

The Pennsylvania State University  
The Graduate School  
Intercollege Graduate Degree Program in Ecology

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

A Dissertation in

Ecology

by

David A. Watts

© 2016 David A. Watts

Submitted in Partial Fulfillment  
of the Requirements  
for the Degree of

Doctor of Philosophy

August 2016

The dissertation of David A. Watts was reviewed and approved\* by the following:

Eric Post  
Professor of Biology  
Dissertation Advisor  
Chair of Committee

Tomás Carlo-Joglar  
Associate Professor of Biology

Margot Kaye  
Associate Professor of Forest Ecology

Tracy Langkilde  
Professor and Head of Biology

Erica Smithwick  
Associate Professor of Geography

David Eissenstat  
Professor of Woody Plant Physiology  
Chair of the Intercollege Graduate Degree Program in Ecology

\*Signatures are on file in the Graduate School

## 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.

## TABLE OF CONTENTS

List of Figures .....	ix
List of Tables .....	xiii
Acknowledgements.....	xv
Chapter 1 General overview .....	1
Evidence for global change in the Arctic.....	1
Recent trends in arctic plant communities .....	3
Terrestrial biophysical changes.....	3
Niches of arctic plants.....	6
Consequences for biodiversity .....	13
Organization of dissertation.....	14
References.....	15
Chapter 2 Seed quality responses to drivers of global change vary widely across arctic plant species .....	34
Abstract.....	34
Introduction.....	35
Methods .....	39
West Greenland climate projections .....	39
Study site and experimental design.....	40
Study species.....	42
Measuring seed quality .....	43
Data analysis .....	44
Results.....	46
Warming and watering.....	46
Grazing.....	47
Interannual variation .....	48
Discussion.....	49
Effects of simulated global change .....	49
Plant functional type and species-specific responses.....	52
Conclusions.....	54
References.....	55
Chapter 3 The recruitment and spread of an arctic deciduous shrub: Sexual recruitment or clonal growth?.....	71
Abstract.....	71
Introduction.....	72
Methods .....	75
Site selection .....	75
Study species.....	76

Sampling design.....	77
DNA isolation and PCR amplification.....	78
Genotyping and ploidy estimation.....	79
Logistic regression.....	81
Results.....	82
Genotyping and pairwise genetic distances.....	82
Logistic regression and predicted probabilities.....	84
Discussion.....	84
Conclusions.....	90
References.....	91
 Chapter 4 Relationship between plant community diversity and ecosystem function altered by warming and herbivore exclusion.....	 117
Abstract.....	117
Introduction.....	118
Methods.....	121
Study design.....	121
Characterizing diversity.....	122
Richness-biomass relationships.....	125
Results.....	126
Characterizing diversity.....	126
Richness-biomass relationships.....	128
Discussion.....	129
Conclusions.....	134
References.....	135
 Chapter 5 Synthesis.....	 156
Sexual reproduction in the Arctic.....	156
Linking genomes to shrub expansion through life history.....	160
Consequences for arctic communities.....	163
References.....	166
 Appendix Species and site differences influence climate-shrub growth responses in West Greenland.....	 177
Abstract.....	178
Introduction.....	179
Materials and Methods.....	181
Study site.....	181
Field sampling.....	182
Objective 1 – Chronology development.....	183
Objective 2 – Climate analyses.....	184
Results.....	186
Objective 1 – Construction of chronologies.....	186
Objective 2 – Climate-growth relationships.....	186
Discussion.....	188
Conclusions.....	194

Acknowledgements..... 195  
References..... 195



## LIST OF FIGURES

- 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/>). ..... 32
- 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. .... 33
- 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 ( $0.05 < P < 0.1$ ). ..... 66
- 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 ( $0.05 < P < 0.1$ ). ..... 67
- 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 ( $^{\circ}\text{C}$ ) 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. .... 68
- 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/>). ..... 106
- 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. .... 107
- 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..... 108
- 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..... 109
- 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..... 110
- 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. .... 111
- 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. .... 112
- 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). .... 113
- 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..... 114
- 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..... 148
- 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 $q = 0, 1, \text{ and } 2$ , respectively (see Equation 1 and associated text).....	149
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).....	150
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).....	151
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). .....	176
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).....	207
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).....	208
Figure A.3. Residual chronologies and sample size (number of individual shrubs) for Site 1 <i>Betula</i> (top), Site 1/2 <i>Salix</i> (middle), and Site 3 <i>Salix</i> (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). .....	209
Figure A.4. Images of <i>Betula</i> (upper) and <i>Salix</i> (lower) wood samples at 14x and 30x magnification. Note the small (micro) ring of the 2005 insect outbreak. ....	210

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..... 211

## LIST OF TABLES

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 enclosures. Because of their rarity, <i>Potentilla</i> was only sampled for the watering treatment, so dashes indicate zero samples for a treatment. ....	69
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. ....	70
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. ....	115
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. ....	116
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 ( <i>df</i> ), <i>F</i> -, and <i>P</i> -values for the fixed effects site, exclusion, warming, and all two- and three-way interactions, as well as estimated degrees of freedom ( <i>edf</i> ), <i>F</i> , and <i>P</i> -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. ....	152
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 ( <i>df</i> ), and <i>t</i> - and <i>P</i> -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] <sup>2</sup> ) and shrub biomass (shrubs and [shrubs] <sup>2</sup> ). ....	153
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 <i>R</i> <sup>2</sup> ) and fixed plus random factors (conditional <i>R</i> <sup>2</sup> ). ....	154

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 <i>t</i> - and <i>P</i> -values. SEM is the standard error of the mean. ....	155
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.....	212
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 ( $\bar{r}$ ), expressed population signal (EPS), mean sensitivity (MS), autocorrelation of the 1st order for raw data ( $AR_{raw}$ ) and autocorrelation of the 1 <sup>st</sup> order for the residual chronology ( $AR_{res}$ ). ....	213
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). ....	214
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). Individ. 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 <i>z</i> -value.....	215
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 <i>z</i> and <i>p</i> are the <i>z</i> -statistic and <i>p</i> -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 <i>z</i> -value, and parameter estimates are based on restricted maximum likelihood estimation. ....	216

## ACKNOWLEDGEMENTS

It's been a fun journey, and although I'm not at the end, I've relied upon a great deal of support, assistance, and sage counsel from many people and institutions. The guidance from and dialogue with my advisor, Dr. Eric Post, have been second to none. I have come to deeply respect his humble approach to supervision and feel fortunate to have had him as a mentor. My committee members have also been role models in myriad ways. Dr. Margot Kaye has consistently shown me different ways of seeing the same questions, data, and approaches that have been truly eye opening in each instance. Dr. Erica Smithwick has always set the bar incredibly high, and she has done so with optimistic expectations of my success. Dr. Tomás Carlo has been a pleasure to work with; whether we were analyzing data or instructing together, his sheer joy and enthusiasm about the study of life were always infectious. On issues big and small, and at all times, Dr. Tracy Langkilde has been a tremendous pillar of support, and certainly more so than could ever have been expected.

I have also had the good fortune to have been allowed to use the equipment, supplies, and scholarly experience of many generous scientists at Penn State. First on the list has to be Dr. James Marden, along with Dr. Howard Fescemyer and Erica Shearer, who have each been inordinately patient with my continual presence in their lab and my incessant questions. I greatly appreciate the additional encouragement and intellectual support provided by Meghann Devlin-Durante and Drs. Todd LaJeunesse, Drew Wham, and John Parkinson. Finally, I thank Dr. Vladimir Douhovnikoff at Bowdoin College for being so receptive and welcoming to my request to collaborate that I hope to continue to do so into the future.

My lab mates have consistently entertained and enlightened me, so thank you Mike Avery, Didem Ikis, Christian John, and Drs. Farshid Ahrestani, Sean Cahoon, and Jeff Kerby. I wouldn't have as many stories to tell without you. And for their help with cold fieldwork and

frustrating labwork, I am deeply indebted to Dr. Nathan Amador, Lucy Atkins, Janine Mistrick, Carly Hawkins, Kara Kolar, Ryan Fatzinger, Tara Mediavillo, Hugh Wilkens, Tiffany Hidalgo, Lauren Onofrio, and Emily Strohm. I've been fortunate to work with you all. And as for those challenges in the field, I'm probably only alive today because of the efforts of Eric Bear Coplin, Kylie Cospers, Kathy Young, Audrey Jo Mills, Geoff Miller, Paul Smotherman, and Twan Moreno of PFS and CH2MHills Polar Services, Kevin Vermilion of SRI, and Basse Vaengtoft of KISS. And of course I could never actually have gotten to Greenland without the New York Air National Guard's 109<sup>th</sup> Airlift Wing!

I have also been lucky to have had a network of family and friends who, even when wondering why I choose to live in a tent in the Arctic, never doubted me. And most important of all, I have had the immense pleasure of sharing many wilderness moments, hot and cold, wet and dry, buggy and windy, with a woman who shares my love of not just being in nature, but understanding how it works, bit by bit. Amanda, let's continue forever chasing winter!



## **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-18<sup>th</sup> century have resulted in an increase in atmospheric CO<sub>2</sub> 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 20<sup>th</sup> 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) Turill, 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 (Carnieli 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<sub>2</sub> 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

- Arrhenius, S. 1896. On the influence of carbonic acid in the air upon the temperature of the ground. *Philosophical Magazine and Journal of Science* 41:237–276.
- Bell, K. L., and L. C. Bliss. 1980. Plant reproduction in a High Arctic environment. *Arctic and Alpine Research* 12:1–10.
- Bellingham, P. J., and A. D. Sparrow. 2000. Resprouting as a life history strategy in woody plant communities. *Oikos* 89:409–416.

- Bhatt, U. S., D. A. Walker, M. K. Raynolds, J. C. Comiso, H. E. Epstein, G. Jia, R. Gens, J. E. Pinzon, C. J. Tucker, C. E. Tweedie, and P. J. Webber. 2010. Circumpolar Arctic tundra vegetation change is linked to sea ice decline. *Earth Interactions* 14:1–20.
- Bhatt, U. S., D. A. Walker, J. E. Walsh, E. C. Carmack, K. E. Frey, W. N. Meier, S. E. Moore, F.-J. W. Parmentier, E. Post, V. E. Romanovsky, and W. R. Simpson. 2014. Implications of Arctic sea ice decline for the Earth system. *Annual Review of Environment and Resources* 39:57–89.
- Bintanja, R., and F. M. Selten. 2014. Future increases in Arctic precipitation linked to local evaporation and sea-ice retreat. *Nature* 509:479–482.
- Bliss, L. C. 1958. Seed germination in arctic and alpine species. *Arctic* 11:180–188.
- Bliss, L. C. 1971. Arctic and alpine plant life cycles. *Annual Review of Ecology and Systematics* 2:405–438.
- Blok, D., M. M. P. D. Heijmans, G. Schaepman-Strub, A. V. Kononov, T. C. Maximov, and F. Berendse. 2010. Shrub expansion may reduce summer permafrost thaw in Siberian tundra. *Global Change Biology* 16:1296–1305.
- Boelman, N. T., L. Gough, J. R. McLaren, and H. Greaves. 2011. Does NDVI reflect variation in the structural attributes associated with increasing shrub dominance in arctic tundra? *Environmental Research Letters* 6:35501.
- Boggs, C. L., and D. W. Inouye. 2012. A single climate driver has direct and indirect effects on insect population dynamics. *Ecology Letters* 15:502–508.
- Bond, W. J., and J. J. Midgley. 2001. Ecology of sprouting in woody plants: The persistence niche. *Trends in Ecology & Evolution* 16:45–51.
- Bret-Harte, M. S., M. C. Mack, G. R. Shaver, D. C. Huebner, M. Johnston, C. A. Mojica, C. Pizano, and J. A. Reiskind. 2013. The response of Arctic vegetation and soils following



- an unusually severe tundra fire. *Philosophical Transactions of the Royal Society B: Biological Sciences* 368:20120490.
- Bret-Harte, M. S., G. R. Shaver, and F. S. Chapin. 2002. Primary and secondary stem growth in arctic shrubs: Implications for community response to environmental change. *Journal of Ecology* 90:251–267.
- Bret-Harte, M. S., G. R. Shaver, J. P. Zoerner, J. F. Johnstone, J. L. Wagner, A. S. Chavez, R. F. Gunkelman, S. C. Lippert, and J. A. Laundre. 2001. Developmental plasticity allows *Betula nana* to dominate tundra subjected to an altered environment. *Ecology* 82:18–32.
- Brutel-Vuilmet, C., M. Ménégoz, and G. Krinner. 2013. An analysis of present and future seasonal Northern Hemisphere land snow cover simulated by CMIP5 coupled climate models. *The Cryosphere* 7:67–80.
- Büntgen, U., L. Hellmann, W. Tegel, S. Normand, I. Myers-Smith, A. V. Kirilyanov, D. Nievergelt, and F. H. Schweingruber. 2014. Temperature-induced recruitment pulses of Arctic dwarf shrub communities. *Journal of Ecology* 103:489–501.
- Cahoon, S. M. P., P. F. Sullivan, G. R. Shaver, J. M. Welker, and E. Post. 2012. Interactions among shrub cover and the soil microclimate may determine future Arctic carbon budgets. *Ecology Letters* 15:1415–1422.
- Callaghan, T. V., M. Johansson, R. D. Brown, P. Y. Groisman, N. Labba, V. Radionov, R. S. Bradley, S. Blangy, O. N. Bulygina, T. R. Christensen, J. E. Colman, R. L. H. Essery, B. C. Forbes, M. C. Forchhammer, V. N. Golubev, R. E. Honrath, G. P. Juday, A. V. Meshcherskaya, G. K. Phoenix, J. Pomeroy, A. Rautio, D. A. Robinson, N. M. Schmidt, M. C. Serreze, V. P. Shevchenko, A. I. Shiklomanov, A. B. Shmakin, P. Sköld, M. Sturm, M. Woo, and E. F. Wood. 2011. Multiple effects of changes in Arctic snow cover. *AMBIO* 40:32–45.

- Campioli, M., L. E. Street, A. Michelsen, G. R. Shaver, T. Maere, R. Samson, and R. Lemeur. 2009. Determination of leaf area index, total foliar N, and normalized difference vegetation index for Arctic ecosystems dominated by *Cassiope tetragona*. *Arctic, Antarctic, and Alpine Research* 41:426–433.
- Cardinale, B. 2014. Overlooked local biodiversity loss. *Science* 344:1098–1098.
- Comiso, J. C. 2011. Large decadal decline of the Arctic multiyear ice cover. *Journal of Climate* 25:1176–1193.
- Cooper, E. J., I. G. Alsos, D. Hagen, F. M. Smith, S. J. Coulson, and I. D. Hodkinson. 2004. Plant recruitment in the High Arctic: Seed bank and seedling emergence on Svalbard. *Journal of Vegetation Science* 15:115.
- Cooper, E. J., S. Dullinger, and P. Semenchuk. 2011. Late snowmelt delays plant development and results in lower reproductive success in the High Arctic. *Plant Science* 180:157–167.
- Daniëls, F. J. A., and J. G. de Molenaar. 2011. Flora and vegetation of Tasiilaq, formerly Angmagssalik, Southeast Greenland: A comparison of data between around 1900 and 2007. *AMBIO* 40:650–659.
- Daniëls, F. J. A., J. G. de Molenaar, M. Chytrý, and L. Tichý. 2011. Vegetation change in Southeast Greenland? Tasiilaq revisited after 40 years. *Applied Vegetation Science* 14:230–241.
- Densmore, R., and J. Zasada. 1983. Seed dispersal and dormancy patterns in northern willows: ecological and evolutionary significance. *Canadian Journal of Botany* 61:3207–3216.
- Derksen, C., and R. Brown. 2012. Spring snow cover extent reductions in the 2008–2012 period exceeding climate model projections. *Geophysical Research Letters* 39:L19504.
- Dobrowski, S. Z. 2011. A climatic basis for microrefugia: The influence of terrain on climate. *Global Change Biology* 17:1022–1035.

- Dornelas, M., N. J. Gotelli, B. McGill, H. Shimadzu, F. Moyes, C. Sievers, and A. E. Magurran. 2014. Assemblage Time Series Reveal Biodiversity Change but Not Systematic Loss. *Science* 344:296–299.
- Dullinger, S., and K. Hülber. 2011. Experimental evaluation of seed limitation in alpine snowbed plants. *PLoS ONE* 6:e21537.
- Elmendorf, S. C., G. H. R. Henry, R. D. Hollister, R. G. Björk, A. D. Bjorkman, T. V. Callaghan, L. S. Collier, E. J. Cooper, J. H. C. Cornelissen, T. A. Day, A. M. Fosaa, W. A. Gould, J. Grétarsdóttir, J. Harte, L. Hermanutz, D. S. Hik, A. Hofgaard, F. Jarrad, I. S. Jónsdóttir, F. Keuper, K. Klanderud, J. A. Klein, S. Koh, G. Kudo, S. I. Lang, V. Loewen, J. L. May, J. Mercado, A. Michelsen, U. Molau, I. H. Myers-Smith, S. F. Oberbauer, S. Pieper, E. Post, C. Rixen, C. H. Robinson, N. M. Schmidt, G. R. Shaver, A. Stenström, A. Tolvanen, Ø. Totland, T. Troxler, C.-H. Wahren, P. J. Webber, J. M. Welker, and P. A. Wookey. 2012a. Global assessment of experimental climate warming on tundra vegetation: Heterogeneity over space and time. *Ecology Letters* 15:164–175.
- Elmendorf, S. C., G. H. R. Henry, R. D. Hollister, R. G. Björk, N. Boulanger-Lapointe, E. J. Cooper, J. H. C. Cornelissen, T. A. Day, E. Dorrepaal, T. G. Elumeeva, M. Gill, W. A. Gould, J. Harte, D. S. Hik, A. Hofgaard, D. R. Johnson, J. F. Johnstone, I. S. Jónsdóttir, J. C. Jorgenson, K. Klanderud, J. A. Klein, S. Koh, G. Kudo, M. Lara, E. Lévesque, B. Magnússon, J. L. May, J. A. Mercado-Díaz, A. Michelsen, U. Molau, I. H. Myers-Smith, S. F. Oberbauer, V. G. Onipchenko, C. Rixen, N. M. Schmidt, G. R. Shaver, M. J. Spasojevic, Þ. E. Þórhallsdóttir, A. Tolvanen, T. Troxler, C. E. Tweedie, S. Villareal, C.-H. Wahren, X. Walker, P. J. Webber, J. M. Welker, and S. Wipf. 2012b. Plot-scale evidence of tundra vegetation change and links to recent summer warming. *Nature Climate Change* 2:453–457.
- Elton, C. S. 1927. *Animal Ecology*. Macmillan, New York, NY, USA.

- Epstein, H. E., M. K. Reynolds, D. A. Walker, U. S. Bhatt, C. J. Tucker, and J. E. Pinzon. 2012. Dynamics of aboveground phytomass of the circumpolar Arctic tundra during the past three decades. *Environmental Research Letters* 7:15506.
- Eskelinen, A., and R. Virtanen. 2005. Local and regional processes in low-productive mountain plant communities: The roles of seed and microsite limitation in relation to grazing. *Oikos* 110:360–368.
- Euskirchen, E. S., M. S. Bret-Harte, G. J. Scott, C. Edgar, and G. R. Shaver. 2012. Seasonal patterns of carbon dioxide and water fluxes in three representative tundra ecosystems in northern Alaska. *Ecosphere* 3:1–19.
- Fenner, M., and K. Thompson. 2005. *The Ecology of Seeds*. Cambridge University Press, Cambridge, UK.
- Festa-Bianchet, M., J. c. Ray, S. Boutin, S. d. Côté, and A. Gunn. 2011. Conservation of caribou (*Rangifer tarandus*) in Canada: An uncertain future. *Canadian Journal of Zoology* 89:419–434.
- Field, C. B., D. B. Lobell, H. A. Peters, and N. R. Chiariello. 2007. Feedbacks of terrestrial ecosystems to climate change. *Annual Review of Environment and Resources* 32:1–29.
- Frost, G. V., and H. E. Epstein. 2014. Tall shrub and tree expansion in Siberian tundra ecotones since the 1960s. *Global Change Biology* 20:1264–1277.
- Frost, G. V., H. E. Epstein, D. A. Walker, G. Matyshak, and K. Ermokhina. 2013. Patterned-ground facilitates shrub expansion in Low Arctic tundra. *Environmental Research Letters* 8:15035.
- Galen, C., and M. L. Stanton. 1991. Consequences of emergence phenology for reproductive success in *Ranunculus adoneus* (Ranunculaceae). *American Journal of Botany* 78:978–988.

- Galen, C., and M. L. Stanton. 1993. Short-term responses of alpine buttercups to experimental manipulations of growing season length. *Ecology* 74:1052–1058.
- Galen, C., and M. L. Stanton. 1995. Responses of snowbed plant species to changes in growing-season length. *Ecology* 76:1546–1557.
- Gough, L., H. Bass, and J. R. McLaren. 2015. Effects of increased soil nutrients on seed rain: A role for seed dispersal in the greening of the Arctic? *Arctic, Antarctic, and Alpine Research* 47:27–34.
- Graae, B., R. Ejrnæs, S. Lang, E. Meineri, P. Ibarra, and H. Bruun. 2011. Strong microsite control of seedling recruitment in tundra. *Oecologia* 166:565–576.
- Graae, B. J., I. G. Alsos, and R. Ejrnaes. 2008. The impact of temperature regimes on development, dormancy breaking and germination of dwarf shrub seeds from arctic, alpine and boreal sites. *Plant Ecology* 198:275–284.
- Graae, B. J., R. Ejrnæs, F. L. Marchand, A. Milbau, A. Shevtsova, L. Beyens, and I. Nijs. 2009. The effect of an early-season short-term heat pulse on plant recruitment in the Arctic. *Polar Biology* 32:1117–1126.
- Grenfell, B. T., K. Wilson, B. F. Finkenstädt, T. N. Coulson, S. Murray, S. D. Albon, J. M. Pemberton, T. H. Clutton-Brock, and M. J. Crawley. 1998. Noise and determinism in synchronized sheep dynamics. *Nature* 394:674–677.
- Grinnell, J. 1917. The niche-relationships of the California thrasher. *The Auk* 34:427–433.
- Grubb, P. J. 1977. The maintenance of species-richness in plant communities: The importance of the regeneration niche. *Biological Reviews* 52:107–145.
- Gussarova, G., I. G. Alsos, and C. Brochmann. 2012. Annual plants colonizing the Arctic? Phylogeography and genetic variation in the *Euphrasia minima* complex (Orobanchaceae). *Taxon* 61:146–160.

- Hansen, B. B., V. Grøtan, R. Aanes, B.-E. Sæther, A. Stien, E. Fuglei, R. A. Ims, N. G. Yoccoz, and Å. Ø. Pedersen. 2013. Climate events synchronize the dynamics of a resident vertebrate community in the High Arctic. *Science* 339:313–315.
- Hedhly, A., J. I. Hormaza, and M. Herrero. 2009. Global warming and sexual plant reproduction. *Trends in Plant Science* 14:30–36.
- Herben, T., B. Šerá, and J. Klimešová. 2015. Clonal growth and sexual reproduction: Tradeoffs and environmental constraints. *Oikos* 124:469–476.
- Hoyle, G. L., S. E. Venn, K. J. Steadman, R. B. Good, E. J. McAuliffe, E. R. Williams, and A. B. Nicotra. 2013. Soil warming increases plant species richness but decreases germination from the alpine soil seed bank. *Global Change Biology* 19:1549–1561.
- Hudson, J. M. G., G. H. R. Henry, and W. K. Cornwell. 2011. Taller and larger: Shifts in Arctic tundra leaf traits after 16 years of experimental warming. *Global Change Biology* 17:1013–1021.
- Hutchinson, G. E. 1957. Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology* 22:415–427.
- Inouye, D. W. 2000. The ecological and evolutionary significance of frost in the context of climate change. *Ecology Letters* 3:457–463.
- Inouye, D. W. 2008. Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology* 89:353–362.
- IPCC, 2013: *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.* Stocker, T. F., D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, and P. M. Midgley, editors. 1535 pages. Cambridge University Press, Cambridge, UK and New York, NY, USA.

- Jia, G. J., H. E. Epstein, and D. A. Walker. 2009. Vegetation greening in the Canadian Arctic related to decadal warming. *Journal of Environmental Monitoring* 11:2231–2238.
- Johnson, R. H. 1910. *Determinate evolution in the color-pattern of the lady-beetles*. Carnegie Institution of Washington, Washington, D.C., USA.
- Jónsdóttir, I. S. 2011. Diversity of plant life histories in the Arctic. *Preslia* 83:281–300.
- Klimeš, L. 2008. Clonal splitters and integrators in harsh environments of the Trans-Himalaya. *Evolutionary Ecology* 22:351–367.
- Kudo, G. 1991. Effects of snow-free period on the phenology of alpine plants inhabiting snow patches. *Arctic and Alpine Research* 23:436–443.
- Lacey, E. P., and D. Herr. 2000. Parental effects in *Plantago lanceolata* L. III. Measuring parental temperature effects in the field. *Evolution* 54:1207–1217.
- Lang, S. I., J. H. C. Cornelissen, G. R. Shaver, M. Ahrens, T. V. Callaghan, U. Molau, C. J. F. Ter Braak, A. Hölzer, and R. Aerts. 2012. Arctic warming on two continents has consistent negative effects on lichen diversity and mixed effects on bryophyte diversity. *Global Change Biology* 18:1096–1107.
- Lantz, T. C., S. V. Kokelj, S. E. Gergel, and G. H. R. Henry. 2009. Relative impacts of disturbance and temperature: Persistent changes in microenvironment and vegetation in retrogressive thaw slumps. *Global Change Biology* 15:1664–1675.
- Lenoir, J., B. J. Graae, P. A. Aarrestad, I. G. Alsos, W. S. Armbruster, G. Austrheim, C. Bergendorff, H. J. B. Birks, K. A. Bråthen, J. Brunet, H. H. Bruun, C. J. Dahlberg, G. Decocq, M. Diekmann, M. Dynesius, R. Ejrnæs, J.-A. Grytnes, K. Hylander, K. Klanderud, M. Luoto, A. Milbau, M. Moora, B. Nygaard, A. Odland, V. T. Ravolainen, S. Reinhardt, S. M. Sandvik, F. H. Schei, J. D. M. Speed, L. U. Tveraabak, V. Vandvik, L. G. Velle, R. Virtanen, M. Zobel, and J.-C. Svenning. 2013. Local temperatures

- inferred from plant communities suggest strong spatial buffering of climate warming across Northern Europe. *Global Change Biology* 19:1470–1481.
- Macias-Fauria, M., B. C. Forbes, P. Zetterberg, and T. Kumpula. 2012. Eurasian Arctic greening reveals teleconnections and the potential for structurally novel ecosystems. *Nature Climate Change* 2:613–618.
- McInerny, G. J., and R. S. Etienne. 2012a. Ditch the niche – is the niche a useful concept in ecology or species distribution modelling? *Journal of Biogeography* 39:2096–2102.
- McInerny, G. J., and R. S. Etienne. 2012b. Pitch the niche – taking responsibility for the concepts we use in ecology and species distribution modelling. *Journal of Biogeography* 39:2112–2118.
- McInerny, G. J., and R. S. Etienne. 2012c. Stitch the niche – a practical philosophy and visual schematic for the niche concept. *Journal of Biogeography* 39:2103–2111.
- McManus, K. M., D. C. Morton, J. G. Masek, D. Wang, J. O. Sexton, J. R. Nagol, P. Ropars, and S. Boudreau. 2012. Satellite-based evidence for shrub and graminoid tundra expansion in northern Quebec from 1986 to 2010. *Global Change Biology* 18:2313–2323.
- Milbau, A., B. J. Graae, A. Shevtsova, and I. Nijs. 2009. Effects of a warmer climate on seed germination in the subarctic. *Annals of Botany* 104:287–296.
- Molau, U., and G. R. Shaver. 1997. Controls on seed production and seed germinability in *Eriophorum vaginatum*. *Global Change Biology* 3:80–88.
- Moles, A. T., and M. Westoby. 2006. Seed size and plant strategy across the whole life cycle. *Oikos* 113:91–105.
- Mondoni, A., G. Rossi, S. Orsenigo, and R. J. Probert. 2012. Climate warming could shift the timing of seed germination in alpine plants. *Annals of Botany* 110:155–164.



- Moulton, C. A., and L. Gough. 2011. Effects of soil nutrient availability on the role of sexual reproduction in an Alaskan tundra plant community. *Arctic, Antarctic, and Alpine Research* 43:612–620.
- Müller, E., E. J. Cooper, and I. G. Alsos. 2011. Germinability of arctic plants is high in perceived optimal conditions but low in the field. *Botany* 89:337–348.
- Myers-Smith, I. H., B. C. Forbes, M. Wilmking, M. Hallinger, T. Lantz, D. Blok, K. D. Tape, M. Macias-Fauria, U. Sass-Klaassen, E. Lévesque, S. Boudreau, P. Ropars, L. Hermanutz, A. Trant, L. S. Collier, S. Weijers, J. Rozema, S. A. Rayback, N. M. Schmidt, G. Schaepman-Strub, S. Wipf, C. Rixen, C. B. Ménard, S. Venn, S. Goetz, L. Andreu-Hayles, S. Elmendorf, V. Ravolainen, J. Welker, P. Grogan, H. E. Epstein, and D. S. Hik. 2011. Shrub expansion in tundra ecosystems: Dynamics, impacts and research priorities. *Environmental Research Letters* 6:45509.
- Myers-Smith, I. H., and D. S. Hik. 2013. Shrub canopies influence soil temperatures but not nutrient dynamics: An experimental test of tundra snow-shrub interactions. *Ecology and Evolution* 3:3683–3700.
- Naito, A. T., and D. M. Cairns. 2011a. Patterns and processes of global shrub expansion. *Progress in Physical Geography* 35:423–442.
- Naito, A. T., and D. M. Cairns. 2011b. Relationships between Arctic shrub dynamics and topographically derived hydrologic characteristics. *Environmental Research Letters* 6:45506.
- Olofsson, J., M. te Beest, and L. Ericson. 2013. Complex biotic interactions drive long-term vegetation dynamics in a subarctic ecosystem. *Philosophical Transactions of the Royal Society B: Biological Sciences* 368.
- Ooi, M. K. J. 2012. Seed bank persistence and climate change. *Seed Science Research* 22:S53–S60.

- Osterkamp, T. E. 2007. Characteristics of the recent warming of permafrost in Alaska. *Journal of Geophysical Research: Earth Surface* 112:F02S02.
- Pajunen, A. m., J. Oksanen, and R. Virtanen. 2011. Impact of shrub canopies on understorey vegetation in western Eurasian tundra. *Journal of Vegetation Science* 22:837–846.
- Pajunen, A., R. Virtanen, and H. Roininen. 2012. Browsing-mediated shrub canopy changes drive composition and species richness in forest-tundra ecosystems. *Oikos* 121:1544–1552.
- Philipp, M., J. Böcher, O. Mattsson, and S. R. J. Woodell. 1990. A quantitative approach to the sexual reproductive biology and population structure in some arctic flowering plants: *Dryas integrifolia*, *Silene acaulis* and *Ranunculus nivalis*. *Meddelelser om Grønland, Bioscience* 34:3–60.
- Post, E., and M. C. Forchhammer. 2002. Synchronization of animal population dynamics by large-scale climate. *Nature* 420:168–171.
- Post, E., M. C. Forchhammer, M. S. Bret-Harte, T. V. Callaghan, T. R. Christensen, B. Elberling, A. D. Fox, O. Gilg, D. S. Hik, T. T. Hoye, R. A. Ims, E. Jeppesen, D. R. Klein, J. Madsen, A. D. McGuire, S. Rysgaard, D. E. Schindler, I. Stirling, M. P. Tamstorf, N. J. C. Tyler, R. van der Wal, J. Welker, P. A. Wookey, N. M. Schmidt, and P. Aastrup. 2009. Ecological dynamics across the Arctic associated with recent climate change. *Science* 325:1355–1358.
- Ropars, P., and S. Boudreau. 2012. Shrub expansion at the forest–tundra ecotone: Spatial heterogeneity linked to local topography. *Environmental Research Letters* 7:15501.
- le Roux, P. C., R. Virtanen, R. K. Heikkinen, and M. Luoto. 2012. Biotic interactions affect the elevational ranges of high-latitude plant species. *Ecography* 35:1048–1056.
- Rowland, J. C., C. E. Jones, G. Altmann, R. Bryan, B. T. Crosby, L. D. Hinzman, D. L. Kane, D. M. Lawrence, A. Mancino, P. Marsh, J. P. McNamara, V. E. Romanvosky, H. Toniolo, B. J. Travis, E. Trochim, C. J. Wilson, and G. L. Geernaert. 2010. Arctic landscapes in

- transition: Responses to thawing permafrost. *Eos, Transactions American Geophysical Union* 91:229–230.
- Sandvik, S. M., E. Heegaard, R. Elven, and V. Vandvik. 2004. Responses of alpine snowbed vegetation to long-term experimental warming. *Ecoscience* 11:150–159.
- Scherrer, D., and C. Körner. 2010. Infra-red thermometry of alpine landscapes challenges climatic warming projections. *Global Change Biology* 16:2602–2613.
- Schuur, E. A. G., K. G. Crummer, J. G. Vogel, and M. C. Mack. 2007. Plant species composition and productivity following permafrost thaw and thermokarst in Alaskan tundra. *Ecosystems* 10:280–292.
- Screen, J. A., and I. Simmonds. 2010. The central role of diminishing sea ice in recent Arctic temperature amplification. *Nature* 464:1334–1337.
- Serreze, M. C., and R. G. Barry. 2011. Processes and impacts of Arctic amplification: A research synthesis. *Global and Planetary Change* 77:85–96.
- Serreze, M. C., and J. A. Francis. 2006. The Arctic amplification debate. *Climatic Change* 76:241–264.
- Shepherd, A., E. R. Ivins, G. A. V. R. Barletta, M. J. Bentley, S. Bettadpur, K. H. Briggs, D. H. Bromwich, R. Forsberg, N. Galin, M. Horwath, S. Jacobs, I. Joughin, M. A. King, J. T. M. Lenaerts, J. Li, S. R. M. Ligtenberg, A. Luckman, S. B. Luthcke, M. McMillan, R. Meister, G. Milne, J. Mouginot, A. Muir, J. P. Nicolas, J. Paden, A. J. Payne, H. Pritchard, E. Rignot, H. Rott, L. S. Sørensen, T. A. Scambos, B. Scheuchl, E. J. O. Schrama, B. Smith, A. V. Sundal, J. H. van Angelen, W. J. van de Berg, M. R. van den Broeke, D. G. Vaughan, I. Velicogna, J. Wahr, P. L. Whitehouse, D. J. Wingham, D. Yi, D. Young, and H. J. Zwally. 2012. A reconciled estimate of ice-sheet mass balance. *Science* 338:1183–1189.

- Shevtsova, A., B. J. Graae, T. Jochum, A. Milbau, F. Kockelbergh, L. Beyens, and I. Nijs. 2009. Critical periods for impact of climate warming on early seedling establishment in subarctic tundra. *Global Change Biology* 15:2662–2680.
- Stendel, M., J. H. Christensen, and D. Petersen. 2008. Arctic climate and climate change with a focus on Greenland. Pages 13–43 *in* H. Meltofte, T. R. Christensen, B. Elberling, M. C. Forchhammer, and M. Rasch, editors. *High-Arctic Ecosystem Dynamics in a Changing Climate*. Academic Press, London, UK.
- Stroeve, J. C., M. C. Serreze, M. M. Holland, J. E. Kay, J. Malanik, and A. P. Barrett. 2011. The Arctic's rapidly shrinking sea ice cover: A research synthesis. *Climatic Change* 110:1005–1027.
- Sturm, M., T. Douglas, C. Racine, and G. E. Liston. 2005a. Changing snow and shrub conditions affect albedo with global implications. *Journal of Geophysical Research* 110:G01004.
- Sturm, M., J. P. McFadden, G. E. Liston, F. S. Chapin III, C. H. Racine, and J. Holmgren. 2001a. Snow-shrub interactions in arctic tundra: A hypothesis with climatic implications. *Journal of Climate* 14:336.
- Sturm, M., C. Racine, and K. Tape. 2001b. Climate change: Increasing shrub abundance in the Arctic. *Nature* 411:546–547.
- Sturm, M., J. Schimel, G. Michaelson, V. E. Romanovsky, J. M. Welker, S. F. Oberbauer, G. E. Liston, and J. Fahnestock. 2005b. Winter biological processes could help convert arctic tundra to shrubland. *BioScience* 55:17–26.
- Tape, K. D., M. Hallinger, J. M. Welker, and R. W. Ruess. 2012. Landscape heterogeneity of shrub expansion in Arctic Alaska. *Ecosystems* 15:711–724.
- Tape, K., M. Sturm, and C. Racine. 2006. The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. *Global Change Biology* 12:686–702.

- Tremblay, B., E. Lévesque, and S. Boudreau. 2012. Recent expansion of erect shrubs in the Low Arctic: Evidence from Eastern Nunavik. *Environmental Research Letters* 7:35501.
- Vallejo-Marín, M., M. E. Dorken, and S. C. H. Barrett. 2010. The ecological and evolutionary consequences of clonality for plant mating. *Annual Review of Ecology, Evolution, and Systematics* 41:193–213.
- Vankoughnett, M., and P. Grogan. 2014. Nitrogen isotope tracer acquisition in low and tall birch tundra plant communities: A 2 year test of the snow-shrub hypothesis. *Biogeochemistry* 118:291–306.
- Vellend, M., L. Baeten, I. H. Myers-Smith, S. C. Elmendorf, R. Beauséjour, C. D. Brown, P. D. Frenne, K. Verheyen, and S. Wipf. 2013. Global meta-analysis reveals no net change in local-scale plant biodiversity over time. *Proceedings of the National Academy of Sciences* 110:19456–19459.
- Verbyla, D. 2008. The greening and browning of Alaska based on 1982–2003 satellite data. *Global Ecology and Biogeography* 17:547–555.
- Vihma, T. 2014. Effects of Arctic sea ice decline on weather and climate: A review. *Surveys in Geophysics* 35:1175–1214.
- Virtanen, R., H. Henttonen, and K. Laine. 1997. Lemming grazing and structure of a snowbed plant community: A long-term experiment at Kilpisjärvi, Finnish Lapland. *Oikos* 79:155–166.
- Vors, L. S., and M. S. Boyce. 2009. Global declines of caribou and reindeer. *Global Change Biology* 15:2626–2633.
- Wagner, J., U. Ladinig, G. Steinacher, and I. Larl. 2012. From the flower bud to the mature seed: Timing and dynamics of flower and seed development in high-mountain plants. Pages 135–152 *in* C. Lütz, editor. *Plants in Alpine Regions*. Springer, Vienna, Austria.

- Wahren, C.-H. A., M. D. Walker, and M. S. Bret-Harte. 2005. Vegetation responses in Alaskan arctic tundra after 8 years of a summer warming and winter snow manipulation experiment. *Global Change Biology* 11:537–552.
- Walck, J. L., S. N. Hidayati, K. W. Dixon, K. Thompson, and P. Poschlod. 2011. Climate change and plant regeneration from seed. *Global Change Biology* 17:2145–2161.
- Walker, D. A., H. E. Epstein, G. J. Jia, A. Balsler, C. Copass, E. J. Edwards, W. A. Gould, J. Hollingsworth, J. Knudson, H. A. Maier, A. Moody, and M. K. Raynolds. 2003. Phytomass, LAI, and NDVI in northern Alaska: Relationships to summer warmth, soil pH, plant functional types, and extrapolation to the circumpolar Arctic. *Journal of Geophysical Research: Atmospheres* 108:8169.
- Walker, D. A., H. E. Epstein, M. K. Raynolds, P. Kuss, M. A. Kopecky, G. V. Frost, F. J. A. Daniëls, M. O. Leibman, N. G. Moskalenko, G. V. Matyshak, O. V. Khitun, A. V. Khomutov, B. C. Forbes, U. S. Bhatt, A. N. Kade, C. M. Vonlanthen, and L. Tichý. 2012. Environment, vegetation and greenness (NDVI) along the North America and Eurasia Arctic transects. *Environmental Research Letters* 7:15504.
- Walker, M. D., C. H. Wahren, R. D. Hollister, G. H. R. Henry, L. E. Ahlquist, J. M. Alatalo, M. S. Bret-Harte, M. P. Calef, T. V. Callaghan, A. B. Carroll, H. E. Epstein, I. S. Jónsdóttir, J. A. Klein, B. Magnússon, U. Molau, S. F. Oberbauer, S. P. Rewa, C. H. Robinson, G. R. Shaver, K. N. Suding, C. C. Thompson, A. Tolvanen, Ø. Totland, P. L. Turner, C. E. Tweedie, P. J. Webber, and P. A. Wookey. 2006. Plant community responses to experimental warming across the tundra biome. *Proceedings of the National Academy of Sciences of the United States of America* 103:1342–1346.
- Weintraub, M. N., and J. P. Schimel. 2005. Nitrogen cycling and the spread of shrubs control changes in the carbon balance of Arctic tundra ecosystems. *BioScience* 55:408–415.

- Winkler, E., and M. Fischer. 2002. The role of vegetative spread and seed dispersal for optimal life histories of clonal plants: a simulation study. *Evolutionary Ecology* 15:281–301.
- de Witte, L. C., G. F. J. Armbruster, L. Gielly, P. Taberlet, and J. Stöcklin. 2012. AFLP markers reveal high clonal diversity and extreme longevity in four key arctic-alpine species. *Molecular Ecology* 21:1081–1097.
- Zamin, T. J., and P. Grogan. 2012. Birch shrub growth in the low Arctic: The relative importance of experimental warming, enhanced nutrient availability, snow depth and caribou exclusion. *Environmental Research Letters* 7:34027.
- Zamin, T. J., and P. Grogan. 2013. Caribou exclusion during a population low increases deciduous and evergreen shrub species biomass and nitrogen pools in low Arctic tundra. *Journal of Ecology* 101:671–683.

Annual J-D 1986-2015      L-OTI(°C) Anomaly vs 1951-1980      0.51

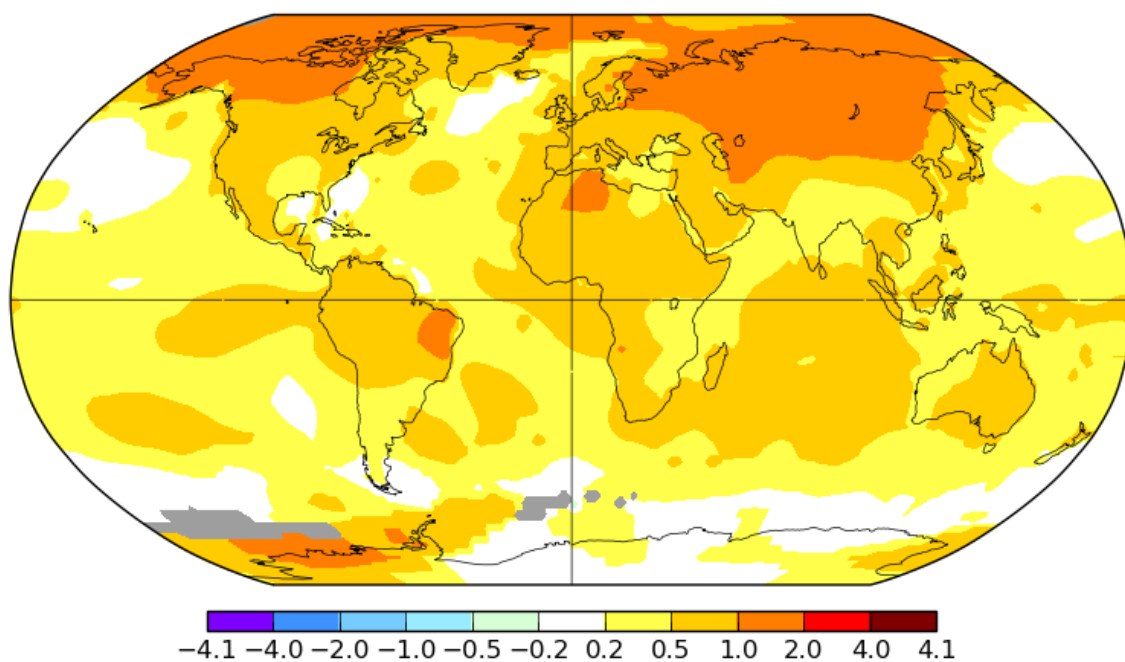


Figure 1.1. 1986-2015 temperature anomaly relative to the 1951-1980 climate normal. Map created using GISTEMP on the NASA Goddard Institute for Space Studies web-based tool (<http://data.giss.nasa.gov/gistemp/>).



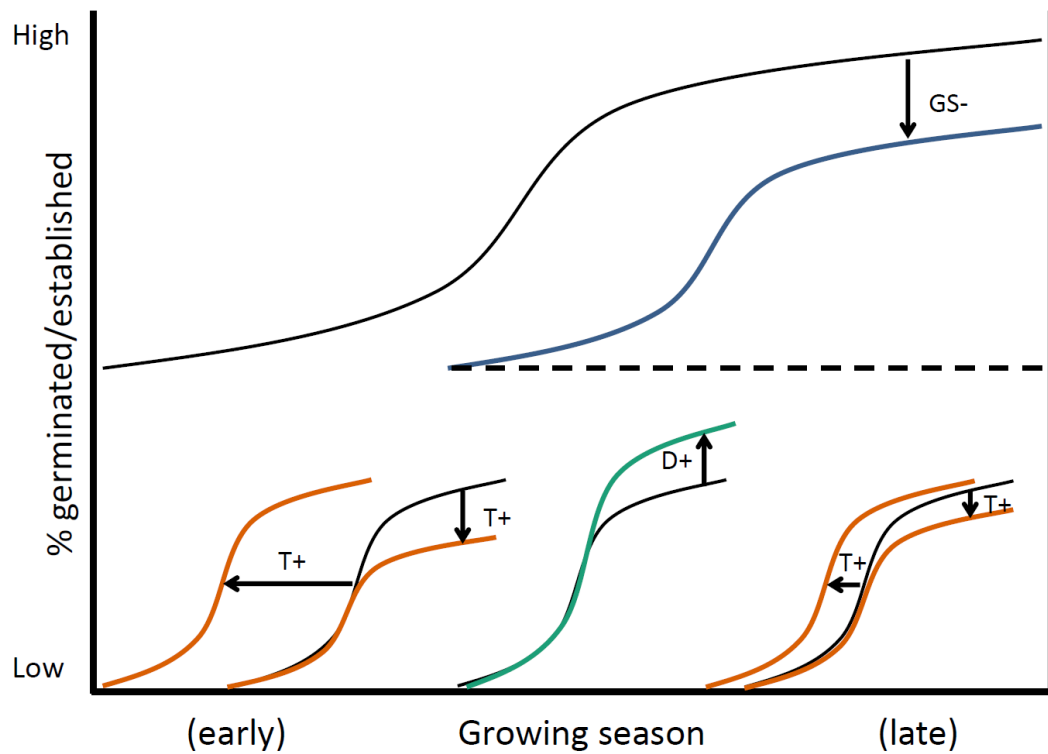


Figure 1.2. Summary of how changes in or during the growing season affect seed germination (G) and seedling establishment (E). Increases in temperature (T+) can lead to advancement in the timing of G and E as well as declines in the cumulative total G and E. These changes occur primarily in early- rather 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<sup>1</sup>

#### 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,

---

<sup>1</sup> To be submitted to *Climate Change Responses*

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 CO<sub>2</sub> 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. 2008, 2009, 2011, Milbau et al. 2009, Shevtsova et al. 2009). Where such information has been 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 species (Molau 1993). 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 hexagones (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:

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

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:

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

in which the outcome is the proportion of the number of seeds that germinated,  $Y_{ij}^{germ}$ , out of the total number of seeds in the cohort for each sample,  $Y_{ij}^{cohort}$ . 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<sub>5</sub>) from May 1 through August 18 were



454.4, 282.6, and 372.5. Not only did 2013 have fewer GDD<sub>5</sub> 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 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 with 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.

### References

- Alsos, I. G., S. Spjelhøvik, and T. Engelsen. 2003. Seed bank size and composition of *Betula nana*, *Vaccinium uliginosum*, and *Campanula rotundifolia* habitats in Svalbard and northern Norway. *Canadian Journal of Botany* 81:220.
- Arft, A. M., M. D. Walker, J. Gurevitch, J. M. Alatalo, M. S. Bret-Harte, M. Dale, M. Diemer, F. Gugerli, G. H. R. Henry, M. H. Jones, R. D. Hollister, I. S. Jónsdóttir, K. Laine, E. Lévesque, G. M. Marion, U. Molau, P. Mølgaard, U. Nordenhäll, V. Raszhivin, C. H. Robinson, G. Starr, A. Stenström, M. Stenström, Ø. Totland, P. L. Turner, L. J. Walker,

- P. J. Webber, J. M. Welker, and P. A. Wookey. 1999. Responses of tundra plants to experimental warming: Meta-analysis of the International Tundra Experiment. *Ecological Monographs* 69:491–511.
- Baskin, C. C., and J. M. Baskin. 1998. *Seeds: Ecology, biogeography, and evolution of dormancy and germination*. Academic Press, San Diego, CA, USA.
- Baskin, C. C., O. Zackrisson, and J. M. Baskin. 2002. Role of warm stratification in promoting germination of seeds of *Empetrum hermaphroditum* (Empetraceae), a circumboreal species with a stony endocarp. *American Journal of Botany* 89:486–493.
- Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:48.
- Beckman, N. G., R. Dybzinski, and G. D. Tilman. 2013. Neighborhoods have little effect on fungal attack or insect predation of developing seeds in a grassland biodiversity experiment. *Oecologia* 174:521–532.
- Billings, W. D. 1987. Constraints to plant growth, reproduction, and establishment in arctic environments. *Arctic and Alpine Research* 19:357–365.
- Bliss, L. C. 1958. Seed germination in arctic and alpine species. *Arctic* 11:180–188.
- Bliss, L. C. 1971. Arctic and alpine plant life cycles. *Annual Review of Ecology and Systematics* 2:405–438.
- Blok, D., U. Sass-Klaassen, G. Schaepman-Strub, M. M. P. D. Heijmans, P. Sauren, and F. Berendse. 2011. What are the main climate drivers for shrub growth in northeastern Siberian tundra? *Biogeosciences Discuss.* 8:771–799.
- Bret-Harte, M. S., G. R. Shaver, and F. S. Chapin. 2002. Primary and secondary stem growth in arctic shrubs: Implications for community response to environmental change. *Journal of Ecology* 90:251–267.



- Briske, D. D., and J. D. Derner. 1998. Clonal biology of caespitose grasses. Pages 106–135 in G. P. Cheplick, editor. *Population Biology of Grasses*. Cambridge University Press, Cambridge, UK.
- Briske, D. D., and I. Noy-Meir. 1998. Plant responses to grazing: A comparative evaluation of annual and perennial grasses. Pages 13–26 in V. P. Papanastasis and D. Peter, editors. *Ecological Basis of Livestock Grazing in Mediterranean Ecosystems*. Official Publications of the European Communities, Luxembourg.
- Bykova, O., I. Chuine, X. Morin, and S. I. Higgins. 2012. Temperature dependence of the reproduction niche and its relevance for plant species distributions. *Journal of Biogeography* 39:2191–2200.
- Cappelen, J. 2013. Greenland - Danish Meteorological Institute historical climate data collection 1873-2012. Page 75. Danish Meteorological Institute, Copenhagen, Denmark.
- Chapin, F. S., M. S. Bret-Harte, S. E. Hobbie, and H. Zhong. 1996. Plant functional types as predictors of transient responses of arctic vegetation to global change. *Journal of Vegetation Science* 7:347–358.
- Cooper, E. J. 2006. Reindeer grazing reduces seed and propagule bank in the High Arctic. *Canadian Journal of Botany* 84:1740–1752.
- Cooper, E. J., I. G. Alsos, D. Hagen, F. M. Smith, S. J. Coulson, and I. D. Hodkinson. 2004. Plant recruitment in the High Arctic: Seed bank and seedling emergence on Svalbard. *Journal of Vegetation Science* 15:115.
- Diggle, P. K. 1997. Extreme preformation in alpine *Polygonum viviparum*: An architectural and developmental analysis. *American Journal of Botany* 84:154–169.
- Donohue, K., and J. Schmitt. 1998. Maternal environmental effects in plants: Adaptive plasticity? Pages 137–158 in T. Mousseau and C. Fox, editors. *Maternal Effects as Adaptations*. Oxford University Press, Oxford, UK.

- Dormann, C. F., and S. J. Woodin. 2002. Climate change in the Arctic: using plant functional types in a meta-analysis of field experiments. *Functional Ecology* 16:4–17.
- Douhovnikoff, V., G. R. Goldsmith, K. D. Tape, C. Huang, N. Sur, and M. S. Bret-Harte. 2010. Clonal diversity in an expanding community of arctic *Salix* spp. and a model for recruitment modes of arctic plants. *Arctic, Antarctic, and Alpine Research* 42:406–411.
- Elmendorf, S. C., G. H. R. Henry, R. D. Hollister, R. G. Björk, A. D. Bjorkman, T. V. Callaghan, L. S. Collier, E. J. Cooper, J. H. C. Cornelissen, T. A. Day, A. M. Fosaa, W. A. Gould, J. Grétarsdóttir, J. Harte, L. Hermanutz, D. S. Hik, A. Hofgaard, F. Jarrad, I. S. Jónsdóttir, F. Keuper, K. Klanderud, J. A. Klein, S. Koh, G. Kudo, S. I. Lang, V. Loewen, J. L. May, J. Mercado, A. Michelsen, U. Molau, I. H. Myers-Smith, S. F. Oberbauer, S. Pieper, E. Post, C. Rixen, C. H. Robinson, N. M. Schmidt, G. R. Shaver, A. Stenström, A. Tolvanen, Ø. Totland, T. Troxler, C.-H. Wahren, P. J. Webber, J. M. Welker, and P. A. Wookey. 2012. Global assessment of experimental climate warming on tundra vegetation: Heterogeneity over space and time. *Ecology Letters* 15:164–175.
- Eskelinen, A., and R. Virtanen. 2005. Local and regional processes in low-productive mountain plant communities: The roles of seed and microsite limitation in relation to grazing. *Oikos* 110:360–368.
- Fenner, M., and K. Thompson. 2005. *The Ecology of Seeds*. Cambridge University Press, Cambridge, UK.
- Fierer, N., and J. P. Schimel. 2002. Effects of drying–rewetting frequency on soil carbon and nitrogen transformations. *Soil Biology and Biochemistry* 34:777–787.
- Fournier, D. A., H. J. Skaug, J. Ancheta, J. Ianelli, A. Magnusson, M. N. Maunder, A. Nielsen, and J. Sibert. 2012. AD Model Builder: Using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. *Optimization Methods and Software* 27:233–249.

- Gabrielsen, T. M., and C. Brochmann. 1998. Sex after all: high levels of diversity detected in the arctic clonal plant *Saxifraga cernua* using RAPD markers. *Molecular Ecology* 7:1701–1708.
- Galen, C., and M. L. Stanton. 1991. Consequences of emergence phenology for reproductive success in *Ranunculus adoneus* (Ranunculaceae). *American Journal of Botany* 78:978–988.
- Germain, R. M., and B. Gilbert. 2014. Hidden responses to environmental variation: Maternal effects reveal species niche dimensions. *Ecology Letters* 17:662–669.
- Graae, B., R. Ejrnæs, S. Lang, E. Meineri, P. Ibarra, and H. Bruun. 2011. Strong microsite control of seedling recruitment in tundra. *Oecologia* 166:565–576.
- Graae, B. J., I. G. Alsos, and R. Ejrnaes. 2008. The impact of temperature regimes on development, dormancy breaking and germination of dwarf shrub seeds from arctic, alpine and boreal sites. *Plant Ecology* 198:275–284.
- Graae, B. J., R. Ejrnæs, F. L. Marchand, A. Milbau, A. Shevtsova, L. Beyens, and I. Nijs. 2009. The effect of an early-season short-term heat pulse on plant recruitment in the Arctic. *Polar Biology* 32:1117–1126.
- Graae, B., S. Pagh, and H. Bruun. 2004. An experimental evaluation of the arctic fox (*Alopex lagopus*) as a seed disperser. *Arctic, Antarctic, and Alpine Research* 36:468–473.
- Gremer, J. R., A. Sala, and E. E. Crone. 2010. Disappearing plants: Why they hide and how they return. *Ecology* 91:3407–3413.
- Grubb, P. J. 1977. The maintenance of species-richness in plant communities: The importance of the regeneration niche. *Biological Reviews* 52:107–145.
- Harper, J. L. 1977. *Population Biology of Plants*. Academic Press.
- Henry, G. H. R., and U. Molau. 1997. Tundra plants and climate change: The International Tundra Experiment (ITEX). *Global Change Biology* 3:1–9.

- Herben, T., B. Šerá, and J. Klimešová. 2015. Clonal growth and sexual reproduction: Tradeoffs and environmental constraints. *Oikos* 124:469–476.
- Hilbe, J. M. 2011. *Negative Binomial Regression*. Second edition. Cambridge University Press, New York, NY, USA.
- Hobbie, S. E., and F. S. Chapin. 1998. An experimental test of limits to tree establishment in Arctic tundra. *Journal of Ecology* 86:449–461.
- Hobbie, S. E., and L. Gough. 2004. Litter decomposition in moist acidic and non-acidic tundra with different glacial histories. *Oecologia* 140:113–124.
- Holm, S. 1979. A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics* 6:65–70.
- Inouye, D. W. 2008. Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology* 89:353–362.
- Klady, R. A., G. H. R. Henry, and V. Lemay. 2011. Changes in high arctic tundra plant reproduction in response to long-term experimental warming. *Global Change Biology* 17:1611–1624.
- Kudo, G., and A. Hirao. 2006. Habitat-specific responses in the flowering phenology and seed set of alpine plants to climate variation: implications for global-change impacts. *Population Ecology* 48:49–58.
- Kuijper, D. P. J., J. P. Bakker, E. J. Cooper, R. Ubels, I. S. Jónsdóttir, and M. J. J. E. Loonen. 2006. Intensive grazing by barnacle geese depletes High Arctic seed bank. *Canadian Journal of Botany* 84:995–1004.
- Lacey, E., S. Smith, and A. Case. 1997. Parental effects on seed mass: Seed coat but not embryo/endosperm effects. *American Journal of Botany* 84:1617–1617.
- Laine, K., E. Malila, and M. Siuruainen. 1995. How is annual climatic variation reflected in the production of germinable seeds of arctic and alpine plants in the northern Scandes? Pages

- 89–96. Global Change and Arctic Terrestrial Ecosystems. European Commission, Luxembourg.
- McGraw, J. B., and M. C. Vavrek. 1989. The role of buried viable seeds in arctic and alpine plant communities. Pages 91–105 in M. A. Leck, V. T. Parker, and R. L. Simpson, editors. Ecology of Soil Seed Banks. Elsevier, San Diego, CA, USA.
- Meineri, E., J. Spindelböck, and V. Vandvik. 2013. Seedling emergence responds to both seed source and recruitment site climates: A climate change experiment combining transplant and gradient approaches. *Plant Ecology* 214:607–619.
- Menzel, A., T. H. Sparks, N. Estrella, E. Koch, A. Aasa, R. Ahas, K. Alm-Kübler, P. Bissolli, O. 'ga Braslavská, A. Briede, F. M. Chmielewski, Z. Crepinsek, Y. Curnel, Å. Dahl, C. Defila, A. Donnelly, Y. Filella, K. Jatzak, F. Måge, A. Mestre, Ø. Nordli, J. Peñuelas, P. Pirinen, V. Remišová, H. Scheifinger, M. Striz, A. Susnik, A. J. H. Van Vliet, F.-E. Wielgolaski, S. Zach, and A. Zust. 2006. European phenological response to climate change matches the warming pattern. *Global Change Biology* 12:1969–1976.
- Milbau, A., B. J. Graae, A. Shevtsova, and I. Nijs. 2009. Effects of a warmer climate on seed germination in the subarctic. *Annals of Botany* 104:287–296.
- Molau, U. 1993. Relationships between flowering phenology and life history strategies in tundra plants. *Arctic and Alpine Research* 25:391–402.
- Molau, U., U. Nordenhäll, and B. Eriksen. 2005. Onset of flowering and climate variability in an alpine landscape: a 10-year study from Swedish Lapland. *American Journal of Botany* 92:422–431.
- Molau, U., and G. R. Shaver. 1997. Controls on seed production and seed germinability in *Eriophorum vaginatum*. *Global Change Biology* 3:80–88.
- Moles, A. T., and M. Westoby. 2004a. Seedling survival and seed size: a synthesis of the literature. *Journal of Ecology* 92:372–383.

- Moles, A. T., and M. Westoby. 2004b. What do seedlings die from and what are the implications for evolution of seed size? *Oikos* 106:193–199.
- Moulton, C. A., and L. Gough. 2011. Effects of soil nutrient availability on the role of sexual reproduction in an Alaskan tundra plant community. *Arctic, Antarctic, and Alpine Research* 43:612–620.
- Olofsson, J., and L. Oksanen. 2002. Role of litter decomposition for the increased primary production in areas heavily grazed by reindeer: A litterbag experiment. *Oikos* 96:507–515.
- Paradis, M., C. Mercier, and S. Boudreau. 2014. Response of *Betula glandulosa* seedlings to simulated increases in nutrient availability, temperature and precipitation in a lichen woodland at the forest–tundra ecotone. *Plant Ecology* 215:305–314.
- Pedersen, C. 2010, May. The response of arctic vegetation to climate warming in an ungulate grazing system. Doctoral dissertation, The Pennsylvania State University, University Park, Pennsylvania.
- Pedersen, C. B., and P. Aastrup. 2000. Muskoxen in Angujaartorfiup Nunaa, West Greenland: Monitoring, spatial distribution, population growth, and sustainable harvest. *Arctic* 53:18–26.
- Post, E. 2013. *Ecology of climate change: The importance of biotic interactions*. Princeton University Press, Princeton, NJ.
- Post, E., M. C. Forchhammer, N. C. Stenseth, and T. V. Callaghan. 2001. The timing of life–history events in a changing climate. *Proceedings of the Royal Society of London B: Biological Sciences* 268:15–23.
- Post, E. S., C. Pedersen, C. C. Wilmers, and M. C. Forchhammer. 2008. Phenological sequences reveal aggregate life history response to climatic warming. *Ecology* 89:363–370.

- R Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Sadras, V. O. 2007. Evolutionary aspects of the trade-off between seed size and number in crops. *Field Crops Research* 100:125–138.
- Sandvik, S. M. 2001. Somatic and demographic costs under different temperature regimes in the late-flowering alpine perennial herb *Saxifraga stellaris* (Saxifragaceae). *Oikos* 93:303–311.
- Shevtsova, A., B. J. Graae, T. Jochum, A. Milbau, F. Kockelbergh, L. Beyens, and I. Nijs. 2009. Critical periods for impact of climate warming on early seedling establishment in subarctic tundra. *Global Change Biology* 15:2662–2680.
- Silvertown, J. 1989. The paradox of seed size and adaptation. *Trends in Ecology & Evolution* 4:24–26.
- Skaug, H. J., D. A. Fournier, A. Nielsen, A. Magnusson, and B. Bolker. 2013. Generalized linear mixed models using AD Model Builder. R package version 0.7.4.
- Stamati, K., P. Hollingsworth, and J. Russell. 2007. Patterns of clonal diversity in three species of sub-arctic willow (*Salix lanata*, *Salix lapponum* and *Salix herbacea*). *Plant Systematics and Evolution* 269:75–88.
- Steltzer, H., R. A. Hufbauer, J. M. Welker, M. Casalis, P. F. Sullivan, and R. Chimner. 2008. Frequent sexual reproduction and high intraspecific variation in *Salix arctica*: Implications for a terrestrial feedback to climate change in the High Arctic. *Journal of Geophysical Research* 113:G03S10.
- Stendel, M., J. H. Christensen, and D. Petersen. 2008. Arctic climate and climate change with a focus on Greenland. Pages 13–43 in H. Meltofte, T. R. Christensen, B. Elberling, M. C. Forchhammer, and M. Rasch, editors. *High-Arctic Ecosystem Dynamics in a Changing Climate*. Academic Press, London, UK.

- Teller, B. J., C. Campbell, and K. Shea. 2014. Dispersal under duress: Can stress enhance the performance of a passively dispersed species? *Ecology* 95:2694–2698.
- Thing, H. 1984. Feeding ecology of the West Greenland caribou (*Rangifer tarandus groenlandicus*) in the Sisimiut-Kangerlussuaq region. *Danish Review of Game Biology* 12:1–52.
- Wager, H. G. 1938. Growth and survival of plants in the Arctic. *Journal of Ecology* 26:390–410.
- Wagner, J., U. Ladinig, G. Steinacher, and I. Larl. 2012. From the Flower Bud to the Mature Seed: Timing and Dynamics of Flower and Seed Development in High-Mountain Plants. Pages 135–152 in C. Lütz, editor. *Plants in Alpine Regions*. Springer, Vienna, Austria.
- Walck, J. L., S. N. Hidayati, K. W. Dixon, K. Thompson, and P. Poschlod. 2011. Climate change and plant regeneration from seed. *Global Change Biology* 17:2145–2161.
- Walker, D. A., M. K. Raynolds, F. J. A. Daniëls, E. Einarsson, A. Elvebakk, W. A. Gould, A. E. Katenin, S. S. Kholod, C. J. Markon, E. S. Melnikov, N. G. Moskalenko, S. S. Talbot, B. A. Yurtsev, and the other members of the CAVM Team. 2005. The Circumpolar Arctic vegetation map. *Journal of Vegetation Science* 16:267.
- Walker, M. D., C. H. Wahren, R. D. Hollister, G. H. R. Henry, L. E. Ahlquist, J. M. Alatalo, M. S. Bret-Harte, M. P. Calef, T. V. Callaghan, A. B. Carroll, H. E. Epstein, I. S. Jónsdóttir, J. A. Klein, B. Magnússon, U. Molau, S. F. Oberbauer, S. P. Rewa, C. H. Robinson, G. R. Shaver, K. N. Suding, C. C. Thompson, A. Tolvanen, Ø. Totland, P. L. Turner, C. E. Tweedie, P. J. Webber, and P. A. Wookey. 2006. Plant community responses to experimental warming across the tundra biome. *Proceedings of the National Academy of Sciences of the United States of America* 103:1342–1346.
- Welling, P., A. Tolvanen, and K. Laine. 2004. The Alpine Soil Seed Bank in Relation to Field Seedlings and Standing Vegetation in Subarctic Finland. *Arctic, Antarctic, and Alpine Research* 36:229–238.



- Wookey, P. A., A. N. Parsons, J. M. Welker, J. A. Potter, T. V. Callaghan, J. A. Lee, and M. C. Press. 1993. Comparative responses of phenology and reproductive development to simulated environmental change in sub-arctic and high arctic plants. *Oikos* 67:490–502.
- Wookey, P. A., C. H. Robinson, A. N. Parsons, J. M. Welker, M. C. Press, T. V. Callaghan, and J. A. Lee. 1995. Environmental constraints on the growth, photosynthesis and reproductive development of *Dryas octopetala* at a high Arctic polar semi-desert, Svalbard. *Oecologia* 102:478–489.

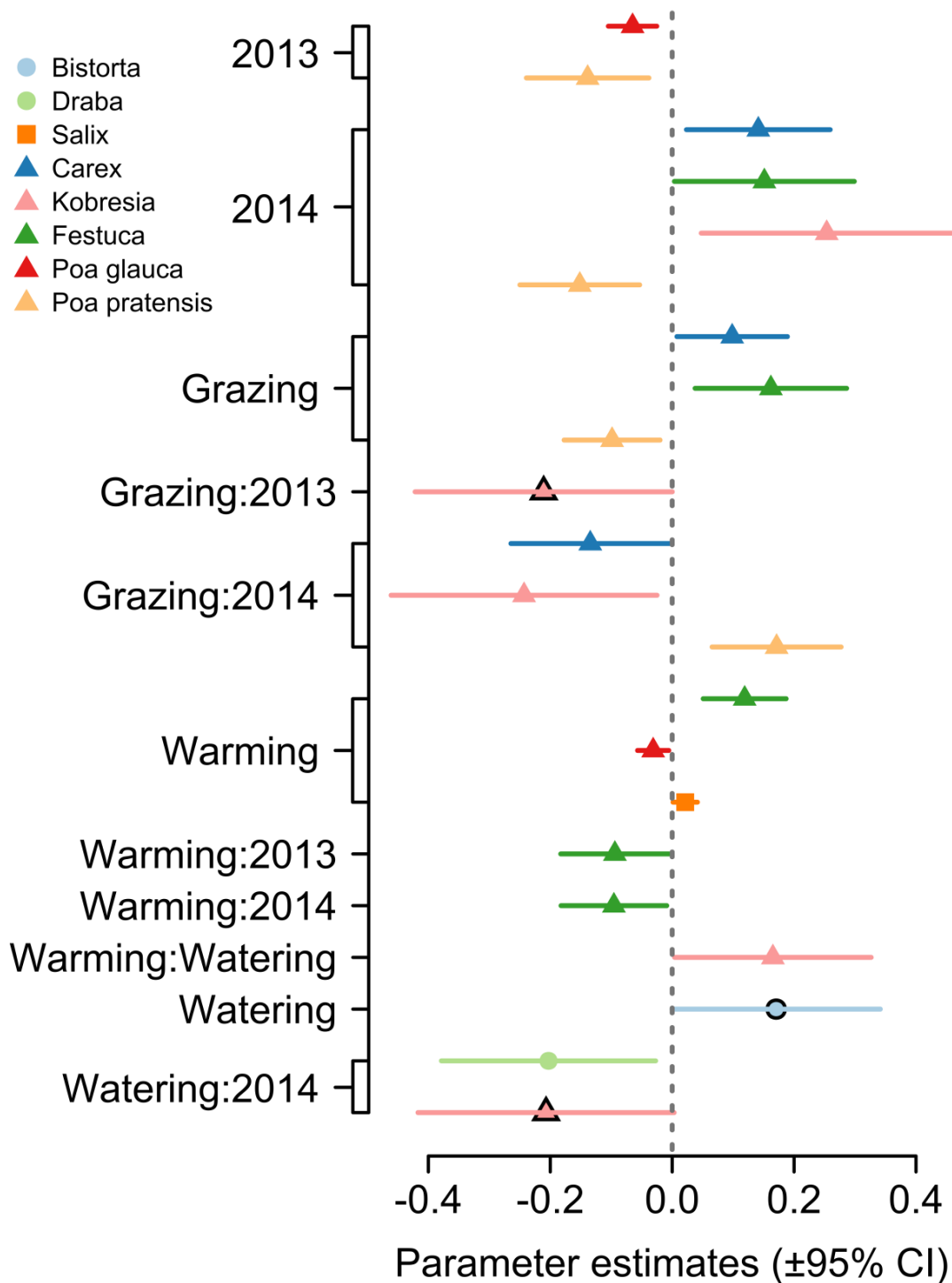


Figure 2.1. Parameter estimates for the effects of warming, watering, grazing and year on seed mass. A colon between factors indicates an interaction between two primary factors. Colors indicate species, while symbol represents plant functional type (circles are forbs, squares are deciduous shrubs, and triangles are graminoids). Symbols with black outlines indicate marginally significant effects after adjusting for familywise error rate ( $0.05 < P < 0.1$ ).

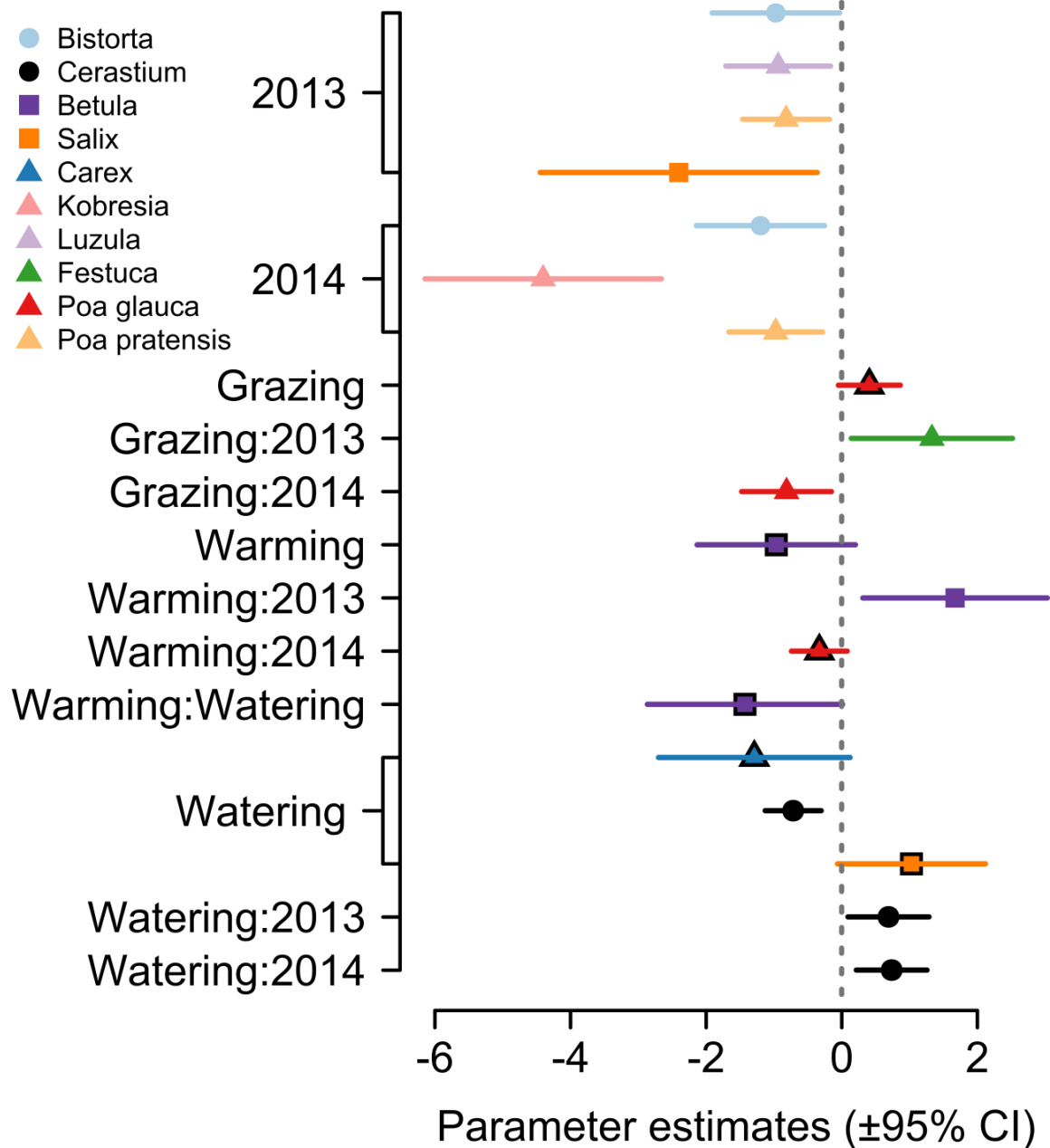


Figure 2.2. Parameter estimates for the effects of warming, watering, grazing and year on the proportion of germinated seeds. A colon between factors indicates an interaction between two primary factors. Colors indicate species, while symbol represents plant functional type (circles are forbs, squares are deciduous shrubs, and triangles are graminoids). Symbols with black outlines indicate marginally significant effects after adjusting for familywise error rate ( $0.05 < P < 0.1$ ).

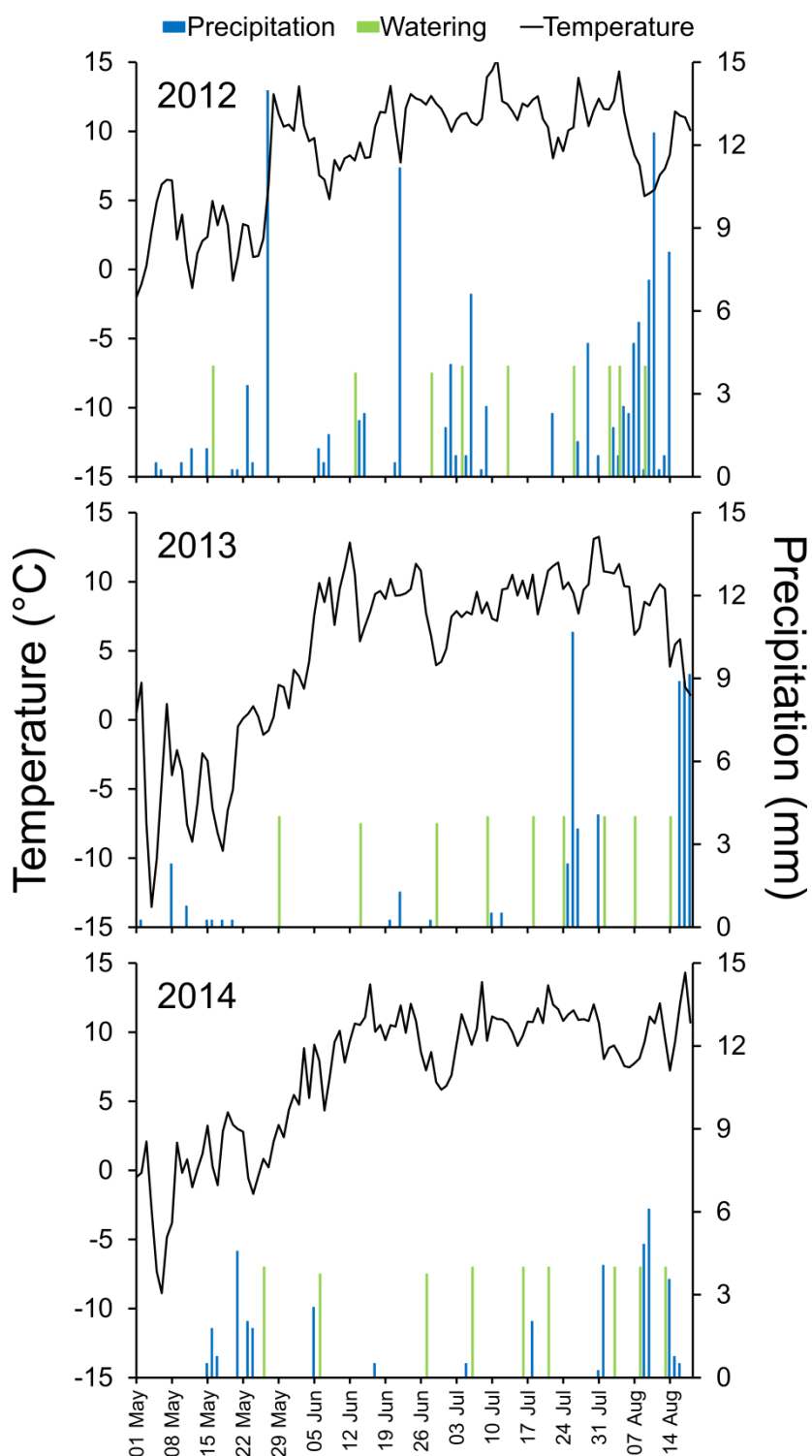


Figure 2.3. Environmental variables from a meteorological station measured throughout the growing season for each of 2012, 2013, and 2014. Black lines represent average daily air temperature ( $^{\circ}\text{C}$ ) measured at 2 m, and blue bars are total daily precipitation (mm). Green bars show dates 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.

Species	Treatment						Total
	Warmed			Ambient			
	Unwatered		Watered	Unwatered		Watered	
	Grazed	Exclosed	Grazed	Grazed	Exclosed	Grazed	
<i>Betula</i>	29	15	14	53	19	18	148
<i>Bistorta</i>	27	14	13	52	14	9	129
<i>Carex</i>	38	28	8	57	29	13	173
<i>Cerastium</i>	31	16	7	50	14	16	134
<i>Draba</i>	37	16	14	51	15	16	149
<i>Festuca</i>	44	12	18	67	8	17	166
<i>Kobresia</i>	16	6	6	28	6	9	71
<i>Luzula</i>	24	4	11	46	2	13	100
<i>Poa glauca</i>	33	21	14	56	20	16	160
<i>Poa pratensis</i>	33	18	15	48	18	12	144
<i>Potentilla</i>	--	--	--	58	--	32	90
<i>Salix</i>	25	15	29	59	15	40	183

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.

<b>Species</b>	<b>Site (variance)</b>	<b>NB2 dispersion (<math>\theta</math>)</b>
<i>Betula</i>	6.26E-09	0.869
<i>Bistorta</i>	1.03E-08	2.255
<i>Carex</i>	2.10E-07	0.707
<i>Cerastium</i>	1.84E-08	8.082
<i>Draba</i>	2.79E-02	1.455
<i>Festuca</i>	1.01E-08	1.559
<i>Kobresia</i>	7.23E-08	10.007
<i>Luzula</i>	2.09E-09	1.066
<i>P. glauca</i>	1.94E-02	2.899
<i>P. pratensis</i>	9.49E-02	1.399
<i>Potentilla</i>	3.00E-08	0.703
<i>Salix</i>	5.86E-09	0.400

### Chapter 3

## The recruitment and spread of an arctic deciduous shrub: Sexual recruitment or clonal growth?<sup>2</sup>

### 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.

---

<sup>2</sup> 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 CO<sub>2</sub>, 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

$$S_R = \sqrt[3]{\pi \left(\frac{D_b}{2}\right)^2 \times L_R} \quad [1]$$

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

$$S_G = \sqrt[3]{\pi(L_G \times W_G \times H_G)} \quad [2]$$

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  $\mu$ L 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  $\mu$ L 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 MgCl<sub>2</sub>, 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 (Duhovnikoff 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:

$$G_e = 1/\sum g_i^2 \quad [3]$$

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) (Duhovnikoff 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 3.3). 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 ( $\chi^2 = 0.663$ ,  $df = 4$ ,  $P = 0.412$ ).

### **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 statured 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

- Argus, G. W. 2004. A guide to the identification of *Salix* (willows) in Alaska, the Yukon Territory and adjacent regions. Ontario, Canada.
- Arnaud-Haond, S., C. M. Duarte, F. Alberto, and E. A. Serrão. 2007. Standardizing methods to address clonality in population studies. *Molecular Ecology* 16:5115–5139.
- Balloux, F., L. Lehmann, and T. de Meeûs. 2003. The population genetics of clonal and partially clonal diploids. *Genetics* 164:1635–1644.
- Barker, J. H. A., A. Pahlich, S. Trybush, K. J. Edwards, and A. Karp. 2003. Microsatellite markers for diverse *Salix* species. *Molecular Ecology Notes* 3:4–6.
- Barsoum, N. 2001. Relative contributions of sexual and asexual regeneration strategies in *Populus nigra* and *Salix alba* during the first years of establishment on a braided gravel bed river. *Evolutionary Ecology* 15:255–279.
- Bartoń, K. 2015. MuMIn: Multi-Model Inference, R package version 1.15.1.
- Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:48.
- Beck, P. S. A., and S. J. Goetz. 2011. Satellite observations of high northern latitude vegetation productivity changes between 1982 and 2008: Ecological variability and regional differences. *Environmental Research Letters* 6:45501.
- te Beest, M., J. J. L. Roux, D. M. Richardson, A. K. Brysting, J. Suda, M. Kubešová, and P. Pyšek. 2012. The more the better? The role of polyploidy in facilitating plant invasions. *Annals of Botany* 109:19–45.
- Bennike, O., and S. Björck. 2002. Chronology of the last recession of the Greenland Ice Sheet. *Journal of Quaternary Science* 17:211–219.

- Billings, W. D. 1987. Constraints to plant growth, reproduction, and establishment in arctic environments. *Arctic and Alpine Research* 19:357–365.
- Bishop, S. C., and F. S. Chapin. 1989. Establishment of *Salix alaxensis* on a gravel pad in Arctic Alaska. *Journal of Applied Ecology* 26:575–583.
- Bliss, L. C. 1956. A comparison of plant development in microenvironments of arctic and alpine tundras. *Ecological Monographs* 26:303–337.
- Bliss, L. C. 1971. Arctic and alpine plant life cycles. *Annual Review of Ecology and Systematics* 2:405–438.
- Blok, D., U. Sass-Klaassen, G. Schaepman-Strub, M. M. P. D. Heijmans, P. Sauren, and F. Berendse. 2011a. What are the main climate drivers for shrub growth in northeastern Siberian tundra? *Biogeosciences Discuss.* 8:771–799.
- Blok, D., G. Schaepman-Strub, H. Bartholomeus, M. M. P. D. Heijmans, T. C. Maximov, and F. Berendse. 2011b. The response of Arctic vegetation to the summer climate: Relation between shrub cover, NDVI, surface albedo and temperature. *Environmental Research Letters* 6:35502.
- Boelman, N. T., L. Gough, J. R. McLaren, and H. Greaves. 2011. Does NDVI reflect variation in the structural attributes associated with increasing shrub dominance in arctic tundra? *Environmental Research Letters* 6:35501.
- Boudreau, S., P. Ropars, and K. A. Harper. 2010. Population dynamics of *Empetrum hermaphroditum* (Ericaceae) on a subarctic sand dune: Evidence of rapid colonization through efficient sexual reproduction. *Am. J. Bot.* 97:770–781.
- Boulangeat, I., D. Georges, C. Dentant, R. Bonet, J. Van Es, S. Abdulhak, N. E. Zimmermann, and W. Thuiller. 2014. Anticipating the spatio-temporal response of plant diversity and vegetation structure to climate and land use change in a protected area. *Ecography* 37:1230–1239.

- Boulanger-Lapointe, N., E. Lévesque, S. Boudreau, G. H. R. Henry, and N. M. Schmidt. 2014. Population structure and dynamics of Arctic willow (*Salix arctica*) in the High Arctic. *Journal of Biogeography* 41:1967–1978.
- Bret-Harte, M. S., G. R. Shaver, and F. S. Chapin. 2002. Primary and secondary stem growth in arctic shrubs: Implications for community response to environmental change. *Journal of Ecology* 90:251–267.
- Bret-Harte, M. S., G. R. Shaver, J. P. Zoerner, J. F. Johnstone, J. L. Wagner, A. S. Chavez, R. F. Gunkelman, S. C. Lippert, and J. A. Laundre. 2001. Developmental plasticity allows *Betula nana* to dominate tundra subjected to an altered environment. *Ecology* 82:18–32.
- Budde, K. B., L. Gallo, P. Marchelli, E. Mosner, S. Liepelt, B. Ziegenhagen, and I. Leyer. 2011. Wide spread invasion without sexual reproduction? A case study on European willows in Patagonia, Argentina. *Biological Invasions* 13:45–54.
- Büntgen, U., L. Hellmann, W. Tegel, S. Normand, I. Myers-Smith, A. V. Kirilyanov, D. Nievergelt, and F. H. Schweingruber. 2014. Temperature-induced recruitment pulses of Arctic dwarf shrub communities. *Journal of Ecology* 103:489–501.
- Cain, M. L., B. G. Milligan, and A. E. Strand. 2000. Long-distance seed dispersal in plant populations. *American Journal of Botany* 87:1217–1227.
- Callaghan, T. V., S. Jonasson, and R. W. Brooker. 1997. Arctic clonal plants and global change. Pages 381–403 in J. Van Groenendael and H. de Kroon, editors. *The ecology and evolution of clonal plants*. Backhuys Publishers, Leiden.
- Cappelen, J. 2013. Greenland - Danish Meteorological Institute historical climate data collection 1873-2012. Page 75. Danish Meteorological Institute, Copenhagen, Denmark.
- Caraco, T., and C. K. Kelly. 1991. On the adaptive value of physiological integration in clonal plants. *Ecology* 72:81–93.

- Castro, S., J. Loureiro, C. Santos, M. Ater, G. Ayensa, and L. Navarro. 2007. Distribution of flower morphs, ploidy level and sexual reproduction of the invasive weed *Oxalis pes-caprae* in the western area of the Mediterranean region. *Annals of Botany* 99:507–517.
- Chapin, F. S., M. S. Bret-Harte, S. E. Hobbie, and H. Zhong. 1996. Plant functional types as predictors of transient responses of arctic vegetation to global change. *Journal of Vegetation Science* 7:347–358.
- Christie, K. S., J. P. Bryant, L. Gough, V. T. Ravolainen, R. W. Ruess, and K. D. Tape. 2015. The role of vertebrate herbivores in regulating shrub expansion in the Arctic: A synthesis. *BioScience* 65:1123–1133.
- Christie, K. S., R. W. Ruess, M. S. Lindberg, and C. P. Mulder. 2014. Herbivores influence the growth, reproduction, and morphology of a widespread arctic willow. *PLoS ONE* 9:e101716.
- Clark, J. S., M. Lewis, J. S. McLachlan, and J. HilleRisLambers. 2003. Estimating population spread: What can we forecast and how well? *Ecology* 84:1979–1988.
- Clark, L. V., and M. Jasieniuk. 2011. polysat: an R package for polyploid microsatellite analysis. *Molecular Ecology Resources* 11:562–566.
- Costa, J., V. Ferrero, J. Loureiro, M. Castro, L. Navarro, and S. Castro. 2014. Sexual reproduction of the pentaploid, short-styled *Oxalis pes-caprae* allows the production of viable offspring. *Plant Biology* 16:208–214.
- Densmore, R., and J. Zasada. 1983. Seed dispersal and dormancy patterns in northern willows: Ecological and evolutionary significance. *Canadian Journal of Botany* 61:3207–3216.
- Douhovnikoff, V., and R. S. Dodd. 2003. Intra-clonal variation and a similarity threshold for identification of clones: Application to *Salix exigua* using AFLP molecular markers. *TAG Theoretical and Applied Genetics* 106:1307–1315.

- Douhovnikoff, V., G. R. Goldsmith, K. D. Tape, C. Huang, N. Sur, and M. S. Bret-Harte. 2010. Clonal diversity in an expanding community of arctic *Salix* spp. and a model for recruitment modes of arctic plants. *Arctic, Antarctic, and Alpine Research* 42:406–411.
- Douhovnikoff, V., and E. L. G. Hazelton. 2014. Clonal growth: Invasion or stability? A comparative study of clonal architecture and diversity in native and introduced lineages of *Phragmites australis* (Poaceae). *American Journal of Botany* 101:1577–1584.
- Douhovnikoff, V., J. R. McBride, and R. S. Dodd. 2005. *Salix exigua* clonal growth and population dynamics in relation to disturbance regime variation. *Ecology* 86:446–452.
- Dudley, L., and C. Galen. 2007. Stage-dependent patterns of drought tolerance and gas exchange vary between sexes in the alpine willow, *Salix glauca*. *Oecologia* 153:1–9.
- Dudley, L. S. 2006. Ecological correlates of secondary sexual dimorphism in *Salix glauca* (Salicaceae). *American Journal of Botany* 93:1775–1783.
- Dytham, C., J. M. J. Travis, K. Mustin, and T. G. Benton. 2014. Changes in species' distributions during and after environmental change: Which eco-evolutionary processes matter more? *Ecography* 37:1210–1217.
- Ellstrand, N. C., and M. L. Roose. 1987. Patterns of genotypic diversity in clonal plant species. *American Journal of Botany* 74:123–131.
- Elmendorf, S. C., G. H. R. Henry, R. D. Hollister, R. G. Björk, A. D. Bjorkman, T. V. Callaghan, L. S. Collier, E. J. Cooper, J. H. C. Cornelissen, T. A. Day, A. M. Fosaa, W. A. Gould, J. Grétarsdóttir, J. Harte, L. Hermanutz, D. S. Hik, A. Hofgaard, F. Jarrad, I. S. Jónsdóttir, F. Keuper, K. Klanderud, J. A. Klein, S. Koh, G. Kudo, S. I. Lang, V. Loewen, J. L. May, J. Mercado, A. Michelsen, U. Molau, I. H. Myers-Smith, S. F. Oberbauer, S. Pieper, E. Post, C. Rixen, C. H. Robinson, N. M. Schmidt, G. R. Shaver, A. Stenström, A. Tolvanen, Ø. Totland, T. Troxler, C.-H. Wahren, P. J. Webber, J. M. Welker, and P. A.

- Wookey. 2012a. Global assessment of experimental climate warming on tundra vegetation: Heterogeneity over space and time. *Ecology Letters* 15:164–175.
- Elmendorf, S. C., G. H. R. Henry, R. D. Hollister, R. G. Björk, N. Boulanger-Lapointe, E. J. Cooper, J. H. C. Cornelissen, T. A. Day, E. Dorrepaal, T. G. Elumeeva, M. Gill, W. A. Gould, J. Harte, D. S. Hik, A. Hofgaard, D. R. Johnson, J. F. Johnstone, I. S. Jónsdóttir, J. C. Jorgenson, K. Klanderud, J. A. Klein, S. Koh, G. Kudo, M. Lara, E. Lévesque, B. Magnússon, J. L. May, J. A. Mercado-Díaz, A. Michelsen, U. Molau, I. H. Myers-Smith, S. F. Oberbauer, V. G. Onipchenko, C. Rixen, N. M. Schmidt, G. R. Shaver, M. J. Spasojevic, P. E. Þórhallsdóttir, A. Tolvanen, T. Troxler, C. E. Tweedie, S. Villareal, C.-H. Wahren, X. Walker, P. J. Webber, J. M. Welker, and S. Wipf. 2012b. Plot-scale evidence of tundra vegetation change and links to recent summer warming. *Nature Climate Change* 2:453–457.
- Elven, R., D. F. Murray, V. Y. Razzhivin, and B. A. Yurtsev, editors. 2011. Annotated checklist of the Panarctic Flora (PAF): Vascular plants.
- Eriksson, O. 1996. Regional dynamics of plants: A review of evidence for remnant, source-sink and metapopulations. *Oikos* 77:248–258.
- Forbes, B. C., M. Macias-Fauria, and P. Zetterberg. 2010. Russian Arctic warming and “greening” are closely tracked by tundra shrub willows. *Global Change Biology* 16:1542–1554.
- Fraser, R. H., I. Olthof, M. Carrière, A. Deschamps, and D. Pouliot. 2011. Detecting long-term changes to vegetation in northern Canada using the Landsat satellite image archive. *Environmental Research Letters* 6:45502.
- Freckleton, R. P., and A. R. Watkinson. 2002. Large-scale spatial dynamics of plants: Metapopulations, regional ensembles and patchy populations. *Journal of Ecology* 90:419–434.



- Freedman, B., N. Hill, J. Svoboda, and G. Henry. 1982. Seed banks and seedling occurrence in a High Arctic oasis at Alexandra Fjord, Ellesmere Island, Canada. *Canadian Journal of Botany* 60:2112–2118.
- Frost, G. V., and H. E. Epstein. 2014. Tall shrub and tree expansion in Siberian tundra ecotones since the 1960s. *Global Change Biology* 20:1264–1277.
- Frost, G. V., H. E. Epstein, D. A. Walker, G. Matyshak, and K. Ermokhina. 2013. Patterned-ground facilitates shrub expansion in Low Arctic tundra. *Environmental Research Letters* 8:15035.
- Gabrielsen, T. M., and C. Brochmann. 1998. Sex after all: High levels of diversity detected in the arctic clonal plant *Saxifraga cernua* using RAPD markers. *Molecular Ecology* 7:1701–1708.
- Gartner, B. L., F. S. C. III, and G. R. Shaver. 1986. Reproduction of *Eriophorum vaginatum* by seed in Alaskan tussock tundra. *Journal of Ecology* 74:1–18.
- Goetz, S. J., H. E. Epstein, U. S. Bhatt, G. J. Jia, J. O. Kaplan, H. Lischke, Q. Yu, A. Bunn, A. H. Lloyd, D. Alcaraz-Segura, P. S. A. Beck, J. C. Comiso, M. K. Reynolds, and D. A. Walker. 2011. Recent changes in arctic vegetation: Satellite observations and simulation model predictions. Pages 9–36 in G. Gutman and A. Reissell, editors. *Eurasian Arctic Land Cover and Land Use in a Changing Climate*. Springer, Netherlands.
- Graae, B., R. Ejrnaes, S. Lang, E. Meineri, P. Ibarra, and H. Bruun. 2011. Strong microsite control of seedling recruitment in tundra. *Oecologia* 166:565–576.
- Graae, B. J., R. Ejrnaes, F. L. Marchand, A. Milbau, A. Shevtsova, L. Beyens, and I. Nijs. 2009. The effect of an early-season short-term heat pulse on plant recruitment in the Arctic. *Polar Biology* 32:1117–1126.
- Hadfield, J. D. 2010. MCMC methods for multi-response generalized linear mixed models: The MCMCglmm R package. *Journal of Statistical Software* 33.

- Hallinger, M., M. Manthey, and M. Wilmking. 2010. Establishing a missing link: Warm summers and winter snow cover promote shrub expansion into alpine tundra in Scandinavia. *New Phytologist* 186:890–899.
- Hanley, S., J. Barker, J. V. Ooijen, C. Aldam, S. Harris, I. Åhman, S. Larsson, and A. Karp. 2002. A genetic linkage map of willow (*Salix viminalis*) based on AFLP and microsatellite markers. *Theoretical and Applied Genetics* 105:1087–1096.
- Hautala, H., A. Tolvanen, and C. Nuortila. 2001. Regeneration strategies of dominant boreal forest dwarf shrubs in response to selective removal of understorey layers. *Journal of Vegetation Science* 12:503–510.
- Higgins, S. I., R. Nathan, and M. L. Cain. 2003. Are long-distance dispersal events in plants usually caused by nonstandard means of dispersal? *Ecology* 84:1945–1956.
- 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.
- Hudson, J. M. G., and G. H. R. Henry. 2010. High Arctic plant community resists 15 years of experimental warming. *Journal of Ecology* 98:1035–1041.
- Hutchings, M. J., and D. K. Wijesinghe. 1997. Patchy habitats, division of labour and growth dividends in clonal plants. *Trends in Ecology & Evolution* 12:390–394.
- Jones, M. h, C. Bay, and U. Nordenhäll. 1997. Effects of experimental warming on arctic willows (*Salix* spp.): A comparison of responses from the Canadian High Arctic, Alaskan Arctic, and Swedish Subarctic. *Global Change Biology* 3:55–60.
- Jónsdóttir, I. S., and M. A. Watson. 1997. Extensive physiological integration: An adaptive trait in resource-poor environments? Pages 109–136 in J. Van Groenendael and H. de. Kroon, editors. *The ecology and evolution of clonal plants*. Backhuys Publishers, Leiden.

- Kikuchi, S., W. Suzuki, N. Ban, A. Kanazashi, and H. Yoshimaru. 2005. Characterization of eight polymorphic microsatellites in endangered willow *Salix hukaoana*. *Molecular Ecology Notes* 5:869–870.
- King, R. A., S. L. Harris, A. Karp, and J. H. A. Barker. 2010. Characterisation and inheritance of nuclear microsatellite loci for use in population studies of the allotetraploid *Salix alba*–*Salix fragilis* complex. *Tree Genetics & Genomes* 6:247–258.
- Kinlan, B. P., and S. D. Gaines. 2003. Propagule dispersal in marine and terrestrial environments: A community perspective. *Ecology* 84:2007–2020.
- Klady, R. A., G. H. R. Henry, and V. Lemay. 2011. Changes in high arctic tundra plant reproduction in response to long-term experimental warming. *Global Change Biology* 17:1611–1624.
- Klimeš, L. 2008. Clonal splitters and integrators in harsh environments of the Trans-Himalaya. *Evolutionary Ecology* 22:351–367.
- Lauron-Moreau, A., F. E. Pitre, L. Brouillet, and M. Labrecque. 2013. Microsatellite markers of willow species and characterization of 11 polymorphic microsatellites for *Salix eriocephala* (Salicaceae), a potential native species for biomass production in Canada. *Plants* 2:203–210.
- Levin, D. A. 1975. Minority cytotype exclusion in local plant populations. *Taxon* 24:35–43.
- Lian, C., K. Nara, H. Nakaya, Z. Zhou, B. Wu, N. Miyashita, and T. Hogetsu. 2001. Development of microsatellite markers in polyploid *Salix reinii*. *Molecular Ecology Notes* 1:160–161.
- Lian, C., R. Oishi, N. Miyashita, K. Nara, H. Nakaya, B. Wu, Z. Zhou, and T. Hogetsu. 2003. Genetic structure and reproduction dynamics of *Salix reinii* during primary succession on Mount Fuji, as revealed by nuclear and chloroplast microsatellite analysis. *Molecular Ecology* 12:609–618.

- Lin, J., J. P. Gibbs, and L. B. Smart. 2009. Population genetic structure of native versus naturalized sympatric shrub willows (*Salix*; Salicaceae). *American Journal of Botany* 96:771–785.
- Magnusson, A., and I. Stewart. 2014. plotMCMC: MCMC diagnostic plots, version 2.0-0.
- Meineri, E., J. Spindelböck, and V. Vandvik. 2013. Seedling emergence responds to both seed source and recruitment site climates: A climate change experiment combining transplant and gradient approaches. *Plant Ecology* 214:607–619.
- Meirmans, P. G., and P. H. Van Tienderen. 2004. genotype and genodive: Two programs for the analysis of genetic diversity of asexual organisms. *Molecular Ecology Notes* 4:792–794.
- Milbau, A., B. J. Graae, A. Shevtsova, and I. Nijs. 2009. Effects of a warmer climate on seed germination in the subarctic. *Annals of Botany* 104:287–296.
- Millennium Ecosystem Assessment. 2005. *Ecosystems and human well-being: Biodiversity synthesis*. World Resources Institute, Washington, D.C.
- Miller, G. H., J. Brigham-Grette, R. B. Alley, L. Anderson, H. A. Bauch, M. S. V. Douglas, M. E. Edwards, S. A. Elias, B. P. Finney, J. J. Fitzpatrick, S. V. Funder, T. D. Herbert, L. D. Hinzman, D. S. Kaufman, G. M. MacDonald, L. Polyak, A. Robock, M. C. Serreze, J. P. Smol, R. Spielhagen, J. W. C. White, A. P. Wolfe, and E. W. Wolff. 2010. Temperature and precipitation history of the Arctic. *Quaternary Science Reviews* 29:1679–1715.
- Myers-Smith, I. H., B. C. Forbes, M. Wilmking, M. Hallinger, T. Lantz, D. Blok, K. D. Tape, M. Macias-Fauria, U. Sass-Klaassen, E. Lévesque, S. Boudreau, P. Ropars, L. Hermanutz, A. Trant, L. S. Collier, S. Weijers, J. Rozema, S. A. Rayback, N. M. Schmidt, G. Schaeppman-Strub, S. Wipf, C. Rixen, C. B. Ménard, S. Venn, S. Goetz, L. Andreu-Hayles, S. Elmendorf, V. Ravolainen, J. Welker, P. Grogan, H. E. Epstein, and D. S. Hik. 2011. Shrub expansion in tundra ecosystems: Dynamics, impacts and research priorities. *Environmental Research Letters* 6:45509.

- Myers-Smith, I. H., and D. S. Hik. 2012. Uniform female-biased sex ratios in alpine willows. *American Journal of Botany* 99:1243–1248.
- Naito, A. T., and D. M. Cairns. 2011a. Patterns and processes of global shrub expansion. *Progress in Physical Geography* 35:423–442.
- Naito, A. T., and D. M. Cairns. 2011b. Relationships between Arctic shrub dynamics and topographically derived hydrologic characteristics. *Environmental Research Letters* 6:45506.
- Naito, A. T., and D. M. Cairns. 2015. Patterns of shrub expansion in Alaskan arctic river corridors suggest phase transition. *Ecology and Evolution* 5:87–101.
- Nakagawa, S., and H. Schielzeth. 2013. A general and simple method for obtaining  $R^2$  from generalized linear mixed-effects models. *Methods in Ecology and Evolution* 4:133–142.
- Narayan, L., R. S. Dodd, and K. L. O’Hara. 2015. A genotyping protocol for multiple tissue types from the polyploid tree species *Sequoia sempervirens* (Cupressaceae). *Applications in Plant Sciences* 3:1400110.
- Nathan, R., G. G. Katul, H. S. Horn, S. M. Thomas, R. Oren, R. Avissar, S. W. Pacala, and S. A. Levin. 2002. Mechanisms of long-distance dispersal of seeds by wind. *Nature* 418:409.
- Normand, S., N. E. Zimmermann, F. M. Schurr, and H. Lischke. 2014. Demography as the basis for understanding and predicting range dynamics. *Ecography* 37:1149–1154.
- Parisod, C., R. Holderegger, and C. Brochmann. 2010. Evolutionary consequences of autopolyploidy. *New Phytologist* 186:5–17.
- Poole, K. G., C. Cuyler, and J. Nyman. 2013. Evaluation of caribou *Rangifer tarandus groenlandicus* survey methodology in West Greenland. *Wildlife Biology* 19:225–239.
- Puschenreiter, M., M. Türktaş, P. Sommer, G. Wieshammer, G. Laaha, W. W. Wenzel, and M.-T. Hauser. 2010. Differentiation of metallicolous and non-metallicolous *Salix caprea*

- populations based on phenotypic characteristics and nuclear microsatellite (SSR) markers. *Plant, Cell & Environment* 33:1641–1655.
- R Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Reisch, C., S. Schurm, and P. Poschlod. 2007. Spatial genetic structure and clonal diversity in an alpine population of *Salix herbacea* (Salicaceae). *Annals of Botany* 99:647–647.
- Schickhoff, U., M. D. Walker, and D. A. Walker. 2002. Riparian willow communities on the Arctic Slope of Alaska and their environmental relationships: A classification and ordination analysis. *Phytocoenologia* 32:145–204.
- Schmidt, N. M., C. Baittinger, and M. C. Forchhammer. 2006. Reconstructing century-long snow regimes using estimates of High Arctic *Salix arctica* radial growth. *Arctic, Antarctic, and Alpine Research* 38:257–262.
- Schuelke, M. 2000. An economic method for the fluorescent labeling of PCR fragments. *Nature Biotechnology* 18:233–234.
- Shevtsova, A., B. J. Graae, T. Jochum, A. Milbau, F. Kockelbergh, L. Beyens, and I. Nijs. 2009. Critical periods for impact of climate warming on early seedling establishment in subarctic tundra. *Global Change Biology* 15:2662–2680.
- Stamati, K., S. Blackie, J. W. S. Brown, and J. Russell. 2003. A set of polymorphic SSR loci for subarctic willow (*Salix lanata*, *S. lapponum* and *S. herbacea*). *Molecular Ecology Notes* 3:280–282.
- Stamati, K., P. Hollingsworth, and J. Russell. 2007. Patterns of clonal diversity in three species of sub-arctic willow (*Salix lanata*, *Salix lapponum* and *Salix herbacea*). *Plant Systematics and Evolution* 269:75–88.
- Steinger, T., C. Körner, and B. Schmid. 1996. Long-term persistence in a changing climate: DNA analysis suggests very old ages of clones of alpine *Carex curvula*. *Oecologia* 105:94–99.

- Steltzer, H., R. A. Hufbauer, J. M. Welker, M. Casalis, P. F. Sullivan, and R. Chimner. 2008. Frequent sexual reproduction and high intraspecific variation in *Salix arctica*: Implications for a terrestrial feedback to climate change in the High Arctic. *Journal of Geophysical Research* 113:G03S10.
- Sturm, M., J. P. McFadden, G. E. Liston, F. S. Chapin III, C. H. Racine, and J. Holmgren. 2001. Snow-shrub interactions in arctic tundra: A hypothesis with climatic implications. *Journal of Climate* 14:336.
- Suda, J., A. Krahulcová, P. Trávníček, and F. Krahulec. 2006. Ploidy level versus DNA ploidy level: An appeal for consistent terminology. *Taxon* 55:447–450.
- Suda, Y., and G. Argus. 1968. Chromosome numbers of some North American *Salix*. *Brittonia* 20:191–197.
- Suda, Y., and G. W. Argus. 1969. Chromosome numbers of some North American arctic and boreal *Salix*. *Canadian Journal of Botany* 47:859–862.
- Suominen, O., and J. Olofsson. 2000. Impacts of semi-domesticated reindeer on structure of tundra and forest communities in Fennoscandia: A review. *Annales Zoologici Fennici* 37:233–249.
- Tamstorf, M. P., P. Aastrup, and L. C. Cuyler. 2005. Modelling critical caribou summer ranges in West Greenland. *Polar Biology* 28:714–724.
- Tape, K. D., M. Hallinger, J. M. Welker, and R. W. Ruess. 2012. Landscape heterogeneity of shrub expansion in Arctic Alaska. *Ecosystems* 15:711–724.
- Tape, K., M. Sturm, and C. Racine. 2006. The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. *Global Change Biology* 12:686–702.
- Thomas, L. K., L. Tölle, B. Ziegenhagen, and I. Leyer. 2012. Are vegetative reproduction capacities the cause of widespread invasion of Eurasian Salicaceae in Patagonian River landscapes? *PLoS ONE* 7:e50652.

- Tolvanen, A., J. Schroderus, and G. H. R. Henry. 2001. Age- and stage-based bud demography of *Salix arctica* under contrasting muskox grazing pressure in the High Arctic. *Evolutionary Ecology* 15:443–462.
- Travis, J. M. J., M. Delgado, G. Bocedi, M. Baguette, K. Bartoń, D. Bonte, I. Boulangeat, J. A. Hodgson, A. Kubisch, V. Penteriani, M. Saastamoinen, V. M. Stevens, and J. M. Bullock. 2013. Dispersal and species' responses to climate change. *Oikos* 122:1532–1540.
- Tremblay, B., E. Lévesque, and S. Boudreau. 2012. Recent expansion of erect shrubs in the Low Arctic: Evidence from Eastern Nunavik. *Environmental Research Letters* 7:35501.
- Venn, S. E., and J. W. Morgan. 2009. Patterns in alpine seedling emergence and establishment across a stress gradient of mountain summits in south-eastern Australia. *Plant Ecology & Diversity* 2:5–16.
- Wagner, B., and O. Bennike. 2012. Chronology of the last deglaciation and Holocene environmental changes in the Sisimiut area, SW Greenland based on lacustrine records. *Boreas* 41:481–493.
- Weijers, S., F. Wagner-Cremer, U. Sass-Klaassen, R. Broekman, and J. Rozema. 2013. Reconstructing High Arctic growing season intensity from shoot length growth of a dwarf shrub. *The Holocene* 23:721–731.
- Welling, P., A. Tolvanen, and K. Laine. 2004. The alpine soil seed bank in relation to field seedlings and standing vegetation in subarctic Finland. *Arctic, Antarctic, and Alpine Research* 36:229–238.
- Wickham, H. 2009. *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York.
- Young, A. B., D. A. Watts, A. H. Taylor, and E. Post. 2016. Species and site differences influence climate-shrub growth responses in West Greenland. *Dendrochronologia* 37:69–78.



Zalatan, R., and K. Gajewski. 2006. Dendrochronological potential of *Salix alaxensis* from the Kuujjua River area, western Canadian Arctic. *Tree-Ring Research* 62:75–82.

Zuur, A. F., E. N. Ieno, and C. S. Elphick. 2010. A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* 1:3–14.

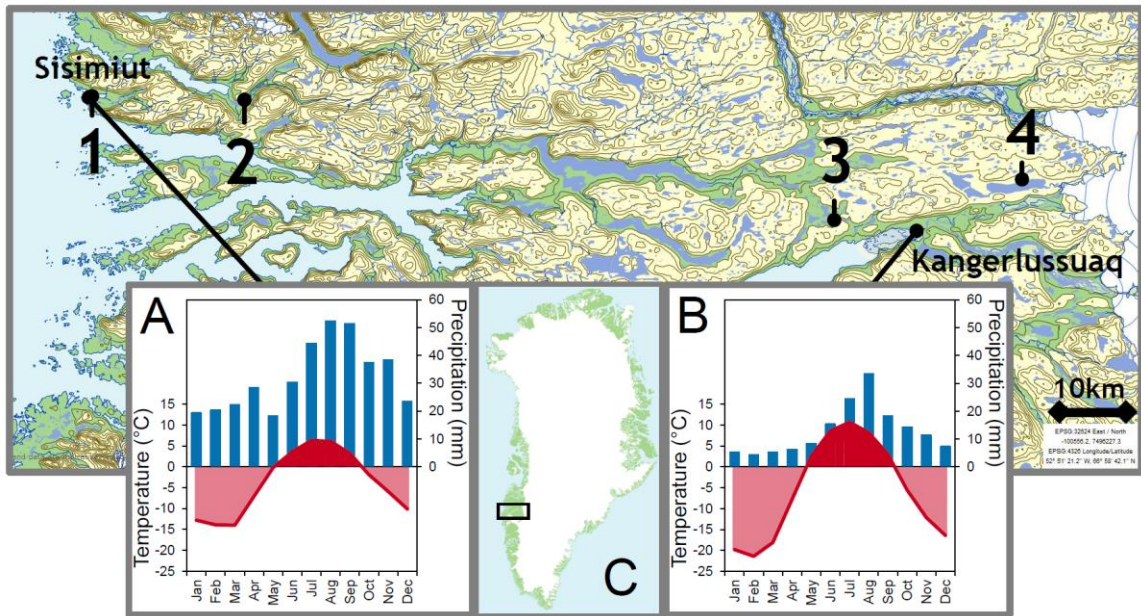


Figure 3.1. Climographs for the (A) Sisimiut and (B) Kangerlussuaq meteorological stations and topographic map of the West Greenland region and its location in Greenland (C). Numbers on the main map indicate the four site locations, and contour lines represent 100 m intervals. Climographs are based on 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/>).

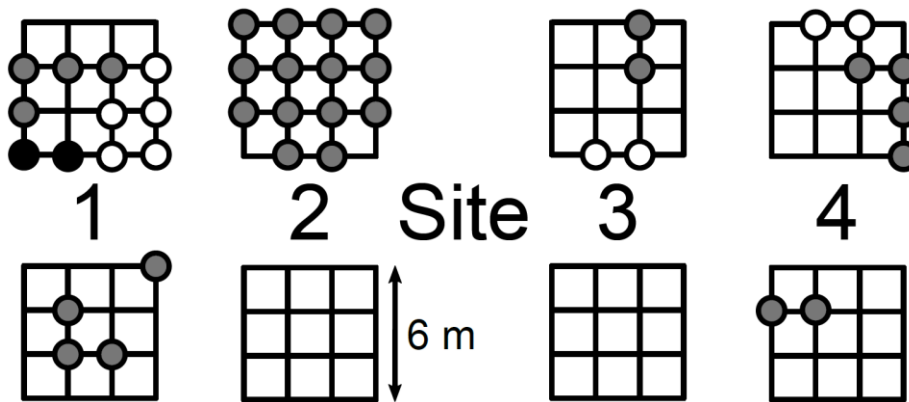


Figure 3.2. Layout of the study's sampling design. 16 samples per plot were collected at each of the intersections a 6x6 m grid. All plots at each of the four sampling sites, indicated by numbers, were at least 25 m apart. Shown here are the least (lower set) and most (upper set) clonal plots at each site.

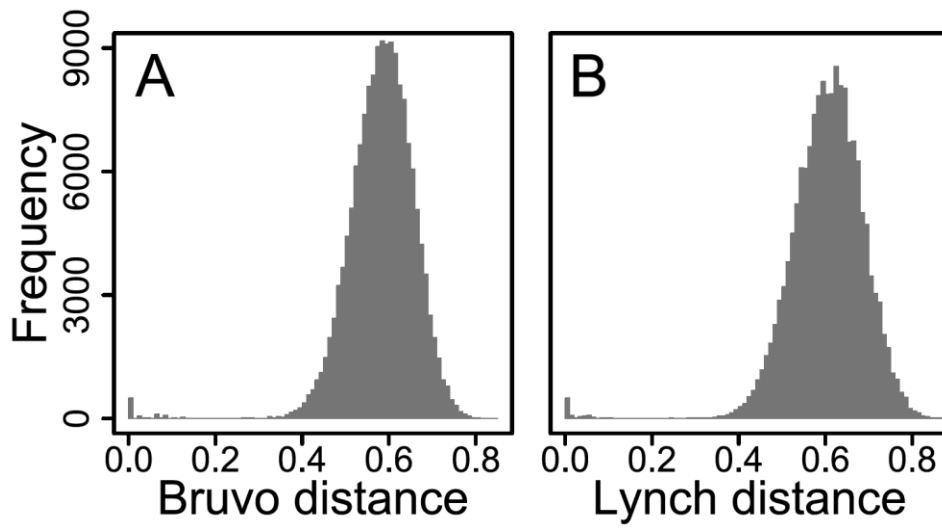


Figure 3.3. Histograms of pairwise genetic distances among all sample pairs. Both Bruvo (A) and Lynch (B) distance metrics show bimodal distributions with distinguishable tails, indicating sample pairs belonging to the smaller mode represent the same genotype.

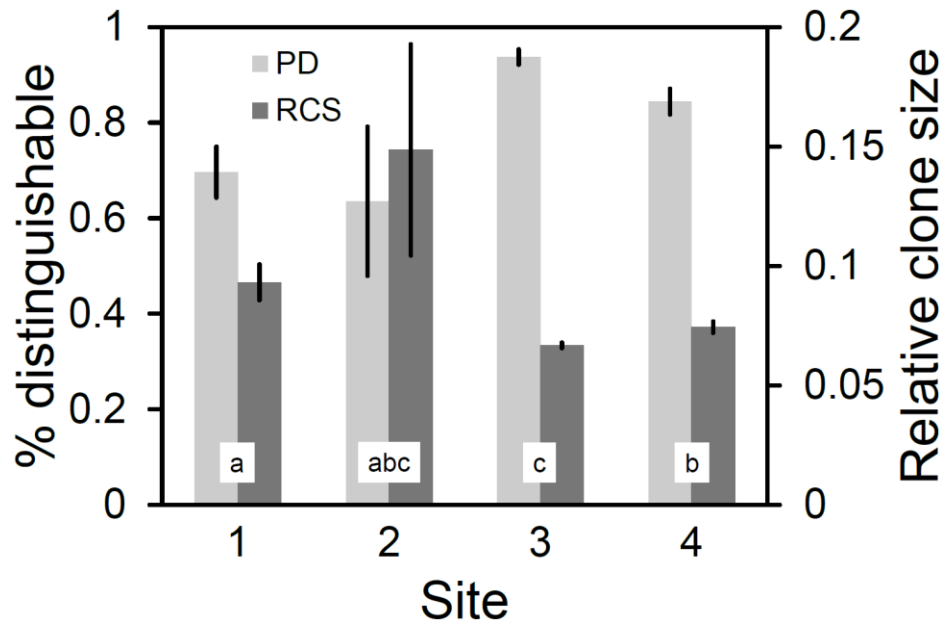


Figure 3.4. Indicators of clonality for each of the four sampling sites. Percent (or proportion) distinguishable (PD) and relative clone size (RCS) are shown on the left and right y-axes, respectively. PD and RCS are both calculated here at the plot level. Error bars represent one standard error of the mean; letters indicate results from *post hoc* pairwise comparisons of sites.

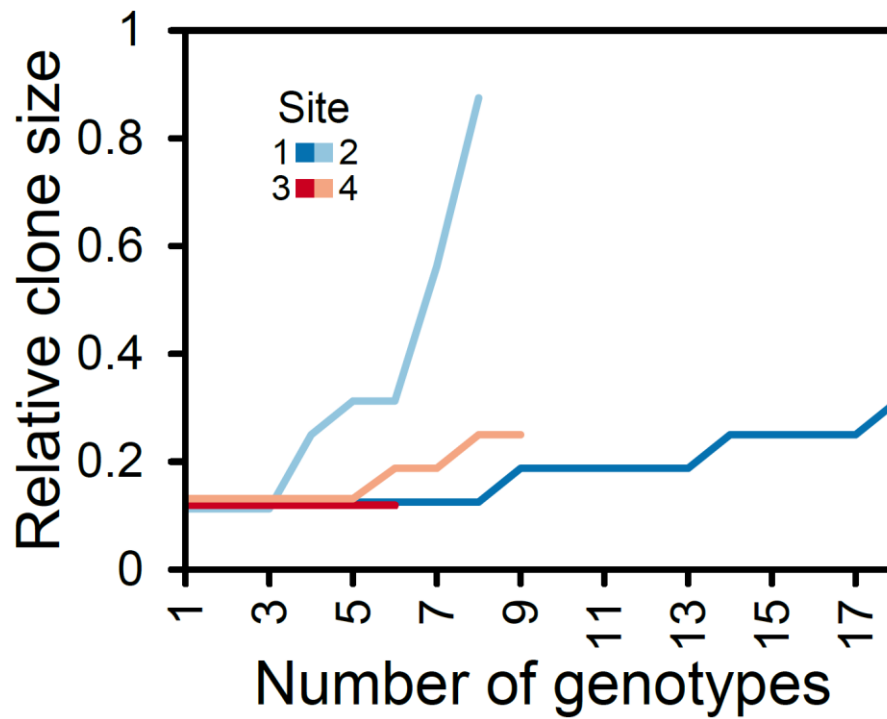


Figure 3.5. Relative clone sizes (RCS) for each of the four sampling sites. RCS here was calculated at the genotype level after excluding unique genotypes only represented by single sample, so only clonal genotypes are displayed here. Blue lines indicate coastal, maritime sites, and red lines indicate inland, continental sites. Lines have been slightly shifted in the y-dimension to preclude visual overlap.

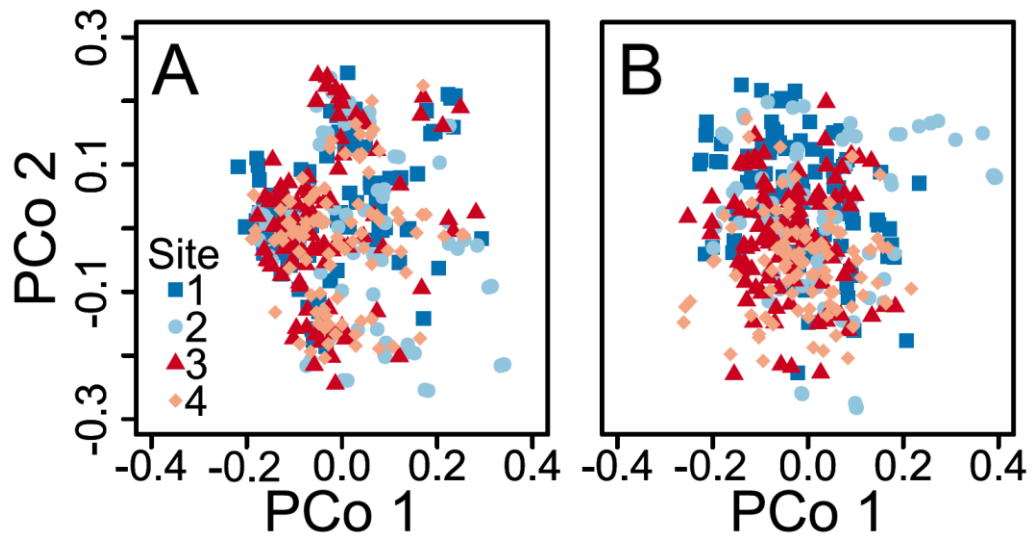


Figure 3.6. Principal coordinate (PCo) axes from analyses of pairwise genetic distances across all four sampling sites. Shown here are the results based on the Bruvo (A) and Lynch (B) distance metrics, each of which reveals nearly complete overlap between all four sites. Blue symbols indicate coastal, maritime sites, and red symbols indicate inland, continental site.

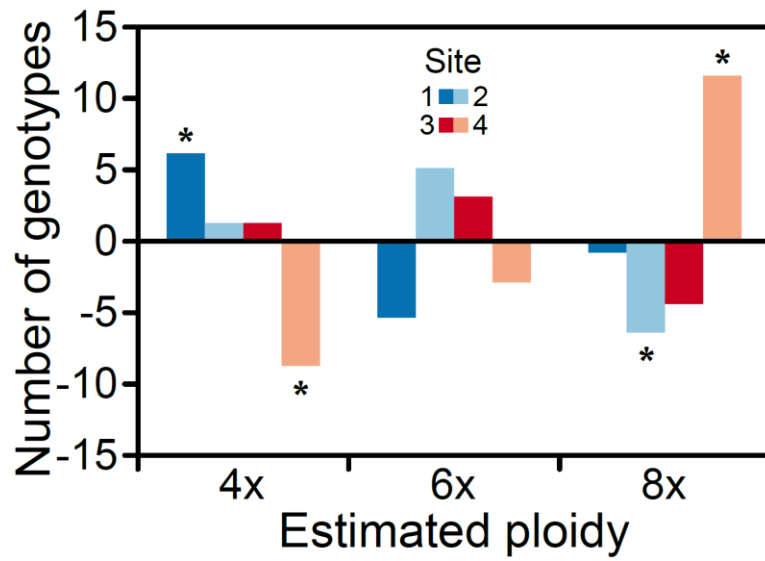


Figure 3.7. Estimated ploidy level for each of the four sampling sites. The number of genotypes represents the difference between observed and expected for the three aggregated ploidy levels (see text for details). Asterisks indicate significant differences based on a chi-squared ( $\chi^2$ ) test. Blue bars indicate coastal, maritime sites, and red bars indicate inland, continental sites.



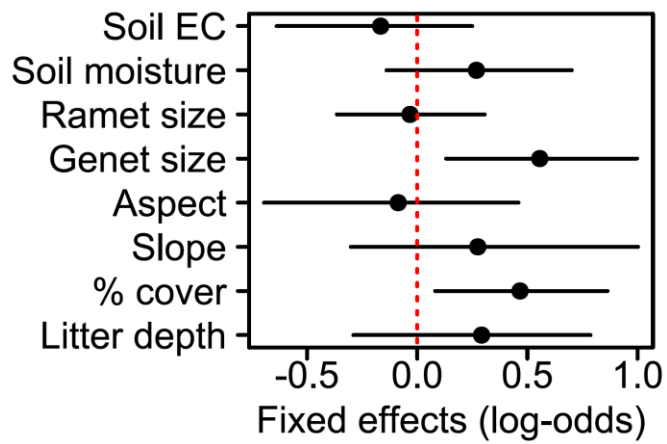


Figure 3.8. Log-odds of the fixed effects predictors of clonality. Error bars represent 95% credible intervals from Bayesian logistic regression modeling. Only the credible intervals for genet size and percent cover do not overlap zero (red dashed line).

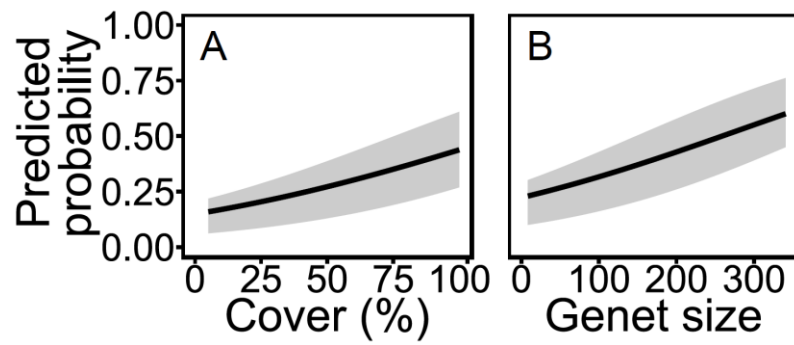


Figure 3.9. Predicted probabilities of clonality for percent cover and genet size, revealing declines in the probability of a given genotype being clonal as the predictors approached minimal values. Shaded curves denote 95% confidence intervals. See text for details on the calculation of genet size.

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.

<b>Locus</b>	<b>Repeat motif</b>	<b># of alleles</b>	<b>Reference</b>
Cha475	[GT] <sub>12</sub> [GA]	33	[1]
Cha580	[CT] <sub>10</sub> [CA] <sub>19</sub>	7	[1]
SB24	[TG] <sub>21</sub> AG[TG] <sub>3</sub> AG[TG] <sub>3</sub> AG[TG] <sub>3</sub> AGTGAG[TG] <sub>3</sub>	52	[2]
SB196	[GCC] <sub>9</sub>	12	[2]
SB199	[TG] <sub>11</sub> CG[TG] <sub>6</sub>	34	[2]
SB201	[CT] <sub>4</sub> CC[CT] <sub>3</sub> [CA] <sub>22</sub>	21	[2]
SB233	[TA] <sub>2</sub> [TGTGCG] <sub>4</sub> [TG] <sub>9</sub>	29	[2]
SB243	[GCC] <sub>3</sub> ATCAT TCCCC[GCC] <sub>4</sub>	17	[2]

References: [1] Hoshikawa et al. 2009, [2] Barker et al. 2003

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.

Fixed effects							$R^2$	df	$\Delta$ AICc	BIC
Aspect (plot)	Percent cover	Genet size	Litter depth	Soil moisture	Soil EC	Slope (plot)				
	0.443	0.467	0.482	0.224			0.288	6	0.00	455.12
	0.407	0.486	0.489				0.282	7	0.24	451.44
	0.365	0.453				0.391	0.279	7	1.45	452.66
	0.446	0.458	0.472	0.244	-0.093		0.290	5	1.62	460.66
	0.375	0.467	0.268			0.142	0.284	6	1.71	456.83
-0.072	0.422	0.452	0.484	0.225			0.289	5	1.81	460.85
	0.419	0.455	0.341	0.211		0.069	0.289	5	1.89	460.92
	0.411	0.483					0.271	8	1.96	449.23

## Chapter 4

### **Relationship between plant community diversity and ecosystem function altered by warming and herbivore exclusion<sup>3</sup>**

#### **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

---

<sup>3</sup> To be submitted to *Proceedings of the Royal Society B: Biological Sciences*

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<sup>2</sup> circular plots were established inside and outside of three permanent circular fenced areas that excluded large herbivores from approximately 800 m<sup>2</sup> 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 exclosure 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), exclosed + 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:

$${}^qD \equiv \left( \sum_{i=1}^S p_i^q \right)^{1/(1-q)} \quad [1]$$

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  $q = 0, 1, \text{ and } 2$ , 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. Secondly, 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  $304.3 \pm 23.0$  pin hits (mean across all treatments  $\pm 1$  SE). Beginning in 2006, this value increased monotonically through 2014, the year with the greatest aboveground biomass ( $1690.8 \pm 125.2$  pin hits). The year 2015 was the only exception to this otherwise monotonic increase. Mean ( $\pm 1$  SE) plot-level aboveground biomass across all years was  $96.6 \pm 2.9$ ,  $120.6 \pm 4.3$ ,  $91.5 \pm 3.0$ , and  $96.6 \pm 3.5$  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.

### References

- T Allouche, O., M. Kalyuzhny, G. Moreno-Rueda, M. Pizarro, and R. Kadmon. 2012. Area–heterogeneity tradeoff and the diversity of ecological communities. *Proceedings of the National Academy of Sciences* 109:17495–17500.
- Al-Mufti, M. M., C. L. Sydes, S. B. Furness, J. P. Grime, and S. R. Band. 1977. A quantitative analysis of shoot phenology and dominance in herbaceous vegetation. *Journal of Ecology* 65:759.
- Arft, A. M., M. D. Walker, J. Gurevitch, J. M. Alatalo, M. S. Bret-Harte, M. Dale, M. Diemer, F. Gugerli, G. H. R. Henry, M. H. Jones, R. D. Hollister, I. S. Jónsdóttir, K. Laine, E. Lévesque, G. M. Marion, U. Molau, P. Mølgaard, U. Nordenhäll, V. Raszhivin, C. H. Robinson, G. Starr, A. Stenström, M. Stenström, Ø. Totland, P. L. Turner, L. J. Walker, P. J. Webber, J. M. Welker, and P. A. Wookey. 1999. Responses of tundra plants to experimental warming: Meta-analysis of the International Tundra Experiment. *Ecological Monographs* 69:491–511.
- Axmanová, I., M. Chytrý, J. Danihelka, P. Lustyk, M. Kočí, S. Kubešová, M. Horsák, M. M. Cherosov, and P. A. Gogoleva. 2013. Plant species richness–productivity relationships in a low-productive boreal region. *Plant Ecology* 214:207–219.
- Axmanová, I., M. Chytrý, D. Zelený, C.-F. Li, M. Vymazalová, J. Danihelka, M. Horsák, M. Kočí, S. Kubešová, Z. Lososová, Z. Otýpková, L. Tichý, V. B. Martynenko, E. Z.

- Baisheva, B. Schuster, and M. Diekmann. 2012. The species richness–productivity relationship in the herb layer of European deciduous forests. *Global Ecology and Biogeography* 21:657–667.
- Balvanera, P., A. B. Pfisterer, N. Buchmann, J.-S. He, T. Nakashizuka, D. Raffaelli, and B. Schmid. 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters* 9:1146–1156.
- Berger, W. H., and F. L. Parker. 1970. Diversity of planktonic Foraminifera in deep-sea sediments. *Science* 168:1345–1347.
- Billings, W. D., and H. A. Mooney. 1968. The ecology of arctic and alpine plants. *Biological Reviews* 43:481–529.
- Bret-Harte, M. S., E. A. García, V. M. Sacré, J. R. Whorley, J. L. Wagner, S. C. Lippert, and F. S. Chapin. 2004. Plant and soil responses to neighbour removal and fertilization in Alaskan tussock tundra. *Journal of Ecology* 92:635–647.
- Bret-Harte, M. S., M. C. Mack, G. R. Goldsmith, D. B. Sloan, J. DeMarco, G. R. Shaver, P. M. Ray, Z. Biesinger, and F. S. Chapin. 2008. Plant functional types do not predict biomass responses to removal and fertilization in Alaskan tussock tundra. *Journal of Ecology* 96:713–726.
- Bret-Harte, M. S., G. R. Shaver, J. P. Zoerner, J. F. Johnstone, J. L. Wagner, A. S. Chavez, R. F. Gunkelman, S. C. Lippert, and J. A. Laundre. 2001. Developmental plasticity allows *Betula nana* to dominate tundra subjected to an altered environment. *Ecology* 82:18–32.
- Cahoon, S. M. P., P. F. Sullivan, E. Post, and J. M. Welker. 2012a. Large herbivores limit CO<sub>2</sub> uptake and suppress carbon cycle responses to warming in West Greenland. *Global Change Biology* 18:469–479.



- Cahoon, S. M. P., P. F. Sullivan, G. R. Shaver, J. M. Welker, and E. Post. 2012b. Interactions among shrub cover and the soil microclimate may determine future Arctic carbon budgets. *Ecology Letters* 15:1415–1422.
- Cappelen, J. 2013. Greenland - Danish Meteorological Institute historical climate data collection 1873-2012. 75 pages. Danish Meteorological Institute. Copenhagen, Denmark.
- Cardinale, B. J., D. M. Bennett, C. E. Nelson, and K. Gross. 2009. Does productivity drive diversity or vice versa? A test of the multivariate productivity–diversity hypothesis in streams. *Ecology* 90:1227–1241.
- Cardinale, B. J., J. P. Wright, M. W. Cadotte, I. T. Carroll, A. Hector, D. S. Srivastava, M. Loreau, and J. J. Weis. 2007. Impacts of plant diversity on biomass production increase through time because of species complementarity. *Proceedings of the National Academy of Sciences* 104:18123–18128.
- Cayuela, L., N. J. Gotelli, and R. K. Colwell. 2015. Ecological and biogeographic null hypotheses for comparing rarefaction curves. *Ecological Monographs* 85:437–455.
- Chao, A., N. Gotelli, T. C. Hsieh, E. Sander, K. H. Ma, R. K. Colwell, and A. M. Ellison. 2014. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecological Monographs* 84:45–67.
- Colwell, R. K., A. Chao, N. J. Gotelli, S.-Y. Lin, C. X. Mao, R. L. Chazdon, and J. T. Longino. 2012. Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. *Journal of Plant Ecology* 5:3–21.
- Cornelissen, J. H. C., T. V. Callaghan, J. M. Alatalo, A. Michelsen, E. Graglia, A. E. Hartley, D. S. Hik, S. E. Hobbie, M. C. Press, C. H. Robinson, G. H. R. Henry, G. R. Shaver, G. K. Phoenix, D. Gwynn Jones, S. Jonasson, F. S. Chapin, U. Molau, C. Neill, J. A. Lee, J. M. Melillo, B. Sveinbjörnsson, and R. Aerts. 2001. Global change and arctic ecosystems: is

lichen decline a function of increases in vascular plant biomass? *Journal of Ecology* 89:984–994.

- Delignette-Muller, M. L., and C. Dutang. 2015. *fitdistrplus*: An R package for fitting distributions. *Journal of Statistical Software* 64:34.
- Dorrepaal, E., J. H. C. Cornelissen, and R. Aerts. 2006. Changing leaf litter feedbacks on plant production across contrasting sub-arctic peatland species and growth forms. *Oecologia* 151:251–261.
- Elmendorf, S. C., G. H. R. Henry, R. D. Hollister, R. G. Björk, A. D. Bjorkman, T. V. Callaghan, L. S. Collier, E. J. Cooper, J. H. C. Cornelissen, T. A. Day, A. M. Fosaa, W. A. Gould, J. Grétarsdóttir, J. Harte, L. Hermanutz, D. S. Hik, A. Hofgaard, F. Jarrad, I. S. Jónsdóttir, F. Keuper, K. Klanderud, J. A. Klein, S. Koh, G. Kudo, S. I. Lang, V. Loewen, J. L. May, J. Mercado, A. Michelsen, U. Molau, I. H. Myers-Smith, S. F. Oberbauer, S. Pieper, E. Post, C. Rixen, C. H. Robinson, N. M. Schmidt, G. R. Shaver, A. Stenström, A. Tolvanen, Ø. Totland, T. Troxler, C.-H. Wahren, P. J. Webber, J. M. Welker, and P. A. Wookey. 2012a. Global assessment of experimental climate warming on tundra vegetation: Heterogeneity over space and time. *Ecology Letters* 15:164–175.
- Elmendorf, S. C., G. H. R. Henry, R. D. Hollister, R. G. Björk, N. Boulanger-Lapointe, E. J. Cooper, J. H. C. Cornelissen, T. A. Day, E. Dorrepaal, T. G. Elumeeva, M. Gill, W. A. Gould, J. Harte, D. S. Hik, A. Hofgaard, D. R. Johnson, J. F. Johnstone, I. S. Jónsdóttir, J. C. Jorgenson, K. Klanderud, J. A. Klein, S. Koh, G. Kudo, M. Lara, E. Lévesque, B. Magnússon, J. L. May, J. A. Mercado-Díaz, A. Michelsen, U. Molau, I. H. Myers-Smith, S. F. Oberbauer, V. G. Onipchenko, C. Rixen, N. M. Schmidt, G. R. Shaver, M. J. Spasojevic, Þ. E. Þórhallsdóttir, A. Tolvanen, T. Troxler, C. E. Tweedie, S. Villareal, C.-H. Wahren, X. Walker, P. J. Webber, J. M. Welker, and S. Wipf. 2012b. Plot-scale

- evidence of tundra vegetation change and links to recent summer warming. *Nature Climate Change* 2:453–457.
- Euskirchen, E. S., A. D. McGuire, D. W. Kicklighter, Q. Zhuang, J. S. Clein, R. J. Dargaville, D. G. Dye, J. S. Kimball, K. C. McDonald, J. M. Melillo, V. E. Romanovsky, and N. V. Smith. 2006. Importance of recent shifts in soil thermal dynamics on growing season length, productivity, and carbon sequestration in terrestrial high-latitude ecosystems. *Global Change Biology* 12:731–750.
- Gillman, L. N., and S. D. Wright. 2006. The influence of productivity on the species richness of plants: A critical assessment. *Ecology* 87:1234–1243.
- Gough, L., H. Bass, and J. R. McLaren. 2015. Effects of increased soil nutrients on seed rain: A role for seed dispersal in the greening of the Arctic? *Arctic, Antarctic, and Alpine Research* 47:27–34.
- Graae, B., R. Ejrnæs, S. Lang, E. Meineri, P. Ibarra, and H. Bruun. 2011. Strong microsite control of seedling recruitment in tundra. *Oecologia* 166:565–576.
- Grace, J. B., P. B. Adler, E. W. Seabloom, E. T. Borer, H. Hillebrand, Y. Hautier, A. Hector, W. S. Harpole, L. R. O'Halloran, T. M. Anderson, J. D. Bakker, C. S. Brown, Y. M. Buckley, S. L. Collins, K. L. Cottingham, M. J. Crawley, E. I. Damschen, K. F. Davies, N. M. DeCrappeo, P. A. Fay, J. Firn, D. S. Gruner, N. Hagenah, V. L. Jin, K. P. Kirkman, J. M. H. Knops, K. J. La Pierre, J. G. Lambrinos, B. A. Melbourne, C. E. Mitchell, J. L. Moore, J. W. Morgan, J. L. Orrock, S. M. Prober, C. J. Stevens, P. D. Wragg, and L. H. Yang. 2012. Response to comments on “Productivity is a poor predictor of plant species richness.” *Science* 335:1441–1441.
- Graham, J. H., and J. J. Duda. 2011. The humpbacked species richness-curve: A contingent rule for community ecology. *International Journal of Ecology* 2011.

- Grime, J. P. 1973. Control of species density in herbaceous vegetation. *Journal of Environmental Management* 1:151–167.
- Gross, K., and B. J. Cardinale. 2007. Does species richness drive community production or vice versa? Reconciling historical and contemporary paradigms in competitive communities. *The American Naturalist* 170:207–220.
- Henry, G. H. R., and U. Molau. 1997. Tundra plants and climate change: The International Tundra Experiment (ITEX). *Global Change Biology* 3:1–9.
- Hill, M. O. 1973. Diversity and evenness: A unifying notation and its consequences. *Ecology* 54:427.
- Hillebrand, H., J. M. Cowles, A. Lewandowska, D. B. Van de Waal, and C. Plum. 2014. Think ratio! A stoichiometric view on biodiversity–ecosystem functioning research. *Basic and Applied Ecology* 15:465–474.
- Hillebrand, H., D. S. Gruner, E. T. Borer, M. E. S. Bracken, E. E. Cleland, J. J. Elser, W. S. Harpole, J. T. Ngai, E. W. Seabloom, J. B. Shurin, and J. E. Smith. 2007. Consumer versus resource control of producer diversity depends on ecosystem type and producer community structure. *Proceedings of the National Academy of Sciences* 104:10904–10909.
- Hobbie, S. E., and F. S. Chapin. 1998. The response of tundra plant biomass, aboveground production, nitrogen, and CO<sub>2</sub> flux to experimental warming. *Ecology* 79:1526–1544.
- Hobbie, S. E., and L. Gough. 2004. Litter decomposition in moist acidic and non-acidic tundra with different glacial histories. *Oecologia* 140:113–124.
- Hooper, D. U., F. S. Chapin, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, D. M. Lodge, M. Loreau, S. Naeem, B. Schmid, H. Setälä, A. J. Symstad, J. Vandermeer, and D. A. Wardle. 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs* 75:3–35.

- Hsieh, T. C., K. H. Ma, and A. Chao. 2015. iNEXT: An R package for interpolation and extrapolation of species diversity (Hill numbers).
- Jost, L. 2006. Entropy and diversity. *Oikos* 113:363–375.
- Jost, L. 2010. The relation between evenness and diversity. *Diversity* 2:207–232.
- Kaarlejärvi, E., A. Eskelinen, and J. Olofsson. 2013. Herbivory prevents positive responses of lowland plants to warmer and more fertile conditions at high altitudes. *Functional Ecology* 27:1244–1253.
- Kassen, R., A. Buckling, G. Bell, and P. B. Rainey. 2000. Diversity peaks at intermediate productivity in a laboratory microcosm. *Nature* 406:508–512.
- Klanderud, K. 2005. Climate change effects on species interactions in an alpine plant community. *Journal of Ecology* 93:127–137.
- Klanderud, K. 2010. Species recruitment in alpine plant communities: the role of species interactions and productivity. *Journal of Ecology* 98:1128–1133.
- Lasky, J. R., M. Uriarte, V. K. Boukili, D. L. Erickson, W. John Kress, and R. L. Chazdon. 2014. The relationship between tree biodiversity and biomass dynamics changes with tropical forest succession. *Ecology Letters* 17:1158–1167.
- Lefcheck, J. S. 2015. piecewiseSEM: Piecewise structural equation modeling in R for ecology, evolution, and systematics. *Methods in Ecology and Evolution*.
- Lohbeck, M., L. Poorter, M. Martínez-Ramos, and F. Bongers. 2015. Biomass is the main driver of changes in ecosystem process rates during tropical forest succession. *Ecology* 96:1242–1252.
- Longino, J. T., and R. K. Colwell. 2011. Density compensation, species composition, and richness of ants on a Neotropical elevational gradient. *Ecosphere* 2:1–20.

- Lovett Doust, L. 1981. Population dynamics and local specialization in a clonal perennial (*Ranunculus repens*): I. The dynamics of ramets in contrasting habitats. *Journal of Ecology* 69:743–755.
- Matesanz, S., A. Escudero, and F. Valladares. 2009. Impact of three global change drivers on a Mediterranean shrub. *Ecology* 90:2609–2621.
- Michalet, R., R. W. Brooker, L. A. Cavieres, Z. Kikvidze, C. J. Lortie, F. I. Pugnaire, A. Valiente-Banuet, and R. M. Callaway. 2006. Do biotic interactions shape both sides of the humped-back model of species richness in plant communities? *Ecology Letters* 9:767–773.
- Naeem, S., D. E. Bunker, A. Hector, M. Loreau, and C. Perrings. 2009. The ecological and social implications of changing biodiversity: An overview of a decade of biodiversity and ecosystem functioning research. Pages 3–13 *in* S. Naeem, D. E. Bunker, A. Hector, M. Loreau, and C. Perrings, editors. *Biodiversity, Ecosystem Functioning, and Human Wellbeing: An Ecological and Economic Perspective*. Oxford University Press, Oxford, UK.
- Nakagawa, S., and H. Schielzeth. 2013. A general and simple method for obtaining  $R^2$  from generalized linear mixed-effects models. *Methods in Ecology and Evolution* 4:133–142.
- Normand, S., C. Randin, R. Ohlemüller, C. Bay, T. T. Høy, E. D. Kjær, C. Körner, H. Lischke, L. Maiorano, J. Paulsen, P. B. Pearman, A. Psomas, U. A. Treier, N. E. Zimmermann, and J.-C. Svenning. 2013. A greener Greenland? Climatic potential and long-term constraints on future expansions of trees and shrubs. *Philosophical Transactions of the Royal Society B: Biological Sciences* 368.
- Oberbauer, S. F., and T. E. Dawson. 1992. Water relations of arctic vascular plants. Pages 259–279 *in* F. S. Chapin III, R. L. Jefferies, J. F. Reynolds, G. R. Shaver, and J. Svoboda,

- editors. *Arctic Ecosystems in a Changing Climate: An Ecophysiological Perspective*. Academic Press, San Diego, CA, USA.
- Olofsson, J., M. te Beest, and L. Ericson. 2013. Complex biotic interactions drive long-term vegetation dynamics in a subarctic ecosystem. *Philosophical Transactions of the Royal Society B: Biological Sciences* 368.
- Olofsson, J., and L. Oksanen. 2002. Role of litter decomposition for the increased primary production in areas heavily grazed by reindeer: A litterbag experiment. *Oikos* 96:507–515.
- Olofsson, J., L. Oksanen, T. Callaghan, P. E. Hulme, T. Oksanen, and O. Suominen. 2009. Herbivores inhibit climate-driven shrub expansion on the tundra. *Global Change Biology* 15:2681–2693.
- Olsen, S. L., and K. Klanderud. 2014. Exclusion of herbivores slows down recovery after experimental warming and nutrient addition in an alpine plant community. *Journal of Ecology* 102:1129–1137.
- Patil, G. P., and C. Taillie. 1982. Diversity as a concept and its measurement. *Journal of the American Statistical Association* 77:548–561.
- Pedersen, C. 2010, May. The response of arctic vegetation to climate warming in an ungulate grazing system. Doctoral dissertation, The Pennsylvania State University, University Park, Pennsylvania.
- Pedersen, C., and E. Post. 2008. Interactions between herbivory and warming in aboveground biomass production of arctic vegetation. *BMC Ecology* 8:17.
- Post, E. 2013a. *Ecology of climate change: The importance of biotic interactions*. Princeton University Press, Princeton, NJ, USA.
- Post, E. 2013b. Erosion of community diversity and stability by herbivore removal under warming. *Proceedings of the Royal Society B: Biological Sciences* 280.

- Post, E., and C. Pedersen. 2008. Opposing plant community responses to warming with and without herbivores. *Proceedings of the National Academy of Sciences* 105:12353–12358.
- Post, E. S., C. Pedersen, C. C. Wilmer, and M. C. Forchhammer. 2008. Phenological sequences reveal aggregate life history response to climatic warming. *Ecology* 89:363–370.
- R Core Team. 2015. R: A language and environment for statistical computing, Vienna, Austria. <https://www.r-project.org/>.
- Reyes-Fox, M., H. Steltzer, M. J. Trlica, G. S. McMaster, A. A. Andales, D. R. LeCain, and J. A. Morgan. 2014. Elevated CO<sub>2</sub> further lengthens growing season under warming conditions. *Nature* 510:259–262.
- Rundqvist, S., H. Hedenås, A. Sandström, U. Emanuelsson, H. Eriksson, C. Jonasson, and T. V. Callaghan. 2011. Tree and shrub expansion over the past 34 years at the tree-line near Abisko, Sweden. *AMBIO* 40:683–692.
- Schmid, B., P. Balvanera, B. J. Cardinale, J. Godbold, A. B. Pfisterer, D. Raffaelli, M. Solan, and D. S. Srivastava. 2009. Consequences of species loss for ecosystem functioning: Meta-analyses of data from biodiversity experiments. Pages 14–29 *in* S. Naeem, D. E. Bunker, A. Hector, M. Loreau, and C. Perrings, editors. *Biodiversity, Ecosystem Functioning, and Human Wellbeing: An Ecological and Economic Perspective*. Oxford University Press, New York, NY, USA.
- Shannon, C. E. 1948. A mathematical theory of communication. *The Bell System Technical Journal* 27:379–423, 623–656.
- Simpson, E. H. 1949. Measurement of diversity. *Nature* 163:688.
- Spehn, E. M., A. Hector, J. Joshi, M. Scherer-Lorenzen, B. Schmid, E. Bazeley-White, C. Beierkuhnlein, M. C. Caldeira, M. Diemer, P. G. Dimitrakopoulos, J. A. Finn, H. Freitas, P. S. Giller, J. Good, R. Harris, P. Högberg, K. Huss-Danell, A. Jumpponen, J. Koricheva, P. W. Leadley, M. Loreau, A. Minns, C. P. H. Mulder, G. O'Donovan, S. J.



- Otway, C. Palmborg, J. S. Pereira, A. B. Pfisterer, A. Prinz, D. J. Read, E.-D. Schulze, A.-S. D. Siamantziouras, A. C. Terry, A. Y. Troumbis, F. I. Woodward, S. Yachi, and J. H. Lawton. 2005. Ecosystem effects of biodiversity manipulations in European grasslands. *Ecological Monographs* 75:37–63.
- Stein, A., K. Gerstner, and H. Kreft. 2014. Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecology Letters* 17:866–880.
- Sturm, M., J. Schimel, G. Michaelson, V. E. Romanovsky, J. M. Welker, S. F. Oberbauer, G. E. Liston, and J. Fahnestock. 2005. Winter biological processes could help convert arctic tundra to shrubland. *BioScience* 55:17–26.
- Svenning, J.-C., and B. Sandel. 2013. Disequilibrium vegetation dynamics under future climate change. *American Journal of Botany* 100:1266–1286.
- Tape, K., M. Sturm, and C. Racine. 2006. The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. *Global Change Biology* 12:686–702.
- terHorst, C., and P. Munguia. 2008. Measuring ecosystem function: consequences arising from variation in biomass-productivity relationships. *Community Ecology* 9:39–44.
- Thuiller, W., M. Guéguen, D. Georges, R. Bonet, L. Chalmandrier, L. Garraud, J. Renaud, C. Roquet, J. Van Es, N. E. Zimmermann, and S. Lavergne. 2014. Are different facets of plant diversity well protected against climate and land cover changes? A test study in the French Alps. *Ecography* 37:1254–1266.
- Tilman, D., and J. Knops. 1997. The influence of functional diversity and composition on ecosystem processes. *Science* 277:1300–1302.
- Tóthmérész, B. 1995. Comparison of different methods for diversity ordering. *Journal of Vegetation Science* 6:283–290.
- Tuomisto, H. 2010. A consistent terminology for quantifying species diversity? Yes, it does exist. *Oecologia* 164:853–860.

- Tuomisto, H. 2012. An updated consumer's guide to evenness and related indices. *Oikos* 121:1203–1218.
- Vellend, M., L. Baeten, I. H. Myers-Smith, S. C. Elmendorf, R. Beauséjour, C. D. Brown, P. D. Frenne, K. Verheyen, and S. Wipf. 2013. Global meta-analysis reveals no net change in local-scale plant biodiversity over time. *Proceedings of the National Academy of Sciences* 110:19456–19459.
- Viola, D. V., E. A. Mordecai, A. G. Jaramillo, S. A. Sistla, L. K. Albertson, J. S. Gosnell, B. J. Cardinale, and J. M. Levine. 2010. Competition–defense tradeoffs and the maintenance of plant diversity. *Proceedings of the National Academy of Sciences* 107:17217–17222.
- Waide, R. B., M. R. Willig, C. F. Steiner, G. Mittelbach, L. Gough, S. I. Dodson, G. P. Juday, and R. Parmenter. 1999. The relationship between productivity and species richness. *Annual Review of Ecology & Systematics* 30:257–300.
- Walker, M. D., C. H. Wahren, R. D. Hollister, G. H. R. Henry, L. E. Ahlquist, J. M. Alatalo, M. S. Bret-Harte, M. P. Calef, T. V. Callaghan, A. B. Carroll, H. E. Epstein, I. S. Jónsdóttir, J. A. Klein, B. Magnússon, U. Molau, S. F. Oberbauer, S. P. Rewa, C. H. Robinson, G. R. Shaver, K. N. Suding, C. C. Thompson, A. Tolvanen, Ø. Totland, P. L. Turner, C. E. Tweedie, P. J. Webber, and P. A. Wookey. 2006. Plant community responses to experimental warming across the tundra biome. *Proceedings of the National Academy of Sciences of the United States of America* 103:1342–1346.
- Weis, J. J., B. J. Cardinale, K. J. Forshay, and A. R. Ives. 2007. Effects of species diversity on community biomass production change over the course of succession. *Ecology* 88:929–939.
- Wilsey, B. J., D. R. Chalcraft, C. M. Bowles, and M. R. Willig. 2005. Relationships among indices suggest that richness is an incomplete surrogate for grassland biodiversity. *Ecology* 86:1178–1184.

- de Witte, L. C., and J. Stöcklin. 2010. Longevity of clonal plants: why it matters and how to measure it. *Annals of Botany* 106:859–870.
- Wood, S. N. 2004. Stable and efficient multiple smoothing parameter estimation for generalized additive models. *Journal of the American Statistical Association* 99:673–686.
- Wood, S. N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models: Estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)* 73:3–36.
- Zhang, Y., H. Y. H. Chen, and P. B. Reich. 2012. Forest productivity increases with evenness, species richness and trait variation: A global meta-analysis. *Journal of Ecology* 100:742–749.

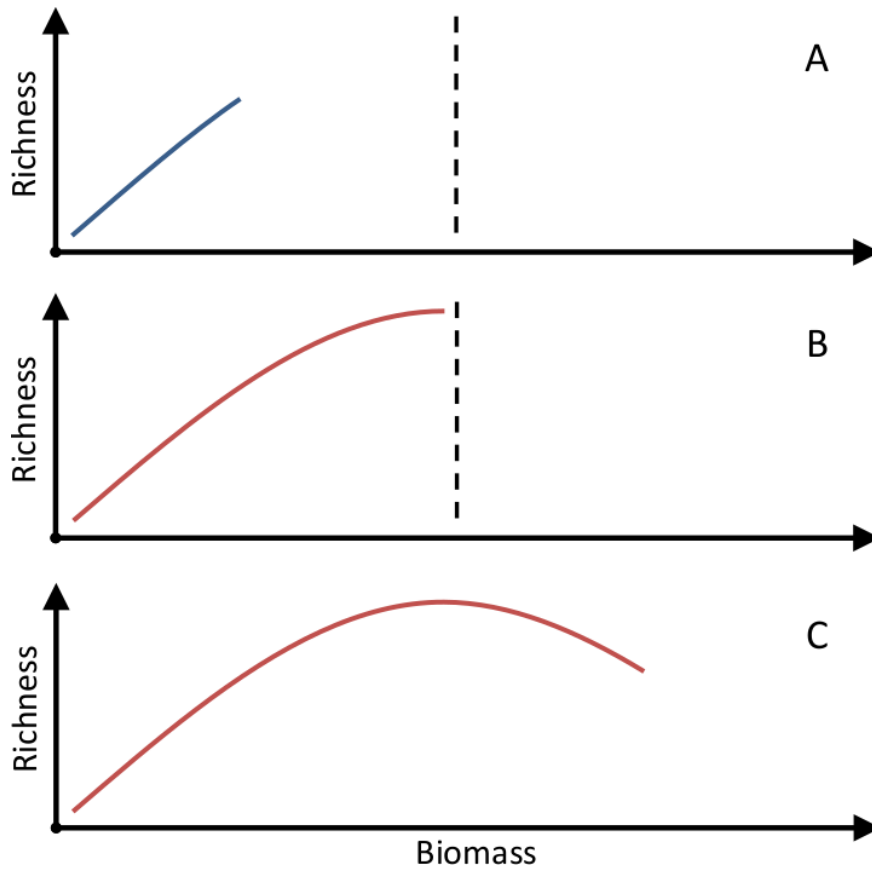


Figure 4.1. Hypothesized relationship between standing aboveground biomass and taxonomic richness. (A) A large disturbance, such as an outbreak of phytophagous insects, would reduce standing biomass to below the prior limit seen under historical climates (dashed bar). (B) Persistent herbivory may maintain 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.

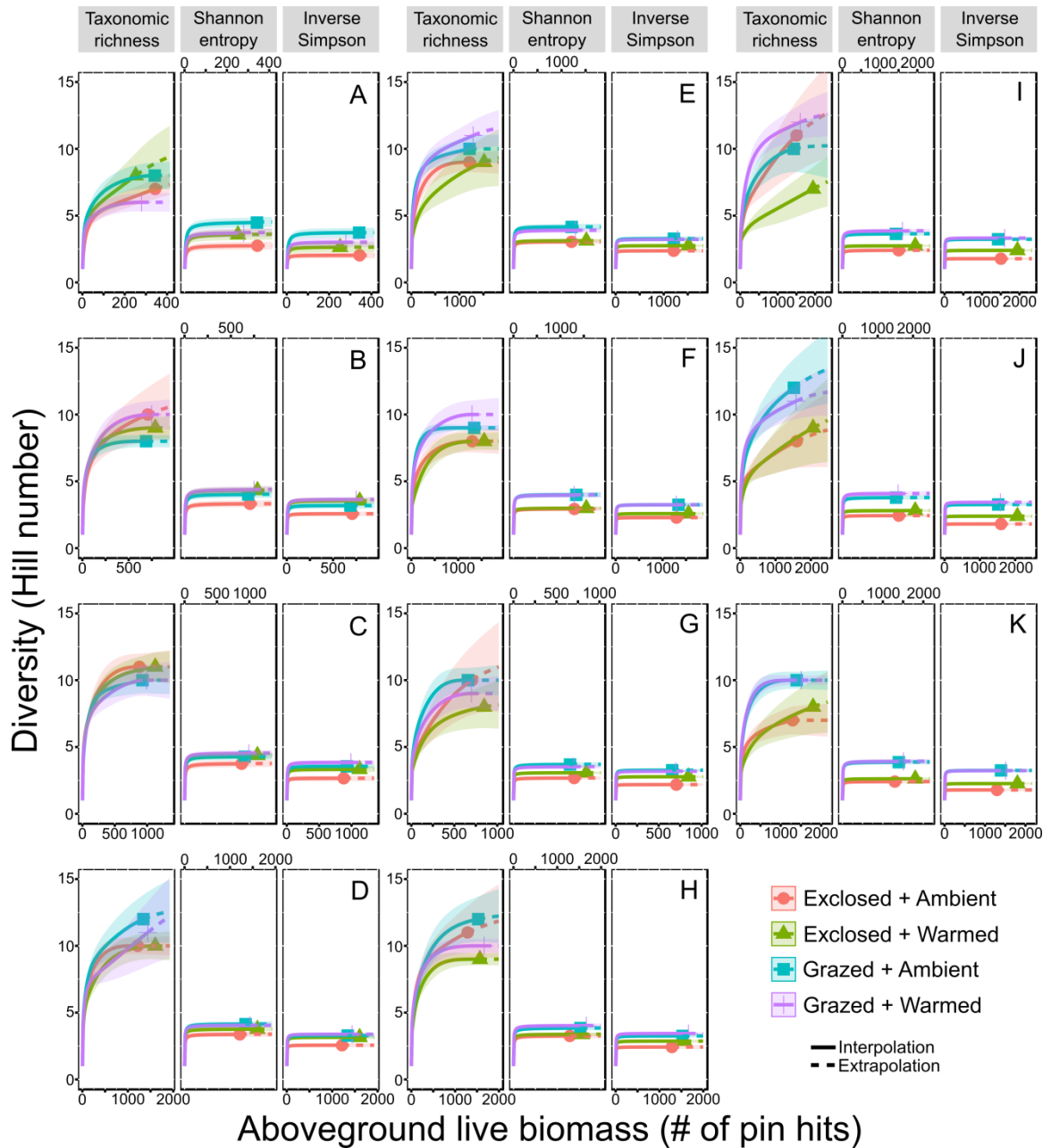


Figure 4.2. Rarefaction and extrapolation profiles for the four warming and herbivore exclusion treatments. Shown here are the individual years 2005 through 2015 (A through K). Note that the x-axes are scaled to be 1.2 times the total of the treatment with the maximal biomass for a given year. Taxonomic 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).

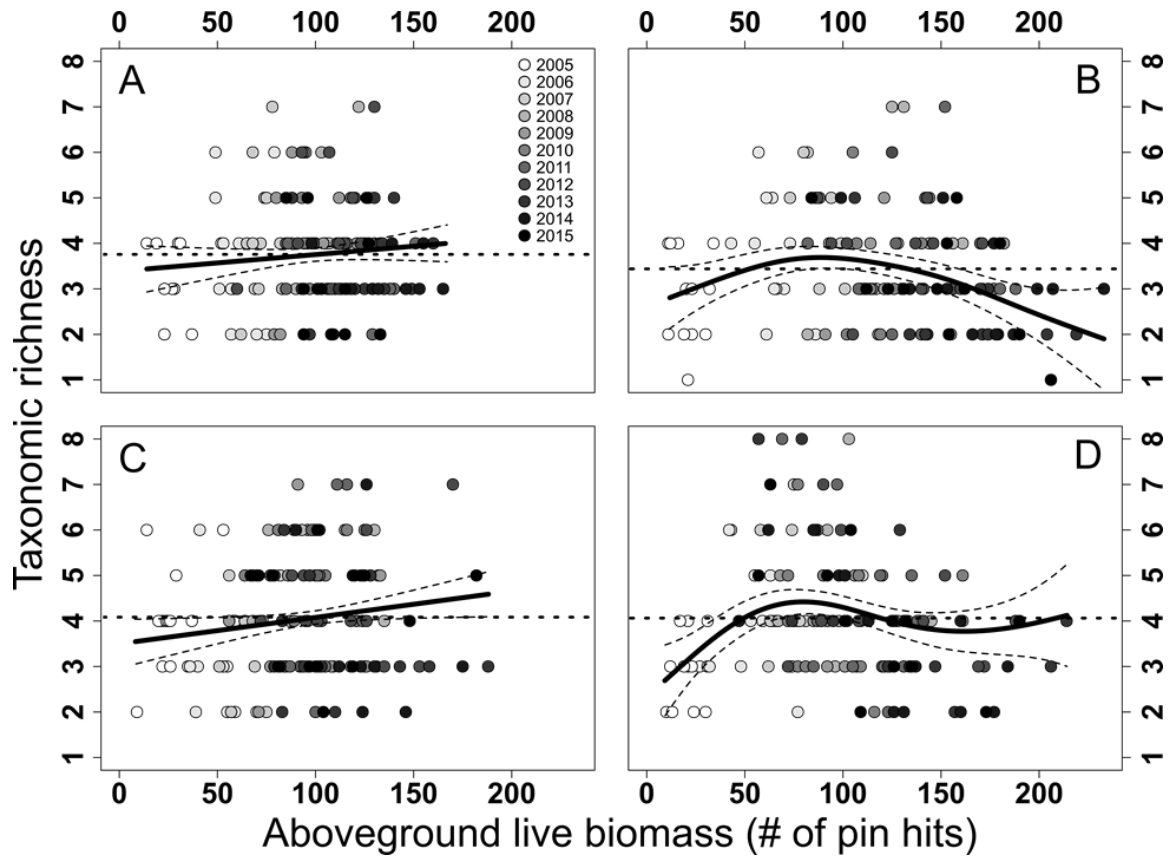


Figure 4.3. Generalized additive mixed model of total biomass and taxonomic richness. Smoothing splines are shown here separated by treatment: excluded + ambient, excluded + warmed, grazed + ambient, and grazed + warmed (A through D). Both warmed treatments as well as the grazed + ambient treatment contained significant smooths (see Table 4.1), though only the linear mixed effects model for the excluded + warmed treatment had a significant second-order polynomial term for biomass (see Table 4.2).

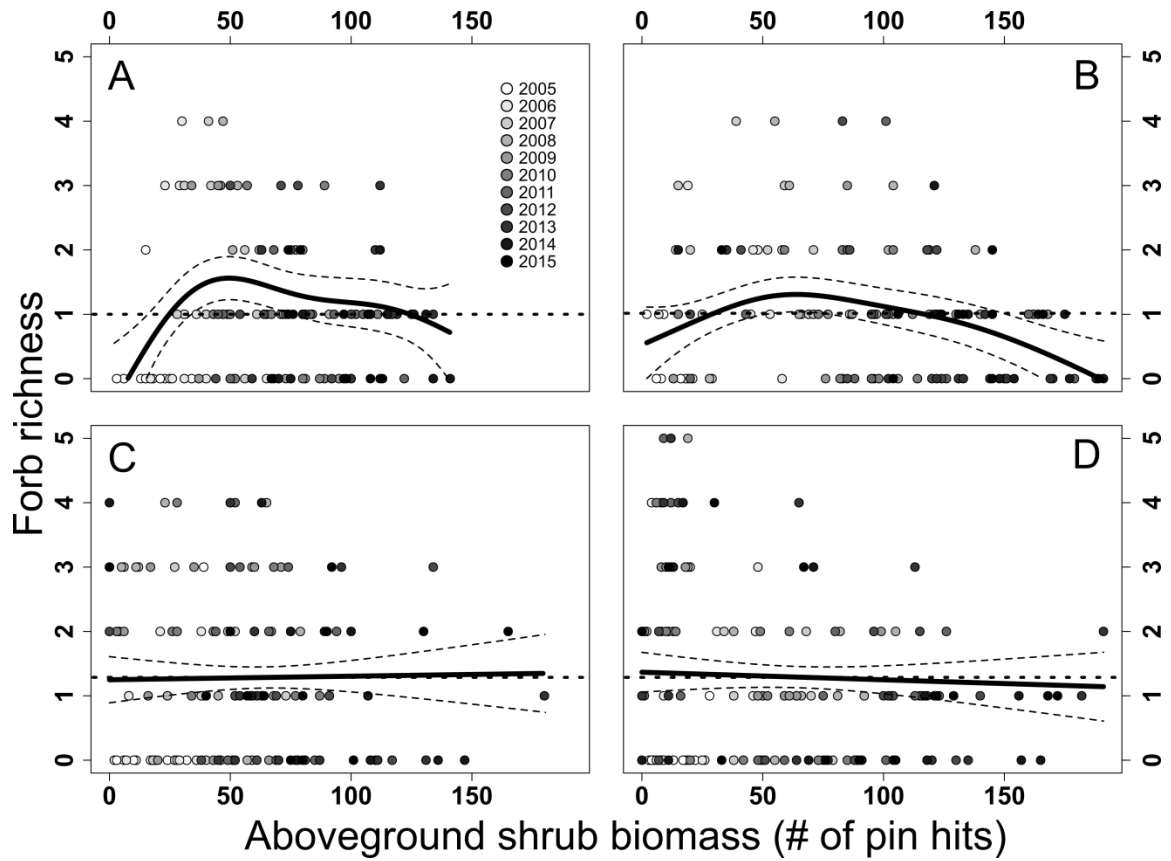


Figure 4.4. Generalized additive mixed model of shrub biomass and forb richness. Smoothing splines are shown here separated by treatment: excluded + ambient, excluded + warmed, grazed + ambient, and grazed + warmed (A through D). Both excluded treatments contained significant smooths (see Table 4.1), 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 excluded + ambient (EA), excluded + warmed (EW), grazed + ambient (GA), and grazed + warmed (GW) treatments. SEM is the standard error of the mean.

<b>Parameter</b>	<b><i>df/edf</i></b>	<b><i>F</i></b>	<b><i>P</i></b>
<i>(A) Total</i>			
Site	2	3.974	0.019
Exclusion	1	9.398	0.002
Warming	1	3.009	0.083
Site*Exclusion	2	3.716	0.025
Site*Warming	2	3.675	0.026
Exclusion*Warming	1	4.787	0.029
Site*Exclusion*Warming	2	4.159	0.016
s(EA)	1.000	1.702	0.193
s(EW)	2.767	5.857	0.001
s(GA)	1.000	4.868	0.028
s(GW)	3.554	5.227	0.001
<i>(B) Forbs</i>			
Site	2	13.496	0.000
Exclusion	1	10.352	0.001
Warming	1	25.383	0.000
Site*Exclusion	2	3.171	0.043
Site*Warming	2	9.895	0.000
Exclusion*Warming	1	28.905	0.000
Site*Exclusion*Warming	2	11.570	0.000
s(EA)	3.646	4.133	0.003
s(EW)	3.447	8.923	0.000
s(GA)	1.000	0.352	0.553
s(GW)	1.000	0.032	0.858



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]<sup>2</sup>) and shrub biomass (shrubs and [shrubs]<sup>2</sup>).

Treatment	Parameter	Estimate	SEM	<i>df</i>	<i>t</i> -value	<i>P</i>
<i>(A) Total</i>						
EA	Live	1.828	1.149	117	1.591	0.114
	(Live) <sup>2</sup>	-1.716	1.072	117	-1.601	0.112
	Litter	-0.045	0.020	117	-2.247	0.027
EW	Live	-0.503	1.188	117	-0.423	0.673
	(Live) <sup>2</sup>	-3.437	1.133	117	-3.034	0.003
	Litter	-0.059	0.020	117	-2.983	0.004
GA	Live	3.217	1.270	127	2.533	0.013
	(Live) <sup>2</sup>	0.396	1.187	127	0.334	0.739
	Litter	-0.014	0.018	127	-0.738	0.462
GW	Live	2.675	1.248	127	2.144	0.034
	(Live) <sup>2</sup>	-1.197	1.086	127	-1.102	0.272
	Litter	-0.071	0.019	127	-3.755	0.000
<i>(B) Forbs</i>						
EA	Shrubs	0.317	1.073	117	0.296	0.768
	(Shrubs) <sup>2</sup>	-2.205	0.897	117	-2.458	0.015
	Litter	-0.039	0.016	117	-2.361	0.020
EW	Shrubs	-0.456	1.002	117	-0.456	0.649
	(Shrubs) <sup>2</sup>	-3.677	0.876	117	-4.195	0.000
	Litter	-0.054	0.015	117	-3.688	0.000
GA	Shrubs	3.013	1.329	127	2.267	0.025
	(Shrubs) <sup>2</sup>	-1.146	1.071	127	-1.070	0.287
	Litter	-0.029	0.014	127	-2.051	0.042
GW	Shrubs	2.328	1.655	127	1.407	0.162
	(Shrubs) <sup>2</sup>	0.341	1.141	127	0.298	0.766
	Litter	-0.082	0.017	127	-4.893	0.000

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  $R^2$ ).

<b>Treatment</b>	<b>Parameters</b>	<b>Marginal <math>R^2</math></b>	<b>Conditional <math>R^2</math></b>
<i>(A) Total</i>			
EA	Litter	0.033	0.195
EW	Live, (Live) <sup>2</sup> , Litter	0.151	0.405
GA	Live	0.036	0.427
GW	Live, Litter	0.143	0.414
<i>(B) Forbs</i>			
EA	Shrubs, (Shrubs) <sup>2</sup> , Litter	0.064	0.343
EW	Shrubs, (Shrubs) <sup>2</sup> , Litter	0.177	0.487
GA	Shrubs, Litter	0.029	0.462
GW	Litter	0.155	0.325

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.

<b>Parameter</b>	<b>Estimate</b>	<b>SEM</b>	<b><i>t</i>-value</b>	<b><i>P</i></b>
<i>(A) Total</i>				
(Intercept)	1.184	0.061	19.270	0.000
Site 2	0.225	0.083	2.729	0.007
Site 3	0.158	0.072	2.201	0.028
Grazed	0.260	0.085	3.066	0.002
Warmed	0.150	0.086	1.735	0.083
Site 2*Grazed	-0.105	0.116	-0.908	0.364
Site 3*Grazed	-0.262	0.101	-2.604	0.009
Site 2*Warmed	-0.297	0.119	-2.509	0.012
Site 3*Warmed	-0.238	0.103	-2.312	0.021
Grazed*Warmed	-0.266	0.121	-2.188	0.029
Site 2*Grazed*Warmed	0.433	0.169	2.571	0.010
Site 3*Grazed*Warmed	0.371	0.144	2.581	0.010
<i>(B) Forbs</i>				
(Intercept)	-1.288	0.238	-5.407	0.000
Site 2	0.904	0.285	3.177	0.002
Site 3	1.245	0.240	5.195	0.000
Grazed	0.950	0.295	3.218	0.001
Warmed	1.563	0.310	5.038	0.000
Site 2*Grazed	0.005	0.381	0.012	0.991
Site 3*Grazed	-0.658	0.325	-2.027	0.043
Site 2*Warmed	-1.618	0.399	-4.051	0.000
Site 3*Warmed	-1.342	0.341	-3.940	0.000
Grazed*Warmed	-2.196	0.408	-5.376	0.000
Site 2*Grazed*Warmed	2.206	0.559	3.949	0.000
Site 3*Grazed*Warmed	2.103	0.464	4.532	0.000

## 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 (Klady 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<sup>2</sup>). 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

- Anderson, N. J., K. P. Brodersen, D. B. Ryves, S. McGowan, L. S. Johansson, E. Jeppesen, and M. J. Leng. 2008. Climate versus in-lake processes as controls on the development of community structure in a Low-Arctic lake (South-West Greenland). *Ecosystems* 11:307–324.
- Aronson, J., C. Murcia, G. H. Kattan, D. Moreno-Mateos, K. Dixon, and D. Simberloff. 2014. The road to confusion is paved with novel ecosystem labels: A reply to Hobbs et al. *Trends in Ecology & Evolution* 29:646–647.
- te Beest, M., J. J. L. Roux, D. M. Richardson, A. K. Brysting, J. Suda, M. Kubešová, and P. Pyšek. 2012. The more the better? The role of polyploidy in facilitating plant invasions. *Annals of Botany* 109:19–45.
- Bennike, O. 2000. Palaeoecological studies of Holocene lake sediments from west Greenland. *Palaeogeography, Palaeoclimatology, Palaeoecology* 155:285–304.
- Bennike, O., and S. Björck. 2002. Chronology of the last recession of the Greenland Ice Sheet. *Journal of Quaternary Science* 17:211–219.
- Bliss, L. C. 1956. A comparison of plant development in microenvironments of arctic and alpine tundras. *Ecological Monographs* 26:303–337.
- Bliss, L. C. 1958. Seed germination in arctic and alpine species. *Arctic* 11:180–188.
- Bliss, L. C. 1962. Adaptations of arctic and alpine plants to environmental conditions. *Arctic* 15:117–144.
- Bliss, L. C. 1971. Arctic and alpine plant life cycles. *Annual Review of Ecology and Systematics* 2:405–438.
- Boelman, N. T., L. Gough, J. Wingfield, S. Goetz, A. Asmus, H. E. Chmura, J. S. Krause, J. H. Perez, S. K. Sweet, and K. C. Guay. 2015. Greater shrub dominance alters breeding

- habitat and food resources for migratory songbirds in Alaskan arctic tundra. *Global Change Biology* 21:1508–1520.
- Bret-Harte, M. S., M. C. Mack, G. R. Goldsmith, D. B. Sloan, J. DeMarco, G. R. Shaver, P. M. Ray, Z. Biesinger, and F. S. Chapin. 2008. Plant functional types do not predict biomass responses to removal and fertilization in Alaskan tussock tundra. *Journal of Ecology* 96:713–726.
- Bret-Harte, M. S., G. R. Shaver, and F. S. Chapin. 2002. Primary and secondary stem growth in arctic shrubs: Implications for community response to environmental change. *Journal of Ecology* 90:251–267.
- Bret-Harte, M. S., G. R. Shaver, J. P. Zoerner, J. F. Johnstone, J. L. Wagner, A. S. Chavez, R. F. Gunkelman, S. C. Lippert, and J. A. Laundre. 2001. Developmental plasticity allows *Betula nana* to dominate tundra subjected to an altered environment. *Ecology* 82:18–32.
- Brooks, W. S. 1968. Comparative adaptations of the Alaskan redpolls to the Arctic environment. *The Wilson Bulletin* 80:253–280.
- Cahoon, S. M. P., P. F. Sullivan, E. Post, and J. M. Welker. 2012. Large herbivores limit CO<sub>2</sub> uptake and suppress carbon cycle responses to warming in West Greenland. *Global Change Biology* 18:469–479.
- Chapin, F. S., M. S. Bret-Harte, S. E. Hobbie, and H. Zhong. 1996. Plant functional types as predictors of transient responses of arctic vegetation to global change. *Journal of Vegetation Science* 7:347–358.
- Christie, K. S., J. P. Bryant, L. Gough, V. T. Ravolainen, R. W. Ruess, and K. D. Tape. 2015. The role of vertebrate herbivores in regulating shrub expansion in the Arctic: A synthesis. *BioScience* 65:1123–1133.

- Christie, K. S., M. S. Lindberg, R. W. Ruess, and J. A. Schmutz. 2014a. Spatio-temporal patterns of ptarmigan occupancy relative to shrub cover in the Arctic. *Polar Biology* 37:1111–1120.
- Christie, K. S., R. W. Ruess, M. S. Lindberg, and C. P. Mulder. 2014b. Herbivores influence the growth, reproduction, and morphology of a widespread arctic willow. *PLoS ONE* 9:e101716.
- Den Herder, M., R. Virtanen, and H. Roininen. 2004. Effects of reindeer browsing on tundra willow and its associated insect herbivores. *Journal of Applied Ecology* 41:870–879.
- Díaz, S., and M. Cabido. 2001. Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution* 16:646–655.
- Dobeš, C., A. Milosevic, D. Prohaska, S. Scheffknecht, T. F. Sharbel, and K. Hülber. 2013. Reproductive differentiation into sexual and apomictic polyploid cytotypes in *Potentilla puberula* (Potentilleae, Rosaceae). *Annals of Botany* 112:1159–1168.
- Donnelly, A., A. Caffarra, and B. O’Neill. 2011. A review of climate-driven mismatches between interdependent phenophases in terrestrial and aquatic ecosystems. *International Journal of Biometeorology* 55:805–817.
- Douhovnikoff, V., G. R. Goldsmith, K. D. Tape, C. Huang, N. Sur, and M. S. Bret-Harte. 2010. Clonal diversity in an expanding community of arctic *Salix* spp. and a model for recruitment modes of arctic plants. *Arctic, Antarctic, and Alpine Research* 42:406–411.
- Drees, B., and F. J. A. Daniëls. 2009. Mountain vegetation of south-facing slopes in continental West Greenland. *Phytocoenologia* 39:1–25.
- Ehrich, D., J.-A. Henden, R. A. Ims, L. O. Doronina, S. T. Killengren, N. Lecomte, I. G. Pokrovsky, G. Skogstad, A. A. Sokolov, V. A. Sokolov, and N. G. Yoccoz. 2011. The importance of willow thickets for ptarmigan and hares in shrub tundra: The more the better? *Oecologia* 168:141–151.



- Elmendorf, S. C., G. H. R. Henry, R. D. Hollister, R. G. Björk, A. D. Bjorkman, T. V. Callaghan, L. S. Collier, E. J. Cooper, J. H. C. Cornelissen, T. A. Day, A. M. Fosaa, W. A. Gould, J. Grétarsdóttir, J. Harte, L. Hermanutz, D. S. Hik, A. Hofgaard, F. Jarrad, I. S. Jónsdóttir, F. Keuper, K. Klanderud, J. A. Klein, S. Koh, G. Kudo, S. I. Lang, V. Loewen, J. L. May, J. Mercado, A. Michelsen, U. Molau, I. H. Myers-Smith, S. F. Oberbauer, S. Pieper, E. Post, C. Rixen, C. H. Robinson, N. M. Schmidt, G. R. Shaver, A. Stenström, A. Tolvanen, Ø. Totland, T. Troxler, C.-H. Wahren, P. J. Webber, J. M. Welker, and P. A. Wookey. 2012a. Global assessment of experimental climate warming on tundra vegetation: Heterogeneity over space and time. *Ecology Letters* 15:164–175.
- Elmendorf, S. C., G. H. R. Henry, R. D. Hollister, R. G. Björk, N. Boulanger-Lapointe, E. J. Cooper, J. H. C. Cornelissen, T. A. Day, E. Dorrepaal, T. G. Elumeeva, M. Gill, W. A. Gould, J. Harte, D. S. Hik, A. Hofgaard, D. R. Johnson, J. F. Johnstone, I. S. Jónsdóttir, J. C. Jorgenson, K. Klanderud, J. A. Klein, S. Koh, G. Kudo, M. Lara, E. Lévesque, B. Magnússon, J. L. May, J. A. Mercado-Díaz, A. Michelsen, U. Molau, I. H. Myers-Smith, S. F. Oberbauer, V. G. Onipchenko, C. Rixen, N. M. Schmidt, G. R. Shaver, M. J. Spasojevic, Þ. E. Þórhallsdóttir, A. Tolvanen, T. Troxler, C. E. Tweedie, S. Villareal, C.-H. Wahren, X. Walker, P. J. Webber, J. M. Welker, and S. Wipf. 2012b. Plot-scale evidence of tundra vegetation change and links to recent summer warming. *Nature Climate Change* 2:453–457.
- Elzinga, J. A., A. Atlan, A. Biere, L. Gigord, A. E. Weis, and G. Bernasconi. 2007. Time after time: Flowering phenology and biotic interactions. *Trends in Ecology & Evolution* 22:432–439.
- Field, C. B., D. B. Lobell, H. A. Peters, and N. R. Chiariello. 2007. Feedbacks of terrestrial ecosystems to climate change. *Annual Review of Environment and Resources* 32:1–29.

- Flora of North America Editorial Committee, editors. 1993+. *Flora of North America North of Mexico*. 19+ volumes. New York, NY, USA and Oxford, UK.
- Forrest, J. R. K. 2015. Plant–pollinator interactions and phenological change: What can we learn about climate impacts from experiments and observations? *Oikos* 124:4–13.
- Graae, B., R. Ejrnæs, S. Lang, E. Meineri, P. Ibarra, and H. Bruun. 2011. Strong microsite control of seedling recruitment in tundra. *Oecologia* 166:565–576.
- Hegland, S. J., A. Nielsen, A. Lázaro, A.-L. Bjerknes, and Ø. Totland. 2009. How does climate warming affect plant-pollinator interactions? *Ecology Letters* 12:184–195.
- Henden, J.-A., N. G. Yoccoz, R. A. Ims, and K. Langeland. 2013. How spatial variation in areal extent and configuration of labile vegetation states affect the riparian bird community in arctic tundra. *PLoS ONE* 8:e63312.
- Herben, T., B. Šerá, and J. Klimešová. 2015. Clonal growth and sexual reproduction: Tradeoffs and environmental constraints. *Oikos* 124:469–476.
- Hobbs, R. J., E. Higgs, C. M. Hall, P. Bridgewater, F. S. Chapin, E. C. Ellis, J. J. Ewel, L. M. Hallett, J. Harris, K. B. Hulvey, S. T. Jackson, P. L. Kennedy, C. Kueffer, L. Lach, T. C. Lantz, A. E. Lugo, J. Mascaro, S. D. Murphy, C. R. Nelson, M. P. Perring, D. M. Richardson, T. R. Seastedt, R. J. Standish, B. M. Starzomski, K. N. Suding, P. M. Tognetti, L. Yakob, and L. Yung. 2014. Managing the whole landscape: Historical, hybrid, and novel ecosystems. *Frontiers in Ecology and the Environment* 12:557–564.
- Hörandl, E. 2010. The evolution of self-fertility in apomictic plants. *Sexual plant reproduction* 23:73–86.
- Høye, T. T., E. Post, N. M. Schmidt, K. Trøjelsgaard, and M. C. Forchhammer. 2013. Shorter flowering seasons and declining abundance of flower visitors in a warmer Arctic. *Nature Climate Change* 3:759–763.

- Inouye, D. W. 2008. Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology* 89:353–362.
- Kevan, P. G. 1972. Insect pollination of High Arctic flowers. *Journal of Ecology* 60:831–847.
- Klady, R. A., G. H. R. Henry, and V. Lemay. 2011. Changes in high arctic tundra plant reproduction in response to long-term experimental warming. *Global Change Biology* 17:1611–1624.
- Kudo, G. 1991. Effects of snow-free period on the phenology of alpine plants inhabiting snow patches. *Arctic and Alpine Research* 23:436–443.
- Suzuki, S., and G. Kudo. 2000. Responses of alpine shrubs to simulated environmental change during three years in the mid-latitude mountain, northern Japan. *Ecography* 23:553–564.
- Lavorel, S., S. Díaz, J. H. C. Cornelissen, E. Garnier, S. P. Harrison, S. McIntyre, J. G. Pausas, N. Pérez-Harguindeguy, C. Roumet, and C. Urcelay. 2007. Plant functional types: Are we getting any closer to the Holy Grail? Pages 149–164 *in* J. G. Canadell, D. E. Pataki, and L. F. Pitelka, editors. *Terrestrial Ecosystems in a Changing World*. Springer Berlin Heidelberg.
- Legault, G., and A. E. Weis. 2013. The impact of snow accumulation on a heath spider community in a sub-Arctic landscape. *Polar Biology* 36:885–894.
- Leishman, M. R., G. J. Masters, I. P. Clarke, and V. K. Brown. 2000. Seed bank dynamics: The role of fungal pathogens and climate change. *Functional Ecology* 14:293–299.
- McKinney, A., and K. Goodell. 2010. Shading by invasive shrub reduces seed production and pollinator services in a native herb. *Biological Invasions* 12:2751–2763.
- Miller-Rushing, A. J., T. T. Høye, D. W. Inouye, and E. Post. 2010. The effects of phenological mismatches on demography. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:3177–3186.

- Molau, U., and G. R. Shaver. 1997. Controls on seed production and seed germinability in *Eriophorum vaginatum*. *Global Change Biology* 3:80–88.
- Mondoni, A., G. Rossi, S. Orsenigo, and R. J. Probert. 2012. Climate warming could shift the timing of seed germination in alpine plants. *Annals of Botany* 110:155–164.
- Moulton, C. A., and L. Gough. 2011. Effects of soil nutrient availability on the role of sexual reproduction in an Alaskan tundra plant community. *Arctic, Antarctic, and Alpine Research* 43:612–620.
- Myers-Smith, I. H., B. C. Forbes, M. Wilmsking, M. Hallinger, T. Lantz, D. Blok, K. D. Tape, M. Macias-Fauria, U. Sass-Klaassen, E. Lévesque, S. Boudreau, P. Ropars, L. Hermanutz, A. Trant, L. S. Collier, S. Weijers, J. Rozema, S. A. Rayback, N. M. Schmidt, G. Schaeppman-Strub, S. Wipf, C. Rixen, C. B. Ménard, S. Venn, S. Goetz, L. Andreu-Hayles, S. Elmendorf, V. Ravolainen, J. Welker, P. Grogan, H. E. Epstein, and D. S. Hik. 2011. Shrub expansion in tundra ecosystems: Dynamics, impacts and research priorities. *Environmental Research Letters* 6:45509.
- Norrmann, G. A., C. L. Quarin, and B. L. Burson. 1989. Cytogenetics and reproductive behavior of different chromosome races in six *Paspalum* species. *Journal of Heredity* 80:24–28.
- Olofsson, J., L. Oksanen, T. Callaghan, P. E. Hulme, T. Oksanen, and O. Suominen. 2009. Herbivores inhibit climate-driven shrub expansion on the tundra. *Global Change Biology* 15:2681–2693.
- Pallardy, S. G. 2008. *Physiology of Woody Plants*. 3rd edition. Academic Press, San Diego, CA, USA.
- Pandit, M. K., M. J. O. Pockock, and W. E. Kunin. 2011. Ploidy influences rarity and invasiveness in plants. *Journal of Ecology* 99:1108–1115.

- Post, E., and M. C. Forchhammer. 2008. Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. *Philosophical Transactions of the Royal Society B: Biological Sciences* 363:2369–2375.
- Post, E., and C. Pedersen. 2008. Opposing plant community responses to warming with and without herbivores. *Proceedings of the National Academy of Sciences* 105:12353–12358.
- Price, M. V., D. R. Campbell, N. M. Waser, and A. K. Brody. 2008. Bridging the generation gap in plants: Pollination, parental fecundity, and offspring demography. *Ecology* 89:1596–1604.
- Ramsey, J., and D. W. Schemske. 1998. Pathways, mechanisms, and rates of polyploid formation in flowering plants. *Annual Review of Ecology and Systematics* 29:467–501.
- Rich, M. E., L. Gough, and N. T. Boelman. 2013. Arctic arthropod assemblages in habitats of differing shrub dominance. *Ecography* 36:994–1003.
- Schafer, M., and P. M. Kotanen. 2003. The influence of soil moisture on losses of buried seeds to fungi. *Acta Oecologica* 24:255–263.
- Schafer, M., and P. M. Kotanen. 2004. Impacts of naturally-occurring soil fungi on seeds of meadow plants. *Plant Ecology* 175:19–35.
- Serapiglia, M. J., F. E. Gouker, J. F. Hart, F. Unda, S. D. Mansfield, A. J. Stipanovic, and L. B. Smart. 2014. Ploidy level affects important biomass traits of novel shrub willow (*Salix*) hybrids. *BioEnergy Research*:1–11.
- Shevtsova, A., B. J. Graae, T. Jochum, A. Milbau, F. Kockelbergh, L. Beyens, and I. Nijs. 2009. Critical periods for impact of climate warming on early seedling establishment in subarctic tundra. *Global Change Biology* 15:2662–2680.
- Sokolov, V., D. Ehrich, N. G. Yoccoz, A. Sokolov, and N. Lecomte. 2012. Bird communities of the Arctic shrub tundra of Yamal: Habitat specialists and generalists. *PLoS ONE* 7:e50335.

- Sturm, M., J. P. McFadden, G. E. Liston, F. S. Chapin III, C. H. Racine, and J. Holmgren. 2001. Snow-shrub interactions in arctic tundra: A hypothesis with climatic implications. *Journal of Climate* 14:336.
- Suding, K. N., and L. J. Goldstein. 2008. Testing the Holy Grail framework: Using functional traits to predict ecosystem change. *The New Phytologist* 180:559–562.
- Tape, K. D., R. Lord, H.-P. Marshall, and R. W. Ruess. 2010. Snow-mediated ptarmigan browsing and shrub expansion in Arctic Alaska. *Ecoscience* 17:186–193.
- Tyler, G. 2001. Relationships between climate and flowering of eight herbs in a Swedish deciduous forest. *Annals of Botany* 87:623–630.
- Virtanen, R., H. Henttonen, and K. Laine. 1997. Lemming grazing and structure of a snowbed plant community: A long-term experiment at Kilpisjärvi, Finnish Lapland. *Oikos* 79:155–166.
- Wagner, B., and O. Bennike. 2012. Chronology of the last deglaciation and Holocene environmental changes in the Sisimiut area, SW Greenland based on lacustrine records. *Boreas* 41:481–493.
- Wahren, C.-H. A., M. D. Walker, and M. S. Bret-Harte. 2005. Vegetation responses in Alaskan arctic tundra after 8 years of a summer warming and winter snow manipulation experiment. *Global Change Biology* 11:537–552.
- Walck, J. L., S. N. Hidayati, K. W. Dixon, K. Thompson, and P. Poschod. 2011. Climate change and plant regeneration from seed. *Global Change Biology* 17:2145–2161.
- Walker, B., A. Kinzig, and J. Langridge. 1999. Plant attribute diversity, resilience, and ecosystem function: The nature and significance of dominant and minor species. *Ecosystems* 2:95–113.
- Walker, M. D., C. H. Wahren, R. D. Hollister, G. H. R. Henry, L. E. Ahlquist, J. M. Alatalo, M. S. Bret-Harte, M. P. Calef, T. V. Callaghan, A. B. Carroll, H. E. Epstein, I. S. Jónsdóttir,

J. A. Klein, B. Magnússon, U. Molau, S. F. Oberbauer, S. P. Rewa, C. H. Robinson, G. R. Shaver, K. N. Suding, C. C. Thompson, A. Tolvanen, Ø. Totland, P. L. Turner, C. E. Tweedie, P. J. Webber, and P. A. Wookey. 2006. Plant community responses to experimental warming across the tundra biome. *Proceedings of the National Academy of Sciences of the United States of America* 103:1342–1346.

Zamin, T. J., and P. Grogan. 2013. Caribou exclusion during a population low increases deciduous and evergreen shrub species biomass and nitrogen pools in low Arctic tundra. *Journal of Ecology* 101:671–683.

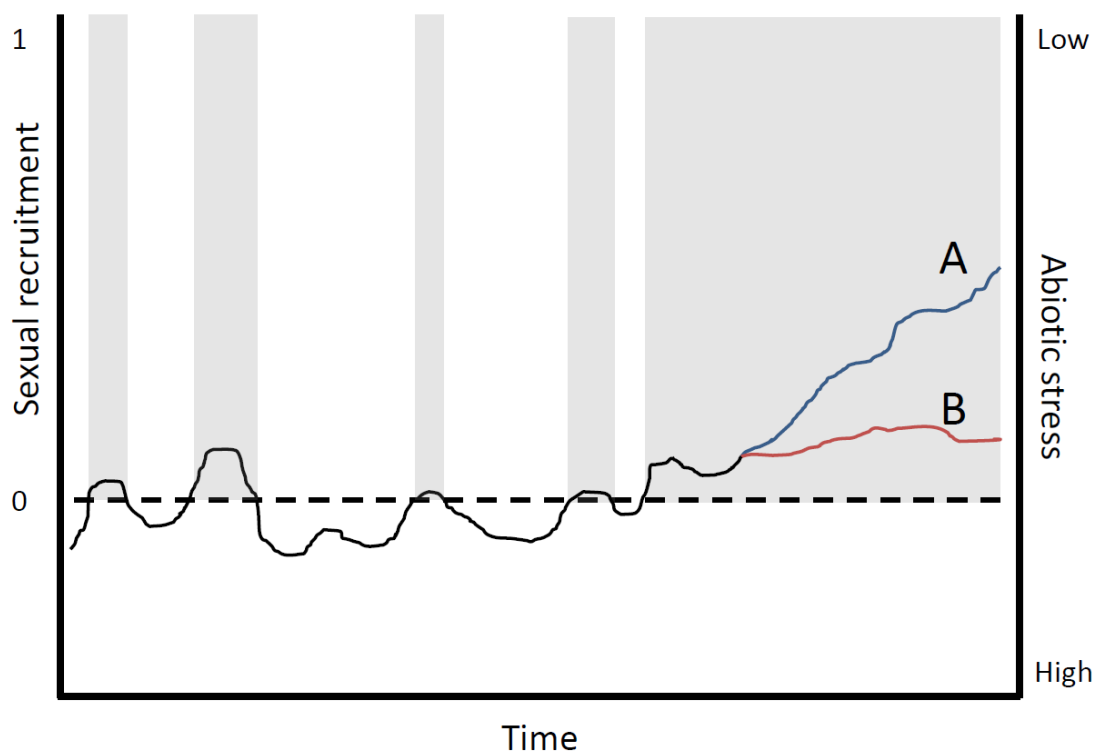


Figure 5.1. Conceptual model of the probability of successful sexual recruitment over time (e.g. decades to centuries) as abiotic stress varies. Historic abiotic stress is indicated by the solid black line, and a theoretical threshold above which sexual recruitment is possible because abiotic stress 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

Amanda B. Young<sup>1\*</sup>, David A. Watts<sup>2,3</sup>, Alan H. Taylor<sup>1,3</sup>, Eric Post<sup>2,3</sup>

<sup>1</sup>Department of Geography

<sup>2</sup>The Polar Center and Department of Biology

<sup>3</sup>Ecology Intercollege Graduate Degree Program

Pennsylvania State University

University Park, PA 16802, USA

\*Corresponding Author

Phone: +1(814) 863-7702

Fax: (814) 863-7943

E-mail: aby113@psu.edu

Published in *Dendrochronologia* 37 (2016) 69-78

<http://dx.doi.org/10.1016/j.dendro.2015.12.007>

### 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,  $\delta^{18}\text{O}$ ,  $\text{CH}_4$ , and  $\text{NO}_2$  [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 Poschod, 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 m<sup>2</sup> 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 ( $\sim 90^\circ$  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 ( $\bar{r}$ ), 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 *Betula* (87.1%) and *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 *E. occulta* make up the largest proportion, are important in the diet of Lapland longspurs (*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. *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 *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 *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 *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). *Empetrum nigrum* ssp. *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, *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 ( $\sim 1 \text{ m}^2$ ). 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.

### Acknowledgements

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.

### References

- Alley, R., 2000. The Younger Dryas cold interval as viewed from central Greenland. *Quaternary Science Reviews* 19, 213-226.
- Andersen, K., Axuma, N., Barnola, J.-M., Bigler, M., Biscaye, P., Caillon, N., Chappellaz, J., Clausen, H., Dahl-Jensen, D., Fischer, H., Flückiger, J., Fritzsche, D., Fujii, Y., Goto-Azuma, K., Grønvold, K., Gundestrup, N., Hansson, M., Huber, C., Hvidberg, S., Johnsen, S., Jonsell, U., Jouzel, J., Kipfstuhl, S., Landais, A., Leuenberger, M., Lorrain, R., Masson-Delmotte, V., Miller, H., Motoyama, H., Narita, H., Popp, T., Rasmussen, S., Raynaud, D., Rothlisberger, R., Ruth, U., Samyn, D., Schwander, J., Shoji, H., Siggard-Andersen, M.-L., Steffensen, J., Stocker, T., Sveinbjörnsdóttir, A., Svensson, A., Takata, M., Tison, J.-L., Thorsteinsson, T., Watanabe, O., Wilhelms, F., White, J., 2004. High resolution record of Northern Hemisphere climate extending into the last interglacial period. *Nature* 43, 147-151.

- Avery, M., Post, E., 2013. Record of a *Zoophthora* sp. (Entomophthoromycota: Entomophthorales) pathogen of the irruptive noctuid moth *Eurois occulta* (Lepidoptera) in West Greenland. *Journal of Invertebrate Pathology* 114,292-294.
- Bär, A., Bräuning, A., Löffler, J., 2006. Dendroecology of dwarf shrubs in the high mountains of Norway – A methodological approach. *Dendrochronologia* 24, 17–27.
- Bär, A., Pape, R., Bräuning, A., Löffler, J., 2008. Growth-ring variations of dwarf shrubs reflect regional climate signals in alpine environments rather than topoclimatic differences. *Journal of Biogeography* 35, 625-636.
- Bartoń, K., 2012. MuMIn: multi-model inference. R Package, version 1.9.13. URL <https://cran.r-project.org/package=MuMIn>.
- Bhatt, U., Walker, D., Raynolds, M., Comiso, J., Epstein, H., Jia, G., Gens, R., Pinzon, J., Tucker, C., Tweedie, C., Webber, P., 2010. Circumpolar Arctic tundra vegetation change is linked to sea ice decline. *Earth Interactions* 14, 1-20.
- Blok, D., Sass-Klaassen, U., Schaepman-Strub, G., Heijmans, M., Sauren, P., Berendse, F., 2011. What are the main climate drivers for shrub growth in Northeastern Siberian tundra? *Biogeosciences* 8, 1169-1179.
- Blok, D., Weijers, S., Welker, J. M., Cooper, E. J., Michelsen, A., Löffler, J., Elberling, B., 2015. Deepened winter snow increases stem growth and alters stem  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  in evergreen dwarf shrub *Cassiope tetragona* in high-arctic Svalbard tundra. *Environmental Research Letters* 10, 044008.
- Blunier, T., Barnett, B., Bender, M., Hendricks, M., 2002. Biological oxygen productivity during the last 60,000 years from triple oxygen isotope measurements. *Global Biogeochemical Cycles* 16, 3-1-3-13.

- Bradley, R. S., 2011. High-resolution paleoclimatology, in: Hughes, M. K., Swetnam, T. W., Diaz, H. F. (Eds.), *Dendroclimatology: Progress and Prospects*. Springer Netherlands, pp. 3-15.
- Bret-Harte, M.S., Shaver, G., Zoerner, J., Johnstone, J., Wagner, J., Chaves, A., Gunkelman, R., Lippert, S., Laundre, J., 2001. Developmental plasticity allows *Betula nana* to dominate tundra subjected to an altered environment. *Ecology* 82, 18-32.
- Bret-Harte, M.S., Shaver, G.R., Chapin, F.S. III., 2002. Primary and secondary stem growth in arctic shrubs: implications for community response to environmental change. *Journal of Ecology* 90, 251-267.
- Bret-Harte, M.S., Mack, M., Goldsmith, G., Sloan, D., DeMarco, J., Shaver, G., Ray, P., Biesinger, Z., Chapin, F.S. III., 2008. Plant functional types do not predict biomass response to removal and fertilization in Alaskan tussock tundra. *Journal of Ecology* 96, 713-326.
- Bunn, A., 2008. A Dendrochronology Program Library in R (dplR). *Dendrochronologia* 26, 115-124.
- Buchwal, A., Rachlewicz, G., Fonti, P., Cherubini, P., Gärtner, H., 2013. Temperature modulates intra-plant growth of *Salix polaris* from a High Arctic site (Svalbard). *Polar Biology* 36, 1305-1318.
- Buras, A., Hallinger, M., Wilmking, M., 2012. Can shrubs help to reconstruct historical glacier retreats? *Environmental Research Letters* 7, 044031.
- Burnham, K. P., Anderson, D. R., 2004. Multimodel inference: understanding AIC and BIC in model selection. *Sociological Methods and Research* 33, 261-304.
- Böcher, T., 1979. Birch woodlands and tree growth in southern Greenland. *Holarctic Ecology* 2, 218-221.

- Cairns, D., Lafon, C., Mouton, M., Stuteville, R., Young, A., Moen, J., 2012. Comparing two methods for aging trees with suppressed, diffuse-porous rings (*Betula pubescens* ssp. *czerepanovii*). *Dendrochronologia* 30, 252-256.
- Chylek, P., Folland, C., Frankcombe, L., Dijkstra, H., Lesins, G., Dubey, M., 2012. Greenland ice core evidence for spatial and temporal variability of the Atlantic Multidecadal Oscillation. *Geophysical Research Letters* 39, L09705
- Cooper, E., Dullinger, S., Semenchuk, P., 2011. Late snowmelt delays plant development and results in lower reproductive success in the High Arctic. *Plant Science* 180, 157-167.
- De Groot, W., Thomas, P., Wein, R., 1997. *Betula nana* L. and *Betula glandulosa* Michx. *Biological Flora of the British Isles*. *Journal of Ecology* 85, 241-264.
- Dowdeswell, J., White, J., 1995. Greenland ice core records and rapid climate change. *Philosophical Transactions: Physical Science and Engineering* 352, 359-371.
- Elven, R., Murray, D., Razzhivin, V., Yurtsev, B. 2011. Annotated Checklist of the Panarctic Flora (PAF) Vascular plants version 1.0. URL <https://nhm2.uio.no/paf/>.
- Ernakovich, J. G., Hopping, K. A., Berdanier, A. B., Simpson, R. T., Kachergis, E. J., Steltzer, H., Wallenstein, M. D., 2014. Predicted responses of arctic and alpine ecosystems to altered seasonality under climate change. *Global Change Biology* 20, 3256-3269.
- Flückiger, J., Blunier, T., Stauffer, B., Chappellaz, J., Spahni, R., Kawamura, K., Schwander, J., Stocker, T., Dahl-Jensen, D., 2004. N<sub>2</sub>O and CH<sub>4</sub> variations during the last glacial epoch: Insights into global processes. *Global Biogeochemical Cycles* 18, GB1020.
- Forbes, B., Macias Fauria, M., Zetterberg, P., 2010. Russian Arctic warming and 'greening' are closely tracked by tundra shrub willows. *Global Change Biology* 16, 1542-1554.
- Forchhammer, M., Christensen, T., Hansen, B., Tamstorf, M., Schmidt, N., Høye, T., Nabe-Nielsen, J., Rasch, M., Heltofte, H., Elberling, B., Post, E., 2008. Zackenberg in a circumpolar context. *Advances in Ecological Research* 40, 499-544.

- Fox, A., Francis, I., Madsen, J., Stroud, J., 1987. The breeding biology of the Lapland Bunting *Calcarius lapponicus* in West Greenland during two contrasting years. *IBIS* 129, 541-552.
- Freckleton, R. P., 2010. Dealing with collinearity in behavioural and ecological data: model averaging and the problems of measurement error. *Behavioural Ecology and Sociobiology* 65, 91-101.
- Fredskild, B., Ødum, S., 1990. The Greenland mountain birch zone, an introduction. *Meddelelser om Grønland, Bioscience* 33, 3-7.
- Fritts, H., 1976. *Tree Rings and Climate*. New York, NY: Academic Press. 567 pp.
- Grissino-Mayer, H. D., 2001. Evaluating crossdating accuracy: A manual and tutorial for the computer program COFECHA. *Tree-Ring Research* 57, 205-221.
- Hallinger, M., Manthey, M., Wilmking, M., 2010. Establishing a missing link: warm summers and winter snow cover promote shrub expansion into alpine tundra in Scandinavia. *New Phytologist* 186, 890-899.
- Hijmans, R., Cameron, S., Parra, J., Jones, P., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. *Journal of Climatology* 25, 1965-1978.
- Hollesen, J., Buchwal, A., Rachlewicz, G., Hansen, B., Hansen, M., Stecher, O., Elberling, B., 2015. Winter warming as an important co-driver for *Betula nana* growth in western Greenland during the past century. *Global Change Biology* 21, 2410-2423.
- Holmes, R. L., 1986. User's manual for program COFECHA, in: Holmes, R. L., Adams, R. K., and Fritts, H. C. (Eds.), *Tree-ring chronologies of western North America: California, eastern Oregon, and northern Great Basin*. Laboratory of Tree-Ring Research, University of Arizona, Tucson, pp. 41-49.
- Inouye, D., 2000. The ecological and evolutionary significance of frost in the context of climate change. *Ecology Letters* 3, 457-463.

- Jørgensen, R., Hallinger, M., Ahlgimm, S., Friemel, J., Kollmann, J., Meilby, H., 2014. Growth response to climate change over 120 years for *Alnus viridis* and *Salix glauca* in West Greenland. *Journal of Vegetation Science* 26, 155-165.
- Keuper, F., Parmentier, F. J. W., Blok, D., van Bodegom, P. M., Dorrepaal, E., van Hal, J. R., van Logtestijn, R. S. P., Aerts, R., 2012. Tundra in the rain: responses to three years of experimentally doubled summer precipitation in Siberian shrub and Swedish bog tundra. *AMBIO* 41, 269-280.
- Klein Tank, A., Wijngaard, J., Können, G., Böhm, R., Demarée, G., Gocheva, A., Mileta, M., Pashiardis, S., Hejkrlik, L., Kern-Hansen, C., Heino, R., Bessemoulin, P., Müller-Westermeier, G., Tzanakou, M., Szalai, S., Pálsdóttir, T., Fitzgerald, D., Rubin, S., Capaldo, M., Maugeri, M., Leitass, A., Bukantis, A., Aberfeld, R., Van Engelen, A., Forland, E., Miletus, M., Coelho, F., Mares, C., Razuvaev, V., Nieplova, E., Cegnar, T., António Lopez, J., Dahlström, B., Moberg, A., Kirchhofer, W., Ceylan, A., Pachaliuk, O., Alexander, L., Petrovic, P., 2002. Daily dataset of 20<sup>th</sup>-Century surface air temperature and precipitation series for the European climate assessment. *International Journal of Climatology* 22, 1441-1453.
- Kolishchuk, V., 1990. Dendroclimatological study of prostrate woody plants. In: Cook, E., Kairiukstis, L. (Eds.) *Methods of Dendrochronology. Applications in the environmental sciences*. Kluwer, Dordrecht, Boston, London, pp. 51-55.
- Kuivinen, K., Lawson, M., 1982. Dendroclimatic analysis of birch in South Greenland. *Arctic and Alpine Research* 14, 243-250.
- Kummerow, J., Ellis, B. A., Kummerow, S., Chapin, F. S. III., 1983. Spring growth of shoots and roots in shrubs of an Alaskan muskeg. *American Journal of Botany* 70, 1509–1515.



- Macias-Fauria, M., Forbes, B., Zetterberg, P., Kumpula, T., 2012. Eurasian Arctic greening reveals teleconnections and the potential for structurally novel ecosystems. *Nature Climate Change* 2, 613-618.
- Mann, M., Bradley, R., Hughes, M., 1998. Global-scale temperature patterns and climate forcing over the past six centuries. *Nature* 392, 779-787.
- Masson-Delmotte, V., Swingedouw, D., Landais, A., Seidenkrantz, M-S., Gauthier, E., Bichet, V., Massa, C., Perren, B., Jomelli, V., Adalgeirsdottir, G., Christensen, J., Arneborg, J., Bhatt, U., Walker, D., Elberling, B., Gillet-Chaulet, F., Ritz, C., Gallée, H., van den Broeke, M., de Vernal, A., Vinther, B., 2012. Greenland climate change: From the past to the future. *WIREs Climate Change* 3, 427-449.
- Meinardus, C., Weinert, B., Löffler, J., Lundberg, A., Brauning, A., 2011. The potential of the dwarf shrub *Betula nana* L. as a climate indicator above the tree line in the southern Norwegian Scandes. *TRACE* 9, 181-186.
- Myers-Smith, I., Forbes, B., Wilmking, M., Hallinger, M., Lantz, T., Blok, D., Tape, K., Macias-Fauria, M., Sass-Klaassen, U., Lévesque, E., Boudreau, S., Popars, P., Hermanutz, L., Trant, A., Collier, L., Weijers, S., Rozema, J., Rayback, S., Schmidt, N., Schaepman-Strub, G., Wipf, S., Rixen, C., Ménard, C., Venn, S., Goetz, S., Andreu-Hayles, L., Elmendorf, S., Ravolainen, V., Welker, J., Epstein, H., Hik, D., 2011. Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. *Environmental Research Letters* 6, 045509.
- Myers-Smith, I., Elmendorf, S., Beck, P., Wilmking, M., Hallinger, M., Blok, D., Tape, K., Rayback, S., Macias-Fauria, M., Forbes, B., Speed, J., Boulanger-Lapointe, N., Rixen, C., Lévesque, E., Schmidt, N., Baittinger, C., Trant, A., Hermanutz, L., Collier, L., Dawes, M., Lantz, T., Weijers, S., Jørgensen, R., Buchwal, A., Buras, A., Naito, A., Ravolainen, V., Schaepman-Strub, G., Wheeler, J., Wipf, S., Guay, K., Hick, D., Vellend,

- M., 2015a. Climate sensitivity of shrub growth across the tundra biome. *Nature Climate Change* 5, 887-891.
- Myers-Smith, I., Hallinger, M., Blok, D., Sass-Klaassen, U., Rayback, S., Weijers, S., Trant, A., Tape, K., Naito, A., Wipf, S., Rixen, C., Dawes, M., Wheeler, J., Buchwal, A., Baittinger, C., Macias-Fauria, M., Forbes, B., Levesque, E., Boulanger-Lapointe, N., Beil, I., Ravolainen, V., Wilmking, M., 2015b. Methods for measuring arctic and alpine shrub growth: A review. *Earth-Science Reviews* 140, 1-13.
- Nadelhoffer, K., Shaver, G., Fry, B., Giblin, A., Johnson, L., McKane, R., 1996.  $^{15}\text{N}$  natural abundances and N use by tundra plants. *Oecologia* 107, 386–394.
- Naito, A., Cairns, D., 2011. Relationships between arctic shrub dynamics and topographically-derived hydrologic characteristics. *Environmental Research Letters* 6, 045506.
- Nakagawa, S., Schielzeth, H., 2013. A general and simple method for obtaining  $R^2$  from generalized linear mixed-effects models. *Methods in Ecology and Evolution* 4, 133-142.
- Oberbauer, S. F., Dawson, T. E., 1992. Water relations of Arctic vascular plants. In: Chapin, F. S. III, Jefferies, R. L., Reynolds, J. F., Shaver, G. R., Svoboda, J. (Eds.) *Arctic Ecosystems in a Changing Climate: An Ecophysiological Perspective*. Academic Press, San Diego, pp. 259-279.
- Patterson, A.E., 1959. Distinguishing annual rings in diffuse porous tree species. *Journal of Forestry* 57, 126.
- Paradis, M., Mercier, C., Boudreau, S., 2014. Response of *Betula glandulosa* seedlings to simulated increases in nutrient availability, temperature and precipitation in a lichen woodland at the forest–tundra ecotone. *Plant Ecology* 215, 305–314
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R Core Team., 2014. nlme: Linear and nonlinear mixed effects models. R package version 3.1-118. URL <http://CRAN.R-project.org/package=nlme>.

- Post, E., 2013a. Ecology of Climate Change: The Importance of Biotic Interactions. Princeton University Press., Princeton, NJ. 373 pp.
- Post, E., 2013b. Erosion of community diversity and stability by herbivore removal under warming. Proceedings of the Royal Society of London, B 280, 20122722
- Post, E., Pedersen, C., 2008. Opposing plant community responses to warming with and without herbivores. PNAS 105, 12353-12358
- Post, E., Pedersen, C., Wilmers, C., Forchhammer, M., 2008. Phenological sequences reveal aggregate life history response to climate. Ecology 89, 363-370.
- Post, E., Forchhammer, M., Bret-Harte, M., Callaghan, T., Christensen, T., Elberling, B., Fox, A., Gilg, O., Hik, D., Høye, T., Ims, R., Jeppesen, E., Klein, D., Madsen, J., McGuire, A., Rysgaard, S., Schindler, D., Stirling, I., Tamstorf, M., Tyler, N., van der Wal, R., Welker, J., Wookey, P., Schmidt, N., Aastrup, P., 2009. Ecological dynamics across the arctic associated with recent climate change. Science 325, 1355-1358.
- Rayback, S., Henry, G., 2006. Reconstruction of summer temperature for a Canadian high Arctic site from retrospective analysis of the dwarf shrub, *Cassiope tetragona*. Arctic, Antarctic, and Alpine Research 38, 228-238.
- R Core Team., 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.
- Schweingruber, F., Poschlod, P., 2005. Growth rings in herbs and shrubs: life span, age determination and stem anatomy. Forest, Snow and Landscape Research 79, 195-415.
- Schweingruber, F., Hellmann, L., Tegel, W., Braun, S., Nievergelt, D., Büntgen, U., 2013. Evaluating the wood anatomical and dendroecological potential of Arctic dwarf shrub communities. IAWA Journal 34, 485-497.

- Schmidt, N., Baittinger, C., Forchhammer, M., 2006. Reconstructing century-long snow regimes using estimates of High Arctic *Salix arctica* radial growth. *Arctic, Antarctic, and Alpine Research* 38, 257-262.
- Schmidt, N., Baittinger, C., Kollmann, J., Forchhammer, M., 2010. Consistent dendrochronological response of the dioecious *Salix arctica* to variation in local snow precipitation across gender and vegetation types. *Arctic, Antarctic, and Alpine Research* 42, 471-475.
- Stamati, K., Hollingsworth, P., Russell, J., 2007. Patterns of clonal diversity in three species of sub-arctic willow (*Salix lanata*, *Salix lapponum* and *Salix herbacea*). *Plant Systematics and Evolution* 269, 75-88.
- Stendel, M., Christensen, J., Petersen, D., 2008. Arctic Climate and Climate Change with a Focus on Greenland. *Advances in Ecological Research*, 13–43.
- Stokes, M.A., Smiley, T.L., 1968. *An Introduction to Tree-ring Dating*. University of Arizona Press, Tucson, AZ., 73pp.
- Tape, K., Sturm, M., Racine, C., 2006. The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. *Global Change Biology* 12, 686-702.
- Tremblay, B., Levesque, E., Boudreau, S., 2012. Recent expansion of erect shrubs in the low Arctic: evidence from Eastern Nunavik. *Environmental Research Letters* 7, 035501.
- Trenberth, K. E., Jones, P. D., Ambenje, P., Bojariu, R., Easterling, D., Klein Tank, A., Parker, D., Rahimzadeh, F., Renwick, J. A., Rusticucci, M., Soden, B., Zhai, P., 2007. Observations: Surface and Atmospheric Climate Change, in: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K. B., Tignor, M., Miller, H. L. (Eds.), *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, pp. 234-336.

- Walker, D. A., Raynolds, M. K., Daniëls, F. J. A., Einarsson, E., Elvebakk, A., Gould, W. A., Katenin, A. E., Kholod, S. S., Markon, C. J., Melnikov, E. S., Moskalenko, N. G., Talbot, S. S., Yurtsev, B. A., and the other members of the CAVM Team., 2005. The Circumpolar Arctic vegetation map. *Journal of Vegetation Science* 16, 267-282.
- Walker, M., Wahren, C.H., Hollister, R., Henry, G., Ahlquist, L., Alatalo, J., Bret-Harte, M., Calef, M., Callaghan, T., Carroll, A., Epstein, H., Jonsdottir, I., Klein, J., Magnusson, B., Molau, R., Oberbauer, S., Rewa, S., Robinson, C., Shaver, G., Suding, K., Thompson, C., Tolvanen, A., Totland, O., Turner, P., Tweedie, C., Webber, P., Wookey, P., 2006. Plant community responses to experimental warming across the tundra biome. *PNAS* 103, 1342-1346.
- Weijers, S., Alsos, I., Eidesen, P., Broekman, R., Loonen, M., Rozema, J., 2012. No divergence in *Cassiope tetragona*: persistence of growth response along a latitudinal temperature gradient and under multi-year experimental warming. *Annals of Botany* 110, 653-665.
- Wigley, T., Briffa, K., Jones, P., 1984. On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. *Journal of Climate and Applied Meteorology* 23, 201-213.
- Wilson, J.W., 1964. Annual Growth of *Salix arctica* in the High-Arctic. *Annals of Botany* 28, 71-76.
- Wipf, S., 2010. Phenology, growth, and fecundity of eight subarctic tundra species in response to snowmelt manipulations. *Plant Ecology* 207, 53-66.
- Young, A. B., Cairns, D. M., Lafon, C. W., Moen, J., 2014. Geometrid moth outbreaks and their climatic relations in northern Sweden. *Arctic, Antarctic, and Alpine Research* 46, 659-668.
- Zalatan, R., Gajewski, K., 2006. Dendrochronological potential of *Salix alaxensis* from the Kuujjua River area, Western Canadian Arctic. *Tree-Ring Research* 62, 75-82.

Zang, C., Biondi, F., 2012. Dendroclimatic calibration in R: The bootRes package for response and correlation function analysis. *Dendrochronologia* 31, 68-74.

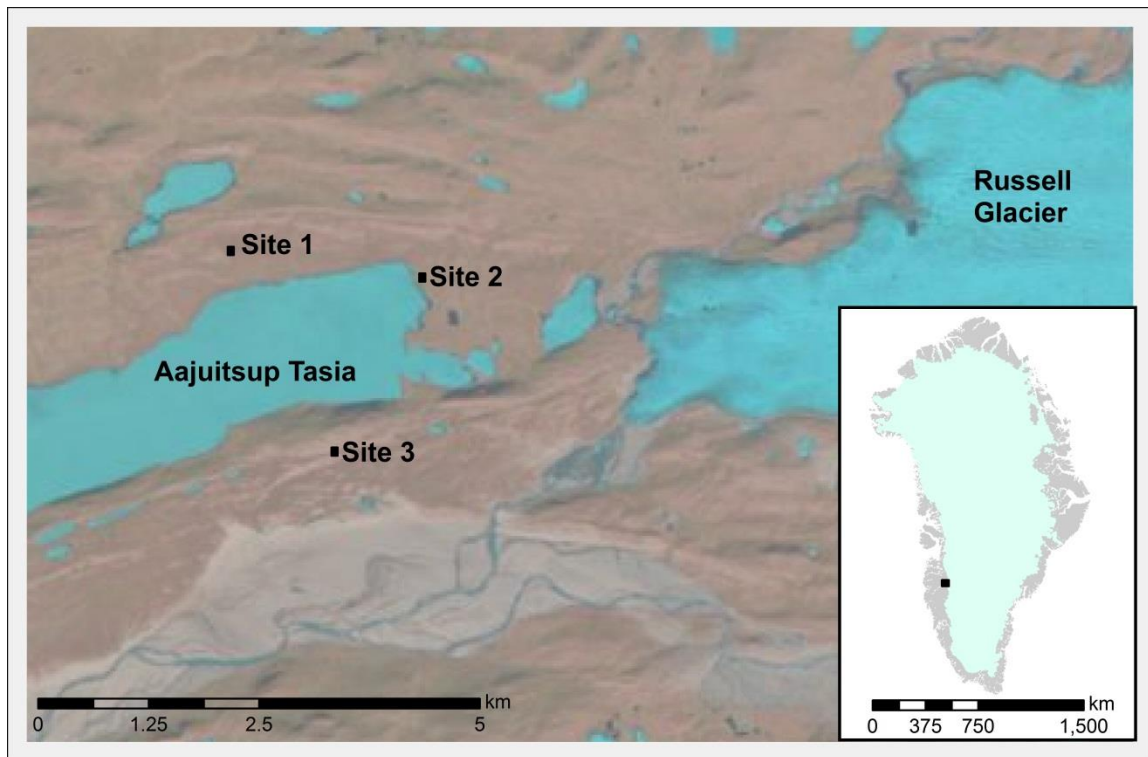


Figure A.1. Map of sites located on the eastern end of Long Lake (Aajuitsup Tasia), roughly 2-5 km from Russell Glacier, West Greenland. Data Source: Landsat 5 (NASA), Cryosphere Atlas (National Snow and Ice Data Center).

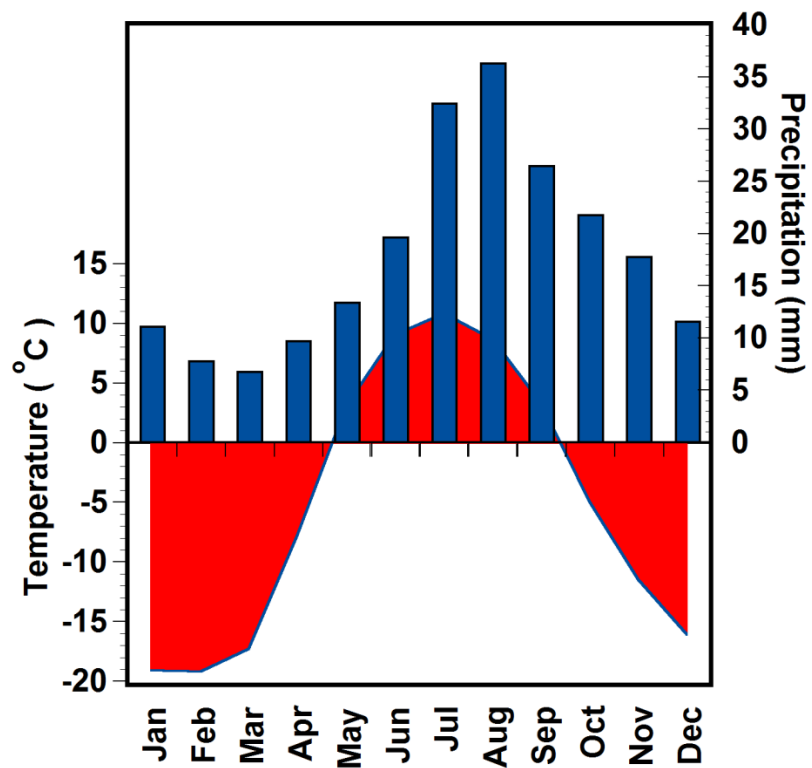


Figure A.1. Climograph of Kangerlussuaq, West Greenland, with average monthly temperature in °C (red), and average total monthly precipitation in mm (blue). Data from Klein Tank et al., 2002, via KNMI's Climate Explorer website ([climexp.knmi.nl](http://climexp.knmi.nl)).



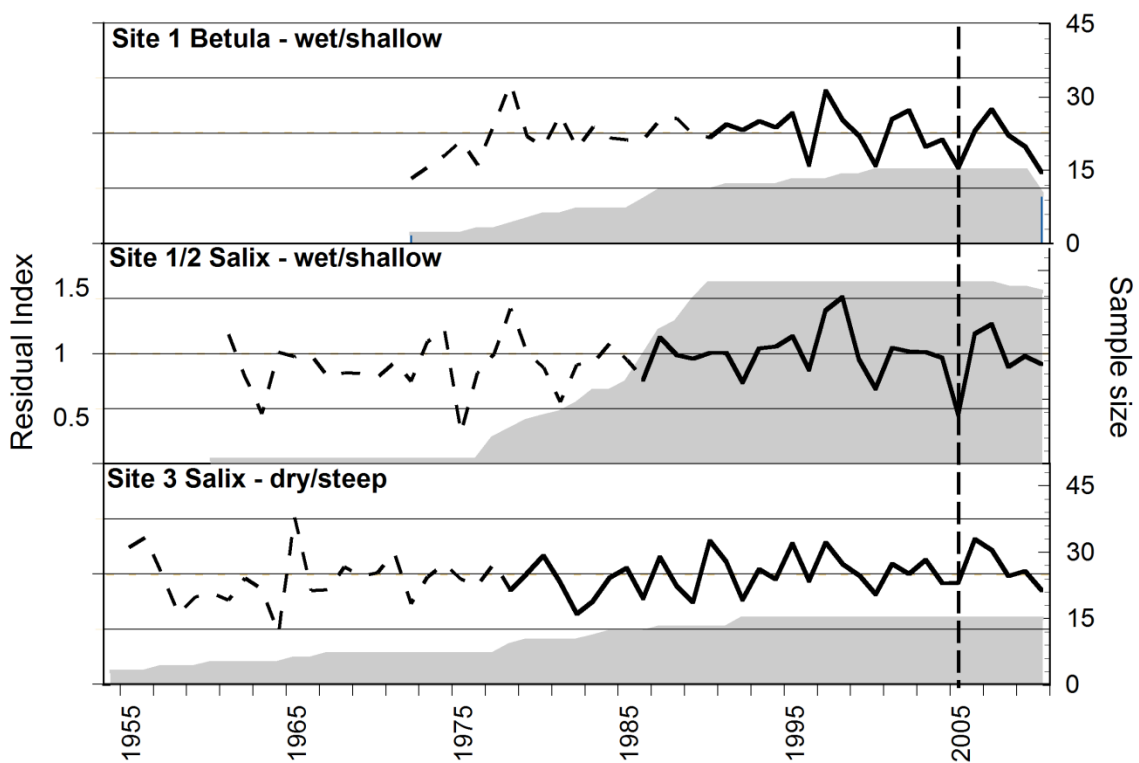


Figure A.3. Residual chronologies and sample size (number of individual shrubs) for Site 1 *Betula* (top), Site 1/2 *Salix* (middle), and Site 3 *Salix* (bottom). Solid lines on the residual chronology represent the portions that have a running expressed population signal (rEPS) > 0.85. A known insect outbreak occurred in 2005 (vertical dashed line).

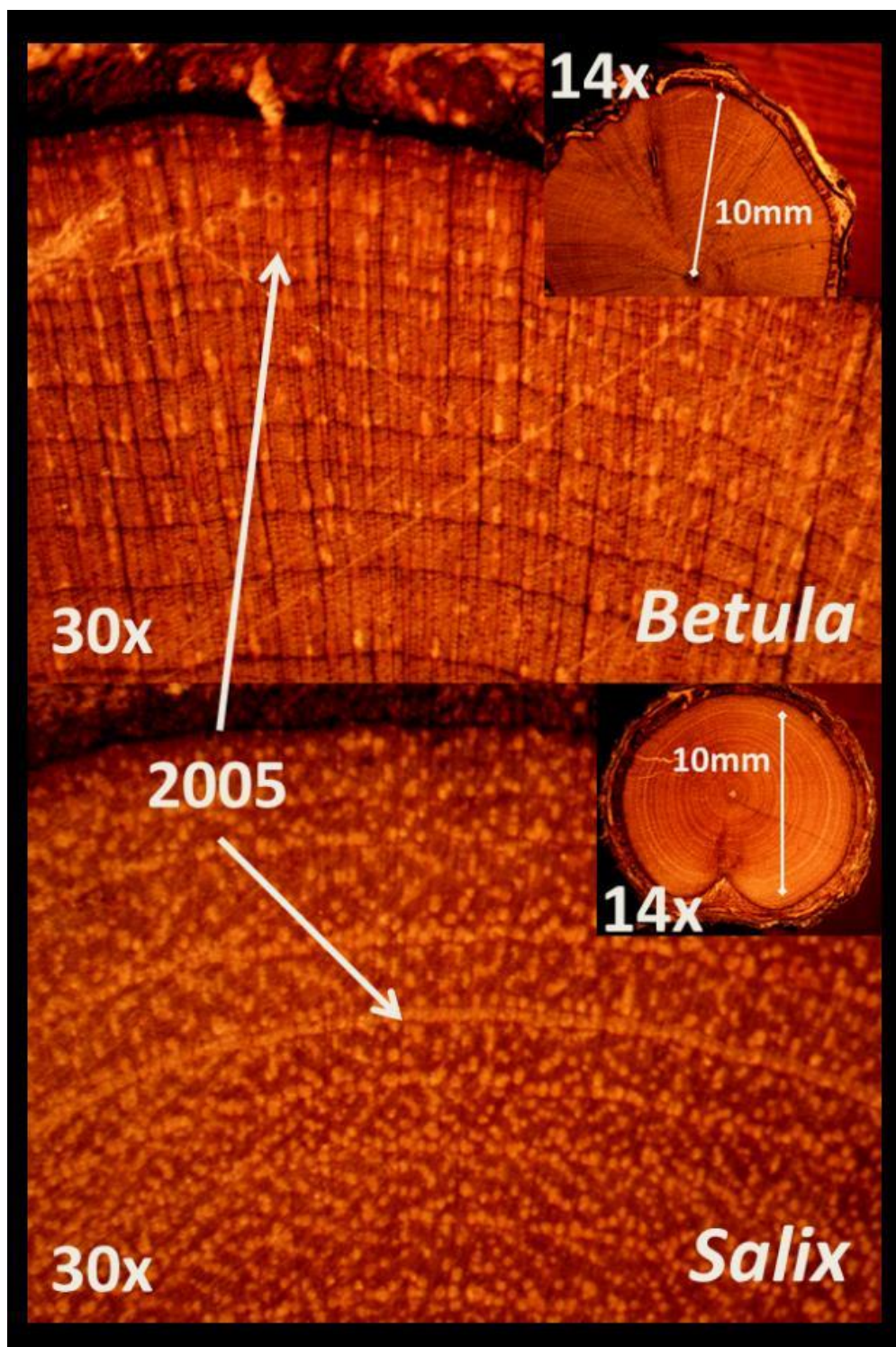


Figure A.4. Images of *Betula* (upper) and *Salix* (lower) wood samples at 14x and 30x magnification. Note the small (micro) ring of the 2005 insect outbreak.

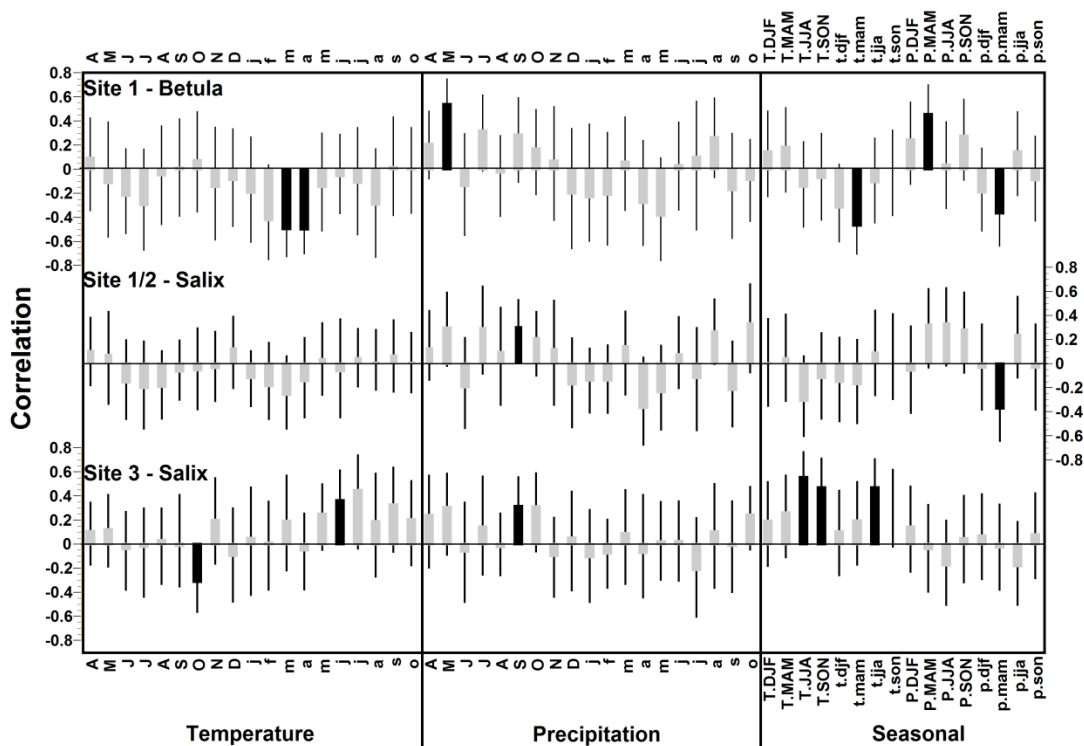


Figure A.5. Correlations (grey bars) and significant correlations (black bars) between ring width series and climate parameters (monthly and seasonal mean temperature and total precipitation). Type I error rates were set at  $\alpha = 0.05$ . Analysis was conducted over a 20 month period encompassing 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.

<b>Site</b>	<b>Latitude</b>	<b>Longitude</b>	<b>Elevation</b>	<b>Slope</b>	<b>Aspect</b>	<b>Topography</b>
1	67.10486	50.34396	240	4	S	Long steady slope
2	67.10152	50.29398	218	4	WSW	Small rolling hills
3	67.08510	50.33027	382	30	S	Steep hillside

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 ( $\bar{r}$ ), expressed population signal (EPS), mean sensitivity (MS), autocorrelation of the 1st order for raw data ( $AR_{raw}$ ) and autocorrelation of the 1<sup>st</sup> order for the residual chronology ( $AR_{res}$ ).

Site	Species	Interval	# shrubs	# paths	$\bar{r}$	EPS	MS	$AR_{raw}$	$AR_{res}$
1	<i>Betula</i>	1971-2010	15	33	0.288	0.809	0.344	0.392	0.075
1/2	<i>Salix</i>	1961-2010	42	92	0.307	0.918	0.389	0.427	-0.183
3	<i>Salix</i>	1954-2010	13	28	0.201	0.737	0.333	0.475	-0.050
<b>rEPS</b>									
<b>&gt;0.85</b>									
1	<i>Betula</i>	1988-2010	15	33	0.393	0.907	0.350	0.387	-0.020
1/2	<i>Salix</i>	1977-2010	42	92	0.307	0.943	0.388	0.426	0.108
3	<i>Salix</i>	1981-2010	13	28	0.214	0.813	0.316	0.443	-0.073

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).

Site	Species	Ring width		% 2005
		<i>All Years</i>	<i>2005 outbreak</i>	
1	<i>Betula</i>	0.204 (0.093)	0.106 (0.049)	100
1/2	<i>Salix</i>	0.242 (0.138)	0.089 (0.060)	100
3	<i>Salix</i>	0.565 (0.344)	0.598 (0.428)	71.4

*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.

Site	Species	Climate Variables	Indiv. (Obs.)	$R^2$	$\Delta\log\text{Lik}$	$\Delta\text{AICc}$	$\Delta\text{BIC}$
1	<i>Betula</i>	t.mam, P.MAM, p.jja	15 (399)	0.13	-36.51	67.02	55.05
1/2	<i>Salix</i>	p.mam, p.jja, p.djf, P.SON, T.JJA, P.JJA, T.SON, t.djf, p.son	42 (1112)	0.21	-93.86	169.73	124.72
3	<i>Salix</i>	t.jja, P.MAM	13 (380)	0.11	-27.36	50.73	42.84

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.

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



## VITA

David A. Watts

### EDUCATION

The Pennsylvania State University	2016
Ph.D. Ecology	
Texas A&M University	2009
M.S. Rangeland Ecology and Management	
University of California, Los Angeles	2006
B.S. Ecology, Behavior, and Evolution; History	

### PUBLICATIONS AND SELECT MANUSCRIPTS IN PROGRESS

Young, A. B., **Watts, D. A.**, Taylor, A. H., and Post, E. 2016. Species and site differences influence climate-shrub growth responses in West Greenland. *Dendrochronologia* 36:69-78.

**Watts, D. A.** and Moore, G. W. 2011. Water-use dynamics of an invasive reed, *Arundo donax* L., from leaf to stand. *Wetlands* 31:725-734.

Moore, G. W., **Watts, D. A.**, and Goolsby, J. A. 2010. Ecophysiological responses of giant reed (*Arundo donax*) to herbivory. *Invasive Plant Science and Management* 3:521-529.

**Watts, D. A.** and Baltzer, J. L. Land ownership impacts within a UNESCO Biosphere Reserve: changes in forest tree communities across ecological gradients. *Submitted*.

**Watts, D. A.** and Post, E. Relationship between plant community diversity and ecosystem function altered by warming and herbivore exclusion. *In Prep*.

**Watts, D. A.**, Douhovnikoff, V., and Post, E. The recruitment and spread of an arctic deciduous shrub: Sexual recruitment or clonal growth? *In Prep*.

**Watts, D. A.**, Mediavillo, T. M., and Post, E. Ploidy level varies along gradients in an expanding arctic shrub population. *In Prep*.

**Watts, D. A.** and Post, E. Seed quality responses to drivers of global change vary widely across arctic plant species. *In Prep*.

Gamm, C. M., Sullivan, P.F., Young, A. B., **Watts, D. A.**, Buchwal, A., Cahoon, S. M. P., Welker, J. M., Eissenstat, D.M., and Post, E. Declining growth of Arctic shrubs in a warming climate: Species-specific effects of drought and herbivory in West Greenland. *In Prep*.

### SELECT GRANTS AND AWARDS

2015	PSU Ecology Program J. Brian Horton Memorial Award
2013-2016	J. Lloyd Huck Dissertation Research Grant
2013	Arctic Institute of North America Grant-in-Aid
2012-2015	NASA Pennsylvania Space Grant Consortium Seed Grant
2010-2011	PSU University Graduate Fellowship
2008-2009	USGS/Texas Water Resources Institute Research Grant
2006-2007	Willie Mae Harris Agricultural Fellowship
2006-2007	Hoblitzelle Farm Endowment Scholarship

### PROFESSIONAL ASSOCIATIONS

2015-2016	International Association for Landscape Ecology, U.S. Regional Chapter
2014-2016	Arctic Institute of North America
2012-2016	American Geophysical Union
2007-2016	Ecological Society of America