

Growth of aspen and white spruce on naturally saline sites in northern Alberta: Implications for development of boreal forest vegetation on reclaimed saline soils

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²Current address: Bulkley Valley Research Centre, Box 4274, Smithers, British Columbia V0J 2N0; and

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Lilles, E. B., Purdy, B. G., Macdonald, S. E. and Chang, S. X. 2012. **Growth of aspen and white spruce on naturally saline sites in northern Alberta: Implications for development of boreal forest vegetation on reclaimed saline soils.** *Can. J. Soil Sci.* **92**: 213–227. We examined height and basal area growth over time for trembling aspen and white spruce in plots along a salinity gradient at six naturally saline sites in northern Alberta, as a benchmark for forest productivity on reclaimed saline sites. We measured root distributions and analyzed foliage for ions, nutrients and carbon and nitrogen stable isotope ratios. Both species grew on soil conditions previously considered unsuitable for forest vegetation [pH >8.5; electrical conductivity > 10 dS m⁻¹, sodium adsorption ratio > 13 at depth (50–100 cm)] yet there was little evidence of nutritional toxicities or deficiencies. Aspen basal area growth decreased 50% as salinity increased, but aspen was commercially productive (site index = 22) on soils with electrical conductivity of 7.8 dS m⁻¹ at 50–100 cm depth. Growth of white spruce seemed to be unaffected by salinity level differences, but 78% of white spruce site indexes were less than 13 and would be considered non-productive. Both species showed growth declines over time, compared with non-saline reference growth curves, and rooted primarily in the forest floor and top 20 cm of soil. This suggests that rooting limitations may constrain longer-term productivity of forests established on sites with salinity at depth.

Key words: Salinity gradient, salt tolerance, forest growth, stem analysis, boreal forest, reclamation

Lilles, E. B., Purdy, B. G., Macdonald, S. E. et Chang, S. X. 2012. **Croissance du tremble et de l'épinette blanche sur des sites salins naturels dans le nord de l'Alberta : implications pour la croissance de la forêt boréale sur des sols salins restaurés.** *Can. J. Soil Sci.* **92**: 213–227. Les auteurs ont examiné la hauteur et la croissance de la surface terrière de trembles et d'épinettes blanches poussant sur des parcelles situées le long d'un gradient de salinité, à six sites naturellement salinisés du nord de l'Alberta, en vue d'établir des points de comparaison pour la productivité forestière sur les sites salins restaurés. Ils ont pour cela mesuré la distribution des racines et analysé le feuillage afin d'établir la concentration d'ions et d'éléments nutritifs ainsi que le ratio des isotopes stables de carbone et d'azote. Les deux essences croissaient sur des sols qu'on pensait jusque là impropres à la végétation forestière (pH > 8,5; conductivité électrique > 10 dS par mètre, ratio d'adsorption du sodium > 13 à une profondeur de 50 à 100 cm). Pourtant, les arbres présentaient peu d'indices de toxicité ou de carence nutritives. La croissance de la surface terrière du tremble diminue de 50 % avec la hausse de la salinité, mais l'espèce demeure commercialement productive (indice du site = 22) sur les sols dont la conductivité électrique est de 7,8 dS par mètre, à une profondeur de 50 à 100 cm. La croissance de l'épinette blanche ne semble pas touchée par la variation du degré de salinité, mais dans 78 % des cas, les sites où poussait cette espèce avait un indice inférieur à 13. Ils seraient donc jugés improductifs. Les deux essences voient leur croissance faiblir dans le temps, comparativement aux courbes de référence obtenues sur les sites non salinisés; leur enracinement se situe principalement au niveau du tapis forestier et des 20 premiers centimètres de sol. On en déduit que le plus faible enracinement pourrait limiter la productivité à long terme des forêts établies sur des sites dont le sol est salinisé en profondeur.

Mots clés: Gradient de salinité, tolérance au sel, croissance forestière, analyse des souches, forêt boréale, restauration

Saline soils are rare in the Canadian boreal forest, but they do exist in regional or local areas where, for example, ground water passes through marine sedimentary materials and then surfaces (Purdy et al. 2005). These areas host plant communities dominated by herbs, graminoids and shrubs with varying levels of

salt tolerance. Although most boreal forest species are considered salt-sensitive, boreal mixedwood forest communities do exist on saline sites. Specifically, they grow on saline areas where electrical conductivity in the topsoil is below 4 dS m⁻¹, soil water is available throughout the growing season and nutrient availability is high (Lilles et al. 2010). These forest stands growing

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Abbreviations: BAI, basal area increment; BH age, age at breast height; SAR, sodium adsorption ratio

on soils with salinity at depth are of great interest to reclamation research because industrial activities, including oil sands mining and other oil and gas development, can create substantial areas of salt-affected soils (Webster and Innes 1981; Barbour et al. 2007). The challenge in meeting regulatory requirements is to rehabilitate salt-affected sites to support boreal forest vegetation. Information about vegetation development is needed to guide reclamation programs today, but it would take 50–100 yr to experimentally evaluate forest growth on reclaimed saline sites. Naturally saline forested sites can serve as a benchmark for understanding boreal vegetation response to saline soils and for predicting productivity of forests in natural and reclaimed saline sites.

White spruce [*Picea glauca* (Moench) Voss] and aspen (*Populus tremuloides* Michx.) are the dominant tree species on mesic sites in the boreal mixedwood forest region of western Canada. They are sought for lumber and pulp, and they provide habitat for a variety of wildlife, while influencing the understory plant community (Mills and Macdonald 2005; Macdonald and Fenniak 2007) through effects on light availability (Constable and Lieffers 1996), forest microclimate and litter input (Hannam et al. 2004). For future fiber production, and to meet government regulations and societal expectations, landscapes reclaimed after oil sands mining are required to support forest productivity equivalent to what existed prior to mining (Alberta Environment 2010). There is concern regarding prospects for aspen and white spruce productivity on reclaimed saline soils because long-lived woody species can be quite sensitive to salinity (Maas 1986; Allen et al. 1994). Furthermore, some oil sands mining processes result in increased Na^+ and Cl^- and among the common salts NaCl is the most harmful to boreal species (e.g., Nguyen et al. 2006).

Survival and growth of boreal species generally decrease with increasing salinity (McKenzie et al. 1993; Maynard et al. 1996) and neither white spruce nor aspen is known to be exceptionally salt tolerant. In one study, every aspen seedling growing in a 2 dS m^{-1} hydroponic NaCl salinity treatment died within 1 mo (Khasa et al. 2002), and in other studies white spruce seedlings had reduced growth at electrical conductivities as low as 0.5 dS m^{-1} with a Na_2CO_3 solution and 3.0 dS m^{-1} with fertilizer salts (Phillion and Bunting 1983; Maynard et al. 1996). However, there is some evidence of salt tolerance in these species. For example, greenhouse-grown white spruce seedlings survived in 2 dS m^{-1} , 4 dS m^{-1} , and 6 dS m^{-1} hydroponic NaCl salinity treatments better than red alder (*Alnus rubra* Bong.) and lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) (Khasa et al. 2002). White spruce survived (albeit with leaf damage and water stress) for 4 wk in hydroponic solutions with electrical conductivities as high as 6.55 dS m^{-1} (Renault et al. 1998). Aspen tolerates drought (Abrams 1988) and thus

may be able to survive water deficit caused by salinity. Aspen may have an advantage over evergreen species in saline soils because it is deciduous, and if ions accumulate to harmful levels in leaves they can be shed and regrown (Renault et al. 1999). The degree to which these species can withstand salinity-caused water deficit, ion toxicity or nutritional imbalance over long time periods in the field, however, is unknown.

The saline soil environment encountered in natural soils is much different than in greenhouse pot experiments because in the field salinity increases with depth and may fluctuate with hydrologic conditions over the growing season or across years (Lieffers and Shay 1983; Close 2007). During reclamation of saline soils, non-saline peat and peat mineral mixes are placed on top of saline-sodic overburden materials creating an environment where the highest salinity is encountered at depth and salinity may fluctuate over time (Kessler et al. 2010). In both situations, assessing tree root response to variation in salinity with depth and assessing tree growth response over many decades are critical for understanding how forests develop on soils with salinity at depth.

The goal of this study was to improve our understanding of potential forest productivity on saline soils by examining tree growth in mature stands of white spruce and aspen growing naturally in different levels of salinity. The salinity gradients and soil characteristics at these sites were described by Lilles et al. (2010), and here we build upon that foundation by providing insight into the long-term effects of salinity on white spruce and aspen growth, root distribution, nutritional status, ion toxicity and stable isotope ratios. We hypothesized that productivity of aspen and white spruce would decrease with increases in salinity along natural salinity gradients and that foliar chemistry or foliar stable isotope ratios would provide insight into response mechanisms to salinity. We further hypothesized that shallow rooting depth of aspen and white spruce would facilitate avoidance of salinity on sites with saline soils at depth. We interpret tree responses to salinity in natural systems to support decisions regarding rehabilitation of salt-affected sites which target boreal forest vegetation for reclamation after oil sands development.

MATERIALS AND METHODS

Site Description

This study was conducted at six naturally saline sites in northern Alberta, Canada, with forests dominated by white spruce (Benchmark, Clearwater, Salt Plains) or aspen (Child Lake, Salt Pan Lake, Zama Marsh) and understory plant communities typical of the boreal forest region (Table 1). At each site there was a distinct boundary between forest vegetation and vegetation dominated by grasses and shrubs. This boundary corresponded with a decrease in topsoil electrical conductivity from >4 dS m^{-1} (grass and shrub vegetation)

Table 1. Summary information for the high (H), medium (M), and low (L) salinity plots at the six study sites (modified from Lilles et al. 2010)

Site	N Lat./W Long.	Relative elevation (m) ^z	Salinity level	Lower subsurface soil EC ^y (dS m ⁻¹)	Lower subsurface soil SAR ^y	Soil subgroup ^x	Plant community type ^w	Soil water regime ^v	Soil nutrient regime ^v
Benchmark	59°47'36.73"	0.4	H	10.1	25.4	Gleyed Gray Solodized Solonetz	Sw/feather moss	Subhygric	Med ^v -rich
Clearwater	56°44'58.31"	0.8	M	5.2	41.5	Gray Solodized Solonetz ^y	Sw/feather moss	Mesic	Med-rich
		3.4	L	3.7	34.5	Gray Solod	Sw/feather moss	Mesic	Med-rich
		1.7	H	18.7	70.3	Lignic Folisol	Sw-Sb/labrador tea/horsetail	Subhygric	Med-rich
Salt Plains	59°58'02.06"	2.4	M	4.2	22.8	Lignic Folisol	Sw-Sb/labrador tea/horsetail	Subhygric	Med-rich
		3.0	L	2.2	15.8	Lignic Folisol	Sw/feather moss	Subhygric	Med-rich
		1.0	H	22.8	63.2	Humic Regosol	Sw/buffalo-berry	Mesic	Rich
Child Lake	58°25'31.73"	1.1	M	5.1	35.1	Humic Regosol	Sw/buffalo-berry	Subhygric	Rich
		1.0	L	3.2	22.9	Humic Regosol	Sw/feather moss	Subhygric	Rich
		0.6	H	15.0	21.8	Dark Gray Solodized Solonetz	Aw/saskatoon-pin cherry	Mesic	Rich
Salt Pan Lake	59°49'15.03"	0.3	M	9.7	16.4	Gleyed Gray Solodized Solonetz	Aw/buffalo-berry	Mesic	Rich
		0.2	L	7.8	9.1	Gleyed Gray Luvisol	Aw/buffalo-berry	Mesic	Rich
		1.3	H	3.5	12.5	Eluviated Eutric Brunisol	Aw/saskatoon-pin cherry	Mesic	Med-rich
Zama Marsh	59°06'09.1"	1.6	M	2.1	8.8	Eluviated Eutric Brunisol	Aw/buffalo-berry	Submesic	Med-rich
		1.3	L	1.7	10.9	Eluviated Eutric Brunisol	Aw/buffalo-berry	Submesic	Med
		0.1	H	8.8	16.7	Gleyed Gray Solodized Solonetz	Aw/saskatoon-pin cherry	Subhygric	Rich
	118°03'42.4"	0.0	M	8.2	12.7	Gleyed Gray Solodized Solonetz	Aw-Sw/buffalo-berry	Subhygric	Rich
		-0.4	L	5.4	9.5	Solonchic Luvisol	Aw-Sw/buffalo-berry	Subhygric	Rich

^zRelative elevation measured in m relative to the nearest open water in a saline spring, wetland or river.

^yEC, electrical conductivity; SAR, sodium adsorption ratio, Med, medium.

^xSee Soil Classification Working Group (1998).

^wSee Beckingham and Archibald (1996); Sw—white spruce, Aw—white spruce, Sb—black spruce.

^vSee Leskiw (2006).

to $<4 \text{ dS m}^{-1}$ (forest vegetation; Lilles et al. 2010). At each site, sampling was conducted in three $5 \times 20 \text{ m}^2$ plots located along a transect situated perpendicular to the forest edge and extending from the boundary further into the forest interior. Based on preliminary investigation, plots were located to represent the variation along the gradient of salinity at each site. Soil sampling and analysis revealed that salinity consistently increased with depth and decreased with distance from the forest edge even though absolute electrical conductivity measurements and other soil characteristics varied greatly among sites (Lilles et al. 2010). For example, Regosolic, Solonchic, Luvisolic, Brunisolic, Gleysolic and Organic soil orders (Soil Classification Working Group 1998) were identified at the six sites (Table 1). The salinity at 50–100 cm soil depth could be as high as 23 dS m^{-1} for white spruce or 15 dS m^{-1} for aspen and still support forest vegetation; each site had some soil with a sodium adsorption ratio (SAR) >12 , and some sites had SAR >20 (Table 1; Lilles et al. 2010). Sodium chloride salts dominated at every site except Zama Marsh where sodium chloride and sodium sulfate salts co-dominated (Close 2007).

To compare tree growth rates and foliar parameters within and among sites with very different absolute values of salinity, we characterized salinity of the three plots at each site as: high (closest to the forest edge), medium, and low (farthest from the forest edge). High, medium, and low levels of salinity were determined with an EM-38 (Geonics Ltd., Mississauga, ON) in the field and later confirmed by results of soil measurements (Lilles et al. 2010).

Soil Sampling and Analysis

Soils were sampled in 2005 or 2006 depending on the site. In each of the three plots at each site we evaluated three soil profiles: one in the center of the plot, and one about 5 m to either side of it. For each horizon we measured depth, recorded morphological features and collected soil samples. The three profiles per plot were considered subsamples of our experimental unit (the plot); thus we bulked samples into one per horizon per plot. Horizon depths and bulk densities by horizon were then used for converting soil data by horizon to soil data by fixed depth layers. We wanted to examine results by fixed depth because we were interested in soil properties that plant roots would encounter at different depths, irrespective of which horizons existed at that depth. The type of horizon and horizon thicknesses varied among sites and plots, making it impossible to compare among plot locations or study sites using data by horizon. The depths we chose were those typically used in reclamation practices: (1) the forest floor or LFH (composed of litter, partially decomposed litter material, and highly decomposed and humified humus horizons that lie above the mineral soil surface), (2) surface soil (0–20 cm), (3) upper subsurface soil (20–50 cm), and (4) lower subsurface soil (50–100 cm). The organic soils

at Clearwater were compared with mineral soils at the other sites by considering the forest floor to be the L and F horizons while other organic horizons began at 0-cm depths.

Samples were air dried (water contents of air-dried soil samples were measured to express properties on an oven-dry basis) and ground to pass through a 2-mm sieve. Electrical conductivity on all samples was measured with an Accumet AP 65 portable conductivity meter (Fisher Scientific, Ottawa, ON) in a saturation paste extract (Sparks 1996) without adding $(\text{NaPO}_3)_6$. Soluble Na^+ , Ca^{2+} and Mg^{2+} concentrations (in mg L^{-1}) were measured with a SpectrAA 880 (Varian Inc., Mississauga, ON) atomic absorption spectrometer on the saturation extracts and used to calculate the SAR as per Carter (1993). Soluble Cl^- and SO_4^{2-} concentrations were measured on the saturation extracts with a Dionex Corp. DX600 (Sunnydale, CA) ion chromatograph.

Tree Sampling

In each plot, four trees were selected for sampling using a stratified random sampling method. Trees were stratified by canopy dominance and health; candidate trees were dominant canopy trees not overtopped by a neighboring stem, free from disease, damage, or rot, and safe to fell. Two trees that met these criteria were randomly selected to be felled for stem analysis and two additional trees were cored twice with an increment borer at 1.3 m in height for tree ring analysis. Salt Plains was in a Special Preservation Zone of a National Park, so we were unable to fell trees. Instead we cored four trees per plot. In a few instances, to find a tree that met our criteria we had to go just outside the $5 \text{ m} \times 20 \text{ m}$ plot, but with the same salinity level as the plot concerned.

During tree felling, stems were cut between 0.3 m (stump height) and 1.3 m (breast height). After felling, stem length was measured and stem cross-section samples were cut and collected at 0.3, 1.3, 2.3 and 3.3 m and every meter thereafter to the top of the tree. Stem cross-sections were oven dried at 65°C and the diameter at 1.3 m was re-measured to adjust future calculations for shrinkage. Tree cores were air dried, mounted onto wooden blocks, and sanded with progressively finer grades of sandpaper, ending with 600 grit, so tree rings could be seen clearly. A dissecting microscope was used to view tree rings and cross date all samples within a site (Yamaguchi 1991). Each sample was dated along two radii for correct ring counting.

Ring Width Measurements

Ring widths were measured on the four breast height samples from each salinity level at each site. A Velmex microscope-sliding stage system (Velmex Inc., Bloomfield, NY) was used to measure tree ring widths. The inner and outer radius of each ring was measured for two average radii per sample to increase the accuracy

of ring width measurement. These were used to calculate the area of wood in each ring, or the basal area increment (BAI) using Eq. 1:

$$\text{BAI} = \pi(R_n^2 - R_{n-1}^2) \quad (1)$$

where R is the tree radius and n is the year (Kolb and McCormick 1993; Hogg et al. 2002).

Tree ring widths decrease with tree age because the circumference increases; calculating the BAI is one way to account for that change, enabling comparison of growth rates in trees of different ages. BAI is expressed as area before drying. It took 5–10 yr of growth beyond breast height age for the BAI of juvenile trees to reach the average BAI level of older trees. Thus, to compare trees at all sites, the 1990s was the only decade with a full sample set for aspen (some high-salinity trees at Child Lake only reached breast height in 1984). There was not a full sample set for the 1990s for white spruce, and for the 1980s and 1970s, there were many years with poor growth, so the 1960s were used as the best decade for comparisons among white spruce trees of differing ages. The 1960s included years of poor, medium and good growth similar to the 1990s. The annual BAI values for each tree were averaged across the 10 yr from 1990 to 1999 inclusive for aspen and from 1960 to 1969 for white spruce so that a single (mean) value of basal area growth per year for each tree was used in subsequent analyses.

Basal area growth data were analyzed with ANOVA using the model in Eq. 2:

$$Y_{ijk} = \mu + \text{Site}_i + \text{Treatment}_j + \text{Treatment} \times \text{Site}_{ij} + e_{k(ij)} \quad (2)$$

where Y_{ijk} is the value for the k th tree in the i th site of the j th salinity level, which is equal to the overall mean (μ), plus the effect of the i th site (e.g., Child Lake, Salt Pan Lake or Zama Marsh for aspen), the j th treatment (high, medium or low salinity), the interaction of the i th site and the j th treatment, and the random error among trees within a treatment at a site ($e_{k(ij)}$). Because we were interested in examining differences among sites and among salinity levels at each site, both Site and Treatment were considered fixed effects and the general linear model procedure in the SAS software package (v 9.1; SAS Institute Inc., Cary, NC) was appropriate to analyze the data. Aspen basal area increment data were square-root transformed before analysis to meet homogeneity of variance assumptions of ANOVA, but spruce basal area increment variances remained heterogeneous even after square-root (and logarithmic) transformations, so the original data were analyzed with the SAS mixed procedure, and the heterogeneous variances were compensated for in the model (SAS Institute, Inc.). In both cases untransformed data are presented in figures and tables. When there were significant effects in the model at $\alpha=0.05$, least squared means were compared with a comparison-wise $\alpha=0.05$.

Stem Analysis

After cross dating, tree age and height were recorded for each stem cross-section. The age at breast height (BH age) was used because of difficulty in obtaining absolute age in the boreal forest (Gutsell and Johnson 2002; Peters et al. 2002). To account for the problem in stem analysis of underestimating actual tree height at a given age, we adjusted the data with Carmean's (1972) algorithm for each tree separately (Dyer and Bailey 1987; Chen et al. 2002). These data were plotted to create age-height growth curves for each tree, which were then compared visually to provincial average growth curves for white spruce and aspen in Alberta (Huang et al. 1994), except for white spruce at Benchmark and Salt Plains which were compared with growth curves for the Northern Mixedwood natural region, as recommended by Wang and Huang (2000). Site index [height (m) at 50 yr BH age] was calculated from growth curves using the equation for a straight line between the age-height points on either side of 50 yr old; the mean site index for the two trees in each plot is reported. A SAS program published by Huang et al. (1994) with parameters from Wang and Huang (2000) for the Northern Mixedwood natural region was used to estimate the site index for trees at Salt Plains. Total height and BH age were inputs into the model; the mean site index for four trees per plot is reported. When tree cores were taken through or next to the pith, allowing accurate aging of additional trees, these age-height points were added to the tree height growth data. Site index could not be calculated for the high salinity level at Child Lake because those trees were <50 yr old when felled. No statistical analysis was performed on stem analysis data because of the small sample size (two trees per salinity level per site).

Foliage Sampling and Analysis

Foliar samples were collected from four trees per salinity level (=plot) per site in summer 2006 except at Salt Plains where we were only able to obtain foliage from two trees at high and medium salinity levels and three trees at the low salinity level. Aspen trees at Zama Marsh were defoliated by forest tent caterpillar in early summer, so leaves were collected in August after regrowth. For felled trees at Zama Marsh, Benchmark and Clearwater, foliage was collected from the top third of the crown. For all other trees, sun-lit leaves were collected with a pruning pole from as high as possible in the crown, or by shaking the stem hard enough with a rope attached to the upper main stem of the tree, for small twigs and branches (with leaves attached) to fall off. Leaves were air dried and 100 were counted for each tree to determine unit leaf weight. When <100 leaves were collected, we counted all leaves collected from the tree. All leaves were oven dried at 65°C, weighed, ground with a Wiley mill and then sub-sampled and finely ground with an electric ball grinder.

Foliar concentrations of sodium (Na), the macronutrients phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg) and sulfur (S), and the micronutrients manganese (Mn), iron (Fe), aluminum (Al), zinc (Zn) and copper (Cu) were determined by the Analytical Services Laboratory at the Northern Forestry Centre (Canadian Forest Service) in Edmonton, AB. Approximately 500 mg of leaf material per sample was digested with a CEM MARS Xpress microwave digestion system (Matthews, NC) and then measured on a Spectro Cirrus Inductively Coupled Plasma Atomic Emission Spectrophotometer (Kleve, Germany). Extractable foliar Cl concentration was determined by a DI 300 ion chromatography (Dionex Corporation, Sunnyvale, CA) on filtered water samples obtained by combining two successive 1-h extractions of 0.05 g samples with hot water (Franklin and Zwiazek 2004). Foliar C and N concentrations were determined by the Dumas combustion method on a Carlo Erba (now CE Elantech Inc., Lakewood, NJ) NA1500 Elemental Analyzer (Carter 1993) on approximately 6 mg of samples. All foliar elemental concentrations were expressed on an oven-dry weight basis.

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were determined using a Finnigan Delta Plus Advantage isotopic ratio mass spectrometer (Thermoquest, Bremen, Germany) with a ConFlo III universal interface. A Costech ECS 4010 elemental analyzer (Valencia, CA) was used as a peripheral to combust the samples (approximately 6 mg each) according to the Dumas method (Carter 1993). Stable isotope composition is expressed as a ratio relative to a standard, which is Vienna PeeDee Belemnite for carbon and atmospheric N_2 for nitrogen, according to Eq. 3:

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N} (\%) = 1000 \times (R_{\text{sample}}/R_{\text{standard}} - 1) \quad (3)$$

where R is the abundance ratio of the heavier isotope to the lighter isotope (Dawson et al. 2002).

Data for each variable measured on the foliar samples were analyzed with ANOVA using the same general linear model as for the basal area increment data (Eq. 2). To account for analyses of the 16 foliar variables the ANOVA effects were assessed for significance using a Bonferroni adjustment of $\alpha = 0.05/16 = 0.003$. For variables with a significant effect of site, treatment or their interaction, least squared means were used for multiple comparisons with a further adjustment of α (e.g., for three comparisons among salinity levels $\alpha = 0.003/3 = 0.001$). Variables that did not meet the homogeneity of variance assumption of ANOVA (Cl, S, $\delta^{15}\text{N}$) were square root transformed, and then analyzed. Transformation was unsuccessful for foliar sulfur and $\delta^{15}\text{N}$ which were then analyzed with SAS proc mixed with compensation for heterogeneous variances, as described above. In all cases, the original, untransformed data are presented. Some of the data did not meet the assumption of normality, but none were severely non-normal, so ANOVA was still used.

Root Sampling and Analysis

Root distributions from the mineral soil surface to a depth of 100 cm were sampled using an 8-cm-diameter Riverside auger in 20-cm increments. Three replicate cores were collected from within each plot for each forest stand sampled and bulked prior to root extraction. For forest floor root distributions, blocks of LFH were excavated immediately above a core sampling location, and the dimensions recorded. Samples were stored at 4°C until processing. Soil samples were placed on a fine mesh and washed to remove soil from the roots. For samples with high clay content, cores were soaked in water and then frozen to facilitate segregation of roots and soil particles. Dead roots were removed from the samples as much as possible. Roots isolated in the soil wash were scanned using a high-resolution scanner and WinRhizo software (Régent Instruments, Québec City, QC) to determine the root length density.

RESULTS

Tree Basal Area Growth Rates

There were no differences ($P = 0.46$) in white spruce basal area growth among salinity levels (Fig. 1). Surprisingly, individual trees with the fastest basal area growth rate at Clearwater and Salt Plains (13.9 and $6.8 \text{ cm}^2 \text{ yr}^{-1}$, respectively) were growing at the high salinity level, and at Benchmark the second fastest growing tree ($5.6 \text{ cm}^2 \text{ yr}^{-1}$) was at the high salinity level. In contrast, aspen basal area growth was significantly affected by salinity level ($P < 0.001$) with the lowest aspen basal area growth rate occurring at the highest salinity level at every site (Fig. 1). Aspen in the high-salinity plots were growing between 2.2 and $3.2 \text{ cm}^2 \text{ yr}^{-1}$, or about 50% of the 4.5 to $6.2 \text{ cm}^2 \text{ yr}^{-1}$ growth rate achieved by those growing in the low-salinity plots (Fig. 1). White spruce trees showed much more variation in growth than did aspen, especially at the Clearwater site (Fig. 1).

Basal area growth differed among sites for both species; higher white spruce basal area growth rates occurred at Clearwater than at Benchmark or Salt Plains ($P = 0.004$) and higher aspen basal area growth rates occurred at Child Lake than at Zama Marsh ($P = 0.036$). There was no site by treatment interaction for white spruce ($P = 0.31$) or aspen ($P = 0.15$). Although presented data only compare basal area growth in the 1960s for white spruce and 1990s for aspen, examination of earlier and later annual rings in these trees showed the same trends (data not shown).

White spruce height growth and site index were similar among salinity levels at Benchmark and Salt Plains, but tended to increase with decreasing salinity at Clearwater (although one tree in the low-salinity plot was growing at the same slow rate as trees in the high-salinity plot: Table 2; Fig. 2). The height growth rates of most white spruce trees at Benchmark decreased at about 50 yr BH age in comparison to expected growth

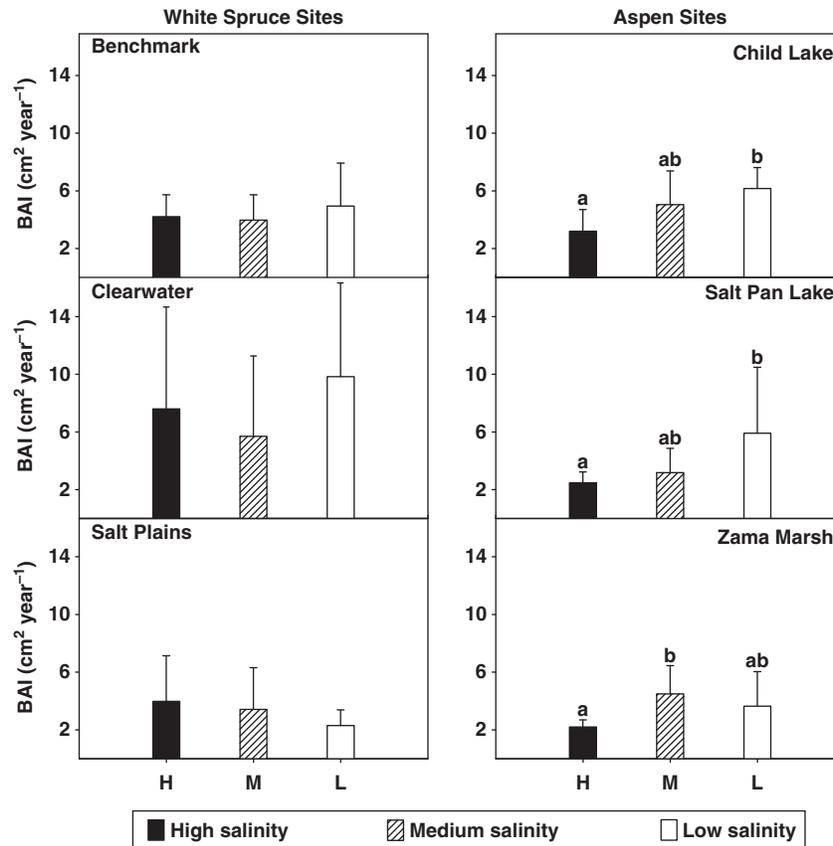


Fig. 1. White spruce and aspen basal area growth rates (means and 95% confidence intervals) for high, medium, and low-salinity plots at each study site. For each site, plots with the same letter were not significantly different at the $\alpha = 0.05$ level.

curves; this suggests a possible increase in growth limitation(s) with tree age. White spruce trees at Salt Plains differed in stand age among salinity levels, but seemed to span the same range of low site indexes (Fig. 2). In contrast to Benchmark and Salt Plains, height growth over time of white spruce at Clearwater followed the same pattern as those in the province-wide

data set, and two trees were following the growth curve for a site index of 16 or higher (Fig. 2).

Aspen height growth rates seemed to be affected by salinity after the juvenile stage of growth. Aspen in high-salinity plots at each site had juvenile height growth similar to aspen in low-salinity plots (Fig. 2); however, their height growth rates seemed to decrease by age 20 at Salt Pan Lake, and age 36 at Zama Marsh. The trees growing at the high salinity level at Child Lake were still young but their growth rates also seemed to have decreased in recent years (Fig. 2). Salinity related decreases in growth with age were reflected in site index; the site index of high-salinity plots at Salt Pan Lake was 5.1 m lower than in the low-salinity plots, and at Zama Marsh site index also tended to decrease with increasing salinity (Table 2).

Table 2. Site index (height at a breast height age of 50), and land capability rating (in bold) from 1 (high capability) to 5 (non-productive) (Leskiw 2004), of white spruce and aspen in high, medium and low-salinity plots at each site

Species	Site	Salinity level		
		High	Medium	Low
White spruce	Benchmark	12.1 (5)	12.4 (5)	12.8 (5)
	Clearwater	10.4 (5)	14.3 (4)	16.3 (3)
	Salt Plains	5.6 (5)	5.7 (5)	7 (5)
Aspen	Child Lake ^z		19.5 (2)	22.3 (1)
	Salt Pan Lake	11.5 (5)	15.1 (3)	16.6 (3)
	Zama Marsh	12.8 (5)	14.4 (4)	16.3 (3)

^zSite index could not be calculated for the high salinity level at Child Lake because those trees were less than 50 yr old when felled.

Foliar Nutrient and Salt Ion Concentrations and ¹⁵N and ¹³C Abundances

We found several significant differences in white spruce and aspen foliar nutrient concentrations among sites, but few differences were related to salinity level. The N, Ca, Mn and Fe concentrations differed among white spruce sites and N, K, Ca, Mg, S, Mn and Al concentrations differed among aspen sites (Table 3).

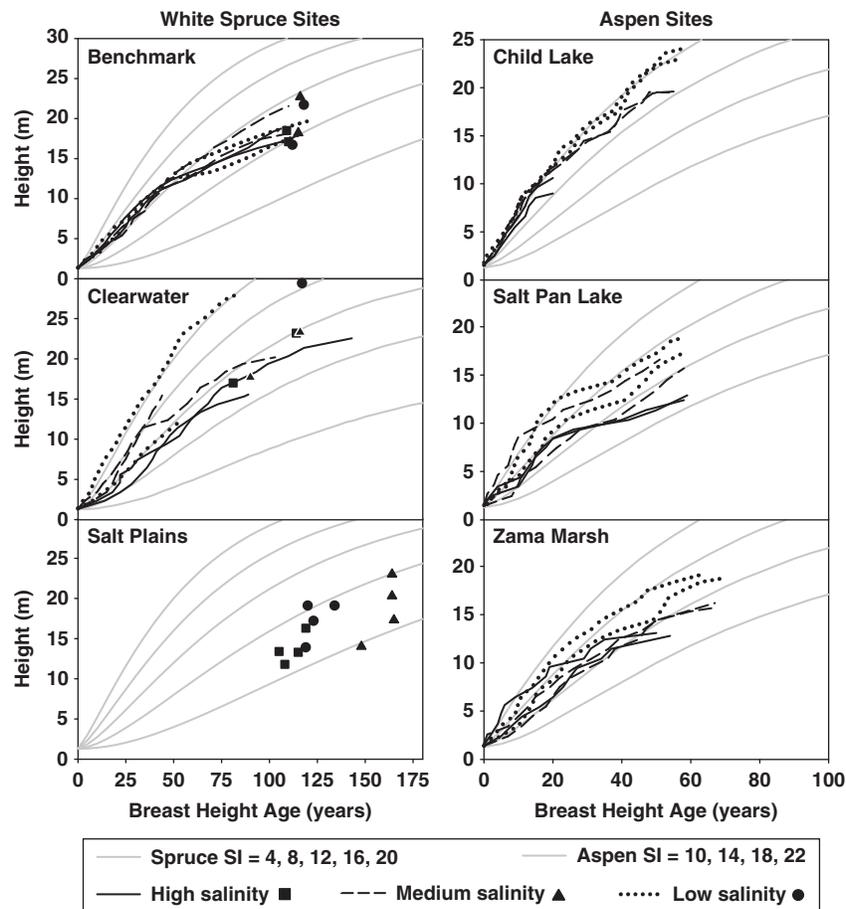


Fig. 2. White spruce and aspen age-height growth curves for the high, medium, and low-salinity plot at each site based on stem analysis of two trees per plot. Additional points are the age and height of cored trees (two trees per plot at Benchmark and Clearwater and four trees per plot at Salt Plains). Gray lines are Alberta standard growth curves for comparison.

For aspen, there were also significant treatment effects or site by treatment interactions for foliar N, P, S and Cl concentrations (Table 3). Foliar N and P concentrations in aspen were similar across sites and treatments except for very high concentrations of both nutrients in three trees at the medium salinity level at Salt Pan Lake (data not shown). Leaves from these trees were light weight and turned a dark color quickly after collection. We suspect a pathogen had infected these trees, causing altered nutrient concentrations in their foliage. At Salt Pan Lake, trees in the low-salinity plot had lower foliar sulfur concentrations than in the other two plots (Fig. 3); the low-salinity plots also had lowest sulfur concentrations in the soil solution (Fig. 4). There were differences among sites in how aspen foliar Cl concentration varied with salinity level (Fig. 3). At the Salt Pan site, medium and low-salinity plots had lower foliar Cl, while at the Zama Lake site the low-salinity plot had highest foliar Cl (Fig. 3).

Unexpectedly, large differences in soil sodium adsorption ratios among plots within sites (Table 1) seemed to

have little effect on foliar Na concentrations; we found no significant differences in foliar Na concentrations due to treatment (Table 3). Significant differences in foliar Na concentrations among aspen sites were due to higher values at Zama Marsh than at Child Lake or Salt Pan Lake (Fig. 3). Zama Marsh also had the highest topsoil SAR of the three sites (see Lilles et al. 2010). Most white spruce and aspen had foliar Na concentrations near typical background (0.2 mg g^{-1}) levels (Fig. 3). Unlike the majority of trees at Clearwater, a few individual trees in the medium salinity plot at that site had foliar Na concentration above background levels. These high concentrations of foliar sodium did not seem to be related to reduced tree growth or discolored needles, but did correspond with these individual trees also having higher than average foliar chloride.

Most foliar Cl concentrations in this study were below injurious levels for both white spruce and aspen (Fig. 3). Foliar chloride did accumulate to possibly toxic levels for aspen in the low-salinity plot at Zama Marsh

Table 3. Results of analysis of variance testing for effects of salinity level, site and interactions on foliar concentrations of salt ions, macronutrients, micronutrients, and carbon and nitrogen stable isotope ratios from the six naturally saline sites for white spruce and aspen^z

Variable	White spruce			Aspen		
	Trmt	Site	Trmt × Site	Trmt	Site	Trmt × Site
Na	0.68	0.49	0.57	0.30	< 0.0001 ^y	0.08
Cl	0.99	0.91	0.67	0.002	< 0.0001	< 0.0001
C	0.92	0.72	0.61	0.65	0.09	0.05
N	0.25	0.0004	0.36	< 0.0001	< 0.0001	< 0.0001
P	0.15	0.85	0.53	0.05	0.37	< 0.0001
K	0.84	0.22	0.81	0.01	0.003	0.02
Ca	0.18	0.003	0.31	0.08	0.001	0.92
Mg	0.22	0.24	0.2	0.42	< 0.0001	0.58
S	0.21	0.05	0.9	0.0002	< 0.0001	< 0.0001
Mn	0.09	0.001	0.52	0.15	< 0.0001	0.02
Fe	0.16	0.0003	0.19	0.24	0.74	0.47
Al	0.52	0.005	0.39	0.17	< 0.0001	0.07
Zn	0.47	0.02	0.47	0.95	0.09	0.21
Cu	0.11	0.04	0.03	0.56	0.08	0.17
δ ¹³ C	0.45	0.37	0.49	0.12	0.01	0.74
δ ¹⁵ N	0.26	0.14	0.01	< 0.0001	0.03	0.009

^zTrmt, treatment; Na, sodium; Cl, chloride; C, carbon; N, nitrogen; P, phosphorus; K, potassium; Ca, calcium; Mg, magnesium; S, sulfur; Mn, manganese; Fe, iron; Al, aluminum; Zn, zinc; Cu, copper; δ¹³C, carbon stable isotope ratio; δ¹⁵N, nitrogen stable isotope ratio.

^yP values in bold are significant at the (Bonferroni-adjusted) $\alpha = 0.003$ level.

(Fig. 3). Soil solution Cl⁻ and the water table were also higher in the low-salinity plot than in the other Zama Marsh plots (Fig. 4 and Table 1), but this did not seem to be related to reduced growth; in fact, that plot had the tallest trees at Zama Marsh. Only at Salt Pan Lake did increased foliar Cl correspond with slower growth of aspen in the high-salinity plot (Figs. 1–3). Soil solution Cl⁻ did not seem to be related to foliar Cl concentrations consistently across sites (compare Fig. 3 and Fig. 4).

Among the isotope ratios we assessed, only aspen foliar δ¹⁵N varied significantly with salinity level (Table 3). Aspen growing in high-salinity plots were enriched in ¹⁵N, while those growing in medium and low-salinity plots had similar nitrogen isotope ratios to that of the atmosphere, or were slightly depleted in ¹⁵N (Fig. 5). Two unusually high values for trees in low-salinity plots at Child Lake were enriched in ¹⁵N as much as, or more than, high-salinity trees; these values caused high variation in δ¹⁵N for the low-salinity treatment. Otherwise, there was a striking difference in δ¹⁵N between aspen growing in high versus medium/low salinity. Foliar δ¹³C values were similar among sites and treatments for both species (Table 3).

Root Growth and Distribution

In both aspen and white spruce stands, the majority of roots were distributed either in the forest floor (LFH) or in the top 20 cm of mineral soil (Fig. 6). For white spruce, >90% of the root length (Fig. 6) was distributed within the LFH and top 20 cm of soil for all sites; fines roots occurred to a maximum depth of 40–60 cm at all sites. Aspen roots were distributed in a similar pattern to white spruce, but with slightly higher root

length densities and with increased rooting at depth, especially at Salt Pan Lake, the site with coarse-textured soils (Fig. 6). Root distribution patterns and densities were similar among salinity levels within each study site.

DISCUSSION

Although white spruce growth seemed unaffected by the different salinity levels, and the trees we studied seemed to be less sensitive to salinity than previously reported (McKenzie et al. 1993; Maynard et al. 1996), Clearwater was the only site with a land capability rating above non-productive. Characteristics like long leaf lifespan (Greenway et al. 1992; Munson et al. 1995; Claveau et al. 2002), high leaf mass per leaf area (Claveau et al. 2005), and high plasticity in crown morphology (Messier et al. 1999) that help white spruce survive in low resource availability conditions in the forest understory could also help it survive in unfavorable soils. Khalsa et al. (2002) also found that white spruce was slow growing, yet had high survivorship in a comparative salinity experiment.

The decrease in growth rates of mature aspen as soil salinity increased concurs with the response in aspen and hybrid poplar seedlings in field (McKenzie et al. 1993) and greenhouse (Khalsa et al. 2002) trials. Growth rates of aspen in the high-salinity plots were similar to growth rates in pest- and pathogen-stressed aspen stands near Grande Prairie, Alberta, from 1990 to 1998 (~2.7 cm² yr⁻¹; Hogg et al. 2002). The fastest growth rates of aspen at our sites were higher than growth rates in healthy aspen stands near Grande Prairie from the same time period (~3.8 cm² yr⁻¹; Hogg et al. 2002), suggesting that soils with medium and low salinity at depths of 50–100 cm and with water and nutrient

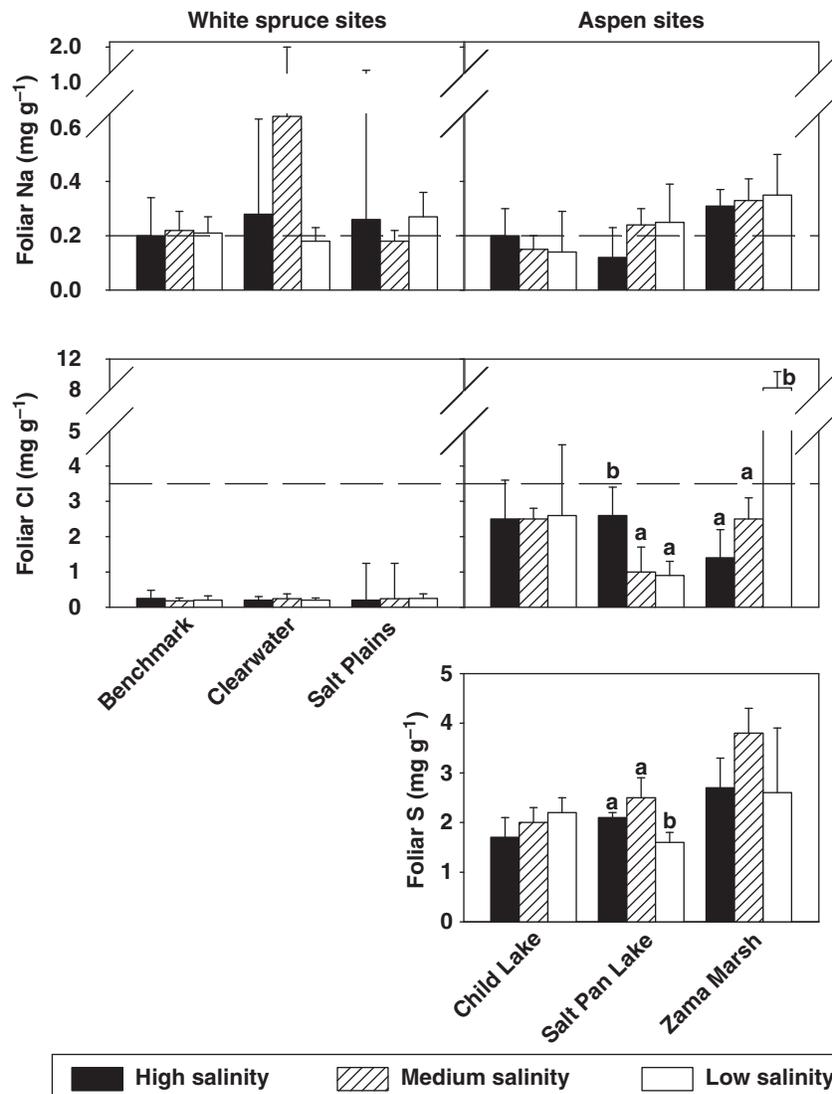


Fig. 3. Foliar sodium and chloride concentrations (mean and 95% confidence interval) in high, medium and low-salinity plots at the three white spruce sites (left side) and foliar sodium, chloride and sulfur at the three aspen sites (right side). Lowercase letters within sites indicate significant differences at the Bonferroni-adjusted alpha level (0.003).

regimes similar to those in this study can support healthy, productive aspen stands. Interestingly, aspen growth declined with age, compared with reference growth curves, in every stand except at the low-salinity plot at Child Lake. Research in short-term greenhouse and field trials would never reveal this pattern because it becomes apparent only once trees were over 15 yr old, and even later in some stands. The fact that salinity affected aspen growth more strongly with time is highly pertinent for oil sands revegetation planning; it suggests that early measures of productive growth for aspen established over saline-sodic overburden or oil sand tailings may persist in the long term.

The obvious differences between white spruce and aspen growth in response to saline soils at our study sites

correspond with differences in their basic biology. Aspen is a shade-intolerant species, able to grow quickly above-ground and deeply below-ground to exploit light, water and nutrients in early successional environments (Gale and Grigal 1987). White spruce is shade tolerant, and can withstand lower light and nutrient conditions for years in the understory, growing slowly but persistently (Nienstaedt and Zasada 1990). In a saline environment, aspen could grow 22 m tall in 50 yr, but basal area growth was reduced by 50% at higher salinity levels. Generally white spruce grew slowly, but growth was not reduced by increasing salinity, and white spruce was able to survive on soils with higher levels of salinity and sodicity than aspen was found on. The high variation in white spruce growth rates, as compared

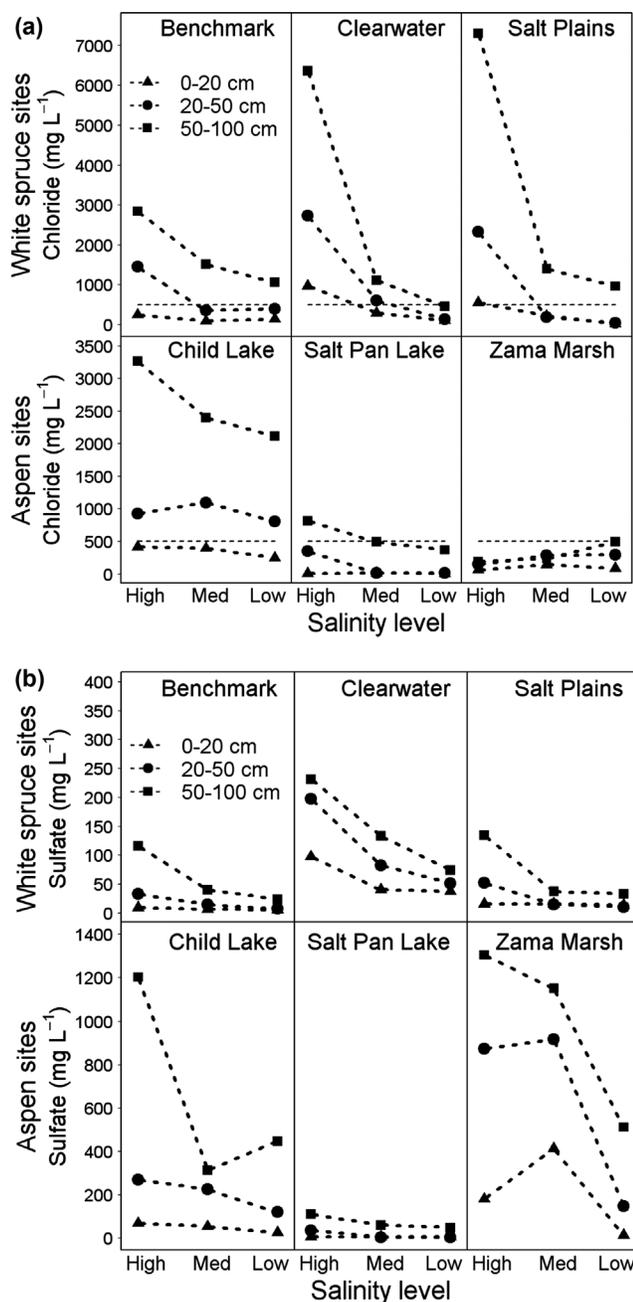


Fig. 4. Soluble chloride (a) and sulfate (b) in the surface soil (0–20 cm), upper subsurface soil (20–50 cm), and lower subsurface soil (50–100 cm) in high, medium, and low-salinity plots for the three white spruce and three aspen sites.

with aspen, was predictable considering that aspen is a clonal species, but it was remarkable that aspen grew at similarly slow rates in three very different aspen sites and in pest- and pathogen-stressed stands (Hogg et al. 2002). Perhaps different aspen genotypes were similarly affected by salinity or stress levels that were near the limit of their tolerance.

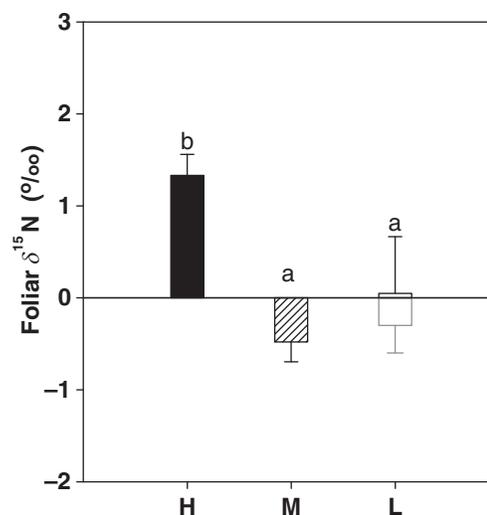


Fig. 5. Foliar $\delta^{15}\text{N}$ (mean and 95% confidence interval), the only foliar parameter significantly affected by treatment only, averaged across the three aspen sites for the high (H), medium (M), and low (L) salinity plots. Plots with the same letter were not significantly different at $\alpha = 0.001$.

The average root distribution of aspen is typically deeper than that of white spruce (Gale and Grigal 1987) with aspen roots mostly located in mineral soil, whereas white spruce roots are primarily in F and H horizons of the forest floor (Strong and La Roi 1983). Root distribution with depth and root length density were similar across all study sites, although root length and root depth were higher in aspen stands, especially for upper mineral soils sampled. Aspen is known to deplete soil water more quickly and to a greater depth than most conifers (Peterson and Peterson 1995) and greater water use by aspen was recorded at our study sites (Close 2007). Water depletion during the growing season in saline soils would, therefore, likely be more of a disadvantage for aspen than white spruce. Rooting habits are adaptable to different soil conditions, but resource allocation to root responses represents additional stress on the tree (Gale and Grigal 1987). Since aspen had greater root length at intermediate soil depths, drought stress and any accompanying growth reductions are likely to be greater for aspen than for white spruce in soils in which salinity increases with depth, as they did at our study sites (Lilles et al. 2010), and as they most likely will after oil sands reclamation (Kessler et al. 2010).

Neither aspen nor white spruce showed evidence of salinity-related nutrient stress in these saline soils, and both largely avoided salt ion accumulation in their foliage. Similarities in foliar $\delta^{13}\text{C}$ values in aspen and white spruce across treatments suggest that they did not experience salinity-related water deficit, as water stress would have caused stomatal closure, increased water-use efficiency and decreased discrimination against ^{13}C

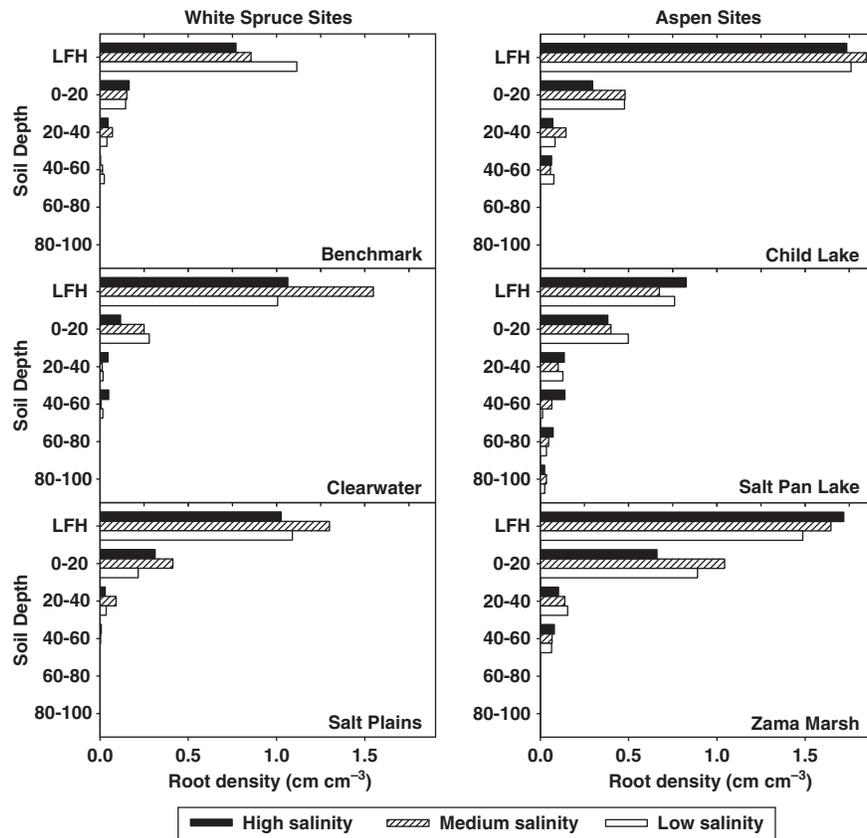


Fig. 6. Distribution of root length (<5 mm diameter) with soil depth in high, medium, and low-salinity plots at the three white spruce sites (left side) and the three aspen sites (right side). Average values presented were derived from bulk samples of three soil cores per plot.

during photosynthesis (Choi et al. 2007). Foliar $\delta^{15}\text{N}$ in aspen was affected by salinity level, but foliar N was not, so ^{15}N discrimination was most likely occurring within the soil and was not a direct indicator of salinity stress (Close 2007). How did these species circumvent these common effects of saline soil? Chloride in particular is the most deleterious ion for many woody plants and most likely to accumulate in foliar tissues (Greenway and Munns 1980; Shannon et al. 1994) and in many of our sites soil solution Cl^- was above the 25% soil concentration threshold (500 mg L^{-1} ; Cain et al. 2000). It is possible that these trees were exhibiting some degree of salt tolerance. They may have been excluding both chloride and sodium by selective membrane permeability or by active ion pumping (Allen et al. 1994). Root tissues could have compartmentalized ions in vacuoles (Jacoby 1999) to protect the foliage, the tissues with the highest photosynthetic capacity (Greenway et al. 1992; Brooks et al. 1996). In laboratory experiments, jack pine (*Pinus Banksiana* Lamb.) and red-osier dogwood (*Cornus sericea* Michx.) showed some ability to restrict Na and Cl ion accumulation in roots and prevent translocation to shoots (Renault et al. 2001; Franklin and Zwiazek 2004) and in white spruce this ability was

enhanced by ectomycorrhizal colonization (Muhsin and Zwiazek 2002; Nguyen 2006). Our results suggest that aspen might share this ability.

It is possible that we did not see foliar Na or Cl ion accumulation because of our sampling methods. Sodium and chloride concentrations increase in spruce needles over time and decrease needle life span (Kayama et al. 2003). Since we only collected foliage that was ≤ 3 yr old, we might have missed needles with injurious concentrations of salt ions. Even if white spruce did accumulate salt ions in its older foliage, the apparent exclusion of sodium and chloride from its younger needles was probably an important factor allowing white spruce to survive at these saline sites (Allen et al. 1994). Investigation into the concentration of salt ions in older foliage and in roots at these sites could elucidate whether mature white spruce and aspen do exhibit some mechanism(s) for salt tolerance, or if they predominantly avoid salts.

One possible mechanism for avoidance of salt stress in trees that has not been explored in previous work is salinity avoidance by very shallow rooting. The majority of other studies on tree salt tolerance have been greenhouse experiments where tree roots are constrained to

a small pot, or have occurred where salt was applied to existing tree roots (e.g., along roadsides). Neither scenario successfully mimics naturally saline boreal forest soils where electrical conductivity of surface soil is $<4 \text{ dS m}^{-1}$, but which have much more saline subsurface soils. Rooting primarily or exclusively in the surface soil could have allowed white spruce and aspen to avoid high levels of subsoil Cl^- and Na^+ and prevent foliar injury or nutrient deficiency.

The majority of roots, including fine roots, were confined to the forest floor and the top 20 cm of mineral soil for white spruce among all sites and salinity levels in this study. Whereas aspen did have higher root length at depth compared with white spruce, the pattern was pronounced only at the study site with coarse-textured soil (Salt Pan Lake). Both species thus avoided salinity at depth by means of shallow rooting, but it does not appear to be specifically in response to saline soils as the rooting pattern was similar across the salinity gradient. The shallow rooting depths measured in this study were indicative of rooting restrictions when compared with other boreal sites of similar stand type and age which found greater rooting at depth (Stone and Kalisz 1991; Van Rees 1997). The reduction in height growth rate over time in most sites could have been due to restrictions on rooting; maturing trees ran out of space in the "favorable" soil zone so they then reduced their growth and photosynthesis accordingly, thereby preventing nutrient deficiency or drought stress symptoms. Placement of additional clean, non-saline capping material during reclamation of saline tailings or overburden would increase the favorable rooting zone, while adding to the cost of reclamation, but the long-term benefit could be a more productive or commercially valuable forest.

These naturally saline sites provide evidence that aspen and white spruce can establish on soils that are moderately to extremely saline at depth, given a natural LFH layer, a medium-rich to rich nutrient regime, mesic to subhygric conditions and at least 20 cm of a natural mineral soil profile with an electrical conductivity $<4 \text{ dS m}^{-1}$ (Lilles et al. 2010). However, the low productivity of most of these stands implies that forestry operations may not be feasible on saline soils in the boreal forest, at least for white spruce. There was one productive aspen stand at Child Lake suggesting that if soil water and nutrient availabilities are not limiting, sites with low to moderate salinity in the lower subsurface soil (e.g., 7.8 dS m^{-1} at Child Lake) could support productive aspen forests. Where revegetation has occurred over soils with salinity at depth, stands should be watched carefully as they age, because growth limitations associated with salinity may not be evident in juvenile trees.

While the evidence that boreal forest communities can grow on naturally saline soils may seem promising, these communities are rare, and may be difficult to establish on engineered soils; generally where high salinity is

found, trees are not. Some recommendations for boreal forest reclamation practices on saline soils can, however, be drawn from this research. Evidently, electrical conductivity of the topsoil should be $<4 \text{ dS m}^{-1}$ in constructed soils if treed forest communities are desired; lower soil electrical conductivity will be required for establishment of productive forest stands, which meet commercial forestry requirements. Caution should be used when reclaiming saline soils because we do not fully understand the interactions between climate, soil water availability, soil salinity and saline ground water. The assumption that vegetation will respond similarly to natural and reclaimed saline soils has not been proven. The forests examined in this research may be surviving through a delicate balance of evapotranspiration, precipitation and water table fluctuations. Higher saline ground water tables or more frequent drought could both seriously affect stability of these forest stands, either through direct supply of saline ground water (e.g., high water table) or through capillary rise and concentration of salts (e.g., drought). Some saline soils in this study appeared to be grassland soils and may not have been forested in drier periods (i.e., before 1850). Thus, this documentation of aspen and white spruce trees surviving on saline soils should not be considered a panacea for salt-affected soil reclamation.

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