Relative impacts of disturbance and temperature: persistent changes in microenvironment and vegetation in retrogressive thaw slumps

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Abstract

In the Low Arctic, a warming climate is increasing rates of permafrost degradation and altering vegetation. Disturbance associated with warming permafrost can change micro-climate and expose areas of ion-rich mineral substrate for colonization by plants. Consequently, the response of vegetation to warming air temperatures may differ significantly from disturbed to undisturbed tundra. Across a latitudinal air temperature gradient, we tested the hypothesis that the microenvironment in thaw slumps would be warmer and more nutrient rich than undisturbed tundra, resulting in altered plant community composition and increased green alder (*Alnus viridis* subsp. *fruticosa*) growth and reproduction. Our results show increased nutrient availability, soil pH, snow pack, ground temperatures, and active layer thickness in disturbed terrain and suggest that these variables are important drivers of plant community structure. We also found increased productivity, catkin production, and seed viability of green alder at disturbed sites. Altered community composition and enhancement of alder growth and reproduction show that disturbances exert a strong influence on deciduous shrubs that make slumps potential seed sources for undisturbed tundra. Overall, these results indicate that accelerated disturbance regimes have the potential to magnify the effects of warming temperature on vegetation. Consequently, understanding the relative effects of temperature and disturbance on Arctic plant communities is critical to predicting feedbacks between northern ecosystems and global climate change.

Keywords: climate change, disturbance ecology, green alder, ground ice, Low Arctic, Mackenzie delta, permafrost, shrub encroachment, tall shrub, thermokarst

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Introduction

Across the rapidly warming circumpolar north (Hassol, 2004) there is growing evidence that tundra vegetation is responding to increasing temperatures (Chapin *et al.*, 1995; Stow *et al.*, 2004; Tape *et al.*, 2006). Climate envelope models predict that additional greenhouse warming will result in large shifts in species distributions (Iverson & Prasad, 2001; Pearson & Dawson, 2003). However, these models typically neglect factors such as disturbance (Davis *et al.*, 1998), which may mediate both species and community level responses

by altering dispersal and establishment (Forbes *et al.*, 2001; White & Jentsch, 2001).

In the Low Arctic disturbances are related primarily to fluvial activity, thawing permafrost (thermokarst), or resource development (Gill, 1973; Pearce *et al.*, 1998; Walker & Walker, 1991; Forbes *et al.*, 2001; Lantz & Kokelj, 2008). Although generally smaller than the large wildfires of boreal regions (Walker & Walker, 1991), Arctic disturbances can be numerous and widespread (Jorgenson *et al.*, 2001; Lantz & Kokelj, 2008). Because both climate induced permafrost degradation and industrial activity are expected to increase the size and frequency of disturbances (Jorgenson *et al.*, 2001; Holroyd & Retzer, 2005; Anisimov & Reneva, 2006; Lantz & Kokelj, 2008), understanding the ecological

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dynamics of disturbed terrain is critical to predicting the response of Arctic vegetation to global climate change.

Deciduous shrubs can respond to warming Arctic temperatures on decadal time scales (Chapin *et al.*, 1995; Bret-Harte *et al.*, 2002; Epstein *et al.*, 2004; Tape *et al.*, 2006; Walker *et al.*, 2006). In this paper, we explore community and population responses, focusing on green alder [*Alnus viridis* subsp. *fruticosa* (Ruprecht) Nyman], a deciduous shrub likely to show improved growth and recruitment in response to warming and disturbance. Green alder is found in disturbed and undisturbed terrain throughout many parts of the Low Arctic and Subarctic and is a particularly successful colonizer of mineral soils and newly exposed substrates (Gilbert & Payette, 1982; Matthews, 1992). Green alder cover in Alaska has also increased over the last 50 years on disturbed and undisturbed sites (Tape *et al.*, 2006).

Across the Low Arctic and Subarctic, degradation of ice-rich permafrost on sloping terrain can cause the development of retrogressive thaw slumps, disturbances which consist of a headwall of exposed ground ice and a footslope of viscous, thawed sediments (Burn & Lewkowicz, 1990, Fig. 1). As the ground ice in an active slump melts, the headwall retreats upslope (retrogressively) and the disturbance grows. In the Mackenzie delta region, thaw slumps are numerous and individual disturbances may be several hectares in size. The growth rates and areal extents of slumps have increased significantly over the past 50 years (Lantz & Kokelj, 2008). Research on the revegetation of tundra slumps has largely focused on describing the initial stages of succession, thus outside of the boreal region
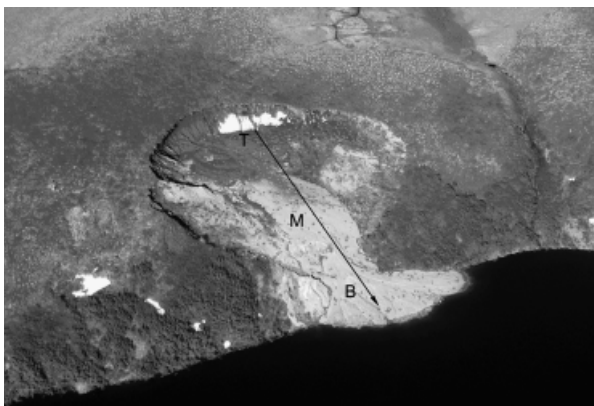
little is known about their long-term effects on abiotic conditions and vegetation (Kerfoot, 1969; Lambert, 1976; Burn & Friele, 1989; Bartleman *et al.*, 2001). The abundance of thaw slumps of various ages across the Low Arctic-Subarctic Transition in the Mackenzie delta region presents a unique opportunity to investigate the effect of temperature and disturbance on species and community level responses.

In this paper, we test the hypotheses that slumping: (1) alters abiotic conditions, (2) changes plant community composition, (3) increases green alder growth and reproduction, and (4) has a larger influence on vegetation and microenvironment than differences in regional temperature. To test these predictions, we described regional variability in summer air temperatures across the Low Arctic and Subarctic Transition Zones and compared abiotic conditions, plant community composition, and the response of green alder among active slumps, stable slumps, and undisturbed tundra in both the Low Arctic and Subarctic Transition Zones.

Materials and methods

Study area

Our study area in northwestern Canada is located between the latitudes of 68°16′N and 69°33′N and the longitudes of 133°00′W and 135°00′W (Fig. 2). This upland terrain adjacent to the Mackenzie River delta is characterized by rolling hills (30–150 m relief) and thousands of small lakes. The near-surface permafrost is ice-rich and most upland soils are clayey silts (Mackay, 1963). Winters are long and cold with subzero monthly mean air temperatures persisting from October to April. Across the region average summer temperature and total annual precipitation decrease with proximity to the Beaufort Sea (Ritchie, 1984; Burn, 1997).

Slump sampling

To compare the relative effects of regional temperature and retrogressive thaw slumping on abiotic and biotic site conditions, we selected 28 thaw slumps from the Inuvik area to northern Richards Island (Fig. 2). We divided these slumps into two response groups intended to reflect differences in regional climate. Southerly sites were within the northern portion of the Subarctic Transition Zone and sites to the north were within the Low Arctic Zone (Timoney *et al.*, 1992). Within each latitudinal zone we selected active slumps which showed signs of recent activity ($n = 7$), and stable slumps where shrubby vegetation was well-established ($n = 7$). Ring counts of green alder indicated that the stable slumps have been inactive for 29–83 years
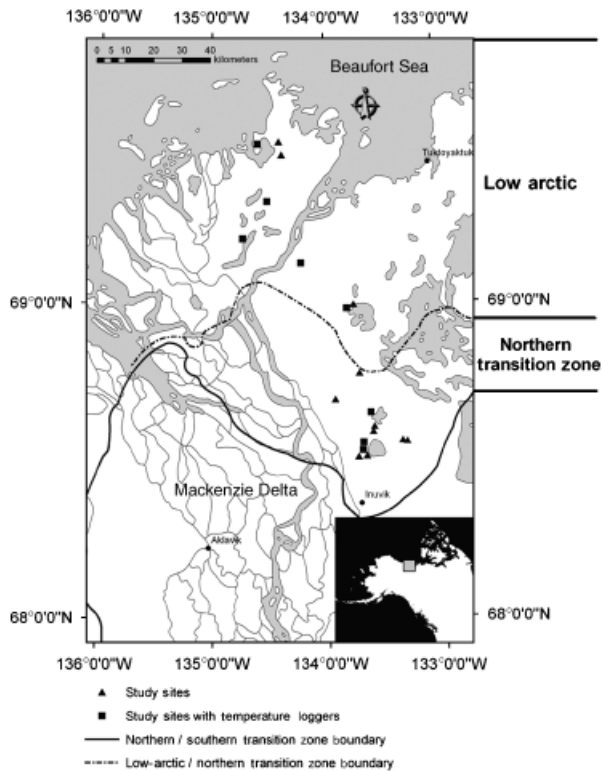

Fig. 1 Active retrogressive thaw slump showing evidence of soil movement. The areal extent of this disturbance is approximately 0.5 ha. Orientation of ground-based line transects with respect to the slump are shown by the arrow. Slump positions where point data were collected are indicated by the letters: T, top; M, middle; and B, bottom.

Fig. 2 Map of the study region showing study sites, study sites with temperature loggers, and vegetation zones *sensu* Timoney *et al.* (1992). Inset map shows the position of the study area in North America.

(mean = 56.9). Within each slump we established a line transect from the upper headwall to the lake shore on a bearing roughly perpendicular the headwall of the slump (Fig. 1). Slump surfaces ranged from flat to gently sloping (<10°). We also established 26 transects in undisturbed tundra across both zones.

Abiotic data. In March of 2006, we recorded winter snow depth along each transect at 5 m intervals using a graduated avalanche probe. We also measured the temperature at the base of the snow pack (subnivian temperature) at 10 m intervals using a thermistor attached to the base of a wooden dowel. In late August of 2006, active layer depth (the surface layer of earth materials that annually thaws and refreezes) was measured at the top, middle, and bottom of each slump and on three hummock tops along each undisturbed transect by pushing a graduated steel probe into the ground to depth of refusal.

To measure anion (NO_3^-, PO_4^-, SO_4^-) and cation (K^+, Ca^{2+}, Mn^{2+}, NH^{4+}, Mg^{2+}) supply rates we installed PRS™ nutrient probes (Western Ag. Innovations Inc., Saskatoon, SK, Canada) at slump and control sites in June of 2006. The charged PRS ion exchange membranes

attract anions or cations present in the soil solution and provide an index that is useful for the comparison of differences in plant available nutrients. These data are presented in milliequivalents/cm² exchange membrane/burial period (66 days). On each undisturbed transect we installed two anion and two cation probes in mineral soil on two hummock tops ($n = 8$/site). On active and stable slump sites two pairs of anion and cation probes were placed in the top, middle, and bottom of each slump ($n = 12$/site). Probes were installed between June 21 and 22 and removed between August 26 and August 27, 2006. At each probe site we also measured percent soil moisture ([(wet weight−dry weight)/dry weight] × 100) in June and August, organic layer thickness, and soil pH.

We measured air temperatures at eight sites along the north–south transect (Fig. 2). At each site thermistors attached to data loggers were installed in radiation shields mounted 1.5 m above the ground surface. At four sites, we also measured near-surface ground temperatures at a single point within: (1) undisturbed tundra, (2) an active slump, and (3) a stable slump. Ground temperatures were measured from September 2005 to August 2006 by placing thermistors attached to a dowel into a small diameter hole augered to 5 and 100 cm depths. At all sites, temperatures were logged every hour (Onset Computing, Pocasset, MA, USA, HOBO™, TMC6-HD H08-006-04, H08-030-08RS1). In winter, the onset of rapid cooling at 100 cm depth indicates the overlying active-layer has frozen and heat is being extracted by conduction. The rapid decline of 100-cm temperatures was used to estimate the date that the active layer had frozen.

Vegetation sampling. We measured plant community composition by visually estimating percent cover in quadrats positioned at 5 or 10 m intervals along each transect. Although slump length varied, we sampled a minimum of seven quadrats per slump. The percent cover of all tall shrubs was estimated using 5 m² quadrats. Cover of dwarf shrubs, herbs, forbs, mosses and lichens was estimated using a 0.5 m² plot randomly nested within the 5 m² plot. Vascular plant nomenclature used throughout this paper follows Porsild & Cody (1980).

The growth and life history of green alder were assessed on stable slumps and undisturbed tundra. Alder quadrats were selected by randomly choosing up to three shrub quadrats (5 m²) where alder cover was >0%. In each 5 m² plot, we excavated and mapped all stems rooted within the plot and obtained stem cross sections from above the top of the root collar. Subsequently we recorded stem ages by counting growth rings on a minimum of two radii.

We compared alder growth using three response variables: (1) vertical growth (stem height/stem age), (2) radial growth (stem basal diameter/stem age), and (3) stem basal area ($cm^2 m^{-2}$). Alder reproduction was examined using: (1) alder presence–absence, (2) catkin production (catkins m^{-2}), and (3) percent germination (number of germinants/total number of seeds × 100). Catkins collected from August 28 to 29, 2005 were air dried at room temperature until they released their seeds. Seeds were used in germination trials where 100 seeds were placed on moist filter paper in petri dishes. Dishes were kept moist at room temperature under 12 h of full spectrum light for 3 weeks and germinants were counted and removed every 3 days.

Statistical analysis

To explore the relationship between mean summer temperature and position along the Low Arctic-Subarctic Transition we used linear regression analysis. To test abiotic and alder response variables for significant differences and interactions between latitudinal zones and site type (active slumps, stable slumps, and controls) we used a general linear model containing both fixed and random effects (PROC MIXED; SAS, 2004). Latitudinal zone and site type were treated as fixed effects and individual sites and position within the slump were treated as random factors. 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 χ^2 test (Morrell, 1998). In each model random terms were retained if they significantly improved likelihood. To estimate the error degrees of freedom for all F-tests of fixed effects we used the Kenward–Rogers approximation (SAS, 2004). The following response variables were log transformed: tall shrub cover, vertical growth, basal area, shoot density, stems/clone catkins m^{-2}, and seed viability to meet the assumptions of normality and equal variance.

To explore differences in plant community composition among undisturbed tundra, active slumps, and stable slumps in both the Low Arctic and Subarctic Transition Zones, we used PRIMER (Clarke & Gorley, 2001) to perform an NMDS ordination of a Bray–Curtis distance matrix calculated from percent cover data. We set PRIMER to repeat this analysis 20 times and selected the two dimensional ordination that best represented the multidimensional distance matrix [i.e., exhibited the least stress (Legendre & Legendre, 1998)]. To reduce noise and stress, we $\log(1 + x)$ transformed percent cover data. Subsequently, we used ANOSIM to test the null hypothesis that species composition did not differ among the six types that represented different combinations of latitudinal zone and disturbance type. 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}

Table 1 Pair-wise comparisons of plant community composition between site types using the ANOSIM procedure

Comparison	Site type: disturbance (Zone)	R_{ANOSIM}	P-value
Between Latitudinal Zones	Active Slump (L.A.)–Active Slump (T.Z.)	0.124	0.072
	Stable Slump (L.A.)–Stable Slump (T.Z.)	0.125	0.91
	Control (L.A.)–Control (T.Z.)	0.15	**0.009**
Between Controls and Active Slumps	Control (T.Z.)–Active Slump (L.A.)	0.956	**0.001**
	Control (T.Z.)–Active Slump (T.Z.)	0.773	**0.001**
	Control (L.A.)–Active Slump (L.A.)	0.501	**0.001**
	Control (L.A.)–Active Slump (T.Z.)	0.384	**0.001**
Between Controls and Stable Slump	Control (T.Z.)–Stable Slump (L.A.)	0.983	**0.001**
	Control (T.Z.)–Stable Slump (T.Z.)	0.931	**0.001**
	Control (L.A.)–Stable Slump (T.Z.)	0.56	**0.002**
	Control (L.A.)–Stable Slump (L.A.)	0.528	**0.002**
Between Active and Stable Slump	Active Slump (L.A.)–Stable Slump (T.Z.)	0.478	**0.003**
	Active Slump (L.A.)–Stable Slump (L.A.)	0.408	**0.016**
	Active Slump (T.Z.)–Stable Slump (T.Z.)	0.355	**0.005**
	Stable Slump (L.A.)–Active Slump (T.Z.)	0.251	**0.04**

R_{ANOSIM} values >0.75 indicate well separated groups, values between 0.5 and 0.75 describe overlapping but distinguishable groups, and values <0.25 represent groups that cannot be separated (Clarke & Gorley, 2001). The Transition Zone and Low Arctic are abbreviated as T.Z. and L.A.

statistic ranges from zero to one and expresses the similarity between groups (Clarke & Gorley, 2001; Table 1). The significance of the R_{ANOSIM} statistic was calculated by performing 9999 randomizations of the original data (Clarke & Gorley, 2001).

Results

Regional air temperature conditions

Data from 2005 showed a northward decrease in the average June–August air temperature from 10.8 °C at Inuvik (67°37N, 133°45W) to 6.8 °C at the Beaufort Coast (69°30N, 134°32). This corresponds to a decrease in mean summer temperature of ~ 3 °C/degree latitude, or 4 °C across the study area (Fig. 3, $F_{1,6}$ $F = 83.55$, $r^2 = 0.93$, $P < 0.001$). Temperature records from 1970 to 2005 showed that the more northern community of Tuktoyaktuk (68°18′N, 133°28′W) is 3.3 °C colder than Inuvik (SD = 0.4) and demonstrated that the summer temperature gradient we observed was not unique to 2005.

Snow pack, ground temperature, and active layer depth

Abiotic conditions in active and stable slumps were markedly different from undisturbed tundra in both the Low Arctic and the Subarctic Transition Zones. Snow depth, subnivian temperature, and active layer depth all showed significant increases in disturbed terrain
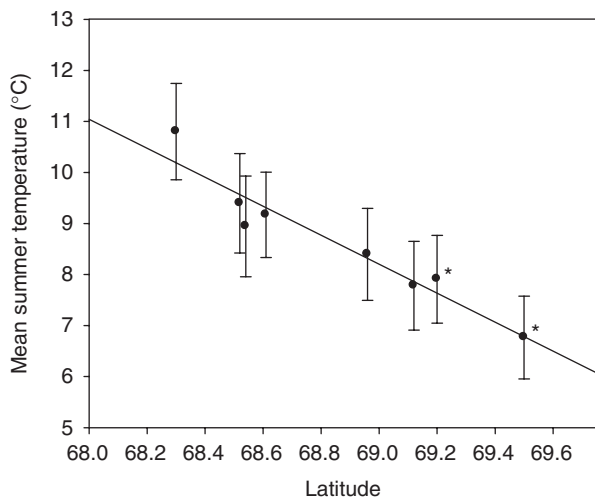

Fig. 3 Mean growing season temperature and latitude for eight sites in the Mackenzie delta uplands, June–August 2005 ($r^2 = 0.933$, $P < 0.001$). Error bars show the 95% confidence intervals of the means. Data indicated with asterisks (69°30′N, 133°34′W and 69°11′N, 134°42′W) provided by Dr. Chris Burn (Carleton University).

(Fig. 4). In the Low Arctic, late winter snow pack on active and stable slumps was significantly greater than on controls and subnivian temperatures were approximately 10 °C higher (Fig. 4a and b). In the Transition Zone, snow pack at stable slumps was significantly greater than active slumps and controls (Fig. 4a). Although Transition Zone snow thicknesses in active slumps were similar to controls, the average temperature at the base of snow pack in both slump types was greater than in controls (Fig. 4a and b). In the Transition Zone, snow and subnivian temperatures on undisturbed tundra were significantly greater than in the Low Arctic (Fig. 4a and b). Mean active layer depth in undisturbed terrain was also greater in the Transition Zone than in the Low Arctic and thaw depths on active and stable slumps were significantly greater than controls in both zones (Fig. 4c). Continuous temperature data from disturbed and undisturbed terrain at four sites showed that completion of active layer freezeback ranged from November 8 in undisturbed tundra to April 8 in an active slump (Fig. 5). The completion of active layer freezeback was delayed by 51–139 days on active slumps and 28–120 days on stable slumps compared with adjacent undisturbed tundra (Fig. 5).

Soils and nutrient availability

The soils at most active slumps had little or no organic layer following disturbance (Fig. 4d). Undisturbed controls were characterized by thicker soil organic layers (Fig. 4b). On stable slumps, leaf litter and moss accumulation contributed to a thicker surface organic layer than on active slumps (Fig. 4d). Although mean organic thickness was lower on stable slumps compared with controls in both the Low Arctic and the Transition Zone, this difference was only significant in the Low Arctic ($P < 0.05$, Fig. 4d).

Soil moisture in June and August did not differ with disturbance type or latitudinal zone. Sulfate and calcium availability on active and stable disturbances were significantly elevated with respect to controls, regardless of position along the latitudinal gradient (Fig. 6a and b). Conversely, plant available nitrate concentrations were similar on controls and active slumps, but higher on stable slumps (Fig. 6c). Soil pH on active and stable slumps was elevated with respect to the controls within both zones (Fig. 6d). Plant available concentrations of other soil nutrients (PO_4^-, Mn^{2+}, NH^{4+}, and Mg^{2+}) did not differ among site types.

Plant community composition

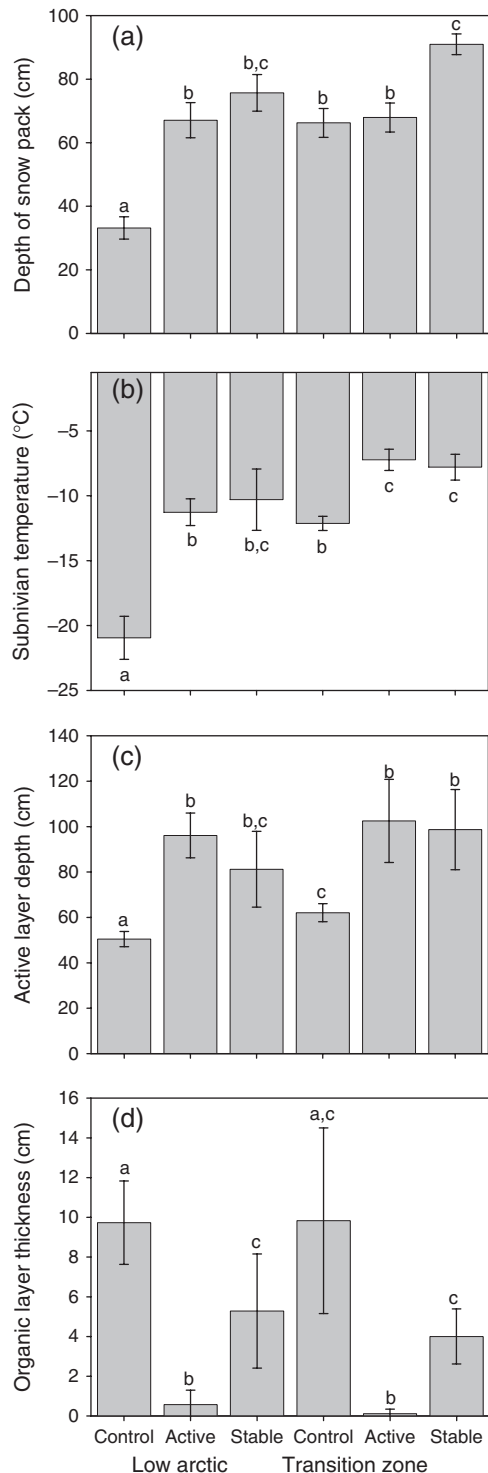Undisturbed tundra in both the Low Arctic and the Subarctic Transition Zones was characterized by an
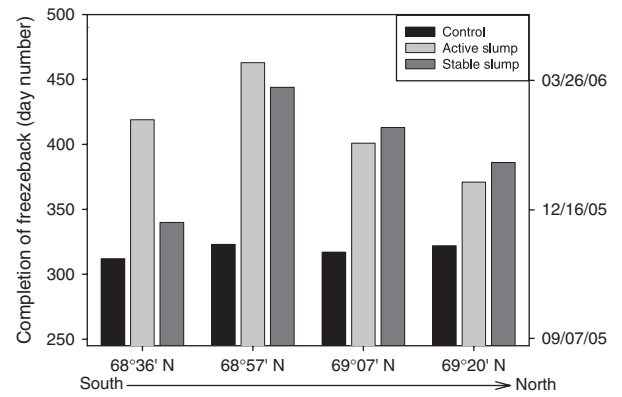
Fig. 5 Timing of 100 cm depth cooling (indicative of active layer freezeback) at four sites in the study region. At each site ground temperatures were measured at single point within: (1) undisturbed tundra, (2) an active slump, and (3) a stable slump. Grouped bars show freezeback dates at controls, active and stable slumps at a given site. Dates on the *y*-axis are in day number starting January 1, 2005. Corresponding Calendar Dates are shown at the right.

abundance of dwarf shrubs including: Labrador tea (*Ledum decumbens* (Ait.) Lodd), cranberry (*Vaccinium vitis-idaea* L.), and cloudberry (*Rubus chamaemorus* (L.). Scrub birch (*Betula glandulosa* Michx.) was also abundant at undisturbed sites. In contrast, active slumps in both zones were generally dominated by mosses and herbaceous species, including *Calamagrostis canadensis* (Michx) Beauv., *Arctagrostis latifolia* (R.Br) Grieseb, and mastodon flower (*Senecio congestus* (R.Br.) DC. Scrub birch was also found on slumps because occasionally, disturbance did not completely remove the tundra vegetation. Stable slumps in both the Transition Zone and Low Arctic were typified by an abundance of tall shrubs including alder, willows (primarily *Salix pulchra* Cham. and *Salix glauca* L.) and scrub birch.

The vegetation on active and stable slumps had significantly different species composition than the surrounding undisturbed tundra (Fig. 7; R_{ANOSIM} values 0.38–0.98; Table 1). Of the 69 species or species groups we encountered at the study sites, 16 (28%) were found exclusively on active or stable slumps and 12 (17%) were found only at control sites. Species that were unique to active slumps included: mastodon flower, Tilesius wormwood (*Artemisia tilesii* Ledeb), and fireweed (*Epilobium angustifolium* L.). Between 29 and 73 years following stabilization, slumps still had significantly different species composition than controls (R_{ANOSIM} values 0.53–0.98; Table 1). In addition to dominance by green alder and willow, these sites also had high cover of deciduous shrubs that were otherwise
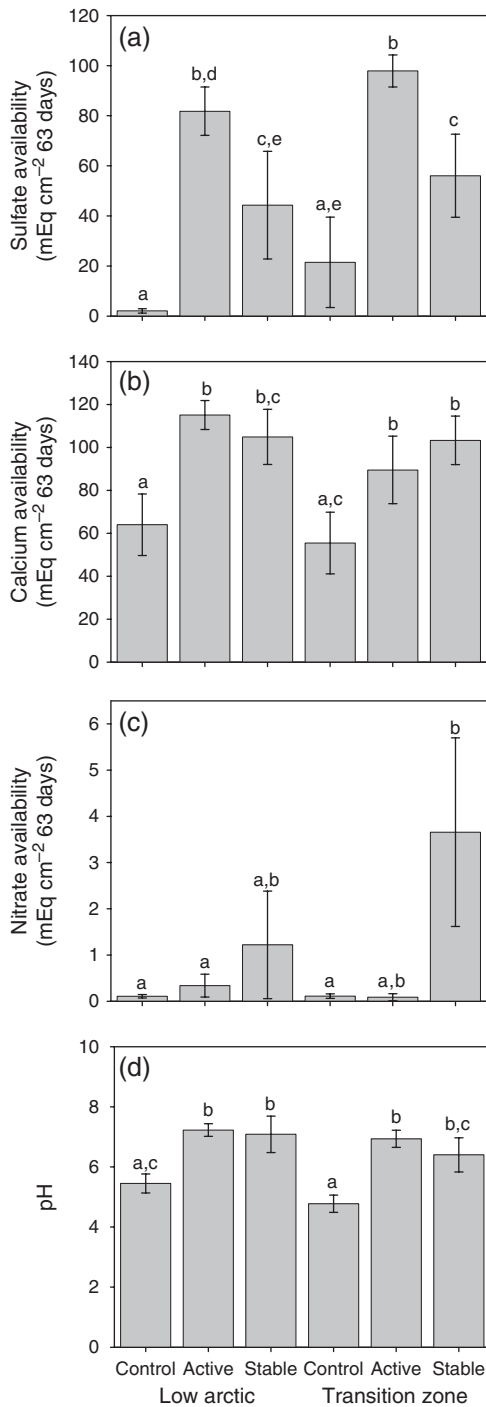

Fig. 4 Mean abiotic variables measured on active slumps (Active), stable slumps (Stable), and undisturbed controls (Control) in the Low Arctic and Transition Zones: (a) snow pack depth, (b) active layer depth, (c) subnivian temperature, and (d) organic layer thickness. Error bars show the 95% confidence intervals of the mean (untransformed). Bars with different letters are significantly different ($P \leq 0.05$, Mixed Model ANOVA and Tukey's Adjusted LSD).

Fig. 6 Mean abiotic variables measured on active slumps (Active), stable slumps (Stable) and undisturbed controls (Control) in the Low Arctic and the Transition Zones: (a) plant available sulfate, (b) plant available calcium, (c) plant available nitrate, and (d) pH. Error bars show the 95% confidence intervals of the mean (untransformed). Bars with different letters are significantly different ($P \leq 0.05$, Mixed Model ANOVA and Tukey's Adjusted LSD).
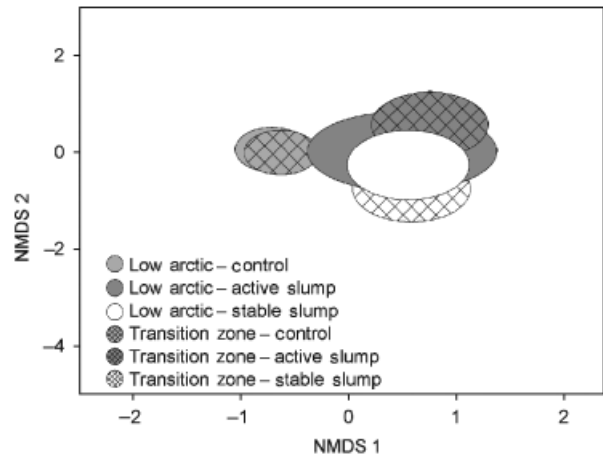

Fig. 7 Non-metric multidimensional scaling ordination of plant community composition based on Bray–Curtis similarity matrix. (a) Grayscale ellipses in the upper panel show the differences in species composition and variability between site type. Ellipses were defined using the mean NMDS scores (x and y) for each site type $\pm$ SD.

rare [*Rosa acicularis* (Lindl.)], or completely absent (*Ribes triste* (Pall), *Sheperdia canadensis* (L.) Nutt., *Spirea beauverdiana* Schneid) in controls. Although less pronounced, there were also differences in species composition between active and stable slumps evidenced by R_{ANOSIM} values between 0.25 and 0.48 (Table 1). Conversely, plant communities on the same site type (i.e., active slumps, stable slumps, or controls), on either side of the Low Arctic boundary were virtually indistinguishable from one other ($R_{ANOSIM} \leq 0.15$, Table 1). The magnitude of differences in plant community composition among treatments is illustrated in the NMDS ordination in Fig. 7.

Green alder growth and reproduction

Green alder exhibited increased growth and reproduction on stable slumps compared with controls (Fig. 8). In both zones, disturbed sites had a greater proportion of plots with alder present, and higher vertical growth, radial growth, basal area, catkin production, and seed viability (Fig. 8). On stable slumps, alder vertical growth, mean basal area and catkin production were up to four times greater than on controls in both zones. On undisturbed sites only alder presence/absence and seed viability increased at more southerly sites (Fig. 8). There were no significant interactions between zone and disturbance for any of the response variables measured.
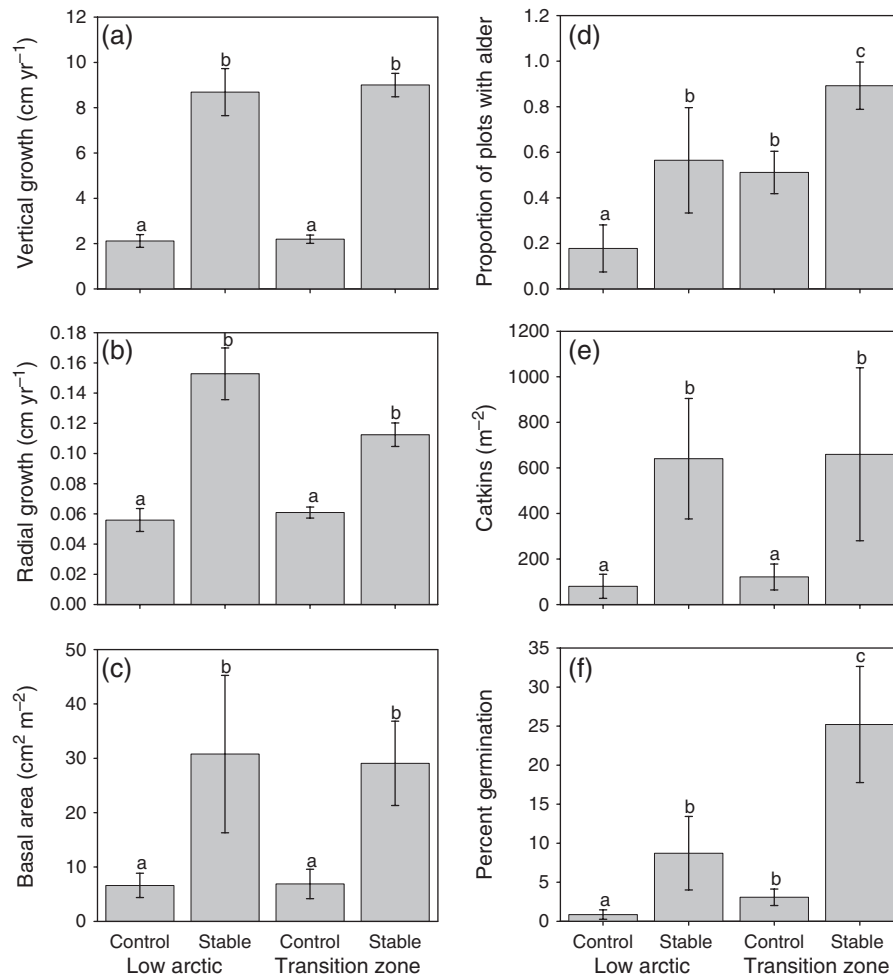
Fig. 8 Mean growth and reproduction of green alder measured on stable slumps (Stable) and undisturbed controls (Control) in the Low Arctic and Transition Zones: (a) vertical growth, (b) radial growth, and (c) basal area, (d) proportion of plots with alder (e) catkin production, (f) percent germination. Error bars show the 95% confidence intervals of the mean (untransformed). Bars with different letters are significantly different ($P \leq 0.05$, Mixed Model ANOVA and Tukey's Adjusted LSD).

Discussion

Snow pack, ground temperature, and active layer depth

Thaw slumps were markedly different environments than undisturbed tundra. They were characterized by warmer soils, deeper snow pack, and later freezeback than undisturbed tundra. The absence of surface organics, combined with the low albedo of these moist exposed surfaces resulted in active layer thicknesses that were close to double those observed in undisturbed tundra. The concave morphology of slumps and tall shrub cover in older slumps likely also promoted snow accumulation (Sturm et al., 2005; Pomeroy et al., 2006), inhibiting ground heat loss, delaying freezeback, and elevating minimum near-surface ground temperatures compared with the adjacent tundra (Kokelj et al., in

press). Similar interactions between vegetation, snow and ground temperatures have been reported by Johnstone & Kokelj (2008) on drilling mud sumps in the Mackenzie delta region and by Mackay & Burn (2002) at an experimentally drained lake on Richards Island, NWT.

Overall, slumping had a much larger influence on the microenvironment than did air temperature differences across the latitudinal gradient (Figs 4–6). Regional variation in ground temperatures and active layer depth on undisturbed sites in the delta uplands is driven in part by climate gradients associated with proximity to the Beaufort Sea coast. In spring and early summer, the persistence of sea ice cools air near the coast (Ritchie, 1984; Burn, 1997) resulting in colder permafrost (Mackay, 1974) and thinner active layers in the northern part of the study area (Palmer, 2007). Winter air tempera-

tures across the study area are similar (Burn, 1997), but deeper snow pack in the Transition Zone (Ritchie, 1984, Fig. 4a, Palmer, 2007), inhibits ground heat loss resulting in warmer subnivian temperatures compared with the Low Arctic Zone near the coast.

Nutrient availability and soils

Soil pH and plant available nutrients (Ca^{2+} and SO_4^-) were elevated on slumps (Fig. 6) because soluble materials sequestered in frozen tills are liberated by thawing (Kokelj & Burn, 2005). Plant available Ca^{2+} and SO_4^- persist in high concentrations in slump soils because they are the dominant ions in the tills derived from carbonate and shale bedrock of the Mackenzie basin and leaching takes at least several decades (Duk-Rodkin & Lemmen, 2000; Kokelj *et al.*, 2005). Higher nitrate concentrations on stable slumps compared with undisturbed tundra and active slumps may be driven by the dominance of nitrogen fixing green alder and soapberry (*Sheperdia canadensis* (L.) Nutt.) on older disturbances (Rhoades *et al.*, 2001, 2008). Elevated pH on active and stable slumps is likely driven by increased concentration of Ca^{2+} and limited organic acid deposition from a thinner organic layer (Bohn *et al.*, 2001). No regional trends in plant available nutrients were apparent between the Low Arctic and Transition Zones. Nutrient availability among controls across the region is probably similar because the soils are of similar age and parent materials, and remain unfrozen for similar amounts of time each year.

Altered microenvironmental conditions and slump reinitiation

Altered abiotic conditions in stable thaw slumps suggest that the effects of disturbance persist for decades to centuries. There are a number of factors influencing near-surface conditions in thaw slumps, but our data suggest that the depth of snow pack is critical. Because, the concave morphology of thaw slumps can likely be sustained for centuries, elevated snow accumulation and distinct abiotic conditions may also persist. Sustained differences in the thaw slump microenvironment may also be related to the recurrent nature of this form of thermokarst. Modelling studies indicate that the thermal disturbance resulting from a lakeside thaw slump can cause the unfrozen zone (talik) beneath a lake to migrate laterally. If the talik grows into ice-rich ground, it may lead to lake-bottom subsidence and cause slump reinitiation at the shoreline (Kokelj *et al.*, 2009). These models also suggest that, once initiated, slumps likely cycle between periods of activity and stability on multidecadal timescales (Kokelj *et al.*,

2009). These predictions are corroborated by observations that slump reinitiation frequently occurs at the lakeshore and that most slumps are multiaged (Lantuit & Pollard, 2008; Kokelj *et al.*, 2009).

Persistence of changes in plant community composition

Our data also show that shrub dominated vegetation can persist in thaw slumps for close to a century. In Low Arctic tundra, community stability is thought to be linked to the duration of disturbance effects on soils and thermal regime (Walker *et al.*, 1987; Walker & Walker, 1991; Forbes *et al.*, 2001). Where disturbance causes transient changes in thermal conditions and soils, often its impact on vegetation cannot be detected after several decades (Vavrek *et al.*, 1999; Kemper, 2005). Conversely, where disturbances cause long-term alteration of ground thermal regime, pH, and nutrient availability, changes in community composition can last for decades (Walker *et al.*, 1987; Forbes *et al.*, 2001; Racine *et al.*, 2004; Johnstone & Kokelj, 2008). This is consistent with our observations of thaw slumps, where soil chemistry, snow depth, ground temperatures, and vegetation all remain distinct from undisturbed sites for close to a century.

Although differences in snow pack and ground temperatures may persist for more than a century, it is unclear if the shrub dominated vegetation in slumps is stable or successional. In most boreal and temperate environments tall shrub communities are either transient (persisting for 20–50 years) or are maintained by repeated disturbance (Foote, 1983; Pickett & White, 1985; Morneau & Payette, 1989; Chapin *et al.*, 1994). However, in the Low Arctic and Subarctic some shrublands show no sign of imminent replacement (Barbour & Billings, 2000). In thaw slumps, shrub-dominated terrain is likely to be maintained by decadal or centennial slump reinitiation (Kokelj *et al.*, 2009). It is also possible that in the absence of repeated disturbance, slumps will remain dominated by tall shrubs. In subalpine meadows Anthelme *et al.*, (2002) suggest that the persistence of green alder through clonal reproduction inhibits succession.

There is also the possibility that tall shrubs on stable slumps will be replaced by dwarf shrub or herbaceous tundra. Succession in the Arctic is slow (Svoboda & Henry, 1987), but chronosequences on river alluvium suggest that persistent tall shrub communities are eventually succeeded by dwarf shrub or herbaceous tundra (Bliss and Cantlon, 1957). Because each of these trajectories (e.g., stable tall shrub, tall shrub $\Rightarrow$ dwarf-shrub, or tall shrub $\Rightarrow$ dwarf-shrub $\Rightarrow$ herbaceous tundra) have different feedbacks to climate, uncertainty regard-

ing the speed and direction of Low Arctic succession clearly requires additional investigation.

Green alder

Our data show that areas disturbed by thaw slumping have a much larger impact on green alder than the regional climate gradient. The proportion of plots with alder, alder growth, and alder reproduction were all significantly greater on slumps than controls. The uniformity of alder growth variables across the regional temperature gradient on disturbed and undisturbed sites indicates that (like other tundra plants) the growth of established alders is constrained by site-specific factors such as nutrient availability and competition (Chapin et al., 1995; Gough, 2006). This is supported by observations that increases in growth and catkin production on thaw slumps did not differ between the northern and southern portions of our study area.

Enhanced alder growth and reproduction on thaw slumps is related in part to the increased opportunity for colonization on exposed nonacidic substrates (Forbes et al., 2001). Like many deciduous shrubs, green alder is likely better adapted than stress tolerant evergreen shrubs to capitalize on the reduced competition, improved microenvironmental conditions, and increased nutrient availability (Kielland, 1994; Chapin et al., 1995; Gough, 2006). Slump morphology and increased snow pack may also provide protection from winter desiccation and snow abrasion (Sturm et al., 2005). The proliferation of deciduous shrubs on stable slumps is also consistent with shifts in dominance of plant functional groups observed on other forms of natural and anthropogenic disturbance and in response to experimental warming and nutrient addition (Walker et al., 1987; Chapin et al., 1995; Vavrek et al., 1999; Forbes et al., 2001; Racine et al., 2004; Walker et al., 2006; Johnstone & Kokelj, 2008).

Implications

Our results suggest that disturbances may have a larger and more immediate impact on Low Arctic ecosystems than temperature warming alone (Rupp et al., 2000; Turner et al., 2003; Stow et al., 2004). Slumps are widespread across the western Canadian Arctic and although they are relatively small, their frequency and aerial extents are increasing (Wolfe et al., 2001; Lantuit & Pollard, 2008; Lantz & Kokelj, 2008). As the number and size of slumps increases, these disturbances will likely have a growing influence on vegetation dynamics in the Low Arctic. Substrates exposed by thaw slumps provide opportunities for rapid colonization and movement of species beyond their present geographic ranges (Staniforth & Scott, 1991; Landhäusser & Wein, 1993). Our results also suggest that these disturbed sites may act as highly productive seed sources within large areas of undisturbed terrain.

Forbes et al. (2001) have described Arctic disturbances as 'dynamic focal points,' where persistence of alternative stable states following perturbation can exert a long-term influence on a range of biotic and abiotic processes in the disturbance and on the surrounding terrain. Tall shrubs like green alder can significantly increase snow depth, active layer depth, and nutrient availability (Epstein et al., 2004; Schimel et al., 2004; Sturm et al., 2005; Rhoades et al., 2008). Thus, changes in their population ecology catalyzed by increases in thermokarst activity may also lead to changes in permafrost conditions, wildlife habitat, and ecosystem function (Walsh et al., 1997; Forbes et al., 2001; McGuire et al., 2006). Changes in microenvironment following thaw slumping likely also lead to slump reinitiation on multidecadal time scales. Because vegetation exerts strong controls on regional ecosystem processes (Chapin et al., 2000; Thompson et al., 2004; Chapin et al., 2005), understanding the effects of disturbance on short-term and long-term successional trajectories is also a critical component of efforts to understand the effects of climate change on the Arctic.

References

Anisimov O, Reneva S (2006) Permafrost and changing climate: the Russian perspective. *Ambio*, **35**, 169–175.

Anthelme F, Cornillon L, Brun JJ (2002) Secondary succession of *Alnus viridis* (Chaix) DC. in Vanoise National Park, France: coexistence of sexual and vegetative strategies. *Annals of Forest Science*, **59**, 419–428.

Barbour MG, Billings WD (2000) *North American Terrestrial Vegetation*. Cambridge University Press, Cambridge, UK.

Bartleman AP, Miyanishi K, Burn CR, Cote MM (2001) Development of vegetation communities in a retrogressive thaw slump near Mayo, Yukon Territory: a 10-year assessment. *Arctic*, **54**, 149–156.

Bliss LC, Cantlon JE (1957) Succession on river alluvium in northern Alaska. *American Midland Naturalist*, **58**, 452–469.

Bohn HL, McNeal BL, O'Connor GA (2001) *Soil Chemistry*. Wiley, New York.

Bret-Harte MS, Shaver GR, Chapin FS (2002) Primary and secondary stem growth in Arctic shrubs: implications for community response to environmental change. *Journal of Ecology*, **90**, 251–267.

Burn CR (1997) Cryostratigraphy, paleogeography, and climate change during the early Holocene warm interval, western Arctic coast, Canada. *Canadian Journal of Earth Sciences*, **34**, 912–925.

Burn CR, Friele PA (1989) Geomorphology, vegetation succession, soil characteristics and permafrost in retrogressive thaw slumps near Mayo, Yukon Territory. *Arctic*, **42**, 31–40.

Burn CR, Lewkowicz AG (1990) Retrogressive thaw slumps. *Canadian Geographer*, **34**, 273–276.

Chapin FS, McGuire AD, Randerson J *et al.* (2000) Arctic and Boreal ecosystems of western North America as components of the climate system. *Global Change Biology*, **6**, 211–223.

Chapin FS, Shaver GR, Giblin AE, Nadelhoffer KJ, Laundre JA (1995) Responses of Arctic tundra to experimental and observed changes in climate. *Ecology*, **76**, 694–711.

Chapin FS, Sturm M, Serreze MC *et al.* (2005) Role of land-surface changes in Arctic summer warming. *Science*, **310**, 657–660.

Chapin FS, Walker LR, Fastie CL, Sharman LC (1994) Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. *Ecological Monographs*, **64**, 149–175.

Clarke KR, Gorley RN (2001) *Primer v5: Users Manual/Tutorial*. Primer-E Ltd, Plymouth, MA.

Davis AJ, Jenkinson LS, Lawton JH, Shorrocks B, Wood S (1998) Making mistakes when predicting shifts in species range in response to global warming. *Nature*, **391**, 783–786.

Duk-Rodkin A, Lemmen DS (2000) Glacial history of the Mackenzie region. In: *The Physical Environment of the Mackenzie Valley, Northwest Territories: A Base Line for the Assessment of Environmental Change. Geological Survey of Canada Bulletin 547* (eds Dyke LD, Brooks GR), pp. 41–48. Geological Survey of Canada, Ottawa, ON.

Epstein HE, Beringer J, Gould WA *et al.* (2004) The nature of spatial transitions in the Arctic. *Journal of Biogeography*, **31**, 1917–1933.

Foote MJ (1983) *Classification, description, and dynamics of plant communities after fire in the taiga of interior Alaska*. U.S.D.A. Forest Service Research Paper: PNW-307.

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

Gilbert H, Payette S (1982) Écologie des populations d'aulne vert (*Alnus crispa* (Ait.) Pursh) á la limite des forêts, Québec nordique. *Géographie Physique et Quaternaire*, **36**, 109–124.

Gill D. (1973) Modification of northern alluvial habitats by river development. *Canadian Geographer*, **17**, 138–153.

Gough L (2006) Neighbor effects on germination, survival, and growth in two Arctic tundra plant communities. *Ecography*, **29**, 44–56.

Hassol SJ (2004) *Arctic Climate Impact Assessment: Impacts of Warming Climate*. Cambridge University Press, Cambridge.

Holroyd P, Retzer H (2005) *A peak into the future: The potential landscape impacts from gas development in northern Canada*. The Pembina Institute for Appropriate Development, Calgary, AB.

Iverson LR, Prasad AM (2001) Potential changes in tree species richness and forest community types following climate change. *Ecosystems*, **4**, 186–199.

Johnstone JF, Kokelj SV (2008) Environmental conditions and vegetation recovery at abandoned-drilling mud sumps in the Mackenzie Delta region, NWT, Canada. *Arctic*, **61**, 199–211.

Jorgenson MT, Racine CH, Walters JC, Osterkamp TE (2001) Permafrost degradation and ecological changes associated with a warming climate in central Alaska. *Climatic Change*, **48**, 551–579.

Kemper JT (2005) *Short and long-term effects of winter seismic exploration on Low Arctic plant communities of the Kendall Island migratory bird sanctuary, Northwest Territories*. Masters Thesis, University of Alberta, Edmonton, Alberta.

Kerfoot DE (1969) *The geomorphology and permafrost conditions of Garry Island, N.W.T.* Ph.D. Dissertation, University of British Columbia, Vancouver, BC.

Kielland K (1994) Amino-acid-absorption by Arctic plants – implications for plant nutrition and nitrogen cycling. *Ecology*, **75**, 2373–2383.

Kokelj SV, Burn CR (2005) Geochemistry of the active layer and near-surface permafrost, Mackenzie delta region, Northwest Territories, Canada. *Canadian Journal of Earth Sciences*, **42**, 37–48.

Kokelj SV, Jenkins RE, Milburn D, Burn CR, Snow N (2005) The influence of thermokarst disturbance on the water quality of small upland lakes, Mackenzie Delta region, Northwest Territories, Canada. *Permafrost and Periglacial Processes*, **16**, 343–353.

Kokelj SV, Lantz TC, Kanigan J, Smith SS, Coutts R (2009) On the origin and polycyclic behaviour of tundra thaw slumps, Mackenzie Delta region, Northwest Territories, Canada. *Permafrost and Periglacial Processes*, **20**.

Lambert JDH (1976) Plant succession on an active tundra mud slump, Garry-Island, Mackenzie-river-delta, Northwest-Territories. *Canadian Journal of Botany*, **54**, 1750–1758.

Landhäusser SM, Wein RW (1993) Postfire vegetation recovery and tree establishment at the Arctic treeline – climate-change vegetation-response hypotheses. *Journal of Ecology*, **81**, 665–672.

Lantuit H, Pollard WH (2008) Fifty years of coastal erosion and retrogressive thaw slump activity on Herschel Island, southern Beaufort sea, Yukon Territory, Canada. *Geomorphology*, **95**, 84–102.

Lantz TC, Kokelj SV (2008) Increasing rates of retrogressive thaw slump activity in the Mackenzie Delta region, N.W.T., Canada. *Geophysical Research Letters*, **35**, 1–5.

Legendre P, Legendre L (1998) *Numerical Ecology*. Elsevier, Amsterdam.

Mackay JR (1963) *The Mackenzie Delta Area, N.W.T.* Department of Mines and Technical Surveys, Ottawa, ON.

Mackay JR (1974) Seismic shot holes and ground temperatures, Mackenzie Delta area, N.W.T. *Geological Survey of Canada Paper*, **74**, 389–390.

Mackay JR, Burn CR (2002) The first 20 years (1978–1979 to 1998–1999) of active-layer development, Illisarvik experimental drained lake site, western Arctic coast, Canada. *Canadian Journal of Earth Sciences*, **39**, 1657–1674.

Matthews RF (1992) Fire Effects Information System: *Alnus viridis* ssp. *crispa*. U.S. Department of Agriculture, Forest Service. Rocky Mountain Research Station, Fire Sciences Laboratory. http://www.fs.fed.us/database/feis/

McGuire AD, Chapin FS, Walsh JE, Wirth C (2006) Integrated regional changes in Arctic climate feedbacks: implications for the global climate system. *Annual Review of Environment and Resources*, **31**, 61–91.

Morneau C, Payette S (1989) Postfire lichen spruce woodland recovery at the limit of the boreal forest in northern Quebec. *Canadian Journal of Botany*, **67**, 2770–2782.

Morrell CH (1998) Likelihood ratio testing of variance components in the linear mixed-effects model using restricted maximum likelihood. *Biometrics*, **54**, 1560–1568.

Palmer MJ (2007) *Vegetation, snow cover and air and near-surface ground temperatures across treeline in the uplands east of the Mackenzie Delta, Northwest Territories.* Masters Thesis, Carleton University, Ottawa, ON.

Pearce CM, Mclennan D, Cordes LD (1988) The evolution and maintenance of white spruce woodlands on the Mackenzie Delta, N.W.T., Canada. *Holarctic Ecology*, **11**, 248–258.

Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography*, **12**, 361–371.

Pickett ST, White PS (1985) *The Ecology of Natural Disturbance and Patch Dynamics.* Academic Press, Orlando, FL.

Pomeroy JW, Bewley DS, Essery RLH *et al.* (2006) Shrub tundra snowmelt. *Hydrological Processes*, **20**, 923–941.

Porsild AE, Cody WJ (1980) *Vascular Plants of Continental Northwest Territories, Canada.* National Museum of Natural Sciences, National Museums of Canada, Ottawa.

Racine C, Jandt R, Meyers C, Dennis J (2004) Tundra fire and vegetation change along a hillslope on the Seward Peninsula, Alaska, USA. *Arctic Antarctic and Alpine Research*, **36**, 1–10.

Rhoades C, Binkley D, Oskarsson H, Stottlemyer R (2008) Soil nitrogen accretion along a floodplain terrace chronosequence in northwest Alaska: influence of the nitrogen-fixing shrub *Shepherdia canadensis*. *Écoscience*, **15**, 223–230.

Rhoades C, Oskarsson H, Binkley D, Stottlemyer R (2001) Alder (*Alnus crispa*) effects on soils vary with ecosystem type along the Agashashok river, northwest Alaska. *Écoscience*, **8**, 89–95.

Ritchie JC (1984) *Past and Present Vegetation of the Far Northwest of Canada.* University of Toronto Press, Toronto, ON.

Rupp TS, Chapin FS, Starfield AM (2000) Response of Subarctic vegetation to transient climatic change on the Seward Peninsula in north-west Alaska. *Global Change Biology*, **6**, 541–555.

SAS (2004) *SAS version 9.1.3. Help and Documentation.* SAS Institute, Cary, NC.

Schimel JP, Bilbrough C, Welker JA (2004) Increased snow depth affects microbial activity and nitrogen mineralization in two Arctic tundra communities. *Soil Biology & Biochemistry*, **36**, 217–227.

Staniforth RJ, Scott PA (1991) Dynamics of weed populations in a northern sub-arctic community. *Canadian Journal of Botany*, **69**, 814–821.

Stow DA, Hope A, McGuire D *et al.* (2004) Remote sensing of vegetation and land-cover change in Arctic tundra ecosystems. *Remote Sensing of Environment*, **89**, 281–308.

Sturm M, Schimel J, Michaelson G *et al.* (2005) Winter biological processes could help convert Arctic tundra to shrubland. *Bioscience*, **55**, 17–26.

Svoboda J, Henry GHR (1987) Succession in marginal Arctic environments. *Arctic and Alpine Research*, **19**, 373–384.

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

Thompson C, Beringer J, Chapin FS, McGuire AD (2004) Structural complexity and land-surface energy exchange along a gradient from Arctic tundra to boreal forest. *Journal of Vegetation Science*, **15**, 397–406.

Timoney KP, Laroi GH, Zoltai SC, Robinson AL (1992) The high sub-arctic forest-tundra of northwestern Canada - position, width, and vegetation gradients in relation to climate. *Arctic*, **45**, 1–9.

Turner MG, Romme WH, Tinker DB (2003) Surprises and lessons from the 1988 Yellowstone fires. *Frontiers in Ecology and the Environment*, **1**, 351–358.

Vavrek MC, Fetcher N, McGraw JB, Shaver GR, Chapin FS, Bovard B (1999) Recovery of productivity and species diversity in tussock tundra following disturbance. *Arctic Antarctic and Alpine Research*, **31**, 254–258.

Walker DA, Cate D, Brown J, Racine C (1987) *Disturbance and recovery of Arctic Alaskan tundra terrain: A review of recent investigations. CRREL Report 87-11.* US Army Corps of Engineers. Cold Regions Research and Engineering Laboratory, Hanover, NH.

Walker DA, Walker MD (1991) History and pattern of disturbance in Alaskan Arctic terrestrial ecosystems - a hierarchical approach to analyzing landscape change. *Journal of Applied Ecology*, **28**, 244–276.

Walker MD, Wahren CH, Hollister RD *et al.* (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.

Walsh NE, McCabe TR, Welker JM, Parsons AN (1997) Experimental manipulations of snow-depth: effects on nutrient content of caribou forage. *Global Change Biology*, **3** (Suppl. 1), 158–164.

White PS, Jentsch A (2001) The search for generality in studies of disturbance and ecosystem dynamics. *Progress in Botany*, **62**, 400–450.

Wolfe SA, Kotler E, Dallimore SR (2001) *Surficial Characteristics and the Distribution of Thaw Landforms (1970 to 1999), Shingle Point to Kay Point, Yukon Territory. Geological Survey of Canada, Open File 4088.* Geological Survey of Canada, Ottawa, ON.