaq near Long Lake (Aajuitsup Tasia, 67.1 °N, 50.29 °W; Figure A.1). The climate has frigid winters, cool summers, and low annual precipitation. Five months (May-September) have mean monthly temperatures above freezing (Figure A.2; Klein Tank et al., 2002 [KNMI]). Most precipitation falls during the summer and estimates of total annual precipitation range from 131 to 338 mm,
with a mean of 149 mm (Figure A.2). Daily temperature measurements have been collected at the Kangerlussuaq airport (67.02 °N, 50.70 °W) since 1949 but missing values are common before 1973. Consequently, only data for the 1973-2010 period were used in our analysis. Missing monthly values from the data set (January-July in 1999) were interpolated using mean monthly temperatures for that month in the prior and subsequent 2 years. There were no missing values in the total monthly precipitation data for the period of 1977-2010, which was the period used for our analyses.

The study area is dominated by Low Arctic shrubland, a matrix of shrubs and patches of tundra forbs and grasses that create the mix of vegetation typical in terrain composed of mountain complexes of non-carbonate substrate (Walker et al., 2005). Common shrubs include three deciduous species (Salix, Betula, and Vaccinium uliginosum L.) and two evergreen species (Rhododendron groenlandicum (Oeder) Kron & Judd, and R. lapponicum (L.) Wahlenb.) In this study, we focused on Salix and Betula because they are locally dominant and also have circumpolar distributions. Salix is a highly polymorphic, dioecious erect shrub that is widespread throughout the Arctic, with the degree of polymorphism varying by region (Elven et al., 2011). It can attain heights between approximately 1.2 and 6 m tall, depending on habitat, and is an important food source for a variety of herbivores, including insects, birds, and mammals (Elven et al., 2011). Betula is a circumboreal-polar monoecious dwarf shrub that can grow in a variety of conditions, with maximum heights ranging from 0.4 to 1.20 m (Elven et al., 2011).

Field sampling

In May of 2011, we collected shrub samples from three sites around Long Lake (Figure A.1). Long Lake is surrounded by a system of ridges running largely east-west; our goal was to sample the landscape to capture some of this heterogeneity. Therefore, we sampled two sites
(Sites 1 and 3) on south facing aspects with large differences in slope and one on a southwest facing aspect (Site 2). Sites 1 and 2 are on gently sloping, low lying terrain near the northern and northeastern shores of Long Lake, respectively (Table A.1). These sites consist of a matrix of _Betula_ interspersed between taller _Salix_ individuals, with several centimeters of litter accumulation beneath the shrub canopies. Site 3, in contrast, is on a steep, dry slope with sandy soils and negligible surface litter, and there is little vegetation other than _Salix_ (Table A.1). At all sites, we observed no obvious signs of locally heavy recent herbivory like feces or direct damage to plants. At each of Sites 1 and 2, we sampled _Salix_ and _Betula_ within one 10 X 100 m belt transect. Each transect was divided into ten 10 m² quadrats, and _Salix_ and _Betula_ were sampled in every other quadrat. This approach reduced the likelihood that sampled stems from different quadrats would be from the same clone, since both species can spread vegetatively from adventitious roots or shoots (De Groot et al., 1997; Stamati et al., 2007). We identified individual plants based on their margins and branching patterns and measured the largest (by basal diameter) stem for each individual. We then sampled the individuals with the five largest stems of each species from every other quadrat in each transect. Based on this approach, we deemed it highly unlikely that two samples represent the same individual. Because _Betula_ was not present at Site 3, only _Salix_ was sampled there. At this site, we collected the twenty largest stems of _Salix_ from a population of spatially separated (>3 m between the edges of the clones) individuals. Stems selected for sampling were cut-off at the root collar for laboratory analysis.

**Objective 1 – Chronology development**

Samples were air dried and sanded to a high polish using progressively finer grades of sandpaper (120-1000 grit) until the cellular structures of the rings were visible under a binocular microscope. The ring boundaries of _Betula_ were faint, so samples were stained with
phloroglucinol to enhance boundary definition (Patterson, 1959). Samples were visually cross-dated using pointer years (Stokes and Smiley, 1968) along two to four clearly distinguishable radii per sample (~90° apart). A minimum of two radii per sample were used to identify partial and fully missing rings. After visual cross-dating, ring widths were measured with a Velmex measuring system and the program Measure J2X (VoorTech Consulting, 2007). The ring width measurements were then used to statistically evaluate visual cross-dating using COFECHA (Holmes, 1986; Grissino-Mayer, 2001). We then calculated the mean interseries correlation statistic (rbar), expressed population signal (EPS), and mean sensitivity (MS) for each chronology using the dplR package (Bunn, 2008). EPS was calculated annually for each chronology with a 10 year window to identify periods with a running EPS (rEPS) >0.85 (Wigley et al., 1984).

Ring width chronologies were developed by standardizing values in each sample to remove age-related growth trends (Fritts, 1976) using dplR (Bunn, 2008). Standardization functions included negative exponential (n = 41), linear regression (n = 67), and horizontal means (n = 45), with the choice of function based on best fit for each series. A standardized chronology was then developed for each species at each site and a pre-whitened residual chronology with the first order (i.e., lag-one) autocorrelation removed was used to identify climate-ring width relationships.

**Objective 2 – Climate analyses**

The relationship between shrub ring width and climate was determined by calculating correlation coefficients between the residual site-level chronologies and mean monthly temperature, total monthly precipitation, and seasonal temperature and precipitation using the bootRes package (Zang and Biondi, 2012). bootRes provides bootstrapped confidence intervals
estimates for evaluating the significance of correlation coefficients. Correlation coefficients were calculated for the periods in each chronology with an EPS >0.85.

In addition to the traditional site chronology and development of correlation coefficients run on ring width data with autocorrelation removed, linear mixed effects models (LMM) with a first order autoregressive covariance structure were used to detect significant climatic variables influencing shrub ring growth for each of the species and sites using the nlme (Pinheiro et al. 2014) package in R version 3.1.2 (R Core Team, 2014). This second analytical approach allowed us to substantiate the results of the correlation analysis using an approach that accounted for individual variation (Myers-Smith et al., 2015b). Standardized time series for two radii from each individual were averaged and used as the response variable in the LMM so that each individual, not each radius, would serve as a replicate. These data were normally distributed for Salix from Site 3 and for Betula; for Salix from Site 1/2, it was necessary to log+1 transform the standardized data to yield normality. Seasonal climate variables in each model were used as fixed effects after determining that collinearity was absent among these predictors (Freckleton, 2010), and we included individual stem as a random factor (Schmidt et al., 2006). The submodels were ranked by the sample size adjusted Akaike Information Criterion (AICc) (Burnham and Anderson, 2004), and we performed model averaging with the MuMIn package (Bartoń, 2012) on all submodels within two AICc of the best submodel. The model selection process was conducted using maximum likelihood estimation, and the reported effect sizes (parameter estimates) were based on restricted maximum likelihood estimation. We initially assessed quadrat as a higher level random factor for Sites 1 and 2, but because the variance estimate was near zero, we excluded it from our final models. Climate data from the period 1977-2010 were used for the LMM because of missing precipitation values in earlier years.
Results

Objective 1 – Construction of chronologies

*Betula* and *Salix* are fully and semi-diffuse-porous species, respectively, and had clearly visible annual growth rings. Chronologies were successfully developed for *Betula* from Site 1 and *Salix* at Sites 1, 2, and 3. Due to the similarity in site conditions and the strong correlation between chronologies (Pearson’s $r = 0.654 \ [p = <0.001]$, Gleichläufigkeit [glk] of 0.86), the *Salix* samples from Sites 1 and 2 were combined into a single chronology.

There were two main challenges in cross-dating the samples. First, the three chronologies were short (40, 50, and 57 years for *Betula* 1, *Salix* 1/2, and *Salix* 3 chronologies, respectively; see Table A.2). Moreover, the portions with an EPS $>0.85$ were even shorter (23, 34, and 30 years for chronologies, as above; see Table A.2, Figure A.3), and the rings were very narrow (*Betula $\bar{x} = 0.204$ mm, *Salix $\bar{x} = 0.334$ mm; Table A.3). Second, multiple growth reductions (pointer years) were present in most of the samples and occurred in 2005, 2000, 1996, and 1981/82 and served as markers for cross-dating (Table A.3, Figures A.3 and A.4).

Mean inter-series correlations from COFECHA for the chronologies were moderate, from 0.48-0.60 (rbar range: 0.26-0.33) and stronger for portions that had an EPS $>0.85$ (rbar range: 0.27-0.41; Table A.2). The chronologies had mean sensitivities that ranged from 0.33-0.39 (Table A.2), suggesting that they are suitable for climate-growth analysis as these values are in the range used in previous studies on arctic shrubs (Schmidt et al., 2006; Jørgensen et al., 2014).

Objective 2 – Climate-growth relationships

Growth of both shrubs responded to climate, but each species differed in how climate influenced growth. The significant correlation coefficients ($p <0.05$, see Figure 5) demonstrate
that *Betula* ring widths had a negative response to the current year’s spring temperature, whereas *Salix* responded to current year’s summer temperature, but only at one site. *Salix* growth at this same site was also negatively correlated with mean monthly temperature for October of the previous year (Figure 5). Additionally, *Salix* at both sites had a positive correlation with September precipitation in the previous year, and *Betula* growth responded positively to the previous year’s May precipitation. Both *Salix* and *Betula* showed negative growth responses to current year’s spring precipitation despite the lack of responses to monthly precipitation.

Linear mixed effects models (LMM) broadly corroborated those significant climate responses found with correlations for all three of the chronologies (Table A.4). Moreover, in each of the three LMMs, the climate factor with the highest z-value was also significant in the correlation analyses (Table A.5); however, the significant climate variables were not always the same in both analyses. *Betula* at Site 1 showed nearly the same patterns as the correlations, with current year’s spring temperature and previous year’s spring and current year’s summer precipitation influencing growth. Also, the effect size of the former factor was an order of magnitude greater than the latter two.

The full model for *Salix* at Site 1/2 revealed a large number of significant climate factors that influence growth, though only one of those factors had a large effect size (Table A.5). Previous summer temperature had the largest (and negative) effect on growth, with previous autumn and current year’s winter temperatures having the next largest effect sizes. Though these factors were not significant in the correlation analysis, the upper limit of the confidence interval for previous summer temperature was only slightly above zero (Figure A.5). Growth in *Salix* at Site 3 was influenced solely by the current year’s summer temperature and the previous year’s spring precipitation (Table A.5), and the effect size of the former was nearly twice that of the latter. The results of these LMMs generally confirm those of the correlation analysis, with the LMM for *Salix* at Site 1/2 revealing additional climate parameters that significantly influenced
growth, though the effect sizes for these parameters were small compared to values reported in a recent synthesis (Myers-Smith et al., 2015a).

**Discussion**

*Betula* and *Salix* shrubs from West Greenland can successfully be cross-dated and used for dendroclimatological analysis without using serial (Kolishchuk, 1990; Hallinger et al., 2010, Myers-Smith et al., 2015b) or microtome cross-sectioning (Cairns et al., 2012). The longest chronology with an EPS >0.85 was 33 years and extends back to 1977 (*Salix*, Site 1/2), 4 years less than the unbroken instrumental temperature record and the same length as the instrumental precipitation record. Because we sampled while the soil was still frozen, we could not sample belowground tissues that may have had a record of earlier growth. Excavation would have caused significant damage to the samples and disturbance to the site. Though the samples we collected do not extend beyond the instrumental climate record, *Betula* and *Salix* growth rings have the potential for climate reconstructions in West Greenland since the oldest individual stem in this study is 55 years old, while some individuals from the Disko Bay area north of our study region were approximately 75 years old (Jørgensen et al., 2014). Furthermore, conspecifics in Norway live to be over 90 and 70 years old for *Betula* and *Salix*, respectively (Meinardus et al., 2011; Buras et al., 2012). Future sampling during the growing season when the soils are not frozen would likely yield longer chronologies.

Ring widths in the wood samples had relatively high mean sensitivities (MS) (Table A.2), because of the frequency of very narrow and partially missing rings. The years with very narrow rings corresponded with irruptive outbreaks of the moth *Eurois occulta* L. (Lepidoptera: Noctuidae) in the region. Documented outbreaks occurred in 2004/2005 (Post and Pedersen, 2008) and in 2010/2011 (Avery and Post, 2013), shortly before samples were collected in May.
2011. In 2004/2005, the defoliation led to large leaf biomass reductions in \textit{Betula} (87.1%) and \textit{Salix} (97.8%) (Post and Pedersen, 2008). There was a reduction of ring growth in 2005 in both species at Sites 1 and 1/2, and during both 2004 and 2005 at Site 3, which corresponded to the outbreak observed by Post and Pedersen (2008) in 2004/2005 (Table A.3, Figures A.3 and A.4).

In addition to the direct evidence of recent outbreaks, there is indirect evidence of an outbreak in the early 1980s (Fox et al., 1987). Moth larvae, of which \textit{E. occulta} make up the largest proportion, are important in the diet of Lapland longspurs (\textit{Calcarius lapponicus} L.) (Fox et al., 1987). In 1979, there was a high density of moth larvae on the landscape, and they comprised a major portion of nestlings’ diet (Fox et al., 1987). By comparison, in 1984, overall breeding output was lower than in 1979, partly because moth larvae were far less abundant in 1984 (Fox et al., 1987). These results suggest that a large decline in the moth population may have occurred at some time in the interim. Our ring width record show narrow and partially missing rings in 1981 for both species at Sites 1 and 1/2 and in 1982 at Site 3, suggesting an outbreak occurred during these years. This highlights the potential for future research not only on climate reconstruction using shrub growth rings, but also on the assessment of possible relationships between outbreaks and climate, and even the possibility of exploring the spatial synchrony (Young et al., 2014) of these outbreaks throughout West Greenland.

Throughout the Arctic, numerous species of shrubs exhibit positive growth responses to summer temperatures (Rayback and Henry, 2006; Bär et al., 2008; Hallinger et al., 2010; Forbes et al., 2010; Blok et al., 2011; Buras et al., 2012; Macias-Fauria et al., 2012; Weijers et al., 2012; Buchwal et al., 2013, Jørgensen et al., 2014), though there are exceptions in the High Arctic (e.g. \textit{Salix}; Schmidt et al., 2006; Zalatan and Gajewski, 2006). A recent synthesis demonstrated that the responses of arctic shrubs to climatic variability are dominated by correlations with summer temperature, most of which are positive relationships (Myers-Smith et al., 2015a). In our study area, only \textit{Salix} responds positively to summer temperatures, and only on dry south facing slopes.
Moreover, although Salix on gentle slopes showed a negative response to the previous year’s summer temperature, this parameter is a comparatively poor predictor. If we had made use of a limited set of climate predictors in our LMM (e.g. Myers-Smith et al., 2015a), previous summer temperatures would not have shown up in our final model.

Instead, the Salix in the flat site (Site 1/2) primarily showed very weak responses to precipitation in several different seasons (Table A.5). The negative association between growth and current year’s spring precipitation may indicate that springs with particularly heavy snowfall reduce growth (Schmidt et al., 2006, Schmidt et al., 2010), likely through a shortened growing season (Ernakovich et al., 2014). Interestingly, higher snowfall during the winter correlated positively with growth, suggesting that greater snow cover may have had a small insulating effect. Additionally, there was a small but significant positive association between precipitation during the summer months and ring width. A recent synthesis demonstrated that shrub growth was associated, both positively and negatively, with precipitation in some models, though the association with summer precipitation was only ever negative if significant (Myers-Smith et al., 2015). Nonetheless, the greatest increase in shrub abundance in response to warming occurred at wetter sites (Elmendorf et al., 2012). It may also be that greater summer precipitation increased growth via a lengthened, or at least not shortened (Ernakovich et al., 2014), growing season by reducing the advancement of senescence caused in part by seasonal declines in soil moisture (Oberbauer and Dawson, 1992).

Similarly to Salix in most of the Arctic, Betula from Siberia (Blok et al., 2011) and Norway (Meinardus et al., 2011) have shown a positive growth response to the current year’s early summer temperatures. In contrast, Betula at our site showed no response to the current year’s summer temperatures and had a negative response to current year’s spring temperatures. Multiple potential mechanisms could be responsible for this pattern. Although we did not observe frost rings in our samples, we speculate that warm temperatures in the spring before leaves flush
may increase the susceptibility of shrubs to spring frost events, potentially reducing annual growth (Inouye, 2000, Blok et al., 2015). Phenological differences between the species may be important here, as Betula opens its first leaves earlier in the spring (~3 days) compared with Salix (Post, 2013a). Although the mean differences in the dates of the first emergence of leaves are small, there may be years with exceptionally warm springs during which Betula leaves emerge enough before Salix leaves that they might be significantly more susceptible to frost (Inouye, 2000). Moreover, because these data reflect differences in the onset of emergence, rather than peak leaf out, differences between the species in the duration of the leaf out process may also be important in influencing growth responses to spring temperatures (Post et al., 2008).

Alternatively, if warm springs lead to a lower near surface soil moisture later in the growing season, Betula may be more sensitive to this relative drought. Though both Betula and Salix can be deeply rooted compared with evergreen shrubs (Kummerow et al., 1983), Betula is more shallowly rooted than Salix and appears to acquire more of its resources near the soil surface (Nadelhoffer et al., 1996). Finally, because we did not sample Betula at a dry, warm site, it is possible that the differences between these two species are simply the product of the lack of spatial variation in the sampling of Betula; the spatial variation in climate-growth responses that is clearly evident in the Salix may also be present in Betula. There may be sites where Betula growth does respond positively to summer temperatures, as has been shown elsewhere (e.g. Blok et al., 2011). One potential cause of this variation among sites could be differences in the degree to which microsite variation buffers some individuals against broad scale climatic influence.

Many shrub species throughout the Arctic show little growth response to precipitation (Bär et al., 2008; Hallinger et al., 2010; Weijers et al., 2012), except where shrubs are growing in unusual microsite conditions (Bär et al., 2008; Hallinger et al., 2010). However, the results for Betula species are more ambiguous, with reports of both no significant response (Paradis et al., 2014) and positive (Blok et al., 2011; Keuper et al., 2012) growth responses to precipitation. Our
chronologies from Sites 1 and 1/2 show a seasonal negative correlation with spring seasonal precipitation of the current year, while Site 3 does not. Furthermore, the LMM for \textit{Salix} at Site 1/2 revealed not only the same negative response to spring precipitation, but also significant responses to precipitation in both the current and prior year. The LMM for Site 3 showed that only the previous spring’s precipitation significantly influenced \textit{Salix} growth. Site 3 is on a dry, warm south-facing slope, whereas Sites 1 and 1/2 are on relatively flat terrain that would remain comparatively wet and cool. Precipitation in the spring months falls largely as snow, and the negative correlation with spring precipitation on the shallow sloped sites could have been due to lower angles of insolation than that of Site 3. Snow may persist longer on these sites in the spring, which could delay the onset of leaf out and decrease the length of the growing season, thereby reducing shrub growth (Bär et al., 2008; Wipf, 2010; Cooper et al., 2011). It should be noted, however, that many of these significant precipitation effects in the LMM had small effect sizes when compared with seasonal temperature effects (Table A.5). Finally, though there were some differences between the results of the traditional correlation analysis and LMM approach, the most important seasonal climate parameter (in terms of increasing goodness-of-fit while maintaining parsimony) in the LMM also appeared to have similar importance in the correlation analysis.

Understanding how topographic position mediates the growth of shrubs is important in interpreting their responses to climatic variability and change. Due to the short stature of most arctic shrubs (<1 m), they are highly influenced by microsite conditions (e.g. aspect, elevation, landscape curvature). \textit{Empetrum nigrum} ssp. \textit{hermaphroditum} Hagerup. in Norway growing on south facing slopes experienced reduced growth due to heat stress during the warmest days of summer, while those on the north facing slopes benefited from these high temperatures (Bär et al., 2008). The timing of response may also shift due to elevation. For example, \textit{Juniperus nana} Willd. growing at higher elevation showed positive monthly responses earlier in the summer
(June) than individuals growing at low elevation (August), possibly due to high elevation individuals’ need to develop as soon as conditions are adequate, while low elevation individuals experience a longer growing season (Hallinger et al., 2010).

Observations over the last 12 years in the study area (Post, 2013b) have shown an increase in the cover of both shrub species at small scales (~1 m²). At large scales, remote sensing data revealed large increases in both peak and time-indexed NDVI, which are estimates of total biomass and gross primary productivity, respectively (Masson-Delmotte et al., 2012). Much of these landscape-scale increases in biomass and productivity have been driven by an increase in woody plant abundance associated with increases in temperature in arctic and subarctic regions (Tape et al., 2006; Bhatt et al., 2010; Forbes et al., 2010; Naito and Cairns, 2011; Tremblay et al., 2012). Projections of climate change for West Greenland show increases in both temperature and precipitation, the latter occurring through both larger and more frequent precipitation events, particularly during the growing season (Stendel et al., 2008).

Under these conditions, our results indicate that individual Salix ramets would benefit from these changes in climate more than those of Betula (Bret-Harte et al., 2001; Hollesen et al., 2015). However, microsite conditions as well as precipitation timing would influence annual growth (Bär et al., 2008; Blok et al., 2011). Although both species are deciduous shrubs, they have key differences in their life history strategies. Betula allocates carbon to both short and long shoots, so growth may not produce an even ring width in all ramets each year (Bret-Harte et al., 2001; Bret-Harte et al., 2002). On the other hand, Salix has only one type of shoot, and carbon is not partitioned, so annual ring widths are similar among ramets and relatively uniform (Bret-Harte et al., 2002). The positive correlation between Salix ramet growth and summer temperature (Site 3), and the absence of a similar association in Betula ramets, may reflect differences in allocation patterns. Physiological integration, which allows for genets to share resources among ramets through translocation, may be stronger in Betula than Salix. Hence, growth in any given
ramet might poorly correlate with temperatures during the growing season because of the heterogeneity of other limiting resources (e.g. nutrients) or microtopographic influence on climate. In these instances, secondary growth may not be as reliable an indicator of the response to changes in climate as, for example, primary growth. Despite their different life history strategies, both species had a similar response to insect outbreaks. In the end, understanding how species-specific responses (cf. Bret-Harte et al., 2008) influence the way plant populations change over time is vital for reliable predictions of vegetation dynamics in a rapidly changing Arctic.

**Conclusions**

We suggest that an increase in *Betula* cover in a warmer climate may derive from increasing numbers of stems (ramets) in a genet (Bret-Harte et al., 2002) rather than an increase in the size of individual stems, as evidenced by the lack of a response to summer temperatures and the negative response to warmer springs. For *Salix*, warmer summers will elicit greater stem growth on dry, south-facing slopes. The processes contributing to the community level expansion of arctic shrubs are highly complex (Myers-Smith et al., 2011), and accounting for the intra- and interspecific variation in secondary growth is needed to understand how communities are likely to change at multiple scales. Additionally, we found that serial sectioning was not necessary to capture the patterns of growth at these sites, mainly due to the occurrence of pointer rings created by periodic irruptive outbreaks of the moth, *E. occulta*. Our analysis demonstrates the continued potential for using shrub growth for climate reconstructions based on longer lived individuals and more spatially extensive sampling or studies of moth outbreak dynamics.
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We are grateful to members of the Post Lab for hosting A.B.Y. in the field, Alison Donnelly for field assistance, and Abby Dolinger for laboratory assistance in sample preparation. Two anonymous reviewers also provided helpful comments to an earlier draft of the manuscript. Financial support for this research was provided by the Pennsylvania State University’s Department of Geography, a University Graduate Fellowship awarded to D.A.W., and NSF grant PLR 1107381 to E.P. to conduct the fieldwork.

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Zalatan, R., Gajewski, K., 2006. Dendrochronological potential of Salix alaxensis from the
Kujujua River area, Western Canadian Arctic. Tree-Ring Research 62, 75-82.
Figure A.1. Map of sites located on the eastern end of Long Lake (Aajuitsup Tasia), roughly 2-5 km from Russell Glacier, West Greenland. Data Source: Landsat 5 (NASA), Cryosphere Atlas (National Snow and Ice Data Center).
Figure A.1. Climograph of Kangerlussuaq, West Greenland, with average monthly temperature in °C (red), and average total monthly precipitation in mm (blue). Data from Klein Tank et al., 2002, via KNMI’s Climate Explorer website (climexp.knmi.nl).
Figure A.3. Residual chronologies and sample size (number of individual shrubs) for Site 1 Betula (top), Site 1/2 Salix (middle), and Site 3 Salix (bottom). Solid lines on the residual chronology represent the portions that have a running expressed population signal (rEPS) >0.85. A known insect outbreak occurred in 2005 (vertical dashed line).
Figure A.4. Images of *Betula* (upper) and *Salix* (lower) wood samples at 14x and 30x magnification. Note the small (micro) ring of the 2005 insect outbreak.
Figure A.5. Correlations (grey bars) and significant correlations (black bars) between ring width series and climate parameters (monthly and seasonal mean temperature and total precipitation). Type I error rates were set at $\alpha = 0.05$. Analysis was conducted over a 20 month period encompassing the previous year (Capitals) and the current year (lower case) for the portion of each chronology with a rEPS $>0.85$. 
Table A.1. Site locations and microsite conditions, including latitude and longitude (decimal degrees), elevation (m), slope (degrees), aspect, and a description of the topography of the terrain.

<table>
<thead>
<tr>
<th>Site</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Elevation</th>
<th>Slope</th>
<th>Aspect</th>
<th>Topography</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>67.10486</td>
<td>50.34396</td>
<td>240</td>
<td>4</td>
<td>S</td>
<td>Long steady slope</td>
</tr>
<tr>
<td>2</td>
<td>67.10152</td>
<td>50.29398</td>
<td>218</td>
<td>4</td>
<td>WSW</td>
<td>Small rolling hills</td>
</tr>
<tr>
<td>3</td>
<td>67.08510</td>
<td>50.33027</td>
<td>382</td>
<td>30</td>
<td>S</td>
<td>Steep hillside</td>
</tr>
</tbody>
</table>
Table A.2. Summary statistics for site chronologies for the entire series and the portion of the series with a running EPS (rEPS) >0.85. Listed are species, time interval, number of shrubs used in the analyses (# shrubs), total number of radii (# paths), mean interseries correlation statistic (rbar), expressed population signal (EPS), mean sensitivity (MS), autocorrelation of the 1st order for raw data (AR_{raw}) and autocorrelation of the 1st order for the residual chronology (AR_{res}).

<table>
<thead>
<tr>
<th>Site</th>
<th>Species</th>
<th>Interval</th>
<th># shrubs</th>
<th># paths</th>
<th>rbar</th>
<th>EPS</th>
<th>MS</th>
<th>AR_{raw}</th>
<th>AR_{res}</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Betula</td>
<td>1971-2010</td>
<td>15</td>
<td>33</td>
<td>0.288</td>
<td>0.809</td>
<td>0.344</td>
<td>0.392</td>
<td>0.075</td>
</tr>
<tr>
<td>1/2</td>
<td>Salix</td>
<td>1961-2010</td>
<td>42</td>
<td>92</td>
<td>0.307</td>
<td>0.918</td>
<td>0.389</td>
<td>0.427</td>
<td>-0.183</td>
</tr>
<tr>
<td>3</td>
<td>Salix</td>
<td>1954-2010</td>
<td>13</td>
<td>28</td>
<td>0.201</td>
<td>0.737</td>
<td>0.333</td>
<td>0.475</td>
<td>-0.050</td>
</tr>
</tbody>
</table>

rEPS >0.85

<table>
<thead>
<tr>
<th>Site</th>
<th>Species</th>
<th>Interval</th>
<th># shrubs</th>
<th># paths</th>
<th>rbar</th>
<th>EPS</th>
<th>MS</th>
<th>AR_{raw}</th>
<th>AR_{res}</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Betula</td>
<td>1988-2010</td>
<td>15</td>
<td>33</td>
<td>0.393</td>
<td>0.907</td>
<td>0.350</td>
<td>0.387</td>
<td>-0.020</td>
</tr>
<tr>
<td>1/2</td>
<td>Salix</td>
<td>1977-2010</td>
<td>42</td>
<td>92</td>
<td>0.307</td>
<td>0.943</td>
<td>0.388</td>
<td>0.426</td>
<td>0.108</td>
</tr>
<tr>
<td>3</td>
<td>Salix</td>
<td>1981-2010</td>
<td>13</td>
<td>28</td>
<td>0.214</td>
<td>0.813</td>
<td>0.316</td>
<td>0.443</td>
<td>-0.073</td>
</tr>
</tbody>
</table>
Table A.3. Comparison of average ring widths between all years excluding 2005 and the average 2005 insect outbreak ring for each site. Also shown are the mean ring widths (and standard deviations) in mm and the percent of samples with reduced growth in 2005 (% 2005).

<table>
<thead>
<tr>
<th>Site</th>
<th>Species</th>
<th>Ring width</th>
<th>% 2005</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td><strong>All Years</strong></td>
<td><strong>2005 outbreak</strong></td>
</tr>
<tr>
<td>1</td>
<td>Betula</td>
<td>0.204 (0.093)</td>
<td>0.106 (0.049)</td>
</tr>
<tr>
<td>1/2</td>
<td>Salix</td>
<td>0.242 (0.138)</td>
<td>0.089 (0.060)</td>
</tr>
<tr>
<td>3</td>
<td>Salix</td>
<td>0.565 (0.344)</td>
<td>0.598 (0.428)</td>
</tr>
</tbody>
</table>

Bracketed values are the standard deviation of the mean.
Table A.4. Site specific linear mixed effects models (LMM) of seasonal climate variables that significantly influenced the growth of shrub rings. A t or p as the initial letter in the parameter name indicates temperature or precipitation, respectively, and lowercase letters for the climate variables represent the current year, while capitalized letters represent the previous year (djf/DJF = winter, mam/MAM = spring, jja/JJA = summer, and son/SON = autumn). Indiv. is the number of individual shrubs included in each model, while Obs. is the total number of ring width observations. $R^2$ is Nakagawa & Schielzeth's (2013) marginal $R^2_{GLMM}$, which summarizes the variance explained by the fixed factors. logLik is the log-likelihood statistic, AICc is the sample-size adjusted Akaike’s Information Criterion, and BIC is Bayesian Information Criterion, and these are reported as the difference ($\Delta$) between the full and intercept-only models using maximum likelihood estimation. Climate variables are fixed factors and are listed in descending order of their $z$-value.

<table>
<thead>
<tr>
<th>Site</th>
<th>Species</th>
<th>Climate Variables</th>
<th>Indiv. (Obs.)</th>
<th>$R^2$</th>
<th>ΔlogLik</th>
<th>ΔAICc</th>
<th>ΔBIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Betula</td>
<td>t.mam, P.MAM, p.jja</td>
<td>15 (399)</td>
<td>0.13</td>
<td>-36.51</td>
<td>67.02</td>
<td>55.05</td>
</tr>
<tr>
<td>1/2</td>
<td>Salix</td>
<td>p.mam, p.jja, p.djf, P.SON, T.JJA, P.JJA, T.SON, t.djf, p.son</td>
<td>42 (1112)</td>
<td>0.21</td>
<td>-93.86</td>
<td>169.73</td>
<td>124.72</td>
</tr>
<tr>
<td>3</td>
<td>Salix</td>
<td>t.jja, P.MAM</td>
<td>13 (380)</td>
<td>0.11</td>
<td>-27.36</td>
<td>50.73</td>
<td>42.84</td>
</tr>
</tbody>
</table>
Table A.5. Parameter estimates (effect sizes) for fixed climate factors for full site specific linear mixed effects models (LMM) of shrub growth rings, with all significant factors included. A t or p as the initial letter in the parameter name indicates temperature or precipitation, respectively, and lowercase letters for the climate variables represent the current year, while capitalized letters represent the previous year (djf/DJF = winter, mam/MAM = spring, jja/JJA = summer, and son/SON = autumn). Adj. SE is the adjusted standard error of the mean, and z and p are the z-statistic and p-value of each fixed factor, respectively. Because all parameters in each final model had an importance value of 1, climate variables are instead listed in descending order of their z-value, and parameter estimates are based on restricted maximum likelihood estimation.

<table>
<thead>
<tr>
<th>Site</th>
<th>Species</th>
<th>Parameter</th>
<th>Estimate</th>
<th>Adj. SE</th>
<th>z-value</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Betula</td>
<td>(Intercept)</td>
<td>0.50000</td>
<td>0.13040</td>
<td>1.420</td>
<td>0.155</td>
</tr>
<tr>
<td></td>
<td></td>
<td>t.mam</td>
<td>-0.02799</td>
<td>0.00581</td>
<td>3.662</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td></td>
<td>P.MAM</td>
<td>0.00233</td>
<td>0.00063</td>
<td>3.385</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>p.jja</td>
<td>0.00105</td>
<td>0.00035</td>
<td>3.236</td>
<td>0.001</td>
</tr>
<tr>
<td>1/2</td>
<td>Salix</td>
<td>(Intercept)</td>
<td>1.12000</td>
<td>0.17980</td>
<td>4.745</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td></td>
<td>p.mam</td>
<td>-0.00289</td>
<td>0.00025</td>
<td>10.963</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td></td>
<td>p.jja</td>
<td>0.00118</td>
<td>0.00014</td>
<td>8.503</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td></td>
<td>p.djf</td>
<td>0.00395</td>
<td>0.00046</td>
<td>8.181</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td></td>
<td>P.SON</td>
<td>0.00145</td>
<td>0.00017</td>
<td>7.247</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td></td>
<td>T.JJA</td>
<td>-0.06633</td>
<td>0.00931</td>
<td>6.484</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td></td>
<td>P.JJA</td>
<td>0.00106</td>
<td>0.00017</td>
<td>5.888</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td></td>
<td>T.SON</td>
<td>0.02444</td>
<td>0.00472</td>
<td>4.376</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td></td>
<td>t.djf</td>
<td>0.00711</td>
<td>0.00188</td>
<td>3.242</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>p.son</td>
<td>-0.00032</td>
<td>0.00017</td>
<td>2.163</td>
<td>0.031</td>
</tr>
<tr>
<td>3</td>
<td>Salix</td>
<td>(Intercept)</td>
<td>-0.16650</td>
<td>0.15650</td>
<td>0.501</td>
<td>0.616</td>
</tr>
<tr>
<td></td>
<td></td>
<td>t.jja</td>
<td>0.11390</td>
<td>0.01555</td>
<td>6.429</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td></td>
<td>P.MAM</td>
<td>0.00225</td>
<td>0.00055</td>
<td>3.020</td>
<td>0.003</td>
</tr>
</tbody>
</table>
VITA

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