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Cumulative impacts and feedbacks of a gravel road on shrub tundra ecosystems in the Peel Plateau, Northwest Territories, Canada

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Abstract

Gravel highways in the continuous permafrost zone provide critical transportation links that are increasingly vulnerable to the impacts of climate warming and permafrost thaw. To examine if the physical effects associated with the construction, maintenance, and use of gravel roads alter vegetation and permafrost conditions, we measured vegetation, soils, and near-surface ground temperatures at tall and dwarf shrub tundra sites adjacent to and distant from the Dempster Highway in the Northwest Territories of Canada. We found that alder growth and recruitment were significantly enhanced adjacent to the highway. Where alder shrubs had formed closed canopies, we observed dramatic alterations to plant community composition, soil properties, and ground temperatures. Tall shrub sites adjacent to the road exhibited less understory vegetation, greater litter and organic layer thickness, higher nutrient availability, and thicker snowpack than all other site types. Our results show that in shrub tundra ecosystems the conditions generated by the maintenance and use of a gravel road can drive ecological feedbacks that magnify changes to vegetation communities and soils. We found that where the road facilitated shrub dominance, feedbacks were initiated that enhanced snow accumulation and altered ground temperatures and soil chemistry. In turn, these changes likely promoted enhanced shrub recruitment and growth. Shrub proliferation adjacent to highways is an important consideration for the planning and maintenance of this form of infrastructure. To improve our understanding of the spatial heterogeneity of shrub proliferation, research exploring the relationships between biophysical landscape features and shrub development is also needed.

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Introduction

Gravel highways and roads are commonly constructed in regions underlain by continuous permafrost because they are less costly to construct and easier to maintain than paved surfaces (GNWT, 2012; Walker et al., 1987). These surfaces provide critical transportation corridors between northern communities in Canada and the South. Northern roads are increasingly vulnerable to environmental changes, including changing precipitation regimes and permafrost degradation (Burn and Kokelj, 2009; Moritz et al., 2002; Romanovsky et al., 2010; Tape et al., 2006). Gravel roads alter surface and subsurface conditions, which influence the surface energy balance, near-surface ground thermal properties, and the temperature regime of the underlying and adjacent permafrost. Road embankments modify local hydrology and create a physical barrier that fragments the landscape. During initial construction, the removal of vegetation and establishment of culverts for stream and river crossings alters local hydrology and increases soil erosion (Claridge and Mirza, 1981; Myers-Smith et al., 2006). In permafrost terrain a thaw bulb several meters deep can develop below the toe of the road embankment within a few decades of construction, leading to subsidence of the embankment and adjacent land (Hayley, 2005; Lingnau, 1985). The development and maintenance of gravel roads also requires large quantities of gravel. The extraction of borrow materials from areas of ice-rich permafrost can lead to challenges in the construction and maintenance of some quarries. Roads affect adjacent terrain by increasing dust deposition and runoff, altering soil properties, and impacting plant physiology (Auerbach et al., 1997; Eller, 1977). Roadside gravel deposition, trash, and vehicular pollution are other factors that may affect adjacent vegetation (Walker et al., 1987). Anecdotal evidence suggests that changes in vegetation structure adjacent to many northern roads have been extensive. These changes have the potential to alter ground temperatures adjacent to roadbeds by influencing snowpack (Marsh et al., 2010; Sturm et al., 2001a). Maintenance of permafrost in the road embankment is critical to long-term stability and research is needed to examine the feedbacks between gravel roads, vegetation change, snow accumulation, and near-surface ground thermal regime in the Arctic.

The Dempster Highway is a 740 km gravel road between Dawson City, Yukon, and Inuvik, Northwest Territories. This highway is a critical transportation link between the Beaufort Delta Region and southern Canada. The Dempster Highway begins at 64°N, and traverses boreal spruce forest, woodlands, tundra, and a variety of wetlands before terminating south of the treeline at 68°N (Western Arctic Handbook Society, 2007). In the Peel Plateau region of the Northwest Territories, the Dempster Highway descends 850 m from the Richardson Mountains across a fluvially incised plateau consisting of ice-rich morainal deposits (Fulton, 1995). This area is characterized by spruce forest at lower elevations and dwarf shrub tundra at higher elevations (GNWT, 2007). Residents in nearby communities have expressed concerns about the impacts of the road on vegetation and terrain stability (Gill et al., 2014; Kershner, 2010; Scott, 2011). The Peel Plateau is also an important area for harvesting country foods, including wild berries, and development impacts on the abundance and distribution of berry patches are a concern to Teetl'it Gwich'in harvesters from Fort McPherson, Northwest Territories (Parlee et al., 2005).

Several studies in the western Arctic have investigated the impacts of gravel roads on moist sedge tussock and dwarf shrub tundra (Auerbach et al., 1997; Myers-Smith et al., 2006; Walker and Everett, 1987). However, to date no studies have explored the impact of gravel roads on tall shrub tundra, such as is found along parts of the northern portion of the Dempster Highway. The Dalton Highway in Alaska has been shown to alter acidic and nonacidic tundra plant community composition, decrease species richness and soil moisture, and increase soil pH, bulk density, snow accumulation, and the rate of snowpack melt (Auerbach et al., 1997; Myers-Smith et al., 2006; Walker and Everett, 1987; Walker et al., 1987). The Dalton Highway has also contributed to altered vegetation structure, deeper snowpack, and increased active layer thickness adjacent to the road (Auerbach et al., 1997; Myers-Smith et al., 2006). In the Peel Plateau, the Dempster Highway has likely facilitated similar ecological changes, but the long-term impacts of this road have not been quantitatively investigated (Smith, 2009). Exploring the ecological feedbacks associated with the Dempster Highway in the Peel Plateau will contribute to a more thorough understanding of the regional impact of all-weather roads.

In this study, we used space for time substitution to examine the impacts of 35 years of ongoing use and maintenance of a gravel road on shrub tundra vegetation, soils, and permafrost conditions in the Peel Plateau region. Our primary objective was to examine if the physical disturbance associated with the road and its ongoing use and maintenance, including the effects of dust deposition and altered drainage, have affected vegetation composition and structure, and whether these changes have impacted permafrost conditions. To examine how the effects of the road may be mediated by vegetation type, we compared biotic and abiotic conditions at sites adjacent to the road with undisturbed tundra, and sampled in areas of tall shrub tundra and dwarf shrub tundra. We hypothesized that the effects of the road would be greatest in tall shrub tundra, where feedbacks between tall shrubs and the road amplify the effects on vegetation, soils, and ground temperature underneath tall shrubs.

Methods

STUDY AREA

This study was conducted in the Peel Plateau region of the Northwest Territories, in a 70 km^2 area approximately halfway between Fort McPherson and the Yukon border (Fig. 1). This terrain ranges in elevation from 150 to 600 m above sea level. Deeply incised creek valleys drain to the Peel River via the Vittrekwa River south of the highway and Stony Creek north of the highway (Kokelj

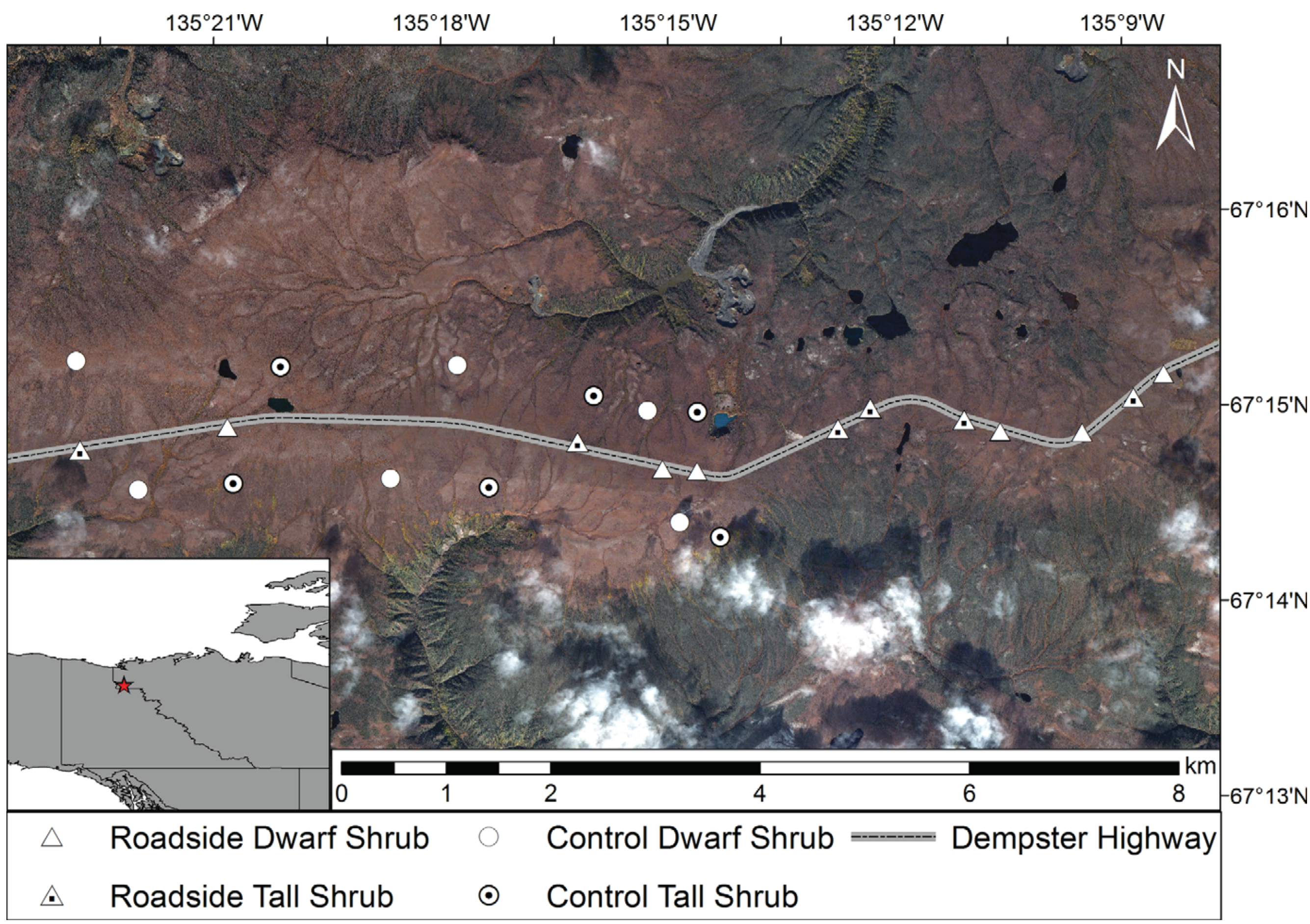

FIGURE 1. Quickbird (2008) satellite image of the study area showing sites along the Dempster Highway classified by disturbance and vegetation type. Inset map at bottom left shows the position of the study area in northwestern Canada (red star).

et al., 2013). The region is underlain by continuous permafrost (Smith and Burgess, 2000). Active layer development varies with soil conditions and vegetation type, and thicknesses range from about 50 to 100 cm (Hughes et al., 1981). Bedrock is composed of Cretaceous sandstone, which is overlain by ice-rich moraine and glaciolacustrine silt and clay deposits (Hadlari, 2006). In this area, the Dempster Highway is a two-lane all-weather road that sits atop a 1.2- to 2.4-m-thick raised gravel embankment constructed of glaciofluvial materials and surfaced with quarried limestone or glaciofluvial materials (Hayley, 2005; Lingnau, 1985; MacLeod, 1979). The embankment is designed to reduce heat transfer to underlying permafrost and maintain a frozen foundation, which prevents settlement and road surface cracking as the ground heaves seasonally (GNWT, 2007; Hayley, 2005; McGregor et al., 2008).

The study area lies at the northern edge of the boreal forest, and is a heterogeneous landscape with spruce forest at lower elevations, transitioning to patchy tundra dominated by tall shrubs (*Salix* spp., *Alnus viridis, Betula glandulosa*) at intermediate elevations, and dwarf shrubs (*Rhododendron subarcticum, Vaccinium* spp., *Empetrum nigrum, Rubus chamaemorus, Arctostaphylos* spp.) and sedges (*Eriophorum* spp. and *Carex* spp.) at higher elevations (Meikle and Waterreus, 2008). The regional climate is characterized by long cold winters with average air temperatures below 0 °C from October through April. The mean annual air temperature at Fort McPherson is –7.3 °C and mean annual precipitation is 310 mm (Burn and Kokelj, 2009). Convective rainfall events commonly deposit 20–30 mm of rainfall over periods of a few hours. A shallow permafrost table can rapidly transfer surface water to streams, causing roadside washouts. Rapid saturation of the active layer can also result in the loss of shear strength resulting in active-layer detachment slides and retrogressive thaw slumps (Kokelj et al., 2013). Human disturbances in this region include seismic cut lines created in the 1970s, off-road vehicle tracks, and gravel quarries and pull-outs along the road. In the study area, old borrow pits are not actively quarried, but are used to store and distribute gravel excavated from active pits further west along the highway. The closest active quarries are at Midway Lake, 1 km west of the study area, and at Frog Creek, 70 km east of the study area. Traffic on the highway includes large transportation trucks and recreational vehicles including cars and trucks, motorcycles, bicycles, and all-terrain vehicles (Western Arctic Handbook Society, 2007). Road maintenance occurs regularly in the summer and consists of additional gravel deposition, grading, culvert replacement, and the application of calcium and water to control dust (Scott, 2011). In winter, the road remains open and snow removal occurs, although winter winds can result in snow drifting and road closures.

SITE SELECTION

To examine the impact of the road on tundra vegetation and soils, we focused on the zone of most intense impacts, within 15 m of the toe of the embankment (Walker and Everett, 1987). We selected study sites directly adjacent to the Dempster Highway (15 m from the embankment), and in undisturbed tundra at least 500 m from the highway, where dust deposition and hydrological alterations are negligible (Auerbach et al., 1997; Santelmann and Gorham, 1988). To explore the role of vegetation in mediating the impacts of the road, we used 2008 Quickbird satellite imagery to select sites that are dominated by tall shrubs and sites dominated by dwarf shrubs with sparse cover of tall shrubs. A total of 24 sites were sampled, including six roadside sites dominated by tall shrubs, six roadside sites dominated by dwarf shrubs, six undisturbed sites dominated by tall shrubs, and six undisturbed sites dominated by dwarf shrubs (Figs. 1 and 2). Throughout this paper, these sites are referred to as: roadside tall shrub, roadside dwarf shrub, control tall shrub, and control dwarf shrub. All sites were at least 300 m apart, were distributed on both the north and south sides of the highway, and occurred at similar elevations on the plateau (Fig. 1).

BIOTIC RESPONSE VARIABLES

In July 2012, we established a 200 m transect parallel to the highway on flat terrain (0°–3° slope). Transects excluded hydrologic features such as water tracks, creeks, and ponds. Along each transect, we measured plant community composition by visually estimating the percent cover of tall shrub and tree species inside 10 randomly located 5 m^2 plots. The cover of understory species was estimated using 0.0625 m^2 subplots. To assess the impact of the road on green alder (*Alnus viridis*) growth and population dynamics, we made detailed measurements of this species in three sample plots along each transect (72 plots in total). To avoid bias, we sampled the same three plots (#3, 5, 7) on each transect regardless of the alder cover. Since alders were never present in the selected plots at control dwarf shrub sites, this site type is excluded from this component of our study. In each 5 m^2 plot sampled for alder we measured the height and basal diameter of all stems within the plot. To determine the number of individuals in the plot and their ages we traced each stem back to a root crown and collected a stem section above the top of the root collar. Stem sections were dried, sanded, and examined under a dissecting microscope to record stem age by counting growth rings on two radii. The diameter of each stem section was also measured using calipers. We used this data to estimate alder growth rates (vertical growth = stem height ÷ age; radial growth = stem basal diameter ÷ age). To assess the rate of alder proliferation over time, we made alder stem counts using 2008 Quickbird satellite imagery and 1972 air photos within a 200 × 200 m buffer at each site.

ABIOTIC RESPONSE VARIABLES

To measure ground temperatures, we installed HOBO data loggers (U23 Pro v2, Onset Computing) under representative vegetation at five roadside tall shrub sites, five control tall shrub sites, and five control dwarf shrub sites. Each data logger was attached to two thermistors (U23-002, Onset Computing) anchored along a PVC tube inserted and positioned at 10 cm and 100 cm below the ground. Temperatures were logged every hour for one year before data collection in August 2012. Thermistors were not installed at roadside dwarf shrub sites.

In March 2012, we measured snowpack thickness at each site along a 75 m snow transect parallel to the highway by inserting a graduated avalanche probe every 5 m. To measure active layer thickness, in late August 2012 we inserted a graduated soil probe to the depth of refusal at 10 random locations along the 200 m transect. In hummocky terrain, active layer measurements were taken in the center of the hummock tops in order to minimize the effects of within-site microtopographic variation. Two measurements of litter and organic layer thickness were also made in the same 10 locations using a metal ruler inserted into the soil to visually demarcate horizons. To measure the supply rate of plant-available nutrients, we used Plant Root Simulator (PRS) nutrient probes (Western Ag Innovations, Saskatoon, Saskatchewan, Canada). PRS probes consist of paired cation and anion exchange resin membranes and provide nutrient supply rates in milliequivalents cm^{-2} exchange membrane

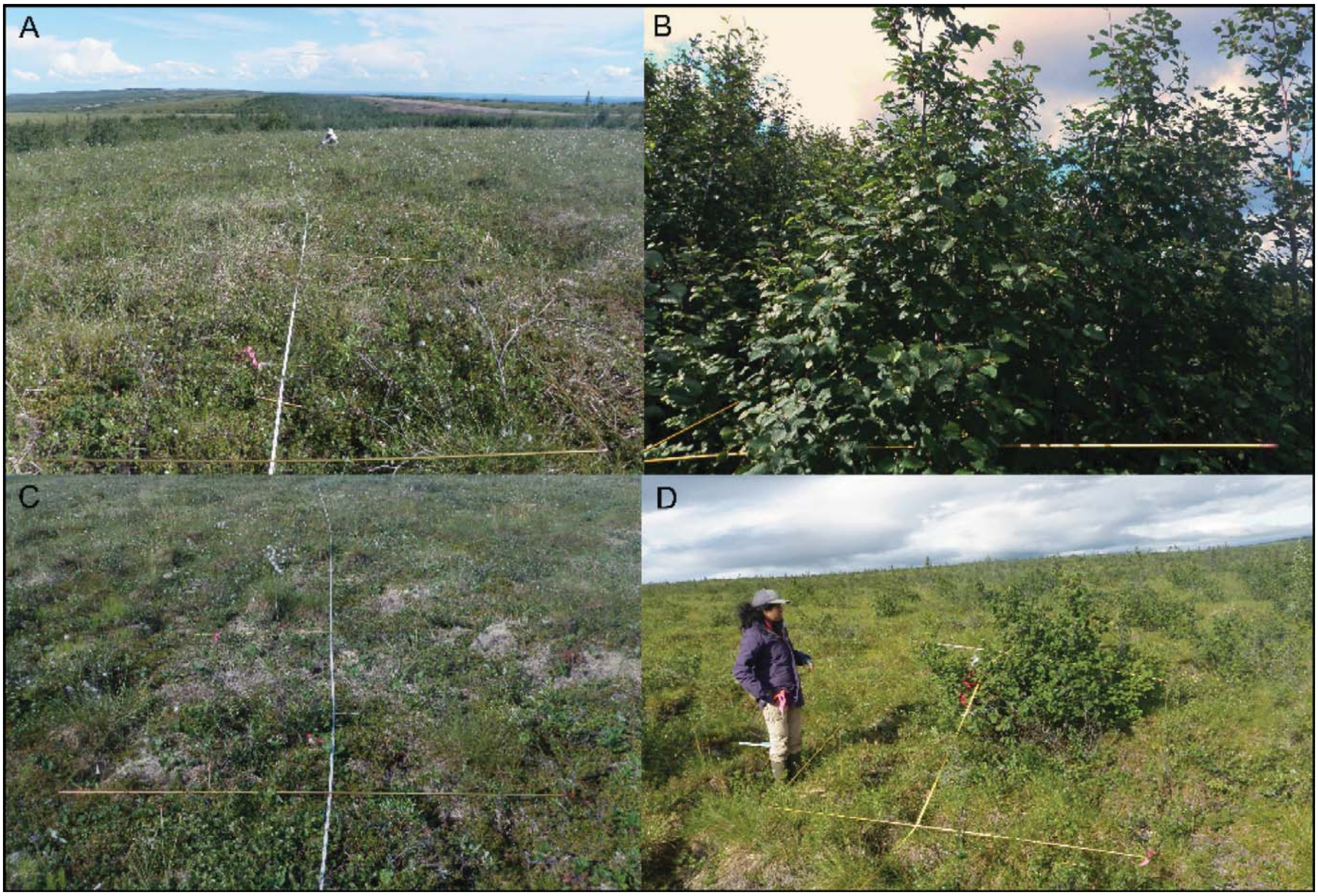

FIGURE 2. Plant community composition at four site types: (A) roadside dwarf shrub, (B) roadside tall shrub, (C) control dwarf shrub, and (D) control tall shrub sites.

per days of burial (Western Ag Innovations Inc., 2012). In 2012, we installed 6 pairs of probes at each of our four site types (n = 24) for 30 days (23 July–23 August 2012). In 2011, we deployed probes at four roadside tall shrub sites, three control dwarf shrub sites, and three control tall shrub sites between 22 July and 22 August 2011. All probes were inserted to a depth of 15 cm. To measure soil pH, we collected 100 cm^3 organic soil samples from between hummocks at two locations along each transect. In the lab, we mixed 10 mL of soil with 40 mL of deionized water, agitated the solution for three minutes, and left it standing for two hours before measuring the pH.

STATISTICAL ANALYSIS

To explore differences in community composition among site types (roadside tall shrub, roadside dwarf shrub, control tall shrub, and control dwarf shrub), we used PRIMER (Plymouth Marine Laboratories, Plymouth, U.K.) to perform a nonmetric multidimensional scaling (NMDS) ordination of a Bray-Curtis resemblance matrix calculated using percent cover data (Clarke and Gorley, 2001). To reduce noise prior to analysis, abundance data was log(1 + x) transformed, and rare species (occurred in fewer than two subplots) were removed (Clarke, 1993). The NMDS analysis was repeated 25 times and the two-dimensional ordination plot with the least stress was automatically selected by PRIMER. To test for differences in vegetation community composition among site types, we performed an analysis of similarity (ANOSIM, an analog of a univariate ANOVA) on the resemblance matrix. The significance of the R_{ANOSIM} statistic was calculated by performing 999 randomizations of the original data. To determine the contribution of each species or species group to pairwise dissimilarities between site types and similarities within site types, we performed a similarity percentage (SIMPER) analysis of log(1 + x) transformed cover data (Clarke and Gorley, 2001).

To test whether the road significantly altered biotic and abiotic response variables, we used the PROC MIXED procedure in SAS (SAS Institute, Cary, North Carolina, U.S.A.). PROC MIXED is a linear mixed effects model that uses maximum likelihood to estimate variance components (Littell et al., 2006). We set disturbance (road-disturbed or control) and vegetation type (tall shrub or dwarf shrub) as fixed factors, and plot and site as random factors, and used the Kenward-Roger approximation to estimate degrees of freedom (Kenward and Roger, 1997). To examine the importance of random spatial variation in our models, we removed random terms one at a time and compared models using Akaike information criteria (AIC) (Johnson and Omland, 2004). We retained the plot and site terms for models of alder height and age, and used a model with site as the only random factor for all other variables. Multiple comparisons were made using the least squares means (LS MEANS) procedure to detect significant differences in least squares means (α = 0.05, Tukey-Kramer adjusted p-values). Residuals were plotted to check for deviations from normality.

Results

BIOTIC RESPONSES

The presence of the road had a strong impact on alder abundance and growth. Alder cover was significantly greater at roadside tall shrub sites than at all other site types, including control tall shrub sites ($p < 0.001$). Other deciduous shrubs (*Betula glandulosa*, *Spiraea beauverdiana,* and *Salix* spp.) were not influenced by the road and had similar abundances across site types. Alders at roadside tall shrub sites were significantly younger, taller, and faster growing compared to controls (Fig. 3). Alders at roadside dwarf shrub sites were slightly younger and shorter, but were faster growing than at roadside tall shrub sites; however, the differences were not significant (Fig. 3). Both roadside site types had a higher proportion of young individuals than control sites, where the population was dominated by individuals >25 yr (Figs. 3 and 4). Alders were not encountered in surveys of control dwarf shrub sites, but recent alder recruitment was evident at dwarf shrub sites adjacent to the road. Comparisons of alder stem counts made using 1972 air photos and 2008 Quickbird satellite images confirm that alder proliferation within 100 m of the road has occurred more rapidly than in undisturbed tundra (Fig. 5).

The plant community at roadside tall shrub sites was distinct from all other site types (Fig. 6, R_{ANOSIM} values 0.315–0.640, Table 1). These differences were driven primarily by a higher abundance of alders and a lower abundance of acrocarpous mosses, lichens, peat mosses, and dwarf shrubs (*Empetrum nigrum, Rhododendron subarcticum,* and *Vaccinium vitis-idaea*) at roadside tall shrub sites (Appendix Table A1).

TABLE 1

Pairwise comparisons of plant community composition between site types using the ANOSIM procedure. R_{ANOSIM} values > 0.75 indicate well-separated groups, values between 0.25 and 0.75 describe overlapping but distinguishable groups, and values < 0.25 represent groups that cannot be separated. Readily distinguishable sites are indicated in bold (Clarke and Gorley, 2001).

		Tall Shrub		Dwarf Shrub	
		Roadside	Control	Roadside	Control
Dwarf Shrub	Control	**0.640**	**0.265**	**0.333**	
	Roadside	**0.345**	0.196		
Tall Shrub	Control	**0.315**			
	Roadside				

Roadside and control dwarf shrub sites were also distinguished from each other by a lower abundance of lichens, acrocarpous mosses and *Petasites* spp. at the road, and a higher abundance of *E. vaginatum* and most dwarf shrubs at the road (Table A1). The only site types with similar community composition were control tall shrub and roadside dwarf shrub sites (Table 1); although there were fewer alders at the latter, both had understory vegetation dominated by sedges and dwarf shrubs. The magnitude of differences in plant community composition among site types is shown visually in an NMDS ordination (Fig. 6). At the road, the abundance of species harvestable for

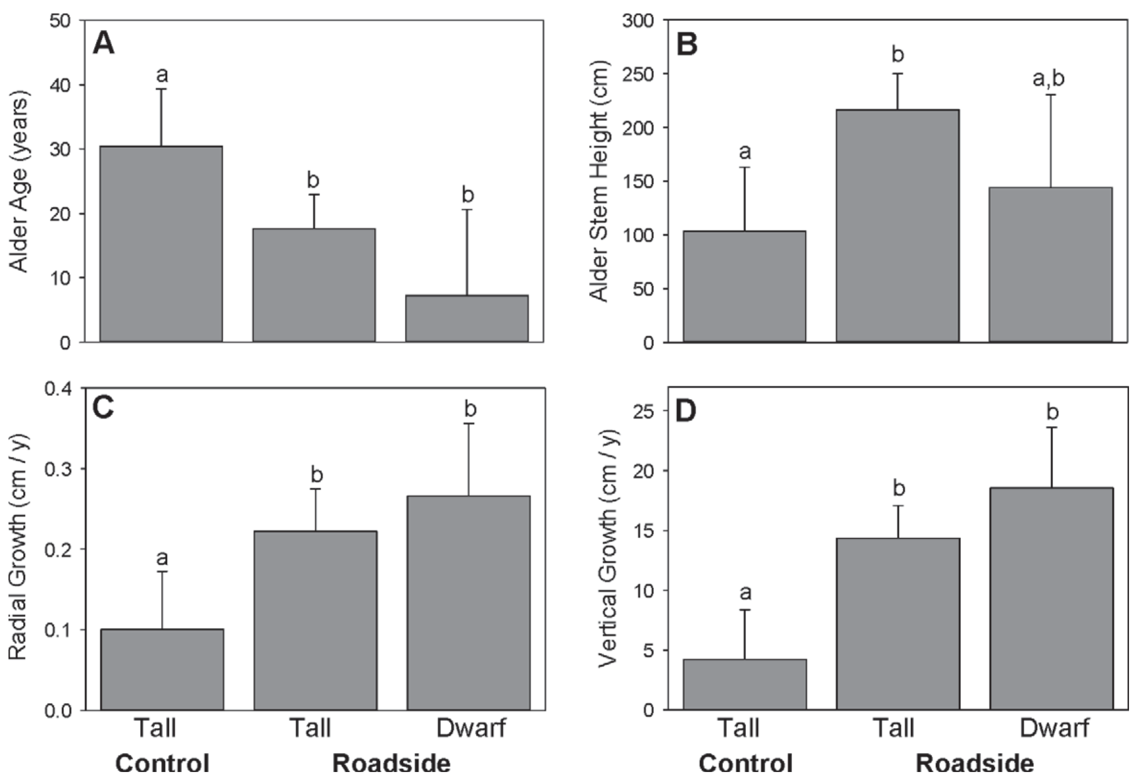

FIGURE 3. Alder response variables measured in undisturbed tall shrub tundra (control tall shrub) and beside the Dempster Highway (roadside tall shrub), and in dwarf shrub tundra beside the highway (roadside dwarf shrub): (A) average age (years), (B) stem height (cm), (C) radial growth rate (cm/year), and (D) vertical growth rate (cm/year). Alders did not occur in the sampled plots at undisturbed dwarf shrub sites. Bars show means for each site type and error bars are 95% confidence intervals of the mean (untransformed). Bars sharing the same letter are not significantly different ($\alpha = 0.05$, mixed model and Tukey adjusted least squares means procedure).

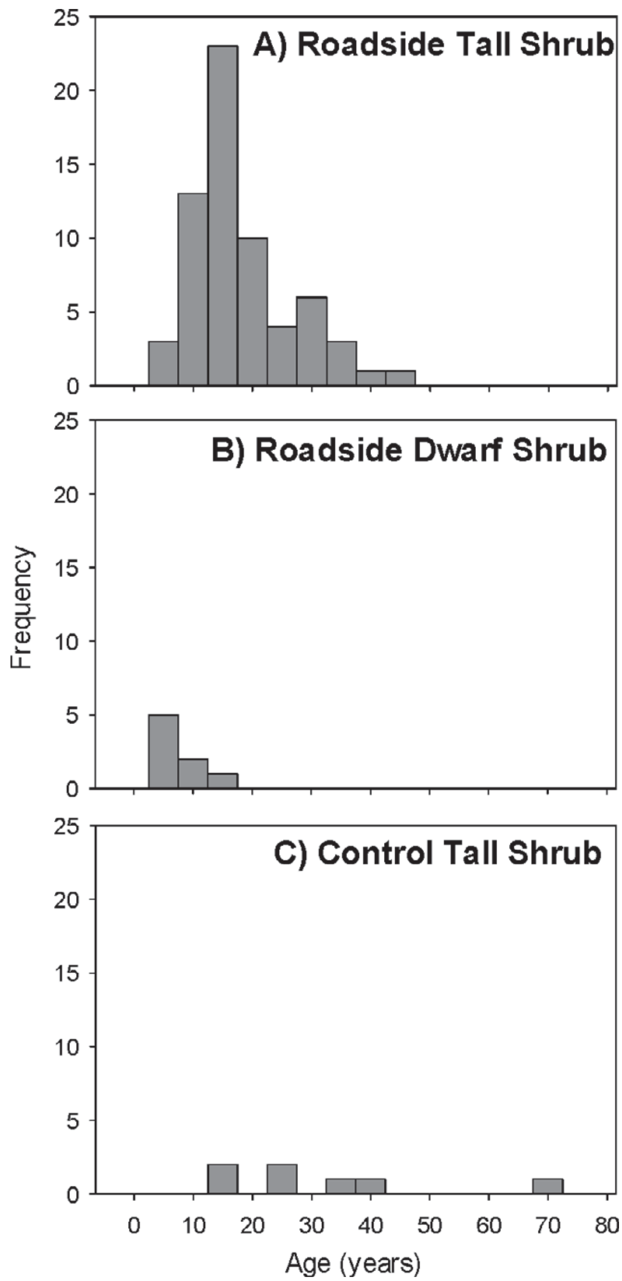

FIGURE 4. Alder age distributions at (A) roadside tall shrub tundra sites, (B) roadside dwarf shrub sites, and (C) control tall shrub sites. Alders did not occur in the sampled plots at undisturbed dwarf shrub sites. Bars indicate number of individual alders in each age category.

edible berries was lower at tall shrub compared to dwarf shrub sites (Table A1). Away from the road, berry plants were also less abundant at tall shrub sites.

ABIOTIC RESPONSES

Ground temperatures were higher at roadside sites compared to controls. At 10 cm depth, average daily temperatures were warmer at roadside tall shrub sites than at control tall and dwarf shrub sites, except in the summer (July-August) when soils were slightly cooler underneath roadside tall shrubs (Fig. 7). Temperatures at 10 cm depth under tall shrubs in undisturbed tundra were also warmer in the winter and spring than in undisturbed dwarf shrub tundra. Roadside tall shrub ground temperatures at 100 cm depth were also higher than controls and remained close to zero throughout the entire year. Minimum temperatures at tall and dwarf shrub control sites were 5–10 °C lower than at roadside sites, and freezeback was completed by 27 February and 1 February, respectively (Fig. 7).

Abiotic parameters including snow, active layer, litter, and organic soil thicknesses all varied with the patterns of alder cover, with higher values at roadside sites compared to controls, and at tall shrub sites compared to dwarf shrub sites (Fig. 8, Appendix Table A2). Snowpack thickness at roadside tall shrub sites was significantly greater than at both dwarf shrub site types (Fig. 8, part b, $p \leq 0.05$). Snowpack thickness was similar among all other site types. Active layer thickness was also highest at roadside tall shrub sites, but these differences were not significant. The greatest active layer thicknesses (>120 cm) occurred at roadside tall shrub sites under thick alder patches, but since our transects crossed through alder thickets to more open areas, measurements also included shallower active layers (Fig. 8, part c). Organic soil and litter thickness were both influenced by the effects of the road on vegetation. Both parameters were greatest at roadside and control tall shrub sites (Fig. 8, parts d and e). Soil pH in both roadside site types was higher than the controls, but the differences were only significant where tall shrubs dominated (Fig. 8, part f).

Soil chemistry was also significantly impacted by the road, but in some cases the differences were mediated by vegetation type (Fig. 9). Total nitrogen, calcium, magnesium, and sulfur all showed higher levels near the road, but significant differences were limited to tall shrub sites. Vegetation type also had a significant effect on sulfur and total nitrogen supply rates, showing the highest levels at roadside tall shrub sites (Fig. 9; tests Appendix Table A2).

Discussion

Differences in plant community composition and alder age structure between control and roadside tall shrub sites indicate that the presence of the Dempster Highway has contributed to significant changes in the vegetation beside the road. At tall shrub sites adjacent to the road, young alders formed closed canopies that often exceeded 3 m in height. Differences in alder response variables among sites indicate that environmental changes following road construction facilitated both alder growth and recruitment near the embankment. Alder populations near the road were between two and three times faster-growing than at control sites and were dominated by individuals recruited in the last two decades. Increased deciduous shrub cover and biomass have been observed in other studies of gravel roads in tundra ecosystems (Myers-Smith et al., 2006), but the changes were much less pronounced than the shifts evident next to the Dempster Highway.

At roadside sites where tall shrubs dominated, moss, lichen, and forb cover were significantly reduced, likely in response to increased shading and litter deposition from the closed canopy. Dwarf shrub and forb cover was also reduced at roadside tall shrub sites, including several culturally important berry species (*E. nigrum, R. chamaemorus, V. uliginosum,* and *V. vitis-ideae*). Of these, *R. chamaemorus* (cloudberry) was the only edible berry observed flowering under the alder canopies, but it almost never produced fruits. Dust deposition and increased soil alkalinity likely contributed to reduced cover of mosses, lichens, forbs, and dwarf shrubs (Auerbach et al., 1997; Santelmann and Gorham, 1988; Appendix Table A2). These findings are supported by previous studies on the effects of

FIGURE 5. Vegetation adjacent to the Dempster Highway on the Peel Plateau, Northwest Territories, Canada. Shrub proliferation, particularly of *Alnus viridis*, since the 1970s has been most extensive adjacent to the road.

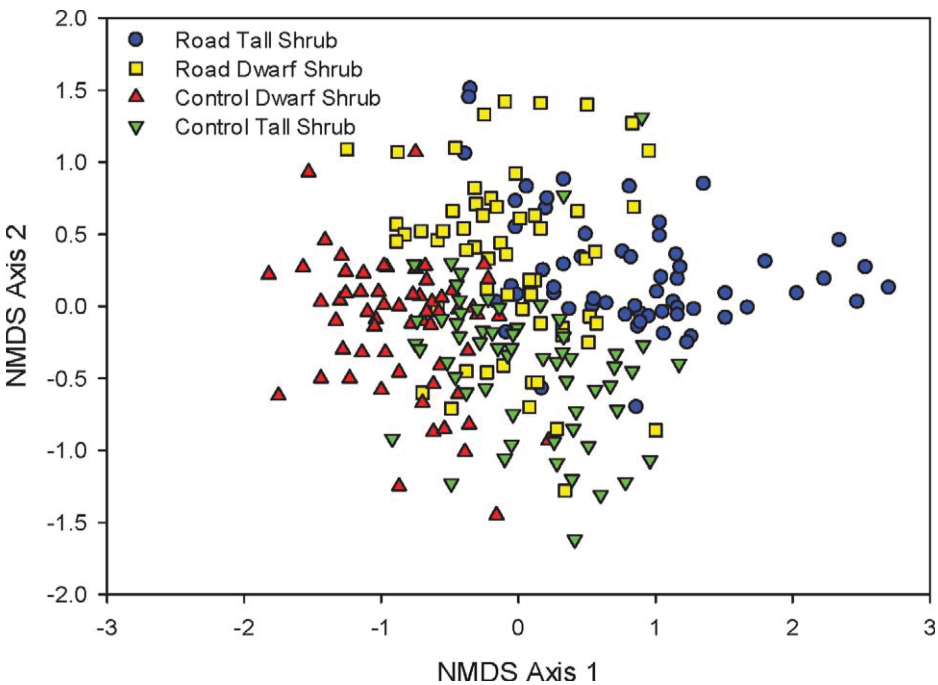

FIGURE 6. Nonmetric multidimensional scaling ordination of plant community composition based on Bray-Curtis similarity matrix. Symbols plotted are individual plots sampled at road-disturbed and undisturbed sites in tall and dwarf shrub dominated tundra. Plots that are in close proximity to each other in this ordination space have similar species composition.

gravel roads on tundra plant communities, which documented decreases in peat mosses and lichens and an increase in graminoids (Myers-Smith et al., 2006). Even where tall shrubs have not come to dominate the plant community, the road has facilitated vegetation change, promoting sedge growth and reducing the cover of mosses, lichens, and forbs. These differences were likely caused by increased soil alkalinity and shading from a vigorous sedge canopy (Everett, 1980; Farmer, 1993). Similar differences in plant communities were found between tall shrub– and dwarf shrub–dominated sites undisturbed by the road, but the contrasts were smaller because alders did not form closed canopies away from the road.

Vegetation change beside the highway was likely facilitated by several processes: microsite disturbance, increased nutrient availability, and elevated moisture. Greater dust deposition beginning within the first few years of road use and increased microbial activity and nutrient mineralization driven by prolonged freezeback beside the embankment likely enhanced deciduous shrub growth (Lantz et al., 2009, 2010; Zimov et al., 1993). Road construction itself may have also promoted shrub recruitment by creating microsites for establishment (Blok et al., 2011; Lantz et al., 2013; Tape et al., 2012), as a swath wider than the current embankment was likely disturbed during construction. Increased

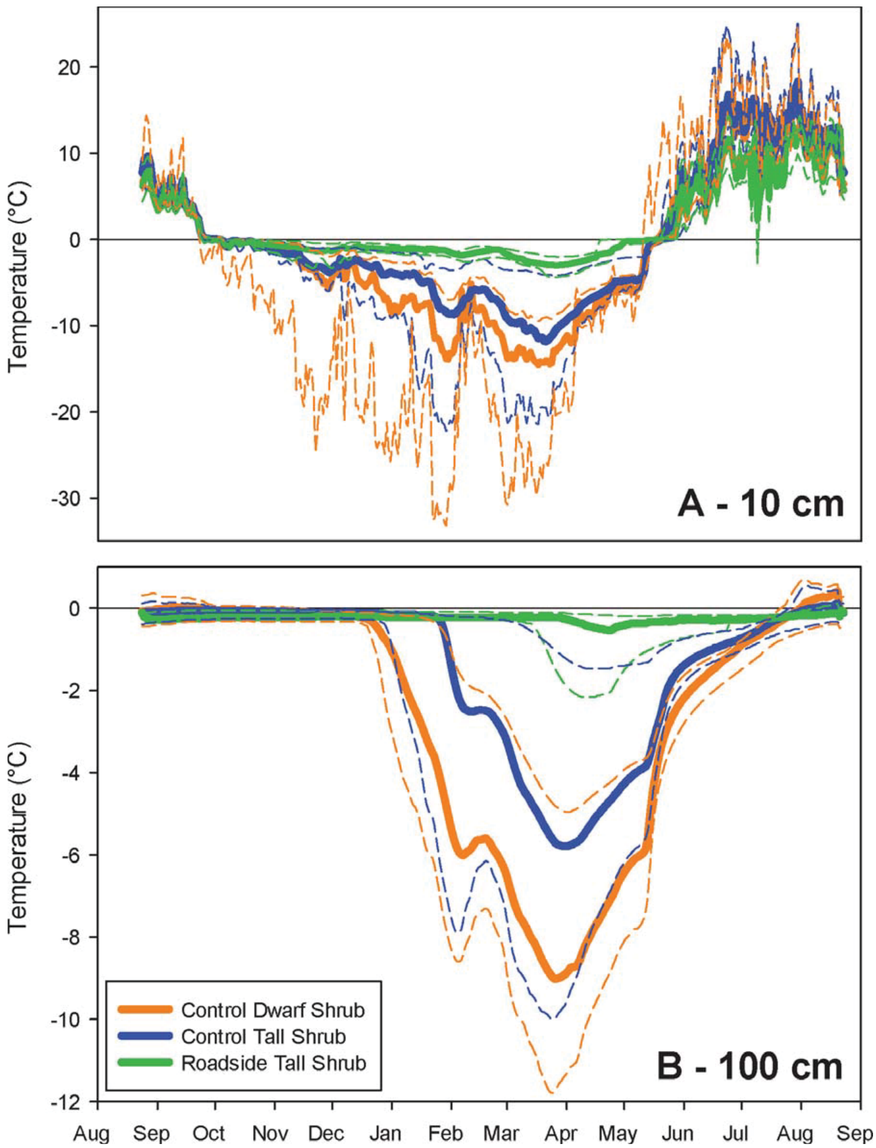

FIGURE 7. Median, maximum, and minimum temperatures at (A) 10 cm depth and (B) 100 cm depth from August 2011 to August 2012 at disturbed tall shrub (roadside tall shrub), undisturbed tall shrub (control tall shrub), and undisturbed dwarf shrub (control dwarf shrub) tundra sites. Solid lines show median daily temperature across site type, and upper and lower broken lines show daily maximum and minimum temperatures, respectively.

snow accumulation and impeded drainage due to presence of the road embankment may have also facilitated vegetation change. Deep snowpack protects shrub vegetation from desiccation by winter winds and, in conjunction with higher soil moisture content adjacent to the road, slows ground heat loss in winter and delays freezeback of the active layer (Zhang and Stamnes, 1998). In summer, warmer soil temperatures likely promoted active layer thaw and increased moisture and nutrient availability. Collectively, these conditions are highly favorable for tall shrub establishment and growth (Lantz et al., 2009; Sturm et al., 2001a; Tape et al., 2012). These effects were likely enhanced over time as terrain adjacent to the road embankment subsided due to thaw of near-surface permafrost (Hayley, 2005).

Canopy-forming alders did not dominate all sites adjacent to the road, suggesting that shrub proliferation is also mediated by existing biophysical conditions. Local differences in soil composition, moisture, slope, aspect, and mechanical disturbance at the time of construction likely also influenced shrub recruitment and growth. This is not surprising, since shrub proliferation in undisturbed environments throughout the Arctic has been heterogeneous (Fraser et al., 2014; Tape et al., 2012). Field studies in other areas that link tall shrub expansion to mesic soil environments (Blok et al., 2011; Lantz et al., 2013; Tape et al., 2012) suggest that heterogeneous changes in soil moisture adjacent to the road may have facilitated shrub proliferation in some areas and not others. Further investigation is required to assess the factors facilitating or constraining shrub proliferation adjacent to the Dempster Highway. Research using historical air photos should be conducted to map vegetation change and examine the relationships between areas of shrub proliferation and landscape-scale variation in biophysical variables.

Our findings indicate that vegetation development adjacent to the highway initiates biotic and abiotic feedbacks that affect ground temperatures. Near-surface ground temperatures beneath areas of tall shrub 15 m from the road embankment were significantly higher than in control areas, and freezeback was delayed more than 3 months. It is known that thawing of near-surface permafrost and terrain subsidence can occur immediately adjacent to road embankments, but terrain more than 10 m away from the toe of the embankment is typically considered unimpacted (Hayley, 2005; Walker and Everett, 1987). Anomalously high ground temperatures and delayed freezeback at our roadside sites were likely

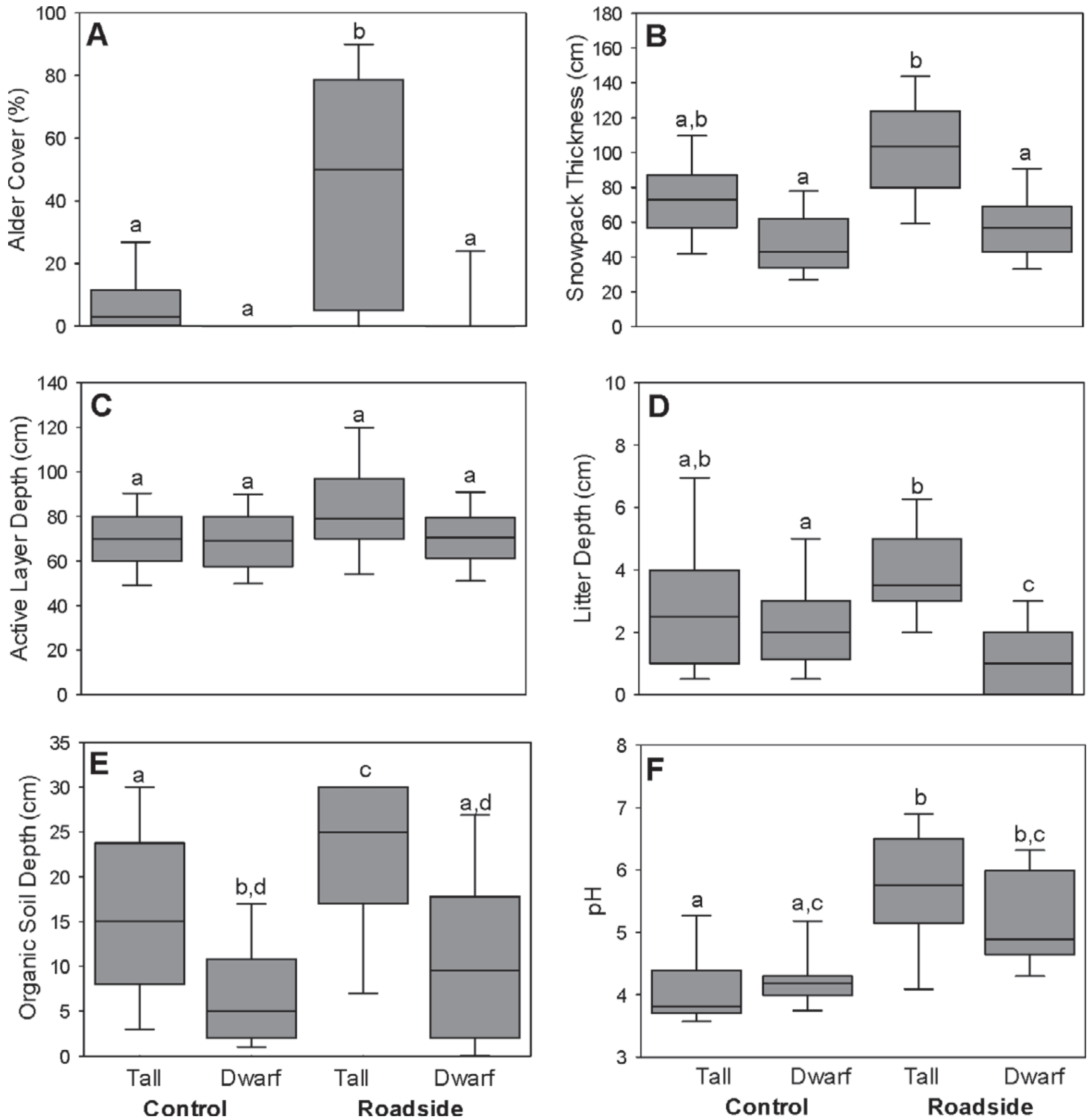

FIGURE 8. Biotic and abiotic response variables measured in undisturbed tall shrub tundra (control tall shrub) and dwarf shrub tundra (control dwarf shrub), and in disturbed tall shrub tundra (roadside tall shrub) and dwarf shrub tundra (roadside dwarf shrub): (A) alder cover (%), (B) snowpack thickness (cm), (C) active layer thickness (cm), (D) litter thickness (cm), (E) organic layer thickness (cm), and (F) soil pH. The solid black line inside the box shows the median, the ends of the box represent the 25th to 75th percentiles, and whiskers show the 10th and 90th percentiles. Boxes sharing the same letter are not significantly different (α = 0.05, mixed model and Tukey adjusted least squares means procedure).

caused by the higher latent heat content of wet soils, by a thicker active layer, and by the early and thick accumulation of snow.

Our conceptual model (Fig. 10), supported by field observations, suggests that the initial thermal disturbance resulting from road construction and increased snow accumulation is accentuated by shrub proliferation. In particular, progressive shrub growth may expand the lateral extent of snow drifting and ground surface warming, further strengthening the feedbacks described above (Fig. 10; Essery and Pomeroy, 2004). Warmer ground temperatures observed beyond subsided areas immediately adjacent to the road suggest that by trapping snow, the proliferation of roadside alders has increased the intensity and spatial extent of the thermal disturbance that would normally be associated with a gravel road in continuous permafrost (Fig. 10). Tall alders trap snow and limit compaction of the snowpack, which insulates the ground and inhibits ground heat loss in winter (Sturm et al., 2001a). The dense alder canopy may have a cooling effect in summer when shading reduces ground temperatures (Fig. 7, part a; Blok et al., 2010; Chapin et al., 2005; Lantz et al., 2013; Sturm et al., 2001a, 2005). However, the shading effect of the alders on ground temperatures is greatly offset by the influence that deep snow has on ground heat loss in winter. The hypothesis that higher ground temperatures are promoted by shrub-snow interactions is supported by our observation of warmer temperatures in control tall shrub tundra compared to control dwarf

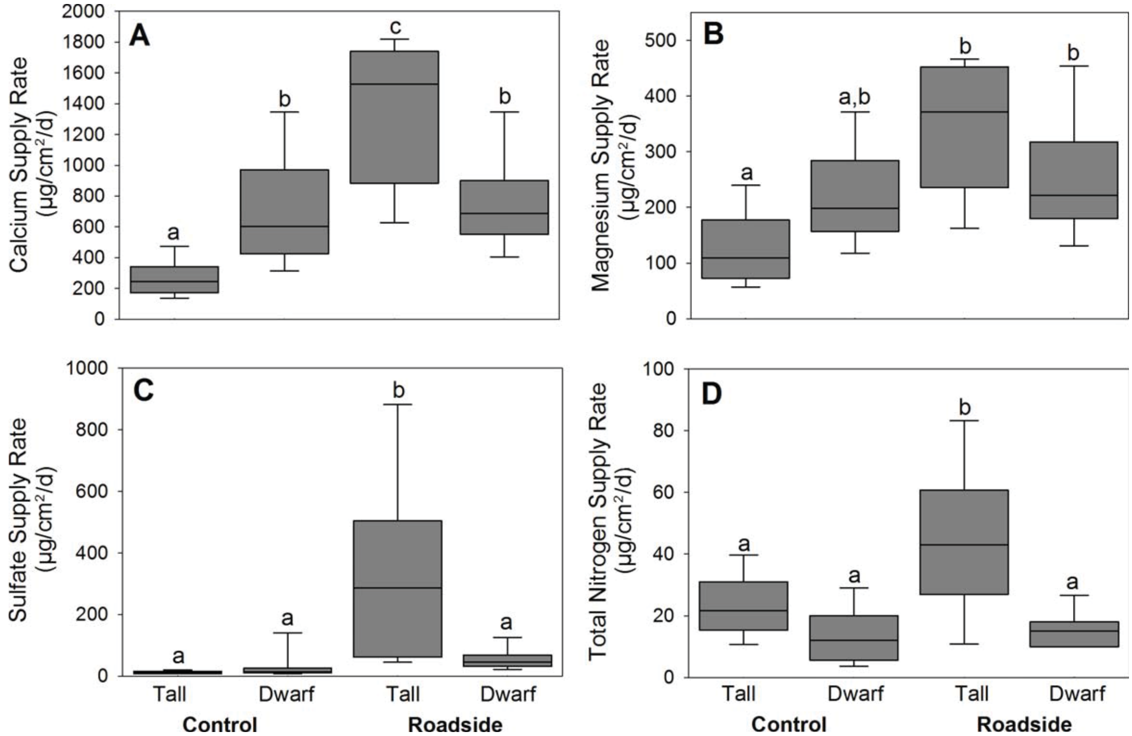

FIGURE 9. Plant-available nutrient supply rate (µg/cm²/d) at undisturbed tall shrub tundra (control tall shrub) and dwarf shrub tundra (control dwarf shrub), and in disturbed tall shrub tundra (roadside tall shrub) and dwarf shrub tundra (roadside dwarf shrub): (A) calcium, (B) magnesium, (C) sulfate, and (D) total nitrogen. The solid black line inside the box shows the median, the ends of the box represent the 25th to 75th percentiles, and whiskers show the 10th and 90th percentiles. Boxes sharing the same letter are not significantly different ($\alpha = 0.05$, mixed model and Tukey adjusted least squares means procedure).

shrub tundra (Fig. 7). Although we did not find significantly thicker active layers at roadside tall shrub sites, ground temperatures were higher at these sites and thaw depths greater than 120 cm were only observed under roadside shrubs.

Shrub proliferation adjacent to the road also created a positive feedback with soil chemistry, as dust and nutrient deposition adjacent to the road were more pronounced where tall shrubs dominated (Fig. 10). Previous research suggests that the dust load is greater closer to the road (Everett, 1980), but taller vegetation likely also traps more dust, leading to greater increases in levels of Ca, Mg, and S at roadside sites covered with tall shrubs. Alder growth is enhanced by increased micronutrients deposited in road dust and runoff (calcium, sulfur, magnesium) and increased pH (Lantz et al., 2009; Sturm et al., 2001b). Since alders have the ability to fix nitrogen, their proliferation also altered available soil nitrogen (Mitchell and Ruess, 2009; Rhoades et al., 2001).

The first order effects of gravel roads on tundra ecosystems are well known: heat transfer to adjacent ground that results in permafrost thaw, altered plant communities, increased soil pH, and microsite disturbance due to road construction and maintenance (Hayley, 2005; Walker and Everett, 1987). Our results show that the conditions generated by the maintenance and use of the road interact with local ecosystem processes to generate feedbacks between biotic and abiotic conditions that enhance dust deposition and snow accumulation and magnify the effects of the road on vegetation communities and substrate properties. In this study, we found that where the road facilitated shrub dominance, taller vegetation enhanced snow accumulation and altered ground temperatures and soil chemistry. In turn, these changes promoted enhanced shrub recruitment and growth (Fig. 10). When vegetation near the road is altered, but does not result in establishment of tall shrubs, disturbance feedbacks are much less pronounced because snow and dust are distributed more sparsely without tall shrubs acting as a windbreak. Tall shrub expansion has clearly been facilitated by the Dempster Highway, and the changes we observed are consistent with other forms of disturbance that also promote shrub growth (Forbes et al., 2001; Johnstone and Kokelj, 2009; Kemper and Macdonald, 2009; Lantz et al., 2009, 2010, 2013; Marsh et al., 2005). The surface of all-weather roads directly impacts a relatively small area, but the extent of hydrological changes, dust redistribution, shrub proliferation, and changes to ground thermal regime extend the effects of roads across a significantly larger area (Walker and Everett, 1987).

The ecological changes we documented, as well as feedbacks with ground thermal conditions, have significant implications for the long-term stability and maintenance of transportation corridors through tundra environments. The stability of northern infrastructure relies on frozen ground in, and adjacent to, the road embankment (Andersland and Ladanyi, 2004; Couture et al., 2000). Growing evidence indicates that anthropogenic and natural disturbances facilitate the establishment and proliferation of tall shrubs (Forbes et al., 2001; Johnstone and Kokelj, 2009; Kemper and Macdonald, 2009; Lantz et al., 2009, 2010, 2013; Marsh et al., 2005). Tall shrub proliferation on disturbances such as drilling mud sumps, roads, and slumps has been shown to contribute to increased snow accumulation, higher ground temperatures, permafrost degradation, and subsidence (Johnstone and Kokelj, 2009; Kanigan and Kokelj, 2008; Kokelj et al., 2010; Lantz and Kokelj, 2008). The implica-

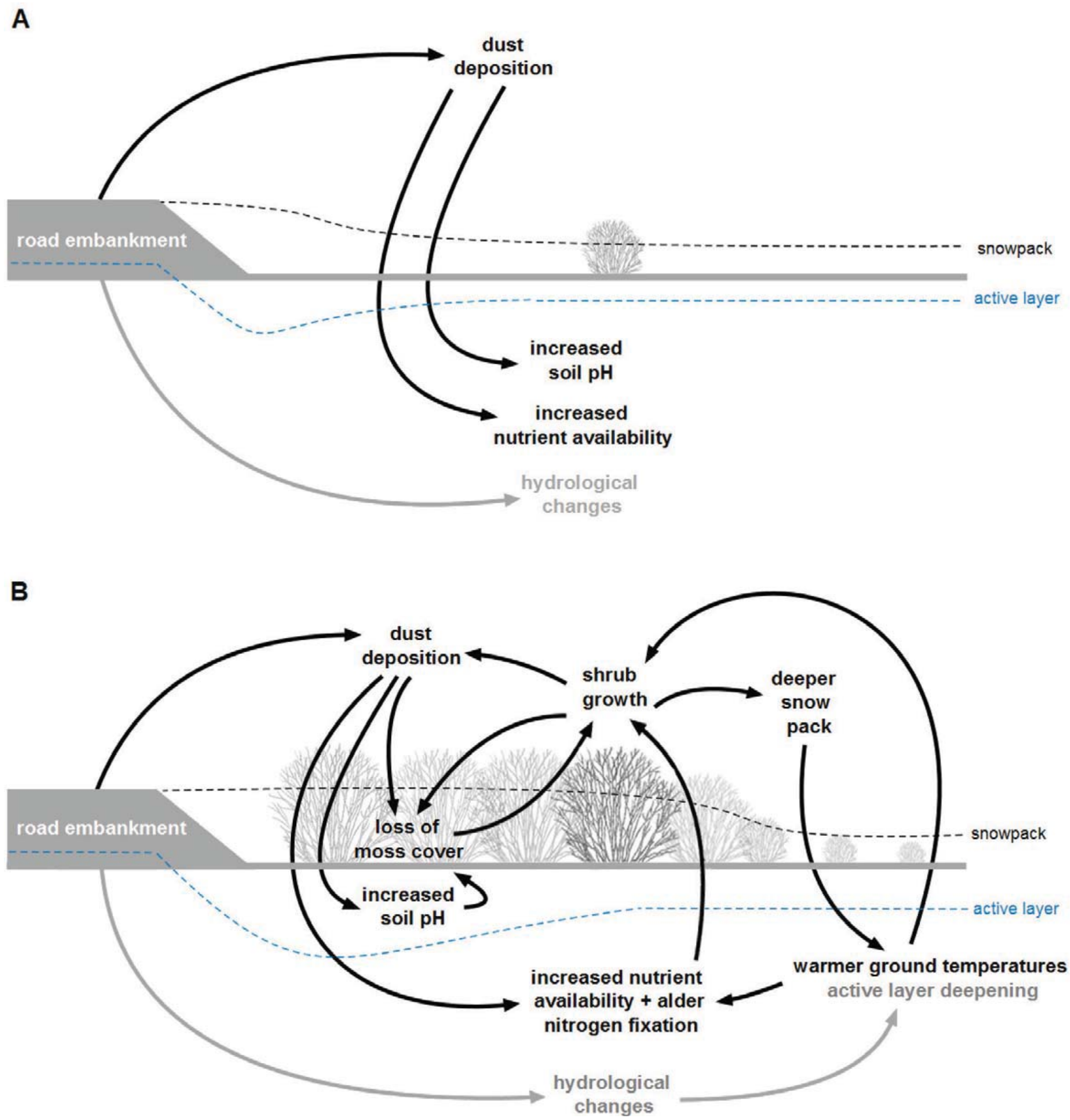

FIGURE 10. Cross section of a gravel highway showing the development of ecological feedbacks in tundra ecosystems (A) immediately following gravel road construction, and (B) after 35 years. Construction of the embankment causes hydrological changes (particularly water pooling adjacent to the road) and traps snow, leading to warmer ground temperatures, thicker active layers, and increasing nutrient availability, promoting shrub growth near the embankment. When tall shrubs become dominant, several feedbacks are strengthened: tall shrubs act as a windbreak to increase dust deposition; soil nutrient availability increases; mosses and acidophilous plants are reduced as soil pH and shading increase; and tall shrub growth is promoted through enhanced nutrient availability and reduced competition. Tall shrubs acting as a windbreak may also increase the depth and lateral extent of snow accumulation, insulating the ground and potentially leading to higher ground temperatures and thicker active layers beyond areas immediately adjacent to the road; this in turn promotes tall shrub growth by increasing nutrient availability, soil moisture, and rooting depth. Black text and arrows are processes observed in our study of the Dempster Highway; gray are hypothesized or known to occur in other studies of gravel roads in Arctic tundra.

tions of ground warming and permafrost thaw adjacent to roads include an increase in ground settlement and loss of ground bearing capacity and soil creep resistance (Couture et al., 2000). To better understand the implications for roadbed stability, our network of ground temperature monitoring sites adjacent to the Dempster Highway can be used to parameterize numerical models that investigate the effects of vegetation, embankment configuration, and snowpack on ground temperatures. Our findings make it clear that the long-term management of gravel roads in the Arctic, including the proposed Mackenzie Valley Highway (GNWT, 2005) and the Inuvik-Tuktoyaktuk Highway, should consider the effects of roads on vegetation, soils, snow accumulation, and ground thermal conditions. Active vegetation management (regular shrub cutting) should be considered as a potential method to maintain permafrost conditions in and around infrastructure constructed in tundra environments. Future work at the sites described here will involve shrub removal experiments to assess the impacts and feasibility of this management strategy.

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APPENDIX

TABLE A1

Results of the SIMPER analysis showing the top six species or species groups that make the greatest contribution to the between-group Bray-Curtis dissimilarity for comparisons of interest. The mean cover (log transformed) of each species at the site types being compared is shown in the second and third columns. The last column shows cumulative dissimilarity associated with the species listed.

Species or species group	Abundance site type 1	Abundance site type 2	Cumulative % dissimilarity
Roadside (tall shrub) and roadside (dwarf shrub)			
Alnus viridis	2.96	0.49	11.69
Acrocarpous mosses	1.37	2.24	20.52
Eriophorum vaginatum	0.45	1.91	28.45
Rubus chamaemorus	1.89	2.16	35.14
Empetrum nigrum	0.95	1.85	41.58
Rhododendron subarcticum	1.67	2.39	47.74
Roadside (tall shrub) and control (tall shrub)			
Alnus viridis	2.96	1.41	9.51
Lichens	0.17	1.97	17.65
Acrocarpous mosses	1.37	1.86	25.74
Rubus chamaemorus	1.89	2.33	32.65
Vaccinium vitis-idaea	1.54	2.82	39.21
Sphagnum spp.	0	1.57	45.74
Roadside (dwarf shrub) and control (tall shrub)			
Acrocarpous mosses	2.24	1.86	8.35
Eriophorum vaginatum	1.91	0.74	16.29
Lichens	1.28	1.97	24
Sphagnum spp.	0.3	1.57	30.79
Rubus chamaemorus	2.16	2.33	37.26
Empetrum nigrum	1.85	0.94	43.66
Roadside (tall shrub) and control (dwarf shrub)			
Lichens	0.17	3.56	12.2
Alnus viridis	2.96	0.17	22.62
Acrocarpous mosses	1.37	2.69	30.36
Rubus chamaemorus	1.89	1.02	36.21
Rhododendron subarcticum	1.67	2.82	41.85
Vaccinium vitis-idaea	1.54	2.6	47.14
Roadside (dwarf shrub) and control (dwarf shrub)			
Lichens	1.28	3.56	10
Eriophorum vaginatum	1.91	0.61	17.57
Acrocarpous mosses	2.24	2.69	24.99
Rubus chamaemorus	2.16	1.02	31.93
Empetrum nigrum	1.85	1.54	37.44
Vaccinium vitis-idaea	1.95	2.6	42.78
Control (tall shrub) and control (dwarf shrub)			
Lichens	1.97	3.56	8.53
Acrocarpous mosses	1.86	2.69	16.06
Rubus chamaemorus	2.33	1.02	23.48
Sphagnum spp.	1.57	0.77	30.51
Alnus viridis	1.41	0.17	36.17
Empetrum nigrum	0.94	1.54	41.72

TABLE A2

Results of mixed model ANOVAs of fixed effects for biotic and abiotic response variables. Vegetation type has two levels: tall shrub and dwarf shrub, and Disturbance includes two levels: road-disturbed and undisturbed. Numbers shown in bold are significant effects ($\alpha < 0.05$).

Response variable	Effect	*p*	*F* value	Degrees of freedom
Active layer depth	Vegetation type	0.1640	2.03	1, 32
	Disturbance	0.1446	2.28	1, 23
	Vegetation × Disturbance	0.2765	1.23	1, 32
Litter depth	Vegetation type	**<.0001**	33.88	1, 20
	Disturbance	0.8207	0.05	1, 20
	Vegetation × Disturbance	**0.0013**	13.90	1, 20
Organic soil depth	Vegetation type	**<.0001**	56.68	1, 20
	Disturbance	**0.0013**	13.87	1, 20
	Vegetation × Disturbance	0.2536	1.38	1, 20
Snow depth	Vegetation type	**0.0008**	16.94	1, 16
	Disturbance	**0.0506**	4.47	1, 16
	Vegetation × Disturbance	0.3715	0.85	1, 16
Snow density	Vegetation type	0.0526	4.39	1, 16
	Disturbance	0.6725	0.19	1, 16
	Vegetation × Disturbance	0.4108	0.71	1, 16
Soil pH	Vegetation Type	0.4464	0.60	1, 20
	Disturbance	**<.0001**	27.42	1, 20
	Vegetation × Disturbance	0.1774	1.95	1, 20
Nitrogen supply rate	Vegetation type	**<.0001**	25.32	1, 57
	Disturbance	**0.0063**	8.04	1, 57
	Vegetation × Disturbance	**0.0170**	6.04	1, 57
Calcium supply rate	Vegetation type	0.4340	0.64	1, 20
	Disturbance	**<.0001**	31.27	1, 20
	Vegetation × Disturbance	**<.0001**	25.13	1, 20
Magnesium supply rate	Vegetation type	0.8328	0.05	1, 20
	Disturbance	**0.0006**	16.33	1, 20
	Vegetation × Disturbance	**0.0068**	9.13	1, 20
Sulfate supply rate	Vegetation type	**0.0159**	6.84	1, 22
	Disturbance	**0.0022**	12.02	1, 22
	Vegetation × Disturbance	**0.0067**	8.99	1, 22
Alder height*	Vegetation type	0.1369	2.35	1, 28
	Disturbance	**0.0028**	10.49	1, 32
Alder age*	Vegetation type	0.1708	1.99	1, 24
	Disturbance	**0.0233**	5.83	1. 26
Alder vertical growth*	Vegetation type	0.1697	2.08	1, 15
	Disturbance	**0.0008**	15.94	1, 19
Alder radial growth*	Vegetation type	0.4233	0.68	1, 14
	Disturbance	**0.0176**	7.11	1, 15
Alder cover	Vegetation type	**<.0001**	49.23	1, 20
	Disturbance	**<.0001**	27.66	1, 20
	Vegetation × Disturbance	**0.0002**	20.15	1, 20

*No tests for interactions were performed since alders were not present at undisturbed dwarf shrub sites.