



Nitrogen fertilization improves the growth of lodgepole pine and white spruce seedlings under low salt stress through enhancing photosynthesis and plant nutrition



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ABSTRACT

The effectiveness of nitrogen (N) fertilization in improving tree growth in saline forest soils is poorly understood. Hence, in this study, the interactive effect of N fertilization and salt stress on seedling physiology and growth was examined to improve our understanding of possible mechanisms for fertilization to mitigate salt stress. We compared physiological characteristics, growth, and foliar and root nutrient concentrations in lodgepole pine (*Pinus contorta*) and white spruce (*Picea glauca*) seedlings planted in a peat-mineral soil mix during a three months study with N fertilization (0 and 300 mg N seedling⁻¹) and salinity (0, 50, 100, 150 mmol L⁻¹ NaCl) in a greenhouse experiment. Nitrogen fertilization significantly increased net photosynthetic rates (P_n) and N concentrations in needles and roots, resulting in improved seedling height and root collar diameter growth and total seedling biomass for both species when seedlings were subjected to low salinity (50 mmol L⁻¹ NaCl), while it did not help tree growth under high salinity (150 mmol L⁻¹ NaCl). The physiological responses to combined salt stress and N fertilization did not differ between the two species; however, fertilization improved the growth of pine seedlings more than that of spruce seedlings under different salinity levels. The results suggest that the effectiveness of N fertilization in mitigating the salinity effect on seedling growth was species specific. Our study demonstrates that N fertilization improves tree growth through enhanced photosynthesis and N nutrition under low salinity and provides valuable insights into strategies to manage N nutrition in saline boreal forest soils.

1. Introduction

Soil salinity is often a major abiotic stress influencing plant survival, growth and development, and site productivity (Boyer, 1982; Andrews et al., 1998; Renault et al., 1999; Rodrigue and Burger, 2004). High soil salinity can decrease osmotic potential, induce nutrient imbalance, and cause ion toxicity (Munns, 1993; Jacoby, 1994; Cornillon and Palloix, 1997; Munns and Tester, 2008). In addition, high salinity influences plant water uptake and nitrogen (N) metabolism, including N uptake and assimilation, and amino acid and protein synthesis (Aslam et al., 1984; Botella et al., 1997; Dluzniewska et al., 2007). Although saline soils are rare in the boreal forest region in Canada, saline areas do exist locally within the region (Purdy et al., 2005; Lilles et al., 2012). In particular, salt-affected soils after land reclamation in the oil sands occupy substantial areas, which are located in the boreal forest region of Alberta, Canada (Barbour et al., 2007). Therefore, understanding the responses of lodgepole pine (*Pinus contorta*) and white spruce (*Picea glauca*), two common boreal tree species, to salinity has significant

implications for successful reestablishment of boreal forest stands in salt-affected soils, as most boreal tree species are salt-sensitive (Allen et al., 1994; Lilles et al., 2012).

The reconstruction of the landscape after oil sands surface mining may increase salinity in reclaimed soils in the Athabasca oil sands region (AOSR) (Barbour et al., 2007). Salts, mainly sodium chloride (NaCl) and sodium sulfate (Na₂SO₄), may migrate from saline processed tailings sand or marine shale overburden, that are produced from oil sands mining and are generally buried below the cover soil (Barbour et al., 2007). Sometimes salts are introduced into the cover soil when the saline overburden material is improperly mixed with the non-saline cover soil. The upward movement of salts from the saline overburden layers into the cover soil can raise the electrical conductivity (EC) level up to 6.0 dS m⁻¹ in the lower part of peat-mineral soil mix (PMM) used as a cover soil (Kessler et al., 2010). According to the guidelines for reclamation to forest vegetation in the AOSR, if soil EC is greater than 4 dS m⁻¹, the soils are unfavorable for survival and growth of plants, and the establishment of a forest ecosystem (Alberta Environment, 2010).

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However, the response of boreal plant species to soil salinity is not well understood; therefore, information about plant physiological and growth responses to salinity will be valuable in guiding the revegetation of saline soils in the oil sands.

Nutrient availability, especially N availability, is often reported to be one of the major limiting factors for tree growth and site productivity in the boreal forest region. The situation is even worse in the oil sands region, because oil sands mining and related activities may lead to substantial loss of soil organic carbon (C) and N due to the loss of fertile topsoil and mechanical mixing of surface soils with infertile subsurface soils (Ussiri and Lal, 2005; Shrestha and Lal, 2011). Previous studies have shown that N availability was limiting tree growth in reclaimed sites (Duan et al., 2015), and fertilization has been shown to promote tree growth in sites with low productivity in the AOSR (Duan and Chang, 2015). Although fertilization has been widely recognized as an important management practice to supply nutrients for seedling establishment and to promote plant growth (Khasa et al., 2005; Pinno et al., 2012; Sloan and Jacobs, 2013), it is not clear whether N fertilization may alleviate or aggravate growth limitation of trees planted in reclaimed saline soils with a low N availability. Previous studies have reported that N fertilization could ameliorate salt stress of many annual herbaceous species (Villa-Castorena et al., 2003; Chen et al., 2010). Many studies have focused on responses of plants to salt stress or fertilization separately, and little information is available on the interactive effects of salinity and N availability on boreal tree species. Information regarding the interactive effects of salt stress and N fertilization on plant performance will be useful for improving current reclamation practices to reestablish plant communities on reclaimed saline sites.

The aim of this study was to evaluate the physiological and growth responses of lodgepole pine and white spruce seedlings to salinity and N fertilization in a boreal forest soil in Alberta, Canada. We hypothesized that (1) increased N availability would ameliorate salt stress and improve plant growth by maintaining the integrity of the physiology of the plant, as salinity will reduce photosynthesis and root water uptake; and (2) the physiological and growth responses of lodgepole pine and white spruce seedlings to combined soil salinity and N fertilization would be similar, as the mechanism for increased N to ameliorate salt stress will work in the same way despite that the two species have different N requirement and salt tolerance.

2. Materials and methods

2.1. Soil preparation, plant materials and growth conditions

A mineral soil (0–50 cm) sample was collected, after removing the forest floor layer, from a boreal forest site (56°09'N, 111°52'W) near Fort McMurray, Alberta. The soil was passed through a 2 mm sieve and stored at 4 °C for later use. The PMM was formed by mixing the mineral soil with commercial peat moss and perlite with a 5:4:1 ratio on a volume basis to mimic cover soils used for reclamation in the AOSR oil sands region.

One-year-old container-grown (415D styroblocks™, Beaver Plastics Ltd., Acheson, Canada) lodgepole pine and white spruce seedlings were produced from the Smoky Lake Forest Nursery of Coast to Coast Reforestation Inc. in Alberta. Seedlings that had gone through a chilling process were placed in a freezer at –3 °C for a six-week cold storage period prior to the greenhouse experiment. Seedlings were planted in pots with a 15 cm diameter and a 17 cm height in early January 2014. The bottom of the pots was lined with a nylon mesh to prevent soil from falling through the holes. An aluminum pan was placed under each pot to collect leachates during irrigation events, and the leachates were poured back to the pots to prevent nutrient loss. Seedlings were placed in a controlled-environment greenhouse. Environmental conditions in the greenhouse were maintained with a day-time temperature of 24 °C and night-time temperature of 18 °C, and 65% relative humidity. The

photoperiod in the greenhouse was 18 h (6 am to 12 pm), and photosynthetic photo flux density was 300–350 $\mu\text{mol m}^{-2} \text{s}^{-1}$. The pots were periodically rotated to minimize the edge effect during the experiment.

2.2. Experimental design

The experiment used a $2 \times 4 \times 2$ factorial design with two N fertilization rates, four salinity levels and two tree species, and each treatment was replicated five times. Seedlings were grown in the greenhouse for two weeks to allow them to recover from cold storage and break dormancy before the application of N fertilizer and salinity treatments. Half of the seedlings for each tree species were applied with N fertilizer (supplied as urea, 300 mg N seedling⁻¹, equivalent to 200 kg N ha⁻¹, N300), and the other half were not fertilized (N0) as control. Nitrogen fertilizer was split-applied over three times in a 20-day interval at the rate of 100 mg N seedling⁻¹ at each application. All the seedlings were subjected to deionized water (S0), 50 (S50), 100 (S100) and 150 (S150) mmol L⁻¹ NaCl. Salinity treatments were also applied over three times in a 20-day interval at the rate of 300 mL deionized water or NaCl solution per application one week after N fertilizer addition. During the experiment, the seedlings were irrigated with 200 mL deionized water every two days to maintain the soil moisture content to 70% of water holding capacity.

2.3. Seedling physiological measurements

The seedlings were grown in the greenhouse for three months. Net photosynthetic rate (P_n), and transpiration rate (E) were measured in needles in the upper part of the seedling before harvesting using a LI-6400XT portable photosynthesis system with a conifer chamber (LI-COR Inc., Lincoln, NE). The reference CO₂ concentration was 400 $\mu\text{mol mol}^{-1}$; photosynthetic photon flux density was 400 $\mu\text{mol m}^{-2} \text{s}^{-1}$; relative humidity was 30%; leaf temperature was 20 °C; and the CO₂ flow rate was 200 $\mu\text{mol s}^{-1}$ in the conifer chamber. The measurements were conducted between 9:00 and 12:00 am to maintain consistency between measurement periods. After those measurements, the needles were detached from the branches and scanned, and the SigmaScan Pro 5.0 software (Systat Software Inc., San Jose, CA) was used to calculate the total leaf area. Shoot water potential (Ψ_w) was measured in the distal 10-cm shoot using a Scholander-type pressure chamber (PMS Instrument Company, Albany, OR) before harvesting as described in Wan et al. (1999). Root hydraulic conductance was determined with a high pressure flow meter (HPFM) (Dynamax Inc., Houston, TX) after Ψ_w measurement as described in Tyree et al. (1995). Briefly, the stem of seedlings was excised 2 cm above the root collar, and the whole intact root system was connected to the HPFM system through the cut stem. Root systems were gradually pressurized by the pressurized water tank from 0 to 0.5 MPa to obtain a pressure-flow relationship. Root hydraulic conductivity (L_p) was calculated by dividing the root hydraulic conductance value by root dry weight.

2.4. Seedling growth measurements

The height and root collar diameter (RCD) of seedlings were measured with a meter stick and a digital vernier caliper (Traceable™, Thermo Fisher Scientific Inc., Waltham, MA), respectively, two weeks after planting and before harvesting. Height and RCD increments were calculated as the differences of height or RCD between the two measurements. The seedlings were harvested, washed with deionized water three times and separated into current-year and 1-year-old needles, stems and roots. After being oven-dried at 65 °C for 48 h, the dry weight of each component was determined.

2.5. Total N and ¹³C abundance in seedlings

The oven-dried current-year and 1-year-old needles and roots were

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