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Temporal variations and spatial patterns in saline and waterlogged peat fields
1. Survival and growth of salt marsh graminoids

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Abstract

A cutover bog contaminated with seawater in New Brunswick, Canada remained barren 5 years after peat extraction operations ceased despite the proximity of natural seed sources. The aim of the study was to identify abiotic stresses impeding plant establishment and test transplanting of salt-tolerant wetland plants. The site consisted of long cambered rectangular fields that sloped down (2%) to the drainage ditches on both sides. Across this slope, zones were delineated based on moisture gradient as: Up-areas (drier), Mid-areas (moist) and Low-areas (wet). *Juncus balticus* was transplanted to these zones in August 2004 whereas *Spartina pectinata* was reintroduced in June 2005. Plant material was collected from nearby marshes. Survival of *J. balticus* in August 2005 was poorest at the Low-areas probably because of the early season flooded conditions of that zone. *S. pectinata* survival in June 2006 was good in all zones having better adaptation to early season waterlogged conditions. Early season waterlogged conditions resulted from a perched water table (May–June) and were alleviated only upon the complete thaw of the frozen peat layer on 8 July. Thereafter, important changes in peat characteristics occurred: lowered water table depths that increased redox potentials, decreased moisture content (θ) that increased dry bulk density (ρ), and increased electrical conductivity (EC) that decreased pH. Waterlogged conditions were of greater magnitude and duration at the Low-areas but salinity levels were highest in the Up-areas and Mid-areas. We conclude that local conditions of waterlogging (especially in the Low-areas) and high salinity and low pH (notably in the Up- and Mid-areas) favoured the survival of *S. pectinata* in all areas and *J. balticus* in Up- and Mid-areas only.

Keywords: Frozen ground layer; *Juncus balticus*; pH; Redox potentials; *Spartina pectinata*; Water table

1. Introduction

The province of New Brunswick is Canada's leading *Sphagnum* peat producer and majority of the peat deposits currently under commercial extraction operations are coastal bogs (GNB, 2006) at mean sea level elevation (NRC, 2001). Restoration of mined peatlands to natural wetland ecosystems is one of the aims of the province's Peat Mining Policy. However, seawater contamination of coastal cutover bogs (*e.g.* Mouneimne and Price, 2007) may prevent regeneration of salt intolerant bog plant communities (Tester and Davenport, 2003; White and Broadley, 2001). Evaporation during the growing season further intensifies salinity stress when salts are deposited on the bare surface of peat fields, as is commonly observed in salinity-affected soils (Qadir et al., 2000; Rowell, 1994). Where salinity is a problem, planting strategies must consider timing sensitive life stages, even for halophytes (*e.g.* germination and seedling) to avoid periods of high salinity stress (Zedler et al., 2003). Transplanting grown plants having greater tolerance to stresses may also overcome periods of high salinity stress (Fraser and Kindscher, 2001; Forbes and Jefferies, 1999). However, little is known about the viability of plants in saline acidic soils. This includes halophytes found in local salt marshes that could potentially be useful in restoring a plant cover. While salt marshes undergo regular cycles of tidal flooding and drainage (Harvey and Nuttle, 1995), bogs generally flood less frequently and flooding can be prolonged when the frost table persists and drainage is limited. These conditions can be severely stressful to vascular plants and tolerances vary among wetland plants (Pennings and Callaway,

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1992). Flooded, saturated or waterlogged soils create an oxygen-deficient root medium (Pezeshki, 2001) causing anoxia (Blom and Voesenek, 1996; Ernst, 1990). In such soils the limited supply of oxygen is rapidly depleted by roots, microorganisms and soil reductants and the reduced state is indicated by decreasing redox potentials (E_hs) (Koncalova, 1990; Ponnamperuma, 1972).

Despite the proximity of natural seed sources and introduction of seeds and fertilizer (Chiasson, L., peat producer, personal communication), the study site is devoid of vegetation 5 years after seawater contamination and the termination of peat-extraction operations. Preliminary transplantation trials of several species in summer 2004 showed *Juncus balticus* Willd. and *Spartina pectinata* Link to have the greatest potential. Both species are rhizomatous perennial wetland plants that can grow on the irregularly flooded zone of salt and brackish marshes (Tiner, 1987). They can revegetate disturbed sites with periodic flooding (NRCS, 2000a), although *S. pectinata* is intolerant of frequent flooding (NRCS, 2000b). However, it is not known how both species respond to a combination of prolonged spring flooding, acidic, saline and perennially saturated conditions of a cutover bog. The purpose of this study is to identify how these stresses affect plant survival and growth. The specific objectives are to determine (1) the temporal and spatial patterns of moisture content, salinity, pH and redox potentials of the residual peat layer (0–20 cm) and (2) plant response to these variables.

2. Materials and methods

2.1. The study site

The study site is located on Pokesudie Island, in the Acadian Peninsula of New Brunswick, Canada (47°48′N, 64°46′W). The site was originally a domed and ombrogenous maritime bog (Rampton et al., 1984). Undisturbed bogs and marshes border the study site and are potential natural seed sources. Peat extraction operations began in the 1960s (Daigle et al., 1993) and continued until a storm surge in 21 January 2000 contaminated the peat with seawater and rendered it unfit for horticultural use (Mouneimne and Price, 2007). Currently, drainage is very poor, since pumps used to remove water during peat extraction operations are no longer operating. Twenty-two hectares out of the 150 ha that had been mined was contaminated with seawater. This section was still barren at the beginning of our trial, in contrast to the adjacent uncontaminated bog areas that have some spontaneous regeneration.

The peat is predominantly composed of *Sphagnum* remnants with patches of sedge peat, underlain by wood peat. A thin layer of gyttja overlies the sand substrate. Peat extraction operations left behind long rectangular fields (300–400 m long, 30 m wide), bordered by drainage ditches. The seawater-contaminated area under study comprise 17 parallel fields oriented perpendicular to the adjacent north seashore. The surface and bottom topography is irregular and the remaining peat has a variable thickness of 1–2 m. The fields were cambered along the centerline to direct drainage toward ditches, and the study area portion of each field now have a slope of about 2%. This slope created a moisture gradient that was divided into zones designated as Up-areas, Mid-areas, and Low-areas.

The nearest meteorological station is Bas Caraquet (47°48′N, 64°49′W) but the nearest with climate normals (1971–2000) is Bathurst (47°37′N, 65°45′W); both are coastal locations. Daily mean temperature for January and July at Bathurst is −11 and 19.3 °C, respectively and total precipitation is 1059 mm, (314 mm snow). Annual total degree-days above 5 °C are 1678, and 156, 325, 442 and 408 for May, June, July and August, respectively with the June to August representing 70% of the total (Environment Canada, 2004).

2.2. Preparation of transplant materials

Collection and transplantation of *J. balticus* sods were done on 25 July–8 August 2004. *S. pectinata* was planted at the same time but resulted in extremely low survival the following season (2005). Therefore, *S. pectinata* was collected and re-planted on the Up- and Mid-areas on 4–9 June 2005. Low-areas were re-planted later, 19–21 June 2005 because flooded conditions impeded the reintroduction. Transplanting was done on the day of collection.

Sods of *J. balticus* (11 cm × 15 cm) were collected from a marsh close to the study area that has been isolated from the sea by a service road. This area is currently non-saline and does not undergo tidal flooding events. The rootzone in this marsh corresponds to a ∼13 cm thick distinct soil layer containing organic matter overlying sand. A sod of *J. balticus* containing 28.5 ± 5.6 (mean ± S.D.) number of stems per sod with height 37.5 ± 3.6 cm was planted per planting spot as explained in Section 2.3. *S. pectinata* was collected from the upper-most zone of a nearby undisturbed salt marsh. Dense clumps *of S. pectinata* of height 48.8 ± 7.8 cm were split into ‘J-section’ individual plants (NRCS, 2000b) and about half of the length of the leaves were trimmed-off to reduce transpiration and for ease of handling. Three individuals (or stems) were planted together as a group at each spot as explained in Section 2.3.

2.3. Experimental design

To test the effect of location (Up-, Mid- and Low-areas) on peat characteristics (salinity, pH, moisture content, bulk density, redox potential), and plant growth and survival, we carried out a factorial design experiment in the seawater contaminated and waterlogged area of the cutover bog. Ten experimental blocks of 17 m × 7 m were randomly selected from either side of the longitudinal central ridge of the 17 cambered fields. The length of each block (17 m) was parallel to the longitudinal ridge of the field. Two parallel plant rows were spaced 30 cm apart within each Location. The upper row on the Up-area was 1 m from the longitudinal ridge of the field. The lower rows on the Up-area and Mid-areas were 2 m apart, respectively, from the upper row of the adjacent Locations. Each pair of 17 m rows was divided into four equal sections of 3 m lengths for plants, with 1 m length of undisturbed spaces in between and on both ends of each pair of rows. There were 10 sods (*J. balticus*) or groups of plants (*S. pectinata*) per row, a total of 20 sub-units per Location. Sods were transplanted on a randomly selected section at each Location. For each block, two water wells were installed: one at the Up-area and the other at the Low-area. The undisturbed 1-m length spaces were reserved areas for destructive peat sampling to measure moisture content (θ), electrical conductivity (EC), pH, and dry bulk density (ρ) which required an undisturbed spot at each sampling. Peat samples were obtained from each of the three Locations (factor 1); at four Depths (factor 2): 0–5, 5–10, 10–15 and 15–20 cm in all the 10 blocks, five times during the entire study period 30 May, 26 June, 12 July, 29 July, and 9 August.

Survival counts were done a year after transplantation; 11 August 2005 for *J. balticus* and 10 June 2006 for *S. pectinata*. Survival was expressed as percentage of total number of sods (20) planted for *J. balticus*. On 12 August 2005, a whole plant sample was removed from each Location for both species (except for *J. balticus* Low-areas which had insufficient survival) for a separate study on ion accumulation. Therefore, the percentage survival of *S. pectinata* on 10 June 2006 was based on 19 instead of 20 spots per location. At the end of the study period three randomly selected sods or groups of plants from each Location in all the 10 blocks were used to determine the number of stems per sod, number of flowers per stem, number of leaves per stem, and plant height.

2.4. Peat parameters

Since under waterlogged conditions plants are shallow-rooted (Cronk and Fennessy, 2001), peat samples were collected from 0–5, 5–10, 10–15 and 15–20 cm depths, layer by layer beginning at the surface. Sampling tubes were made of 6.1 cm diameter galvanized steel pipe. At each sampling point one core sample was for θ and ρ and three aggregate cores were for EC and pH measurements. All samples were extruded immediately after extraction and stored in sealed plastic bags, stored in the refrigerator and analyzed within a week of collection. Moisture content was expressed as % dry weight basis (Farnham and Finney, 1965) because peat in the upper surface of fields during May and early June was in a flowable state in some blocks and could not be sampled as a solid unit of a precise volume that would allow moisture content to be expressed as % volume volume^{-1}. Dry bulk density (ρ) was calculated by dividing the oven dry mass of a sample by its field volume. Total number of samples of ρ was reduced to $N = 562$ instead of $N = 600$ (3 Locations × 4 Depths × 10 blocks × 5 times) due to sample volume accuracy problems in 30 May (36 samples) and 26 June (2 samples) measurements.

For EC and pH, a sample was vacuum-filtered (Fisherbrand Qualitative P8-creped coarse porosity and fast flowrate filter paper) while simultaneously pressing the sample by hand using a jar. The filtrate was then tested for EC using YSI Model 33, S-C-T Meter (Yellow Springs Instrument Co., Inc.) and pH using Fisher Scientific Accumet pH meter 10. Filtrates were frozen at the study site laboratory and shipped to the University of Waterloo for ion analysis later.

Redox potentials (E_h) were measured in situ using an Orion 9678 BNWP redox/ORP electrode (Thermo Scientific Inc.). The probe was inserted into the peat immediately after making a hole with a wooden dowel, at 12 cm depth at three random points within plant rows in each Location in all the 10 blocks, four times during the study: 24 June, 8 July, 21 July and 5 August. The probe was checked with a standard ferrous-ferric solution (Light, 1972) before each use. The corresponding in situ pH was measured using Orion S175CD spear tip electrode (Thermo Scientific Inc.). ORP readings were adjusted to pH 7 (Bohn, 1971) and to standard hydrogen electrode, and corrected for temperature (25 °C) (Kölling, 2000) for final E_h values. The temperature used for each measurement period was the average of data-logger readings at the meteorological station from 9:30 a.m. to 4:00 p.m. which was the entire duration of field measurements.

2.5. Hydrological parameters

Wells were installed on 25 May 2005 by driving them into the peat until obstructed by the frozen layer. Twelve water table (WT) measurements were taken from 26 May to 15 August 2005. The wells were made of 50 mm (i.d.) ABS pipes, 950 mm in length fitted with a wooden cone tip of length 76 mm and perforated throughout their lengths at 3.8% porosity. The pipes (wells) were lined with fine nylon netting on its outer side before installation, to prevent peat particles from entering them. After each WT measurement, the wells were driven into the peat until obstructed by the frozen layer and its depth was measured.

A pit measuring 1 m × 1 m wide was dug to a depth that reached the WT in an unsaturated but saline part of a field. Core samples were taken in 5 cm increments from the surface down to the WT using the same metals cylinders described earlier. Moisture content was determined gravimetrically as described earlier. Measurements were made on 9 July and 6 August 2005. The pit was kept covered with plywood sheets between these dates, and 5 cm of peat was scraped off the pit face before resampling. The capillary fringe (CF), a saturated zone above the water table where water is retained by capillary forces (Hornberger et al., 1998) was determined from the θ profile (Ronen et al., 1997).

An automated meteorological station recorded every 20 min precipitation from a tipping bucket rain gauge, net radiation with a REBS Q*8 net radiometer, and ground heat flux with a pair of REBS HFT-1 heat flux plates (Campbell Scientific, Inc.). The air temperature sensor malfunctioned; thus, mean air temperature was obtained from the nearest (3.5 km) coastal weather station at Bas Caraquet. Total evaporation (mm) was calculated according to Priestley and Taylor (1972), as described in Price (1996).

2.6. Statistical analysis

A two-way factorial ANOVA was done to determine the effect of: Location and Depth on EC and θ at each time of measurement, and Location and Time of measurement on E_h. Transformations log(x) were performed to achieve normal distribution and homogeneity of variances, and rank (Conover and Iman, 1981) where these could not be achieved especially for two-way ANOVAs and are indicated on the ANOVA tables. One-way ANOVAs were done to determine the effect of Location on plant parameters (% survival, number of stems per sod, number of flowers per

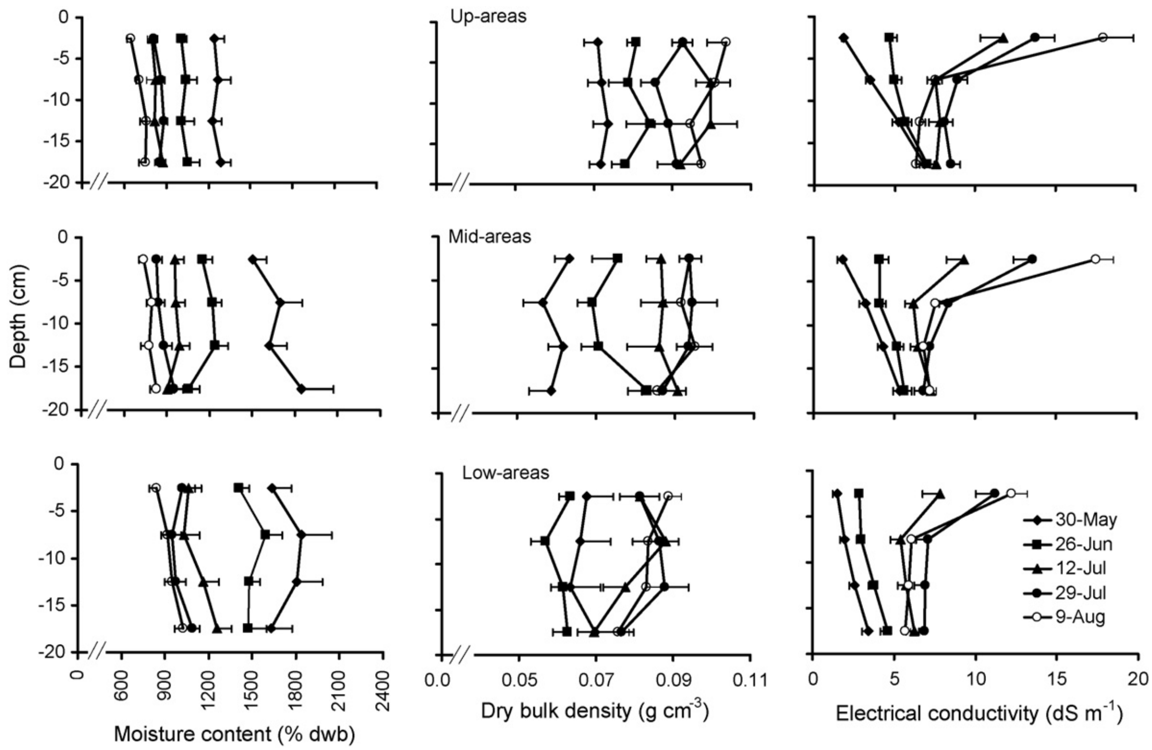

Fig. 1. Moisture content, dry bulk density and electrical conductivity at various locations, depths and times during the study period. + or − standard error bars are shown. $N = 10$ for each point except for 30 May and 26 June (explained in Section 2.4).

sod, number of leaves per stem and height), When the assumptions for ANOVA were not fulfilled, non-parametric ANOVA, Kruskal–Wallis (K–W) test was applied. Where K–W test was significant, one-way ANOVA of ranks was performed. Significant ANOVAs were followed with multiple comparisons (Least Significant Difference). ANOVAs were performed using SPSS (SPSS 14.0 for Microsoft Windows, SPSS Inc., Chicago, USA). Regression curves were derived for θ and ρ, θ and EC, and EC and pH using Microsoft Excel.

3. Results

3.1. Peat characteristics

The range and magnitude of moisture content (θ) in the Up-areas (∼600–1400%) were less than those of Mid- and Low-areas (∼700–2200%) (Fig. 1). During the early part of the season (30 May), θ was high, ∼12–20 times peat oven dry weight, and decreased to ∼6–10 times peat oven-dry weight in all Locations by August. Difference in θ was related to Location on the cambered field surface (two-way ANOVA, d.f. = 2; $F = 15.1$, 31.9, 14.1, 7.58, and 23.3 for 30 May, 26 June, 12 July, 29 July and 9 August, respectively; $P < 0.001$). The Up-areas were always the driest and the Low-areas the wettest, while the Mid-areas were intermediate, but similar to Low-areas on 30 May and Up-areas on 29 July (post hoc (LSD), $P = 0.05$). Significant differences in θ with peat Depth was found only at the end of study period (9 August) (two-way ANOVA, d.f. = 3, $F = 3.84$, $P = 0.012$), the two uppermost layers being drier than the underlying peat (post hoc (LSD), $P = 0.05$).

Dry bulk density (ρ) ranged from ∼0.05 to 0.11 g cm^{-3}, highest at the Up-areas (Fig. 1), and lowest at Low-areas, opposite to that of θ. Dry bulk density of the surface peat increased as the season progressed, and was inversely related with θ ($R^2 = 0.89$) (Fig. 2).

Electrical conductivity increased as the season progressed, most substantially at the surface (0–5 cm depth) (Fig. 1). Differences in EC were a function of Location on the cambered field surface (d.f. = 2; $F = 24.8$, 11.3, 8.32 and 17.3 for 26 June, 12 July, 29 July and 9 August, respectively; $P = <0.0001$) and peat Depth (d.f. = 3, $F = 54.1$, 13.2, 8.4, 25.0 and 53.2 for 26 June, 12 July, 29 July and 9 August, respectively; $P < 0.0001$). The Up-areas always had the highest EC and the Low-areas had the lowest, while the Mid-areas had intermediate EC but matched the Up-areas towards the later part of the study period (29 July and 9 August) ($P = 0.05$). The vertical distribution of EC displayed the same general pattern at Up-, Mid- and Low-areas. Before 26 June, EC increased with depth, thereafter, EC decreased with depth, punctuated by a sharp rise in EC in the 0–5 cm layer. Over the entire study period, a negative relationship was found between EC and pH, and θ and EC (Fig. 2).

3.2. Hydrologic parameters

There were 33 rainfall events from 3 May to 15 August which totaled 212 mm. Most rainfall (139.3 mm) occurred before 21 June or during the pre-thaw period, whereas between 21 June and 19 July there was only 16 mm, and between 19 July and 15 August, 55.8 mm. Total rainfall for 3–31 May, June, July and

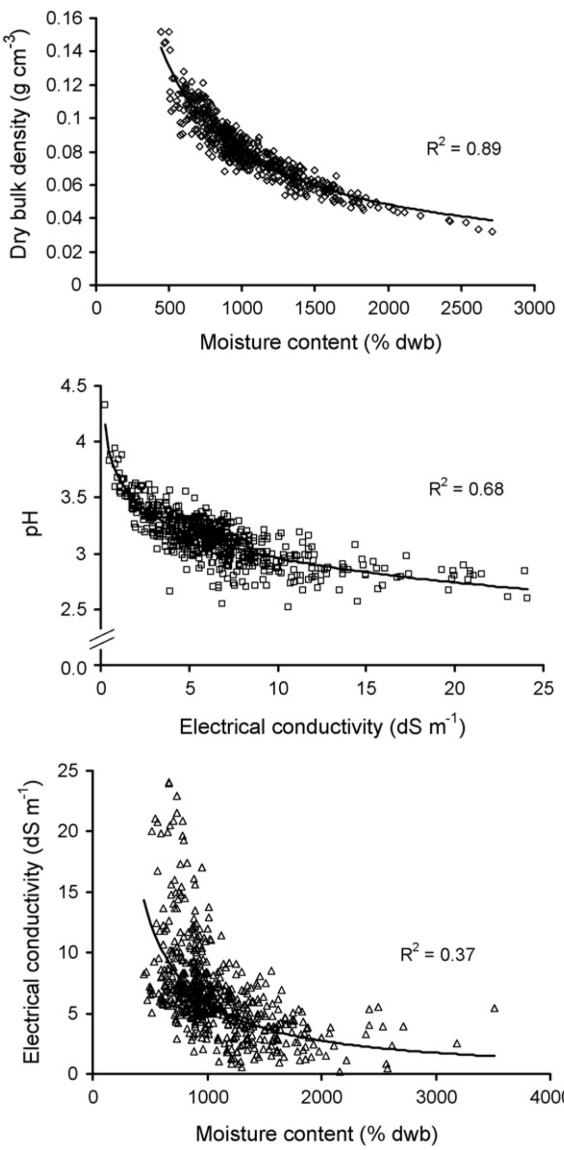

Fig. 2. Dry bulk density of peat increased as peat became drier ($N = 562$), pH decreased as EC increased ($N = 600$) and EC decreased as peat became wetter ($N = 600$).

1–15 August at the study site was 69.2, 74.4, 37.7 and 30.4 mm, respectively. Compared with the Bathurst monthly climate normals of 78.5, 83.5, 99.0 and 101.6 mm, respectively, June and July were drier. Considering that rainfall at the study site was short of 2 days in May and 16 days in August, Bas Caraquet rainfall during the study period which were 76.7, 76.4, 44.5 and 108.5 for May, June, July and August, respectively could be compared with climate normals; May to July were drier and August wetter at Bas Caraquet weather station, which could represent rainfall in the experimental area. The average daily temperature for May, June, July and August at Bas Caraquet (which represented temperature in the experimental area) in 2005 were 7.6, 16.4, 19.7 and 19.8 °C, respectively which differed from the Bathurst climate normals by 2.3, −0.6, −0.4 and −1.6 °C, respectively. Thus, July with the maximum degree-days was also the driest warm month. Total evaporation during the study period was estimated to be 311 mm, ∼100 mm greater than precipitation.

The average WT depth was greater at Up-areas than at Low-areas (Fig. 3) which decreased from -8.5 ± 1.7 and -1.6 ± 1.2 cm, to -51.5 ± 2.5 and -40.7 ± 2.4 cm, respectively on 26 May and 15 August, respectively. Water table variability increased as the frost table disappeared, which was about 30 June in the Low-areas, and 8 July in the Up-areas.

The capillary fringe (CF) determined from moisture profiles of unsaturated areas extended 40–50 cm above the WT.

Average θ of the 0–20 cm peat layer decreased with WT depth as the season progressed and exhibited a curvilinear relationship (study period, $R^2 = 0.62$) showing greater sensitivity in θ when the WT was high (Fig. 4).

3.3. Redox potentials

After 8 July when the frost table had thawed, and WTs were lower, E_h increased with very few blocks approaching partially aerated conditions (+400 mV) (Fig. 5) but most were below the level where oxygen disappears (+330 mV) but above the level where manganese is reduced (+200 mV) (Ponnamperuma, 1984 in Laanbroek, 1990). However, during the pre-thaw period, Low-areas were at the levels where iron is reduced (+120 mV) (Ponnamperuma, 1984 in Laanbroek, 1990). Variation among blocks was greatest at Low-areas and the minimum E_h values

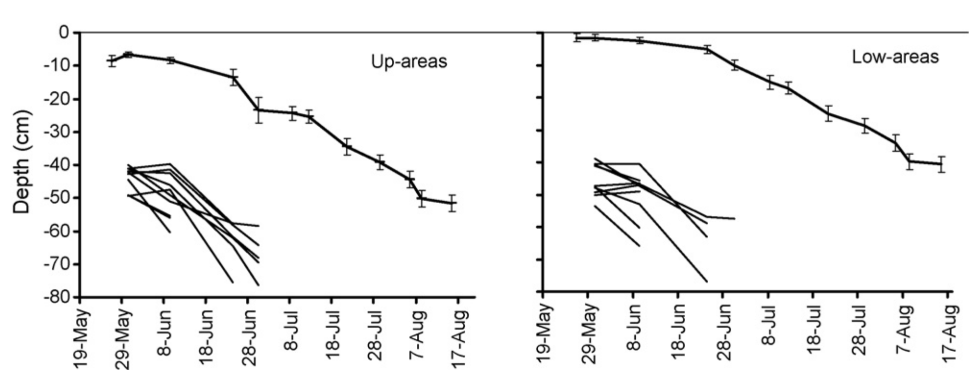

Fig. 3. Average depth of water table (top curves with standard error bars) and depths of frozen layer (a curve for each of the 10 blocks because of decreasing N with time) at Up-areas and Low-areas during the study period.

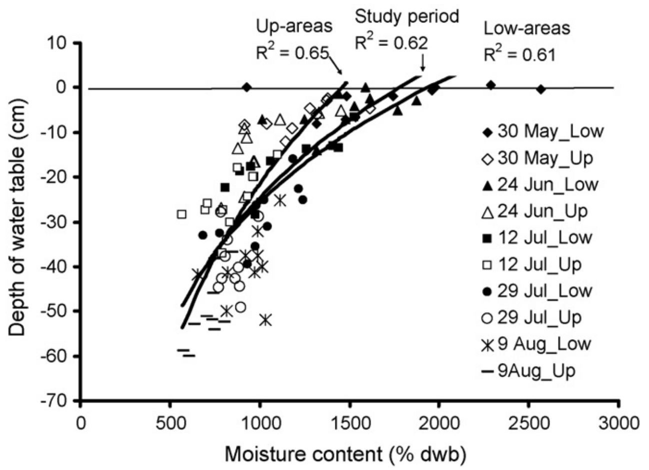

Fig. 4. Relationship between water table depth and average surface moisture content (0–20 cm) for the entire study period ($N = 20$ for each date of measurement), Up-areas ($N = 50$) and Low-areas ($N = 50$).

were exhibited by some blocks at this Location. Location on the cambered field surface (d.f. = 2, $F = 6.46$, $P = 0.002$) and Time of measurement (d.f. = 3, $F = 83.6$, $P < 0.0001$) (two-way ANOVA by ranks) had significant effects on E_h. Overall, E_h (untransformed means are given instead of rank means) at the Up- and Mid-areas were higher (200.1 and 207.8 mV, respectively) than at the Low-areas (167.8 mV) ($P = 0.05$) and E_hs (231.7 and 253.8 mV) during post-thaw (for 21 July and 5 August, respectively) were higher than during pre-thaw period (180.9 mV for 24 June and 127.9 mV for 8 July) ($P = 0.05$).

3.4. Plant responses

Survival of *J. balticus* on 12 August 2005 at the Up-areas (68.9%) and Mid-areas (58.5%) were not significantly different but both were higher than at the Low-areas (27.5%) (Fig. 6, Table 1a). The number of flowers per stem was highest at the Up-areas (0.34), lowest (0.07) at the Low-areas and not different to either Locations (0.2) at Mid-areas (Fig. 6, Table 1a). No significant difference was found between Locations for number of stems per sod and stem height (Fig. 6, Table 1a).

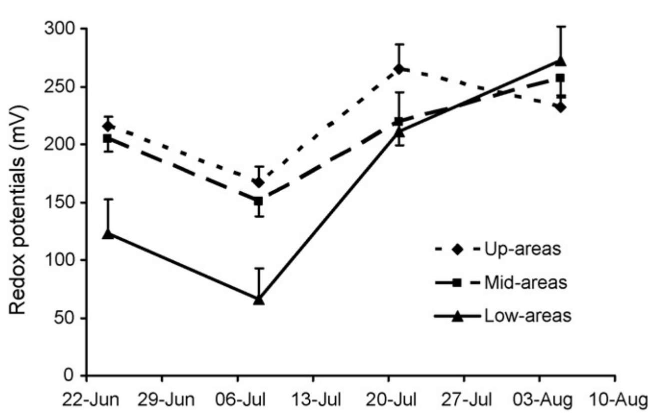

Fig. 5. Redox potentials (±S.E.) at 12 cm depth at the three Locations on four occasions during the study period.

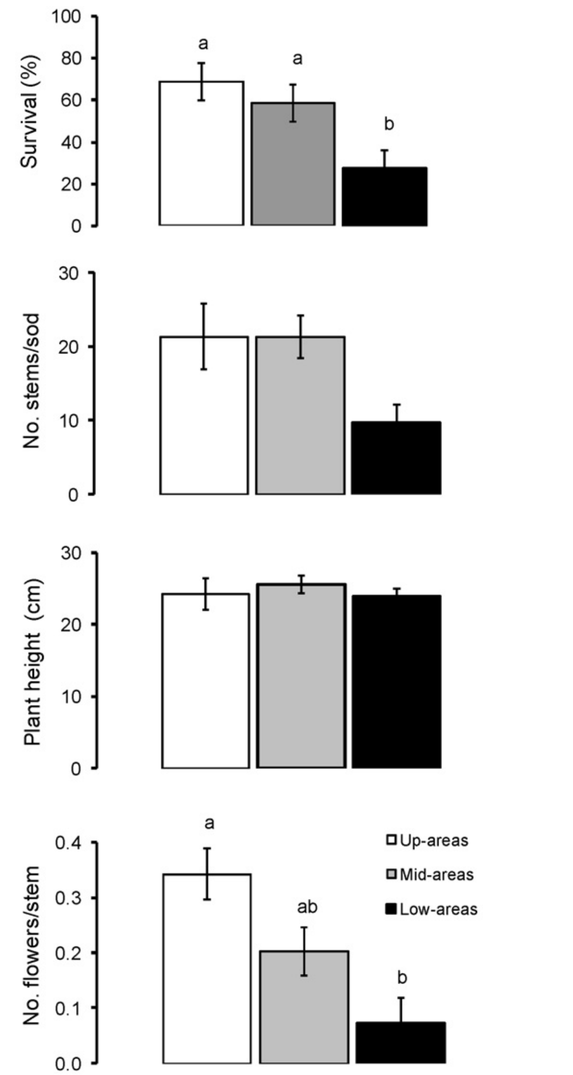

Fig. 6. *Juncus balticus* survival ± S.E. and other plant parameters ± S.E. on 11 August 2005. For number of stems and flowers per stem, and plant height, $N = 30$, 27 and 21 for Up-areas, Mid-areas and Low-areas, respectively. Means indicated by the same letters are not significantly different ($P = 0.05$).

S. pectinata survival on 10 June 2006 was high and was not significantly different among Locations, which was 89, 92 and 84% at Up-, Mid- and Low-areas, respectively. Similarly, Location on the cambered field surface did not affect the number stems per planting spot, number of leaves per stem or plant height (Fig. 7, Table 1b).

Spontaneous regeneration of *Agrostis* spp., *Eleocharis* spp. and *Juncus buffonius* occurred on some sods at Mid- and Low-areas where *J. balticus* died. *Agrostis* and *Eleocharis* came with the sod but *J. buffonius* was introduced in the study area 2 years earlier (L. Chiasson, personal communication) and grows in the non-saline waterlogged areas of the cutover bog.

4. Discussion

The thaw period marked notable changes in peat characteristics and hydrology. A frozen peat layer persisted until the last week of June (Fig. 3). During this period, WT was very

Table 1
Analysis of variance (one-way ANOVA) comparing different plant parameters by Location

Source	d.f.	Survival (%)			d.f.	Number of stems per sod			Plant height (cm)			Number flowers per stem (rank)		
		MS	*F*	*P*		MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
(a) *Juncus balticus*														
Block	9				9									
Location	2	4570	6.13	0.006	2	354	3.02	0.069	7.03	0.275	0.762	211.8	4.71	0.019
Error	18	745			14	117			25.6			44.9		
Total	29				25									

Survival (%) (K–W test)	Source	d.f.	Number of stems per planting spot			Plant height (cm)			Number leaves per stem		
			MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
(b) *Spartina pectinata*											
χ^2: 1.41											
d.f.: 2	Block	9									
AS: 0.494	Location	2	0.226	0.083	0.921	5.52	0.513	0.605	0.115	0.047	0.954
	Error	18									
	Total	29									

MS = mean square; AS = asymptotic significance.

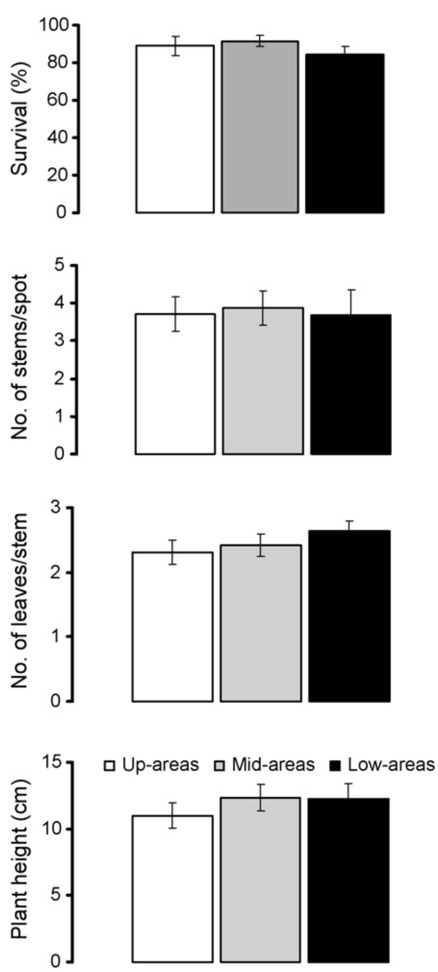

Fig. 7. *Spartina pectinata* survival ± S.E. and other plant parameters ± S.E. on 10 June 2006. There is no significant difference among Locations in all parameters ($P = 0.05$).

high because frost restricted drainage. Consequently θ was also high (>1000%) (Fig. 1). These conditions were exacerbated at low elevation areas where water collected. Some blocks at Low-areas had flooded conditions early in the season where θ exceeded ∼2000% dwb (Fig. 2). Low-areas maintained the highest θ throughout the study period. Immediately after thaw, θs in the Up- and Mid-areas were <1000%, but at Low-areas this was achieved only at the end of the season (Fig. 1).

Bulk density (ρ) increased as the peat dried and θ decreased (Fig. 2). Price (1997) also noted that peak bulk density occurred during drier periods, as peat volume decreased. The change in volume in very wet peat is equivalent to the volume of water lost (Kennedy and Price, 2005). The reduction in pore volume prolongs saturated conditions (Whittington and Price, 2006) which can stress plants or divert plant energy from growth and reproduction towards expression of tolerance to continued saturated conditions. Although θ decreased as the season progressed, ρ increased and thus saturated or near-saturated conditions were maintained at all Locations. While E_h increased following ground thaw, aerated conditions were never achieved (Fig. 5).

Early in the season, before complete thaw, EC increased with Depth (Fig. 1). Since soil freezes from the top down (Zhang and Shijie, 2001), downward solute redistribution occurs by ion exclusion from the ice grid, convective transport towards the frost front, and diffusion owing to developing concentration gradients between the top frozen layer and unfrozen layer below (Stähli and Stadler, 1997). Chagué-Goff and Fyfe (1997) observed this phenomenon in a Canadian sub-artic plateau bog where the concentration of solutes was enriched immediately above the permafrost table (at 0.68 m deep). There was a distinct increase in EC (8–15 dS m^{-1}) following ground thaw (between 26 June and 12 July), particularly in the 0–5 cm layer. During the study period evaporation was 100 mm greater than precipitation causing an upward flow of water and solutes, and, leaving salts behind on the soil surface (Qadir et al., 2000; Rowell, 1994).

The uppermost layer thus became strongly saline and can be unsuitable even for salt tolerant species at the early stages of growth (Zedler et al., 2003). However, transplanting rhizomatous mature halophytes which reproduce vegetatively have the advantage of having their roots and rhizomes below this highly saline surface layer.

The concomitant reduction in pH as EC increased (Fig. 2) is due to the high cation exchange capacity of *Sphagnum* peat and its pore water (Thomas and Pearce, 2004; Bates, 2000; Smidsrod and Painter, 1984; Clymo, 1963) with Na^+ and other cations displacing H^+ ions thus reducing pH (Vitt, 2000; Ours et al., 1997; Pugh et al., 1996; Reeve et al., 1996; Kilham, 1982). pH affects the bioavailability of many nutrients and toxic elements (Hinsinger et al., 2003). In a study by Armstrong and Armstrong (1999) in relation to the *Phragmites* die-back in Europe, phytotoxins butyric and caproic acids present in die-back sites were found innocuous at pH 6 but highly toxic to over-wintered *Phragmites* plantlets at pH 4.5. They found proto and metaxylem blockages in the roots, lignification and suberization of apices and stunted growth of roots. Roem et al. (2002) did a field experiment to simulate atmospheric deposition of nitrogen and sulphur that cause eutrophication and acidification of heathlands in the Netherlands. They found that at pH < 5 and with elevated concentrations of Al, the germination of several heathland species decreased significantly thus affecting species diversity of the ecosystem. In an earlier hydroculture study, De Graaf et al. (1997) found that low pH resulted in Al toxicity that led to poor root development, yellowish leaves and reduced Mg and P in heathland plants. Thus, seawater contamination in a bog produced two stresses: salinity itself and the intensification of acidic conditions. The planting guide (NRCS, 2000a,b) does not mention the suitable pH range for *J. balticus*. However, Stoughton and Marcus (2000) found that among the 33 species they studied only *J. balticus* significantly increased in plant density in plots with pH < 6.4. Given that *J. balticus* has some tolerance for both salinity and low pH, the greatest stressor to its survival at this site was the flooded conditions early in the season.

As the season progressed, WT dropped dramatically (Fig. 3) with the Low-areas maintaining shallower WT. During mid-summer (July), the period of maximum degree-days above 5 °C and most conducive to plant growth, WT dropped to 40–50 cm below the surface in Up-areas, and surface θs to ~800% (Fig. 1). However, Up-areas were not moisture-limited, because of a high CF which in combination with decreasing ρ was responsible for continued poor aeration (low E_h). WT had a strong influence on surface θ (Fig. 4). In general, warmer temperature, lower WT and rise in E_h provided improved conditions for plant growth by July.

Very low survival of *J. balticus* (Fig. 6) at Low-areas was primarily due to very high θs (>1400%) with E_h values <250 mV as a direct result of very shallow WT especially prior to complete thaw (Fig. 1), which was a critical time for shoot emergence. This confirmed the findings of Wierda et al. (1997) and Runhaar et al. (1997) that the spring water table depth is a dominant factor in determining plant species distribution in wetlands. Low survival suggested limited metabolic adaptation of its rhizomes to flooding. This adaptation is expressed by the ability to conserve carbohydrate reserves until shoot emergence in the beginning of the season (Crawford, 1992; Barclay and Crawford, 1983) and minimal accumulation of ethanol, a potentially toxic product of glycolytic fermentation especially upon re-exposure of rhizomes to air (Monk et al., 1984; Rumpho and Kennedy, 1983). Barclay and Crawford (1982) studied the responses of rhizomes of 23 wetlands species to total anoxia for 7 days at 22 °C and found that these could be grouped into three different levels of tolerance. Species related to the plants in our study *Juncus effusus* L. and *J. conglomeratus* belonged to the least tolerant – species killed by anoxia, while *Spartina anglica* C. E. Hubbard was more tolerant and belonged to the group – species surviving but showing no shoot extension under anoxia. In a further study (Barclay and Crawford, 1983) of three wetland species with large carbohydrate reserves, each representing different tolerance levels, they found that after 4 days in anaerobic conditions, the least tolerant species *Glyceria maxima* showed a rapid decline in total non-structural carbohydrates than when grown in air while this did not occur under both growing conditions in more tolerant (*Phalaris arundinacea*) and most tolerant (*Scirpus maritima*) species. Monk et al. (1984) subjected five wetland species with large carbohydrate reserves that belonged to the groups of more and most tolerant to anoxia, and a dryland species intolerant to anoxia *Iris germanica*, to 8 days without oxygen and thereafter re-introduced them to air for another 9 days. In wetland species ethanol accumulation increased but reached a plateau within 2–4 days of anoxia and decreased to the levels of control (aerobic condition) upon re-exposure to air. The lowest accumulation was in *Acorus calamus* followed by *Typha latifolia*. Whereas in *I. germanica*, there was a steady increase in ethanol accumulation during anoxia which decreased upon re-exposure to air but its level did not reach those of control. In its natural setting, *J. balticus* zone is located beyond the upper region (*S. pectinata* zone) of the salt marshes with relatively drier and lower salinity conditions. Sprouting earlier and growing in relatively drier conditions implies that its metabolic adaptation to flooded conditions is limited compared to *S. pectinata*. Of the few that survived at Low-areas, their sexual reproduction was impaired as shown by significant reduction in the production of flowers per stem (Fig. 6).

High θs were maintained at the Low-areas even after thaw, which left plants little chance of recovery from waterlogging. However, at the Up- and Mid-areas where plant survival was greater, EC levels were high (Fig. 1). This could prevent germination even of halophyte seeds (Zedler et al., 2003), or survival of seedlings that managed to germinate unless sufficient and frequent precipitation during the post-thaw dilutes or leaches salts downward. However, the normal soil-water deficit that prevails in July does not generally promote leaching. Therefore seeding is unlikely to succeed as a major revegetation technique for the study site as was already shown by experience (Chiasson, L., personal communication), so transplanting grown plants is the most reliable method.

In contrast to *J. balticus* which did not grow well in the Low-areas, *S. pectinata* was not affected by its Location on the cambered field surface. Hence, we would expect that when grown together, *J. balticus* would likely colonize in the Up-areas and *S. pectinata* would dominate the Mid- and Low-areas. Thus, there would be a zonation of the two species in a small gradient of 2% with 4–8 cm difference in elevation base on water stress tolerance as it occurs in salt marshes (Rand, 2000; Pennings and Callaway, 1992). Zedler (2000) views this as the importance of microtopography and that in salt marshes a difference of only 10 cm can shift composition to alternative plant assemblages. The suitability or otherwise, of a Location could be based on water stress tolerance of a species and was illustrated by the WT–θ relationship during the entire study period (Fig. 4). For example, the Low-areas curve described WT–θ relationship in a Location or zone unsuitable for *J. balticus* (Fig. 4). However, long-term salinity tolerance in the Up-areas that can be investigated by future studies would eventually determine the dominant species.

Of the two species tested *S. pectinata* appeared to be more tolerant of salinity because of its higher survival % especially in the Up-areas (Fig. 7). The mechanism for salt tolerance may be manifested in the distribution of salts in the above- and below ground parts of plant which is an important survival strategy in halophytes and this is presented in a separate forthcoming paper. In order to promote plant diversity, there is a need to search for other species that may perform similar to or better than *J. balticus* and *S. pectinata* under the current conditions of the study site and investigate the potential of those species that regenerated spontaneously.

5. Conclusions

The thaw period was the time when major changes in peat characteristics occurred which could be categorized into pre- and post-thaw characteristics. During pre-thaw period the frozen ground layer kept the water table near the surface which created flooded and reduced conditions especially in the lower elevation areas near the ditches. These conditions were unfavourable to the survival of *J. balticus*. At post-thaw, the water table dropped dramatically and consequently, moisture content decreased but bulk density increased. Increase in bulk density maintained saturated or anaerobic conditions stressful to plants. After thaw, EC increased significantly especially at the 0–5 cm surface with concomitant decrease in pH which, in combination with spring flooding precluded germination of seeds or survival of seedlings and thus explained the current lack of spontaneous regeneration. However, adverse condition at the surface is avoided by transplanted grown plants because their roots are located below this surface and thus make transplantation a more reliable method for revegetation than seeding. *S. pectinata* which showed higher survival at all locations tested was found more tolerant than *J. balticus* to the harsh environment of the seawater contaminated bog.

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