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Response of green alder (*Alnus viridis* subsp. *fruticosa*) patch dynamics and plant community composition to fire and regional temperature in north-western Canada

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ABSTRACT

Aim Feedbacks between climate warming and fire have the potential to alter Arctic and sub-Arctic vegetation. In this paper we assess the effects and interactions of temperature and wildfire on plant communities across the transition between the Arctic and sub-Arctic.

Location Mackenzie Delta region, Northwest Territories, Canada.

Methods We sampled air temperatures, green alder (*Alnus viridis* ssp. *fruticosa*) cover, growth, reproduction and age distributions, and overall plant community composition on burned and unburned sites across a latitudinal gradient.

Results Mean summer temperature across the study area decreased by 3 °C per degree of increasing latitude (6 °C across the study area). In the northern part of the study area, where seed viability was low, alder was less dominant than at southern sites where seed viability was high. The age structure of alder populations across the temperature gradient was highly variable, except in the northern part of the forest–tundra transition, where populations were dominated by young individuals. Alder growth and reproduction were significantly greater on burned sites (38–51 years following fire) than on unburned sites. North to south across the temperature gradient, vegetation changed from a community dominated by dwarf shrubs and fruticose lichens to one characterized by black spruce (*Picea mariana*), alder and willows (*Salix* spp.). Regardless of the position along the temperature gradient, burned sites were dominated by tall shrubs.

Main conclusions Temperature limitation of alder abundance and reproduction, combined with evidence of recent recruitment on unburned sites, indicates that alder is likely to respond to increased temperature. Elevated alder growth and reproduction on burned sites shows that wildfire also has an important influence on alder population dynamics. The magnitude of alder's response to fire, combined with observations that burns at the southern margin of the low Arctic are shrub dominated, suggest that increases in the frequency of wildfire have the potential to alter northern vegetation on decadal scales. By creating new seedbeds, fire provides opportunities for colonization that may facilitate the northward movement of tall shrubs. Feedbacks between the global climate system and low Arctic vegetation make understanding the long-term impact of increasing fire frequency critical to predicting the response of northern ecosystems to global change.

Keywords

Alnus viridis, climate change, climate feedbacks, disturbance, fire, forest tundra, global change, shrub encroachment, succession, tall shrubs.

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INTRODUCTION

There is growing evidence that tall shrubs are becoming a more dominant component of low Arctic ecosystems, but the mechanisms driving landscape-level shrub encroachment are not well understood (Silapaswan *et al.*, 2001; Sturm *et al.*, 2001; Jia *et al.*, 2003; Stow *et al.*, 2004; Tape *et al.*, 2006). Observed changes in shrub cover in the western Arctic may be linked to recent increases in temperature, which have been among the most rapid in the world (Hassol, 2004; Parry *et al.*, 2007). In high-latitude ecosystems, where growth and sexual reproduction in plants are limited by a short summer growing season, increases in temperature have the potential to favour many suppressed deciduous trees and tall shrubs by improving their growth and reproduction (Landhäusser & Wein, 1993; Hobbie & Chapin, 1998; Bret-Harte *et al.*, 2001; Meunier *et al.*, 2007). At fine scales, experimental evidence also shows that climate warming is likely to promote the growth of shrubs (Parsons *et al.*, 1994; Chapin *et al.*, 1995; Bret-Harte *et al.*, 2001, 2002; Walker *et al.*, 2006).

Across landscapes dominated by long-lived vegetation, the spread of tall shrubs may also be facilitated by wildfire (Bliss & Matveyeva, 1992; Landhäusser & Wein, 1993; Racine *et al.*, 2004). In tundra and forest tundra, fires expose new seedbeds, increase nutrient availability and create opportunities for the establishment of species in communities where recruitment is otherwise infrequent (Zasada *et al.*, 1983; Hobbie & Chapin, 1998; Gough, 2006). Models and empirical studies suggest that increases in the frequency of fire and other disturbances are likely to have greater consequences for the distribution and abundance of woody species than increased temperatures alone (Landhäusser & Wein, 1993; Bergeron *et al.*, 1998; Rupp *et al.*, 2000; Cullen *et al.*, 2001; Stow *et al.*, 2004; Lantz *et al.*, 2009). Evidence that fire frequency is increasing in response to climate warming (Gillett *et al.*, 2004; McCoy & Burn, 2005) makes understanding the independent and combined effects of fire and temperature on northern vegetation critical in predicting the rate and nature of vegetation change at high latitudes.

The overall goal of this research was to evaluate the independent and combined effects of temperature and fire on the upland vegetation of the low Arctic and sub-Arctic. Our sampling focused on plant community composition and populations of green alder (*Alnus viridis* subsp. *fruticosa* (Ruprecht) Nyman). We chose alder as a focal species because it is likely to respond to increasing temperatures and altered fire regimes. Alder is found across the Northern Hemisphere, and subspecies of *Alnus viridis* are common in many parts of the low Arctic and sub-Arctic (Furrow, 1979, 1997; Tolmachev *et al.*, 2000). In the North American Arctic and sub-Arctic, green alder is a particularly successful colonizer of newly exposed substrates and mineral soils (Gilbert & Payette, 1982; Matthews, 1992; Rhoades *et al.*, 2001). Green alder can also be abundant in undisturbed Arctic tundra, where its northern limit extends to within several kilometres of the Arctic Ocean (Gilbert & Payette, 1982; McLeod, 2001). Photographic evidence also shows that over the last 50 years alder cover

has increased on disturbed and undisturbed sites in Alaska (Tape *et al.*, 2006).

We examined variability in summer air temperature and its relationship to the dominance, seed viability and population age structure of alder across a latitudinal gradient extending from the sub-Arctic forest–tundra to the low Arctic (Fig. 1). We also examined alder cover, growth and reproduction, and plant community composition on burned and unburned sites in the central portion of this gradient. By sampling alder populations and plant community composition across a regional temperature gradient on burned (38–51 years ago) and unburned sites, we tested the hypothesis that fire has a larger relative influence on alder population dynamics and plant community composition than temperature alone. We expected that alder cover, growth and reproduction would be greater on burned sites than unburned sites, but would show little variation across the regional temperature gradient. We also expected that plant community composition would show greater differences between burned and unburned sites compared with differences between unburned sites across the temperature gradient.

MATERIALS AND METHODS

Study area

Our study area in north-western Canada covers approximately 25,000 km² of upland terrain east of the Mackenzie River Delta (Fig. 1). This landscape is characterized by low rolling hills (30–150 m) and thousands of small lakes (Mackay, 1963). Soils are primarily clayey silts underlain by continuous permafrost and fine-grained tills are ice rich (Mackay, 1963; Aylsworth *et al.*, 2000; Kokelj & Burn, 2004; Soil Landscapes of Canada Working Group, 2007).

The climate of this region is defined by long cold winters, with mean air temperatures of less than 0 °C from October to April. Previous studies in this region show a roughly linear decrease in summer temperatures with increasing latitude (Ritchie, 1984; Burn, 1997). Temperature decreases are paralleled by a shift from continuous forest, through forest tundra, to low Arctic tundra (Black & Bliss, 1980; Ritchie, 1984). Both white spruce (*Picea glauca* (Moench) Voss) and black spruce (*Picea mariana* (Mill) B.S.P.) are common in the southern part of our study area (Ritchie, 1984). Moving northwards, spruce woodlands give way to tundra characterized by a mix of ericaceous shrubs (*Ledum decumbens* (Ait) Lodd., *Vaccinium* spp. and *Arctostaphylos* spp.), willows (*Salix* spp.), green alder and dwarf birch (*Betula glandulosa* Michx.). At the northern end of our study area, vegetation becomes increasingly dominated by sedges (*Carex* spp. and *Eriophorum* spp.) and ericaceous shrubs (Lantz *et al.*, 2010).

Field sampling

To confirm regional temperature differences we installed thermistors at 10 sites across the study area (Fig. 1).

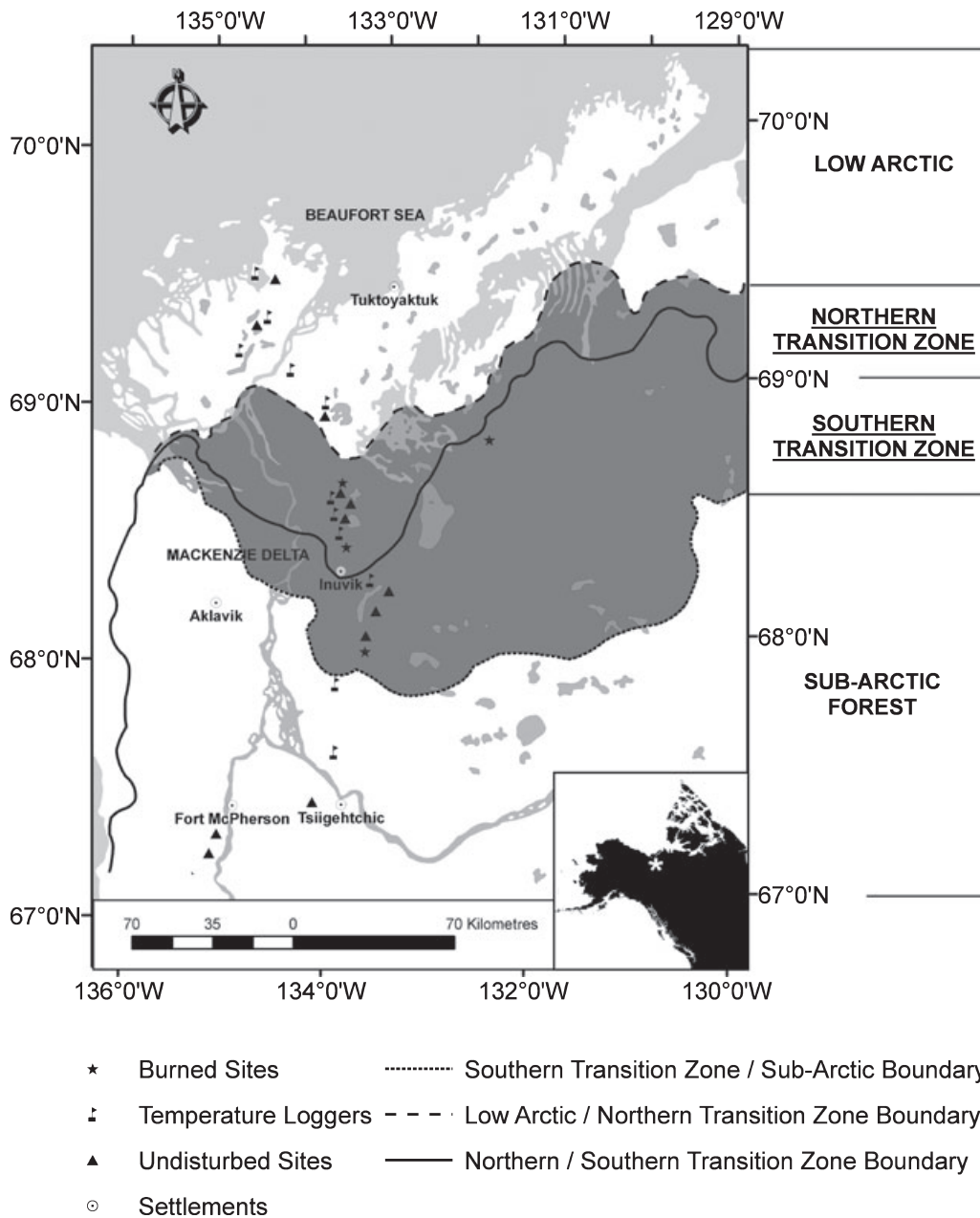


Figure 1 Map of the study region in north-western Canada, showing water (pale grey), settlements, burned and unburned study sites, temperature loggers and the boundaries of the vegetation zones *sensu* Timoney *et al.* (1992). The intensively sampled portion of the study area (the northern and southern transition zones) is shaded darker grey. The inset map at the bottom right shows the position of the study area in North America.

Thermistors attached to data loggers were placed in radiation shields mounted 1.5 m above the ground surface and temperatures were recorded every hour from June to August 2005 (HOBO®, H08-030-08, RS1; Onset Computer Corporation, Pocasset, MA, USA).

In the summers of 2004 and 2005 we sampled alder cover, growth and reproduction and plant community composition on burned and unburned sites. Our study area extended from the northern limit of the boreal forest into the southern portion of the low Arctic. Study sites were grouped a priori using vegetation zones defined by Timoney *et al.* (1992). These

zones included: (1) sub-Arctic forest (tree:upland tundra cover (t:utc) > 1000:1), (2) southern forest–tundra transition zone (t:utc > 1:1), (3) northern forest–tundra transition zone (t:utc < 1:1), and (4) low Arctic (t:utc < 1:1000). The majority of our sampling was conducted in the northern and southern forest–tundra transition zones in the central part of this region. In each of these zones we selected two burned and three unburned sites and established two to five transects at each site. In order to describe sites where the vegetation had recovered post-fire, we selected fires initiated between 1954 and 1968 (38–51 years ago) (Wein, 1975). We also established

two to four transects at three unburned sites within both the sub-Arctic and low Arctic zones (Fig. 1). Unburned sites showed no visible evidence of recent fire, but have probably all burned within the last 100–1000 years. Estimates suggest that the fire return interval in the southern transition zone ranges between 80 and 200 years, but is considerably longer in the northern transition. Data from the study area are limited, but estimates of fire return interval from ecosystems analogous to the northern transition zone range from 180 to 1500 years (Rowe *et al.*, 1974; Racine *et al.*, 1985; Payette *et al.*, 1989; Murphy & Witten, 2006). All transects were placed within homogeneous terrain and topography by establishing a 200-m line transect along a random azimuth.

At each transect in the southern and northern transition zones we collected community composition data at 10 points randomly selected at distances along each transect. For each vegetation stratum we estimated percentage cover inside a quadrat centred on these points. Cover of trees was estimated using 100-m² quadrats ($n = 10$ per transect), tall shrubs using 5-m² quadrats ($n = 10$ per transect) and low shrubs, dwarf shrubs, herbs and moss using 0.05-m² quadrats ($n = 10$ per transect). Individual estimates were made for most species, but the cover of the following groups was estimated together [grasses (Poaceae), sedges (Cyperaceae), mosses, liverworts and lichens]. Nomenclature for vascular plants follows Porsild & Cody (1980) and Catling *et al.* (2005).

On unburned sites across the entire study area, and burned sites in the southern and northern transition zones, we also measured alder growth and reproduction along transects. The alders we measured were selected by randomly choosing up to three shrub quadrats (5 m²) per transect where alder cover was > 0%. In all shrub quadrats we excavated and mapped all stems that were rooted within the quadrat and obtained stem cross-sections at the top of the root collar. We dried, sanded and used a dissecting microscope to record stem ages. The ages of alder seedlings were estimated by examining stem thin sections using a compound microscope. Between the 27th and 30th of August 2005 we also obtained catkin samples from a number of individuals within burned sites and unburned sites in each vegetation zone. Catkins used to test seed viability were air dried at room temperature until they released their seeds. Subsequently these seeds were used in germination trials where lots of 100 seeds were placed on moist filter paper in Petri dishes. Dishes were kept moist at 21 °C under 12 h of full-spectrum light per day for 3 weeks and germinants were counted and removed every 3 days.

The following alder response variables were compared among burned and unburned sites in the northern and southern transition zones: (1) alder cover (%), (2) vertical growth (stem height/stem age), (3) radial growth (stem basal diameter/stem age), (4) catkins m⁻², (5) seed viability (number of germinants/total number of seeds × 100), and (6) abundance of recruits (percentage of stems < 5 years old per quadrat). On unburned sites across the entire study area we compared alder dominance (number of quadrats per transect

with alder), percentage seed viability and population age structure.

Statistical analysis

Alder and regional temperature

To explore the relationship between mean summer temperature and latitude we used linear regression analysis. Given the strength of the linear relationship between air temperature and latitude across the study area (Fig. 2; $F_{1,8} = 293$, $r^2 = 0.9734$, $P < 0.001$) we used this regression to interpolate the mean summer temperature at sample sites located between our temperature loggers. Subsequently, we used these collected and interpolated data points as independent variables in regression models. We compared linear and nonlinear models of the dominance (number of quadrats per transect with alder) and seed viability of alder using Akaike's information criterion (AIC), AIC weights and r^2 values (Anderson *et al.*, 2000; R Development Core Team, 2006). We also examined residual plots to ensure that models met the assumptions of equal variance and normality. To contrast alder population age structure across the study area and to test for deviations from static age structures that have been described in other species (Hett & Loucks, 1976; Payette *et al.*, 1990; Szeicz & MacDonald, 1995) we fitted negative exponential models to 10-year age class frequency distributions. These simple models ($y = y_i e^{-bx}$) assumed that the number of individuals of a given age (y) is a function of age (x), a constant recruitment rate (y_i) and fixed mortality rate (b) (Hett & Loucks, 1976).

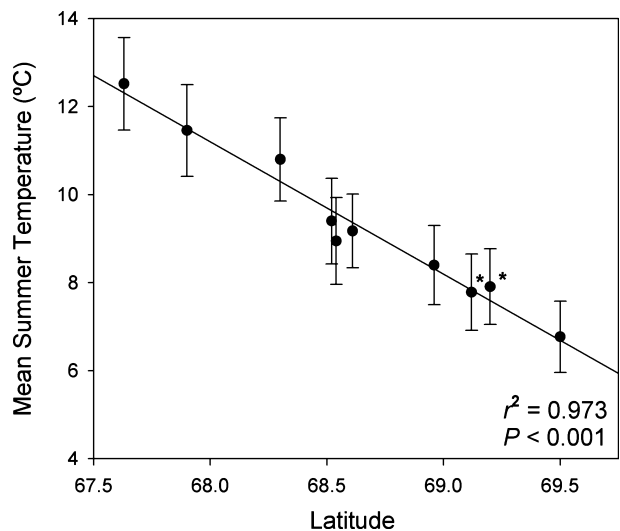


Figure 2 Regression of mean growing season temperature and latitude for 10 sites in the Mackenzie Delta uplands, June–August 2005 ($r^2 = 0.973$, $P < 0.001$, $y = 219.4 - 3.06x$). Error bars are 95% confidence intervals of the mean. Data marked with asterisks (69°30' N, 133°34' W and 69°11' N, 134°42' W) were provided by Dr Chris Burn (Carleton University, Ottawa).

Impact of fire and regional temperature on alder

To test for significant differences and interactions among vegetation zones and fire history in the central portion of the study area, we used linear mixed effects models (PROC MIXED; SAS, 2004). This technique uses restricted maximum likelihood to estimate variance components with both fixed and random effects and is particularly useful for unbalanced and spatially nested datasets (Buckley *et al.*, 2003; Littell, 2006). In our models we treated vegetation zones and fire history as fixed effects. We also included spatial covariance in our models by incorporating: (1) sites, (2) transects (within sites), and (3) quadrats (within transects) as random effects. In all of our models we assumed a simple covariance structure by using the variance components option for random effects. To assess the importance of random factors in our model we tested their significance by removing terms one at a time and comparing the difference between the log likelihoods of the reduced and complete models using a chi-square test (Morrell, 1998). Individual transects were the only random factor that had a significant effect on our models, and all analyses presented here include transects as the only random factor. To estimate the error degrees of freedom for all *F*-tests of fixed effects we used the Kenward–Roger approximation (SAS, 2004). To meet the assumptions of normality and equal variance, the following response variables were log transformed: alder cover, vertical growth, radial growth, catkins m^{-2} and seed viability.

Impact of fire and regional temperature on plant community composition

To explore differences in plant community composition at burned and unburned sites across the northern and southern transition zones we used PRIMER to perform a non-metric multi-dimensional scaling (NMDS) ordination of a Bray–Curtis distance matrix calculated from percentage cover data (Clarke & Gorley, 2001). We set PRIMER to repeat this analysis 20 times and selected the best two-dimensional representation of the original distance matrix (i.e. the least stress) (Legendre & Legendre, 1998). To reduce noise and stress we $\log(1 + x)$ -transformed percentage cover data. Subsequently, we used analysis of similarities (ANOSIM) to test the null hypothesis that species composition did not differ among burned and unburned sites in each vegetation zone. ANOSIM is roughly analogous to a one-way ANOVA and uses ranked Bray–Curtis dissimilarities to test for significant differences in species composition between groups (Legendre & Legendre, 1998). The R_{ANOSIM} statistic ranges from 0 to 1 and expresses the similarity between groups (Clarke & Gorley, 2001). The significance of the R_{ANOSIM} statistic was calculated by performing 9999 randomizations of the original data. To identify the species making the largest contribution to differences among burned and unburned sites in each vegetation zone, we used the SIMPER function in PRIMER to calculate the percentage contribution of each species and

species group to the Bray–Curtis dissimilarities among site types (combinations of fire history and vegetation zone) (Clarke & Gorley, 2001).

RESULTS

Regional temperature

Moving south to north across our study area in 2005 the average June–August temperature decreased from a mean of 12.5 °C at 67°37' N to a mean of 6.8 °C at 69°30' N. This represents a decrease in mean temperature of approximately 3 °C per degree of latitude, or 6 °C across the entire study area (Fig. 2). Within the intensively sampled northern and southern transition zones, the mean temperature changed by approximately 3 °C. Environment Canada temperature records from 1970 to 2005 showed that summer temperatures in the more northerly community of Tuktoyaktuk (68°18' N, 133°28' W) were 3.3 °C colder than Inuvik (SD = 0.4), and

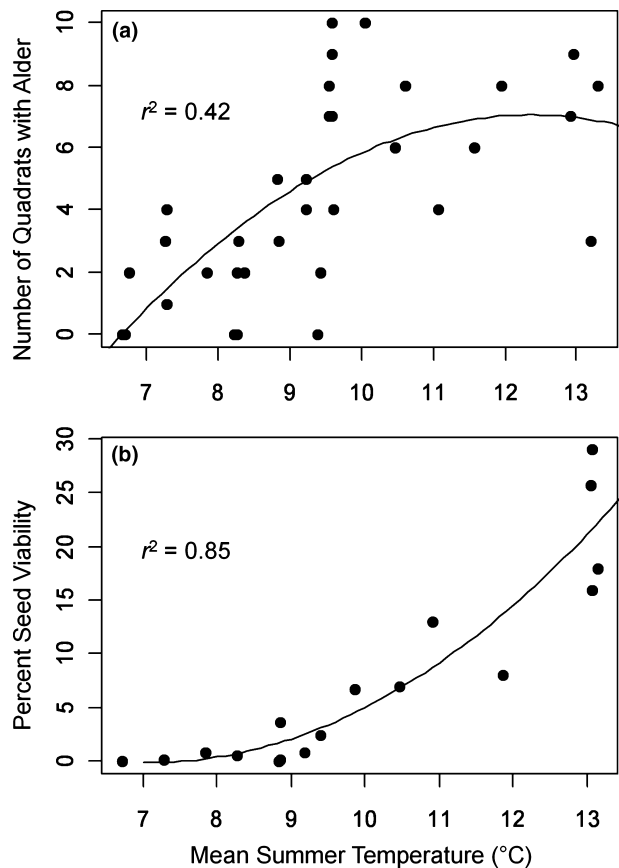


Figure 3 Alder (*Alnus viridis* subsp. *fruticosa*) characteristics measured on unburned sites across the entire study area in the Mackenzie Delta uplands. (a) Number of quadrats per transect with alder present versus average summer temperature ($F_{2,31} = 13.16$, $P < 0.001$, $r^2 = 0.42$, $n = 32$). (b) Percentage seed viability versus average summer temperature ($F_{2,14} = 44.62$, $P < 0.001$, $r^2 = 0.85$, $n = 16$).

4.6 °C (SD = 1.5) degrees colder than Fort Macpherson (67°24' N, 134°51' W) (Environment Canada, 2006). Thus the summer temperature gradient we observed was not unique to 2005.

Green alder

On unburned sites across the entire study area, alder dominance and seed viability decreased with lower summer temperatures at more northerly sites. The best model of alder dominance versus mean growing season temperature was nonlinear. This model predicts a decline in the presence of alder with reduced summer temperatures in the northern part of the study area but little change in the southern part of the study area (Fig. 3a). Seed viability also declined with lower temperatures at more southerly latitudes and the best model describing this change was also nonlinear (Fig. 3b).

The age structures of alder populations across the temperature gradient were highly variable. Uneven age distributions in the low Arctic, southern transition zone and sub-Arctic were predominantly unimodal, but varied from symmetric to positive or negatively skewed. None of these age structures could be described using a negative exponential model. In the northern transition zone, highly skewed age distributions were dominated by stems in the youngest age classes (Fig. 4). Negative exponential models of population age structures in the northern transition zone had r^2 values ranging from 0.18 to 0.56, but were all statistically significant (Fig. 4). Populations were also generally smaller in the low Arctic and the sub-Arctic forest than in the northern and southern transition zones.

Alder cover, growth, catkin production and seed viability were significantly greater on burned sites than on unburned sites (Fig. 5). Except for the percentage of recruits/quadrat, differences between burns and controls within a zone were consistently greater than differences among controls across the

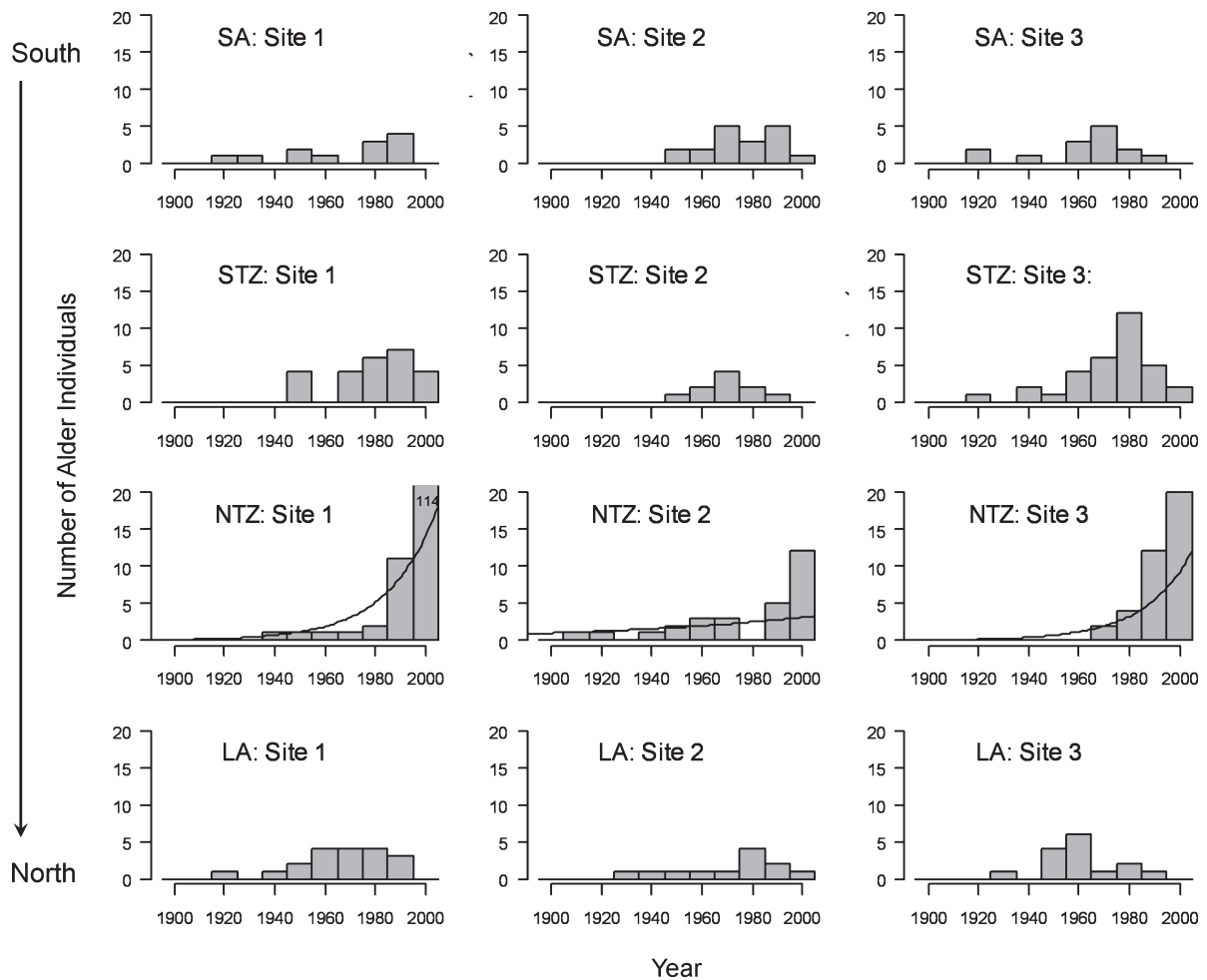


Figure 4 Alder (*Alnus viridis* subsp. *fruticosa*) age distributions on unburned sites across the study area in the Mackenzie Delta uplands. Histograms show the number of individuals by 10-year age class in 12 populations (three from each vegetation zone). Rows of histograms are arranged by vegetation zone from south to north. Vegetation zones are abbreviated as follows: SA, sub-Arctic; STZ, southern transition zone; NTZ, northern transition zone; LA, low Arctic. Statistically significant negative exponential models are plotted as solid lines (NTZ, Site 1: $F_{2,12} = 5.03$, $P < 0.05$, $r^2 = 0.18$, $n = 16$; NTZ, Site 2: $F_{2,12} = 17.73$, $P < 0.01$, $r^2 = 0.56$; NTZ, Site 3: $F_{2,12} = 5.02$, $P < 0.05$, $r^2 = 0.18$).

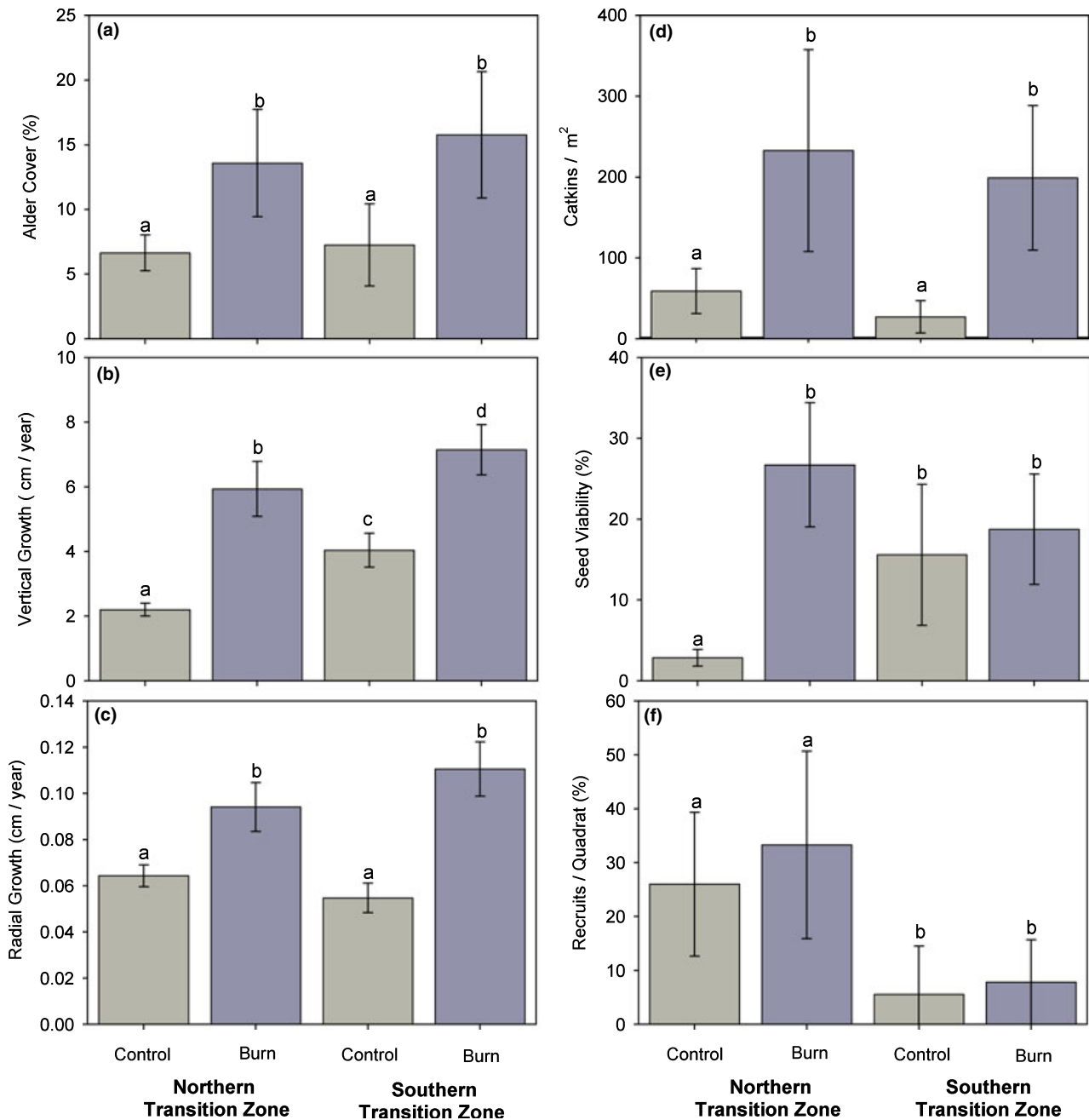


Figure 5 Alder (*Alnus viridis* subsp. *fruticosa*) characteristics measured on unburned controls (light grey bars) and burned sites (dark grey bars) across the northern and southern transition zone in the Mackenzie Delta uplands. Response variables include: (a) percentage alder cover within shrub quadrats, (b) vertical growth, (c) radial growth, (d) catkin production, (e) percentage seed viability, (f) percentage recruits. Bars represent mean for each treatment and error bars are 95% confidence intervals of the mean (untransformed). Bars sharing the same letter are not significantly different ($P \leq 0.05$, mixed model ANOVA and Tukey's adjusted least significant difference).

regional temperature gradient. Seed viability, vertical growth and the percentage of recruits were the only variables that differed between controls across the regional temperature gradient (Fig. 5). Both seed viability and vertical growth were higher on controls in the southern transition zone than in the northern transition zone (Fig. 5d,b). Conversely, the percentage of alder recruits was significantly higher on controls in the northern transition zone than in sites in the southern

transition zone (Fig. 5f). The percentage of recruits was also greater on northern than southern burns (Fig. 5f).

Plant community composition

Plant community composition on unburned sites changed significantly with latitude (Fig. 6, Tables 1 & 2). In the southern transition zone, unburned sites were characterized

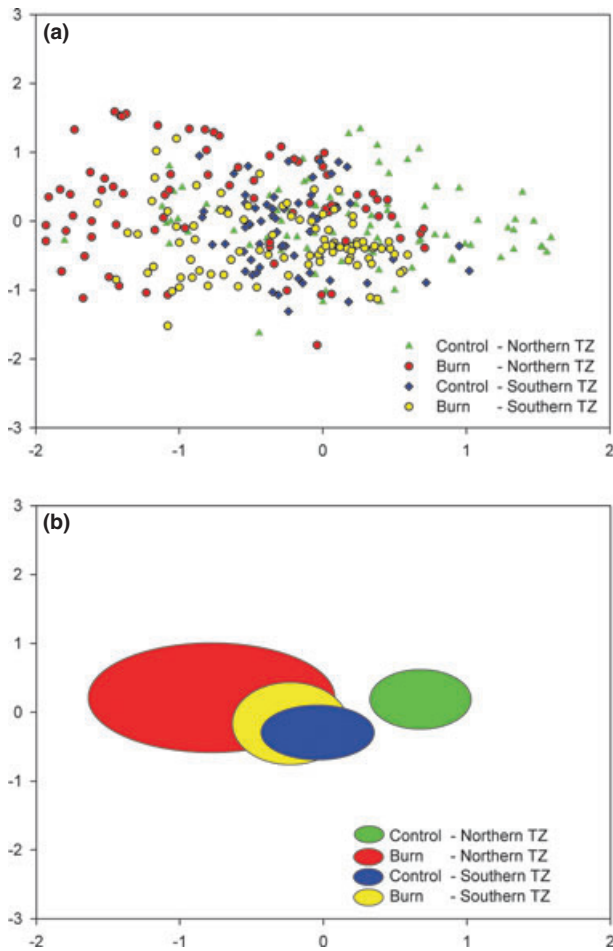


Figure 6 Non-metric multi-dimensional scaling (N-MDS) ordination of plant community composition based on Bray–Curtis distance. The figure shows the two-dimensional solution exhibiting the least stress (0.23). The symbols plotted in (a) are the NMDS scores for quadrats within each site type. Site types include burned (Burn) and unburned (Control) areas of the southern and northern transition zones (abbreviated as TZ). The ellipses plotted in (b) are defined using the mean NMDS scores (x and y) for each treatment \pm standard deviation. Pairwise comparisons of site types using the analysis of similarity (ANOSIM) procedure show significant differences among site types (Table 1).

by an abundance of black spruce, alder and willows (*Salix glauca* L. and *Salix pulchra* Cham.), cranberry (*Vaccinium vitis-idaea* L.) and mosses. Unburned sites in the northern transition zone were characterized by an abundance of northern Labrador tea (*Ledum decumbens*), dwarf birch (*Betula glandulosa*) and fruticose lichens (Table 2e).

Plant community composition 38–51 years following fire was similar, regardless of regional temperature (Fig. 6, Table 1), and burned sites in the southern transition zone were characterized by a similar suite of species as southern controls. These sites all shared an abundance of alder and diamondleaf willow (*Salix pulchra* Cham.) (Table 2f). Pairwise comparisons between burned and control sites in the southern transition zone and burned sites in the northern transition

Table 1 Pairwise comparisons of plant community composition between site types in the Mackenzie Delta uplands using the analysis of similarity (ANOSIM) procedure.

	Northern transition zone		Southern transition zone	
	Burn	Control	Burn	Control
Southern transition zone				
Control	0.25	0.56	0.22	
Burn	0.23	0.47		
Northern transition zone				
Control	0.58			
Burn				

Comparisons are based on a Bray–Curtis distance matrix. Values of $R_{ANOSIM} > 0.75$ indicate that site types are well separated, values between 0.5 and 0.75 describe overlapping but distinguishable groups, and values < 0.25 are characteristic of groups that can barely be separated. $P < 0.001$ for all comparisons.

zone using the ANOSIM procedure all generated R_{ANOSIM} statistics of ≤ 0.25 (Table 1). These differences are also reflected in the NMDS ordination of sites, which shows that unburned sites in the northern transition zone are overlapping but clearly separable from the other site types, while all other site types overlap considerably (Fig. 6).

Burned sites in the northern transition zone had significantly different species compositions from unburned sites (Fig. 6, Table 1, $R_{ANOSIM} = 0.58$). This difference was driven primarily by an abundance of alder and diamondleaf willow on burned sites. On unburned sites in the northern transition zone, willow and alder were less abundant, and dwarf birch (*Betula glandulosa*), fruticose lichens and northern Labrador tea (*Ledum decumbens*) generally dominated (Table 2a).

DISCUSSION

Regional temperature and alder population dynamics

Concurrent decreases in alder dominance and seed viability at northern sites suggest that low growing season temperatures influence the abundance of alder by limiting the availability of viable seed. Alder age structure data indicate that recent recruitment on unburned sites has been infrequent in populations in the low Arctic, southern transition and sub-Arctic zones. In 2005 most alder populations in the low Arctic produced little or no viable seed, suggesting that at the northern edge of its range alder recruitment is limited by temperature. Low alder dominance in the low Arctic indicates that the small populations in this part of the study area probably originated in warm years when conditions for seed production, germination and survival were favourable (Gilbert & Payette, 1982).

This conclusion is consistent with observational evidence showing that low temperatures limit reproduction in many

Table 2 Results of the SIMPER analysis of plant community composition for site types in the Mackenzie Delta uplands.

Species or species group	Log (% cover) site type 1	Log (% cover) site type 2	Dissimilarity (%)	Cumulative dissimilarity (%)
(a) Control (northern TZ) and burn (northern TZ)				
Fruticose lichens	0.85	0.08	8.78	8.78
<i>Betula glandulosa</i>	0.94	0.45	8.73	17.51
<i>Alnus viridis</i>	0.36	0.84	8.07	25.58
<i>Salix pulchra</i>	0.08	0.74	7.77	33.35
<i>Ledum decumbens</i>	0.89	0.60	7.63	40.98
(b) Burn (northern TZ) and control (southern TZ)				
<i>Picea mariana</i>	0.01	0.9	9.5	9.5
Mosses	0.26	0.93	9.09	18.59
<i>Alnus viridis</i>	0.84	0.56	7.84	26.43
<i>Salix pulchra</i>	0.74	0.53	6.8	33.23
<i>Vaccinium vitis-idaea</i>	0.6	0.75	6.73	39.96
(c) Burn (northern TZ) and burn (southern TZ)				
<i>Betula glandulosa</i>	0.45	1.19	11.58	11.58
<i>Alnus viridis</i>	0.84	0.47	9.53	21.11
<i>Vaccinium vitis-idaea</i>	0.6	0.72	8.49	29.6
<i>Salix pulchra</i>	0.74	0.89	8.18	37.78
Moss	0.26	0.69	7.75	45.53
(d) Control (northern TZ) and burn (southern TZ)				
<i>Salix alaxensis</i>	0.08	0.89	9.71	9.71
Fruticose lichens	0.85	0.26	8.7	18.41
<i>Betula glandulosa</i>	0.94	1.19	8.03	26.44
<i>Vaccinium vitis-idaea</i>	0.89	0.72	7.69	34.13
Mosses	0.53	0.69	7.19	41.32
(e) Control (northern TZ) and control (southern TZ)				
<i>Picea mariana</i>	0.01	0.9	9.72	9.72
Fruticose lichens	0.85	0.52	8.63	18.35
Mosses	0.53	0.93	8.16	26.51
<i>Betula glandulosa</i>	0.94	0.49	7.12	33.63
<i>Alnus viridis</i>	0.36	0.56	6.09	39.72
(f) Burn (southern TZ) and control (southern TZ)				
<i>Betula glandulosa</i>	1.19	0.49	10.26	10.26
Mosses	0.69	0.93	9.03	19.29
<i>Picea mariana</i>	0.36	0.9	8.9	28.19
<i>Alnus viridis</i>	0.47	0.56	7.57	35.76
<i>Salix pulchra</i>	0.89	0.53	7.11	42.87

The table shows the top five species (or species groups) that make the greatest contribution to the between-group Bray–Curtis dissimilarity for each pairwise comparison. The mean cover (log transformed) of each species at the site types being compared is shown in the second and third columns. TZ, transition zone.

trees and shrubs at high latitudes. In black spruce (*Picea mariana*), white spruce (*Picea glauca*) and larch (*Larix laricina* (Du Roi) Koch) both seed production and viability decline with reduced temperature near their northern limits, where populations often persist through vegetative growth (Elliott, 1979; Black & Bliss, 1980; Sirois, 2000; McLeod, 2001; Meunier *et al.*, 2007). Observations of low pollen or seed viability in populations of dwarf birch (*Betula glandulosa*), willows (*Salix* spp.) and alder near their range limits suggest that temperature limitation of reproduction and high mortality of recruits may determine the northern extent of many shrubs in the low Arctic (Weis & Hermanutz, 1993; Hobbie & Chapin, 1998).

In the southern transition zone and the sub-Arctic forest, where temperatures do not limit seed viability, small popula-

tions with infrequent recruitment are probably limited by factors other than temperature. A decrease in the number of alder recruits on warmer southern sites suggests that site-specific factors (e.g. competition with spruce, birch and poplar, and lower microsite and nutrient availability) may be more important than temperature. Experimental evidence from other workers shows that competition and substrate and nutrient availability can limit recruitment in spite of the presence of viable seed (Hobbie & Chapin, 1998). It is likely that reduced alder recruitment on burned sites in the southern transition zone was caused by a lack of suitable microsites and competition with spruce and other woodland species. Elevated vertical growth of alder on controls in the southern transition zone is also indicative of higher competition for light than at

northern sites. Studies by Johnstone & Kasischke (2005) and Johnstone & Chapin (2006) have shown that lower-severity fires with thicker post-fire organic layers can also limit recruitment in small-seeded deciduous species. It is possible that residual organics at southern sites were an important factor limiting recent alder recruitment.

Alder recruitment and regional warming

Temperature limitation in northern alder populations raises the possibility that recent warming (Lantz & Kokelj, 2008) has altered the population dynamics of this species. Populations sampled in the northern transition zone showed high levels of recruitment and were dominated by stems originating in the last two decades. Age distributions in these populations showed a good fit with negative exponential models, indicating that alder recruitment was higher in the northern transition zone than anywhere else in the study area. While it is possible that higher recruitment in these populations was driven by conditions favouring greater survival at these sites, we hypothesize that differences in static age distributions reflect a recent response to changes in summer conditions.

Summer temperatures in the Mackenzie Delta region have increased by more than 2 °C over the period of record (Environment Canada, 2005; Lantz & Kokelj, 2008). Using historical temperature averages and the regression shown in Fig. 3(b) to estimate potential changes in seed viability suggests that the probability of successful germination may have increased by approximately 7% in the northern transition zone. This probable increase in seed viability offers a reasonable explanation for the high proportion of alder recruits in the northern transition zone, and suggests that future warming will continue to facilitate the expansion of alder in the Arctic. In northern Quebec, Gilbert & Payette (1982) attributed expansion of the alder population in the early 19th century to changes in seed germination caused by climate warming during that period. Recent changes in recruitment are also consistent with observations of increased shrub cover (particularly alder) at sites across the Arctic (Thorpe *et al.*, 2002; Tape *et al.*, 2006).

Fire and the proliferation of tall shrubs

The magnitude of the effects of fire on alder reproduction suggests that fire may have an even greater role in mediating the spread of alder than temperature changes. In the southern boreal forest, alder is often among the first species to colonize after fire (Haessler *et al.*, 1990; Matthews, 1992). Our results show that near the edge of its range, where it is frequently found on unburned sites, alder cover and reproduction are also strongly affected by fire. The response of alder is related primarily to the opportunity for colonization created when fire exposes new seedbeds and stimulates shoot production in meristems not killed by the fire (Gilbert & Payette, 1982; Zasada *et al.*, 1983; de Groot & Wein, 2004). Intense wildfires can also increase air and soil temperatures (Yoshikawa *et al.*,

2003; Hart *et al.*, 2005), deepen active layers (Fetcher *et al.*, 1984; Mackay, 1995), enhance nutrient availability by increasing nutrient mineralization (Smithwick *et al.*, 2005) and release ions trapped in frozen soils (Kokelj & Burn, 2005). Our observation that willow and birch were dominant on old burns at the southern edge of the low Arctic suggests that fire will also facilitate the spread of other deciduous shrubs.

Predicted and observed increases in fire frequency in our study area (Kasischke & Turetsky, 2006; Kochtubajda *et al.*, 2006) and elsewhere (Gillett *et al.*, 2004; McCoy & Burn, 2005) suggest that fire will facilitate alder expansion by providing both available substrates and sources of viable seed. A single alder plant on a burned site in the northern transition zone contributes approximately 39 times the amount of viable seed as an individual at an unburned site. In contrast, a 1.5 °C difference in mean summer temperature (the average temperature difference between the northern and southern transition zones) corresponded to a 3.3-fold difference in viable seed production. Fossil pollen and charcoal evidence from the Brooks Range, Alaska, indicates that transition from herb to shrub tundra in the early Holocene was concurrent with an increased fire return interval (Higuera *et al.*, 2008). In addition to changes in fire frequency (Gillett *et al.*, 2004), recent evidence suggests that both thermokarst activity (Jorgenson *et al.*, 2001; Lantz & Kokelj, 2008) and anthropogenic disturbance (Forbes *et al.*, 2001; Holroyd & Retzer, 2005) are becoming more common in the Arctic. Increased dominance of tall shrubs on thaw slumps (Lantz *et al.*, 2009), old seismic tracks (Kemper & Macdonald, 2009) and drilling mud sumps (Johnstone & Kokelj, 2008) suggest that increases in these forms of disturbance will also contribute to the spread of tall shrubs.

Fire, regional warming and alternative successional trajectories

Increasing fire frequency is also likely to drive short-term changes in vegetation at the community level. Approximately 40 years post-fire, burned plant communities in the northern and southern transition zones most closely resemble the unburned 'forest-tundra like' sites in the southern transition zone. This suggests that tundra vegetation in the northern transition zone is following a similar successional trajectory as post-fire forest-tundra communities. Based on observations of tundra plant community composition 22 years after fire, Landhäusser & Wein (1993) suggested that post-fire increases of tall shrubs and deciduous trees represented the initial stages of the northward movement of the tree line in response to increasing regional temperature. Our observation that unburned sites in the northern transition zone have not reverted to tundra, but resemble burned and unburned sites in the southern transition zone, are consistent with this interpretation. Although mean total spruce cover (*Picea glauca* and *P. mariana*) on northern burns (c. 10%) was less than on southern burns (c. 15%) and controls (c. 16%), its presence in both areas suggests that communities of tall shrubs

will eventually succeed to spruce woodland as envisioned by Landhäusser & Wein (1993). With continued climate warming, it is likely that increased fire frequency will facilitate the northward movement of the boreal forest.

Implications

Evidence that regional warming is increasing northern fire frequency (Kasischke & Turetsky, 2006; Kochtubajda *et al.*, 2006) makes understanding the combined effects of fire and climate change a critical component of efforts to predict the response of the Arctic to global change. Our results indicate that temperature and fire both have an important influence on northern vegetation, but that they act at different spatial and temporal scales. In the short term, fire has a larger impact on alder populations and plant communities than regional temperature differences, but it is constrained by the spatial extent of each fire. Although probably smaller, the effects of increasing temperature in our study area would impact on an area roughly 20 times larger than the total area affected by fire.

In the short term, changes in abundance of tall shrubs in the low Arctic are likely to modify regional warming (Chapin *et al.*, 2000; Epstein *et al.*, 2004; Sturm *et al.*, 2005), alter snow pack (Pomeroy *et al.*, 1995; Sturm *et al.*, 2005; Johnstone & Kokelj, 2008), change active layer depth and nutrient dynamics (Rhoades *et al.*, 2001; Schimel *et al.*, 2004; Sturm *et al.*, 2005; Grogan & Jonasson, 2006; Kokelj *et al.*, 2009) and modify important animal habitats (Walsh *et al.*, 1997). In the long term, if succession on burned sites leads to encroachment of forest–tundra into the low Arctic, increasing fire frequency will decrease albedo, alter soil carbon sinks and drive large feedbacks to the global climate system (Chapin *et al.*, 2000, 2005). Consequently, understanding the interaction between temperature changes and fire regimes on the short- and long-term responses of vegetation will be critical in predicting the future trajectory of northern ecosystems.

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