

Ecological impacts of roads in Canada's north

by

Emily A Cameron
B.Sc., Queen's University, 2009

A Thesis Submitted in Partial Fulfillment
of the Requirements for the Degree of

MASTER OF SCIENCE

in the School of Environmental Studies

© Emily A Cameron, 2015
University of Victoria

All rights reserved. This thesis may not be reproduced in whole or in part, by photocopy or other means, without the permission of the author.

Supervisory Committee

Ecological impacts of roads in Canada's north

by

Emily A Cameron
B.Sc., Queen's University, 2009

Supervisory Committee

Dr. Trevor C. Lantz, School of Environmental Studies
Supervisor

Dr. Brian Starzomski, School of Environmental Studies
Departmental Member

Abstract

Supervisory Committee

Dr. Trevor Lantz, School of Environmental Studies

Supervisor

Dr. Brian Starzomski, School of Environmental Studies

Departmental Member

Arctic ecosystems are experiencing rapid changes as a result of climate warming and more frequent natural and human-caused disturbances. Disturbances can have particularly large effects on high-latitude ecosystems because ecosystem structure and function is controlled by strong feedbacks between soil conditions, vegetation, and ground thermal regime. My MSc. research used fieldwork and broad-scale GIS data to investigate post-disturbance ecosystem recovery along roads in two permafrost zones (discontinuous and continuous). In the first of two case studies, I focussed on tall shrub proliferation along the Dempster Highway at the Peel Plateau, NT. To explore the drivers of tall shrub proliferation and to quantify shrub expansion in this region of continuous permafrost, greyscale air photos (1975) and Quickbird satellite imagery (2008) were used to map landcover change within a 1.2 km buffer next to the road and inside a buffer 500 m away from the road. Extensive tall shrub proliferation in the study area indicates that warming air temperatures and disturbance both facilitate vegetation change in tundra environments. My findings also indicate that accelerated shrub expansion adjacent to the road was caused by increased 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. These observations also support previous work that illustrates that tall shrub expansion next to the highway promotes strong positive feedbacks to ongoing shrub growth and proliferation.

In a second case study I examined ecosystem recovery in an area of discontinuous permafrost 30 years after construction and abandonment of a winter access road in

Nahanni National Park Reserve. Ecosystem recovery was studied by comparing disturbed (road) and undisturbed (adjacent to the road) sites in spruce muskeg, black spruce parkland, deciduous forest, and alpine treeline terrain. Field data showed that disturbances to discontinuous permafrost terrain can lead to large and persistent changes to ecosystem composition and structure. In spruce muskeg, permafrost thaw triggered by road construction dramatically increased soil moisture and facilitated a transition from spruce muskeg to sedge wetland. At alpine treeline the removal of stabilizing vegetation and organic soil during construction slowed subsequent ecosystem recovery. These findings are consistent with resilience theory that predicts that changes to key environmental factors will increase the likelihood of regime shifts. In terrain types where disturbance fundamentally alters ecosystem processes, the management of disturbance impacts in NNPR will be extremely difficult. Overall, this thesis contributes to our understanding of effects of disturbance on vegetation and abiotic conditions, and provides insight into the future of high-latitude ecosystems in a warmer climate with increased disturbance.

Table of Contents

Supervisory Committee	ii
Abstract	iii
Table of Contents	v
List of Tables	vii
List of Figures	viii
Acknowledgments.....	xi
Chapter 1- Introduction.....	1
Critical Context.....	3
The Dempster Highway (Highway 8).....	3
Prairie Creek Winter Access Road	4
Drivers of shrub proliferation	4
Ecosystem feedbacks of tall shrubs	5
Drivers of contemporary permafrost configuration	6
Uncertainty in the response of discontinuous permafrost to disturbance	7
Effects of vegetation structure on ground conditions	8
Effects of soils on ground conditions.....	9
Vegetation response to changing permafrost conditions	9
Chapter 2 - Drivers of tall shrub proliferation at the Dempster Highway, NWT	11
Introduction.....	12
Methods.....	13
Study Area	13
Airphoto Analysis	15
Experimental Site Selection.....	18
Response Variables.....	18
GIS Data.....	19
Statistical Analysis.....	19
Results.....	21
Discussion.....	29
Conclusions.....	32
Chapter 3 – Ecosystem recovery after the abandonment of a winter access road in Nahanni National Park Reserve, NWT	34
Introduction.....	35
Methods.....	37
Study Area	37
Response Variables.....	40
Statistical Analysis.....	41
Results.....	43
Discussion.....	53
Disturbance effects at the Prairie Creek road	53
Resilience of discontinuous permafrost	55
Implications for management	56
Conclusions.....	58

Chapter 4 – Project Summary 59

 Synthesis 62

 Limitations of case study 1: The Dempster Highway, NT. 63

 Limitations of case study 2: Prairie Creek winter access road, NT. 64

 Future Research 64

Bibliography 67

List of Tables

- Table 2-1: Results from the SIMPER analysis of pairwise comparisons of community composition among all three site types. The top eight species or species groups that contributed to between-group dissimilarity for pairwise comparisons of site types. Mean cover is $\log(x+1)$ transformed..... 24
- Table 2-2: Mixed model results for comparisons of biotic and abiotic response variables between site types. Site type has two levels: stable dwarf shrub and tall shrub expansion. Significant p-values are shown in bold text..... 25
- Table 2-3: Mixed model results for comparisons of GIS-derived response variables. Site type has two levels: stable dwarf shrub and tall shrub expansion. Significant p-values are shown in bold text..... 28
- Table 3-1: A_{NOSIM} statistic for pairwise comparisons of plant community composition between control and disturbed sites in the four terrain types. R_{ANOSIM} values below 0.25 are considered to be indistinguishable based on their species composition (Clarke & Gorley 2001). 44
- Table 3-2: Results from the SIMPER analysis of community composition at disturbed and undisturbed sites in the 4 terrain types. The top seven species or species groups that contributed to between-group dissimilarity for comparisons of control and disturbed terrain types are shown. Mean cover is $\log(x+1)$ transformed. 45
- Table 3-3: Mixed model results for biotic and abiotic response variables. Site has 4 levels: black spruce parkland, spruce muskeg, deciduous forest, and alpine treeline. Disturbance has two levels: control and disturbed. Significant p-values are bold. 49

List of Figures

Figure 2-1: Map showing the study area and study sites adjacent to the Dempster. Study sites were classified by the degree of tall shrub proliferation. Inset map at the bottom right indicates the position of the study area (box) in northern Canada. 14

Figure 2-2: Historical black and white 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. 17

Figure 2-3: (A) Relative landcover change (%) and (B) landcover change area (km²) adjacent to the Dempster highway and more than 500m from the Dempster highway. Note the large increase in the cover of water and tall shrubs adjacent to the Dempster. . 21

Figure 2-4: Non-metric multidimensional scaling (NMDS) ordination of plant community composition based on a Bray-Curtis similarity matrix. Symbols represent subplots sampled in 3 site types adjacent to the Dempster highway. 22

Figure 2-5: Scatterplot showing the principal components scores (PC1 and PC2) for each site. The arrows show the direction of increasing values for shrub height, organic soil thickness, soil moisture, and active layer thickness. Only variables with significant loadings were plotted ($\alpha=0.01$). 23

Figure 2-6: Biotic and abiotic response variables measured in stable dwarf shrub (Stable Dwarf) and tall shrub expansion (Tall Expansion) sites adjacent to the Dempster highway: (A) Average site elevation (m), (B) Average embankment height (m), (C) Average organic soil thickness (cm), (D) Average gravimetric soil moisture (%), (E) Average active layer thickness (cm), (F) Average soil pH, (G) Average litter depth (cm), and (H) Maximum shrub canopy cover height (cm). 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 ($\alpha=0.05$). 26

Figure 2-7: Abiotic response variables derived from GIS for stable dwarf shrub sites (Stable Dwarf) and tall shrub expansion sites (Tall Expansion) adjacent to the Dempster Highway: (A) Average elevation (m), (B) Average topographic wetness index (unitless), (C) Average untransformed area solar radiation (watt hours per m²), (D) Average slope (degrees). Bars show the mean of 1000 random points for each site type. Error bars illustrate the 95% confidence interval of the mean. Three asterisks (***) indicate that the contrast is significantly different ($\alpha=0.05$). 27

Figure 2-8: Relative elevation of the highway embankment and adjacent terrain obtained from total station surveys at A) tall shrub expansion and B) stable dwarf shrub sites. Each plot shows the average x (meters from toe of embankment) and y (relative elevation in meters) position of the highway embankment at 4 points: (a) embankment shoulder, (b) toe of the embankment, (c) minimum elevation adjacent to the embankment, and (d) first point away from the road where the ground begins to level. Error bars indicate the 95% confidence interval of the mean height of these points. Dashed lines show the position (x and y) of the embankment..... 28

Figure 2-9: Topographic wetness index (A) derived from a LIDAR digital elevation model and a QuickBird satellite image of the same area (B). Darker blue regions on the topographic wetness index represent areas of higher potential wetness. Areas of tall shrub proliferation adjacent to the Dempster are shown as green polygons. 29

Figure 3-1: Map of the study area showing field sites in each terrain type along the Prairie Creek access road. Green shading indicates vegetated areas, and white indicates unvegetated areas. Inset map at the bottom left shows the position of the study area in Northwestern Canada. The black outline indicates the boundaries of Nahanni National Park Reserve expansion and the shaded box shows the extent of the upper map. 38

Figure 3-2: Photos of characteristic vegetation communities of each terrain type: black spruce parkland, spruce muskeg, deciduous forest, and alpine treeline. Aerial views of the terrain types are in the left column, photos of the control transects are in the middle column, and photos of disturbed transects are in the right column. 39

Figure 3-3: Non-metric multidimensional scaling ordination of plant community composition based on a Bray-Curtis similarity matrix. Symbols represent control and disturbed plots in the four terrain types. 44

Figure 3-4: Size class distribution of canopy trees in spruce muskeg terrain. Control and disturbed sites that have significantly different size distributions are marked with three asterisks ($\alpha=0.05$)..... 46

Figure 3-5: Size class distribution of canopy trees in deciduous woodland terrain. Control and disturbed sites that have significantly different size distributions are marked with three asterisks ($\alpha=0.05$). Note that the scale on the y-axis differs between the upper and lower graphs..... 47

Figure 3-6: Size class distribution of canopy trees in black spruce parkland terrain. Control and disturbed sites that have significantly different size distributions are marked with three asterisks ($\alpha=0.05$)..... 48

Figure 3-7: Abiotic and biotic response variables measured in control and disturbed transects in black spruce parkland, spruce muskeg, deciduous woodland, and alpine terrain types: (A) volumetric soil moisture (%), (B) organic soil thickness (cm), (C) active layer thickness (cm), (D) litter depth (cm), (E) maximum understory height, and

(F) maximum shrub height (cm). Bars show means for each site type, and error bars are 95% confidence intervals of the mean. Significant differences in biotic and abiotic factors between control and disturbed terrain types are indicated with three asterisks ($\alpha=0.05$, LS Means procedure, Tukey adjusted p-values). 51

Figure 3-8: Near-surface ground temperatures recorded at 10cm and 100cm below the ground surface from August 2012 to August 2013 at disturbed (red) and undisturbed (blue) sites in black spruce parkland, spruce muskeg, deciduous forest, and alpine treeline terrain types. Lines show the daily mean temperatures ($^{\circ}\text{C}$). The dashed reference line shows 0°C 52

Acknowledgments

This project was made possible by the contributions of many people. Thanks to my supervisor, Trevor Lantz, for his support and advice throughout this project. Brian Starzomski and Karen Harper also provided thoughtful comments and feedback on this work.

For help and support in the field, lab, and elsewhere, I would like to extend a hearty thank you in no particular order to: Harneet Gill, Audrey Steedman, Mat Whitelaw, Kaylah Lewis, Aaron Donohue, Claire Marchildon, Krista Chin, Brendan O'Neill, Marcus Phillips, Mike Sutor, Doug Tate, Jon Tsetso, Sharon Snowshoe, Peter Snowshoe, Christine Firth, Becky Segal, Abra Martin, Chanda Brietzke, Meg Sullivan, Christine Twerdoclib, Shannon McFayden, Rosanna Breiddal, and Jamie Pope.

Chapter 1- Introduction

Arctic ecosystems are experiencing rapid changes as a result of climate warming and anthropogenic disturbances (Chapin et al., 2004; Cheng and Wu, 2007; Forbes et al., 2001; Hudson and Henry, 2009; Tape et al., 2012; Walker and Walker, 1991). Permafrost is a key determinant of pattern and process in arctic ecosystems and is particularly vulnerable to the effects of these changes (Euskirchen et al., 2010; Romanovsky et al., 2010). It is anticipated that permafrost degradation will affect hydrology, nutrient cycling, species distributions, and profoundly influence the global carbon cycle by liberating large quantities of soil carbon into positive feedbacks to climate warming (Grosse et al., 2011; Jorgenson et al., 2001; McGuire et al., 2006; Natali et al., 2011; Quinton et al., 2011; Schuur et al., 2008; Sturm et al., 2005a; Walker et al., 2003, 2006; Wookey et al., 2009).

Towards the southern extent of discontinuous permafrost, perennially frozen ground underlies less than 90% of the landscape and is typically shallow, warm, and strongly influenced by local conditions (Shur and Jorgenson, 2007; Smith and Riseborough, 2002). Further north, continuous permafrost is thicker and colder, and occurs under all terrestrial surfaces (Beilman et al., 2001; Camill, 1999; Smith et al., 2010a). Although permafrost is sensitive to air temperatures, vegetation and surface conditions (snow pack, albedo, evapotranspiration, soil moisture, etc.) also influence the state of permafrost by mediating surface energy balances (Iwahana, 2005; Lantz et al., 2010a; Liston et al., 2002; Pomeroy et al., 2008; Sturm et al., 2005b). In the discontinuous permafrost zone, the persistence of frozen ground is especially dependent on vegetation and organic material that buffers the ground from warm air temperatures (Camill and Clark, 2000; Shur and Jorgenson, 2007; Walker et al., 2003).

Research shows that disturbances such as roads, seismic lines, fires, and right of ways can strongly influence the thermal state of permafrost because the effects of disturbance on biotic and abiotic surface conditions facilitate increases in ground temperature (Burn, 1998, 2000; Chapin and Shaver, 1981; Gill et al., 2014; Smith and

Riseborough, 2010; Smith et al., 2008; Williams et al., 2013). However, after disturbance events, vegetation succession patterns and the development of organic soil can also reduce soil temperatures, increasing the likelihood of permafrost recovery (Burn, 2000; Calmels et al., 2012; Jorgenson et al., 2010b). At present, the relationship between disturbance and variable vegetation recovery is not fully understood.

Efforts to predict future permafrost configurations in the Arctic as a whole requires an understanding of how climate warming and disturbance interact with vegetation and variable biophysical conditions in thaw sensitive terrain (Bauer and Vitt, 2011; Camill et al., 2001; Jorgenson et al., 2010b). Regionally specific studies are therefore needed to characterize the relationship between disturbance effects, vegetation succession patterns, and biophysical factors that mediate permafrost conditions.

The overarching goal of my MSc. research is to explore variation in the response of vegetation to disturbance in the subarctic. This thesis consists of two standalone research projects that focus on the ecological effects of roads built in permafrost regions.

Chapter 2 explored the ecological impacts of the Dempster Highway in a zone of continuous permafrost where it crosses the Peel Plateau, NWT. In this chapter I examined the nature and causes of vegetation change adjacent to the road. In this project, field and remote sensing data were used to assess the biophysical factors that promote tall shrub proliferation. My specific research questions were as follows:

- **What is the magnitude of landcover transformation next to the Dempster Highway?**
- **What biophysical factors are associated with tall shrub proliferation?**

This component of my research included mapping landscape change adjacent to the Dempster between 1975 and 2008, extensive fieldwork, and GIS data collection.

In Chapter 3 I explored ecosystem recovery trajectories along the Prairie Creek Winter Access Road, in Nahanni National Park Reserve (NNPR), NT. The Prairie Creek road was constructed and abandoned in 1981-82 and crosses a zone of

discontinuous permafrost. This research examined post-disturbance ecological recovery in four different terrain types. In this component of my thesis I sought to identify biophysical factors that mediate or constrain ecosystem recovery in thaw-sensitive terrain. Data collected from the Prairie Creek winter access road were used to explore the following question:

- **How do post-disturbance biotic and abiotic conditions following road abandonment affect ecosystem recovery in discontinuous permafrost?**

This component of my thesis involved extensive field sampling in black spruce parkland, alpine treeline, deciduous forest, and spruce muskeg terrain types in NNPR.

Both case studies are valuable in that they are regionally specific, and investigate disturbance-initiated feedbacks to ground surface conditions in different zones of permafrost. The results of each case study will contribute to our understanding of the response of thaw-sensitive ecosystems to disturbance and will inform management that seeks to minimize the effects of northern infrastructure.

In the final chapter of this thesis, I discuss the implications of the results presented in both Chapters 2 and 3, and provide an overall synthesis of the work as a whole.

Avenues for future research are also discussed. The remainder of this chapter provides additional background information relevant to the thesis.

Critical Context

The Dempster Highway (Highway 8)

The Dempster Highway is an all-weather two-lane road that connects Dawson City, YK with Inuvik, NT. The Dempster Highway was approved for construction in 1958 and was opened to traffic in 1979. It is currently the only all-season road into Canada's western arctic. As the road is constructed over a region of continuous permafrost, the roadbed consists of a raised gravel berm designed to maintain underlying permafrost by reducing heat transfer from the road to the ground. At the Peel Plateau, frequent maintenance of the Dempster is required to resurface, widen, and repair the road. Roadside water bodies are periodically drained prior to winter

freezing. The application of dust palliatives, such as calcium chloride and light watering of the road surface, are undertaken along the Dempster and other arctic gravel roads to suppress dust (Jones et al., 2001; Thompson and Visser, 2007; Walker and Everett, 1987). In the winter, road management focuses on snow removal from the surface of the road.

Prairie Creek Winter Access Road

Aboriginal Affairs and Northern Development Canada (AANDC) guidelines indicate that winter access roads are typically constructed in winter months once the ground is frozen. Dozers are used to level the surface of the ground and to clear and pack snow so that ground freezing is enhanced and the ground surface is protected. Trees and brush are cleared from the route. Water may also be used to build up ice for the road bed. These types of roads should only be used once the ground is frozen since ground ice increases soil strength (Indian and Northern Affairs, 2010). Opening and closing dates for winter access roads are typically determined by air temperatures and snow depth (Indian and Northern Affairs, 2010).

In 1981, a winter road was built in the region to access a silver and base metal mine near Prairie Creek. This particular road was intended to haul minerals and supplies to and from the mine during the winter. This road traverses the eastern portion of NNPR and was abandoned in 1982. The road remained unused until 2014, when Canadian Zinc obtained permits to resume road operation and maintenance. Approximately 64km of the 180km Prairie Creek Access Road pass through NNPR. The road spans numerous terrain types, ranging from high elevation alpine tundra to low-lying peatlands. This road also crosses the main Nahanni karst belt (Ford, 2011). Spillage of hazardous substances during road use should be avoided as access to karst aquifers may cause aquifer contamination (Ford, 2011).

Drivers of shrub proliferation

Tall shrub tundra, or low shrub subzone, is characterized by shrubs that are between 40-400 cm tall (Lantz et al., 2010a). Similar rates of tall shrub proliferation across the arctic have been attributed to warming air temperatures, and predicted increases in

winter precipitation are also expected to enhance shrub growth (Blok et al., 2015; Fraser et al., 2014; Sturm et al., 2001a; Tape et al., 2012; Wahren et al., 2005). Additionally, landscape-level disturbances, such as thermokarst and tundra fires, and anthropogenic disturbances such as sumps, roads, and seismic lines have been associated with increased rates of tall shrub proliferation because these disturbances improve growing conditions for tall shrubs by exposing previously frozen nutrient-rich mineral soil as a substrate for colonization, and by enhancing ground temperatures, nutrient availability, and soil moisture balances (Frost et al., 2013; Johnstone and Kokelj, 2008; Kemper and Macdonald, 2009a; Kokelj and Jorgenson, 2013; Lantz et al., 2009, 2010a; Tape et al., 2012). Once established, tall shrubs induce several positive feedbacks that are thought to promote additional proliferation (Buckeridge et al., 2009; Gill et al., 2014; Lantz et al., 2013; Myers-Smith et al., 2011; Sturm et al., 2005a; Wookey et al., 2009).

Ecosystem feedbacks of tall shrubs

Tall shrubs have a different effect on snow cover and ground temperature than mature trees and other types of vegetation. Shrubs tend to trap snow, which increases ground temperatures by insulating the ground from winter heat loss (Shur and Jorgenson, 2007; Sturm et al., 2005a). Warmer winter soil temperatures allow for winter microbial activity with the net result being greater nutrient availability (Buckeridge and Grogan, 2008; Sturm et al., 2005a). Additionally, deeper snow prevents shrub tissue damage from harsh winter conditions and increases spring runoff (Blok et al., 2015; Hiemstra et al., 2002; Liston et al., 2002). Tall shrubs with more complex structures decrease albedo and increase radiation absorbed by the canopy (Chapin et al., 2005; Pomeroy et al., 2008, 2006; Sturm et al., 2005a). The impact of shrubs on surface energy balance is particularly important in the spring, when rapid snowmelt around the shrubs extends the shrub growing season (Liston et al., 2002; Pomeroy et al., 2006). In this manner, shrubs have the potential to alter the structure and function of ecosystems (Sturm et al., 2001a, 2005a).

Drivers of contemporary permafrost configuration

At the continental scale, the current configuration of permafrost is associated with mean annual air temperatures (Brown, 1960). At its southern margin, discontinuous permafrost underlies <90% of the ground and is relatively warm (generally above -3°C) and only a few meters thick (Smith et al., 2010a). As mean annual air temperatures decrease at higher latitudes, permafrost becomes continuous, thicker, and colder (Smith and Riseborough, 2002; Smith et al., 2010a).

The continental distribution of permafrost has been responsive to past climate changes (Anisimov and Nelson, 1997; Jorgenson and Osterkamp, 2005; Marchenko et al., 2007; Vitt et al., 2000). Presently, there is also evidence that the latitudinal and elevational configuration of permafrost is changing, with the southern permafrost boundaries shifting north in response to warmer mean annual air temperatures (Halsey et al., 1995; Marchenko et al., 2007; Nelson et al., 2002). Permafrost distribution models that use climate warming as a driver of permafrost distribution forecast a large range contraction in areas underlain by continuous permafrost within the next century (Anisimov and Reneva, 2006; Nelson et al., 2002).

The degree of thaw, however, is not expected to be uniform across the polar region (Smith et al., 2005, 2010a). Data collected from boreholes drilled during the International Polar Year (IPY) suggests that long-term climate warming will decrease both the total area of terrain underlain by permafrost and the extent of continuous permafrost (Romanovsky et al., 2010; Smith et al., 2010a). As the continuous permafrost boundary shifts north, the area underlain by extensive and sporadic discontinuous permafrost zones will increase (Anisimov and Nelson, 1997; Halsey et al., 1995; Nelson et al., 2002; Smith et al., 2010a). In many places the permafrost that remains will not be in equilibrium with current climate conditions, but will continue to exist in locations where surface conditions such as vegetation cover and soil type facilitate its persistence (Shur and Jorgenson, 2007).

Uncertainty in the response of discontinuous permafrost to disturbance

Regions of discontinuous permafrost are areas where 50-90% of the ground is frozen year-round for two consecutive years (Beilman et al., 2001; Smith and Riseborough, 2002). In some regions, areas of discontinuous permafrost are in disequilibrium with current climate conditions and would not form under the present-day climate (Camill and Clark, 1998, 2000; Jorgenson et al., 2010b; Shur and Jorgenson, 2007). Discontinuous permafrost persists in these locations because local factors prevent thaw (Shur and Jorgenson, 2007). Local factors that can mediate the persistence of discontinuous permafrost in a warm climate include elevation, aspect, soil moisture, snow cover, and soil conditions, as well as biotic factors such as vegetation cover. These local environmental factors insulate discontinuous permafrost from warmer air temperatures, ultimately slowing its thaw (Camill and Clark, 2000; Halsey et al., 1995; Shur and Jorgenson, 2007; Vitt et al., 2000). Despite the insulation provided by local environmental factors, relatively warm, thin discontinuous permafrost is particularly vulnerable to horizontal energy fluxes from nearby permafrost-free terrain as well as vertical energy fluxes (Beilman and Robinson, 2003; Kwong and Gan, 1994; McClymont et al., 2013; Quinton and Baltzer, 2013).

The response of discontinuous permafrost to terrain disturbances that alter biotic and abiotic conditions is poorly understood. As discontinuous permafrost is considered to be relict of a colder historical climate, it is assumed that once it thaws, it is not capable of regenerating (Arseneault and Payette, 1997; Camill and Clark, 1998, 2000; Shur and Jorgenson, 2007; Wookey et al., 2009). However, there is substantial evidence to show that vegetation succession following disturbance and a gradual thickening of the organic soil layer can promote lower soil temperatures, which make discontinuous permafrost more resilient to transient climate warming (Burn, 2000; Calmels et al., 2012; Jorgenson et al., 2010b). The observation of discontinuous permafrost aggradation after post-disturbance ecosystem recovery emphasizes the importance of vegetation's impact on ground temperatures, as it illustrates that ecosystem and permafrost recovery following disturbance can occur in a warmer climate (Calmels et al., 2012).

Effects of vegetation structure on ground conditions

Tree and shrub cover also influence permafrost conditions (Camill and Clark, 2000). Data collected during the International Polar Year reveal that forested sites have less annual variation in ground temperature when compared with the relatively barren tundra (Romanovsky et al., 2010; Smith et al., 2010a). It is likely that these differences are caused by ground shading from forest canopies, which limits the effects of solar radiation on the ground (Pomeroy et al., 2008, 2006). The three dimensional structure of the vegetation community also affects the degree of shading by the vegetation canopy, and any change in vegetation community composition may impact the amount of solar radiation that reaches the ground (Pomeroy et al., 2008). Black spruce canopies have also been shown to promote the persistence of discontinuous permafrost because they shade the ground and increase evapotranspiration, resulting in a reduction of surface soil moisture (Shur and Jorgenson, 2007; Walker et al., 2003). Removal of surface vegetation, especially trees, can reduce evapotranspiration and increase soil moisture (Iwahana, 2005; Kopp et al., 2014; Vitt et al., 2000; Yoshikawa et al., 2002).

Snow pack also strongly impacts heat transfer between the ground and the air and deep snow has a strong insulative effect on ground thermal conditions (Burn, 2000; Smith et al., 2005; Taylor et al., 2006). The impact of snow on ground temperatures has been experimentally determined with snow addition and removal experiments. Deep winter snow embankments increased winter soil temperatures by roughly 50% compared with areas where snow was removed (Natali et al., 2011). The impact of snow on ground temperatures is impressive on a local scale: it is possible that the mean annual ground temperatures are 1-4⁰C higher than the air temperatures (Osterkamp, 2003). In the winter, mature black spruce trees impede snowfall to the ground, thereby reducing the insulating effects of snowfall on the ground (Shur and Jorgenson, 2007). As such, winter ground temperatures in the boreal forest are influenced by vegetation canopy complexity and by the amount of winter precipitation in that region because the amount of snow trapped by the forest canopy

affects ground cooling, active layer freeze back, and ultimately, ground temperatures (Kanigan et al., 2009; Palmer et al., 2012).

Effects of soils on ground conditions

Disturbances to the soil profile can also strongly influence ground temperatures (Harper and Kershaw, 1997). The impact of the organic layer on soil thermal conductivity was particularly evident in a study undertaken by Woo & Xia (1996). Here, the researchers showed that the latent heat requirement to melt ice-rich organic soil is relatively high. Once thawed and saturated, the thermal conductivity of the organic soil is much lower than that of saturated mineral soil and takes longer to freeze back (Woo and Xia, 1996). Other studies also show that different components of the soil profile have different heat capacities, with peat being the least conductive component of the soil profile (Nicolosky et al., 2007). As such, soils with deep surface organic soils buffer frozen soil profiles against heat transfer from warm air (Camill and Clark, 2000; Osterkamp, 2003; Woo et al., 2007).

Soil moisture can also influence active layer thickness, ground temperatures and ground thaw rates because increased soil moisture slows latent heat loss and freezeback (Burn, 1992, 1998; Quinton and Baltzer, 2013; Romanovsky and Osterkamp, 2000; Woo et al., 2006; Wright, 2009). The magnitude of soil moisture effects vary across permafrost zones: in areas underlain by continuous permafrost high soil moisture affects ground temperatures for several weeks before freeze up. In areas of discontinuous permafrost high soil moisture can affect temperatures over the duration of the winter (Romanovsky and Osterkamp, 2000).

Vegetation response to changing permafrost conditions

As ground temperature, active layer depth and nutrient availability change in response to warmer air temperatures, vegetation structure and composition are also likely to change (Euskirchen et al., 2009; Walker et al., 2006). By altering permafrost conditions and other biophysical factors that affect vegetation, disturbance may also trigger non-linear ecosystem responses that result in unanticipated successional

trajectories and alternative stable states. Plant communities unsuited to cold, wet soils underlain by permafrost are expected to thrive in more appropriate conditions caused by permafrost thaw (Johnstone and Kokelj, 2008; Jorgenson et al., 2010a; Kemper and Macdonald, 2009a; Kershaw and Gill, 1979). Conversely, altered hydrology patterns caused by thermokarst during permafrost peat plateau collapse have been observed to drive transitions to a wet bog/fen type ecosystem (Camill, 1999; Jorgenson et al., 2001). Vegetation-driven feedbacks that emerge as permafrost degrades can also change ecosystem function by affecting surface energy balances, ground heat exchange, nutrient cycling, as well as carbon and methane-related biogeochemical processes (Buckeridge et al., 2009; Chapin et al., 2005; Chasmer et al., 2011; Euskirchen et al., 2010; Gill et al., 2014; Jorgenson and Osterkamp, 2005; Lantz et al., 2013; Pomeroy et al., 2008; Shur and Jorgenson, 2007; Sturm et al., 2001a).

Chapter 2 - Drivers of tall shrub proliferation at the Dempster Highway, NWT

Emily A Cameron¹ and Trevor C. Lantz^{1,2}

1. School of Environmental Studies, University of Victoria
2. Author for correspondence
3. EAC and TCL conceived the study; EAC collected the data; EAC analyzed the data; EAC and TCL wrote the manuscript.

Introduction

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

Recent research also shows that disturbances can transform Arctic vegetation by facilitating shrub growth and proliferation in areas where shrubs were not previously dominant. Disturbances such as thaw slumps, lake drainage, tundra fire, and frost heave all facilitate rapid conversion to tall shrubs (Frost et al., 2013; Landhäusser and Wein, 1993; Lantz et al., 2009, 2010b; Mackay and Burn, 2002). Field studies of seismic lines, roads, and drilling mud sumps indicate that human-caused disturbance also stimulate tall shrub growth (Auerbach et al., 1997; Gill et al., 2014; Johnstone and Kokelj, 2008; Kemper and Macdonald, 2009b).

Evidence from plot-scale warming experiments (Bret-Harte et al., 2001; Chapin et al., 1995; Elmendorf et al., 2012b; Walker et al., 2006) 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 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., 2012; 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). Some evidence suggests that shrub proliferation at disturbed sites may also be facilitated by

changes to hydrology (Johnstone and Kokelj 2008, Gill et al 2014), but additional research is required to understand drivers of shrub proliferation.

A recent study of shrub proliferation adjacent to the Dempster highway indicates that linear disturbances provide an excellent opportunity to study the edaphic factors that mediate tall shrub expansion (Gill et al., 2014). Historical images of the Dempster (1975) that precede its official opening to traffic in 1979 allow comparisons of vegetation structure prior to prolonged disturbance from road use. Inspection of these images suggests that patchy shrub expansion is related to variation in hydrological changes associated with the construction of the highway. To test the hypothesis that increases in tall shrub density are linked to hydrological changes following road construction, we compared biophysical factors between areas where shrub density increased since 1975 with areas where the vegetation structure has not changed since 1975.

Insight into drivers of tall shrub proliferation is critical to our ability to forecast the nature and extent of Arctic vegetation change. Understanding the drivers of shrub encroachment is important for infrastructure management because shrub-snow feedbacks can increase ground temperatures and lead to permafrost thaw, which threatens road stability and increases the cost of road maintenance and repair (Gill et al., 2014). 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 regimes (Buckeridge et al., 2010; Chapin et al., 2005; Lantz et al., 2009; Schuur et al., 2008; Sturm et al., 2005a).

Methods

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 2-1). This section of the highway is bounded to the west by the Richardson Mountains and by the Peel River to the east. 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).

Within shrub tundra communities, *Rubus chamaemorus* (L.), *Betula glandulosa* (Michx.), and *Vaccinium* spp (L.) dominate the understory, and *Alnus fruticosa* ((Ruprecht)Nyman) and *Salix* spp. are patchily distributed across the landscape (Stanek et al., 1981).

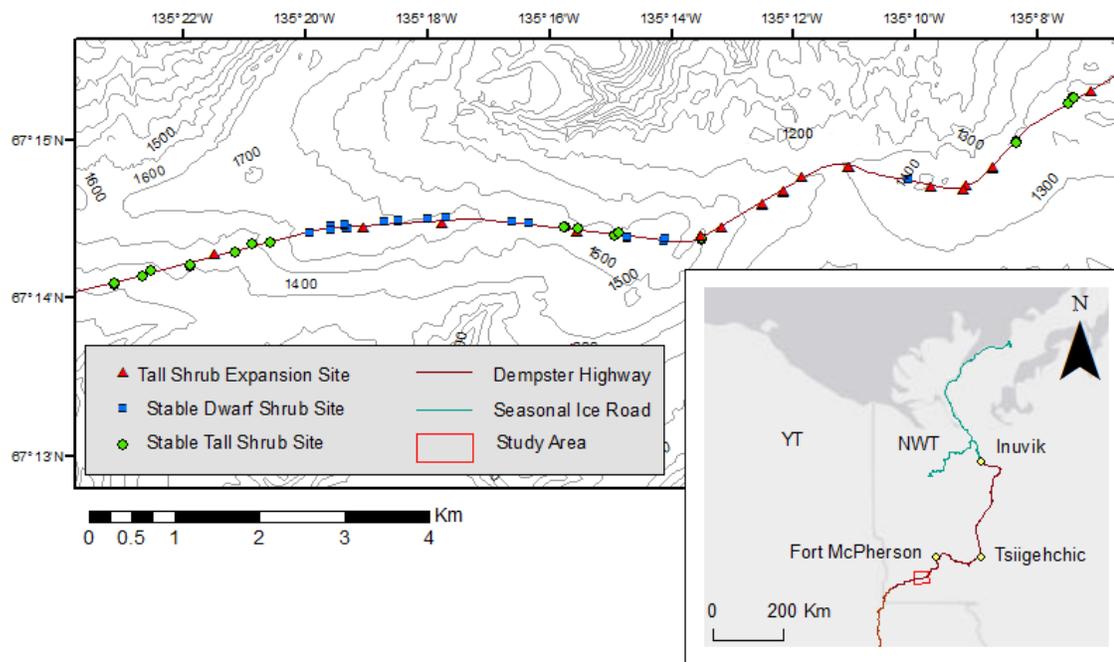


Figure 2-1: Map showing the study area and study sites adjacent to the Dempster. Study sites were classified by the degree of tall shrub proliferation. Inset map at the bottom right indicates the position of the study area (box) in northern Canada.

The climate in this 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 , and in this region, mean annual air temperatures have increased by 0.77°C per decade since the 1970's (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). Across our study area, the highway crosses numerous small drainages and water tracks. Despite relatively low regional precipitation, a large proportion of snow and rain is mobilized as slope runoff because the underlying permafrost acts as an aquiclude and the shallow active layer has a limited capability to absorb water (Hinzman et al., 2003; Kokelj, 2001; Roots et al., 2004; Woo, 1986).

The northern Dempster highway was constructed between 1959 and 1979, and passes over continuous permafrost (O'Neill et al., 2015; Smith et al., 2005; Tunnicliffe et al., 2009). The Peel Plateau region is characterized by glacio-fluvial, glacio-lacustrine and ice-rich morainal sediments that overlay cretaceous sandstones, marine shales, and conglomerate bedrock (Duk-Rodkin and Hughes; Hadlari, 2006; Norris; Stanek et al., 1981). Differences in soil conditions, hydrology, vegetation communities, and climate affect near surface ground thermal regimes and contribute to variation in active layer thickness, which is typically less than one meter in this region (Hughes et al., 1981; Kokelj et al., 2013; O'Neill et al., 2015; Zhang, 2005).

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 0.6m and the timing of image acquisition increased colour contrast between *Salix* spp, *Alnus fruticosa*, and ericaceous dwarf shrubs. Greyscale aerial photos (1975) were scanned at 1200 dpi, but had an effective pixel size of 0.6m, and were processed in the computer program Summit Evolution to create soft copy stereo models. In Summit Evolution, absolute orientation of stereo models was completed using 2008 Quickbird imagery and a digital elevation model with a grid size of 20x20 m (NRCan/RNCAN, 2013). The average root mean square (RMS) error of stereomodels was 3.67m, but ranged from 0.7 to 5.5 m.

To compare land cover in both time periods, mapping was completed inside buffers adjacent to the road (road buffer) and distant from the highway (control buffer). The road buffer extended 22m past the toe of the road embankment on both sides of the road. The road surface was not included in the buffer, and the buffer width of 22 m from the road was maintained in instances where the road had been widened. Control buffers located 500 m away from the Dempster on both sides of the road were also 22 m wide. Both the control and road buffers had a total length of 14 km on either side of the road, and covered an area of approximately 0.6 km². In both sets of imagery, tall shrubs, dwarf shrubs, and water were mapped when their area exceeded 1m² (Figure 2-2). Mapping was

undertaken by one person and was completed onscreen while viewing softcopy stereo (1975) or Quickbird images (2008). Based on data in Lantz et al. (2013), we estimate that mapping error rates were less than 6%. 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:

$$\text{Landcover Change} = \frac{\text{Percent Cover 2008} - \text{Percent Cover 1975}}{\text{Percent Cover 1975}}$$

Maps of land cover from each time period were also used to map areas of landscape change and stability (Figure 2-2). 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.

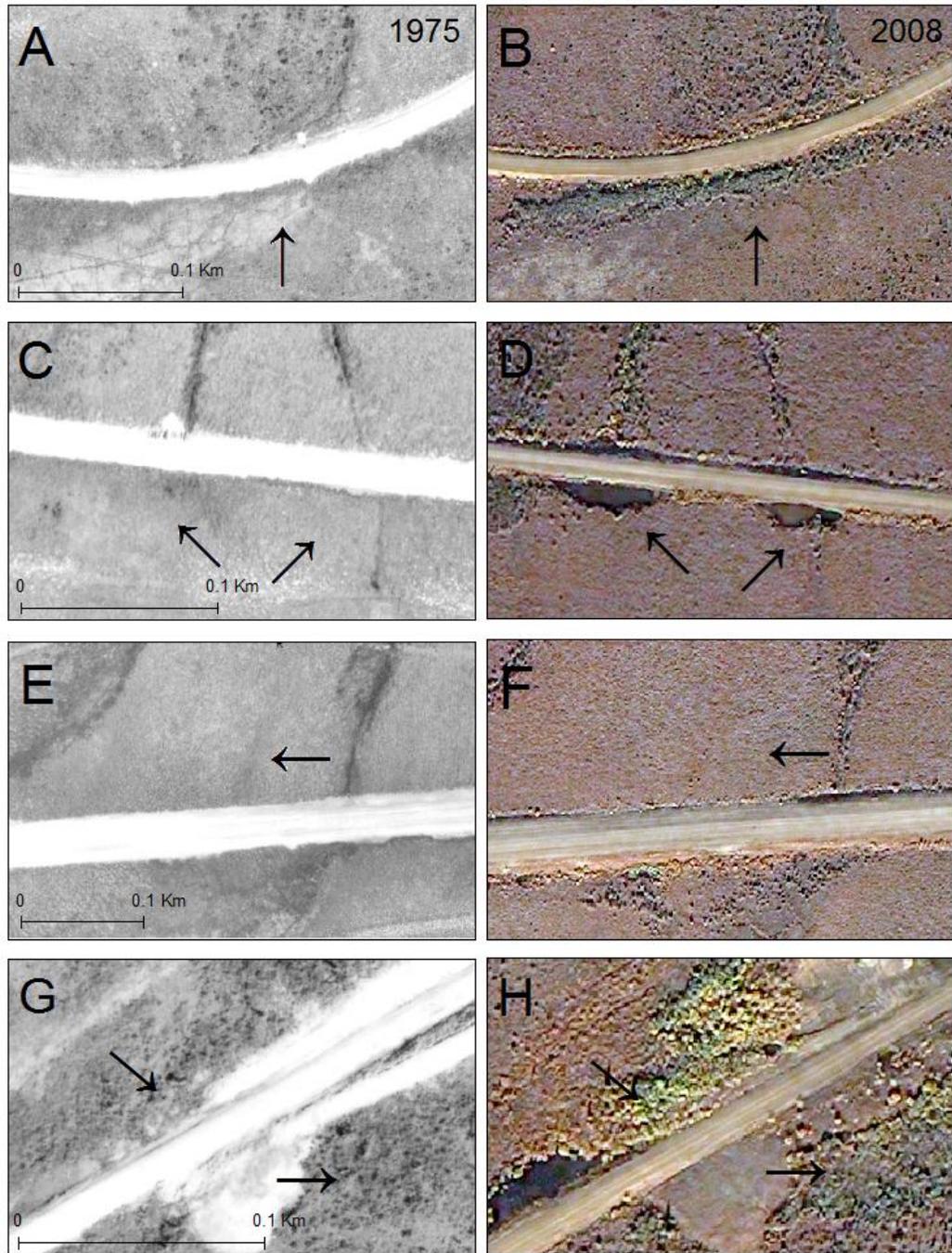


Figure 2-2: Historical black and white air photos (1975) and contemporary satellite imagery (2008) of the same location. Images A and B illustrate a transition from dwarf shrub tundra to tall shrub tundra (arrows). Images C and D demonstrate an increase in ponding adjacent to the Dempster highway (arrows). 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.

Experimental Site Selection

To contrast biotic and abiotic conditions beside the road at: 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 ($>1,600\text{m}^2$) tall shrub proliferation. Stable dwarf shrub sites were located in polygons larger than $1,850\text{m}^2$ 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. Field sites were separated from each other by at least 300m and were distributed across the north and south sides of the road. Fifteen roadside field sites in each vegetation category ($n=45$) were located between 11-14 m from the toe of the road embankment and consisted of 3 subplots 3m from the center of the site on 120^0 , 240^0 , and 360^0 bearings ($n=135$).

Response Variables

Within each subplot, the percent cover of shrubs and trees was estimated inside a 5m^2 quadrat. The percent cover of understory vegetation was estimated using a 0.625m^2 quadrat randomly nested within the larger plot. Gravimetric soil moisture was measured in each subplot at every site by collecting a 250cm^3 composite active layer sample. All soil samples were collected on the same day to minimize weather-related variability in soil moisture. No precipitation had occurred for 48 hours prior to sample collection on August 25, 2013. In hummocky terrain, soil was sampled from the top of the hummock in order to decrease within-site soil variability. Wet soil samples were weighed to the nearest tenth of a gram, and then dried at 90°C for 48 hours in an oven. Gravimetric soil moisture (percent) was calculated with the following formula from (Auerbach et al., 1997):

$$([(wet\ weight-dry\ weight)/dry\ weight] \times 100).$$

A portion of the 250cm^3 composite active layer sample was used to measure soil pH of each subplot by vigorously mixing 10mg of soil with 30mL 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 5m² subplot, 6 active layer measurements were acquired by pushing a graduated soil probe to the depth of refusal. Measurements were restricted to hummock tops in hummocky terrain. A metal ruler was inserted into a small hole to measure litter and organic soil thickness.

At each site, a total station (Nikon NIVO 5M+) was used to measure the relative geometry of the embankment from a bench mark, whose location was established with a GPS unit (Garmin etrex 20). At each site we used the total station to measure position and elevation at the shoulder of the road, the toe of the embankment, and the high and low points within the first 5 meters beyond the toe of the embankment.

GIS Data

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 of the Peel Plateau. The LIDAR DEM had a horizontal resolution of 1m and a vertical resolution of <1m. We used ArcGIS and this DEM to calculate aspect, slope, area solar radiation (ASR) and elevation. A topographical wetness index (TWI) raster was also calculated in ArcGIS using the following formula provided by Sørensen et al., 2006:

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

Subsequently, we used ArcGIS to select 1000 random points in stable dwarf shrub and tall shrub expansion patches (n=2000) beside the road. To reduce the likelihood of mapping error, the following constraints were applied to sample selection: 1) points were separated by at least 1m, and 2) random points were allocated to areas of tall shrub expansion and stable dwarf shrub tundra when the area of these sites was greater than 100m².

Statistical Analysis

To compare vegetation community composition among tall shrub expansion, stable dwarf shrub, and stable tall shrub sites, a non-metric multidimensional scaling (NMDS) ordination of a Bray-Curtis resemblance matrix was performed with the PRIMER software program (Plymouth Marine Laboratories, Plymouth, UK). To reduce noise, percent cover data were log(x+1) transformed, and species present in fewer than two

subplots were removed from analysis (Clarke, 1993). PRIMER was set to repeat the NMDS analysis 25 times, and the two-dimensional ordination with the least amount of stress was selected. 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 explore the interrelationships among response variables measured in the field, we used the statistical program R to perform a principal components analysis (PCA) (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). Significance of variable loadings was calculated as $p \leq 0.01$.

To test for significant differences in 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 all models, site type (tall shrub expansion, stable dwarf shrub) was included as a fixed factor, and site and subplot were treated as random factors. The Kenward-Roger approximation was used to estimate the degrees of freedom in these models (Kenward and Roger, 1997). The importance of including random spatial variation in the models was explored by removing random terms one at a time, and then selecting models with the lowest Akaike information criteria (AIC) (Buckley et al., 2003; Johnson and Omland, 2004; Morrell, 1998). Site was retained as the only random factor for all abiotic factor models except for active layer thickness, where site and subplot were included as random factors. No random terms were retained for elevation or embankment height. Residuals were plotted to ensure normality, and no transformations were necessary. To examine differences in the response variables derived from GIS data we used the same statistical approach. No

random factors were considered in the analysis. To meet the assumption of normality, area solar radiation (ASR) was log-transformed.

Results

Disturbance associated with the construction and maintenance of the Dempster highway has accelerated vegetation change adjacent to the road (Figure 2-3). Shrub proliferation was more extensive adjacent to the Dempster, where the relative cover of tall shrubs increased by 525%. In areas more than 500m from the road, relative tall shrub cover only increased by 34%. The road also had a significant impact on hydrology, and was associated with a 1209% increase in the relative cover of water adjacent to the road. Relative water cover only increased by 0.06% at the buffer 500m from the road. Tall shrub expansion and increases in the cover of water were accompanied by concomitant decreases of dwarf shrub area (Figure 2-3). 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 2-2).

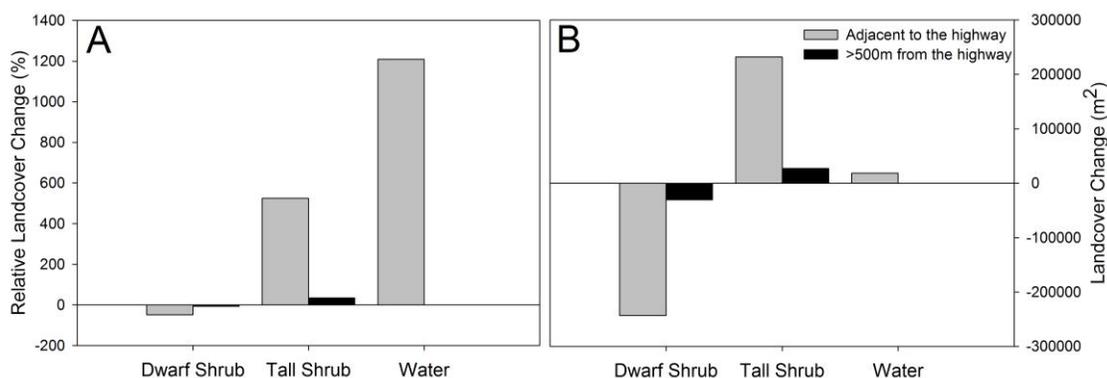


Figure 2-3: (A) Relative landcover change (%) and (B) landcover change area (km²) adjacent to the Dempster highway and more than 500m from the Dempster highway. Note the large increase in the cover of water and tall shrubs adjacent to the Dempster.

Plant community composition adjacent to the road depended on site type (Table 2-1, Figure 2-4). At sites where tall shrub expansion occurred, the vegetation was significantly different from stable dwarf shrub sites ($R_{ANOSIM} = 0.89$, $p < 0.001$), and was characterized

by greater cover of *A. fruticosa* and litter, and lower cover of *R. chamaemorus*, *L. decumbens*, *E. nigrum*, and *V. vitis-idaea* when compared with stable dwarf shrub sites. The vegetation at stable tall shrub sites also differed significantly from stable dwarf shrub sites ($R_{ANOSIM} = 0.93$, $p < 0.001$). This difference was driven by increased cover of *A. fruticosa*, *Salix* spp, and litter and diminished cover of *R. chamaemorus* and ericaceous shrubs at stable tall shrub sites. Community composition in 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. at stable tall shrub sites, and greater *A. fruticosa* cover in tall shrub expansion sites (Table 2-1). To investigate drivers of tall shrub proliferation the remainder of this analysis explores differences in biophysical factors between tall shrub expansion and stable dwarf shrub sites.

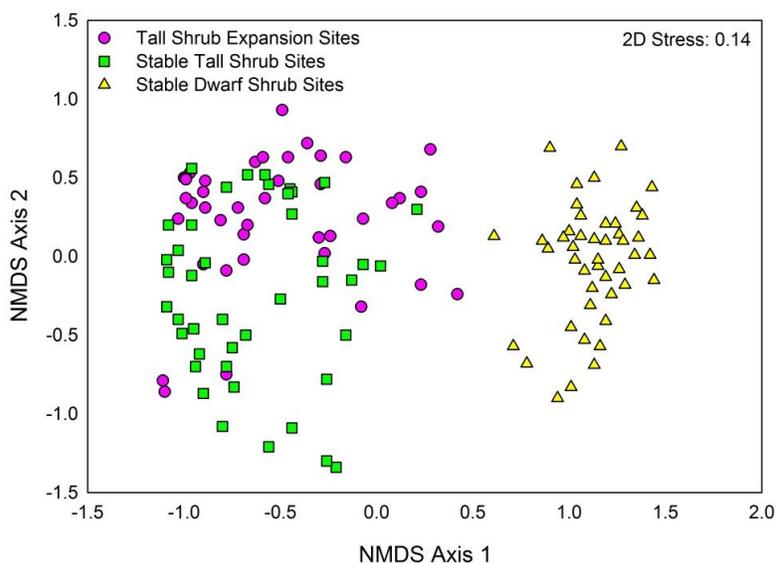


Figure 2-4: Non-metric multidimensional scaling (NMDS) ordination of plant community composition based on a Bray-Curtis similarity matrix. Symbols represent subplots sampled in 3 site types adjacent to the Dempster highway.

Biotic and abiotic response variables measured adjacent to the road also varied between site types (Figure 2-5). The principle component analysis shows that elevated soil moisture, increases in shrub height and organic soil thickness were correlated with each other and strongly associated with tall shrub expansion sites. Deeper active layers were strongly associated with stable dwarf shrub sites and were negatively correlated with

increased shrub height and organic soil thickness and to a lesser degree, soil moisture (Figure 2-5).

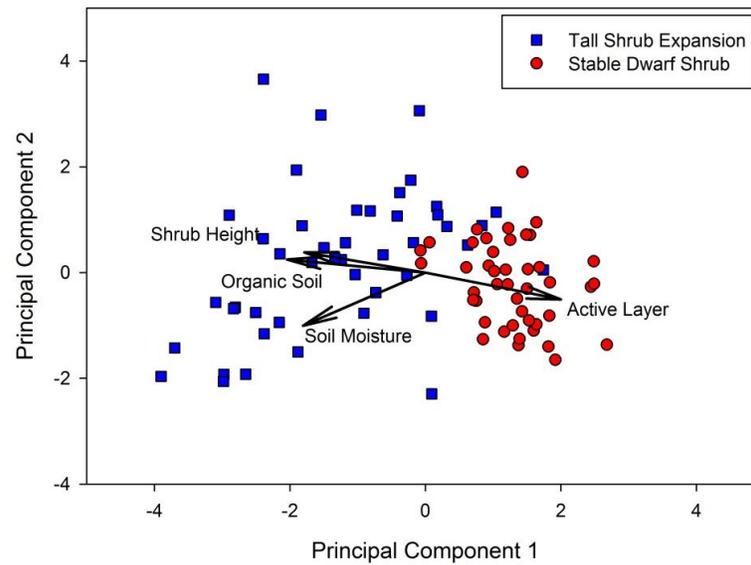


Figure 2-5: Scatterplot showing the principal components scores (PC1 and PC2) for each site. The arrows show the direction of increasing values for shrub height, organic soil thickness, soil moisture, and active layer thickness. Only variables with significant loadings were plotted ($\alpha=0.01$).

Table 2-1: Results from the SIMPER analysis of pairwise comparisons of community composition among all three site types. The top eight species or species groups that contributed to between-group dissimilarity for pairwise comparisons of site types. Mean cover is $\log(x+1)$ transformed.

Species or Species Group	Mean Cover Tall Shrub Expansion	Mean Cover Stable Dwarf Shrub	Cumulative % Dissimilarity
<i>Alnus fruticosa</i>	3.90	0.02	15.61
Litter	4.21	0.81	29.50
<i>Rubus chamaemorus</i>	0.81	2.37	37.44
<i>Ledum decumbens</i>	0.5	2.23	45.15
<i>Empetrum nigrum</i>	0.76	2.15	52.47
<i>Vaccinium vitis-idaea</i>	0.61	2.15	59.63
<i>Cyperaceae</i> spp.	0.24	1.70	66.34
<i>Betula glandulosa</i>	0.85	2.31	72.69
Species or Species Group	Mean Cover Tall Shrub Expansion	Mean Cover Stable Tall Shrub	Cumulative % Dissimilarity
<i>Salix</i> spp.	1.15	2.67	15.20
<i>Alnus fruticosa</i>	3.9	2.57	28.03
<i>Equisetum</i> spp.	0.87	0.94	36.98
<i>Poaceae</i> spp.	0.56	1.01	44.32
<i>Betula glandulosa</i>	0.85	0.79	50.56
<i>Rubus chamaemorus</i>	0.81	0.25	56.32
<i>Vaccinium vitis-idaea</i>	0.61	0.6	62.01
<i>Empetrum nigrum</i>	0.76	0.28	67.30
Species or Species Group	Mean Cover Stable Tall Shrub	Mean Cover Stable Dwarf Shrub	Cumulative % Dissimilarity
Litter	4.10	0.81	12.89
<i>Alnus fruticosa</i>	2.57	0.02	22.76
<i>Salix</i> spp.	2.67	0.41	32.35
<i>Rubus chamaemorus</i>	0.25	2.37	41.11
<i>Empetrum nigrum</i>	0.28	2.15	49.02
<i>Ledum decumbens</i>	0.39	2.23	56.76
<i>Vaccinium vitis-idaea</i>	0.60	2.15	63.86
<i>Betula glandulosa</i>	0.79	2.31	70.52

Comparisons of individual response variables revealed significant differences between sites types (Table 2-2, Figure 2-6). The average elevation of dwarf shrub sites was 46m higher than tall shrub expansion sites, but the average embankment height was not significantly different between stable dwarf and tall shrub expansion sites (Figure 2-6A). 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 (Figures 2-6C, 2-6D, Table 2-2). Active layer thickness at tall shrub expansion sites was significantly lower when compared with stable dwarf shrub sites (Figure 2-6E), but soil pH and average litter depth were similar between sites types (Figure 2-6F and 2-6G). 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 (Figure 2-6G and Table 2-2).

Table 2-2: Mixed model results for comparisons of biotic and abiotic response variables between site types. Site type has two levels: stable dwarf shrub and tall shrub expansion. Significant p-values are shown in bold text.

Response Variable	Effect	F Value	P Value	Degrees of Freedom
Litter	Site Type	3.8	0.0614	1,28
Organic Soil Depth	Site Type	27.36	<0.0001	1,28
Volumetric Soil Moisture	Site Type	12.75	0.0013	1,28
Soil pH	Site Type	0.3	0.5912	1,28
Active Layer Thickness	Site Type	49.56	<0.0001	1,88
Elevation	Site Type	76.01	<0.0001	1,88
Embankment Height	Site Type	0.51	0.4759	1,88
Tall Shrub Height	Site Type	415.34	<0.0001	1,28
Understory Height	Site Type	0.38	0.5441	1,28

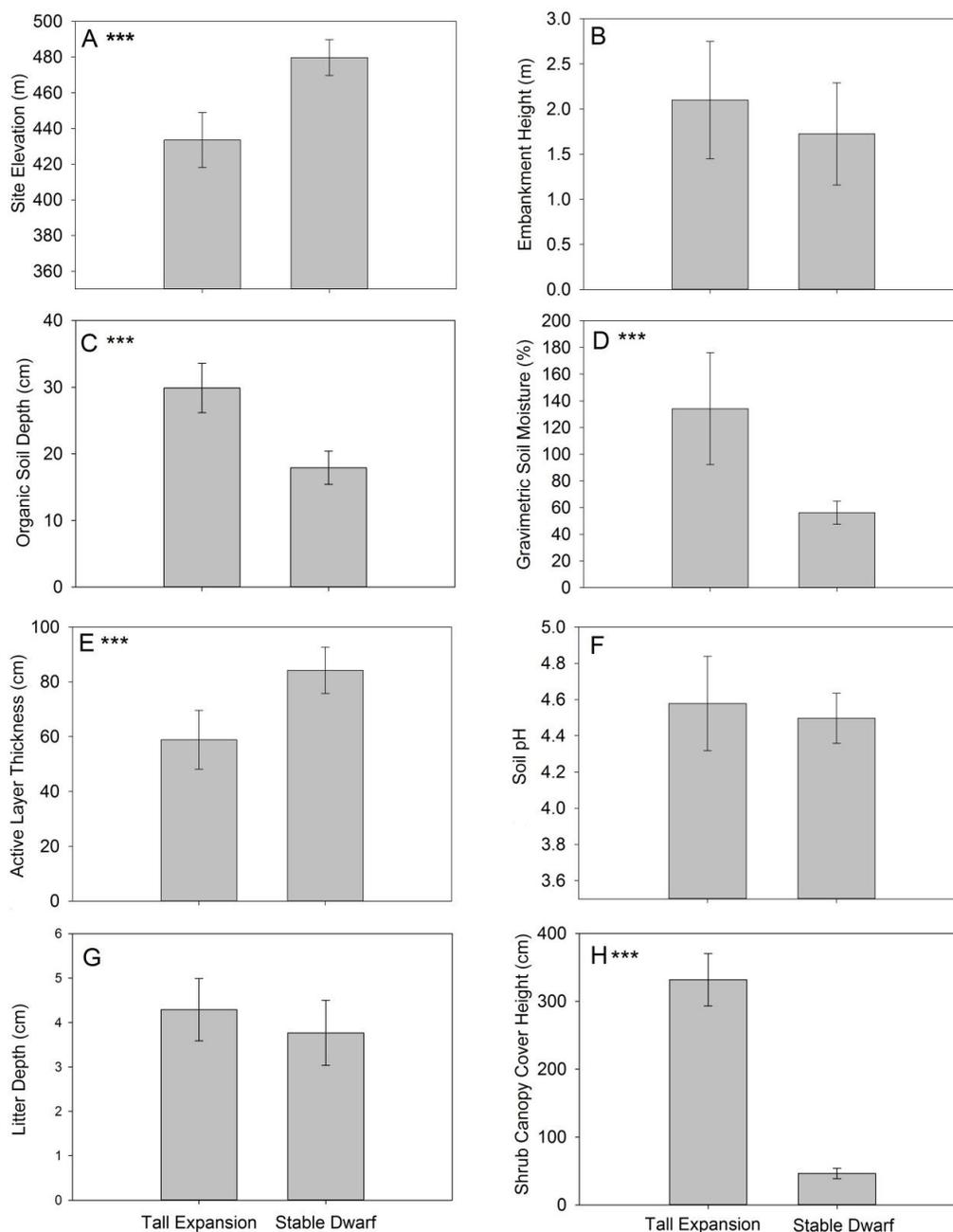


Figure 2-6: Biotic and abiotic response variables measured in stable dwarf shrub (Stable Dwarf) and tall shrub expansion (Tall Expansion) sites adjacent to the Dempster highway: (A) Average site elevation (m), (B) Average embankment height (m), (C) Average organic soil thickness (cm), (D) Average gravimetric soil moisture (%), (E) Average active layer thickness (cm), (F) Average soil pH, (G) Average litter depth (cm), and (H) Maximum shrub canopy cover height (cm). 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 ($\alpha=0.05$).**

Abiotic variables derived from GIS also revealed differences between stable dwarf and tall shrub expansion sites (Table 2-3, Figure 2-7). Stable dwarf shrub sites occurred at higher elevations than tall shrub expansion sites beside the road (Figure 2-7A) and the topographic wetness (TWI) index was significantly higher at tall shrub expansion sites than stable dwarf shrub sites (Figures 2-7B, 2-9). Slope was not significantly different between site types (Figure 2-7D), but the incidence of area solar radiation (ASR) was higher at tall shrub expansion sites (Figure 2-7C).

Topographic profiles of the embankment obtained with a total station revealed small depressions immediately adjacent to the road (Figure 2-8).

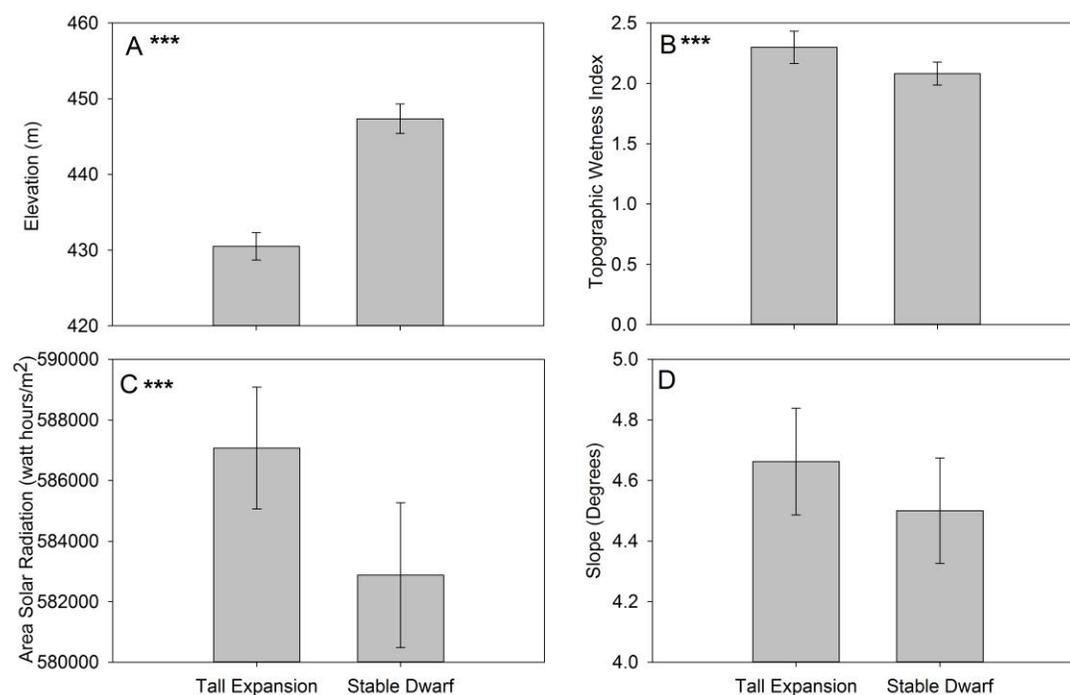


Figure 2-7: Abiotic response variables derived from GIS for stable dwarf shrub sites (Stable Dwarf) and tall shrub expansion sites (Tall Expansion) adjacent to the Dempster Highway: (A) Average elevation (m), (B) Average topographic wetness index (unitless), (C) Average untransformed area solar radiation (watt hours per m²), (D) Average slope (degrees). Bars show the mean of 1000 random points for each site type. Error bars illustrate the 95% confidence interval of the mean. Three asterisks (*) indicate that the contrast is significantly different ($\alpha=0.05$).**

Table 2-3: Mixed model results for comparisons of GIS-derived response variables. Site type has two levels: stable dwarf shrub and tall shrub expansion. Significant p-values are shown in bold text.

Response Variable	Effect	F Value	P Value	Degrees of Freedom
Elevation	Site Type	154.78	<0.0001	1, 1998
Topographic Wetness Index	Site Type	6.81	0.0091	1, 1998
Area Solar Radiation	Site Type	8.56	0.0035	1, 1998
Slope	Site Type	1.65	0.1985	1, 1998

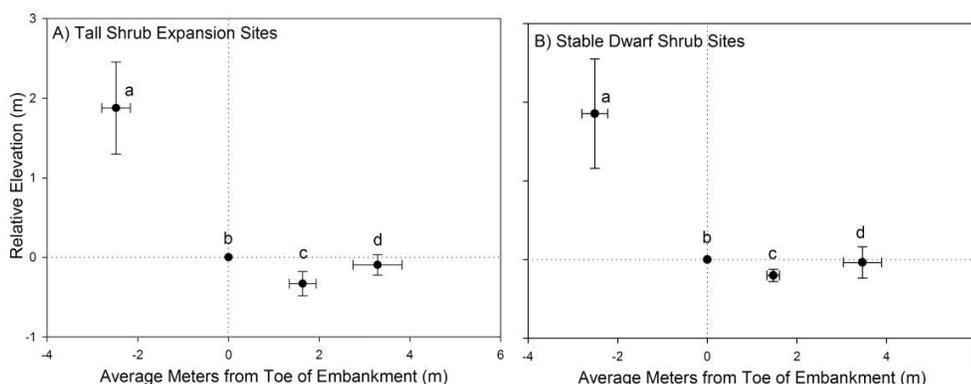


Figure 2-8: Relative elevation of the highway embankment and adjacent terrain obtained from total station surveys at A) tall shrub expansion and B) stable dwarf shrub sites. Each plot shows the average x (meters from toe of embankment) and y (relative elevation in meters) position of the highway embankment at 4 points: (a) embankment shoulder, (b) toe of the embankment, (c) minimum elevation adjacent to the embankment, and (d) first point away from the road where the ground begins to level. Error pars indicate the 95% confidence interval of the mean height of these points. Dashed lines show the position (x and y) of the embankment.



Figure 2-9: Topographic wetness index (A) derived from a LIDAR digital elevation model and a QuickBird satellite image of the same area (B). Darker blue regions on the topographic wetness index represent areas of higher potential wetness. Areas of tall shrub proliferation adjacent to the Dempster are shown as green polygons.

Discussion

Rapid tall shrub proliferation next to the Dempster 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 (Epstein

et al., 2004a, 2004b; Fraser et al., 2014; Jia et al., 2003; Lantz et al., 2013; McManus et al., 2012; Tape et al., 2006). Both plot-scale warming experiments (Elmendorf et al., 2012a, 2012b; Walker et al., 2006) and shrub dendrochronology studies (Forbes et al., 2010; Fraser et al., 2014; Myers-Smith et al., 2015) strongly indicate that pan-arctic tall shrub expansion has been driven by increases in air temperatures. Serreze et al. (2000) have documented recent, disproportionately large temperature increases in Canada's western subarctic and it is likely that direct and indirect effects of warmer air temperatures have also contributed to the shrub expansion we observed at all sites on the Peel Plateau.

Accelerated shrub proliferation adjacent to the road was likely caused by the effects of elevated soil moisture on both establishment and growth. This is evidenced by higher gravimetric soil moisture readings at tall shrub expansion sites next to the road. Our air photo analysis also revealed increases in standing water next to the road, and topographic wetness index values along the Dempster indicated that tall shrub expansion sites had higher potential soil moisture compared to stable dwarf shrub sites. Generally, patches of stable dwarf shrub tundra persisted at the crest of elevated ridges along the plateau, where soils were drier, more exposed to snow scouring from winter winds, and received less incoming solar radiation (Blok et al., 2015). The idea that dry soils limit tall shrub proliferation is also supported by our observation that shrub patches in 1975 were constrained to drainages and water tracks. *Alnus viridis* spp. *fruticosa* is also known to favour relatively wet soil conditions since higher soil moisture allows for increased rates of N mineralization and accelerated shrub growth rates (Binkley et al., 1994; Furlow, 1979; Hendrickson et al., 1982; Myers-Smith et al., 2015). Evidence from this study of moisture-facilitated tall shrub proliferation is also consistent with Tape et al.'s (Tape et al., 2006) observation that shrub expansion in Alaska occurred preferentially in wet, high resource environments.

Our observations from the Peel Plateau raise the possibility that temperature-induced shrub expansion across the circumpolar north has also been mediated by soil moisture. Fine and broad scale change detection studies show that shrub proliferation has been

patchy (Bhatt et al., 2010; Fraser et al., 2014; Lantz et al., 2013; Tape et al., 2006). It is possible that these patterns are the result of spatial variation on soil moisture, since dendrochronology (Myers-Smith et al., 2015), plot-based studies (Elmendorf et al., 2012b), and air photo analysis (Tape et al., 2006) also indicate that rapid shrub growth occurs in wet areas. However, additional research on the links between edaphic conditions and shrub encroachment is needed to test this hypothesis and scale up our findings to identify locations susceptible to shrub proliferation.

Increased soil moisture beside the road was likely caused by increased snow accumulation next to the 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 (Burn et al., 2009; Fortier et al., 2011; Hiemstra et al., 2002; Hinkel and Hurd, 2006). Deeper snow increases localized spring run-off and likely elevates soil moisture (Hinkel and Hurd, 2006; Wahren et al., 2005). Increased snow pack also insulates the ground, reduces winter cooling, and can promote permafrost degradation (Alfaro et al., 2009; Burn et al., 2009; Fortier et al., 2011; Hinkel and Hurd, 2006). Increased ground temperatures can result in subsidence next to the road as thaw consolidation takes place, creating depressions adjacent to the road (Alfaro et al., 2009; Fortier et al., 2011; Hinkel and Hurd, 2006). This is evidenced in our data by a dip in relief beside the road, and by increases in standing water that pool in these roadside depressions.

Recent research on the Dempster and elsewhere also suggests that positive feedbacks initiated by shrub proliferation can accelerate 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 (Gill et al., 2014; Sturm et al., 2001b). On the Peel Plateau, temperatures beneath patches of tall shrubs have been shown to be significantly warmer during the winter, and freezeback 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, which create favourable conditions for subsequent tall shrub growth (Buckeridge and Grogan, 2008; Buckeridge et al., 2010; Mikan et al., 2002; Romanovsky and Osterkamp, 2000; Schimel et al., 2004; Viereck et al., 1983; Wahren et al., 2005). A larger shrub canopy also enhances road dust interception, which increases nutrient availability and promotes shrub growth (Gill et al., 2014). It is likely that all of these feedbacks also contributed to accelerated shrub growth next to the Dempster.

Despite reports of increased 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 and thick organic soil layers reduced ground thaw and limited active layer development (Blok et al 2010). However, Gill et al. (2014) reported elevated permafrost temperatures beneath shrub canopies beside the road, which suggests that winter conditions have a larger impact on ground thermal regime than summer processes (Gill et al., 2014; Palmer et al., 2012; Romanovsky and Osterkamp, 2000; Sturm et al., 2001b). 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. These findings suggest that road design in permafrost environments should consider hydrological conditions and snow accumulation patterns prior to construction. Additional research on the impact of tall shrub proliferation on the balance between winter and summer heat flux is also needed.

Conclusions

We draw the following conclusions based on the results of this study:

1. Construction and maintenance of the Dempster highway has intensified the effects of a warming climate on tall shrub growth and proliferation.
2. Increases in soil moisture facilitated rapid tall shrub proliferation adjacent to the Dempster.
3. Increases in soil moisture and changes to water drainage patterns likely occurred as a result of snow accumulation next to the road.

4. Tall shrubs create positive feedbacks that promote subsequent tall shrub proliferation.
5. Hydrology and snow accumulation patterns are essential to consider prior to road construction in permafrost environments.

Chapter 3 – Ecosystem recovery after the abandonment of a winter access road in Nahanni National Park Reserve, NWT

Emily A Cameron¹ and Trevor C. Lantz^{1,2}

1. School of Environmental Studies, University of Victoria
2. Author for correspondence
3. EAC and TCL conceived the study; EAC collected the data; EAC analyzed the data; EAC and TCL wrote the manuscript.

Introduction

Recent high latitude temperature increases have been double the global average, and Canada's western arctic has experienced disproportionately more warming than other northern regions (ACIA, 2005; IPCC, 2007; Serreze et al., 2000). Across the arctic, warming air temperatures have been accompanied by increases in permafrost temperature (Kokelj and Jorgenson, 2013; Romanovsky et al., 2010; Smith et al., 2010a; Throop et al., 2012) and there is widespread concern about the long-term persistence of discontinuous permafrost (Romanovsky et al., 2010; Shur and Jorgenson, 2007; Smith et al., 2010a). Permafrost degradation and range retractions are predicted to be most severe at the southern margin of discontinuous permafrost, where perennially frozen ground is in disequilibrium with the current climate (Camill and Clark, 1998, 2000; Halsey et al., 1995; Jorgenson et al., 2010b; Shur and Jorgenson, 2007; Throop et al., 2012). In these environments, permafrost is normally maintained by surface conditions (vegetation, organic deposits, soil moisture, etc.) that insulate frozen ground from warmer air temperatures (Camill and Clark, 2000; Halsey et al., 1995; Shur and Jorgenson, 2007; Vitt et al., 2000).

Since discontinuous permafrost is buffered from thaw by local conditions, frozen ground may be somewhat resilient to recent warming. Holling (1973) first described resilience as the capacity of an ecosystem to absorb perturbations and sustain function, structure, identity, and feedbacks. When the effects of disturbance on biotic and abiotic processes exceed the resilience of the system, disturbances can result in a persistent change of state (Chapin et al., 2009; Holling, 1973). Resilience theory predicts that changes to environmental factors with strong feedbacks to ecosystem function are particularly likely to drive regime shifts (Folke et al., 2004; Gunderson, 2000; Thrush et al., 2009). Recent observations suggest that in some regions warmer air temperatures are already exceeding resilience thresholds and causing permanent permafrost degradation that results in large ecological transitions (Chasmer et al., 2011; Grosse et al., 2011; Schuur et al., 2008). Shifting permafrost boundaries will have strong impacts on terrestrial and aquatic ecosystems because hydrology, nutrient availability, and carbon dynamics are strongly affected by permafrost thaw (Connon et al., 2014; Jorgenson et al., 2001; Lantz et al., 2009; Natali et al., 2011; Quinton et al., 2011). As such, understanding the factors that

affect ecosystem resilience and the nature of ecosystem transitions in areas of discontinuous permafrost is critical to understanding the trajectory of the subarctic.

Field studies in the low arctic suggest that ecosystem resilience in discontinuous permafrost is controlled by the strength of the feedbacks among several processes: 1) organic layer depth, 2) soil moisture, 3) vegetation structure, and 4) snow cover (Harper and Kershaw, 1996, 1997; Jorgenson et al., 2001; Lantz et al., 2009; Smith et al., 2008). Strong feedbacks among biotic and abiotic processes in discontinuous permafrost mean that changes to surface conditions have the potential to affect ecosystem resilience. For example, localized anthropogenic disturbances can intensify the effects of climate warming on discontinuous permafrost by altering the conditions that insulate the ground (Smith et al., 2008). Ecological responses to disturbance also depend on the nature and rate of post-disturbance vegetation succession, which varies with terrain type (Calmels et al., 2012; Sannel and Kuhry, 2008). At Scotty Creek, NWT, Williams et al. (2013) showed that discontinuous permafrost thaw associated with linear disturbances instigated feedbacks to soil moisture and drove persistent changes to the plant community. Similarly, Lantz et al. (2009) showed that disturbances associated with thawing permafrost created feedbacks among vegetation structure, snow pack and ground temperature that perpetuated altered community structure. The examination of variation among post-disturbance ecological recovery trajectories will help identify processes that influence ecosystem resilience in discontinuous permafrost terrain. Yet, to date, few studies have explored the effects of anthropogenic disturbance on vegetation recovery, soils and near surface ground temperatures in the discontinuous permafrost zone.

The Prairie Creek winter access road was built in 1981 within Nahanni National Park Reserve (NNPR) and abandoned the following year. It is located in an area of discontinuous permafrost, which spans alpine treeline, black spruce parkland, forested muskeg, and deciduous woodland. Portions of the road have naturally re-vegetated in the 30 years since it was abandoned and the road provides an excellent opportunity to explore the effect of disturbance on vegetation, soils, and near-surface ground temperature. In this paper we assess ecological responses to disturbance in four terrain types by comparing vegetation, soil, and permafrost conditions, at the roadbed with nearby undisturbed terrain.

Methods

Study Area

This study was conducted in Nahanni National Park Reserve in the southwestern corner of the Northwest Territories, Canada (Figure 3-1). NNPR is one of the largest national parks in Canada (30 050km²). It is situated in the boreal forest within the taiga plains ecozone and is underlain by extensive discontinuous permafrost (Johnson et al., 1995; Smith et al., 2010b). The climate in this region is continental and is characterized by short warm summers and long cold winters. Mean annual temperature and precipitation (2001-2014) at a meteorological station approximately 35km away from our study site were -1.25°C and 146mm, respectively (Environment Canada 2015). The western part of our study area lies in the carbonate and siliciclastic Neoproterozoic – Cambrian rocks of the Mackenzie Mountains (Narbonne and Aitken, 1995). Further east, our study area is situated in the geologically unique North Karst area, which is comprised of middle Devonian limestone overlain with upper Devonian shale and glacio-lacustrine deposits (Ford 2010, 1976). Though evidence of historical glaciation is present, highly developed karst features imply that large parts of NNPR remained unglaciated during the past 300 000 years (Ford, 2010, 1976).

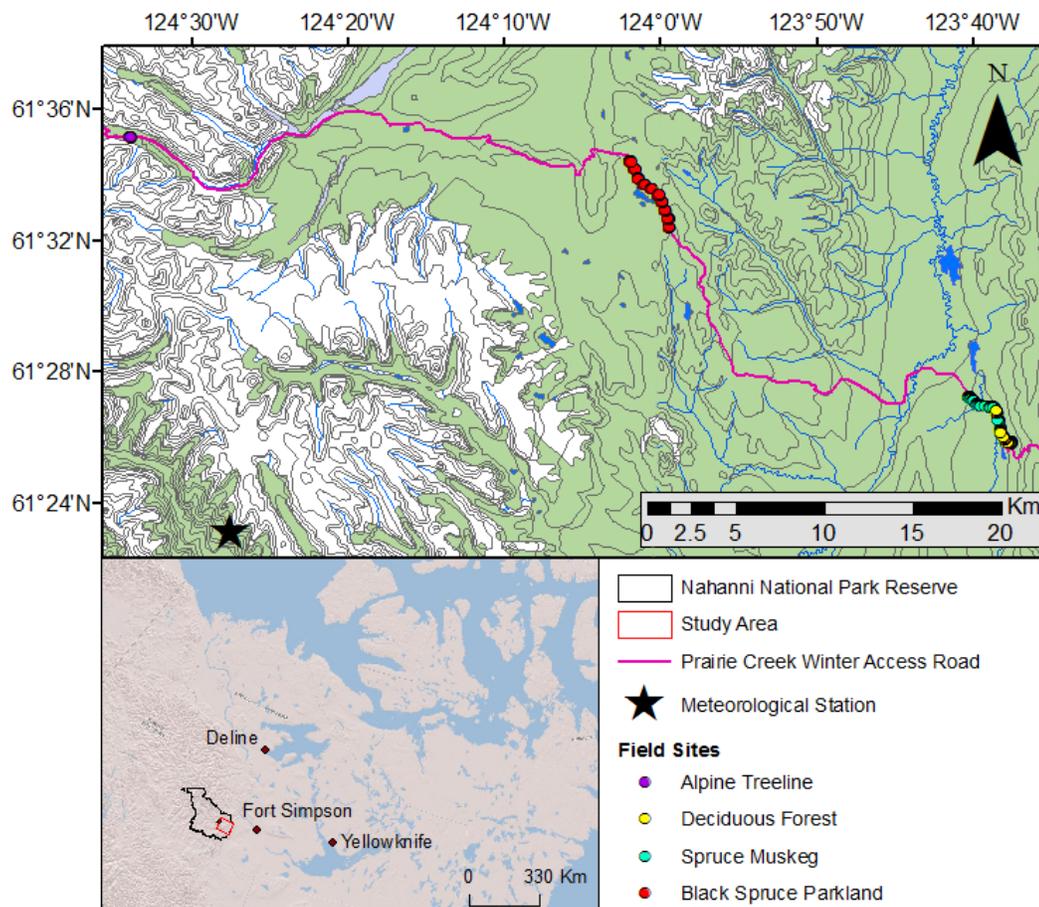


Figure 3-1: Map of the study area showing field sites in each terrain type along the Prairie Creek access road. Green shading indicates vegetated areas, and white indicates unvegetated areas. Inset map at the bottom left shows the position of the study area in Northwestern Canada. The black outline indicates the boundaries of Nahanni National Park Reserve expansion and the shaded box shows the extent of the upper map.

In 1981, a winter road was built in the region to access a silver and base metal mine near Prairie Creek (Figure 3-1). This road traverses the eastern portion of NNPR and was abandoned in 1982. The road remained unused until 2014, when Canadian Zinc obtained permits to resume road operation and maintenance. Approximately 64km of the 180km Prairie Creek Access Road pass through NNPR. The road spans numerous terrain types, ranging from high elevation alpine tundra to low-lying peatlands. The research described

in this paper focussed on four of the dominant terrain types in this part of NNPR (Figure 3-2).

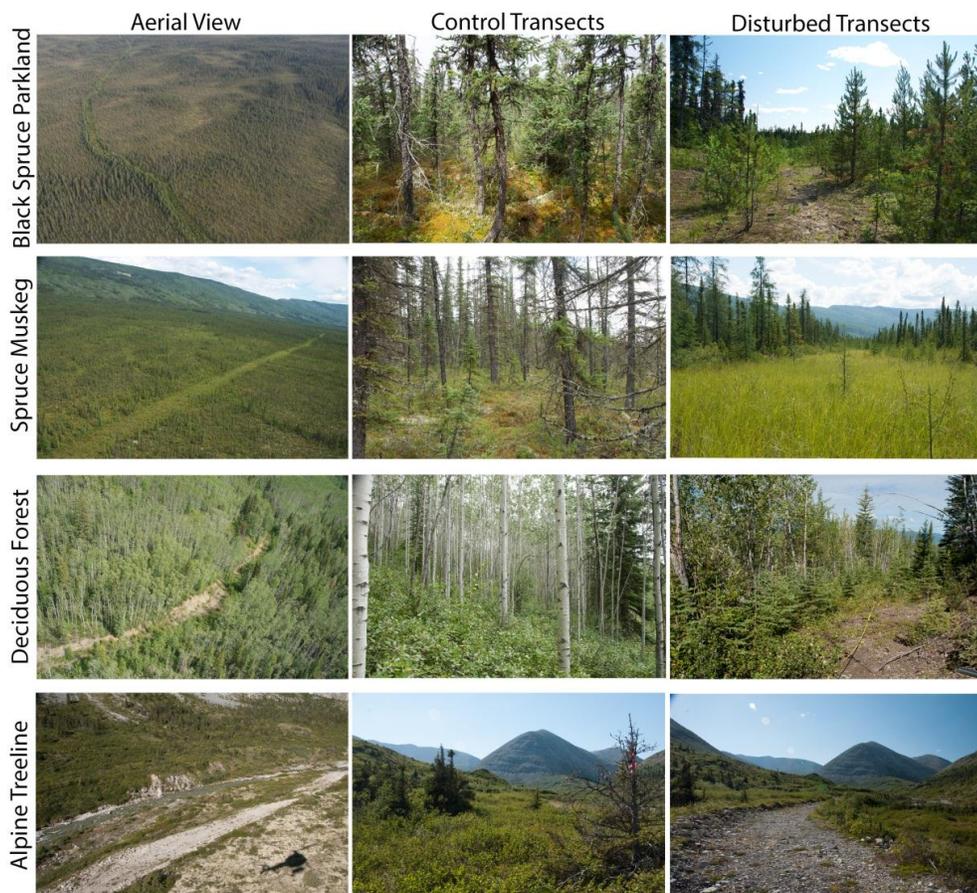


Figure 3-2: Photos of characteristic vegetation communities of each terrain type: black spruce parkland, spruce muskeg, deciduous forest, and alpine treeline. Aerial views of the terrain types are in the left column, photos of the control transects are in the middle column, and photos of disturbed transects are in the right column.

Black spruce parkland is prevalent at mid elevations (696-1005m) and is characterized by a moderately dense canopy of *Betula glandulosa* (Michx.) and *Picea mariana* (Mill.) and an understory dominated by lichens and moss. Spruce-dominated peatlands at lower elevations (271-224m) are distinguished by abundant mosses and sedges, ericaceous shrubs, *B. glandulosa*, *P. mariana*, and *Larix laricina* (DuRoi, Koch). Deciduous forest is common at elevations ranging from 463-221m and is typically dominated by a closed

cover of *Populus tremuloides* (Michx.) and *Populus balsamifera* (L.) interspersed with *Picea glauca* (Moench) and an understory of *Cornus canadensis* (L.), *Linnaea borealis* (Forbes), *Rosa acicularis* (Lindl. S. lat) and *Viburnum edule* (Michx.). Alpine treeline terrain is found at high elevations (1101-1115m) in the Mackenzie Mountains and is characterized by open stands of *P. glauca* and a dense cover of *Ledum groenlandicum* (Oeder), *Vaccinium vitis-idaea* (L.), *Vaccinium uliginosum* (L.), *B. glandulosa*, mosses, and lichens.

Response Variables

To investigate how disturbance affects ecosystems in different terrain types, we compared a suite of biotic and abiotic response variables at sites impacted by the Prairie Creek Access Road and adjacent control sites not impacted by the road. To select sites in alpine treeline, spruce muskeg, deciduous forest, and black spruce parkland, we used a landcover classification (Stow and Wilson, 2006) and field reconnaissance. We established 10 sites in spruce muskeg, 10 sites in black spruce parkland, 8 sites in deciduous woodland terrain, and one site in the alpine treeline terrain (n=29).

At each site, paired line transects were established along the road corridor (disturbed) and in the undisturbed terrain adjacent to the road. Disturbed transects ran along the center of the road for 70m. Undisturbed transects ran parallel to the disturbed transect for 70m, but were located 10 meters from the edge of the roadbed. Data from Smith et al. (2008) and Smith et al. (2005) suggests 10m is far enough from the road bed that disturbance-related thermal effects are negligible.

Community composition at disturbed and undisturbed sites was described by estimating the percent cover of all plants within quadrats placed at 10 meter intervals along each transect. Within a 1m² quadrat, percent cover was evaluated for all species except sedges and grasses, which were grouped at a family level, and lichen and mosses which were identified as functional groups. The cover of tall shrubs (woody species >0.4m tall) was estimated inside a 5m² quadrat centered on the 1m² quadrat. The heights of the tallest shrub and understory plant were recorded within the 5m² and the 1m² quadrat respectively. Canopy cover, stem density, and diameter at breast height (DBH) of trees were recorded within a 25m² plot centered on each 1m² plot.

Within each 5m² quadrat, five measurements of active layer thickness were obtained by pushing an active layer probe into the ground until depth of refusal. To control for variation associated with microtopography, active layer measurements were recorded on hummock tops. Active layer measurements from alpine treeline and deciduous forest terrain were discarded because talus and thick clays made it difficult to probe to the base of the active layer. Organic soil thickness and litter depth were recorded in each 5m² quadrat using a shovel and a small metal ruler. Volumetric soil moisture was measured by averaging 5 measurements taken with a Theta moisture probe (Type ML2x, Delta-T Devices Ltd.).

Near-surface ground temperature was recorded at disturbed and undisturbed sites in each terrain type using data loggers attached to two external temperature probes (HOBO Pro v2 2x External Temperature Data Logger, Onset Computing, Pocasset, MA, USA). These temperature probes were mounted on a PVC pipe that was inserted into a hole such that the probes recorded temperatures 10cm and 100cm below the ground surface. We set the loggers to record ground temperature every two hours for a year. In August 2012, 11 thermistors were installed at disturbed and undisturbed areas in each of the four terrain types. Data was recovered from control and disturbed transects in black spruce parkland (n=2), alpine treeline (n=2), and deciduous forest terrain types (n=2). Due to unforeseen animal encounters in spruce muskeg terrain, we obtained data only from the disturbed transect (n=1).

Statistical Analysis

To examine differences in community composition among control and disturbed sites in the four terrain types, a non-metric multidimensional scaling (NMDS) ordination of a Bray-Curtis resemblance matrix based on percent cover data was performed with the PRIMER software program (Plymouth Marine Laboratories, Plymouth, UK) (Clarke and Gorley, 2001; Clarke and Warwick, 2001). To reduce noise, abundance data was $\log(x+1)$ transformed before NMDS ordination (Clarke, 1993). To minimize the influence of rare species, plants found in fewer than two subplots were excluded from the analysis. Two unvegetated plots in disturbed alpine and black spruce parkland were also deleted from the analysis. To determine whether community composition was significantly different among control and disturbed areas in each terrain type, we used the

ANOSIM (analysis of similarities) function in PRIMER. To test the significance of the R_{ANOSIM} statistic we used PRIMER to conduct 999 permutations on the resemblance matrix. To identify species that made the greatest contribution to pairwise differences among site types, we used PRIMER to perform a SIMPER analysis on the $\log(x+1)$ transformed percent cover data (Clarke and Gorley, 2001).

To compare the forest structure of disturbed and undisturbed sites and to determine if the size distributions of canopy trees were significantly different, we plotted histograms of tree DBH and used a two-sample Kolmogorov-Smirnov test in R (R Core Team, Vienna, Austria). To constrain this analysis to dominant canopy species, tree species were only included in analysis when there were more than 50 individuals within each site type.

To test whether biotic and abiotic variables were significantly altered by the construction of the road, and to assess whether these impacts varied by terrain type, we used linear mixed effects models. This analysis was conducted with the GLIMMIX procedure in SAS version 9.3 (SAS Institute, Cary, NC, USA). Terrain type (Black Spruce Parkland, Spruce Muskeg, Alpine Treeline, and Deciduous Forest) and disturbance level (Control and Disturbed) were included in the models as fixed factors. Transect and plot number were included in the models as random factors. To assess the importance of the spatial nesting of the data we removed random terms from each models one at a time and selected the model with the lowest AIC score (Johnson and Omland, 2004; Morrell 1998, Buckley et al., 2003). Both random factors were retained in the models for soil moisture and active layer thickness, but only transect identity was included in models of organic soil thickness, understory and shrub story maximum height, and litter depth. The Kenward-Roger method was used to estimate degrees of freedom and the Bonferroni corrected LS MEANS procedure was used to perform pairwise comparisons among site types. Residuals were plotted to observe deviations from normal and no transformations were necessary.

Results

Plant community composition varied significantly between disturbed and undisturbed sites in all terrain types (Figure 3-3; Tables 3-1, 3-2), but the magnitude of the difference depended on the terrain type. The largest difference between disturbed and control sites was observed at the alpine treeline ($R_{ANOSIM} = 0.991$, $p < 0.001$). Impacted alpine treeline sites exhibited no cover of *Betula glandulosa*, moss, lichen, ericaceous shrubs, and *Picea glauca*, which were common species at the control site in this terrain type (Table 3-2). *Dryas integrifolia* was the dominant vegetation cover on the mostly barren roadbed (Figure 3-2), but *Salix* spp. was also present in some places. Spruce muskeg sites also exhibited large differences in community composition between control and disturbed sites ($R_{ANOSIM} = 0.645$, $P < 0.001$) that were driven primarily by increases in sedge and litter at disturbed sites. Tall shrubs, predominantly *Salix* spp. and *Betula glandulosa*, were also more abundant at disturbed spruce muskeg sites. Undisturbed spruce muskeg was characterized by *Picea mariana*, moss, and ericaceous shrubs. Distinct vegetation communities were also observed at control and disturbed sites in the deciduous forest ($R_{ANOSIM} = 0.494$, $p < 0.001$). In this terrain, the abandoned roadbed was characterized by higher cover of *P. glauca*, moss, and *Sheperdia canadensis* and lower cover of *Populus tremuloides*, litter, *Viburnum edule*, and *Cornus canadensis* compared with undisturbed sites. Disturbance also impacted plant community composition in black spruce parkland ($R_{ANOSIM} = 0.435$, $p < 0.001$). Disturbed sites had increased cover of *Salix* spp. and reduced cover of *Picea mariana*, *Betula glandulosa*, *Cornus canadensis*, and lichen compared to undisturbed sites.

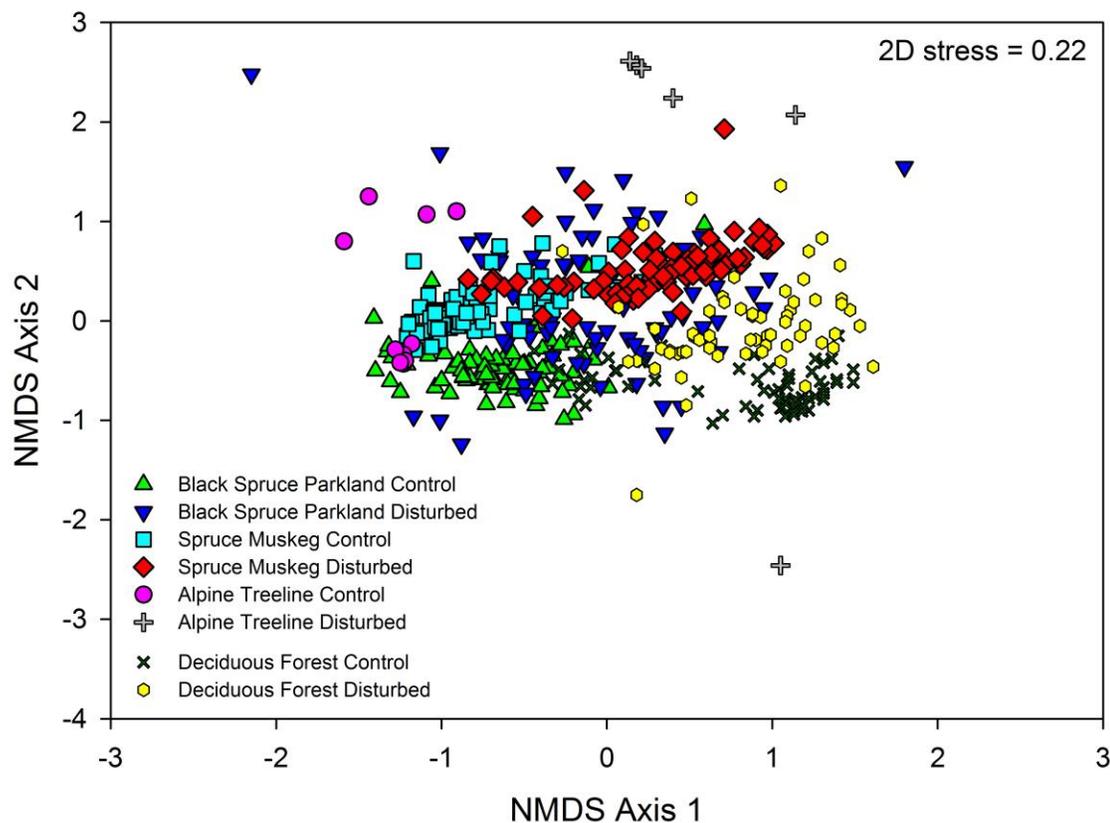


Figure 3-3: Non-metric multidimensional scaling ordination of plant community composition based on a Bray-Curtis similarity matrix. Symbols represent control and disturbed plots in the four terrain types.

Table 3-1: A_{NOSIM} statistic for pairwise comparisons of plant community composition between control and disturbed sites in the four terrain types. R_{ANOSIM} values below 0.25 are considered to be indistinguishable based on their species composition (Clarke and Gorley, 2001).

Terrain Type	R_{ANOSIM} (control vs. disturbed)	P Value
Black Spruce Parkland	0.435	<0.001
Spruce Muskeg	0.645	<0.001
Deciduous Forest	0.494	<0.001
Alpine Treeline	0.991	<0.001

Table 3-2: Results from the SIMPER analysis of community composition at disturbed and undisturbed sites in the 4 terrain types. The top seven species or species groups that contributed to between-group dissimilarity for comparisons of control and disturbed terrain types are shown. Mean cover is log(x+1) transformed.

Terrain Type	Species or Species Group	Mean Cover Control Site	Mean Cover Disturbed Site	Cumulative % Dissimilarity
Black Spruce Parkland	Moss spp.	4.18	2.31	7.20
	<i>Betula glandulosa</i>	2.05	0.72	13.23
	<i>Salix</i> spp.	1.32	2.38	19.01
	<i>Cornus canadensis</i>	1.76	0.72	24.68
	<i>Pinus contorta</i>	0.97	1.81	30.34
	<i>Picea mariana</i>	2.17	1.32	35.95
	Lichen spp.	1.23	0.77	40.38
	Spruce Muskeg	Sedge spp.	1.10	3.02
Moss spp.		3.86	2.18	15.35
Litter		1.66	3.21	22.59
<i>Ledum palustre</i>		1.96	0.13	29.47
<i>Picea mariana</i>		2.31	0.74	36.06
<i>Salix</i> spp.		0.62	1.83	41.58
<i>Betula glandulosa</i>		0.96	1.41	46.76
Deciduous Forest		<i>Populus tremuloides</i>	2.68	0.34
	Moss spp.	1.30	1.58	12.33
	<i>Picea glauca</i>	1.41	2.55	17.22
	Litter	3.90	3.09	21.17
	<i>Cornus canadensis</i>	1.83	0.88	25.01
	<i>Sheperdia canadensis</i>	1.03	1.53	28.73
	<i>Viburnum edule</i>	1.30	0.00	32.37
	Alpine Treeline	<i>Betula glandulosa</i>	3.04	0.00
Moss spp.		2.74	0.00	25.81
Lichen spp.		2.64	0.00	37.58
<i>Dryas integrifolia</i>		0.00	2.41	48.45
<i>Vaccinium vitis-idaea</i>		1.96	0.00	57.08
<i>Ledum groenlandicum</i>		1.79	0.00	65.38
<i>Picea glauca</i>		1.25	0.00	71.28

Road construction significantly affected stand structure at forested sites, but the effects of disturbance also varied by terrain type (Figures 3-4, 3-5, 3-6). Tree size distributions at disturbed sites were log-normal and were characterized by a large number of small individuals (Figures 3-4, 3-5, 3-6). At undisturbed sites tree size distributions depended on terrain type, but typically included a greater number of large individuals. In most terrain types, the dominant species along the road also differed from the nearby forest. In spruce muskeg, large cohorts of *Larix laricina* replaced *Picea mariana* as the dominant tree, which displayed signs of recruitment failure following disturbance (Figure 3-4). At disturbed deciduous woodland sites, *Populus tremuloides* did not regenerate following road abandonment, but was replaced by large cohorts of *Picea glauca* and *Betula papyifera* (Figure 3-5). In black spruce parkland, the same tree species were found on the road and adjacent to the road, but *Pinus contorta* was the dominant tree species on the road, and *Picea mariana* was the dominant tree species at undisturbed sites (Figure 3-6).

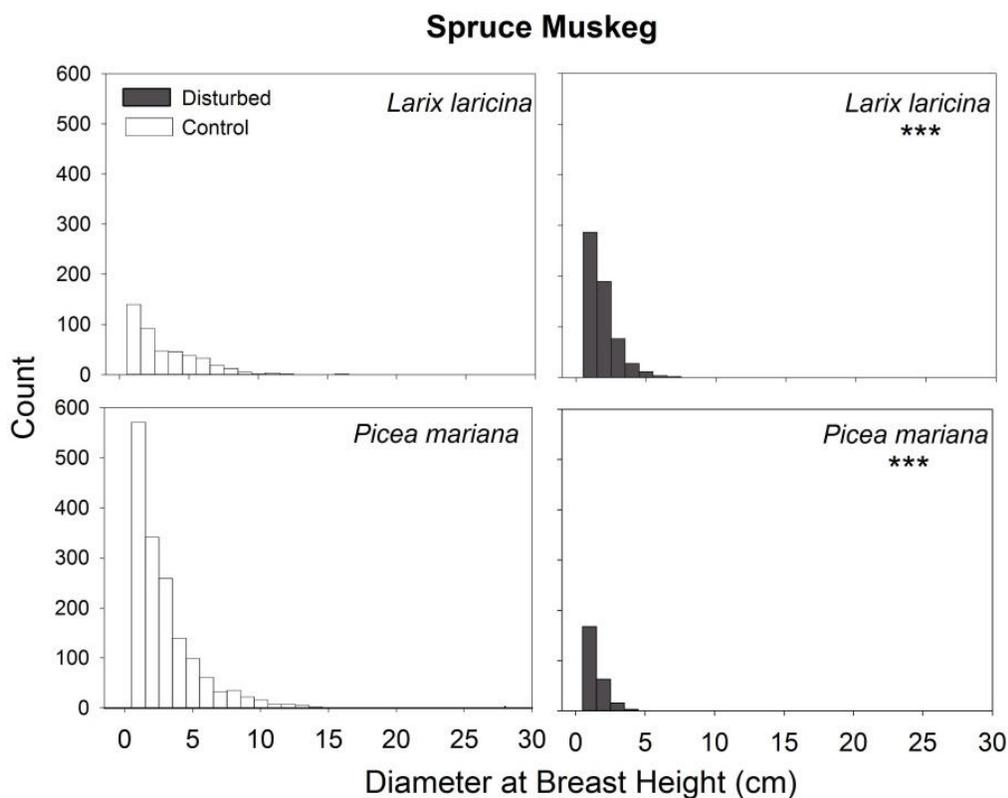


Figure 3-4: Size class distribution of canopy trees in spruce muskeg terrain. Control and disturbed sites that have significantly different size distributions are marked with three asterisks ($\alpha=0.05$).

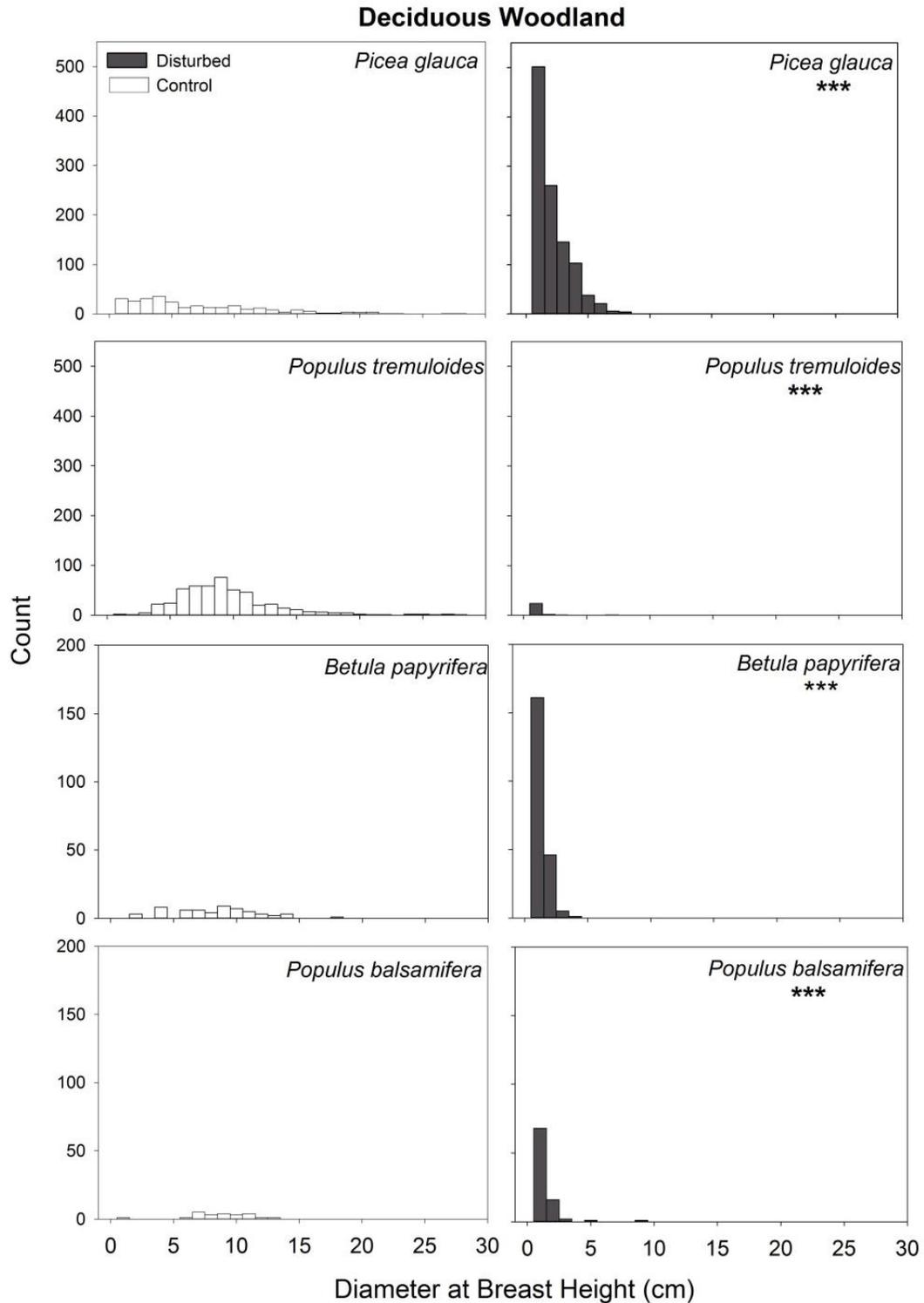


Figure 3-5: Size class distribution of canopy trees in deciduous woodland terrain. Control and disturbed sites that have significantly different size distributions are marked with three asterisks ($\alpha=0.05$). Note that the scale on the y-axis differs between the upper and lower graphs.

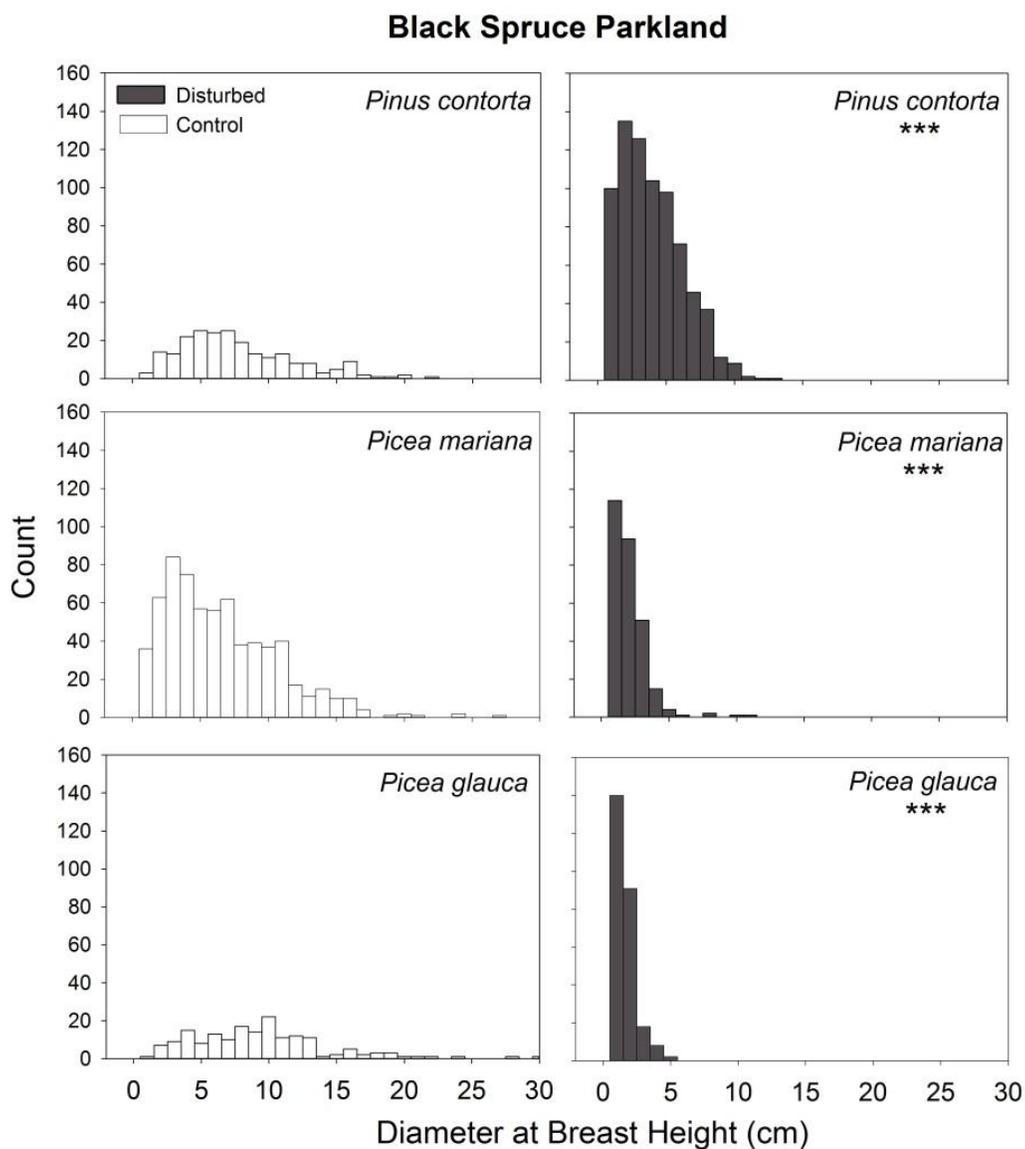


Figure 3-6: Size class distribution of canopy trees in black spruce parkland terrain. Control and disturbed sites that have significantly different size distributions are marked with three asterisks ($\alpha=0.05$).

The presence of the road also had significant effects on the abiotic conditions 30 years after construction (Table 3-3, Figure 3-7). In spruce muskeg, volumetric soil moisture at disturbed sites was approximately double undisturbed levels. Volumetric soil moisture also increased with disturbance in black spruce parkland and deciduous forest, but the

differences were only significant in black spruce parkland. The disturbed site at alpine treeline had lower soil moisture, but the difference was not significant (Figure 3-7A). Organic soil thickness was lower on the roadbed than at undisturbed sites in all terrain types. In black spruce parkland and deciduous forest, organic soil thickness decreased by a factor of 5, and alpine treeline organic soil showed a 116-fold decrease in thickness. At disturbed spruce muskeg sites, there was a moderate but non-significant reduction in organic soil thickness (Figure 3-7B).

Table 3-3: Mixed model results for biotic and abiotic response variables. Site has 4 levels: black spruce parkland, spruce muskeg, deciduous forest, and alpine treeline. Disturbance has two levels: control and disturbed. Significant p-values are bold.

Response Variable	Effect	F Value	P Value	Degrees of Freedom
Soil Moisture	Site	11.31	< 0.0001	3, 464
	Disturbance Level	35.30	< 0.0001	1, 464
	Site * Disturbance Level	52.94	< 0.0001	3, 464
Organic Soil Thickness	Site	74.51	< 0.0001	3, 25
	Disturbance Level	232.3	< 0.0001	1, 439
	Site * Disturbance Level	53.93	< 0.0001	3, 439
Litter Depth	Site	7.52	0.0010	3, 24
	Disturbance Level	9.28	0.0025	1, 439
	Site * Disturbance Level	102.5	< 0.0001	3, 439
Active Layer Thickness	Site	0.41	0.5215	1, 281
	Disturbance Level	6.18	0.0135	1, 281.3
	Site * Disturbance Level	12.25	0.0005	1, 281.3
Understory Height	Site	11.87	< 0.0001	3, 48
	Disturbance Level	35.41	< 0.0001	1, 46
	Site * Disturbance Level	11.08	< 0.0001	3, 48
Shrub Height	Site	7.51	0.0010	3, 49
	Disturbance Level	2.86	0.0914	1, 48
	Site * Disturbance Level	5.95	0.0006	3, 49

Litter depth in most terrain types was also impacted by road construction (Figure 3-7C). Disturbed black spruce parkland and deciduous forest sites both showed significant decreases in litter depth compared to undisturbed sites. At disturbed spruce muskeg sites, the road was associated with a doubling of litter depth, but at alpine treeline sites, litter depth was not significantly impacted (Figure 3-7C). Average active layer thickness at disturbed spruce muskeg sites was significantly higher than at undisturbed sites. Active

layers did not differ between control and disturbed sites in black spruce parkland. Vegetation structure was also strongly impacted by the road. Maximum understory height increased significantly in all disturbed terrain types except for disturbed deciduous forest (Figure 3-7E). Maximum shrub height was significantly lower at disturbed sites at treeline. Maximum shrub height was higher at disturbed black spruce parkland, spruce muskeg, and deciduous woodland, but differences between control and disturbed sites were not significant (Figure 3-7F).

The impact of the road on near-surface ground temperatures varied among terrain types. In black spruce parkland, temperatures beneath the abandoned roadbed were elevated at both 10 and 100cm below ground surface when compared with undisturbed temperatures. Ground temperatures at 100cm beneath the abandoned roadbed in spruce muskeg remained close to zero for the entire winter (Figure 3-8). Near-surface temperatures at 10cm beneath the roadbed indicated that the ground cooled relatively slowly, and was at its coldest, -3.4°C , in late March. Temperature data for undisturbed muskeg is missing because the thermistor was damaged by an animal. However, permafrost was detected in this terrain during active layer probing and drilling during thermistor installation. The presence of hummocks and a black spruce forest type also indicates that permafrost persists under much of the undisturbed spruce muskeg terrain (Bauer and Vitt, 2011; Shur and Jorgenson, 2007; Williams and Burn, 1996). Temperature profiles in deciduous forest did not show appreciable differences between control and disturbed sites. At alpine treeline, temperatures along the road at both 10cm and 100cm below ground surface were higher than undisturbed sites during the summer and colder than controls during the summer (Figure 3-8).

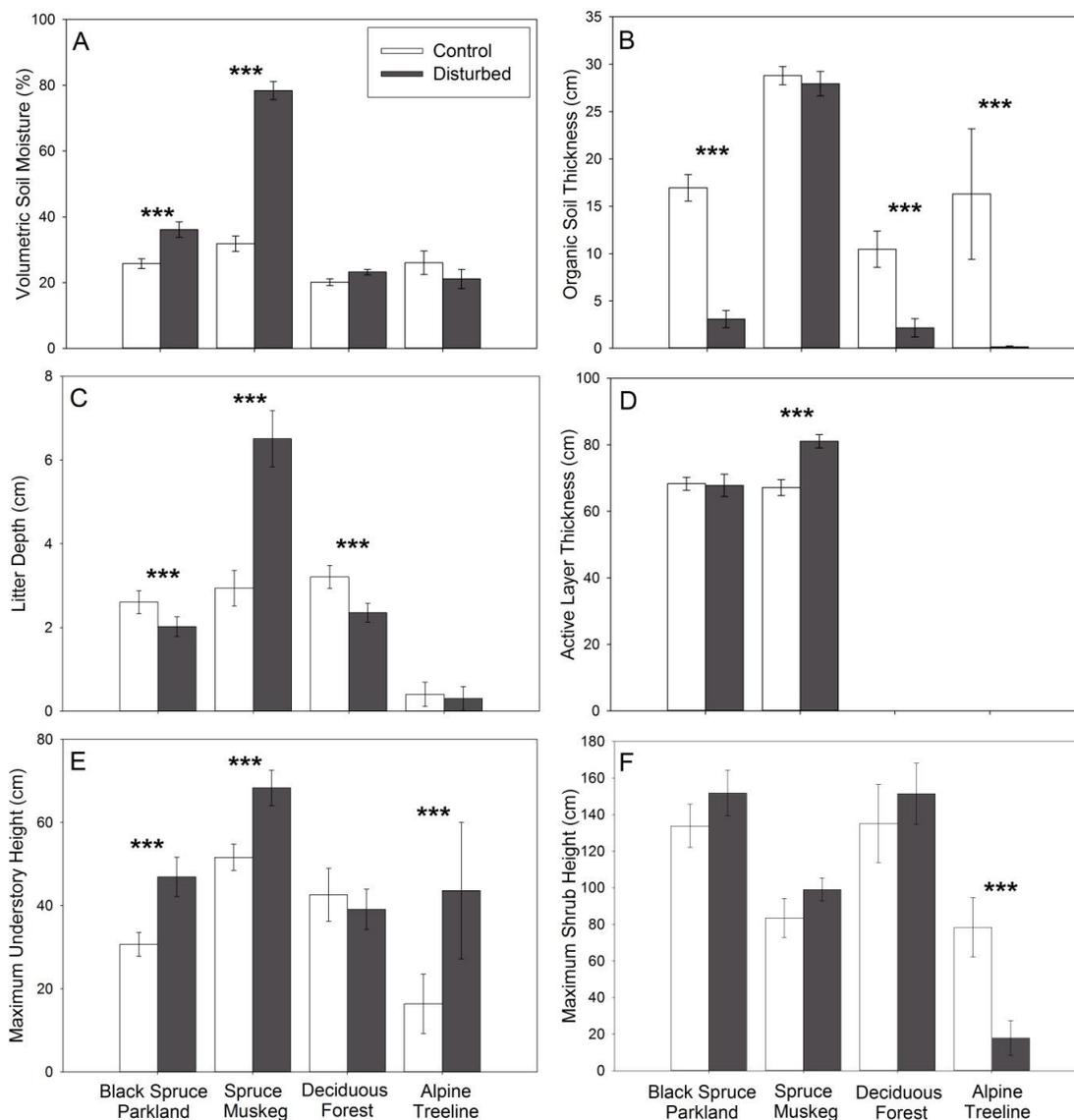


Figure 3-7: Abiotic and biotic response variables measured in control and disturbed transects in black spruce parkland, spruce muskeg, deciduous woodland, and alpine terrain types: (A) volumetric soil moisture (%), (B) organic soil thickness (cm), (C) active layer thickness (cm), (D) litter depth (cm), (E) maximum understory height, and (F) maximum shrub height (cm). Bars show means for each site type, and error bars are 95% confidence intervals of the mean. Significant differences in biotic and abiotic factors between control and disturbed terrain types are indicated with three asterisks ($\alpha=0.05$, LS Means procedure, Tukey adjusted p-values).

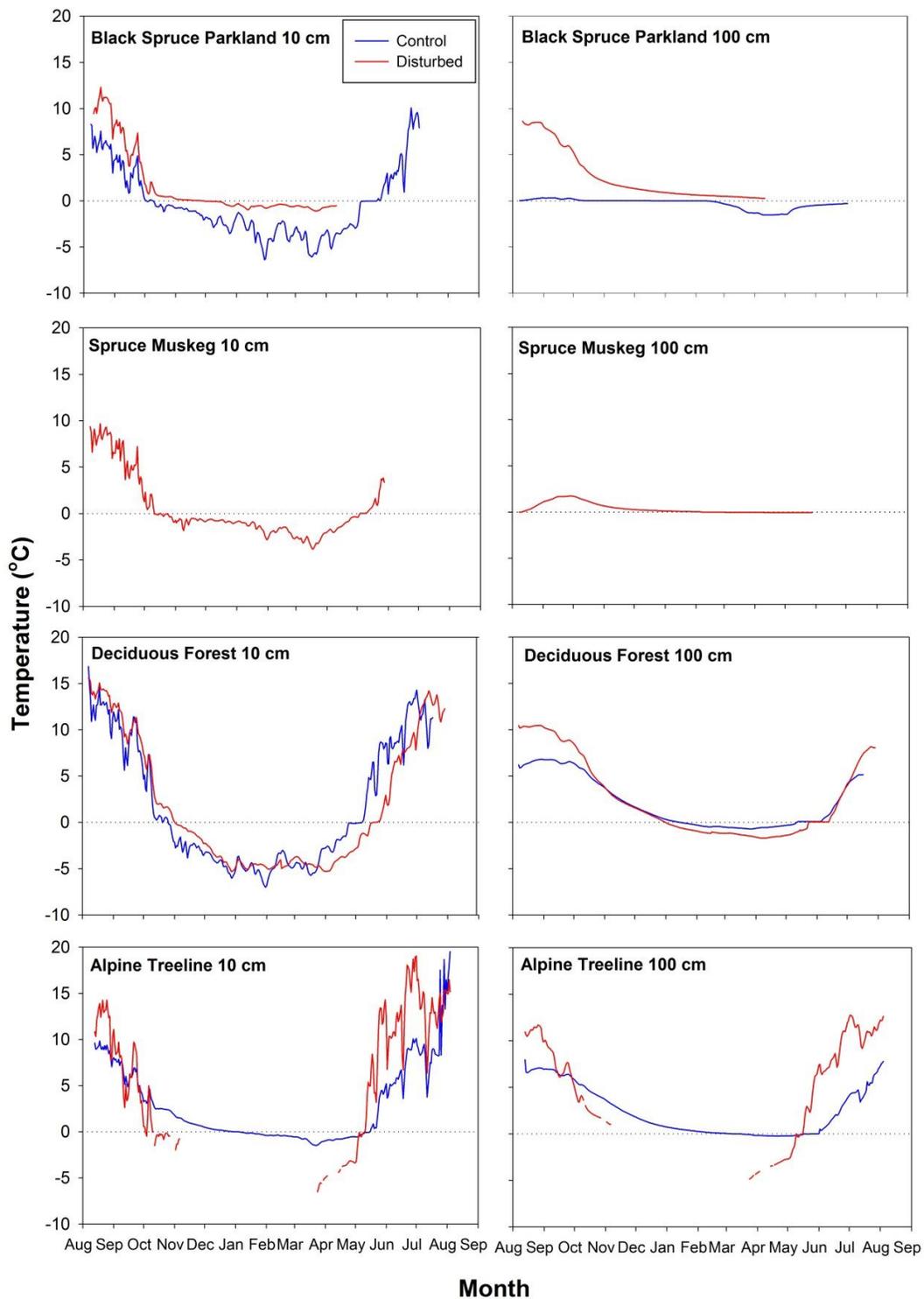


Figure 3-8: Near-surface ground temperatures recorded at 10cm and 100cm below the ground surface from August 2012 to August 2013 at disturbed (red) and undisturbed (blue) sites in black spruce parkland, spruce muskeg, deciduous forest, and alpine treeline terrain types. Lines show the daily mean temperatures (°C). The dashed reference line shows 0°C.

Discussion

Disturbance effects at the Prairie Creek road

Our field data show that disturbances to discontinuous permafrost terrain can lead to persistent changes in ecosystem composition and structure. Thirty years after road abandonment in NNPR, community composition along the road remained significantly different from undisturbed locations in all terrain types. In spruce muskeg, permafrost thaw triggered by road construction significantly increased soil moisture and facilitated a transition from spruce muskeg to sedge wetland. Permafrost thaw was evidenced by warm ground temperatures, thicker active layers, and increased soil moisture at disturbed sites in this terrain type. It is likely that permafrost degradation at muskeg sites was caused by the removal and compaction of organic material, which decreased the insulative capacity of soils and promoted thicker active layers (Chapin and Shaver, 1981; Mackay, 1970). Permafrost degradation and subsequent ground subsidence likely increased soil moisture by bringing the water table closer to the surface of the ground. This is consistent with observations made by Williams et al. (2013) and McClymont et al. (2013) of permafrost degradation, ground subsidence, and increases in soil moisture following linear disturbance in a discontinuous permafrost at Scotty Creek, NWT (2013). Work by Kopp *et al.* (2014) and Zhang *et al.* (2001) also suggest that decreased evapotranspiration associated with the removal of large trees and other vegetation during road construction may have also contributed to increased soil moisture along the road. Increases in soil moisture in this terrain type are likely to limit permafrost recovery because the latent heat effects of water delay ground freeze and may persist over the course of the winter (Jorgenson et al., 2010b; Romanovsky and Osterkamp, 2000). Increased soil moisture and thicker active layers along the road promoted the growth of hydrophilic vegetation. This sedge-dominated community was completely dissimilar to the surrounding black spruce forest and unless soil moisture levels change, it is unlikely that black spruce forest will regenerate along the road (Berg et al., 2009).

Ecosystem recovery at alpine treeline was also strongly influenced by the impacts of the road on soil conditions. Road construction through alpine treeline completely removed organic material and increased seasonal maximum and minimum ground temperatures.

These harsh environmental conditions almost completely limited revegetation along the road (Figure 2). It is likely that the removal of stabilizing vegetation and organic soil during construction in alpine treeline also slowed subsequent vegetation recovery. The very sparse cover of pioneer species we observed is consistent with work by Svoboda and Henry (1987) as well as work by Harper and Kershaw (1996), which shows that succession can be limited in extreme environments. Thicker organic soils provide protection against harsh environmental conditions, reduce water loss, increase nutrients, and stabilize the surface of the ground, all of which are favourable for revegetation in alpine terrain and have been extensively documented (Brink, 1964; Chambers et al., 1990; Tscherko et al., 2003). Other work indicates that existing vegetation may also facilitate subsequent vegetation recovery (Callaway et al., 2002; Rawls et al., 2003).

In black spruce parkland, vegetation composition 30 years following road abandonment indicates that disturbance also facilitated an alternative recovery trajectory. Increased soil moisture, reduced organic soil thickness, and warmer ground temperatures at disturbed sites likely lead to the establishment of a lodgepole pine sere 30 years after road abandonment (Brown, 1975; Johnstone and Chapin, 2006; Viereck, 1983; Ronco, 1967; Sheppard and Noble, 1976). The relative dominance of lodgepole pine recruits over spruce seedlings suggests that pine is likely to persist in the canopy and that succession patterns to spruce forest observed at undisturbed sites may not occur (Gutsell and Johnson, 2002; Johnstone and Chapin, 2003).

In deciduous forest, road construction transformed aspen forest to white spruce stands. In this terrain type, small changes in vegetation structure and composition in deciduous forest corresponded with small changes to soil conditions. Other than a reduction in organic soil thickness, ground conditions were comparable between control and disturbed sites. By clearing dense understory vegetation and litter along the road bed, road construction created favourable microsites for white spruce establishment (Carlson and Groot, 1997; Constabel and Lieffers, 1996; DeLong et al., 1997; Messier et al., 1998; Simard et al., 1998). Nearby white spruce at the control site likely provided the seed for the recruitment of white spruce along the disturbed corridor (Dobbs, 1976; Greene et al.,

2007; Kinugasa and Oda, 2014). The transition from a trembling aspen sere to a conifer sere is a well-documented successional pattern (Mueggler, 1988; Shepperd et al., 2001).

The ecological responses to the Prairie Creek road indicate that discontinuous permafrost terrain is very sensitive to disturbance, and in spruce muskeg where disturbance promoted permafrost thaw, alterations to ecosystem configurations are likely to be permanent. The transformations we observed at alpine treeline and in black spruce parkland are also likely to persist for as long as abiotic conditions remain distinct from the pre-disturbance state. Disturbances to sensitive terrain types will negatively affect habitat for woodland caribou, adversely impact vulnerable and endemic species, and may favour invasive species (Bennett, 2013; James and Stuart-Smith, 2000). The delicate Nahanni North Karst, which has been designated as a UNESCO world heritage site (Parks Canada, 2006), may be negatively affected if disturbances increase erosional processes, or trigger soil compaction that can affect hydrology patterns of the epikarst (Van Beynen and Townsend, 2005).

Resilience of discontinuous permafrost

Sampling along the Prairie Creek road suggests that ecosystems in areas of discontinuous permafrost are susceptible to long-term ecosystem changes when disturbances fundamentally alter soil conditions. Our data show that alternative stable states occurred following road abandonment in terrain where disturbance had large impacts to soil conditions, which initiated feedbacks that facilitated ecosystem change. Differences among the response of terrain types also indicate that the strength of stabilizing feedbacks strongly influence the nature of recovery. Increased soil moisture caused by permafrost degradation in spruce muskeg transformed this ecosystem from a spruce muskeg to a sedge-dominated wetland. Persistent changes in ground temperature and vegetation, and increased soil moisture will likely prevent permafrost re-aggradation. In alpine treeline, ecological recovery was severely impaired when road construction removed organic soil and surface vegetation that had previously moderated harsh environmental conditions. Extreme environmental conditions at alpine sites limited the colonization of pioneer species and will likely prevent ecosystem recovery for centuries (Haugland and Beatty,

2005; Svoboda and Henry, 1987; Willard and Marr, 1971). Conversely, ecological change was dampened in both black spruce parkland and deciduous woodland because smaller alterations to soil conditions did not affect vegetation to the same degree as disturbance in spruce muskeg and alpine treeline.

Our results are consistent with resilience theory, which predicts that changes to key environmental factors increase the likelihood of regime shifts, where an abrupt transition leads to a new ecosystem configuration with different structures and feedbacks (Chapin et al., 2009; Folke et al., 2004; Gunderson, 2000; Thrush et al., 2009). Previous research in high latitude environments shows that when disturbance alters the environmental factors that helped shape undisturbed vegetation communities, changes to vegetation are likely to persist for centuries (Gill et al., 2014; Harper and Kershaw, 1996; Johnstone and Kokelj, 2008; Lantz et al., 2009; Williams et al., 2013). Several previous studies in the subarctic have also described state changes following disturbance. Bauer and Vitt (2011) observed how a permafrost peat plateau transitioned into a continental bog-type ecosystem once permafrost thaw occurred after a forest fire. Intense subarctic fires can also lead to non-equilibrium forest succession where lodgepole pine replaces white spruce forest (Johnstone and Chapin, 2003).

Implications for management

As part of its mandate, Parks Canada seeks to “protect and present examples of Canada’s natural and cultural heritage... in ways that ensure that ecological and commemorative integrity of these places for present and future generations” (Parks Canada, 2002). In NNPR, protecting ecological integrity means that Parks Canada is responsible for the management and mitigation of disturbance impacts caused by the Prairie Creek winter access road. Our field data shows that ecosystem recovery, and likely the success of restoration in NNPR, depends on the magnitude of the impacts to soil conditions and abiotic and biotic processes. In terrain types where disturbance fundamentally alters ecosystem processes, the management of disturbance impacts is likely to be extremely difficult.

Spruce muskeg underlain by permafrost is extremely sensitive to disturbance, and should be actively avoided by infrastructure projects in NNPR. Since the transition from spruce muskeg to sedge wetland is mediated by the effects of permafrost degradation on soil moisture, it is unlikely that management efforts can be used to restore this terrain type after disturbance. It is extremely improbable that permafrost aggradation will occur in the warm and wet soils along the road, and areas on the road are too wet to support spruce recruitment (Chapin et al., 2006; Lloyd et al., 2003). Horizontal heat flows in wet soils may also drive additional permafrost degradation (Quinton et al., 2011; Romanovsky and Osterkamp, 2000; Jorgenson et al., 2013).

Our field data also show that strong feedbacks between vegetation and soil conditions in alpine terrain will make restoration difficult in this terrain type. Sparse cover of early succession grasses and *D. drumondii* along the road suggest that harsh abiotic conditions will continue to restrict vegetation community development. Over time, early successional vegetation may promote vegetation recovery by improving abiotic conditions (Callaway et al., 2002; Chambers et al., 1990, Scalenghe et al., 2002). However, a large body of literature on severe disturbance to alpine tundra that indicates that ecosystem recovery times may vary anywhere from several centuries to millennia (Bell and Bliss, 1973; Harper and Kershaw, 1996; Haugland and Beatty, 2005; Hodkinson et al., 2003; Scalenghe et al., 2002; Whinam and Chilcott, 1999; Willard and Marr, 1971). Based on the extreme sensitivity of alpine terrain, we recommend that it be avoided during infrastructure development in NNPR.

In black spruce parkland, road construction triggered a shift from black spruce to a lodgepole pine forest. Although the replacement of lodgepole pine by black spruce has been observed in some situations (Lotan and Critchfield, 1990), intense initial growth of lodgepole pine strongly suggests that pine stands will be self-replacing (Johnstone 2004, Peet 2000). As such, management of disturbance impacts in this terrain type will have to account for differences in ecological processes that mediate ecosystem function, such as nutrient cycling, vegetation productivity, and habitat quality between spruce and lodgepole pine forests.

Ecosystem recovery in deciduous forest resulted in the development of white spruce forest. Although white spruce and trembling aspen can overlap in xeric forest types, aspen stands typically self-replace after disturbance events expose mineral soil (Greene et al., 2007; Johnstone and Chapin, 2006; Roland et al., 2013; Strong, 2004; Viereck et al., 1983). As such, this successional trajectory was somewhat unanticipated. Based on our observations that disturbance facilitated a normal successional trajectory, linear disturbances are unlikely to affect the long-term ecological integrity of this terrain within NNPR and management of disturbance impacts in this terrain type are moderate.

Since human-caused and natural disturbances are increasing in the subarctic, additional research is required to predict and to manage their impacts, and to preserve ecological integrity within northern national parks. Variation in the effects of road construction among terrain types suggests that efforts to predict ecological responses to warming in discontinuous permafrost will be complicated by the potential for multiple and successional trajectories. Along the Prairie Creek winter access road, none of the terrain types returned to pre-disturbance plant communities. Divergent post-disturbance recovery following road construction emphasizes that ecosystem recovery is not necessarily bound to historical successional trajectories. As air temperatures and disturbance rates continue to increase, we should anticipate persistent changes in ecosystem function in discontinuous permafrost terrain.

Conclusions

Based on the data presented here we draw the following conclusions:

1. Disturbance to discontinuous permafrost terrain has persistent impacts on ecosystem structure and function.
2. Terrain types where disturbance exerts strong effects on soil condition are particularly vulnerable to persistent state changes.
3. Terrain where disturbance initiates strong feedbacks to ground conditions will be difficult to restore.

Chapter 4 – Project Summary

Increases in air temperatures and more frequent disturbances in the circumpolar north are having profound impacts on arctic and subarctic ecosystem structure and function (Chapin et al., 2004; Cheng and Wu, 2007; Forbes et al., 2001; Hudson and Henry, 2009; Tape et al., 2012; Walker and Walker, 1991). Although warmer air temperatures and disturbances affect the north as a whole, post-disturbance feedbacks, ecosystem recovery trajectories, and permafrost vulnerability vary among terrain types and permafrost zones. In areas of discontinuous permafrost, ground temperatures are mediated by local controls and disturbances that affect these controls can drive permafrost thaw and changes to the ecosystem configuration (Forbes et al., 2001; Halsey et al., 1995; Shur and Jorgenson, 2007; Smith et al., 2008; Vitt et al., 2000). Areas of continuous permafrost are generally more resilient to disturbance than discontinuous permafrost because permafrost is typically colder and deeper (Beilman et al., 2001; Camill, 1999; Smith et al., 2010a). However, disturbances in continuous permafrost zones can also precipitate significant ecological change (Frost et al., 2013; Gill et al., 2014; Johnstone and Kokelj, 2008; Lantz et al., 2009; Mackay and Burn, 2002).

Although previous research has explored the impacts of roads on vegetation communities, soils and permafrost, few studies have examined the processes driving variation in ecological responses among terrain types (Chapin and Shaver, 1981; Harper and Kershaw, 1996; Jorgenson et al., 2010a; Kemper and Macdonald, 2009a, 2009b; Smith and Riseborough, 2010; Williams et al., 2013). As such, the overall goal of this thesis was to investigate the nature of ecosystem recovery and post-disturbance feedbacks associated with road construction in both continuous and discontinuous permafrost zones. This research involved independent cases studies, which are presented as chapters 2 and 3 of this thesis.

The first case study (Chapter 2) focused on a zone of continuous permafrost, where the Dempster Highway crosses the Peel Plateau, NT. In similar arctic landscapes, considerable evidence suggests that disturbance can rapidly increase tall shrub abundance (Frost et al., 2013; Gill et al., 2014; Johnstone and Kokelj, 2008; Lantz et al., 2009; Mackay and Burn, 2002). To explore the relationship between disturbance and tall shrub proliferation in the Peel Plateau we collected along the Dempster Highway and examined the following research questions:

- **What is the magnitude of land cover transformation next to the Dempster Highway?**
- **What biophysical factors are associated with tall shrub proliferation?**

To determine the nature of landscape transformations adjacent to the Dempster Highway along the Peel Plateau, NT, greyscale airphotos (1975) and Quickbird satellite imagery (2008) from the same location were used to map areas of tall shrub tundra, dwarf shrub tundra, and water within a 1.2km buffer adjacent to the road as well as within a 1.2km buffer 500m away from the road. Comparisons of landcover maps from 1975 and 2008 showed that areas of tall shrub and standing water increased dramatically adjacent to the road. Away from the road, increases in tall shrub tundra were modest and ponding did not increase. Tall shrub proliferation next to the Dempster was not uniform and there were large areas of dwarf shrub tundra that resisted tall shrub expansion.

To investigate drivers of tall shrub proliferation next to the road, we measured biophysical variables at both tall shrub expansion sites and stable dwarf shrub sites. This analysis used plot scale data and broad scale GIS-derived data. Our results indicated that highway construction and maintenance accelerated major land cover transformations in the immediate vicinity of the road. Roadside tall shrub proliferation occurred preferentially at warmer, lower elevation sites that were characterized by wetter soils and thicker organic soils. Areas that resisted tall shrub

encroachment were located at cooler, higher elevation sites and were characterized by dry soils with thinner organic layers.

Our study of the Dempster Highway also provides insight into drivers of shrub proliferation and suggests that soil moisture is a key determinant of this process. Understanding the mechanisms facilitating shrub expansion in the tundra is vital because tall shrubs influence ground temperatures, and have strong feedbacks to soil nutrients, hydrology, and energy fluxes, which in turn influence vegetation community structure and function (Sturm et al. 2005, Chapin et al. 2005, Wookey et al. 2009, Quinton et al. 2011, Myers-Smith et al. 2011). By impacting ground thermal regimes, tall shrubs may also affect soil carbon storage (Natali et al., 2011; Sturm et al., 2005a). Ultimately, tall shrubs can modify processes that have feedbacks to the global climate system and may compound the effects of climate warming (Schuur et al., 2008).

The case study presented in chapter 3 focused on the Prairie Creek winter access road in Nahanni National Park Reserve (NNPR), NT, within a discontinuous permafrost zone. Since the structure and function of ecosystems in discontinuous permafrost are strongly mediated by feedbacks between environmental conditions, vegetation, and ground thermal regimes, disturbance is likely to have significant impacts on post-disturbance ecosystem function and configuration. Understanding the factors that affect ecosystem resilience in areas of discontinuous permafrost is critical for the management of anthropogenic disturbances in the subarctic. The Prairie Creek road spans black spruce parkland, deciduous forest, alpine treeline, and spruce muskeg terrain and portions of the road have naturally re-vegetated in the 30 years since it was abandoned. In Chapter 3, I explored the following research question with data collected from the Prairie Creek winter access road as it crossed these four terrain types:

- **How do post-disturbance biotic and abiotic conditions following road abandonment affect ecosystem recovery and near-surface ground temperatures in different terrain types?**

The effects of road construction on ecosystem recovery were investigated by comparing data collected from paired disturbed (road) and undisturbed (adjacent to the road) sites in spruce muskeg, black spruce parkland, deciduous forest, and alpine treeline terrain. Our field data indicate that disturbances to discontinuous permafrost terrain lead to large and persistent changes in ecosystem composition and structure in all terrain types. Our results are consistent with resilience theory that predicts that changes to key environmental factors will increase the likelihood of regime shifts. In spruce muskeg, permafrost thaw triggered by road construction dramatically increased soil moisture and facilitated a transition from spruce muskeg to sedge wetland. At alpine treeline, the removal of stabilizing vegetation and organic soil during construction slowed subsequent ecosystem recovery since extreme environmental conditions almost completely limited revegetation along the road. These results also show that in terrain types where disturbance fundamentally alters ecosystem processes, the management of disturbance impacts will be extremely difficult.

Synthesis

This project highlights the importance of understanding differences in feedbacks among terrain types following disturbance. Although increases in soil moisture caused by the Dempster and the Prairie Creek road affected ground conditions and promoted vegetation change, the specific effects of increased soil moisture and the nature of vegetation change depended on the study site/ terrain type. Data from along the Prairie Creek winter road indicates that thaw-sensitive terrain types have specific biophysical controls (ground thermal regimes, soil moisture, existing vegetation) on vegetation community, and that modification of these factors can trigger feedbacks that lead to persistent ecological changes. Data from the Dempster

highway also shows that local controls, such as soil moisture, can lead to significant changes in vegetation structure.

Taken together, the two case studies explored in this thesis provide some insight into similarities between continuous and discontinuous permafrost zones. In both case studies, our data showed that permafrost dynamics strongly influence vegetation communities at undisturbed locations. In discontinuous permafrost linear disturbances are likely to cause irreversible ecological changes once permafrost degrades. Perturbations to continuous permafrost by linear disturbances also cause large ecological changes when elevated soil moisture promotes vegetation change. However, in this environment permafrost may continue to persist under tall shrub canopies.

The results from both studies also indicate that disturbance accelerates vegetation change, and highlights the type of changes we should anticipate in a warmer climate. Ultimately, both thesis chapters suggest that landscape change in face of disturbance and climate warming will not be uniform across the subarctic, but will depend on variation in the abiotic controls that mediate ecological responses to perturbation.

Limitations of case study 1: The Dempster Highway, NT.

In the broad scale GIS analysis presented in Chapter 2, the statistical models did not account for spatial autocorrelation between data points. Since many of the 2000 data points were located in a relatively small area, this approach likely underestimated the variance between treatments (Legendre and Fortin, 1989). To reduce the effects of spatial autocorrelation, we could have used semivariogram analysis to determine an appropriate distance constraint between measurement points, reduced the number of data points used, or constructed models that accounted for spatial autocorrelation (Legendre and Fortin, 1989).

The observational approach used in this chapter strongly indicates that increases in soil moisture drove tall shrub proliferation along the Dempster. However, it is

possible that other factors that we did not measure, such as exposure to harsh winter environmental conditions, as well as differences in area solar radiation may have also promoted tall shrub proliferation. These limitations could be overcome by using an experimental approach to manipulate soil moisture while controlling for other biophysical conditions related to elevation and area solar radiation. Diligent monitoring of new roads built in continuous permafrost areas, such as the Inuvik Tuktoyaktuk Highway, could also be used to improve our understanding of drivers of vegetation change because they give us an idea of conditions prior to extensive tall shrub proliferation.

Limitations of case study 2: Prairie Creek winter access road, NT.

The greatest limitations in the second case study stemmed from time and budgetary constraints. Transect replication was low in alpine terrain because of the prohibitively expensive costs of transportation within the park. Helicopter support from Parks in 2012 allowed us to install 11 thermistors in 4 terrain types. Unfortunately, animal encounters reduced the number of functional thermistors and not all terrain types were adequately represented. In the future, installation of a minimum of 6-8 thermistors in each terrain type would help to mitigate data loss from animal encounters. Since permafrost is defined as ground below 0°C for two or more years (Smith and Riseborough, 2002), it would have been preferable to record near-surface thermal data for more than one year. It would also have been helpful to install deep thermistors to determine the ground temperature at the depth of zero annual amplitude.

Future Research

Thaw-sensitive terrain in the subarctic will likely continue to be impacted by warming air temperatures and disturbance. Variation in the response to disturbance described in this thesis suggests that the recovery of terrain impacted by roads will not be simple. Additional analysis of feedbacks that lead to ecosystem change in both continuous and discontinuous permafrost zones is needed to provide more

information on the resilience of these terrain types, and to help predict thresholds that will initiate future landscape-scale ecological change.

On the Peel plateau, additional work on the Dempster Highway should explore the interrelations among tall shrub proliferation, active layer thickness, and permafrost temperature. Evidence indicates that increased tall shrub cover warms permafrost temperature by trapping insulating snow during the winter (Gill et al., 2014; Sturm et al., 2005a). However our analysis also shows that active layers are thinner under patches of tall shrub expansion, suggesting that increases in organic soil thickness and summer shading from the shrub canopy can decrease summer ground temperatures and reduce active layer thickness. Given that tall shrub proliferation is expected to increase, the relative effects of winter and summer processes on heat flux should be explored in more detail. To better understand the feedbacks associated with tall shrub expansion, Drs. Lantz and Kokelj have recently initiated a shrub removal experiment beside the Dempster. Following shrub removal, ground temperatures and snow accumulation are expected to decrease, and active layer thickness is expected to increase. The construction of the Inuvik-Tuktoyaktuk highway also presents a unique opportunity to monitor biotic and abiotic factors before landscape transformations occur.

Subsequent work in NNPR should explore the abiotic thresholds that precede ecosystem shifts to alternative stable states in thaw sensitive terrain. For example, determining the degree of soil compaction that spruce muskeg is able to withstand before ground subsidence and altered hydrology patterns drive permafrost thaw would be useful for any subsequent infrastructure development in the park. Future work along the Prairie Creek winter access road should also focus on long-term monitoring of thaw-sensitive spruce muskeg terrain. Particular care should be taken to monitor ground temperatures along the roadbed because all-season permits have been submitted to the Mackenzie Valley Land and Water board to render the road fully operational. Subsequent work should also be undertaken to monitor

succession along abandoned portions of the road and to assess the extent of lateral thaw.

Bibliography

- ACIA (2005). *Arctic Climate Impact Assessment: Impacts of Warming Climate* (Cambridge: Cambridge University Press).
- Alfaro, M.C., Ciro, G.A., Thiessen, K.J., and Ng, T. (2009). Case study of degrading permafrost beneath a road embankment. *Journal of Cold Regions Engineering* 23, 93–111.
- Anisimov, O.A., and Nelson, F.E. (1997). Permafrost zonation and climate change in the northern hemisphere: results from transient general circulation models. *Climatic Change* 35, 241–258.
- Anisimov, O., and Reneva, S. (2006). Permafrost and changing climate: the Russian perspective. *Ambio* 35, 169–175.
- Arseneault, D., and Payette, S. (1997). Reconstruction of millennial forest dynamics from tree remains in a subarctic tree line peatland. *Ecology* 78, 1873–1883.
- Auerbach, N.A., Walker, M.D., and Walker, D.A. (1997). Effects of roadside disturbance on substrate and vegetation properties in arctic tundra. *Ecological Applications* 7, 218–235.
- Bauer, I.E., and Vitt, D.H. (2011). Peatland dynamics in a complex landscape: development of a fen-bog complex in the sporadic discontinuous permafrost zone of northern Alberta, Canada. *Boreas* 40, 714–726.
- Beck, P.S.A. (2011). Satellite observations of high northern latitude vegetation productivity changes between 1982 and 2008: ecological variability and regional differences. *Environmental Research Letters* 6, 045501.
- Beilman, D.W., and Robinson, S.D. (2003). Peatland permafrost thaw and landform type along a climatic gradient. In *Proceedings of the 8th International Conference on Permafrost*, (Balkema Zurich), pp. 61–65.
- Beilman, D.W., Vitt, D.H., and Halsey, L.A. (2001). Localized permafrost peatlands in western Canada: definition, distributions, and degradation. *Arctic, Antarctic, and Alpine Research* 33, 70–77.
- Bell, K.L., and Bliss, L.C. (1973). Alpine disturbance studies: Olympic National Park, USA. *Biological Conservation* 5, 25–32.
- Bennett, B. (2013). *Vascular Plants of Nahanni National Park Reserve: Results of a survey August 7-12, 2012*.

Berg, E.E., Hillman, K.M., Dial, R., and DeRuwe, A. (2009). Recent woody invasion of wetlands on the Kenai Peninsula Lowlands, south-central Alaska: a major regime shift after 18 000 years of wet *Sphagnum* –sedge peat recruitment. *Canadian Journal of Forest Research* 39, 2033–2046.

Bhatt, U.S., Walker, D.A., Raynolds, M.K., Comiso, J.C., Epstein, H.E., Jia, G.S., Gens, R., Pinzon, J.E., Tucker, C.J., Tweedie, C.E., et al. (2010). Circumpolar Arctic Tundra Vegetation Change Is Linked to Sea Ice Decline. *Earth Interact Earth Interact* 14, 1–20.

Binkley, D., Stottlemeyer, 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.

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 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in evergreen dwarf shrub *Cassiope tetragona* in high-arctic Svalbard tundra. *Environmental Research Letters* 10, 044008.

Bret-Harte, M.S., Shaver, G.R., Zoerner, J.P., Johnstone, J.F., Wagner, J.L., Chavez, A.S., Gunkelman IV, R.F., 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.

Brink, V.C. (1964). Plant establishment in the high snowfall alpine and subalpine regions of British Columbia. *Ecology* 45, 432–438.

Brown, J. (1975). Fire cycles and community dynamics in lodgepole pine forests. In (D. Baumgartner, Ed.) *Management of Lodgepole Pine Ecosystems: Symposium Proceedings*, pp. 429–456.

Brown, R.J.E. (1960). The distribution of permafrost and its relation to air temperature in Canada and the U. S. S. R. *Arctic* 13, 163–177.

Buckeridge, K.M., and Grogan, P. (2008). Deepened snow alters soil microbial nutrient limitations in arctic birch hummock tundra. *Applied Soil Ecology* 39, 210–222.

Buckeridge, K.M., Zufelt, E., Chu, H., and Grogan, P. (2009). Soil nitrogen cycling rates in low arctic shrub tundra are enhanced by litter feedbacks. *Plant and Soil* 330, 407–421.

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, 407–421.

Buckley, Y.M., Briese, D.T., and Rees, M. (2003). Demography and management of the invasive plant species *Hypericum perforatum*. II. Construction and use of an individual-based model to predict population dynamics and the effects of management strategies. *Journal of Applied Ecology* 40, 494–507.

Burn, C.R. (1992). Recent ground warming inferred from the temperature in permafrost near Mayo, Yukon Territory. In Dixon, J.C., and Abrams, A.D., Eds. *Periglacial Geomorphology*, (New York: John Wiley and Sons), pp. 327–350.

Burn, C.R. (1998). The response (1958-1997) of permafrost and near-surface ground temperatures to forest fire, Takhini River valley, southern Yukon Territory. *Canadian Journal of Earth Sciences* 35, 184–199.

Burn, C.R. (2000). The thermal regime of a retrogressive thaw slump near Mayo, Yukon Territory. *Canadian Journal of Earth Sciences* 37, 967–981.

Burn, C.R., and Kokelj, S.V. (2009). The environment and permafrost of the Mackenzie Delta area. *Permafrost and Periglacial Processes* 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 and Periglacial Processes* 20, 221–227.

Callaway, R.M., Brooker, R.W., Choler, P., Kikvidze, Z., Lortie, C.J., Michalet, R., Paolini, L., Pugnaire, F.I., Newingham, B., Aschehoug, E.T., et al. (2002). Positive interactions among alpine plants increase with stress. *Nature* 417, 844–848.

Calmels, F., Froese, D.G., Clavano, W.R., and Burn, C.R. (2012). Cryostratigraphic record of permafrost degradation and recovery following historic (1898–1992) surface disturbances in the Klondike region, central Yukon Territory. *Canadian Journal of Earth Sciences* 49, 938–952.

Camill, P. (1999). Patterns of boreal permafrost peatland vegetation across environmental gradients sensitive to climate warming. *Canadian Journal of Botany* 77, 721–733.

Camill, P., and Clark, J.S. (1998). Climate change disequilibrium of boreal permafrost peatlands caused by local processes. *The American Naturalist* 151, 207–222.

Camill, P., and Clark, J.S. (2000). Long-term perspectives on lagged ecosystem responses to climate change: permafrost in boreal peatlands and the grassland/woodland boundary. *Ecosystems* 3, 534–544.

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, 461–478.

Carlson, D.W., and Groot, A. (1997). Microclimate of clear-cut, forest interior, and small openings in trembling aspen forest. *Agricultural and Forest Meteorology* 87, 313–329.

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, 121–137.

- Chambers, J.C., MacMahon, J.A., and Brown, R.W. (1990). Alpine seedling establishment: the influence of disturbance type. *Ecology* 71, 1323–1341.
- Chapin, F.S., and Shaver, G.R. (1981). Changes in soil properties and vegetation following disturbance of Alaskan Arctic tundra. *Journal of Applied Ecology* 18, 605–617.
- 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., Peterson, G., Berkes, F., Callaghan, T.V., Angelstam, P., Apps, M., Beier, C., Bergeron, Y., Crépin, A.S., and Danell, K. (2004). Resilience and vulnerability of northern regions to social and environmental change. *Ambio* 33, 344–349.
- Chapin, F.S., Sturm, M., Serreze, M.C., McFadden, J.P., Key, J.R., Lloyd, A.H., McGuire, A.D., Rupp, T.S., Lynch, A.H., Schimel, J.P., et al. (2005). Role of land-surface changes in Arctic summer warming. *Science* 310, 657–660.
- Chapin, F.S., Viereck, L.A., Adams, P., Van Cleve, K., Fastie, C.L., Ott, R.A., Mann, D., and Johnstone, J.F. (2006). Successional processes in the Alaskan boreal forest. In *Alaska's Changing Boreal Forest*, (Oxford: Oxford University Press), pp. 100–120.
- Chapin, F.S., Kofinas, G.P., Folke, C., and Chapin, M.C. (2009). *Principles of ecosystem stewardship: resilience-based natural resource management in a changing world* (Springer Science & Business Media).
- Chasmer, L., Quinton, W., Hopkinson, C., Petrone, R., and Whittington, P. (2011). Vegetation canopy and radiation controls on permafrost plateau evolution within the discontinuous permafrost zone, Northwest Territories, Canada. *Permafrost and Periglacial Processes* 199–213.
- Cheng, G., and Wu, T. (2007). Responses of permafrost to climate change and their environmental significance, Qinghai-Tibet Plateau. *Journal of Geophysical Research: Earth Surface* 112, F02S03.
- Clarke, K.R. (1993). Nonparametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18, 117–143.
- Clarke, K.R., and Gorley, R.N. (2001). *Primer v5: Users Manual / Tutorial* (Plymouth, MA: Primer-E Ltd.).
- Clarke, K.R., and Warwick, R.M. (2001). *Change in marine communities: an approach to statistical analysis and interpretation* (PRIMER-E Limited).
- Connon, R.F., Quinton, W.L., Craig, J.R., and Hayashi, M. (2014). Changing hydrologic connectivity due to permafrost thaw in the lower Liard River valley, NWT, Canada. *Hydrological Processes* 28, 4163–4178.

Constabel, A., and Lieffers, V. (1996). Seasonal patterns of light transmission through boreal mixedwood canopies. *Canadian Journal of Forest Research* 26, 1008–1014.

DeLong, H.B., Lieffers, V.J., and Blenis, P.V. (1997). Microsite effects on first-year establishment and overwinter survival of white spruce in aspen-dominated boreal mixedwoods. *Canadian Journal of Forest Research* 27, 1452–1457.

Dobbs, R.C. (1976). White spruce seed dispersal in central British Columbia. *The Forestry Chronicle* 52, 225–228.

Duk-Rodkin, A., and Hughes, O. Surficial geology, Fort McPherson - Bell River Yukon - Northwest Territories (Geological Survey of Canada).

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 Letters* 15, 164–175.

Elmendorf, S.C., Henry, G.H.R., Hollister, R.D., Bjork, R.G., Boulanger-Lapointe, N., Cooper, E.J., Cornelissen, J.H.C., Day, T.A., Dorrepaal, E., Elumeeva, T.G., et al. (2012b). Plot-scale evidence of tundra vegetation change and links to recent summer warming. *Nature Clim. Change* 2, 453–457.

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. *Journal of Biogeography* 31, 1917–1933.

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. *Global Change Biology* 10, 1325–1334.

Euskirchen, E.S., McGuire, A.D., Rupp, T.S., Chapin, F.S., and Walsh, J.E. (2009). Projected changes in atmospheric heating due to changes in fire disturbance and the snow season in the western Arctic, 2003–2100. *Journal of Geophysical Research: Biogeosciences* 114, G04022.

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. *Canadian Journal of Forest Research* 40, 1336–1346.

Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L., and Holling, C.S. (2004). Regime Shifts, Resilience, and Biodiversity in Ecosystem Management. *Annual Review of Ecology, Evolution, and Systematics* 35, 557–581.

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

Forbes, B.C., Fauria, M.M., and Zetterberg, P. (2010). Russian Arctic warming and “greening” are closely tracked by tundra shrub willows. *Global Change Biology* 16, 1542–1554.

Ford, D. (2010). The South Nahanni: High-Latitude Limestone Landscapes. In *Geomorphological Landscapes of the World*, (Springer Netherlands), pp. 13–20.

Ford, D. (2011). Expanding South Nahanni National Park, Northwest Territories, Canada, to Include and Manage Some Remarkable Sub-Arctic/Arctic Karst Terranes. In *Karst Management*, P.E. van Beynen, ed. (Dordrecht: Springer Netherlands), pp. 415–437.

Ford, D.C. (1976). Evidences of multiple glaciation in South Nahanni National Park, Mackenzie Mountains, Northwest Territories. *Canadian Journal of Earth Sciences* 13, 1433–1445.

Fortier, R., LeBlanc, A.-M., and Yu, W. (2011). Impacts of permafrost degradation on a road embankment at Umiujaq in Nunavik (Quebec), Canada. *Canadian Geotechnical Journal* 48, 720–740.

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, 1151–1168.

Frost, G.V., Epstein, H.E., Walker, D.A., Matyshak, G., and Ermokhina, K. (2013). Patterned-ground facilitates shrub expansion in Low Arctic tundra. *Environmental Research Letters* 8, 015035.

Furlow, J.J. (1979). Systematics of the American species of *Alnus* (Betulaceae). *Rhodora* 81, 1–121.

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, and Alpine Research* 46, 947–961.

Greene, D., Macdonald, S., Haeussler, S., Domenicano, S., Noel, J., Jayen, K., Charron, I., Gauthier, S., Hunt, S., Gielau, E., et al. (2007). The reduction of organic-layer depth by wildfire in the North American boreal forest and its effect on tree recruitment by seed. *Canadian Journal of Forest Research* 37, 1012–1023.

Grosse, G., Harden, J., Turetsky, M., McGuire, A.D., Camill, P., Tarnocai, C., Frohling, S., Schuur, E.A.G., Jorgenson, T., Marchenko, S., et al. (2011). Vulnerability of high-latitude soil organic carbon in North America to disturbance. *Journal of Geophysical Research* 116, G00K06.

Gunderson, L.H. (2000). Ecological Resilience--In Theory and Application. *Annual Review of Ecology and Systematics* 31, 425–439.

- Gutsell, S.L., and Johnson, E.A. (2002). Accurately ageing trees and examining their height-growth rates: implications for interpreting forest dynamics. *Journal of Ecology* 90, 153–166.
- Hadlari, T. (2006). Sedimentology of Cretaceous wave-dominated parasequences, Trevor Formation, Peel Plateau, NWT (Yellowknife, NT: Northwest Territories Geosciences Office).
- Halsey, L.A., Vitt, D.H., and Zoltai, S.C. (1995). Disequilibrium response of permafrost in boreal continental western Canada to climate change. *Climatic Change* 30, 57–73.
- Harper, K.A., and Kershaw, G.P. (1996). Natural revegetation on borrow pits and vehicle tracks in shrub tundra, 48 years following construction of the CANOL No. 1 pipeline, N.W.T., Canada. *Arctic and Alpine Research* 28, 163.
- Harper, K.A., and Kershaw, G.P. (1997). Soil characteristics of 48-year-old borrow pits and vehicle tracks in shrub tundra along the CANOL No. 1 pipeline corridor, Northwest Territories, Canada. *Arctic and Alpine Research* 29, 105–111.
- Haugland, J.E., and Beatty, S.W. (2005). Vegetation establishment, succession and microsite frost disturbance on glacier forelands within patterned ground chronosequences. *Journal of Biogeography* 32, 145–153.
- 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).
- 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, U.S.A. *Arctic, Antarctic, and Alpine Research* 34, 262.
- Hinkel, K.M., and Hurd, J.K. (2006). Permafrost Destabilization and Thermokarst Following Snow Fence Installation, Barrow, Alaska, U.S.A. *Arctic, Antarctic, and Alpine Research* 38, 530–539.
- Hinzman, L., Kane, D., and Yoshikawa, K. (2003). Hydrological variations among watersheds with varying degrees of permafrost. In *Proceedings of the 8th International Conference on Permafrost*, pp. 21–25.
- Hodkinson, I.D., Coulson, S.J., and Webb, N.R. (2003). Community assembly along proglacial chronosequences in the high Arctic: vegetation and soil development in north-west Svalbard. *Journal of Ecology* 91, 651–663.
- Holling, C.S. (1973). Resilience and Stability of Ecological Systems. *Annual Review of Ecology and Systematics* 4, 1–23.
- 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, 2657–2663.

Hughes, O.L., Harington, C.R., Janssens, J.A., Matthews, J.V., Morlan, R.E., Rutter, N.W., and Schweger, C.E. (1981). Upper Pleistocene stratigraphy, paleoecology, and archaeology of the Northern Yukon Interior, Eastern Beringia 1. Bonnet Plume Basin. *Arctic* 34, 329–365.

Indian and Northern Affairs (2010). Northern land use guidelines. Volume 05: access - roads and trails.

IPCC (2007). *Climate Change 2007: The Physical Science Basis*. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel of Climate Change (Cambridge, UK: Cambridge University Press).

Iwahana, G. (2005). Influence of forest clear-cutting on the thermal and hydrological regime of the active layer near Yakutsk, eastern Siberia. *Journal of Geophysical Research* 110, G02004.

James, A.R.C., and Stuart-Smith, A.K. (2000). Distribution of Caribou and Wolves in Relation to Linear Corridors. *The Journal of Wildlife Management* 64, 154–159.

Jia, G.S.J., Epstein, H.E., and Walker, D.A. (2003). Greening of arctic Alaska, 1981–2001. *Geophysical Research Letters* 30, 1029–1033.

Johnson, J.B., and Omland, K.S. (2004). Model selection in ecology and evolution. *Trends in Ecology & Evolution* 19, 101–108.

Johnson, J.D., MacKinnon, A., and Pojar, J. (1995). *Plants of the western boreal forest and aspen parkland* (Edmonton, Alberta: Lone Pine Publishing).

Johnstone, J., and Chapin, F. (2006). Effects of soil burn severity on post-fire tree recruitment in boreal forest. *Ecosystems* 9, 14–31.

Johnstone, J.F., and Chapin, F.S. (2003). Non-equilibrium succession dynamics indicate continued northern migration of lodgepole pine. *Global Change Biology* 9, 1401–1409.

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

Jones, D., Sadzik, E., and Wolmarans, I. (2001). The incorporation of dust palliatives as a maintenance option in unsealed road management systems. In 20th ARRB Conference, (Australia),.

Jorgenson, M.T., and Osterkamp, T.E. (2005). Response of boreal ecosystems to varying modes of permafrost degradation. *Canadian Journal of Forest Research* 35, 2100–2111.

Jorgenson, J.C., Hoef, J.M.V., and Jorgenson, M.T. (2010a). Long-term recovery patterns of arctic tundra after winter seismic exploration. *Ecological Applications* 20, 205–221.

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. *Climatic Change* 48, 551–579.

Jorgenson, M.T., Romanovsky, V., Harden, J., Shur, Y., O'Donnell, J., Schuur, E.A.G., Kanevskiy, M., and Marchenko, S. (2010b). Resilience and vulnerability of permafrost to climate change. *Canadian Journal of Forest Research* 40, 1219–1236.

Kanigan, J.C., and Kokelj, S.V. (2008). Review of current research on drilling-mud sumps in permafrost terrain, Mackenzie Delta region, NWT, Canada. *Delta* 1473–1479.

Kanigan, J.C.N., Burn, C.R., and Kokelj, S.V. (2009). Ground temperatures in permafrost south of treeline, Mackenzie Delta, Northwest Territories. *Permafrost and Periglacial Processes* 20, 127–139.

Kemper, J.T., and Macdonald, S.E. (2009a). Effects of contemporary winter seismic exploration on Low Arctic plant communities and permafrost. *Arctic, Antarctic, and Alpine Research* 41, 228–237.

Kemper, J.T., and Macdonald, S.E. (2009b). Directional change in upland tundra plant communities 20-30 years after seismic exploration in the Canadian low-arctic. *Journal of Vegetation Science* 20, 557–567..

Kenward, M.G., and Roger, J.H. (1997). Small sample inference for fixed effects from restricted maximum likelihood. *Biometrics* 53, 983–997.

Kershaw, G.P., and Gill, D. (1979). Growth and decay of palsas and peat plateaus in the Macmillan Pass–Tsichu River area, Northwest Territories, Canada. *Canadian Journal of Earth Sciences* 16, 1362–1374.

Kimball, J.S., Zhao, M., McGuire, A.D., Heinsch, F.A., Clein, J., Calef, M., Jolly, W.M., Kang, S., Euskirchen, S.E., McDonald, K.C., 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.

Kinugasa, T., and Oda, S. (2014). Effects of vehicle track formation on soil seed banks in grasslands with different vegetation in the Mongolian steppe. *Ecological Engineering* 67, 112–118.

Kokelj, S.A. (2001). Hydrologic overview of the Gwich'in and Sahtu Settlement Areas (Yellowknife, NT: Water Resources Division, Aboriginal Affairs and Northern Development Canada).

Kokelj, S.V., and Jorgenson, M.T. (2013). Advances in thermokarst research: recent advances in research investigating thermokarst processes. *Permafrost and Periglacial Processes* 24, 108–119.

- 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. *Journal of Geophysical Research: Earth Surface* *118*, 681–692.
- Kopp, B.J., Minderlein, S., and Menzel, L. (2014). Soil moisture dynamics in a mountainous headwater area in the discontinuous permafrost zone of northern Mongolia. *Arctic, Antarctic, and Alpine Research* *46*, 459–470.
- Koronatova, N.G., and Milyaeva, E.V. (2011). Plant community succession in post-mined quarries in the northern-taiga zone of West Siberia. *Contemporary Problems of Ecology* *4*, 513–518.
- Kwong, Y.J., and Gan, T.Y. (1994). Northward migration of permafrost along the Mackenzie Highway and climatic warming. *Climatic Change* *26*, 399–419.
- Landhäuser, S.M., and Wein, R.W. (1993). Postfire vegetation recovery and tree establishment at the Arctic treeline - climate-change vegetation-response hypotheses. *Journal of Ecology* *81*, 665–672.
- 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. *Global Change Biology* *15*, 1664–1675.
- Lantz, T.C., Gergel, S.E., and Kokelj, S.V. (2010a). Spatial heterogeneity in the shrub tundra ecotone in the Mackenzie Delta Region, Northwest Territories: implications for Arctic environmental change. *Ecosystems* *13*, 194–204.
- Lantz, T.C., Gergel, S.E., and Henry, G.H.R. (2010b). Response of green alder (*Alnus viridis* subsp. *fruticosa*) patch dynamics and plant community composition to fire and regional temperature in north-western Canada. *Journal of Biogeography* *37*, 1597–1610.
- 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.
- Legendre, P., and Fortin, M. (1989). Spatial pattern and ecological analysis. *Vegetation* *80*, 107–138.
- Liston, G.E., Mcfadden, J.P., Sturm, M., and Pielke, R.A. (2002). Modelled changes in arctic tundra snow, energy and moisture fluxes due to increased shrubs. *Global Change Biology* *8*, 17–32.
- Lloyd, A.H., Yoshikawa, K., Fastie, C.L., Hinzman, L., and Fraver, M. (2003). Effects of permafrost degradation on woody vegetation at arctic treeline on the Seward Peninsula, Alaska. *Permafrost and Periglacial Processes* *14*, 93–101.
- Lotan, J.E., and Critchfield, W.B. (1990). Lodgepole pine. Seed 2, 2.

Mackay, J.R. (1970). Disturbances to the tundra and forest tundra environment of the western Arctic. *Canadian Geotechnical Journal* 7, 420–432.

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. *Canadian Journal of Earth Sciences* 39, 95–111.

Marchenko, S.S., Gorbunov, A.P., and Romanovsky, V.E. (2007). Permafrost warming in the Tien Shan Mountains, Central Asia. *Global and Planetary Change* 56, 311–327.

McClymont, A.F., Hayashi, M., Bentley, L.R., and Christensen, B.S. (2013). Geophysical imaging and thermal modeling of subsurface morphology and thaw evolution of discontinuous permafrost. *Journal of Geophysical Research: Earth Surface* 118, 1826–1837.

McGuire, A.D., Chapin Iii, F.S., Walsh, J.E., and Wirth, C. (2006). Integrated regional changes in arctic climate feedbacks: implications for the global climate system. *Annual Review of Environment and Resources* 31, 61–91.

McManus, Kelly 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. *Global Change Biology* 18, 2313–2323.

Messier, C., Parent, S., and Bergeron, Y. (1998). Effects of overstory and understory vegetation on the understory light environment in mixed boreal forests. *Journal of Vegetation Science* 9, 511–520.

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 Biology and Biochemistry* 34, 1785–1795.

Monz, C.A. (2002). The response of two arctic tundra plant communities to human trampling disturbance. *Journal of Environmental Management* 64, 207–217.

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

Mueggler, W.F. (1988). *Aspen community types of the Intermountain Region* (Utah: Department of Agriculture, Forest Service).

Myers-Smith, I.H., Arnesen, B.K., Thompson, R.M., and Chapin, F.S. (2006). Cumulative impacts on Alaskan arctic tundra of a quarter century of road dust. *Ecoscience* 13, 503–510.

Myers-Smith, I.H., Forbes, B.C., Wilmking, M., Hallinger, M., Lantz, T., Blok, D., Tape, K.D., Macias-Fauria, M., Sass-Klaassen, U., Lévesque, E., et al. (2011). Shrub expansion

in tundra ecosystems: dynamics, impacts and research priorities. *Environmental Research Letters* 6, 045509.

Myers-Smith, I.H., Elmendorf, S.C., Beck, P.S.A., Wilkening, M., Hallinger, M., Blok, D., Tape, K.D., Rayback, S.A., Macias-Fauria, M., Forbes, B.C., et al. (2015). Climate sensitivity of shrub growth across the tundra biome. *Nature Climate Change* 5, 1–5.

Narbonne, G.M., and Aitken, J.D. (1995). Neoproterozoic of the Mackenzie Mountains, northwestern Canada. *Precambrian Research* 73, 101–121.

Natali, S.M., Schuur, E.A.G., Trucco, C., Hicks Pries, C.E., Crummer, K.G., and Baron Lopez, A.F. (2011). Effects of experimental warming of air, soil and permafrost on carbon balance in Alaskan tundra. *Global Change Biology* 17, 1394–1407.

Nelson, F.E., Anisimov, O.A., and Shiklomanov, N.I. (2002). Climate change and hazard zonation in the circum-Arctic permafrost regions. *Natural Hazards* 26, 203–225.

Nicolson, D.J., Romanovsky, V.E., Alexeev, V.A., and Lawrence, D.M. (2007). Improved modeling of permafrost dynamics in a GCM land-surface scheme. *Geophysical Research Letters* 34, L08501.

Norris, D.. Geology of the northern Yukon and northwestern District of Mackenzie (Geological Survey of Canada).

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 and Periglacial Processes* 26, 103–118.

Osterkamp, T.E. (2003). A thermal history of permafrost in Alaska. In *Proceedings of the 8th International Conference on Permafrost*, pp. 863–867.

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. *Canadian Journal of Earth Sciences* 49, 877–894.

Parks Canada (2006). Proposed expansion of Nahanni National Park Reserve. ([Ottawa, Ont.]: Parks Canada).

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, 2347–2363.

Pomeroy, J., Ellis, C., Rowlands, A., Essery, R., Hardy, J., Link, T., Marks, D., and Sicart, J.E. (2008). Spatial variability of shortwave irradiance for snowmelt in forests. *Journal of Hydrometeorology* 9, 1482–1490.

Pomeroy, J.W., Bewley, D.S., Essery, R.L.H., Hedstrom, N.R., Link, T., Granger, R.J., Sicart, J.E., Ellis, C.R., and Janowicz, J.R. (2006). Shrub tundra snowmelt. *Hydrological Processes* 20, 923–941.

Quinton, W.L., and Baltzer, J.L. (2013). The active-layer hydrology of a peat plateau with thawing permafrost (Scotty Creek, Canada). *Hydrogeology Journal* 21, 201–220.

Quinton, W. l., Hayashi, M., and Chasmer, L. e. (2011). Permafrost-thaw-induced land-cover change in the Canadian subarctic: implications for water resources. *Hydrological Processes* 25, 152–158.

Rawls, W.J., Pachepsky, Y.A., Ritchie, J.C., Sobecki, T.M., and Bloodworth, H. (2003). Effect of soil organic carbon on soil water retention. *Geoderma* 116, 61–76.

Roland, C.A., Schmidt, J.H., and Nicklen, E.F. (2013). Landscape-scale patterns in tree occupancy and abundance in subarctic Alaska. *Ecological Monographs* 83, 19–48.

Romanovsky, V., and Osterkamp, T.E. (2000). Effects of unfrozen water on heat and mass transport processes in the active layer and permafrost. *Permafrost and Periglacial Processes* 11, 219–239.

Romanovsky, V.E., Smith, S.L., and Christiansen, H.H. (2010). Permafrost thermal state in the polar Northern Hemisphere during the international polar year 2007–2009: a synthesis. *Permafrost and Periglacial Processes* 21, 106–116.

Ronco, F. (1967). Lessons from artificial regeneration studies in a cutover beetle-killed spruce stand in western Colorado (Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO: USDA Forest Service).

Roots, C.F., Smith, C.A.S., Meikle, J.C., Canada, and Agriculture and Agri-Food Canada (2004). Ecoregions of the Yukon Territory: biophysical properties of Yukon landscapes (Summerland, B.C.: Agriculture and Agri-Food Canada, Research Branch).

Sannel, A.B.K., and Kuhry, P. (2008). Long-term stability of permafrost in subarctic peat plateaus, west-central Canada. *The Holocene* 18, 589–601.

Scalenghe, R., Bonifacio, E., Celi, L., Ugolini, F.C., and Zanini, E. (2002). Pedogenesis in disturbed alpine soils (NW Italy). *Geoderma* 109, 207–224.

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 Biology and Biochemistry* 36, 217–227.

Schuur, E.A.G., Bockheim, J., Canadell, J.G., Euskirchen, E., Field, C.B., Goryachkin, S.V., Hagemann, S., Kuhry, P., Lafleur, P.M., Lee, H., et al. (2008). Vulnerability of permafrost carbon to climate change: implications for the global carbon cycle. *Bioscience* 58, 701–714.

Serreze, M., Walsh, J., Chapin, F.S., Osterkamp, T., Dyurgerov, M., Romanovsky, V., Oechel, W., Morison, J., Zhang, T., and Barry, R. (2000). Observational evidence of recent change in the northern high-latitude environment. *Climatic Change* 46, 159–207.

Sheppard, W., and Noble, D. (1976). Germination, survival, and growth of lodgepole pine under simulated precipitation regimes: a greenhouse study (Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO: USDA Forest Service).

Shepperd, W.D., Bartos, D.L., and Mata, S.A. (2001). Above- and below-ground effects of aspen clonal regeneration and succession to conifers. *Canadian Journal of Forest Research* 31, 739–745.

Shur, Y.L., and Jorgenson, M.T. (2007). Patterns of permafrost formation and degradation in relation to climate and ecosystems. *Permafrost and Periglacial Processes* 18, 7–19.

Simard, M.-J., Bergeron, Y., and Sirois, L. (1998). Conifer seedling recruitment in a southeastern Canadian boreal forest: the importance of substrate. *Journal of Vegetation Science* 9, 575–582.

Smith, M.W., and Riseborough, D.W. (2002). Climate and the limits of permafrost: a zonal analysis. *Permafrost and Periglacial Processes* 13, 1–15.

Smith, S.L., and Riseborough, D.W. (2010). Modelling the thermal response of permafrost terrain to right-of-way disturbance and climate warming. *Cold Regions Science and Technology* 60, 92–103.

Smith, S.L., Burgess, M.M., Riseborough, D., and Mark Nixon, F. (2005). Recent trends from Canadian permafrost thermal monitoring network sites. *Permafrost and Periglacial Processes* 16, 19–30.

Smith, S.L., Burgess, M.M., Riseborough, D.W., and Chartrand, J. (2008). Permafrost and terrain research and monitoring sites of the Norman Wells to Zama pipeline - thermal data collection and case histories, April 1985 to September 2001 (NRCan).

Smith, S. L., Romanovsky, V.E., Lewkowicz, A.G., Burn, C.R., Allard, M., Clow, G.D., Yoshikawa, K., and Throop, J. (2010a). Thermal state of permafrost in North America: a contribution to the international polar year. *Permafrost and Periglacial Processes* 21, 117–135.

Smith, S.L., Lewkowicz, A.G., Burn, C.R., Allard, M., and Throop, J. (2010b). The thermal state of permafrost in Canada-Results from the International Polar Year. In GEO2010, 63rd Canadian Geotechnical Conference and the 6th Canadian Permafrost Conference, Calgary, pp. 1214–1221.

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 and Earth System Sciences Discussions* 10, 101–112.

- Stanek, W., Alexander, K., and Simmons, C.. (1981). Reconnaissance of vegetation and soils along the Dempster Highway, Yukon Territory: I. vegetation types (Victoria, B.C.: Environment Canada, Canadian Forestry Service).
- Stow, N., and Wilson, P. (2006). Aggregated CCRS Land Cover Mapping for the Greater Nahanni Ecosystem (Stow Ecology).
- Stow, D.A., Hope, A., McGuire, D., Verbyla, D., Gamon, J., Huemmrich, F., Houston, S., Racine, C., Sturm, M., Tape, K., et al. (2004). Remote sensing of vegetation and land-cover change in Arctic tundra ecosystems. *Remote Sensing of Environment* 89, 281–308.
- Strong, W.L. (2004). Secondary vegetation and floristic succession within a boreal aspen (*Populus tremuloides* Michx.) clearcut. *Canadian Journal of Botany* 82, 1576–1585.
- Sturm, M., Racine, C., and Tape, K. (2001a). Increasing shrub abundance in the Arctic. *Nature* 411, 546–547.
- Sturm, M., Holmgren, J., McFadden, J.P., Liston, G.E., Chapin III, F.S., and Racine, C.H. (2001b). Snow-shrub interactions in Arctic tundra: a hypothesis with climatic implications. *Journal of Climate* 14, 336–344.
- Sturm, M., Schimel, J., Michaelson, G., Welker, J.M., Oberbauer, S.F., Liston, G.E., Fahnestock, J., and Romanovsky, V. (2005a). Winter biological processes could help convert Arctic tundra to shrubland. *BioScience* 55, 17–26.
- Sturm, M., Douglas, T., Racine, C., and Liston, G.E. (2005b). Changing snow and shrub conditions affect albedo with global implications. *Journal of Geophysical Research* 110, G01004.
- Svoboda, J., and Henry, G.H.R. (1987). Succession in Marginal Arctic Environments. *Arctic and Alpine Research* 19, 373.
- Tape, K., Sturm, M., and Racine, C. (2006). The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. *Global Change Biology* 12, 686–702.
- Tape, K.D., Hallinger, M., Welker, J.M., and Ruess, R.W. (2012). Landscape heterogeneity of shrub expansion in Arctic Alaska. *Ecosystems* 15, 711–724.
- Taylor, A.E., Wang, K., Smith, S.L., Burgess, M.M., and Judge, A.S. (2006). Canadian Arctic Permafrost Observatories: Detecting contemporary climate change through inversion of subsurface temperature time series. *Journal of Geophysical Research: Solid Earth* 111, B02411.
- Thompson, R.J., and Visser, A.T. (2007). Selection, performance and economic evaluation of dust palliatives on surface mine haul roads. *South African Institute of Mining and Metallurgy* 107, 435.

Throop, J., Lewkowicz, A.G., Smith, S.L., and Burn, C.R. (2012). Climate and ground temperature relations at sites across the continuous and discontinuous permafrost zones, northern Canada. *Canadian Journal of Earth Sciences* 49, 865–876.

Thrush, S.F., Hewitt, J.E., Dayton, P.K., Coco, G., Lohrer, A.M., Norkko, A., Norkko, J., and Chiantore, M. (2009). Forecasting the limits of resilience: integrating empirical research with theory. *Proceedings of the Royal Society B: Biological Sciences* 276, 3209–3217.

Torre Jorgenson, M., Harden, J., Kanevskiy, M., O'Donnell, J., Wickland, K., Ewing, S., Manies, K., Zhuang, Q., Shur, Y., Striegl, R., et al. (2013). Reorganization of vegetation, hydrology and soil carbon after permafrost degradation across heterogeneous boreal landscapes. *Environmental Research Letters* 8, 035017.

Tscherko, D., Rustemeier, J., Richter, A., Wanek, W., and Kandeler, E. (2003). Functional diversity of the soil microflora in primary succession across two glacier forelands in the Central Alps. *European Journal of Soil Science* 54, 685–696.

Tunncliffe, J., Kokelj, S.V., and Burn, C.R. (2009). Geomorphic characterization of 'mega-slumps' in the Peel Plateau, NWT. In *Geohydro.*

Van Beynen, P., and Townsend, K. (2005). A Disturbance Index for Karst Environments. *Environmental Management* 36, 101–116.

Viereck, L.. (1983). The effects of fire in black spruce ecosystems of Alaska and Northern Canada. In *The Role of Fire in Northern Circumpolar Ecosystems*, R.. Wien, and D.A. MacLean, eds. (New York: John Wiley and Sons, Ltd.), pp. 201–220.

Viereck, L., Dyrness, C., Van Cleve, K., and Foote, M.J. (1983). Vegetation, soils, and forest productivity in selected forest types in interior Alaska. *Canadian Journal of Forest Research* 13, 703–720.

Vitt, D.H., Halsey, L.A., and Zoltai, S.C. (2000). The changing landscape of Canada's western boreal forest: the current dynamics of permafrost. *Canadian Journal of Forest Research* 30, 283–287.

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, 537–552.

Walker, D.A., and Everett, K.R. (1987). Road dust and its environmental impact on Alaskan taiga and tundra. *Arctic and Alpine Research* 19, 479–489.

Walker, D.A., and Walker, M.D. (1991). History and pattern of disturbance in Alaskan Arctic terrestrial ecosystems: a hierarchical approach to analysing landscape change. *Journal of Applied Ecology* 28, 244–276.

- Walker, D.A., Cate, D., Brown, J., and Racine, C. (1987). Disturbance and recovery of Arctic Alaskan tundra terrain. A review of recent investigations (Hanover, NH: US Army Corps of Engineers, Cold Regions Research and Engineering Laboratory).
- Walker, D.A., Jia, G.J., Epstein, H.E., Reynolds, M.K., Chapin III, F.S., Copass, C., Hinzman, L.D., Knudson, J.A., Maier, H.A., Michaelson, G.J., et al. (2003). Vegetation-soil-thaw-depth relationships along a low-arctic bioclimate gradient, Alaska: synthesis of information from the ATLAS studies. *Permafrost and Periglacial Processes* 14, 103–123.
- Walker, M.D., Wahren, C.H., Hollister, R.D., Henry, G.H.R., Ahlquist, L.E., Alatalo, J.M., Bret-Harte, M.S., Calef, M.P., Callaghan, T.V., Carroll, A.B., et al. (2006). Plant community responses to experimental warming across the tundra biome. *Proceedings of the National Academy of Sciences of the United States of America* 103, 1342–1346.
- Whinam, J., and Chilcott, N. (1999). Impacts of trampling on alpine environments in central Tasmania. *Journal of Environmental Management* 57, 205–220.
- Willard, B.E., and Marr, J.W. (1971). Recovery of alpine tundra under protection after damage by human activities in the rocky mountains of Colorado. *Biological Conservation* 3, 181–190.
- Williams, D., and Burn, C.R. (1996). Surficial characteristics associated with the occurrence of permafrost near Mayo, Central Yukon Territory, Canada. *Permafrost and Periglacial Processes* 7, 193–206.
- Williams, T.J., Quinton, W.L., and Baltzer, J.L. (2013). Linear disturbances on discontinuous permafrost: implications for thaw-induced changes to land cover and drainage patterns. *Environmental Research Letters* 8, 025006.
- Woo, M. (1986). Permafrost hydrology in North America. *Atmosphere-Ocean* 24, 201–234.
- Woo, M.-K., and Xia, Z. (1996). Effects of hydrology on the thermal conditions of the active layer. In *Nordic Hydrology*, (Nordic Association for Hydrology), pp. 129–142.
- Woo, M., Mollinga, M., and Smith, S.L. (2006). Simulating active layer thaw in a boreal environment. *Géographie physique et Quaternaire* 60, 9.
- Woo, M., Mollinga, M., and Smith, S.L. (2007). Climate warming and active layer thaw in the boreal and tundra environments of the Mackenzie Valley. *Canadian Journal of Earth Sciences* 44, 733–743.
- Wookey, P.A., Aerts, R., Bardgett, R.D., Baptist, F., Bråthen, K.A., Cornelissen, J.H.C., Gough, L., Hartley, I.P., Hopkins, D.W., Lavorel, S., et al. (2009). Ecosystem feedbacks and cascade processes: understanding their role in the responses of Arctic and alpine ecosystems to environmental change. *Global Change Biology* 15, 1153–1172.

Wright, T. (2009). Water and energy fluxes from a permafrost peat plateau: examining controls on runoff generation. PhD Thesis. Simon Fraser University.

Yoshikawa, K., Bolton, W.R., Romanovsky, V.E., Fukuda, M., and Hinzman, L.D. (2002). Impacts of wildfire on the permafrost in the boreal forests of Interior Alaska. *Journal of Geophysical Research* *108*, FFR – 4.

Zhang, T. (2005). Spatial and temporal variability in active layer thickness over the Russian Arctic drainage basin. *Journal of Geophysical Research* *110*, D16101.

Zhang, L., Dawes, W., and Walker, G. (2001). Response of mean annual evapotranspiration to vegetation changes at catchment scale. *Water Resources Research* *37*, 701–708.