

Survival and growth of the forage grass *Festuca rubra* in naturally and artificially devegetated sites in a sub-arctic coastal marsh¹

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Abstract: *Festuca rubra* is an abundant supratidal grass on sub-arctic James Bay (Canada) shorelines, forming extensive near-monocultures that are used as forage by nesting and migrating geese. Studies at other, more northern North American locations have shown grubbing by geese can have severe consequences for intertidal and supratidal marshes, but these studies have focussed on plant communities that differ substantially in species composition, physical environment, and extent from James Bay's *Festuca* meadows. In this study, we examined the responses of this grass to natural and simulated goose grubbing in *Festuca* swards heavily used by lesser snow geese, Canada geese, and brant at Akimiski Island in James Bay. We transplanted *Festuca* into plots previously devegetated by geese, into plots where we removed vegetation to simulate goose grubbing, and into intact vegetation (controls). We found shoots transplanted into control and artificially grubbed plots survived well, but those transplanted into previously devegetated areas usually died. Growth initially was reduced in naturally devegetated sites, but the few survivors in the following year performed as well as plants transplanted into intact or artificially grubbed sites. Spot measurements suggested that naturally devegetated sites suffered from degraded soil conditions, such as hypersalinity and increased temperature. These results provide evidence that recovery of *Festuca* swards following loss of vegetation is likely to be difficult, probably as a result of deteriorating soil conditions. Models of goose-plant interactions developed at substantially more northern sites thus seem applicable to the significantly different plant communities of the James Bay shoreline.

Keywords: *Festuca rubra*, grazing, grubbing, habitat degradation, lesser snow geese, supratidal marsh.

Résumé : La fétuque rouge (*Festuca rubra*) est une graminée qui abonde dans la partie supralittorale des rives de la baie James, dans la zone subarctique du Canada. Elle forme des cultures étendues presque monospécifiques qui servent à l'alimentation des oies pendant leur reproduction et leurs migrations. Des études menées dans des régions plus nordiques du continent nord-américain montrent que le déracinement des plantes par les oies peut entraîner des conséquences négatives sévères sur les marais intertidaux et supralittoraux. Les communautés végétales qui ont été étudiées diffèrent toutefois beaucoup (environnement physique, étendue, composition en espèces) de celles que l'on trouve près de la baie James et où domine la fétuque. Dans cet article, nous nous sommes intéressés aux réponses de la fétuque au déracinement naturel et à un déracinement simulé celui fait par les petites oies des neiges, les bernaches du Canada et les bernaches cravants. Dans les prés de fétuques de l'île Akimiski (baie James), nous avons transplanté ces graminées dans des parcelles où la végétation avait été supprimée par les oies, dans des parcelles où nous avions retiré la végétation pour simuler un déracinement par les oies et dans des parcelles témoins où la végétation était intacte. Les pousses de fétuque transplantées dans les parcelles témoins et dans celles simulé un déracinement ont bien survécu. Par contre, celles qui ont été transplantées dans les parcelles où la végétation avait été retirée par les oies sont mortes. Dans les sites où la végétation avait été supprimée de façon naturelle, la croissance des fétuques était réduite au cours de la première saison de croissance. Par contre, l'année suivante, les quelques individus survivants ont eu une croissance comparable aux fétuques transplantées dans les parcelles intactes ou celles simulé un déracinement par les oies. Des mesures ponctuelles suggèrent que les sites où la végétation a été supprimée de façon naturelle ont souffert des mauvaises conditions du sol, notamment d'une trop grande salinité et d'une température trop élevée. Il semble donc que le retour de la végétation dans les prés de fétuque après le déracinement des individus sera dans la plupart des cas difficile, probablement en raison des conditions du sol qui sont détériorées. Les modèles décrivant les interactions entre les oies et la végétation qui ont été développés pour des sites plus septentrionaux pourraient donc s'appliquer aux communautés végétales pourtant très différentes des rives de la baie James.

Mots-clés : broutement, dégradation de l'habitat, déracinement, *Festuca rubra*, marais supralittoral, petite oie des neiges.

Nomenclature: AOU, 1998; Blaney & Kotanen, 2001.

Introduction

Natural disturbance helps to maintain many ecosystems (Sousa, 1984; Pickett & White, 1985); for example,

fires often significantly contribute to the structure and dynamics of forests, savannas, and grasslands (Morgan & Lunt, 1999; Odion & Davis, 2000; Boyd & Bidwell, 2002). However, disturbance also can lead to the loss or degradation of ecosystems. Many of the most severe examples of disturbance result directly or indirectly from human activities such as agriculture, industry, and

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forestry (Jefferies, 1997; Lindenmayer & McCarthy, 2002). The impacts of such disturbances may be far removed from their source of origin. A good example is the effect of tropical deforestation, which reduces northern temperate and boreal migratory bird populations by reducing their wintering habitats (Finch & Stangel, 1993).

Populations of lesser and greater snow geese (*Chen caerulescens caerulescens*, *C. c. atlantica*), Ross's geese (*Chen rossii*), and some races of Canada geese (*Branta canadensis*) have increased in recent decades as a result of agriculture on their overwintering grounds, reduced hunting harvest rates along their migratory pathways, and the creation of wildlife refuges in the United States (Abraham *et al.*, 1996; Abraham & Jefferies, 1997; Jefferies, 1997; Miller, Smeins & Webb, 1998; Jefferies, Henry & Abraham, 2004; Jefferies, Rockwell & Abraham, 2004a,b). In some cases, these increasing populations are having a negative impact on northern staging and breeding areas thousands of kilometres away from the anthropogenic causes of their growth (Jefferies & Rockwell, 2002; Jefferies, Henry & Abraham, 2004; Jefferies, Rockwell & Abraham, 2004a,b). Lesser snow geese of the mid-continent population are a good example because of their rapid rates of increase (Rockwell, Cooch & Brault, 1997) and destructive foraging methods (Jefferies & Rockwell, 2002; Jefferies, Rockwell & Abraham, 2004a). These geese graze above-ground parts of plants during the post-hatch period beginning in mid-June (Abraham & Jefferies, 1997); at moderate intensities, this grazing can be sustainable (Cargill & Jefferies, 1984; Bazely & Jefferies, 1985; Hik, Sadul & Jefferies, 1991). In contrast, in spring and fall, they destructively grub below-ground plant parts (Jefferies, Jensen & Abraham, 1979; Jefferies, Rockwell & Abraham, 2004a). As goose populations have expanded, the intensity of grazing and grubbing has increased, resulting in loss of vegetation on their arctic breeding grounds (Abraham & Jefferies, 1997) and changes in exposed soil such as increased salinity and temperature (Iacobelli & Jefferies, 1991; Srivastava & Jefferies, 1996; McLaren & Jefferies, 2004).

Damage by lesser snow geese to northern plant communities is believed to occur in a series of steps (Abraham & Jefferies, 1997; Jefferies, 1997; Jefferies & Rockwell, 2002; Jefferies, Rockwell & Abraham, 2004a). First, heavy grazing of intertidal saltwater marshes converts their preferred forage, *Puccinellia phryganodes*, to short "grazing lawns" (*sensu* McNaughton, 1984). Together with spring grubbing, excessive grazing eventually converts these lawns to unvegetated mudflats. The geese next utilize supratidal saline and brackish marshes for forage. These marshes undergo damage similar to that in intertidal marshes, with intact vegetation replaced by grazing lawns and ultimately mudflats. Geese also increasingly exploit inland freshwater marshes (Kerbes, Kotanen & Jefferies, 1990; Kotanen & Jefferies, 1997), depleting the forage species in heavily used areas. This pattern of moving further inland from intertidal to supratidal to freshwater marshes has been observed at multiple sites, including La Pérouse Bay, Manitoba, the west coast of Hudson Bay, and the north shore of Akimiski Island in James Bay.

Although consequences of intense foraging by geese have been well documented for arctic intertidal marshes and, to a lesser extent, for freshwater sedge meadows, almost all the work in northern supratidal sites has been conducted at La Pérouse Bay in habitats very different from those at Akimiski Island (Jefferies, Rockwell & Abraham, 2004a). The supratidal at La Pérouse Bay is a very heterogeneous mixture of *Puccinellia phryganodes* / *Carex subspathacea* grazing flats, salt pans, and willows; *Festuca rubra* does occur in small (metre-scale) patches mixed with other grasses, sedges, and dicots, but never forms the extensive (100-m to km scale) near-monocultures that dominate supratidal sites on James Bay. Although snow geese at La Pérouse Bay use *Festuca* as a non-preferred food (Hik, Jefferies & Sinclair, 1992; Gadallah & Jefferies, 1995a,b), it is a minor source of forage compared to both intertidal *Puccinellia* flats and freshwater sedgeland. In contrast, at Akimiski, *Festuca* meadows are rapidly replacing the intertidal flats as the principal source of forage for snow geese near their colony as the intertidal flats are progressively devegetated; *Festuca* meadows also are a preferred foraging habitat for Canada geese. Finally, although numerous studies in temperate Europe have considered interactions between *Festuca rubra* and foraging geese (van der Wal, van de Koppel & Sagel, 1998; Dormann, van der Wal & Bakker, 2000; Bos *et al.*, 2002), these systems differ significantly from ours in climate, herbivore species (different goose species, as well as brown hares and livestock), plant communities (additional important competitors, notably *Phragmites*), and management (most are in managed systems with ongoing or historical agriculture), and studies have focussed on grazing rather than grubbing. Thus, our studies of *Festuca* meadows are necessary both because they extend the current model of goose-plant interactions to a major new North American habitat type and because this habitat represents a key future source of forage for nesting birds.

Our research used experimental transplants to assess whether survival and growth of the dominant supratidal grass, *Festuca rubra*, are possible in areas where loss of *Festuca*-dominated vegetation previously has occurred. We also attempted to determine whether areas completely devegetated by geese in previous years are harder to revegetate than freshly disturbed sites. Comparing artificially grubbed sites with ungrubbed controls allowed us to test the immediate effects of devegetation on the survival and performance of *Festuca* in a fully randomized, replicated, controlled experiment. Comparing these treatments with areas naturally devegetated in previous years allowed us to investigate whether these short-term effects changed over time. Our hypotheses were 1) devegetation should result in an immediate decrease in the survival and growth of transplanted *Festuca* and 2) the negative effects of devegetation on growth and survival should increase over time.

Methods

STUDY SITE

Akimiski Island, Nunavut Territory, Canada (53° N, 81° W) is the largest island in James Bay, which lies at

the southernmost end of Hudson Bay. This 3,800-km² island is located just offshore of the community of Attawapiskat, Ontario, and is roughly 1,000 km to the southeast of the well-known snow goose colony at La Pérouse Bay, Manitoba (58° N, 94° W). Three species of geese nest, stage, or molt on the island in significant numbers: Lesser snow geese, Canada geese, and brant (*Branta bernicla hrota*). Currently, up to 2,000 pairs of lesser snow geese nest in a 20-km stretch along the north shore of the island (Abraham, Leafloor & Lumsden, 1999). An average of 9,947 breeding pairs of Canada geese (*B. c. interior*) nested throughout the island between 1990–2001 (Abraham & Warr, 2003), with about 20% of the nests located on the north shore. Molt-migrant giant Canada geese (*B. c. maxima*) using the island have increased in numbers since the 1970s (Leafloor *et al.*, 1996; Abraham, Leafloor & Lumsden, 1999) and currently number several thousand. Small Canada geese (*B. c. hutchinsii*) occur on the island during fall migration (Thomas & Prevett, 1982), but their current numbers are unknown. During spring migration, brant stage for approximately one month, and single day counts of 10,000 individuals have been recorded; these geese graze intensively in the early growing season, but do not grub vegetation. Habitat damage on the north coast of Akimiski Island is most evident in areas where both lesser snow and Canada geese nest, and in areas used for staging by brant and giant Canada geese as well as by broods of both lesser snow and Canada geese.

This experiment was conducted on the north shore of Akimiski Island in the supratidal marshes along a small river (unofficially called the “Thompson River”: 53° 11' N, 81° 26' W), in an area where both lesser snow geese and Canada geese nest. Supratidal vegetation is dominated by *Festuca rubra*, which forms extensive and nearly pure stands in many areas. In areas heavily used by geese, a mosaic of taller *Festuca* stands (ca 15 cm), shorter grazing lawns (≤ 2 cm), and bare (formerly vegetated) plateaus has been created. Minor species co-occurring with *Festuca* include *Juncus balticus*, *Carex* spp., various herbaceous dicots, and (rarely) *Salix* spp., but these generally contribute < 1% of biomass in the *Festuca* pastures that formed the focus of this study.

EXPERIMENTAL DESIGN

Sixty 1- × 1-m experimental plots were established in June 2001. Forty of these plots were placed in short *Festuca* grazing lawns. Twenty were interspersed in unvegetated soils that had lost their plant cover as a result of goose grubbing in years prior to this study (conservatively, a minimum of 2 y earlier); cover in these areas is believed to have been originally dominated by *Festuca*, based on remnant vegetation, tidal position, and frequency of inundation. Within each 1- × 1-m plot, two circular subplots of 30 cm diameter (707 cm² in area) were created for destructive biomass sampling, one for sampling on 1–2 August 2001 and one for 7–8 July 2002; research in arctic salt marshes has shown this size of subplot to be sufficient to significantly affect revegetation and soil processes (McLaren & Jefferies, 2004). Both subplots in half of the grazing lawn plots were then grubbed by hand.

Goose grubbing was simulated by using a knife to remove vegetation from each circle and hand-pulling any remaining shoots. The end result was a total of three treatments, each with 20 replicate plots: 1) artificial grubbing, 2) natural devegetation, and 3) intact grazing lawn controls. All subplots received five transplants of 2- × 3- × 1.5-cm-deep plugs of *Festuca* collected locally from grazing lawns. This is a highly clonal plant; we assume each of these small plugs likely represented a fragment of a single genet. How (or whether) *Festuca* establishes naturally in devegetated areas is unknown, but regeneration from seed, fragments, and surviving plants are possibilities; this experiment was intended to assess the suitability of disturbed habitats for *Festuca*, rather than to directly imitate the natural revegetation process. Finally, each plot was enclosed in a chicken wire cage to protect the transplants from damage by geese; this was necessary since this experiment was designed to determine whether *Festuca* is potentially able to establish in damaged sites, not whether geese currently can prevent this establishment.

SAMPLING AND ANALYSIS

Biomass and plant status (alive or dead) were determined on 1–2 August 2001 and 7–8 July 2002. Transplants were judged to be dead if they contained no living shoots. The above-ground parts of each surviving transplant were collected and sorted into live and dead material; values of the five transplants per subplot were averaged before analysis. These weights are reported as grams per transplant, since the area covered by each transplant was too small to measure accurately. In addition, any naturally occurring plants, including colonists of *Festuca* or other species, were collected from one quarter of the 30-cm-diameter sampling area (177 cm²) and weighed separately. These values were extrapolated to grams per square metre to facilitate comparison with other studies.

Spot measures of several physical parameters also were made; these were intended to provide a snapshot of physical conditions, rather than a detailed description. Soil salinity, temperature, and water content were measured on 1–2 August 2001 and 7–8 July 2002. Soil salinity was measured with the standard saturated soil-paste method using a conductivity meter (Rhoades, 1996). Daytime soil temperatures were measured using a Barnant 115 Thermocouple Thermometer (Barnant Co., Barrington, Illinois), placing the probe 2.5 cm into the soil. In order to determine percent water content, soil was collected, weighed, and placed in a drying oven at 50–70 °C until completely dry and weighed again.

The number of surviving transplants on each sampling date was analyzed with Kruskal-Wallis tests because the data were highly non-normal. Significant tests were followed with nonparametric *post-hoc* analyses (Bonferroni-corrected Mann-Whitney *U*-tests with familywise $\alpha = 0.05$). All other data were analyzed using one-way analysis of variance (ANOVA) followed by *post-hoc* Tukey-Kramer analyses with familywise $\alpha = 0.05$ when ANOVA results were significant. This approach was adopted after split-plot analyses demonstrated that treatment effects differed significantly between years (treatment × year interaction: $P < 0.05$); one-way analyses also

solved problems resulting from missing data and differences in variance between years. In addition, salinity was log-transformed before analysis to improve homogeneity of variance; proportional data were arcsine-square root transformed before analysis. Bonferroni correction did not alter patterns of significance for the principal (biomass and survival) variables measured; thus, uncorrected overall ANOVA and Mann-Whitney results are presented. Degrees of freedom varied based on the number of samples successfully recovered for each sample period. Means are reported \pm SE.

Results

SURVIVAL OF TRANSPLANTS

Kruskal-Wallis tests demonstrated highly significant differences among treatments in the survival of transplants for both 2001 ($H = 27.76$, $df = 2$, $P < 0.0001$) and 2002 ($H = 22.91$, $df = 2$, $P < 0.0001$). Survival of transplants in intact vegetation and artificially grubbed plots was similar and relatively high, while the survival of transplants in naturally devegetated plots was consistently very low (Figure 1a). *Post-hoc* comparisons confirmed that survival in naturally devegetated plots differed significantly from survival in the other two treatments (Figure 1a).

ABOVE-GROUND BIOMASS OF TRANSPLANTS

The live above-ground biomass of surviving transplants differed among treatments in 2001 ($F_{2, 57} = 37.42$, $P = 0.0001$), but not in 2002 ($F_{2, 41} = 2.34$, $P = 0.109$). *Post-hoc* analyses of data from 2001 found that artificially grubbed plots and intact plots had significantly higher live biomass than the naturally devegetated treatment (Figure 1b). The non-significant differences between treatments in 2002 could be due to a small sample size for surviving transplants in naturally devegetated plots ($n = 5$).

Dead biomass indicates how much tissue senesced before sampling and can indicate whether a plant is suffering increased rates of tissue death. There were significant treatment effects on dead biomass of surviving transplants in 2001 ($F_{2, 57} = 14.40$, $P = 0.0001$) and 2002 ($F_{2, 41} = 9.40$, $P = 0.0004$). *Post-hoc* comparisons for 2001 found that transplants in intact vegetation had the highest amount of dead biomass, transplants in artificially grubbed plots had intermediate values, and transplants in naturally devegetated areas had the lowest values (Figure 1c). In 2002, transplants in intact vegetation again had significantly higher amounts of dead biomass than transplants in artificially grubbed plots or naturally devegetated areas (Figure 1c).

The proportion of above-ground biomass that is alive (= live biomass / [live + dead biomass]) is an indicator of plant vitality and can indicate whether growth exceeds senescence or *vice versa*. ANOVAs revealed significant differences among treatments in both 2001 ($F_{2, 57} = 23.66$, $P = 0.0001$) and 2002 ($F_{2, 41} = 38.36$, $P = 0.0001$). In 2001, *post-hoc* comparisons found that transplants in naturally devegetated areas had a lower proportion of live *Festuca* biomass (0.35 ± 0.77) (mean \pm SE) than plants in either the artificially grubbed plots (0.81 ± 0.24) or in intact vegetation (0.75 ± 0.03). In 2002, all

treatments were significantly different from each other; the naturally devegetated treatments had the highest proportion of live material (0.75 ± 0.02), the artificially grubbed plots had intermediate values (0.63 ± 0.02), and the intact vegetation had the lowest proportion (0.52 ± 0.02).

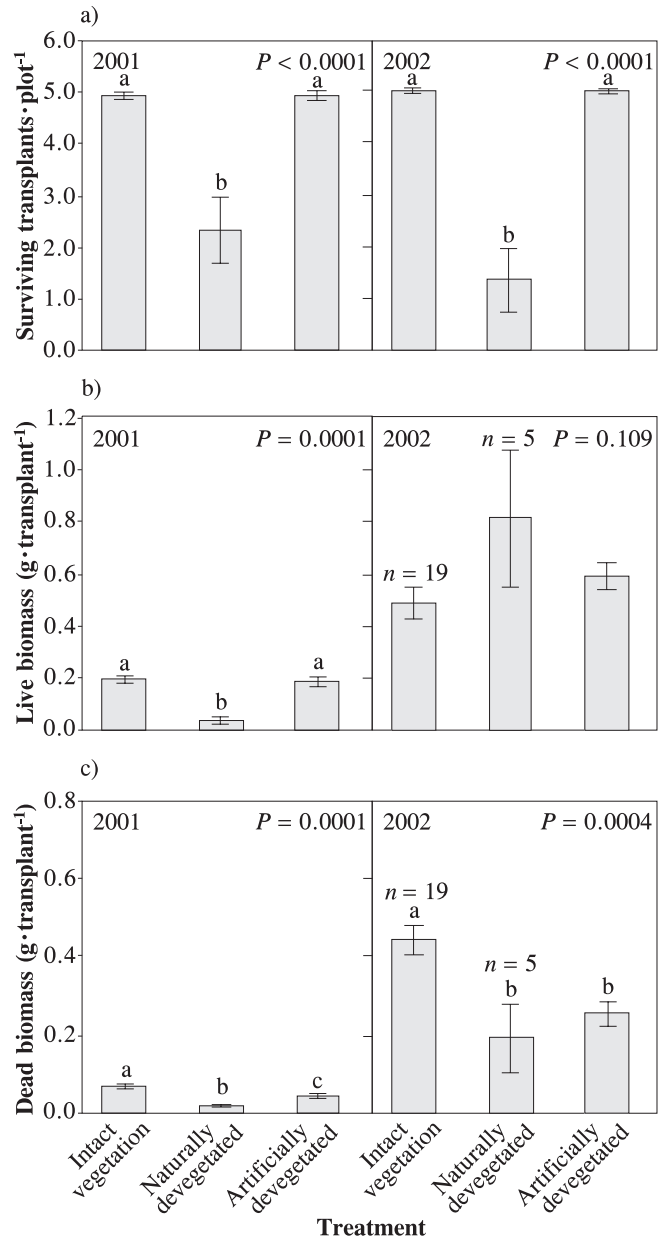


FIGURE 1. Survival and biomass of transplanted *Festuca* in intact vegetation, naturally devegetated plots, and artificially grubbed plots in August 2001 and July 2002. Data are mean \pm SE. a) Number of surviving transplants per plot, out of a total of five planted in June 2001. For each panel, letters above bars indicate results of *post-hoc* analyses (Bonferroni-corrected Mann-Whitney *U*-tests); treatments sharing the same letter are not significantly different ($P > 0.05$). Also shown is significance of a Kruskal-Wallis test comparing all three treatments. b) Live above-ground biomass and c) dead above-ground biomass per *Festuca* transplant; $n = 20$, except as indicated. For each panel, letters above bars indicate results of *post-hoc* analyses (Tukey-Kramer tests); treatments sharing the same letter are not significantly different ($P > 0.05$). Also shown is significance of an ANOVA comparing all three treatments.

Biomass of naturally occurring vegetation within experimental plots, sampled only in 2002, also differed among treatments ($F_{2, 27} = 155.17$, $P < 0.0001$). Plots of intact vegetation had the greatest amounts of naturally occurring *Festuca* biomass ($129.94 \pm 9.45 \text{ g}\cdot\text{m}^{-2}$); non-transplant *Festuca* biomass in naturally revegetated ($0.01 \pm 0.01 \text{ g}\cdot\text{m}^{-2}$) and artificially grubbed ($8.72 \pm 3.57 \text{ g}\cdot\text{m}^{-2}$) treatments was low. Other species, including *Triglochin maritima*, *Senecio congestus*, *Atriplex cf. subspicata*, and *Carex* spp. occurred as regrowth in experimental plots and accounted for $2.92 \text{ g}\cdot\text{m}^{-2}$ in undamaged sites, $4.11 \text{ g}\cdot\text{m}^{-2}$ in artificially grubbed plots, and $0.60 \text{ g}\cdot\text{m}^{-2}$ in naturally revegetated areas; these numbers amount to less than 4% of the biomass of *Festuca* in undisturbed sites.

ENVIRONMENTAL FACTORS

Our environmental measurements are based on a very small number of sampling episodes. Such infrequent samples are not able to provide a detailed description of physical conditions in degraded and intact sites, nor was that the intent. Instead, we present them as point samples of overall trends. They should not be interpreted as direct evidence that the physical conditions described are necessarily the cause of patterns in growth and survival of *Festuca*.

Soil salinity differed significantly among treatments in August 2001 ($F_{2, 15} = 14.19$, $P = 0.0003$); *post-hoc* tests found that naturally revegetated sites ($1.48 \pm 0.75 \text{ g}\cdot\text{L}^{-1}$) were significantly more saline than either intact vegetation ($0.13 \pm 0.02 \text{ g}\cdot\text{L}^{-1}$) or artificially grubbed ($0.26 \pm 0.06 \text{ g}\cdot\text{L}^{-1}$) treatments. Similarly, in July 2002, treatments differed significantly ($F_{2, 15} = 7.87$, $P = 0.0046$); in this case, *post-hoc* tests found that naturally revegetated soils ($4.68 \pm 1.41 \text{ g}\cdot\text{L}^{-1}$) were more saline than intact sites ($1.15 \pm 0.16 \text{ g}\cdot\text{L}^{-1}$), but artificially grubbed plots had intermediate salinity values that did not differ significantly from either of the other treatments ($2.03 \pm 0.49 \text{ g}\cdot\text{L}^{-1}$). Soil moisture also differed between treatments on both sampling dates (2001: $F_{2, 57} = 3.48$, $P = 0.038$; 2002: $F_{2, 57} = 6.19$, $P = 0.004$). *Post-hoc* comparisons for 2001 revealed soil water content in the naturally revegetated areas ($46.65 \pm 1.91\%$) was significantly lower than in artificially grubbed plots ($52.82 \pm 1.73\%$), while intact vegetation ($50.13 \pm 1.27\%$) did not differ from either treatment. In 2002, the naturally revegetated treatment ($32.30 \pm 1.70\%$) had lower soil moisture than both the intact vegetation ($39.10 \pm 1.07\%$) and artificially grubbed ($38.40 \pm 1.66\%$) treatments. Finally, soil temperature differed among treatments in August 2001 ($F_{2, 57} = 7.33$, $P = 0.002$) and July 2002 ($F_{2, 57} = 14.51$, $P < 0.0001$). In general, intact vegetation (2001: $22.55 \pm 0.42 \text{ }^\circ\text{C}$; 2002: $18.10 \pm 0.39 \text{ }^\circ\text{C}$) had significantly cooler soil temperatures than naturally revegetated (2001: $24.97 \pm 0.49 \text{ }^\circ\text{C}$; 2002: $21.59 \pm 0.47 \text{ }^\circ\text{C}$) or artificially grubbed areas (2001: $24.57 \pm 0.53 \text{ }^\circ\text{C}$; 2002: $19.94 \pm 0.51 \text{ }^\circ\text{C}$).

Discussion

Studies in intertidal and supratidal marshes of the sub-arctic/arctic boundary have shown that transplants of forage species are often unable to establish and survive in areas revegetated by lesser snow geese; whether establishment is possible depends on the extent of soil degrada-

tion (Handa & Jefferies, 2000; Handa, Harmsen & Jefferies, 2002; McLaren & Jefferies, 2004). Similarly, we found that transplants of *Festuca rubra* survived well for two seasons in undisturbed control plots and in artificially grubbed plots, but their survival was greatly reduced in older, natural disturbance. These differences may reflect a greater degree of soil degradation in sites that have been revegetated longer, though this requires further study.

As revealed by patterns of live biomass, growth of surviving transplants was also initially better in controls and artificially grubbed plots than in naturally revegetated sites, but in the second year growth of the few surviving transplants in naturally revegetated sites was equal to that in the other treatments. These results must be treated with suspicion given the small sample size in 2002. However, they may in part reflect reduced levels of senescence in grubbed areas: plants in both naturally and artificially revegetated sites had lower levels of dead biomass than plants in intact vegetation in both 2001 and 2002. As well, the proportion of live biomass was reduced relative to intact plots in naturally degraded areas in 2001, but increased in 2002, suggesting senescence may have initially increased, but then declined. We suspect these results indicate that transplants into naturally revegetated areas suffered a severe dieback in the first year, but that those few individuals that did survive (possibly because of chance placement in favourable microsites) may have enjoyed reduced competition compared to plants in freshly disturbed areas and especially in intact swards. Once established, it also is possible that these plants may have gradually improved their own microenvironment, for example by aerating soil through root growth or by trapping water and reducing salinity (Shumway & Bertness, 1994), thereby creating "safety islands" (Urbanska, 1997) for further growth and revegetation. It is uncertain whether the good performance of the survivors can persist, or whether these plants will eventually succumb to adverse physical conditions, similarly to the majority of transplants in the naturally revegetated sites.

Our results suggest that re-establishment of *Festuca* in areas revegetated by geese is likely to be a slow process: not only was transplant survival poor in naturally revegetated areas, but we also observed little natural recolonization in this 2-y study. Handa and Jefferies (2000) also found natural establishment of *Festuca rubra* at La Pérouse Bay to be severely limited in degraded areas, though it was increased by the presence of earlier successional vegetation consisting largely of intertidal species. It is possible that the re-establishment of *Festuca* at Akimiski Island similarly might benefit following colonization by other species, such as those that we recorded volunteering in our plots. Indeed, surviving plants of *Festuca* might themselves act as templates for further revegetation, especially if they ameliorate the environment as speculated above.

Studies of the snow goose colony at La Pérouse Bay, Manitoba, suggest that the soil properties most likely to hinder revegetation of damaged areas include increased bulk density, increased anoxia, reduced water content, and hypersalinity (Iacobelli & Jefferies, 1991; Srivastava & Jefferies, 1996; Handa & Jefferies, 2000; McLaren &

Jefferies, 2004). It takes time for these processes of soil damage to occur, so the degradation of the soil worsens over time (Iacobelli & Jefferies, 1991; Srivastava & Jefferies, 1996; Handa & Jefferies, 2000; McLaren & Jefferies, 2004). This is consistent with our result that substantial transplant establishment was possible in freshly disturbed sites, but not in older naturally revegetated soils. Our spot estimates found that soil water content was lower in soil from naturally revegetated areas than in intact vegetation and that salinity was higher in the naturally revegetated soils than any other treatment. Because these estimates are based on such a small number of samples, they cannot be assumed to be adequate descriptions of the physical environment; however, results from other degraded northern coastal marshes (Iacobelli & Jefferies, 1991; Srivastava & Jefferies, 1996; McLaren & Jefferies, 2004) suggest that these measurements might reflect conditions over much of the summer. Several of these factors potentially could underlie the reduced plant performance in degraded areas; further experimental work with *Festuca* in controlled conditions is required to identify the specific mechanisms involved.

Conclusion

Contrary to our hypothesis 1, revegetation did not result in an immediate decrease in the survival and growth of transplanted *Festuca*; however, as predicted by our hypothesis 2, survival was much reduced in areas revegetated by geese in previous years (though the few survivors performed unexpectedly well), suggesting the effects of revegetation worsen over time. Our results suggest that revegetation of subarctic *Festuca* meadows by geese may be difficult to reverse, as has been documented in other habitats at La Pérouse Bay (Jefferies, Rockwell & Abraham, 2004a). Thus, not only does our paper represent one of the first studies of grubbing by geese in this important coastal habitat, but it also provides independent support for goose-habitat models developed 1,000 km away.

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