ARCTIC ALASKAN SHRUB GROWTH, DISTRIBUTION, AND RELATIONSHIPS TO LANDSCAPE PROCESSES AND CLIMATE DURING THE 20TH CENTURY

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ABSTRACT

The primary change underway in the tundra of Arctic Alaska is the increase in air temperature and expansion of deciduous shrubs since 1980. I explored relationships between shrub expansion and relevant ecosystem properties such as climate, soil characteristics, erosion, and herbivory. *Alnus viridis* ssp. *fruticosa* (Siberian alder) shrubs located along streams, rock outcrops, or other features with active disturbance regimes showed a positive correlation between growth ring widths and March through July air temperature. Climate-growth relationships were much weaker for alder in adjacent tussock tundra. Additionally, tussock tundra sites had different vegetation composition, shallower thaw, lower mean annual ground temperature, lower mean growing season temperature, higher soil moisture, more carbon in mineral soil, and higher C:N values in shrub leaves than nearby non-tussock alder. Growth rings and site characteristics imply that preexisting soil conditions predispose alder shrubs growing in non-tussock tundra to respond rapidly to warming.

Analysis of temporal series of aerial photography from 1950 and 2000 and of Landsat imagery from 1986 and 2009 showed an increase in percent cover of shrubs, primarily in riparian areas. This increase in shrubs is contemporaneous with a decline in peak discharge events from the Kuparuk River and a lengthening of the growing season since 1980, both of which may have caused the decline in sediment deposition observed in 3 of 4 lake sediment cores dated with lead and cesium isotopes. Both alder shrub growth and erosion are particularly sensitive to runoff dynamics during the snowmelt and green-up period, and these dynamics are affected by spring temperatures.

Ptarmigan, moose, and hares forage heavily on shrubs protruding above the deepening snow during the late-winter, and selective browsing on willow vs. alder is likely influencing shrub community composition. The increase in shrubs during the 20th century may represent additional habitat for these herbivores, and herbivore-mediated changes in shrub architecture may have important implications for how shrubs trap snow and ultimately affect surface energy balance.

Evidence from this thesis indicates shrub growth and cover have increased in response to persistent warming, particularly in areas where the organic layer is thinner and active layer deeper.

TABLE OF CONTENTS

Page

LIST OF FIGURES

LIST OF TABLES

Page

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I gratefully acknowledge the contributions of others to this work. In Chapter 1, I designed the study, collected the samples, analyzed all except the shrub rings, interpreted the data, and wrote the initial draft of the paper. Martin Hallinger measured the shrub ring widths and established the climate correlations. Roger Ruess and Jeffrey Welker helped clarify ideas and writing. In Chapter 2, I designed the study, collected the lake sediment cores and analyzed the discharge data, Flett Research Ltd. analyzed the cores, David Verbyla performed the NDVI (Normalized Difference Vegetation Index) analysis, and I interpreted the collective results. Jeffrey Welker provided critical feedback and logistical support. In Chapter 3, I designed the study and collected and analyzed the data. Hans-Peter Marshall assisted with the non-parametric statistics and Roger Ruess helped clarify ideas and writing. Thanks especially to Matthew Sturm, Terry Chapin, and Skip Walker for providing guidance and insight on individual chapters and throughout this process. Funding and additional acknowledgements appear at the end of the individual chapters.

GENERAL INTRODUCTION

The landscape of Arctic Alaska has undergone changes in the last century in response to elevated temperatures, most notably between 1930 and 1950 and from 1970 to present [*Shulski and Wendler*, 2007]. The most detectable of these changes include shrub encroachment into tundra [*Sturm et al.*, 2001; *Tape et al.*, 2006], increased photosynthetic activity [*Bhatt et al.*, 2010; *Goetz et al.*, 2005; *Jia et al.*, 2003], warmer permafrost temperatures [*Osterkamp and Jorgenson*, 2006], and a longer growing season [*Jia et al.*, 2003; *Myneni et al.*, 1997]. The expansion of shrubs is predicted to increase decomposition and release carbon from the soil [*Mack et al.*, 2004], alter herbivore dynamics [*Joly et al.*, 2007], capture more drifting snow [*Sturm et al.*, 2005], enhance albedo-driven snowmelt [*Chapin et al.*, 2005], decrease moss and understory productivity [*Walker et al.*, 2006], and generally alter the structure and function of the tundra ecosystem.

A considerable amount is known about the Arctic Alaskan landscape during the Holocene from paleoenvironmental reconstructions, but those records are limited by the availability and precision of dates in the lake core sediments, and by the reliability of the paleoenvironmental proxy, whether it be oxygen isotopes or pollen abundances [*Oswald et al.*, 1999; *Oswald et al.*, 2003a; *Oswald et al.*, 2003b]. For example, due to the imprecision of the pollen record, temporal variations in shrub abundances since the development of the modern tundra approximately 7,000 cal ya B.P. (calendar years before present) are assumed to be minimal, though short-term fluctuations in shrub pollen abundance are ubiquitous. This thesis draws from 20th century chronologies obtained from lake sediment cores, shrub growth rings, and browsed-shrub architecture to examine the factors controlling shrub growth, distribution, and expansion.

Manipulation experiments dating to the early 1980s have improved our understanding of mechanisms and responses of Arctic vegetation to climate variability [*Chapin et al.*, 1995], though the system responses are often complex [*Bret-Harte et al.*, 2004]. Satellite records also initiated during the early 1980s provide a record of gradually increasing photosynthetic activity over the past 30 years [*Bhatt et al.*, 2010; *Goetz et al.*, 2005; *Jia et al.*, 2003]. Still, the plot studies are manipulations, rather than actual observations of changing vegetation, and can therefore be somewhat difficult to interpret and extrapolate to the landscape scale. Most satellite records contain large pixels that integrate into a single value the spectral response of a complex vegetation mosaic, and are hence difficult to interpret. Furthermore, neither record predates 1980, and thus neither record contains information prior to the onset of the current warming initiated in the 1970s. Repeat photography shows a widespread increase in shrubs since 1950, but the two assessments of shrub cover imply only a connection between warmer temperatures and shrub expansion [*Sturm et al.*, 2001; *Tape et al.*, 2006].

The goal of this thesis is to develop temporal records of shrub growth and other relevant processes from the 20th century to compare with the temperature record. Chapter 1 uses shrub growth rings to show the climatic influence on shrub growth from 1950 to present, and how that is mediated by soil properties. Chapter 2 aligns 20th century trends in shrub distribution, erosion, and discharge to illuminate relationships between these processes. Chapter 3 presents herbivory and snow as prominent factors controlling shrub architecture. These chronologies begin to bridge between paleoecological studies [*Mann et al.*, 2010] and modern ecological studies, such as the vegetation plot studies and NDVI (Normalized Difference Vegetation Index) trends. These records of terrestrial processes improve our understanding of past landscape changes and prediction of future trajectories of landscape changes in the Arctic.

Chapter 1 – Landscape Heterogeneity of Shrub Expansion in Arctic Alaska[1]

Abstract

The most detectable terrestrial change underway in the Arctic in response to elevated temperatures during the 20th century is the encroachment of shrubs into tundra areas, which has been documented primarily using time series of photography, plot studies, and satellite images. Time series of photography permits a glimpse into greening satellite pixels, and it shows that, since 1950, some shrub patches have increased rapidly (hereafter expanding), while others have increased little or not at all (hereafter stagnant). We characterized and compared adjacent expanding and stagnant shrub patches across Arctic Alaska by sampling a wide range of physical and chemical soil and vegetation properties, including shrub growth rings. The sampling was conducted along the Nimiuktuk River in the Brooks Range, and along the Colville and Sagavanirktok Rivers of the North Slope foothills. Expanding patches of *Alnus viridis* ssp. *fruticosa* (Siberian alder) contained shrub stems with thicker growth rings than in stagnant patches. Shrub growth in expanding patches also showed a strong correlation with spring and summer warming, whereas shrubs in stagnant patches showed little correlation with temperature. Expanding patches had different vegetation composition, deeper thaw depth, higher mean annual ground temperature, higher mean growing season temperature, lower soil

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[1] Tape, KD, Hallinger M, Welker J, Ruess RW, in review. Landscape heterogeneity of shrub expansion in Arctic Alaska. *Global Change Biology*

moisture, less carbon in mineral soil, and lower C:N values in shrub leaves. Geographic extrapolation of repeat photography showed that expanding patches composed of clumped or randomly distributed shrubs – higher resource environments – are associated with floodplains, stream corridors, and outcrops. Stagnant patches composed of evenly dispersed shrubs – low resource environments – are associated with flat, though not necessarily level, terrain. Collectively, we interpret these differences as implying that preexisting soil conditions predispose parts of the landscape to a rapid response to climate change. We therefore expect rapid change to continue penetrating the landscape via dendritic floodplains, streams, and scattered rock outcrops.

Introduction

The encroachment of shrubs into tundra landscapes is the most detectable terrestrial change underway in the Arctic. This shift toward a shrubbier arctic has been documented primarily using time-series photography (Sturm *et al.*, 2001, Tape *et al.*, 2006), plot studies (Joly *et al.*, 2007), and satellite images (Bhatt *et al.*, 2010, Goetz *et al.*, 2005, Jia *et al.*, 2003, Myneni *et al.*, 1997). This vegetation shift appears to be associated with elevated temperatures during the 20th century (Hinzman *et al.*, 2005). This causal relationship is based on (1) vegetation responses to plot-level temperature manipulations (Chapin *et al.*, 1995, Walker *et al.*, 2006), (2) correlations between summer air temperature and growth ring widths and shrub height (Blok *et al.*, 2011, Forbes *et al.*, 2010, Walker, 1987), (3) the abundance of shrubs at lower arctic latitudes (Walker *et al.*, 2005), (4) the broad scale of the vegetation shift (Bhatt *et al.*, 2010, Forbes *et al.*, 2010, Goetz *et al.*, 2005, Jia *et al.*, 2003, Myneni *et al.*, 1997, Ukraintseva, 2008, Verbyla, 2008), and (5) the correlation between summer warming and NDVI (Normalized Difference Vegetation Index) values (Raynolds *et al.*, 2008). A shift toward a shrubbier arctic has profound implications, such as increasing drifted snow (Liston *et al.*, 2002) and associated permafrost thaw (Nowinski *et al.*, 2010), inducing positive feedbacks to warming due to the effects of taller shrubs on decreasing albedo (Chapin *et al.*, 2005) and evapotranspiration (Swann *et al.*, 2010), and altering geomorphic processes such as drainage and erosion (Chapter 2). Increasing shrub dominance has the potential to release stored deep soil carbon through thawing and accelerated decomposition (Mack *et* *al.*, 2004, Schuur *et al.*, 2007). Shrub expansion is also reducing primary caribou forage (Joly *et al.*, 2007) and improving forage availability for moose, ptarmigan, and hare (Tape *et al.*, 2010).

Not all arctic landscapes previously dominated by low-stature tundra vegetation currently host tall (> 0.5 m) shrubs. The spatial heterogeneity of greening, characterized by time-series satellite imagery, is primarily derived from satellites with coarser resolution sensors (> 8 km pixels) with high spatial coverage. At the largest scale, greening has occurred primarily in the arctic tundra, while the boreal forest has been in decline, referred to as 'browning' (Bunn & Goetz, 2006, Goetz *et al.*, 2005). From 1982 to 2003, 62% of North American tundra pixels had NDVI slopes near zero, while 12% had strong positive slopes, and 2% had strong negative slopes (Goetz *et al.*, 2005). In Arctic Alaska from 1982-2003, GIMMS (Global Inventory Modeling and Mapping Studies) data showed more greening on the coastal plain than in the North Slope foothills, and no trends across most of the Brooks Range (Verbyla, 2008). Interannual fluctuations in peak-season and time-integrated NDVI produced dissimilar results, explained by graminoids being more sensitive to interannual temperature fluctuations than shrubs (Jia *et al.*, 2006).

Temporal series of coarse satellite imagery, though very convincing in their widespread coverage, understandably lack information about heterogeneity of change within pixels. Though NDVI is strongly controlled by shrub biomass and leaf area (Jia *et al.*, 2002), other functional groups also contribute to the signal. NDVI also does not distinguish whether increases in shrub cover are due to the enhanced growth of individual stems or the initiation of new stems, or both. This patch-scale heterogeneity can be easily underestimated or even overlooked due to the large size of pixels for which a single rate of change is assigned in most satellite greening studies. As longer time series of moderate-scale (*e.g.* Landsat 30 m pixels) and fine-scale sensors (*e.g.* Ikonos <1 m pixels) become available (Munger *et al.*, 2008), what is now sub-pixel variability will be resolved.

Time-series photography (pixel size ~ 10 cm) permits a unique glimpse into those larger NDVI pixels, and shows that, since 1950, some shrub patches have expanded rapidly (hereafter "expanding"), while others have expanded little or not at all (hereafter "stagnant"). We sought to characterize and compare expanding and stagnant shrub patches across Arctic Alaska, based on a wide range of physical and chemical soil and vegetation parameters, including shrub growth rings. Because the recent increase in air temperature in adjacent expanding and stagnant shrub patches is presumably the same, differences in soil conditions between expanding and stagnant patches may explain the differing responses of shrubs to changes in air temperature or precipitation. Spatial extrapolation of diagnostic expanding or stagnant soil and shrub characteristics may permit finer-scale generalizations regarding which parts of the landscape have experienced shrub expansion and associated ecosystem changes.

Materials and Methods

Study Area

Sampling was conducted in the treeless tundra along the Nimiuktuk River in the Brooks Range, and along the Colville and Sagavanirktok Rivers of the North Slope foothills (Figure 1.1). The shrub patches that are the focus of this study were located on slopes leading down to the river valley fills, and contain primarily the 0.5 to 3 m shrubs *Alnus viridis* ssp. *fruticosa* (Siberian alder, hereafter alder), *Betula nana* or *glandulosa* (hereafter birch), and *Salix* spp. (hereafter willow). These tall shrub patches generally occur in riparian areas (Beck *et al.*, in press, Schickhoff *et al.*, 2002, Selkowitz, 2010), and adjacent to rock outcrops. Such restricted distribution of shrubs in an otherwise tundra landscape causes tall shrubs to blend into larger pixels dominated by smaller or non-shrub tundra and be overlooked in coarse vegetation maps, though smaller- and nested-scale fractional cover mapping approaches detect shrubs (Beck *et al.*, in press, Selkowitz, 2010) and describe these communities as "riparian shrublands" (Walker *et al.*, 1994).

Sampling

Twenty-six transects were sampled where repeat photography showed shrub patches that were either expanding (n=10) or stagnant (n=16)(Tape *et al.*, 2006). The first 4 patches were along the Sagavanirktok River and were sampled in early August 2006. The next 8 patches were located along the Nimiuktuk River, a tributary of the Noatak

River, and were sampled in June/July 2008. The last 14 patches were located along the Colville River and were sampled in July/August 2008 (Figure 1.1).

One 80 m transect was placed in each patch, and sampling intervals (hereafter "locations") were established at 0, 20, 60, and 80 m along each transect. Each location consisted of a 1×1 m quadrat nested within a 6×6 m plot (Figure 1.2). The 1×1 m quadrat was used to record vascular species presence and percent cover, the latter using ocular estimates. Non-vascular species were recorded as percent cover of moss or lichen. A diagonal line (8.5 m) was run within the 6×6 m plot such that it did not interfere with the 1×1 m quadrat, and active layer depth was measured with a probe at 1 m intervals along the diagonal.

The remainder of the sampling applies to the 22 shrub patches from the Nimiuktuk and Colville Rivers. From each location an inverted cone of soil was extracted using a shovel. Triplicate volumetric pedons of mineral and organic soils were extracted from the wall of the soil pit using steel cylinders, sharpened on one end and open on both ends (diameter = 3.9 cm, length = 3.5 cm). The cone of soil from the pit was reinserted into the vacancy, such that no surface disturbance was visible. Pedons were bagged in Ziplocs® and weighed on a digital balance in the field. Instantaneous soil temperature was measured at 10 cm depth in 3 locations near the soil pit, using a Campbell Scientific Australia HydroSense™ device. Soil moisture in the top 10 cm was measured at 3 locations using the same device.

Ten shrub leaves at each location, by genus (*Alnus*, *Salix*, and *Betula*), were picked and placed in coin envelopes, with no more than 3 leaves from any single shrub.

Leaf samples, pooled by genus and location (as collected), were stored in coin envelopes. In the laboratory, samples were dried at 40° C, ground using a ball mill, and then analyzed for total C and N, $\delta^{13}C$, and $\delta^{15}N$ using a Elemental Analyzer (Costech) in line with a ThermoFinnigan stable isotope mass spectrometer. Soil samples were freeze-dried at -40° C for 5 days, and bulk density was determined. An equal mass of each of the dried triplicate pedons was then combined into one soil sample per horizon per location for subsequent analyses. Soils were analyzed for pH (saturated soil with de-ionized water), and total C and N (Bran-Luebbe GmbH AutoAnalyzer 3, Norderstedt, Germany).

The largest alder stem at each of the 5 locations per transect was cut near the ground surface (< 0.3 m) and a disc then cut from the stump for shrub growth ring analysis. Discs were dried and polished with progressively finer sandpapers, ending with 800 grit. Two radii were counted from each disc and measured to 0.001 mm precision using a ring width measuring stage (LINTAB 5; Rinn, 1996).

At the eight transects (four pairs of expanding and stagnant) along the Nimiuktuk River, one HOBO® Pendant Temperature/Light Data Logger (#UA-002) was installed at 20 cm above, and 5 cm below the ground surface. Where microtopography was present, neutral locations were chosen. The loggers measured temperature at 1-hr intervals from 7/1/2008 to 9/20/2010.

Repeat photography (Tape *et al.*, 2006) was used to delineate 10 polygons of rapidly expanding shrub patches and 10 polygons of slowly expanding or stagnant shrub patches on SPOT satellite imagery along a 20 km stretch of the Chandler River, which flows into the Colville River. Using the polygons, a supervised classification using ENVI software was applied to the SPOT image to depict landscape positions prone to shrub expansion or stagnation.

Shrub Ring Chronology

The two radii measured for rings on each disc were averaged. Average ring width curves were aligned with other average ring width curves in their corresponding expanding (n = 59) or stagnant (n=40) category to eliminate errors from missing rings or false rings. This precise dating of individual rings was accomplished by maximizing the correlation between the individual shrub ring curves using a combination of purely statistical (Cofecha; Holmes, 1983) and partly visual (TSAPWin; Rinn, 1996) techniques that rely on aligning years of very strong or very weak growth across all shrubs. Averaged ring width curves with < 20% correlation with their associated category mean ring width curve were removed, including 7 of 59 expanding and 10 of 40 stagnant shrubs.

The resulting individual ring width curves typically contained a trend of decreasing ring width values with increasing stem age (Fritts, 1976), independent of climatic influences. This trend can be removed using a variety of detrending approaches. Normally, a trend line (negative exponential, negative linear, and horizontal line regression) is fitted to each individual ring width curve and the ratio of measured ring width to the trend line results in a dimensionless index. However, if the selected trend line decreases toward zero and undershoots the actual ring width measurements, then the procedure introduces the risk of artificial index inflation (Büntgen *et al.*, 2005, Büntgen

& Schweingruber, 2010, Cook & Peters, 1997, Hallinger & Wilmking, 2011). To avoid this potential pitfall, we first power-transformed the ring widths, which produced time series where the annual deviation from the mean was independent of the growth level (Büntgen *et al.*, 2005). Then, indices were calculated as a difference between residuals of the actual ring widths to the expected ring widths. Finally, the variance of the resulting chronologies was stabilized to eliminate the influence of changes in sample size on the resulting chronologies (Cook, 1985, Osborn *et al.*, 1997).

Starting with the power transformation and ending with the standardized expanding and stagnant chronologies, the procedures above were computed with both Negative Exponential Curve Standardization (NECS; negative exponential, negative linear, and horizontal line regression), described above, and Regional Curve Standardization (RCS), described below. Expanding RCS and NECS chronologies and stagnant RCS and NECS chronologies were very similar (E: $P < 0.0001$, $r^2 = 0.80$; S: $P < 0.0001$, $r^2 = 0.52$). Due to the better chronology quality indicated by the higher serial correlation of the RCS than the NECS (Table 1.1), results presented here are from the RCS technique (Briffa *et al.*, 1992, Büntgen *et al.*, 2005, Esper *et al.*, 2003).

RCS aligns the individual ring width curves by cambial age by setting the innermost ring to a biological age of 1. The mean of all age-aligned ring width curves is the regional curve (RC), which describes the overall age-related growth trend for either expanding or stagnant shrubs. Departures from the group RC are interpreted as growth signals that are related to climate or other external forcing. In our study, these departures were power transformed, residuals calculated, variance stabilized, and developed into expanding and stagnant chronologies. The primary difference between the RCS and NECS technique is that the RCS approach detrends each individual growth curve with the same RC, whereas in NECS, each individual growth curve is detrended by a unique curve specific to that shrub.

Serial correlation within standardized expanding and stagnant RCS shrub ring chronologies was 0.76 and 0.57, respectively (Table 1.1). The expressed population signal (EPS), a measure of the common signal strength within a chronology that is a function of sample size and serial correlation, was > 0.85 after 1949 in the expanding chronology, and > 0.85 after 1971 in the stagnant chronology. Every measured shrub disc is included in the raw ring width averages, whereas the expanding and stagnant group chronologies, regional curves, and associated climate relationships were restricted to periods with at least five individual shrub records per group.

Gridded climate data were obtained from the Climate Research Unit (CRU) in East Anglia, Great Britain (www.cru.uea.ac.uk), which was downscaled to 2 km pixels covering the study area by the Scenarios Network for Alaska Planning. To accomplish this, the finer-scale 2 km pixel PRISM (Parameter-elevation Regressions on Independent Slopes Model) mean monthly climate data were overlain and combined with coarse-scale CRU gridded data. A single pixel in the center of the North Slope, containing 4 expanding and 4 stagnant patches, was selected for climate data from 1909 to present. Correlation coefficients between growth and climate data were calculated by applying a bootstrapped routine (Biondi & Waikul, 2004).

Statistics

Transect was considered the sample unit when comparing site characteristics, and the distribution of each environmental variable within the expanding or stagnant category was tested for normality. In four cases (E and S mineral soil C, alder leaf %C and $\delta^{15}N$) the distribution failed all four normality tests (Shapiro-Wilk, Jarque-Bera, Anderson-Darling, and Lilliefors), so one outlier from four environmental variables was removed and normality was satisfied. Transect averages and standard error were calculated and T-tests applied to determine significant differences between expanding and stagnant shrub patches. Paired T-tests were used to compare temperature loggers deployed at the 8 Nimiuktuk transects. When calculating mean thaw depth, 120 cm was assigned to locations where permafrost was >120 cm (beyond the length of the probe) or rocks prohibited measurement. In all stagnant shrub patches, and in only three expanding locations, pronounced microtopography (tussocks) convinced us to use temperature and moisture probes on both high and low microsites. In these cases the high and low values were averaged. Unless otherwise mentioned, means ± standard error are reported.

Ordination

The species data from five 1×1m plots from each transect were averaged across 5 plots to produce one value per transect. The transect species data were imported into PC-Ord© software, where nonmetric multi-dimensional scaling (NMS) ordination technique was applied.

Results

Shrub Rings and Climate

Evidence from shrub rings confirms that shrubs in expanding patches are growing at twice the rate (expanding = 0.43 ± 0.03 mm/yr, stagnant = 0.19 ± 0.02 mm/yr; Figure 1.3) and are better correlated with temperature than shrubs in stagnant patches. The standardized shrub growth ring chronology from the expanding alder patches is positively correlated ($P < 0.05$) with spring and summer temperatures from both the previous year and the current year of ring formation (Figure 1.4a). In contrast, the standardized chronology from the stagnant alder patches shows only a positive correlation with August temperature and a negative correlation with August precipitation from the previous year, and a negative correlation with January temperature from the current year ($P < 0.05$)(Figure 1.4b). Stagnant patches otherwise showed no significant correlations with spring and summer temperatures, and correlations with other monthly temperature data were generally weaker than those observed for expanding patches.

Both expanding and stagnant chronologies show no significant trend over the period when ≥ 5 shrubs are included in each category (Figure 1.5c). Both chronologies contain opposing decadal-scale oscillations, however, that seem to be associated with trends in temperature and the phase of the Arctic Oscillation (Thompson *et al.*, 2000). Prior to 1976, when the AO was not as strong (Thompson *et al.*, 2000) and temperatures were cooler, the stagnant chronology increased significantly and the expanding chronology decreased significantly (both $P < 0.05$) (Figure 1.5c). Since that time the AO has been predominantly positive (Thompson *et al.*, 2000), and the stagnant chronology has declined significantly ($P < 0.05$), while the expanding chronology has increased marginally ($P < 0.15$).

Ring widths from shrubs comprising the stagnant chronology were less correlated with each other (Table 1.1) than were those from the expanding population, indicating a weaker common (climate) signal in the stagnant shrub rings. The stagnant chronology was constructed without 25% (10 of 40) of the shrubs, which were eliminated based on their growth incoherence with the other stagnant shrubs, while only 12% (7 of 59) were eliminated from the expanding group. The remaining expanding shrubs had higher serial correlation than stagnant shrubs (0.76 vs. 0.57), and a much earlier attainment of high chronology quality (1949 vs. 1971, $EPS > 0.85$) (Table 1.1).

Vegetation Composition

Ten consecutive iterations of NMS ordination showed clear differences between species composition and cover within stagnant and expanding shrub patches (Figure 1.6). Expanding patches had lower percent cover of sedge tussocks ($E = 3 \pm 1\%$, $S = 22 \pm 5\%$; $P < 0.01$) and higher percent cover of deciduous shrubs ($E = 33 \pm 2\%$, $S = 25 \pm 3\%$; $P < 0.05$) (Table 1.2), which was most pronounced at the Nimiuktuk sites (Figure 1.6). Other cover categories – forbs, lichens, grasses, litter, moss, evergreen shrubs, soil, sphagnum, rock, and water – were similar in expanding and stagnant sites. Regional differences in flora were also evident between Brooks Range and North Slope sites, and showed > 0.3

Pearson correlation coefficient with leaf chemical properties in birch and alder including $\delta^{13}C$ in birch and C:N and %N in alder (Figure 1.6).

Soil Characteristics

Mineral and organic soils from expanding sites had significantly lower soil moisture than the same horizons from stagnant soils (Table 1.2). Soil temperature at 5 cm depth, averaged over the period from 7/1/2010 to 9/20/2010, was warmer in expanding shrub patches than in stagnant shrub patches ($P < 0.05$), resulting in significantly greater depth of thaw (Table 1.2). Above-zero temperatures were warmer in expanding patches than in stagnant patches ($P < 0.01$), while below-zero temperatures were not significantly different. Temperature at 20 cm above ground was not significantly different between expanding and stagnant patches.

Expanding shrub patches had higher soil organic bulk density than stagnant patches ($P < 0.05$), while the mineral layers had similar bulk density (Table 1.2). Total carbon and nitrogen contents (%) of organic horizons did not differ between expanding and stagnant patches; however, both %C and %N were significantly greater for mineral soils from stagnant patches compared with those from expanding patches (both $P < 0.05$). Soils from expanding sites were less acidic than those from stagnant sites for both organic ($P < 0.05$) and mineral ($P < 0.05$) horizons, though this difference was driven by the 6 unpaired expanding sites along the upper Colville River.

Leaf Chemistry

Nitrogen content of birch leaves was significantly higher in expanding patches compared with stagnant patches; however, no differences in N content were found for either alder or willow between the patch types. Leaf carbon content was higher in stagnant patches only for alder and willow. These patterns translated to lower leaf C:N ratios for alder, willow, (both $P < 0.1$) and birch ($P < 0.05$) leaves from expanding patches compared with stagnant patches (Table 1.2). Willow leaves from expanding patches had marginally lower $\delta^{15}N$ values than corresponding leaves from stagnant patches ($P < 0.1$), while birch and alder leaves from the two patch types had similar $\delta^{15}N$ values. Alder leaves from expanding patches had significantly more depleted $\delta^{13}C$ values than stagnant alder leaves ($P < 0.05$), while birch and willow expanding patch leaves had similar $\delta^{13}C$ values to their corresponding stagnant patch leaves.

Shrub distribution

On the ground, and from aerial photographs, it is clear that shrubs in the expanding patches are usually large, upright, and clumped or randomly distributed, whereas the shrubs in the stagnant patches are smaller, prostrate, and more evenly distributed. None of the parameters we measured capture the spatial distribution, but the difference in the distribution of individuals between expanding and stagnant shrub patches in the repeated photos is obvious (*e.g.* Figure 1.2), and so is mentioned here as a clear, but difficult to quantify, difference.

Textures of expanding and stagnant shrub patches were scaled from repeat photographs to a satellite image by outlining polygons of expanding and stagnant patches, which were then used in a supervised classification of satellite image pixels revealing distinct patterns tied to landscape topography. Expanding patches were found along topographic incisions including streams of various sizes, floodplains, and outcrops, while stagnant patches occupied broader, less-sloping landscape positions (Figure 1.7). The approach does not delineate between new shrubs and those that existed in 1950, but it does help to identify the landscape positions that are being rapidly colonized by tall shrubs, versus areas that are not.

Discussion

Shrub Rings and Climate

Shrub ring width and summer temperatures are commonly correlated at northern high latitude and high elevation locations (Bar *et al.*, 2008, Blok *et al.*, 2011, Forbes *et al.*, 2010, Hallinger *et al.*, 2010). In this study, the summer growth-temperature correlations were only strong in expanding patches (Figure 1.4a). The stagnant chronology, in contrast, was largely independent of spring/summer temperatures (Figure 1.4b). Shallower thaw depth and cooler annual and summer soil temperatures in stagnant patches (Table 1.2) suggests that the organic soils retard heat penetration and dampen the potential effect of warm summers on soil microbial activity. Most of the width of the annual growth ring has been added by August (Blok *et al.*, 2011), so the (negative) correlation between growth and the previous August precipitation is probably due to the persistence of wet soils in stagnant patches. The negative relationship with August precipitation (Figure 1.4b) suggests that high soil moisture inhibits growth in tussock tundra shrubs. Because August precipitation has remained stable throughout the record (Figure 1.5a), and the stagnant shrubs are unresponsive to air temperature (Figure 1.4b), the decline in the stagnant chronology since the 1970s may instead be attributable to factors such as interspecific competition, discussed later.

Positive correlations between March and April air temperatures and growth are particularly interesting because the shrubs are not growing during those months, yet they are sensitive to climatic conditions during that period (Figure 1.4a). Consistently negative correlations with snow depth (precipitation October – April), though non-significant, suggest that earlier snowmelt favors early bud burst and shrub growth. Indeed, the earlier initiation of growing seasons since 1976 (Chapter 2) has positively affected alder growth in this study. Recent evidence from Siberian tundra also indicates a strong correlation between growing season temperatures and growth in *Salix pulchra*, though no correlation was found between growth and pre-snowmelt temperature (Blok *et al.*, 2011). Similarly, bud burst in *Salix pulchra* and *Betula nana*, two common shrub species in expanding sites, is controlled by spring temperatures once snowmelt has occurred (Pop *et al.*, 2000).

The standardized chronologies ostensibly remove the effect of new or juvenile stems growing more rapidly, itself an inherent metric of shrub expansion. It is perhaps not surprising, then, that trends in the standardized chronologies do not portray persistent increases in shrub growth in arctic Alaska. For example, there is only a subtle increase (P

< 0.15) in the standardized expanding chronology since 1976, during a warm period when we would expect shrubs to be thriving (Figure 1.5c).

The raw ring width measurements (Figure 1.5d) contain information about both stem growth rates and stem initiation. During the period when the expanding standardized chronology showed only a subtle increase (> 1976), the raw ring widths of expanding patches showed a clear separation from the stagnant patches, due to the initiation of new stems (Figure 1.5e). Interpreting raw ring widths also has it hazards; in this case, the largest stems were cut from each plot, so the decline in the stagnant raw ring widths is partly attributable to no stems being initiated to boost average ring widths during that period. While the goal of standardized chronologies is typically to establish relationships between climate and stem growth, the raw ring widths are more suggestive of shrub patch dynamics than standardized chronologies.

The shrub patches sampled for this study were selected based on their categorization as “expanding” or “stagnant” in the repeated photographs. The results presented here indicate that expanding shrubs grow faster and are more responsive to climate than stagnant shrubs. However, positive trends in the standardized chronology prior to 1976, and negative trends thereafter, show that the so-called stagnant patches may not be truly stagnant, and therefore the terminology should be interpreted in the context of the shrub ring and site characteristics presented here.

Soil Characteristics

The response of expanding shrub patches, but not adjacent stagnant shrub patches, to warm summers suggests that the effect of air temperature on shrubs is mediated by soil conditions, since adjacent shrubs presumably experienced the same summer air temperatures. Warmer mean soil temperatures and a strong correlation between shrub ring width and air temperature in expanding shrub patches is consistent with recent studies showing that summer temperature positively affects growth (Blok *et al.*, 2011, Forbes *et al.*, 2010, Hallinger *et al.*, 2010). The deeper active layer in the expanding patches indicates that the summer ground heat flux is higher than in the stagnant patches. The warmer summer soil temperatures in expanding patches (Table 1.2) are a result of higher thermal conductivity resulting from lower soil moisture and less organic material.

Soils from expanding patches have higher thermal conductivity in the summer, in spite of their lower moisture content. Drier soils, combined with the warmer soil conditions (Table 1.2), produce higher rates of decomposition and mineralization . The drier soils of expanding shrub patches are partly attributable to the deeper, and sometimes non-existent permafrost permitting greater drainage and lower soil moisture than in the adjacent stagnant patches. Grain size was not examined, but may also be affecting drainage and permafrost conditions.

Differences in soil moisture between expanding and stagnant patches are sufficiently strong that June, July, and August precipitation correlations in the current and preceding year are positive in the expanding patches and negative in the stagnant patches, though only the preceding August stagnant correlation is significant. The strong negative correlation between preceding August precipitation and annual shrub growth in stagnant patches suggests that high soil moisture is inhibiting growth, either through anoxic summer conditions, or through increased cold penetration in the winter from higher ice content. Wet summer soil conditions and high surface organic matter content in stagnant patches prevents soils from warming during summer and limits nutrient turnover and cycling rates.

Enhanced soil physical conditions in expanding patches, along with lower C:N ratios in the leaves (and, presumably, the litter) probably explain the marginally lower C:N ratios in soils of expanding patches ($P < 0.1$). Soil was sampled volumetrically, and the bottom of the organic layer was not recorded. Both expanding and stagnant patches typically had at least a thin organic layer, which, when volumetrically sampled, showed no significant differences between %C and %N of expanding and stagnant organic soils. The greater C and N content in the mineral soils of stagnant patches ($P < 0.05$), however, indicates a deeper presence of organic material at the stagnant sites.

Shrub distribution

Regular spacing of plants is thought to be most prevalent in low-resource environments (Rietkerk & van de Koppel, 2008). Regular spacing of alder shrubs, such as that evident in stagnant patches described here (Figure 1.2), suggests competition for limited resources, as demonstrated by increased nutrient content in stems of neighboring alder shrubs when an individual alder shrub is removed (Chapin *et al.*, 1989). When stagnant patches composed of evenly-spaced shrubs are extrapolated across the landscape using high-resolution satellite images, the result is that stagnant patches – low resource environments – occupy flat, though not necessarily level, terrain. The low resource notion is corroborated by the stagnant shrub rings, which chronicle slow growth that is largely unresponsive to climate. In contrast, expanding patches composed of clumped or randomly distributed shrubs – higher resource environments – are associated with floodplains, stream corridors, and outcrops. These generalizations are corroborated by the expanding shrub rings, which chronicle rapid growth that is responsive to spring and summer temperatures. In some cases (*e.g.* Figure 1.2), there is no topographic expression where shrubs are expanding, but the deeper active layer likely channelizes subsurface flow, a process shown to improve nutrient cycling and productivity for *Eriophorum vaginatum* in smaller drainage features (Chapin *et al.*, 1988). In that study, the authors argued that subsurface flow reduced diffusional constraints on nutrient delivery, increased soil heat flux, and increased microbial activity and nutrient turnover.

The repeat photography extrapolated across satellite imagery in this study is consistent with recent studies utilizing Landsat and finer-scale imagery to characterize the distribution and current expansion of shrubs along stream networks (Beck *et al.*, in press, Munger *et al.*, 2008). Our *in situ* measurements imply that surface organic material at stagnant sites is buffering the soil from persistent warming, and that shallow permafrost is impeding drainage and causing cold, wet soils (Table 1.2, Figure 1.4b). Stream channels dissect the often continuous organic layer, and can be considered corridors along which ecological disturbance can readily propagate (Chapter 2).

A number of studies have shown that NDVI is also increasing in many tussock tundra sites comparable to the stagnant sites described in this study (Goetz *et al.*, 2005, Munger *et al.*, 2008, Verbyla, 2008). The increasing NDVI trend from tussock tundra areas reflects an increase in productivity, which correlates well with temperature and enhanced shrub growth (Forbes *et al.*, 2010), but could also be partially explained by increases in the abundance or productivity of graminoids (Jia *et al.*, 2006, Munger *et al.*, 2008), which have out-paced changes in shrubs in some tussock tundra areas (Joly *et al.*, 2007). The so-called stagnant sites we present here are located between plot studies at Toolik Lake and the Seward Peninsula that document increases in graminoid abundance in recent decades (Joly *et al.*, 2007) or in response to nutrient addition (Chapin *et al.*, 1995, Gough *et al.*, 2002, Hobbie *et al.*, 2005). We speculate that in stagnant patches, graminoids such as *Eriophorum vaginatum* and *Carex aquatilis* (graminoids: S = 21.8%, E = 2.8%; $P < 0.01$) may be more responsive to warming (Chapin, 1980) and out-compete alder for soil nutrients, which may or may not be increased because of the minor soil warming occurring in these highly organic soils. A rapid response to warming from tussock-forming graminoids, for example, would explain the higher NDVI values during warm summers and reconcile those values with the lack of response from (stagnant, tussock tundra) alder to warm summers.

Alder colonization is occurring on recent thaw slumps in the Mackenzie Delta of NW Canada (Lantz *et al.*, 2009). Thaw slumps are threshold responses associated with warming air and subsurface temperatures, which radically alter the immediate environment (mean size = 1.34 ha; Lantz & Kokelj, 2008, Ukraintseva, 2008). The expanding patches in this study seemingly change the landscape more gradually, but do so on a larger scale. Active disturbance regimes are maintained through processes like cryoturbation or the regular input of loess (Bockheim *et al.*, 1998, Walker *et al.*, 2001), which increase nutrient turnover, promote warmer soils, and maintain lower soil organic matter stocks (Walker & Walker, 1991) through higher rates of litter decomposition. Continual inputs of nutrients from ongoing disturbances prevent the accumulation of soil organic material, making the soil more responsive to changes in temperature. In this study, the thermal conductivity of soils – a function of the prevailing disturbance regime – predisposes expanding patches to respond to warmer springs and summers (Figure 1.4). Soils in areas of the landscape with less peat are more responsive to air temperature changes. The peat, in concert with fine-grained soils, also allows shallow permafrost to exist, which makes soils too wet and cold for rapid shrub growth. This is corroborated by the pattern of expanding patches overlapping with floodplains and stream corridors, where peat is lacking and flowing water facilitates the penetration and lateral migration of heat and nutrients.

Trajectories

The relevant time series measurements available for expanding patches are increased shrub coverage, stature and growth derived from repeat photography and shrub growth rings, and increased air temperature from distant stations. Because shrub height and snow depth are so tightly coupled (Liston *et al.*, 2002), we can assume that snow depth has increased over the last century in the expanding shrub patches. This has not led to an increase in snow duration, and, in fact, a lengthening of the growing season has been documented in numerous studies (Chapin *et al.*, 2005, Euskirchen *et al.*, 2007). The imprint of the lengthening growing season on shrubs is evident as positive growth correlations with pre-snowmelt temperature (Figure 1.4a) and concurrently non-significant but negative correlations with snow depth (April and May temperature in previous and current year). In response to increases in air temperature, growing season length, and snow depth, ground temperature has presumably also increased in both types of patches, though preferentially in the expanding patches, because those soils have less organic material and greater thermal conductivity.

It is not clear whether the expanding alder-dominated shrub communities presented here are stable under the current climatic conditions or whether the communities are transitional. Disturbed arctic communities do not necessarily return to their pre-disturbance state (Forbes *et al.*, 2001). The prediction is complicated by the ongoing warming (Serreze & Francis, 2006), and the expanding communities being roughly divided between those associated with outcrops and those associated with drainage corridors. The most notable alder expansion prior to the end of the Little Ice Age occurred approximately 7,000 ya and coincided with paludification and the formation of the modern tundra (Oswald *et al.*, 1999). Alder is a N_2-fixing genus known to enhance production and precede permafrost aggradation during boreal forest upland (Mitchell & Ruess, 2009a, Mitchell & Ruess, 2009b) and floodplain succession (Nossov *et al.*, 2011). It is possible that the current alder expansion in arctic Alaska will enhance production and paludify parts of the landscape with currently thin or nonexistent organic layers. Experimental removal of birch shrubs has been shown to reduce active layer thickness by increasing heat input during the growing season, implying that the addition of shrubs would aggrade permafrost (Blok *et al.*, 2010). Alternatively, alder expansion could facilitate positive feedbacks by drifting snow, trapping Ca-rich loess, increasing available N, releasing soil C, and further promoting conditions conducive to shrub growth. This sequence of events seems likely in expanding patches where rock outcrops lie shallowly beneath the surface. Rocky soils prevent moisture from being held in the soil, which is a prerequisite for permafrost development and paludification. Areas marginal to stream corridors, however, often have finer-grained soils capable of holding more moisture, so the trajectory and outcome of alder expansion in these locations will depend on the balance between soil decomposition and aboveground production.

Conclusion

This study presents localized environmental conditions, vegetation composition, plant ecophysiological traits, and growth metrics that differ between expanding and stagnant shrub patches. Because the air temperature is the same in adjacent expanding and stagnant patches, the diagnostic parameters of expanding shrub patches suggest changes in the soil environment driven by warming air temperatures are directly influencing the shrub expansion. The pattern of expanding shrub patches on the landscape indicates that shrubs are propagating preferentially via floodplains, dendritic stream corridors, and outcrops, where localized disturbance regimes mediate increases in air temperature.

Acknowledgements

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Tables

Table 1.1. Comparison of shrub ring chronologies age-detrended using the RCS (Regional Curve Standardization) and NECS (Negative Exponential Curve Standardization) methods. RCS chronologies had higher serial correlations, and were therefore used for subsequent analyses.

Standardized shrub ring chronologies	Interannual correlation (autocorrelation)	Mean sensitivity (to climate)	Serial Correlation	Average Expressed Population Signal (EPS)
Expand (NECS)	0.27	0.37	0.31	0.88 (1950)
Stagnant (NECS)	0.34	0.27	0.20	0.83 (1981)
Expand (RCS)	0.45	0.37	0.57	0.88 (1949)
Stagnant (RCS)	0.48	0.23	0.76	0.83 (1971)

Table 1.2. Vegetation and soil characteristics of expanding (E) and stagnant (S) shrub patches. Leaf chemistry statistics are within-species comparisons.

Soils	Expanding	Stagnant
Gravimetric soil moisture (%)		
Organic	62 ± 3 **	75 ± 1 **
Mineral	25 ± 2 **	33 ± 1 **
Soil moisture probe, top 10 cm (%)	22.6 ± 3.1 **	32.3 ± 4.1 **
Thaw depth (cm)	88 ± 7.8 †	32 ± 3.6 †
-5 cm ground temp,		
7/1/08 – 9/20/10 (°C)	-1.4 ± 0.4 **	-3.0 ± 0.3 **
> 0 °C	8.9 ± 1.8 †	5.6 ± 1.6 †
< 0 °C	-8.9 ± 1.2	-10.6 ± 0.7
Emergence of +20 cm light sensors from snow	May 13th ± 3.1 days **	May 2nd ± 1.4 days **
Bulk density (g)		
Organic	0.40 ± 0.03 **	0.26 ± .04 **
Mineral	1.23 ± 0.06	1.20 ± 0.02
pH	5.8 ± 0.2 **	5.2 ± 0.1 **
% C		
Organic	15.5 ± 1.0	14.4 ± 0.8
Mineral	6.3 ± 0.8 **	9.9 ± 0.7 **

Table 1.2 Continued…		
% N		
Organic	0.86 ± 0.06	0.75 ± 0.05
Mineral	0.56 ± 0.09 **	0.87 ± 0.10 **
C:N		
Organic	18.4 ± 0.9	19.2 ± 0.5
Mineral	12.7 ± 0.5 *	14.0 ± 0.3 *
Leaf chemistry		
% C		
Alder	47.6 ± 0.1 **	48.3 ± 0.1 **
Birch	48.6 ± 0.2	48.8 ± 0.3
Willow	47.2 ± 0.2 †	48.0 ± 0.1 †
% N		
Alder	2.7 ± 0.1	2.5 ± 0.1
Birch	2.3 ± 0.1 **	2.1 ± 0.1 **
Willow	2.5 ± 0.1	2.6 ± 0.1
C:N		
Alder	17.9 ± 0.5 *	19.1 ± 0.5 *
Birch	21.0 ± 0.7 **	23.6 ± 0.8 **
Willow	19.0 ± 0.5 *	18.4 ± 0.3 *

Table 1.2 Continued…

δ^{15}N		
Alder	-1.3 ± 0.06	-1.2 ± 0.03
Birch	-5.4 ± 0.3	-4.8 ± 0.4
Willow	-2.7 ± 0.3 *	-2.0 ± 0.2
δ^{13}C		
Alder	-27.8 ± 0.1 **	-27.5 ± 0.1 **
Birch	-29.3 ± 0.1	-29.4 ± 0.1
Willow	-28.2 ± 0.1	-27.9 ± 0.1
Growth Form (% cover)		
Shrub deciduous	32.6 ± 1.7 **	24.9 ± 3.1 **
Moss	25.0 ± 3.4	14.6 ± 4.2
Sedge	2.8 ± 0.8 †	21.8 ± 4.6 †
Shrub evergreen	11.0 ± 1.6	14.7 ± 2.6
Litter	14.7 ± 3.5	10.8 ± 2.9
Lichen	7.5 ± 1.8	7.6 ± 2.3
Forb	4.1 ± 0.7	2.7 ± 2.1
Grass	1.9 ± 0.6	2.0 ± 0.8

$P < 0.1$ = *

$P < 0.05$ = **

$P < 0.01$ = †

Figures

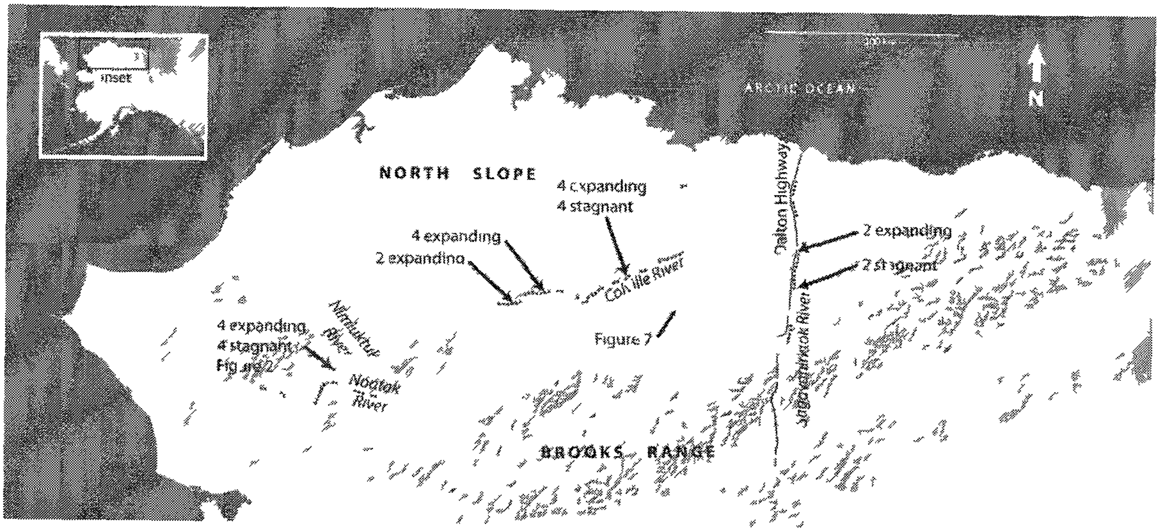

Figure 1.1. Study area and location of 26 shrub patches sampled, indicated as either expanding or stagnant.

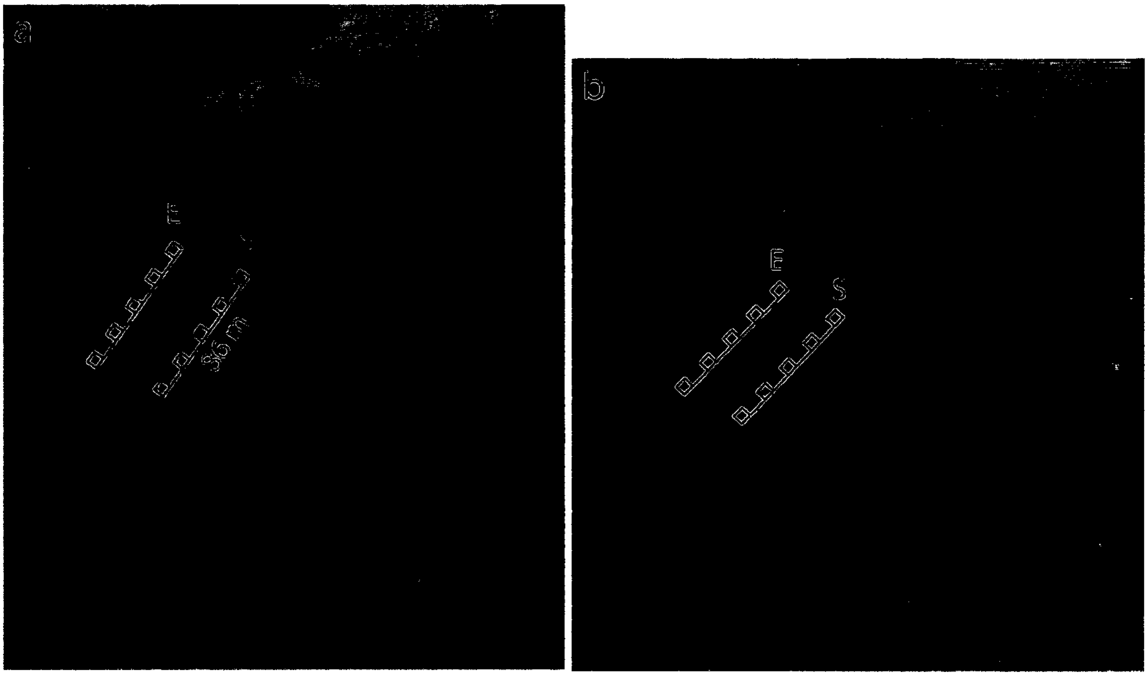

Figure 1.2. Placement of expanding (E) and stagnant (S) transects upon repeat photography (1950 (a) and 2002 (b)) from the Nimiuktuk River (Figure 1.1) (USGS/Navy, Ken Tape). Smaller boxes along the transects are 6×6 m plots (referred to as "locations" in the text), and not shown are the 1×1m quadrats nested in each 6×6 plot.

Figure 1.3. Individual (normal lines) and mean (bold lines) alder shrub growth rates for expanding (green) and stagnant (red) shrubs, showing that expanding shrubs grew twice as fast as stagnant shrubs.

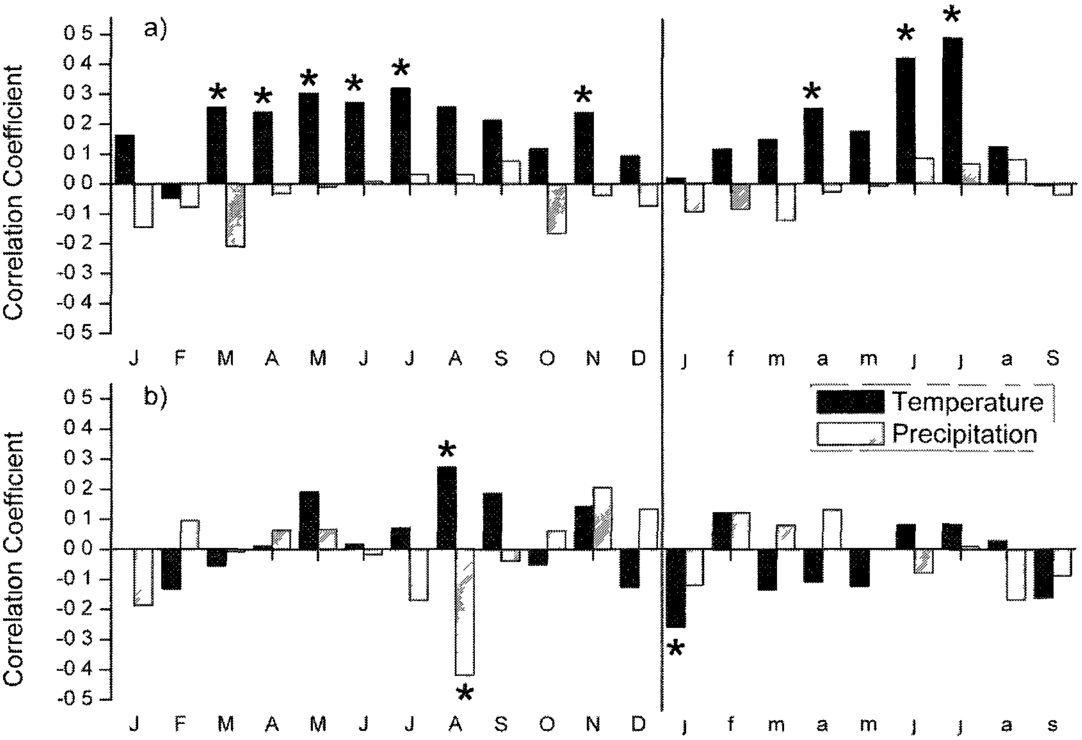

Figure 1.4. Correlation coefficients (* = P < 0.05) between alder shrub chronologies and monthly average temperatures (black columns) or precipitation sums (grey columns) for a) expanding shrub patches (1939-2008) and b) stagnant shrub patches (1953-2008), when >5 shrubs were included in each chronology. Months of the prior growing season are displayed in capital letters, and months of the current growing season are displayed in lowercase letters.

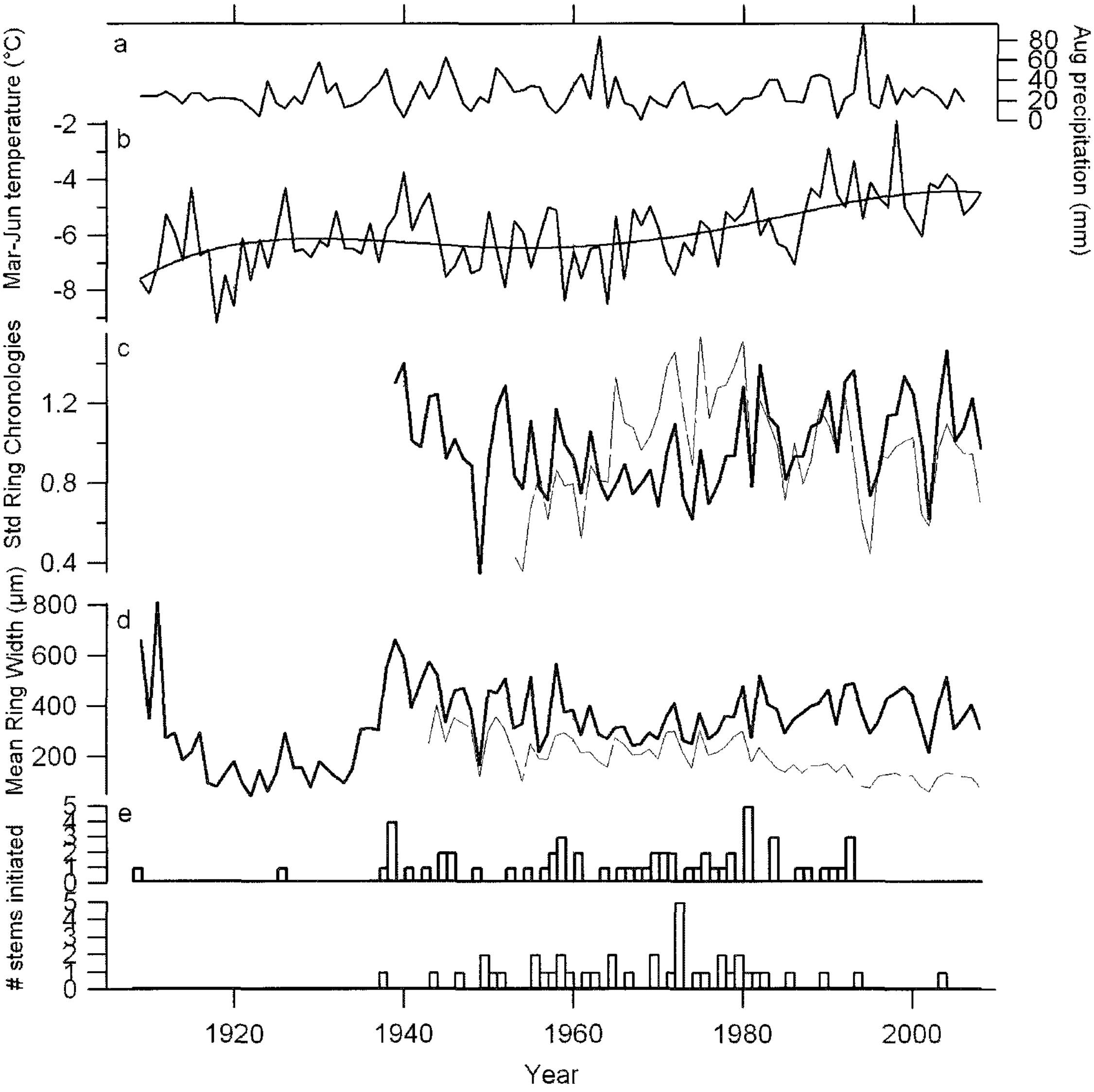

Figure 1.5. Expanding (bold line) and stagnant (normal line) alder shrub chronologies (c, d) and the significantly correlated climate variables (a, b) from Figure 1.4. The polynomial fit for temperature is to emphasize decadal and longer trends. (e) Population structure of sampled expanding (upper histogram) and stagnant (lower histogram) shrubs.

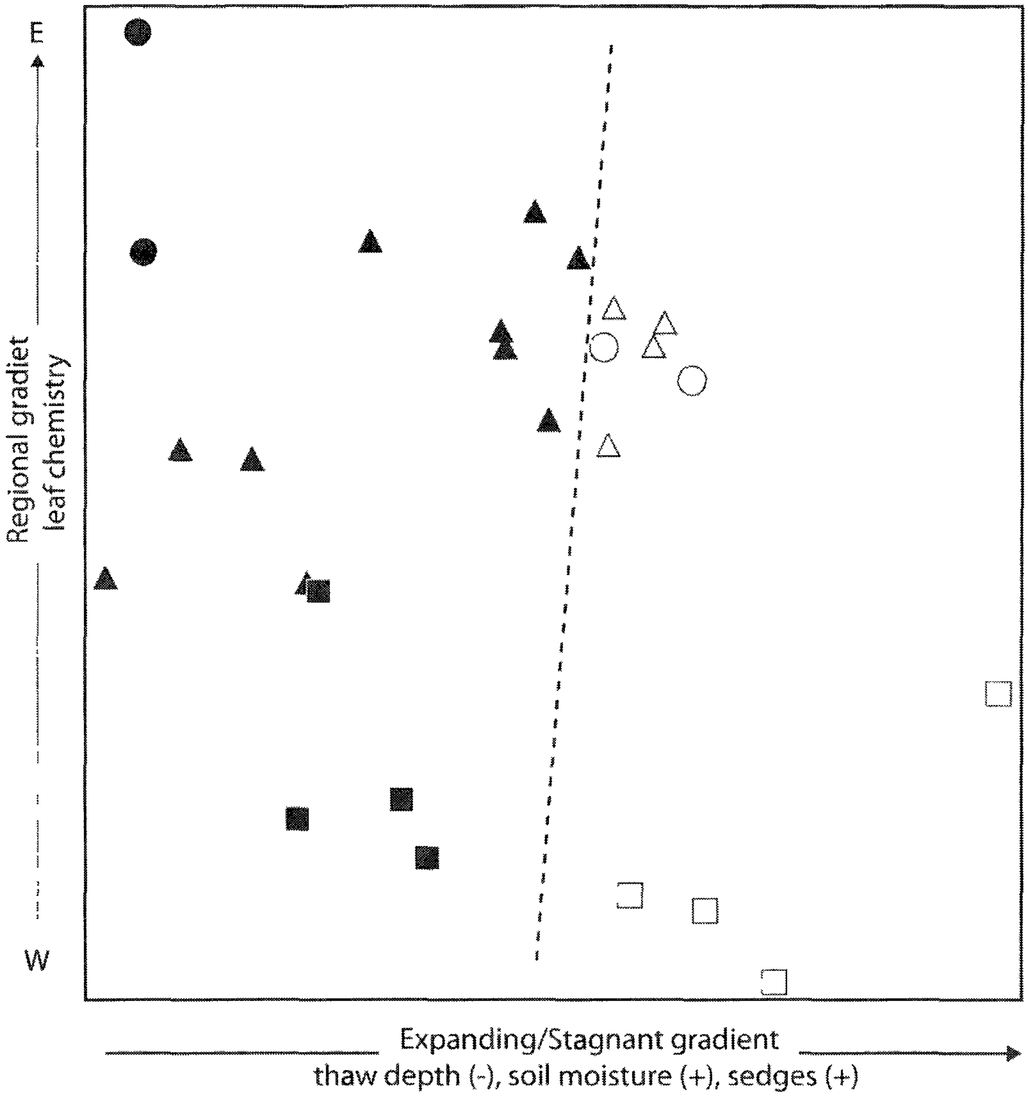

Figure 1.6. Nonmetric Multi-dimensional Scaling (NMS) ordination of floristic cover in 16 expanding (solid) and 10 stagnant (open) shrub patches. Distance in the ordination space is proportional to floristic difference, and dashed line separates expanding from stagnant patches (triangles = Colville River, squares = Nimiuktuk River, circles = Sagavanirktok River).

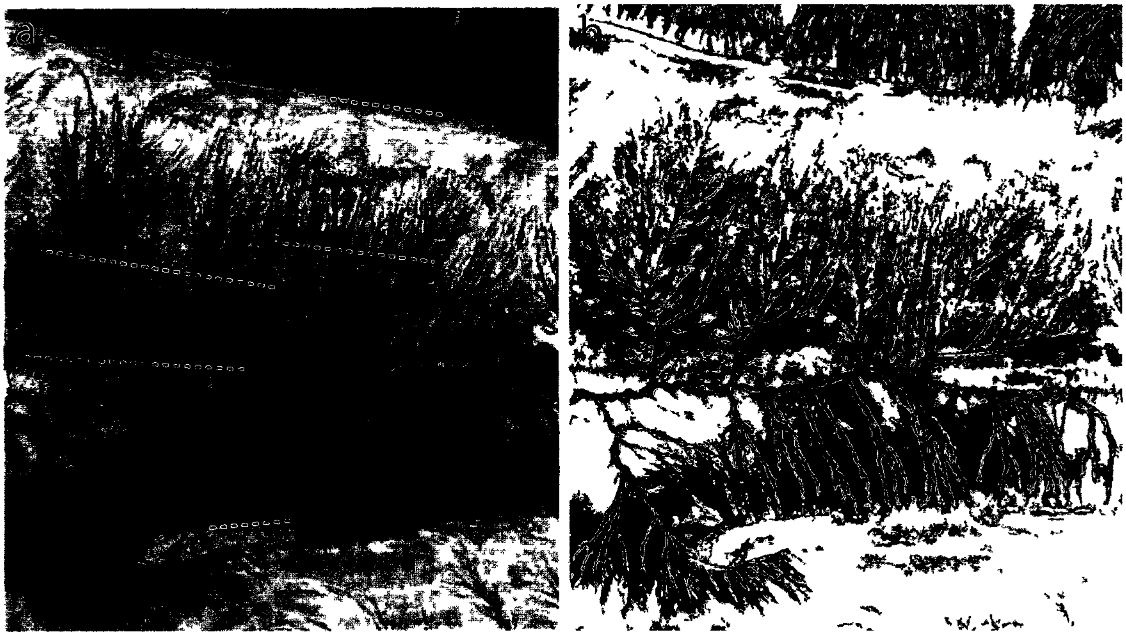

Figure 1.7. (a) False-color SPOT image near the Chandler River showing pattern of tall shrub (red) distribution along streams and near-surface or outcropping sedimentary rock units (dashed lines). (b) Supervised classification of the SPOT image, showing expanding shrub patches (green), stagnant shrub patches (blue), and short- or non-shrub tundra (white) Each image is 5 5 km wide

References

Bar A., Pape R., Brauning A., Loffler 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.

Beck P. S. A., Horning N., Goetz S. J., Loranty M. M., Tape K. D. (in press) The density of shrub cover on the North Slope of Alaska: a circa 2000 baseline map. *Arctic, Antarctic, and Alpine Research.*

Bhatt U. S., Walker D. A., Raynolds M. K., Comiso J. C., Epstein H. E., Jia G., . . . Webber P. J. (2010) Circumpolar arctic tundra vegetation change is linked to sea ice decline. *Earth Interactions,* **14**, 1-20.

Biondi F., Waikul K. (2004) DENDROCLIM2002: A C++ program for statistical calibration of climate signals in tree-ring chronologies. *Computers & Geosciences,* **30**, 303-311.

Blok D., Heijmans M. M. P. D., Schaepman-Strub G., Kononov A. V., Maximov T. C., Berendse F. (2010) Shrub expansion may reduce summer permafrost thaw in Siberian tundra. *Global Change Biology,* **16**, 1296-1305.

Blok D., Sass-Klaassen U., Schaepman-Strub G., Heijmans M. M. P. D., Sauren P., Berendse F. (2011) What are the main climate drivers for shrub growth in Northeastern Siberian tundra? *Biogeosciences Discuss,* **8**, 771-798.

Bockheim J. G., Walker D. A., Everett L. R., Nelson F. E., Shiklomanov N. I. (1998) Soils and cryoturbation in moist nonacidic and acidic tundra in the Kuparuk River basin, Arctic Alaska, USA. *Arctic and Alpine Research,* **30**, 166-174.

Briffa K. R., Jones P. D., Bartholin T. S., Eckstein D., Schweingruber F. H., Karlén W., . . . Eronen M. (1992) Fennoscandian summers from AD 500: temperature changes on short and long timescales. *Climate Dynamics,* **7**, 111-119.

Bunn A. G., Goetz S. J. (2006) Trends in satellite-observed circumpolar photosynthetic activity from 1982 to 2003: The influence of seasonality, cover type, and vegetation density. *Earth Interactions,* **10**, 1-19.

Büntgen U., Esper J., Frank D., Nicolussi K., Schmidhalter M. (2005) A 1052-year tree-ring proxy for Alpine summer temperatures. *Climate Dynamics,* **25**, 141-153.

Büntgen U., Schweingruber F. H. (2010) Environmental change without climate change? *New Phytologist,* **188**, 646-651.

Chapin F. S. (1980) Nutrient allocation and responses to defoliation in tundra plants. *Arctic and Alpine Research,* **12**, 553-563.

Chapin F. S., Fetcher N., Kielland K., Everett K. R., Linkins A. E. (1988) Productivity and nutrient cycling of Alaskan tundra - enhancement by flowing soil-water. *Ecology,* **69**, 693-702.

Chapin F. S., Mcgraw J. B., Shaver G. R. (1989) Competition causes regular spacing of alder in Alaskan shrub tundra. *Oecologia,* **79**, 412-416.

Chapin F. S., Shaver G. R., Giblin A. E., Nadelhoffer K. J., Laundre J. A. (1995) Responses of Arctic tundra to experimental and observed changes in climate. *Ecology,* **76**, 694-711.

Chapin F. S., Sturm M., Serreze M. C., Mcfadden J. P., Key J. R., Lloyd A. H., . . . Welker J. M. (2005) Role of land-surface changes in Arctic summer warming. *Science,* **310**, 657-660.

Cook E. R. (1985) *A time series analysis approach to tree ring standardization,* Tucson, University of Arizona.

Cook E. R., Peters K. (1997) Calculating unbiased tree-ring indices for the study of climatic and environmental change. *Holocene,* **7**, 361-370.

Esper J., Cook E. R., Krusic P. J., Peters K., Schweingruber F. H. (2003) Tests of the RCS method for preserving low-frequency variability in long tree-ring chronologies. *Tree-Ring Research,* **59**, 81-97.

Euskirchen E. S., McGuire A. D., Chapin F. S. (2007) Energy feedbacks of northern high-latitude ecosystems to the climate system due to reduced snow cover during 20th century warming. *Global Change Biology,* **13**, 2425-2438.

Forbes B. C., Ebersole J. J., Strandberg B. (2001) Anthropogenic disturbance and patch dynamics in circumpolar Arctic ecosystems. *Conservation Biology,* **15**, 954-969.

Forbes B. C., Fauria M. M., Zetterberg P. (2010) Russian Arctic warming and 'greening' are closely tracked by tundra shrub willows. *Global Change Biology,* **16**, 1542-1554.

Fritts H. (1976) *Tree rings and climate,* Caldwell, Blackburn Press.

Goetz S. J., Bunn A. G., Fiske G. J., Houghton R. A. (2005) Satellite-observed photosynthetic trends across boreal North America associated with climate and fire disturbance. *Proceedings of the National Academy of Sciences of the United States of America,* **102**, 13521-13525.

Gough L., Wookey P. A., Shaver G. R. (2002) Dry heath arctic tundra responses to long-term nutrient and light manipulation. *Arctic Antarctic and Alpine Research,* **34**, 211-218.

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.

Hallinger M., Wilmking M. (2011) No change without a cause – why climate change remains the most plausible reason for shrub growth dynamics in Scandinavia. *New Phytologist,* **189**, 902-908.

Hinzman L. D., Bettez N. D., Bolton W. R., Chapin F. S., Dyurgerov M. B., Fastie C. L., . . . Yoshikawa K. (2005) Evidence and implications of recent climate change in northern Alaska and other arctic regions. *Climatic Change,* **72**, 251-298.

Hobbie S. E., Gough L., Shaver G. R. (2005) Species compositional differences on different-aged glacial landscapes drive contrasting responses of tundra to nutrient addition. *Journal of Ecology,* **93**, 770-782.

Holmes R. L. (1983) Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bulletin,* **43**, 69-78.

Jia G., Epstein H. E., Walker D. A. (2002) Spatial characteristics of AVHRR-NDVI along latitudinal transects in northern Alaska. *Journal of Vegetation Science,* **13**, 315-326.

Jia G., Epstein H. E., Walker D. A. (2003) Greening of arctic Alaska, 1981-2001. *Geophysical Research Letters,* **30**, doi 10.1029/2003gl018268.

Jia G., Epstein H. E., Walker D. A. (2006) Spatial heterogeneity of tundra vegetation response to recent temperature changes. *Global Change Biology,* **12**, 42-55.

Joly K., Jandt R. R., Meyers C. R., Cole M. J. (2007) Changes in vegetative cover on Western Arctic Herd winter range from 1981 to 2005; potential effects of grazing and climate change. *Rangifer*, 199-206.

Lantz T. C., Kokelj S. V. (2008) Increasing rates of retrogressive thaw slump activity in the Mackenzie Delta region, NWT, Canada. *Geophysical Research Letters,* **35**, doi 10.1029/2007gl032433.

Lantz T. C., Kokelj S. V., Gergel S. E., Henry G. H. R. (2009) Relative impacts of disturbance and temperature: persistent changes in microenvironment and vegetation in retrogressive thaw slumps. *Global Change Biology,* **15**, 1664-1675.

Liston G. E., Mcfadden J. P., Sturm M., Pielke R. A. (2002) Modelled changes in arctic tundra snow, energy and moisture fluxes due to increased shrubs. *Global Change Biology,* **8**, 17-32.

Mack M. C., Schuur E. A. G., Bret-Harte M. S., Shaver G. R., Chapin F. S. (2004) Ecosystem carbon storage in arctic tundra reduced by long-term nutrient fertilization. *Nature,* **431**, 440-443.

Mitchell J., Ruess R. W. (2009a) N_2-fixing alder (*Alnus viridis* spp. *fruticosa*) effects on soil properties across a secondary successional chronosequence in interior Alaska. *Biogeochemistry,* **95**, 215-229.

Mitchell J., Ruess R. W. (2009b) Seasonal patterns of climate controls cver nitrogen fixation by *Alnus viridis* subsp. *fruticosa* in a secondary successional chronosequence in Interior Alaska. *Ecoscience,* **16**, 341-351.

Munger C. A., Walker D. A., Maier H. A., Hamilton T. D. (2008) Spatial analysis of glacial geology, surficial geomorphology, and vegetation in the Toolik Lake region: Relevance to past and future land-cover changes. *9th Int. Permafrost Conf.,* **2**, 1255-1260.

Myneni R. B., Keeling C. D., Tucker C. J., Asrar G., Nemani R. R. (1997) Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature,* **386**, 698-702.

Nossov D. R., Hollingsworth T. N., Ruess R. W., Kielland K. (2011) Development of *Alnus tenuifolia* stands on an Alaskan floodplain: patterns of recruitment, disease and succession. *Journal of Ecology*, doi: 10.1111/j.1365-2745.2010.01792.x.

Nowinski N. S., Taneva L., Trumbore S. E., Welker J. M. (2010) Decomposition of old organic matter as a result of deeper active layers in a snow depth manipulation experiment. *Oecologia,* **163**, 785-792.

Osborn T. J., Briffa K. R., Jones P. D. (1997) Adjusting variance for sample-size in tree-ring chronologies and other regional mean timeseries. *Dendrochronologia,* **15**, 89-99.

Oswald W. W., Brubaker L. B., Anderson P. M. (1999) Late Quaternary vegetational history of the Howard Pass area, northwestern Alaska. *Canadian Journal of Botany-Revue Canadienne De Botanique,* **77**, 570-581.

Pop E. W., Oberbauer S. F., Starr G. (2000) Predicting vegetative bud break in two arctic deciduous shrub species, *Salix pulchra* and *Betula nana*. *Oecologia,* **124**, 176-184.

Raynolds M. K., Comiso J. C., Walker D. A., Verbyla D. (2008) Relationship between satellite-derived land surface temperatures, Arctic vegetation types, and NDVI. *Remote Sens. Environ.,* **112**, 1884-1894.

Rietkerk M., van de Koppel J. (2008) Regular pattern formation in real ecosystems. *Trends in Ecology & Evolution,* **23**, 169-175.

Rinn F. (1996) TSAP Time Series Analysis and Presentation Version 3.0 Reference Manual.

Schickhoff U., Walker M. D., Walker D. (2002) Riparian willow communities on the Arctic Slope of Alaska and their environmental relationships: A classification and ordination analysis. *Phytocoenologia,* **32**, 145-204.

Schuur E. A. G., Crummer K. G., Vogel J. G., Mack M. C. (2007) Plant species composition and productivity following permafrost thaw and thermokarst in alaskan tundra. *Ecosystems,* **10**, 280-292.

Selkowitz D. J. (2010) A comparison of multi-spectral, multi-angular, and multi-temporal remote sensing datasets for fractional shrub canopy mapping in Arctic Alaska. *Remote Sensing of Environment,* **114**, 1338-1352.

Serreze M. C., Francis J. (2006) The arctic amplification debate. *Climatic Change,* **76**, 241-264.

Sturm M., Racine C., Tape K. (2001) Increasing shrub abundance in Arctic. *Nature,* **411**, 546.

Swann A. L., Fung I. Y., Levis S., Bonan G. B., Doney S. C. (2010) Changes in Arctic vegetation amplify high-latitude warming through the greenhouse effect. *Proceedings of the National Academy of Sciences of the United States of America,* **107**, 1295-1300.

Tape K. D., Lord R., Marshall H. P., Ruess R. W. (2010) Snow-mediated ptarmigan browsing and shrub expansion in Arctic Alaska. *Ecoscience,* **17**, 186-193.

Tape K. D., Sturm M., Racine C. (2006) The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. *Global Change Biology,* **12**, 686-702.

Thompson D. W. J., Wallace J. M., Hegerl G. C. (2000) Annular modes in the extratropical circulation. Part II: Trends. *Journal of Climate,* **13**, 1018-1036.

Ukraintseva N. G. (2008) Vegetation response to landslide spreading and climate change in the West Siberian tundra. *9th Int. Conf. on Permafrost,* **2**, 1793-1798.

Verbyla D. (2008) The greening and browning of Alaska based on 1982-3003 satellite data. *Global Ecol. Biogeogr.,* **17**, 547-555.

Walker D. A. (1987) Height and growth rings of *Salix lanata* ssp *richardsonii* along the coastal temperature gradient of northern Alaska. *Canadian Journal of Botany-Revue Canadienne De Botanique,* **65**, 988-993.

Walker D. A., Bockheim J. G., Chapin F. S., Eugster W., Nelson F. E., Ping C. L. (2001) Calcium-rich tundra, wildlife, and the "Mammoth Steppe". *Quaternary Science Reviews,* **20**, 149-163.

Walker D. A., Raynolds M. K., Daniels F. J. A., Einarsson E., Elvebakk A., Gould W. A., . . . Team C. (2005) The circumpolar Arctic vegetation map. *Journal of Vegetation Science,* **16**, 267-282.

Walker D. A., Walker M. D. (1991) History and pattern of disturbance in Alaskan Arctic terrestrial ecosystems: A hierarchical approach to analysing landscape change. *Journal of Applied Ecology,* **28**, 244-276.

Walker M. D., Wahren C. H., Hollister R. D., Henry G. H. R., Ahlquist L. E., Alatalo J. M., . . . Wookey P. A. (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.

Walker M. D., Walker D. A., Auerbach N. A. (1994) Plant communities of a tussock tundra landscape in the Brooks Range Foothills, Alaska. *Journal of Vegetation Science,* **5**, 843-866.

Chapter 2 – 20th Century Erosion in Arctic Alaska: The Influence of Shrubs, Runoff, and Permafrost[1]

Abstract

Recent changes in the climate of Arctic Alaska, including warmer summers and a lengthened growing season, have increased vegetation productivity and permafrost temperatures. In this study, we use (1) time series imagery to examine the landscape pattern of tall shrub distribution and expansion in Arctic Alaska, and (2) lake sediments from watersheds where shrub expansion is occurring to compare 20th century temporal trends between shrub expansion, erosion, and runoff. Landsat TM data from 1986 and 2009 was used to evaluate the expansion of tall shrubs across three regional subscenes in the Arctic foothills in northeast Alaska. We found that tall shrubs occupied floodplains and streams in 1986 and have been expanding their coverage along these corridors. The interaction between shrub expansion and erosion was examined by reconstructing the last 60 to 100 years of erosion from sediment cores in four lakes with shrub expansion in the surrounding watersheds. Three of the four lake cores showed a steadily increasing or fluctuating erosion rate until 1980, after which these cores show a synchronous decline. We postulate that the increase in shrubs since 1980 in landscape positions prone to erosion has contributed to the decline in erosion. A decrease in the magnitude and frequency of runoff events has likely also contributed to the decline in erosion. Our results indicate a general decline in erosion since 1980 that is contemporaneous with

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[1] Tape, KD, Verbyla D, Welker J, in press. 20th Century erosion in Arctic Alaska: The influence of shrubs, runoff, and permafrost. *Journal of Geophysical Research – Biogeosciences.*

shrub expansion and peak runoff decline, punctuated by episodic erosion events in one of four catchments.

Introduction

Recent changes in the climate of Arctic Alaska, including warmer temperatures and a lengthened growing season [*Chapin et al.*, 2005; *Serreze and Francis*, 2006; *Shulski and Wendler*, 2007], are linked with increases in vegetation productivity and permafrost temperatures. Increased vegetation productivity, as measured using time series of satellite vegetation indices such as NDVI (Normalized Difference Vegetation Index) [*Bhatt et al.*, 2010; *Goetz et al.*, 2005; *Jia et al.*, 2003; *Myneni et al.*, 1997], has been partly attributed to the expansion of shrubs, which has been documented using time series of aerial photography [*Sturm et al.*, 2001; *Tape et al.*, 2006], plot studies [*Joly et al.*, 2007], and shrub growth ring chronologies [*Forbes et al.*, 2010; *Hallinger et al.*, 2010].

The evidence of shrub increase from repeat photography is most reliable for tall, dark *Alnus viridis* ssp. *fruticosa* (Siberian alder) shrubs, and evidence from other repeat photography (Figure 2.1), NDVI trends (herein), and vegetation plot studies [*Joly et al.*, 2007] indicate an expansion of *Salix* spp. (willow), and possibly *Betula* spp. (birch) shrubs. Shrub expansion may include clonal reproduction, sexual reproduction [*Douhovnikoff et al.*, 2010], or new shrubs germinating from seeds that have been either frozen or otherwise dormant until recently [*Ebersole*, 1989]. These various modes of shrub propagation are manifest in a heterogeneous spatial pattern of expansion and a shifting dominance within tundra ecosystems. Here, we focus on patterns of shrub propagation (shrubs > 1 m tall; hereafter tall shrubs) and whether it is associated with permafrost aggradation or degradation.

Observations of associated shrub expansion and thermokarst formation in boreal Alaska indicate a coupling between shrub expansion and permafrost dynamics [*Jorgenson and Osterkamp*, 2005; *Jorgenson et al.*, 2010; *Schuur et al.*, 2007]. Repeat photography from the Arctic Alaska foothills suggests that similar associations of shrubs and permafrost degradation are present in the Arctic (Figure 2.1), and growing evidence from the Mackenzie River delta region substantiates this connection [*Lantz et al.*, 2009]. It is sometimes unclear whether the shrub expansion or thermokarst disturbance occurs first, but in either case, snow depth is increased by drifting around shrubs, which increases ground temperatures [*Schimel et al.*, 2004; *Sturm et al.*, 2005b] and facilitates permafrost degradation [*Nowinski et al.*, 2010]. Other feedbacks, such as drainage impoundment increasing thermal conductivity, can also facilitate thermokarst development [*Jorgenson and Osterkamp*, 2005; *Jorgenson et al.*, 2006; *Osterkamp et al.*, 2009].

Borehole evidence shows that permafrost temperatures in Alaska are warming in response to a combination of elevated air temperatures and greater or earlier snowfall during the 2nd and 4th quarters of the 20th century [*Clow and Urban*, 2002; *Lachenbruch*, 1959; *Osterkamp*, 2007a; b; *Shulski et al.*, 2007]. Thawing the top of the ice-rich permafrost [*Jorgenson and Shur*, 2007] can wet the soil, reduce shear strength, and cause subsidence, accelerating processes like soil creep [*Matsuoka*, 2001], ice wedge degradation [*Jorgenson et al.*, 2006], and thermal erosion along gullies [*Osterkamp et al.*, 2009] (Figure 2.1). Permafrost degradation and subsequent erosion could potentially expose and release large amounts organic carbon currently stored in frozen and unfrozen soils, thereby accelerating feedbacks to climate warming [*Tarnocai et al.*, 2009; *Zimov et al.*, 2006].

The increase in erosion is obvious from catastrophic permafrost degradation, such as thaw slumps that muddy the waters of rivers and lakes [*Lamoureux and Lafreniere*, 2009; *Lantz and Kokelj*, 2008]. Reports from northern Alaska and NW Canada using time series of imagery document a deterioration of massive ice wedges and subsequent thermokarst formation on the North Slope coastal plain since 1945 [*Jorgenson et al.*, 2006], and an increase in permafrost related mass movements (hereafter "thaw slumps") in the Arctic Alaskan foothills tundra [*Bowden et al.*, 2008; *Gooseff et al.*, 2009] and Arctic Canada [*Lantuit and Pollard*, 2008; *Lantz and Kokelj*, 2008; *Wolfe et al.*, 2004]. Warm periods from 13,600 to 12,800 calendar years before present (cal yr B.P.) and 11,200 to 10,000 cal yr B.P. caused permafrost degradation and rapid erosion from slopes into stream channels and floodplains of the North Slope [*Mann et al.*, 2010] and Brooks Range [13,500 cal yr B.P. to < 12,600 cal yr B.P.; *B. Gaglioti, Pers. Comm.*]. Alluvial deposition from hillslopes overwhelmed the transport capacity of streams and floodplains, causing them to aggrade [*Mann et al.*, 2010].

The increase in vegetation productivity and shrub expansion, in some cases linked to permafrost degradation, could instead stabilize soil particles [*Lewkowicz and Kokelj*, 2002] (Figure 2.2), reduce summer heat flux, and promote permafrost development [*Blok et al.*, 2010]. In northern Alaska during the early Holocene, rapid alder expansion and associated paludification – the accumulation of organic material resulting from aboveground production outpacing decomposition – was concurrent with the development of a widespread peat layer and the modern tundra [*Mann et al.*, 2002; *Oswald et al.*, 1999; *D A Walker et al.*, 2001]. This association between shrub expansion and soil stabilization is in contrast to the association of shrub expansion and permafrost degradation (Figure 2.1).

Is the current warming and concurrent shrub expansion on older Arctic landscapes associated with increased or decreased erosion? In this study, we explored this question by using (1) time series imagery to examine the landscape pattern of tall shrub distribution and expansion in Arctic Alaska, and (2) lake core sediments from watersheds where shrub expansion is occurring to compare 20th century temporal trends between shrub expansion and erosion.

Methods

Study Area

The vegetation of the Arctic foothills, located on the north side of the Brooks Range, Alaska, is mostly tussock-sedge, dwarf-shrub, moss tundra, with some erect, dwarf-shrub tundra [*D A Walker et al.*, 2005], dissected by riparian corridors ranging in size from floodplains to small streams that often host tall shrubs [*Beck et al.*, in press; *M D Walker et al.*, 1994]. Most of this foothills region is moist acidic tundra (MAT), while moist non-acidic tundra (MNT) is confined to areas of ongoing loess deposition, limestone bedrock, and naturally disturbed systems, such as floodplains, snowbeds, windblown ridges, and recently deglaciated areas. Vegetation succession and possibly changes in climate spurred peat development during the Holocene, and most of the landscape was converted from dry vegetation on mineral-rich loess and till deposits to MAT [*D A Walker et al.*, 1998]. Older MAT surfaces typically have higher NDVI values, resulting from greater biomass [*Munger et al.*, 2008].

The climate of the Alaskan North Slope is dominated by long, cold winters and short, cool summers. Snow covers the landscape for 7 to 9 months [*Benson and Sturm*, 1993], is highly variable in distribution, and melts rapidly, constituting the hydrologic event of the season and the onset of the growing season [*McNamara et al.*, 1998]. Snow drifts can persist into August, though the duration of these residual drifts is likely diminishing in response to warmer and longer summers [*Euskirchen et al.*, 2006].

Soils of the Brooks Range and North Slope of Alaska are dominated by continuous permafrost, often within one meter of the surface, except for talik underneath some large lakes and river floodplains [*West and Plug*, 2008]. Spatial variability of the depth of the active layer and temperature of the permafrost is a function of the air temperature, the thermal properties (e.g. thermal conductivity, heat capacity) of the overlying soil and vegetation, and, when present, snow. Permafrost at the upland/lowland interface (toeslopes and stream channels) is vulnerable to thawing due to the close proximity of the talik, and ecological processes that inhibit the development of peat. Toeslopes and stream channels also receive considerable runoff from upslope, which transfers heat via flowing water [*Jorgenson et al.*, 2010; *Kane et al.*, 2001].

We selected the Chandler River corridor (Figure 2.3) for lake coring because it contains abundant shrubs, and because repeat photography shows a large increase in shrub cover since 1950 [28% to 38% = 36% relative increase; *Tape et al.*, 2006]. The section of the Chandler River basin with abundant shrubs has never been glaciated [*Kaufman and Manley*, 2004], but sediment inputs from weathering Ca-rich rock outcrops provide continual disturbance that prevent peat development near outcrops and along stream channels and floodplains. The primary deciduous shrubs are alder (height = 1-4 m), willow (0.25-4 m), and birch (0.25-1.5 m). The Chandler River and its tributaries had an earlier break-up than other rivers on the North Slope in 2003 [*Tape, unpublished aerial photography from May 2003*], and their floodplains host gallery forests dominated by *Populus balsamifera* along approximately 100 river km, centered around the Ninngolik Valley (personal observation). Large shrubs, a longer growing season, and gallery poplar forests collectively suggest this region to be a good analogue for a future with improved growing conditions across on the North Slope.

Approximately 100 km east of the Chandler River are four subscenes from a single Landsat image, used here. Two subscenes (1 and 2) were only glaciated during maximum glacial extent (regionally the Sagavanirktok advance: >125,000 ya), while the other two subscenes (3 and 4) contain some areas glaciated during the late Wisconsinan advance (regionally the Itkillik advance: 24,000 to 11,500 cal yr B.P.)[*Kaufman and Manley*, 2004].

Detecting Tall Shrubs and their Patterns of Distribution and Expansion

Time series of photography overlapping with the SPOT imagery and the area of the lake cores (Figure 2.3), and time series of Landsat imagery from a non-overlapping area within the general study region (Figure 2.3), were used to establish patterns of shrub distribution and expansion. Repeat photography from 1948 and 2001 was used to manually delineate 10 polygons (approximately 0.04 ha each) of rapidly expanding shrub patches and 10 polygons of slowly expanding or stable shrub patches on SPOT satellite imagery (bands 2, 3, 4; 2.5 m pixel; 12 July 2008) along a 20 km stretch of the Chandler River. The difference in growth rates deduced from widespread repeat photography was confirmed by shrub growth rings from 22 shrub patches across Arctic Alaska. Shrub rings show greater growth in expanding patches responding to warmer spring and summers, while stable patches show slower growth and only weak relationships to climatic influences [*Chapter 1*]. Using the pixel characteristics of the expanding shrub polygons and stable shrub polygons, ENVI software applied the supervised classification to the SPOT image to interpolate areas of shrub expansion (and stability) throughout the SPOT image.

To validate this method, if only qualitatively, additional remote sensing techniques were applied to imagery of the broader study region. Landsat TM data from 1986 and 2009 were used to evaluate the expansion of tall shrubs across four regional subscenes in the Arctic foothills (Figure 2.3). The subscenes were selected as clear-sky areas from a 1986-July-6 and 2009-July-5 Landsat scene (Path73Row11) and were 25 km by 20 km in size. Images were calibrated and NDVI was computed using red and nearinfrared spectral reflectance [*Chander et al.*, 2009] from each subscene. Tall shrub areas, because of relatively high leaf area, typically have the highest NDVI among tundra vegetation types [*Jia et al.*, 2003]. NDVI values were threshholded > 0.6 and considered pixels dominated by tall shrubs [*Olthof et al.*, 2008].

Chandler River Lake Cores

We cored four lakes near the Chandler River on the central North Slope of Alaska (Figure 2.3). Lakes were chosen with watersheds where shrub expansion was either observed using repeat photography or inferred using the SPOT imagery. Additionally, lakes with small watersheds were selected to limit intra-watershed spatial variation of explanatory factors. In August 2009, using two small boats, a piston gravity corer with clear polycarbonate tubing was used to extract sediment cores 30 cm long and 6.7 cm in diameter from near the center of each lake. Because of logistical constraints of transporting intact cores, cores from all four lakes were sectioned in the field at 0.5 cm intervals to 10 cm depth, 1 cm intervals from 10 to 20 cm, and then 2 cm intervals from 20 to 30 cm. Samples were stored in Whirlpak™ bags and refrigerated for 10 days before being frozen.

Lakes 1 (watershed = 2.0 km^2) and 2 (watershed = 1.5 km^2) are thaw ponds with evidence of shrub expansion along stream inlets identified using the SPOT imagery. These two lakes showed eroding polygonal ground along one margin. The inlet to lake 1 is incised <1 m and enters the lake at a gentle gradient. The inlet to lake 2 is a steep-sided gully >3 m deep incised into polygonal ground (Figure 2.4). Alder shrubs 1 to 3 m tall, frost boils, and tussocks are prominent in both watersheds, and smaller willow and birch shrubs are also common. Lakes 3 (watershed = 0.3 km^2) and 4 (watershed = 2.7 km^2) are located on elevated river terraces at the edge of the valley fill. Lake 3 has a 300 m shrub-covered 12° slope adjacent to the west, with gullies and evidence of shrub expansion (Figure 2.5). Lake 4 has no identifiable inlet, and is also located at the edge of the valley fill. There were no signs of erosion along lake 3 and 4 shores. All lakes were 2.5 m at the deepest point, where the cores were taken, and had nearly flat bathymetry (determined by $\geq$20 depth measurements), suggestive of a uniform underlying permafrost table.

The cores were dated assuming constant deposition and decay of ^{210}Pb, and mass depositional rates in the cores were used to infer the last 60 to100 years of erosion in the watersheds. Core analysis and age modeling was conducted by Flett Research Ltd., Manitoba, Canada. Core sections were dried, weighed, and dated using sediment ^{210}Pb activity determined by α-spectroscopy. Typically, spectroscopy was applied to all core sections from 0.0 to 3.0 cm, alternating sections from 3.0 to 6.0 cm, and with decreasing frequency along the remainder of the core. Profiles of sediment ^{210}Pb activity (half-life ~ 22 years) decreased logarithmically with depth to supported (background) levels, which were determined statistically [*Binford*, 1990]. The age at the bottom of a given section was calculated using the constant rate of supply (CRS) model [*Appleby and Oldfield*, 1978], by taking the natural log of the fraction of unsupported ^{210}Pb (measured in disintegrations per minute, (DPM = Becquerels) in the section to the total unsupported ^{210}Pb below that section. Accumulation rates are then calculated by dividing the mass in a given section by the time to deposit that section.

^{137}Cs was used as an independent tracer to validate the ^{210}Pb chronology. The maximum ^{137}Cs activity in a core profile typically corresponds to the date of 1963, the year of maximum ^{137}Cs direct deposition of bomb testing radionuclides from the atmosphere in the northern hemisphere. Elevated ^{137}Cs activity above the maximum ^{137}Cs core section would indicate that the majority of the ^{137}Cs is from terrestrial erosion sources. In such cases, the ^{137}Cs maximum can be delayed to the year 1966, the date when maximum ^{137}Cs soil inventory occurred. To have high confidence in the ^{210}Pb model, it should predict a core date between 1963 and 1966 for the ^{137}Cs peak.

Because the lakes have nearly flat bathymetry, we assume that deposition is uniform over the area of the lake. Using this assumption, we scaled the mass of each 0.5 cm section to the size of the lake (as determined in Google Earth) and calculated the mass deposited in each section, which was then averaged over the period of the section to obtain an annual mass influx. That term was then divided by the area of the watershed to obtain an annual average erosion rate for each watershed (g / m^2 watershed / year). These rates averaged over the watershed area are only relevant if the source of the erosion was approximately uniform. If the erosion instead came from point sources, then the spatially explicit values are misleading. The calculations are also misleading if the deposition in the lake is non-uniform (see initial assumption), though temporal changes in deposition at the core location still reflect changes in watershed erosion. In calculating erosion, we assume aquatic production (in a vertical column above the core area) to be approximately equal between lakes and constant over the period of study. We also assume the eolian deposition onto the lake surface to be negligible.

Core Chronology Statistics

Standard error in the ^{210}Pb activity in each section is converted to standard error in the ^{210}Pb-derived dates ranging from 0.1 years on the recent dates to a maximum of 6.8 years on the oldest date, with a mean of 2.0 years. These are relatively small (all < 10%) and not represented graphically, because they are likely outweighed by unknown potential errors resulting from non-constant ^{210}Pb inputs, and from sediment mixing and ^{210}Pb diffusion in upper sections.

Results

Detecting Tall Shrubs and their Pattern of Distribution and Expansion

The spatial pattern that emerges from extrapolating the repeat photography using a supervised classification of a SPOT image is one of rapidly expanding shrub patches emanating from floodplains, stream channels, and sedimentary rock outcrops. In contrast, slowly expanding or stable shrub patches are located on gentler tussock tundra slopes and upland benches (Figure 2.6). Shrub growth rings confirm that rapidly expanding patches have added more biomass than stable shrub patches during the 20th century [*Chapter 1*].

This landscape pattern of expansion is confirmed and refined by the analysis of paired Landsat imagery. Time series of four Landsat subscenes (1986 and 2009) shows an 18% increase in high NDVI (> 0.6) pixels. This increase is due to tall shrubs expanding on floodplains, along stream channels, and adjacent to rock outcrops (Figure 2.6). Tall shrubs in the Landsat imagery are alder and willow. The Landsat imagery better distinguishes between previously existing tall shrub patches and new tall shrub patches, while the extrapolated repeat photography essentially classifies entire patches of tall clumped shrubs as expanding (Figure 2.6).

One alternative explanation is that the Landsat results might simply be due to interannual variation in canopy production related to climate, with 2009 possibly a more favorable growing season relative to 1986. Under this scenario we would expect the change in NDVI from high NDVI patches that existed in 1986 to be significantly greater in 2009. However, no increase was observed between aforementioned pixels in 1986 and 2009 (Table 2.1), indicating that the observed increase in the time series of adjacent (high NDVI) pixels was not an artifact of a single enhanced growing season, but rather was an increase in the number of high NDVI pixels between 1986 to 2009.

Chandler River Lake Cores

Lake sediment cores 1, 3, and 4 show fluctuating or increasing erosion rates until 1980, after which these cores collectively show a decline (cumulative for 3 lakes: $r = -0.47$, $p < 0.03$; Figure 2.7c), though when lakes are considered individually only the decline in lake 1 is significant. The two lakes located on a river terrace (3 and 4) have similar temporal trends in deposition, showing that between 1904 and 1980 there was a period of increasing erosion ($r^2 = 0.998$, $p < 0.001$ and $r^2 = 0.82$, $p < 0.05$, respectively).

The lake 1 record has a higher temporal resolution revealing more fluctuations prior to 1980.

The record of deposition in lake 2 is unlike that in lakes 1, 3, and 4. Lake 2 deposition is highly episodic, showing an order of magnitude difference between relative maximum and minimum sediment deposition rates (~0.3 to ~0.03 g/cm^2/yr). Even the lower rates in lake 2 are substantially higher than the deposition rates in the other three lakes (~.008 g/cm^2/yr).

Assuming that the lake deposition record can be used to infer average basin erosion rates, we compute that since 1951 (the shortest record in four lakes), watersheds from lakes 1 and 3 were eroded 11.1 and 11.8 g m^{-2} yr^{-1} respectively. The lake 4 watershed, a large area with a small lake and no obvious inputs, eroded 0.25 g m^{-2} yr^{-1}. Using the same computational method, and over the same interval, the watershed of lake 2 eroded 51.6 g cm^{-2} yr^{-1}, more than twice as much erosion per area as the other three lakes combined.

Discussion

Tall shrubs occupy floodplains, gullies, and stream banks, which act as propagation corridors for shrubs across the broader landscape (gullies and streams; Figures 2.1, 2.2, 2.6). Within the Landsat imagery the tall shrub areal expansion rate was +0.78% yr^{-1} between 1986 to 2009. This is a change in tall shrub area of +18%, and it is similar to the 0.68% yr^{-1} areal increase between 1948 to 2002 based from repeat photography reported by *Tape et al.* (2006) for the Arctic foothills.

One consequence of the warmer spring and summer temperatures in the Arctic [*Shulski et al.*, 2007] is that the growing season in the study area has lengthened, asymmetrically toward spring [*Chapin et al.*, 2005]. A longer growing season means that snow drifts disappear earlier in the spring [*Euskirchen et al.*, 2007; *Verbyla*, 2008], a trend possibly accelerated by taller shrubs decreasing albedo and further increasing snowmelt temperatures [*Chapin et al.*, 2005]. The same trend toward earlier snowmelt is evident in the Kuparuk River (which flows across Landsat subscene 1), where gauging since 1971 shows a 1-week earlier peak discharge, from May 10th to May 3rd ($r^2 = 0.143$, $p < 0.01$).

Shrub expansion in northern Alaska often occurs along the perimeter of shrinking residual snow drifts (Figure 2.5), where the growing season has lengthened. Indeed, alder growth rings in expanding patches from Arctic Alaska show positive correlations with current and previous year spring and early summer temperatures, implying a connection between the onset of the growing season and shrub growth [*Chapter 1*]. Correlations between temperature in the first half of the growing season and shrub growth have also been observed in Scandinavia [*Hallinger et al.*, 2010] and Siberia [*Blok et al.*, 2011; *Forbes et al.*, 2010]. High Arctic *Salix arctica* shrubs in Greenland grow more during years of reduced-snow-extent early in the growing season [*Schmidt et al.*, 2006]. Other studies have shown that the relationship in Arctic Alaska between June 1-15 peak NDVI and annual NDVI was not significant, supporting a decoupling of early growing season photosynthesis from peak season photosynthesis [*Verbyla*, 2008], though this may be explained by graminoids being more sensitive to interannual temperature fluctuations than shrubs [*Jia et al.*, 2006].

Erosion in pristine non-periglacial settings with precipitation similar to the Arctic is primarily controlled by topography, lithology, vegetation, and precipitation. Precipitation dislodges soil particles and creates runoff, but typically increases plant growth, which in turn stabilizes soil. The net effect is an inverse relationship between precipitation and erosion, though this relationship is not valid at extremely low precipitation, where plants have difficulty growing and stabilizing (non-periglacial) soils [*Dendy and Bolton*, 1976; *Douglas*, 1967; *Langbein and Schumm*, 1958]. The tundra environment in this study is underlain by continuous permafrost that impedes drainage and causes most soils to be moist or wet [*D A Walker et al.*, 2002], and most plants to not be water limited [*Chapin et al.*, 1989], despite the semi-arid climate. The role of precipitation in controlling erosion in continuous permafrost landscapes is therefore confined to eroding and transporting sediment, and transferring heat. Thermal erosion from permafrost degradation is an additional variable of importance in the Arctic environment [*Mann et al.*, 2010]. When examining temporal trends in erosion in an Arctic watershed, we assume topography and lithology to be constant, and the variables controlling erosion become vegetation, runoff, permafrost, and climate.

An increase in shrub cover and vegetation productivity, specifically in landscape positions where the ground was previously exposed to erosion, coincided with and may have contributed to the decline in erosion observed in lake cores 1, 3, and 4 (Figure 2.7).

Beginning in 1980, alder shrub rings from rapidly expanding shrub patches along streams, gullies, and outcrops in Arctic Alaska became much wider than those from alders in tussock tundra (Figure 2.7a) [*Chapter 1*]. Because only the largest stems were cut and analyzed, the decline in the tussock tundra alder rings is predominantly an age trend of decreasing ring width over the record, including few young stems. The lack of decline in the expanding patches since 1980 is due to wide rings from new stems and to maintained growth of aging stems during warmer and longer summers. Based on these rings, and the strong link between temperature and productivity [*D A Walker et al.*, 2003a], and between temperature and shrub growth [*Chapin et al.*, 1995; *Forbes et al.*, 2010; *D A Walker et al.*, 2003b], the pattern of expanding shrubs along drainages was likely concurrent with the erosion decline around 1980. Increased vegetation cover is correlated with reduced erosion in the high Arctic Canadian archipelago [*Lewkowicz and Kokelj*, 2002], and across North America [*Langbein and Schumm*, 1958]. Surfaces prone to erosion are those landscape positions without peat or other vegetation blanketing the soil [*Mann et al.*, 2010]. Though our study focused on tall shrub expansion along streams and proximal to shrinking residual snow drifts, a general increase in vegetation productivity [*Goetz et al.*, 2005; *Munger et al.*, 2008; *Verbyla*, 2008] is likely stabilizing soil in many landscape positions.

A decrease in the magnitude and frequency of peak runoff events is also contributing to the decline in erosion in lake cores 1, 3, and 4. The largest runoff events of the year occur at snowmelt [*Cockburn and Lamoureux*, 2008; *McNamara et al.*, 1998], and four of the top five peak annual discharge events for the Kuparuk River occurred between 1971 and 1982, with only one similar event occurring since 1982 (Figure 2.7b). We assume the peak discharge events, more so than the cumulative discharge, to be erosive [*Dugan et al.*, 2009]. The decline in the magnitude of peak discharge events is contemporaneous with both the erosion decline and shrub expansion. The decrease in stream and river silt depositional events, as inferred from decreased lake core deposition, is consistent with and could be partly responsible for the increase in vegetation and stabilization of bars along floodplains of rivers and streams [*Tape et al.*, 2006]. One explanation for the decline in peak discharge events is that there is less snow (technically, snow-water equivalent, or SWE), though it is possible that the mere occurrence of snowmelt earlier in the spring, when solar insolation is smaller, is sufficient to explain a slower, and thus less flashy, runoff. Taller shrubs reducing snow surface albedo could also advance the snowmelt date [*Chapin et al.*, 2005; *Sturm et al.*, 2005a].

We consider the erosion trends from lakes 1, 3, and 4 to be slow and steady erosion shaping the landscape, and these trends are probably controlled by changes in vegetation and runoff. In contrast, the erosion trend from lake 2 is episodic, fluctuating tenfold within a decade. Lakes 1 and 2 watersheds have similar topography and are about as similar in vegetation and morphology as two watersheds could be, except that lake 2 has a more incised stream inlet leading up 600 m from the mouth (Figure 2.4). There are no obvious slope failures in the watershed, so the episodic sediment pulses probably emanate from the gully-inlet that is cut through polygonal ground and hosts expanding shrubs (Figure 2.4). Erosion at the lake margin could also be a source of sediment. So, while trends from lakes 1, 3, and 4 indicate recent soil stabilization resulting from increased vegetation, the episodic record of deposition in lake 2 hints at the potential instabilities and heterogeneity in tundra landscapes. More specifically, if the episodic events are from point sources, then the background erosion rates are, relatively speaking, small and unimportant, because the landscape is being shaped by catastrophic events, rather than gradual processes [*Hooke*, 2000].

In three of four watersheds studied here, the addition and enhanced growth of shrubs along streams and gullies since 1980 did not coincide with a destabilization of permafrost in those watersheds. If the permafrost degradation represented by Figure 2.1 were occurring in watersheds of lakes 1, 3, and 4, then an increase, rather than a decrease, in erosion should have been detected, despite concurrent increases in shrubs. The general stability in those three watersheds therefore stands in contrast to Figure 2.1 and recent reports of increasing permafrost degradation. That contrast may be explained by the recent thermal erosion being concentrated in younger, more recently glaciated terrains [*Bowden et al.*, 2008; *Gooseff et al.*, 2009; *Lantz and Kokelj*, 2008], such as in Figure 2.1. Thinner or nonexistent peat layers in the younger terrains may be permitting greater heat flux and permafrost degradation, whereas older terrains with thicker peat layers are most susceptible in limited areas where the peat is not present.

Erosion includes any process that redistributes soil particles, and the coring methods in this study cannot separate erosion due to permafrost degradation from erosion due to water dislodging soil particles. We speculate that the episodic events in lake 2 are the signature of catastrophic thermal erosion, shown to be recently increasing [*Bowden et al.*, 2008; *Gooseff et al.*, 2009; *Lantz and Kokelj*, 2008], though no trend in the episodic signal was observed in this study. This study highlights the need for a more integrated understanding of the factors that control permafrost stability and erosion. Widespread coring of varying terrains is necessary to assess the post-Little Ice Age soil and permafrost stability over large areas, and to correlate erosion trends with landscape and climate variables such as vegetation productivity and runoff events.

Conclusion

Our results indicate a background decline in erosion (collectively, in 3 cores) since 1980, superimposed by episodic erosional events (in 1 core). The background decline in erosion is associated with trends of increasing shrubs and declining peak runoff events. In contrast to the positive feedbacks associated with shrub expansion and climate change [*Chapin et al.*, 2005; *Mack et al.*, 2004; *Sturm et al.*, 2005b; *Swann et al.*, 2010], our results suggest a negative feedback from shrubs stabilizing soil (including carbon), though this response could be reversed by an increase in permafrost-related erosional events, or an increase in decomposition [*Mack et al.*, 2004]. Results from lakes 1, 3, and 4 appear counter to the recent reports of increased thaw slump activity, but results from lake 2 are consistent with these recent reports and probably reflect the episodic contribution of thermal erosion to the erosion regime within that watershed. Determining the relative contribution of enhanced vegetation productivity, changes in the hydrologic regime, and permafrost degradation to erosion trends is a challenging problem that warrants attention in future studies.

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Tables

Table 2.1. Change in mean NDVI from tall shrub pixels within each frame (± standard error) [a]

	Mean NDVI within 1986 high NDVI patches		Mean NDVI within new 2009 high NDVI patches	
	7/6/1986	7/5/2009	7/6/1986	7/5/2009
Frame 1	0.627 ± 0.0002	0.621 ± 0.0004	0.567 ± 0.0004 *	0.616 ± 0.0002 *
Frame 2	0.615 ± 0.0001	0.602 ± 0.0003	0.571 ± 0.0003 *	0.611 ± 0.0001 *
Frame 3	0.627 ± 0.0001	0.614 ± 0.0002	0.569 ± 0.0002 *	0.616 ± 0.0001 *
Frame 4	0.628 ± 0.0001	0.621 ± 0.0003	0.566 ± 0.038 *	0.615 ± 0.014 *

* $p < 0.01$

[a] Within the extent of the 1986 tall shrub pixels the 2009 NDVI values are equal or slightly lower than in 1986. The new tall shrub pixels evident in the 2009 image have, in contrast, changed significantly since 1986, suggesting that those pixels represent new tall shrubs.

Figures

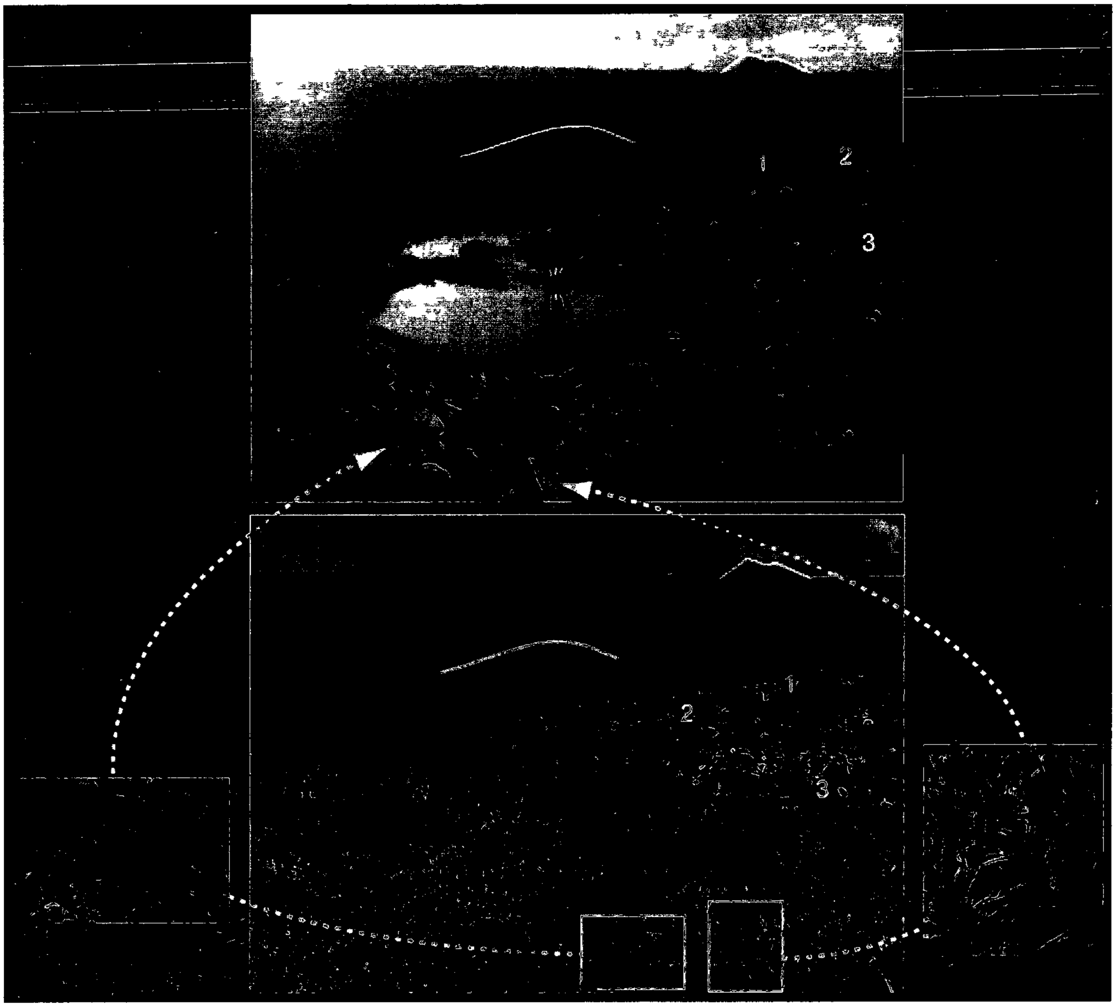

Figure 2.1. Repeat photo pair from the Jago River valley. The old photo (*top*) is from 1957 (George Kunkle & Ed Sable), and the new photo (*bottom*) is from 7/29/2007 (Ken Tape). The camera positions are nearly identical in the two photos, but in the new photo willow shrubs have replaced alpine flora and are obscuring the ponds seen in the old photo. On the left and right are close-up photos of two foreground rocks seen in the old photo. Both rocks have migrated downhill. The left rock has retained its initial orientation. The rock on the right has been forced upright by the large willow shrub growing underneath it. Also, the steep slope to the right of the figure in the old photo has collapsed as the underlying permafrost has thawed. Three large boulders in the old photo are marked in the new photo. The assumption in this study is that, if this gully drained into a lake, then the collapse evident in this photo would be recorded as a sediment pulse in the lake.

Figure 2.2. 1948 (a) and 2001 (b) photographs showing shrub expansion emanating from a drainage along the Nimiuktuk River, in the Noatak basin. An interesting exercise is to imagine a photo taken a half-century prior to 1948 – about the time that the Little Ice Age waned and the current shrub expansion presumably initiated. Such an extrapolation yields a landscape devoid of large shrubs on the facing slope, or along the creek, much like in the old photo from Figure 2.1. This supports the notion of drainages as corridors for rapid expansion and dispersion of shrubs over the landscape.

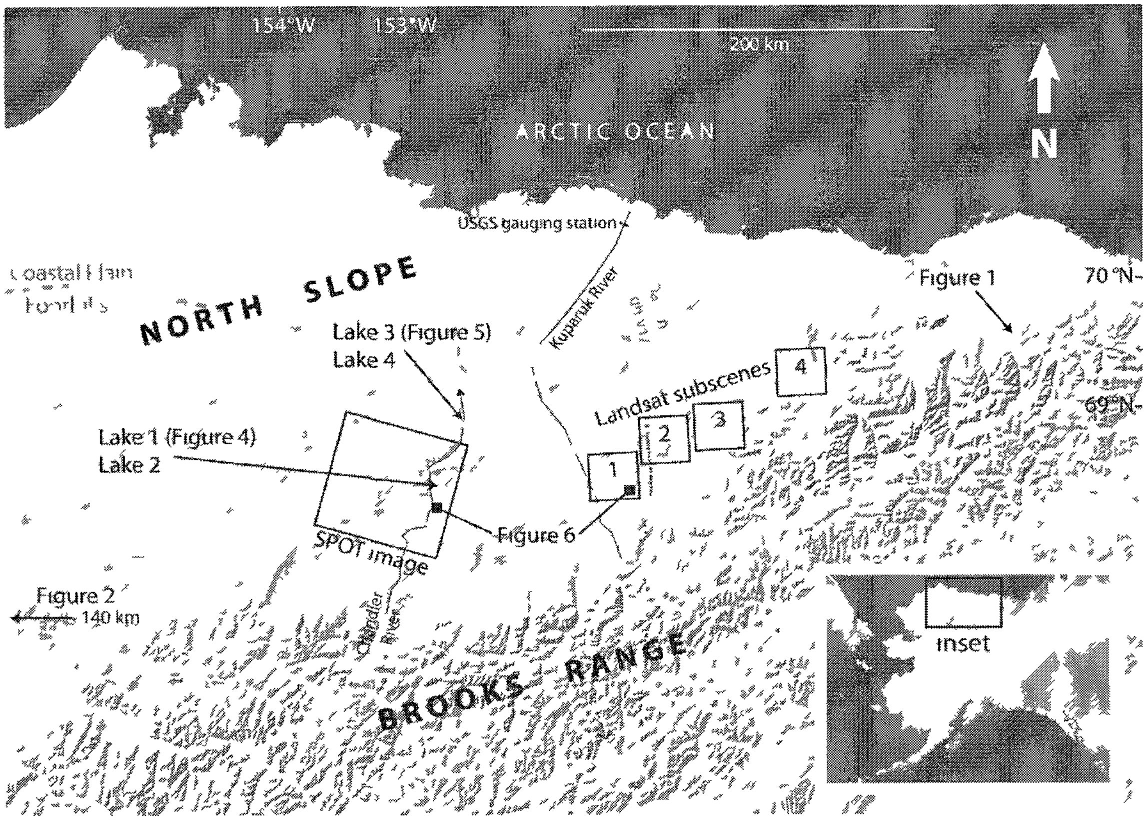

Figure 2.3. Locations of SPOT and Landsat imagery, lakes cored, and repeat photography figures referred to in this chapter.

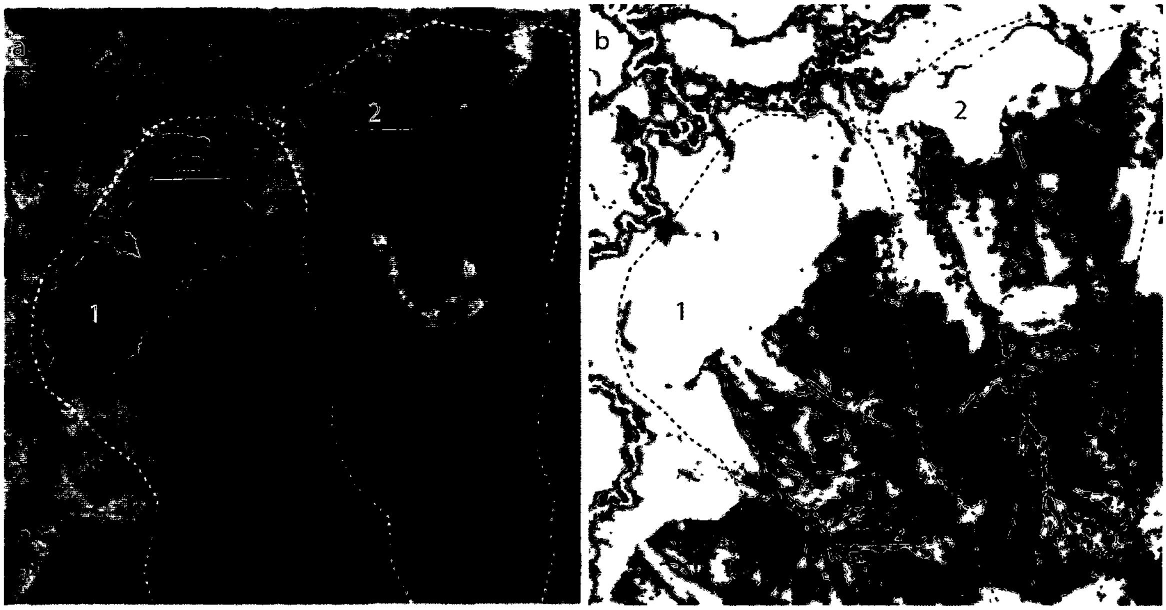

Figure 2.4. (a) A false-color SPOT image showing most of the watersheds for lakes 1 and 2 (dashed line), including the shrub-filled inlets. (b) Supervised classification of (a) into expanding shrub patches (green), low shrub patches (blue), and non-shrub (white) shows the gully-inlet to lake 2 densely vegetated with expanding shrubs. Numbers also denote locations of cores. The image is 2 km wide.

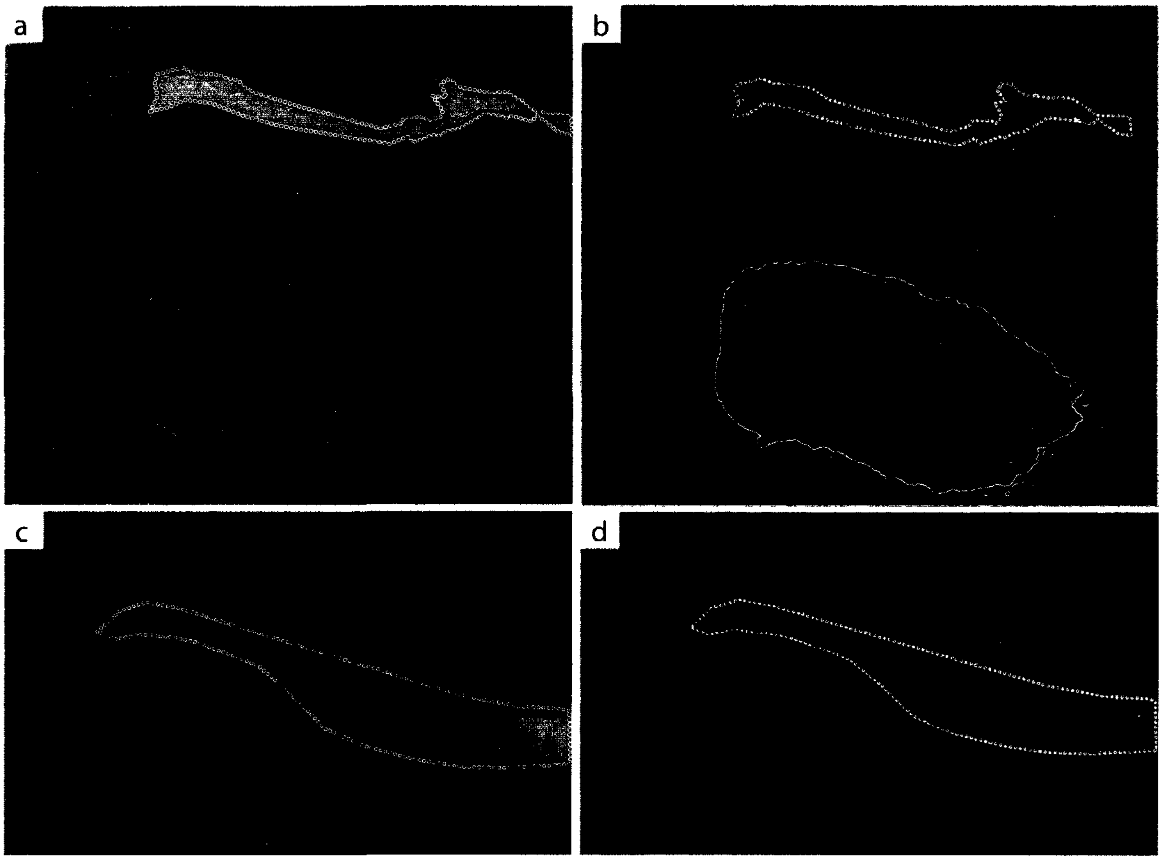

Figure 2.5. A small watershed for lake 3 photographed (a) in 1948-50 (USGS/US Navy) and (b) on August 17, 2004 (© Google Earth), showing a gentle bluff at the edge of the Chandler River valley with shrubby gullies leading down to a lake. Shrub expansion is prominent along the perimeter of the snow drift (dashed lines), one of many such drifts persisting along the valley edge in the larger image (not shown). Shrub expansion along the perimeter of residual snow drifts filling slope breaks (these examples from an underlying geologic stratum) is also evident in repeat photography from other locations, such as (c) and (d), along the nearby Oolamnagavik River [August 11, 1948 and July 27, 2002; reprinted from *Tape*, 2010]. Lake 4 is in a similar setting to Lake 3, 1 km to the north and on the same river terrace.

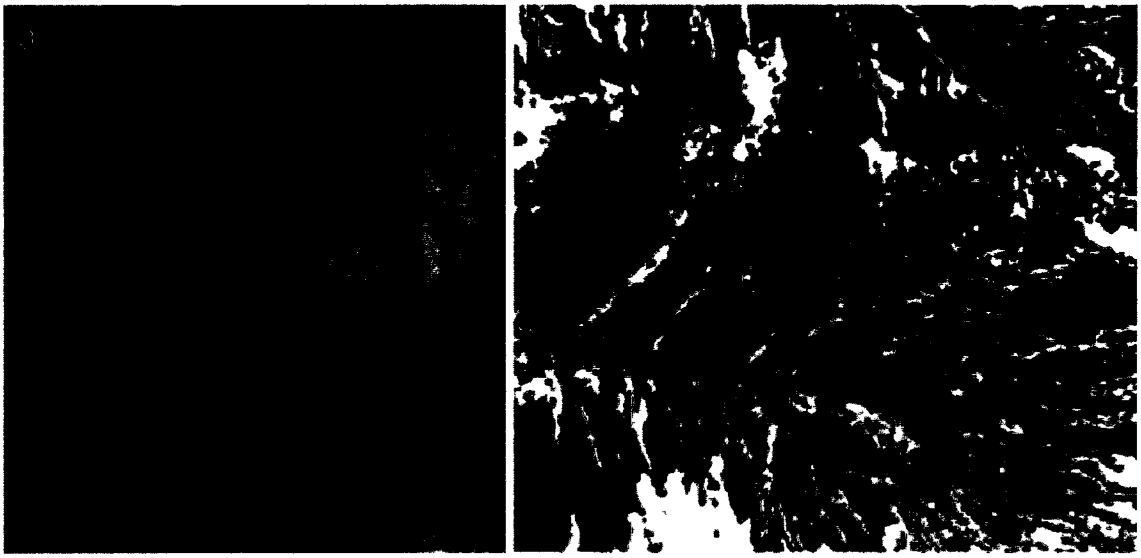

Figure 2.6. Similar pattern of expanding shrubs in two *different areas*, produced using two methods. In (a), magenta indicates tall shrubs (NDVI > 0.6) in 1986, and light green indicates additional tall shrubs in 2009, as evaluated using Landsat imagery (pixels are 30 by 30 m). In (b), SPOT image extrapolation of repeat photography indicates a similar pattern of expanding tall shrubs (green) along stream networks. Images are approximately 4 km wide and locations of (a) and (b) are shown in Figure 2.3.

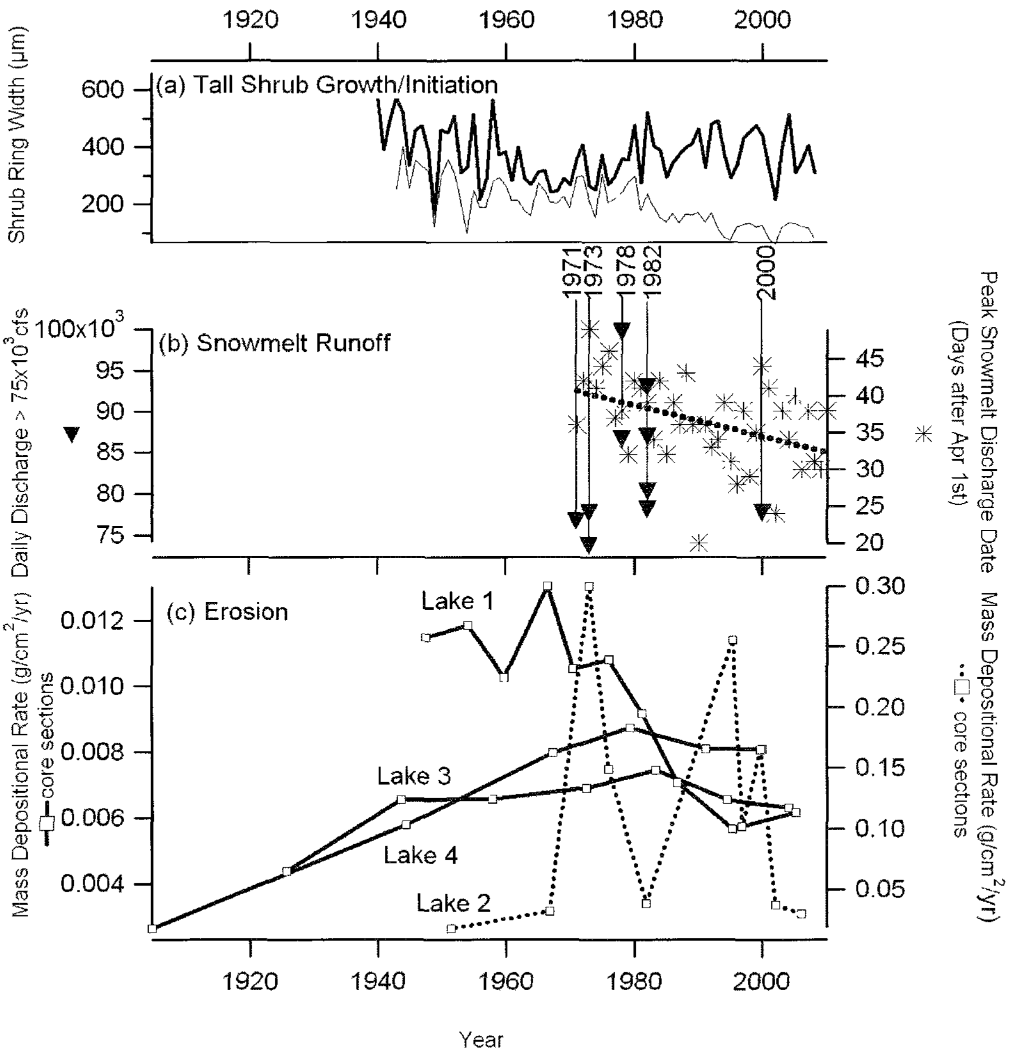

Figure 2.7. (a) Shrub growth ring widths for the largest stem from expanding (thick line) and stable (thin line) shrub patches, only the former strongly correlated with spring/summer temperatures [*Chapter 1*]. (b) A decline in the number of extreme snowmelt discharge events on the Kuparuk River, and a one-week earlier (0.21 days/decade) peak snowmelt discharge indicative of earlier onset of the growing season ($r^2 = 0.143$, $p < 0.01$, discharge data: USGS Open file reports, 1971-2010). (c) Depositional rate in four lakes over the last century. A decline around 1980 in lakes 1, 3, and 4 reflects a decline in erosion in those watersheds. We speculate that trends in shrub growth (a) and a decline in peak discharge events (b) are contributing to trends in erosion (c), except in lake 2, where the deposition is episodic and seemingly independent of trends in (a) or (b).

References

Appleby, P. G., and F. Oldfield (1978), The calculation of lead-210 dates assuming a constant rate of supply of unsupported lead-210 to the sediment, *Catena*, *5*(1), 1-8.

Beck, P. S. A., N. Horning, S. J. Goetz, M. M. Loranty, and K. D. Tape (in press), The density of shrub cover on the North Slope of Alaska: a circa 2000 baseline map, *Arctic, Antarctic, and Alpine Research.*

Benson, C., and M. Sturm (1993), Structure and wind transport of seasonal snow on the Arctic slope of Alaska, *Annals of Glaciology*, *18*, 261-267.

Bhatt, U. S., et al. (2010), Circumpolar arctic tundra vegetation change is linked to sea ice decline, *Earth Interact*, *14*(8), 1-20.

Binford, M. W. (1990), Calculation and uncertainty analysis of ^{210}Pb dates for PIRLA project lake sediment cores, *J Paleolimnol*, *3*(3), 253-267.

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 Biol*, *16*(4), 1296-1305.

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*, 771-798.

Bowden, W. B., M. N. Gooseff, A. Balser, A. Green, B. J. Peterson, and J. Bradford (2008), Sediment and nutrient delivery from thermokarst features in the foothills of the North Slope, Alaska: potential impacts on headwater stream ecosystems, *J Geophys Res-Biogeo*, *113*(G2), doi 10.1029/2007jg000470.

Chander, G., B. L. Markham, and D. L. Helder (2009), Summary of current radiometric calibration coefficients for Landsat MSS, TM, ETM+, and EO-1 ALI sensors, *Remote Sens Environ*, *113*(5), 893-903.

Chapin, F. S., J. B. Mcgraw, and G. R. Shaver (1989), Competition causes regular spacing of alder in Alaskan shrub tundra, *Oecologia*, *79*(3), 412-416.

Chapin, F. S., G. R. Shaver, A. E. Giblin, K. J. Nadelhoffer, and J. A. Laundre (1995), Responses of Arctic tundra to experimental and observed changes in climate, *Ecology*, *76*(3), 694-711.

Chapin, F. S., et al. (2005), Role of land-surface changes in Arctic summer warming, *Science*, *310*(5748), 657-660.

Clow, G. D., and F. E. Urban (2002), Large permafrost warming in northern Alaska during the 1990's determined from GTN-P borehole temperature measurements, *American Geophysical Union, Fall Meeting 2002, abstract #B11E-04*.

Cockburn, J. M. H., and S. F. Lamoureux (2008), Hydroclimate controls over seasonal sediment yield in two ajacent High Arctic watersheds, *Hydrol Process*, *22*(12), 2013-2027.

Dendy, F. E., and G. C. Bolton (1976), Sediment yield-runoff-drainage area relationships in the United States, *Journal of Soil and Water Conservation*, *31*(6), 264-266.

Douglas, I. (1967), Natural and man-made erosion in the humid tropics of Australia, Malaysia and Singapore, *Comm of Surface Waters, Proc Gen Assembly of Bern (Sept-Oct 1967), Int Ass Sci Hydrol*, *75*, 17-30.

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 dodel for recruitment modes of Arctic plants, *Arctic, Antarctic, and Alpine Research*, *42*(4), 406-411.

Dugan, H. A., S. F. Lamoureux, M. J. Lafreniere, and T. Lewis (2009), Hydrological and sediment yield response to summer rainfall in a small high Arctic watershed, *Hydrol Process*, *23*(10), 1514-1526.

Ebersole, J. J. (1989), Role of the seed bank in providing colonizers on a tundra disturbance in Alaska, *Can J Bot*, *67*(2), 466-471.

Euskirchen, E. S., A. D. Mcguire, and F. S. Chapin (2007), Energy feedbacks of northern high-latitude ecosystems to the climate system due to reduced snow cover during 20th century warming, *Global Change Biol*, *13*(11), 2425-2438.

Euskirchen, E. S., et al. (2006), Importance of recent shifts in soil thermal dynamics on growing season length, productivity, and carbon sequestration in terrestrial high-latitude ecosystems, *Global Change Biol*, *12*(4), 731-750.

Forbes, B. C., M. M. Fauria, and P. Zetterberg (2010), Russian Arctic warming and 'greening' are closely tracked by tundra shrub willows, *Global Change Biol*, *16*(5), 1542-1554.

Goetz, S. J., A. G. Bunn, G. J. Fiske, and R. A. Houghton (2005), Satellite-observed photosynthetic trends across boreal North America associated with climate and fire disturbance, *P Natl Acad Sci USA*, *102*(38), 13521-13525.

Gooseff, M. N., A. Balser, W. B. Bowden, and J. B. Jones (2009), Effects of hillslope thermokarst in Northern Alaska, *EOS*, *90*(4), 29-36.

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 Phytol*, *186*(4), 890-899.

Hooke, R. L. (2000), Toward a uniform theory of clastic sediment yield in fluvial systems, *Geol Soc Am Bull*, *112*(12), 1778-1786.

Jia, G., H. E. Epstein, and D. A. Walker (2003), Greening of arctic Alaska, 1981-2001, *Geophys Res Lett*, *30*(20), doi 10.1029/2003gl018268.

Jia, G., H. E. Epstein, and D. A. Walker (2006), Spatial heterogeneity of tundra vegetation response to recent temperature changes, *Global Change Biol*, *12*(1), 42-55.

Joly, K., R. R. Jandt, C. R. Meyers, and M. J. Cole (2007), Changes in vegetative cover on Western Arctic Herd winter range from 1981 to 2005; potential effects of grazing and climate change, *Rangifer*(Special Issue no. 17), 199-206.

Jorgenson, M. T., and T. E. Osterkamp (2005), Response of boreal ecosystems to varying modes of permafrost degradation, *Can J Forest Res*, *35*(9), 2100-2111.

Jorgenson, M. T., Y. L. Shur, and E. R. Pullman (2006), Abrupt increase in permafrost degradation in Arctic Alaska, *Geophys Res Lett*, *33*(2).

Jorgenson, M. T., and Y. Shur (2007), Evolution of lakes and basins in northern Alaska and discussion of the thaw lake cycle, *J Geophys Res-Earth*, *112*(F2), doi 10.1029/2006jf000531.

Jorgenson, M. T., V. Romanovsky, J. Harden, Y. Shur, J. O'Donnell, E. A. G. Schuur, M. Kanevskiy, and S. Marchenko (2010), Resilience and vulnerability of permafrost to climate change, *Can J Forest Res*, *40*(7), 1219-1236.

Kane, D. L., K. M. Hinkel, D. J. Goering, L. D. Hinzman, and S. I. Outcalt (2001), Non-conductive heat transfer associated with frozen soils, *Global Planet Change*, *29*(3-4), 275-292.

Kaufman, D. S., and W. F. Manley (2004), Pleistocene maximum and Late Wisconsin glacier extents across Alaska, U.S.A., in *Quaternary Glaciations—Extent and Chronology, Part II: North America. Developments in Quaternary Science*, edited by J. Ehlers, Gibbard, P.L., pp. 9-27, Elsevier, Amsterdam.

Lachenbruch, A. H. (1959), Dissipation of the temperature of drilling a well in Arctic Alaska, *Geological Survey Bulletin*, *1083-C*, 1-109.

Lamoureux, S. F., and M. J. Lafreniere (2009), Fluvial impact of extensive active layer detachments, Cape Bounty, Melville Island, Canada, *Arct Antarct Alp Res*, *41*(1), 59-68.

Langbein, W. B., and S. A. Schumm (1958), Yield of sediment in relation to mean annual precipitation, *American Geophysical Union Transactions*, *39*, 1076-1984.

Lantuit, H., and W. H. Pollard (2008), Fifty years of coastal erosion and retrogressive thaw slump activity on Herschel Island, southern Beaufort Sea, Yukon Territory, Canada, *Geomorphology*, *95*(1-2), 84-102.

Lantz, T. C., and S. V. Kokelj (2008), Increasing rates of retrogressive thaw slump activity in the Mackenzie Delta region, NWT, Canada, *Geophys Res Lett*, *35*(6), doi 10.1029/2007gl032433.

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 Biol*, *15*(7), 1664-1675.

Lewkowicz, A. G., and S. V. Kokelj (2002), Slope sediment yield in and lowland continuous permafrost environments, Canadian Arctic Archipelago, *Catena*, *46*(4), 261-283.

Mack, M. C., E. A. G. Schuur, M. S. Bret-Harte, G. R. Shaver, and F. S. Chapin (2004), Ecosystem carbon storage in arctic tundra reduced by long-term nutrient fertilization, *Nature*, *431*(7007), 440-443.

Mann, D. H., D. M. Peteet, R. E. Reanier, and M. L. Kunz (2002), Responses of an arctic landscape to late glacial and early Holocene climatic changes: the importance of moisture, *Quaternary Sci Rev*, *21*(8-9), 997-1021.

Mann, D. H., P. Groves, R. E. Reanier, and M. L. Kunz (2010), Floodplains, permafrost, cottonwood trees, and peat: What happened the last time climate warmed suddenly in arctic Alaska?, *Quaternary Sci Rev*, *29*, 3812-3830.

Matsuoka, N. (2001), Solifluction rates, processes and landforms: a global review, *Earth-Sci Rev*, *55*(1-2), 107-134.

McNamara, J. P., D. L. Kane, and L. D. Hinzman (1998), An analysis of streamflow hydrology in the Kuparuk River basin, Arctic Alaska: A nested watershed approach, *J Hydrol*, *206*(1-2), 39-57.

Munger, C. A., D. A. Walker, H. A. Maier, and T. D. Hamilton (2008), Spatial analysis of glacial geology, surficial geomorphology, and vegetation in the Toolik Lake region: Relevance to past and future land-cover changes, *9th Int. Permafrost Conf.*, *2*, 1255-1260.

Myneni, R. B., C. D. Keeling, C. J. Tucker, G. Asrar, and R. R. Nemani (1997), Increased plant growth in the northern high latitudes from 1981 to 1991, *Nature*, *386*(6626), 698-702.

Nowinski, N. S., L. Taneva, S. E. Trumbore, and J. M. Welker (2010), Decomposition of old organic matter as a result of deeper active layers in a snow depth manipulation experiment, *Oecologia*, *163*(3), 785-792.

Olthof, I., D. Pouliot, R. Latifovic, and W. J. Chen (2008), Recent (1986-2006) vegetation-specific NDVI trends in Northern Canada from satellite data, *Arctic*, *61*(4), 381-394.

Osterkamp, T. E. (2007a), Characteristics of the recent warming of permafrost in Alaska, *J Geophys Res-Earth*, *112*(F2), doi 10.1029/2006jf000578.

Osterkamp, T. E. (2007b), Causes of warming and thawing permafrost in Alaska, *EOS*, *88*(48), 522-523.

Osterkamp, T. E., M. T. Jorgenson, E. A. G. Schuur, Y. L. Shur, M. Z. Kanevskiy, J. G. Vogel, and V. E. Tumskoy (2009), Physical and ecological changes associated with warming permafrost and thermokarst in Interior Alaska, *Permafrost Periglac*, *20*(3), 235-256.

Oswald, W. W., L. B. Brubaker, and P. M. Anderson (1999), Late Quaternary vegetational history of the Howard Pass area, northwestern Alaska, *Can J Bot*, *77*(4), 570-581.

Schimel, J. P., C. Bilbrough, and J. A. Welker (2004), Increased snow depth affects microbial activity and nitrogen mineralization in two Arctic tundra communities, *Soil Biol. Biochem.*, *36*(2), 217-227.

Schmidt, N. M., C. Baittinger, and M. C. Forchhammer (2006), Reconstructing century-long snow regimes using estimates of high arctic *Salix arctica* radial growth, *Arct Antarct Alp Res*, *38*(2), 257-262.

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*(2), 280-292.

Serreze, M. C., and J. Francis (2006), The arctic amplification debate, *Climatic Change*, *76*(3), 241-264.

Shulski, M., G. Wendler. (2007), *The Climate of Alaska*, 226 pp., University of Alaska Press, Fairbanks.

Sturm, M., C. Racine, and K. Tape (2001), Increasing shrub abundance in Arctic, *Nature*, *411*(6837), 546.

Sturm, M., T. Douglas, C. Racine, and G. E. Liston (2005a), Changing snow and shrub conditions affect albedo with global implications, *J. Geophys. Res.*, *110*(G1), G01004.

Sturm, M., J. Schimel, G. Michaelson, J. M. Welker, S. F. Oberbauer, G. E. Liston, J. Fahnestock, and V. E. Romanovsky (2005b), Winter biological processes could help convert arctic tundra to shrubland, *Bioscience*, *55*(1), 17-26.

Swann, A. L., I. Y. Fung, S. Levis, G. B. Bonan, and S. C. Doney (2010), Changes in Arctic vegetation amplify high-latitude warming through the greenhouse effect, *P Natl Acad Sci USA*, *107*(4), 1295-1300.

Tape, K. D. (2010), *The Changing Arctic Landscape*, 64 pp., University of Alaska Press, Fairbanks.

Tape, K. D., M. Sturm, and C. Racine (2006), The evidence for shrub expansion in Northern Alaska and the Pan-Arctic, *Global Change Biol*, *12*(4), 686-702.

Tarnocai, C., J. G. Canadell, E. A. G. Schuur, P. Kuhry, G. Mazhitova, and S. Zimov (2009), Soil organic carbon pools in the northern circumpolar permafrost region, *Global Biogeochem Cy*, *23*, doi 10.1029/2008gb003327.

Verbyla, D. (2008), The greening and browning of Alaska based on 1982-3003 satellite data, *Global Ecol. Biogeogr.*, *17*, 547-555.

Walker, D. A., W. A. Gould, H. A. Maier, and M. K. Raynolds (2002), The circumpolar Arctic vegetation map: AVHRR-derived base maps, environmental controls, and integrated mapping procedures, *Int J Remote Sens*, *23*(21), 4551-4570.

Walker, D. A., J. G. Bockheim, F. S. Chapin, W. Eugster, F. E. Nelson, and C. L. Ping (2001), Calcium-rich tundra, wildlife, and the "Mammoth Steppe", *Quaternary Sci Rev*, *20*(1-3), 149-163.

Walker, D. A., et al. (2003a), Phytomass, LAI, and NDVI in northern Alaska: Relationships to summer warmth, soil pH, plant functional types, and extrapolation to the circumpolar Arctic, *J Geophys Res-Atmos*, *108*(D2), doi 10.1029/2001jd000986.

Walker, D. A., et al. (2003b), Vegetation-soil-thaw-depth relationships along a low-Arctic bioclimate gradient, Alaska: Synthesis of information from the ATLAS studies, *Permafrost Periglac*, *14*(2), 103-123.

Walker, D. A., et al. (2005), The circumpolar Arctic vegetation map, *J Veg Sci*, *16*(3), 267-282.

Walker, D. A., et al. (1998), Energy and trace-gas fluxes across a soil pH boundary in the arctic, *Nature*, *394*(6692), 469-472.

Walker, M. D., D. A. Walker, and N. A. Auerbach (1994), Plant communities of a tussock tundra landscape in the Brooks Range Foothills, Alaska, *J Veg Sci*, *5*(6), 843-866.

West, J. J., and L. J. Plug (2008), Time-dependent morphology of thaw lakes and taliks in deep and shallow ground ice, *J Geophys Res-Earth*, *113*(F1), doi 10.1029/2006jf000696.

Wolfe, A. P., G. H. Miller, C. A. Olsen, S. L. Forman, P. T. Doran, and S. U. Holmgren (2004), Geochronology of high latitude lake sediments, in *Long-term Environmental Change in Arctic and Antarctic Lakes*, edited by J. P. Smol, R. Pienitz and M. S. V. Douglas, pp. 19-52, Springer Netherlands.

Zimov, S. A., S. P. Davydov, G. M. Zimova, A. I. Davydova, E. A. G. Schuur, K. Dutta, and F. S. Chapin (2006), Permafrost carbon: Stock and decomposability of a globally significant carbon pool, *Geophys Res Lett*, *33*(20), doi 10.1029/2006gl027484.

Chapter 3 – Snow-Mediated Ptarmigan Browsing and Shrub Expansion in Arctic Alaska[1]

ABSTRACT

Large, late-winter ptarmigan migrations heavily impact the shoot, plant and patch architecture of shrubs that remain above the snow surface. Ptarmigan browsing on arctic shrubs was assessed in the vicinity of Toolik Lake, on the north side of the Brooks Range in Alaska. Data were collected in early May 2007, at maximum snow depth, after the bulk of the ptarmigan migration had passed through the area. In an area of tall shrubs, half of the buds on <u>Salix alaxensis</u> were browsed by ptarmigan. Three percent of the buds that were buried beneath the snow were browsed, 90% of the buds that were less than 30 cm above the maximum snow level were browsed, and 45% of the buds above that height were browsed. Ptarmigan browsing was found to be a major height limiter for tall shrubs, thereby controlling shrub architecture by 'brooming' stems and inducing stump shoots at the snow surface. These data were qualitatively extrapolated by photographing shrub morphology over a region approximately 300 km across a series of north-flowing arctic rivers with headwaters in the Brooks Range. Ptarmigan 'hedging' shrub patches, and shrub growth under a warmer climate, are opposing forces mediated by snow distribution.

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[1] Tape KD, Lord R, Marshall HP, Ruess RW. 2010. Snow-mediated ptarmigan browsing and shrub expansion in Arctic Alaska. *Ecoscience* 17: 186-193

INTRODUCTION

Evidence from repeat photography, remote sensing, and vegetation plot studies suggests that shrubs are increasing in Northern Alaska (Figure 3.1) (Chapin et al., 1995; Myneni et al., 1997; Tape, Sturm & Racine, 2006). Temporal trends in satellite vegetation indices, namely the Normalized Difference Vegetation Index (NDVI), show a generic "greening" in tundra regions (Zhou et al., 2001; Jia, Epstein & Walker, 2003; Goetz et al., 2005; Verbyla, 2008). While it is not clear exactly what this greening actually represents in terms of shifts in plant communities, it is believed that an increase in deciduous shrubs is responsible for much of the greening (Jia, Epstein & Walker, 2004). It has been projected that the increase in shrubs will alter the surface energy balance and carbon balance at high latitudes, with potential for strong positive feedbacks to climate warming (McFadden, Chapin & Hollinger, 1998; Mack et al., 2004; Sturm et al., 2005; Chapin et al., 2005).

One factor that has been largely overlooked in discussions of shrub expansion is the potential interaction between herbivores and changing arctic vegetation. This interaction involves not just how the changing vegetation affects forage availability and quality for herbivores, but how the herbivores affect net primary production, plant architecture, and community composition. Such herbivore effects can be substantial in high-latitude terrestrial ecosystems, and often lead to a reduction in aboveground biomass and slow recovery (Crête & Doucet, 1998; den Herder, Virtanen & Roininen, 2004; Hansen et al., 2007). For example, in southern Greenland, 20% of the increased growth from experimental warming was consumed by caribou (*Rangifer tarandus*) and muskoxen (*Ovibos moschatus*). The biomass reduction was even more extensive for dwarf birch (46%), the main shrub species at the site (Post & Pedersen, 2008). In Norway, fertilization of a tundra heath led to a 4-fold increase in rodent density and an increase in winter grazing, but no change in aboveground plant biomass (Aunapuu et al., 2008). In western Alaska, recent declines in lichens and forbs and increases in shrubs and grasses were attributed to increases in caribou (*Rangifer tarandus*) grazing and possibly climate change (Joly et al., 2007). In interior Alaska, moose can consume 100% of current annual growth of preferred shrub species, which has significant effects on a suite of vegetation characteristics, including canopy structure, age distribution, species composition, and survival (Kielland et al., 1997; Butler & Kielland, 1998; Bowyer & Neville, 2003; Butler & Kielland, 2008). Snowshoe hares (Lepus americanus) also browse shrubs in interior Alaska, especially Salix alaxensis (Bryant et al., 1985). Hare browsing was found to increase plant biomass and decrease plant height (Bryant, 1987). Both moose and hare browsing accelerated succession from willow shrubs to alder shrubs (Bryant, 1987).

Ptarmigan browsing could similarly be a major factor influencing the species composition and canopy structure of shrubs throughout the arctic. Despite the considerable literature on willow ptarmigan (Lagopus lagopus) and rock ptarmigan (Lagopus mutus) diet and behavior (Weeden, 1969; Moss, 1973; Helle, 1981; Pulliainen & Iivanainen, 1981), few studies have examined the impact of ptarmigan on vegetation or how browsing by ptarmigan might interact with snowfall to influence shrub architecture.

Studies from northern Alaska show that ptarmigan, including a fraction of rock ptarmigan among the majority willow ptarmigan (Irving, 1953; Pitelka, 1974), migrate from summer breeding grounds north of the Brooks Range to winter habitat in the boreal forest of the southern Brooks Range. These movement patterns are characterized by one broad southward migration in November, and 2 broad northward migrations in January/February and April/May (Irving et al., 1967). When ptarmigan return to arctic feeding grounds in spring, snow depth restricts access to forage, which forces them to feed almost exclusively on taller shrub species, particularly Salix alaxensis (West & Meng, 1966). This reduces the number of catkins on tall, but not short willows, because the short shrubs are buried by the snow (Williams, Best & Warford, 2007). Browsing of this severity slows the growth of willow shrubs and could affect shrub architecture to such an extent as to retard the greening trend or alter the snow regime, but these direct effects and feedbacks have never been explored explicitly.

The purpose of this study was to examine the interactive effects snow depth and ptarmigan browsing on shrub growth and architecture in arctic Alaska. The project had 2 questions: (1) How does accumulating snow affect ptarmigan browsing on shrub buds, and (2) is there a long-term impact of ptarmigan browsing on shrub architecture? To answer these questions, we excavated snow surrounding Salix alaxensis shrubs near the end of the winter. We then compared browsing of buds on shoots above the snow to buds on shoots buried beneath the snow. A conceptual model is presented that outlines the complex interactions between tall shrubs, snow, and ptarmigan browsing within the framework of changing arctic vegetation.

METHODS

Site description

This study was conducted between April and June 2007 in an area within 1.5 km of the Toolik Lake Field Station (N 68°37.69', W 149°35.61'), in arctic Alaska. The area is broadly classified as tussock-sedge, dwarf-shrub, moss tundra (CAVM, 2003), while the specific areas where shrubs were sampled are classified as riparian shrublands (Walker, Walker & Auerbach, 1994). This includes the shrubs Betula nana, Salix pulchra, Salix lanata, and Salix alaxensis growing in water tracks and peaty-stream floodplains (Walker, Walker & Auerbach, 1994). The former 3 species are typically <1.2 m tall, while the latter regularly grows up to 4 m in height. Ptarmigan prefer willow species, but also feed on Betula nana catkins and foliar buds (Bryant & Kuropat, 1980). The terrain is an amalgamation of glacially-derived sediments, some of which have been reworked by streams or cryoturbation. The area is underlain by permafrost.

The region is dominated by long, cold winters and short, cool summers, with a mean annual temperature of -13 °C. The snow period extends from September to May, but snow depth varies inter-annually and across short distances due to wind and topography. Shrubs also play an important role in affecting snow depth, by trapping blowing snow and increasing snow depth (Sturm et al., 2000). This study was conducted during a year with a steady accumulation of snow, starting in October and ultimately becoming a typical snowpack by the time of the spring ptarmigan migration (Berezovskaya et al., 2008). All vegetation sampled was in pristine areas devoid of anthropogenic disturbance.

Flocks of hundreds of ptarmigan were commonly seen feeding in tall shrub communities, particularly during the late winter. Although caribou (Rangifer tarandus) migrate through the region, heading south in the Fall and north in the Spring, they feed almost exclusively on lichens during the snow-covered months, with shrubs composing a minimal portion of their diet (Boertje, 1984). Moreover, during the spring migration, caribou (*Rangifer tarandus*) typically utilize windswept higher ground where snow is shallow or nonexistent, while avoiding shrubby areas with deep snow (Schaefer, Stevens & Messier, 1996; personal observation). Moose (Alces alces) are rare in the immediate region, and were not seen during the study. Voles (Microtus oeconomus, Microtus miurus) and ground squirrels (Spermophilus parryii) can be abundant, but their browsing on tall shrub buds is negligible. Hares (Lepus americanus and Lepus othus) are beyond their range limit in this region (Rausch, 1951), and were not seen during the study. Therefore, during winter and spring, ptarmigan are the primary herbivore feeding on shrubs in this area.

Sampling

Ptarmigan Browsing on Shrubs, and Protection by Snow

In September 2006, 2 representative shrub patches (2-4 m in diameter) of Betula nana and 2 similarly sized patches of Salix pulchra were selected NE of Toolik Lake. Four ramets (main stems emanating from the base of the plant) of each species were randomly selected within each patch, 2 of which were staked upright to prevent snow burial, while the other 2 were tagged but left untreated. By May 2007, all new shoots on the staked ramets were sticking above the snow, while control ramets remained buried beneath the snow. At least ten new (most recent annual growth) shoots were chosen from the control and experimental ramets, and all buds were counted on each shoot. Bud scars were classified as browsed if the bark was ripped near the bud location, or missing if the bud was not present and no bark was ripped near the bud scar.

In early May 2007, we quantified bud browsing by ptarmigan on all new shoots of Salix alaxensis within 3 large patches (75 m^2) with ramets sticking out of the snow. This was the predominant species that had exposed stems and buds during late spring. Three height classes (strata) were delineated and sampled: buried, low, and high. The "buried" stratum included shoots below the snow (~1 m depth), the "low" stratum included shoots between 0 and 50 cm above the snow surface, and the "high" stratum included shoots greater than 50 cm above the snow surface. When the measurements were made, snow had melted approximately 20 cm from the maximum accumulation. We estimated that when standing on the snow pack, ptarmigan could reach and browse up to approximately

30 cm above the snow surface. Therefore the low stratum was established to include buds readily accessible to ptarmigan while foraging from the ground, in contrast to above this height, where ptarmigan would be browsing while roosting. Shoots of new growth were haphazardly selected and assessed (n=1143 total) in each stratum. On each shoot, all bud locations were counted and classified according to the protocol described above for staked shrubs. Each new shoot was also classified as no stripping (N), low stripping (L), medium stripping (M), or high stripping (H), according to the fraction of bark (green felt) stripped from the stem (N=0%, L=0-10%, M=10-50%, H=50-100%). We also recorded whether or not the shoot was broken.

Ptarmigan Browsing on Dominant Shrub Species

To include more shrub species and a larger area, in late May 2007, thirteen tall individuals of each Salix lanata, Salix pulchra, and Betula nana shrubs were assessed for ptarmigan browsing intensity. Four Salix alaxensis shrubs were similarly assessed (total n = 43 shrubs). The snow was completely melted, and ten new shoots were randomly selected for each shrub. Bud locations on each of ten shoots were classified as browsed, missing, live bud, and whether or not the shoot was broken. For Betula nana, bud locations were only classified as missing or present because the characteristic ptarmigan browse was difficult to identify on this species. The characteristic ripped bark beneath the bud location was more difficult to discern, because the new growth on dwarf birch is not fuzzy or easily ripped.

Ptarmigan Influence on Regional Shrub Architecture

In late winter, spring, and summer of 2007 and 2008, we photographed a variety of shrub and branch morphologies that contained an encrypted record of ptarmigan browsing, to evaluate whether results from Toolik Lake could be extrapolated across arctic Alaska. From these photos, an index of ptarmigan browsing influence on shrub architecture was developed. The index, $\underline{i}$, is the number of broomed shoots or resprouted stump shoots divided by the number of total shoots ($0 < \underline{i} \leq 1$).

During April/May 2007, photographs were taken of ptarmigan-browsed shrubs from Toolik and Galbraith Lake westward to the Itkillik River (15 km), May Creek (25 km), and the Nanushuk River (55 km) while traveling via dog sled. In the summer of 2007, photographs of ptarmigan-browsed shrubs were taken along a section of the Jago River, which is approximately 150 km east of Toolik Lake. A 180 km transect from Anaktuvuk Pass (north-central Brooks Range) to Toolik Lake was skied during the April/May ptarmigan migration of 2008. Along the transect widespread browsing-controlled shrub architecture was photographed. In most cases, it was possible to identify ptarmigan browsing by the signature bark and bud stripping, tracks, and actual observation of the browsing. Moose break shoots rather than plucking individual buds, and moose are at the fringe of their range in these generally low-stature drainage habitats. Some of the area surveyed was also close to the village of Anaktuvuk Pass, where subsistence hunting is important and moose density is very low. Ultimately, only 2 moose were sighted (both at the head of May Creek) in the combined 2 months of spring and summer travel in the northern Brooks Range and southern North Slope foothills, so we assume the browsing to be primarily that of ptarmigan. In some cases drainages were choked with thick aufies during the winter and spring, thus restricting available forage by burying portions of the shrub in layered overflow ice, instead of snow.

STATISTICS

Data were not normally distributed, so differences in browsing rates on Salix alaxensis among strata were tested using the Kolmogorov-Smirnov 2-sample test (KS-test) for independence (e.g. Massey, 1951). The maximum difference between the 3 strata was evaluated using the Kolmogorov distribution. KS-tests were also used for comparing browsing rates among shrub species. Unless otherwise mentioned, means and standard errors of untransformed data are presented throughout the text and in the figures.

RESULTS

Ptarmigan Browsing on Shrubs, and Protection by Snow

Snow protects shoots that are buried, but facilitates access to shoots immediately above the snow level. Buds on Betula nana and Salix pulchra ramets that were buried by snow early in the winter were not browsed, whereas buds on their counterparts that were staked upright were heavily browsed (Salix upright = 55 ± 6 %, Salix buried = 0 ± 0 %, Betula upright = 44 ± 6 %, Betula buried = 0 ± 0%) (Table 3.1). Ptarmigan browsing on current annual Salix alaxensis shoots (n = 1143) examined at maximum snow depth, including bud removal, breaking of new shoots, and bark removal, was highest in the low stratum (90 ± 2 %), lowest in the buried stratum (3 ± 2 %), and moderate in the high stratum (45 ± 2 %) (stratum effect: P< 0.0001) (Figure 3.2 and Table 3.2).

Ptarmigan Browsing on Dominant Shrub Species

The taller shrub species, Salix alaxensis, was subject to heavier browsing than the shorter shrub species. Data from our survey NE of Toolik Lake show that 42 ± 4% of the new buds on Salix alaxensis were browsed by ptarmigan, while browsing on buds of Salix lanata, Salix pulchra, and Betula nana averaged 27 ± 5%, 25 ± 5%, and 20 ± 5%, respectively (species effect: P<0.02)(Table 3.3).

Ptarmigan Influence on Regional Shrub Architecture

Repeated browsing by ptarmigan can have substantial effects on the architecture of shrubs. When browsing intensity is high, all buds on new shoots are removed, except the small buds near the base of the shoot, which are often protected by the branch intersection. In the following year, new shoots originate from surviving buds near the branch intersection, or from the base of the shrub (hereafter stump shoots). Repeated heavy browsing eventually creates a "broom"-like branch architecture (Figure 3.3), and hedged or partially hedged stump shoots (Figure 3.4).

Photographs of shrubs taken during surveys across arctic Alaska showed that branches on tall shrubs (n = 49) were often broomed shoots or stump shoots resulting from intense browsing. Along the Anaktuvuk River, $\underline{i}$ = 0.79 ± .04, and along the Jago

River, $\underline{i}$ = 0.82 ± .03, which means that approximately 80% of the shoots on these shrubs were hedged by ptarmigan. Photographs from Toolik Lake and the surrounding area taken during spring 2007 were unusable, due to deeper snow in 2007 concealing stump shoots.

DISCUSSION

Snow deposition, ptarmigan browsing, and shrub architecture interact in ways that strongly couple trophic dynamics with the physical environment (Figure 3.5). Accumulating snow (1) protects smaller shrubs or those that readily lie down during winter, (2) leaves the taller shrubs exposed above the snow, and (3) enables ptarmigan to access buds higher on the shrub. (4) Ptarmigan populations depend on tall shrubs for forage during the spring. (5) Ptarmigan browsing alters shrub architecture and reduces shrub heights through hedging, which (6) decreases future snow accumulation (Figure 3.5).

Snow timing and distribution mediate the impact of ptarmigan browsing on shrubs. If snow arrives late or is insufficient to bury most of the shrubs, then ptarmigan browsing is spread over a larger number of smaller shrubs of varying heights. This lessens the impact of browsing on individual shrubs. In contrast, during winters with average to deep snow, most shrubs are buried at the time of spring ptarmigan migrations so only the remaining exposed tall shrubs are browsed heavily. Years with average to deep snow may lead to high fidelity of large ptarmigan flocks to exposed shrub patches due to food limitations at the landscape scale. In our study, the taller shrub species, Salix alaxensis, was subject to heavier browsing (42 ± 4%) than the shorter shrub species (27 ± 5%, 25 ± 5%, and 20 ± 5%), because the shorter shrubs were buried by snow during the spring ptarmigan migration, while the tall shrubs had ramets exposed throughout the winter.

Legacies of ptarmigan browsing intensity and snow depth can be inferred from the architecture of shrubs. When deep snow restricts ptarmigan browsing to tall shrubs, and when ptarmigan abundances are high relative to shrub density, ptarmigan maintain shrubs in a hedged or partially hedged growth form (Figure 3.4). The height of the hedge is approximately the browsing height of a ptarmigan above the average snow depth.

Because ptarmigan browsing appears to affect arctic shrubs in a manner similar to how snowshoe hare browsing affects boreal shrubs (Bryant, 1987), it might be expected that much of the associated plant-herbivore dynamics documented for boreal browsing systems apply to ptarmigan browsing on arctic shrubs. Effects of intensive browsing on growth of Salix alaxensis and Salix interior can be seen along the Tanana River in central Alaska, where high moose and snowshoe hare populations maintain "browsing lawns" (similar to hedges here) of shrubs close to the snow surface (personal observation).

Severe snowshoe hare browsing causes Salix alaxensis to revert to stump shoots, which are initially of lower nutritional quality, though they regain nutritional content after several years, when they grow high enough to be available to hares during the winter (Bryant et al., 1985). The stump shoots and hedges resulting from severe hare browsing in central Alaska are also prevalent in arctic Salix alaxensis shrubs (Figure

3.4b). Stump shoots and broomed shoots constituted approximately 80% of the ramets on surveyed shrubs along the Anaktuvuk and Jago Rivers, and most of that 80% were stump shoots, rather than broomed shoots (Figure 3.4b). In the central and eastern Brooks Range and arctic foothills of Alaska, however, hares and moose are rare (Best & Henry, 1994; (personal observation) and the stump shoots and hedges in the study area are instead likely a response to severe ptarmigan browsing. Stump shoots constitute additional shoots, which widen the effective base of the shrub, while the brooming truncates and broadens the branch structure. Combined, these architectural modifications resulting from browsing create a hedged shrub.

Average to deep snow years and associated heavy ptarmigan browsing can trigger another positive feedback that promotes architecture amenable to ptarmigan browsing. Repeated browsing during average to deep snow years produces a thickening of the junction of the broom in the following year (Bowyer & Neville, 2003) and a new shoot from that junction, rather than the new shoot growing well above maximum snow depth and above the reach of ptarmigan standing on the snow. This allows ptarmigan to maintain new growth within reach and control shrub canopy structure to their advantage, in a manner reminiscent of the positive feedback between grazers and graminoids (McNaughton, 1984; Person et al., 2003; Frank, 2007).

Because taller shrubs trap more snow and create deeper snow than shorter shrubs (Sturm et al., 2000), intense ptarmigan browsing has the potential to reduce snow-trapping by shrubs at the landscape scale. Shallower snow in heavily- browsed shrub patches permits higher winter energy exchange between the ground and the atmosphere.

The lower winter ground temperature as a result of shallower snow is a negative feedback to warming and greening (Sturm et al., 2005). Similarly, ptarmigan browsing reducing shrub height may increase winter albedo, another negative feedback to warming and greening (Chapin et al., 2005), but the complexity of snow-shrub interactions confounds these predictions.

The increase in shrub abundance across arctic Alaska (Jia, Epstein & Walker, 2003; Tape, Sturm & Racine 2006) may have fostered an increase in ptarmigan over-winter survival, maternal nutrition, and overall population size. More tall shrubs create more forage above the snow surface available to ptarmigan during the winter. The fact that only 6% of buds on Salix alaxensis remained unbrowsed in the heavily-browsed low stratum suggests that late-winter forage availability may be a factor limiting ptarmigan populations. Territorial behavior of ptarmigan (Moss, 1973) and other birds (Greenberg, Ortiz & Caballero, 1994), and the association of that behavior with food resources also suggest that winter forage is a limiting resource. For example, the Mid-Continent population of the lesser snow goose (Chen caerulescens ssp. caerulescens) has grown 5-7% annually in response to nitrogen fertilizers enhancing the growth of agricultural forage on wintering grounds and along flyways (Abraham, Jefferies & Alisauskas, 2005). The estimated annual 50,000 ptarmigan migrating biannually through Anaktuvuk Pass in 1960-64 (Irving et al., 1967) constitute only a fraction of the total number of ptarmigan passing through a dozen similar meridional migration routes through the Brooks Range, and the current increase in shrubs is a potential mechanism for population growth since that period.

Some of the dramatic greening observed in repeat photography over the last half-century in arctic Alaska is Siberian alders (Alnus viridis spp. fruticosa) colonizing floodplains (Tape, Sturm & Racine, 2006). In the boreal floodplain succession, moose and snowshoe hares facilitate a similar vegetation shift by browsing heavily on willows while avoiding and indirectly cultivating the dominance of the thin-leaf alder (Alnus tenuifolia), an important N_2-fixing species (Bryant, 1987; Uliassi & Ruess, 2002; Butler & Kielland, 2008). Browsing also has both direct (feces) and indirect (litter quality, rhizosphere processes) effects on nutrient cycling processes (Hamilton & Frank, 2001; Butler & Kielland, 2008). It is possible that by browsing willows and avoiding alders (Moss, 1973), ptarmigan are similarly facilitating the spread of Siberian alder and influencing ecosystem N balance, both within and outside of arctic floodplains.

CONCLUSION

Ptarmigan browsing, snow cover, and shrub architecture are tightly interconnected in a complex way. Ptarmigan populations may not only be responding to recent shrub expansion, but they are a major limiter of shrub height in arctic Alaska, and may be affecting arctic floodplain succession. The interactions presented here involve both positive and negative feedbacks to greening, and, though the cumulative impact on the system is unknown, the outcome of the interactions is encrypted in the height and architecture of shrubs across arctic Alaska.

ACKNOWLEDGEMENTS

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Tables

Table 3.1. Mean percent of bud locations browsed per new shoot ± standard error (see Ptarmigan Browsing on Shrubs, and Protection by Snow).

Species	buried by snow (n = 40 shoots)	exposed (n = 40 shoots)
Salix pulchra (n = 2 ramets)	0.0 ± 0	54.6 ± 6
Betula nana (n = 2 ramets) *	0.0 ± 0	43.5 ± 6

* value includes "browsed" and "missing" bud locations

Table 3.2. Percentage of Salix alaxensis shoots in each stratum categorized by the percent of bark stripped (see Ptarmigan Browsing on Shrubs, and Protection by Snow; No stripping = 0%, Low stripping = 0.1-10%, Medium stripping = 10-50%, High stripping = 50-100%). Each row adds up to 100%.

	No stripping	Low stripping	Medium stripping	High stripping
Buried stratum	96%	3.7	0.0	0.2
Low stratum	1.0	30	37	32
High stratum	28	68	3.6	0.2

Table 3.3. Mean percent of bud locations browsed per new shoot on dominant shrub species (Ptarmigan Browsing on Dominant Shrub Species).

shrub species	% bud locations browsed ± standard error
Salix alaxensis	42 ± 4
Salix lanata	27 ± 5
Salix pulchra	25 ± 5
Betula nana	20 ± 5 *

* value includes “browsed” and “missing” buds

Figures

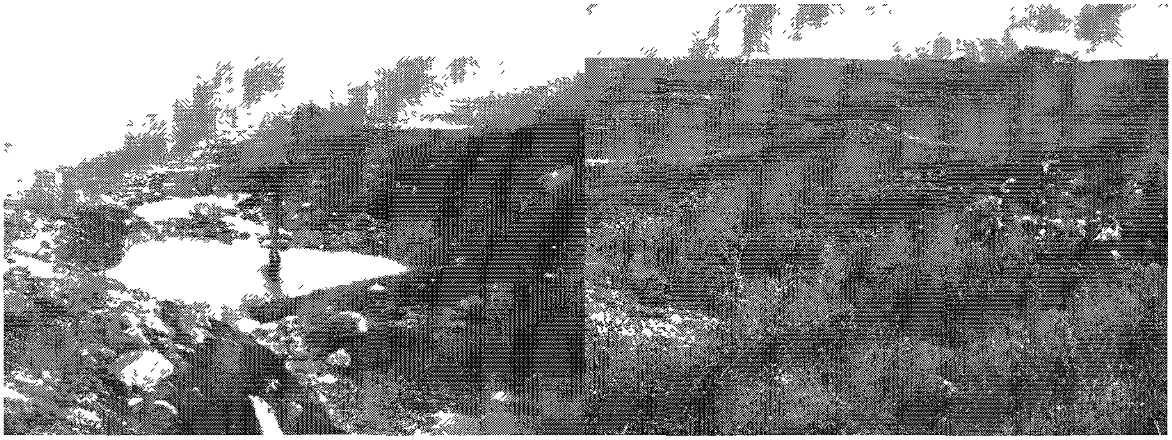

Figure 3.1. Photos taken from the same location near the top of a >10 ka moraine on the west side of the Jago River, (N 69°27.83', W 143°44.73'): (left) From 1957 (George Kunkel), showing no vegetation higher than 0.5 m, and (right) from 2007 (Ken Tape), showing dense stand of Salix alaxensis > 3 m tall. The perspective in the new photo is close, but not exactly the same as in the old photo, because the permafrost is collapsing, making the exact old photo location inaccessible, hanging above the collapse.

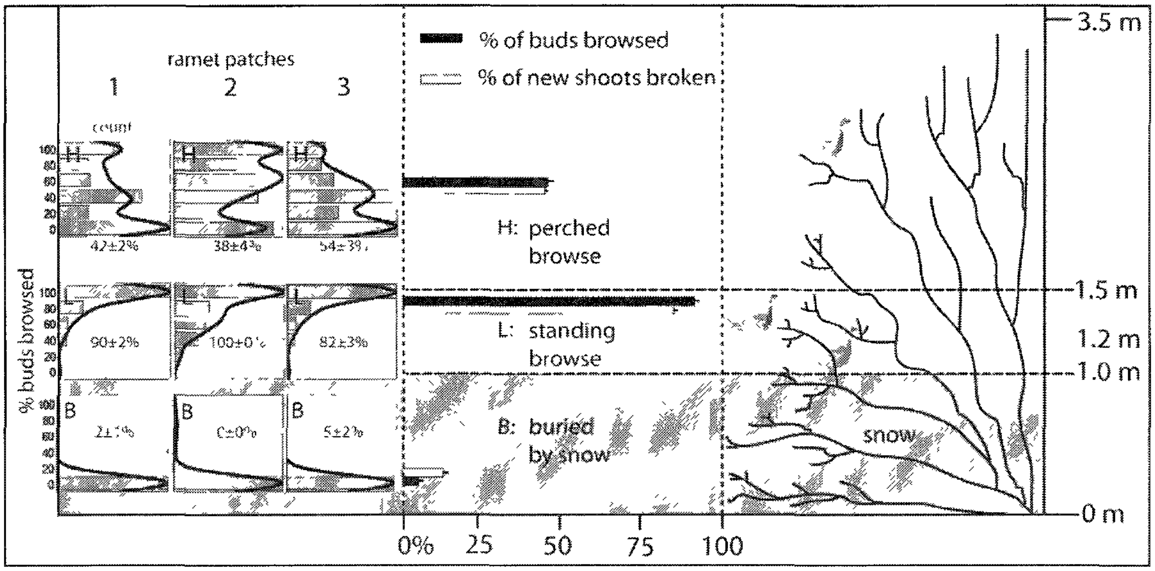

Figure 3.2. Patterns of ptarmigan browsing on 3 Salix alaxensis ramet patches measured during spring migration at Toolik Lake. The curves are non-parametric probability distribution functions, including means and standard error for each patch. Because of the similarity between the browsing distributions of the 3 Salix alaxensis patches (left column), independence of new shoots is assumed for computing means of each height stratum (center column). Ptarmigan browsing on Salix alaxensis is heaviest in the low stratum, where the snow surface permits easy access to the buds.

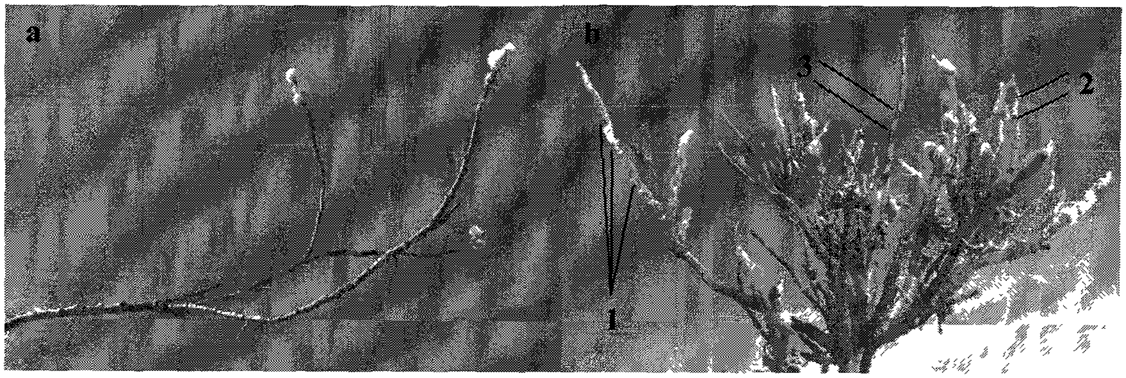

Figure 3.3. Influence of ptarmigan browsing on shoot architecture of Salix alaxensis: (a) Unbrowsed growth form at 3 m tall, and (b) Repeatedly browsed ("broomed") growth form at 1.5 m tall, showing evidence of (1) this year's browsing, (2) last year's browsing, and (3) browsing from at least 3 years ago.

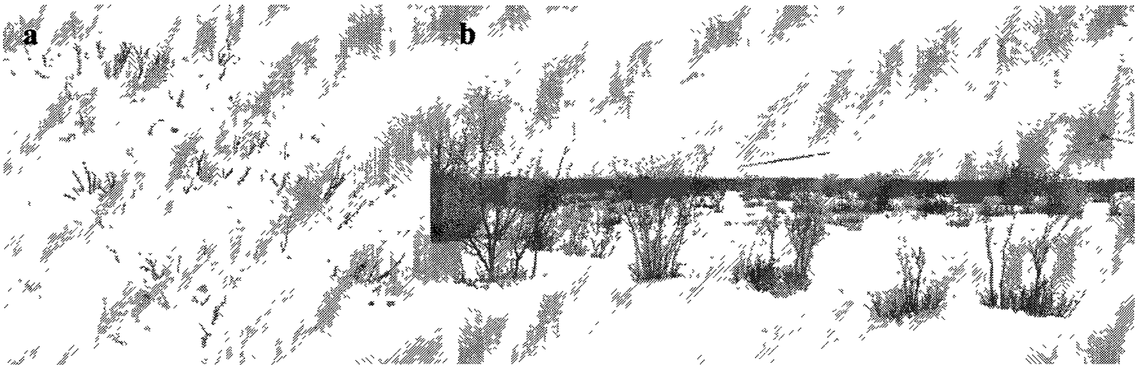

Figure 3.4. Photo (a) shows hedged shrub architecture at maximum snow depth, 15 km east of Anaktuvuk Pass (i ~ 1). In the same valley, photo (b) shows hedged architecture at mean snow depth, but also some ramets growing above the standing browsing level of ptarmigan (i ~ 0.8). The hedged shoots are mostly stump shoots that were initiated by severe browsing events.

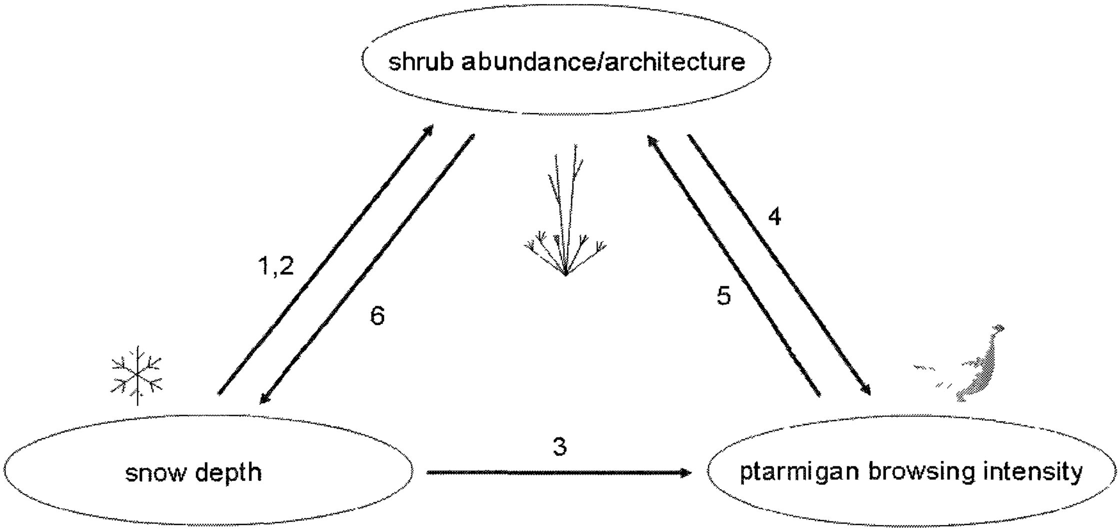

Figure 3.5. Complex interactions between snow, shrubs, and ptarmigan. Numbers correspond to processes described in the Discussion.

LITERATURE CITED

Abraham, K. F., R. L. Jefferies, R. T. Alisauskas, 2005. The dynamics of landscape change and snow geese in mid-continent North America. Global Change Biology, 11:841-855.

Aunapuu, M., J. Dahlgren, T. Oksanen, D. Grellmann, L Oksanen, J. Olofsson, U. Rammul, M. Schneider, B. Johansen, H. O. Hygen, 2008. Spatial patterns and dynamic responses of Arctic food webs corroborate the exploitation ecosystems hypothesis (EEH). The American Naturalist, 171-2: 249-262.

Berezovskaya, S. L., J. E. Derry, D. I. Kane, R. E. Geick, M. R. Lilly, D. M. White, 2008. Snow survey data for the Kuparuk Foothills Hydrology Study: Spring 2008. University of Alaska Fairbanks, Water and Environmental Research Center, Report INE/WERC 08.14, 40 pp.

Best, T. L., T. H. Henry, 1994. Lepus othus. Mammalian Species, 458:1-5.

Boertje, R. D., 1984. Seasonal Diets of the Denali Caribou Herd, Alaska. Arctic, 37-2: 161-165.

Bowyer, R. T. & J. A. Neville, 2003. Effects of browsing history by Alaskan Moose on regrowth and quality of Felt-leaf Willow. Alces, 39: 193-202.

Bryant, J. P. & P. J. Kuropat, 1980. Selection of Winter Forage by Subarctic Browsing Vertebrates: The Role of Plant Chemistry. Annual Review of Ecology and Systematics, 11: 261-285

Bryant, J. P., G. D. Wieland, T. Clausen, P. Kuropat, 1985. Interactions of Snowshoe Hare and Feltleaf Willow in Alaska. Ecology, 66-5: 1564-1573

Bryant, J. P., 1987. Feltleaf Willow-Snowshoe Hare Interactions: Plant Carbon/Nutrient Balance and Floodplain Succession. Ecology, 68-5: 1319-1327

Butler, L. G. & K. Kielland, 2008. Acceleration of vegetation turnover and element cycling by mammalian herbivory in riparian ecosystems. Journal of Ecology, 96: 136-144.

CAVM Team, 2003. Circumpolar Arctic Vegetation Map. Scale 1:7,500,000. Conservation of Arctic Flora and Fauna (CAFF) Map No. 1. U.S. Fish and Wildlife Service, Anchorage, Alaska.

Chapin III, F. S., G. R. Shaver, A. E. Giblin, K. J. Nadelhoffer, J. A. Laundre, 1995. Responses of arctic tundra to experimental and observed changes in climate. Ecology, 76-3: 694-711.

Chapin III, F. S., M. Sturm, M. C. Serreze, J. P. McFadden, A. H. Lloyd, A. D. McGuire, T. S. Rupp, A. H. Lynch, J. P Shimel, J. Baringer, W. L. Chapman, H. E. Epstein, E. S. Euskirchen, L. D. Hinzman, G. Jia, C.-L. Ping, K. D. Tape, C. D. C. Thompson, D. A. Walker, J. M. Welker, 2005. Role of Land-Surface Changes in Arctic Summer Warming. Science, 310-5748: 657-660.

Crête, M., & G. J. Doucet, 1998. Persistent Suppression in Dwarf Birch after Release from Heavy Summer Browsing by Caribou. Arctic and Alpine Research, 30-2: 126-132

Frank, D. A., 2007. Drought effects on above- and belowground production of a grazed temperate grassland ecosystem. Oecologia, 152: 131-139.

Goetz, S. J., A. G. Bunn, G. J. Fiske, R. A. Houghton, 2005. Satellite-observed photosynthetic trends across boreal North America associated with climate and fire disturbance. Proceedings of the National Academy of Sciences, 102-38: 13521-13525.

Greenberg, R., J. S. Ortiz, C. M. Caballero, 1994. Aggressive competition for critical resources among migratory birds in the Neotropics. Bird Conservation International, 4: 115-127.

Hakkarainen, H., R. Virtanen, J. O. Honkanen, H. Roininen, 2007. Willow bud and shoot foraging by ptarmigan in relation to snow level in NW Finnish Lapland. Polar Biology, 30:619-624

Hamilton, EW, III & Frank, DA (2001) Can plants stimulate soil microbes and their own nutrient supply? evidence from a grazing tolerant grass. *Ecology* 82(9):2397-2402.

Hansen, B. B., S. Henriksen, R. Aanes, B. E. Sæther, 2007. Ungulate impact on vegetation in a 2-level trophic system. Polar Biology, 30: 549-558

Helle, E., 1981. Riekon talviravinnon koostumuksesta ja valinnasta Pohjois-Pohjanmaalla (Summary: Preference for different types of winter forage in the willow grouse (Lagopus lagopus L.) in the northern part of Ostrobotnia, Finland). Suom Riista, 28: 15-20

den Herder, M., R. Virtanen, H. Roininen, 2004. Effects of reindeer browsing on tundra willow and its associated insect herbivores. Journal of Applied Ecology, 41: 870-879

Irving, L., 1953. The Naming of Birds by Nunamiut Eskimo Arctic, 6: 35-43.

Irving, L., G. C. West, L. J. Peyton, S. Paneak, 1967. Migration of Willow Ptarmigan in Arctic Alaska. Arctic, 20: 77-85.

Jia, G. J., H. E. Epstein, D. A. Walker, 2003. Greening of arctic Alaska. Geophysical Research Letters, 3020: 20-67.

Jia, G. J., H. E. Epstein, D. A. Walker, 2004. Controls over intra-seasonal dynamics of AVHRR NDVI for the arctic tundra in northern Alaska. International Journal of Remote Sensing, 25-9: 1547-1564.

Joly, K., R. R. Jandt, C. R. Meyers, M. J. Cole, 2007. Changes in vegetative cover on Western Arctic Herd winter range from 1981-2005: potential effects of grazing and climate change. Rangifer, Special Issue 17: 199-207.

Kielland, K. & J. P. Bryant, 1997. Moose herbivory in taiga: effects on biogeochemistry and vegetation dynamics in primary succession. Oikos, 82:377-383.

Mack, M. C., E. A. G. Shur, M. S. Bret-Harte, G. R. Shaver, F. S. Chapin III, 2004. Ecosystem carbon storage in arctic tundra reduced by long-term nutrient fertilization. Nature, 431: 440-443.

Massey, F. J., 1951. The Kolmogorov-Smirnov Test for Goodness of Fit. Journal of the American Statistical Association, 46-253: 68–78.

McFadden, J. P., F. S. Chapin III, D. Y. Hollinger, 1998. Subgrid-scale variability in the surface energy balance of arctic tundra. Journal of Geophysical Research, 103-22: 28947-28961.

McNaughton, S. J., 1984. Grazing Lawns: Animals in Herds, Plant Form, and Coevolution. The American Naturalist, 124-6: 863-886.

Moss, R., 1973. The digestion and intake of winter foods by wild ptarmigan in Alaska. Condor, 75:293-300

Myneni, R. B., C. D. Keeling, C. J. Tucker, G. Asrar, R. R. Nemani, 1997. Increased plant growth in the northern high latitudes from 1981 to 1991. Nature, 38: 698-702.

Person, B. T., M. P. Herzog, R. W. Ruess, J. S. Sedinger, R. M. Anthony, C. A. Babcock, 2003. Feedback dynamics of grazing lawns: coupling vegetation change with animal growth. Oecologia, 135:583-592.

Pitelka, F. A., 1974. An Avifaunal Review for the Barrow Region and North Slope of Arctic Alaska. Arctic and Alpine Research, 6-2: 161-184.

Post, E. & C. Pedersen, 2008. Opposing plant community responses to warming with and without herbivores. Proceedings of the National Academy of Sciences, 105-34: 12353-12358.

Pulliainen, E. & J. Iivanainen, 1981.Winter nutrition of the willow grouse (Lagopus lagopus) in the extreme north of Finland. Annals of Zoology of Fennoscandia, 18:263-269

Rausch, R., 1951. Notes on the Nunamiut Eskimo and mammals of the Anaktuvuk Pass region, Brooks Range, Alaska. Arctic, 3: 147-195

Ripple, W. J. & R. L. Beschta, 2003. Wolf reintroduction, predation risk, and cottonwood recovery in Yellowstone National Park. - Forest Ecology and Management, 184:299–313.

Schaeffer, J. A., S. D. Stevens, F. Messier, 1996. Comparative Winter Habitat Use and Associations among Herbivores in the High Arctic. Arctic, 49-4: 387-391.

Sturm, M., T. Douglas, C. Racine, G.E. Liston, 2005. Changing snow and shrub conditions affect albedo with global implications. Journal of Geophysical Research, 110

Sturm, M., J. Holmgren, J. P. McFadden, G. E. Liston, F. S. Chapin III, C. Racine, 2000. Snow-Shrub Interactions in Arctic Tundra: A Hypothesis with Climatic Implications. Journal of Climate, 14:336-344.

Tape, K., M. Sturm, C. Racine, 2006. The evidence for shrub expansion in Northern Alaska and the pan-Arctic. Global Change Biology, 12: 686-702.

Uliassi, D. D. & R. W. Ruess (2002). Limitations to Symbiotic Nitrogen Fixation in Primary Succession in the Tanana River Floodplain. Ecology, 83-1: 88-103.

Verbyla, D., 2008. The greening and browning of Alaska based on 1982-2003 satellite data. Global Ecology and Biogeography, 17-4: 547-555.

Walker, M. D., D. A. Walker, N. A. Auerbach, 1994. Plant communities of a tussock tundra landscape in the Brooks Range Foothills, Alaska. Journal of Vegetation Science, 5:843-866.

Weeden, R. B., 1969. Foods of rock and willow ptarmigan in central Alaska with comments on interspecific competition. Auk, 86:271-281.

West, G. C. & M. S. Meng, 1966. Nutrition of willow ptarmigan in northern Alaska. Auk, 83:603-615.

Williams, J. B., D. Best, C. Warford, 1980. Foraging Ecology of Ptarmigan at Meade River, Alaska. *The Wilson Bulletin* 92-3: pp. 341-351

Zhou, L., C. J. Tucker, R. K. Kaufman, D. Slayback, N. V. Shabanov, R. B. Myneni, 2001. Variations in northern vegetation activity inferred from satellite data of vegetation index during 1981 to 1999. Journal of Geophysical Research, 106-D17: 20,069-20,083.

GENERAL CONCLUSIONS

Changing vegetation in Arctic Alaska, notably the expansion of deciduous shrubs into tundra areas, has altered the structure and function of these ecosystems. Results from temporal studies of satellite imagery [*Jia et al.*, 2003] and vegetation plot manipulations [*Chapin et al.*, 1995; *Walker et al.*, 2006] imply that warming increases shrub abundance, and therefore that warming of the 2nd and 4th quarters of the 20th century triggered an increase in shrubs, though relationships with snow and other factors complicate this assumption. In general, few records of landscape processes accompany the 20th century record of temperature. Available records for Arctic Alaska include permafrost boreholes, which show that permafrost temperatures were imprinted with 20th century air temperature increases. [*Lachenbruch*, 1959; *Osterkamp*, 2007; *Osterkamp and Jorgenson*, 2006], and repeated old photographs, which, though only snapshots in time, reveal changes in shrub cover [*Tape et al.*, 2006] and permafrost degradation [*Jorgenson et al.*, 2006; *Lantz and Kokelj*, 2008].

This thesis was undertaken to improve the 20th century perspective of landscape change to include not only temperature, but shrub growth, shrub colonization, erosion, and snowmelt magnitude and timing. By creating and aligning new records of landscape processes, factors governing shrub growth and distribution emerged. Sampling shrubs in different landscape positions revealed spatial patterns in these interactions. The cascading effects of air temperature increase during the 20th century on vegetation and subsequent ecosystem interactions shape the landscape slowly to rapidly, and to varying spatial extents. Climate perturbations and the subsequent interactions between, for example, herbivores and shrubs, must be considered within a single framework that includes all components as mechanisms for a systemic perturbation.

In Chapter 1, a chronology of alder shrub growth was developed using shrub rings that spanned the latter half of the 20th century. Alder growth was dictated strongly by growing season temperature in locations with deeper active layer and higher ground heat flux, often adjacent to streams or outcrops. In contrast, in tussock tundra areas, shrubs were unresponsive to growing season temperature or precipitation, most likely because the soils were generally too wet, as suggested by strong negative correlations with August precipitation in the year prior to ring formation. The rapid response of shrubs to warm summers in areas without tussocks and with deeper active layers indicates a predisposition to shrub expansion during recent warming. The lack of response of shrubs in tussock tundra with shallow permafrost to warm spring/summers indicates a resilience of vegetation and permafrost to climate change. Graminoids may outcompete shrubs for additional nutrients available during warm summers in tundra landscapes, resulting in the NDVI increase during warm summers. The NDVI signal correlates well with temperature [*Verbyla*, 2008], though alder growth rings from tussock tundra show no such relationship.

In Chapter 2, a chronology of 20th century erosion in four watersheds was compared to a nearby river discharge record and evidence of shrub expansion in the watersheds and surrounding area. Temporal changes in erosion and the transport of sediment are controlled by the vegetation, runoff, and, in Arctic watersheds, the stability of the underlying permafrost. Because much of the landscape is protected from erosion and temperature perturbations by a thick organic layer, I speculate that most of the erosion is occurring along stream margins, where soil is exposed and shrub expansion is prevalent. A decline in erosion in three watersheds in approximately 1980 may be due to shrub expansion along streams and gullies, or earlier and reduced peak runoff evident in the discharge record. One watershed showed a much higher and episodic record of erosion that is not correlated with climatic or vegetation variables but perhaps resulted from permafrost degradation along the inlet gully. Building on the first study, this study reaffirms that the snowmelt period and ensuing runoff constitutes a dynamic period that is dictating many of the observed climate, vegetation, and geomorphic changes. This study also reiterates the vulnerability of the Arctic landscape along floodplains and streams, where flowing water dissects the otherwise thick organic layer and shallow permafrost.

In Chapter 3, herbivory was observed to be critical in shaping the architecture of tall Arctic willow and birch shrubs. During springtime, thousands of ptarmigan pass through each of many meridional migration routes through the Brooks Range and onto the North Slope. Deepening snow cover as the winter progresses limits the available ptarmigan forage to tall shrubs along floodplains and streams, resulting in heavy browsing on those shrubs. Browsing of buds and new shoots during repeated years leads to shorter shrubs with broomed branches, often forming a hedge approximately the height of a ptarmigan above the average to deep snowpack. Ptarmigan populations may be both responding to increased shrub forage availability and influencing the composition and expansion rate of shrub communities. Like the previous studies, this study highlights conditions during the snowmelt/green-up (migration) period as being critical in shaping the shrub canopy.

The evidence presented in this thesis shows that vegetation and climate are changing in the Arctic, and that vegetation change is concentrated along stream and floodplain corridors where permafrost and vegetation are more sensitive to increases in temperature and precipitation. Although vegetation change is focused along the dendritic pattern of riparian corridors, it is widespread. Changes in temperature, precipitation, and shrubs are penetrating the landscape via these drainage corridors, and gradually spreading into the more resilient tussock tundra through lateral degradation of permafrost.

If we are to predict how the Arctic landscape will evolve in the coming decades to centuries, we must consider the gradual, but widespread changes presented here alongside the patchy, but more dramatic disturbances potentially forthcoming in the form of fire, thaw slumps, or insect outbreaks. In the Alaskan boreal forest it has been shown that climate-driven changes in disturbance regimes are changing the vegetation and ecosystem more rapidly than the direct effect of climate on the ecosystem. For example, the increase in fire severity coupled with permafrost loss in recent decades is reconfiguring forest stands by altering successional trajectories [*Johnstone et al.*, 2010]. In comparison, the ongoing direct effect of climate on boreal vegetation is rather limited; for example, white spruce in average to dry sites are responding negatively to the warming [*Goetz et al.*, 2005], due to drought stress [*Wilmking et al.*, 2004]. This decline in white spruce has so far not resulted in catastrophic changes comparable to those wrought by insect outbreaks, or by severe fires that prevent the return of permafrost and initiate a different vegetation and successional cycle.

In Arctic Alaska, disturbances, such as fire and thaw slumps, may become increasingly important in shaping vegetation composition, permafrost distribution, and associated hydrology. Such changes in landscape structure and accompanying lengthening of the snow-free period will have profound effects on feedbacks of trace gases and energy to the atmosphere. These disturbances radically alter discrete patches of the landscape and often produce sediment pulses similar to those detected using the lake coring method implemented herein. These threshold disturbances are currently very limited in their spatial coverage [*Gooseff et al.*, 2009](one in four watersheds, herein), and few studies have reliably indicated an increasing frequency of such disturbance events [*Lantz and Kokelj*, 2008], though they likely will be crucial mechanisms of change as the continuous permafrost approaches thawing temperatures. The gradual expansion of shrubs via drainage corridors, described herein, remains the dominant type of landscape change in Arctic Alaska.

The Arctic landscape in several decades or centuries could be shaped by ongoing processes like those presented here, or by an increasing prevalence of threshold responses resulting from interactions between climate warming and changing disturbance regimes, such as fire. Both types of change will probably result in the expansion of shrubs, though the resulting ecosystem could vary substantially depending on the relative contributions of gradual and disturbance type change. The limited evidence available now suggests that it will be a combination of the two.

References

Bhatt, U. S., et al. (2010), Circumpolar arctic tundra vegetation change is linked to sea ice decline, *Earth Interact*, *14*(8), 1-20.

Bret-Harte, M. S., E. A. Garcia, V. M. Sacre, 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, *J Ecol*, *92*(4), 635-647.

Chapin, F. S., G. R. Shaver, A. E. Giblin, K. J. Nadelhoffer, and J. A. Laundre (1995), Responses of Arctic tundra to experimental and observed changes in climate, *Ecology*, *76*(3), 694-711.

Chapin, F. S., et al. (2005), Role of land-surface changes in Arctic summer warming, *Science*, *310*(5748), 657-660.

Goetz, S. J., A. G. Bunn, G. J. Fiske, and R. A. Houghton (2005), Satellite-observed photosynthetic trends across boreal North America associated with climate and fire disturbance, *P Natl Acad Sci USA*, *102*(38), 13521-13525.

Gooseff, M. N., A. Balser, W. B. Bowden, and J. B. Jones (2009), Effects of hillslope thermokarst in Northern Alaska, *EOS*, *90*(4), 29-36.

Jia, G., H. E. Epstein, and D. A. Walker (2003), Greening of arctic Alaska, 1981-2001, *Geophys Res Lett*, *30*(20), doi 10.1029/2003gl018268.

Johnstone, J. F., T. N. Hollingsworth, F. S. Chapin, and M. C. Mack (2010), Changes in fire regime break the legacy lock on successional trajectories in Alaskan boreal forest, *Global Change Biol*, *16*(4), 1281-1295.

Joly, K., R. R. Jandt, C. R. Meyers, and M. J. Cole (2007), Changes in vegetative cover on Western Arctic Herd winter range from 1981 to 2005; potential effects of grazing and climate change, *Rangifer*(Special Issue no. 17), 199-206.

Jorgenson, M. T., Y. L. Shur, and E. R. Pullman (2006), Abrupt increase in permafrost degradation in Arctic Alaska, *Geophys Res Lett*, *33*(2), -.

Lachenbruch, A. H. (1959), Dissipation of the temperature of drilling a well in Arctic Alaska, *Geological Survey Bulletin*, *1083-C*, 1-109.

Lantz, T. C., and S. V. Kokelj (2008), Increasing rates of retrogressive thaw slump activity in the Mackenzie Delta region, NWT, Canada, *Geophys Res Lett*, *35*(6), doi 10.1029/2007gl032433.

Mack, M. C., E. A. G. Schuur, M. S. Bret-Harte, G. R. Shaver, and F. S. Chapin (2004), Ecosystem carbon storage in arctic tundra reduced by long-term nutrient fertilization, *Nature*, *431*(7007), 440-443.

Mann, D. H., P. Groves, R. E. Reanier, and M. L. Kunz (2010), Floodplains, permafrost, cottonwood trees, and peat: What happened the last time climate warmed suddenly in arctic Alaska?, *Quaternary Sci Rev*, *29*, 3812-3830.

Myneni, R. B., C. D. Keeling, C. J. Tucker, G. Asrar, and R. R. Nemani (1997), Increased plant growth in the northern high latitudes from 1981 to 1991, *Nature*, *386*(6626), 698-702.

Osterkamp, T. E. (2007), Causes of warming and thawing permafrost in Alaska, *EOS*, *88*(48), 522-523.

Osterkamp, T. E., and J. C. Jorgenson (2006), Warming of permafrost in the Arctic National Wildlife Refuge, Alaska, *Permafrost Periglac*, *17*(1), 65-69.

Oswald, W. W., L. B. Brubaker, and P. M. Anderson (1999), Late Quaternary vegetational history of the Howard Pass area, northwestern Alaska, *Can J Bot*, *77*(4), 570-581.

Oswald, W. W., L. B. Brubaker, F. S. Hu, and D. G. Gavin (2003a), Pollen-vegetation calibration for tundra communities in the Arctic Foothills, northern Alaska, *J Ecol*, *91*(6), 1022-1033.

Oswald, W. W., P. M. Anderson, L. B. Brubaker, F. S. Hu, and D. R. Engstrom (2003b), Representation of tundra vegetation by pollen in lake sediments of northern Alaska, *J Biogeogr*, *30*(4), 521-535.

Shulski, M., G. Wendler. (2007), *The Climate of Alaska*, 226 pp., University of Alaska Press, Fairbanks.

Sturm, M., C. Racine, and K. Tape (2001), Increasing shrub abundance in Arctic, *Nature*, *411*(6837), 546.

Sturm, M., J. Schimel, G. Michaelson, J. M. Welker, S. F. Oberbauer, G. E. Liston, J. Fahnestock, and V. E. Romanovsky (2005), Winter biological processes could help convert arctic tundra to shrubland, *Bioscience*, *55*(1), 17-26.

Tape, K. D., M. Sturm, and C. Racine (2006), The evidence for shrub expansion in Northern Alaska and the Pan-Arctic, *Global Change Biol*, *12*(4), 686-702.

Verbyla, D. (2008), The greening and browning of Alaska based on 1982-3003 satellite data, *Global Ecol. Biogeogr.*, *17*, 547-555.

Walker, M. D., et al. (2006), Plant community responses to experimental warming across the tundra biome, *P Natl Acad Sci USA*, *103*(5), 1342-1346.

Wilmking, M., G. P. Juday, V. A. Barber, and H. S. J. Zald (2004), Recent climate warming forces contrasting growth responses of white spruce at treeline in Alaska through temperature thresholds, *Global Change Biol*, *10*(10), 1724-1736.