# A comparison of growth and physiology in *Picea glauca* and *Populus tremuloides* at different soil temperatures

**Simon M. Landhäusser, Annie DesRochers, and Victor J. Lieffers**

**Abstract**: Trembling aspen (*Populus tremuloides* Michx.) and white spruce (*Picea glauca* (Moench) Voss) seedlings were grown at uniform air temperatures but different soil temperatures (5, 15, and 25°C), and gas-exchange and growth characteristics were examined during active growth and early dormancy. At 5°C, *Populus tremuloides* had no root growth and limited growth in leaf area and shoot mass compared with the large increases in leaf and shoot mass at 25°C. In contrast, *Picea glauca* had some root growth at 5°C and moderate growth of roots at 15 and 25°C; however, there were no differences in aboveground mass at the different soil temperatures. Net assimilation and stomatal conductance in *Populus tremuloides* were reduced with decreasing soil temperatures, while in *Picea glauca* soil temperatures did not affect these gas-exchange variables. In both species, root mass was higher in the dormant period than during the growing period, while root volume remained constant. Generally, the growth variables of *Populus tremuloides* were more suppressed by cold soils than in *Picea glauca*. Root total nonstructural carbohydrates (TNC) decreased between the active growth and dormancy period by nearly 50% in *Populus tremuloides*, while there was no change in TNC in *Picea glauca*. Results suggest a more conservative use of TNC reserves in *Picea glauca* combined with a tolerance to cold soil temperatures compared with *Populus tremuloides*.

**Résumé** : Des semis de peuplier faux-tremble (*Populus tremuloides* Michx.) et d'épinette blanche (*Picea glauca* (Moench) Voss) ont été cultivés à des températures de l'air uniformes mais à différentes températures du sol (5, 15 et 25°C). Les échanges gazeux et les caractéristiques de la croissance ont ensuite été étudiés pendant les périodes de croissance active et de début de dormance. À 5°C dans le cas de *Populus tremuloides*, il n'y avait aucune croissance des racines et un faible accroissement de la surface foliaire et du poids des pousses comparativement à des augmentations importantes du poids des feuilles et des pousses à 25°C. Au contraire dans le cas de *Picea glauca*, les racines croissaient un peu à 5°C et modérément à 15 et 25°C. Cependant, il n'y avait pas de différences dans le poids des structures épigées aux différentes températures du sol. Chez *Populus tremuloides*, l'assimilation nette et la conductance des stomates diminuaient avec une réduction de la température du sol, tandis que chez *Picea glauca*, ces variables reliées aux échanges gazeux n'étaient pas affectées par la température du sol. Chez les deux espèces, le poids des racines était plus élevé pendant la période de dormance que pendant la période de croissance active tandis que le volume de racines demeurait constant. En général, les variables de croissance de *Populus tremuloides* étaient davantage affectées par des sols froids que chez *Picea glauca*. Les hydrates de carbone non structuraux totaux diminuaient de près de 50% dans les racines de *Populus tremuloides* en passant de la période de croissance active à la période de dormance, tandis qu'ils ne variaient pas chez *Picea glauca*. Les résultats semblent indiquer que *Picea glauca* fait une utilisation plus conservatrice des hydrates de carbone non structuraux totaux combinée à une tolérance aux températures froides du sol comparativement à *Populus tremuloides*.

[Traduit par la Rédaction]

## Introduction

In boreal forests, short summers and low solar angles result in low amounts of energy reaching the soil surface (Bonan 1992). This coupled with the build-up of organic matter and thatch on the soil surface slows energy transport into soils (Viereck 1970; Hogg and Lieffers 1991), which keep soil temperatures low relative to soils of temperate regions. Cold soil temperatures are a key factor limiting tree growth (Tryon and Chapin 1983; Bonan 1992). In boreal forests, stand-replacing fires commonly initiate forest regeneration. Fire kills the canopy trees, consumes some or the entire surface organic layer and reduces albedo, contributing to soil warming. After a disturbance removes the previous stand, trembling aspen (*Populus tremuloides* Michx.) can quickly reoccupy mixedwood sites via root suckering (Peterson and Peterson 1992; DeByle and Winokur 1985), while white spruce (*Picea glauca* (Moench) Voss) recruitment might occur immediately after or slowly over time (DeLong 1991; Lieffers et al. 1996). However, because of its slow juvenile growth rates, *Picea glauca* only dominates these sites

Received September, 25, 2000. Accepted July 15, 2001. Published on the NRC Research Press Web site at http://cjfr.nrc.ca on October 18, 2001.

**S.M. Landhäusser,[1] A. DesRochers, and V.J. Lieffers.** Centre of Enhanced Forest Management, Department of Renewable Resources, 4-42 Earth Sciences Building, University of Alberta, Edmonton, AB T6G 2E3, Canada.

[1] Corresponding author (e-mail: simon.landhausser@ualberta.ca).

DOI: 10.1139/cjfr-31-11-1922

later in succession. The decline in dominance of *Populus tremuloides* at the later stages of succession may be related to factors such as age, diseases, insect damage, and changes in site conditions (Peterson and Peterson 1992; DeByle and Winokur 1985).

Soils are likely to become colder as the leaf area and soil organic layers redevelop through time following the disturbance. As species composition gradually shifts from *Populus tremuloides* to *Picea glauca*, average stand soil temperatures decrease (Amacher et al. 2001). *Picea glauca* with its denser canopy and greater leaf area density (Stadt and Lieffers 2000) intercepts more solar radiation during the growing season and snow in winter, which will negatively affect average soil temperatures (Amacher et al. 2001). On a landscape scale, Van Cleve et al. (1983) noted that *Populus tremuloides* is more dominant on sites with warmer soil temperatures. We hypothesize, therefore, that *Populus tremuloides* and *Picea glauca* have different growth and physiological strategies in response to warm and cold soils.

Low soil temperatures have been shown to inhibit shoot and leaf growth (Landhäusser et al. 1996; Landhäusser and Lieffers 1998), root growth and water uptake (Grossnickle and Blake 1985, Grossnickle 1987; Wan et al. 1999), and photosynthesis (Tryon and Chapin 1983; Vapaavuori et al. 1992; Folk et al. 1995; Wan et al. 1999) in several tree species. Since *Picea glauca* is a shade-tolerant evergreen conifer and *Populus tremuloides* is a shade-intolerant deciduous species (Landhäusser and Lieffers 2001), they are likely to have different strategies for photosynthesis, carbon allocation, root and shoot growth, and respiration. In addition, the evergreen mode of *Picea glauca* could allow this species to photosynthesize during the spring and fall period, when leaves in *Populus tremuloides* are not present, suggesting further differences in photosynthesis and carbon allocation between the evergreen *Picea glauca* and the deciduous *Populus tremuloides*.

The objectives of this study were to qualitatively compare growth strategies and physiology of *Picea glauca* and *Populus tremuloides* under different soil temperatures, in the periods of active growth and early dormancy. Specifically we anticipate that *Populus tremuloides* will have higher photosynthetic rates, leaf and root area development, and respiration rates in warm soils compared with *Picea glauca*.

## Materials and methods

Fifty-four *Populus tremuloides* and 66 *Picea glauca* 1-year-old dormant seedlings from a local seed source were obtained from a commercial grower. Their root systems were carefully washed to remove all peat, and seedlings were then planted in sand. The seedlings were grown for a period of 6 weeks in a growth chamber with 18 h light : 6 h dark cycle with a daytime air temperature of 18°C and a night temperature of 16°C. Relative humidity was maintained at 60%. Light intensity was maintained at 350–400 $\mu$mol photons$\cdot$m$^{-2}\cdot$s$^{-1}$ photosynthetically active radiation (PAR) at pot level.

Seedlings were subjected to three soil temperatures of 5, 15, and 25°C. To control soil temperature, self-watering pots (15-cm diameter with a false bottom) were submerged into water baths consisting of watertight plastic boxes (90 × 90 × 20 cm), which maintained soil temperatures at 5, 15, and 25°C. The false bottom accumulated drainage water during waterings, which was removed through a hose to prevent waterlogging of the plants (Landhäusser and Lieffers 1998). The space between the pots in the baths was covered with a white polystyrene board and the soil surface in the pots was covered with 2 cm of perlite to increase albedo and insulate the soil surface. Soil temperature was regulated with thermostats throughout the experiment and monitored periodically using hand-held thermometers.

The pots were watered as needed and fertilized twice a week with full-strength Hoagland's solution (Epstein 1972), and later with 2 g$\cdot$L$^{-1}$ of a commercial fertilizer (20:20:20, N–P–K with chelated micronutrients). During the growing period, the pots were rotated to compensate for possible spatial differences in growth chamber conditions. After 6 weeks, physiological and growth variables were measured on half of the seedlings for both *Populus tremuloides* and *Picea glauca*. Dormancy was induced on the rest of the plants by shortening daylength to 6 h, lowering air temperatures to 11°C during the day and 8°C at night, lowering soil temperature to 5°C, and suspending fertilization for 2 weeks. The plants were then placed in a dark refrigerator at 2°C for another 2 weeks, before measurements of root respiration rates and growth variables were taken. This technique has been successfully used to complete bud development and allow seedlings to reflush.

### Gas exchange and root respiration measurements

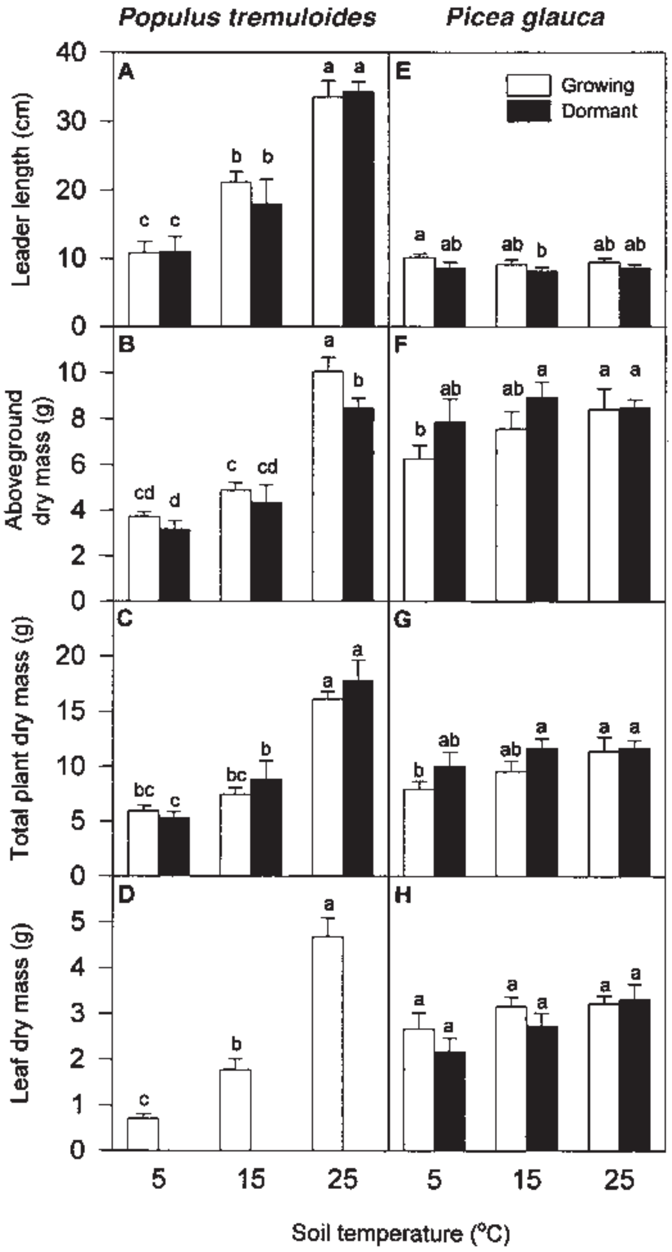
Root respiration rates were measured with a clamp-on chamber (open-system, with a mixing fan and temperature measurement; DesRochers 2000). Sand was gently washed away from roots with deionized water, and excess water was blotted with paper towels. The whole root system was enclosed in the chamber, with the aboveground portions left intact but excluded from the chamber. The chamber was placed in a temperature-controlled chamber (described in Landhäusser et al. 1997), and all measurements were made at constant root temperatures. Respiration rates were measured for each seedling at their respective previous soil temperatures treatments with an open-system infrared gas analyser (CIRAS I, PP Systems, Haverhill, Mass.). Recent studies have shown that respiration is increased by low $CO_2$ concentrations (Qi et al. 1994; Burton et al. 1997; Clinton and Vose 1999). DesRochers (2000) determined that $CO_2$ concentrations in a mixedwood forest soil at 5°C were 3233 ± 609 ppm (mean ± SD; $n = 16$); therefore, $CO_2$ concentration supplied to the chamber was held at 3000 ppm. Roots were acclimated to the measurement temperature for about 30 min, and the respiration chamber was equilibrated for another 20 min before the rates were recorded. Over the range of temperatures, relative humidity was maintained at saturation levels.

Gas exchange on the actively growing *Populus tremuloides* and *Picea glauca* seedlings was measured after 6 weeks. Gas exchange was measured with the above open-system infrared gas analyser with a broadleaf cuvette (Auto cuvette, PP systems, Haverhill, Mass.) on the preformed leaves for *Populus tremuloides* and on the terminal leader with a conifer cuvette (ADC, Hoddesdon, England) for *Picea glauca*. Because of the two different cuvettes, environmental conditions during gas-exchange measurements were somewhat different. For *Populus tremuloides*, light, leaf temperature, and relative humidity were maintained at 1500 $\mu$mol$\cdot$m$^{-2}\cdot$s$^{-1}$ (PAR), 20°C, and 35%, respectively, while for *Picea glauca*, conditions were 1100 $\mu$mol$\cdot$m$^{-2}\cdot$s$^{-1}$, 25°C, and 35%. Projected leaf and needle area were used to calculate physiological variables. Projected leaf area of *Populus tremuloides* was measured with a leaf area meter (LI-3100, LI-COR, Inc., Lincoln, Nebr.), while projected leaf area of *P. glauca* was measured using a computer scanner and imaging software (Sigma Scan 3.0, Jandal Scientific, San Rafael, Calif.).

### Growth variables and tissue analysis

Root volume was measured by water displacement before and after the experiment. Leader length and dry mass of roots, old and new shoots, leaves, and needles were measured for each seedling. Total projected needle area of *Picea glauca* was estimated using a relationship between needle dry mass and projected needle area.

**Fig. 1.** Leader length (A and E) and aboveground (B and F), total plant (C and G), and leaf dry mass (D and H) for *Populus tremuloides* ($n$ = 9) and *Picea glauca* ($n$ = 11) seedlings grown at a soil temperature of 5, 15, and 25°C during the growing season and during dormancy. Different letters above the bars indicate significantly different means ($\alpha$ = 0.05).



Total nonstructural carbohydrates (TNC) and total nitrogen (N) were measured on roots, old shoots, new shoots, leaves, and needles after drying to constant mass at 68°C. All samples were ground in a Wiley mill (40 mesh). For the total nitrogen determination, samples were digested with the Kjeldahl method (Kalra and Maynard 1991) and N was determined with a Technicon autoanalyzer II (Tarrytown, N.Y.). Sugars and starch (TNC) were determined by a colorimetric reaction to phenolsulfuric acid (Smith et al. 1964) after digestion of ground samples in 0.2 M $H_2SO_4$ in a 115°C bath for 1 h (Shepperd and Smith 1993).

### Data analysis

The growth variables, gas-exchange, and root respiration data were analyzed as a randomized 3 × 2 factorial design with 3 soil temperatures (5, 15, and 25°C) and 2 seasons (growing and dormant) as fixed main effects. To test for treatment effects, analysis of variance and least significant difference multiple comparisons were performed with the general linear models procedure of SAS version 6.11 (SAS Institute Inc., Cary, N.C.). A significance level of $\alpha$ = 0.05 was chosen.

## Results

### Growth variables and tissue analysis

Leader length; leaf area (data not shown); and leaf, stem, and root dry mass in *Populus tremuloides* were lower at a soil temperature of 5°C compared with 25°C (all variables $p$ < 0.001) (Figs. 1 and 2). This is in contrast to *Picea glauca*, which had no differences in leader length ($p$ = 0.571), leaf area ($p$ = 0.146; data not shown), and aboveground biomass ($p$ = 0.153) at the different soil temperatures (Figs. 1 and 2). New root growth was also lower in *Picea glauca* at 5°C compared with 25°C ($p$ < 0.001). However, by comparison, root mass in *Picea glauca* increased 7% at 5°C from the initial root size ($p$ = 0.014), while *Populus tremuloides* had no measurable root growth at 5°C compared with the pretreatment measurement ($p$ = 0.832) (Figs. 2A and 2E). At 15°C, *Populus tremuloides* had a 100% increase in root mass, while *Picea glauca* increased root mass by 21% from initial values. At 25°C, root mass in *Populus tremuloides* increased by 350% from initial measurements compared with 59% in *Picea glauca* (Figs. 2B and 2F). However, the increase in new root mass in *Picea glauca* did not result in larger seedlings. Total plant mass of *Picea glauca* was not different among the three soil temperatures ($p$ = 0.250), while mean total plant mass in *Populus tremuloides* increased 71 and 240% for 15 and 25°C, respectively, compared with plants grown at 5°C ($p$ < 0.001) (Figs. 1C and 1G).

In *Populus tremuloides*, root and shoot mass (Figs. 1B and 2B) and root/shoot ratio (Fig. 2D) were overall higher in the dormant than the growing season. At a soil temperature of 5°C, total root mass was not different between the dormant and growing season, while root mass increased by 73% (from 2.6 to 4.5 g between growing and dormant season) at 15°C and by 52% (6.1–9.2 g) at 25°C. However, root volume did not differ between growing and dormant season (Fig. 2C). Similarly to the roots at 5°C soil temperature, shoot mass (excluding leaf dry mass) of *Populus tremuloides* seedlings was not different between the growing and dormant season (3 g), while shoot mass increased by 42% at 15°C and by 57% at 25°C ($p$ < 0.05) (data not shown). Over all soil temperatures, root/shoot ratios were not different in *Populus tremuloides* between the dormant and growing season when leaves were excluded from the shoot mass. With leaves included, the root/shoot ratios in seedlings grown at 5°C were not different between the growing and dormant season, while root/shoot ratios increased in both 15 and 25°C from 0.57 in the growing season to 1.03 during the dormant season resulting in a soil temperature by season interaction ($p$ = 0.032) (Fig. 2D).

**Fig. 2.** New root (A and E) and total root dry mass (B and F), root volume (C and G), and root/shoot ratio (D and H) for *Populus tremuloides* ($n = 9$) and *Picea glauca* ($n = 11$) seedlings grown at a soil temperature of 5, 15, and 25°C during the growing season and during dormancy. Different letters above the bars indicate significantly different means ($\alpha = 0.05$).

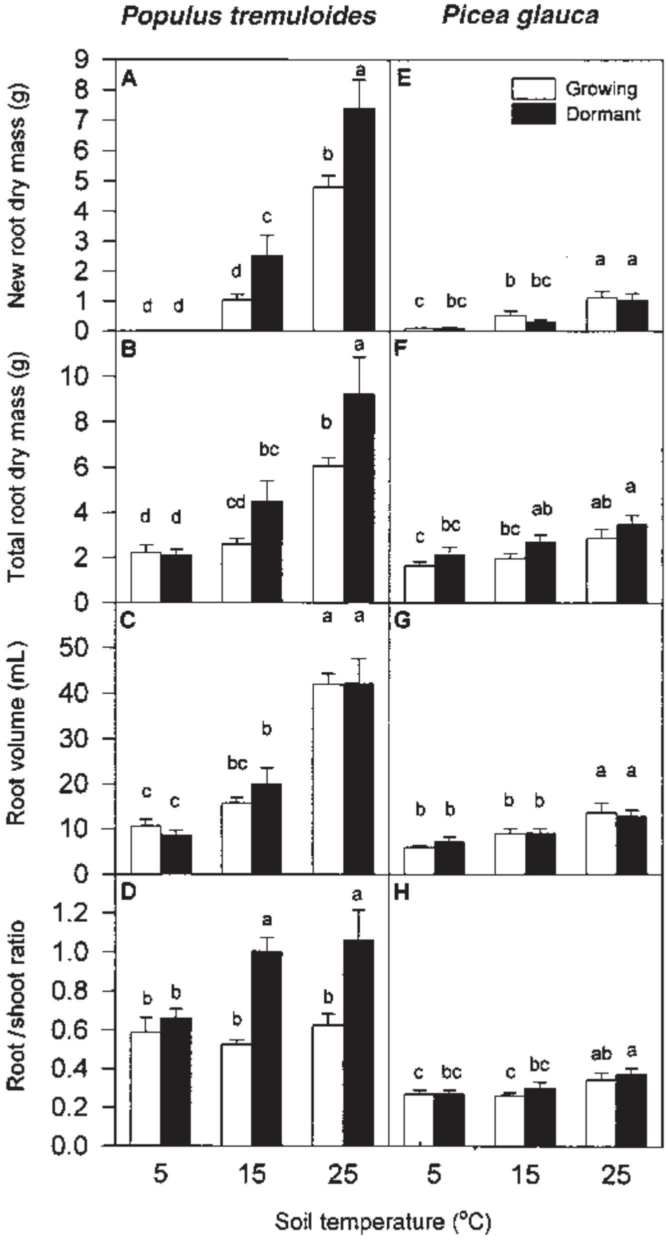
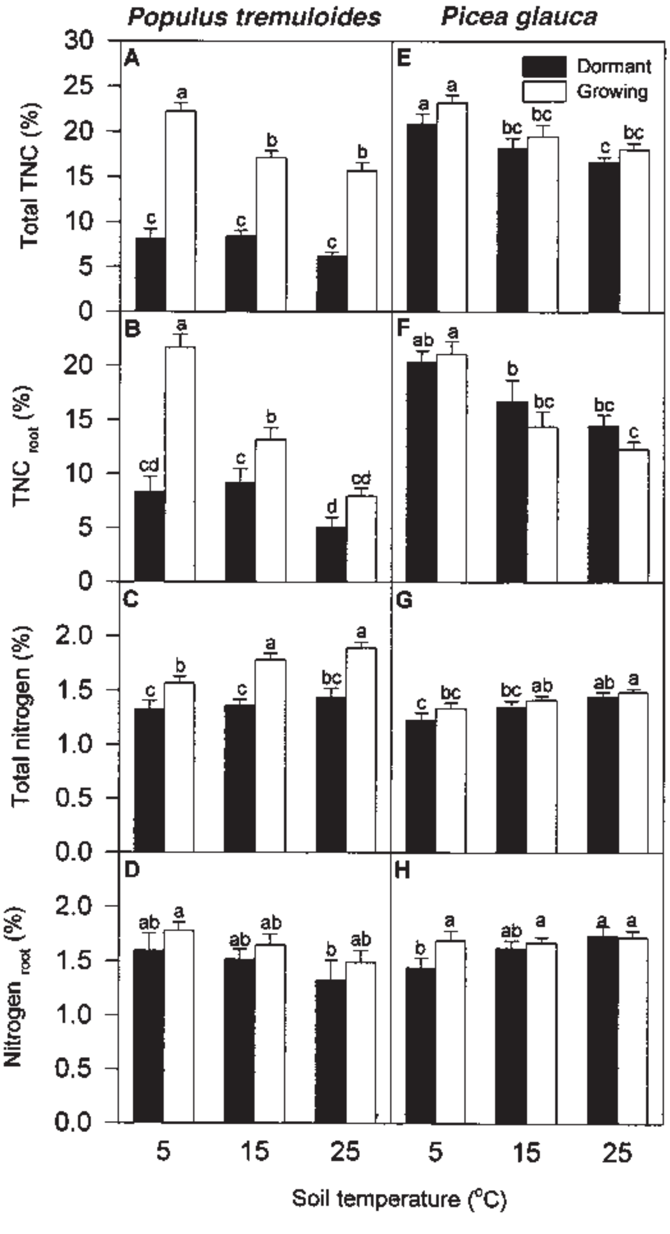


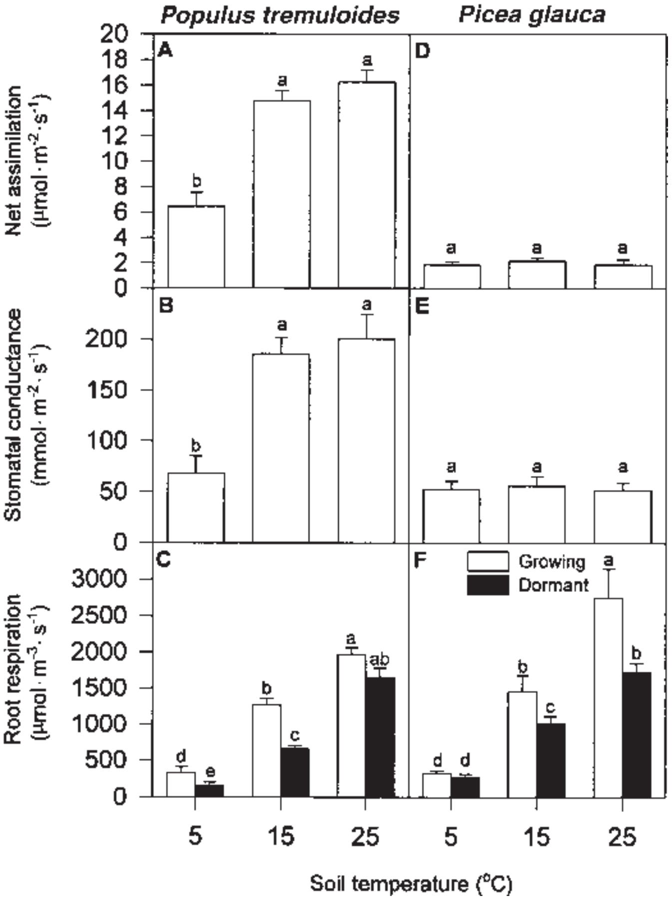
**Fig. 3.** Total nonstructural carbohydrates (TNC) per plant (A and E) and in roots (B and F), and nitrogen concentration per plant (C and G) and in roots (D and H) for *Populus tremuloides* ($n = 9$) and *Picea glauca* ($n = 11$) seedlings grown at a soil temperature of 5, 15, and 25°C during the growing season and during dormancy. Different letters above the bars indicate significantly different means ($\alpha = 0.05$).



Similar responses to season were found in *Picea glauca*, where overall the root mass was higher in the dormant than in the growing season ($p = 0.026$). As in *Populus tremuloides*, root mass was not different among seedlings during the growing and dormant season at a soil temperature of 5°C, but seedlings grown at 15 and 25°C had 42 (1.9–2.7 g) and 21% (2.9–3.5 g) higher root mass in the dormant season than in the growing season (Fig. 2F). Root/shoot ratio in *Picea glauca* was not different for plants between the two seasons ($p = 0.290$); however, plants grown at 25°C soil temperatures had higher root/shoot ratios (0.36) than plants grown at 15 and 5°C (0.28) (Fig. 2H).

The mean TNC (starch and sugars) in *Populus tremuloides* seedlings grown at 5°C during the growing season was 22% of dry mass; this was higher than the 16% at 15 and 25°C (Fig. 3A). At all soil temperatures, TNC concentration for whole plants was reduced between growing and dormant season measurement ($p < 0.001$). At the dormant season measurement, TNC was reduced to 8, 8, and 6% of the plant dry mass for seedlings grown at 5, 15, and 25°C, respec-

**Fig. 4.** Net assimilation (A and D), stomatal conductance (B and E), and root respiration (C and F) for *Populus tremuloides* ($n$ = 9) and *Picea glauca* ($n$ = 11) seedlings grown at a soil temperature of 5, 15, and 25°C during the growing season and during dormancy. Different letters above the bars indicate significantly different means ($\alpha$ = 0.05).



tively. However, because of the smaller decline in TNC between the growing and the dormant season from 16 to 8% (51% reduction) at a soil temperature of 15°C compared with plants at 5 and 25°C with a TNC decline of 64 and 62%, respectively, there was a significant soil temperature by season interaction ($p$ = 0.004). Root TNC (Fig. 3B) showed a similar pattern as in the TNC concentrations on a per plant basis. During the growing season, seedlings grown at 5°C had the highest TNC (22%), compared with 13% at 15°C and 8% at 25°C (Fig. 3B). The TNC concentration in the roots decreased sharply from the growing to the dormant season measurements. However, because of the larger decline in root TNC in seedlings growing at 5°C, from 22 to 8% (62% decline) between the growing and the dormant season, compared with seedlings growing at 15°C (30%) and 25°C (36%), there was a soil temperature by season interaction ($p$ < 0.001). Leaf TNC in *Populus tremuloides* was 29% of dry mass in plants grown at 5°C compared with 22% in leaves of seedlings grown at 15 and 25°C ($p$ = 0.004) (data not shown).

During the growing season, *Picea glauca* seedlings grown at 5°C had 22% TNC compared with 18% for seedlings grown at 15 and 25°C ($p$ < 0.001). There were no differences in TNC between seedlings grown at 15 and 25°C (Fig. 3E). In contrast to *Populus tremuloides*, TNC concentrations in *Picea glauca* were only marginally lower in the dormant season compared with the growing season ($p$ = 0.067). While no differences were detected between measurements from the growing and the dormant season, seedlings at 5°C had higher root TNC than seedlings at 15 and 25°C ($p$ < 0.001); however, root TNCs at 15 and 25°C were not different (Fig. 3F). Leaf TNC in *P. glauca* was not different among the three soil temperatures and was 25, 24, and 22% for 5, 15, and 25°C, respectively ($p$ = 0.155) (data not shown).

In *Populus tremuloides*, N concentration per plant was higher for seedlings grown at 25°C compared with 5°C ($p$ = 0.009) (Fig. 3C). Nitrogen concentrations per plant were 1.45, 1.57, and 1.67% for seedlings grown at 5, 15, and 25°C, respectively, while root nitrogen in *Populus tremuloides* was lower at 25°C compared with 5°C (Fig. 3D). Overall, N concentrations per plant were significantly higher during the growing season compared with the dormant season ($p$ < 0.001), but N concentrations in roots were not different between seasons ($p$ = 0.134).

In *Picea glauca*, seedlings grown at 5°C had lower N concentration per plant (1.28%) compared with seedlings grown at 25°C (1.47%); seedlings grown at 15°C (1.38%) were not different from those grown at 5 or 25°C (Fig. 3G). While *Populus tremuloides* seedlings showed a significant reduction in N concentration per plant between the growing and the dormant season, *Picea glauca* N content per plant showed only a marginal reduction in N concentration between the dormant and growing season ($p$ = 0.080); however, this was not the case in roots ($p$ = 0.124). Root N in *Picea glauca* was not affected by soil temperature ($p$ = 0.107) (Fig. 3H).

## Gas exchange and root respiration measurements

Net assimilation (NA) increased with increasing soil temperatures in *Populus tremuloides* ($p$ < 0.001). Net assimilation was 6.5 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at 5°C, 14.8 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at 15°C, and 16.3 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at 25°C (Fig. 4A). Stomatal conductance ($g_s$) increased with increasing soil temperatures from 68 $mmol \cdot m^{-2} \cdot s^{-1}$ at 5°C, to 186 $mmol \cdot m^{-2} \cdot s^{-1}$ at 15°C, and 200 $mmol \cdot m^{-2} \cdot s^{-1}$ at 25°C ($p$ < 0.001). NA and $g_s$ were not different in *Populus tremuloides* seedlings growing at 15 and 25°C (Figs. 4A and 4B).

In *Picea glauca*, NA ($p$ = 0.719) and $g_s$ ($p$ = 0.931) were not affected by soil temperature. Over all soil temperatures, NA in *Picea glauca* was 1.95 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and $g_s$ was 54 $mmol \cdot m^{-2} \cdot s^{-1}$ (Figs. 4D and 4E).

Root respiration in *Populus tremuloides* ($p$ < 0.001) and *Picea glauca* ($p$ < 0.001) increased with increasing soil temperatures. Overall, respiration rates in *Populus tremuloides* roots were higher during the growing than during the dormant season ($p$ < 0.001); however, at 25°C there was no difference in respiration rates between the two seasons, while at 15 and 5°C, respiration rates were higher in the growing season than in the dormant season, which resulted in a significant season by soil temperature interaction ($p$ = 0.004) (Fig. 4C). Roots in *Picea glauca* also had overall higher respiration rates in the growing compared with the dormant season ($p$ = 0.001); however, respiration rates were not different between growing and dormant season in seedlings grown at 5°C compared with seedlings grown at 15 and 25°C resulting in a significant season by soil temperature interaction ($p = 0.007$) (Fig. 4F).

## Discussion

At cold soil temperature, *Populus tremuloides* root growth was negligible, shoot growth was severely restricted, and gas exchange was only 40% of that when seedlings were grown in warm soil temperatures. Because of its higher net assimilation in warm soils and the sustained addition of new leaves during the growth period, *Populus tremuloides* seedlings grew massively in height relative to the seedlings in cold soils. These results are consistent with earlier studies on root and shoot growth in *Populus tremuloides* and *Populus balsamifera* L. (Tryon and Chapin 1983; Landhäusser et al. 1996; Landhäusser and Lieffers 1998).

In contrast to *Populus tremuloides*, with *Picea glauca*, there was some new root growth at 5°C but only moderate root growth at 15° and 25°C (Figs. 2B and 2F) and no difference in shoot growth with temperature. *Picea glauca* had little differences in NA and $g_s$ in response to soil temperature. Similar results have been reported for *Picea glauca* saplings (Man and Lieffers 1997), *Picea engelmannii* Parry ex Engelm. trees (Day et al. 1990), *Picea sitchensis* (Bong) Carrière (Turner and Jarvis 1975), and for various herbaceous species (Anderson and McNaughton 1973), where net assimilation rates at low soil temperature were comparable with rates at warmer soil temperatures. In contrast, a reduction of NA and $g_s$ with decreasing soil temperature has been reported for *Picea* species (e.g., Neilson and Jarvis 1976; DeLucia 1986; Grossnickle 2000). Day et al. (1990) suggested that these contradictory outcomes could be the result of experimentally chilling actively growing seedlings instead of measuring seedlings, which were hardened to cool root temperatures. Based upon our data and the literature, it appears that NA or $g_s$ in *Picea glauca* increase very steeply with root temperature and reach a plateau with further increase in temperature (analogous to saturation level of a light response curve) (DeLucia 1986). In contrast, NA or $g_s$ in *Populus tremuloides* approached their maxima at 25°C root temperature. Suppressed root growth at cold soil temperatures in conifers has been reported for *Pinus sylvestris* L. (Varpaavuori et al. 1992) and *Picea mariana* (Mill.) BSP (Tryon and Chapin 1983; Landhäusser et al. 1996). Tryon and Chapin (1983) noted that of a group of boreal forest tree species, *Picea mariana* was least sensitive to cold soils (10°C) (based upon root and shoot growth), and *Populus tremuloides* was most sensitive.

The low $g_s$ found in plants grown at cold soils compared with warm soils for *Populus tremuloides* in this study and earlier works (Wan et al. 1999; Wan and Zwiazek 1999) suggests that roots are slow to take up water when cold. In contrast, based upon $g_s$ measures, *Picea glauca* grown at 5°C appears to have similar water uptake as roots grown at 25°C soil temperature (Fig. 4E). While high viscosity of water and reduced permeability of roots are known to slow root water uptake at cold soil temperatures (e.g., Kaufmann 1975; Häussling et al. 1988; Grossnickle 2000), these data suggest that other factors, such as cell metabolism and membrane properties, may also be affected (Zhang and Tyerman 1991). For *Populus tremuloides*, Wan et al. (2001) demonstrated that water channel proteins are important for water uptake. We speculate that water uptake in *Picea glauca* might be more dependent on passive flow than in *Populus tremuloides*, but we cannot explain why $g_s$ of *Picea glauca* did not increase at the warmer soil temperatures in response to the increased root growth. This speculation on different water uptake mechanisms between species is supported by work of Grossnickle and Blake (1985) who found that *Picea glauca* did not show differences in stem water potential ($\Psi$) and $g_s$ with decreasing soil temperatures, while *Populus tremuloides* had significant lower $\Psi$ and $g_s$ at low soil temperatures (Wan et al. 1999).

During the growing season, both *Picea glauca* and *Populus tremuloides* had higher root and total plant TNC at 5°C soil temperature than at 25°C (Fig. 3). The lower TNC concentrations at 25°C were most likely related to increased allocation of carbon to shoots and root structures at the expense of TNC reserves; this was especially so for *P. tremuloides* where total plant mass almost tripled, while in *Picea glauca*, it increased by 18%. The reduced root TNC reserves at the warmer soil temperature in *Picea glauca* and *Populus tremuloides* could also be related to an increase in root respiration with increasing soil temperature (Fig. 4F). Thus, high soil temperature may result in a trade-off between increased root growth and higher respiration cost, especially in *Picea glauca*. For *Picea glauca*, warm soils could be a disadvantage relative to *Populus tremuloides*, since *Picea glauca*'s net assimilation rates did not increase with temperature, while there were substantial increases in root respiration. Because of its evergreen status, this might be partially offset by longer periods of photosynthesis during spring and fall (Man and Lieffers 1997).

*Populus tremuloides* seedlings growing at low soil temperatures had 31% higher leaf TNC concentrations at 5°C soil temperature compared with 15 and 25°C. Accumulations of carbohydrates in leaf tissue have been shown to lead to lower rates of net assimilation in other species (DeLucia 1986; Azcon-Bieto 1983). This reduction in net assimilation rates has been linked to the weakening of the root carbon sink strength causing a carbohydrate feedback inhibition of NA in the leaves (Herold 1980). In *Picea glauca*, this increase in needle TNC concentrations in response to low soil temperatures was not detected. Although our study did not distinguish between sugar and starch concentrations, our ongoing study of seasonal carbohydrates in *Populus tremuloides* suggests that growing season starch concentrations in leaves are negligible.

Total plant and root TNC concentrations in dormant *Populus tremuloides* seedlings were sharply lower than during the growing season. This decline appears to be related to an increase in the density of root tissue during the early dormant period, i.e., there was no change in root volumes, but root mass increased (Figs. 2B and 2C). Presumably, the root TNC was converted into other structural components such as cell walls or into other storage forms than starch such as lipids or hemicellulose (Dickson 1991). As the root mass in the dormant season was greater than that during the growing season, there was likely translocation of resources to the roots from aboveground parts of the plant during this time period. *Picea glauca* root mass did not increase during the dormant period nor did it show a reduction in TNC concentration between the growing and dormant periods.

While the results of this study are based on a short-term experiment, results may suggest three factors affecting our understanding of the ecology of *Picea glauca* and *Populus tremuloides*.

(1) *Picea glauca* has a much more conservative growth and reserve strategy compared with *Populus tremuloides*. Canham et al. (1999) suggest that tree species with indeterminant or lammas growth invest more into structural biomass than into reserves compared with species that terminate shoot elongation earlier. This may also be important in explaining why *Populus tremuloides* is more likely to die under light suppression compared with *Picea glauca* (Kobe 1997; Wright et al. 1998; Landhäusser and Lieffers 2001).

(2) *Populus tremuloides* will have an advantage over *Picea glauca* on sites with warm soils, especially when resources such as light, water, and nutrients are not limiting. Conversely, *Picea glauca* could have an advantage over *Populus tremuloides* in cold soils.

(3) The apparent decline in soil temperature with gradual dominance of *Picea glauca* in mixedwood stands (Amacher et al. 2001) is thus likely to contribute to a growth decline of the *Populus tremuloides* component; decreased growth of *Populus tremuloides* in stands with understory *Picea glauca* has been reported (MacPherson et al. 2001).

## Acknowledgements

This study has been supported by funds from Ainsworth Lumber Inc., Alberta Pacific Forest Industries Inc., Daishowa Marubeni International Ltd., Millar Western Industries Ltd., Slave Lake Pulp Corp., and Weyerhaeuser Canada Ltd., all matched by the Natural Sciences and Engineering Research Council. Sarah Lieffers, Line Blackburn, Geoff Eerkes, and Ben Seaman assisted in the experimental work.

## References

Amacher, M.C., Johnson, A.D., Kutterer, D.E., and Bartos, D.L. 2001. First-year postfire and postharvest soil temperatures in aspen and conifer stands. USDA Forest Serv. Res. Pap. RMRS-RP–27-WWW.

Anderson, J.E., and McNaughton, S.J. 1973. Effects of low soil temperature on transpiration, photosynthesis, leaf relative water content, and growth among elevationally diverse plant populations. Ecology, **54**: 1220–1233.

Azcon-Bieto, J. 1983. Inhibition of photosynthesis by carbohydrates in wheat leaves. Plant Physiol. **73**: 681–686.

Bonan, G.B. 1992. Soil temperature as an ecological factor in boreal forests. *In* System analysis of the global boreal forest. *Edited by* H.H. Shugart, R. Leemans, and G.B. Bonan. Cambridge Press, Cambridge, U.K. pp. 126–143.

Burton, A.J., Zogg, G.P., Pregitzer, K.S., and Zak, D.R. 1997. Effects of measurement $CO_2$ concentration on sugar maple root respiration. Tree Physiol. **17**: 421–427.

Canham, C.D., Kobe, R.K., Latty, E.F., and Chazdon, R.L. 1999. Interspecific and intraspecific variation in tree seedling survival: effects of allocation to roots versus carbohydrate reserves. Oecologia, **121**: 1–11.

Clinton, B.D., and Vose, J.M. 1999. Fine root respiration in mature eastern white pine (*Pinus strobus*) in situ: the importance of $CO_2$ in controlled environments. Tree Physiol. **19**: 475–479.

Day, T.A., DeLucia, E.H., and Smith, W.K. 1990. Effect of soil temperature on stem sap flow, shoot gas exchange and water potential of *Picea engelmannii* (Parry) during snowmelt. Oecologia, **84**: 474–481.

DeByle, N.V., and Winokur, R.P. 1985. Aspen: ecology and management in the western United States. USDA For. Serv. Gen. Tech. Rep. RM–119.

DeLong, C. 1991. Dynamics of boreal mixedwood ecosystems. *In* Northern Mixedwood ‘89. Proceedings of a Symposium, 12–14 Sept. 1989, Fort St. John, B.C. *Edited by* A. Shortreid. Canadian Forestry Service, Pacific Forestry Centre, Victoria, B.C. For. Resour. Dev. Agree. Rep. 164. pp. 30–31.

DeLucia, E.H. 1986. Effects of low root temperature on net photosynthesis, stomatal conductance and carbohydrate concentration in Engelmann spruce (*Picea engelmannii* Parry *ex* Engelm.) seedlings. Tree Physiol. **2**: 527–533.

DesRochers, A. 2000. Aspen (*Populus tremuloides*) clonal root dynamics and respiration. Ph.D. dissertation, University of Alberta, Edmonton.

Dickson, R.E. 1991. Assimilate distribution and storage. *In* Physiology of trees. *Edited by* A.S. Raghavendra. Wiley, New York. pp. 51–85.

Epstein, E. 1972. Mineral nutrition of plants: principles and perspectives. John Wiley & Sons, Inc., London.

Folk, R.S., Grossnickle, S.C., and Russel, J.H. 1995. Gas exchange, water relations and morphology of yellow-cedar seedlings and stockings before planting and during field establishment. New For. **9**: 1–20.

Grossnickle, S.C. 1987. Influence of flooding and soil temperature on the water relations and morphological development of cold-stored black spruce and white spruce seedlings. Can. J. For. Res. **17**: 821–828.

Grossnickle, S.C. 2000. Ecophysiology of northern spruce species: the performance of planted seedlings. National Research Council Research Press, Ottawa, Ont.

Grossnickle, S.C., and Blake, T.J. 1985. Acclimation of cold-stored jack pine and white spruce seedlings: effect of soil temperature on water relations. Can. J. For. Res. **15**: 544–550.

Häussling, C.A., Jorn, C.A., Lehmbecker, G., Hecht-Buchholz, C., and Marschner, H. 1988. Ion and water uptake in relation to root development in Norway spruce (*Picea abies*). J. Plant Physiol. **13**: 486–491.

Herold, A. 1980. Regulation of photosynthesis by sink activity—the missing link. New Phytol. **86**: 133–144.

Hogg, E.H., and Lieffers, V.J. 1991. The impact of *Calamagrostis canadensis* on soil thermal regimes after logging in northern Alberta. Can. J. For. Res. **21**: 387–394.

Kalra, Y.P., and Maynard, D.G. 1991.Method mannual for forest soil and plant analysis. For. Can. North. For. Cent. Inf. Rep. NOR-X-319.

Kaufmann, M.R. 1975. Leaf water stress in Engelmann spruce. Influence of the root and shoot environments. Plant Physiol. **56**: 841–844.

Kobe, R.K. 1997. Carbohydrate allocation to storage as a basis of interspecific variation in sapling survivorship and growth. Oikos, **80**: 226–233.

Landhäusser, S.M., and Lieffers, V.J. 1998. Growth of *Populus tremuloides* in association with *Calamagrostis canadensis*. Can. J. For. Res. **28**: 396–401.

Landhäusser, S.M., and Lieffers, V.J. 2001. Photosynthesis and carbon allocation of six boreal tree species grown in understory and open conditions. Tree Physiol. **21**: 243–250.

Landhäusser, S.M., Wein, R.W., and Lange, P. 1996. Gas exchange and growth of three arctic treeline tree species under different soil temperature and drought preconditioning regimes. Can. J. Bot. **74**: 686–693.

Landhäusser, S.M., Stadt, K.J., and Lieffers, V.J. 1997. Photosynthetic strategies of summergreen and evergreen understory herbs of the boreal mixedwood forest. Oecologia, **112**: 173–178.

Lieffers, V.J., Macmillan, R.B., MacPherson, D., Branter, K., and Stewart, J.D. 1996. Semi-natural and intensive silvicultural systems for the boreal mixedwood forest. For. Chron. **72**: 286–292.

MacPherson, D.M., Lieffers, V.J., and Blenis, P.V. 2001. Productivity of aspen stands with and without a spruce understory in Alberta’s boreal mixedwood forests. For. Chron. **77**: 351–356.

Man, R., and Lieffers, V.J. 1997. Seasonal variations of photosynthetic capacities of white spruce (*Picea glauca*) and jack pine (*Pinus banksiana*) saplings. Can. J. Bot. **75**: 1766–1771.

Neilson, R.E., and Jarvis, P.G. 1976. Photosynthesis in Sitka spruce (*Picea sitchensis* (Bong.) Carr.) IV. Response of stomata to temperature. J. Appl. Ecol. **12**: 879–891.

Peterson, E.B., and Peterson, N.M. 1992. Ecology, management, and use of aspen and balsam poplar in the Prairie Provinces. Forestry Canada, Northwest Region. Northern Forestry Centre, Edmonton Alta. Spec. Rep. 1.

Qi, J., Marshall, J.D., and Mattson, K.G. 1994. High soil carbon dioxide concentrations inhibit root respiration of Douglas fir. New Phytol. **128**: 435–442.

Salisbury, F.B., and Ross, C.W. 1992. Plant physiology. 4th ed. Wadsworth Publishing Co. Inc., Belmont, Calif.

Shepperd, W.D., and Smith, F.W. 1993. The role of near-surface lateral roots in the life cycle of aspen in the central Rocky Mountains. For. Ecol. Manage. **61**: 157–170.

Smith, D., Paulsen, G.M., and Raguse, C.A. 1964. Extraction of total available carbohydrates from grass and legume tissue. Plant Physiol. **39**: 960–962.

Stadt, K.J., and Lieffers, V.J. 2000. MIXLIGHT: a flexible light transmission model for mixed-species forest stands. Agric For. Meteorol. **102**: 235–252.

Tryon, P.R., and Chapin, F.S. 1983. Temperature control over root growth and biomass in taiga forest trees. Can. J. For. Res. **13**: 827–833.

Turner, N.C., and Jarvis, P.G. 1975. Photosynthesis in Sitka spruce (*Picea sitchensis* (Bong.) Carr.) IV. Response to soil temperature. J. Appl. Ecol. **12**: 561–576.

Van Cleve, K., Oliver, L.K., Schlentner, R., Viereck, L.A., and Dyrness, C.T. 1983. Productivity and nutrient cycling in taiga forest ecosystems. Can. J. For. Res. **13**: 747–766.

Vapaavuori, E.M., Rikala, R., and Ryyppö, A. 1992. Effects of root temperature on growth and photosynthesis in conifer seedlings during shoot elongation. Tree Physiol. **10**: 217–230.

Viereck, L.A. 1970. Forest succession and soil development adjacent to the Chena River in interior Alaska. Arct. Alp. Res. **2**: 1–26.

Wan, X., and Zwiazek, J.J. 1999. Mercuric chloride effects on root water transport in aspen seedlings. Plant Physiol. **121**: 939–946.

Wan X., Landhäusser, S.M., Zwiazek, J.J., and Lieffers, V.J. 1999. Root water flow and growth of aspen (*Populus tremuloides*) at low root temperatures. Tree Physiol. **19**: 879–884.

Wan, X., Zwiazek, J.J., Lieffers, V.J., and Landhäusser, S.M. 2001. Hydraulic conductance in aspen (*Populus tremuloides*) seedlings exposed to low soil temperatures. Tree Physiol. **21**: 691–696.

Wright, E.F., Coates, D., Canham, C.D., and Bartemucci, P. 1998. Species variability in growth response to light across climatic regions in northwestern British Columbia. Can. J. For. Res. **28**: 871–886.

Zhang, W.H., and Tyerman, S.D. 1991. Effects of low $O_2$ concentration and azide on hydraulic conductivity and osmotic volume of the cortical cells of wheat roots. Aust. J. Plant Physiol. **18**: 603–613.