Abiotic Stresses to Vegetation Re-establishment in a Cutover Bog Contaminated with Seawater

by

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A thesis
presented to the University of Waterloo
in fulfillment of the
thesis requirement for the degree of
Master of Environmental Studies
in
Geography

Waterloo, Ontario, Canada, 2006

Author's Declaration

I hereby declare that I am the sole author of this thesis. This is the true copy of the thesis, including any required final revisions, as accepted by my examiners.

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Abstract

Part of a cutover bog in Pokesudie Island, New Brunswick, Canada was contaminated with seawater and was still largely devoid of vegetation 5 years after the event and was consequently chosen for study. The study area consisted of rectangular fields with cambered surface that sloped down (2%) to the drainage ditches on both sides. Across this slope zones were created: Up-, Mid- and Low- areas on either side of the centerline of fields. Two field experiments were conducted to determine abiotic stresses to plant re-establishment in terms of hydrology and peat characteristics along this cambered surface. The general objective was to identify microsites or zones that could be suitable to the introduction of wetland halophytes *Juncus balticus* Willd. and *Spartina pectinata* Link obtained from nearby salt marshes.

In the first experiment, cylindrical *J. balticus* sods were transplanted into the Up- and Low- areas, at 1, 3, 5, 10 and 20 d of incubation (in May 2005) with measurements made on the Outer and Inner annular sod sections, replicated over 4 blocks. Moisture (% dry weight basis (dwb)) reached maximum values 1 day after transplantation, 84±0.05 for Outer and 103±0.07 for Inner sod section. Salinity (dS m^{-1}) in sods due to ingress of sodium (Na^{+}) and chloride (Cl^{-}) reached values of the surrounding peat 3 days after transplantation, 3.52±1.06 for Inner sod section and 4.11±0.99 for Outer sod section in Up-areas, and 1.76±0.24 for Inner sod section and 2.57±0.28 for Outer sod section in Low-areas. Maximum decrease in pH was at 5 days after transplantation, in Outer sod section in the Up-areas (from 5.89 to 4.88±0.14) which was much higher than the pH range of 3-4 of the surrounding peat. This was due to the buffering capacity of calcium (Ca^{2+}) and magnesium (Mg^{2+}) in sods which did not change in concentration after 20 days of incubation. Therefore, Inner sod sections were less affected by the surrounding peat compared to the Outer sod sections, suggesting that a larger sod volume may alleviate stressful conditions for a longer time at transplantation and consequently allow greater time for adaptation.

In the second experiment, *J. balticus* and *S. pectinata* were transplanted on the 3 Locations Up-, Mid- and Low- areas, replicated over 10 blocks; and peat characteristics were measured at Depths 0-5, 5-10, 10-15 and 15-20 cm 5 times during the study period May-August 2005. Survival of *J. balticus* was poorest (27.5±8.3 %) in the Low-areas compared to 68.5±8.9 % in the Up- and 58.5±8.7% in the Mid- areas. *S. pectinata* survival was very good at all Locations (89±5.3, 91.6±3.1 and 84.2±4.4 for Up-, Mid- and Low- areas, respectively) having better adaptation to early season waterlogged conditions. Waterlogged conditions resulted from a perched water table during the early part of the growing season (May-June) and were alleviated only upon the complete thaw of the frozen peat layer on 8 July. Thereafter, important changes in hydrology and peat characteristics occurred: water table depths decreased from -8.5±1.7 and -1.6±1.2 cm on 26 May, to -51.5±2.5 and -40.7±2.4 cm by 9 August in Up- and Low-areas, respectively; redox potentials at 12 cm depth increased from 26 June (190.9±8, 175±10.8 and 109.2±29.4 mV) to 9 August (282.8±8, 302.8±14.3 and 312.3±29.6 mV) in the Up-, Mid- and Low-areas, respectively which showed that anaerobic conditions were maintained throughout the study period; decreased moisture content from 1256.8±61.9, 1667.4±126.3 and 1728.6±153 on 30 May, to 851.7±21.2, 874.6±47 and 1008.2±57.5 % dwb on 25 July) which caused increased dry bulk density (from 0.07±0.002, 0.06±0.003 and 0.07±0.01 to 0.09±0.003, 0.09±0.005 and 0.08±0.004) in the Up-, Mid- and Low-areas, respectively; and increased electrical conductivity (salinity) especially on the 0-5cm surface (from 1.9±0.13, 1.8±0.31 and 1.5±0.29 to 18±1.9, 17.5±1.1 and 12.2±1 dS m^{-1}) which also caused decreased pH (from 3.5±0.04, 3.5±0.08 and 3.6±0.01 to 2.85±0.04, 2.85±0.01 and 2.9±0.03) in the Up-, Mid- and Low-areas, respectively. Therefore, spring flooding followed by high surface salinity in summer precludes plant establishment by seeding and explains the current lack of spontaneous revegetation. Waterlogged conditions were of greater magnitude and duration at lower elevation areas unfavourable to *J. balticus* survival but salinity levels were high in the Up- and Mid-areas.

In the subsequent part of the second experiment, plants of *J. balticus* and *S. pectinata* grown in the study area and those collected from marshes were divided into above- and below-ground parts and accumulation of salt ions in plant tissues were determined to understand the species' salt-tolerance mechanism, as well as the accumulation of potentially toxic levels of iron (Fe) and manganese (Mn). Both plant species had similar accumulations (mmol kg^{-1} dry wt,) of Na^+ (474.3±41 and 468.3±31.7, respectively) and Cl^- (314.9±21.9 and 310.5±27.5, respectively) in the above-ground parts but differed in how they managed Na^+. *J. balticus* accumulated more Na^+ in below-ground parts (659.3±88.7) and had limited transport to the above-ground parts, while *S. pectinata* accumulated and excreted Na^+ in the above-ground parts and had less accumulation in the below-ground parts (397.4±25.1). *S. pectinata* maintained (313.1±23.8 in marsh *vs.* 292.4±26.2 in bog) and *J. balticus* increased (84.2±1.2 in marsh *vs*. 531.2±38.6 in bog) K^+-selectivity in the shoots, a key requirement for survival in saline conditions. Compared with their respective marsh plants, *S. pectinata* had more salinity-tolerance than *J. balticus* primarily through its maintenance of Ca^{2+} (21.5±1.7 in marsh *vs*. 35.6±3.8 in bog) compared to a decrease in *J. balticus* (144.7±12.5 in marsh *vs*. 41±3.7 in bog). Furthermore, Fe and Mn uptake in both species decreased but reached critical Fe-deficiency levels (1.1±0.1 mmol kg^{-1} dry wt,) only in *S. pectinata* grown in drier areas.

It is concluded that local conditions of waterlogging (especially in lower elevation areas) and high salinity and low pH (notably in the upper elevation areas) were favourable to the survival of *S. pectinata* in all areas and *J. balticus* only in upper elevation areas. Sod transplanting may alleviate the acidity problem and depending on sod volume may delay the effects of harsh conditions of the cutover bog. However, long-term survival and growth of both species in drier areas may be constrained by deficiency in calcium in *J. balticus* and iron in *S. pectinata*.

Acknowledgements

My most profound gratitude goes to my supervisor, Jonathan S. Price and co-supervisor, Line Rochefort for providing this valuable opportunity to apply my knowledge and skills to analyze and find solutions to an actual ecosystem rehabilitation problem. I am thankful to Stephanie Boudreau who together with my supervisors formed a great team in meticulously reviewing this work and provided me a most satisfying experience in research and scientific writing especially on a subject that combined the different fields of plant science, soil science, hydrology and the application of statistics. Financial assistance awarded for my program of study by the Natural Science and Engineering Research Council, the Ontario Graduate Scholarship, and the University of Waterloo President's Graduate Award and Entrance Scholarship is greatly appreciated. I am thankful for the co-operation extended by laboratories of different departments of the University of Waterloo: Environmental Studies (Ecology & Geomorphology), Chemical Engineering, Chemistry, and Electrical Engineering; Wilfrid Laurier University Environmental Studies; and Sungro Horticulture Ltd., New Brunswick. Maps, technical data, and literature on Pokesudie Bog supplied by the New Brunswick Department of Natural Resources and Energy are greatly appreciated. I most sincerely thank my co-researchers who went out of their way to give me help during the course of my field work: Gerry McIsaac, Cillian Breathnach and Luc Miousse, The scale of field and laboratory work at the study site was made possible with the help a field assistant, Miranda Lewis. Short-term but very sincere help from Sophie Thibault, Fabrice Pellot and Antonio Difebo, and voluntary help from Jolaine Chaisson during the 2004 planting demonstrate the social aspect of revegetation projects and are greatly appreciated. Thanks to Peter Whittington who helped in setting up the meteorological station and Sara Mouneimne for organizing supplies and equipment for departure to New Brunswick. All praise and gratitude are due to my big family who stood by me in pursuit of this academic endeavour.

Dedicated to Canada's wetlands

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Preface

This thesis is based on field experiments that developed from my own (Chapters 3 and 4) and my supervisor's (Chapter 2) concepts to address the issue of re-establishment of vegetation on a saline and waterlogged area of a cutover bog. All the experiments (Chapters 2, 3 and 4) were designed by myself and implemented with the help of a field assistant. This thesis was solely written myself and edited rigourously by my supervisor, Jonathan S. Price; co-supervisor, Line Rochefort and Stéphanie Boudreau. S. Boudreau particularly made certain that my experimental designs were correct, verified the appropriateness of the statistical methods I used and ran the SAS program (not available in our department) for Chapter 2.

Chapters 2, 3 and 4 are in manuscript form (ms 1, ms 2 and ms 3, respectively) ready for submission to journals. Some tables of ANOVA and Post-hoc analysis were not included in the manuscripts for brevity; instead statistical results were included in the text within parentheses (Df, F, *P* values). However, for completeness of the thesis, these omitted tables are given as Appendices.

1. General Introduction

Peatlands cover about 12% of Canada's land area, the equivalent of about 1.1 M ha (Bergeron, 1996) and are mostly concentrated in the boreal ecological zone. About 0.02% of peatlands have been exploited (NAWCCC, 2001). Out of an estimated billion+ tonnes of peat deposits (WEC, 2005), about one million tonnes are extracted annually (NAWCCC, 2001). Canada ranks third worldwide in peat production for horticulture use (Bergeron, 1996). The leading producer in Canada is the province of New Brunswick, where peat mining policy requires exploited peatlands to be restored to natural wetland ecosystems or reclaimed to an alternate economic usage provided the basic peatland function is restored (GNB, 2005). However, ecosystem and wetland functions are numerous (Ehrenfeld, 2000; Mitsch and Gosselink, 2000; Zedler, 2000) and the decision as to what functions should be restored depend not only on scientific knowledge of ecosystem restoration but also on societal values and the political climate (Baird, 2005; Ehrenfeld, 2000; Higgs, 1997). In Canada the goal of peatland restoration is to re-establish self-regulatory mechanisms that will return functional peat accumulating ecosystems (Quinty and Rochefort, 2003). However, in highly disturbed and contaminated ecosystems (*e.g*. mine pits, salinised or eroded soils) where restoration of the original ecosystem is economically prohibitive or impractical, the goal is to establish any functional ecosystem (Ehrenfeld, 2000).

A maritime bog in Pokesudie Island, New Brunswick (Figure 1.1) was contaminated by seawater during a storm surge in January 2000. Salinity in the affected portion of the bog made the peat unsuitable for horticultural substrate so peat extraction was stopped. The abandoned waterlogged and saline portion of the bog remains essentially devoid of vegetation. In contrast, better drained and non-saline areas of the bog have some spontaneous regeneration of vegetation. Freshwater bog plant species cannot grow in the saline area of the bog. Removal of salts from the site is not a practical or an economical option. Therefore, returning any functional wetland ecosystem is the most reasonable management option. The saline and waterlogged area of the bog

was chosen as the study area for my research with the goal of finding plant species to create a different but functional wetland ecosystem. Such a strategy is challenged by a combination of physico-chemical constraints (Wheeler *et al*. 1995) imposed by study area: salinity combined with acidity inherent of *Sphagnum* peat, and waterlogging. The heterogeneous topography left by peat-extraction operations offered opportunities to identify areas or zones that would allow some plant species to establish when the planting method and time are right. This approach falls under the niche theory in ecology (Krebs, 2001) where fundamental and realized niches as applied in wetland rehabilitation are achieved through planting species in suitable microsites by first conducting pilot plantings to identify suitable habitats and subsequently plant more broadly (Cole, 1999 in Zedler, 2000).

Thus, the objectives of my research are:

1) To introduce plants to the study area by transplanting methods suitable for each species when collected from their natural sites. Some species are easily collected and planted manually as sods (*Juncus balticus* Willd.) and some as individual plant sections (*Spartina pectinata* Link).
2) To identify different zones in the salinity-affected areas of the bog that are suitable or unsuitable to each species through measurement of plant parameters and characterize these zones based on hydrological conditions and peat surface characteristics such as moisture content, electrical conductivity, pH and redox potentials.
3) To understand the salt tolerance mechanisms of the two species and verify the uptake of potentially toxic nutrient metals that occur under waterlogged conditions.

Chapter 2 addresses objective (1) which investigates the possible advantages of sod transplanting and the role of intact natural site soil on buffering the harsh conditions of the new

site. Chapter 3 addresses objective (2) and investigates hydrological conditions, peat characteristics and respective plant responses in different zones and thus, identifies and characterizes zones suitable for each species. Chapter 4 addresses objective (3), to understand how species that survive well in certain zones manage the uptake of salt ions, and determine whether waterlogged conditions of the bog promotes or inhibits the uptake of potentially toxic metal nutrients. Thus, all the three chapters cover basic aspects of plant establishment on a disturbed and contaminated ecosystem that include how and where to plant a particular species and how do they manage the contaminant and survive in a particular location and what are the possible constraints to their long-term survival and growth.

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Figure 1.1 Map showing location of Pokesudie Is., New Brunswick (Label added on a Microsoft product screen shot reprinted with permission from Microsoft Corporation)

2. Changes in soil characteristics of marsh sods transplanted into a cutover bog contaminated with seawater

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2.1. Abstract

The study site is part of a cutover bog in Pokesudie Is., New Brunswick, Canada that was contaminated with seawater and is still almost completely devoid of vegetation 5 years after the event. The aim of this study was to evaluate if marsh plants transplanted as sods could become established and what limitations the site imposed. The study site has cambered rectangular fields that sloped towards the drainage ditches on both sides and thus had relatively drier areas along the central ridge-line (Up-areas) and more frequently flooded areas along the ditches (Low-areas). Cylindrical sods of *Juncus balticus* Willd. were collected from a nearby non-saline marsh and transplanted into the Up- and Low- areas, at 1, 3, 5, 10 and 20 days of incubation (in May 2005) and measurements made on the Outer and Inner annular sod sections, replicated in 4 blocks. Moisture content in sods (% dry weight basis (dwb)) reached maximum values 1 day after transplantation, 84±0.05 for Outer and 103±0.07 for Inner sod section. Electrical conductivity (dS m^{-1}) in sods due to ingress of Na^+ and Cl^- reached values of the surrounding peat 3 days after transplantation, 3.52±1.06 for Inner sod section and 4.11±0.99 for Outer sod section in Up-areas, and 1.76±0.24 for Inner sod section and 2.57±0.28 for Outer sod section in Low-areas. Maximum decrease in pH was at 5 days after transplantation, in Outer sod section in the Up-areas (from 5.89 to 4.88±0.14) which was much higher than the pH range of 3-4 of the surrounding peat. The Inner annular sod sections were less affected by the surrounding peat compared to the Outer annular sections (P <0.02), suggesting that a larger sod volume may alleviate stressful conditions for a

longer time at transplantation and consequently allow greater time for adaptation. The Up-areas were more saline than the flooded Low-areas ($P < 0.0001$). The delay in pH response could be due to the buffering capacity of basic cations Ca^{2+} and Mg^{2+} in sods which could alleviate stress related to substrate acidity. Increased EC intensified acidic conditions in both sods and peat, unfavourable to many plants, which could be attributed to the displacement of H^+ by Na^+. NO_3^- in sods decreased to below detection level suggesting denitrification under waterlogged conditions. Therefore, the survival and establishment of *J. balticus* in the Up-areas is dependent on its tolerance to increasing salinity while in Low-areas to flooded conditions, and in both areas to low pH and NO_3^- concentrations.

Keywords: *Juncus balticus*, peatland, pH, plant reintroduction, rehabilitation, salinity, waterlogged

2.2. Introduction

Abiotic stresses to plant re-establishment in cutover bogs occur because of the intensive drainage, the removal of vegetative cover, and the peat extraction process itself which cause major changes in hydrology and microclimate (Price *et al.* 2003, 1998; Price, 1997, 1996). These changes impair natural revegetation of the original *Sphagnum*-dominated bog ecosystem (Poulin *et al.* 2005) primarily due to insufficient moisture at the surface especially during summer. At several cutover coastal bogs in eastern Canada (New Brunswick), contamination by seawater makes restoration more challenging (Mouneimne and Price, 2006). Bog plants, especially *Sphagnum* spp. are not salt-tolerant and hence, re-establishment is difficult. Salt marsh plants (halophytes) may provide an option for stabilization of peat and create marshy habitat for wildlife, but still stresses caused by salinity remain an important filter to plant establishment (Tester and Davenport, 2003; Zedler *et al*. 2003; White and Broadley, 2001). Furthermore, spring flooding and low pH of the residual peat of these coastal bogs create peculiar substrate conditions for plant establishment. In tidal salt marshes salinity and flooding stresses are minimized because flushing and drainage occur periodically (Harvey and Nuttle, 1995). However, tides do not occur in bogs even when located at low elevations and are influenced by the sea only during extreme weather events. Consequently, extended flooding induces hypoxia in plant roots which in turns leads to plant mortality (Pezeshki, 2001; Pezeshki, *et al*. 1993; Ernst, 1990; Koncalova, 1990).

Bogs are naturally acidic but the addition of salt cations can trigger cation exchange and further intensify acidic conditions. *Sphagnum, Sphagnum* peat and its pore water have an effective cation exchange capacity (CEC) (Thomas and Pearce, 2004; Smidsrod and Painter, 1984; Clymo, 1963) causing efficient absorption of cations, such as Na^+ (predominant in seawater) and the release of H^+ that reduces an already low pH (Vitt, 2000; Ours *et al*. 1997, Pugh et al. 1996; Reeve *et al*.1996). In addition, the presence of SO_4^{2-} or Cl^- in peat may produce acids that further decrease pH (Kilham, 1982). Low pH in soils is known to damage plant roots,

increase the bioavailability of toxic elements (Hinsinger *et al*. 2003) and reduce the uptake of cation nutrients (*e.g.* Ca^{2+} and Mg^{2+}) (Marschner, 1995) that can adversely affect plant survival and growth.

Revegetation techniques must take into consideration plant life stages and their susceptibility to abiotic stresses. Transplanting intact sods ensures quicker plant establishment than seeding primarily because the plants are already grown and the intact soil provides the conditions that allow the plants to gradually acclimatize to the new environment (Fraser and Kindsher, 2001; Forbes and Jefferies, 1999). It is preferable to use sods of native plants obtained from nearby natural sites as they are more ecologically adapted and contain seed banks and soil microbes that can boost biodiversity (Mitsch and Gosselink, 2000). *Juncus balticus* Willd. was considered a good candidate species because in preliminary trials of several species in the summer of 2004 it was one of the marsh species with the highest survival on acidic saline peat (personal observation). It is known to tolerate periodic flooding and drought as well as mild to moderate salinities and transplanting of sods or plugs is the surest way to establish a new stand of this species (NRCS, 2000). We wanted to know what changes occur in its sod soil characteristics after transplantation and how long it takes for the sod to acclimatize.

Therefore, the purpose of the study was to determine the rate and magnitude of changes in soil characteristics: moisture content ($\boldsymbol{\theta}$), salinity measured as electrical conductivity (EC), pH, and ion concentrations, in (1) *J. balticus* sods collected from a non-saline marsh and transplanted to a cutover bog contaminated with seawater and (2) the peat surrounding sod transplants.

2.3. The Study Site

The study site is located on Pokesudie Island, in the Acadian Peninsula of New Brunswick, Canada (47^{o} 48'N, 64^{o} 46'W). The mineral substrate is sand immediately overlain by wood peat (some logs and branches still intact), sedge peat, and finally, *Sphagnum* peat. The bottom topography is irregular giving variable thickness to the remaining peat (1 – 2 m). The upper peat surface (0-20 cm) is predominantly *Sphagnum* peat mixed or interspersed with sedge peat. Currently, drainage is very poor, since pumps used to remove water during peat extraction operations are no longer operating. Extraction operations begun in the 1960's (Daigle *et al*. 1993) and continued until a storm surge on 21 January 2000 contaminated the peat with seawater and rendered it unfit for horticultural use. Extraction operations left behind long rectangular fields (300 to 400 m long, 30 m wide) that are cambered along the centerline to direct drainage toward ditches. The 2% slope cambered surface creates zones of different moisture regimes parallel to the ditches, hereafter termed as Up-areas and Low-areas. The study site was still devoid of spontaneously regenerated vegetation 5 years after the termination of extraction activities.

Marsh soils from which sods were collected had a 3.5 cm top layer of organic litter (O horizon) and the A_m horizon was loamy with an organic matter content of 9.5% compared to 93% in peat (Table 1). Peat ranged from very slightly, to moderately decomposed (H3 to H5). Dry bulk density and particle density of sod soil was 0.8 and 2.25 g cm^{-3}, respectively and the corresponding values for peat were 0.07 and 1.38 g cm^{-3}, respectively. Total porosity of sod soil (0.64) was less than that of peat (0.95). The sods had saturated hydraulic conductivity of 2.1 x 10^{-2} cm s^{-1}, whereas in peat it was 2.2 x 10^{-4} cm s^{-1} (see Methods).

The nearest meteorological station is Bas Caraquet (47^{o} 48'N, 64^{o} 49'W) but the nearest one with climate normals (1971-2000) is Bathurst (47^{o} 37'N, 65^{o} 45'W). Daily mean temperature for January and July are -11 and 19.3 ^{o}C, respectively, and total annual precipitation is 1059 (314

snow) mm. Total degree days above 5°C is 1678, May has 156, with greatest values accumulating in June, July and August representing 70% of the total (Environment Canada, 2004).

2.4. Methods

2.4.1. *Juncus balticus sods collection*

Sods were collected from a drained marsh that was non-saline. An area of the marsh was chosen where the species *J. balticus* was dominant. Uniform sized sods were extracted on 21-22 May 2005 using metal cylinders with sharp cutting edge (9.7 cm diameter and 13.3 cm height). The height of the cylinder corresponded to the total thickness of litter and rooting zones, and beneath it was sand where root tips ventured but did not proliferate. Sods were transplanted following the day of collection (23 May 2005). Eighteen sods were randomly selected from the entire sod collection (see Experimental design) to determine *J. balticus* biomass per sod which was 8.8 g ± 0.43 (70°C oven-dry for 72 hours).

2.4.2. *Experimental design*

To test the effect of Location on the cambered surface and Time of sod incubation on sod soil characteristics (θ, EC, pH and ion concentrations), sods were transplanted according to a split-split-plot design. Main treatments were the Location of the sods on the cambered field surface: Up-areas and Low-areas were rows located 1 m and 5 m from the centre of the peat field, respectively. Sub-treatments were the 5 periods of field incubation (Time): 1, 3, 5, 10 and 20 days after transplanting. Sub-sub-treatments were the 2 annular Sod sections: Outer section consisted of 1.5 cm thick outer (external 4.85 cm to 3.35 cm radius) including the bottom 1.5 cm thick layer, and Inner (3.85 cm radius to the 0 center) section. The whole design was replicated in four blocks, each block randomly located in four out of 17 possible peat fields. Three sods were

transplanted for each period of field incubation and randomly selected among the 15 sods when collected for analysis. Consequently 120 sod transplants were used to implement the design (4 blocks x 2 locations x 5 incubation periods x 3 sub-replicates = 120 sods and 40 experimental units). Within each block, sods were aligned 50 cm apart longitudinally on the rows. Sods were positioned into excavated holes and the excavated peat flowed back into place easily due to its high moisture content; sods were level with the surrounding peat.

From all sods collected from the marsh, 12 were also randomly selected to serve as control (incubation time = 0 day; see next section for more details).

On the day of transplantation (Day 0) and each of the subsequent incubation periods, 24 cores of peat of the same size as the sods were also taken 25 cm from plant rows (4 blocks x 2 locations x 6 incubation periods x 3 sub-replicates = 144).

2.4.3. *Sod soil preparation and analysis*

A thickness of 1.5 cm was trimmed off the outer and bottom sections of cylindrical sods using a sharp stainless steel knife which constituted the Outer section sample. The remaining inner section of the sod was the Inner sod sample. Both Sod sections were processed in exactly the same manner but separately. Plant materials (coarse surface litter and roots) were removed by hand from the soil. The 3 sub-replicates soil samples from each sod section were combined to make a composite sample (ICARDA, 2001; Rowell, 1994) in field condition, stored in sealed plastic bags and refrigerated until the next processing step, a week later.

Samples were not dried prior to preparation of saturation extracts because of the hydrophobic property (Valat *et al*. 1991) of organic matter upon drying. From each composite sample, three sub-samples were taken to make 1:2 saturation extracts using deionized water (ICARDA, 2001) which were allowed to stand for 12 hours and then filtered through No. 42 Whatman ashless filter paper by gravity. Filtrates of samples were tested for salinity measured as

EC (dS m^{-1}) and pH. EC was measured using YSI Model 33, S-C-T Meter, Yellow Springs Instrument Co., Inc. while pH was measured with Fisher Scientific Accumet pH meter 10. Filtrates were frozen at the site laboratory and shipped to the University of Waterloo for subsequent ion analysis 6 months later.

Another three sub-samples from each composite sample were taken for gravimetric determination of θ by drying at 105^{o}C for 72 hours and subsequently calculated as percent g g^{-1} oven-dry weight basis (% g g^{-1} dwb) and ratio (g g^{-1}). Moisture content was expressed as % dry weight basis (dwb) (ICARDA, 2001; Farnham and Finney, 1965) because it was to be compared with the surrounding peat which was in a flowable state in some blocks and presented difficulty in obtaining numerous samples quickly with accurate volumes that would allow moisture content to be expressed accurately as % (volume $volume^{-1}$). EC readings obtained from filtrates were then corrected to the original θ of the soil sample, while pH was that of the filtrate. The average of 3 sub-samples for θ, EC and pH represented the value used for statistical analysis.

The twelve control sods extracted from the donor site (Day 0) were also cleaned of plant roots and rhizomes and their soils were combined into a composite sample (ICARDA, 2001; Rowell, 1994). Twelve sub-samples were taken from this composite sample for determination of EC and pH, and 6 sub-samples for θ following the procedures above. Three samples of filtrates were kept for ion analysis.

2.4.4. *Peat samples preparation and analysis*

The three sub-replicates of peat collected from each Location at each incubation period (Time) were combined to make a composite sample, stored in a sealed plastic bag and refrigerated until the next processing step a week later. From each composite sample, ~200 g sub-sample was taken for gravimetric θ determination by the same method above. The rest of the sample was vacuum-filtered while simultaneously pressing the sample by hand using a jar. Fisherbrand filter paper

Qualitative P8-creped (coarse porosity and fast flowrate) was used. The filtrate was then tested for EC and pH. Filtrates were frozen at the study site laboratory and shipped to the University of Waterloo and ion analysis was done 6 months later.

2.4.5. *Ion analysis*

Filtrates were thawed in the refrigerator and subsequently re-filtered through Whatman No. 42 ashless filter paper. Ion analysis was performed for both peat water and sod soil extracts after the longest incubation period (20 days), as well as for sod soil extracts before incubation (Day 0). For peat, filtrate samples from the four blocks were used while for transplanted sods only three experimental blocks were sampled. Major seawater ions Na^{+} and Cl^{-}, minor components Ca^{+2}, Mg^{+2}, Br^{-} and SO_4^{-2} and soil nutrients K^{+} and NO_3^{-} were analyzed by ion chromatography using Dionex DX500. Quality control (QC) comprised approximately 18% of the sample load which included calibration standards, analytical control samples, blanks and third-party standard reference materials. The unit of analysis mg L^{-1} was converted to mmol kg^{-1} fresh soil sample.

2.4.6. *General soil properties*

Organic matter content was determined by loss-on-ignition in a muffle furnace for 4 hours at 550^{o}C (Bengtsson and Enell, 1986). Soil horizons of *J. balticus* drained marsh soil were identified according to Soil Survey Staff (1975). Particle size distribution was determined by hydrometer method (Gee & Bauder, 1986). Von Post scale of humification (H1 to H10) was used to characterize the state of peat decomposition (*e.g*. Malterer et al. 1992). Saturated hydraulic conductivity for the *J. balticus* soil was determined using the Guelph permeameter (for mineral soils) while for peat the bail test method was used (Hvorslev, 1951 cited by Freeze and Cherry, 1979). Dry bulk density was determined by obtaining the mass of a known volume of peat or sod soil after oven-drying at 105^{o}C. Particle density was determined by measuring the volume of a known mass of peat or *J. balticus* sod soil that had been air-dried for a month and oven-dried at

90^{o}C for 24 hours (Munro, 1982). The procedure by Rowell (1994) was modified by dispersing in 50-60 ml toluene, 2-3 g peat or 5-6 g sod soil, allowed to stand covered overnight and subsequently topped up to 100 ml in a volumetric flask. Total porosity was calculated as porosity = 1- (bulk density/particle density).

2.4.7. *Hydrological data*

To measure the average water table and frozen layer depth wells were installed, made of 5 cm inside diameter ABS pipes, 95 cm in length fitted with a wooden cone tip of length 7.6 cm, and perforated throughout their lengths at 3.8% porosity. The wells were lined with fine nylon netting on its outer side before installation to prevent peat particles from entering them. After measuring water table in the wells, they were driven into the peat until obstructed by the frozen layer and its depth was determined (26 May and 9 June). Water table and frozen layer depth was determined for three randomly selected blocks for each of the Up- and Low-areas, sufficient to describe experimental conditions. An automated meteorological station instrumented with data loggers (Campbell Scientific 10X) set at 20 minutes interval, recorded precipitation with a tipping bucket rain gauge and net radiation. Mean air temperature was obtained from the nearest weather station, Bas Caraquet, because of instrument malfunction at the site. Total evaporation (mm) was calculated according to Priestley and Taylor method as described in Price (1996).

2.4.8. *Statistical analysis*

Due to wide differences in the range of values of measured soil parameters between *J. balticus* sod soil from the donor marsh and the receiving peat, the two soils were not compared within the same ANOVA model. Soil characteristics (EC, $\boldsymbol{\theta}$, and pH) for *J. balticus* transplanted sods were analyzed as split-split plot with repeated measures, the repeated factor being the Sod section because of possible non-independence of data between Inner and Outer Sod sections. Soil characteristics of peat surrounding the sods were analyzed as a split-plot design. Ratio moisture

content of peat and EC data for both peat and sod sections were log (x) transformed prior to analysis in order to reduce heterogeneity of variances. Analysis of variance (ANOVA) was done using the SAS System's Mixed Procedure (SAS Statistical System software, v. 8, SAS Institute Inc., Cary, NC, USA). ANOVAs consisted of Fixed Effects (Time, Location and Sod section (for sods) and their interactions) and Slices Effect (SAS terminology). Slices Effect allows the interpretation of differences in means of measurements made in one factor within each level of another factor when there is an interaction between factors. It was necessary to 'decompose interactions' (UT, 2003) because for the practical purpose of revegetation we were interested on the changes in soil characteristics with Time and Location within an interaction.

Relationships between EC, pH and θ were determined with Pearson correlations (2-tails) and regressions using SPSS (SPSS 14.0 for Microsoft Windows, SPSS Inc., Chicago, USA). Data used for correlations were those of Day 1 to Day 20 for sods (when characteristics of the surrounding peat took effect), while for peat, those of Day 0 to Day 20 were used.

Comparison of means of ion concentrations between Up-areas and Low-areas for peat substrate surrounding the transplanted sods was done only at the last incubation period (after 20 days) with paired t-tests. As the ion concentrations of Inner and Outer sections of a sod were found to be similar after 20 days of incubation, values for each individual whole sod were averaged to assess changes in ion concentration over Time with split-plot ANOVA (2 Locations and 2 Time periods Day 0 and Day 20) with samples from 3 randomly selected blocks using the Mixed procedure of SAS (SAS Statistical System software, v. 8, SAS Institute Inc., Cary, NC, U.S.A.).

Sample sizes were determined according to how much could be done within the available time and resources.

2.5. Results

2.5.1. *Hydrological parameters*

Rain events of 23, 74 and 4 mm on 22 and 27 May and 10 June, respectively (Figure 2.1), preceded some sampling days (Day 0, Day 5 and Day 20), and total rainfall for the duration of the study was 105 mm. Temperature rose from about 5 to 25 ^{o}C from Day 0 to Day 12 then declined to between 10-19 ^{o}C for the duration of the study. The total evaporation was 75 mm for the same period.

The water table remained near the ground surface and on average (± standard error) was deeper in Up-areas (-10.2 ± 2.2 cm) than Low-areas (-2.63 ± 2.1 cm). The water table stayed above the frozen peat layer which averaged 42.9 ± 1.3 and 44 ± 1.6 cm for Up-areas and Low-areas, respectively.

2.5.2. *Sod and peat characteristics*

Moisture content in all sods (θ_{sod}) significantly increased over Time with the greatest change between Day 0 and Day 1 (Table 2.2, Figure 2.2a). Inner sod sections always had greater θ_{sod} than Outer sod sections. Location on the cambered field surface had no impact on θ_{sods}, neither for Outer nor Inner sections.

Moisture content of peat (θ_{peat}) was significantly affected by both Location on the cambered field surface and Time of incubation (F = 4.61, Df = 5, P = 0.0003) (Appendix A). θ_{peat} was always greater but more variable in Low-areas than in Up-areas (). Furthermore, θ_{peat} remained much higher than θ_{sods}.

EC of sods was affected in multiple ways by all factors (Table 2.2). EC levels in sods increased rapidly and approached EC values of the surrounding peat one day after transplantation in the Low-areas and 3 days after in the Up-areas (Figure 2.2b). Over Time, EC of sods from Up-

areas remained significantly greater than Low-areas except on Day 5 whose value could have been affected by the rainfall event of 74 mm on Day 4 (Table 2.2). EC of Outer section was higher than EC of Inner sod section but differences were more pronounced at Low-areas. Moreover, after 20 days of incubation EC of the Inner Sod section was not different from the Outer Sod section (Table 2.2).

EC of peat surrounding the sods was affected by both the Location on the cambered peat field and Time of sampling in the season (F = 2.57, Df = 5, $P = 0.05$) (Appendix A), Lower ECs on Days 5 and 10 resulted from the dilution effect of 74 mm rainfall on Day 4 (Figure 2.1 and Figure 2.2b). Overall, the EC of the peat increased throughout the season during the experimentation (Figure 2.2b) and peat from the Up-areas always had higher EC than peat at Low-areas (Effect Slices; F = 16.38, 8.76, 9.43, 12.78, 18.41 and 9 for Day 0, 1, 3, 5, 10 and 20, respectively; Df = 1; $P < 0.006$) (Appendix A).

pH of sods decreased over the incubation period with about half a unit decrease on the first day after transplantation which stabilized on Day 3 in the Low- areas but continued in the Up-areas until Day 5 (Table 2.2, Figure 2.2c). Inner Sod sections had significantly greater pH than Outer sections, but only at Low-areas on the peat fields bordering the former ditches. On the other hand, pH in Low-areas was higher than Up-area for inner sod sections. The pH of peat slightly decreased over time, but both locations on the cambered peat field were not different in pH (Figure 2.2c; F = 3.62, Df = 1, $P = 0.15$) (Appendix A).

Drier soils generally had higher EC as $\boldsymbol{\theta}$ was inversely correlated to EC in sods, (r = -0.3, $P = 0.05$) and in peat (r = -0.5, $P = 0.01$). In contrast, drier sods had lower pH than wetter ones (r = 0 .4, $P = 0.01$) but $\boldsymbol{\theta}$ did not affect pH of peat (r = 0.04, $P = 0.799$). Thus, sods in the Up-areas were generally drier with higher EC and had lower pH. While pH of sods (~ 5 to 6) was much higher than that of the surrounding peat (3 - 4), pH was reduced where EC was higher (Figure 2.3).

2.5.3. *Ion concentrations*

In sods Na^+, Cl^- and Br^- increased significantly after 20 days of incubation while SO_4^{2-} and NO_3^- decreased (Table 2.3, Figure 2.4 and). Major seawater ions Na^+ and Cl^- introduced to the site during the storm in 2000, were found in high concentrations in peat **(**Figure 2.4 and Figure 2.5), but the high variability in ion concentrations between blocks reflects the non-uniform distribution of seawater contamination as was found in Mouneimne and Price (2006). There was no difference between Low- and Up-areas for sods. Paired-t tests also showed no significant difference in ion concentrations in peat at the Up-areas and Low-areas except in SO_4^{2-} (Df = 3 in all 7 pairs, 2 tailed, $P = 0.05$).

2.6. Discussion

Sod soil characteristics were strongly influenced by their Location on the cambered field surface and the length of Time they had been introduced in the peat. The Up-areas were drier but more saline than Low-areas, which were more prone to flooding. Each site, therefore, had certain advantages and disadvantages for transplantation success.

When transplanted, $\boldsymbol{\theta}$ of sods was 50% but increased to 70-100% within a day at both Upper and Lower areas (Figure 2.2a), as water drained into them from the peat. The Inner sod section had consistently higher moisture content than the Outer section. It is uncertain if this was an experimental error (*e.g*. partial drainage upon removal from peat for preparing the samples) or was the true condition of the sod, but it could not be explained it in either case. The relatively high hydraulic conductivity of sods (Table 2.1) facilitated the flow of water and solutes, possibly assisted by macropores associated with the root zone (Reeve *et al*. 1996; Harvey and Nuttle, 1995). Given the relatively high $\boldsymbol{\theta}$ and salinity of peat, and the initially rapid transfer of moisture

(Figure 2.2a) and salt (Figure 2.2b), salt movement to the sods must have occurred primarily by advection rather than molecular diffusion (Van Genuchten and Wierenga, 1986).

The movement of acidic peat water laden with H^+ ions into sods decreased their pH (Figure 2.3) because Na^+ displaces H^+ in organic matter exchange sites (Thomas and Pearce, 2004; Vitt, 2000). Furthermore, the presence of SO_4^{2-}, Cl^- and H^+ in peat forms acids which further decreases pH (Kilham, 1982). However, pH in sods remained well above that in peat (3 - 4) which is important because it protects plants like *J. balticus* from severe stress due to soil acidity (Hinsinger et al. 2003, Marschner, 1995). This can be attributed to the buffering capacity of the sod soil because Ca^{2+} and Mg^{2+} are not easily displaced by H^+ or Na^+ ions (Rowell, 1994) and hence, concentrations of basic cations Ca^{2+} and Mg^{2+} were not significantly different between Day 0 and Day 20 (Figure 2.4).

Changes to the pH and EC Inner annular sod section were retarded compared to the Outer section, suggesting that larger sod volumes delay stresses to the plant. For example, it took 20 days for the EC of the Inner and Outer sections to equalize. Also, the pH of the Inner section remained higher than the Outer sections in the Low-areas throughout the experiment (Table 2.2) because of the overall higher moisture content of the Low-areas.

Among the ions, Na^+ and Cl^- had the highest concentrations in peat and increased significantly in Sod sections over the 20 days of the experiment (Table 2.3, Figure 2.4 and Figure 2.5). This can hamper plant growth either by direct toxicity from Na^+ and Cl^-, ionic imbalance in the plant (*e.g.* Na^+ replacing the essential nutrient K^+), or lowered osmotic potential which causes physiological drought (Hagemeyer, 1997; Tester and Davenport, 2003; Broadley and White, 2001). The effects of an increase in trace amounts of Br^- are unknown. Deficiency of NO_3^- in sods is probably due to denitrification that commonly occurs under reduced (saturated or flooded) soil conditions (Lanbroek, 1990; Poonamperuma, 1972) and may cause nutritional deficiency in plants. However, *J. balticus* is known to have nitrogen-fixing ability (NCRS, 2000) but it is not

known whether this would work in the adverse conditions of the bog. In summary, the survival and establishment of *J. balticus* depends on its tolerance to increasing salinity in the Up-areas, to flooded conditions in the Low-areas, decreasing pH and a possible N-nutrient deficiency.

2.7. Conclusion

The high moisture content and salinity of peat was rapidly transferred to transplanted sods by advection. The increase in salinity in sods was primarily due to the ingress of Na^+ and Cl^-. The delayed effect of peat acidity on sod pH was because of high buffering capacity of Ca^{2+} and Mg^{2+} in sods. The Inner annular sod section was somewhat protected by the Outer annular sod section that directly contacted the peat. This implies that a larger volume of a sod may delay or alleviate stressful conditions and give transplants time to adapt to the new environment, and thus improve chances of successful revegetation.

2.8. Acknowledgment

This study was made possible by the funding of the Natural Science and Engineering Research Council (NSERC) of Canada through discovery grants to J, S, Price and L. Rochefort, and a scholarship (2005-2006) to M. B. Montemayor; and Canadian peat moss producers. We are thankful for information supplied by the New Brunswick Department of Natural Resources and laboratory facilities made accessible for our use by the Sungro Horticulture Canada Ltd, Lameque Is., New Brunswick, the Ecology and Geomorphology laboratories of the Faculty of Environmental Studies, and the Chemical Engineering laboratory of the University of Waterloo. Individuals who have given their time and effort in the field and laboratory work include: Cillian Breathnach, Gerry McIsaac, Miranda Lewis and Peter Whittington, to whom we give our thanks.

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Table 2.1 General soil properties comparing peat and the *J. balticus* sod soil. Mean ± Standard Error, N = number of samples.

	N	*J. balticus* sods	N	Peat
Organic matter content % (LOI)	3	9.5 ± 0.25	3	93.4 ± 0.87
Thickness of soil horizons (cm):	3			-
O		3.5		
A_m		8.9		
Particle size distribution of A_m	3			
horizon: % sand		87.3		
% silt		12.7		
% clay		0		
Von Post Scale of decomposition		-	8	range: H3-H5
Saturated hydraulic conductivity (cm s^{-1})	3	2.1 ± 1.88 x 10^{-2}	3	2.2 ± 0.7 x 10^{-4}
Dry bulk density (g cm^{-3})	3	0.82 ± 0.05	6	.073 ± 0.004
Particle density (g cm^{-3})	3	2.25 ±.02	6	1.38 ± 0.055
Total porosity	3	0.64	6	0.95

See *General Soil Properties* sub-section under the Methods section for details on the determination of each soil property.

Table 2.2 Analysis of Variance (ANOVAs) of ratio moisture content (θ), electrical conductivity (EC), and pH of sods according to Location on the cambered surface, Time of incubation and the annular Sod sections (Inner or Outer) (split-split plot design with repeated measures in Sod sections). Slices Effect are shown once an interaction has been found significant. Bold values indicate significant difference at $P<0.05$.

Effect	Df	θ		EC (log (x))		pH	
		F value	Pr > F	F value	Pr > F	F value	Pr > F
Block	3						
Location	1	2.04	0.25	12.48	**0.04**	12.50	**0.04**
Error (a)	3						
Time	5	26.93	**<.0001**	120.35	**<.0001**	6.81	**0.0002**
Location x Time	5	0.72	0.61	4.05	**0.006**	1.22	0.32
Error (b)	30						
Sod section	1	31.5	**<.0001**	79.21	**<.0001**	31.27	**<.0001**
Location x Sod section	1	0.24	0.63	5.77	**0.02**	7.10	**0.01**
Time x Sod section	5	1.89	0.12	5.93	**0.0004**	2.26	0.07
Location x Time x Sod section	5	0.92	0.48	1.36	0.26	0.84	0.53
Error (c)	36						
Total	95						
Tests of Slices Effect							
Location x Time							
Time within each location:							
Low-areas	5			44.01	**<.0001**		
Up-areas	5			80.39	**<.0001**		
Location within each time:							
Day 0	1			0	1.0		
Day 1	1			6.89	**0.01**		
Day 3	1			8.99	**0.005**		
Day 5	1			3.93	0.05		
Day 10	1			20.94	**<.0001**		
Day 20	1			10.11	**0.003**		

Location x Sod section					
Sod sections within each location:					
Low-areas	1	63.88	**<.0001**	34.08	**.01**
Up-areas	1	21.11	**<.0001**	4.29	.13
Location within each sod sections:					
Inner	1	14.86	**0.0005**	19.3	**.02**
Outer	1	9.80	**0.003**	3.0	.18
Time x Sod section					
Time within each sod sections:					
Inner	5	97.78	**<.0001**		
Outer	5	116.82	**<.0001**		
Sod section within each time:					
Day 0	1	0	1.000		
Day 1	1	17.73	**0.0002**		
Day 3	1	40.96	**<.0001**		
Day 5	1	22.34	**<.0001**		
Day 10	1	25.75	**<.0001**		
Day 20	1	1.87	0.1799		

Table 2.3 Analysis of Variance (ANOVA split-plot design) of ion concentrations in sods (mmol kg^{-1} fresh soil) according to Location on the cambered field surface and Time of incubation. Bold values indicate significant difference at $P<0.05$.

Effect	Df	Na^+		K^+		Mg^{2+}		Ca^{2+}		Cl^-		Br^-		SO_4^-	
		F value	Pr > F	F value	Pr > F	F value	Pr > F	F value	Pr > F	F value	Pr > F	F value	Pr > F	F value	Pr > F
Block	2														
Location	1	4.55	0.17	1.98	0.29	5.19	0.15	2.29	0.27	4.26	0.17	1.00	0.42	3.37	0.21
Error (a)	2														
Time	1	32.8	**0.005**	0.43	0.55	1.89	0.24	1.12	0.35	51.8	**0.002**	121.5	**0.0004**	25.6	**0.007**
Location x Time	1	3.49	0.13	1.05	0.36	1.02	0.37	0.50	0.52	3.32	0.14	1.50	0.29	1.81	0.25
Error (b)	4														
Total	11														

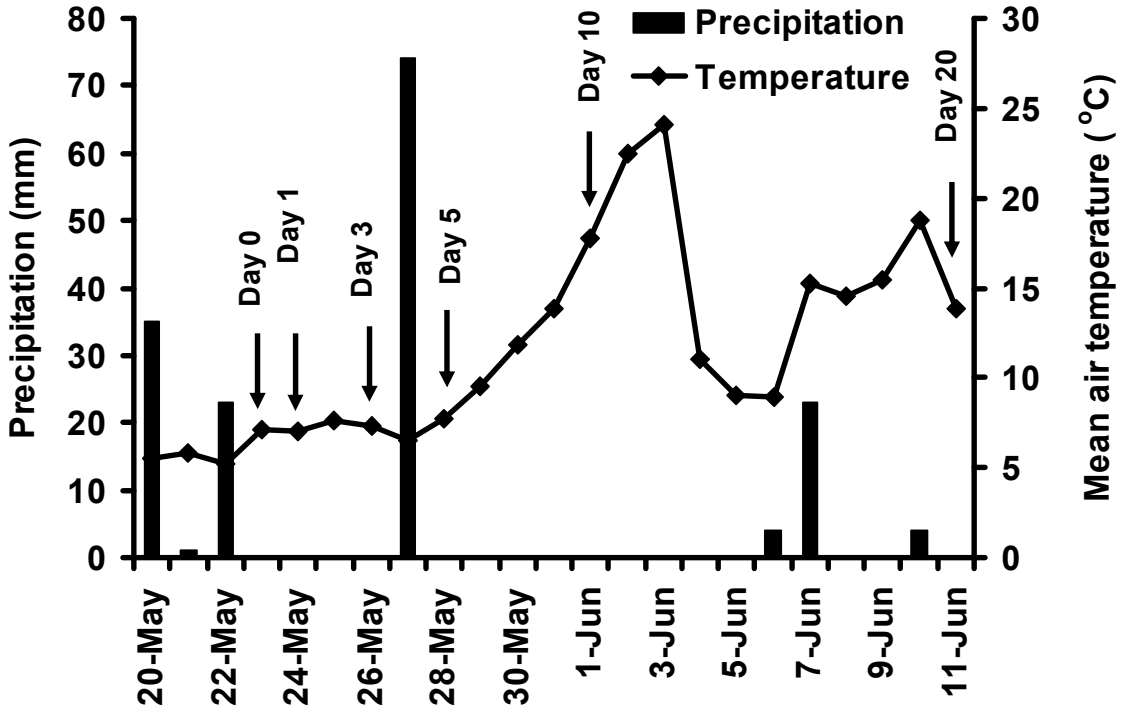

Figure 2.1 Precipitation and daily mean air temperature 3 days before the beginning and through to the end of the experiment in 2005.

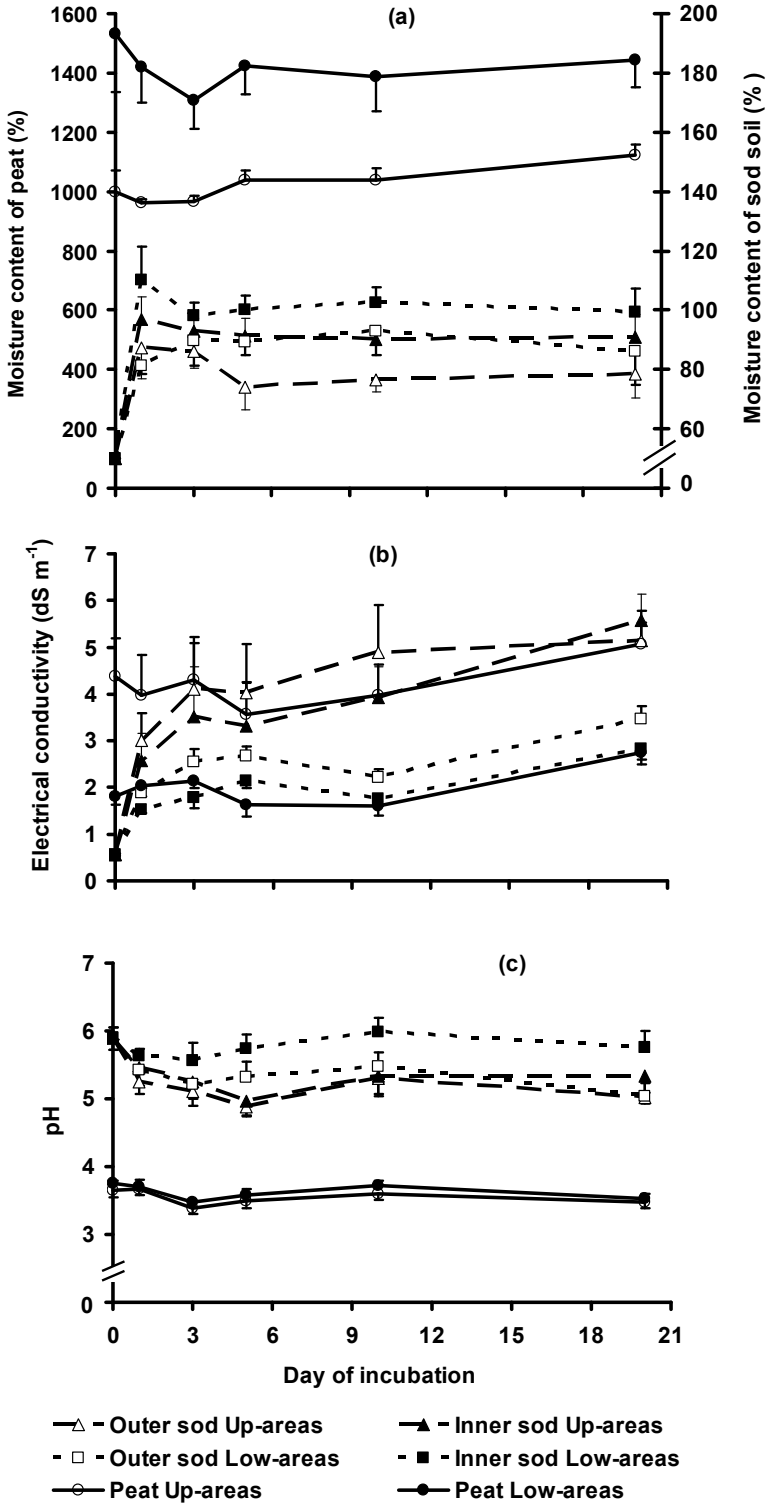

Figure 2.2 Changes over time in (a) moisture content % g g^{-1} dwb (note second y-axis) (b) electrical conductivity and (c) pH of sod soil and peat, at Up-areas and Low-areas. Either + or - standard error bars are shown to avoid overlapping

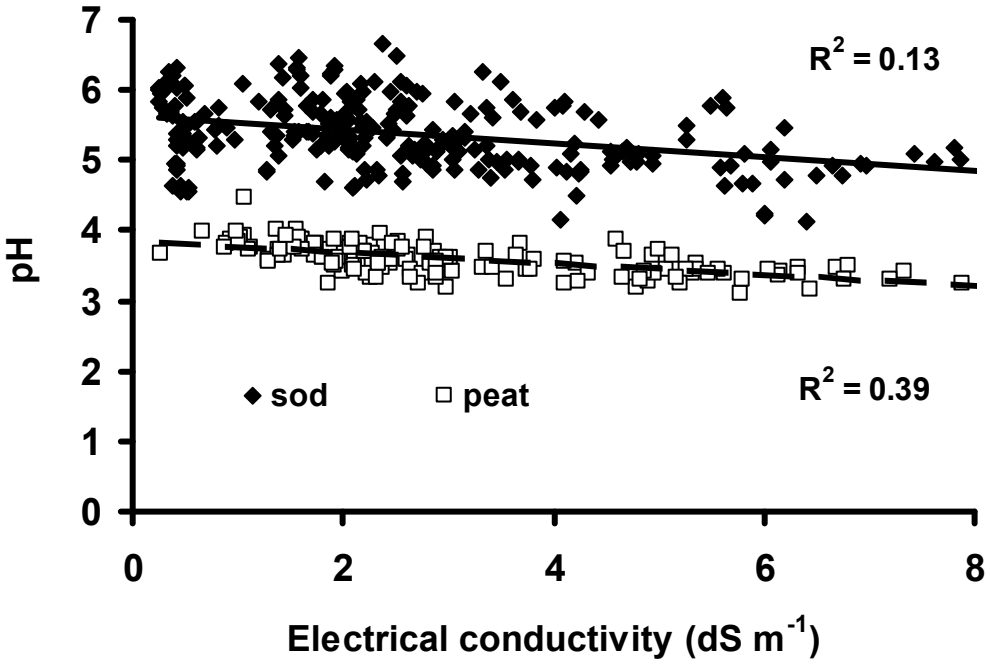

Figure 2.3 Increased electrical conductivity decreased pH in peat (pore water) (N = 96), and in sod (corrected electrical conductivity and pH of paste extract) (N = 132).

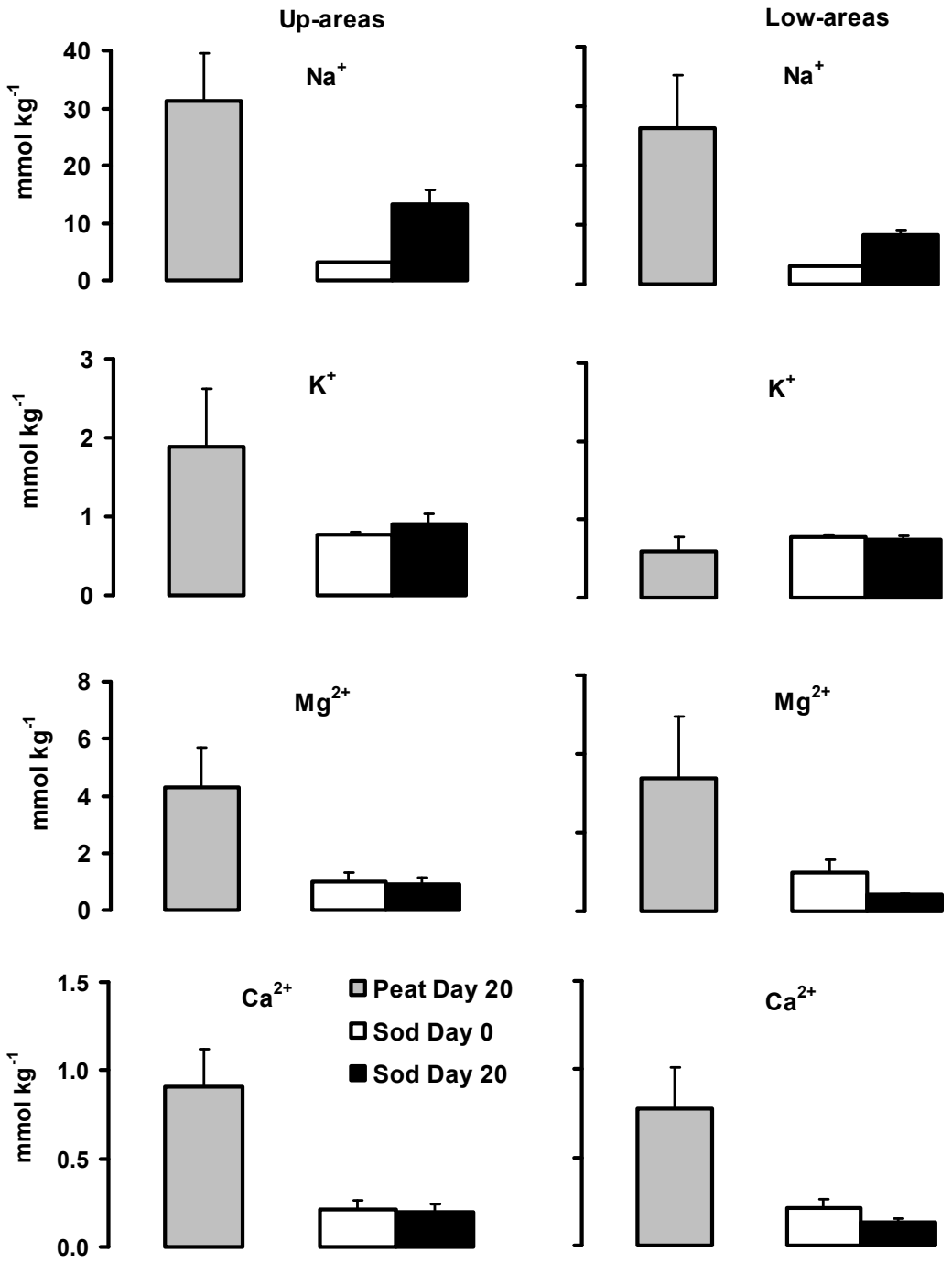

Figure 2.4 Major cation concentrations+SE in sods from the marsh (Day 0) and after 20 days of incubation in peat, and in peat at 20 days after sod transplanting (mmol kg^{-1} fresh soil).

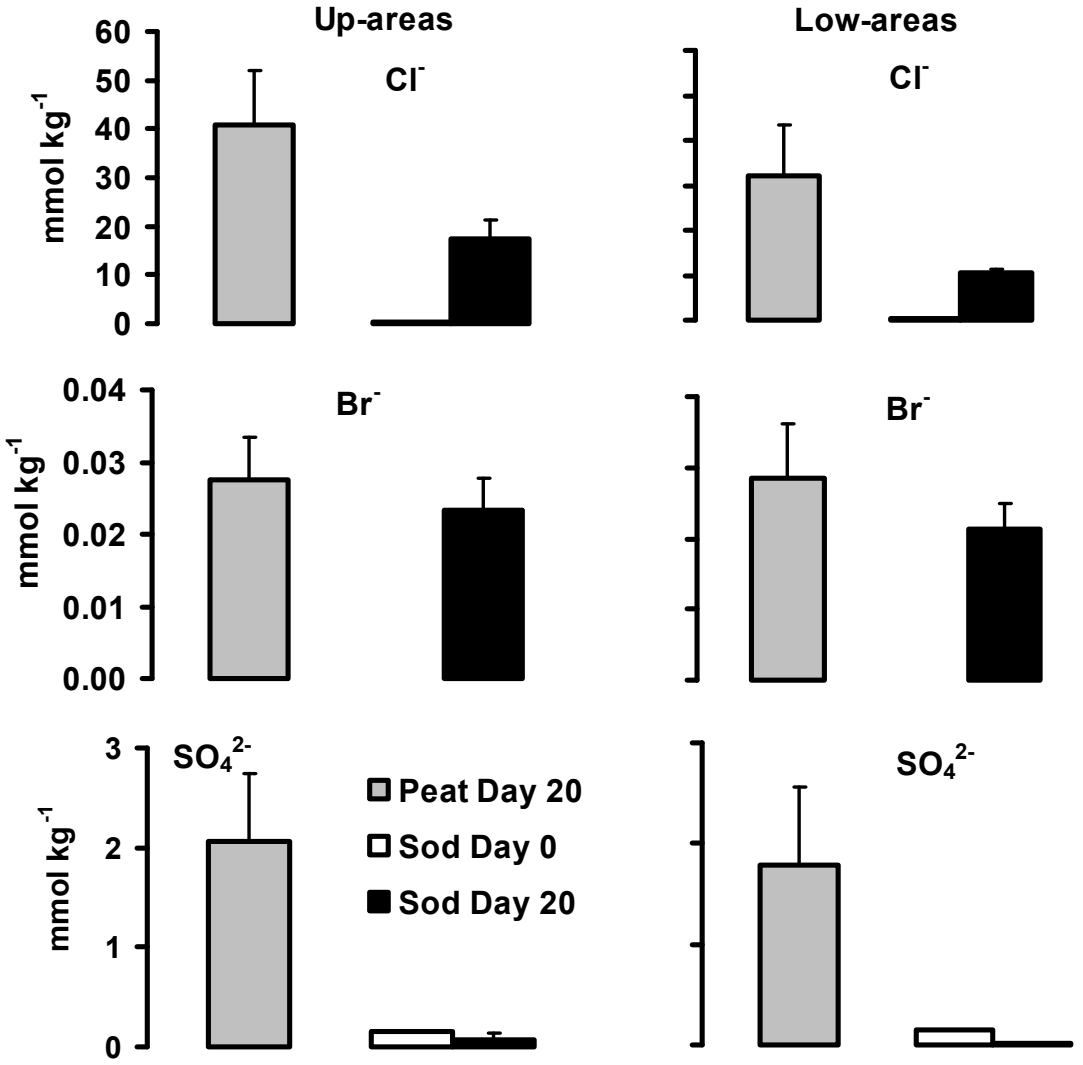

Figure 2.5 Major anion concentrations+SE in sods from the marsh (Day 0) and after 20 days of incubation in peat, and in peat at 20 days after sod transplanting (mmol kg^{-1} fresh soil. NO_3^- which was 4.63+0.21 mmol kg^{-1} fresh soil at Day 0 and below detection level in sods at Day 20 is not shown. NO_3^- in peat was below detection level at both days.

3. Temporal variations and spatial patterns in saline and waterlogged peat fields: I - survival and growth of salt marsh graminoids

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3.1. Abstract

A cutover bog contaminated with seawater on Pokesudie Is., New Brunswick, Canada remained barren five years after extraction operations ceased despite the proximity of natural seed sources. The aim of this paper 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* Willd. was transplanted to these zones in August 2004 whereas *Spartina pectinata* Link was reintroduced in June 2005. Plant material was collected from nearby marshes. Percentage of survival of *J. balticus* in August 2005 was poorest (27.5±8.3) at the Low-areas compared to Up- and Mid-areas (68.5±8.9 and 58.5±8.7, respectively) because of the early season waterlogged conditions of that zone. *S. pectinata* survival in June 2006 was good in all zones (89±5.3, 91.6±3.1 and 84.2±4.4 for Up-, Mid- and Low-areas, respectively) having better adaptation to early season waterlogged conditions. Early season waterlogged conditions resulted from a perched water table (May-June) which were alleviated only upon the complete thaw of the frozen peat layer on 8 July. Thereafter, important changes in hydrology and peat characteristics occurred: water table depths decreased from -8.5±1.7 and -1.6±1.2 cm on 26 May to -51.5±2.5 and -40.7±2 cm by 15 August in Up- and Low-areas, respectively; redox potentials at 12 cm depth increased from 26 June (190.9±8, 175±10.8 and 109.2±29.4 mV) to 9 August (282.8±8, 302.8±14.3 and 312.3±29.6 mV) in the Up-, Mid- and Low- areas, respectively which showed

that anaerobic conditions were maintained throughout the study period; decreased moisture content from 1256.8±61.9, 1667.4±126.3 and 1728.6±153 on 30 May to 851.7±21.2, 874.6±47 and 1008.2±57.5 % dwb on 25 July) which caused increased dry bulk density (from 0.07±0.002, 0.06±0.003 and 0.07±0.01 to 0.09±0.003, 0.09±0.005 and 0.08±0.004) in the Up-, Mid- and Low-areas, respectively; and increased electrical conductivity (salinity) especially on the 0-5cm surface (from 1.9±0.13, 1.8±0.31 and 1.5±0.29 to 18±1.9, 17.5±1.1 and 12.2±1 dS m^{-1}) which also caused decreased pH (from 3.5±0.04, 3.5±0.08 and 3.6±0.01 to 2.85±0.04, 2.85±0.01 and 2.9±0.03) in the Up-, Mid- and Low- areas, respectively. It is concluded 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: bulk density, ground thaw, *Juncus balticus*, redox potential, *Spartina pectinata*, watertable

3.2. Introduction

Spontaneous recolonisation of moss *Sphagnum* spp. communities on cutover bogs is poor (Lavoie *et al.* 2003) because of water-stress conditions during summer (Price, 1997, 1996), However, restoration measures can alleviate the stress (Price *et al*. 2003, 1998). In coastal peatland environments, seawater contamination (*e.g*. Mouneimne and Price, 2006) may prevent regeneration of salt intolerant bog communities (Tester and Davenport, 2003; White and Broadley, 2001). Evaporation further intensifies the salinity stress when salts are deposited on the soil surface, 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 (*e.g*. germination and seedling) to avoid periods of high salinity stress (Zedler *et al.* 2003). Transplanting grown plants can overcome this (Fraser and Kindscher, 2001; Forbes and Jefferies, 1999) especially when sod volumes are relatively large (Montemayor *et al*. submitted ms 1). 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, 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).

Our study site is devoid of vegetation five years after the termination of peat-extraction operations despite the proximity of natural seed sources and active introduction of seeds and phosphate fertilizer (Chaisson, L., peat producer, personal communication). 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.

3.3. The Study Site

The study site is located on Pokesudie Island, in the Acadian Peninsula of New Brunswick, Canada (47^{o} 48'N, 64^{o} 46'W). The site was originally a domed and ombrogenous (Rampton *et al*. 1984) maritime bog identified as Bog 600 by the New Brunswick Department of Natural Resources (GNB, 2006). Undisturbed bogs and marshes border the study site and are potential natural seed sources. Peat extraction operations began in the 1960's (Daigle *et al*. 1993) and continued until a storm surge in 21 January 2000 contaminated the peat with seawater and operations were closed down (Mouneimne and Price, 2006). Currently, drainage is very poor, since pumps used to remove water during peat extraction operations are no longer operating. Twenty-two ha 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 substrate is predominantly composed of *Sphagnum* remnants with patches of sedge peat, underlain by woody peat. A thin layer of gyttja overlies the sand substrate. Peat extraction operations left behind long rectangular fields (300-400m long, 30 m wide), bordered by drainage ditches. The seawater-contaminated area under study comprise 17 fields oriented perpendicular to the sea. The bottom topography is irregular and the remaining peat has a variable thickness of 1 – 2 m. The fields were cambered along the centreline to direct drainage toward ditches, and the study area part of each field now have a slope of about 2%. This slope created a moisture gradient that we 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). 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).

3.4. Methods

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 planted later 19 – 21 June 2005 because flooded conditions impeded the reintroduction. Transplanting was done on the day of collection. Spring melt caused water and sediment to smother some plants. At a few locations flood water washed over the crests of cambered fields and caused some minor uprooting of plants.

All observations were made during the period 03 May to 15 August, 2005 except for the survival of *S. pectinata* on 10 June 2006.

3.4.1. *Preparation of transplant materials*

Sods of *J. balticus* (11 x 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 root zone in this marsh corresponds to a ~13 cm distinct soil layer containing organic matter overlying sand. *S. pectinata* was collected from the upper-most zone of a nearby undisturbed salt marsh. Dense clumps *of S. pectinata* 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 explained below.

3.4.2. *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. Ten experimental blocks of 17 x 7 m were randomly selected from cambered field surfaces, on either side of the central ridge in the seawater contaminated and waterlogged area of the cutover bog. The length of each block (17 m) was parallel to the longitudinal ridge of the field. Locations on the cambered surface in a block were: Up-area, Mid-area and Low-area (factor 1 with 3 levels). 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 row on the Up-area and Mid-area locations were 2 m apart, respectively, from the upper row of the adjacent Locations. Each pair of rows was divided into four equal sections of 3 m lengths for planting, with 1 m length of undisturbed spaces in between and on both ends of each pair of rows. There were 10 sods or groups of plants 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 ($\boldsymbol{\theta}$), electrical conductivity (EC), pH, and dry bulk density ($\boldsymbol{\rho}$) which required an undisturbed spot at each sampling. Peat samples were obtained from each Location (factor 1): Up-area, Mid-area, Low-area; at four Depths: 0-5, 5-10, 10-15 and 15-20 cm (factor 2) in all the 10 blocks, five times during the entire study period 30 May, 26 June, 12 July, 29 July, and 9 August.

Survival of *J. balticus* sods was counted on 11 August 2005 while for *S. pectinata* survival count was done on 10 June 2006, a year after transplantation. 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 and flowers per sod or group of plants, number of leaves per stem, and plant height.

3.4.3. *Peat parameters*

Since under waterlogged conditions plants are shallow-rooted (Cronk and Fennesy, 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 $\boldsymbol{\theta}$ and $\boldsymbol{\rho}$ and three aggregate cores were for EC and pH measurements. All samples were extruded immediately after extraction and stored in sealed plastic bags. All samples were stored in the refrigerator and analyzed within a week of collection. Moisture content was determined gravimetrically by oven-drying the sample at 105^{o}C for 72 h,

and was expressed as percentage dry weight basis (% dwb) for graphs, and ratio (weight weight^{-1}) for statistical analysis. Moisture content was expressed as % dry weight basis (ICARDA, 2001; 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 ($\boldsymbol{\rho}$) was calculated by dividing the oven dry mass of a sample by its field volume. Total number of samples of $\boldsymbol{\rho}$ was reduced to N= 562 instead of N=600 (3 Locations x 4 Depths x 10 blocks x 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 a university laboratory, and ion analysis was done in January 2006.

Redox potentials (E_h) were measured in-situ using an oxidation-reduction probe (ORP) (VWR International Inc.) inserted into the peat at 12 cm depth at each location in all the 10 blocks, four times during the study. The probe was checked with a standard ferrous-ferric solution (Light, 1972) before each use.

3.4.4. *Hydrological parameters*

Wells were installed on 25 May 2005 by driving them into the peat until obstructed by the frozen layer. Water table (WT) measurements were taken about every 8 days 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. The pipes were 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 pipes were driven into the peat until obstructed by the frozen layer and thaw depth was measured.

A pit measuring 1 x 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. Measurements were made on 9 July and 6 August 2005. The pit was kept covered with plywood sheets between these dates, and five 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 minutes) precipitation with 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. The air temperature sensor malfunctioned and 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).

3.4.5. *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) and rank (Conover and Iman, 1981) especially for two-way ANOVAs where needed were performed and are indicated on the ANOVA tables. One-way ANOVAs were done to determine the effect of Location on plant parameters (% survival, no. of stems per sod, no. of flowers per sod, no. of leaves per stem. and height), When the assumptions for ANOVA were not fulfilled, non-parametric ANOVA, Kruskal-Wallis (K-W) test was applied. 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.

3.5. Results

3.5.1. *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 %) (Figure 3.1). 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 (Df = 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; $P < 0.001$) (Appendix B.1). 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 ($P = 0.05$, Appendix B.1). Significant differences in θ with peat Depth was found only at the end of study period (9 August) (Df = 3, F 3.84, $P = 0.012$), the two uppermost layers being drier than the underlying peat ($P = 0.05$, Appendix B.1).

Dry bulk density (ρ) ranged from 0.05 to 0.11 g cm^{-3}, highest at the Up-areas (Figure 3.1), and lowest at Low-areas, opposite to that of θ. Dry bulk density of the surface peat increased as the season progressed, inversely related with θ ($R^2 = 0.89$) (Figure 3.2a).

Electrical conductivity of peat water increased as the season progressed, most substantially at the surface (0-5 cm depth) (Figure 3.1). Differences in EC were a function of Location on the cambered field surface (Df = 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 (Df = 3, F = 54.1, 13.2, 8.4, 25.0 and 53.2 for 26 June, 12 July, 29 July and 9 August, respectively; $P < 0.0001$) (Appendix B.2). On 30 May there was an interaction between these two factors (Df = 6, F = 3.9,

$P < 0.001$). 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) ($P = 0.05$, Appendix B.2). 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 (Figure 3.2b and Figure 3.2c).

3.5.2. *Hydrological parameters*

There were 33 rainfall events from 3 May to 15 August with a total of 212 mm. Most rainfall events (139.3 mm) occurred before 21 June, 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 03-31 May, June, July and 01-15 August at the study site was 69.2, 74.4, 37.7 and 30.4 mm, respectively. Compared with the Bathurst 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 can be compared with climate normals; May- July were drier and August wetter at Bas Caraquet weather station which can represent rainfall in the experimental area. The average daily temperature for May, June, July and August at Bas Caraquet (representing temperature in the experimental area) in 2005 were 7.6, 16.4, 19.7 and 19.8 ^{o}C, respectively which differed from the Bathurst climate normals by 2.3, -0.6, -0.4 and -1.6 ^{o}C, respectively. 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 (Figure 3.3), decreasing from -8.5±1.7 and -1.6±1.2 cm, to -51.5±2.5 and -40.7±2.4 cm, respectively from 26 May to 15 August, respectively. Water table variability increased as the frost table disappeared,

which was about 28 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 (Figure 3.4). The material is wood peat which is the common base for the whole bog and its range of saturated moisture contents (~800-1100 % dwb) is lower than that of *Sphagnum* peat (~1200 % dwb) in this profile. A regression analysis of ρ with saturated θ_s (N = 29) for wood peat obtained from this moisture profile showed a negative relationship between the two factors $\rho = 85.77\theta^{-1.01}$ ($R^2 = 0.81$) a trend similar to *Sphagnum* peat of the waterlogged areas (Figure 3.2a).

Moisture content of the 0-20 cm peat layer decreased with WT depth as the season progressed (Figure 3.5). The individual relationships at each time of measurements were all linear: WT = 0.0053 θ – 12.5 ($R^2 = 0.4$), WT = 0.017 θ- 30.7 ($R^2 = 0.6$), WT = 0.023 θ – 44.2 ($R^2 = 0.7$), WT = 0.035 θ - 66.8 ($R^2 = 0.4$) and WT = 0.043 θ – 80 ($R^2 = 0.5$) for 30 May, 24 June, 12 Jul, 29 July and 9 August, respectively with the strongest relationship just after the thaw, on 12 July. Collectively, the data exhibited a curvilinear relationship (Study period, $R^2 = 0.62$) showing greater sensitivity in θ when the WT was high (Figure 3.5).

3.5.3. *Redox potentials*

Redox potentials (E_h) on and before 8 July were anaerobic being <+330mV on at all three Locations (Figure 3.6). After 8 July when the frost table had thawed, and WTs were lower, E_h increased with some blocks approaching aerated conditions (+400 mV) but most just approached the level where oxygen disappears (+330 mV). Variation among blocks was greatest at Low-areas and the minimum E_h values were exhibited by some blocks at this Location. Location on the cambered field surface (Df = 2, F = 6.55, $P = 0.002$) and Time of measurement (Df = 3, F = 83.6, $P < 0.0001$) had significant effects on E_h (Appendix B.3). Overall, E_h at the Up- and Mid- areas were higher than at the Low-areas ($P = 0.05$) and E_h during post-thaw were higher than during pre-thaw period ($P = 0.05$) (Appendix B.3).

3.5.4. *Plant responses*

Survival of *J. balticus* on 12 August 05 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%) (Figure 3.7, Table 3.1a). The same trend was found with the number of flowers per sod, averaging 7.5, 4.7 and 1.4, respectively (Figure 3.7, Table 3.1a). No significant difference was found between Locations for number of stems per sod and stem height (Figure 3.7, Table 3.1a).

S. pectinata survival on 10 June 06 was high and was not significantly different among Locations which was 89, 92 and 84 % at Up-, Mid- and Low- areas. Similarly, Location on the cambered field surface did not affect the number stems per planting spot, leaves per stem or plant height (Figure 3.8, Table 3.1b).

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 two years earlier (L. Chaisson, personal communication) and grows in the non-saline waterlogged areas of the cutover bog.

3.6. Discussion

The thaw period marked notable changes in peat characteristics and hydrology. A frozen peat layer persisted until the last week of June (Figure 3.3). During this period WT was very high because frost restricted drainage. Consequently $\boldsymbol{\theta}$ was also high (>1000%) (Figure 3.1). These conditions were exacerbated at low elevation areas where water collected. Some blocks at Low-areas had flooded conditions early in the season where $\boldsymbol{\theta}$ exceeded ~2000% dwb (Figure 3.2a). Low-areas maintained the highest $\boldsymbol{\theta}$ throughout the study period. Immediately after thaw, $\boldsymbol{\theta}$**s** in the Up- and Mid- areas were < 1000%, but at Low-areas this was achieved only at the end of the season (Figure 3.1).

Bulk density ($\boldsymbol{\rho}$) increased as the peat dried and $\boldsymbol{\theta}$ decreased (Figure 3.2a). 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 $\boldsymbol{\theta}$ decreased as the season progressed, $\boldsymbol{\rho}$ increased and thus saturated or near-saturated conditions were maintained at all Locations. While E_h increased following ground thaw, fully aerated conditions were never achieved (Figure 3.6). It is noted that high organic matter content and low pH also promote reduced conditions in the bog (Lanbroek, 1990).

Early in the season, before complete thaw, EC increased with Depth (Figure 3.1). Soil freezes from the top down (Zhang and Shijie, 2001) and 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). Chague-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 suitable only for salt tolerant species. However, transplants have the great advantage of having their roots below this highly saline surface layer and halophytes with their roots and rhizomes located at lower salinity levels can reproduce vegetatively (Zedler *et al.* 2003).

The concomitant reduction in pH as EC increased (Figure 3.2c) is due to the high cation exchange capacity of *Sphagnum* peat and its pore water (Thomas and Pearce, 2004, Bates, 2000; Smidrod and Painter, 1984; Clymo, 1963) with Na^+ and other cations displacing H^+ ions thus reducing pH (Sjȍrs and Gunnarsson, 2002; 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 and the physiology of the roots and rhizosphere microorganisms (Hinsinger *et al*. 2003). Thus, seawater contamination in a bog produced two stresses: salinity itself and the intensification of acidic conditions. The planting guide (NRCS, 2000) 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 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 (Figure 3.3) with the Low-areas maintaining shallower WT. During mid-summer (July), the period of maximum degree-days above 5^oC and most conducive to plant growth, WT dropped to 40-50 cm below the surface in Up-areas, and surface moisture contents to ~800 % (Figure 3.1) . However, Up-areas were not moisture-limited, because of the capillary fringe (CF) (Figure 3.4).A high CF in combination with decreasing dry bulk density was responsible for continued poor aeration (low E_h). WT had a strong influence on surface moisture content (Figure 3.5). In general, warmer temperatures, lower WT and rise in E_h provided improved conditions for plant growth in mid-season (July).

High plant mortality (72.5%) for *J. balticus* in the Low-areas was primarily due to very high moisture contents (>1400%) especially prior to complete thaw (Figure 3.1) which was a critical time for shoot emergence. High moisture contents 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 (Figure 3.1). This could affect

germination or the long-term growth of plants, 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, 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-$\boldsymbol{\theta}$ relationship of the entire study period (Figure 3.5). For example, the Low-areas curve described WT-$\boldsymbol{\theta}$ relationship in a location unsuitable for *J. balticus* (Figure 3.5). However, long-term salinity tolerance in the Up-areas would eventually determine the dominant species.

The very low survival of *J. balticus* (Figure 3.7) at Low-areas suggests limited metabolic adaptation to flooding (Crawford, 1989; Perata and Alpi, 1983) or carbohydrate shortage (Crawford, 1993). Species with larger rhizomes (*e.g. Spartina* spp.) and hence more carbohydrate storage are able to survive anoxia longer than species wit thin rhizomes (*e.g. Juncus* spp.) (Barclay and Crawford, 1982). 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 (mid-May) and growing in relatively drier conditions implies that its metabolic adaptation to flooded conditions or carbohydrate storage 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 (Figure 3.7).

Of the two species tested *S. pectinata* appeared to be more tolerant of salinity because of its higher survival % especially in the Up-areas (Figure 3.8). 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. There is a need to investigate the pattern of ion accumulation in *J. balticus* and *S. pectinata* plant parts. Also, 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.

3.7. Conclusion

The thaw period was the time when major changes in peat characteristics occurred which can 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*. Over time, the water table dropped dramatically and consequently moisture content decreased but bulk density increased. Increased bulk density maintained saturated or anaerobic conditions which prolonged adverse effects on the survival and growth of plants. EC increased significantly with concomitant decrease in pH after thaw especially at the 0-5 cm surface which in combination with spring flooding precluded germination of seeds or survival of seedlings and thus explains 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.

3.8. Acknowledgement

This study was made possible by the funding of the Natural Science and Engineering Research Council (NSERC) of Canada through discovery grants to J, S, Price and L. Rochefort, and a scholarship (2005-2006) to M. B. Montemayor; and the Canadian peat moss producers. We are thankful for information materials supplied by the New Brunswick Department of Natural Resources through Jacques Thibault, information about the bog from Laurie Chaisson, and laboratory facilities made accessible for our use by the Sungro Horticulture Canada Ltd, Lameque Is., New Brunswick and the Ecology and Electrical Engineering laboratories of the University of Waterloo. Individuals who have given help in the field or laboratory work include: Cillian Breathnach, Gerry McIsaac, Miranda Lewis, Sophie Thibault, Fabrice Pellot, Jolaine Chaisson, Luc Miousse and Peter Whittington, to whom we give our thanks.

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Table 3.1 Analysis of Variance (One-way ANOVA) comparing different plant parameters by location

(a) *Juncus balticus*

Source	Df	Survival (%)			Df	No. stems per sod			Plant height (cm)			No. flowers per sod log(x)		
		MS	F	*P*		MS	F	*P*	MS	F	*P*	MS	F	*P*
Block	9				9									
Location	2	4570	6.13	**0.006**	2	354	3.02	0.069	7.03	0.275	0.762	0.61	4.61	**0.021**
Error	18	745			14	117			25.6			0.13		
Total	29				25									

(b) *Spartina pectinata*

	Survival (%) (K-W test)	Source	Df	No. of stems per planting spot			Plant height (cm)			No. leaves per stem		
χ^2	1.41			MS	F	*P*	MS	F	*P*	MS	F	*P*
Df	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									

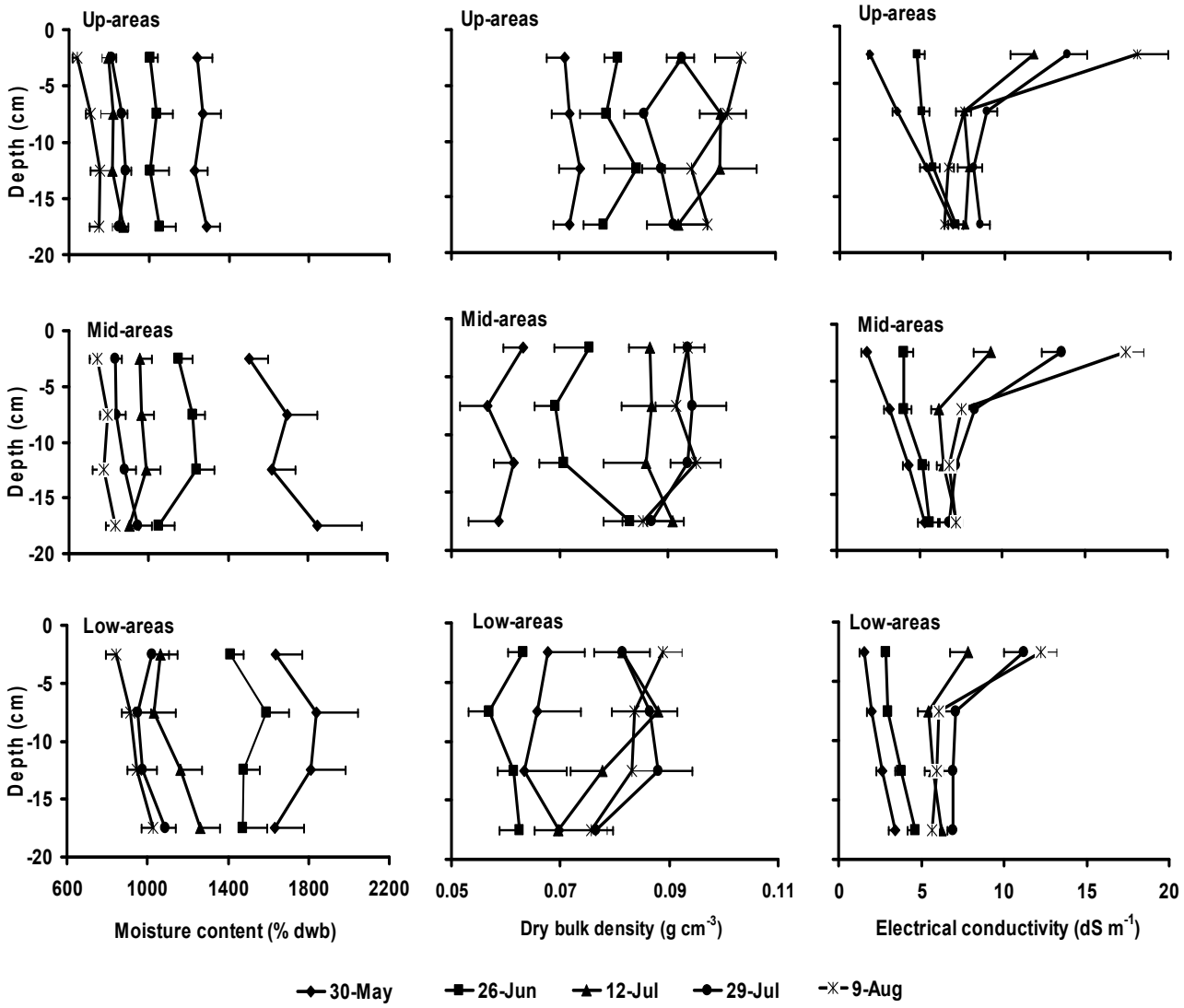

Figure 3.1 Average moisture content, dry bulk density and electrical conductivity at various Locations, Depths and times during the study period. Bars show + or – standard error. N = 10 for each point except for 30 May and 26 June measurements (explained in Peat parameters subsection under the Methods section).

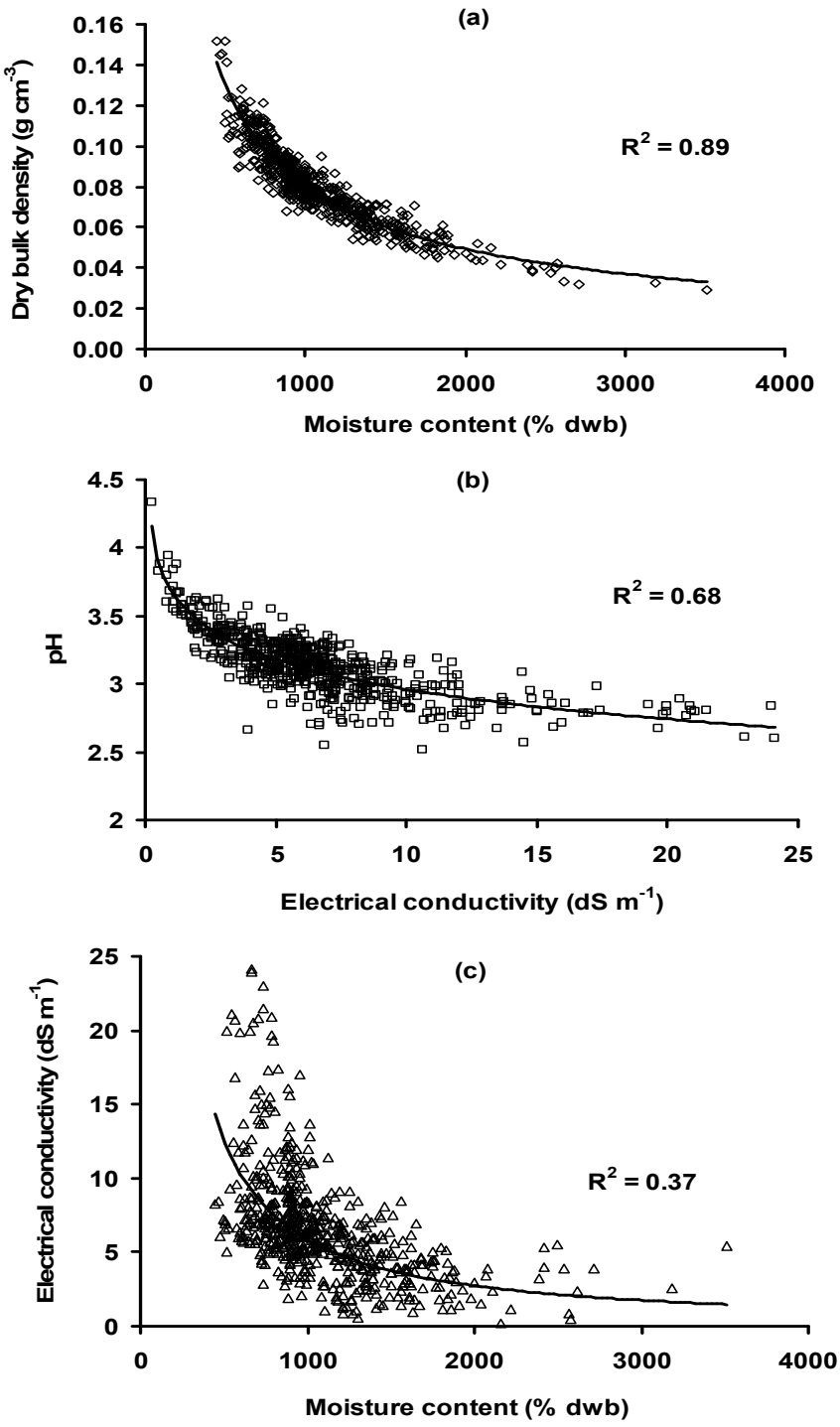

Figure 3.2 Dry bulk density in peat increased as peat became drier (a) (N=562), pH decreased as EC increased (b) (N=600) and EC decreased as peat became wetter (c) (N = 600).

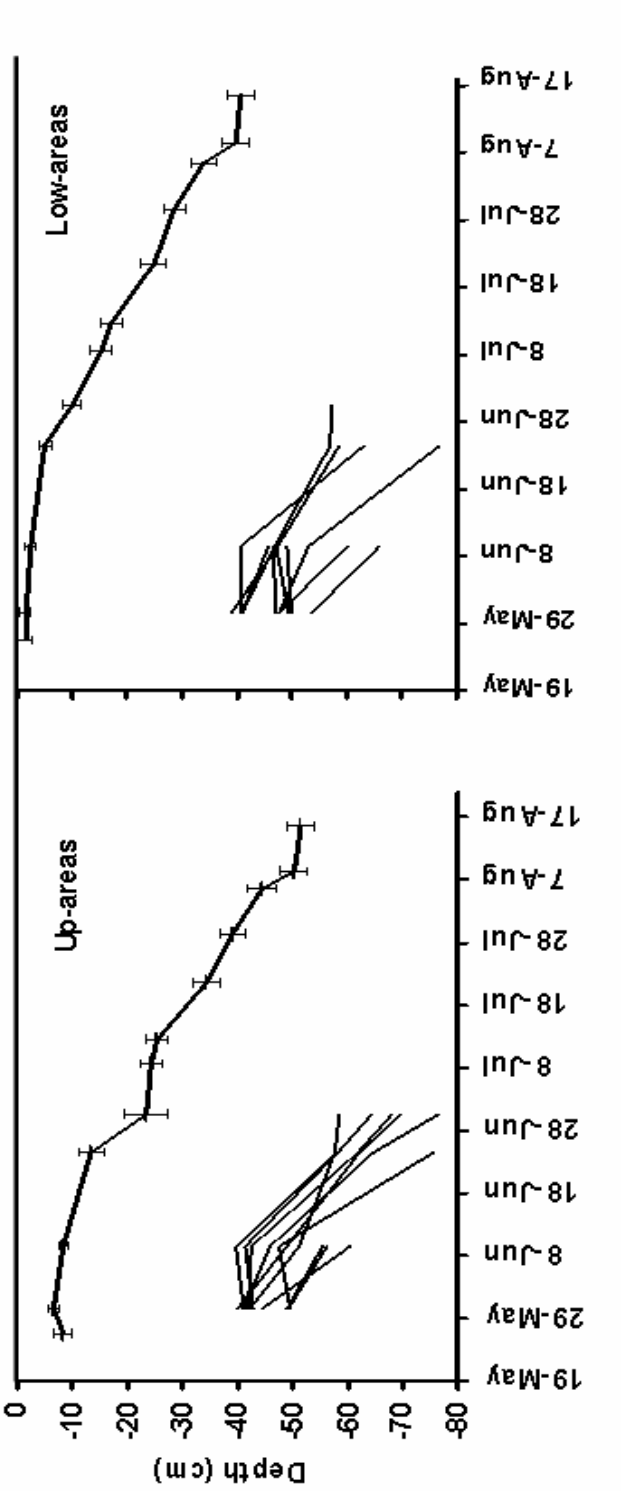

Figure 3.3 Average depth of water table (top curves with standard error bars) and depths of frozen layer (a curve for each of the 10 blocks) at Up-areas and Low-areas during the study period.

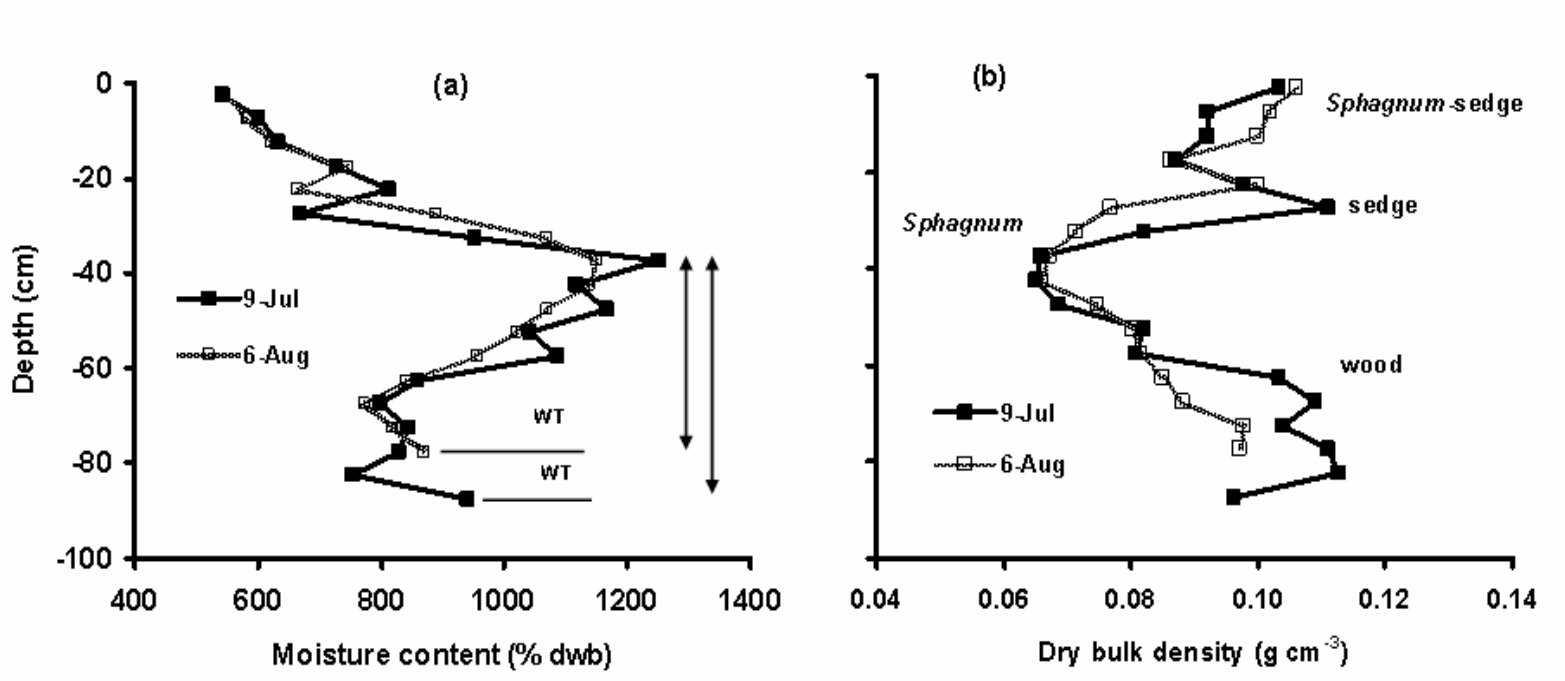

Figure 3.4 Moisture profile and corresponding dry bulk density of peat in unsaturated areas. Double headed arrows show approximate capillary fringe with a rise of 40-50 cm. Patches of sedge peat in *Sphagnum* peat on the upper layers and wood peat consisting of different parts of trees and sand contamination in the bottom layers caused large variations

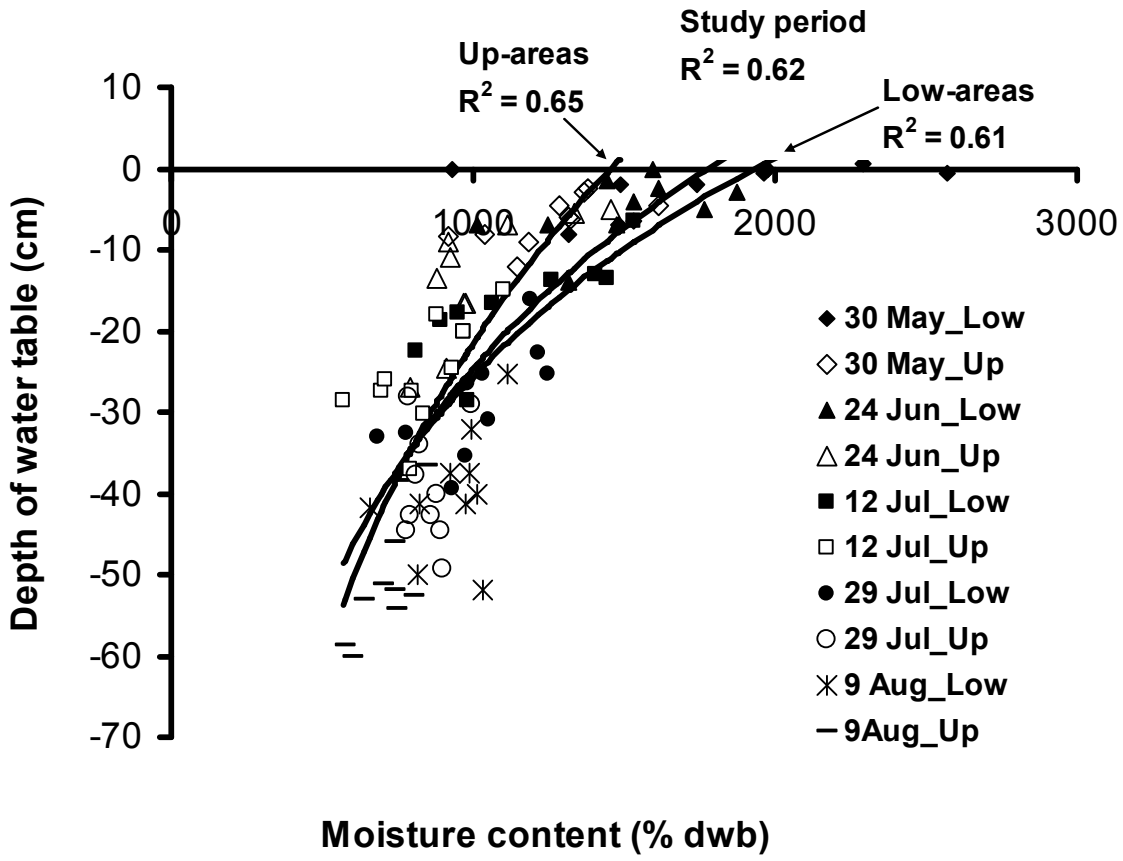

Figure 3.5 Relationship between water table depth and average surface moisture content (0-20 cm) for the entire study period (N = 20 for each date of measurement), Up-areas (N = 50) and Low-areas (N = 50).

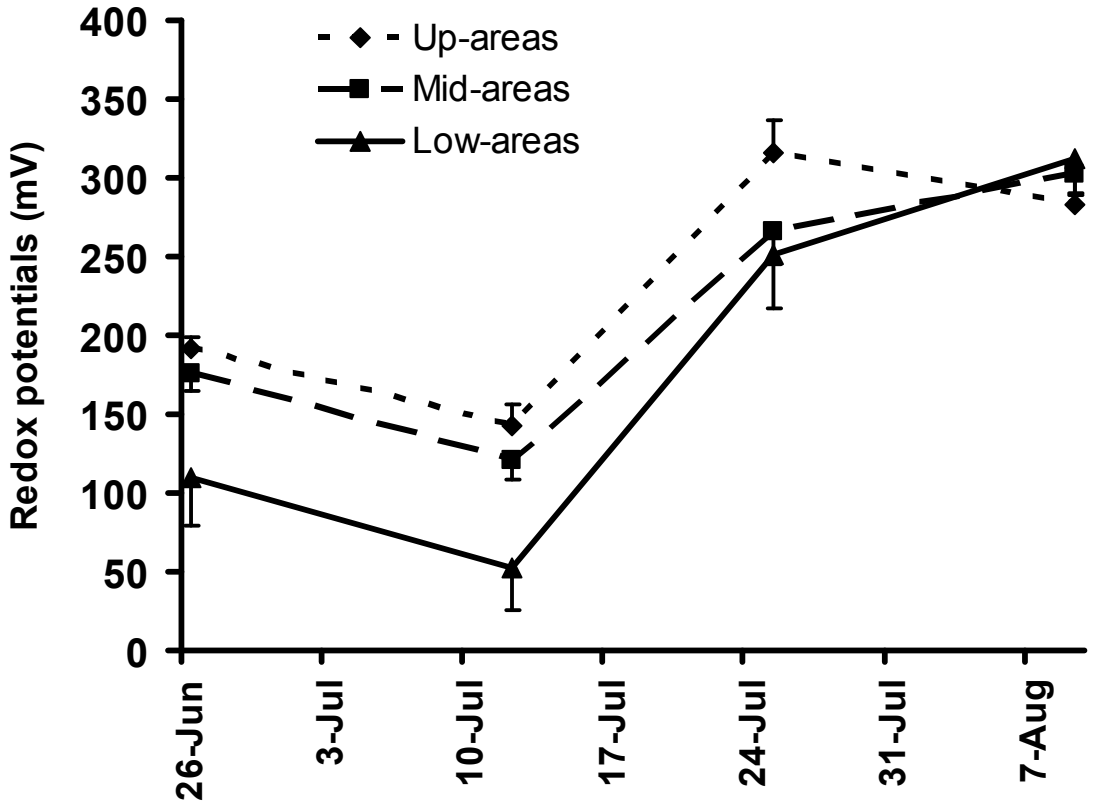

Figure 3.6 Redox potentials at 12 cm depth at the three Locations on four occasions during the study period. Bars show + or - standard error.

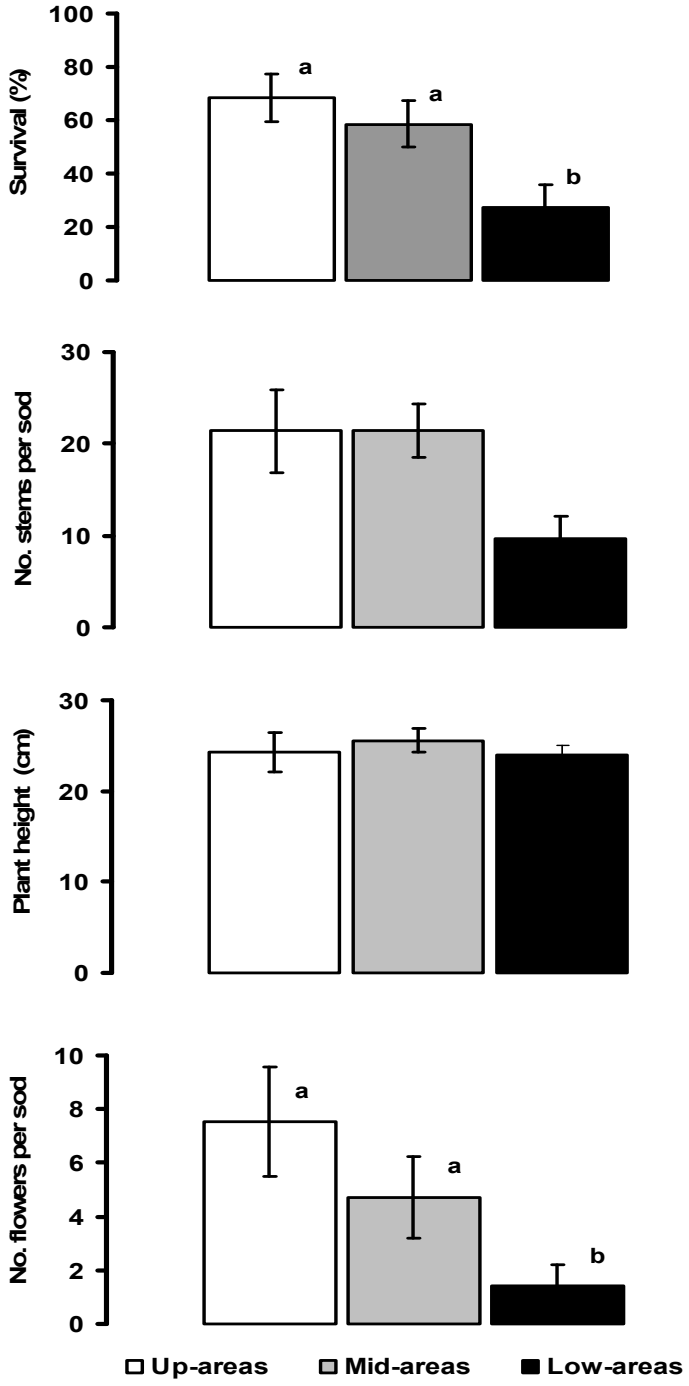

Figure 3.7 ***J. balticus*** **survival and other plant parameters 11 August 05. For no. of stems and flowers per sod, and plant height, N = 30, 27 and 21 for Up-areas, Mid-areas and Low-areas, respectively. Means indicated by the same letters are not significantly different (*P* = 0.05). Standard error bars are shown.**

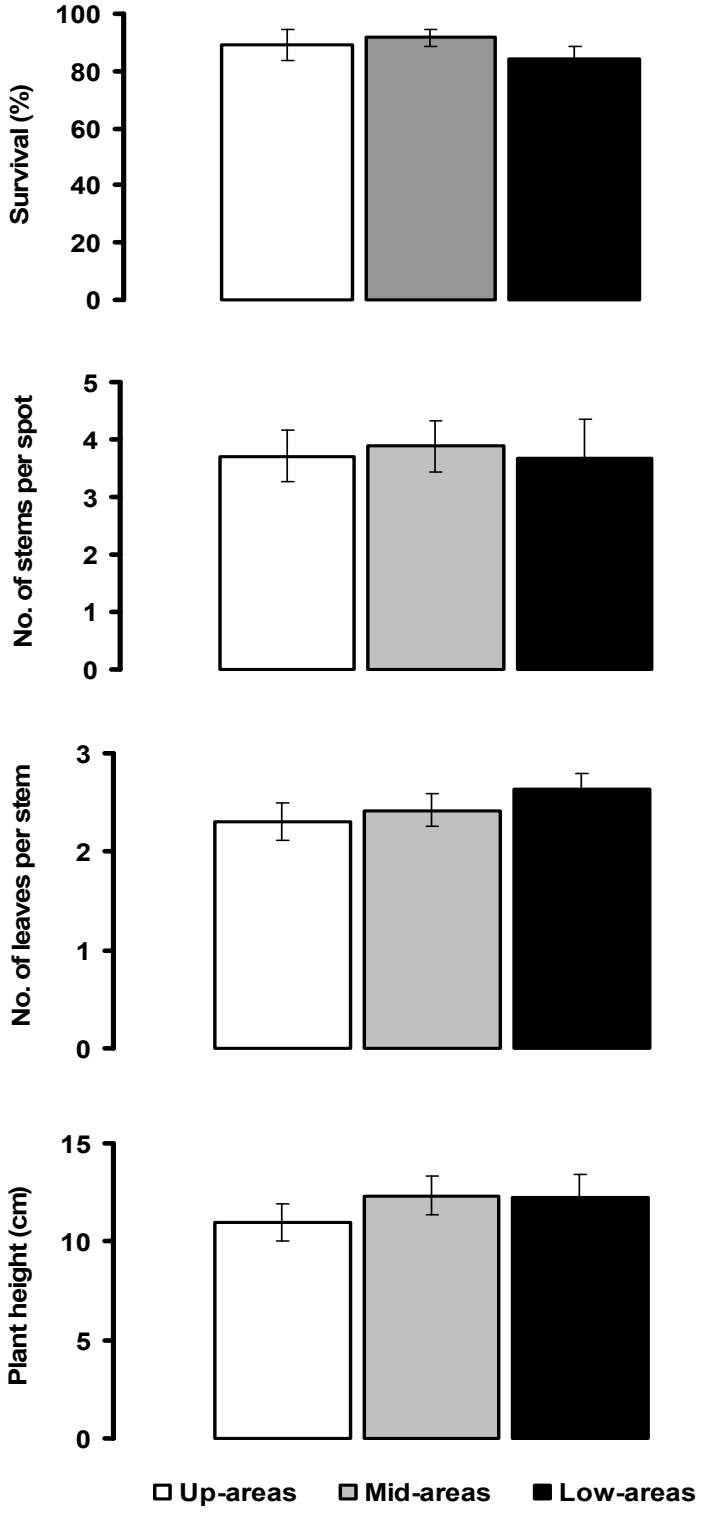

Figure 3.8 ***S pectinata*** **survival and other plant parameters on 10 June 06. There is no significant difference between Locations in all parameters. Standard error bars are shown.**

4. Temporal variations and spatial patterns in saline and waterlogged peat fields: II – ion accumulation in salt marsh graminoids

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4.1. Abstract

In an earlier study (Montemayor *et al*. submitted ms 2), survival of *Spartina pectinata* Link and *Juncus balticus* Willd. was assessed after transplantation in a cutover bog that had been contaminated by seawater. The aim of this paper is to understand the mechanism of salinity tolerance for both species by determining ion accumulation in the above- and below-ground parts of the plants from donor sites (nearby salt marshes) and those grown in the cutover bog. More specifically, to determine if the varied conditions in moisture and salinity of the cutover peat fields have an effect on ion concentrations (mmol kg^{-1} dry wt.) in peat water and plant tissues. *J. balticus* and *S. pectinata* grown in the cutover bog had similar accumulations of Na^+ (474.3±41 and 468.3±31.7, respectively) and Cl^- (314.9±21.9 and 310.5±27.5, respectively) in the shoots but differed in how they managed Na^+. *J. balticus* accumulated Na^+ in below-ground parts (659.5±88.7) and had limited transport to the above-ground parts, while *S. pectinata* accumulated and excreted Na^+ in the above-ground parts and had less (397.4±25.1) in the below-ground parts. Compared with corresponding plants from the marshes, *S. pectinata* maintained (313.1±23.8) and *J. balticus* increased,(531.2.5±38.6) K^+-selectivity in the shoots, a key requirement for survival in saline conditions. *S. pectinata* had more salinity-tolerance than *J. balticus* primarily through its increase in Ca^{2+} concentrations in the shoots (37.9±4.5) while there was a decrease in *J. balticus* (39.8±4.9) compared with corresponding marsh plants (21.5±1.7 and 144.7±12.5, respectively) . Fe in the shoots of *S. pectinata* was greater when grown in wetter locations and was at critical

deficiency level (1.1±0.1) in drier locations. Thus, although an earlier study found *J. balticus* to have the best survival in drier locations and *S. pectinata* at all locations, their long-term survival in drier areas is constrained by limited salinity tolerance in the former and Fe deficiency in the latter.

Keywords: reduced soil conditions, macro-nutrients, micro-nutrients, salinity tolerance, nutrient uptake, nutrient deficiency

4.2. Introduction

Establishing a vegetation cover on an abandoned cutover bog contaminated with seawater (Mouneimne and Price, 2006) requires transplantation of salt tolerant plants such as *Juncus balticus* Willd. and *Spartina pectinata* Link (Montemayor *et al*. submitted ms 2). Such halophytes (Tester and Davenport, 2003; White and Broadley, 2001) such as these can survive and grow under saline conditions and accumulate Na^+, K^+ and Ca^{2+} (Moghaieb *et al*. 2004). Excessive accumulation of Na^+ and Cl^- inhibits growth and can cause damage to many plants (Tester and Davenport, 2003). However, halophytes can manage the accumulation of salt ions by various means. For example, Na^+ transport to the shoots which are susceptible to salt damage can be regulated and accumulated in or excluded at the roots. It can also be transported to but excreted through the leaves, and accumulation capacity can be increased through succulence (Tester and Davenport, 2003); while some plants can restrict Cl^- transport from the roots to the shoots (White and Broadley, 2001).

In saturated and reduced conditions common to wetlands with predominantly mineral soils, essential micronutrients like Fe and Mn become readily bioavailable, but their excessive accumulation can be toxic to plants (Pezeshki, 2001; Neue *et al*. 1998, Ernst, 1990; Lanbroek, 1990).

Juncus balticus Willd. and *Spartina pectinata* Link, which are native to brackish and salt marshes, were found to be suitable for transplantation to the seawater contaminated cutover bog of this study (Montemayor *et al*. submitted ms 2). While the marshes have mineral soil (pH 6 -7) and are periodically influenced by tides, the cutover bog has poorly drained, acidic (pH 2.4 – 4) organic soil influenced only by meteoric processes (Montemayor *et al*. submitted ms 2). Both species are rhizomatous perennials with varying degrees of tolerance to salinity and flooding (NRCS, 2000a and b; Tiner, 1987).

Both species were planted along the cambered surface of peat fields on zones of different moisture levels designated as Up-areas, Mid-areas and Low-areas (Montemayor *et al*. submitted ms 2). The thawing period of a frozen ground layer influenced peat moisture contents. Average moisture contents (% dry weight basis) ± standard error of the 0-20 cm upper surface of peat for 26 June (pre-thaw period) were 1027±62, 1166±57 and 1488±80 and for 29 July (post-thaw period) were 852±21, 875±47 and 1008±58 for Up-areas, Mid-areas and Low-areas, respectively. Redox potentials mostly indicated anaerobic conditions throughout the season with few blocks reaching as low as -50 mV and as high as 450 mV (approaching aerated conditions). Survival 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 very low at Low-areas (27.5%).

The general aim of this study is to understand the salt-tolerance mechanisms of plants that survived well. Specifically, the objectives are (1) to determine the concentrations of Na^+, K^+, Ca^{2+}, Mg^{2+}, Cl^- and SO_4^{2-} in the above- and below ground parts of *J. balticus* and *S. pectinata* transplanted on a seawater contaminated cutover bog and relate these to long-term plant survival, (2) to determine whether or not Fe and Mn uptake by plants considered to reach potentially toxic levels under the waterlogged and reduced soil conditions would exceed concentrations in plants from natural sources and (3) to determine concentrations of these ions in peat water at pre- and post- thaw periods which have different levels of reduced conditions.

4.3. Study Site

The study site is a cutover bog located on Pokesudie Island, in the Acadian Peninsula of New Brunswick, Canada (47^o 48'N, 64^o 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 (300-400m long, 30 m wide) with cambered surfaces along the longitudinal centreline, bordered by drainage ditches. Five years after the

closing of operations, the ditches are partially filled with eroded peat and the cambered surfaces in the middle of fields now have a slope of about 2%. This slope creates a moisture gradient that we divided into zones designated as Up-areas, Mid-areas, and Low-areas. Details of the study site and climatic data can be found in Montemayor *et al*. submitted ms 2.

4.4. Methods

J. balticus was planted as sods of volume 2145 cm^3. *S. pectinata* was planted as bare root J-section (NRCS, 2000b) individual plants at three individuals per planting spot. Collection of plants and transplanting were carried out beginning of August 2004 according to the experimental design below whereas *S. pectinata* was re-planted at the beginning of June, 2005. More details on the plantation can be found in Montemayor *et al.* submitted ms 2.

4.4.1. *Experimental design*

To determine the effect of Locations with varied moisture and salinity levels as created by the topography of the cutover peat fields (Up-areas, Mid-areas, Low-areas) on ion concentrations in plant tissues, one whole plant sample was collected from each Location of the 10 experimental blocks as described in Montemayor *et al.* ms 2. Plant samples of *J. balticus* were not collected from the Low-areas and from two blocks in the Up- and Mid- areas because of very low survival %. Plant samples were collected on 11 August 2005, which was after one full growing season for *J. balticus* and 2 months of incubation for *S. pectinata*. To determine the effect of Location (topography of Up-, Mid- and Low-areas) and Depth of peat layer on ion concentration in peat at pre- and post-thaw periods, samples were collected from each Location at Depths 0-5, 5-10, 10-15 and 15-20 cm from five randomly selected experimental blocks on 26 June 2005 and 29 July 2005. Peat core samples were taken from the 1-m wide undisturbed spaces between planted row sections as described in Montemayor *et al*. submitted ms 2.

Plant samples of both species were also taken from the same marshes the planted species were collected from (N=3 sods for *J. balticus* and N=6 individual plants from 6 different clumps for *S. pectinata*) so that ion accumulation between plant parts from the study and natural plant source sites could be compared as: Bog above-ground parts, Bog below-ground parts, Marsh above-ground parts and Marsh below-ground parts.

4.4.2. *Peat samples preparation*

Ion concentrations in peat water were measured in filtrates obtained through vacuum-filtering while simultaneously pressing the sample by hand using a jar. Fisherbrand filter paper Qualitative P8-creped (coarse porosity and fast flowrate) was used. Filtrates were frozen at the study site laboratory and shipped to the University of Waterloo and were kept frozen until ion analysis. Filtrates were thawed in the refrigerator and re-filtered through Whatman No. 42 ashless filter paper for ion analysis in January 2006. Filtrates were analyzed for concentrations of total Na, K, Ca, Mg, Fe and Mn, and anions Cl^-, Br-, NO_3^- and SO_4^{2-} by methods described in the Ion analysis section.

4.4.3. *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^{o}C for 72 h. Dried plants were placed in brown paper bags and shipped to the University of Waterloo and processed in December 2005. 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 length pieces using 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^{o}C, cooled, digested with 5 ml 2N HCl, topped with deionized water to 50 ml and filtered through Whatman No. 42 ashless filter paper (ICARDA, 2001). The extracts were analyzed in January 2007 for cations Na^+, K^+, Ca^{2+}, Mg^{2+}, Fe and Mn; and for anions SO_4^{2-}, NO_3^-, and Br^-.(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 are written as total iron Fe and total manganese 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^{o}C for at least 2 h until the volume was reduced to about 25 ml, and 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.

4.4.4. *Ion analysis*

Total element and cation concentrations in plant tissues and peat water were analyzed using Perkin-Elmer 3100 atomic absorption spectrometer and anions by ion chromatography using Dionex DX500. 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, to mmol g^{-1} oven-dry weight (dry wt.) for plants, for statistical analysis.

4.4.5. *Statistical analysis*

A two-way ANOVA with fixed factors: Location on the cambered peat field and Depth of peat layer was performed for ion concentrations in peat water. For ion concentrations in plants transplanted in the bog a two-way ANOVA with fixed factors was performed: Location on the cambered field surface and Plant part (above- and below-ground).

To test differences in ion concentrations among plant parts from the bog and from the marshes, a One-way ANOVA was done.

Log(x) and rank (Conover and Iman, 1981) transformations were applied where required in order to fulfill ANOVA assumptions (normal distribution and homogeneity of variances). Significant ANOVAs were followed by multiple comparisons of means (Least Significant Difference (LSD))

4.5. Results

4.5.1. *Juncus balticus*

Concentrations of K^+, Ca^{2+}, Mg^{2+} and Mn in plants grown in the bog 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; F = 49.7, 37.1, 38.1, 14.1, 7.13, 27.1 and 4.41, P = <0.0001, <0.0001, <0.0001, <0.001, 0.012, <0.0001, and 0.045, for K^+(log(x)), Ca^{2+}(Rank), Mg^{2+}, Mn (log(x)), Na^+, Fe(log(x)), and SO_4^{2-}, respectively) (Appendix C.1). There was no difference in Cl^- (Df = 1, F = 0.19, P = 0.665) (Appendix C.1). As no significant interaction was found according to topography (location of Up and Mid- areas), data on the concentrations of plant parts were pooled together (Figure 4.1).

Comparison of ion concentrations in plants grown in the cutover bog and collected from the marsh, Na^+ in both plant parts, K^+ in the above-ground parts and SO_4^{2-} in the below-ground parts of plants grown in the bog were greater than those from the marsh (One-way ANOVA; Df = 3 for all three ions; F = 13.8, 35.3 and 7.76 for Na^+, K^+ and SO_4^{2-}, respectively; P = <0.0001 for all three ions) (Appendix C.4, Post-hoc in Figure 4.1). Ca^{2+} and Mn in both plants parts, Fe in the above-ground parts and Mg^{2+} in the below-ground parts of plants grown in the bog were less than those from the marsh (One-way ANOVA; Df = 3; F = 28.3, 17.1, 14.3 and 17.6 for Ca^{2+} (Rank), Mn (log(x)), Fe (Rank) and Mg^{2+}, respectively; P <0.0001 for all four ions) (Appendix C.4; Post-hoc in Figure 4.1). Cl^- in the above- and below- ground parts of plants grown in the bog were not

different but were greater than those from the marsh (Df = 3, F = 19.9, $P < 0.0001$) (Appendix C.4; Post-hoc in Figure 4.1).

4.5.2. *Spartina pectinata*

All ion concentrations were greater in the above- than in the below-ground parts in plants grown in the cutover bog (Two-way ANOVA; Df = 1; F = 9.07, 27.1, 99.7, 100.3, 47.03, 18.7 and 9.2, $P = 0.004$, <0.0001, 0.0001, <0.0001, <0.0001, <0.0001 and 0.004 for Na^+, K^+ (log(x)), Ca^{2+} (log(x)), Mg^{2+}, Mn (log(x)), Cl^- and SO_4^{2-}, respectively) (Appendix C.2), except for Fe(rank), where there was no difference between *S. pectinata* plant parts (Two-way ANOVA, Df = 1, F = 0.273, $P = 0.603$) (Appendix C.2). Among all the ions, only Fe was affected by the Location on the cambered field 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, $P = 0.003$) (Appendix C.2). Here also ion concentrations of the three locations could be pooled together (Figure 4.2).

Na^+, Ca^{2+}, Mg^{2+} and Cl^- in the above-ground parts and SO_4^{2-} in both above- and below-ground parts of plants grown in the bog were greater than those from the marsh (One-way ANOVA; Df = 3; F = 11.6, 9.92, 39.3, 19.1 and 19.7 for Na^+, Ca^{2+}(log(x)), Mg^{2+}(log(x)), Cl^- and SO_4^{2-}, respectively; P <0.0001 for all five ions) (Appendix C.5, Post-hoc in Figure 4.2). Mn and Fe were less in both above- and below-ground parts of plants in the bog than those in plants from the marsh. (Df = 3; F = 29.6 and 11.9 for Mn (log(x)) and Fe (rank), respectively; P <0.0001 for both ions) while K^+ (log(x)) remained about the same in plants from both sites (Df = 3, F = 9.92, $P < 0.0001$) (Appendix C.5; Post-hoc in Figure 4.2).

4.5.3. *Peat water*

Concentrations of total elements and anions generally increased between 26 June and 29 July, with substantial increases on the uppermost layer (0-5 cm) except for Fe (Figure 4.3).

Na and Cl^- concentrations in peat 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.

During the pre-thaw period (26 June), concentrations were significantly different among the three Locations on cambered field surface except for Fe and Mn (Table 4.1). The Up-areas had the highest and the Low-areas the lowest concentrations and the Mid-areas were either intermediate or were not different from either (P = 0.05, Appendix C.3). After the peat thawed (29 July), there was no significant difference between Locations in all ions except Mg (Figure 4.1) where the Up- and Mid-areas had higher concentrations compared to the Low-areas (P = 0.05, Appendix C.3).

Before the complete thaw of peat, concentrations of Na, Mg, Cl^- and SO_4^{2-}, increased with Depth of peat layer but decreased with Depth for Fe (P = 0.05, Appendix C.3, Figure 4.3). No difference between Depths was found for K, Ca and Mn (Table 4.1). By 29 July, all concentrations decreased with Depth with the greatest concentrations on the 0-5 cm peat surface (P = 0.05, Appendix C.3; Figure 4.3). There was no interaction between Location on the cambered field surface and Depth of peat layer at both times of measurement (Table 4.1). Overall, except for Fe, ion concentrations were greater at post-thaw than at pre-thaw period (Figure 4.3).

4.6. Discussion

J. balticus and *S. pectinata* transplanted into the seawater-contaminated bog were similar in their expression of salt tolerance with respect to the accumulation of Na^+ and Cl^- in their above-ground tissues at concentrations typical of halophytes (White and Broadley, 2001; Dionisio-Sese and Tobita, 1998). However, both species differed in the way salts were partitioned in the above- and below-ground tissues. For *J. balticus*, there

was greater accumulation of Na^+ in the below ground tissues, while Cl^- accumulation was not different between above- and below-ground tissues (Figure 4.1). Greater accumulation of Na^+ in the below-ground tissues suggests salt tolerance in *J. balticus* was through regulation or minimization of Na^+ transport to the shoots. In contrast, Na^+ and Cl^- accumulation in *S. pectinata* were greater in the above-ground tissues (Figure 4.2) which suggests another salt-tolerance mechanism; the excretion of salts through the leaves (Tester and Davenport, 2003). The amount of Na^+ accumulated in the above-ground tissues of both species (average 471 mmol kg^{-1} dry biomass) (Figure 4.1 and Figure 4.2), was about 17-36 % of that in salt-intolerant plants and slightly higher than in other salt-tolerant species (~400 mmol kg^{-1} dry biomass) adapted to wet soils (Dionisio-Sese and Tobita, 1998). Cl^- accumulation in the shoots (average 313 mmol kg^{-1}) was similar for both species and were below the maximum range (422 - 1408 mmol kg^{-1} dry biomass) of toxicity reported for other Cl^- -tolerant plants (White and Broadley, 2001).

Halophytes employ multiple but coordinated mechanisms to express salt tolerance because accumulation of salts in plant tissues has its limits. Some mechanisms necessary to supplement salt accumulation are: salt exclusion at the roots and thus limiting transport to the shoots and salt excretion from the leaves through salt hairs and salt glands (Tester and Davenport, 2003). The greater accumulation of Na^+ in the below-ground tissues of *J. balticus* suggests a salt-tolerance mechanism achieved through several processes that could include the exclusion of Na^+ from the root at the site of initial entry, the prevention of Na^+ entry into the xylem from the root cortex, retrieval of Na^+ from the xylem and accumulated in mature roots or recirculation of Na^+ back to the roots by the phloem (Tester & Davenport, 2003). The greater accumulation of Na^+ in the above-ground tissues

without the plant characteristic of succulence suggests salt excretion mechanism through the leaves. This requires a substantial loss of water via transpiration and is therefore restricted to plants in habitats where there is plenty of water (Tester and Davenport, 2003), which is the case for the *S. pectinata*.

The K^+:Na^+ ratio in *J. balticus* was 1.1 and 0.37 for the above- and below-ground parts, respectively. The K^+:Na^+ ratio in *S. pectinata* was 0.67 and 0.52 for above- and below-ground parts which are not as disparate as in *J. balticus*. Na^+ interferes with K^+ uptake (Pezeshki *et al*. 1987) and maintenance of high K^+ is essential for plant survival in saline conditions because it sustains the osmotic gradient for the uptake of water (osmoregulation) (Hu and Schmidalter, 2005; Moghaieb et al. 2004) and maintains metabolic plant processes activated by it (Bhandal and Malik, 1988). Maintenance high K^+:Na^+ ratio is more important for many species than the maintenance of low Na^+ concentration (Tester and Davenport, 2003). However, in some species Na^+ can replace K^+ in both these functions (Marschner, 1995) and this could perhaps be the case with *S. pectinata* having a lower K^+:Na^+ ratio in the above-ground parts compared with *J. balticus* as it has a better survival in the contaminated cutover bog then *J. balticus*.

Lower K^+ concentrations were found in plants of *J. balticus* from the marshes (Figure 4.1). Under the non-saline conditions of the *J. balticus* marsh, the need for increased K^+ accumulation for osmoregulation was not needed. On the contrary, K^+ concentration in *S. pectinata* from the salt marsh was higher and similar to those from the bog suggesting response to saline conditions indicated by the high concentrations of Na^+ and Cl^- in plant tissues (Figure 4.2).

Therefore, in terms of Na^+, K^+ and Cl^-, *J. balticus* and *S. pectinata* planted in the bog did express salinity tolerance with different combination of mechanisms.

Ca^{2+} and Mg^{2+} are essential plant nutrients and in saline conditions their function in plants can include osmoregulation, and maintenance of sufficient Ca^{2+} levels is known to increase salt tolerance (Marschner, 1995). In *J. balticus* grown in the bog Ca^{2+} and Na^+ concentrations exhibited an inverse pattern of accumulation – elevated Na^+ was associated with lower Ca^{2+}, and vice-versa (Figure 4.1). In contrast, Ca^{2+} and Na^+ concentrations in *S. pectinata* had a direct relationship (Figure 4.2). Furthermore, *S. pectinata* transplanted in the bog had higher Ca^{2+} concentrations in above-and below-ground tissues than those from the salt marsh while the opposite occurred in *J. balticus* (Figure 4.1 and Figure 4.2). This difference in Ca^{2+} accumulation of the two species when grown in their natural sites and transplanted to the bog reflects another difference in their salt tolerance mechanism. The decrease in Ca^{2+} concentration in *J. balticus* could be due to the effect of Na^+ which 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). This trend was not found with *S. pectinata* which increased its Ca^{2+} concentrations when grown in the bog, thus, *S. pectinata* can be considered to be able to express more salinity tolerance than *J. balticus* with respect to Ca^{2+}.

Fe concentration in plants grown in the bog remained lower than in plants from the marshes especially in *S. pectinata* and in the above-ground parts of *J. balticus* (Figure 4.1 and Figure 4.2). However, except for *S. pectinata* in Up-areas, Fe concentrations were above the critical deficiency in leaves, 0.89-2.7 mmol Fe kg^{-1} dry wt. (Marschner, 1995).

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.* submitted ms). Fe concentration in *S. pectinata* was highest at Low-areas which have the most reduced conditions (Montemayor *et al*. submitted ms 2) suggesting uptake of Fe(II) or Fe^{2+}. Fe has a high affinity for ligands and form complexes, *e.g*., with dissolved organic matter (organic anion) abundant in peat water (Rowell, 1994; Reeve *et al*. 1996) or Cl^-. In bogs, Fe(III) is greater than Fe(II) (Steinmann and Shotyk, 1997), whereas plants have preference for the latter (Marschner, 1995). However, graminaceous species (*e.g*. *S. pectinata*) secrete Fe^{3+}-chelators from their roots and the resulting ferric-chelate complexes, (Fe(III)) are then reabsorbed into the roots (Strategy I) (Schmidt, 1999). This mechanism which is employed under Fe-deficiency conditions in aerobic soils (Schmidt, 1999) did not seem to be very effective in *S. pectinata* grown in the cutover bog. Another factor could be that when Fe was readily available (pre-thaw period) the plants were just beginning to grow and at post-thaw when plants rapidly pick-up growth reduced conditions were of levels (> 120 mV) unsuitable for Fe reduction. Another explanation could be the greater Fe content in marsh (mineral) soils (Jones, 1971) compared to the cutover bog. The greater accumulation of Fe in the below-ground parts of *J. balticus* comparable to that in the marsh is difficult to explain because although the formation of iron plaques on the roots can restrict uptake of ions to the shoots, under the acidic conditions of the bog (pH ~3) these are not expected to be stable (Ernst, 1990). It could be that *J. balticus* employs Strategy II uptake, *i.e*., reductive detachment of Fe from its

ligand and subsequent transport of Fe^{2+} across the root plasma membrane but subsequent transport to the above-ground parts is slow due to some other factor.

Mn accumulation of *J. balticus* and *S. pectinata* grown in the bog was less than those from the marshes (Figure 4.1 and Figure 4.2) and there was more accumulation in the above-ground than in the below-ground parts. Although reduced conditions (E_h ~225 mV) in the cutover bog during the pre-thaw period were conducive to the formation of readily bioavailable Mn^{2+} ions (Lanbroek, 1990; Ponnamperuma, 1972) or Mn(II) salinity might have decreased the solubility of micronutrients (*e.g*. Fe and Mn) (Grattan and Grieve 1999). Mn^{2+} is competitive with Ca^{2+} and Mg^{2+} (Marschner, 1995) and it could be that the abundance of Mg in peat (Figure 3) and consequently in the above-ground parts of plants explain the decrease in Mn accumulation. There were opposing trends between the accumulation of Fe and Mn in the above- 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 bog were above critical deficiency in fully expanded leaves, 0.18-0.36 mmol Mn kg^{-1} dry wt. (Marschner, 1995).

SO_4^{2-} was in greater concentration in plants grown in the cutover bog than those from the marshes (Figure 4.1 and Figure 4.2). Salt marshes (source of *S. pectinata*) are usually low in SO_4^{2-} because reduced conditions favour the formation of sulphides (Giblin and Wider, 1992) and the marsh soil from where *J. balticus* was taken was also low in SO_4^{2-} compared to the cutover bog peat water (Montemayor *et al*. submitted ms 1). These explain the lower concentrations in plants from the marshes. Most studies focus on the common S-deficiency in plants (Marschner, 1995) or the effect of sulfate salinity (Na_2SO_4). There is a dearth of information as to the effect of chloride salinity or low pH on SO_4^{2-} plant uptake although in general, low pH has less effect on the uptake of anions (Marschner, 1995).

The long-term survival and growth of *J. balticus* which can only grow best in drier areas may be adversely affected by a deficiency in Ca^{2+}, and *S. pectinata* in drier areas, by deficiency in

Fe. However, the decrease in the uptake of cations cannot be fully attributed to salinity because the very low pH of the bog could have its own contributing effect (Marschner, 1995). In general, uptake rates of cations decrease with low pH in contrary to the uptake of anions which is less affected (Marschner, 1995). In a study by Gloser and Gloser (2000) they found that the uptake rates of Mg^{2+} and Ca^{2+} were decreased at pH 3.5-4.5. Future studies can isolate the individual effects of salinity and pH with experiments at both seawater- contaminated and uncontaminated areas.

4.7. Conclusions

The long-term survival of *J. balticus* and *S. pectinata* on the drier areas of the cutover bog which have the greatest salinity is constrained by a lower salinity tolerance in *J. balticus* due to its decreased Ca^{2+} accumulation, and Fe deficiency in *S. pectinata.* Despite the reduced conditions of the cutover bog, toxic accumulation levels of Fe and Mn did not occur which could due to the individual or combined influence of salt ions, organic acids, low pH, or increase in redox potentials after the thaw period. Thus, over the long-term *S. pectinata* which grows best at higher moisture contents required for its salt excretion mechanism and better uptake of Fe, may successfully establish in the Mid- and Low- areas. *J. balticus* which can only grow in the drier Up- and Mid-areas may establish in patches depending on some window of opportunity, where salinity levels may be slightly lower, or during times when there are slight but frequent rains, or by planting their sods deeper than 5 cm.

4.8. Acknowledgement

This study was made possible by the funding of the Natural Science and Engineering Research Council (NSERC) of Canada through discovery grants to J, S, Price and L. Rochefort, and a scholarship (2005-2006) to M. B. Montemayor; and Canadian peat moss producers. We are thankful for information materials supplied by the New Brunswick Department of Natural Resources through Jacques Thibault, information about the bog from Laurie Chaisson, and laboratory facilities made accessible for our use by the Sungro Horticulture Canada Ltd, Lameque Is., New Brunswick, the Ecology, Chemistry, and Chemical Engineering laboratories of the University of Waterloo, and the Environmental Studies laboratory of the Wilfrid Laurier University. Individuals who have given their time and effort in the field and laboratory work include: Cillian Breathnach, Gerry McIsaac, Miranda Lewis, Peter Whittington and Antonio Difebo, to whom we give our thanks.

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Table 4.1 Analysis of Variance (Two-way ANOVA) of ion concentrations (mmol L^{-1}) in peat water at different peat Depths and Locations on the cambered field surface, 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	**<.0001**	0.223	22.03	**<.0001**	.449	6.41	**.003**	0.741	16.7	**<.0001**
Error (a)	8												
Depth	3	1125	5.25	**0.003**	0.01	1.023	0.391	.088	1.26	.299	0.211	4.74	**0.006**
Location x Depth	6	27.5	0.128	.992	0.01	0.952	0.467	.006	.081	.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	.142	.868	0.019	2.85	0.068	0.003	0.489	0.616	0.121	4.18	**0.021**
Error (a)	8												
Depth	3	11883	5.82	**.002**	0.262	38.3	**<.0001**	0.185	30.3	**<.000l**	0.223	7.71	**<.0001**
Location x 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												

		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	**<.0001**	2524	11.4	**<.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 x 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	**<.0001**	1048	3.98	**0.013**
Location x 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

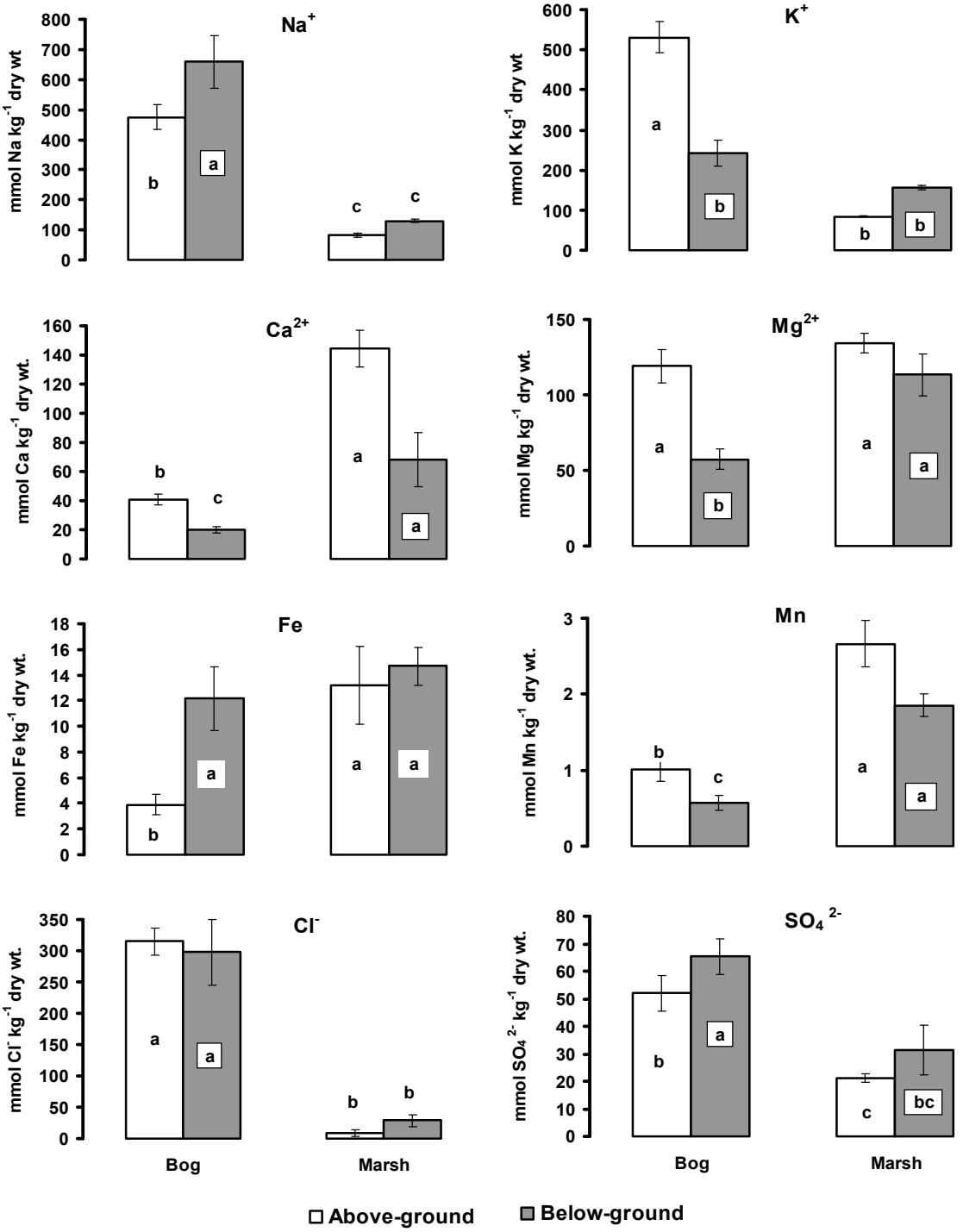

Figure 4.1 Mean ion concentrations±SE (mmol kg^{-1} dry weight) in the above- and below- ground parts of *J. balticus*, grown in the bog (study area) and collected from the marsh. Bog N = 16, Marsh N = 3. Means indicated by the same alphabet are not significantly different (*P*=0.05).

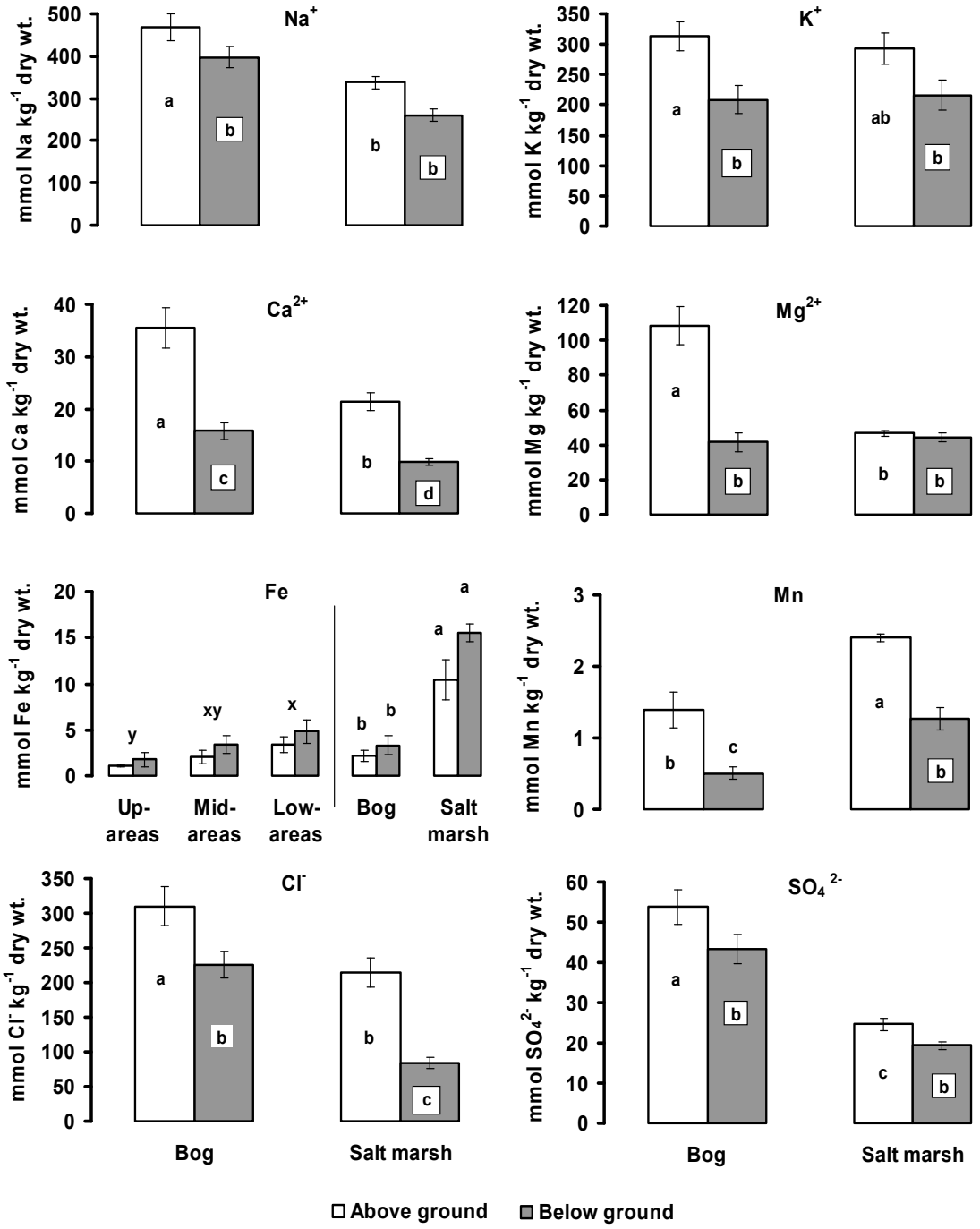

Figure 4.2 Mean ion concentrations±SE (mmol kg^{-1} dry weight) in the above- and below ground parts of *S. pectinata* grown in the bog (study area) and collected from the marsh. Bog N = 30, Marsh = 6. Means indicated by the same alphabet are not significantly different (*P*=0.05).

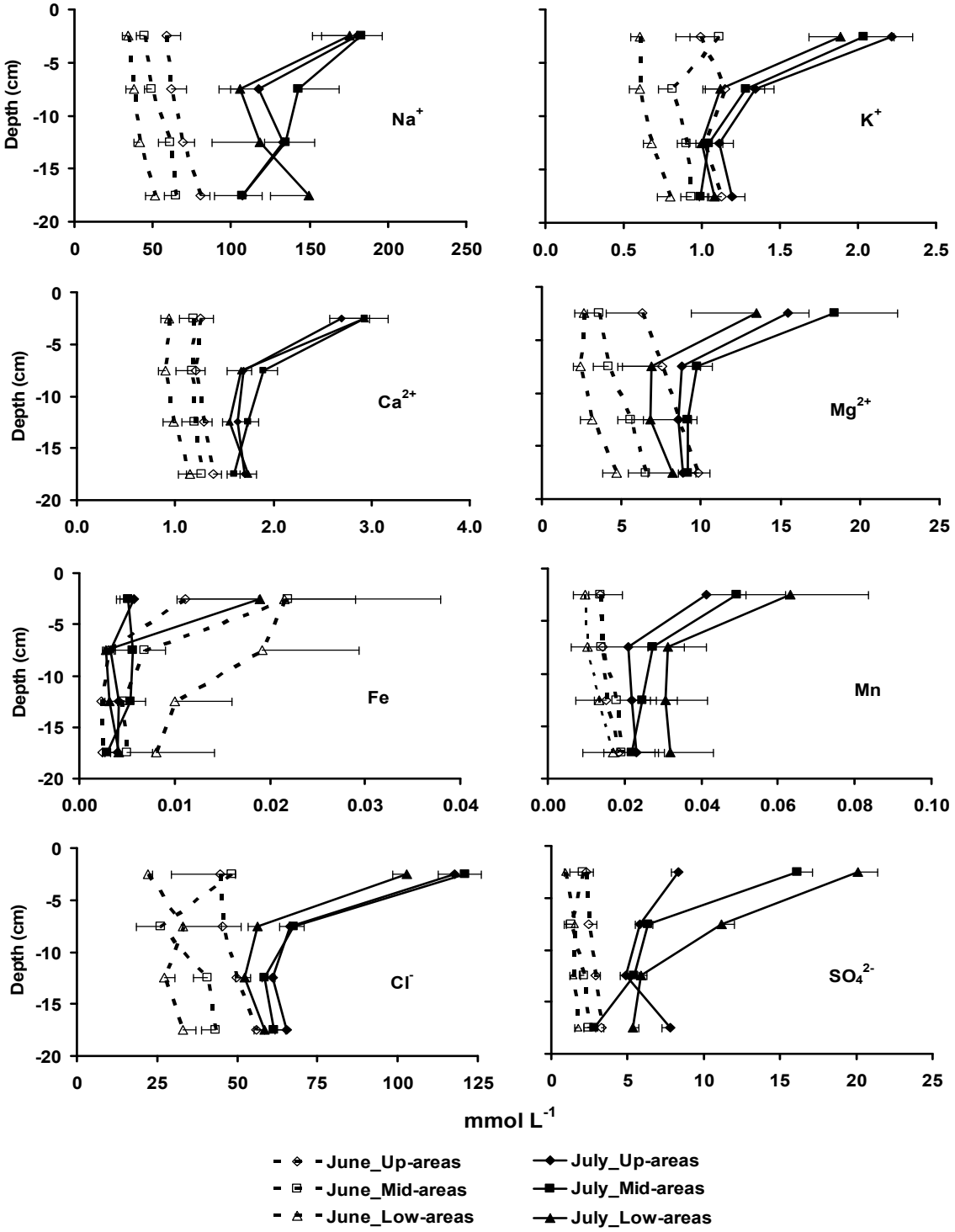

Figure 4.3 Major elements and anion concentrations±SE in peat water (mmol L^{-1}) on 26 June and 29 July at four Depths and three Locations. N = 5 for each point.

5. General Discussion, Conclusions, and Recommendations

Abiotic stresses to plant establishment in the cutover bog were spring flooding, continued saturated conditions, salinity, and acidity. The presence of a frozen ground layer and its thaw, the cambered surface of peat fields, and summer evaporation influenced the temporal and spatial variations of these stressors. In addition, a stressor influenced the other such that moisture content influenced salinity which in turn influenced acidity.

Spring flooding was caused by the frozen ground layer that did not allow vertical drainage. Plant responses to spring flooded conditions were evident in the high mortality of *J. balticus* in lower elevation areas near the ditches. This showed that *J. balticus* is not tolerant to spring flooding probably due to its insufficient carbohydrate storage or intolerance to metabolic by-products of carbohydrate utilization for respiration. Saturated and anaerobic conditions persisted even after thaw of the frozen layer due to the capillary rise of water from the watertable and the increase in dry bulk density of peat as its moisture content decreased over time. These conditions could be stressful to plants that survived and could divert plant energy towards expression of tolerance to waterlogged conditions from growth and reproduction. The moisture regime of an area suitable or unsuitable to a species could be described well by a watertable-moisture content relationship. *S. pectinata* with greater survival at all locations tested was found more tolerant to flooding than *J. balticus*.

Salinity underwent a vertical redistribution from an increase with depth at pre-thaw period to a decrease with depth at post-thaw period with maximum values at the 0-5 cm surface during this period. Spring flooding at pre-thaw period followed by high salinity on the surface during summer would preclude plant establishment through seeding and explains the current lack of spontaneous regeneration of vegetation despite the proximity of natural seed sources.

Transplanting of grown plants places roots below this highly saline surface and thus

avoidance is facilitated. Salinity was greatest at higher elevation areas towards the centerline of the cambered surface of peat field. Both species maintained basic halophyte characteristics which are the accumulation of Na^+ and Cl^- below toxic levels and the maintenance of K^+. There were differences in the levels of salt-tolerance even among halophytes; *S. pectinata* was more salt-tolerant than *J. balticus* because of its increased accumulation of Ca^{2+}. Greater Na^+ accumulation in the below-ground parts of *J. balticus* suggested that it managed Na^+ by limiting its transport to the more sensitive above-ground parts. In contrast, *S. pectinata* accumulated more Na^+ in the above-ground parts and its being a non-succulent, and its high survival in flooded low elevation areas suggested that it excreted salts through the leaves via transpiration. Increased salinity further intensified acidity and thus made stressful conditions worse for plants. Fe and Mn decreased in both species but reached critical Fe-deficiency level only in *S. pectinata* grown in drier areas indicating that this could be a long-term constraint to its growth on these areas.

Transplanting natural sods from the marsh to the seawater-contaminated bog provided some advantages despite the rapid transfer of salinity (high concentrations of Na^+ and Cl^-) through water movement from peat to the sods. The advantages primarily were the protection of plant roots from very acidic peat because basic cations Mg^{2+} and Ca^{2+} in sods did not allow rapid change in pH and a larger volume of sod delayed the transport of salts into its inner volume.

To successfully establish vegetation in the study area requires the delineation of different zones or microsites on the basis of surface moisture content-water table relationship for the growing season, and salinity. From a broader ecological perspective, the study area should be developed not in isolation from the immediate adjacent areas which are non-saline. The three moisture-based categories above are also present in non-saline areas. There are high elevation areas adjacent to the study area where the surface is beyond the influence of or is least influenced by the water table. In these areas the spring snowmelt drains away as surface runoff towards the low elevation wet areas (study area) while the frozen ground layer decreases in depth over time

but does not completely thaw. These areas are non-saline and have two categories – dry and very dry which can be described by surface moisture contents particularly those in July. Thus the study and its immediate adjacent areas are composed of roughly eight microsites which will support different species base on water requirements and tolerance to salinity. Moist and wet non-saline areas already have sparse spontaneous regeneration of vegetation. Preliminary trials in 2004 showed promising species for each microsite not covered in this study. Further away from the study and its adjacent area and separated by a road is another portion of the cutover bog which is non-saline. This area requires different categorization because the remnant peat layer is much thinner (~ 1 m or less) than the study area. Here the water table disappears soon after thaw in the high elevation areas. This area of the cutover bog requires a separate study.

Management of snowmelt flow is important in maintaining microsite delineation and vegetation establishment. Haphazard erosion and sedimentation caused by snowmelt flow can be minimized by connecting fields with snowmelt channels, some of them have already been formed by the snowmelt breaking through the crests of cambered fields. Thus, within the waterlogged area, the crests of the cambered surface would appear as islands on which vegetation would remain relatively protected from flooding, erosion and sedimentation.

S. pectinata should be planted now in the Mid- and Low- elevation areas. However, Zedler (2000) cautions against *en masse* planting in wetlands restoration or rehabilitation projects because it can attract wildlife before the plants are truly established. In natural succession, colonization occurs in patches, a pattern with its inherent ecological wisdom. Thus, revegetation of the entire cutover bog should be done in phases.

Future studies may consider:

1) the long-term survival and growth of plants with respect to nutritional deficiency and methods to address this
2) the effect of acidity without salinity on plant survival and growth

3) the effect of different established plant species on surface salinity after 5, 10, etc. years

4) continued search for other plant species tolerant to the harsh conditions of the bog to boost plant diversity

5) physical structures to manage snowmelt and

6) community participation in revegetation activities to cultivate ‘place awareness’ (Bluell, 1995) or the cultural aspect of ecosystem restoration or rehabilitation.

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Appendix A

Analysis of Variance (ANOVAs) of moisture content (θ) electrical conductivity (EC) and pH of peat according to Location on the cambered surface and Time of incubation (split-plot design). Slices Effect are shown once an interaction has been found significant. Bold values indicate significant difference at $P<0.05$.

Effect	Df	θ (log (x))		EC (log (x))		pH	
		F value	Pr > F	F value	Pr > F	F value	Pr > F
Block	3						
Location	1	25.38	**0.02**	13.65	**0.03**	3.62	0.15
Error (a)	3						
Time	5	8.37	**<0.0001**	20.22	**<0.0001**	15.3	**<0.0001**
Location x Time	5	4.61	**0.003**	2.57	**0.05**	0.21	0.96
Error (b)	30						
Total	47						
Tests of Effect Slices							
Location x Time							
Time within each location:							
Low-areas	5	5.93	**0.0006**	15.56	**<.0001**		
Up-areas	5	7.05	**0.0002**	7.22	**0.0002**		
Location within each time:							
Day 0	1	37.05	**<.0001**	16.38	**0.0003**		
Day 1	1	29.10	**<.0001**	8.76	**0.006**		
Day 3	1	17.81	**0.0002**	9.43	**0.005**		
Day 5	1	19.36	**0.0001**	12.78	**0.001**		
Day 10	1	16.26	**0.0003**	18.41	**0.0002**		
Day 20	1	12.38	**0.0014**	9	**0.005**		

Appendix B.1

Analysis of Variance (Two-way ANOVA) comparing ratio moisture content (θ), (log(x+1)) of peat by Location on the cambered field surface and Depth of peat from surface at different Times during the period of study - factorial design.

a)

		30 May			26 June			12 July			29 July			9 August		
Source	Df	Mean Square	F	*P*	Mean Square	F	*P*	Mean Square	F	*P*	Mean Square	F	*P*	Mean Square	F	*P*
Blocks	9															
Location	2	0.171	15.1	**0.0001**	0.231	31.9	**0.0001**	0.132	14.1	**0.0001**	0.044	7.58	**0.001**	0.108	23.3	**0.0001**
Error (a)	18															
Depth	3	0.005	0.465	0.708	0.006	0.806	0.493	0.006	0.655	0.581	0.006	1.069	0.365	0.018	3.84	**0.012**
Location x Depth	6	0.004	0.382	0.889	0.004	0.588	0.739	0.006	0.681	0.665	0.003	0.555	0.765	0.002	0.328	0.921
Error (b)	81															
Total	119															

b) Multiple comparisons (LSD). Means indicated by the same letter are not significantly different (*P*=0.05).

Factor	30 May	26 June	12 July	29 July	9 August
Location					
Up-areas	1.13 b	1.04 c	0.96 c	0.98 b	0.91 c
Mid-areas	1.23 a	1.09 b	1.02 b	0.98 b	0.94 b
Low-areas	1.25 a	1.19 a	1.08 a	1.04 a	1.01 a
Depth (cm)					
0-5					0.92 b
5-10					0.95 ab
10-15					0.96 a
15-20					0.98 a

Appendix B.2

Analysis of Variance (Two-way ANOVA) comparing electrical conductivity (dS m^{-1}) of peat by Location on the cambered field surface and Depth from the peat surface at different times during the study period – factorial design

a)

		30 May			26 June			12 July (Rank)			29 July (Rank)			9 August (Rank)		
Source	Df	Mean Square	F	*P*	Mean Square	F	*P*	Mean Square	F	*P*	Mean Square	F	P	Mean Square	F	*P*
Block	9															
Location	2	39.7	32	**<0.0001**	41.9	24.8	**<0.0001**	10373	11.3	**<0.0001**	5926	8.32	**<0.0001**	8119	17.3	**<0.0001**
Error (a)	18															
Depth	3	67.3	54.1	**<0.0001**	22.4	13.2	**<0.0001**	7687	8.4	**<0.0001**	17785	25.0	**<0.0001**	25055	53.2	**<0.0001**
Location x Depth	6	4.85	3.9	**0.001**	0.44	0.26	0.955	214.3	0.234	0.964	286.6	0.40	0.876	287.1	0.61	0.72
Error (b)	81															
Total	119															

b) Multiple comparisons (LSD). Means indicated by the same letter are not significantly different (*P*=0.05).

Factor	26 June	12 July (Rank)	29 July (Rank)	9 August (Rank)
Location				
Up-areas	5.6 a	77.0 a	72.1 a	64.0 a
Mid-areas	4.74 b	59.7 b	61.6 a	72.7 a
Low-areas	3.56 c	44.8 c	47.8 b	44.8 b
Depth (cm)				
0-5	3.89 c	83.4 a	96.4 a	102.5 a
5-10	4.02 c	47.8 b	54.9 b	56.7 b
10-15	4.88 b	51.3 b	45.1 b	42.2 c
15-20	5.75 a	59.5 b	45.7 b	40.7c

Appendix B.3

Analysis of variance (Two-way ANOVA) comparing redox potentials (mV) by Location and Time (Rank transformed)

(a)

Source	Df	Mean Square	F	*P*
Blocks	9			
Location	2	2492	6.55	**0.002**
Error (a)	18			
Time	3	31812	83.6	**<0.0001**
Location x Time	6	412.6	1.08	0.376
Error (b)	81			
Total	119			

(b) Multiple comparisons (LSD). Means indicated by the same letter are not significantly different (*P*=0.05)

Location		Time	
Up-areas	67.6 a	24 June	42.5 c
Mid-areas	61.9 a	8 July	24.1 d
Low-areas	52.0 b	22 July	82.6 b
		05 Aug	92.8 a

Appendix C.1

Analysis of Variance (Two-way ANOVA) comparing electrical conductivity (dS m^{-1}) of peat by Location on the cambered field surface and Depth from the peat surface at different times during the study period – factorial design

a)

		30 May			26 June			12 July (Rank)			29 July (Rank)			9 August (Rank)		
Source	Df	Mean Square	F	*P*	Mean Square	F	*P*	Mean Square	F	*P*	Mean Square	F	P	Mean Square	F	*P*
Block	9															
Location	2	39.7	32	**<0.0001**	41.9	24.8	**<0.0001**	10373	11.3	**<0.0001**	5926	8.32	**<0.0001**	8119	17.3	**<0.0001**
Error (a)	18															
Depth	3	67.3	54.1	**<0.0001**	22.4	13.2	**<0.0001**	7687	8.4	**<0.0001**	17785	25.0	**<0.0001**	25055	53.2	**<0.0001**
Location x Depth	6	4.85	3.9	**0.001**	0.44	0.26	0.955	214.3	0.234	0.964	286.6	0.40	0.876	287.1	0.61	0.72
Error (b)	81															
Total	119															

b) Multiple comparisons (LSD). Means indicated by the same letter are not significantly different (*P*=0.05).

Factor	26 June	12 July (Rank)	29 July (Rank)	9 August (Rank)
Location				
Up-areas	5.6 a	77.0 a	72.1 a	64.0 a
Mid-areas	4.74 b	59.7 b	61.6 a	72.7 a
Low-areas	3.56 c	44.8 c	47.8 b	44.8 b
Depth (cm)				
0-5	3.89 c	83.4 a	96.4 a	102.5 a
5-10	4.02 c	47.8 b	54.9 b	56.7 b
10-15	4.88 b	51.3 b	45.1 b	42.2 c
15-20	5.75 a	59.5 b	45.7 b	40.7c

Appendix C.2

Analysis of Variance (Two-way ANOVA) of ion concentrations (mmol g^{-1}) in *S. pectinata* according to Plant parts and the three Locations on the cambered field surface.

Source	Df	Na			K			Ca			Mg		
		MS	F	*P*	MS	F	*P*	MS	F	*P*	MS	F	*P*
						log(x)			log(x)			log(x)	
Block	9												
Location	2	0.024	2.88	0.065	0.028	1.42	0.251	0.022	1.15	0.325	0.049	1.84	0.169
Error (a)	18												
Plant part	1	0.075	9.07	**0.004**	0.538	27.1	**0.0001**	1.91	99.7	**<0.0001**	2.65	100.3	**<0.0001**
Location x Plant part	2	0.009	1.04	0.359	0.001	0.042	0.959	0.083	4.35	0.018	0.036	1.37	0.263
Error (b)	27												
Total	59												
			Fe			**Mn**			**Cl^-**			**SO_4^{2-}**	
			Rank			log(x)							
Block	9												
Location	2	1727	6.49	**0.003**	0.004	0.067	0.935	0.002	0.457	0.636	0.019	1.58	0.216
Error (a)	18												
Plant part	1	72.6	0.273	0.603	2.68	47.03	**<0.0001**	0.099	18.7	**<0.0001**	0.113	9.2	**0.004**
Location x Plant part	2	55.05	0.207	0.814	0.036	0.625	0.539	0.002	0.33	0.72	0.009	0.706	0.499
Error (b)	27												
Total	59												

Appendix C.3

Multiple comparison of means (LSD) of ions concentrations in different peat Depths on 26 June and 29 July, and at different Locations on the cambered field surface on 26 June. Transformations either log(x) or rank are indicated.

	Na	K	Ca	Mg	Fe	Mn	Cl^-	SO_4^{2-}
26 June		log(x)	log(x)	log(x)	Rank	log(x)	Rank	Rank
Location								
Up-areas	67.7a	0.023 a	1.29a	0.845 a			42.7 a	41.4 a
Mid-areas	54.9b	-0.045b	1.21a	0.647 b			30.4 b	29.9 b
Low-areas	41.4c	-0.184c	0.997b	0.46 c			16.8 c	18.6 c
Depth (cm)								
0-5	46.1 b			0.538 b	43.3 a		27.4 b	24.4 b
5-10	49.6 ab			0.575 b	33.2 ab		22.4 b	22.9 b
10-15	57.4 a			0.69 ab	24.1 ab		33.3 ab	34.2 ab
15-20	65.5 a			0.8 a	21.4 b		36.8 a	38.4 a
29 July		log(x)	log(x)	log(x)	log(x)	log(x)	Rank	Rank
Location								
Up-areas				0.99 a				
Mid-areas				1.03 a				
Low-areas				0.879 b				
Depth (cm)								
0-5	179.8a	0.303 a	0.445 a	1.15 a	-2.19 a	-1.39 a	48.0 a	41.9 a
5-10	121.7b	0.088 b	0.24 b	0.898 b	-2.47 b	-1.67 b	26.8 b	23.9 b
10-15	128.7b	0.016 c	0.212 b	0.896 b	-2.42 b	-1.71 b	20.0 b	24.2 b
15-20	121.3b	0.032bc	0.22 b	0.923 b	-2.48 b	-1.7 b	24.5 b	29.1 b

Means followed by the same letter are not significantly different ($P = 0.05$).

Appendix C.4

Analysis of Variance (One-way ANOVA) of ion concentrations (mmol g^{-1} dry wt.) in *J. balticus* Plant parts grown in the bog and collected from the marsh (4 categories)

Source	Df	MS	F	*P*	MS	F	*P*	Df	MS	F	*P*	Df	MS	F	*P*
		Na			**K (Rank)**				**Ca (Rank)**				**Mg**		
Treatment	3	0.452	13.8	**<0.0001**	1150.7	35.3	**<0.0001**		1022.7	28.3	**<0.0001**		0.012	17.6	**<0.0001**
Error	34														
Total	37														
		Fe (Rank)			**Mn** (log(x))				**Cl^-**				**SO_4^{2}**		
Treatment	3	842	14.3	**<.0001**	0.638	17.1	**<0.0001**	3	0.116	19.9	**<0.0001**	3	0.002	7.76	**<0.0001**
Error	34							28				32			
Total	37							31*				35*			

*some samples missed by Chem. Engg. lab.

Appendix C.5

Analysis of Variance (One-way ANOVA) of ion concentrations (mmol g^{-1} dry wt.) in *S. pectinata* Plant parts grown in the bog and collected from the marsh (4 categories)

Source	Df	MS	F	*P*	MS	F	*P*	Df	MS	F	*P*	Df	MS	F	*P*
		Na			**K (log(x))**				**Ca (log(x))**				**Mg (log(x))**		
Treatment	3	0.091	11.6	**<0.0001**	0.199	9.92	**<0.0001**		0.877	44.7	**<0.0001**		0.951	39.3	**<0.0001**
Error	68														
Total	71														
		Fe (Rank)			**Mn** (log(x))				**Cl**$^-$				**SO_4^{2}**		
Treatment	3	3572.7	11.9	**<0.0001**	1.44	29.6	**<0.0001**	3	0.087	19.1	**<0.0001**	3	0.003	19.7	**<0.0001**
Error	68							62				62			
Total	71							65*				65*			

*some samples missed by Chem. Engg. lab.