

# Relationship between vegetation and soil seed banks in an arctic coastal marsh

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## Summary

**1** The effects of habitat degradation on the soil seed bank at La Pérouse Bay, Manitoba are described. Foraging by lesser snow geese leads to loss of vegetation, coupled with changes in soil abiotic conditions and an increase in salinity.

**2** The density of seeds and the relative abundance in the seed bank of species characteristic of undisturbed sites decrease following degradation, while the relative abundance of invasive species increases. Vegetation loss had the greatest impact on seed banks of stress-tolerant species and the least impact on species with many widely dispersed seeds.

**3** The above-ground vegetation and below-ground seed bank were less similar in undamaged plots than in disturbed plots. In spite of the low degree of similarity, redundancy analysis of the data indicated that approximately half of the variation in the soil seed bank could be explained by the vegetation data and vice versa.

**4** More recently degraded soils had richer soil seed banks than those from older disturbances. Site-specific factors not only influenced the species present but also the time lag between loss of vegetation and loss of the seed bank. Seed banks in these impacted and fragmented sites do not recover quickly.

**5** Seed banks in sandy beach-ridges were less affected by degradation due to the greater proportion of ruderals present in the original vegetation and the absence of the high soil salinities that are characteristic of degraded salt-marsh soils.

*Key-words:* beach-ridges, disturbance, lesser snow geese, redundancy analysis, salt-marsh, seed bank, stress

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## Introduction

Regeneration strategies of plants (Grubb 1977) are shaped by patterns of disturbance and stress, which act as selection forces over evolutionary time and can correspond approximately to the ruderal, stress-tolerator and competitor strategies in Grime's life history-based classification (1977, 1979). Seeds frequently persist in soil as a 'memory' of former vegetation (Bakker *et al.* 1996a), as they are often more tolerant of adverse conditions than their adult counterparts and, once buried in soil, they may escape from agents of disturbance, disease and predation. The presence of seeds in disturbed habitats (Grime 1979) is determined by the relationships between the original plant assemblages, propagule production and seed reserves in the soil. All will be affected by disturbance and stress, and the soil seed bank will decline as a function of the time that has lapsed since the vegetation was destroyed (Bakker *et al.* 1996a).

The highest similarity in species composition between vegetation and the soil seed bank is predicted when recruitment is tightly coupled with disturbance, and secondary succession follows the initial colonization (Pierce & Cowling 1991) as seen in early, frequently disturbed, successional communities in both coastal dunes (Pierce & Cowling 1991) and an alpine herb field (Chambers 1993). In later stages, the vegetation was composed of mostly long-lived species, while the seed bank was dominated by short-lived species (Chambers 1993).

In some northern and alpine habitats such as Mont Jacques-Cartier in Quebec (Morin & Payette 1988), vegetation and seed bank are correlated, but they are only loosely coupled in other arctic, subarctic and subalpine communities (Whipple 1978; Diemer & Prock 1993; Ingersoll & Wilson 1993; Staniforth *et al.* 1998). In wetlands similar correlations were found in freshwater marshes (Leck & Graveline 1979; Parker & Leck 1985; Leck & Simpson 1987), coastal salt-marshes (Hopkins & Parker 1984) and inland marshes (van der Valk & Davis 1978; Pederson 1981), but not in an Appalachian sphagnum bog (McGraw 1987), salt pans (Ungar &

Riehl 1980) or over 10 years in a tidal freshwater marsh on the Delaware River (Leck & Simpson 1995).

Methods used to determine the similarity between species composition of standing vegetation and seeds buried in the soil include qualitative assessment based on the presence and absence of species (Morin & Payette 1988), percentage similarity (Ingersoll & Wilson 1993; Ungar & Woodell 1996), comparisons of frequencies (Leck & Simpson 1987; Diemer & Prock 1993; Leck & Simpson 1995), Sørensen's similarity index (van der Valk & Davis 1976; Grandin & Rydin 1998), correlation coefficients (Spearman's correlation coefficient in Leck & Simpson 1995; Grandin & Rydin 1998; Staniforth *et al.* 1998; Kendall's rank correlation coefficient in Pierce & Cowling 1991; community coefficient in Pierce & Cowling 1991), the  $\chi^2$  goodness of fit test (Rydgren & Hestmark 1997) and the Mantel test (Jutila 1998). More recently, multivariate statistics have been used to summarize and assess the relationship (Bray & Curtis ordination, Jutila 1998; [detrended] correspondence analysis, Pierce & Cowling 1991; Looney & Gibson 1995; Rydgren & Hestmark 1997; Grandin & Rydin 1998; unweighted pair group mean cluster analysis, Ungar & Woodell 1996). The difficulties that arise due to the different scales used in measuring vegetation (frequency and cover estimates) and the seed bank (density per unit area) can be circumvented by comparing separate ordinations of the vegetation and the seed bank (Pierce & Cowling 1991; Looney & Gibson 1995), or by converting data to the presence or absence of species (Rydgren & Hestmark 1997). Grandin & Rydin (1998) simply noted the difference of scale in their ordinations and made comparisons based on the axes rather than absolute similarity values. Many other studies have used multiple methods.

Redundancy analysis (RDA) (van den Wollenberg 1977), a method largely neglected by ecologists (Jongman *et al.* 1987), is an appropriate alternative where spatial environmental gradients are short, as in this study, and linear responses of species are expected (ter Braak 1994). A form of reduced rank regression, RDA can be viewed as a constrained version of principal component analysis (PCA) (ter Braak 1994; Skinner *et al.* 1998). Canonical correlation analysis (CANCOR) may seem to be a more logical choice, as it would produce correlations and regressions for the degree of similarity between vegetation and seed bank, and vice versa, in one ordination (Skinner *et al.* 1998). However, its stringent requirements regarding the ratio of samples to species are fulfilled by few ecological data sets (Jongman *et al.* 1987). Two reciprocal RDA ordinations can, however, be viewed as equivalent to CANCOR and used to assess the effects of gradients of disturbance, stress on plants and other potentially important environmental variables that affect the relationships.

A study of the seed and vegetation dynamics was undertaken in both undamaged and degraded areas of an arctic coastal marsh where herbivory by lesser snow

geese (*Anser caerulescens caerulescens* L.) has led to a gradient of loss of vegetation and habitat degradation. The questions posed were as follows: (1) What is the effect of loss of vegetation on the soil seed bank? (2) To what extent can the below-ground seed bank be predicted from the above-ground vegetation and vice versa?

## Methods

### SITE AND VEGETATION DESCRIPTION

La Pérouse Bay (58°44' N, 94°28' W) is located 32 km east of Churchill, Manitoba, on the coast of the Hudson Bay lowlands. Permafrost, which is continuous in the Churchill region (Rouse *et al.* 1997), is found at depths of 25–30 cm below the surface of coastal salt-marshes in mid-summer (Wilson & Jefferies 1996). The soils of intertidal and supratidal marshes are regosolic static cryosols (Agriculture Canada Expert Committee on Soil Survey 1987) characterized by a gley mineral horizon (Cg) and a surface Ah horizon that is very shallow close to the coast (Wilson & Jefferies 1996). Surface soils of the beach-ridges where *Leymus mollis* grows, consist of undifferentiated sand and fine gravel (< 2 mm) with the presence of organic matter in the upper 15 cm.

Due to impeded drainage and the low salinity of tidal waters, an inverse salinity gradient exists with highest soil salinities recorded inland from the sea coast in the upper intertidal marsh or in the supratidal marsh (< two tidal inundations every 3 years) (Jefferies *et al.* 1979).

The salinity gradient is further modified by the foraging activities of a breeding colony of lesser snow geese, that has been increasing exponentially at a rate of about 7% per annum from an estimated 1300 breeding pairs in 1968 to 44 500 pairs in 1997 (Cooke *et al.* 1995; K.F. Abraham, K. Ross & R.F. Rockwell, unpublished aerial survey). Removal of live marsh vegetation and the insulating layer of litter by geese leads to increased soil surface temperatures and rates of evapotranspiration and hypersaline conditions, and substantially increased rates of soil erosion result (Srivastava & Jefferies 1996). Similar changes have accompanied pulling of lyme grass (*L. mollis*) shoots by geese on a nearby beach-ridge, which extends along the western coast of La Pérouse Bay for 3 km.

Undamaged intertidal flats are covered with a graminoid sward consisting of *Puccinellia phryganodes* and *Carex subspathacea* (all nomenclature follows Cody [1996] unless indicated) with associated dicotyledonous species including *Potentilla egedii*, *Plantago maritima*, *Ranunculus cymbalaria* and *Stellaria humifusa*. *Salicornia borealis* (Wolff & Jefferies 1987a,b) and *Senecio congestus* invade *Puccinellia*–*Carex* swards as degraded areas become increasingly saline. *Salicornia borealis* also colonizes degraded areas of the supratidal marsh where the vegetation previously consisted of low shrubs, *Salix brachycarpa* and *Salix myrtilifolia*, and two caespitose grasses, *Calamagrostis deschampsoides* and *Festuca*

*rubra*. On the beach-ridges, extensive stands of *L. mollis* have been replaced by ruderal species, such as *Matricaria ambigua*. General descriptions and locations of these communities, together with maps, are given in Jefferies *et al.* (1979) and Jano *et al.* (1998).

#### COLLECTION OF SEED BANK AND VEGETATION DATA

The soil seed bank and vegetation were sampled in intertidal, supratidal and inland salt-marshes, and on the beach-ridge. Sampling areas were chosen *a priori* based on the presence of selected indicator species for each type of community (e.g. *S. borealis* is characteristic of degraded, highly saline soils and *P. egedii* is restricted to undamaged salt-marsh vegetation). On the beach-ridge, closed swards of *L. mollis* were characteristic of undamaged plots and abundant *M. ambigua* indicated loss of lyme grass. Samples were collected from two long-term exclosures (exclosed since 1982), and 10 plots where loss of vegetation and soil degradation had occurred (degraded plots) on the intertidal marsh in the western section of La Pérouse Bay. Where large patches (> 9 m<sup>2</sup>) of intact vegetation remained, cores were taken from five undamaged and five degraded paired plots in the eastern area. Twenty undamaged and 20 degraded plots blocked into two sites of 10 plots each were sampled in the supratidal marsh, and samples were also taken from two long-term exclosures (exclosed since 1984) and two paired degraded plots in an inland salt-marsh 3 km from the coast. Lastly, 10 undamaged and 10 degraded paired plots were sampled on the beach-ridge. Each set of paired plots, as well as each of the 10 degraded plots on the western intertidal flats and each set of 20 paired undamaged and degraded vegetation plots in the supratidal marsh, were separated by at least 25 m.

The soil seed bank was sampled from supratidal areas after spring melt in June 1997 and from other areas at the same time of year in 1998. At each plot, 10 soil cores (diameter, 6.7 cm; depth, 6 cm) were taken randomly along a 1-m transect, separated into two layers and pooled within layers to give two samples of approximately 1 L of soil for each plot. The distribution of seeds in the soil profile can be used as an indicator of seed longevity of individual species (Thompson *et al.* 1997) and, where an organic horizon was visible usually 2–3 cm in depth, cores were separated into an upper organic and a lower mineral layer: otherwise the mineral horizon was separated into two equal portions. Seed banks were assessed using a modified seedling emergence technique (ter Heerdt *et al.* 1996). The seeds were concentrated by washing soils through a series of sieves (2 mm, 220 µm) using a Honda water pump before being spread out in trays (27 cm × 53 cm) on top of sterile silica sand, covered with ventilated cloches, and placed in a common garden at La Pérouse Bay Field Station. Trays were monitored and watered, usually twice a day, and shaded from bright sunlight. Seedlings were removed as soon as they could be identified, or transplanted into small flower pots

(10 cm in diameter), filled with a peat-marl mixture and grown until (except in a few cases) identification was possible. After approximately 6 weeks, soils in trays were dried, crumbled, and then watered and monitored for an additional 6 weeks before a subsample of soil from each tray (10% by mass) was checked under a dissection microscope for apparently viable seeds that had failed to germinate. However, very few intact seeds were found.

Percentage cover values were estimated for above-ground vegetation in late July and early August 1998 in the same plots where soil seed bank samples were collected. Vegetation abundance was estimated by selecting only a randomly chosen subset of the same plots used to sample the seed bank in the supratidal marsh ( $n = 15$  for undamaged plots and  $n = 10$  plots for degraded areas) and on the beach-ridge ( $n = 6$  plots each for undamaged and degraded areas). At each sampled plot a grid (1 m × 2 m separated into 10 cm × 10 cm cells) was used to estimate cover values. A pin was lowered at a random point within each 10 cm × 10 cm square ( $n = 200$  points per plot) and all species touching the pin were recorded.

#### COLLECTION OF ENVIRONMENTAL DATA

Soil samples were collected in August 1998 and 1999 in order to determine the distribution of particle sizes and salinity as these environmental variables are known to affect the distribution and growth of plants (Jefferies *et al.* 1979; Srivastava & Jefferies 1995b). Three plots were picked randomly from each of the undamaged and degraded sites sampled in the intertidal and supratidal salt-marsh, and on the beach-ridge. Where only two plots were available, such as exclosures in the western intertidal marsh, both were sampled.

Proportions of sand, silt and clay in mineral soils were determined using the hydrometer method to measure particle-size distribution (Sheldrick & Wang 1993). This measure was inappropriate for soils of the inland marsh that were rich in organic matter. Data for soils from the eastern intertidal salt-marsh were taken from Handa (1998).

Each year the soils were very dry in late July and early August. Due to the difficulty of extracting pore water, a known volume of water was added to a known mass of soil and the sodium concentration present in the water of amended soil (g Na per g dry soil) was used as an index of salinity (Srivastava & Jefferies 1995a). Sodium content of the extract was measured using a Perkin-Elmer atomic absorption spectrophotometer (model 3110) in flame-emission mode.

#### DATA ANALYSES

The relationship between the soil seed bank and above-ground vegetation was examined using RDA (Rao 1964; van den Wollenberg 1977). For the vegetation RDA, a centred and normed PCA was used initially to summarize the soil seed bank and environmental data in order

to increase the sample-to-predictor variable ratio. PCA was used rather than detrended correspondence analysis (DCA) or non-centred components analysis using varimax rotation as it resulted in an analysis with higher explanatory power. All variables were converted to a standardized scale as relative frequency out of 100%. The resulting first eight postnormalized PCA axes were then used to constrain the vegetation ordination. The biplot scores for the species in the seed bank data and the three environmental variables (percentage silt and sand in the particle-size distribution, sodium concentration) were projected onto the vegetation ordination using matrix multiplication where:

$$S = P \times R$$

where  $S$  represents a matrix with the species in the seed bank and the soil variables as its rows and the four RDA axes as columns,  $R$  represents eight principle component axes (rows) (four RDA axes (columns)), and  $P$  represents the species in the seed bank and the soil variables as predictors of species in the vegetation (rows) (eight principle component axes (columns)).

Resulting scores were postnormalized. Although percentage silt and sand are correlated, both soil variables were used because when a RDA was executed using the original variables rather than the summarized PCA axes, these two variables had inflation factors between 5 and 7 indicating that both contribute useful information independent of each other. An inflation factor of 30 indicates complete redundancy. For species found in both the vegetation and the seed bank, a Euclidean distance among the first four RDA axes was calculated between the position of the species in the vegetation ordination and the position of the endpoint for the biplot arrow. This represented the same species as a constraining variable in the seed bank based on the equation:

$$ED = [(v_1 - s_1)^2 + (v_2 - s_2)^2 + (v_3 - s_3)^2 + (v_4 - s_4)^2]^{1/2}$$

where ED is the Euclidean distance,  $v$  is the species scores in the vegetation species ordination,  $s$  is the species score in the constraining seed bank variables and subscripts 1–4 denote the RDA axes.

The same procedure was followed to predict seed bank data from vegetation and soil data. Comparison of the results of the RDA to random expectation based on Monte Carlo simulation (1000 permutations) was used to test for significance based on the  $F$ -statistic (ter Braak 1986). The statistical program used for these analyses was CANOCO Version 4 (ter Braak & Smilauer 1998).

## Results

### VEGETATION

The vegetation consisted of 33 species that were subjectively assigned to the plant species assemblage type with which they had the closest association (Jefferies

*et al.* 1979), based on long-term observations of the vegetation at La Pérouse Bay and elsewhere in the Hudson Bay lowlands (Table 1). Vegetation of undamaged salt-marshes included both a lower lying graminoid sward, and islands of willow-grassland each associated with characteristic dicotyledonous species (Table 1). *Salicornia borealis* invasion of devegetated hypersaline mudflats was accompanied by *Spergularia marina* and *Atriplex patula* whereas unconsolidated sediments in brackish ponds and streams within the delta of the Mast River and Wawao Creek were colonized by *Hippuris tetraphylla*. The 'weedy' assemblage consisted of ruderal species that were not tolerant of high soil salinity while the beach-ridge vegetation was dominated by *L. mollis*.

Loss of vegetation and degradation of habitat resulted in a substantially lower vegetation cover for all plots (Table 1) and shifts in relative abundance of salt-marsh or beach-ridge assemblages to more ruderal species (Fig. 1). In intertidal, supratidal and inland salt-marshes, vegetation changed from graminoid swards with relatively high dicotyledonous species diversity to plots with low plant biomass that were invaded by weedy species, such as *S. congestus* (Table 1).

Eventually, the only vegetation that persisted in damaged marsh sites was a monoculture of *S. borealis*. Among undamaged sites, the eastern intertidal plots had a high cumulative vegetation cover (100.2%), but extremely low dicotyledonous species diversity (Table 1). Disturbance of beach-ridges led to replacement of the dominant *L. mollis*, a tall grass, by short vegetative cover composed mostly of *M. ambigua*.

### SOIL SEED BANK

In general, total soil seed bank densities were highest in plots in the western intertidal marsh and the beach-ridge followed by plots in the supratidal, inland and eastern intertidal marshes (Table 2). Loss of vegetation and soil degradation did not significantly affect seed density in soils within each marsh, except for the supratidal marsh (Fig. 2e, Wilcoxon rank-sum test, but n.s. for all other cases). In addition, in this marsh there were also significant differences in seed abundance among sites.

However, there were clear differences in seed abundance with soil depth in the western intertidal marsh and the beach-ridge where seed densities were three to 10 times more abundant in the upper soil sections. In contrast, differences between upper and lower sections in seed density were non-significant in the eastern intertidal marsh.

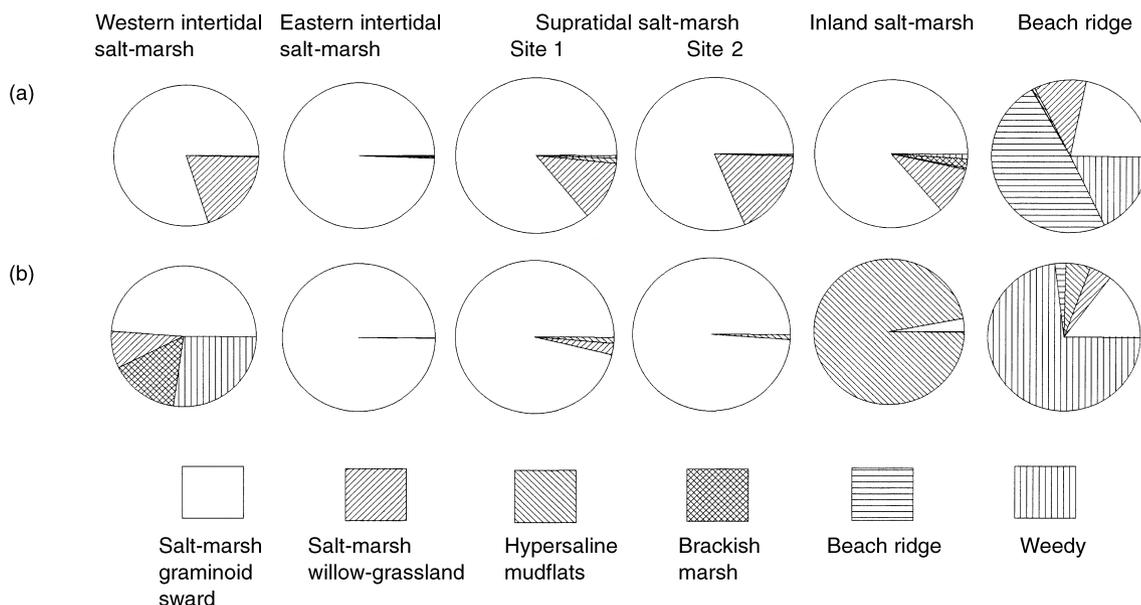
Overall, 23 species, of which very few were monocotyledonous, were found in the seed banks and each was assigned to the assemblage group with which it was most closely associated in the above-ground vegetation (Table 2). The small achenes (around 1.2 mm in length) of *R. cymbalaria* were abundant in soil under intertidal salt-marsh graminoid swards whereas seeds of *S. borealis*, an annual tolerant of high salinity, were an indicator of

**Table 1** Percentage cover ( $\pm$  standard error) of species in vegetation of undamaged and degraded plots. The undamaged plots in the western intertidal marsh and inland salt-marsh have been excluded from goose grazing since 1982 and 1985, respectively. Species abbreviations are given in parentheses

Species	Western intertidal salt-marsh		Eastern intertidal salt-marsh		Inland salt-marsh	
	Undamaged sites ( $n = 2$ )	Degraded sites ( $n = 10$ )	Undamaged sites ( $n = 5$ )	Degraded sites ( $n = 5$ )	Undamaged sites ( $n = 2$ )	Degraded sites ( $n = 2$ )
<b>Salt-marsh graminoid sward</b>						
<i>Carex subspathacea</i> (CS)	82.50	9.55 $\pm$ 3.48	1.00 $\pm$ 0.88	0.90 $\pm$ 0.78	46.25	0
<i>Potentilla egedii</i> (PE)	82.00	0.20 $\pm$ 0.20	1.60 $\pm$ 0.40	0.10 $\pm$ 0.10	20.75	0
<i>Puccinellia phryganodes</i> (PP)	26.75	7.05 $\pm$ 4.29	92.30 $\pm$ 2.50	9.20 $\pm$ 3.97	55.50	1.00
<i>Stellaria longipes</i> (SL)	26.00	0.20 $\pm$ 0.11	0	0	0	0
<i>Puccinellia nuttaliana</i> (PN)	10.50	0	0	0	8.75	0
<i>Ranunculus cymbalaria</i> (RC)	6.75	1.50 $\pm$ 0.40	0.80 $\pm$ 0.12	0	5.25	0
<i>Plantago maritima</i> (PM)	0	0	3.90 $\pm$ 3.31	1.00 $\pm$ 1.00	1.00	0
<i>Stellaria humifusa</i> (SH)	2.00	0	0.10 $\pm$ 0.10	0	1.00	0
<b>Salt-marsh willow-grassland</b>						
<i>Festuca rubra</i> (FR)	53.75	0.05 $\pm$ 0.05	0	0	11.75	0
<i>Calamagrostis deschampsoides</i> (CD)	4.75	2.10 $\pm$ 0.62	0	0	0	0
<i>Salix brachycarpa</i> (SaB)	0	1.00 $\pm$ 1.00	0	0	0	0
<i>Salix</i> sp. (Ssp)	0.25	0	0	0	0	0
<i>Parnassia palustris</i> (PaP)	0	0.05 $\pm$ 0.05	0	0	0.25	0
<i>Lomatogonium rotatum</i> (LR)	0	0.05 $\pm$ 0.05	0	0	4.25	0
<b>Hypersaline mudflats</b>						
<i>Salicornia borealis</i> (SB)	0.25	0	0.10 $\pm$ 0.10	0	0.75	32.50
<i>Spergularia marina</i> (SM)	0	0	0.10 $\pm$ 0.10	0	0	0.75
<b>Brackish marsh</b>						
<i>Salix candida</i> (SaC)	0	0	0	0	1.25	0
<i>Euphrasia arctica</i> (EA)	0	0	0	0	1.00	0
<i>Salix planifolia</i> (SaP)	0	0	0	0	0.75	0
<i>Triglochin palustris</i> (TP)	0.25	5.85 $\pm$ 2.86	0.30 $\pm$ 0.20	0	0	0
<b>Brackish ponds and streams</b>						
<i>Hippuris tetraphylla</i> (HT)	0	0.05 $\pm$ 0.05	0	0	0	0
<b>Weedy</b>						
<i>Senecio congestus</i> (SC)	0.25	10.25 $\pm$ 3.85	0	0	1.00	0
<i>Juncus bufonius</i> (JB)	0	0.10 $\pm$ 0.10	0	0	0	0
<i>Achillea nigrescens</i> (AN)	0	0	0	0	0.75	0
<b>Other</b>						
Unknown species 1 (UK1)	0	0.05 $\pm$ 0.05	0	0	2.75	0
<b>Total</b>	<b>296.00</b>	<b>38.05</b>	<b>100.20</b>	<b>11.20</b>	<b>163.00</b>	<b>34.25</b>

Table 1 Continued

Species	Supratidal salt-marsh				Beach-ridge	
	Undamaged sites		Degraded sites		Undamaged sites	Degraded sites
	Site 1 (n = 5)	Site 2 (n = 10)	Site 1 (n = 5)	Site 2 (n = 5)	(n = 2)	(n = 2)
Salt-marsh graminoid sward						
<i>Carex subspathacea</i> (CS)	37.00 ± 5.9	53.45 ± 5.30	0.30 ± 0.20	2.20 ± 0.84	0	0.08 ± 0.08
<i>Potentilla egedii</i> (PE)	10.20 ± 4.0	7.35 ± 1.06	0.10 ± 0.10	0	0	0
<i>Puccinellia phryganodes</i> (PP)	11.60 ± 0.8	9.95 ± 1.82	7.40 ± 3.93	6.90 ± 2.85	0.08 ± 0.08	1.25 ± 0.81
<i>Stellaria longipes</i> (SL)	0	0	0	0	27.50 ± 4.87	6.00 ± 2.21
<i>Puccinellia nuttalliana</i> (PN)	0	0	0	0	0	0.08 ± 0.08
<i>Ranunculus cymbalaria</i> (RC)	0.30 ± 0.2	0.45 ± 0.16	0	0	7.08 ± 1.80	5.92 ± 1.55
<i>Plantago maritima</i> (PM)	2.50 ± 1.0	0.15 ± 0.08	0	0	0	0
<i>Dupontia fisheri</i> (DF)	0	0.80 ± 0.45	0	0	0	0.42 ± 0.27
<i>Koenigia islandica</i> (KI)	0	0	0	0	0	0.17 ± 0.17
<i>Stellaria humifusa</i> (SH)	0	0	0	0	0	0.17 ± 0.17
Salt-marsh willow-grassland						
<i>Festuca rubra</i> (FR)	8.00 ± 2.4	13.25 ± 3.93	0.20 ± 0.20	0	0.50 ± 0.26	0.42 ± 0.20
<i>Calamagrostis deschampsoides</i> (CD)	0.10 ± 0.1	1.30 ± 0.35	0	0	11.91 ± 4.86	3.42 ± 1.92
<i>Salix brachycarpa</i> (SaB)	0.40 ± 0.2	0	0	0	0.08 ± 0.08	0.25 ± 0.17
<i>Salix</i> sp. (Ssp)	0.40 ± 0.4	1.25 ± 0.37	0	0	1.92 ± 0.44	0.08 ± 0.08
<i>Parnassia palustris</i> (PaP)	0	0.25 ± 0.20	0	0	0	0
<i>Lomatogonium rotatum</i> (LR)	0	0.20 ± 0.08	0	0	1.92 ± 0.98	0.17 ± 0.17
<i>Senecio pauperculus</i> (SP)	0	0	0	0	0.42 ± 0.33	0.08 ± 0.08
<i>Rhinanthus minor</i> (RB)	0	0	0	0	0.17 ± 0.17	0
Hypersaline Mudflats						
<i>Salicornia borealis</i> (SB)	0.40 ± 0.5	0	0.10 ± 0.10	0.10 ± 0.10	0	0
<i>Spergularia marina</i> (SM)	0.10 ± 0.1	0	0	0	0.08 ± 0.08	0
<i>Atriplex patula</i> (AP)	0	0	0	0	0.67 ± 0.21	5.08 ± 3.40
Brackish marsh						
<i>Euphrasia arctica</i> (EA)	0	0.05 ± 0.05	0	0	0.17 ± 0.17	0
<i>Triglochin palustris</i> (TP)	0	0.20 ± 0.13	0	0	0.08 ± 0.08	0
Beach-ridge						
<i>Leymus mollis</i> (LM)	0	0	0	0	72.58 ± 9.76	0
<i>Potentilla norvegica</i> (PoN)	0	0	0	0	3.33 ± 1.74	0.50 ± 0.41
<i>Minuartia rubella</i> (MR)	0	0	0	0	1.25 ± 1.25	1.50 ± 0.60
<i>Hordeum jubatum</i> (HJ)	0	0	0	0	0.42 ± 0.42	0.17 ± 0.17
Weedy						
<i>Senecio congestus</i> (SC)	0	0	0	0	4.08 ± 1.12	0.92 ± 0.40
<i>Juncus bufonius</i> (JB)	0.30 ± 0.2	0	0	0	0	0
<i>Matricaria ambigua</i> (MA)	0.10 ± 0.1	0	0	0	23.50 ± 5.36	68.67 ± 5.62
<i>Rumex occidentalis</i> (RO)	0	0.10 ± 0.07	0	0	0.33 ± 0.25	0.08 ± 0.08
<i>Achillea nigrescens</i> (AN)	0	0	0	0	0.25 ± 0.17	0
Other						
Unknown species 1 (UK1)	0	0	0	0	0.25 ± 0.17	1.34 ± 0.95
Total	71.40	88.75	8.10	9.20	158.58	96.8



**Fig. 1** Relative abundance of assemblages of plant species (see Table 1 for composition) found in the above-ground vegetation. (a) Undamaged plots, (b) degraded plots.

hypersaline mudflat sediments. Species characteristic of brackish marsh, brackish ponds and streams, and freshwater ponds and streams, which occur geographically close to the sampled salt-marsh plots, were also found in the seed bank, suggesting that some seeds that dispersed to the plots were incorporated into the seed bank (Table 2). The weedy assemblage that consisted of mostly ruderal species that colonize disturbed soils, but are not highly salt tolerant, was mainly represented in the seed bank by *Juncus bufonius*, a widely distributed annual species with many records of a persistent seed bank (Thompson *et al.* 1997). Only four species found here appeared to be members of long-term persistent seed banks, i.e. *R. cymbalaria*, *Hippuris* spp., *J. bufonius* and an unidentified member of Rosaceae that is not found in the La Pérouse Bay flora at present (Table 2). It should be noted that the seed banks all of the dominant species (*P. phryganodes* and *C. subspathacea* in the salt-marsh, *L. mollis* on the beach-ridge) are extremely small or absent because of irregular flowering and fruit set, grazing and sterility.

Soil degradation caused seed banks in the supratidal marsh and, to a lesser extent on the beach-ridge, to show shifts in relative abundance of seeds of different assemblages towards more ruderal species (Fig. 3); that is comparable with changes in the vegetation (Fig. 1).

The seed bank in other habitats showed little change (Fig. 3). The western intertidal marsh was dominated by seeds typical of the graminoid sward (Table 2), except in the lower layers of the soil in undamaged plots where an assemblage, typical of brackish ponds and streams, and consisting mostly of *Hippuris* spp., formed 67% of the seed bank. Seeds representative of plants from hypersaline mudflats, the vegetation typical of degraded salt-marshes, had the greatest relative abundance in plots in the inland salt-marsh. They made up most of

the seed bank where soil was degraded (60% and 90% at this location), as well as that in the upper organic layers of undamaged plots (97%). In contrast, the weedy assemblage formed a significant proportion of the seed bank in the mineral layers of plots where vegetation was undamaged and in the organic layers where soil was degraded (Table 2).

The soil seed density was so low in the eastern intertidal sites that it was difficult to determine the affinities of seeds to current plant assemblages. The only species to have a density of at least 100 seeds  $m^{-2}$  was *R. cymbalaria*, which was found in the top soil layer of undamaged plots.

#### VEGETATION ORDINATION CONSTRAINED BY SEED BANK

Overall, the eight seed bank variables (PCA axes one to eight) and the three soil variables (salinity, silt and sand percentages) explained 49.5% ( $P < 0.005$ ) of the variation in the species data. The first two axes collectively contained 39.5% and the first three axes accounted for 45.9% of the variability. Tests on both the first axis ( $F$ -ratio = 19.21,  $P = 0.001$ ) and the total configuration ( $F$ -ratio = 6.14,  $P = 0.001$ ) showed a high level of significance. For the eight modified seed bank and environmental variables, the first eight PCA axes explained 99.7% of the variance with 73.7% contained within the first two axes. The first RDA axis separated the more silty salt-marsh plots from the sandier beach-ridge (Fig. 4a). The second RDA axis represented a disturbance gradient with salinity (sodium concentration) showing the highest correlation, although proportion of sand was also important. The placement of plots along the disturbance gradient corresponded well with *a priori* assignment with three of the long-term exclosures

**Table 2** Density of species found in seed bank (seeds m<sup>-2</sup> ± SE). Each sample (\*) contains 10 pooled soil cores. Samples of varying thickness (+); all samples of same thickness (+ +)

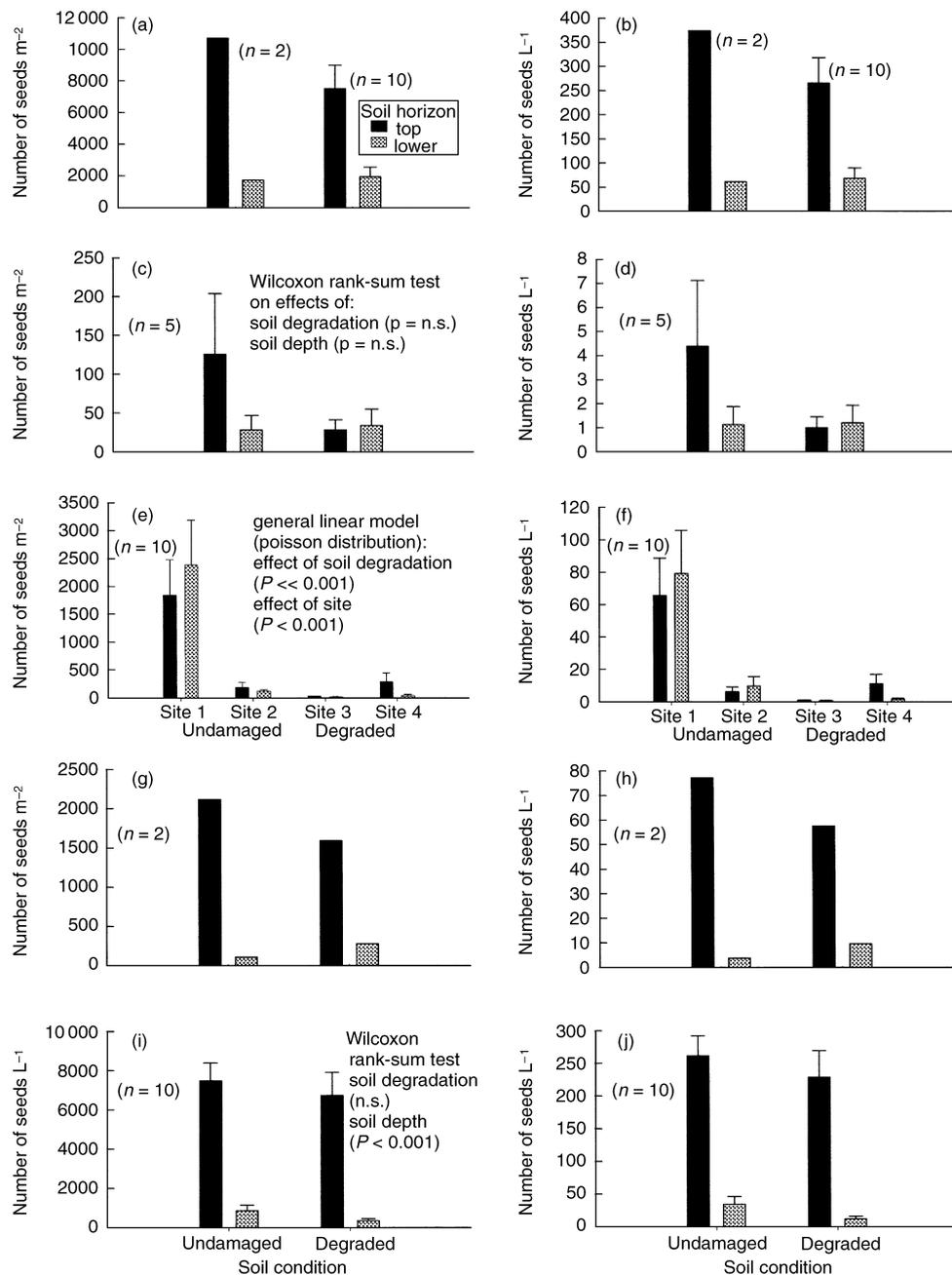
Species	Western intertidal salt-marsh				Eastern intertidal salt-marsh			
	Undamaged (n = 2* for each layer)		Degraded (n = 10* for each layer)		Undamaged (n = 5* for each layer)		Degraded (n = 5* for each layer)	
	Top layer (3 cm) + +	Lower layer (2.5–3 cm) +	Top layer (2.2–3.0 cm) +	Lower layer (2.5–3.0 cm) +	Top layer (3.0 cm) + +	Lower layer (2.0–3.0 cm) +	Top layer (3.0 cm) + +	Lower layer (2.5–3.0 cm) +
<b>Salt-marsh graminoid sward</b>								
<i>Ranunculus cymbalaria</i> (RC)	9380	471	7100 ± 1500	1900 ± 594	120 ± 80.0	0	17.1 ± 11.4	0
<i>Potentilla egedii</i> (PE)	257	0	5.71 ± 5.71	2.86 ± 2.86	0	0	0	0
<i>Carex subspathacea</i> (CS)	343	0	2.86 ± 2.86	0	0	0	0	0
<i>Stellaria longipes</i> (SL)	71.4	0	2.86 ± 2.86	0	0	0	0	0
<b>Salt-marsh willow-grassland</b>								
<i>Salix</i> spp. (Ssp)	14.3	28.6	11.4 ± 6.32	8.57 ± 7.18	0	17.1 ± 11.4	5.71 ± 5.71	22.8 ± 16.6
<i>Festuca rubra</i> (FR)	85.7	0	5.71 ± 2.81	5.71 ± 3.81	0	5.71 ± 5.71	0	0
<b>Hypersaline mudflats</b>								
<i>Salicornia borealis</i> (SB)	28.6	0	0	2.86 ± 2.86	0	0	0	0
<i>Spergularia marina</i> (SM)	14.3	0	0	0	0	0	0	0
<i>Atriplex patula</i> (AP)	0	14.3	0	0	0	0	0	0
<b>Brackish ponds and streams</b>								
<i>Hippuris</i> spp. (Hsp)	171	1160	266 ± 83.5	22.8 ± 14.0	5.71 ± 5.71	0	5.71 ± 5.71	11.4 ± 7.00
<b>Weedy</b>								
<i>Juncus bufonius</i> (JB)	0	0	51.4 ± 38.3	0	0	0	0	0
<i>Senecio congestus</i> (SC)	314	71.4	5.71 ± 3.81	0	0	5.71 ± 5.71	0	0
<i>Achillea nigrescens</i> (AN)	0	0	2.86 ± 2.86	0	0	0	0	0
<i>Matricaria ambigua</i> (MA)	14.3	0	0	2.86 ± 2.86	0	0	0	0
<b>Other</b>								
Unknown species 1 (UK1)	0	0	68.6 ± 53.06	14.3 ± 7.68	0	0	0	0
<b>Total</b>	<b>10700</b>	<b>1740</b>	<b>7520 ± 1480</b>	<b>1960 ± 607</b>	<b>126 ± 78.0</b>	<b>28.6 ± 18.1</b>	<b>28.6 ± 12.8</b>	<b>34.3 ± 21.0</b>

Table 2 Continued

Species	Supratidal salt-marsh							
	Undamaged ( $n = 10^*$ for each layer)				Degraded ( $n = 10^*$ for each layer)			
	Site 1		Site 2		Site 3		Site 4	
	Organic (2.1–3.5 cm) +	Mineral (2.0–3.5 cm) +	Organic (2.3–3.7 cm) +	Mineral (2.0–3.5 cm) +	Top layer (2.0–4.5 cm) +	Lower layer (1.5–4.6 cm) +	Top layer (1.6–3.7 cm) +	Lower layer (1.6–3.4 cm) +
<b>Salt-marsh graminoid sward</b>								
<i>Ranunculus cymbalaria</i> (RC)	948 ± 425	1820 ± 772	134 ± 89.2	97.1 ± 24.5	0	0	11.42 ± 6.32	8.57 ± 4.36
<i>Potentilla egedii</i> (PE)	17.1 ± 6.32	0	2.86 ± 2.86	11.43 ± 8.73	0	0	0	0
<i>Stellaria longipes</i> (SL)	0	5.71 ± 3.81	2.86 ± 2.86	0	1.43 ± 1.43	0	5.71 ± 3.81	0
<b>Salt-marsh willow-grassland</b>								
<i>Salix</i> spp. (Ssp)	68.6 ± 17.1	5.71 ± 3.81	14.3 ± 7.68	0	0	0	17.1 ± 12.2	0
<i>Festuca rubra</i> (FR)	14.3 ± 7.68	8.57 ± 6.10	5.71 ± 5.71	0	0	0	0	0
<i>Primula</i> spp. (Psp)	0	0	2.86 ± 2.86	0	0	0	0	0
<b>Hypersaline mudflats</b>								
<i>Salicornia borealis</i> (SB)	54.3 ± 20.6	0	8.57 ± 4.36	2.86 ± 2.86	8.57 ± 6.10	11.4 ± 11.4	234 ± 139	22.86 ± 22.86
<i>Spergularia marina</i> (SM)	0	0	0	0	0	0	2.86 ± 2.86	2.86 ± 2.86
<b>Brackish ponds and streams</b>								
<i>Hippuris</i> spp. (Hsp)	37.1 ± 17.1	91.4 ± 53.0	0	8.57 ± 6.10	0	0	0	2.86 ± 2.86
<i>Ranunculus gmelinii</i> ssp. <i>purshii</i> (RG)	0	2.86 ± 2.02	0	0	0	0	0	0
<b>Freshwater ponds and streams</b>								
<i>Carex aquatilis</i> (CA)	0	0	5.71 ± 3.81	0	0	0	0	0
<b>Weedy</b>								
<i>Juncus bufonius</i> (JB)	694 ± 534	434 ± 369	0	0	0	0	0	0
<i>Senecio congestus</i> (SC)	8.57 ± 4.36	17.1 ± 11.4	0	0	2.86 ± 2.86	0	0	0
<i>Achillea nigrescens</i> (AN)	0	0	0	0	0	0	8.57 ± 8.57	0
<i>Matricaria ambigua</i> (MA)	0	0	0	0	2.86 ± 2.86	0	0	0
<b>Other</b>								
Rosaceae (ROS)	0	5.71 ± 5.71	8.57 ± 6.10	0	7.14 ± 3.84	0	0	0
Unknown species 1 (UK1)	0	0	0	0	1.43 ± 1.43	0	0	0
<b>Total</b>	<b>1843 ± 637</b>	<b>2390 ± 810</b>	<b>186 ± 90</b>	<b>120.0 ± 25.5</b>	<b>24.28 ± 6.04</b>	<b>11.4 ± 11.4</b>	<b>280 ± 157</b>	<b>37.14 ± 25.22</b>

Table 2 Continued

Species	Inland salt-marsh				Beach-ridge			
	Undamaged ( $n = 2^*$ for each layer)		Degraded ( $n = 2^*$ for each layer)		Undamaged ( $n = 10^*$ for each layer)		Degraded ( $n = 10^*$ for each layer)	
	Organic (2.4–3.0 cm) +	Mineral (2.0–3.0 cm) +	Organic (2.5–3.5 cm) +	Mineral (3.0 cm) ++	Organic (2.5–4.0 cm) +	Mineral (1.0–3.5 cm) +	Organic (2.5–4.5 cm) +	Mineral (1.5–4.0 cm) +
<b>Salt-marsh graminoid sward</b>								
<i>Ranunculus cymbalaria</i> (RC)	28.6	28.6	42.8	0	1960 ± 631	137 ± 74.3	471 ± 150	34.3 ± 10.2
<i>Potentilla egedii</i> (PE)	0	0	0	0	2.86 ± 2.86	0	0	0
<i>Stellaria longipes</i> (SL)	0	0	0	0	237 ± 82.1	20.0 ± 8.57	42.8 ± 14.3	14.3 ± 8.78
<i>Carex subspathacea</i> (CS)	0	0	0	0	0	22.8 ± 22.8	0	0
<b>Salt-marsh willow-grassland</b>								
<i>Salix</i> spp. (Ssp)	14.3	0	42.8	28.6	2.86 ± 2.86	8.57 ± 6.10	5.71 ± 3.81	2.86 ± 2.86
<i>Festuca rubra</i> (FR)	0	0	14.3	0	468 ± 186	208 ± 130	8.57 ± 6.10	2.86 ± 2.86
<i>Senecio pauperculus</i> (SP)	0	0	0	0	0	2.86 ± 2.86	0	0
<b>Hypersaline mudflats</b>								
<i>Salicornia borealis</i> (SB)	2040	14.3	943	243	2.86 ± 2.86	0	0	0
<i>Spergularia marina</i> (SM)	14.3	0	14.3	0	42.8 ± 28.3	5.71 ± 5.71	137 ± 131	2.86 ± 2.86
<i>Atriplex patula</i> (AP)	14.3	0	42.8	0	843 ± 444	74.3 ± 58.9	1010 ± 753	8.57 ± 6.10
<b>Brackish ponds and streams</b>								
<i>Hippuris</i> spp. (Hsp)	0	0	14.3	0	0	0	2.86 ± 2.86	0
<b>Brackish marsh</b>								
<i>Triglochin palustris</i> (TP)	0	14.3	0	0	0	0	0	0
<b>Beach-ridges</b>								
<i>Saxifraga oppositifolia</i> (SO)	0	0	0	0	0	0	0	2.86 ± 2.86
<b>Weedy</b>								
<i>Juncus bufonius</i> (JB)	0	28.6	443	0	0	2.86 ± 2.86	42.8 ± 34.4	2.86 ± 2.86
<i>Senecio congestus</i> (SC)	0	14.3	28.6	0	951 ± 152	131 ± 44.5	388 ± 85.1	60.0 ± 53.8
<i>Achillea nigrescens</i> (AN)	0	0	0	0	0	0	2.86 ± 2.86	0
<i>Matricaria ambigua</i> (MA)	0	0	0	0	2880 ± 633	234 ± 107	4570 ± 1040	203 ± 67.4
<b>Other</b>								
Unknown species 1 (UK1)	0	0	0	0	106 ± 41.7	5.71 ± 35.6	11.4 ± 4.67	0
<b>Total</b>	<b>2114</b>	<b>100.0</b>	<b>1586</b>	<b>271</b>	<b>7490 ± 886</b>	<b>854 ± 286</b>	<b>6700 ± 1190</b>	<b>334 ± 96.9</b>

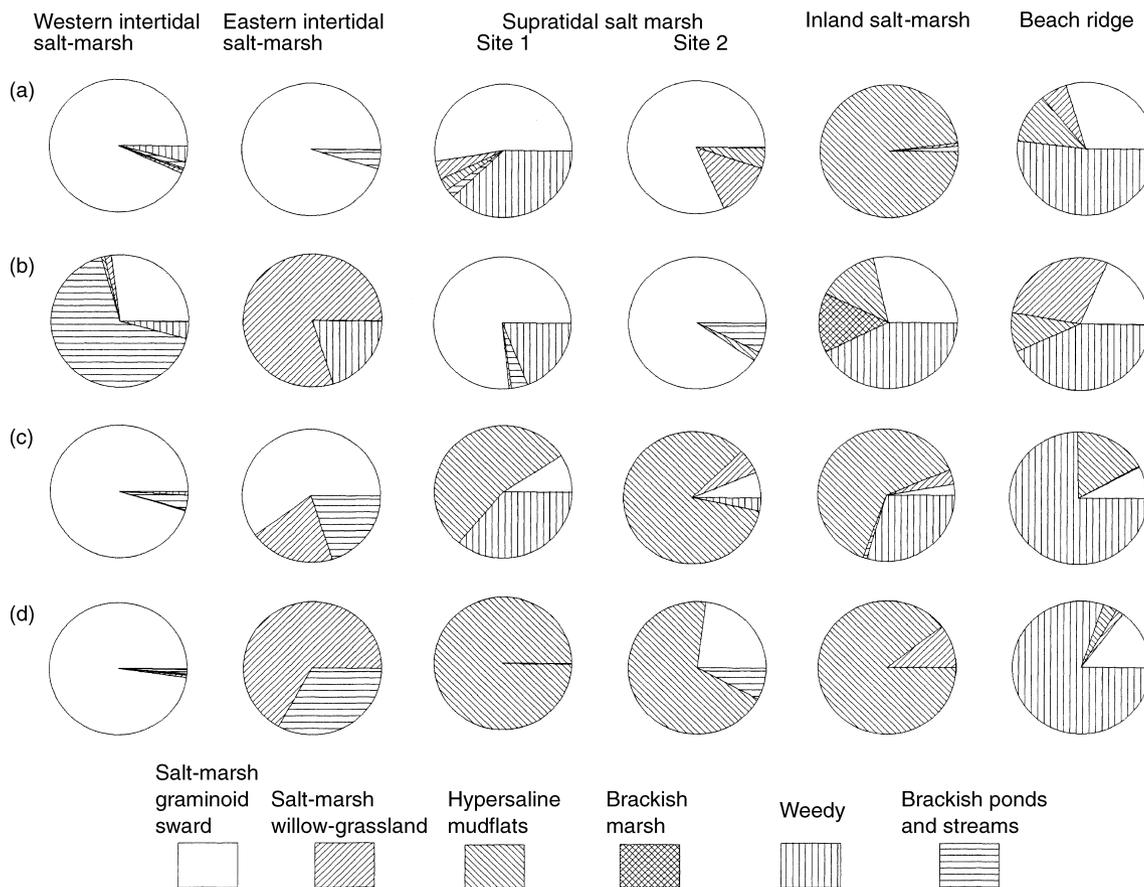


**Fig. 2** Seed bank density (all species pooled) of undamaged and degraded salt-marsh sites expressed per unit area and per unit volume. (a, b) Western intertidal plots; range is 9100–12 300 seeds  $m^{-2}$  for upper layers of soil in enclosed plots and 1600–1880 seeds  $m^{-2}$  for lower layers of soil in enclosed plots. (c, d) Eastern intertidal salt-marsh plots, (e, f) supratidal marsh, (g, h) inland marsh; range is given for upper and lower layers of soil in enclosed plots, and upper and lower layers of soil in damaged plots, respectively: 800–3400 seeds  $m^{-2}$ , 86–110 seeds  $m^{-2}$ , 940–2200 seeds  $m^{-2}$  and 260–285 seeds  $m^{-2}$ . (i, j) beach-ridge plots. Density was calculated originally per unit volume due to the unequal sampling of depth and then converted into the less accurate per unit area. Sample sizes are contained in parentheses.

well separated from all the degraded plots and undamaged supratidal plots. The eastern intertidal plots where vegetation was intact and one inland enclosure formed a group on the third axis (not shown). These plots have moderately high plant cover but low species diversity, which suggests partial damage or recent colonization and development of a graminoid sward in the case of the enclosure, possibly due to trampling and grazing by caribou in 1994 and 1996. Competitive exclusion is an unlikely explanation as it is a process usually restricted

to the higher successional willow-grassland sites covered with swards of *F. rubra* and *C. deschampsoides*, rather than grazed *Puccinellia*–*Carex* swards.

The species–variable biplot (Fig. 4b) shows the distribution of the species found in the vegetation and the distribution of the constraining species found in the seed bank. Some species, including *J. bufonius*, *P. egedii*, *M. ambigua*, *A. patula* and *S. borealis*, occupy similar positions in the two distributions and the multidimensional Euclidean distance is short (Table 3) whereas species



**Fig. 3** Relative abundance of plant assemblages (see Table 2) found in the soil seed bank in the organic or top layer (a, c) and mineral or lower layer (b, d) of undamaged and degraded soils, respectively. The presence of an organic layer depends upon the salt-marsh zonation and the site condition.

**Table 3** Euclidean distance among first four redundancy analysis (RDA) axes calculated between position of species in the species ordination and in the constraining variables

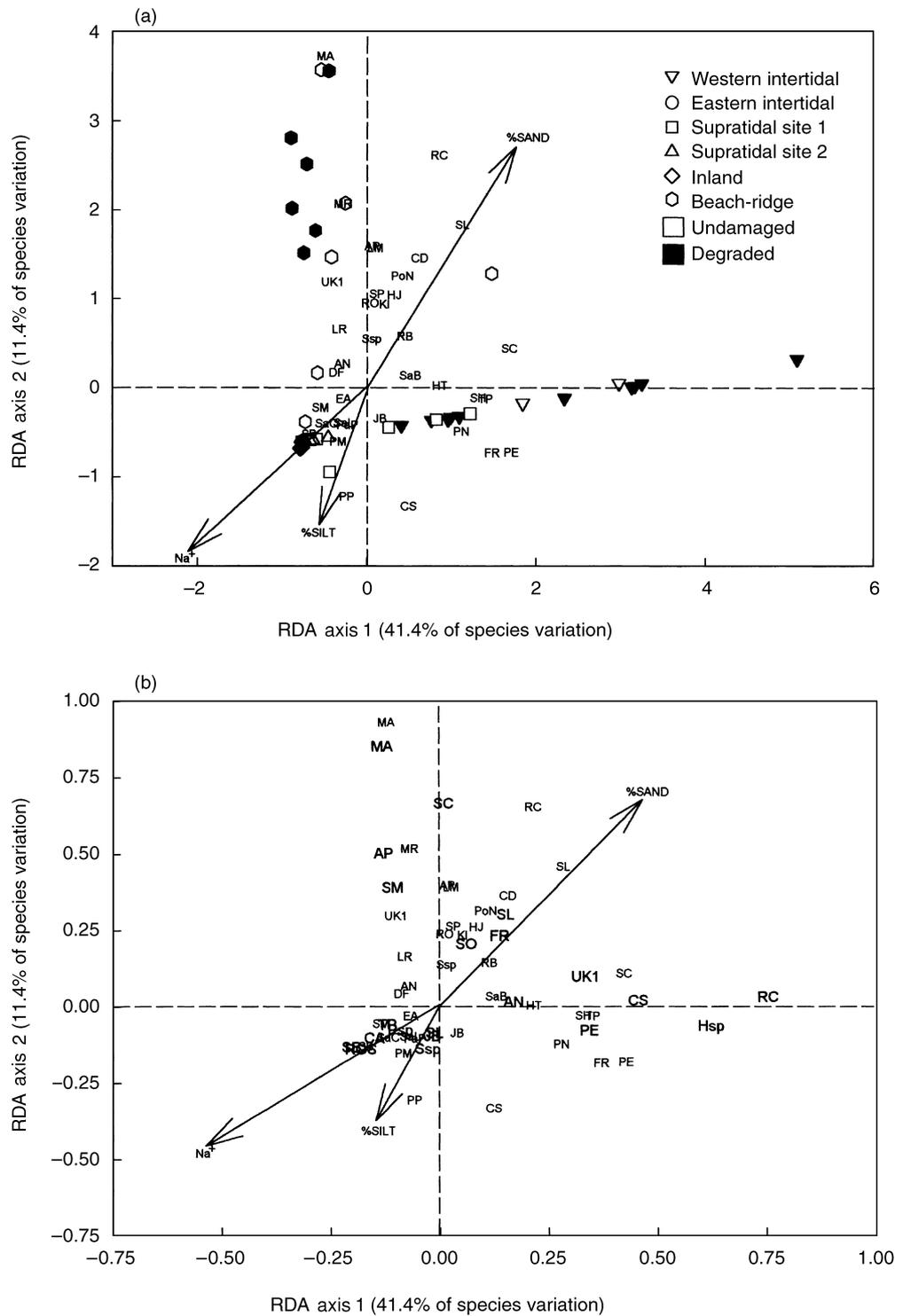
Species	Euclidean distance in seed bank RDA	Rank in seed bank RDA	Euclidean distance in vegetation RDA	Rank in vegetation RDA
<i>Juncus bufonius</i>	0.088187	1	0.053299	1
<i>Potentilla egedii</i>	0.182975	2	0.216858	3
<i>Matricaria ambigua</i>	0.191915	3	0.117689	2
<i>Atriplex patula</i>	0.196805	4	0.465001	5
<i>Salicornia borealis</i>	0.273251	5	0.494135	6
<i>Stellaria longipes</i>	0.333149	6	0.29502	4
<i>Hippuris</i> spp.	0.428626	7	0.568504	10
<i>Achillea nigrescens</i>	0.443124	8	0.584276	11
<i>Salix lanata</i>	0.486874	9	0.567008	9
<i>Salix</i> spp.	0.549631	10	0.614478	12
<i>Carex subspathacea</i>	0.576832	11	0.669819	14
<i>Spergularia marina</i>	0.582876	12	0.536944	7
Unknown species 1	0.659066	13	0.63975	13
<i>Triglochin palustris</i>	0.762462	14	0.544449	8
<i>Festuca rubra</i>	0.795892	15	1.023676	16
<i>Senecio congestus</i>	0.804974	16	0.974186	15
<i>Ranunculus cymbalaria</i>	0.864135	17	1.13357	17

such as *S. congestus* and *R. cymbalaria* occur further apart. Caution must be used when interpreting the Euclidean distance for *Hippuris* spp., *Achillea nigrescens*, *Salix lanata*, *Salix* spp. and *Triglochin palustris* due to their very low incidence in the vegetation and/or the seed bank.

#### SEED BANK ORDINATION CONSTRAINED BY VEGETATION

Modified vegetation and soil variables were slightly better predictors of the soil seed bank than vice versa,





**Fig. 5** Redundancy analysis (RDA) based on density of species in the soil seed bank constrained by percentage cover of species in the vegetation and three soil variables (sand, silt and salinity,  $\text{Na}^+$ ). Vegetation and soil factors were summarized using a principle component analysis (PCA) and the resulting first eight PCA axes were used as constraining variables. The positions of species in the vegetation and soil variables were projected back through matrix multiplication. (a) Sample-variable biplot; (b) species ordination. Species in the vegetation are shown in small upper case letters and are not represented by biplot arrows for the sake of clarity. Species present in the seed bank are shown in large upper case letters. See Tables 1 & 2 for abbreviations.

ordination). Other major differences were that the seed banks of the degraded western intertidal plots contained species characteristic of undamaged vegetation, while the two exclosures in the inland

marsh had seed banks typical of degraded soils. The ranking of Euclidean distance was similar in the two ordinations (Table 3), with greater consistency at the extremes (Fig. 5b).

## Discussion

### EFFECT OF THE LOSS OF VEGETATION ON THE SOIL SEED BANK

The combination of disturbance and physical stress on plants has a major effect on vegetation, as predicted by Grime (1979). The RDA vegetation ordination (Fig. 4) clearly delineated undamaged areas from areas where soil was degraded. As expected, salinity stress was positively correlated with disturbance, and disturbed salt-marsh plots were appreciably more saline than beach-ridge plots.

Loss of vegetation led to a decline in the density of the soil seed bank. While total seed number was not significantly different in the western intertidal and inland salt-marshes, and on the beach-ridge where vegetation is relatively intact, density decreased when spatial and temporal scales of degradation were greater (Fig. 2), and the soils of the more degraded inland and eastern intertidal salt-marshes thus contain fewer seeds. This pattern was not always apparent on a smaller scale as the loss of seeds from the soil following vegetation damage was non-linear and exhibited a threshold associated with soil erosion. Vegetation loss also led to decreasing relative abundance of seeds of species characteristic of intact vegetation and an increase in invasive species (weedy species or annuals typical of hypersaline mudflats). Even species with long-term persistent seed banks are vulnerable to local extinction due to erosion, and our plots reflect different stages in this process. Most soil degradation in the western intertidal marsh and the supratidal marsh occurred at about the same time (1988–90), and the former now has low values for vegetation cover while still retaining this relatively rich seed bank. Processes appear to have been slower in the latter, possibly because there is organic matter in the soil that is less easy to erode. In the supratidal salt-marsh, site differences in the seed bank were apparent where the vegetation was undamaged, but were not apparent in degraded areas.

The inland enclosures also have undamaged vegetation but seed banks here are very poor and are composed mostly of *S. borealis*, an indicator of disturbance and high salinity. Degradation which was already apparent during the late 1970s and rapid run-off of melt water may have strongly affected seed accumulation, despite its continuing production. Although *S. borealis* is present at low frequencies in enclosed plots, it is the dominant species in the surrounding degraded soils, and, hence, may have dispersed high numbers of seeds there.

Most of the degradation on the beach-ridge occurred between 1973 and 1984 (remote-sensing data, Jano *et al.* 1998), and loss of vegetation was associated with loss of soil. However, the reduced effect of vegetation loss on the seed banks here may be due to the greater number of free seeding ruderal species and the lack of hypersaline conditions (Srivastava & Jefferies 1996).

### REGENERATION STRATEGIES OF PLANTS IN UNDAMAGED AND DEGRADED HABITATS

The effect of loss of vegetation on the soil seed bank is influenced by the regeneration strategies of plants (Grubb 1977). Stress-tolerant species are often long-lived clonal plants (Grime 1979). The undamaged salt-marsh is composed mostly of perennial vegetation and the species with the highest cover frequencies, *C. subspathacea*, *P. phryganodes*, *P. egedii* and *S. humifusa* (Table 1) are all salt-tolerant plants. They are capable of extensive stoloniferous or rhizomatous growth and *P. phryganodes* and *C. subspathacea* can also disperse and establish from plant fragments, including individual leaves, shoot systems and tillers (Chou *et al.* 1992).

The most common species in the soil seed bank when the vegetation is undamaged are *R. cymbalaria*, *Hippuris* spp. and *P. egedii* (Table 2). Seeds of *J. bufonius*, an annual rush, are sometimes present in high densities but their distribution is patchy. Of these species, only *P. egedii* is common in salt-marsh vegetation, but the only seeds that are present in substantial densities in all zones and at all soil depths are those of *R. cymbalaria* (up to 9380 seeds m<sup>-2</sup>) and *Hippuris* spp. (up to 1160 seeds m<sup>-2</sup>). Species characteristic of the undamaged salt-marsh tend to spread clonally and do not therefore contribute to the soil seed bank apart from *R. cymbalaria*, which is a minor component of the vegetation.

Staniforth *et al.* (1998) found very high numbers of seeds of *J. bufonius* and *S. marina* in salt-marsh sediments at Churchill. These two species formed 92% of the total seed bank, which had a mean of 39 204 seeds m<sup>-2</sup>, possibly because the soils are sandier and of lower salinity (average of 10 g of solute per litre of soil solution; Staniforth *et al.* 1998) than at La Pérouse Bay.

Salinity and desiccation may limit seed viability and ability to germinate, despite large annual production. Colonizers can be categorized as stress-tolerators (*sensu* Grime 1977) because of the build up of salinity and the drying out of soils away from drainage channels in summer. Patches of bare sediment appear as geese grub for roots and rhizomes, and these are invaded by weedy species that invest heavily in seed production, such as *S. borealis*. Due to the extremely high soil salinity (up to 120 g of solute per litre) (Iacobelli & Jefferies 1991) in all marsh zones late in the growing season and the high rates of soil erosion, salt-tolerant plants dominate both the above-ground vegetation and the soil seed bank (Tables 1 & 2). *Salicornia borealis* is at the limit of its distribution in northern coastal sites in Canada (Wolff & Jefferies 1987a,b) and, as an annual plant with an annual non-overlapping seed bank (Chang 2000), it may be at risk. The seed bank in a heavily grazed salt-marsh in South Wales dominated by *Puccinellia maritima* was similarly composed of only two salt-tolerant ruderal species, in this case *Salicornia europaea* and *Suaeda maritima* (Ungar & Woodell 1996).

Beach-ridge sites have a distinct vegetation, composed, with the exception of *L. mollis*, of ruderals. This may be

due to the greater physical abrasion from wind, wave and ice action combined with the less stable, sandy substrate producing a habitat that was more disturbed than that of the salt-marsh until the establishment of the lesser snow goose colony in the mid-1950s (Cooke *et al.* 1995). Species common to both the vegetation and the seed bank are *M. ambigua*, *Stellaria longipes*, *R. cymbalaria*, *A. patula* and *S. marina*.

Seeds of the biennial composite *S. congestus* possess a pappus and are widely dispersed. Although this species can tolerate only low levels of salinity, its seeds are widely distributed and entrapped at the soil surface. Although it was found most frequently in degraded intertidal sites, its highest density was under undamaged vegetation on the western intertidal and beach-ridge plots where the vegetation and the larger particle size of sandy soils, respectively, help to retain larger seeds.

The Euclidean distances given in Table 3 can be interpreted as a measure of the degree of coupling of species between vegetation and the seed bank. Of the well-coupled species, only *P. egedii* was found in undamaged salt-marshes and production of large numbers of both stolons and seeds may reinforce the link between the seed bank and mature plants. The others are all weedy species typical either of degraded areas (*M. ambigua*, *A. patula* and *S. borealis*) or of areas that are disturbed but still retain intact soil (*J. bufonius* and *S. longipes*) whose seeds may be dispersed close to the parent plant or transported over long distances. In contrast, seeds of *S. congestus* and *R. cymbalaria* were often found where they were absent from the vegetation. Seeds of species with persistent seed banks may be expected to be found far from parent plants, although they may be lost during disturbance. *Juncus bufonius*, which has many records of a large, persistent seed bank (Thompson *et al.* 1997), might have been expected to show a large Euclidean distance. In fact, the distance was short because of depletion of the seed bank due to disturbance, thereby confirming the difficulty of regeneration of species in degraded areas from a persistent seed bank.

Similar responses to disturbance of shifts in species composition from long-lived, stress-tolerant species that propagate through vegetative mechanisms to short-lived, ruderal species that form seed banks have been recorded in salt-marshes (Hopkins & Parker 1984; Ungar & Woodell 1996), subarctic coastal habitats (Staniforth *et al.* 1998) and arctic and alpine systems (Freedman *et al.* 1982; Chambers 1993).

#### RELATIONSHIP BETWEEN THE SEED BANK AND VEGETATION

The degree of similarity between the species composition of vegetation and the soil seed bank is predicted to increase with disturbance due to greater relative abundance of annuals in the vegetation (Hutchings & Russell 1989; Chambers 1993; Ungar & Woodell 1996), and to decrease with 'stress' due to lower seed production

and greater investment in clonal growth in perennial species (Diemer & Prock 1993). The degree of similarity was indeed less in plots where the vegetation was undamaged (compare positions in Figs 4 & 5). Much of this reflects the poor contribution of the dominant species to the seed bank (cf. Ungar & Woodell 1996). Of these, *P. phryganodes* is a sterile triploid that has never been known to set viable seed in North America (Bowden 1961; Sadul 1987) and *C. subspatheacea* only sets seed where it is protected from grazing, although both species spread by clonal propagation (Chou *et al.* 1992).

Other species were over-represented in the soil seed bank compared with their abundance in the vegetation. Soil seed banks that were similarly dominated by a few species have been shown in other studies, including a polar desert in the High Arctic (Freedman *et al.* 1982), a salt-marsh near Churchill (Staniforth *et al.* 1998), a high subalpine site in the Oregon Cascade Mountains (Ingersoll & Wilson 1993), a salt-marsh in California (Hopkins & Parker 1984), a shoreline in Nova Scotia (Wisheu & Keddy 1991) and dune vegetation in South Africa (Pierce & Cowling 1991). Some species were found in the seed bank but were absent in the present-day vegetation, possibly due to lack of suitable 'safe' sites for germination and establishment (van der Valk & Davis 1976, 1978, 1979; Keddy & Reznicek 1982; Smith & Kadlec 1983). Despite the low similarity, roughly half of the seed bank data could nevertheless be predicted from the vegetation data and vice versa, although these values are slightly inflated (sample to variable ratio is below the ideal, 6 : 1 vs. 10 : 1).

#### THE POTENTIAL ROLE OF SEED SOURCES IN REVEGETATION AT LA PÉROUSE BAY

Handa's (1998) study of revegetation potential if goose populations at La Pérouse Bay were controlled concluded that restoration of the dominant graminoids, followed by other species, was possible in younger, intertidal marshes (i.e. while a source of propagules remained), but would be extremely difficult in older marshes where vegetation had been absent for a number of years.

The loss of vegetation and soil degradation in the inland marshes has occurred on such a large scale and over a long period of time that even enclosed areas, with apparently high seed production, only accumulate seeds of the opportunists *S. borealis* and *J. bufonius*. The *S. borealis* assemblage represents a 'lost sere', as this annual has roots less than 1 cm in length and all litter is blown or washed away, exposing the mineral substrate and preventing accumulation of organic material. Revegetation is thus unlikely.

Revegetation from natural seed sources may be limited by the dominance of 'weedy' species in the seed bank of disturbed environments, as well as the transient or only short-term persistence of seeds of target species (i.e. those in communities present before disturbance)

in a range of ecosystems, including grasslands (Thompson 1986; Bakker *et al.* 1996b; Hutchings & Booth 1996; Bekker *et al.* 2000), arctic and alpine sites (Freedman *et al.* 1982; Chambers 1993) and wetlands (Staniforth *et al.* 1998; Wisheu & Keddy 1991; Ungar & Woodell 1996). In a review on European grasslands and heathlands, Bakker & Berendse (1999) state that many species of interest in restoration projects are not present in the soil seed bank and have limited ranges of dispersal. This is not surprising as the high levels of stress and disturbance in degraded habitats select for survival and persistence of species with ruderal or stress-tolerant life strategies (Grime 1977).

Thus, the probability of restoring from extant seed sources many species that are under threat of local extinction decreases with the passage of time. The alternative practice of introducing species to habitats is currently under debate (van Groenendael *et al.* 1998) and would be very difficult and expensive to apply to vast areas, such as the Hudson Bay lowlands. Management practices should therefore aim at reinstating suitable habitats for the establishment of species while regeneration from natural sources is still tenable.

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