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Recovery of Tundra Vegetation Three Decades after Hydrocarbon Drilling with and without Seeding of Non-Native Grasses

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ABSTRACT. Oil and gas exploration conducted in the 1970s left a legacy of abandoned test wells with sumps, containing drilling waste, in the Mackenzie Delta region of Canada's Northwest Territories. One to two years after the test wells were decommissioned, a set of sites were seeded with non-native grasses and fertilized to test whether these treatments could accelerate vegetation recovery and prevent erosion. We sampled seeded and unseeded sumps and adjacent tundra vegetation in the Mackenzie Delta region three decades later to examine the impact of post-disturbance seeding treatments on site recovery. Plant species composition and environmental data were collected at 12 sump sites (6 seeded and fertilized and 6 unseeded and unfertilized) in lowland and upland tundra. Multivariate analyses using NMDS and perMANOVA indicated that in the lowlands, seeding and fertilization treatments had small but significant effects on plant species composition that differentiated seeded from unseeded sump caps. Plant communities on sump caps for all treatment types were significantly different from surrounding undisturbed tundra, even after more than 30 years of recovery. Seeded non-native grasses were found on both seeded and unseeded sumps, but not in the surrounding undisturbed tundra. Undisturbed tundra appears resistant to the spread of introduced agronomic grasses, but disturbed areas, such as sumps, provide areas of suitable habitat where non-native plants can persist.

Key words: revegetation treatments; low Arctic tundra; plant invasion; oil and gas exploration; Kendall Island Bird Sanctuary; long-term monitoring

RÉSUMÉ. L'exploration pétrolière et gazière effectuée dans les années 1970 a laissé des puits abandonnés et des bassins à boue contenant des résidus de forage dans la région du delta du Mackenzie, dans les Territoires du Nord-Ouest au Canada. Un à deux ans après que les puits ont été mis hors service, un ensemble de sites a été fertilisé et ensemencé avec des graminées non indigènes afin de vérifier si ces traitements pouvaient accélérer le rétablissement de la végétation et empêcher l'érosion du sol. Dans le but d'examiner l'incidence des traitements d'ensemencement sur la récupération des sites après trois décennies, nous avons échantillonné des bassins à boue ensemencés et non ensemencés, ainsi que la végétation de la toundra adjacente non perturbée dans la région du delta du Mackenzie. Sur 12 sites de bassins à boue (six sites ensemencés et fertilisés et six sites non ensemencés et non fertilisés) situés en basse et haute toundra arctique, des données environnementales ont été récoltées et des relevés de végétation ont été effectués. Les analyses multivariées (NMDS et perMANOVA) ont indiqué que les traitements d'ensemencement et de fertilisation ont eu un impact petit, mais significatif sur les communautés végétales au sommet des bassins à boue en basse toundra arctique. Les communautés végétales présentes au sommet des bassins à boue de tous types étaient significativement différentes de celles trouvées dans la toundra non perturbée environnante, même plus de 30 ans après l'abandon des puits. De plus, des graminées non indigènes ont été trouvées sur les bassins à boue ensemencés et non ensemencés, mais pas dans la toundra adjacente non perturbée. La toundra non perturbée semble résistante à la propagation d'espèces introduites de graminées, alors que les zones perturbées telles que les bassins à boue fournissent des habitats plus favorables à la persistance de plantes non indigènes.

Mots clés : traitements de revégétalisation; basse toundra arctique; invasion par les plantes; exploration pétrolière et gazière; Refuge d'oiseaux de l'île Kendall; surveillance à long terme

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INTRODUCTION

Understanding disturbance impacts on ecological communities is central to our theoretical and applied understanding of ecosystem structure and function (Turner, 2010). Disturbance is the primary factor that triggers the

reorganization of plant communities and initiates a pattern of successional recovery. Initial conditions related to the characteristics of a disturbance and the early patterns of colonization and recovery can affect the pathway of succession that is realized at a given site and thus influence future ecosystem attributes (e.g., Lantz et al., 2013). As a result,

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understanding the role played by management interventions in early post-disturbance recovery is a key element in developing restoration strategies for human-disturbed systems (Cargill and Chapin, 1987; Forbes and Jefferies, 1999).

Growing resource demands continue to stimulate an expanding interest in industrial exploitation of high-latitude environments such as Arctic tundra, with consequent implications for ecosystem disturbance and restoration needs (Forbes and Jefferies, 1999). Tundra vegetation is characterized by low species diversity, simple community structure, and low annual productivity (Bliss et al., 1973). Vegetation growth is limited by a short growing season, low precipitation and temperature, and low availability of soil nutrients, especially nitrogen and phosphorus (Billings, 1987). Consequently, recovery of tundra vegetation from disturbances is often slow (Forbes et al., 2001), and there is interest in developing strategies to accelerate vegetation recovery following industrial disturbances (e.g., Deshaies et al., 2009). Methods for enhancing vegetation recovery in tundra habitats have frequently included fertilizer applications, seeding treatments, or a combination of the two (e.g., Densmore, 1992; Jorgenson et al., 2003; Deshaies et al., 2009). Seeding treatments frequently use non-native, grass cultivars as a more economical alternative to seeding with indigenous species (Jorgenson et al., 2003). In the short term, seeding with non-native species helps to overcome limits on viable seed dispersal during the initial colonization period and the rapid growth of agronomic species may increase litter cover and aid in erosion control on disturbed sites (McKendrick, 1987; Younkin and Martens, 1987). However, establishment of native plant species may be hampered by competition with seeded, non-native species, thereby altering the successional recovery of the native plant community (Cargill and Chapin, 1987; Younkin and Martens, 1987; Densmore, 1992). Seeded non-native species may also spread from treated areas into adjacent natural areas (Conn et al., 2008). The potential for negative interactions between native and non-native species has led to a general suggestion that, if seeding is necessary, management should seed with only indigenous species (Kershaw and Kershaw, 1987; Kidd et al., 2006).

The pace and structure of vegetation recovery after disturbance have implications in tundra environments for the indirect effects of disturbance on near-surface ground temperatures and terrain stability (Kokelj et al., 2010). Sites underlain by ice-rich permafrost, or perennially frozen ground, can thaw and subside when the vegetation is removed or even compacted (Bliss and Wein, 1972; Burn and Kokelj, 2009; Jorgenson et al., 2010). Thawing of permafrost and the resulting changes in surface drainage alter soil conditions for plant growth, while at the same time plant community composition and structure affect permafrost stability through surface cover or effects on snow interception (Kanigan and Kokelj, 2010; Kokelj et al., 2010). Once initiated, these interactions can be sustained over several years or decades and can substantially alter trajectories of vegetation recovery (Jorgenson et al., 2010; Lantz et al., 2013). Thus, early interventions that can alter the interacting effects of vegetation and permafrost thaw on disturbance recovery are of substantial interest for managing the impacts of oil and gas extraction in the North. Decadal-scale field experiments can provide an assessment of the longer-term impacts of management practices on ecosystem recovery that are critical for developing best practices for environmental management.

Here we examine the long-term effects of early revegetation treatments on plant communities several decades after initial disturbance from hydrocarbon drilling in low Arctic tundra. Revegetation treatments consisted of sowing seeds of five non-native grass species and applying fertilizer to soils on test wells one to two years after abandonment (Younkin and Martens, 1976). Measurements of vegetation composition 30 years later provided an opportunity to examine the longer-term outcomes of these early intervention treatments. In particular, we hypothesized that if early revegetation treatments affected the rate of vegetation recovery from disturbance, then we should see a pattern of increased vegetation cover in treated areas compared to untreated areas. As seeding with agronomic species may also have altered the pathway of vegetation succession, we also expected divergent patterns of plant community composition in areas subject to revegetation treatments compared to untreated areas. We accounted for local site effects on community composition by using a comparison of disturbed areas to adjacent undisturbed tundra as a reference point for community recovery. We also tested whether the revegetation treatments have led to persistent populations of seeded non-native grass species in treated areas or their expansion into surrounding undisturbed tundra. The results of this study document some of the long-term effects of revegetation treatments and disturbance on plant communities, providing information that is needed to inform future management of industrial disturbances in tundra habitats.

METHODS

Study Area and History

This study focuses on low Arctic tundra of the Mackenzie Delta Region (MDR), north of Inuvik in the Northwest Territories (NWT), Canada. Sites were located within and adjacent to the Kendall Island Bird Sanctuary and to the east of Parson's Lake (Table 1). The region experiences a typical growing season length of three to four months (Burn and Kokelj, 2009). Mean daily temperatures at Inuvik, approximately 100 km south of the Kendall Island Bird Sanctuary, average 14.2°C in July and –27.6°C in January (Environment Canada, 2010). Most of the underlying terrain consists of ice-rich permafrost, with active layer depths ranging from 35 cm to 65 cm below the mineral soil surface (Burn and Kokelj, 2009). Two types of tundra communities, lowland and upland, characterize much of the MDR. Lowland tundra forms mainly on saturated, alluvial soils and

TABLE 1. Locations of sump sites with well names divided into the traditional name of the land (e.g., Taglu) and the site name (e.g., C42).
Rig release date is the day the well was decommissioned.

Terrain	Treatment	Well nam	e	Rig release date	Latitude	Longitude
Lowland	Unseeded and unfertilized	Taglu	C42	18 November 72	69.3514	-134.9472
		Kumak	E58	08 June 77	69.2915	-135.2487
		Taglu	D43	11 September 73	69.3705	-134.9501
		Taglu	H54	05 April 77	69.3889	-134.9683
	Seeded and Fertilized	Titalik	K26	20 February 73	69.0917	-135.1042
		Unipkat ¹	I22	06 March 73	69.1937	-135.3409
		Toapolock ¹	O54	01 April 74	69.2326	-134.9753
		Kumak	C58	19 October 73	69.2850	-135.2317
Upland	Unseeded and unfertilized	Parsons ¹	F09	19 April 72	68.9745	-133.5293
		Kumak	K16	13 July 75	69.2591	-135.0662
	Seeded and Fertilized	Kumak	J06	16 May 74	69.2600	-135.0161
		Kamik ¹	D58	14 March 75	68.9537	-133.4976

¹ Sites outside the Kendall Island Bird Sanctuary.

the vegetation is dominated by wet sedge/shrub meadows (Bliss and Matveyeva, 1992; Johnstone and Kokelj, 2008). Upland tundra is characterized by well-drained, morainal sediments that support a shrub-heath tundra of slow-growing deciduous or evergreen shrubs (Bliss and Matveyeva, 1992; Aylsworth et al., 2000).

Study sites were located at test wells in the MDR used for oil and gas exploration in the 1970s (Table 1). A drilling mud sump, a large pit excavated in the frozen ground, was constructed at each site to dispose of drilling wastes, largely mixtures of salt, water, and drill cuttings of ground rock and soil (Serverson-Baker, 2004). When the well was decommissioned, the drilling waste was allowed to freeze and was then capped with the excavated subsoil (AMEC Earth & Environmental, 2005). This mound on the land-scape is called a capped sump, referred to hereafter as a sump (Serverson-Baker, 2004). Sumps were intended to keep drilling waste frozen in the permafrost and to facilitate recovery of the active layer (seasonal thaw layer) to a depth similar to that in the surrounding tundra (Kokelj et al., 2010).

A revegetation experiment was established in the MDR in the 1970s to test the effects of seeding and fertilization treatments on post-disturbance vegetation recovery (Younkin and Martens, 1976). Younkin and Martens (1976) aerially applied a mix of grass seed and fertilizer to a set of 22 recently capped sumps in 1974–75. Seeding treatments used a 2:2:2:1:1 mixture (by weight) of five non-native grass species: Festuca rubra L. cultivar "Boreal" (boreal creeping red fescue), Poa pratensis L. cultivar "Nugget" (Nugget Kentucky bluegrass), Phleum pratense L. (climax timothy or Engmo timothy), Phalaris arundinacea L. (Frontier reed canary grass), and Lolium perenne L. (Prolific spring rye) applied at approximately 55 kg/ha (50 lb/acre). During seeding, sites were also fertilized with a 14-28-14 mixture of N-P₂O₅-K₂O (nitrogen-phosphate-potash) applied at 440 kg/ha (400 lb/acre). Seeding and fertilization treatments were applied aerially by helicopter to disturbed areas in late May and early June in the first or second year after the test wells were decommissioned (Younkin and Martens, 1976).

For simplicity, we refer to the joint application of seed and fertilizer by Younkin and Martens (1976) as a "seeding treatment."

Approximately 30 years later, we returned to a subset of Younkin and Martens' (1976) sites to compare the post-disturbance recovery of vegetation on sumps with and without the seeding treatment. We selected 12 sump sites (6 unseeded and 6 seeded) for study in 2008 on the basis of four criteria: 1) sumps were decommissioned in 1972–77; 2) sites in lowland tundra were accessible from the river channel (< 1 km distant); 3) sumps were located on Crown land to provide permission of access; and 4) seed applications were applied to the entire sump (seeded sites). We identified eight sites in lowland tundra (4 seeded and 4 unseeded) and an additional four sites in upland tundra (2 seeded and 2 unseeded). All sites were accessed by boat along the Mackenzie River, except for two sites (1 seeded, 1 unseeded) in upland tundra near Parson's Lake, which were accessed by helicopter (Table 1). The site nomenclature follows the coding used in the regulatory process and is consistent with Younkin and Martens (1976).

Field Measurements

Surveys of vegetation and environmental conditions were conducted in July and August 2008, with a randomized order of sampling for the 12 sites. Sampling occurred along two perpendicular transects at each site, each of which started at the cap center and extended at least 30 m into the surrounding undisturbed tundra. The transects were 100–200 m in length, depending on the shape of the sump, and were divided into three zones of disturbance: a) cap (heavily disturbed), b) perimeter (moderately disturbed), and c) undisturbed control areas in the surrounding tundra. The cap zone consisted of an elevated area created from soil overburden piled on the top of the sump, and the perimeter zone was a transitional zone between the cap and undisturbed tundra. The cap and perimeter make up the sump. Zone boundaries were determined from elevation, active layer depth (i.e., depth of thaw), the presence of a surface organic layer, and indicators of disturbance, including pilings and materials left from exploration activities.

Plant community composition was measured as the frequency of species occurrence in 12 (0.5 \times 0.5 m) quadrats that were randomly positioned along the two transects within each zone. The minimum distance between quadrats was 0.5 m, and no restriction was placed on the positioning of quadrats with respect to zone edges. In each sampling quadrat, we recorded the presence of all vascular plant species, as well as our visual estimates of surface cover (%) of total vegetation, lichen, moss, plant litter, water, and bare soil. Standing (attached) dead plant material was included in the estimates of vegetation cover, and fallen or unattached dead vegetation was measured as litter. We also noted any instances where non-native vascular plants were present at the site but not recorded within the sampling quadrats. Vascular species nomenclature follows the Integrated Taxonomic Information System. Nonnative plants were identified, but seeded cultivars could not be conclusively separated from previously introduced varieties of Poa pratensis and Festuca rubra for lack of reliable distinguishing features (Porsild and Cody, 1980). The 55 plant specimens that could not be conclusively identified to species (25 Cyperaceae, 11 Poaceae, 8 Salicaceae, and 11 unknown herbaceous dicots) were excluded from subsequent analyses. All but two (Carex sp. and Calamagrostis sp.) of these specimens were believed to represent species observed at only a single site and thus contribute little to assessing resemblances among communities (McCune and Grace, 2002).

Environmental conditions were assessed in the field by measuring elevation, active layer depth, organic layer depth, and soil conductivity along the same transects used for vegetation sampling. Elevation data were collected every 5 m along each transect using a Trimble R3 differential GPS system (L1 GPS receiver, A3 L1 GPS antenna). Active layer depth was measured every 10 m along each transect by pushing a 120 cm calibrated steel probe into the soil to the depth of refusal. Soil cores were collected using a soil corer (5 cm diameter) in three randomly selected vegetation quadrats per zone along each transect (n = 18/ site). The organic layer depth was measured from the sampled core and included all the organic material above the mineral soil and below the base of the surface litter or live moss. A sample of the mineral soil was collected from 5 cm below the surface of the mineral soil. These soil samples were analyzed for electrical conductivity, an indicator of soil salinity (Corwin and Lesch, 2003), at the Taiga Environmental Laboratory, Yellowknife, NWT.

Statistical Analysis

At each of the 12 sites, we averaged environmental and cover data and summed species frequency data of all quadrats within each zone (cap, perimeter, and adjacent tundra) to obtain a single value (n = 36). This procedure avoided pseudo-replication of data and allowed comparison of

environmental and species data collected across different subsamples within a zone. Our analyses assumed that the sampled sites represented independent replicates of sump and seeding treatments. Although the sump locations per se were unlikely to have been randomly selected, their distribution in the outer Mackenzie Delta suggests that they were selected without bias from available terrestrial habitats during well exploration in the 1970s. Unless otherwise mentioned, all analyses were conducted in R version 3.0.2 (R Core Team, 2013).

Species Distributions: We used a suite of analysis tools to test for seeding treatment and disturbance zone effects. Seeding treatments were considered the main plot effect and disturbance zones as the split-plot effect in a split-plot sampling design. In some cases, low sample sizes (either 8 or 4 sites within a terrain type) prevented explicit consideration of treatment interactions within the split-plot design, and we focused our assessment on the main effects only. First, we used contingency table analysis and Fisher's Exact Test to test whether the factors of seeding treatment and disturbance zone significantly influenced the odds of encountering non-native species (Quinn and Keough, 2002). Because non-native species were observed only at low densities (a few individuals inside or outside of sampling quadrats), response data were counts of sites × zones where non-natives were present. In order to distinguish clearly between the effects of seeding treatment and disturbance zone in a two-dimensional contingency table, we performed our analyses of seeding and zone effects separately while pooling data across terrain types and levels of the other factor.

Environmental Variables: We used four environmental variables to assess differences between treatments in terrain conditions for lowland sites only (sample sizes were too low at upland sites): relative elevation, organic layer thickness, active layer depth, and soil conductivity. We used a split-plot MANOVA in SPSS version 17.0 (SPSS Inc., Chicago, Illinois) to test for the effects of both seeding treatment and zone on environmental variables. We transformed the relative elevation and salinity data using a $\log_{10} (x + 1)$ transformation, which made all the variables spherical. The data were then normalized using Z-scores prior to analysis.

Plant Community Composition: We first used ordination to describe patterns of plant species composition observed at the sump sites and then applied a suite of tests to assess the effects of seeding treatments on specific plant community responses. We performed non-metric multidimensional scaling (NMDS) analysis to ordinate sites on the basis of shared species abundances (R-based approach), using the Bray-Curtis association metric calculated from summed frequencies across quadrats (Faith et al., 1987) with the "metaMDS" function from the "vegan" library (Oksanen et al., 2013). Our "best" solution was found from 20 independent runs starting from random configurations and with 200 iterations per run. The number of ordination axes used in the final solution was determined by comparing stress vs. dimensionality against randomized outcomes

(McCune and Grace, 2002). We used vector overlays to determine the extent to which the environmental variables influenced species distribution, as well as to determine which variables most strongly correlated to certain plots.

We performed three separate NMDS ordinations to investigate differences in species composition using data from 1) lowland tundra sites only, 2) upland tundra sites only, and 3) lowland and upland sites combined. To reduce species turnover associated with the presence of rare species or sparsely vegetated plots, we reduced the species used in our final NMDS ordinations to those that occurred in at least two study plots (McCune and Grace, 2002). In addition, three outlier species, Deschampsia caespitosa (L.) Beauv., Festuca richardsonii Hook., and Salix reticulata L., were removed because their presence substantially increased the stress of the final NMDS plot, their removal did not qualitatively alter the ordination results, and they were not found to be indicator species in any seeding treatment, zone, or terrain grouping. Pearson correlation coefficients between environmental variables and NMDS scores were calculated using 999 permutations to assess relationships between relative site differences in species composition and environmental variables.

We used indicator species analysis (Dufrêne and Legendre, 1997) with the function "indval" from the library "labdsv" (Roberts, 2013) to determine which species were indicators of seeding treatments or disturbance zones. A perfect indicator of the group is one that is always present and is exclusive to that group (Dufrêne and Legendre, 1997). The indicator value (IV) for a species was calculated by taking the relative abundance and frequency of each species and running a Monte Carlo test with 4999 randomizations to identify significant indicator species. An indicator species has a high IV and a low probability (p < 0.05) of obtaining an IV of equal or higher value by chance when the data are randomly reshuffled (McCune and Grace, 2002).

Treatment Effects on Vegetation: We applied parametric analyses of variance (ANOVA) to test for treatment effects on species richness and total plant species cover. These parametric analyses incorporated a mixed model, split-plot design, in which sites were considered random factors (B(A)) nested within the seeding treatment (A) (Quinn and Keough, 2002). The seeding treatment was treated as a fixed factor with two levels, seeded and unseeded. The within-subject, or split-plot, factor was the zone of the sump (C), which was also considered a fixed factor with three levels: cap, perimeter, and undisturbed control. Pairwise comparisons using a Tukey's honest significant difference (Tukey HSD) were performed to assess patterns of significant differences between the three zones (cap, perimeter, and undisturbed) (Quinn and Keough, 2002). Assumptions of normality, equal variance, and covariance of the groups were assessed using tests of sphericity (Quinn and Keough, 2002). Species richness data were log₁₀ transformed for analysis to meet the assumptions of ANOVA.

For upland sites, the sample size was too small (n = 4 sites total) to run the analysis as a split-plot design. Thus we tested for a seeding treatment effect using a one-way ANOVA with data from the cap, the zone expected to show the greatest difference among the seeded and unseeded sites. In the case of no seeding treatment effect, a second ANOVA was used to test for a disturbance zone effect, ignoring the seeding treatments. This analysis design did not permit testing for an interaction between zone and seeding treatments at upland sites.

We used Multi-Response Permutation Procedures (MRPP), a multivariate randomization test (Mielke and Berry, 2007), to test for significant differences in species composition between lowland and upland sites. We used Bray-Curtis association and 5000 permutations for each run. We then examined treatment effects on vegetation composition separately for each terrain type. We used a permutation multivariate analysis of variance (perMANOVA) to test for the treatment × zone effect on the species composition in lowlands and uplands separately, with seeding treatments as a main plot effect and disturbance zones as a split-plot effect. We ran these analyses on the Bray-Curtis association matrix of species abundances. PerMANOVA analyses were conducted using the functions "Adonis" from the "vegan" library, to obtain the within-subject effects (zones) and the interaction seeding treatment × zones, and "nested.npmanova" from the "BiodiversityR" library (Kindt and Coe, 2005), to obtain the correct between-subject treatment effect (seeding treatment). Because seeding treatment was applied mostly on cap zones, which is where we hypothesized seeding effect would be the greatest, we used a perMANOVA to investigate more precisely the effects of seeding treatment on species composition of sump caps in both lowlands and uplands.

RESULTS

Species Distributions

Quadrat sampling at the sump sites identified a total of 94 species representing 56 genera in 25 plant families (online Appendix 1). Of the three non-native species encountered, two (Festuca rubra and Poa pratensis) were grass species seeded by Younkin and Martens (1976), and the third, F. trachyphylla (Hack.) Krajina, was a naturalized species previously observed along pipelines, roadsides, and riverbanks of the upper Mackenzie River (Government of the Northwest Territories, 2012) (Table 2). Both Festuca rubra and Poa pratensis had also been previously introduced to the NWT (Porsild and Cody, 1980), and thus their presence on sump caps cannot be unambiguously attributed to the seeding treatment. Although there was a tendency for non-native species to be associated with one another geographically, there was no significant difference from a null expectation of no difference in the odds of observing non-natives at seeded vs. unseeded sites (Fisher's exact test

TABLE 2. Observations of non-native species at 12 sump sites, summarized by seeding treatment and disturbance zone. There was no difference in the odds of observing non-natives at seeded vs. unseeded sites (Fisher's exact test p=0.19). No non-native species were found in the undisturbed zones of any sampled sumps. The three disturbance zones differed significantly in the odds of encountering a non-native species (Fisher's exact test p=0.004). Superscripts indicate the species observed in each group.

Treatment and zone	Sites with non-natives	Sites without non-natives		
Unseeded:				
Cap	2^1	4		
Perimeter	1^{2}	5		
Undisturbed	0	6		
Seeded:				
Cap	51,2,3	1		
Perimeter	51,2	1		
Undisturbed	0	6		

¹ Festuca rubra.

p = 0.19). However, no seeded or alien/exotic species were found in the undisturbed zones of any sampled sumps, and there was a significant effect of disturbance zone on the odds of encountering a non-native species (Fisher's exact test p = 0.004).

Environmental Variables

Results for statistical analyses of treatment effects on environmental variables are shown in Table 3. These variables (elevation, active layer depth, soil conductivity, and organic layer depth) did not differ between seeded and unseeded sites in lowland tundra. However, there was a significant difference between zones at these sites. As expected, elevation differed significantly between zones, with highest elevations recorded in the cap, followed by the perimeter and then the undisturbed zones.

Active layer followed a similar pattern. In the lowland sites, active layer depth was 89% thicker in the cap and 56% thicker in the perimeter than in the undisturbed zone. Organic layer depths varied at each site and showed inconsistent differences between the zones either because of frequent flooding in the area, or because of very wet marshy conditions in which we could not take a soil core sample. (For example, standing water at sites H54 and I22 resulted in no data for the perimeter and undisturbed zones.) Nevertheless, there was a trend at the lowland sites for organic layer depths to be shallower on sump caps than in perimeter and undisturbed zones.

Three sites in lowland tundra (E58, K26, and C58) had observations of high soil conductivity that suggested the soils were severely saline (> 4 dS/m). In addition to these sites, the cap and perimeter zones of lowland sites D43 and O54 and upland sites D58 and J06 had saline soil patches,

where salt crusts had formed on the soil surface and little vegetation was present. Across all lowland sites, the mean soil conductivity for the sump cap, perimeter, and undisturbed zones were significantly different (Table 3). The undisturbed zone was the only zone that consistently had a mean salinity within the range of non-saline soils (0-2 dS/m) (Wentz, 2001). The perimeter zone had several observations of high soil conductivity and was significantly different from both the cap and the undisturbed zone (Fig. 1).

Plant Community Composition and Environmental Characteristics

Ordination of the combined lowland and upland species (65 species) resulted in a three-dimensional NMDS solution that captured ~82% of the variation in the original ranked distance matrix. The three axes accounted for 48%, 30%, and 5% of the variation, respectively (Fig. 2). Interpretation of the ordination was based on the first two dimensions, as the third explained a comparatively small proportion of the variance. Sites in upland and lowland terrain occupied different areas of multivariate space in the NMDS ordination (Fig. 2a), indicating consistent differences in vegetation community composition. An exception to this pattern was upland site J06, which had a cap community more similar to lowland tundra sites than to other upland tundra locations (Fig. 2a).

No effect of seeding treatment was apparent in the combined ordination of upland and lowland sites (Fig. 2b). Similarly, the three zones of the sumps (cap, perimeter, and undisturbed) did not show consistent patterns in vegetation community composition in the ordination of all sites together (Fig. 2c). Perimeter and undisturbed zones overlapped almost completely in NMDS space, and caps partially overlapped these two zones. Significant differences in vegetation composition between upland and lowland sites (online Appendix 1) were confirmed in a MRPP test (A = 0.254, p < 0.001). Further statistical analyses of seeding and zone effects were conducted for lowlands and uplands separately.

Elevation was the main environmental gradient associated with the distribution of sample sites in the multidimensional space of the combined lowland and upland ordination (Fig. 2d, online Appendix 2). Logically, upland sites were associated with higher elevation and lowland sites with lower elevations. Upland sites were also correlated with higher lichen cover, while lowland sites were associated with thicker active layers, greater bare soil cover, and greater moss cover compared to upland sites (Fig. 2d, online Appendix 2). High moss cover was mostly associated with unseeded caps, whereas caps in general were associated with low total (vascular) vegetation cover.

Analyzing lowland sites alone permitted a more detailed assessment of potential effects of seeding treatments on community composition. Ordination of lowland sites (8 sites × 3 zones by 40 species) resulted in a two-dimensional

² Poa pratensis.

³ Festuca brachyphylla.

TABLE 3. Summary of results of statistical analyses to test for effects of seeding treatment and disturbance zone on a) environmental variables, b) plant community composition, and c) species richness and total vegetation cover in lowland and upland tundra sites. Test results are summarized by the F statistic and associated probability (p) value, along with degrees of freedom for the numerator (DF_n) and denominator (DF_d) of the F statistic. Significant effects are shown in bold type $(\alpha = 0.05)$.

Dataset	Type of analysis	Fixed effects	DF_n , DF_d	F statistic	p value
a) Environmental variables:					
Lowlands (all)	split-plot MANOVA	Treatment	4, 3	2.298	0.260
· /	1 1	Zone	8, 20	17.337	< 0.001
		Treatment × Zone	8, 20	1.149	0.375
Lowlands - Relative elevation	split-plot ANOVA	Zone	2, 12	1405.76	< 0.001
Lowlands – Active layer depth	split-plot ANOVA	Zone	2, 12	8.32	0.005
Lowlands – Soil conductivity	split-plot ANOVA	Zone	2, 12	944.04	< 0.001
Lowlands – Organic layer depth	split-plot ANOVA	Zone	2,12	318.10	0.057
o) Plant community composition:					
Lowlands (all)	perMANOVA	Treatment	1, 6	0.67	0.2
20 Wallas (all)	1	Zone	2, 12	7.29	< 0.001
		Treatment × Zone	2, 12	1.98	0.120
Lowlands (caps only)	perMANOVA	Treatment	1, 6	1.70	0.050
Uplands (all)	perMANOVA	Treatment	1, 2	0.47	0.9
1	1	Zone	2, 4	3.40	0.005
		Treatment × Zone	2, 4	0.49	0.9
Uplands (caps only)	perMANOVA	Treatment	1,2	0.57	0.9
e) Species richness and total vegetation co	over:				
Lowlands – Richness	split-plot ANOVA	Treatment	1,6	0.71	0.430
	1 1	Zone	2, 12	8.88	0.004
		Treatment × Zone	2, 12	2.36	0.140
Lowlands - Vegetation cover	split-plot ANOVA	Treatment	1, 6	7.13	0.037
2		Zone	2, 12	5.75	0.018
		Treatment × Zone	2,12	1.93	0.190
Uplands – Richness	ANOVA	Treatment	1,10	0.03	0.867
•		Zone	2,9	0.81	0.475
Uplands - Vegetation cover	ANOVA	Treatment	1,10	3.03	0.112
		Zone	2,9	1.59	0.257

NMDS solution that captured approximately 81% of the original variation (Fig. 3). The distributions of seeded and unseeded sites only partially overlapped in the multivariate space of our ordination, suggesting differences in community composition between these two groups across all zones (Fig. 3a). However, seeded site C58 fully overlapped with the unseeded sites, and seeding treatment effects were non-significant in the perMANOVA test (Table 3). Different species were selected as indicator species of unseeded and seeded lowland sites, including the seeded grass *Festuca rubra*, which was an indicator species of lowland seeded sites (Table 3, online Appendix 1).

In general, cap zones in lowland terrain occupied a position distinct from that of the perimeter and undisturbed zones (Fig. 3b). Disturbance zone had a significant effect on species composition that did not interact with the seeding treatment (Table 3). Six indicator species of cap zones in lowland sites were identified, whereas no indicator species were found identified for either the perimeter or undisturbed zones (Table 4, online Appendix 1). Seeded and unseeded caps occupied different areas of the ordination space (Fig. 3b) and these differences in community composition were confirmed with a perMANOVA test comparing caps alone (Table 3).

Within the lowland ordination, undisturbed and perimeter zones tended to occupy low scores along Axis 1, while caps were positioned at high values. Within a single site

(Fig. 3c), the perimeter and undisturbed zones were often more similar in composition to each other than they were to the cap zone. Moreover, perimeters often occupied an intermediate position between the cap and undisturbed zones. For example, the undisturbed and perimeter zones of site E58 were very close in ordination space, while the cap zone is quite distinct (Fig. 3c). Seeded caps were positioned closer than unseeded caps to undisturbed and perimeter zones (Fig. 3b), indicating that communities supported by seeded caps were more similar to those of perimeter and undisturbed zones than communities of unseeded caps. However, results from the perMANOVA test (Table 3) did not confirm this trend, as the interaction between seeding treatment and zones was not significant.

While relative differences among disturbance zones were largely reflected in site positions along Axis 1, Axis 2 of the lowland ordination appeared to represent primarily differences in environmental conditions among sites (Fig. 3d, online Appendix 2). Sites K26 and I22, two sites exposed to frequent flooding from the river channel, were positioned at high values on Axis 2 and were associated with thick organic layers, high moss cover, and low vascular vegetation cover (Fig. 3d). Cap zones, and particularly unseeded caps, generally occupied lower scores along Axis 2 and high scores on Axis 1. This quadrant of the ordination was associated with higher values of canopy height, active layer depth, and relative elevation (Fig. 3d).

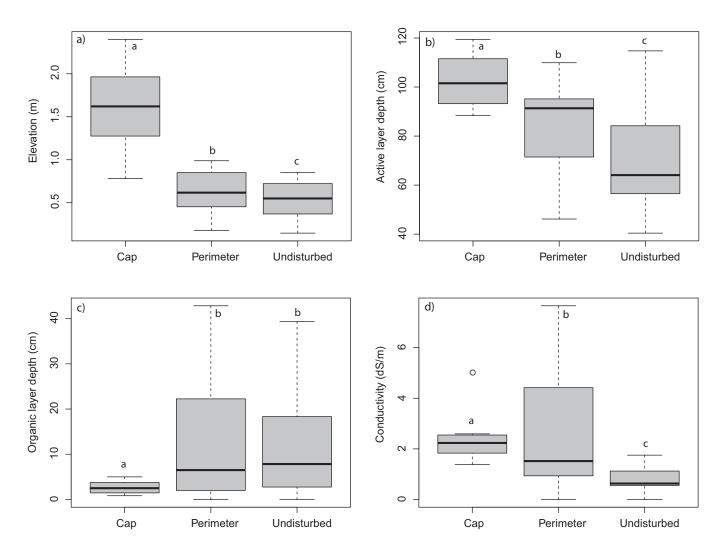


FIG. 1. Boxplots of untransformed environmental variables, by disturbance zone, in eight lowland sites. Variables shown are a) relative elevation, b) active layer depth, c) organic layer depth, and d) soil conductivity. Boxes encompass the theoretical 25%-75% quartiles of the data, and the median is indicated by the thick black line through the center of each box. Whiskers extending from the box encompass the full range of data. For a given variable, bars that share a letter are not significantly different from each other (p < 0.05). Differences in organic layer depths between zones were marginally significant (p = 0.057).

Ordination of upland sites alone (4 sites \times 3 zones by 48 species) resulted in a two-dimensional NMDS solution that captured approximately 76% of the original variation (Fig. 4). There was no significant difference in species composition between seeded and unseeded sites (Fig. 4a, Table 3). Nevertheless, indicator species analysis identified two native species as indicators of seeded sites and one native species as an indicator of non-seeded sites (Table 5). As in the lowland sites, undisturbed and cap zones occupied distinct areas of ordination space, and the space occupied by the perimeter zones was intermediate (Fig. 4b). The per-MANOVA test confirmed these patterns as significant differences in species composition among zones at the upland sites (Table 3). Indicator species were identified for cap and undisturbed zones, but not for the perimeter zone (Table 5). When upland caps were tested alone, the perMANOVA results indicate no significant interactions between seeding treatment and zone and no significant effect of the seeding treatment (Table 3).

Within the upland ordination, undisturbed zones were generally found at high values along Axis 1 and were associated with greater lichen cover and a thicker organic layer (Fig. 4d). In contrast, cap zones were found at low values of Axis 1 and were associated with deep active layers, and high salinity (Fig. 4d). The position of samples along both axes also indicates general differences in environmental variables among sites. For example, Sites D58 and F09 appear to be associated with higher levels of salinity, active layer depth, and lichen cover than sites K16 and J06. The perimeter of site J06 stands out as being very different from perimeters of the other upland sites; its association with very low lichen cover and thick active layer (Fig. 4d) may explain why it was more similar to lowlands sites in the total NMDS diagram (Fig. 2a).

Species Richness and Total Vegetation Cover

In lowland sites, species richness differed according to the zones (Table 3, Fig. 5a), but was not affected by seeding

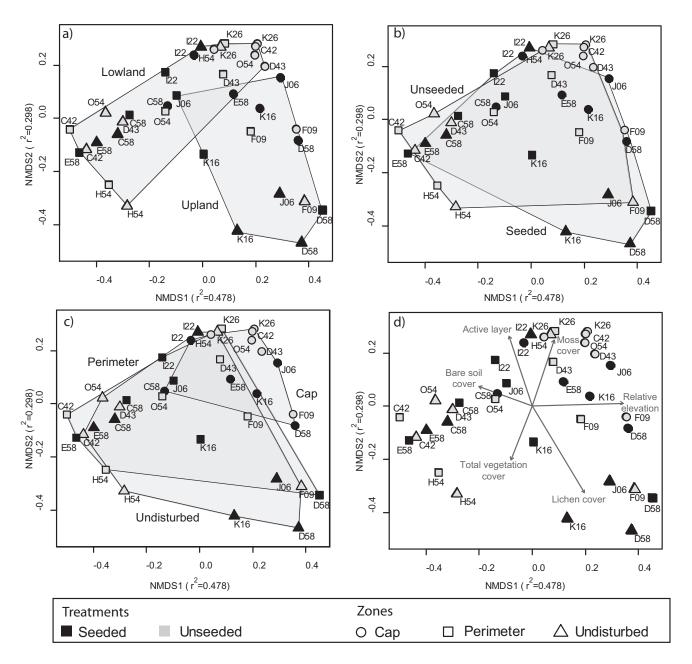


FIG. 2. Distribution of lowland and upland sites in a three-dimensional NMDS ordination (stress of 9.44, 200 iterations, using Bray-Curtis distance) of sample units based on community composition. For ease of interpretation, and because Axis 3 explained only ~5% of the total variation, only Axes 1 and 2 are represented. Each point represents a sample unit of a plot within one of three disturbance zones in a site: cap (circles), perimeter (squares), or undisturbed (triangles). Grey color indicates unseeded sites and black, seeded sites. Each point within a site is labeled with its unique name. Light grey polygons indicate a) groups of lowland and upland sites, b) groups of seeded or unseeded sites, or c) the three zones (cap, perimeter, and undisturbed). d) Vectors represent environmental variables that were strongly correlated with Axes 1 and 2 of the ordination (p < 0.2). Ordination scores of all the environmental variables are available in online Appendix 2.

treatment or the interaction of zones and seeding treatment (Table 3). Species richness was significantly higher in caps than in undisturbed areas (HSD post-hoc test, p < 0.05) and was intermediate in perimeter zones (Fig. 5a). Total vegetation cover was higher in seeded sites than in unseeded sites, regardless of disturbance zone (Table 3, Fig. 5b). Vegetation cover differed among zones at lowland sites (Table 3) in a pattern opposite to that of species richness, with a trend of higher vegetation cover in undisturbed zones, intermediate

cover in perimeters, and lowest cover in cap zones (Fig. 5b). However, none of the pair-wise differences between the zones were significant in the post-hoc test (HSD post-hoc test, p > 0.05).

At upland sites, we found no differences in species richness (Fig. 5c) due to either seeding treatment or disturbance zones (Table 3). Total vegetation cover at upland sites (Fig. 5d) was also similar between seeded and unseeded sites and among disturbance zones (Table 3).

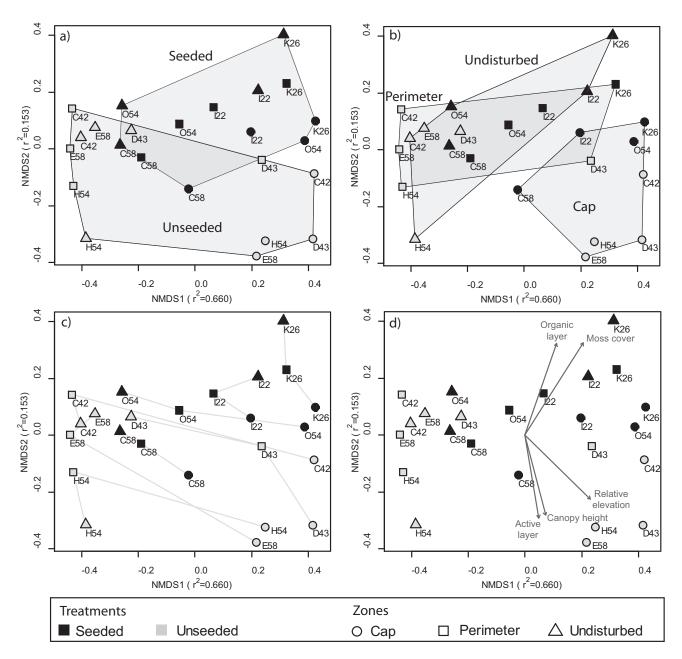


FIG. 3. Distribution of lowland sites in a two-dimensional NMDS ordination (stress of 10.81, 200 iterations, using Bray-Curtis distance) of sample units based on community composition. Light grey polygons indicate a) groups of seeded or unseeded sites, or b) the three zones (cap, perimeter, and undisturbed). c) Lines connect the cap, perimeter, and undisturbed zones within seeded or unseeded sites. d) Vectors represent environmental variables that were strongly correlated with Axes 1 and 2 of the ordination (p < 0.2).

DISCUSSION

In the Mackenzie Delta region, applications of nonnative seed and fertilizer appear to be associated with small but detectable differences in plant community composition of disturbed sumps after 30 years of recovery from disturbance. Two of the non-native grass species (*Festuca rubra* and *Poa pratensis*) used in the seeding treatments (Younkin and Martens, 1976) were found on both seeded and unseeded sumps, although never as a dominant species. Moreover, *F. rubra* was a significant indicator of lowland seeded sites. It is likely that the third non-native species, *F. brachyphylla*, became established on sumps via dispersal from naturalized populations. Non-native grasses were encountered only on sump caps and perimeters, which suggests that sumps were more susceptible to colonization by non-native species than the surrounding undisturbed tundra. Previous research found that seeded species *F. rubra* cultivar "Arctared" and *P. pratensis* cultivar "Nugget" were able to invade surrounding unseeded, disturbed areas from adjacent seeded patches 12 years after the seeding treatment (Younkin and Martens, 1987). Thirty years later, we found no evidence that these populations had invaded undisturbed tundra surrounding the sumps. However, the persistence of these non-native populations on sumps suggests that these disturbed patches have the potential to act

TABLE 4. Indicator species at lowland sites: Results of analysis using 4999 randomizations on frequency data from quadrat sampling. One analysis compared the seeding treatments (seeded and unseeded) and another, the disturbance zones of the sump (cap, perimeter, and undisturbed). The indicator value (IV) and p value (p) are shown for each significant indicator species.

	IV	p
Seeding treatment:		
Seeded:		
Equisetum arvense	0.72	0.004
Parnassia palustris	0.66	0.006
Salix alaxensis	0.65	0.004
Hedysarum alpinum	0.60	0.005
Festuca rubra¹	0.46	0.016
Artemisia tilesii	0.38	0.040
Unseeded:		
Equisetum variegatum	0.45	0.046
Calamagrostis lapponica	0.42	0.012
Zones:		
Cap:		
Arctagrostis latifolia	0.71	< 0.001
Lomatogonium rotatum	0.57	0.018
Oxytropis deflexa	0.63	0.005
Parnassia palustris	0.52	0.027
Pyrola grandiflora	0.57	0.019
Salix alaxensis	0.62	0.004
Perimeter: – none		
Undisturbed: – none		

¹ Seeded species.

as sources for population spread of non-natives into native tundra if environmental conditions become more favorable for these species, or as disturbance patches are created in surrounding areas.

Seeding treatments are often applied following industrial disturbance with the aim of speeding up processes of plant community recovery and soil stabilization (Forbes and Jefferies, 1999; Jorgenson et al., 2003). In lowland tundra, multivariate analyses of plant community composition across all disturbance zones found no effects of seeding treatments, but did identify significant differences in the composition of seeded and unseeded sump caps. Moreover, the distribution of sites in the lowland ordination suggested that seeded caps were more similar in composition to undisturbed and perimeter zones even though the interactions between seeding treatment and zone were not significantly different. Indicator species of seeded lowland sites included a preference of several native herbaceous plants, such as Equisetum arvense (field horsetail), Parnassia palustris (marsh grass-of-Parnassus), Hedysarum alpinum (alpine sweetvetch), and Artemisia tilesii (Tilesius' wormwood), for seeded sump caps. These species are typical of the rich, mesic, calcareous or sandy soils found along the shores of rivers and lakes (Porsild and Cody, 1980). The association of these species with seeded sites could indicate a long-term effect of the fertilizer and seeding treatment, but it may also simply reflect underlying differences in soil conditions of seeded and unseeded sites. It is notable that both indicators of non-seeded sites, Equisetum variegatum and Calamagrostis lapponica, are both typically found in moist habitats (Porsild and Cody, 1980).

TABLE 5. Indicator species at upland sites: Results of analysis using 4999 randomizations on frequency data from quadrat sampling. Details as in Table 4.

	IV	p
Seeding treatment:		
Seeded:		
Salix glauca	0.79	0.022
Pyrola grandiflora	0.78	0.017
Unseeded:		
Alnus viridis	0.87	0.008
Zones:		
Cap:		
Epilobium angustifolium	0.74	0.023
Perimeter:		
– none		
Undisturbed:		
Polygonum viviparum	0.93	0.015
Ledum palustre subsp. decumbens	0.84	0.018
Arctostaphylos rubra	0.79	0.008
Empetrum nigrum	0.68	0.045

Thus, although there is some indication that seeding (and fertilization) treatments applied early after disturbance may have altered patterns of plant community composition observed after over 30 years of recovery, these results must be interpreted with some caution. The low sample size (4 seeded and 4 unseeded sites within the lowland terrain) increases the likelihood that differences may be due to chance differences in environmental conditions among sites. Some evidence for this effect is apparent in the relatively distinct regions of ordination space occupied by all zones of seeded vs. unseeded sites in the ordination graph (Fig. 3a). If it were not for site C58, we would likely conclude that seeded and unseeded sites differed because of pre-existing environmental conditions, as consistent differences among sites in both disturbed and undisturbed zones are unlikely to arise from seeding treatments applied to the sump caps. Similarly, patterns of increased vegetation cover were observed at lowland seeded sites across all disturbance zones (Fig. 5b), rather than having an isolated effect on the cap zone where the treatment was applied. Once we take the environmental differences among sites into account, perhaps the most compelling evidence for a seeding treatment effect comes from the closer proximity of seeded caps to perimeter and undisturbed zones at the same site, compared to the larger distances between caps and undisturbed zones at unseeded sites (Fig. 3c). We found little evidence for an effect of seeding treatments at the upland sites, but of course the very low sample sizes at upland sites limits the power of our test to detect what are likely subtle differences in community composition.

Regardless of terrain type or seeding treatment, plant community composition on sump caps remained substantially different from that of the surrounding undisturbed tundra after 30 years of recovery. Plant communities on sump caps are largely dominated by pioneer species, including forbs, grasses, and tall shrubs (Tables 4 and 5) capable of long-distance dispersal and rapid growth such as *Salix alaxensis*. This pattern is consistent with findings

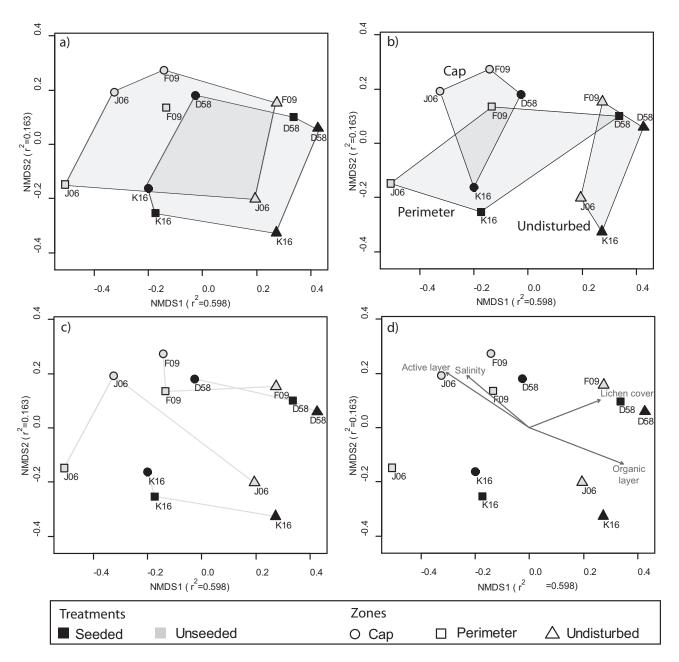


FIG. 4. Distribution of upland sites in a two-dimensional NMDS ordination (stress of 7.77, 200 iterations, using Bray-Curtis distance) of sample units based on community composition. Symbols and other details are the same as in Figure 3.

of increased abundance of pioneer species in tundra communities after industrial disturbance in other studies (e.g., Hernandez, 1973; Harper and Kershaw, 1996; Kemper and Macdonald, 2009; Lantz et al., 2009). Soil disturbance creates opportunities for new plant colonization on the sump caps, where competition is reduced and there is open soil suitable for seedling establishment. In some cases, as observed here for lowland sites, the creation of a pioneer community on sump caps has led to increased species richness on sump caps compared to undisturbed tundra. Plant communities on these caps share many species with communities occurring in natural disturbances (such as thaw slumps and point bars) in the MDR (Pearce, 1986; Lantz et al., 2009). Seed sources for many sump colonizers likely

originate in these naturally disturbed areas (Cargill and Chapin, 1987).

The persistence of distinct plant communities on sump caps after three decades of recovery is consistent with results of Johnstone and Kokelj (2008) in the MDR and other studies demonstrating slow recovery of tundra vegetation following industrial disturbance that span multiple decades (Harper and Kershaw, 1996; Forbes et al., 2001; Jorgenson et al., 2010; Rydgren et al., 2011). In contrast, other research in the MDR has documented rapid rates of vegetation recolonization and recovery following disturbances of tundra by fire, thaw slumps, drainage of lakes, and abandonment of gravel quarries (Lantz et al., 2009, 2010, 2013; Marsh et al., 2009). Differences in rates

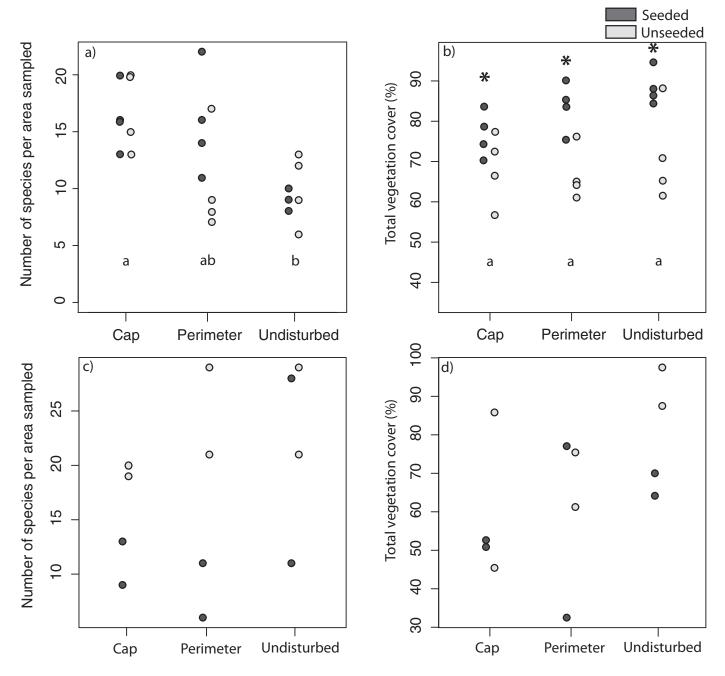


FIG. 5. Observed richness (a, c) and total vegetation cover (b, d) across disturbance zones for seeded and unseeded sites in lowland (a, b; n = 4 sites per treatment) and upland tundra (c, d; n = 2 sites per treatment). Values for seeded sites are shown in dark grey and unseeded sites are shown in light grey. Richness estimates are based on a total sample area of 3 m² (12 × 0.25 m² subsamples) per zone × site. Zones that share a letter (indicated in the bottom of panels a and b) were not significantly different in a Tukey HSD post-hoc test on log-transformed data ($\alpha = 0.05$). Asterisks at the top of the panels indicate a significant effect of seeding treatment. Points were offset slightly to avoid overlap.

of vegetation recovery may be explained by a) whether the assessment focuses on development of total vegetation cover or on the specifics of community composition, and b) whether the disturbance is associated with a change in environmental conditions that may contribute to a persistent shift in the vegetation community (e.g., Lantz et al., 2009). Our results indicate minor or non-significant effects of disturbance on total vegetation cover after 30 years, but large and significant effects of disturbance on community composition.

Persistent differences in environmental conditions may be preventing or slowing the recovery of plant communities after sump abandonment to a composition similar to that of undisturbed tundra. Previous research on sumps within the MDR indicates that the construction of a raised sump cap is associated with changes in soil drainage, temperature regime, snow accumulation, and soil salinity (Kanigan and Kokelj, 2010). Given the strong effect of moisture and soil drainage on vegetation communities throughout the tundra (Bliss and Matveyeva, 1992), it has been argued that sump

caps will support distinct vegetation communities as long as these features remain elevated above the surrounding tundra (Johnstone and Kokelj, 2008). In addition, increased soil salinity within the cap and perimeter zones (Fig. 1; see also Kanigan and Kokelj, 2010) has been associated with a combination of drilling waste leakage and permafrost degradation (Kokelj and Burn, 2005; Kokelj et al., 2010). High levels of salt stress can alter plant community recovery by reducing the potential colonization and growth of salt-intolerant species (McLaren and Jefferies, 2004). We observed particularly high levels of soil conductivity at three sites in lowland tundra, as well as patches of unvegetated, saltencrusted soil at multiple sites; these observations suggest that high salinity is likely affecting plant community composition at several of the sumps in this study. As a result, the recovery of plant communities on sump caps to a composition similar to that of undisturbed tundra will likely be tied to the recovery of environmental conditions, through gradual processes such as erosion, permafrost aggradation, and soil leaching (Burn and Kokelj, 2009).

Overall, the results of this study provide valuable information on decadal-scale effects of revegetation treatments on plant community recovery from disturbance. The shortterm goals of the seeding treatments in this study were to prevent surface soil erosion caused by precipitation and runoff and, where possible, restore the tundra ecosystem to its natural state (Younkin and Martens, 1976). Non-native species were used because seed was readily available and affordable (Younkin and Martens, 1976). Our analysis suggests that after three decades of recovery, seeding treatments likely had some impact on restoring the tundra to its natural state in the lowland sites; however, plant communities on both seeded and unseeded sumps remained significantly different from those of the surrounding undisturbed tundra. In addition, we found no evidence that seeding reduced permafrost degradation, as almost all sumps we surveyed had evidence of thermokarst (ponded water), increased active layer thickness, or subsidence (large tension cracks in the soil). Surface erosion from runoff did not appear to be a significant issue at any sumps, except where meandering river channels were cutting into the riverbanks adjacent to sumps (e.g., at I22). A greater issue in sump recovery is the impact of tall shrubs, commonly found on sump caps, which trap blowing snow in winter (Johnstone and Kokelj, 2008; Lantz et al., 2013). The trapping of snow can increase winter temperatures in the soil, thus increasing thermal erosion and subsidence and destabilizing the sump surface (Kokelj et al., 2010). Correlations of the environmental variables and species cover in the ordinations (data not shown) found no evidence that early seeding treatments affected the distribution of tall shrubs on sump caps. In addition, the seeding treatment has added one potentially long-term negative effect to the impacts of industrial disturbance on plant communities: the addition of non-native species.

The multi-decadal effects of disturbance on plant communities in the MDR suggest that management intervention

to reduce the effects of industrial disturbance is warranted. Although early seeding treatment may have hastened the recovery of plant community composition on seeded sump caps, seeding treatments were unable to compensate for the overriding disturbance effect, which was clearly evident three decades later. Given the high cost of applying revegetation treatments and potential risks associated with the spread of non-native species, we would argue that seeding sumps with non-native species represents an unwarranted and ecologically risky practice. Alternative intervention treatments, such as removal of tall shrubs from the sump caps to maintain the thermal integrity of the sump (Kanigan and Kokelj, 2010), may have a stronger effect on recovery than artificial seeding. In addition, prior to the creation of a sump, the soil organic layer (topsoil) can be stockpiled for reuse in post-disturbance restoration to provide a source of buried seeds and rhizomes for the regeneration of native species (Densmore, 1994). Natural revegetation would reduce the risk of artificially establishing new populations of non-native species that can persist in disturbed areas, as observed here, for several decades.

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APPENDICES

The following appendices are available in a supplementary file to the online version of this article at:

http://arctic.journalhosting.ucalgary.ca/arctic/index.php/arctic issue/view/280

APPENDIX 1. List of species observed in our study organized by family, genus, and species.

APPENDIX 2. Axis loadings of environmental and surface cover variables on NMDS 1 and NMDS 2.

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