# Seed bank and vegetation relationships in Ritchie's vegetation zones on the Churchill River Estuary

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**Abstract**

In 1957, Ritchie described the vegetation patterns in the southern part of Beech Bay on the Churchill River estuary, Churchill, Manitoba. He recognized five successional zones developing in the vegetation between the estuary and the forest; these included the meadow, shrub, invading forest, closed forest and black spruce open forest. The purpose of this project was to investigate and describe relationships between the standing vegetation and the surface soil seed banks of these four vegetation zones at Ritchie's study site on Beech Bay**.** The null hypothesis was that composition and diversity of the seed bank would reflect that and be similar to the standing vegetation, which acted as a seed source, as it developed towards a white spruce forest. The alternative hypothesis was that the seed bank composition and diversity would remain constant even with increasing complexity and diversity of the standing vegetation as it develops towards a white spruce forest because seed banks are primarily composed of pioneer species. Attempts to germinate dormant, buried seeds from soil samples collected from the four zones resulted in 448 seedlings of 16 different taxa. The majority of seedlings were those of *Juncus arcticus* and were found in soils sampled from the invading forest zone. The findings of this study supported the alternative hypothesis i.e. that the seed bank diversity and its species composition were similar throughout the successional stages with the exception of the meadow.

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## ***Introduction***

Seeds of many plants have large food reserves that allow them to remain dormant during dispersal and to persist on or in the soil until environmental conditions are conducive to successful germination (Thompson, 1987). Dormant seeds in the soil make up the "seed bank" which can be described in terms of its diversity, composition and density. It has been suggested the seed bank reflects the standing vegetation but its similarity in composition decreases if the vegetation experiences succession. Seed banks tend to be comprised of seeds of pioneer species because pioneer species produce large numbers of seeds that retain viability for long durations of time (Bliss, 1962; Thompson, 1978; Fox, 1983; McGraw and Vavrek, 1989; Warr *et al.*, 1993; Falinska, 1998; Grandin, 2001; Amiaud and Touzard, 2004).

Previous studies have shown that as succession proceeds through an area the seed bank retains many viable seeds from the pioneer stage of succession (Thompson, 1978; Fox, 1983; Falinska, 1998; Staniforth *et al*., 1998; Grandin, 2001; Amiaud and Touzard, 2004). Thompson (1978) reviewed nine seed bank studies from North America. A consistent finding was the persistence of seeds of early successional species through all successional stages. Fox (1983) studied the montane tundra in Alaska and found a high representation of graminoids in the seed bank which were rarely observed in the vegetation cover. In addition, he found a number of species represented in the vegetation which were not in the seed bank. Falinska (1998) conducted a 20-year study of the seed banks of a 15 hectare unforested site at different successional stages. She found seeds in the seed bank of the forest community from an earlier successional stage (meadow) that were now absent or very rare. Staniforth *et al.* (1998) investigated the seed bank/standing vegetation relationship at Bird Cove, near Churchill, Manitoba. Ninety-seven percent of

the emergents from the seed bank were of three pioneer species; *Juncus bufonius, Senecio congestus, Spergularia marina*. There was little correlation observed between the seed bank and the standing vegetation in the Bird Cove region. Grandin (2001) studied the seed banks of Baltic coastal habitats at different successional stages. He found a decreasing trend of seed bank/standing vegetation similarity as successional age increased. The highest similarities were in areas that were frequently disturbed and did not proceed to the next successional stage. Amiaud and Touzard (2004) studied the seed banks of old fields and grasslands on the French Atlantic coast. They found that the similarity between the seed bank to the standing vegetation decreased with increasing successional age. There were a number of species represented in the seed bank that were not represented in the standing vegetation of later successional stages.

Ritchie (1957) divided the southern part of Beech Bay, Churchill, Manitoba, into five distinct vegetation zones; meadow, shrub, invading forest, closed forest and black spruce open forest. These zones develop increasing complexity from the estuary to a climax closed-canopy white spruce (*Picea glauca*) forest community. This successional pathway is caused largely by topographical changes that result from isostatic rebound, and from the accumulation of organic matter (Handa *et al.*, 2002).

One of the ways to study the past and potential vegetation in an area is to determine the composition of seed banks and to follow how they change as succession proceeds. Unfortunately, seed banks of the Hudson Bay lowland region are largely unexplored and the few studies conducted have provided mixed results. Archibold (1984) found no seed bank in the tundra near Churchill, however Staniforth *et al.* (1998) found

that there was a seed bank as large as 250 000 seeds/m² in certain coastal ecosystems at Bird Cove, near Churchill.

The purpose of this project was to investigate and describe the relationships between the standing vegetation and the soil seed bank along a successional gradient in the Beech Bay area. The null hypothesis was that composition and diversity of the seed bank would reflect that and be similar to the standing vegetation, which acted as a seed source, as it developed towards a white spruce forest. Previous research has shown that the seeds that are most viable in the seed bank are often those of early successional species (Bliss, 1960; Thompson, 1987; Warr *et al.*, 1993; Falinska, 1998; Grandin, 2001).

Therefore, the alternative hypothesis was that the seed bank composition and diversity would remain constant even with increasing complexity and diversity of the standing vegetation as it develops towards a white spruce forest because seed banks are primarily composed of pioneer species. These hypotheses were tested by determining the composition of the standing vegetation and comparing it to that of the seed bank found in soil samples in each of the four vegetation zones; meadow, shrub zone, invading forest, and closed-canopy forest.

## ***Methods***

### ***Site Description***

The study site consisted of the southern portion of Beech Bay on the eastern shore of the Churchill River estuary (51º 44' N, 94º 03' W) and about 5 km south of the town of Churchill, Manitoba (Figure 1). The climate of the area is high subarctic ecoclimatic region. The mean monthly temperature ranges from 12.0 º C in July to – 26.7 º C in January. The mean annual precipitation is 431.6 mm; 264.4 mm fall as rain and 191.0 mm as snow. Prevailing winds are from the northwest at an average speed of 20.5 km/h (Environment Canada, 2004).

**Figure 1: Churchill, Manitoba area**

*Ritchie's Vegetation Zones*

In 1957, Ritchie published a paper describing five plant communities along a successional gradient on Beech Bay; the meadow zone, the shrub zone, the invading forest zone, the closed forest zone and the black spruce open forest zone (Ritchie, 1957) (Figure 2). The pioneer was the meadow zone. Isostatic rebound has been exposing new terrain along the shores of the estuary at a rate between 8.0 – 9.0 mm/year (Tushingham, 1992). The exposure of new terrain by isostatic rebound allows for the colonization of terrestrial vegetation. This is a form of allogenic succession (Ricklefs, 2001). As

succession proceeds and the vegetation communities develop into the invading forest and forest zones, peat accumulates and the soil pH drops. These changes allow acidophilic species to inhabit the area. This type of succession is known as autogenic succession. The establishment of the Misi Falls dam at South Indian Lake lowered water levels in the Churchill River, especially during spring runoff. There is no indication that the successional sequence is still in an adjustment phase as a result of lowered water levels.

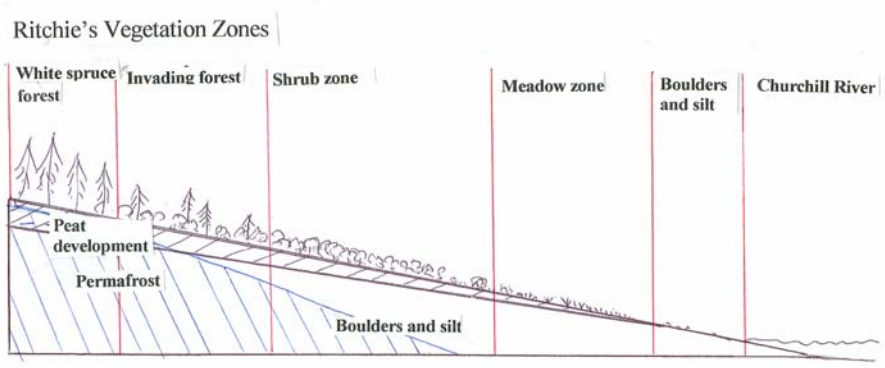


**Figure2: Ritchie's Vegetation Zones**

The meadow zone is located between the tidal mudflats of the estuary and the shrub zone. Intermittent boulders and bedrock dot the landscape of this zone, and the vegetation is dominated by *Puccinellia* spp and other graminoids. The vegetation forms extensive mats within this zone, but there are also areas of exposed mud with little or no vegetation. Bare areas may not yet have been colonized by vegetation, they may have been heavily grazed by geese (Srivastava and Jefferies, 2002) or they may be local areas high salinity. There are intermittent pools and fast moving streams flowing westward across this zone towards the estuary. The streams have a rocky base of flat limestone pebbles that appear to be continuous throughout the zone, regardless of the presence of streams.

Further inland, taller grasses, sedges (*Carex* spp., *Eriophorum angustifolium*) and woody shrubs (*Salix arctophila, Salix brachycarpa, Salix candida, Salix glauca, Salix planifolia*, *Betula glandulosa*) form the shrub zone. Hummock topography begins to develop in this zone. Depressions were wet and often water-filled. They often included aquatic or semi-aquatic vegetation such as *Carex aquatilis* and *Carex rariflora*. The tops of the hummocks were drier and dominated by *Empetrum nigrum* but *Salix arctophila, Salix brachycarpa, Salix candida, Salix glauca, Salix planifolia* and *Betula glandulosa* were common on the slopes of the hummocks. The result was an area of small pools with numerous islands of woody vegetation. The approximate height of hummocks was 40 cm. The pools of standing water were approximately 4 m wide and contained 10 cm depth of standing water and 30 cm depth of soft mud.

The invading forest zone had a dense shrub composition of *Salix brachycarpa*, *Salix candida*, *Salix reticulata*, *Salix planifolia*, *Salix glauca* and *Betula glandulosa*. The intermittent occurrence of tree species (*Larix laricina, Picea glauca*) was characteristic of the zone. The trees were, approximately, less than 5m in height and sparsely distributed. The invading forest was a later seral stage than the shrub zone, therefore, its hummock development was more advanced than that of the shrub area.

The forest zone had a closed-canopy of white spruce (*Picea glauca*) and tamarack (*Larix laricina*). The hummocks were well developed but were of various sizes, shapes and heights. Several plant associations occurred at different positions on the hummocks. The tops of hummocks were dry and often associated with lichen species, especially *Cladina* spp. The hummocks were bordered by deep pools of standing water.

Ritchie's fifth seral stage, the open black spruce forest zone, was not available for study because of the presence of human disturbance in this area.

***Field sampling***

Field sampling was performed between July 26th and August 8th, 2004. The time period was ideal since most of the plants were in flower, allowing for easier identification, and they had not yet set seed. The time of sampling meant that the seed banks in the soil samples were most likely at their minimal density, i.e. post germination but before seed set.

A 100 x 100 m plot was established in each of Ritchie's four vegetation zones (meadow, shrub, invading forest and closed forest) by visually comparing the vegetation in the field to his original descriptions and his actual locations. There was field evidence (decomposed tree stumps) that suggested that we were in the precise location as that used by Ritchie in 1957. Ritchie (1957) had felled several trees along a transect line to obtain their ages.

Once each 100 x 100 m plot had been established, we used a random number table to determine the locations for twenty-five sample sites (50 x 50 cm) within each plot. Percent cover values for all understory and overstory plant species were estimated using absolute values at each sample site. UTM coordinates were recorded at each sample site with the use of a GPS unit. The plant nomenclature used in this study followed that of Porsild and Cody (1980). A cylindrical soil sample (5 cm deep and 10 cm in diameter) was taken from the substrate surface at each sample site and placed into a sealable plastic bag. The soil sample was later used to determine the composition of the seed bank.

A larger soil sample (approx. 20 cm deep and 10 cm in diameter) was taken at every fifth sample site for the purpose of soil analysis. These samples were also placed

into sealable plastic bags. The bags were stored in cool, dark conditions until soil analysis could be performed in the laboratory.

## ***Laboratory Procedures***

### *Seed Bank Samples*

The seed bank soil samples were spread out to dry on a laboratory bench approximately two weeks after sampling had been completed. Once dry, the soils were stored in a cold storage room at 5º C in the dark for five weeks. The soil samples were then sieved with a 2.38mm sieve to remove twigs and large rocks. A 20 ml sub sample was removed and weighed from each field sample and placed in a 90 mm x 15 mm Petri dish. The dish was watered with distilled water and placed into an environmental chamber. This procedure was repeated for each of the 100 field samples (4 plots with 25 sample locations each). The conditions in the environmental chamber were set at 25º C and simulated daylight for 14 hours; and for 10º C in darkness for 10 hours. The samples were checked on alternate days for germinating seeds and to ensure presence of adequate moisture. Seedlings were transplanted into pots and placed in the greenhouse. Each seedling was monitored until such a time that it could be identified. After a prolonged period of no new germinations (1 week) the samples were placed into cold storage (5º C) for 4 weeks to stratify any remaining seeds and a second germination trial was performed under the same conditions.

### *Soil Analysis*

Twenty soil samples, five from the surfaces of each vegetation zone, were collected for the purpose of soil analysis. Salinity, pH, organic content and moisture contents were measured. Soil samples were kept in a cool (5º C), dark environment until analysis could be performed.

*Moisture Content*

A sub-sample of known weight from each of the 20 soil samples was placed into a drying can. The cans were placed into the drying oven at 105 º C for 24 hours. The cans were allowed to cool and reweighed. The moisture content was calculated from the formula:

$$\frac{\text{Mass of moist sample} - \text{Mass of ovendry sample}}{\text{Mass of ovendry sample}} = x\ 100 = \%\ \text{Moisture Content}$$

*Organic Content (Loss on Ignition Method)*

An oven-dry sub-sample of known weight from each of the 20 soil samples was placed into a crucible. The crucibles were placed in an oven set at 550 º C for one hour. The crucible and contents were allowed to cool and then reweighed. The organic matter content of each sample was calculated with the following formula:

$$\frac{\text{Mass of ovendry samples} - \text{Mass of incinerated samples}}{\text{Mass of ovendry samples}} = x\ 100 = \%\ \text{organic matter}$$

*pH*

pH was calculated using the procedure for soil pH determination in 0.01 M $CaCl_2$ (Scott, 2003).

*Salinity*

Salinity was determined using the 1:2 Extract Method (Scott, 2003).

The values calculated for each of the variables were grouped according to their community origin. The mean for each variable was calculated for each community.

## ***Statistical Analysis***

The percent cover vegetation data gathered in the field and the numbers of seedling emergents from seed bank samples were recorded for each species at each sampling site and entered into PC-ORD© 4.25. This computer software package was used for statistical ordination and classification of standing vegetation communities. Diversity indices for the standing vegetation and seed bank samples were also calculated with this software package.

In all statistical tests used in this study, the critical *p*- value was set at $p<0.05$.

### *Ordination*

Ordination methods allowed the summarization of data and identification of variation due to environmental conditions. Detrended Correspondence Analysis (DCA) grouped sample locations and species on a two-dimensional graph. DCA was chosen as the most appropriate ordination since there was a concentration of sampling sites at either end of the ordination axis. A Detrended Correspondence Analysis removed the arch effect of a Correspondence Analysis and reduced the compression of sampling sites at either ends of the x-axis (Gauch, 1982). The closer sample locations or species were to each other on the graph the most closely associated they were too each other.

### *Classification of vegetation communities*

Two-way indicator species analysis (TWINSPAN) was chosen for the classification of sampling sites into vegetation communities. TWINSPAN used reciprocal averages of the sample data (Gauch, 1982). The species that represented the extremes of the reciprocal average axis were used to divide the axis in two near the middle. The

classification was continually divided until there were no longer a minimum number of preset species to form a community or the maximum number of divisions had been reached (Gauch, 1982). For this study, a maximum number of four communities were chosen with a maximum number of three indicator species needed to form a community.

*Diversity indices*

Diversity indices were calculated for each sample site and a mean was calculated for each plot. The characterization of the sample sites into specific communities for this analysis followed the findings of the TWINSPAN analysis described above. Species richness, evenness, Simpson's and Shannon's diversity indices were compared between communities using a one-way analysis of variance (ANOVA). If homogeneity of variance fell below $p<0.05$ a post-hoc test that does not assume equal variance was applied (Tamhane's) otherwise Tukey's post-hoc test was applied.

Richness is a measure of the number of different species in a community. The higher the value the more species are found in the community.

Evenness is a measure of the relative abundance of each species. The closer an evenness value approaches the number 1, then the more species are equally abundant within the community.

Simpson's diversity index (Equation 1) measures the probability that two randomly selected individuals will belong to the same species. A greater value indicates a higher diversity (Pielou, 1975).

$\sum p_i^{\,2} = \lambda$, where $p_i$ = 1/species richness

**Equation 1: Simpson's Diversity Index**

Shannon's diversity index (Equation 2) also relates the richness and evenness of a community to give a measure of overall diversity. Here the higher the value indicates

higher diversity. This diversity index is generally a more useful index when using proportional or percent cover data (Pielou, 1975).

$H' = -\sum p_i \log p_i$ , where $p_i$ = 1/species richness

**Equation 2: Shannon's Diversity Index**

Both types of diversity values will be reported in this study. The data for the standing vegetation was gathered using percent cover and the germination data was gathered in frequencies of individuals.

*Soil Characteristics*

The means and standard deviations of each soil variable were calculated for each vegetation zone. These means were tested for differences with the Kruskall-Wallis test. Differences between the soil characteristics of vegetation communities were isolated using the Mann-Whitney U-test.

Spearman's correlation coefficient was used to determine any correlations between soil variables in the vegetation zones. The Spearman's correlation coefficient was also used to investigate any correlation between the soil characteristics and the vegetation diversity indices.

*Relative Abundance*

The relative abundance of species within each zone was calculated and summarized in Table 1. For each separate vegetation zone, the average percent cover was calculated for each species. The average percent cover for each species was divided against the sum of all the averages for each species in the zone.

*Seed Bank/Standing Vegetation Relationship*

The seed bank and standing vegetation relationship was tested for similarity in terms of diversity using the Mann-Whitney U-test. The diversity values for each

vegetation origin was calculated for each sample site. These values were entered into SPSS 10.1 and a Mann-Whitney U-test tested for differences between the vegetation origins.

## ***Results and Discussion***

### ***Standing Vegetation***

A total of 66 species were observed in the standing vegetation during the sampling period. However, only thirty-two reached levels at or above 1% relative abundance. The species and their relative abundance are listed in Table 1. Species that did not reach levels at or above 1% in relative abundance are listed in Appendix 1. Nine species were observed in the meadow zone, twenty-four in the shrub zone, thirty-seven in the invading forest zone and forty-two in the forest zone.

*Confirmation of Vegetation zones*

Figure 3 shows the DCA plot of the sample location based on the standing vegetation composition. The meadows sample sites were towards the extreme right of the plot. The invading forest sample sites were located between the shrub and forest locations on the right hand side of the plot. Figure 4 is a DCA plot of the species found in the standing vegetation.

**Table 1: Mean relative abundance values for plant species found in Ritchie's Vegetation zones**

| Species | Ritchie's Zone | | | | |
|---|---|---|---|---|---|
| | DCA plot abbreviation | Meadow (n=25) | Shrub (n= 26) | Invading Forest (n=31) | Forest (n=18) |
| *Aster junciformis* | Astejunc | | **0.03** | | |
| *Betula glandulosa* | Betuglan | | 0.03 | **0.28** | 0.03 |
| *Calamagrostis neglecta* | Calanegl | | 0.02 | 0.01 | |
| *Carex aquatilis* | Careaqua | | 0.15 | 0.06 | 0.03 |
| *Carex gynocrates* | Caregyno | | | 0.01 | 0.01 |
| *Carex rariflora* | Carerari | | 0.06 | 0.02 | |
| *Carex subspathacea* | Caresubs | 0.13 | | | |
| *Empetrum nigrum* | Empenigr | | | 0.10 | 0.05 |
| *Equisetum arvense* | Equiarve | | | 0.01 | **0.06** |
| *Eriophorum angustifolium* | Erioangu | | 0.05 | | |
| *Festuca brachyphylla* | Festbrac | 0.02 | 0.03 | | |
| *Juncus arcticus* | Juncuarct | | | 0.08 | 0.01 |
| *Larix laricina* | Larilari | | | 0.02 | **0.09** |
| *Ledum groenlandicum* | Ledugroe | | | | 0.04 |
| *Myrica gale* | Myrigale | | | 0.02 | |
| *Oxycoccus microcarpus* | Oxycmicr | | | | 0.01 |
| *Petasites sagittatus* | Petasagi | | | 0.01 | 0.01 |
| *Picea glauca* | Piceglau | | | 0.02 | 0.05 |
| *Plantago maritima* | Planmari | 0.01 | | | |
| *Potentilla egedii* | Poteeged | 0.22 | | | |
| *Primula stricta* | Primstr | | 0.02 | | |
| *Puccinellia phryganodes* | Puccphry | **0.63** | | | |
| *Rubus acaulis* | Rubuacau | | 0.02 | 0.02 | 0.01 |
| *Salix brachycarpa* | Salibrac | | 0.03 | | |
| *Salix candida* | Salicand | | **0.21** | 0.01 | 0.02 |
| *Salix glauca* | Saliglau | | 0.22 | **0.11** | |
| *Salix planifolia* | Saliplan | | 0.01 | | 0.01 |
| *Salix reticulata* | Salireti | | | | 0.02 |
| *Vaccinium uliginosum* | Vacculig | | | | 0.07 |
| *Vaccinium vitis-idaea* | Vaccviti | | | | 0.03 |
| Lichen spp. | Lichen | | | 0.01 | |
| Moss spp. | Moss | | 0.10 | 0.17 | 0.41 |

Indicator species for each zone (as identified by TWINSPAN) are shown in bold.

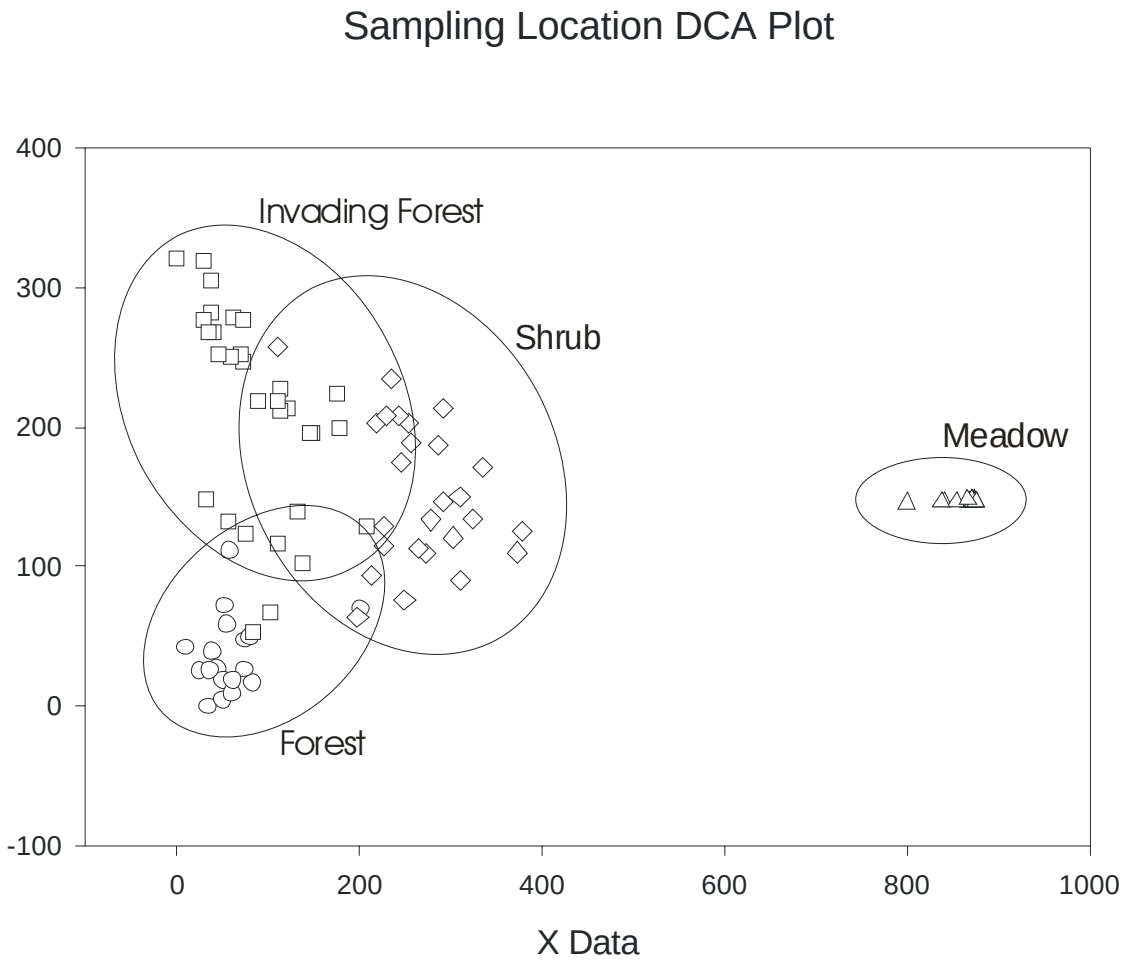


**Figure 3: Standing vegetation Detrended Correspondence Analysis (DCA) plot of sample locations based on species percent coverage**

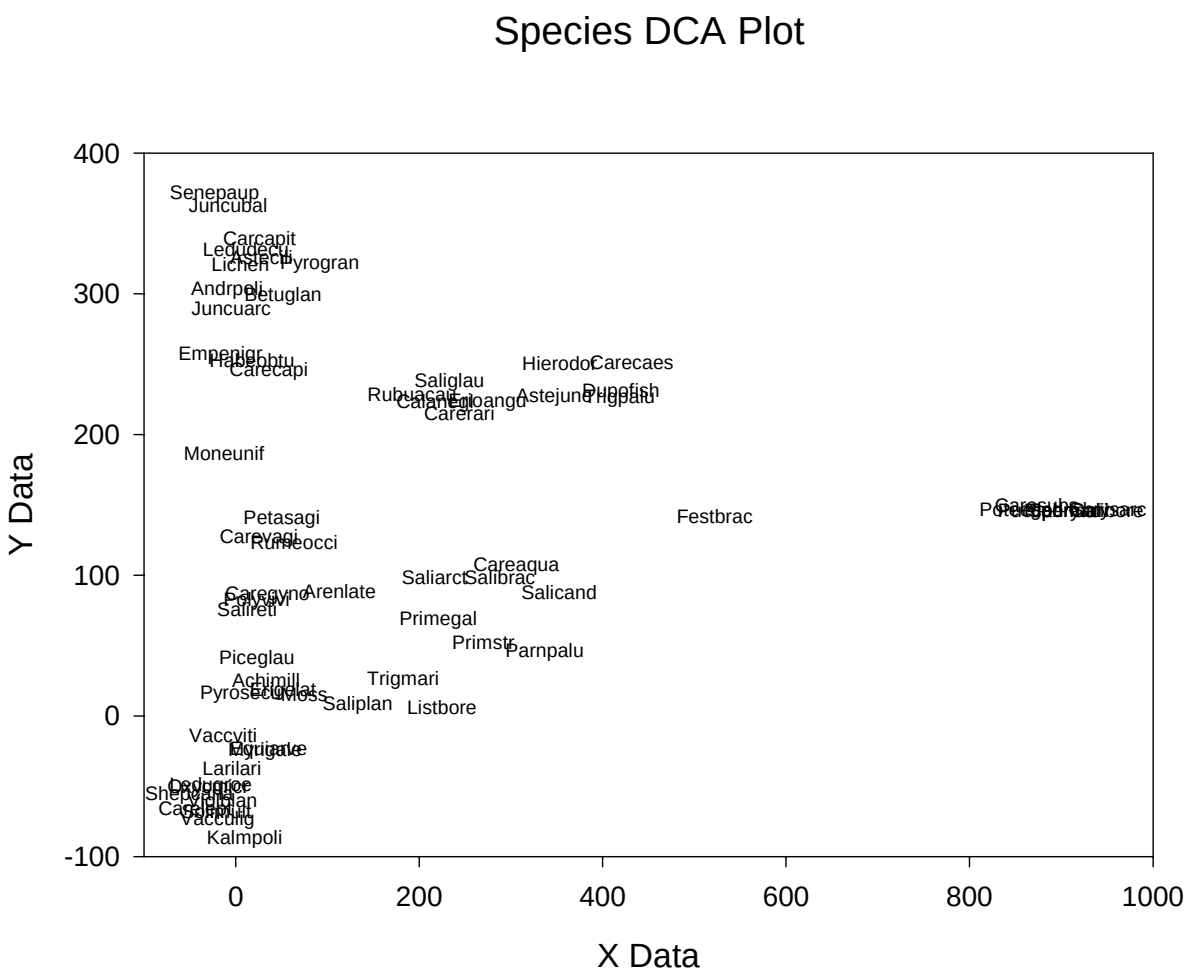


**Figure 4: Standing vegetation Detrended Correspondence Analysis (DCA) plot of species based on species percent cover**

*Characterization of sampling sites*

Two-way indicator species analysis (TWINSPAN) on the data from the 100 sampling sites revealed four communities. Further division of these communities was considered unnecessary because they coincided with Ritchie's zones. Figure 5 illustrates the division of Ritchie's zones.

The first community was the meadow community and included all samples gathered in the 100 x 100 m meadow plot (i.e. samples M1-M25). These sample sites were defined by the presence of *Puccinellia phryganodes.* This species occurred in no other community across the study area.

The second community was the shrub community and it included all 25 samples gathered in the 100 x 100 m shrub plot (i.e. samples S1-S25) plus one sample site that was located in the Invading forest plot (i.e. I11). This sample, (I11) was determined by TWINSPAN to be more closely resemble the characteristics of the shrub community. The presence of *Aster junciformis* and *Salix candida* defined sample sites of this community.

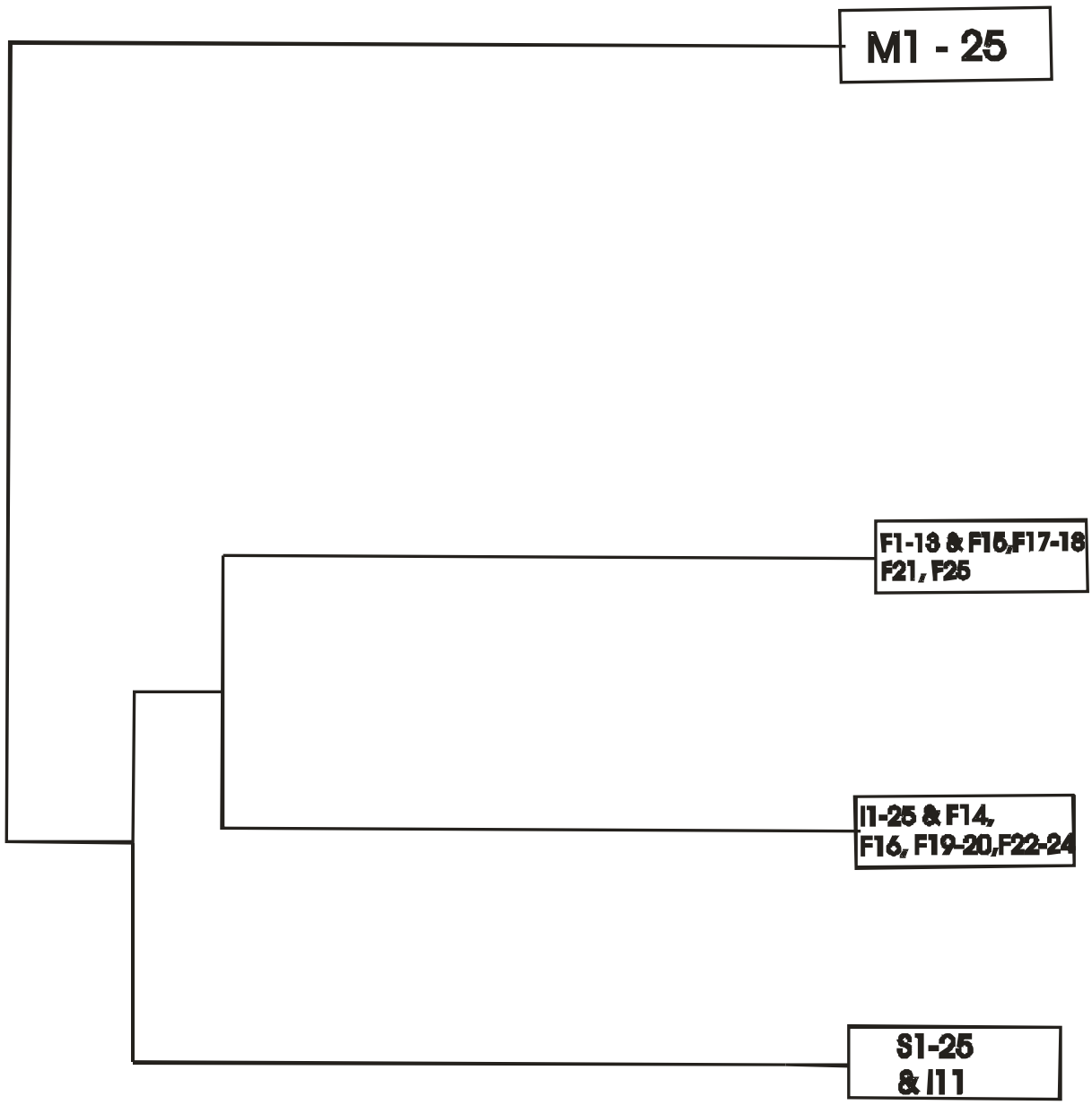


**Figure 5: Standing Vegetation TWINSPAN communities**

The third community was the Invading forest community and was defined by the presence of *Betula glandulosa* and *Salix glauca*. This community was made up of all samples gathered within the invading forest plot, except for sample I11 which more closely resembled the shrub community. It also included samples from the forest plot (F14, F16, F19, F20, F22, F23 & F24). The total number of samples for this community was thirty-one. The remaining eighteen samples were left with the definition of being the forest community. The sample sites in the forest plot were identified with the presence of *Equisetum arvense* and *Larix laricina*.

*Diversity indices*

Species evenness remained statistically similar through all vegetation zones. However, species richness increased as successional stage increased in complexity. This increase also results in the increase in Simpson's and Shannon's diversity indices as succession proceeds from the meadow through to the forest zone.

Analysis of variance found significant differences between the diversity indices and the standing vegetation zones. The differences between the vegetation zones and the diversity indices are summarized in Table 2. Species richness had the highest mean in the forest zone. The shrub and invading forest zones were similar in their species richness values whereas that of the meadow zone was the lowest. The meadow zone was the only zone determined to be statistically different (less even) in terms of species evenness (Table 2). The meadow zone was only zone found to be significantly different (less diverse) from all others in terms of Simpson's and Shannon's diversity indices (Table 2). The invading forest and the forest zone had the highest in mean diversity (Table 2).

**Table 2: Comparison mean diversity values for species in the standing vegetation of estuarine plant communities**

| | | Richness | Evenness | Simpson's Index | Shannon's Index* |
|---|---|---|---|---|---|
| Sample Size (n) | Levene Statistic p-value | <0.001 | <0.001 | <0.001 | 0.995 |
| 25 | Meadow | 3.52a± 1.05 | 0.57± 0.23 | 0.41a± 0.20 | 0.71a± 0.31 |
| 26 | Shrub | 7.77b± 2.18 | 0.68± 0.12 | 0.65b± 0.13 | 1.38b± 0.31 |
| 31 | Invading Forest | 9.35b±3.32 | 0.68±0.08 | 0.68b± 0.10 | 1.48bc± 0.35 |
| 18 | Forest | 12.89c± 3.14 | 0.69± 0.10 | 0.72b± 0.10 | 1.71c± 0.30 |

Means values within each column followed by the same letter are not significantly different ($p$>0.05, Tukey and Tamhane). *denotes when Tukey's post-hoc test was applied.

*Characterization of Soil Profiles*

*Meadow Zone*

A soil profile showed a 4cm Oh horizon underlain by a 12cm deep B horizon. The B horizon was underlain by 30cm of wet grey clay (C horizon) below which the limestone pebble layer was located. Semi-fossilized plant remains (possibly *Potamogeton* spp.) were found attached to the pebbles. The soil profile was characterized as a Gleyed Regosol (Agriculture Canada, 1998).

*Shrub Zone*

A profile dug through a hummock showed an Om horizon underlain by sandy/clay grit with signs of oxidation caused by prolonged fluctuations of water levels (Ahg horizon). Limestone pebbles, similar to those in the meadow, were found at a depth of 30 cm. The soil profile of the hummock was classified as a Gleyed Regosol (Peaty Phase) (Agriculture Canada, 1998).

*Invading Forest Zone*

A profile dug through a hummock showed a black/brown Om horizon underlain by brown/grey clay (Ahg and Bmy horizons). There was a grey sandy clay layer with a discontinuous red oxidation (Cgy horizon). On July 28$^{th}$ 2004 the temperature at the Cgy horizon at a depth of 35 cm was close to 0º C but no permafrost was encountered. The soil profile in the invading forest hummock has been classified as a Eutric Turbic Cryosol (Agriculture Canada, 1998).

*Forest Zone*

Soil profiles dug through hummocks showed deep layers of living feather mosses (10 cm) underlain by decomposing moss and peat layers. The layers of living feather moss were deepest towards the sides of hummocks (~ 15 cm) and were shallowest on their tops (~ 8cm). The organic soil layers (Of, Om and Oh horizons) were deepest (20 cm) in the centers of hummock profiles and tapered in depth towards the sides. The Om

horizon was underlain by a thin Bmg horizon this was underlain by a thicker layer (4 cm) of clay and sand (Cgy horizon). Oxidation occurred within this layer at 30-35 cm from the surface of the hummock. Permafrost was encountered at approximately 40 cm depth within the hummocks but not in the pools (Cz horizon). A disorganized layer of pebbles was also found at this depth. Similar pebbles were encountered in the hollows and pools at a depth of approximately 20 cm. The forest hummock profile was characterized as a Histic Eutric Turbic Cryosol (Agriculture Canada, 1998).

*Soil characteristics*

Mean soil characteristics were compared between plant communities (Kruskall - Wallis) and the results showed significant differences between Moisture content, Organic content and Salinity. There were no significant differences between vegetation zones and pH (Table 3). The general trends in soil characteristics were that salinity and pH decreased with successional position, however, organic content and moisture contents showed increases with successional position (Table 4).

Spearman's correlation coefficient analysis of the soil characteristics showed that the soil moisture ($r$ = 0.520, $p$> 0.01, n = 20) and organic contents ($r$ = 0.769, $p$> 0.01, n = 20) had significant positive correlations with successional position. Further analyses showed that soil moisture and soil organic contents were significantly and positively correlated ($r$ = 0.703, $p$> 0.01, n = 20). There was a positive correlation between salinity and pH ($r$ = 0.546, $p$> 0.05, n = 20) but a negative correlation between salinity and organic content ($r$= -0.597, $p$> 0.01, n = 20). There was a strong negative correlation between pH and Organic Content ($r$= -0.731, $p$> 0.01, n = 20).

Organic content was positively correlated to the species richness, Simpson's and Shannon's diversity the vegetation zones (Table 5). Both pH and Salinity were negatively correlated to richness, Simpson's and Shannon's diversity (Table 5).

**Table 3: Kruskall-Wallis test results for differences in Vegetation Zone soil characteristics**

| | Moisture Content | Organic Content | pH | Salinity |
|---|---|---|---|---|
| Chi-Square | 11.629 | 15.663 | 7.234 | 16.279 |
| df | 3 | 3 | 3 | 3 |
| *p* | 0.009 | 0.001 | 0.065 | 0.001 |

**Table 4: Mann-Whitney U-test results for Soil Characteristics from vegetation zones**

| | | Salinity (mmhos/cm) | Organic Content (%) | Moisture Content (%) | Ph |
|---|---|---|---|---|---|
| 5 | Meadow | $50.13_{a}$± 10.12 | $17.13_{a}$± 3.64 | $132.85_{a}$± 38.06 | 7.06± 0.13 |
| 5 | Shrub | $10.39_{b}$± 6.29 | $62.06_{b}$± 11.52 | $451.78_{b}$± 191.28 | 6.57±0.61 |
| 5 | Invading Forest | $1.15_{c}$± 0.83 | $57.84_{b}$± 22.15 | $358.50_{ab}$± 142.74 | 6.23±.78 |
| 5 | Forest | $0.76_{c}$± 0.84 | $83.79_{c}$± 5.97 | $504.57_{b}$± 189.96 | 6.08±0.34 |

Mean values within each column followed by the same letter are not significantly different ($p>0.05$)

**Table 5: Spearman's Correlation Coefficients between Standing Vegetation Diversity and physical soil properties (n=4)**

| | Richness | Simpson's Diversity index | Shannon's Diversity index |
|---|---|---|---|
| Organic Content | r =0.712, p<0.01 | r =0.478, p<0.05 | r =0.558, p<0.05 |
| pH | r =-0.607, p<0.01 | r =-0.591, p<0.01 | r =-0.582, p<0.01 |
| Salinity | r =-0.758, p<0.01 | r =-0.731, p<0.01 | r =-0.738, p<0.01 |

***Seed Bank Germinations***

Two germination trials were conducted resulting in a total of 448 seedlings in 18 different taxa from 70 of the 100 Petri dishes. Two-hundred and fifty-two germinated in the first trial and 196 seeds germinated in the second trial. Nearly 70% of the seedlings were those of *Juncus arcticus* (Figure 6). The highest germination frequencies occurred in samples from Ritchie's invading forest zone (Figure 7). Table 6 summarizes the number and species of emerging seedlings for the germination trials. The number of seeds per meter square was also calculated and is displayed on Table 6. The procedure for calculating the number of seeds per meter square is shown in Appendix 2.

Kruskall-Wallis and Analysis of Variance found no significant differences between the seed bank diversity indices for any vegetation zone (Table 7). Mean diversity values are also displayed in Table 7.

The greatest numbers of seedlings of *Juncus arcticus* (291 individuals) occurred in seed samples from the invading forest (Table 6). The invading forest also had the highest occurrence of *Juncus arcticus* in its standing vegetation (8%) (Table 1) when compared to other vegetation zones.

**Table 6: Seedlings that emerged from 20 ml soil samples during germination trials.**

| Species | Ritchie's Vegetation Zone | | | | Total |
|---|---|---|---|---|---|
| | Meadow (n=25) | Shrub (n= 26) | Invading Forest (n=31) | Forest (n=18) | (n=100) |
| *Betula glandulosa* | 0 | 4 | 1 | 0 | 5 |
| *Carex* spp. | 2 | 8 | 3 | 3 | 16 |
| *Empetrum nigrum* | 0 | 0 | 2 | 3 | 5 |
| *Epilobium palustre* | 0 | 3 | 0 | 0 | 3 |
| *Juncus arcticus* | 3 | 10 | 291 | 9 | 313 |
| *Potentilla egedii* | 1 | 0 | 0 | 0 | 1 |
| *Ranunculus cymbalaria* | 3 | 0 | 0 | 0 | 3 |
| *Salicornia borealis* | 2 | 0 | 0 | 0 | 2 |
| *Senecio congestus* | 0 | 3 | 0 | 0 | 3 |
| *Spergularia marina* | 26 | 2 | 2 | 1 | 31 |
| *Festuca brachyphylla* | 3 | 0 | 0 | 0 | 3 |
| *Juncus bufonius* | 1 | 0 | 0 | 0 | 1 |
| *Arenaria lateriflora* | 0 | 0 | 4 | 0 | 4 |
| *Erigeron elatus* | 0 | 0 | 1 | 0 | 1 |
| | | | | | |
| Asteraceae (unidentified) | 0 | 1 | 0 | 0 | 1 |
| Unidentified dicots | 2 | 0 | 2 | 2 | 6 |
| Poaceae (unidentified) | 4 | 1 | 4 | 1 | 10 |
| Unidentified monocots | 4 | 3 | 22 | 11 | 40 |
| Totals | 51 | 35 | 333 | 30 | 448 |
| #of seeds per $m^2$ | 5 100 | 3 365 | 26 855 | 4 167 | 11 200 |

**Table 7: Kruskall-Wallis test results testing for differences between seed bank diversity and vegetation community**

| Diversity Indices | Richness | Evenness | Simpson's Diversity Index | Shannon's Diversity Index |
|---|---|---|---|---|
| Kruskall-Wallis p-value | 0.3 | 0.52 | 0.60 | 0.60 |
| Community | | | | |
| Meadow | 1.28±1.28 | 0.36±0.46 | 0.21±0.27 | 0.33±0.45 |
| Shrub | 1.00±1.06 | 0.37±0.48 | 0.19±0.25 | 0.28±0.37 |
| Invading Forest | 1.45±1.06 | 0.27±0.37 | 0.15±0.22 | 0.25±0.36 |
| Forest | 1.06±0.80 | 0.21±0.40 | 0.11±0.21 | 0.16±0.32 |

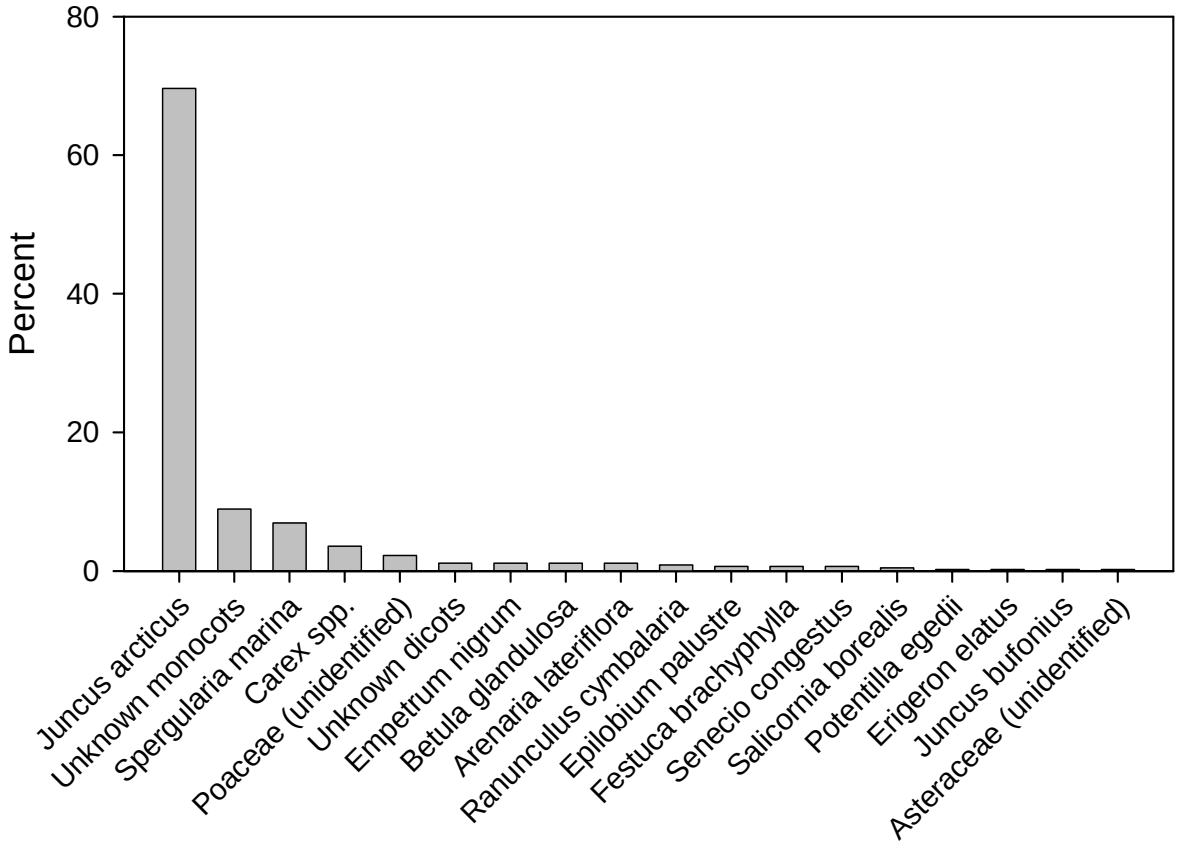


**Figure 6: Percent species frequency in soil seed bank, n = 448.**

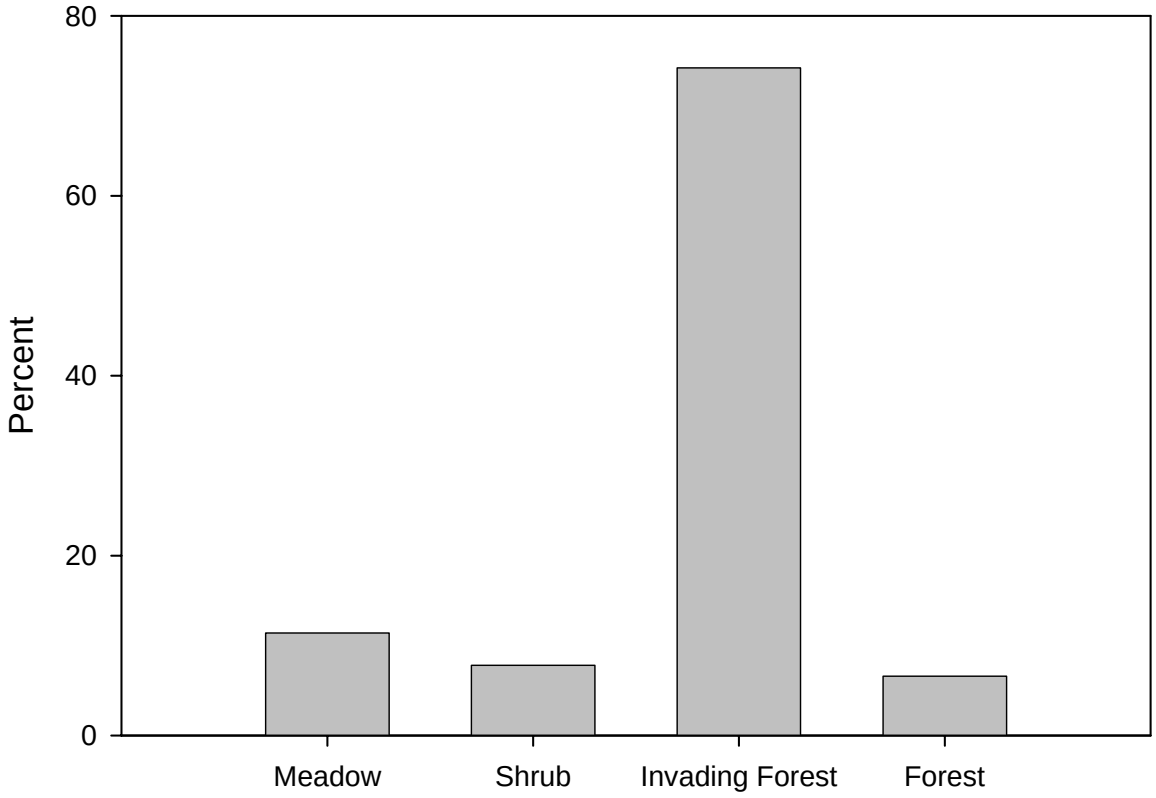


**Figure 7: Percentage of seeds germinating from soils collected in each of four vegetation zones on the Churchill River Estuary, n = 448.**

***Seed Bank/Standing Vegetation relationship***

Comparisons between the seed bank and the standing vegetation showed that species richness, Simpson's and Shannon's diversity indices were significantly different ($p < 0.05$) in all vegetation zones (Table 8). Species evenness was not significantly different between the seed bank and standing vegetation in the meadow and shrub zone (Table 8).

The species composition of the seed bank revealed four species (6% of all species observed in the study) not observed in the standing vegetation (Appendix 1). The species were *Epilobium palustre*, *Juncus bufonius*, *Ranunculus cymbalaria*, and *Senecio congestus*. Eight species (11% of all species observed in the study) were common to both the seed bank and the standing vegetation (Appendix 2). Fifty-six species (80% of all species observed in the study) found in the standing vegetation were not observed in the seed bank samples (Appendix 2). Unidentified *Carex* spp., *Juncus* spp, and *Poaceae* spp. from the seed bank may have included species observed in the standing vegetation but could not be positively identified.

**Table 8: Comparison of Standing Vegetation and Seed Bank diversity indices in Vegetation zones[1].**

| Vegetation Zone | | Richness | Evenness | Simpson Diversity Index | Shannon's Diversity Index |
|---|---|---|---|---|---|
| Meadow | Standing Vegetation | 3.52± 1.05 | 0.57± 0.23 | 0.41± 0.2 | 0.71± 0.31 |
| | Seed Bank | 1.25± 1.23 | 0.36± 0.46 | 0.21± 0.26 | 0.33± 0.44 |
| | *p* | < 0.001 | 0.144 | 0.006 | 0.001 |
| Shrub | Standing Vegetation | 8.04± 2.18 | 0.68± 0.12 | 0.66± 0.13 | 1.4± 0.31 |
| | Seed Bank | 1.00± 1.05 | 0.37± 0.48 | 0.19± 0.25 | 0.28± 0.37 |
| | *p* | < 0.001 | 0.08 | < 0.001 | < 0.001 |
| Invading Forest | Standing Vegetation | 9.17± 3.31 | 0.68± 0.08 | 0.68± 0.1 | 1.71± 0.35 |
| | Seed Bank | 1.45± 1.03 | 0.27± 0.37 | 0.15± 0.22 | 0.25± 0.36 |
| | *p* | < 0.001 | < 0.001 | < 0.001 | < 0.001 |
| Forest | Standing Vegetation | 12.9± 3.14 | 0.69± 0.1 | 0.72± 0.1 | 1.71± 0.3 |
| | Seed Bank | 1.1± 0.84 | 0.21± 0.4 | 0.11± 0.21 | 0.16± 0.32 |
| | *p* | < 0.001 | 0.002 | < 0.001 | < 0.001 |

1: Mann-Whitney U-test

*Meadow zone*

The standing vegetation of the meadow zone was dominated by *Puccinellia phryganodes*. This is a salt-tolerant species common to sub-arctic coastal salt marshes and salt flats (Scoggan, 1959). This species has been described as a sterile triploid and therefore does not reproduce by seed (Srivastava and Jefferies, 2002). This would account for its absence from the seed bank.

*Spergularia marina* was the dominant species in the meadow seed bank. This species is common throughout North America in saline environments. The Beech Bay area is at its extreme northern limit of its natural range. It had a relative abundance score of less than 1% in the standing vegetation of the meadow zone. Seeds of this species have a dormancy period and need light for germination (Carter and Unger, 2004). The meadow zone may experience seasonal meltwater flooding every spring and associated silt deposition may bury the seeds and prevent their germination. Seeds may accumulate in the meadow seed bank because of the lack of suitable conditions for germination. As an annual species, *Spergularia marina* produces numerous seeds which eventually became disproportionately higher in numbers in the seed bank than are mature plants in the standing vegetation.

The meadow zone is the pioneer seral stage of a primary successional sequence in the Beech Bay area. The vegetative reproductive strategy of the dominant species in the meadow zone (*Puccinellia phryganodes*) means that species composition and diversity of its seed bank and standing vegetation were significantly different.

*Shrub Zone*

The standing vegetation of the shrub zone was dominated by *Salix candida*, *Salix glauca* and *Carex aquatilis*. The willow species (*Salix* spp.) produce many seeds annually. The seeds of this genus do not remain viable for long and so do not accumulate in the seed bank (Baskin and Baskin, 2001).

*Juncus arcticus* had the highest number of seeds in the seed bank of the shrub zone. This species was not observed in the standing vegetation. *Juncus* spp. produce many small seeds which can remain viable for up to five years (Jensen, 2004; Berger *et al*., 2004). In this study, the seeds may have been blown in from the invading forest zone, or were washed to the shrub area by streams flowing from the invading forest through the shrub zone to the estuary (Wolters and Bakker, 2002).

Whereas seeds of *Juncus arcticus* had started to colonize the shrub zone, the occurrence of two individuals of *Spergularia marina* in the seed bank of the same zone were possibly due to relicts of the previous seral stage (meadow zone).

A surprising occurrence in the seed bank was that of seeds of *Epilobium palustre*. This species was not observed in the standing vegetation in any sample plot, in any vegetation zone. This species has been characterized as a species common to marshy ground, wet peaty meadows and margins of ponds (Scoggan,1959). The composition of the shrub zone fits this description so it is surprising that it had been absent from all quadrats.

Species composition and diversity of the standing vegetation and the seed bank in the shrub zone were both significantly different.

*Invading Forest Zone*

The invading forest was dominated by *Betula glandulosa* and *Salix glauca*. There was also a strong presence of moss in this vegetation zone.

The seed bank of the invading forest was dominated by *Juncus arcticus.* This species accounted for almost 70% of total germination for all plots and 87% of all germination from the invading forest seed bank. This species accounted for 8% of the relative abundance in the standing vegetation of the invading forest.

*Juncus* spp. are early successional species that are common in seed banks (Schott and Hamburg, 1997; Wolters and Bakker, 2002; Jensen, 2004). The seeds of this genus are numerous per individual and can remain viable in the seed bank for as long as five years until conditions favor germination. Studies have shown that seeds of *Juncus* spp. persisted in seed banks long after the vegetation had proceeded to another successional stage in which *Juncus* spp. was absent ( Wolters and Bakker, 2002; Berger *et al.*, 2004). It has also been shown that *Juncus* spp. required a disturbance and light for successful germination (Berger *et al.*, 2004; Jensen, 2004). Such conditions were unlikely in the invading forest zone. Tall thick shrubs that shaded the ground covered this zone. The accumulation of fast growing moss a shaded understory may be inhibiting to the germination of the majority of *Juncus arcticus* seeds. Therefore, the seeds may have accumulated.

The species composition and diversity indices of the invading forest standing vegetation and its seed bank were significantly different.

*Forest Zone*

Feather mosses made up the dominant vegetation in the standing vegetation of the forest zone. The indicator species for this zone were *Larix laricina* and *Equisetum arvense*. Both species were absent from the seed bank. *Larix laricina* was a late successional species relative to the successional sequence and is rarely found in seed banks. Literature has shown that in successful germination, *Larix laricina* requires a cold stratification period of 30-60 days (Baskin and Baskin, 2001). This study had a cumulative stratification period over 60 days. *Equisetum arvense* is a horsetail that reproduces by spores and not seeds. Its tiny gametophytes may not have been noticed in my germination trials.

*Juncus arcticus* was the most frequent species in the forest zone seed bank. This species was also found in the standing vegetation however the abundance of emergent seedlings do not correspond well with the standing vegetation. Seeds of *Juncus arcticus* may have been deposited in this zone when the forest zone resembled the composition and environment of the invading forest zone. Species associated with the forest zone colonized the area as the moss stratum developed. At that time, *Juncus arcticus* was outcompeted and was almost extirpated from the area. Seeds remained in the soil and contributed to its seed bank even though the conditions have changed to prevent successful germination (Amiaud and Touzard, 2004).

The forest zone was different in species composition and diversity between the standing vegetation and seed bank variables. The number of species found in the forest zone seed bank and the standing vegetation were significantly different. The forest zone had the highest species richness (12.89) in the standing vegetation whereas the species

richness of the seed bank was the second lowest (1.06). The standing vegetation was mostly composed of late successional species that did not produce seeds that are usually found in seed banks (e.g. *Picea glauca* and *Larix laricina*).

***Conclusions***

- The null hypothesis was not supported by my findings.
    - The seed banks and the standing vegetation zones of the Beech Bay area were significantly different to each other in terms of diversity indices regardless of successional age.
    - The species composition of the seed bank was also different to that of the standing vegetation in all vegetation zones.
- The alternative hypothesis was validated in part by the results of this study.
    - No significant differences were observed amongst diversity indices of seed banks in the four zones.
    - There were differences in the species composition of the seed banks.
    - *Spergularia marina* was a pioneer species of saline environments and as such, was well adapted to the soil conditions of the meadow zone (salinity = 50.13 mmhos/cm).
    - *Juncus arcticus* was also an early successional species that was common in seed banks. *Juncus arcticus* was outcompeted in the standing vegetation as the soil and environmental conditions changed to allow for other species to colonize but its viable seeds remained in the seed bank.

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# Appendix 1

**Species in Standing Vegetation that did not reach 1% relative abundance**

*Achillea millefolium*
*Andromeda polifolia*
*Arenaria lateriflora*
*Aster ciliolatus*
*Carex caespitosus*
*Carex capillaris*
*Carex capitata*
*Carex leptalea*
*Carex vaginata*
*Chrysanthemum arcticum*
*Dupontia fisheri*
*Erigeron elatus*
*Habenaria obtusata*
*Hierochloë odorata*
*Kalmia polifolia*
*Ledum decumbens*
*Listera borealis*
*Moneses uniflora*
*Parnassia palustris*
*Polygonum viviparum*
*Primula egaliksensis*
*Pyrola grandiflora*
*Pyrola secunda*
*Rumex arcticus*
*Salicornia borealis*
*Salix arctophila*
*Senecio pauperculus*
*Shepherdia canadensis*
*Solidago multiradiata*
*Spergularia marana*
*Triglochin maritimum*
*Triglochin palustre*
*Viola blanda*

# Appendix 2

### Table 1a: Species found in Seed Bank and Standing Vegetation

*Betula glandulosa*
*Empetrum nigrum*
*Potentilla egedii*
*Festuca brachyphylla*
*Spergularia mariana*
*Arenaria lateriflora*
*Erigeron elatus*
*Salicornia borealis*

### Table 1b: Species found in Seed Bank, not in Standing Vegetation

*Epilobium palustre*
*Juncus bufonius*
*Ranunculus cymbalaria*
*Senecio congestus*

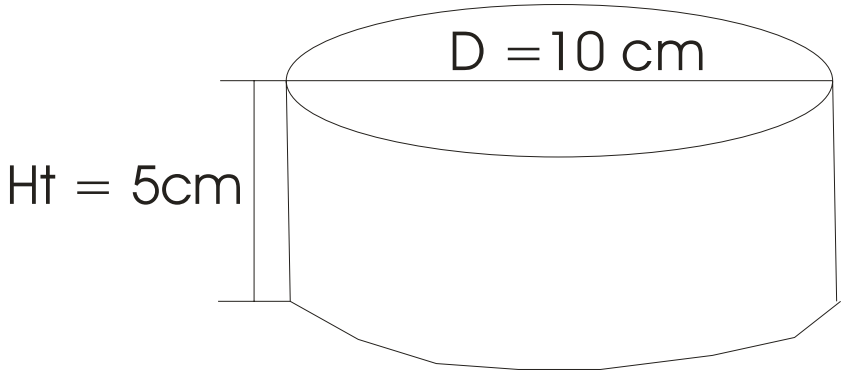
### Table 1c: Species not found in Seed Bank, but observed in Standing Vegetation

*Achillea millefolium*
*Andromeda polifolia*
*Aster ciliolatus*
*Aster junciformis*
*Calamagrostis neglecta*
*Carex aquatilis*
*Carex caespitosus*
*Carex capillaris*
*Carex capitata*
*Carex gynocrates*
*Carex leptalea*
*Carex rariflora*
*Carex subspathacea*
*Carex vaginata*
*Chrysanthemum arcticum*
*Dupontia fisheri*
*Equisetum arvense*
*Eriophorum angustifolium*
*Habenaria obtusata*
*Hierochloe odorata*
*Parnassia palustris*
*Petasites sagittatus*
*Picea glauca*
*Plantago maritima*
*Polygonum viviparum*
*Primula egaliksensis*
*Primula stricta*
*Puccinellia phryganodes*
*Pyrola grandiflora*
*Pyrola secunda*
*Rubus acaulis*
*Rumex arcticus*
*Salix arctophila*
*Salix brachycarpa*
*Salix candida*
*Salix glauca*
*Salix planifolia*
*Salix reticulata*
*Senecio pauperculus*
*Sheperdia canadensis*
*Kalmia polifolia*
*Larix laricina*
*Ledum decumbens*
*Ledum groenlandicum*
*Listera borealis*
*Moneses uniflora*
*Myrica gale*
*Oxycoccus microcarpus*
*Solidago multiradiata*
*Triglochin maritimum*
*Triglochin palustre*
*Vaccinium uliginosum*
*Vaccinium vitis-idaea*
*Viola blanda*

## Appendix 3

**Procedure for calculating number of seeds per meter squared**

*Dimensions of sampling can*




Volume of can = ht x $\pi(r^2)$ = 5cm x $\pi(25cm^2)$ = 392.7 $cm^3$ = 392.7 ml

Surface area of can = $\pi r^2$ = 78.54 $cm^2$

Volume used in germination trials = 20 ml = 20 $cm^3$

$$\frac{20ml}{392.7\ ml} = \frac{4.0\ cm^2}{78.54\ cm^2}$$

*Number of seeds per meter square*

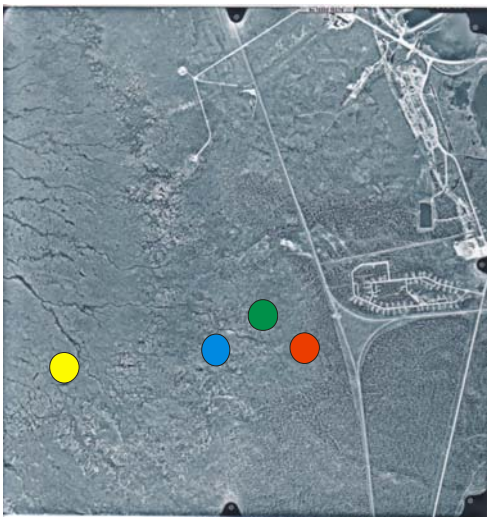
4.0 $cm^2$ = 0.0004 $m^2$

$$\frac{\#\text{ of seeds per 20 ml sample}}{0.0004\ m^2} = \frac{\#\text{ of seeds per } m^2}{1\ m^2}$$

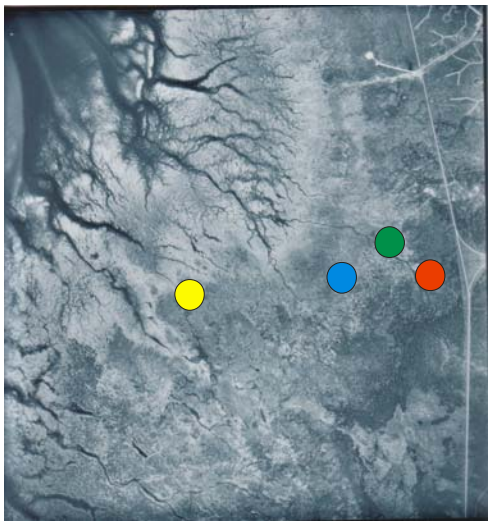
## Appendix 4

*Evidence of Successional Change in the Beech Bay area*

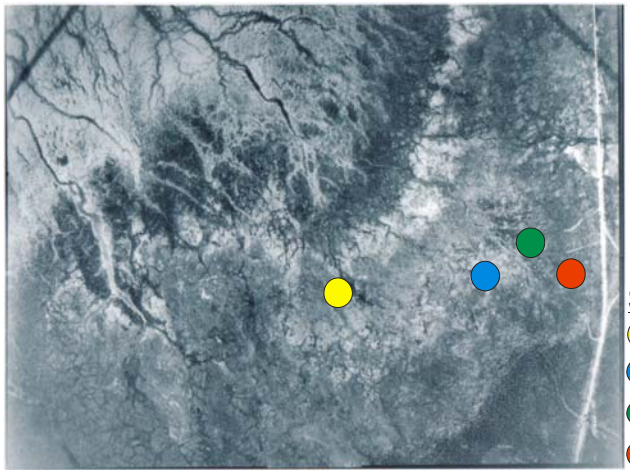
The following aerial photos from 1993, 1955 and 1929 respectively illustrate the successional change in the Beech Bay area over a period of 64 years. The approximate sampling areas are indicated on the photos. The treeline is visible near the railroad tracks and the position of the treeline appears to be changing position indicating that the current position is relatively recent.



**1993 airphoto of study area**



**1955 airphoto of study area**




**1929 airphoto of study area**