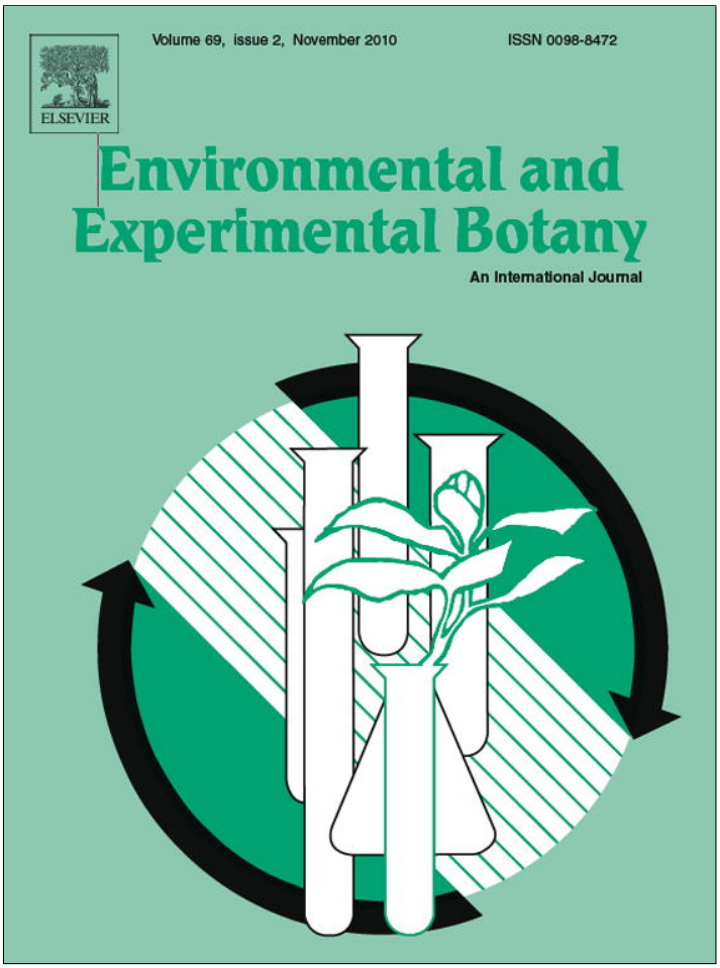

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Temporal variations and spatial patterns in saline and waterlogged peat fields: II. Ion accumulation in transplanted salt marsh graminoids

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ABSTRACT

Our earlier study in New Brunswick, Canada showed that *Spartina pectinata* Link survived very well after transplantation in a barren cutover bog that was contaminated by seawater, in all combinations of salinity and moisture content tested. However, the survival of *Juncus balticus* Willd. was adversely affected in areas with very high moisture contents. The main aim of this current study was to understand the salinity tolerance of both species grown in salinized peat fields by determining how much salt ions, especially Na^+ and Cl^- were accumulated in the above-ground and below-ground parts of these plants. A second aim of this paper was to determine the accumulation of potentially toxic metals Fe and Mn. *S. pectinata* had significantly greater concentrations of Na^+ and Cl^- in the above- than in the below-ground parts. In contrast, *J. balticus* had Na^+ concentration significantly greater in the below- than in the above-ground parts while for Cl^-, there was no significant difference. These contrasting patterns of Na^+ accumulation demonstrated typical characteristics of a halophyte (*S. pectinata*) and a glycophyte tolerant to salinity (*J. balticus*) described in literature. Fe and Mn concentrations in both species were low but only Fe approached deficiency levels in plants.

1. Introduction

Establishing a vegetation cover within a short period, on an abandoned cutover bog contaminated with seawater, requires transplantation of suitable wetland plants. Montemayor et al. (2008) found *Spartina pectinata* Link and to some extent *Juncus balticus* Willd. to have good survival rate under high salinity, low pH, and slightly anaerobic conditions of the cutover bog. The accumulation of salt ions in different parts of salt-tolerant wetland plants under these conditions is not known. How salt ions are partitioned between the above-ground and below-ground parts can provide indications on the tolerance of plant species to salinity. This information gives some understanding of plant species survival and growth under saline conditions. Consequently, such knowledge provides guidance in the selection of appropriate species to revegetate a site characterized with definite or predictable spatial patterns and temporal variations in salinity.

Vegetation that can complete their life cycles at salinities $\geq$300 mmol L^{-1} NaCl are called halophytes (Flowers et al., 1977). Some glycophytes (plants that establish in non-saline environments) can tolerate salinities lower than those tolerated by halophytes (Moghaieb et al., 2004; Poljakoff-Mayber and Lerner, 1999; Flowers et al., 1977). Flowers et al. (1977) further distinguished halophytes from glycophytes by their ability to accumulate ions to high concentrations, particularly in the leaf cells. Halophytes growing under saline conditions accumulate high concentrations of inorganic ions in their tissues. These inorganic ions play a major role in osmotic adjustment or osmotic regulation that maintains the plant's ability to uptake water and to sustain turgor (Moghaieb et al., 2004; Bradley and Morris, 1991; Flowers, 1985; Greenway and Munns, 1980).

Excessive accumulation of Na^+ and Cl^- inhibits plant growth and can cause damage to many plants (Tester and Davenport, 2003; White and Broadley, 2001) but halophytes and salt-tolerant glycophytes manage salt ions by various means to avoid injury, especially to the shoots. Halophytes respond positively to NaCl and accumulate salt concentrations equaling or exceeding those of sea water in their leaves without detriment (Flowers et al., 1977). Since the shoots are susceptible to salt damage Na^+ can be accumulated in, or be excluded from, the roots; a typical response of salt-tolerant glycophytes (Tester and Davenport, 2003; Poljakoff-Mayber and Lerner, 1999). Typical of halophytes is the regulation of Na^+ accumulation in the shoots by excretion from the leaves through salt-secreting glands (Marcum, 1999; Marcum and Murdoch, 1992; Bradley and Morris, 1991; Rozema et al., 1981; Atkinson et al., 1967), compartmentalization in the vacuole (Yeo, 1981), and succulence (Tester and Davenport, 2003; Albert, 1975). Salt glands

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remove both salt and water from the leaves and the loss of water restricts these plants to habitats with abundant water such as salt marshes (Tester and Davenport, 2003). In saline environments, plants may take up Na^+ at the cost of K^+ and Ca^{2+}, both essential nutrients (Alam, 1999; Cramer et al., 1987); K^+ activates about 50 enzymes (Bhandal and Malik, 1988) and Ca^{2+} is responsible for cell membrane integrity that prevents passive accumulation of Na^+ and Cl^- (Alam, 1999; Lauchli, 1990; Cramer et al., 1987; Lynch et al., 1987). Thus, the maintenance of the uptake of both K^+ and Ca^{2+} is key to plant survival in saline environments.

In saturated and reduced conditions common to wetlands, essential micro-nutrients like Fe and Mn can be readily bioavailable. Excessive accumulation of Fe or Mn can result in toxicity especially in plants lacking an avoidance mechanism. Iron plaque formation consequent to radial oxygen loss (ROL) from the roots is an avoidance mechanism (Pezeshki, 2001; Neue et al., 1998; Ernst, 1990; Lanbroek, 1990; Jones, 1971).

Therefore, the objectives of this paper were to determine the accumulation of salt ions as well as of potentially toxic metals Fe and Mn in transplanted *S. pectinata* and *J. balticus*. These plant species grew well in certain locations on the cambered peat fields characterized by certain ranges in salinity, pH, and moisture contents found in our earlier study, *i.e.*, Montemayor et al. (2008). Specifically, the objectives were to determine (1) the concentrations of Na^+, K^+, Ca^{2+}, Mg^{2+}, Cl^-, SO_4^{2-}, Fe and Mn in the above-ground and below-ground tissues and, (2) the concentrations of these ions in the seawater-contaminated peat fields, early in the season when the underlying frozen ground layer is still present, and later when it is completely thawed.

2. Study area and methods

This current study is a continuation of our previous study (Montemayor et al., 2008). The study site is a cutover bog located on Pokesudie Island, in the Acadian Peninsula of New Brunswick, Canada (47°48′N, 64°46′W). It was contaminated by seawater during a storm surge in January 2000 and thereafter peat extraction operations were closed down. Mechanized peat extraction operations created long rectangular fields (300–400 m long, 30 m wide) with cambered surfaces along the longitudinal centre line, bordered by drainage ditches. Five years after the closing of operations, the fields were mostly barren and the ditches were partially filled with eroded peat. The cambered surfaces in the middle of fields had a slope of about 2% towards the side ditches. This slope created a moisture gradient that was divided into three zones and named as Up-areas, Mid-areas, and Low-areas. These zones correspond to relative dry, moist and wet areas, respectively.

The previous study had a factorial design experiment and was consequently maintained in this current study. The first factor in this experimental design was Location (Up-areas, Mid-areas, and Low-areas). The second factor was Depth of the peat from the surface (0–5, 5–10, 10–15, and 15–20 cm). In order to have 10 replicates, 10 fields were randomly selected from a total of 17 separate and independent fields at the site. Thus, each replicate was located on an independent long rectangular field. Details of the study site and climatic data can be found in Montemayor et al. (2008).

Collection of plants and transplanting were carried out on 25 July–8 August 2004. However, *S. pectinata* was re-planted on 4–9 June 2005 in the Up-areas and Mid-areas, and 19–21 June 2005 in the Low-areas. It was not suitable to transplant *S. pectinata* at the end of the growing season. *S. pectinata* plants were obtained from the uppermost edge of its zone in a salt marsh and *J. balticus* plants from a non-saline marsh. Both marshes were within 2 km distance of the study site. *S. pectinata* was planted as bare rhizome J-section (NRCS, 2000) individual plants at three individuals per planting spot. *J. balticus* was planted as sods of volume 2145 cm^3 at one sod per planting spot. For each plant species, there was a pair of parallel planted rows per Location spaced 30 cm apart and each row had 10 planted spots spaced 30 cm apart. Hence, there were 20 planted spots per Location for each species. Each planted row in each Location was 2 m away from the corresponding row in the adjacent Location. In each Location, a pair of parallel planted rows was separated from the adjacent pair of parallel planted rows by a 1 m undisturbed area reserved for peat sampling. More details on the planting layout can be found in Montemayor et al. (2008).

Our earlier study (Montemayor et al., 2008) found two distinct periods that differentiated peat characteristics. These were the pre-thaw and post-thaw period of the underlying frozen peat layer. Changes in peat characteristics upon the thaw of the frozen peat layer were: lowered water table depths that significantly increased redox potentials ($P = 0.05$), decreased moisture content that increased dry bulk density ($R^2 = 0.9$), and increased electrical conductivity that decreased pH ($R^2 = 0.7$). Moisture content increased from Up-areas to Down-areas. A notable effect of Depth was found in electrical conductivity which increased with Depth at pre-thaw period but the trend reversed at post-thaw period. A highly significant increase in electrical conductivity was found at the 0–5 cm Depth. Plant survival at the start of the following growing season (June 2006) of *S. pectinata* was high 89, 91.6, and 84.2% for Up-areas, Mid-areas, and Low-areas, respectively. *J. balticus* survived relatively well at the Up-areas (68.5%) and Mid-areas (58.5%) but survival was poor at Low-areas (27.5%).

2.1. Experimental design

Our previous study (Montemayor et al., 2008) reported the physical conditions of the peat and the survival of the two transplanted plant species. This current study reports the chemical characteristics of the peat and the ion accumulation in the two transplanted plant species in the same experiment. Thus, this current study, being a continuation of the previous study (Montemayor et al., 2008) maintained the original factorial design experiment consisting of two factors. This current study tested the effect of Location (Up-areas, Mid-areas, and Low-areas) as the first factor and Depth (0–5, 5–10, 10–15, and 15–20 cm) as the second factor, on ion concentration in peat water during two periods (pre-thaw and post-thaw of the underlying frozen peat layer).

In order to determine the effect of Location and Depth of peat on ion concentration in peat water, at pre-thaw and post-thaw periods, peat core samples were collected from each Location at Depths 0–5, 5–10, 10–15, and 15–20 cm from five (out of a total of 10 from the previous study) randomly selected replicates on 26 June, 2005 (pre-thaw period) and 29 July, 2005 (post-thaw period). The total number of core samples was 3 Locations × 4 Depths × 5 replicates × 2 periods = 120. Peat core samples were taken from the 1-m wide undisturbed spaces between pairs of parallel planted rows within each Location as described in Montemayor et al. (2008).

In order to determine the effect of Locations (Up-areas, Mid-areas, and Low-areas) on ion concentrations in plant tissues, plants from one planted spot (3 individual plants for *S. pectinata* and a whole sod for *J. balticus*) were collected from each of the three Locations within each of the 10 replicates. A planted spot was selected at random. Hence, for *S. pectinata*, there were 3 Locations × 10 replicates = 30 planted spots, each spot consisting of three individual plants. However, for *J. balticus*, the Low-areas, and two replicates each for Up- and Mid-areas were not sampled because of their very low survival rate. Thus for *J. balticus*, there were 2 Location × 8 replicates = 16 planted spots or sods. Plant samples were collected on 11 August 2005, which was one full growing season for *J. balticus* and 2 months of incubation for *S. pectinata*.

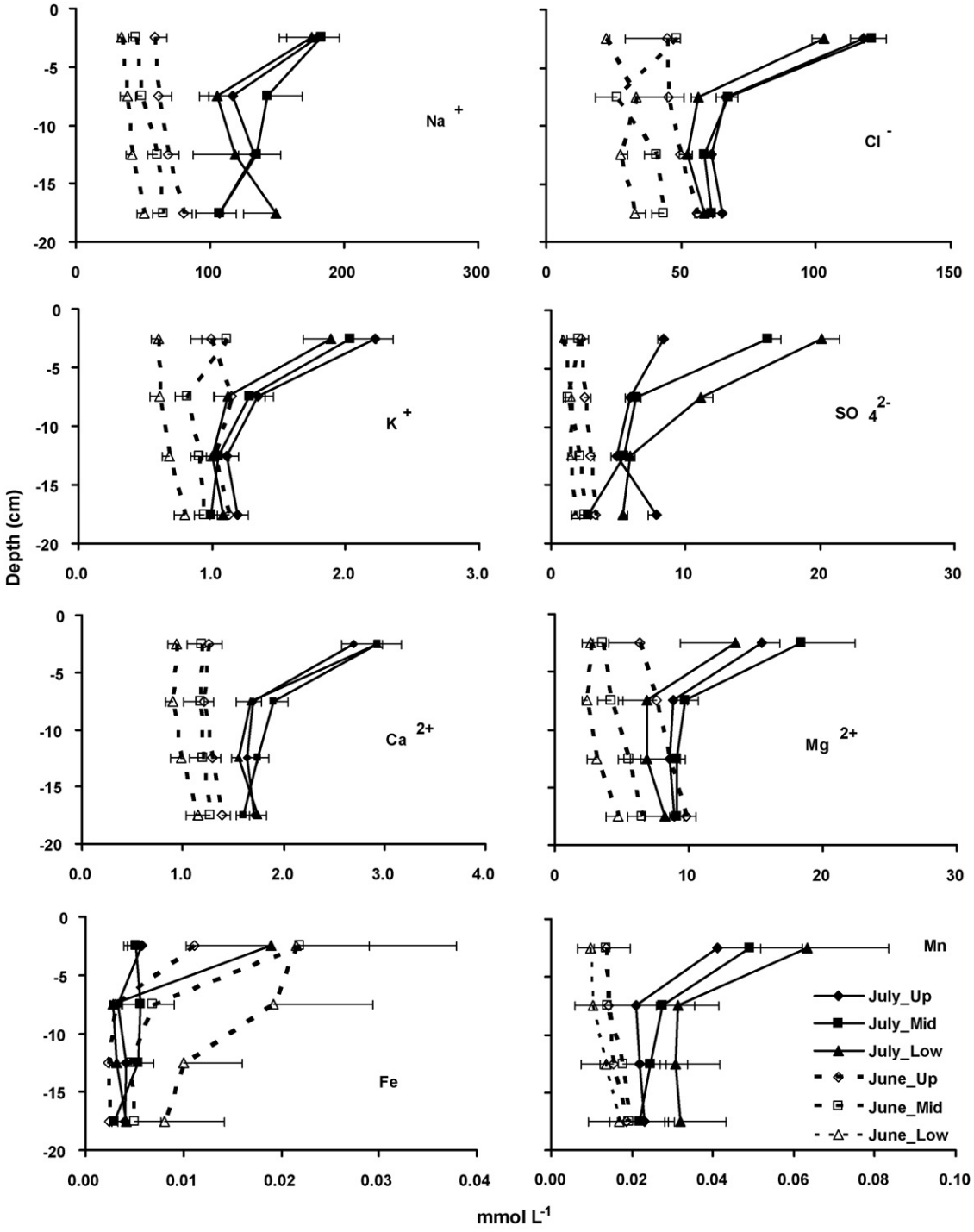

Fig. 1. Ion concentrations in peat water (mmol L^{-1}) on 26 June and 29 July at four depths and three locations. + or − standard error bars are shown. $N = 5$ for each point.

2.2. Peat water sample extraction

Peat water was extracted from the peat core samples by simultaneous gentle pressing and vacuum-filtering (Fisherbrand Qualitative P8-creped coarse porosity and fast flowrate filters). Ion concentrations in the peat water and its electrical conductivity were measured as described in Montemayor et al. (2008). Filtrates were re-filtered through Whatman No. 42 ashless filter paper and analyzed for total Na, K, Ca, Mg, Fe and Mn; and for Cl^-, and SO_4^{2-} (see ion analysis below).

2.3. Plant tissues preparation

Plants were cleaned of peat, washed with tap water and finally rinsed with deionized water, allowed to air dry for a day and then dried in the oven at 70 °C for 72 h. Oven-dried plants were divided into above-ground parts (stems, leaves, flowers) and below-ground parts (rhizomes and roots) and then cut into 2-cm long pieces with stainless steel scissors. A small sample (0.5–1.0 g) of each plant part was ashed in a muffle furnace for 5 h at 550 °C, cooled, digested with 5 mL 2N HCl, topped with deionized water to 50 mL and filtered

Table 1
Analysis of variance (two-way ANOVA) of ion concentrations (mmol L^{-1}) in peat at different depths and locations on the cambered peat fields on 26 June and 29 July.

Source	Df	Na			K			Ca			Mg		
		MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
26 June					log(*x*)						log(*x*)		
Blocks	4												
Location	2	3462	16.1	**<0.0001**	0.223	22.03	**<0.0001**	0.449	6.41	**0.003**	0.741	16.7	**<0.0001**
Error (a)	8												
Depth	3	1125	5.25	**0.003**	0.01	1.023	0.391	0.088	1.26	0.299	0.211	4.74	**0.006**
Location × Depth	6	27.5	0.128	0.992	0.01	0.952	0.467	0.006	0.081	0.998	0.006	0.143	0.99
Error (b)	36												
Total	59												
29 July					log(*x*)			log(*x*)			log(*x*)		
Blocks	4												
Location	2	289.3	0.142	0.868	0.019	2.85	0.068	0.003	0.489	0.616	0.121	4.18	**0.021**
Error (a)	8												
Depth	3	11,883	5.82	**0.002**	0.262	38.3	**<0.0001**	0.185	30.3	**<0.0001**	0.223	7.71	**<0.0001**
Location × Depth	6	1654	0.81	0.57	0.002	0.292	0.938	0.003	0.43	0.86	0.005	0.175	0.982
Error (b)	36												
Total	59												

Source	Df	Fe			Mn			Cl^-			SO_4^{2-}		
		MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
26 June		Rank			log (*x*)			Rank			Rank		
Blocks	4												
Location	2	453	1.79	0.179	0.248	1.61	0.211	3244	15.8	**<0.0001**	2524	11.4	**<0.0001**
Error (a)	8												
Depth	3	1485	5.85	**0.002**	0.075	0.485	0.694	588.2	2.87	**0.047**	825.8	3.72	**0.018**
Location × Depth	6	69.9	0.276	0.946	0.002	0.015	1.0	50.7	0.247	0.958	27.5	0.124	0.993
Error (b)	36												
Total	59												
29 July		log(*x*)			log(*x*)			Rank			Rank		
Blocks													
Location	2	0.031	0.51	0.61	0.043	0.357	0.701	386.7	1.95	0.154	636	2.41	0.101
Error (a)													
Depth	3	0.273	4.52	**0.007**	0.343	2.82	**0.049**	2314	11.7	**<0.0001**	1048	3.98	**0.013**
Location × Depth	6	0.119	1.97	0.089	0.003	0.022	1.0	18.3	0.092	0.997	62.7	0.238	0.962
Error (b)	48												
Total	59												

MS = mean square.

through Whatman No. 42 ashless filter paper (Ryan et al., 2001). The extracts were analyzed for cations Na^+, K^+, Ca^{2+}, Mg^{2+}, Fe and Mn; and for the SO_4^{2-} anion (see below for technical instrument). Most plants preferentially uptake Fe in the form of Fe^{2+} chelates (Fe(II)) (Marschner, 1995) but graminaceous (Poaceae) species (*e.g. S. pectinata*) may uptake chelated-Fe^{3+} (Fe(III)) (Schmidt, 1999). Mn(II) is the predominant form in plants but can also be in Mn(III) and Mn(IV) forms. Hence, Fe and Mn in plant tissues were determined and written as total iron Fe and Mn.

For Cl^- analysis, a small amount of plant material (0.5 g) was boiled in 70 mL deionized water (Khan et al., 2001; Naidoo and Naidoo, 2001) in a 100-mL beaker covered with watch glass, at 100 °C for at least 2 h until the volume was reduced to about 25 mL; then cooled. The extract was poured into 50-mL volumetric flasks and topped up with deionized water and filtered through Whatman No. 2 qualitative filter paper.

2.4. Ion analysis

Cation concentrations in plant tissues and peat water were analyzed using a Perkin-Elmer 3100 atomic absorption spectrometer and anions by ion chromatography using a Dionex DX500, following application note 133. Quality control (QC) comprised approximately 18% of the sample load which included calibration standards, analytical control samples, blanks and third-party standard reference materials. Results in mg L^{-1} were converted to mmol L^{-1} for peat water and for plants, to mmol g^{-1} oven-dry weight (dry wt.) for statistical analysis and mmol kg^{-1} dry wt. for graphs.

2.5. Statistical analysis

A two-way ANOVA with fixed factors (Location on the cambered peat field and Depth of peat) was performed for ion concentrations in peat water. For ion concentrations in plants, a two-way ANOVA with fixed factors was performed (Location on the cambered peat surface (Up-areas, Mid-areas and Low-areas) and Plant part (above-ground and below-ground)). Log(*x*) transformation was applied where required to fulfill ANOVA assumptions (normal distribution and homogeneity of variances) and rank transformation where these assumptions could not be achieved (Conover and Iman, 1981). Significant ANOVAs were followed by multiple comparisons of means (Least Significant Difference). All ANOVAs were performed using SPSS statistical software (SPSS 14.0 for Microsoft Windows, SPSS Inc., Chicago, USA).

3. Results

3.1. Salt ions, Fe and Mn in peat

Ion concentrations in peat generally increased upon thaw of the frozen layer with significant increases in the uppermost layer

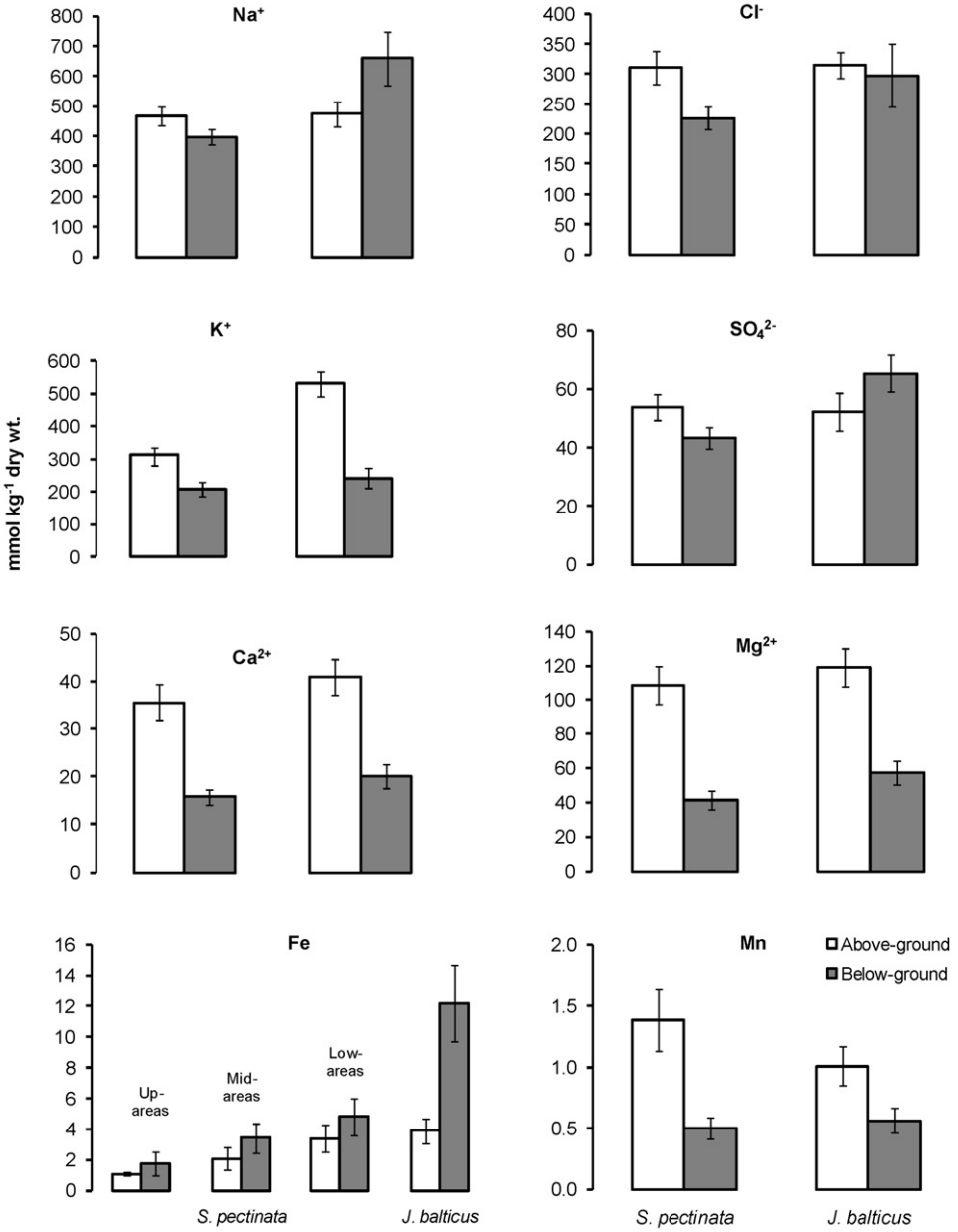

Fig. 2. Mean ion concentrations ± SE (mmol kg^{-1} dry wt.) in the above- and below-ground parts of *S. pectinata* and *J. balticus*. $N = 30$ for *S. pectinata* and $N = 16$ for *J. balticus*. Means are not significantly different among locations for all ions except for Fe in *S. pectinata* ($P = 0.05$). Means are significantly different between plant parts for all ions except Cl^- in *J. balticus* and Fe in *S. pectinata* ($P = 0.05$).

(0–5 cm) except for Fe (Fig. 1) which had the reverse trend. Na^+ and Cl^- concentrations in pore water reached 100 to 175, and 50 to 120 mmol L^{-1}, respectively while Fe and Mn concentrations were less than 0.02 and 0.06 mmol L^{-1}, respectively and showed the greatest variability. Electrical conductivity (Y) showed a positive linear relationship with total ion concentration (X), such that $Y = 0.03X + 2.59$ ($R^2 = 0.7$).

During the pre-thaw period (sampled 26 June), ion concentrations were significantly different among the three Locations on the cambered field surface except for Fe and Mn (Table 1). The Up-areas had the highest and the Low-areas had the lowest concentrations, while the Mid-areas were either intermediate or were not different from either (Post hoc, $P = 0.05$). After the peat thawed (sampled 29 July), there was no significant difference between Locations in all ions except Mg (Table 1) where the Up- and Mid-areas had higher concentrations compared to the Low-areas (Post hoc, $P = 0.05$).

Before the complete thaw of peat (26 June), concentrations of Na^+, Mg^{2+} Cl^- and $SO_4{}^{2-}$, increased with Depth of peat layer but decreased with Depth for Fe (Post hoc, $P = 0.05$; Fig. 1). No difference between Depths was found for K^+, Ca^{2+} and Mn (Table 1). In contrast, by 29 July, all ion concentrations decreased with Depth with the greatest concentrations on the 0–5 cm peat surface layer (Post hoc, $P = 0.05$; Fig. 1). There was no interaction between Location on the cambered peat surface and Depth of peat layer at both times of measurement (Table 1).

3.2. Salt ions, Fe and Mn in S. pectinata

All ion concentrations were greater in the above-ground than in the below-ground parts (Fig. 2) (two-way ANOVA; Df = 1; Na^+ $F = 9.07$, $P = 0.004$; K^+ ($\log(x)$) $F = 27.1$, $P = <0.0001$; Ca^{2+} ($\log(x)$) $F = 99.7$, $P = 0.0001$; Mg^{2+} $F = 100.3$, $P = <0.0001$; Mn ($\log(x)$)

$F = 47.03$, $P = <0.0001$; Cl^- $F = 18.7$, $P = <0.0001$; and SO_4^{2-} $F = 9.2$, $P = 0.004$), except for Fe (rank), where there was no difference between *S. pectinata* plant parts (two-way ANOVA, Df = 1, $F = 0.273$, $P = 0.603$) (Fig. 2). Among all the ions, only Fe was affected by the Location on the cambered peat surface where concentrations were greatest in plants grown at Low-areas and the least at the Up-areas. Fe concentration in plants in the Mid-areas was not different from either of the other two Locations (Df = 2, $F = 6.49$, $P = 0.003$) (Fig. 2).

The Na^+:K^+ratio in the above-ground and below-ground parts were 1.5 and 1.9, respectively.

3.3. Salt ions, Fe and Mn in *J. balticus*

Concentrations of K^+, Ca^{2+}, Mg^{2+} and Mn in plants were greater in the above-ground parts than the below-ground parts. On the contrary, Na^+, Fe and SO_4^{2-} concentrations were greater in the below-ground parts (two-way ANOVA, Df = 1; Na^+ $F = 7.13$, $P = 0.012$; K^+ (log(x)) $F = 49.7$, $P = <0.0001$; Ca^{2+} (rank) $F = 37.1$, $P = <0.0001$; Mg^{2+} $F = 38.1$, $P = <0.0001$; Fe (log(x)) $F = 27.1$, $P = <0.0001$; Mn (log(x)) $F = 14.1$, $P = 0.001$; Cl^- $F = 0.192$, $P = 0.665$; and SO_4^{2-} $F = 4.41$, $P = 0.045$) (Fig. 2).

The Na^+:K^+ ratio in the above-ground parts was 0.89 while in the below-ground parts, it was 2.72.

4. Discussion

S. pectinata and *J. balticus* transplanted into the seawater-contaminated bog differed in the way salt ions were partitioned in the above- and below-ground parts. Na^+ and Cl^- accumulation in *S. pectinata* were greater in the above-ground parts (Fig. 2) suggesting salt-tolerance is achieved by excretion of salts through the leaves, a characteristic of true halophytes (Marcum, 1999; Bradley and Morris, 1991; Rozema et al., 1981; Atkinson et al., 1967). In contrast, in *J. balticus*, there was greater accumulation of Na^+ in the below-ground parts, while Cl^- accumulation was not different between above-ground and below-ground parts (Fig. 2). Greater accumulation of Na^+ in the below-ground parts suggested that salt tolerance in *J. balticus* was through regulation or minimization of Na^+ transport to the shoots. Glycophytes respond to salinity by ion exclusion (Greenway, 1973); the majority of species is leaf excluders and may accumulate high levels of Na^+ in their roots and stems (Flowers et al., 1977).

As expected, the salinity of the site was primarily due to Na^+ and Cl^- (Fig. 1) which are the major constituents of seawater (Rowell, 1994). The mean (of the three Locations) maximum concentration of Na^+ which was at the soil surface (0–5 cm depth) was 180 mmol L^{-1} while that of Cl^- was 114 mmol L^{-1}, a total of 294 mmol L^{-1} NaCl, a concentration that is around the limit (300 mmol L^{-1}) that defines the growth medium of a halophyte (Flowers et al., 1977).

Some *Spartina* species are known to absorb high concentrations of Na^+ in the shoots and eventually secrete it through salt glands. *Spartina anglica* secreted 60% of the absorbed Na^+ (Rozema et al., 1981). Half of the ions (Cl^-, SO_4^{2-}, Na^+, K^+, Mg^{2+}, and Ca^{2+}) taken up by *Spartina alterniflora* Loisel was secreted from the shoots (Bradley and Morris, 1991). The study of Vasquez et al. (2006) suggested that about half of the NaCl entering *S. alterniflora* leaves was excreted. Ion secretion through the leaves of *Sporobolus virginicus* was thought to have controlled shoot Na^+ and Cl^- accumulation so that it did not exceed levels required for osmotic adjustment (Marcum and Murdoch, 1992; Naidoo and Naidoo, 1998). Salt secretion through the transpiration stream requires a substantial loss of water and is therefore restricted to plants in habitats characterized by the presence of abundant water, *e.g.*, salt marshes (Tester and Davenport, 2003). Greater accumulation of Na^+ in the below-ground than in the above-ground tissues of *J. balticus* suggested a salt-tolerance mechanism such as accumulation in the root vacuoles (Hajibagheri and Flowers, 1989) or accumulation in the mature roots (Tester and Davenport, 2003). This pattern of Na^+ accumulation was similar to those found by Rozema (1976) for *J. maritimus* and *J. gerardii* grown at 150 mM NaCl. *J. maritimus* had 3000 and 4500 Na^+ ppm dry weight in the shoots, and in both rhizomes and roots, respectively. Similarly, *J. gerardii* had 4500 and 7000 ppm Na^+ in the shoots, and in both rhizomes and roots, respectively.

The result of our study showed that *S. pectinata* accumulated about 450 mmol Na^+ kg^{-1} dry wt. in the above-ground parts after 2 months of incubation in the field, while a study by Vasquez et al. (2006) found that *S. alterniflora* grown for 12 weeks in the greenhouse at 300 mmol L^{-1} NaCl accumulated about 1100 mmol Na^+ kg^{-1} dry wt. In our study Cl^- accumulation in the above-ground parts (~300 mmol kg^{-1}) was similar for both species and were below the maximum range (422–1408 mmol kg^{-1} dry wt.) of toxicity reported for other Cl^--tolerant plants (White and Broadley, 2001).

Ions with the greatest concentrations in both above-ground and below-ground parts of both *S. pectinata* and *J. balticus* were Na^+ and Cl^- suggesting that these ions had a major contribution to maintaining the osmotic gradient for the uptake of water (osmotic adjustment or osmoregulation). Salt tolerance through the accumulation of Na^+ and Cl^- for osmotic adjustment in halophytes was found in *Sporolus virginicus* (L.) Kunth (Bell and O'Leary, 2003; Marcum and Murdoch, 1992) and *S. alterniflora* (Vasquez et al., 2006). The maintenance of low Na^+ and high K^+, *i.e.*, a low Na^+:K^+ ratio is essential for plant survival in saline environments. In our current study, the Na^+:K^+ ratio in the above-ground parts of *S. pectinata* was of 1.5 while that of *J. balticus* was 0.89. In the below-ground parts, the respective ratios were 1.9 and 2.7. These results did not agree well with the generalization that Gramineae, Juncaceae, and Cyperaceae plants have characteristics of low Na^+ and high K^+ in the shoots, *i.e.*, a low Na^+:K^+ ratio (Albert and Popp, 1977). While this was true with *Juncus geradii* with a Na^+:K^+ ratio of 0.56 (Albert and Popp, 1977) this was still less than that of *J. balticus* (0.89) in our study, *S. anglica* was found to have a very high ratio of 2.17, unusual for a monocot (Gorham et al., 1980); *Spartina longispica* grown 180 mmol L^{-1} NaCl had a Na^+:K^+ ratio of 2.02 (Glenn, 1987). These ratios were greater than that of *S. pectinata* (1.5) in our current study A ratio pattern seems to be evident that *Spartina* species have leaf or shoot Na^+:K^+ ratios greater than unity and *Juncus* species have less than unity, indicating a very different mechanism for managing Na^+.

Na^+ interferes with K^+ uptake (Pezeshki et al., 1987) and maintenance of high K^+ is essential for plant survival in saline conditions because it helps sustain osmotic adjustment or osmoregulation (Hu and Schmidhalter, 2005; Moghaieb et al., 2004; Glenn, 1987) and maintains metabolic plant processes activated by it (Bhandal and Malik, 1988). Thus, salt-tolerant plants have the capacity to maintain or increase K^+ uptake. Rozema (1976) found that K^+ had the greatest contribution to osmotic adjustment compared to Na^+ and Cl^- in *J. maritimus* and *J. gerardii* grown in solutions of increasing salinity up to 300 mmol L^{-1} NaCl and of 6.8 ± 0.3 pH. In our study *S. pectinata* K^+ concentration in the above-ground parts was about the same as Cl^-, the second highest accumulation after Na^+ (Fig. 2). In *J. balticus* K^+ concentration in the above-ground parts was the second highest after Na^+, followed by Cl^- (Fig. 2). Thus, there is a strong suggestion from these results that K^+ played a major role in the overall salinity tolerance of the species.

The pattern of Ca^{2+} and Mg^{2+} accumulation in both species were similar (Fig. 2). Ca^{2+} and Mg^{2+} are essential plant nutrients and in saline conditions their function in plants can include osmoregulation. Maintenance of sufficient Ca^{2+} levels is known to increase

salt tolerance (Marschner, 1995). It is known that Na^+ reduces the binding of Ca^{2+} to plasma membranes, inhibits influx and increases efflux of Ca^{2+}, and causes a depletion of internal Ca^{2+} stores in the cell compartments (Hu and Schmidhalter, 2005; Hagemeyer, 1997). However, in a sand culture experiment with fresh and 50% seawater and at different levels of flooding at pH 7.2 by Rozema and Blom (1977), they found that in *J. gerardii*, salinity had no significant effect on its K^+, Ca^{2+} and Mg^{2+}content. In contrast, a study by Cooper (1984) found that *J. gerardii* grown in 340 mmol L^{-1} NaCl solution showed a decrease in K^+ and $Ca^{2+,}$ and increase in Na^+ in the shoots. We find it difficult to reconcile these results that have mostly been derived from greenhouse studies using mineral soils or growth solution with almost neutral pH, to our current study on acidic (pH range: 2.5–4.3) peat fields (Montemayor et al., 2008). In general, uptake rates of cation nutrients decrease with low pH (Marschner, 1995) and Gloser and Gloser (2000) found that the uptake rates of Mg^{2+} and Ca^{2+} were decreased at pH 3.5–4.5. The current study design did not allow any of these to be verified. A future study could separate the effects of salinity from low pH (they have a negative relationship), under waterlogged conditions on the uptake of Mg^{2+} and Ca^{2+} by wetland plants.

Except for *S. pectinata* in Up-areas, Fe concentrations in the above-ground parts were above the critical deficiency in leaves, 0.89–2.7 mmol Fe kg^{-1} dry wt. (Marschner, 1995) (Fig. 2). Fe concentrations in the above-ground parts of *J. balticus* were much less than shoot Fe concentration associated with 10% yield reduction in *Juncus effusus*, 13.6 mmol g^{-1} dry wt. (Snowden and Wheeler, 1995) (Fig. 2). Reduced conditions that were suitable for the reduction of Fe into readily bioavailable Fe^{2+} (E_h = 120 mV) (Lanbroek, 1990; Ponnamperuma, 1972) in peat occurred during the pre-thaw period but mostly in the Low-areas near the ditches (Montemayor et al., 2008). Thus, Fe concentration in *S. pectinata* was highest in shoots of plants from Low-areas (Fig. 2). Furthermore, Fe was the only ion which had greater concentrations in peat during the pre-thaw compared with the post-thaw period (Fig. 1).

Plants uptake iron as ferric (Fe^{3+}) chelates or, after reduction as ferrous (Fe^{2+}) ions (Bienfait, 1985). The generally low Fe concentration in the shoots of both species despite favourable conditions for its availability such as low pH (Sarkar and Jones, 1982) and reduced conditions during the pre-thaw period (although short) could probably be explained by low Fe concentrations in the peat. However, *in J. balticus*, an additional explanation would be greater accumulation in its below-ground parts (Fig. 2). We have not checked iron plaque formation on the roots which could restrict uptake of ions to the shoots, but under the acidic conditions of the cutover bog (pH ~3) this was not expected to be stable (Ernst, 1990). Perhaps, Fe availability in the cutover bog was very limited since Fe in salt marsh soils are several orders of magnitude more than those found in bogs as indicated by the studies of Weiss et al. (2005), Steinmann and Shotyk (1995), and Jones (1971). In a study of bog iron chemistry by Steinmann and Shotyk (1995) they found that there was a prevalent trivalent oxidation state of iron (Fe^{3+}) by complexation with the peat water's humic substances in the bog. We have not found a study whether this form of iron is readily available for plant uptake or not. Cooper (1982) did hypothesize that Na^+ may antagonize the uptake and metabolism of Fe and Mn.

Similar to Fe, Mn accumulation of *J. balticus* and *S. pectinata* was low (Fig. 2). Reduced conditions (E_h ~225 mV) (Lanbroek, 1990; Ponnamperuma, 1972) in the cutover bog conducive to the formation of readily bioavailable Mn^{2+} were limited only during the pre-thaw period and thus offered limited bioavailability to plants for the rest of the season (Montemayor et al., 2008). Mn^{2+} is competitive with Ca^{2+} and Mg^{2+} (Marschner, 1995) and the salinity of the peat could have influenced the possible low uptake of Fe and Mn as well (Grattan and Grieve, 1999). Cooper (1984) found that Mn shoot content in *J. gerardii* grown in saline solution of 340 mmol L^{-1} NaCl was significantly less than that grown in non-saline nutrient solution. There were opposing trends between the accumulation of Fe and Mn in the above-ground and below-ground parts of the plants which could be due to the competition between Fe and other metals (Kobayashi et al., 2003). However, Mn concentrations of both species grown in the cutover bog were above critical deficiency in fully expanded leaves, 0.18–0.36 mmol Mn kg^{-1} dry wt. (Marschner, 1995).

Plants uptake the micronutrient sulphur through the roots in the form of SO_4^{2-} but excessive uptake of this nutrient can be toxic (Rennenberg, 1984). Conditions in the cutover bog (Montemayor et al., 2008) did not reach the level where SO_4^{2-} could be reduced to sulphide (E_h 75 to −150 mV) (Lanbroek, 1990; Ponnamperuma, 1972) so it could be assumed that SO_4^{2-} was readily available to plants throughout the study period. Plants usually have no avoidance mechanism against excess sulphur so that uptake increases with availability. However, there are known plant mechanisms to avoid toxicity such as storage in the vacuole, translocation, emission, and metabolic processes (Rennenberg, 1984). It is not known how much SO_4^{2-} is detrimental to plant growth since most studies are on crops and focus on its deficiency (Marschner, 1995).

In summary, the ion accumulation pattern (mmol g^{-1} dry wt.) in descending order in *S. pectinata* above-ground parts was $Na^+ > Cl^- = K^+ > Mg^{2+} > SO_4^{2-} > Ca^{2+} >$ Fe > Mn, while that in *J. balticus* above-ground parts was $K^+ > Na^+ > Cl^- > Mg^{2+} > SO_4^{2-} > Ca^{2+} >$ Fe > Mn. The Na^+:K^+ ratio in the above-ground parts for *S. pectinata* was 1.5 while for *J. balticus* was 0.89. The ion accumulation pattern in descending order in the below-ground parts of *S. pectinata* was $Na^+ > Cl^- = K^+ > SO_4^{2-} > Mg^{2+} > Ca^{2+} >$ Fe > Mn, while that in *J. balticus* was $Na^+ > Cl^- > K^+ > SO_4^{2-} > Mg^{2+} > Ca^{2+} >$ Fe > Mn. The greater accumulation of Na^+ in the above-ground compared with the below-ground parts of *S. pectinata* indicated that it is a halophyte. The greater accumulation of Na^+ in the below-ground compared with the above-ground parts of *J. balticus* indicated that it is a glycophyte tolerant to some levels of salinity lower than that which halophytes can thrive on.

The differentiation between halophytes and salt-tolerant glycophytes is important in the revegetation of saline sites that have zones or areas defined by different salinity levels. Plant species can be planted in zones where they would most likely survive and grow. This approach would make revegetation efforts more efficient.

5. Conclusion

For revegetation of saline acidic peatlands, *S. pectinata*, a halophyte would be most suitable in areas that are saline (up to 300 mmol NaCl L^{-1}) and waterlogged but of slightly reduced conditions (E_h > 225 mV). It can be planted in areas that are flooded at the beginning of the growing season (the pre-thaw period). *J. balticus*, a salt-tolerant glycophyte would be suitable in areas with relatively lower salinity levels and moisture contents (<1000% dry weight basis). It certainly cannot be planted in areas that are flooded at the beginning of the growing season (the pre-thaw period). Thus, the principle of vegetation zonation due to salinity and moisture gradients as it occurs in natural salt marshes is also applicable to revegetation of disturbed salinized peatlands.

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