ENVIRONMENTAL RESEARCH
LETTERS

LETTER • OPEN ACCESS

Drivers of tall shrub proliferation adjacent to the Dempster Highway, Northwest Territories, Canada

To cite this article: Emily A Cameron and Trevor C Lantz 2016 *Environ. Res. Lett.* **11** 045006

Environmental Research Letters

OPEN ACCESS

RECEIVED
31 December 2015

REVISED
10 March 2016

ACCEPTED FOR PUBLICATION
29 March 2016

PUBLISHED
19 April 2016

LETTER

Drivers of tall shrub proliferation adjacent to the Dempster Highway, Northwest Territories, Canada

Emily A Cameron and Trevor C Lantz
School of Environmental Studies, University of Victoria, Canada
E-mail: tlantz@uvic.ca

Keywords: shrub tundra, global change, disturbance, Low Arctic, green alder, biomass, air photographs
Supplementary material for this article is available online

Abstract
Arctic ecosystems are undergoing rapid changes as a result of climate warming and more frequent disturbances. Disturbances can have particularly large effects on high-latitude ecosystems when ecosystem structure and function is controlled by strong feedbacks between soil conditions, vegetation, and ground thermal regime. In this study we investigated the impact of road construction and maintenance on vegetation structure and biomass along the Dempster Highway where it crosses the Peel Plateau in the Northwest Territories. To explore drivers of tall shrub proliferation and to quantify shrub proliferation in this region of continuous permafrost, greyscale air photos (1975) and Quickbird satellite imagery (2008) were used to map landcover change within two 0.6 km^2 belts next to the road and two 0.6 km^2 belts 500 m away from the road. Maps showing areas where: 1) tall shrubs expanded, and 2) dwarf shrub tundra resisted invasion were then used to select field sites where a suite of biophysical variables were measured. Rapid tall shrub proliferation and greater biomass adjacent to the road indicate that disturbance can facilitate vegetation change in tundra environments. Our field data also suggests that increased shrub proliferation adjacent to the road was caused by greater soil moisture. Tall shrub proliferation adjacent to the road occurred at lower elevation sites characterized by wetter soils with thicker organic layers. Areas that resisted tall shrub encroachment were located at higher elevations and had drier soils with thin organic layers. Our observations also support previous work illustrating that tall shrub expansion next to the highway promotes strong positive feedbacks to ongoing shrub growth and proliferation.

1. Introduction

The structure and function of arctic ecosystems is changing in response to recent climate warming (Camill *et al* 2001, Jorgenson *et al* 2001, Cary *et al* 2006, Hudson and Henry 2009, Euskirchen *et al* 2010). Analyses of the normalized difference vegetation index (NDVI) show that the productivity of tundra vegetation has increased significantly in the past several decades (Jia *et al* 2003, Stow *et al* 2004, Kimball *et al* 2007, Beck 2011, Fraser *et al* 2014). Plot-based studies and observations from repeat photography link changes in NDVI with increased growth and reproduction of deciduous shrubs (Jia *et al* 2003, Tape *et al* 2006, Elmendorf *et al* 2012b, Lantz *et al* 2013).

Recent research also shows that disturbances can transform Arctic vegetation. Disturbances such as thaw slumps, lake drainage, tundra fire, and frost-heave all facilitate rapid shrub expansion in areas where shrubs were not previously dominant (Mackay and Burn 2002, Lantz *et al* 2009, 2010a, 2013, Frost *et al* 2013). Field studies of seismic lines, roads, and drilling mud sumps indicate that human-caused disturbances also stimulate tall shrub growth (Auerbach *et al* 1997, Johnstone and Kokelj 2008, Kemper and Macdonald 2009a, Gill *et al* 2014).

Evidence from plot-scale warming experiments (Chapin *et al* 1995, Bret-Harte *et al* 2001, Walker *et al* 2006, Elmendorf *et al* 2012a) combined with shrub dendrochronology studies (Forbes *et al* 2010, Myers-Smith *et al* 2015) attribute shrub proliferation in undisturbed areas to warming air temperatures. Some evidence also indicates that the effect of temperature on tall shrub proliferation is mediated by soil

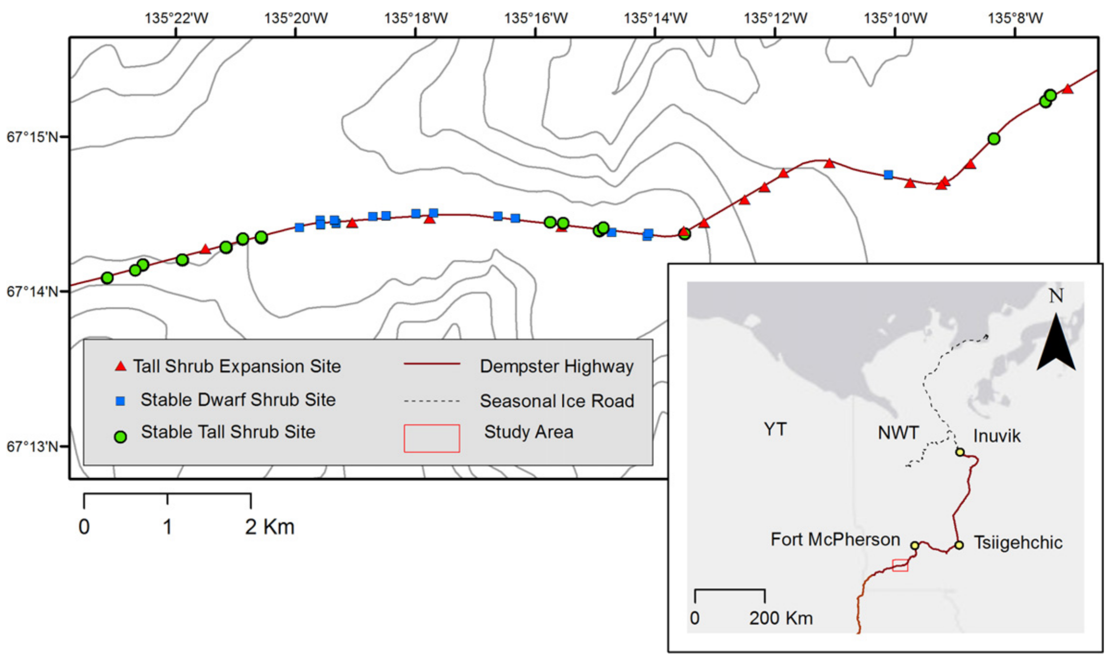

Figure 1. Map showing the study area and study sites adjacent to the Dempster Highway. Study sites were classified by the degree of tall shrub proliferation (see figure 2). Inset map at the bottom right indicates the position of the study area (box) in northern Canada.

moisture. Analysis of tall shrub growth rings and vegetation composition in permanent plots both show that increased shrub growth has been favoured at relatively wet sites (Elmendorf *et al* 2012b, Myers-Smith *et al* 2015). Tape *et al* (2006) also observed rapid tall shrub expansion in wet, high resource environments and snow depth manipulation experiments suggest that moisture facilitates shrub growth (Wahren *et al* 2005). Other studies also suggest that shrub proliferation at disturbed sites may also be mediated by changes to hydrology (Johnstone and Kokelj 2008, Naito and Cairns 2011b, Gill *et al* 2014), but additional field studies are required to test this hypothesis.

Linear disturbances provide an excellent opportunity to study the edaphic factors that mediate tall shrub proliferation because they typically traverse a range of ground conditions. Historical images of the Dempster Highway from 1975 that precede its official opening to traffic in 1979 and Quickbird imagery from 2008 allow comparisons of vegetation structure before and after prolonged disturbance from road use. Inspection of these images suggests that patchy shrub proliferation is related to variation in hydrological changes along the highway corridor. To test the hypothesis that increases in tall shrub density are linked to hydrological changes following road construction, we compared current (2013) biophysical factors between areas where shrub density increased between 1975 and 2008 with areas where the vegetation structure did not change during this period.

Insight into the causes of tall shrub proliferation is critical to our ability to forecast the nature and extent of Arctic vegetation change. Understanding the drivers of shrub proliferation is important for infrastructure management because shrub-snow feedbacks can increase ground temperatures and lead to permafrost thaw, which threatens terrain stability and increases the cost of infrastructure maintenance and repair (Gill *et al* 2014, O'Neill *et al* 2015). Understanding the factors that facilitate or constrain shrub proliferation is also significant because vegetation change can affect carbon storage, nutrient cycling, energy fluxes, hydrology, and ground thermal regime (Chapin *et al* 2005, Sturm *et al* 2005, Schuur *et al* 2008, Lantz *et al* 2009, Buckeridge *et al* 2010).

2. Methods

2.1. Study area

This research was conducted in the northern portion of the Peel Plateau ecoregion, along a 14 km stretch of the Dempster Highway in the Northwest Territories (figure 1). This section of the highway is bounded to the west by the Richardson Mountains and by the Peel River valley to the east. The Dempster Highway was constructed between 1959 and 1979 and passes over continuous permafrost (Smith *et al* 2005, Tunnicliffe *et al* 2009, O'Neill *et al* 2015). This area is situated at the edge of the boreal forest in the taiga plains ecozone (Roots *et al* 2004) and has elevations that range from 150 to 600 m above sea level. Vegetation communities vary with elevation with black spruce forest transitioning into shrub-dominated communities at higher elevations (Roots *et al* 2004). In our study area, tall shrub tundra is dominated by patches of *Alnus fruticosa* ((Ruprecht) Nyman) that are between 40 and 400 cm tall. *Rubus chamaemorus* (L.), *Betula glandulosa* (Michx.), and *Vaccinium* spp (L.) are present in

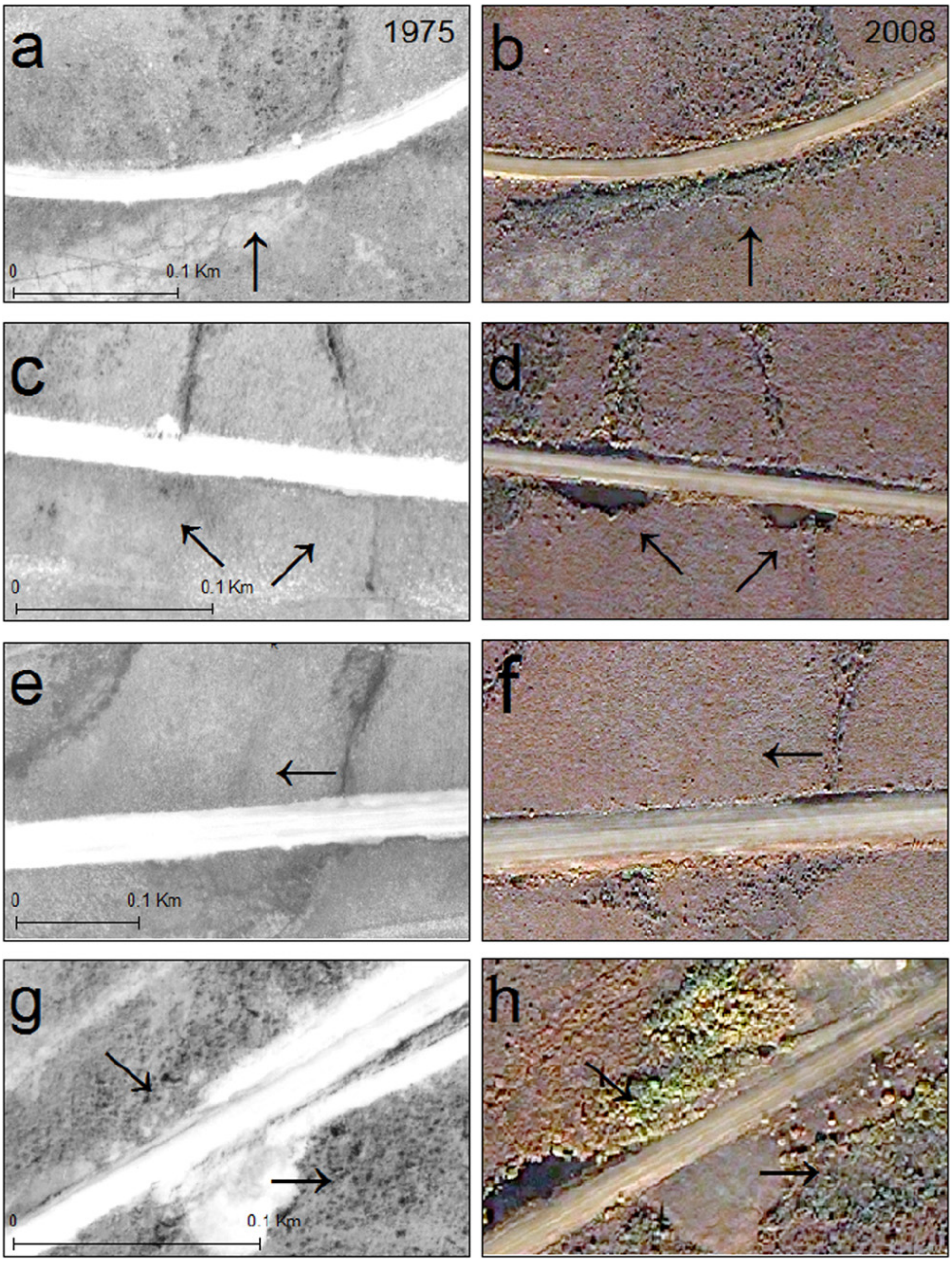

Figure 2. Historical greyscale air photos (1975) and contemporary satellite imagery (2008) of the same location. Images (a) and (b) illustrate a transition from dwarf shrub tundra to tall shrub tundra (arrows). Images (c) and (d) demonstrate an increase in ponding adjacent to the Dempster Highway (arrows). Images (e) and (f) indicate a stable patch of dwarf shrub tundra (arrows). Images (g) and (h) show a stable patch of tall shrub tundra. Arrows in (g) and (h) show the same shrub patches in both time periods.

the understory. Dwarf shrub tundra in this location is characterized by vegetation less than 40 cm tall, which is dominated by *Empetrum nigrum* (L.), *Ledum decumbens* (Aiton), *Rubus chamaemorus, Betula glandulosa*, and *Vaccinium* spp. Tall and dwarf shrub tundra at our study site is analogous to erect shrub tundra in the circumpolar vegetation map (Walker *et al* 2005).

The climate in this area is area is characterized by short cool summers and long cold winters. In Fort McPherson, the mean annual air temperature is −6.2 °C, and the mean summer air temperature is 13.3 °C. In this region, mean annual air temperatures have increased by 0.77 °C per decade since the 1970s (Burn and Kokelj 2009, Kokelj *et al* 2013). Mean annual precipitation in Fort McPherson is 310 mm, approximately half of which occurs as snow (Burn and Kokelj 2009). Precipitation in this region has increased in frequency and magnitude since 2005 (Kokelj *et al* 2015).

2.2. Airphoto analysis

To map land cover change in the study area, greyscale aerial photos from 1975 were compared with pan-sharpened Quickbird imagery acquired in September, 2008. Quickbird imagery had a resolution of 0.6 m. Greyscale aerial photos from 1975 (1:15 000) were scanned at 1200 dpi, but had an effective pixel size of

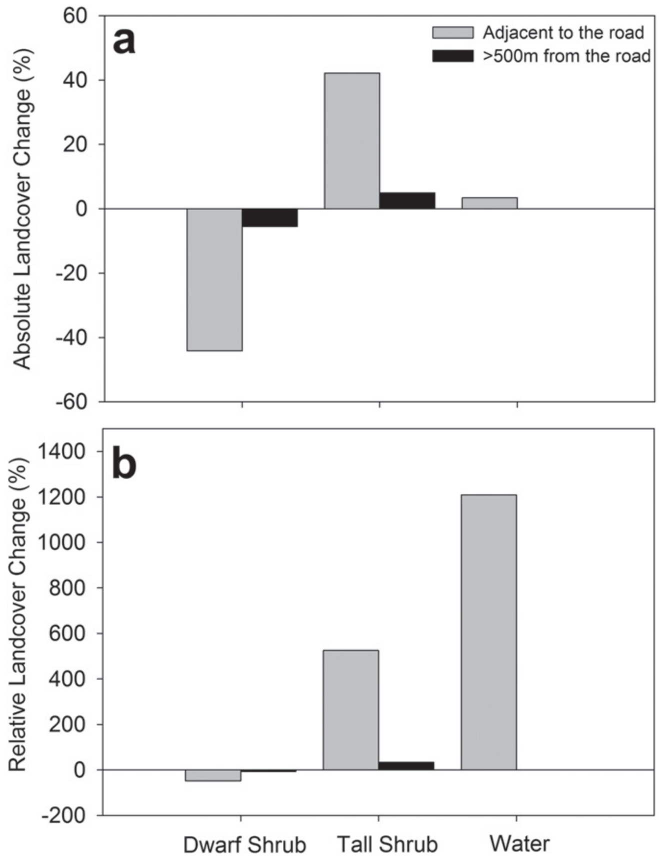

Figure 3. (a) Absolute landcover change (%) and (b) relative landcover change (%) adjacent to the Dempster Highway and more than 500 m from the Dempster Highway. Note the large increase in the cover of water and tall shrubs adjacent to the Dempster.

0.6 m, and were processed using the computer program Summit Evolution (version 6.4, DAT/EM Systems International, Alaska) to create soft copy stereo models. Vegetation mapping was completed inside 14 km belts on both sides of the road. Two of these were located adjacent to the road (road belts) and two were positioned away from the highway (control belts). The road belts extended 22 m past the toe of the road embankment. Control belts located 500 m away from the Dempster on both sides of the road were also 22 m wide. Both the control and road belts covered a total area of approximately 1.2 km^2. In both sets of imagery, tall shrubs, dwarf shrubs, and water were mapped when their area exceeded 1 m^2 (figure 2). Mapping was undertaken by one person and was completed onscreen while viewing softcopy stereo (1975) or Quickbird images (2008). Absolute change in tall shrub, dwarf shrub, and water cover was calculated from the area of each land cover type in 1975 and 2008 as:

$$\text{Absolute landcover change} = \left[\frac{\text{Area 2008} - \text{Area 1975}}{\text{Total area}}\right] * 100. \quad (1)$$

Relative change in tall shrub, dwarf shrub, and water cover was calculated from the area of each land cover type in 1975 and 2008 as:

$$\text{Relative landcover change} = \left[\frac{\text{Percent cover 2008} - \text{Percent cover 1975}}{\text{Percent cover 1975}}\right] * 100. \quad (2)$$

Maps of land cover from each time period were also used to map areas of landscape change and stability (figure 2). This was accomplished by using the RIKS Map Comparison Toolkit (version 3.3, Netherlands Environmental Assessment agency, The Netherlands) to produce maps showing areas of stable tall shrub cover, stable dwarf shrub cover, and tall shrub expansion.

2.3. Field sampling

To contrast biotic and abiotic conditions beside the road in: (1) areas of dwarf shrub that transitioned to tall shrub with (2) areas of dwarf shrub that resisted invasion, we used maps of land cover change to select field sites and verified these locations in the field. To minimize the effects of mapping error we selected the largest possible areas that exhibited extensive (>1600 m^2) tall shrub proliferation. Stable dwarf shrub sites were located in polygons larger than 1850 m^2 that had resisted all tall shrub proliferation. Stable tall shrub sites were areas that remained dominated by tall shrubs from 1975 onwards, and were only included in vegetation community analysis.

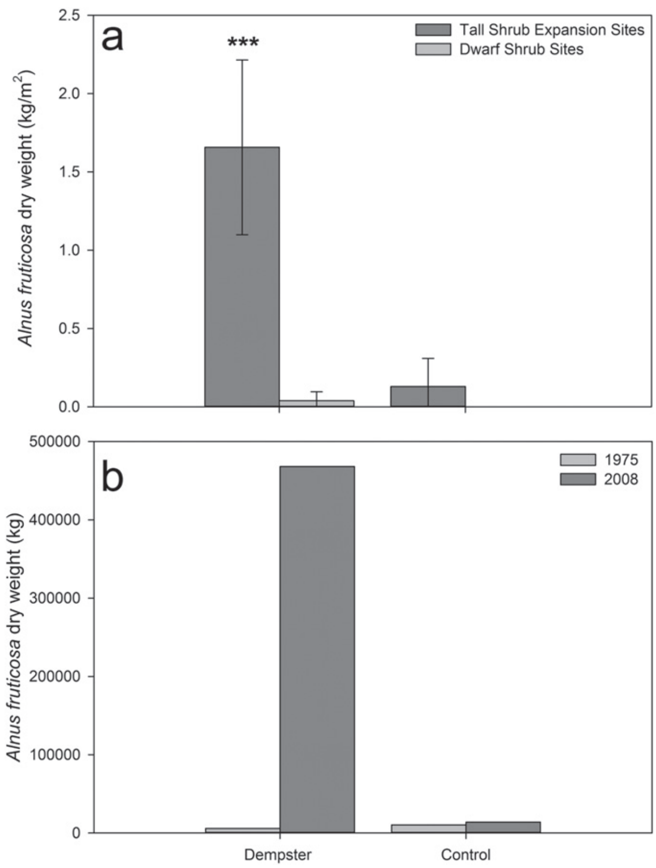

Figure 4. (a) Average *Alnus fruticosa* biomass (kg m^{-2}) at tall shrub expansion and dwarf shrub sites adjacent to the Dempster Highway, and at tall shrub expansion sites >500 m from the highway. Bars show means for each site type, and error bars represent the 95% confidence interval of the mean. Three asterisks (***) indicate that the contrast is significantly different ($\alpha = 0.05$). (b) Estimated dry *Alnus fruticosa* biomass (kg) in 1975 and 2008 at tall shrub expansion and dwarf shrub sites adjacent to the Dempster Highway and >500 m from the highway. Estimates from both time periods were calculated using average *Alnus fruticosa* biomass (kg m^{-2}) at tall shrub expansion and dwarf shrub sites adjacent to the Dempster Highway, and at tall shrub expansion sites >500 m from the highway. Changes in biomass across the study area were obtained by multiplying plot-based estimates (kg m^{-2}) with the area of tall shrub tundra in the belt adjacent to the Dempster Highway, and the belt more than 500 m from the highway.

Field sites were separated from each other by at least 300 m and were distributed across the north and south sides of the road. Fifteen roadside field sites in each vegetation type were located between 11 and 14 m from the toe of the road embankment and consisted of three subplots (5 m^2) that were 3 m from the center of the site on 120°, 240°, and 360° bearings ($n = 135$).

At each subplot, the percent cover of shrubs and trees was estimated inside a 5 m^2 quadrat. The percent cover of understory vegetation was estimated using a 0.625 m^2 quadrat randomly nested within the larger subplot. Gravimetric soil moisture was measured inside the 5 m^2 quadrat at each subplot by collecting a 250 cm^3 composite active layer sample. Soil samples were weighed to the nearest tenth of a gram, and then dried at 90 °C for 48 h in an oven. Gravimetric soil moisture (percent) was calculated using the following formula presented in Auerbach *et al* (1997):

$$\text{Gravimetric soil moisture} = ([(\text{wet weight} - \text{dry weight})/\text{dry weight}] * 100). \quad (3)$$

A portion of the 250 cm^3 composite active layer sample was used to measure the soil pH of each subplot by vigorously mixing 10 mg of soil with 30 ml of deionized water. The soil mixture was left to stand for two hours before measuring soil pH with a pH meter (Oakton Model 510 pH meter, YSI Environmental 2006). Within each 5 m^2 subplot, six active layer measurements were acquired by pushing a graduated soil probe to the depth of refusal. In hummocky terrain measurements were restricted to hummock tops. A metal ruler was inserted into a small hole to measure litter and organic soil thickness at each 5 m^2 subplot.

2.4. Biomass

To estimate the biomass associated with the shrub canopy, we installed 24 transects parallel to the road at locations that were distinct from the field sites used to characterize biotic and abiotic conditions. Transect locations were selected using the vegetation maps of each belt. Twelve transects were located in tall shrub ($n = 6$) and dwarf shrub vegetation ($n = 6$) adjacent

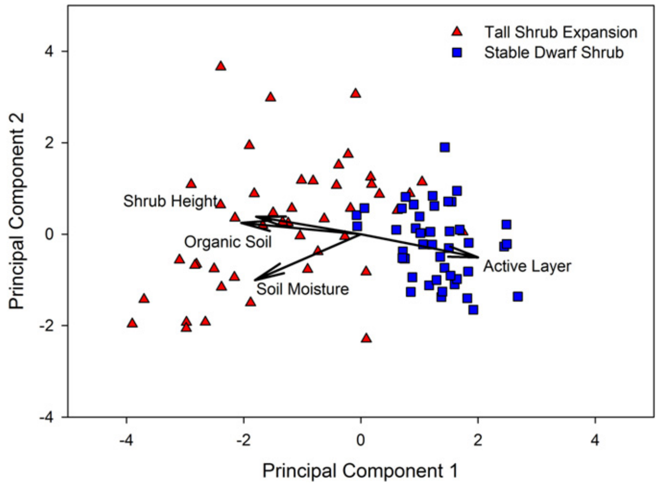

Figure 5. Scatterplot showing the principal components scores (PC1 and PC2) for each site. The arrows show variables with significant loadings ($\alpha < 0.01$) on PC1 and PC2.

Table 1. Mixed model results for comparisons of biotic and abiotic response variables between site types. Site type has two levels: stable dwarf shrub (DS) and tall shrub expansion (TS). Significant p-values are shown in bold text. The table shows means and their 95% confidence intervals.

Response variable	Mean TS	Mean DS	Effect	F	P	d.o.f
Litter (cm)	4.2 ± 0.7	3.7 ± 0.7	Site Type	3.8	0.0614	1,28
Organic soil depth (cm)	29.9 ± 3.7	17.9 ± 2.5	Site Type	27.36	**<0.0001**	1,28
Gravimetric soil moisture (%)	134.2 ± 41.9	56.2 ± 8.7	Site Type	12.75	**0.0013**	1,28
Soil pH	4.6 ± 0.3	4.5 ± 0.1	Site Type	0.3	0.5912	1,28
Active layer thickness (cm)	58.8 ± 10.8	84.2 ± 8.4	Site Type	49.56	**<0.0001**	1,88
Elevation (m)	433.6 ± 15.4	479.8 ± 10.1	Site Type	76.01	**<0.0001**	1,88
Embankment height (m)	2.1 ± 0.7	1.7 ± 0.6	Site Type	0.51	0.4759	1,88
Tall shrub height (cm)	331.8 ± 38.7	46.4 ± 7.6	Site Type	415.34	**<0.0001**	1,28
Understory height (cm)	19.7 ± 7.8	22.1 ± 5.8	Site Type	0.38	0.5441	1,28

to the Dempster Highway and twelve transects were located 500 m away from the highway in tall shrub ($n = 6$) and dwarf shrub vegetation ($n = 6$). Transects were 200 m long, and were located at least 300 m apart. Along each transect, three points were selected at random distances and the basal diameter of each *Alnus fruticosa* ramet was measured within a 5 m^2 quadrat centered on the transect point. Since no tall shrubs were observed at dwarf shrub transects within the control belt, this category was excluded from subsequent analysis. We measured a total of 435 *Alnus* ramets. On average, there were 34 ramets sampled in each subplot. To estimate *Alnus fruticosa* biomass, we used the generalized allometric equation derived by Berner *et al* (2015) relating *Alnus* basal diameter to dry biomass (kg m^{-2}). To estimate *Alnus* dry biomass (kg) in tall shrub and dwarf shrub belts adjacent and away from the Dempster in 1975 and 2008, we multiplied our plot-scale estimates of *Alnus* dry biomass (kg m^{-2}) with the area (m^2) of tall shrub tundra in each belt.

2.5. GIS analysis

To examine associations between biophysical factors and roadside tall shrub proliferation at a broader-scale, we compared maps of vegetation change with biophysical parameters derived from a LiDAR DEM (2013) of the Peel Plateau. The LiDAR DEM had a horizontal resolution of 1m and a vertical resolution of <1 m. We used ArcGIS and this DEM to calculate elevation, aspect, slope, and area solar radiation (ASR). ASR is calculated based on latitude, elevation, and surface orientation. A topographical wetness index (TWI) raster was also calculated in ArcGIS using the following formula provided by Sörensen *et al* (2006), where flow accumulation is based on the local upslope area that flows into each cell:

$$\text{TWI cell value} = \ln \{(([\text{flow accumulation}] + 1) * \text{pixel width}) / (\text{slope})\}. \tag{4}$$

To characterize elevation, aspect, slope, ASR, and TWI, we used ArcGIS to select 1000 random points in areas beside the road mapped as stable dwarf shrub and tall shrub expansion ($n = 2000$). To reduce the likelihood of mapping error, the following constraints were applied to point selection: (1) random points were allocated to areas of tall shrub expansion and

Table 2. Mixed model results for comparisons of GIS-derived response variables. Site type has two levels: stable dwarf shrub (DS) and tall shrub expansion (TS). Significant *p*-values are shown in bold text.

Response variable	Mean TS	Mean DS	Effect	*F*	*P*	d.o.f
Elevation (m)	430.5 ± 1.8	447.4 ± 1.9	Site Type	154.78	**<0.0001**	1, 1998
Topographic wetness index	2.3 ± 0.1	2.08 ± 0.09	Site Type	6.81	**0.0091**	1, 1998
Area Solar Radiation (W h m^{-2})	587 075 ± 2010	582 878 ± 2387	Site Type	8.56	**0.0035**	1, 1998
Slope (°)	4.7 ± 0.2	4.5 ± 0.2	Site Type	1.65	0.1985	1, 1998

stable dwarf shrub tundra that were greater than 100 m^2 and (2) all points were separated by at least 1m.

2.6. Statistical analysis

To compare vegetation community composition among tall shrub expansion, stable dwarf shrub, and stable tall shrub sites, a non-metric multidimensional scaling ordination of a Bray–Curtis resemblance matrix was performed with the PRIMER software program (Plymouth Marine Laboratories, Plymouth, UK). To determine if the community composition among site types was significantly different, we used PRIMER to perform an ANSOIM (analysis of similarities) with 999 permutations on the resemblance matrix. To determine the species that made the largest contribution to differences among site types, PRIMER was used to perform a SIMPER analysis on log($x + 1$) transformed cover data at all sites (Clarke and Gorley 2001).

To test for significant differences in biomass and abiotic and biotic conditions at tall shrub expansion and stable dwarf shrub sites, we used the GLIMMIX procedure in SAS (version 9.3) to create linear mixed models (SAS Institute, Cary, NC, USA). In models for abiotic and biotic conditions, site type (tall shrub expansion, stable dwarf shrub) was included as a fixed factor, and site and subplot were treated as random factors. In biomass models, transect identity (roadside tall shrub, control tall shrub, roadside dwarf shrub) was treated as a fixed factor, and transect number was treated as a random factor. In both cases the Kenward–Roger approximation was used to estimate the degrees of freedom in these models (Kenward and Roger 1997).

To explore the interrelationships among biotic and abiotic variables measured in the field, we used the statistical program R to perform a principal components analysis (R Core Team 2013). A correlation matrix was selected because abiotic factors were measured on different scales. To assess the significance of variable loadings on PC 1 and PC 2, we used R to perform 1000 permutations of a bootstrapped sample (Peres-Neto *et al* 2003).

3. Results

Disturbance associated with the construction and maintenance of the Dempster Highway has caused vegetation change adjacent to the road between 1975 and 2008 (figure 3). Shrub proliferation was more extensive adjacent to the Dempster, where the absolute increase in tall shrub cover was 42% (figure 3(a)) and the relative increase in tall shrub cover was 525% (figure 3(b)). In areas more than 500 m from the road, the absolute increase was only 5% (figure 3(a)), and the relative increase in tall shrub cover was 34% (figure 3(b)). The road had a significant impact on hydrology and large ponds were frequently visible on the modern images (figure 2). The absolute increase in the cover of water adjacent to the road was 3.4%. More than 500 m from the road, the absolute increase in the cover of water was negligible. Tall shrub expansion and increases in the cover of water were accompanied by concomitant decreases in the area of dwarf shrub (figure 3(a)). Although the area of dwarf shrub tundra decreased from 1975 to 2008, large patches of stable dwarf shrub tundra persisted adjacent to the Dempster (figure 2).

Average tall shrub biomass adjacent to the road was close to 13 times greater per square meter than tall shrub biomass in the control belt (figure 4, $F_{2,15} = 17.36, p < 0.001$). Average tall shrub biomass (kg m^{-2}) at dwarf shrub sites adjacent to the road and tall shrub sites away from the road was not significantly different (figure 4(a)). By combining our air photo estimates of the change in areal cover of shrubs with the allometric measurements made in the field, we estimate that increases in tall shrub biomass next to the road were 106 times greater than increases in shrub biomass 500 m away from the road (figure 4(b)). From 1975 to 2008, tall shrub biomass at the Dempster increased by a factor of 81.2, whereas at the control belt, tall shrub biomass only increased by a factor of 1.3 (figure 4(b)).

At sites where tall shrub expansion occurred, the vegetation was significantly different from stable dwarf shrub sites ($R_{ANOSIM} = 0.89, p < 0.001$) (figure S1, table S1). Tall shrub expansion sites were characterized by greater cover of *A. fruticosa* and litter, and lower cover of *R. chamaemorus*, *L. decumbens*, *E. nigrum*, and *V. vitis-idaea* than stable dwarf shrub sites. The vegetation at stable tall shrub sites differed significantly from stable dwarf shrub sites ($R_{ANOSIM} = 0.93, p < 0.001$). This difference was driven by greater cover of *A. fruticosa*, *Salix* spp, and litter and lower cover of *R. chamaemorus* and ericaceous shrubs at stable tall shrub sites. Vegetation community composition at stable tall shrub tundra and tall shrub tundra expansion sites was nearly indistinguishable ($R_{ANOSIM} = 0.12$, $p < 0.001$), with the main differences being greater *Salix* spp. cover at stable tall shrub sites, and greater *A. fruticosa* cover in tall shrub expansion sites (table S1).

Biotic and abiotic response variables measured adjacent to the road in 2013 varied between site types (figure 5). The principle component analysis shows that higher soil moisture, greater shrub height and thicker organic soils were strongly associated with tall shrub expansion sites and correlated with each other. Deeper active layers were strongly associated with stable dwarf shrub sites and were negatively correlated with greater shrub height and thick organic soil and to a lesser degree, soil moisture (figure 5). Comparisons of field-measured biotic and abiotic response variables revealed significant differences between sites types (table 1, figure S2). The average elevation of dwarf shrub sites was 46 m higher than tall shrub expansion sites, but the average embankment height did not differ (table 1, figure S2(a)). Soil conditions also showed significant differences between site types. Tall shrub expansion sites were 2.3 times wetter and had organic soils horizons close to twice as thick as stable dwarf shrub sites (table 1, figures S2(c), S2(d)). Active layer thickness at tall shrub expansion sites was significantly lower when compared with stable dwarf shrub sites (table 1, figure S2(e)), but soil pH and average litter depth were similar between sites types (table 1, figures S2(f) and S2(g)). Maximum shrub height was 7 times greater at tall shrub expansion sites than stable dwarf shrub sites, but maximum understory height did not differ between site types (table 1, figure S2(h)).

Abiotic variables derived from GIS revealed differences between stable dwarf and tall shrub expansion sites (table 2, figure S3). Stable dwarf shrub sites occurred at higher elevations than tall shrub expansion sites beside the road (table 2, figure S3(a)) and the topographic wetness (TWI) index was significantly higher at tall shrub expansion sites than stable dwarf shrub sites (table 2, figures S3(b)). The incidence of ASR was higher at tall shrub expansion sites (table 2, figure S3(c)), but slope was not significantly different between site types (table 2, figure S3(d)).

4. Discussion

Rapid tall shrub proliferation next to the Dempster Highway suggests that abiotic changes associated with road construction and maintenance have intensified the effects of a warming climate on shrub growth and reproduction. Increases in shrub cover of approximately 0.8% per year at undisturbed sites in the Peel Plateau are consistent with other studies that have documented tall shrub proliferation across the Low Arctic (Jia *et al* 2003, Tape *et al* 2006, McManus *et al* 2012, Lantz *et al* 2013, Fraser *et al* 2014). Both plot-scale warming experiments (Walker *et al* 2006, Elmendorf *et al* 2012a) and shrub dendrochronology studies (Forbes *et al* 2010, Myers-Smith *et al* 2015) strongly indicate that pan-arctic tall shrub expansion has been driven by increases in air temperatures. Rapid temperature increases in Canada's western subarctic have been reported (IPCC 2013) and it is likely that the direct and indirect effects of warmer air temperatures have contributed to the shrub expansion we observed at sites on the Peel Plateau. Large increases in the biomass of tall shrubs adjacent to the road between 1975 and 2008 show that abiotic changes associated with disturbance drive significantly larger changes in tall shrub productivity than the effects of warmer air temperatures alone. This clearly indicates that tundra disturbances can have a disproportionately large impact on ecosystem configuration relative to the size of the disturbance-affected area (Lantz *et al* 2010, Frost *et al* 2013).

Greater shrub proliferation and biomass adjacent to the road was likely caused by the effects of elevated soil moisture on *Alnus* establishment and growth. We observed higher gravimetric soil moisture readings at tall shrub expansion sites next to the road, and TWI values along the Dempster indicated that tall shrub expansion sites had higher soil moisture compared to stable dwarf shrub sites. Our air photo analysis also revealed increases in standing water next to the road between 1975 and 2008, suggesting that changes to soil moisture regimes were pronounced adjacent to the Dempster. In contrast, minute increases in standing water at sites away from the road during this same time period corresponded with much smaller changes to tall shrub proliferation and biomass away from the road. Generally, patches of stable dwarf shrub tundra persisted at the crest of elevated ridges along the plateau, where soils were drier and vegetation was more exposed to snow scouring from winter winds (Blok *et al* 2015). The idea that dry soils limit tall shrub proliferation is supported by our observation that shrub patches in 1975 were constrained to drainages and water tracks. *Alnus fruticosa* is known to favour mesic to moist soil conditions since higher soil moisture allows for increased rates of N mineralization and accelerated shrub growth rates (Furlow 1979, Hendrickson *et al* 1982, Binkley *et al* 1994, Myers-Smith *et al* 2015). Blowing snow that accumulates in drainages and water tracks can also protect shrubs from wind and desiccation damage (Ropars *et al* 2015, Swanson 2015). Our field evidence that tall shrub proliferation is facilitated by elevated soil moisture is consistent with Tape *et al*'s (2006) observation that shrub expansion in Alaska occurred preferentially in wet, high resource environments.

Increased soil moisture and altered drainage patterns beside the road was likely caused by increased snow accumulation next to the road embankment. Research in other areas of the subarctic and arctic has shown that obstructions, such as trees, roads, and snow fences promote snow drift formation and can significantly increase maximum winter snow depth (Hiemstra *et al* 2002, Hinkel and Hurd 2006, Burn *et al* 2009, Fortier *et al* 2011). Deeper snow increases localized spring run-off and likely elevates soil moisture (Wahren *et al* 2005, Hinkel and Hurd 2006). Deeper snow pack also insulates the ground, reduces winter cooling, and can promote permafrost degradation and thicker active layers (Hinkel and Hurd 2006, Alfaro *et al* 2009, Burn *et al* 2009, Fortier *et al* 2011). Warmer ground temperatures can result in subsidence and thaw consolidation that creates depressions adjacent to the road (Hinkel and Hurd 2006, Alfaro *et al* 2009, Fortier *et al* 2011). Soil moisture beside the Dempster may also have been increased where the road blocked existing drainages or culverts failed.

It is likely that positive feedbacks initiated by the establishment of shrubs beside the road also contributed to ecosystem change. Gill *et al* (2014) showed that shrub colonization beside the Dempster increases the size of the snow drift, which in turn insulates the ground against winter air temperatures. On the Peel Plateau, temperatures beneath patches of tall shrubs are significantly warmer during the winter, and freeze-back occurs much later when compared with patches of dwarf shrubs (Gill *et al* 2014, O'Neill *et al* 2015). Warmer ground temperatures and increases in soil moisture affect the timing and duration of ground freeze, have strong impacts on microbial activity, nutrient cycling, and decomposition rates, and create favourable conditions for tall shrub growth (Viereck *et al* 1983, Romanovsky and Osterkamp 2000, Mikan *et al* 2002, Schimel *et al* 2004, Wahren *et al* 2005, Buckeridge and Grogan 2008, Buckeridge *et al* 2010). As well as providing larger inputs of high quality litter, the proliferation of *Alnus*, a minerotrophic shrub, has been associated with favourable conditions for organic soil development (Zasada 1986, Buckeridge *et al* 2010, Frost *et al* 2013). Thicker organic soils affect ground thermal properties (Dyrness 1982), and a larger shrub canopy enhances road dust interception, which increases nutrient availability and promotes shrub growth (Gill *et al* 2014).

Despite reports of warmer ground temperatures at tall shrub sites adjacent to the Dempster (Gill *et al* 2014), we found that active layer thickness was significantly reduced at roadside tall shrub expansion sites. It is likely that summer shading by the tall shrub canopy, thick organic soil layers, and increased soil moisture reduced summer ground thaw and limited active layer development (Blok *et al* 2010). However, Gill *et al*'s (2014) observation of elevated permafrost temperatures beneath shrub canopies beside the road, indicates that winter conditions have a larger impact on ground thermal regime than summer processes (Romanovsky and Osterkamp 2000, Sturm *et al* 2001, Palmer *et al* 2012, Gill *et al* 2014). Additional research on the impact of tall shrub proliferation on the balance between winter and summer heat flux is needed, but the results from our study, as well as work by O'Neill *et al* (2015) and Gill *et al* (2014) indicate that continued shrub growth has the potential to facilitate permafrost degradation and compromise the structural integrity of the Dempster Highway.

Although our study area was relatively small, we believe that the Peel Plateau is representative of erect shrub tundra across the Arctic. This terrain type makes up about 18% of the arctic and includes large areas of: the Seward Peninsula, the Tuktoyaktuk Coastlands, the Hudson's Bay Lowlands and eastern Russia (Walker *et al* 2005). Our findings suggest that disturbances affecting hydrological conditions and snow accumulation patterns in this terrain type will have strong impacts on vegetation structure and biomass. Our observations from the Peel Plateau also suggest that temperature-induced shrub proliferation in other areas of erect shrub tundra may have been mediated by soil moisture. Fine and broad-scale change detection studies show that shrub proliferation has been patchy (Tape *et al* 2006, Bhatt *et al* 2010, Lantz *et al* 2013, Fraser *et al* 2014), and it is possible that this pattern of shrub proliferation is related to spatial variation in soil moisture. Shrub dendrochronology (Myers-Smith *et al* 2015), plot-based studies (Elmendorf *et al* 2012b), modelling studies (Naito and Cairns 2011a, 2011b), and air photo analysis (Tape *et al* 2006) also suggest that rapid shrub growth preferentially occurs in mesic-moist areas.

5. Conclusions

(1) Construction and maintenance of the Dempster Highway has intensified the effects of a warming climate on tall shrub growth and proliferation.

(2) Rapid tall shrub proliferation adjacent to the Dempster was facilitated by increases in soil moisture.

(3) Greater tall shrub biomass adjacent to the Dempster shows that disturbances can have a disproportionately large impact on ecosystem configuration relative to the size of the disturbed area.

Acknowledgments

This research was supported by the Natural Sciences and Engineering Research Council of Canada, the Canada Foundation for Innovation, the NWT Cumulative Impact Monitoring Program, and the Northern Scientific Training Program (NSTP). Logistical support was provided by the Aurora Research Institute in Inuvik. For assistance in the field and lab, the authors would like to thank: Christine Firth, Peter Snowshoe, the Tetlit Gwich'in Renewable Resources Council, Mat Whitelaw, Harneet Gill, Audrey Steedman, Kaylah Lewis, Krista Chin, Claire Marchildon, Becky Segal, Chanda

Brietzke, Abra Martin, Brendan O'Neill, and Marcus Phillips. The authors would like to thank Karen Harper, Brian Starzomski, Janet Jorgenson, and an anonymous reviewer for helpful commentary on previous drafts of this manuscript.

References

Alfaro M C, Ciro G A, Thiessen K J and Ng T 2009 Case study of degrading permafrost beneath a road embankment *J. Cold Reg. Eng.* **23** 93–111

Auerbach N A, Walker M D and Walker D A 1997 Effects of roadside disturbance on substrate and vegetation properties in arctic tundra *Ecological Appl.* **7** 218–35

Beck P S A 2011 Satellite observations of high northern latitude vegetation productivity changes between 1982 and 2008: ecological variability and regional differences *Environ. Res. Lett.* **6** 045501

Berner L T, Alexander H D, Loranty M M, Ganzlin P, Mack M C, Davydov S P and Goetz S J 2015 Biomass allometry for alder, dwarf birch, and willow in boreal forest and tundra ecosystems of far northeastern Siberia and north-central Alaska *Forest Ecology Manage.* **337** 110–8

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

Binkley D, Stottlemyer R, Suarez F and Cortina J 1994 Soil nitrogen availability in some arctic ecosystems in northwest Alaska: responses to temperature and moisture *Écoscience* **1** 64–70 (www.jstor.org/stable/42902331)

Blok D, Heijmans M M P D, Schaepman Strub G, Kononov A V, Maximov T C and Berendse F 2010 Shrub expansion may reduce summer permafrost thaw in Siberian tundra *Glob. Change Biol.* **16** 1296–305

Blok D, Weijers S, Welker J M, Cooper E J, Michelsen A, Löffler J and Elberling B 2015 Deepened winter snow increases stem growth and alters stem δ^{13}C and δ^{15}N in evergreen dwarf shrub *Cassiope tetragona* in high-arctic Svalbard tundra *Environ. Res. Lett.* **10** 044008

Bret-Harte M S, Shaver G R, Zoerner J P, Johnstone J F, Wagner J L, Chavez A S, Gunkelman R F IV, Lippert S C and Laundre J A 2001 Developmental plasticity allows Betula nana to dominate tundra subjected to an altered environment *Ecology* **82** 18–32

Buckeridge K M and Grogan P 2008 Deepened snow alters soil microbial nutrient limitations in arctic birch hummock tundra *Appl. Soil Ecology* **39** 210–22

Buckeridge K M, Zufelt E, Chu H and Grogan P 2010 Soil nitrogen cycling rates in low arctic shrub tundra are enhanced by litter feedbacks *Plant Soil* **330** 407–21

Burn C R and Kokelj S V 2009 The environment and permafrost of the Mackenzie Delta area *Permafrost Periglacial Process.* **20** 83–105

Burn C R, Mackay J R and Kokelj S V 2009 The thermal regime of permafrost and its susceptibility to degradation in upland terrain near Inuvik, N.W.T *Permafrost Periglacial Process.* **20** 221–7

Camill P, Lynch J A, Clark J S, Adams J B and Jordan B 2001 Changes in biomass, aboveground net primary production, and peat accumulation following permafrost thaw in the boreal peatlands of Manitoba, Canada *Ecosystems* **4** 461–78

Cary G J, Keane R E, Gardner R H, Lavorel S, Flannigan M D, Davies I D, Li C, Lenihan J M, Rupp T S and Mouillot F 2006 Comparison of the sensitivity of landscape-fire-succession models to variation in terrain, fuel pattern, climate and weather *Landscape Ecology* **21** 121–37

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

Chapin F S *et al* 2005 Role of land-surface changes in Arctic summer warming *Science* **310** 657–60

Clarke K R and Gorley R N 2001 *Primer v5: Users Manual/Tutorial* (Plymouth, MA: Primer-E)

Dyrness C T 1982 *Control of Depth to Permafrost and Soil Temperature by Forest Floor in Black Spruce/Feather Moss Communities* vol 396 (Portland, OR: US Department of Agriculture)

Elmendorf S C, Henry G H R, Hollister R D, Björk R G, Bjorkman A D, Callaghan T V, Siegwart Collier L and Cooper E J 2012a Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time *Ecology Lett.* **15** 164–75

Elmendorf S C *et al* 2012b Plot-scale evidence of tundra vegetation change and links to recent summer warming *Nat. Clim. Change* **2** 453–7

Epstein H E, Beringer J, Gould W A, Lloyd A H, Thompson C D, Chapin F S, Michaelson G J, Ping C L, Rupp T S and Walker D A 2004a The nature of spatial transitions in the Arctic *J. Biogeography* **31** 1917–33

Epstein H E, Calef M P, Walker M D, Chapin F S and Starfield A M 2004b Detecting changes in arctic tundra plant communities in response to warming over decadal time scales *Glob. Change Biol.* **10** 1325–34

Euskirchen E S, McGuire A D, Chapin F S and Rupp T S 2010 The changing effects of Alaska's boreal forests on the climate system *Can. J. Forest Res.* **40** 1336–46

Forbes B C, Fauria M M and Zetterberg P 2010 Russian Arctic warming and 'greening' are closely tracked by tundra shrub willows *Glob. Change Biol.* **16** 1542–54

Fortier R, LeBlanc A-M and Yu W 2011 Impacts of permafrost degradation on a road embankment at Umiujaq in Nunavik (Quebec), Canada *Can. Geotechnical J.* **48** 720–40

Fraser R H, Lantz T C, Olthof I, Kokelj S V and Sims R A 2014 Warming-induced shrub expansion and lichen decline in the Western Canadian Arctic *Ecosystems* **17** 1151–68

Frost G V, Epstein H E, Walker D A, Matyshak G and Ermokhina K 2013 Patterned-ground facilitates shrub expansion in low arctic tundra *Environ. Res. Lett.* **8** 015035

Furlow J J 1979 Systematics of the American species of Alnus (Betulaceae) *Rhodora* **81** 1–121 (www.jstor.org/stable/23310969)

Gill H K, Lantz T C, O'Neill B and Kokelj S V 2014 Cumulative impacts and feedbacks of a gravel road on shrub tundra ecosystems in the Peel Plateau, Northwest Territories, Canada *Arctic Antarctic Alpine Res.* **46** 947–61

Hendrickson O, Robinson J B and Chatarpaul L 1982 *The Microbiology of Forest Soils: a Literature Review* (Chalk River, Ontario: Environment Canada, Canadian Forestry Service) PI-X-19

Hiemstra C A, Liston G E and Reiners W A 2002 Snow redistribution by wind and interactions with vegetation at upper treeline in the Medicine Bow Mountains, Wyoming, USA *Arctic Antarctic Alpine Res.* **34** 262

Hinkel K M and Hurd J K 2006 Permafrost destabilization and thermokarst following snow fence installation, Barrow, Alaska, USA *Arctic Antarctic Alpine Res.* **38** 530–9

Hudson J M G and Henry G H R 2009 Increased plant biomass in a high arctic heath community from 1981 to 2008 *Ecology* **90** 2657–63

IPCC 2013 *Climate Change 2013: The Physical Science Basis, Contribution of Working Group 1 to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* ed T F Stocker *et al* (Cambridge: Cambridge University Press)

Jia G S J, Epstein H E and Walker D A 2003 Greening of arctic Alaska, 1981–2001 *Geophys. Res. Lett.* **30** 1029–33

Johnstone J F and Kokelj S V 2008 Environmental conditions and vegetation recovery at abandoned drilling mud sumps in the Mackenzie Delta region, Northwest Territories, Canada *Arctic* **61** 199–211 (www.jstor.org/stable/40513206)

Jorgenson M T, Racine C H, Walters J C and Osterkamp T E 2001 Permafrost degradation and ecological changes associated

with a warming climate in central Alaska *Clim. Change* **48** 551–79
Kemper J T and Macdonald S E 2009a Directional change in upland tundra plant communities 20–30 years after seismic exploration in the Canadian low-arctic *J. Vegetation Sci.* **20** 557–67
Kenward M G and Roger J H 1997 Small sample inference for fixed effects from restricted maximum likelihood *Biometrics* **53** 983–97
Kimball J S *et al* 2007 Recent climate-driven increases in vegetation productivity for the western arctic: evidence of an acceleration of the northern terrestrial carbon cycle *Earth Interact.* **11** 1–30
Kokelj S V, Lacelle D, Lantz T C, Tunnicliffe J, Malone L, Clark I D and Chin K S 2013 Thawing of massive ground ice in mega slumps drives increases in stream sediment and solute flux across a range of watershed scales: fluvial impacts of thermokarst *J. Geophys. Res.: Earth Surf.* **118** 681–92
Kokelj S V, Tunnicliffe J, Lacelle D, Lantz T C, Chin K S and Fraser R 2015 Increased precipitation drives mega slump development and destabilization of ice-rich permafrost terrain, northwestern Canada *Glob. Planet. Change* **129** 56–68
Lantz T C, Gergel S E and Henry G H R 2010a Response of green alder (Alnus viridis subsp. fruticosa) patch dynamics and plant community composition to fire and regional temperature in north-western Canada *J. Biogeography* **37** 1597–610
Lantz T C, Kokelj S V, Gergel S E and Henry G H R 2009 Relative impacts of disturbance and temperature: persistent changes in microenvironment and vegetation in retrogressive thaw slumps *Glob. Change Biol.* **15** 1664–75
Lantz T C, Marsh P and Kokelj S V 2013 Recent shrub proliferation in the Mackenzie Delta uplands and microclimatic implications *Ecosystems* **16** 47–59
Mackay J R and Burn C R 2002 The first 20 years (1978–1979 to 1998–1999) of ice-wedge growth at the Illisarvik experimental drained lake site, western Arctic coast, Canada *Can. J. Earth Sci.* **39** 95–111
McManus M, Morton D C, Masek J G, Wang D, Sexton J O, Nagol J R, Ropars P and Boudreau S 2012 Satellite-based evidence for shrub and graminoid tundra expansion in northern Quebec from 1986 to 2010 *Glob. Change Biol.* **18** 2313–23
Mikan C J, Schimel J P and Doyle A P 2002 Temperature controls of microbial respiration in arctic tundra soils above and below freezing *Soil Biol. Biochemistry* **34** 1785–95
Myers-Smith I H *et al* 2015 Climate sensitivity of shrub growth across the tundra biome *Nat. Clim. Change* **5** 1–5
Naito A T and Cairns D M 2011a Patterns and processes of global shrub expansion *Prog. Phys. Geography* **35** 423–42
Naito A T and Cairns D M 2011b Relationships between Arctic shrub dynamics and topographically derived hydrologic characteristics *Environ. Res. Lett.* **6** 045506
O'Neill H B, Burn C R, Kokelj S V and Lantz T C 2015 'Warm' tundra: atmospheric and near-surface ground temperature inversions across an alpine tree line in continuous permafrost, western Arctic, Canada *Permafrost Periglacial Process.* **26** 103–18
Palmer M J, Burn C R, Kokelj S V and Allard M 2012 Factors influencing permafrost temperatures across tree line in the uplands east of the Mackenzie Delta, 2004–2010 *Can. J. Earth Sci.* **49** 877–94
PARC Technical Bulletin No. 04-01 Summerland, British Columbia Volume 313
Peres-Neto P R, Jackson D A and Somers K M 2003 Giving meaningful interpretation to ordination axes: assessing loading significance in principal component analysis *Ecology* **84** 2347–63
R Core Team 2013 *R: A Language and Environment For Statistical Computing* (Vienna, Austria: R Foundation for Statistical Computing) (www.R-project.org/)
Romanovsky V and Osterkamp T E 2000 Effects of unfrozen water on heat and mass transport processes in the active layer and permafrost *Permafrost Periglacial Process.* **11** 219–39
Roots C F, Smith C A S and Meikle J C 2004 Ecoregions of the Yukon Territory: biophysical properties of Yukon landscapes *PARC Technical Bulletin No. 04-01, vol 313* Summerland, British Columbia
Ropars P, Lévesque E and Boudreau S 2015 How do climate and topography influence the greening of the forest-tundra ecotone in northern Québec? A dendrochronological analysis of Betula glandulosa *J. Ecology* **103** 679–90
Schimel J P, Bilbrough C and Welker J M 2004 Increased snow depth affects microbial activity and nitrogen mineralization in two arctic tundra communities *Soil Biol. Biochemistry* **36** 217–27
Schuur E A G *et al* 2008 Vulnerability of permafrost carbon to climate change: implications for the global carbon cycle *Bioscience* **58** 701–14
Smith S L, Burgess M M, Riseborough D and Mark Nixon F 2005 Recent trends from Canadian permafrost thermal monitoring network sites *Permafrost Periglacial Process.* **16** 19–30
Sörensen R, Zinko U and Seibert J 2006 On the calculation of the topographic wetness index: evaluation of different methods based on field observations *Hydrology Earth Syst. Sci. Discuss.* **10** 101–12
Stow D A *et al* 2004 Remote sensing of vegetation and land-cover change in arctic tundra ecosystems *Remote Sens. Environ.* **89** 281–308
Sturm M, Holmgren J, McFadden J P, Liston G E, Chapin F S III and Racine C H 2001 Snow-shrub interactions in arctic tundra: a hypothesis with climatic implications *J. Clim.* **14** 336–44
Sturm M, Schimel J, Michaelson G, Welker J M, Oberbauer S F, Liston G E, Fahnestock J and Romanovsky V 2005 Winter biological processes could help convert arctic tundra to shrubland *BioScience* **55** 17–26
Swanson D K 2015 Environmental limits of tall shrubs in Alaska's arctic national parks *PloS One* **10** e0138387
Tape K, Sturm M and Racine C 2006 The evidence for shrub expansion in Northern Alaska and the Pan-Arctic *Glob. Change Biol.* **12** 686–702
Tunnicliffe J, Kokelj S V and Burn C R 2009 Geomorphic characterization of 'mega-slumps' in the Peel Plateau, NWT *Geohydro* vol 2011
Viereck L, Dyrness C, Van Cleve K and Foote M J 1983 Vegetation, soils, and forest productivity in selected forest types in interior Alaska *Can. J. Forest Res.* **13** 703–20
Wahren C-H A, Walker M D and Bret-Harte M S 2005 Vegetation responses in Alaskan arctic tundra after 8 years of a summer warming and winter snow manipulation experiment *Global Change Biology* **11** 537–52
Walker D A *et al* 2005 The circumpolar Arctic vegetation map *J. Vegetation Sci.* **16** 267–82
Walker M D *et al* 2006 Plant community responses to experimental warming across the tundra biome *Proc. Natl Acad. Sci. USA* **103** 1342–6
Zasada J 1986 Forest ecosystems in the Alaskan taiga natural regeneration of trees and tall shrubs on forest sites in interior Alaska *Ecological Stud.* **57** 44–73