Effects of Contemporary Winter Seismic Exploration on Low Arctic Plant Communities and Permafrost

J. Todd Kemper*†‡ and
S. Ellen Macdonald*

*Department of Renewable Resources, University of Alberta, Edmonton, Alberta, T6G 2H1, Canada
†Present address: Alberta Natural Heritage Information Centre, Alberta Tourism Parks and Recreation, 9820–106 Street, Edmonton, Alberta, T5K 2J6, Canada
‡Corresponding author: Todd.Kemper@gov.ab.ca

Abstract

We studied effects of oil and gas exploration, using the most recent seismic exploration technologies, on tundra plant communities and soils in four vegetation types in the Low Arctic of western Canada, two to three years post-disturbance. For all four vegetation types, seismic lines had less vascular plant cover and more bare ground than adjacent "reference" tundra. For the two upland tundra vegetation types, mosses and lichens were less abundant on seismic lines than in reference plots. There were no apparent differences in organic layer thickness between seismic lines and reference areas, but active layer depth (at the time of sampling) was significantly greater on seismic lines for the upland tundra and one of the wetland vegetation types. Diversity and richness were lower, and community composition was different, on seismic lines (as compared to reference plots) in upland tundra vegetation types but not in wetland types. The results suggest that (1) upland vegetation types are less resistant to seismic disturbance, (2) active layer depth increases following seismic disturbance, and (3) impacts from modern seismic techniques in upland tundra are similar to, or somewhat greater than, the initial impacts observed from the earliest phases of winter exploration ~30 years ago.

Introduction

The exploration for, and development of, buried petroleum resources is one of the largest sources of anthropogenic disturbance across the circumpolar Arctic (Forbes, 1997; Forbes et al., 2001). To date the most extensive type of disturbance associated with petrochemical exploration in the western Canadian Arctic has been 2-dimensional (2D) winter seismic exploration, in which heavy vehicles are driven single-file across the tundra in winter months. The largest available body of knowledge concerning winter seismic impacts comes from a suite of publications that followed a two-winter (January–May, 1984 and 1985) seismic program in Alaska, documenting impacts and recovery through a decade thereafter (Felix and Raynolds, 1989a; Felix et al., 1992; Emers et al., 1995; Emers and Jorgenson, 1997). The most recent published accounts for low-arctic Canada report on the short-term impacts of exploration that occurred in the late 1960s and 1970s (e.g. Bliss and Wein, 1972; Kerfoot, 1972a, 1972b; Hernandez, 1973).

Impacts to vegetation from seismic exploration programs are primarily related to off-road vehicle travel and include mechanical damage/mortality of plants (Hernandez, 1973; Felix and Raynolds, 1989a), compression of live or standing dead vegetation (Hernandez, 1973; Rickard and Brown, 1974), damage to/compression of the soil organic layer (Felix and Raynolds, 1989a), melting of permafrost (Bliss and Wein, 1972; Felix et al., 1992), and, potentially, rutting of trails and subsequent changes in drainage (Chapin and Shaver, 1981; Forbes et al., 2001). Vegetation types are expected to show varying responses to such disturbance as a function of: pre-disturbance floristic composition and vegetation stature (Felix and Raynolds, 1989a; Forbes et al., 2001); soil moisture (Webber and Ives, 1978; Forbes et al., 2001);

terrain topography and microtopography (Hernandez, 1973; Raynolds and Felix, 1989); and the intensity of the disturbance (Walker et al., 1987; Emers et al., 1995). Communities composed of fast-growing, rhizomatous species could be expected to quickly recolonize the narrow swaths disturbed by seismic exploration (Fahrig et al., 1994; Kotanen, 1997; Forbes and Jeffries, 1999), while those with species dependant on seed dispersal and germination are likely to require longer periods for recovery (Cargill and Chapin, 1987; Emers et al., 1995). If the disturbance is severe enough to change underlying resource gradients, a return to the pre-disturbance vegetation type may not be possible (Walker et al., 1987; Forbes et al., 2001). In arctic tundra ecosystems, disturbances that affect the permafrost have the potential to dramatically alter soil moisture, which is an important determinant of plant community composition and productivity (Truett and Kertell, 1992).

In the Low Arctic of Canada, particularly in the Mackenzie Delta area, there has been a recent resurgence in exploration activities, which is expected to continue to increase into the foreseeable future. Modern seismic exploration programs differ from those of previous exploration periods in several ways, including: the types of vehicles used; the primary energy source used (vibration vs. dynamite); operational procedures (clearing trails with bulldozers vs. "walking down" vegetation); and environmental technologies (e.g., low pressure tires). Many, or most, of these changes have been introduced specifically to minimize environmental impacts, yet published, peer-reviewed investigations of their efficacy are currently unavailable. Although impacts of seismic exploration disturbance may be reduced through the above-mentioned environmental technologies and operating procedures, the potential for effects to accumulate through space and time is of considerable concern to land

managers (Abele et al., 1984; Walker, 1996; National Research Council, 2003).

The objectives of this study were to: (1) document the effects of modern 2D winter seismic exploration activity on low-arctic vegetation types and permafrost; and (2) compare tundra vegetation types in terms of their resistance (susceptibility to impact) and short-term (two to three growing seasons) resilience (ability to recover from impact) to seismic disturbance.

Material and Methods

STUDY AREA AND SITE SELECTION

The study area was centered on the Kendall Island Bird Sanctuary, Northwest Territories, Canada, and also included adjacent islands of the Mackenzie Delta and upland terrain on Richards Island (~69°00 to 69°24′N, 135°35′ to 134°05′W). The area sits atop two major natural gas deposits and has been explored for oil and gas since 1965. The study area is entirely north of latitudinal treeline, and is within the Tuktoyaktuk Coastlands division of the Arctic Coastal Plain physiographic region of Canada (Rampton, 1988).

Sampling took place during the growing seasons (July and August) of 2002 and 2003. We chose sample sites using a map of 2D seismic programs that are registered with the National Energy Board of Canada. For this study we focused on seismic lines that were in the second or third growing season post-disturbance. We sampled in a total of one hundred seventy-eight 1 m^2 quadrats at 28 sample sites distributed throughout the region and selected to equally represent several broad "habitat types" (upland tundra, sedge/willow tundra, and polygonal tundra) that were initially delineated using Landsat TM imagery. Quadrats were located in a paired design wherein one was placed on a seismic line and the other was situated ~50 m away in "reference" tundra of a similar vegetation type. Pairs within a site were separated from one another by >50 m, and each pair was considered to be an independent "block" (including one quadrat each for the "seismic" and "reference" treatments). There were 89 such blocks in total.

Because disturbance response is known to vary among plant community types (at a finer grain than the broad "habitat types" that could be discerned from Landsat imagery) we grouped the blocks by vegetation type. This was accomplished by a Hierarchical Agglomerative clustering analysis of vascular species composition data from the reference quadrats. Four distinct plant vegetation types were found two upland (referred to here as the "Medium Shrub–Heath type" and "Low Shrub–Heath type"), and two wetland/riparian (referred to here as the "Wet Graminoid type" and "Tall Shrub–Herb type"). The Medium Shrub–Heath and Low Shrub–Heath types were dominated by ericaceous and/or deciduous shrubs, with relatively diverse herbaceous vegetation consisting of forbs, sedges, and grasses. The Wet Graminoid type was dominated almost entirely by sedges (*Carex* sp. and *Eriophorum* sp.) along with prostrate willow species. The Tall Shrub–Herb vegetation type occurred largely along channels and backwaters in the delta and was dominated by relatively tall (>1.5 m) deciduous shrubs (primarily *Salix lanata* ssp. *richardsonii*), with *Equisetum* sp., and wetland sedges dominating the herbaceous layer. Further details of these are available in Kemper (2005). A complete species list is found in the Appendix.

The final breakdown of sites and quadrats following the cluster analysis was as follows: 6 sites (40 quadrats) in the Medium Shrub–Heath (MSH) vegetation type, 3 sites (10 quadrats) in the Low Shrub–Heath (LSH) vegetation type, 12 Sites (56 quadrats) in the Tall Shrub–Herb (TSH) vegetation type, and 9 sites (72 quadrats) in the Wet Graminoid (WG) vegetation type.

SAMPLING

Within each quadrat we estimated the cover of all living vascular plants by species, total cover of lichens, total cover of mosses, and total "cover" of bare ground. Visual estimates of cover were made to within 1% from 1 to 10% cover, to within 5% from 11 to 40% cover, and to within 10% for cover > 40%. Bare ground included exposed organic or mineral soils as well as areas where the predominant ground cover (mosses) appeared dead such that open sites, available for colonization, were present. In wetland areas the "bare ground" designation also included standing water that was devoid of emergent vegetation. Nomenclature is as per Porsild and Cody (1980).

The depth of the soil organic layer was measured by cutting two shallow trenches immediately outside each quadrat at opposite corners, and measuring the distance from the ground surface to the mineral horizon or to permafrost. Thaw depth (active layer depth at time of sampling) was measured by pushing a stainless steel probe into the soil at four points along a diagonal transect across each quadrat until permafrost was reached. The depth of penetration was marked on the probe, and measured after removal.

STATISTICAL ANALYSIS

Because of low sample size the two upland vegetation types (Medium Shrub–Heath and Low Shrub–Heath) were grouped for analysis. Analyses were performed separately for the TSH and WG vegetation types. Richness of vascular plants was calculated as the total number of species occurring within each quadrat. Species diversity of vascular plants per quadrat was calculated using the Shannon Index (H'), and evenness per quadrat was calculated using Shannon's Equitability Index (E_H).

Effects of seismic exploration were assessed using mixed linear models (PROC MIXED in SAS v.8.02; Littell et al., 1996). Prior to analysis each variable was tested for normality and homogeneity of variance. Where moderate to strong departures from normality existed, and wherever heterogeneity of variance was encountered, suitable transformations were applied. For each mixed linear model "site" and "block" (paired seismic-reference quadrats nested within site) were considered random effects and treatment (seismic vs. reference) the fixed effect. Two models were tested, one including the treatment * site interaction term (Equation 1), and one without it (Equation 2). The basic equations for these models were:

$$Y_{ijkl} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + \gamma_k(j) + \varepsilon_{ijkl} \qquad (1)$$

$$Y_{ijkl} = \mu + \alpha_i + \beta_j + \gamma_k(j) + \varepsilon_{ijkl} \qquad (2)$$

where Y_{ijkl} is the dependant variable, μ is the overall mean, α_i is the fixed effect of treatment level i, β_j is the random effect of site j, $(\alpha\beta)_{ij}$ is the random effect of interaction between treatment and site, $\gamma_{k(j)}$ is the random effect of sample unit k within site j, and ε_{ijkl} is the residual error.

Of these, the model which provided the lowest value of Akaike's Information Criterion (AIC) was chosen for the test of the treatment (fixed) effect. Denominator degrees of freedom were calculated using the Kenward Roger method (Kenward and Roger, 1997), which inflates the variance/covariance matrix of fixed and random effects and then performs a Satterthwaite

denominator degrees of freedom calculation to produce a more accurate F test for small sample sizes.

In some instances the assumption of homoscedasticity could not be met because the variance among quadrats on seismic lines exceeded the variance of controls by several orders of magnitude. In these instances the data were tested by applying a Wilcoxon–Signed Rank test on the paired difference between seismic and reference quadrats of each block.

To detect differences in vascular plant composition between seismic lines and reference quadrats we used Non-metric Multidimensional Scaling (NMS), and Multi Response Permutation Procedures (MRPP). Both analyses were performed using percent cover data (untransformed) for all vascular plant species that occurred in >5% of quadrats within a vegetation type. For the three vegetation type groupings we used NMS to ordinate quadrats in species space using Sørensen (Bray-Curtis) distance as the community resemblance measure. Before performing the ordinations each distance matrix was screened for outliers. For each ordination, preliminary runs on the data were performed using the "NMS Autopilot–slow and thorough" function of PC-ORD v. 4.25 (McCune and Mefford, 1999), to assess the dimensionality of the data, and select an optimum dimensionality and starting configuration for the final ordinations. The final ordinations were performed with no step-down in dimensionality, 500 iterations, and with 999 Monte-Carlo permutations to assess the significance of the reduction in stress of the final solution. The final solution was not subjected to rotation.

MRPP were used to complement the ordinations by providing a statistical test of species composition differences between seismic lines and reference tundra. To maximize compatibility with the NMS ordinations the distance matrices used in the MRPP analyses were created using Sørensen distance and were rank transformed prior to analysis (McCune et al., 2000). To calculate δ, the average within group distance was weighted by n/sum(n), the default procedure in PC-ORD (McCune and Mefford, 1999).

Finally, we used Indicator Species Analysis (Dufrêne and Legendre, 1997) to determine whether any species were strongly negatively or positively associated with seismic lines. Treatment (seismic vs. reference) was used as the grouping variable, and 999 Monte-Carlo permutations were used to test for significance of the calculated indicator values.

Results

PLANT COVER AND BARE GROUND

Vascular plant cover was significantly lower on seismic lines than in reference tundra for all vegetation types (Table 1). The magnitude of this effect was greatest in the upland vegetation types (Medium Shrub–Heath and Low Shrub–Heath combined; MSH/LSH), where vascular plant cover was reduced by 59.5% ± 13.8 (95% CL) on average. The Tall Shrub–Herb vegetation type had the second largest difference, with seismic lines having, on average, 27% less cover than in reference quadrats. The smallest effect on vegetation cover was seen in the Wet Graminoid type, where seismic lines had 18% less vascular plant cover than reference tundra.

In the upland (MSH/LSH) vegetation types, moss cover on seismic lines was significantly less than in reference tundra with a mean difference of 17.10% less cover along seismic lines (Table 1). For the Tall Shrub–Herb and Wet Graminoid vegetation types there were no significant differences in moss cover between seismic lines and reference tundra (Wilcoxon Signed Rank test). Lichens were only present in the upland vegetation types, where their cover was significantly reduced along seismic lines, with an average decrease of 5% cover, from 12% total cover in reference tundra to 7% total cover along seismic lines.

The decrease in plant cover on seismic lines coincided with significant increases in cover of bare ground for each vegetation type. The Wet Graminoid vegetation type experienced the smallest increase in bare ground with a median increase of only 2% cover followed by the Tall Shrub–Herb sites with a median increase of 4% cover. The Medium Shrub–Heath and Low Shrub–Heath communities experienced the largest median increase in bare ground cover at 20%.

THAW DEPTH AND ORGANIC LAYER DEPTH

Thaw depth was significantly greater (deeper) on seismic lines in the Medium Shrub–Heath/Low Shrub–Heath and the Wet Graminoid vegetation types, but not significantly different from reference tundra in the Tall Shrub–Herb type (Table 1). Again, the magnitude of the effect was greatest in the MSH/LSH vegetation types, where thaw depth increase on seismic lines averaged 6.6 cm and least in the WG vegetation type, averaging 2.4 cm. In the TSH vegetation type the variability in thaw depth response was much greater than for the other communities, and there was no significant difference between seismic lines and reference tundra. No significant differences in organic layer depth were observed between seismic lines and reference tundra for any of the vegetation types (Table 1).

VASCULAR PLANT COMMUNITIES

There was a significant decrease in vascular plant species richness along seismic lines in the Medium Shrub–Heath/Low Shrub–Heath vegetation type, but no differences in the other vegetation types (Table 1). In the MSH/LSH vegetation type quadrats on seismic lines had on average 1.88 fewer species than controls; mean species richness for control quadrats in this vegetation type was 11.32 species. Mean species richness for reference tundra in the Tall Shrub–Herb vegetation type was 5.91 species/quadrat, while that of undisturbed Wet Graminoid tundra was 4.13 species/quadrat.

Shannon Index diversity (vascular plants only) was significantly lower on seismic lines than in reference tundra for the MSH/LSH vegetation type ($F_{1,40.1} = 3.67$, $p = 0.0623$). In the Tall Shrub–Herb (TSH) vegetation type Shannon Index values were significantly higher on seismic lines than in reference quadrats ($F_{1,41.8} = 5.61$, $p = 0.0221$). No significant difference in vascular plant diversity was found between seismic lines and reference tundra in the Wet Graminoid (WG) vegetation type. Equitability (E_H) of vascular plant communities along seismic lines was not significantly different from that of reference tundra in the MSH/LSH ($F_{1,41} = 0.41$, $p = 0.5273$) and WG ($F_{1,33} = 0.01$, $p = 0.9178$) vegetation types, but was significantly higher along seismic lines than in reference communities for the TSH vegetation type ($F_{1,43.9} = 9.07$, $p = 0.0043$). Mean equitability (E_H value) for seismic line communities in the TSH type was 0.6552 ± 0.03621 (SE), as compared to 0.5719 ± 0.03621 for reference communities.

For the Non-metric Multidimensional Scaling (NMS) ordination of quadrats from the MSH and LSH communities a three-dimensional solution produced the strongest reduction in stress ($p = 0.001$) over randomized data and was selected for the final ordination. The first three axes explained 83.4% of variation in the species data, with the most variation explained by axes 1 and 3

TABLE 1

Mean (or median[†]) paired difference (seismic–reference) for vegetation, soil, and permafrost properties. Except where indicated, treatment effects were tested via mixed linear models, with a null hypothesis of no difference between seismic and reference values.

	Medium Shrub-Heath/Low Shrub-Heath					Tall Shrub-Herb					Wet Graminoid				
	diff	95%CI	df	F (or S[†])	P	diff	95%CI	df	F (or S[†])	P	diff	95%CI	df	F (or S[†])	P
Total Vascular Cover (%)	−59.5	13.8	1,37	75.91	<0.0001	−26.9	12.71	1,24	19.02	2E–04	−18.36	6.751	1,35	30.49	<0.0001
Total Moss Cover (%)	−17.1	12.683	1,7.95	9.69	0.015	−2.37[†]	—	—	24	0.478	−4.02[†]	—	—	51[†]	0.302
Total Bare Ground (%)	20[†]	—	—	−105[†]	<0.0001	4[†]	—	—	−119[†]	1E–04	2[†]	—	—	−98.5[†]	0.03
Shannon Index (H′)	−0.162	0.1704	1,40.8	3.67	0.062	0.16	0.1362	1,41.8	5.65	0.022	−0.062	0.132	1,35	0.91	0.346
Species Richness m^{-2}	−1.88	1.1546	1,40.1	10.83	0.002	0.21*	0.7635	1,26.8	0.32	0.574	−0.25	0.659	1,35	0.59	0.446
Organic Layer Thickness (mm)	−3.24	18.966	1,41	0.12	0.732	13.17	38.74	1,18.9	0.51	0.485	4.3889	25.83	1,26	0.12	0.728
Thaw Depth (cm)	6.61*	3.27	1,24	24.36	<0.0001	3.03	11.44	1,10.1	0.35	0.569	2.37*	2.22	1,35	4.36	0.044

[†] Median paired difference: data were tested via Wilcoxon-Signed Rank test (S), testing a null hypothesis of a median difference of zero.

* Data were log- or ln-transformed prior to testing: means and 95%CIs calculated from back-transformed data.

(31.0 and 27.8%, respectively). Quadrats from seismic lines tended to separate from the control quadrats primarily along axis 1, indicating differences in community composition (Figs. 1a and 1b). The final stress for the ordination was 13.74, and final instability 0.0001.

The Multi Response Permutation Procedures (MRPP) test for the upland vegetation types supported the ordination results, revealing significant differences in species composition between seismic lines and reference tundra ($A = 0.059597$, $p = 0.0008$) in these vegetation types. The Indicator Species Analysis (ISA) revealed three species that were negatively associated with quadrats on seismic lines in the upland vegetation types: *Betula glandulosa*, *Vaccinium vitis-idaea*, and *Pyrola grandiflora* (Table 2). *Betula glandulosa* and *Vaccinium vitis-idaea* both had reduced cover on seismic lines, but only slightly reduced quadrat frequency as compared to controls. *Pyrola grandiflora* was present in almost half of the control quadrats but present in only one seismic line quadrat.

The NMS ordination of quadrats from the TSH type sites also revealed a three-dimensional solution. The three axes of the

final ordination explained 85.4% of variation in the species data, with axes 2 and 3 explaining the most variation (44.7 and 23.2%, respectively). There did not appear to be a separation of quadrats from seismic lines and controls along any axis (Figs. 1c and 1d). Final stress for the solution was 11.53; the instability criterion of 10^{-4}, however, was not met within 500 iterations (final instability = 0.00018).

The MRPP test also failed to detect significant differences in species composition between seismic lines and reference tundra in this vegetation type ($A = 0.014832$, $p = 0.1211$), and no species had either a negative or positive associations with seismic lines in the ISA (Table 2).

For the NMS ordination of quadrats from the Wet Graminoid type (WG) community a three-dimensional solution again provided the best reduction in stress over randomized data ($p = 0.001$) and was used for the final ordination. The three axes in the solution explained 85.4% of the variance in the species data, with axis 1 explaining the greatest portion (54.0%). There was no discernable separation between quadrats from seismic lines and

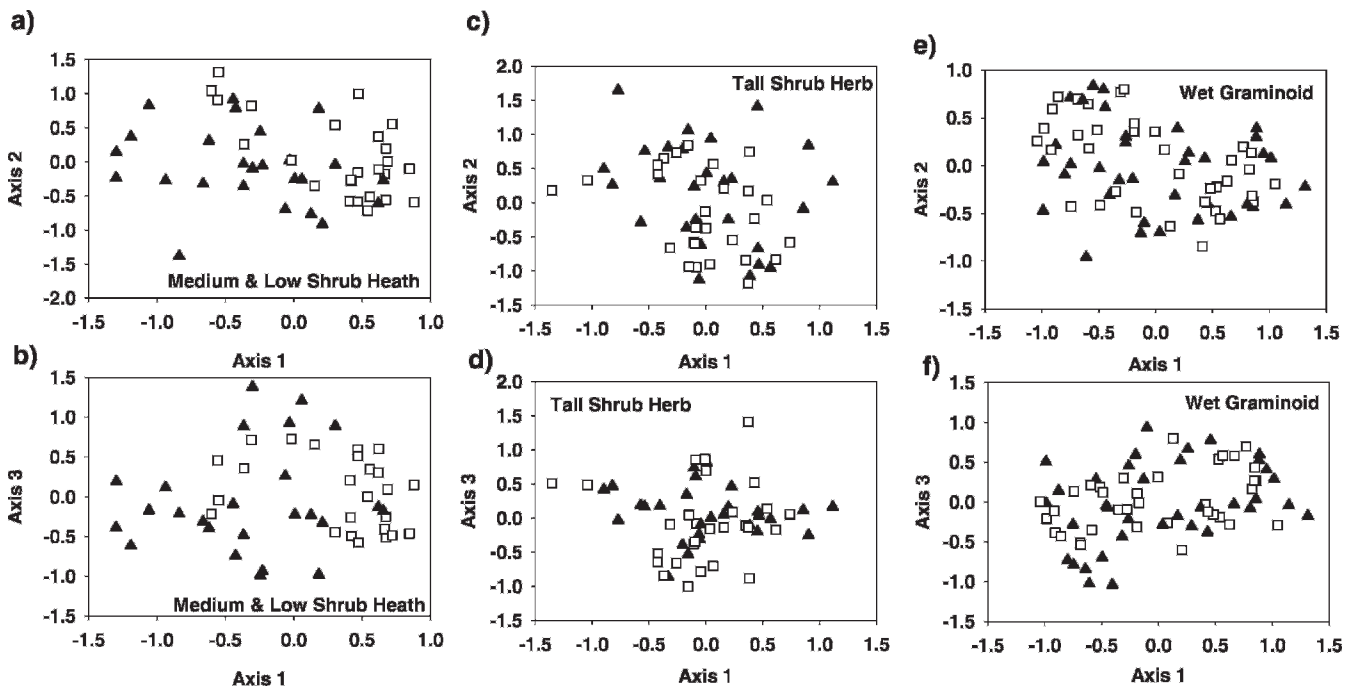
FIGURE 1. Results of Non-metric Multidimensional Scaling ordination showing the locations of quadrats in species space for (a) and (b) Medium Shrub–Heath/Low Shrub–Heath type communities, (c) and (d) Tall Shrub–Herb type communities, and (e) and (f) Wet Graminoid type communities. Closed triangles represent quadrats from seismic lines, open squares represent quadrats from reference tundra.

TABLE 2

Results of Indicator Species Analysis for quadrats on seismic lines (seismic) and in reference tundra for the Medium Shrub Heath/Low Shrub Heath (MSH/LSH), Tall Shrub Herb (TSH), and the Wet Graminoid (WG) vegetation types. Cover= average % cover (when present), Freq = quadrat frequency, IV = Indicator value, P = significance of IV.

Vegetation type	Indicator Species	Cover (reference)	Cover (seismic)	Freq. (reference)	Freq. (seismic)	IV	P
MSH/LSH	*Betula glandulosa*	17.6%	6.3%	0.88	0.80	65.8	0.024
	Vaccinium vitis-idaea	21.3%	6.3%	0.88	0.80	64.1	0.008
	Pyrola grandiflora	1.8%	0.5%	0.40	0.04	36.0	0.003
TSH	None	—	—	—	—	—	—
WG	None	—	—	—	—	—	—

reference tundra in the ordination space (Figs. 1e and 1f). Final stress for the solution was 12.22; the instability criterion of 10^{-4}, however, was not met within 500 iterations (final instability = 0.0027).

The MRPP test corroborated the ordination results, revealing no significant differences in species composition between seismic lines and reference tundra in the WG vegetation type ($A = -0.00216$, $p = 0.4617$). The Indicator Species Analysis also did not detect any species with significant associations (either positive or negative) with seismic lines in the WG sites (Table 2).

Discussion

The most prominent effect of recent winter seismic exploration in all vegetation types was a modest but significant decrease in living plant cover and increase in the amount of bare ground. The removal of vegetation and exposure of darker organic or mineral soils resulted in a prominent visible disturbance at most sites that persisted at least two to three growing seasons post-disturbance. These effects were accompanied by significant increases in thaw depth, although there were no effects on organic layer depth. Disturbances that alter the thermal equilibrium of soils can affect permafrost stability and increase soil moisture, potentially altering the species composition of recovering sites (Billings, 1973; Walker et al., 1987; Walker and Walker, 1991; Shirazi et al., 1998). Likely both direct vegetation damage and impacts on edaphic characteristics underlie the observed vegetation responses to seismic exploration activities.

RELATIVE RESISTANCE AND RESILIENCE OF PLANT COMMUNITIES

Vegetation types clearly differed in their resistance to winter seismic disturbance. Impacts appeared to be greatest in the upland vegetation types (Medium Shrub–Heath and Low Shrub–Heath), were somewhat less in the Tall Shrub–Herb type, and were least in the Wet Graminoid type. Reports of impacts following previous exploration periods have also suggested that upland vegetation types are the least resistant to disturbance by winter seismic exploration activities (Bliss and Wein, 1972; Hernandez, 1973). Compared to other vegetation types in this study, seismic lines in the upland communities experienced the greatest decrease in vascular plant and moss cover; the greatest increase in bare ground cover and thaw depth; reductions in lichen cover, vascular plant species richness, and diversity; and significant differences in species composition. In the Tall Shrub–Herb vegetation type there was a significant reduction in total vascular plants cover accompanied by increased cover of bare ground, but diversity of vascular plants was greater on seismic lines than in reference tundra. Effects in the Wet Graminoid vegetation type were limited to decreases in vascular plant cover and increased cover of bare ground.

The apparent resistance of the Wet Graminoid vegetation type probably relates to several factors. The flat topography of these areas facilitates travel, with less potential for ground disturbance due to vehicles losing traction or churning up slopes (Hernandez, 1973). The saturated soils of these communities should also provide a very hard frozen platform for vehicle travel, which may reduce impacts to below-ground biomass. The Wet Graminoid vegetation type may also have inherently greater short-term resilience to winter vehicle disturbance; even in instances where the above-ground biomass is damaged or removed, the underground rhizomes probably remain intact, allowing for relatively rapid recolonization. Bliss and Wein (1972) reported that the rhizome mass of both *Carex aquatilis* and *Eriophorum angustifolium* survived two years of winter road travel in similar wetlands, and that revegetation was relatively rapid thereafter. Compression of vegetation into contact with the soil in wet low-arctic soils, which have higher nutrient turnover rates than do soils of drier upland sites (Ebersole, 1987; Chapin et al., 1988), may provide a nutrient flush that facilitates rapid revegetation (Rickard and Brown, 1974). The rhizomatous sedges that dominate these communities (*Eriophorum angustifolium*, *Carex aquatilis*) are well adapted to rapidly revegetate narrow seismic lines from the edge inwards. These communities are typically found in low-lying positions, often in close proximity to the Beaufort Sea coast or to major stream channels, and are likely subject to high frequencies of natural disturbance through flooding, ice scouring, and driftwood deposition. They may, therefore, be adapted for rapid recovery following disturbance.

In the Tall Shrub–Herb vegetation type the decrease in vascular plant cover was primarily due to effects on the dominant upright shrub species, with underlying herbaceous plants and prostrate shrubs being relatively unaffected. Similar reductions in cover of dominant shrub species following winter seismic in riparian areas have been reported from Alaska's north slope (Felix and Raynolds, 1989a). Given the height of these shrubs, large portions likely remain above the snow level in winter and could be damaged/broken off by vehicle passage. Reduced dominance of these shrub species, with a concomitant increase in evenness, led to the higher Shannon Index and Equitability Index values measured on seismic lines. No new species were observed colonizing these sites. Although the decrease in vascular (shrub) cover was relatively large, the relatively small increase in the amount of bare ground likely provided little opportunity for new colonists or for substantive changes in relative abundances. Thus, there were no significant impacts of seismic exploration on community composition in the Tall Shrub–Herb communities. The relatively small increase in cover of bare ground on seismic lines in the TSH vegetation type may also play a role in the apparent lack of seismic effects on thaw depth in these communities. Variability in thaw

depth was much greater in the TSH than in other vegetation types. The TSH vegetation type occurs close to the relatively warm, shallow waters of delta stream channels; this may have had a stronger influence on permafrost depth than insulation by vegetation or the organic layer.

The magnitude of the effects in upland tundra vegetation types (Medium Shrub–Heath and Low Shrub–Heath) was surprising, given recent technological changes aimed at reducing impacts of seismic exploration activity. The difference in vascular plant cover that we recorded between seismic lines and controls (59.5% lower on seismic lines) is higher than reported from other studies, including those from the very first period of winter seismic activities in this region. Hernandez (1973) reported vascular plant cover values for winter seismic lines (from 1967 to 1971) that ranged from 32.9 to 44.3% lower than cover at adjacent controls. Bliss and Wein (1972) similarly reported total plant cover values that were 34% lower on winter seismic lines than controls (87.1% vs. 121.2%, respectively). Both of these studies involved upland shrub–heath vegetation in the same general area as our present research, and should be directly comparable. If the results presented here are representative of the situation elsewhere, then it would appear that the intended improvements in technology and/or technique have had an unintended negative consequence. One intriguing possibility is that the high impacts we observed could indicate that vehicles used for Vibroseis cause more damage than do those used in drilled dynamite programs; most of the seismic lines we surveyed had used Vibroseis (though at least one was shot using dynamite) while the older studies (Bliss and Wein, 1972; Hernandez, 1973) were of lines on which dynamite was used exclusively. Raynolds and Felix (1989) noted that seismic surveys that used vibration as the energy source appeared to cause more damage than surveys where drills and dynamite were used. As with our study, however, sample sizes were too small for them to test this observation.

The high percentage of bare ground in the upland tundra vegetation types indicates an abundance of open sites that had yet to be occupied by colonizing or regenerating species. The difference in species composition between seismic lines and reference tundra in these communities suggests either the presence of particularly sensitive species in these communities, or an influx of colonizers from outside the range of normal community assemblage. The ISA results support the former conclusion. All three species determined to be negatively associated with seismic lines in this study have been reported to be particularly sensitive to winter seismic in other studies (Hernandez, 1973; Felix and Raynolds, 1989a). These species, along with several others that were not significant indicators but did have significantly lower cover or frequency on seismic lines (e.g., *Ledum decumbens*, *Empetrum nigrum*, *Cassiope tetragona*), are likely not true "indicators" of undisturbed conditions but rather are species incapable of recovering from disturbance within the period of this study. The result determining *Pyrola grandiflora* as a significant "indicator" of undisturbed tundra is somewhat surprising given the modest reduction in average cover, and is likely driven by the dramatic decrease in frequency of this species within seismic line quadrats.

The standing vegetation crop (Walker et al., 2003) and soil organic mat (Haag and Bliss, 1974; Hinzman et al., 1996) are important insulators of permafrost. The removal of vegetation and exposure of darker colored substrates presumably altered the energy budget of sites on seismic lines (Haag and Bliss, 1974) and led to the measured increases in thaw depth. Permafrost degradation results in increases in available rooting volume and can also lead to increased soil moisture (Hinzman et al., 1996) and

release of soluble cations, notably Na^+, into the soil solution (Kokelj et al., 2002). Species-specific responses to these changes would translate into changes in community composition (Chapin and Shaver, 1981; Felix et al., 1992; McKane et al., 2002). Disturbances to the soil organic layer also have the potential to exert direct effects on plant community development, as this layer contains both the soil seed bank and underground rhizome mass upon which revegetation depends (McGraw, 1980; Gartner et al., 1983; Ebersole, 1989). Topography (Hernandez, 1973; Raynolds and Felix, 1989) and snow depth (Felix and Raynolds, 1989b) have also been identified as important determinants of the extent of damage from winter seismic. Because of their high topographic position and relief, the upland vegetation types would likely experience a greater degree of wind scouring and a subsequent decrease in snow depth. This may also help explain their sensitivity to seismic exploration activities.

It is unclear how long the observed disturbances to the soil thermal regime will persist. Abele et al. (1984) reported initial recovery of thaw depth (the point at which thaw depth began to decrease below vehicle tracks) within 2 to 3 years; sites with the most disturbed thermal regimes recovered natural thaw depths within 10 years. However, the two study sites used by Abele et al. (1984) were flat (a drained lake basin and a uniform area of weakly polygonal ground) sedge-dominated tundra, and their results are likely not applicable to other community types or locations. Other studies have reported that thaw depths on seismic lines continued to increase over time (Felix et al., 1992) with some impacts lasting eight years or more with no sign of recovery (Emers et al., 1995). Because tundra ecosystems are underlain by permafrost and are incompletely drained, even small changes in microtopography can dramatically change soil moisture gradients (Peterson and Billings, 1980), with potentially long-term effects.

One of the core concepts of arctic disturbance ecology is that, while the degree of disturbance depends on the type and severity of impact, natural recovery is slow (Rickard and Brown, 1974; Reynolds and Tenhunen, 1996). If the results reported here are typical of the response of upland plant communities, it seems likely that the effects of seismic programs which are, individually, small will accumulate through time in upland areas as exploration activities continue. If we are to understand and reduce such effects, seismic programs must be sufficiently documented (location, type of survey, snow depth, vehicles used) and their impacts monitored (vegetation cover/composition) over the long term. If cumulative effects management is to be effective, this information needs to be compiled in a single location and available to all stakeholders.

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APPENDIX

Complete list of species found in the study along with the mean paired difference (seismic line minus reference) and the mean cover value on seismic lines and in reference tundra for each of the four vegetation types studied.

	Medium Shrub Heath			Low Shrub Heath			Tall Shrub Herb			Wet Graminoid Tundra		
	Paired diff.	Line Mean	Control Mean	Paired diff.	Line Mean	Control Mean	Paired diff.	Line Mean	Control Mean	Paired diff.	Line Mean	Control Mean
Equisetaceae												
Equisetum arvense L.	—	—	—	—	—	—	0.63	10.96	10.34	1.44	1.76	0.32
Equisetum scirpoides Michx.	—	—	—	—	—	—	−1.96	1.07	3.04	—	—	—
Equisetum variegatum Schleich.	—	—	—	—	—	—	−9.95	6.36	16.30	−1.56	5.53	7.08
Gramineae												
Arctagrostis latifolia (R.Br.) Griseb. ssp. *latifolia*	0.18	0.48	0.30	0.06	0.56	0.50	0.14	0.23	0.09	−0.01	0.00	0.01
Calamagrostis canadensis (Michx.) Beauv.	0.10	0.10	0.00	—	—	—	—	—	—	—	—	—
Calamagrostis neglecta (Ehrh.) Gaertn., Mey. and Schreb.	0.20	0.25	0.05	—	—	—	—	—	—	0.33	0.33	0.00
Dupontia fisheri R. Br.	—	—	—	—	—	—	0.11	0.11	0.00	0.00	0.54	0.54
Festuca rubra L. ssp. *richardsonii* (Hook) Hultén	—	—	—	—	—	—	0.75	0.93	0.18	—	—	—
Hierochloë alpina (Sw.) R. & S.	−0.18	0.03	0.20	—	—	—	—	—	—	—	—	—
Hierochloë pauciflora R. Br.	—	—	—	—	—	—	—	—	—	0.08	0.08	0.00
Poa arctica R. Br.	0.25	0.25	0.00	−0.06	0.00	0.06	—	—	—	—	—	—
Graminae sp.	0.13	0.20	0.08	—	—	—	−0.05	0.00	0.05	−0.72	0.44	1.17
Cyperaceae												
Carex aquatilis Wahlenb.	—	—	—	—	—	—	1.18	2.88	1.70	−5.47	20.81	26.28
Carex capillaris L. ssp. capillaris	—	—	—	—	—	—	—	—	—	0.06	0.06	0.00
Carex consimilis Holm	−3.30	3.70	7.00	0.50	5.13	4.63	−0.04	0.07	0.11	—	—	—
Carex podocarpa R. Br.	−0.75	0.00	0.75	—	—	—	—	—	—	—	—	—
Carex rariflora (Wahlenb.) Sm.	—	—	—	0.00	19.38	19.38	—	—	—	—	—	—
Carex rotundata Wahlenb.	—	—	—	2.94	3.19	0.25	−0.32	0.00	0.32	—	—	—
Carex scirpoidea Michx.	—	—	—	−0.88	0.00	0.88	—	—	—	—	—	—
Carex vaginata Tausch	0.10	0.10	0.00	−0.13	0.00	0.13	—	—	—	—	—	—
Eriophorum angustifolium Honck.	—	—	—	−1.13	0.00	1.13	0.38	1.34	0.96	−9.60	20.32	29.92
Eriophorum russeolum Fr.	—	—	—	−1.63	1.88	3.50	0.07	0.14	0.07	−0.21	0.79	1.00
Eriophorum vaginatum L.	0.45	9.50	9.05	−5.00	0.63	5.63	—	—	—	−0.17	0.00	0.17
Juncaceae												
Luzula nivalis (Laest.) Beurl.	—	—	—	—	—	—	—	—	—	0.42	0.42	0.00
Liliaceae												
Tofieldia pusilla (Michx.) Pers.	−0.03	0.00	0.03	−0.25	0.00	0.25	—	—	—	—	—	—
Orchidaceae												
Habenaria obtusata (Pursh) Richards.	—	—	—	—	—	—	0.00	0.04	0.04	—	—	—
Salicaceae												
Salix alaxensis (Anderss.) Cov.	—	—	—	—	—	—	−0.50	0.00	0.50	—	—	—
Salix arctica Pall. s. lat.	—	—	—	−0.88	0.38	1.25	−0.32	0.57	0.89	0.78	6.97	6.19
Salix arctophila Cockerell	—	—	—	—	—	—	0.46	0.46	0.00	0.47	0.64	0.17
Salix farriae Ball	—	—	—	—	—	—	0.13	0.14	0.02	0.11	0.11	0.00
Salix fuscescens Anderss.	—	—	—	0.63	0.63	0.00	—	—	—	—	—	—
Salix glauca L. s. lat.	−3.40	1.80	5.20	−1.13	3.13	4.25	0.11	0.50	0.39	—	—	—
Salix lanata L. ssp. richardsonii (Hook.) Skvortsov	—	—	—	−0.06	0.00	0.06	−11.32	28.82	40.14	−3.64	3.78	7.42
Salix ovalifolia Trautv. var. arcolitoralis (Hult.) Argus	—	—	—	—	—	—	−0.07	0.04	0.11	−0.03	0.00	0.03
Salix pulchra Cham.	−0.20	0.00	0.20	0.38	0.38	0.00	—	—	—	—	—	—
Salix reticulata L.	—	—	—	0.06	0.06	0.00	−0.09	0.02	0.11	—	—	—
Betulaceae												
Alnus crispa (Ait.) Pursh	−3.43	1.28	4.70	−2.38	0.88	3.25	−2.61	0.79	3.39	—	—	—
Betula glandulosa Michx.	−12.30	6.43	18.73	−1.63	2.25	3.88	—	—	—	—	—	—
Polygonaceae												
Polygonum viviparum L.	—	—	—	−0.06	0.00	0.06	0.21	0.55	0.34	−0.01	0.19	0.21
Caryophyllaceae												
Stellaria longipes Goldie s. str.	−0.03	0.08	0.10	−0.06	0.00	0.06	−0.02	0.00	0.02	—	—	—
Ranunculaceae												
Anemone parviflora Michx.	—	—	—	—	—	—	−0.04	0.02	0.05	—	—	—
Caltha palustris L. var. *arctica* (R.Br.) Huth.	—	—	—	—	—	—	−0.02	0.02	0.04	—	—	—
Ranunculus lapponicus L.	−0.15	0.00	0.15	—	—	—	—	—	—	—	—	—

	Medium Shrub Heath			Low Shrub Heath			Tall Shrub Herb			Wet Graminoid Tundra		
	Paired diff.	Line Mean	Control Mean	Paired diff.	Line Mean	Control Mean	Paired diff.	Line Mean	Control Mean	Paired diff.	Line Mean	Control Mean
Cruciferae												
Cardamine digitata Richards.	0.03	0.08	0.05	−0.06	0.00	0.06	—	—	—	—	—	—
Cardamine pratensis L. s. lat.	—	—	—	−0.19	0.00	0.19	—	—	—	−0.11	0.03	0.14
Saxifragaceae												
Parnassia palustris L.	—	—	—	—	—	—	−0.09	0.00	0.09	—	—	—
Rosaceae												
Dryas integrifolia M. Vahl	−0.13	0.03	0.15	−3.06	0.56	3.63	−0.07	0.05	0.13	—	—	—
Rubus chamaemorus L.	0.33	2.50	2.18	−0.13	0.31	0.44	—	—	—	—	—	—
Leguminosae												
Hedysarum alpinum L.	—	—	—	—	—	—	0.66	3.43	2.77	—	—	—
Lupinus arcticus Wats.	−0.80	0.20	1.00	0.06	0.13	0.06	—	—	—	—	—	—
Onagraceae												
Epilobium angustifolium L.	0.03	0.03	0.00	—	—	—	—	—	—	—	—	—
Empetraceae												
Empetrum nigrum L.	−9.33	3.03	12.35	0.00	0.13	0.13	—	—	—	—	—	—
Pyrolaceae												
Pyrola grandiflora Radius	−0.70	0.00	0.70	−0.50	0.06	0.56	−0.09	0.04	0.13	—	—	—
Orthilia secunda (L.) House	−0.10	0.03	0.13	−0.06	0.00	0.06	—	—	—	—	—	—
Ericaceae												
Andromeda polifolia L.	0.18	0.40	0.23	1.50	4.00	2.50	—	—	—	—	—	—
Arctostaphylos alpina (L.) Spreng.	−2.60	2.05	4.65	—	—	—	−0.07	0.00	0.07	—	—	—
Arctostaphylos rubra (Rehd. & Wils.) Fern.	0.80	0.80	0.00	−2.50	0.88	3.38	−3.61	0.91	4.52	—	—	—
Cassiope tetragona (L.) D.Don	−1.90	0.45	2.35	−5.88	1.31	7.19	—	—	—	—	—	—
Ledum decumbens (Ait.) Lodd.	−9.78	7.53	17.30	−1.00	0.13	1.13	—	—	—	—	—	—
Rhododendron lapponicum (L.) Wahlenb.	—	—	—	−0.31	0.00	0.31	—	—	—	—	—	—
Vaccinium uliginosum L. s. lat.	−0.85	1.55	2.40	−5.00	7.13	12.13	—	—	—	—	—	—
Vaccinium vitis-idaea L. var. minus Lodd.	−17.05	6.13	23.18	0.00	0.56	0.56	—	—	—	—	—	—
Primulaceae												
Primula stricta Hornem.	—	—	—	—	—	—	−0.02	0.00	0.02	−0.01	0.00	0.01
Polemoniaceae												
Polemonium acutiflorum Willd.	—	—	—	—	—	—	0.02	0.02	0.00	—	—	—
Scrophulariaceae												
Castilleja elegans (Ostenf.) Malte	—	—	—	—	—	—	−0.07	0.02	0.09	0.03	0.03	0.00
Pedicularis arctica R. Br.	−0.03	0.00	0.03	−0.13	0.00	0.13	—	—	—	—	—	—
Pedicularis capitata Adams	0.05	0.18	0.13	−0.06	0.06	0.13	—	—	—	—	—	—
Pedicularis lanata Cham. & Schlecht.	−0.13	0.00	0.13	−0.25	0.00	0.25	—	—	—	−0.01	0.01	0.03
Pedicularis lapponica L.	−0.08	0.00	0.08	—	—	—	—	—	—	—	—	—
Pedicularis sudetica Willd.	—	—	—	0.38	0.38	0.00	0.02	0.25	0.23	0.03	0.54	0.51
Pedicularis verticillata L.	—	—	—	—	—	—	0.07	0.09	0.02	—	—	—
Lentibulariaceae												
Pinguicula villosa L.	0.03	0.03	0.00	—	—	—	—	—	—	—	—	—
Pinguicula vulgaris L.	−0.03	0.00	0.03	—	—	—	—	—	—	−0.56	0.00	0.56
Valerianaceae												
Valeriana capitata Pall.	—	—	—	—	—	—	0.00	0.04	0.04	—	—	—
Asteraceae												
Aster sibiricus L.	—	—	—	—	—	—	−0.16	0.02	0.18	—	—	—
Petasites frigidus (L.) Fries	0.33	1.33	1.00	−0.13	0.75	0.88	—	—	—	—	—	—
Saussurea angustifolia (Willd.) DC.	0.05	1.33	1.28	1.00	2.13	1.13	—	—	—	—	—	—
Senecio atropurpureus (Ledeb.) Fedtsch.	−0.18	0.03	0.20	−0.25	0.13	0.38	—	—	—	—	—	—
TOTAL COVER	−64.15	51.88	116.03	−27.00	57.31	84.31	−26.30	61.16	87.46	−18.36	63.39	81.75
MOSS COVER	−15.20	28.10	43.30	−14.88	45.63	60.50	−2.38	42.73	45.11	−4.03	48.74	52.76
LICHEN COVER	−8.28	9.35	17.63	1.38	10.50	9.13	—	—	—	0.01	0.01	0.00
BARE GROUND	25.10	25.25	0.15	17.38	18.38	1.00	9.54	17.25	7.71	6.08	17.06	10.97