

Landscape Heterogeneity of Shrub Expansion in Arctic Alaska

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ABSTRACT

The expansion of shrubs into tundra areas is a key terrestrial change underway in the Arctic in response to elevated temperatures during the twentieth century. Repeat 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 stable). We characterized and compared adjacent expanding and stable shrub patches across Arctic Alaska by sampling a wide range of physical and chemical soil and vegetation properties, including shrub growth rings. Expanding patches of *Alnus viridis* ssp. *fruticosa* (Siberian alder) contained shrub stems with thicker growth rings than in stable patches. Alder growth in expanding patches also showed strong correlation with spring and summer warming, whereas alder growth in stable 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 moisture, less carbon in mineral soil, and lower C:N values in soils and shrub leaves. Expanding patches—higher resource environments—were associated with floodplains, stream corridors, and outcrops. Stable patches—lower resource environments—were associated with poorly drained tussock tundra. Collectively, we interpret these differences as implying that preexisting soil conditions predispose parts of the landscape to a rapid response to climate change, and we therefore expect shrub expansion to continue penetrating the landscape via dendritic floodplains, streams, and scattered rock outcrops.

Key words: Arctic Alaska; shrub; climate; dendrochronology; soil.

INTRODUCTION

The encroachment of shrubs into tundra landscapes is a prominent change linked to the warming Arctic climate. This shift toward a shrubbier arctic has been documented primarily using time-series photography (Sturm and others 2001; Tape and

others 2006), plot studies (Joly and others 2007), and satellite images (Myneni and others 1997; Jia and others 2003; Goetz and others 2005; Bhatt and others 2010). This vegetation shift appears to be associated with elevated temperatures during the twentieth century (Hinzman and others 2005). This causal relationship is based on (1) vegetation responses to plot-level temperature manipulations (Chapin and others 1995; Walker and others 2006), (2) correlations between summer air temperature and growth ring widths and shrub height (Walker 1987; Forbes and others 2010; Blok and others 2011), (3) the abundance of shrubs at lower arctic latitudes (Walker and others 2005), (4) the broad

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scale of the vegetation shift (Myneni and others 1997; Jia and others 2003; Goetz and others 2005; Ukraintseva 2008; Verbyla 2008; Bhatt and others 2010; Forbes and others 2010), and (5) the correlation between summer warming and Normalized Difference Vegetation Index (NDVI) values (Raynolds and others 2008). A shift toward a shrubbier arctic has profound implications, such as increasing drifted snow (Liston and others 2002), inducing positive feedbacks to warming due to the effects of taller shrubs decreasing albedo (Chapin and others 2005), increasing evapotranspiration (Swann and others 2010), and altering geomorphic processes such as drainage and erosion (Tape and others 2011). Increasing shrub dominance has the potential to release stored deep soil carbon through thawing and accelerated decomposition (Mack and others 2004; Schuur and others 2007). Shrub expansion is also reducing primary caribou forage through the loss of lichens (Joly and others 2007), meanwhile improving shrub forage availability for moose, ptarmigan, and hare (Tape and others 2010).

Shrub expansion is expected to be spatially and temporally variable. The spatial heterogeneity of greening, characterized by time-series satellite imagery, is primarily derived from satellites with coarser resolution sensors (>8-km pixels) that have high spatial coverage. At the largest scale, greening has occurred preferentially in the arctic tundra, while the boreal forest has been in decline, referred to as “browning” (Goetz and others 2005; Bunn and Goetz 2006). 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 and others 2005). In Arctic Alaska from 1982 to 2003, Global Inventory Modeling and Mapping Studies (GIMMS) 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 and others 2006).

Temporal series of coarse satellite imagery, though very convincing in its widespread coverage, understandably lacks information about heterogeneity of change within pixels. Though NDVI is strongly controlled by shrub biomass and leaf area (Jia and others 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 to

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 (for example, Landsat 30 m pixels) and fine-scale sensors (for example, Ikonos <1 m pixels) become available (Munger and others 2008), what is now sub-pixel variability will be resolved.

Repeat 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 “stable”) (Naito and Cairns 2011). We sought to compare expanding and stable 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 above adjacent expanding and stable shrub patches was presumably the same, differences in soil conditions between expanding and stable patches may explain the differing responses of shrubs observed in repeat photography. If present, diagnostic characteristics of expanding or stable soils and shrubs could 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 Arctic tundra along the Nimiuktuk River in the Brooks Range, and along the Colville and Sagavanirktok Rivers of the North Slope foothills (Figure 1). The shrub patches that are the focus of this study were located on slopes leading down to the river valley fills, and contained primarily 0.5–3-m tall 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 or near riparian areas (Schickhoff and others 2002; Selkowitz 2010; Beck and others 2011), and adjacent to rock outcrops. Such restricted distribution of shrubs in an otherwise tundra landscape causes tall shrubs to blend into larger pixels that are dominated by smaller or non-shrub tundra and thus to be overlooked in coarse vegetation maps, though approaches that use smaller- and nested-scale fractional cover mapping can detect shrubs (Selkowitz 2010; Beck and others 2011) and describe these

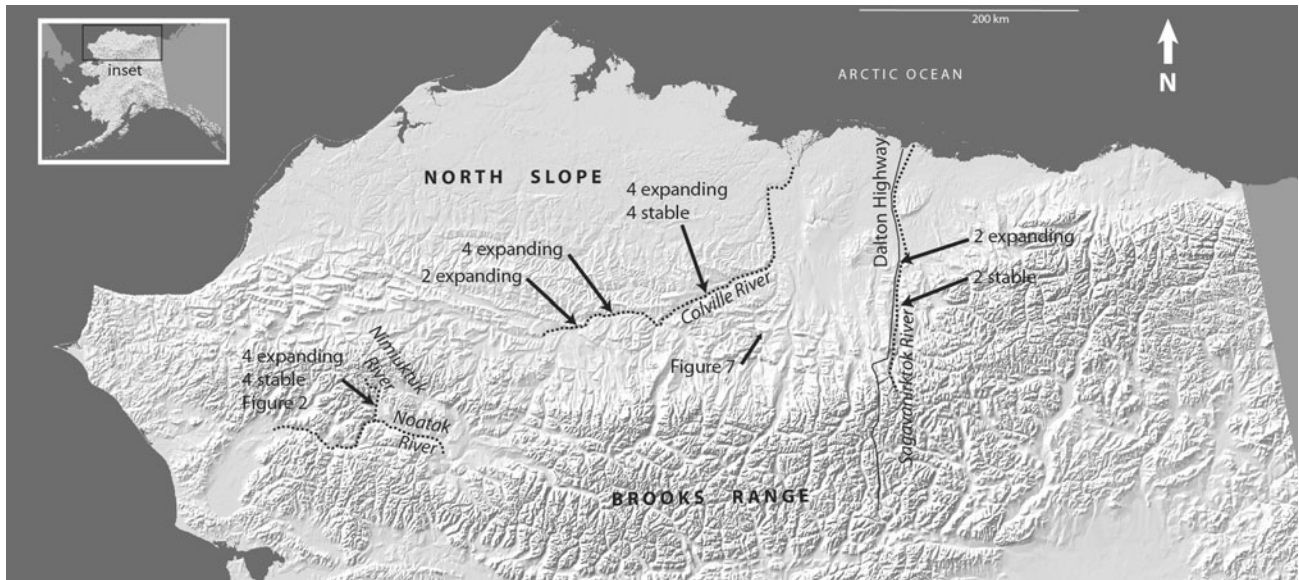


Figure 1. Study area and location of 26 shrub patches sampled, indicated as either expanding or stable (background relief: USGS).

communities as “riparian shrublands” (Walker and others 1994), “Upland Tall Alder Shrub” and “Upland Shrubby Tussock Tundra” (Jorgenson and Heiner 2003).

Sampling

Twenty-six transects were sampled where repeat photography showed shrub patches that were either expanding ($n = 16$) or stable ($n = 10$) (Tape and others 2006). The first four patches (2 E, 2 S) were along the Sagavanirktok River and were sampled in early August 2006. The next eight patches (4 E, 4 S) were located along the Nimiuktuk

River, a tributary of the Noatak River, and were sampled in June/July 2008. The last 14 patches (10 E, 4 S) were located along the Colville River and were sampled in July/August 2008 (Figure 1).

One 80-m transect was placed in each patch, and sampling intervals (hereafter “locations”) were established at 0, 20, 40, 60, and 80 m along each transect. Each location consisted of a 1×1 m quadrat nested within a 6×6 m location (Figure 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 (8.5 m) was run within the 6×6 m plot

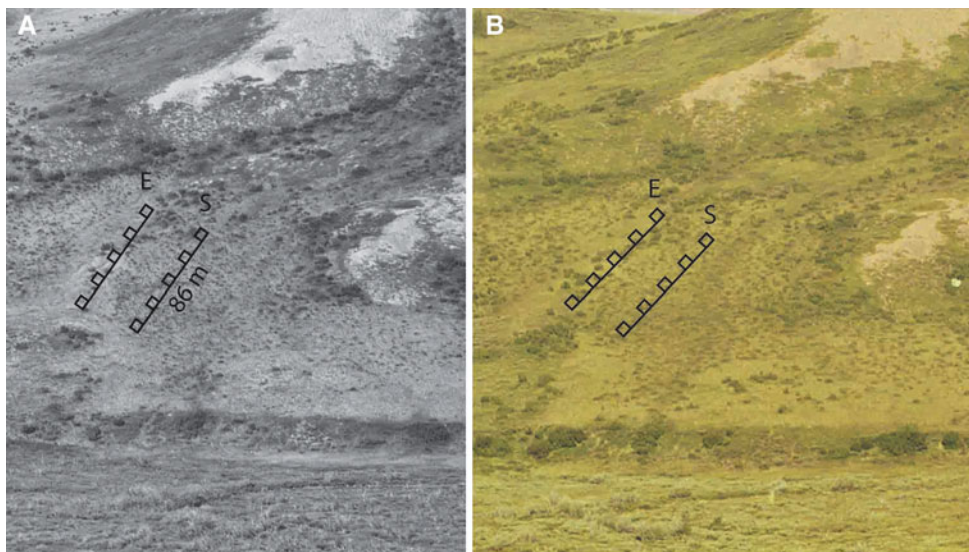


Figure 2. Placement of expanding (E) and stable (S) transects upon repeat photography (A 1950 and B 2002) from the Nimiuktuk River (Figure 1) (USGS/Navy, Ken Tape). Smaller boxes along the transects are 6×6 m plots (referred to as “locations” in the text), and not shown are the 1×1 m quadrats nested in each 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, with the depth of extraction being 70 cm, unless frozen ground or rocky substrate interfered. 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 three locations near the soil pit, using a Campbell Scientific Australia HydroSense™ device. Soil moisture in the top 10 cm was measured at three 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 three 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, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$ 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 %C and %N (Bran-Luebbe GmbH AutoAnalyzer 3, Nordestedt, Germany).

The largest alder stem at each of the five 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 stable) along the Nimiuktuk River, HOBO® Pendant Temperature/Light Data Loggers (#UA-002) were 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-h intervals from 7/1/2008 to 9/20/2010.

Repeat photography from 1948 and 2001 (Tape and others 2006) was used to delineate 10 polygons of rapidly expanding shrub patches and 10 polygons of slowly expanding or stable shrub patches (approximately 0.04 ha each) on SPOT satellite imagery (bands 2, 3, 4; 2.5 m pixel; July 12, 2008) along a 20-km stretch of the Chandler River, which flows into the Colville River. Using the spectral and textural pixel characteristics within the expanding and within the stable polygons, a supervised classification using ENVI software was applied to the SPOT image to depict landscape positions with pixel characteristics similar to either expanding or stable shrub polygons.

Shrub Ring Chronologies

Shrubs usually build one layer of wood each year, which appears in cross section as a distinct ring. These annual ring widths were measured along two radii (from the pith to the circumference) on the sanded and polished surface of each stem, and then averaged to create the “growth curve” for that stem. The growth curve from each stem was aligned with other growth curves within their corresponding expanding ($n = 59$) or stable ($n = 40$) category to eliminate errors from missing rings or false rings (cross dating). This 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. Growth curves with less than 20% correlation with their associated category mean ring width curve were removed, including 7 of 59 expanding and 10 of 40 stable shrubs.

Growth curves typically contained a trend of decreasing ring width values with increasing stem age and circumference (Fritts 1976), independent of climatic influences. This trend can be removed using a variety of approaches. Normally, a trend line (negative exponential, negative linear, and horizontal line regression) is fitted to each growth 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 (Cook and Peters 1997; Büntgen and others 2005; Büntgen and Schweingruber 2010; Hallinger and 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 and others 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 and others 1997).

Starting with the power transformation and ending with the standardized expanding and stable 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 stable 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), results presented here are from the RCS technique (Briffa and others 1992; Esper and others 2003; Büntgen and others 2005).

RCS aligns the individual ring width curves according to 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 stable 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 stable 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 stable RCS shrub ring chronologies was 0.76 and 0.57, respectively (Table 1). The expressed population signal (EPS), which is a combined measure of sample size and serial correlation that represents the common signal strength within a chronology, was greater than 0.85 after 1949 in the expanding chronology, and greater than 0.85 after 1971 in the stable chronology. EPS below 0.85 is thought to represent a strong signal strength among radial growth of woody plants within a chronology (Cook and Kairiukstis 1990). Every measured shrub disc is included in the raw ring width averages, whereas the expanding and stable group chronologies and associated climate relationships were calculated as soon as at least five individual shrub records were available per group ($E \geq 1939$, $S \geq 1953$).

Gridded climate data were obtained from the Climate Research Unit (CRU) in East Anglia, Great Britain (www.cru.uea.ac.uk), and were downscaled to 2-km pixels covering the study area by the Scenarios Network for Alaska Planning (www.sna-p.uaf.edu). To accomplish this, the finer-scale 2-km pixel Parameter-elevation Regressions on Independent Slopes Model (PRISM) mean monthly climate data were overlaid and combined with coarse-scale CRU gridded data. For simplicity, a single pixel in the center of the North Slope, containing four expanding and four stable patches, was selected for climate data from 1909 to present. The average correlation coefficients between annual growth increments and monthly climate data were calculated for the shrub chronologies for every year by applying a bootstrapped routine (Biondi and Waikul 2004).

Statistics

Transect was considered the sample unit when comparing site characteristics, and the distribution of each environmental variable within the expanding or stable category was tested for normality. In four cases (E and S mineral soil C, alder

Table 1. Comparison of Shrub Ring Chronologies Age-Detrended Using the RCS and NECS (Negative Exponential Curve Standardization) Methods

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

leaf %C and $\delta^{15}\text{N}$) 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 errors were calculated and *t* tests applied to determine significant differences between expanding and stable shrub patches. Paired *t* tests were used to compare temperature loggers deployed at the eight Nimiuktuk transects. When calculating mean thaw depth, 120 cm was assigned to locations where permafrost was greater than 120 cm (beyond the length of the probe) or rocks prohibited measurement. In all stable 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 \pm standard errors are reported.

Ordination

The species data from five 1 \times 1 m plots from each transect were averaged across five plots to produce one value per transect. The transect species data were imported into PC-Ord[®] software, where the non-metric 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 = $0.43 \pm 0.03 \text{ mm y}^{-1}$, stable = $0.19 \pm 0.02 \text{ mm y}^{-1}$; Figure 3) and are better correlated with temperature than shrubs in stable

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 4A). In contrast, the standardized chronology from the stable 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 4B). Stable 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.

Shrub ring records of the stable standardized chronology were less correlated with each other (Table 1) than were shrub ring records from the expanding population, indicating a weaker common (climate) signal in the stable shrub rings. The stable chronology was constructed without 25% (10 of 40) of the shrubs, which were eliminated based on their growth incoherence with the other stable shrubs, whereas only 12% (7 of 59) were eliminated to create the expanding chronology. The remaining expanding shrubs had higher serial correlation than stable shrubs (0.76 vs. 0.57), and a much earlier attainment of high chronology quality (1949 vs. 1971, EPS > 0.85; Table 1).

Both expanding and stable standardized chronologies contain opposing decadal-scale oscillations that seem to be associated with decadal temperature trends. Prior to 1976, when temperatures were cooler, the stable chronology increased significantly and the expanding chronology decreased significantly (both $P < 0.05$) (Figure 5C). Since that time, temperatures have been warmer, and the

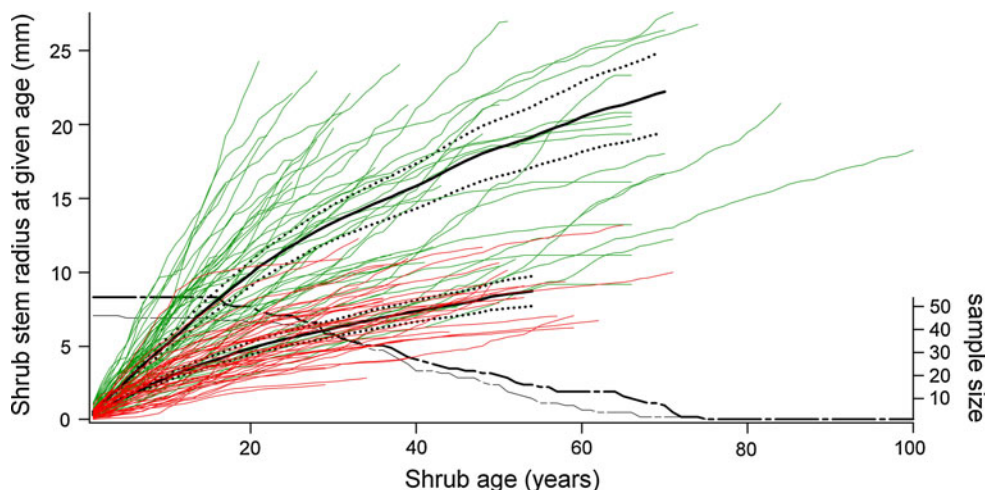


Figure 3. Individual (normal lines) and mean (bold lines) cumulative growth rates (dotted lines \pm SE) for expanding (green) and stable (red) alder stems, showing that expanding shrubs grew twice as fast as stable shrubs. In this graph, shrub growth rates are compared by aligning all shrubs starting at the age of 1. (Color figure online).

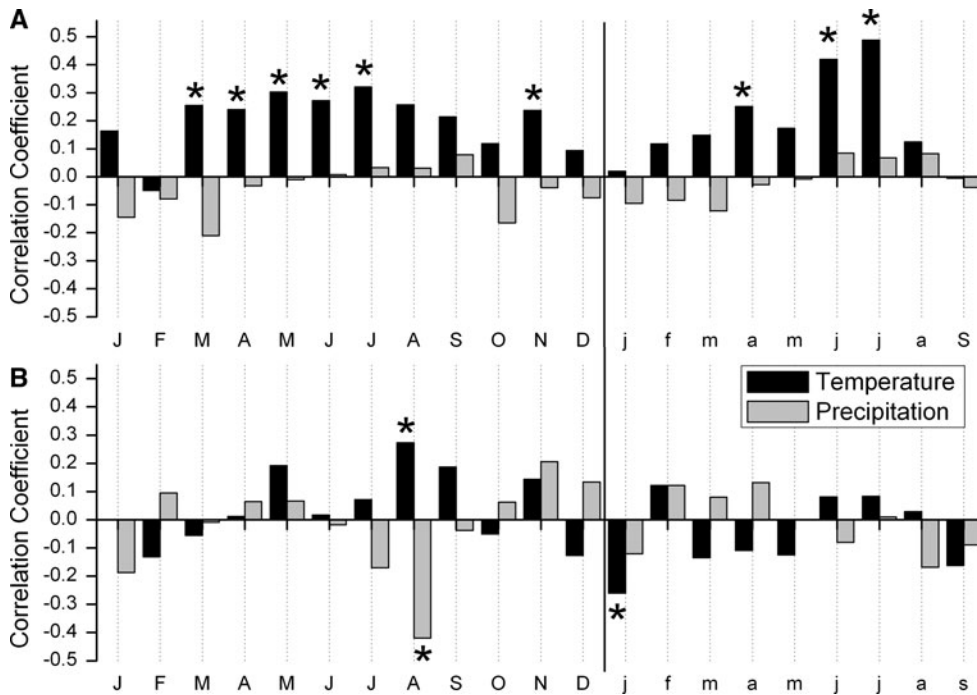


Figure 4. Correlation coefficients ($*P < 0.05$) between alder shrub chronologies and monthly average temperatures (black columns) or precipitation sums (gray columns) for **A** expanding shrub patches (1939–2008) and **B** stable shrub patches (1953–2008). Months of the prior growing season are displayed in capital letters, and months of the current growing season are displayed in lowercase letters.

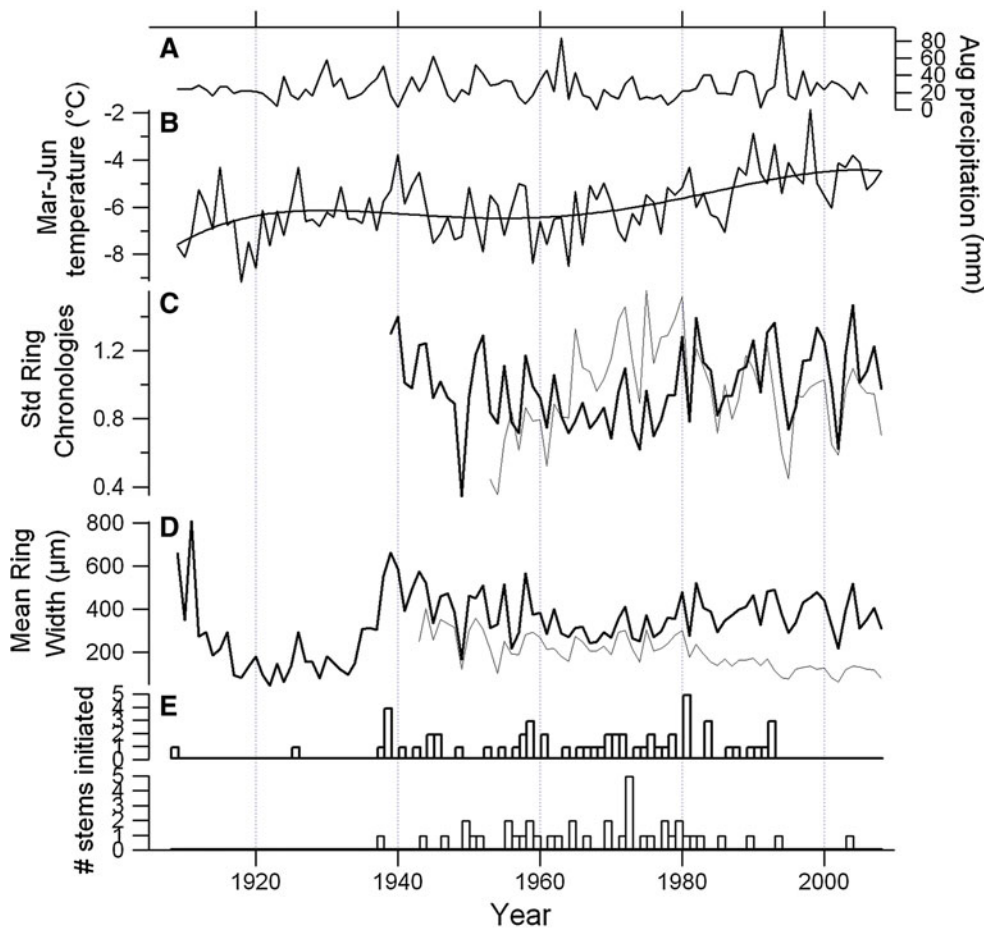


Figure 5. Expanding (bold line) and stable (normal line) alder shrub chronologies (c, d) and the significantly correlated climate variables (a, b) from Figure 4. The polynomial fit for temperature is to emphasize decadal and longer trends. (e) Population structure of sampled expanding (upper histogram) and stable (lower histogram) shrubs.

stable chronology has declined significantly ($P < 0.05$), whereas the expanding chronology has increased marginally ($P < 0.15$). The expanding and stable raw chronologies were similar prior to about 1980, after which time they abruptly diverge (Figure 5D).

Vegetation Composition

Ten consecutive iterations of NMS ordination showed clear differences between species composition and cover within stable and expanding shrub patches (Figure 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 2), which was most pronounced at the Nimiuktuk sites (Figure 6). Other cover categories—forbs, lichens, grasses, litter, moss, evergreen shrubs, soil, sphagnum, rock, and surface water—were similar in expanding and stable sites. Regional differences in flora were also evident along an east–west gradient, and showed a greater than 0.3

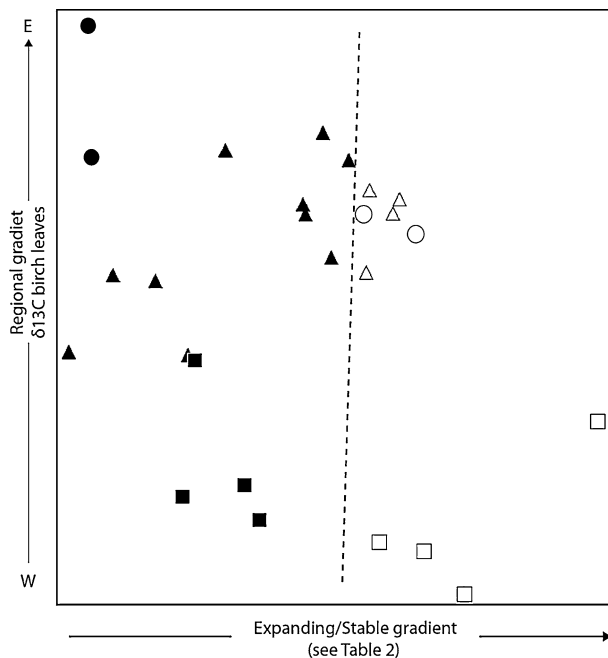


Figure 6. NMS ordination of floristic cover in 16 expanding (*filled*) and 10 stable (*open*) shrub patches. Distance in the ordination space is proportional to floristic difference, and the *dashed line* separates expanding from stable patches (*triangles* Colville River, *squares* Nimiuktuk River, *circles* Sagavanirktok River). The environmental variables correlated with the horizontal axis explain the floristic differences between expanding and stable patches, and are listed in Table 2.

Pearson correlation coefficient with $\delta^{13}\text{C}$ in birch leaves (Figure 6).

Soil Characteristics

Mineral and organic soils from expanding sites had significantly lower soil moisture than the same horizons from stable soils (Table 2). Soil temperature at 5-cm depth, averaged over the period from 7/1/2008 to 9/20/2010, was warmer in expanding shrub patches than in stable shrub patches ($P < 0.05$), contributing to significantly greater depth of thaw (Table 2). Above-zero temperatures were warmer in expanding patches than in stable patches ($P < 0.01$), whereas below-zero temperatures were not significantly different. Above-zero, below-zero, and annual average temperatures at 20 cm above ground were not significantly different between expanding and stable patches, though stable patches emerged from the snow 11 days earlier, on average ($P < 0.05$; Table 2).

Expanding shrub patches had higher soil organic bulk density than stable patches ($P < 0.05$), whereas the mineral layers had similar bulk density (Table 2). Carbon and nitrogen contents (%) of organic horizons did not differ between expanding and stable patches; however, both %C and %N were significantly greater for mineral soils from stable patches compared with those from expanding patches (both $P < 0.05$). Soils from expanding sites were less acidic than those from stable sites for both organic ($P < 0.05$) and mineral ($P < 0.05$) horizons, though this difference was driven by the six unpaired expanding sites along the upper Colville River (Figure 1).

Leaf Chemistry

Nitrogen content of birch leaves was significantly higher ($P < 0.05$) in expanding patches compared with stable patches; however, no differences in N content were found for either alder or willow between the patch types. Leaf carbon content was higher in stable 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 stable patches (Table 2). Willow leaves from expanding patches had marginally lower $\delta^{15}\text{N}$ values than corresponding leaves from stable patches ($P < 0.1$), whereas birch and alder leaves from the two patch types had similar $\delta^{15}\text{N}$ values. Alder leaves from expanding patches had significantly more depleted $\delta^{13}\text{C}$ values than stable alder leaves ($P < 0.05$), whereas birch and willow

Table 2. Vegetation and Soil Characteristics of Expanding (E) and Stable (S) Shrub Patches

	Expanding	Stable
<i>Soils</i>		
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) (<i>n</i> = 16 E, 10 S)	88 ± 7.8**	32 ± 3.6**
-5 cm ground temp (<i>n</i> = 4 E, 4 S)		
7/1/2008–9/20/2010 (°C)	-1.4 ± 0.4*	-3.0 ± 0.3*
>0°C (summer)	8.9 ± 1.8**	5.6 ± 1.6**
<0°C (winter)	-8.9 ± 1.2	-10.6 ± 0.7
+20 cm air temp (<i>n</i> = 4 E, 4 S)		
7/1/2008–9/20/2010 (°C)	-3.0 ± 0.2	-3.1 ± 0.3
>0°C (summer)	11.8 ± 0.8	12.6 ± 0.9
<0°C (winter)	-15.9 ± 0.6	-14.9 ± 1.0
Emergence of +20 cm light sensors from snow (<i>n</i> = 4 E, 4 S)	May 13th ± 3.1 days*	May 2nd ± 1.4 days*
Bulk density (g/cm ³)		
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*
% 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 [†]
<i>Leaf chemistry (within genus comparisons for birch and willow, species for alder)</i>		
% 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 [†]
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
<i>Growth form (% cover)</i>		
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**

Table 2. continued

	Expanding	Stable
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

* $P < 0.05$, ** $P < 0.01$, † $P < 0.1$.

Unless otherwise noted, the sample unit for statistical purposes is 14 expanding patches/transects and eight stable patches/transects, which are averages calculated from at least 15 samples per transect, depending on the parameter. Significant differences were calculated using the Student's t test, except for the ground temperature and light sensor measurements, which used the paired t test.

expanding patch leaves had similar $\delta^{13}\text{C}$ values to their corresponding stable patch leaves. Particularly in the case of willow, some caution is advised in interpreting the leaf chemistry results, because different species abundances and chemical signatures in expanding or stable patches could account for the observed differences between patches.

Shrub Distribution and Landscape Patterns

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 stable patches are smaller, prostrate, and more evenly distributed. None of the in situ parameters we measured captured the spatial distribution of indi-

vidual shrubs, but the difference in pixel spectral and textural characteristics between expanding and stable shrub patches was detectable using satellite imagery, and so is mentioned here.

Textures of expanding and stable shrub patches along the Chandler River (where SPOT imagery and repeat photography were both available) were scaled from repeat photographs to a satellite image by outlining polygons of expanding and stable 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, whereas stable patches occupied broader, less-sloping landscape positions (Figure 7). The results of the satellite image extrapolation highlight the landscape positions

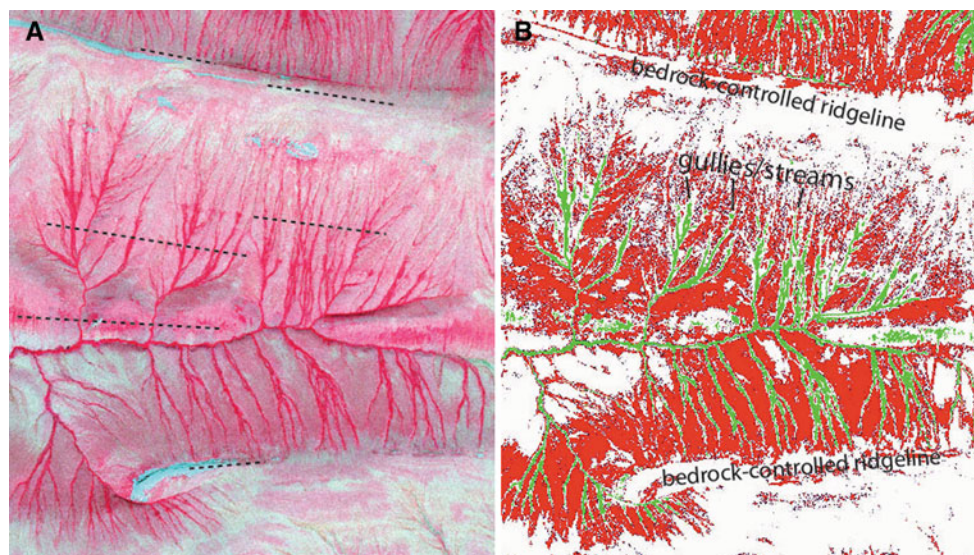


Figure 7. **A** Color-infrared SPOT image near the Chandler River showing pattern of tall shrub (dark red) distribution along streams and near-surface or outcropping sedimentary rock units (dashed lines). **B** Supervised classification of the SPOT image, showing expanding alder patches (green), stable alder patches (red), and short- or non-shrub tundra (white). Each image is 5.5-km wide, with a center point at 68.917°N, 151.765°E; north is up. (Color figure online).

associated with the suite of expanding and stable patch and site characteristics in Table 2.

DISCUSSION

Shrub Rings and Climate

Shrub ring width and summer temperatures are commonly correlated at northern high latitude and high elevation locations (Bar and others 2008; Forbes and others 2010; Hallinger and others 2010; Blok and others 2011). In this study, the summer growth–temperature correlations were only strong in expanding patches (Figure 4A); the shrub ring chronology from stable patches was uncorrelated with temperature (Figure 4B). Shallower thaw depth and cooler annual and summer soil temperatures in the stable patches (Table 2) suggest that the tussock tundra soils retard heat penetration and dampen the potential effect of warm summers on soil processes, such as microbial activity. Most of the width of the annual growth ring has been added by August (Blok and others 2011), so the negative correlation with previous August precipitation (Figure 4B) suggests that high soil moisture inhibits growth in tussock tundra shrubs. Because August precipitation has remained stable throughout the record (Figure 5A), and because the stable shrubs are unresponsive to air temperature (Figure 4B), the decline in the raw and standardized stable chronologies since the 1970s may instead be attributable to factors such as interspecific competition.

Positive correlations between March and April air temperatures and growth are particularly interesting because alder shrubs are not growing during those months, yet they are sensitive to climatic conditions during that period (Figure 4A). In shrub tundra within our study area the rapid increase in AVHRR-derived NDVI that is associated with leaf-out began in early May in the years 1995–1999 (Jia and others 2004), which is similar to the May 13th average snow-free date in the expanding patches. Most of the expanding shrubs sampled for shrub rings were greater than 2 m in height, so it is possible that taller shrubs protrude above the snow and that pre-snowmelt warm temperatures prime the forthcoming growth spurt. These pre-snowmelt temperature correlations may signify the earlier disappearance of snow since 1976, and its correlation with alder growth in this study.

The widespread expansion of shrubs in Arctic Alaska and nearby Arctic Canada has been shown using different time series imagery and methods (Tape and others 2006; Naito and Cairns 2011;

Lantz and others, unpublished), so we expected a strong positive trend in the standardized expanding chronology. However, the standardized chronologies ostensibly remove the effect of new or juvenile stems growing more rapidly, and therefore the standardized chronologies may not reflect shrub patch dynamics as well as the spatial metrics used to document shrub expansion. In this case, the expanding standardized chronology showed only a subtle increase ($P < 0.15$) since 1976 (Figure 5C), during a warm period when shrub expansion was observed regionally (Tape and others 2011).

The raw ring width measurements (Figure 5D) contain information about both stem growth rates and stem initiation. During the period when the expanding standardized chronology showed only a subtle increase (after 1976), the raw ring widths of expanding patches showed a clear divergence from the stable patches, due partly to the initiation of new stems ($n = 24$ E, $n = 12$ S; Figure 5E). Interpreting raw ring widths also has its hazards; in this case, the largest stems were cut from each plot, so the decline in the stable raw ring widths after 1980 is partly attributable to few stems being initiated to boost average ring widths during that period. Although the goal of standardized chronologies is typically to establish relationships between climate and stem growth, the raw ring widths can be more suggestive of shrub patch dynamics than standardized chronologies.

Soil Characteristics

Adjacent expanding and stable shrub patches presumably experienced the same above-canopy air temperatures, and similar lower-canopy annual and seasonal air temperatures were also recorded (Table 2). This suggests that the positive response of expanding shrubs, but not adjacent stable shrubs, to warm summers is mediated by soil conditions, including the layer of organic material or vegetation less than 20 cm. The warmer summer soil temperatures and deeper active layer in the expanding patches (Table 2) indicates that the ground thermal conductivity and summer ground heat flux is higher than in the stable patches. The strong negative correlation between preceding August precipitation and annual shrub growth in stable 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 and cold summer soil conditions in stable patches limits nutrient turnover and cycling rates. Warmer and drier soil conditions in expanding patches, along

with lower C:N ratios in the leaves (and, presumably, the litter) probably explain the marginally higher nutrient availability evident in lower C:N ratios of these soils ($P < 0.1$).

Shrub Distribution and Landscape Patterns

When stable patches were polygonized and extrapolated across the landscape using a supervised classification of high-resolution satellite images, the result was that these lower resource environments occupied flat, though not necessarily level, terrain (Figure 7). Regular spacing of alder shrubs, such as that evident in stable patches described here (Figure 2), suggests competition for limited resources (Rietkerk and van de Koppel 2008), as demonstrated by increased nutrient content in stems of neighboring alder shrubs when an individual alder shrub is removed (Chapin and others 1989). The low resource notion is corroborated by the stable patch 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, gullies, and outcrops. These generalizations are corroborated by the expanding shrub rings, which chronicle rapid growth that is responsive to spring and summer temperatures, and by other studies showing shrub expansion in this area occurring preferentially along drainage features (Naito and Cairns 2011). In some cases (for example, Figure 2), there is no topographic expression where shrubs are expanding, but the deeper active layer channelizes subsurface flow. Channelization of subsurface flow was also shown to improve nutrient cycling and productivity for *Eriophorum vaginatum* in smaller drainage features (Chapin and others 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, similar to this study (Table 2).

A number of studies have shown that NDVI is also increasing in many tussock tundra sites comparable to the stable sites described in this study (Goetz and others 2005; Munger and others 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 and others 2010), but could also be partially explained by increases in the abundance or productivity of

graminoids (Jia and others 2006; Munger and others 2008), which have out-paced changes in shrubs in some tussock tundra areas (Joly and others 2007). The so-called stable 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 and others 2007) or in response to nutrient addition (Chapin and others 1995; Gough and others 2002; Hobbie and others 2005). We speculate that in stable 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 thus may out-compete alder for soil nutrients. 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 limited response from (stable, tussock tundra) alder to warm summers.

CONCLUSION

This study presents localized environmental conditions, vegetation composition, plant ecophysiological traits, and growth metrics that differ between expanding and stable shrub patches. Because the air temperature is presumably the same in adjacent expanding and stable patches, the diagnostic characteristics of expanding shrub patches suggest that 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 soil conditions mediate the response of shrubs to increased air temperatures.

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