Root Growth, Plug Cohesion, Mineral Nutrition, and Carbohydrate Content of 1+0 *Picea mariana* Seedlings in Response to a Short-Day Treatment

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Abstract

A short-day (SD) treatment was applied to containerized 1+0 black spruce (*Picea mariana* [Mill.] B.S.P.) with the objective of increasing root mass and root-plug cohesion. The SD treatment resulted in the induction of bud formation, cessation of height growth, and significant increases in carbohydrate content (sucrose, pinitol, and starch), root nutrient contents, and root dry mass. Allometric models showed that given the same shoot mass, the average seedling grown under the SD treatment had 25 percent more root mass than those in the control treatment, which led to a significant improvement in root-plug cohesion. Seedling quality evaluation before delivery to the planting site showed that 91 percent of 1+0 black spruce seedlings subjected to SD treatments conformed to quality standards compared with 71 percent for those subjected to the control treatment. These results indicate that the use of an SD treatment may improve the profitability of forest nurseries by increasing the quality and quantity of shippable seedlings.

Introduction

More than 150 million forest seedlings are grown annually in Québec, Canada (Lamhamedi and others 2007). Nearly 2,500 different stock types are produced in 24 forest nurseries (18 private and 6 government) using different production scenarios. Most (90 percent) of the seedlings are container grown and the remainder produced are bareroot seedlings. Nursery managers must work within environmental constraints beyond their control, which can reduce the morphophysiological quality of the seedlings. The most notable constraints include climatic extremes and interannual variability as well as the very short growing season in northern forest nurseries.

Before being planted, seedlings grown in Québec forest nurseries are subjected to a morphophysiological evaluation for 25 norms (Veilleux and others 2008). These norms are specific to each stock type and production scenario. Evaluation of 1+0 and 2+0 containerized seedlings is conducted both in the autumn and spring preceding delivery to the planting site. Foliar nitrogen (N) concentration and rooting sufficiency are among the 25 quality norms that are evaluated. During the evaluation, a seedling is deemed to have insufficient root development if the root-plug breaks, either partially or completely, is incomplete after extraction from the container cavity, or exhibits two or more discontinuous sections of undamaged roots separated by more than 5.0 mm (0.2 in). The seedling is also rejected if more than 33 percent of the roots on the periphery of the root plug are dead or decaying (Veilleux and others 2008). An assessment of data from the 24 Québec forest nurseries between 2003 and 2006 indicated that large portions of seedlings were rejected because of failure to meet nine principal norms. Among these norms, the proportion of black spruce seedlings grown in 67-50 containers (67 cavities, 50 cm^3 [3 in^3]/cavity) had insufficient root development that reached an average of 54.3 percent during the autumn before delivery (Lamhamedi and others 2007). This level of insufficient root development varies significantly among nursery growers.

Several cultural techniques have been modified, at an operational scale, to improve seedling root growth and plug cohesion (Landis and others 1989, 1990). These techniques include container design, cavity volume and arrangement (Landis and others 1990), the use of peat and compost-based growing media with the desired physicochemical characteristics (Bernier and others 1995, Heiskanen 1993, Veijalainen and others 2008), and the optimization of irrigation and fertilization regimes (Lamhamedi and others 2006, Landis and others 1989).

In addition, short-day (SD) treatments may be applied early in the growing season to improve root dry mass and plug cohesion. In general, this treatment is used at an operational scale for several coniferous species produced in North American and Scandinavian forest nurseries to induce bud formation, control height growth, and improve frost tolerance (Bigras and others 2001, Colombo 1996, Colombo and others 2001, Hawkins and Shewan 2000, Kohmann and Johnsen 2007, Krasowski and others 1993, MacDonald and Owens 2006, Rostad and others 2006, Turner and Mitchell 2003). The treatment is also used to improve seedling performance under xeric conditions (Luoranen and others 2007) and to combat other stresses on the plantation site (Tan 2007).

Our hypothesis was that an SD treatment, applied for a limited time during the active growing phase, increases root-plug cohesion and root mass by inducing a greater allocation of biomass to root growth and development. This shift in allocation toward the root system has generally been inferred from instantaneous shoot/root ratio assessments (Hawkins and Draper 1988, Krasowski and Owens 1991), but to our knowledge has not been quantified continuously with allometric models in response to early SD treatments applied during rapid shoot elongation. A need also exists to increase our knowledge about the effect of SD treatments on tissue carbohydrate and nutrient contents. The general objectives of the present study were to (1) evaluate the effects of SD treatments during the active growing season on shoot and root growth, plug cohesion, mineral nutrition, carbohydrate content, and bud formation of 1+0 black spruce seedlings produced under tunnel conditions in a forest nursery; and (2) quantify the effects of SD treatments on dry-matter allocation between shoots and roots through the use of allometric models.

Materials and Methods

Plant Material and Experimental Design

Black spruce seeds (seedlot: EPN-V1-LEV-2-2; production code GI05EPN05-C06) were sown at the end of March 2006 into 67-50 containers (IPL 67-50, Saint-Damien, Québec, Canada; 67 cavities, 50 cm^3 [3 in^3]/cavity; cavity depth: 8.7 cm [3.4 in]; cavity diameter: 3.2 cm [1.3 in]; 864 seedlings/m^2 [80 seedlings/ft^2]). The cavities were filled with a moist, peat-based substrate adjusted to a bulk density of 0.09 g/cm^3 (0.0002 oz/in^3). The percentage of large (10-mesh sieve), medium (20-mesh sieve), short (40- and 100-mesh sieves), and fine particles (200-mesh sieve) represented 12, 29, 60, and 11 percent of the growing medium, respectively. The containers were installed in a standard production tunnel (figure 1) at Serres et Pépinière Girardville, a private forest nursery located in the Saguenay-Lac St. Jean region of Québec, Canada (latitude 49° 01’ 06”; longitude 72° 30’ 42”). The tunnel, with an average capacity of 250,000 seedlings, was covered with milk-white polyethylene, 100 mm thick (4 mil = 400 gauge = 0.004 inches), which transmitted 50 to 55 percent of incident light (multi-layer greenhouse cover film, type UVA/White 45 percent, (Ginegar Plastic Products Ltd, Kibbutz, Israel). The cover could be retracted along both sides to facilitate aeration and modify the air temperature inside the tunnel. After seed germination was complete (early May), the germinants were thinned to one per cavity. No germinants were transplanted to empty cavities.

The SD treatment was applied during the most rapid period of shoot elongation as a cultural technique to increase root growth and improve plug cohesion. It was applied between June 30 and July 18, 2006, and consisted of modifying the photoperiod to light/dark: 8hr/16hr. This treatment differs from the typical SD treatment in Québec, which is applied in forest nurseries toward the end of the growing season (mid-August) to improve hardening processes and frost tolerance. A black polyethylene cover, positioned approximately 40 cm (16 in) above the shoot tips, was manually installed above the seedlings and removed each day to create the dark period. The containers of seedlings subjected to the control treatment were grown under natural light conditions where the day length varied between 15.3 and 16 hr per day (Saguenay: 48° 25’ 00” N., 71° 04’ 00” W., Québec, Canada). The two treatments (SD and control) were installed along the length of a standard production tunnel in five randomized complete blocks (figure 1). In each block, the group of 6 containers subjected to the control treatment was isolated from the 11 containers subjected to SD treatment by a wall of white polystyrene foam to prevent incident light from reaching the neighboring containers during the dark periods implicit to the SD treatment (figure 1). In each block, 5 of the 6 control containers and 10 of the 11 SD containers were sampled for growth and mineral nutrition and the remaining container in each was used to assess bud formation.

Growth and Environmental Conditions

Seedlings in both treatments were grown using standard nursery cultural techniques for the production of 1+0 black spruce in Québec. The irrigation regime optimized substrate water contents during the different growth phases (Bergeron and others 2004; Lamhamedi and others 2003). The seedlings were irrigated with sprinklers arranged in a square pattern (7.3 by 7.3 m, [24.0 by 24.0 ft]) (Rain-Jet, model 66U, Harnois, Québec, Canada). Substrate water content was monitored by gravimetry. Covering the range of the sprinkler distribution and both treatments, 12 containers were randomly selected and weighed two or three times per week. Average substrate water content ranged between 20 and 50 percent (v/v) during

Figure 1. (a) Production of black spruce seedlings in a standard production tunnel at Serres et Pépinière Girardville (Québec, Canada). (b) Short-day (SD) and control treatments were installed along the length of a standard production tunnel in five randomized complete blocks. (c) Control containers in each block were grouped and were not covered with the black plastic during SD treatment; they were isolated from the containers subjected to SD treatment by a wall of white polystyrene foam to prevent incident light from reaching the neighboring containers during the periods of darkness implicit to the SD treatment. (Photos by: Mohammed S. Lamhamedi, 2006)

the growing season. The control of substrate water content was identical for both treatments and at no time were any of the seedlings subjected to water stress (Bergeron and others 2004).

Seedlings in both treatments were fertilized twice weekly using the approach developed for Québec forest nursery production and *PLANTEC* software (Girard and others 2001). This approach is adapted to the seedlings' demand for nutrients as well as the established growing standards specific to black spruce seedlings (Girard and others 2001, Langlois and Gagnon 1993). The quantities of N, phosphorous (P), and potassium (K) applied per seedling from May 5 to September 26, 2006, were 18 mg (0.0006 oz), 15 mg (0.0005 oz), and 18 mg (0.0006 oz), respectively. During each fertilization session, seedlings also received micronutrient elements. As the growing season progressed, N concentration in the substrate progressively decreased from 143 to 8 ppm and the electrical conductivity (EC) decreased from 188 to 70 μS/cm.

Temperatures in the growing medium surrounding the roots and at the substrate surface were continuously monitored (soil temperature probe model 107B, Campbell Scientific, Edmonton, Alberta, Canada) under both the SD and control treatments. Air temperature and relative air humidity inside the tunnel at 2.0 m (6.5 ft) above the ground surface were measured with a Vaisala RH and Temperature Probe (model HMP35C, Campbell Scientific, Edmonton, Alberta, Canada). A data acquisition system (model CR10X, Campbell Scientific, Edmonton, Alberta, Canada) was used to record the data.

Growth, Mineral Nutrition, and Bud Formation Measurements

Seedling growth, substrate fertility, and tissue mineral content were evaluated from June through early November. Seedlings and substrate subjected to the SD treatment were sampled 10 times and those in the control treatment were sampled 5 times based on previous study methodologies (Lamhamedi and others 2003). Three of the samples for the control treatment were taken after completion of the SD treatment. On the first sampling date, a container was randomly chosen from the first block. On subsequent sampling dates, a container was systematically sampled from the same position in the other four blocks. In each of these containers, 50 of the 67 seedlings were randomly selected and gently extracted, for a total of 250 seedlings/treatment/date. All sampled seedlings were healthy without any visible damage.

The height and root-collar diameter (50 seedlings/block/treatment), root and shoot dry mass (5 composite samples of 10 seedlings/block/treatment), and tissue mineral content

(1 composite sample of 50 seedlings/block/treatment) were measured. Root and shoot tissues were oven-dried for 48 hr at 60 °C (140 °F) before determination of dry mass. After grinding and acid digestion, each composite sample was analyzed for N using the Kjeldahl method and for P, K, calcium (Ca), and magnesium (Mg) by inductively coupled argon plasma analysis (Parkinson and Allen 1975, Walinga and others 1995). The mineral nutrient composition is expressed as content (concentration x dry mass) per seedling (or tissue type) for each element to accurately reflect seedling mineral nutrient uptake and accumulation (Timmer and Miller 1991). Given that seedling tissue was pooled for analyses, nutrient composition was based on the average seedling (or tissue) mass. Substrate fertility (N-NO_3, N-NH_4, $N_{mineral}$ P, K, Ca, and Mg), pH (H_2O), and EC were determined on one composite sample from each treatment (50 root plugs/ composite sample/block) on each sampling date.

Between June 29 and August 10, 2006, the 9 seedlings in the center row of a randomly selected container in each of five blocks within each treatment (total of 45 seedlings/ treatment) were monitored for bud formation. The same seedlings were evaluated three times weekly until a white terminal bud was visible on all of the monitored seedlings (stage II development, per Lesser and Parker 2004). On May 11, 2007, before delivery to the planting site, bud-break status of seedlings subjected to both treatments was evaluated. Bud break was considered to have occurred when green needles were visible under the bud scale cap (Wilkinson 1977). Before being dispatched to the planting site (May 14 and 15, 2007), 120 seedlings were randomly selected from five blocks of each treatment (24 seedlings/block/treatment) and subjected to an assessment of the 25 quality criteria (including insufficient root development, height, diameter, foliar N concentration, forks, and height/diameter) established by the ministère des Ressources naturelles MRN du Québec (Veilleux and others 2008). This assessment of seedling quality, carried out by a team of evaluators accredited by the MRNF, not only determines the level of uniformity of each seedling lot, but it is also used to calculate the compensation the nursery receives for producing the seedlings.

Carbohydrate Analyses

From each treatment/block, 10 seedlings were randomly selected before (June 27, 2006) and after (July 18, 2006) application of the SD treatment. Seedling roots were washed to remove the substrate, then separated from the shoots and stored at 4 °C (39 °F). For each composite sample (roots and shoots; 10 seedlings), the following carbohydrates were extracted with 80 percent hot ethanol and quantified by high-performance liquid chromatography (model 2414, Waters, Milford, MA, United States): glucose, fructose, sucrose, raffinose, and the sugar alcohols, pinitol and inositol. Individual sugars were identified based on retention times relative to known standards. Starch concentrations in roots and shoots were measured on a spectrophotometer (model Spectronic 20, Bausch & Lomb Incorporated, Aliso Viejo, CA, United States).

Statistical Analyses and Dry-Matter Allocation Between Roots and Shoots

Statistical analyses of morphophysiological variables were conducted with the MIXED procedure of SAS (SAS Institute, Cary, NC, United States). The assumption of normality of the error terms was respected for all of the variables and the assumptions of normality and homogeneity of variance were verified. Independence between the sampling dates was presumed and growth variables were measured on different seedlings on each date. The treatment effect was considered significant at 10 percent to account for spatial variability of resources (Lamhamedi and others 2006) in each cavity and an inherent variability in seedling growth resulting from a bulk collection of open-pollinated seeds.

To quantify the effect of each treatment on biomass partitioning between roots and shoots, an allometric equation was developed from individual seedling data pooled over all sampling dates after the application of SD treatments using natural logarithmic transformation:

$$\ln(y_{ij}) = b_{00} + b_{01}trt + b_{10}\ln(x_{ij}) + b_{11}\ln(x_{ij}) * trt + u_i + \varepsilon_{ij}$$

Where:

- y_{ij} : shoot dry mass measured for seedling j, from block i,
- x_{ij} : root dry mass measured for seedling j, from block i,
- trt : 1 if seedling was subjected to « short day » and 0 if not,
- b_{00} : intercept for control seedlings,
- b_{01} : addition component for treatment intercept ($b_{00}+b_{01}$ = intercept for short-day seedlings),
- b_{10} : slope for control seedlings,
- b_{11} : addition component for treatment slope ($b_{10}+b_{11}$ = slope for short-day seedlings),
- u_j : random effect of block j ~ $N(0,\sigma_u^2)$,
- e_{ij} : residual error, ~ $N(0,\sigma^2)$.

Parameters b_{10} and b_{11} describe the partitioning of biomass between shoots and roots and are a measure of the ratio of their relative growth rates during the exponential growth phase (Ledig and others 1970).

Results

Environment Variables

During the germination and active growing periods (mid-April to late July 2006), mean air temperature ranged from 13 °C (55 °F) to 29 °C (84 °F) (figure 2). During the period of bud formation and natural hardening (early August to late September 2006), the average daily temperature inside the tunnel decreased progressively, varying from 23 °C (73 °F) to 6 °C (43 °F). Relative humidity fluctuated between 65 and 85 percent (figure 2). Average maximum temperatures, 2.0 m (6.5 ft) above the ground and at the substrate surface were similar for the two treatments. Night temperatures at the substrate surface were always higher under SD treatment, however, than under the control treatment (figure 3). In general, substrate temperatures in the rooting zone under the SD treatment were also warmer than those of the control treatment (figure 3).

Seedling Growth, Bud Formation, Bud Break, and Uniformity

With the exception of total seedling dry mass ($p = 0.3127$), all growth variables had a significant date by treatment interaction ($p < 0.0001$). SD treatment resulted in the cessation of height growth ($p = 0.0031$) within 2 weeks of

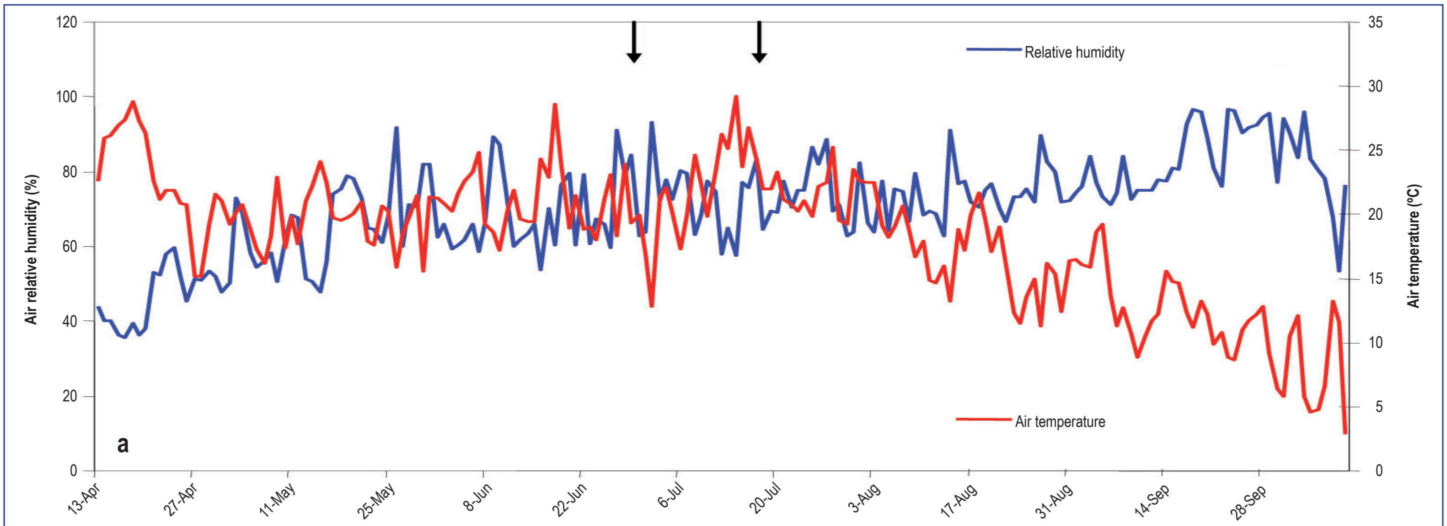

Figure 2. Variations of daily mean air temperature and relative humidity during the growth of 1+0 black spruce seedlings produced under tunnel conditions in a forest nursery. Arrows indicate the beginning and end of the short-day treatment.

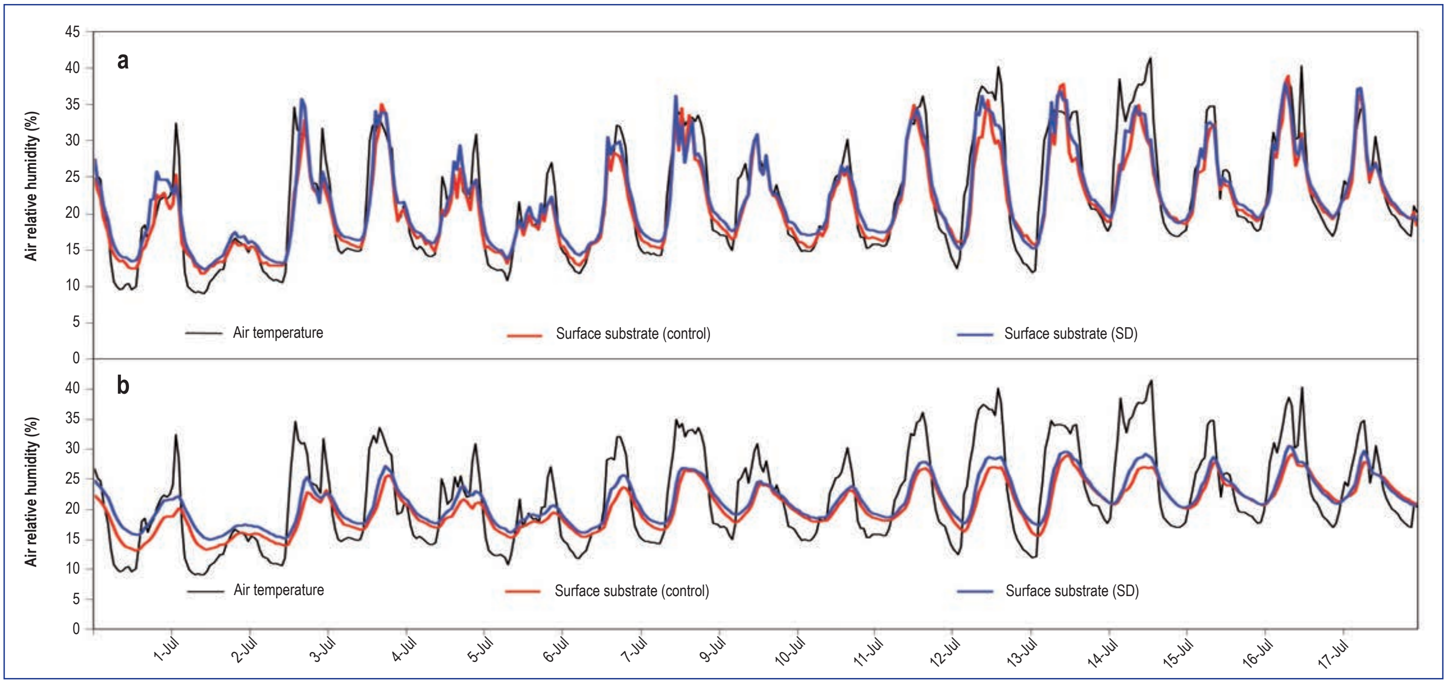

Figure 3. (a) Hourly air temperatures 2 m above and at the substrate surface. (b) Hourly air (2 m) and substrate temperatures for 1+0 black spruce containerized seedlings subjected to control and short-day (SD) treatments.

application, an increase in root mass with time ($p < 0.0001$), and a reduction ($p = 0.0026$) in shoot and total mass of the 1+0 black spruce seedlings (figure 4). Unlike height, the effect of SD treatment on root-collar diameter was not evident after 2 weeks (figure 4) despite slight differences between the two treatments in mid-September ($p = 0.0569$).

All seedlings in the SD treatment formed visible white buds after 2 weeks of treatment, whereas bud formation of seedlings in the control treatment occurred during a prolonged period (mid-July to mid-August) as a function of natural environmental conditions (figure 5). Few seedlings (< 1 percent) broke bud after bud formation despite the favorable environmental conditions for shoot growth during summer and autumn of 2006. After spending the winter outside under the snow, seedlings that had been subjected to the SD treatment broke bud sooner than those grown under the control treatment (figure 5). In addition, the percentage of 1+0 black spruce seedlings that conformed to the 25 MRN norms was higher under the SD treatment (91 percent) than under the control treatment (71 percent).

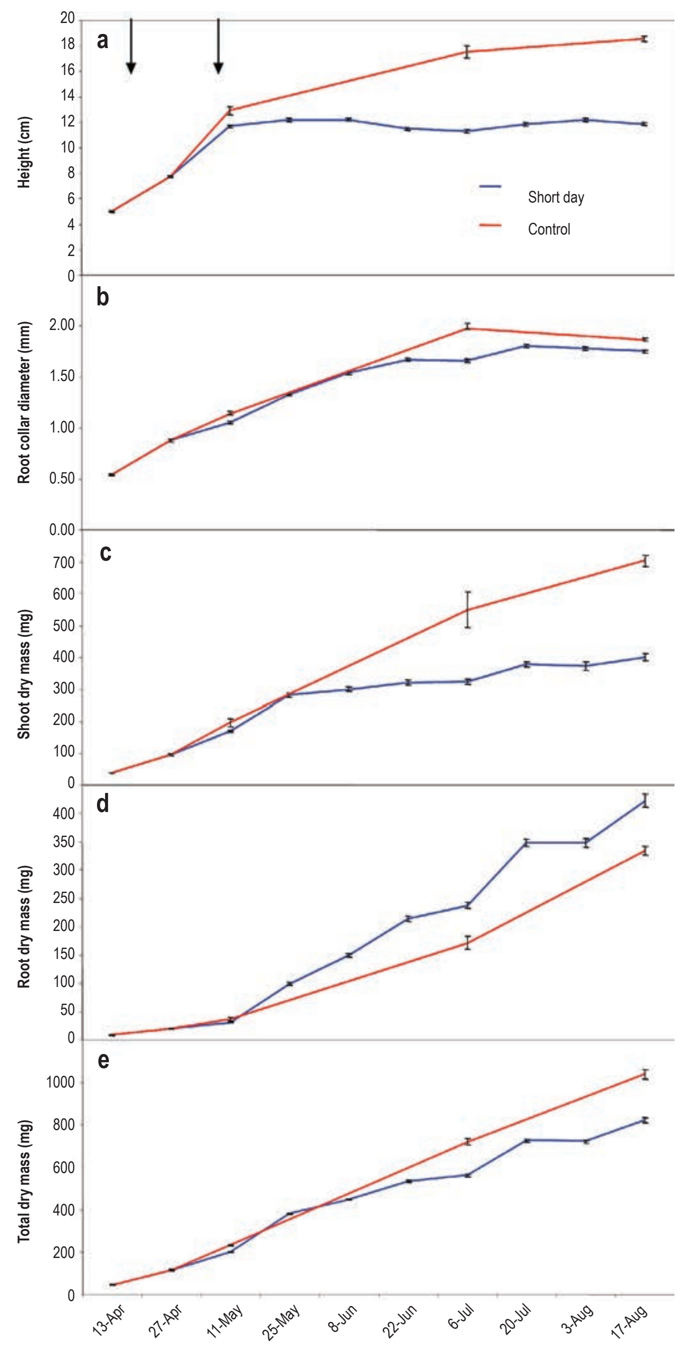

Figure 4. (a) Seasonal changes in height, (b) root-collar diameter, (c) shoot dry mass, (d) root dry mass, and (e) total seedling dry mass of 1+0 black spruce seedlings subjected to the control and short-day (SD) treatments (n = 250 ± SE). Arrows indicate the beginning and end of the SD treatment.

Allocation of Dry Matter Between Shoots and Roots

The allometric models showed that significantly more dry matter was allocated to root growth under the SD treatment than under the control treatment ($p < 0.0001$). Seedlings grown under the SD treatment had a 25-percent increase in root mass compared with seedlings with similar shoot mass that were grown under the control treatment (figures 6 and 7).

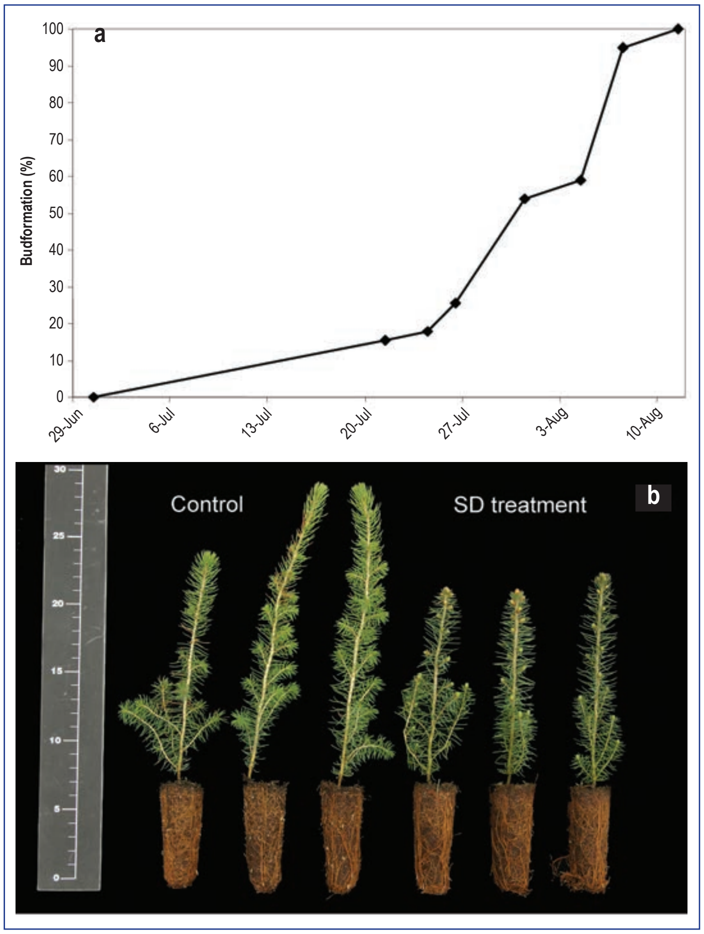

Figure 5. (a) The percentage of bud formation over time in the control seedlings. The seedlings subjected to a short-day (SD) treatment had all formed buds by the end of the SD treatment (July 18, 2006). (b) After spending the winter outside under the snow, seedlings subjected to the SD treatment broke bud sooner than those grown under the control treatment (May 14, 2007).

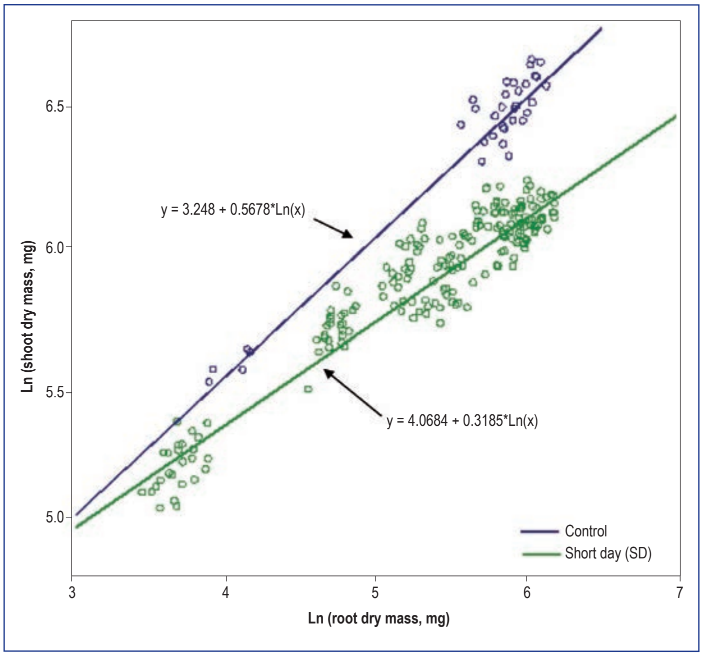

Figure 6. Allometric models of dry-matter allocation between shoots and roots of seedlings subjected to the control and short-day treatments.

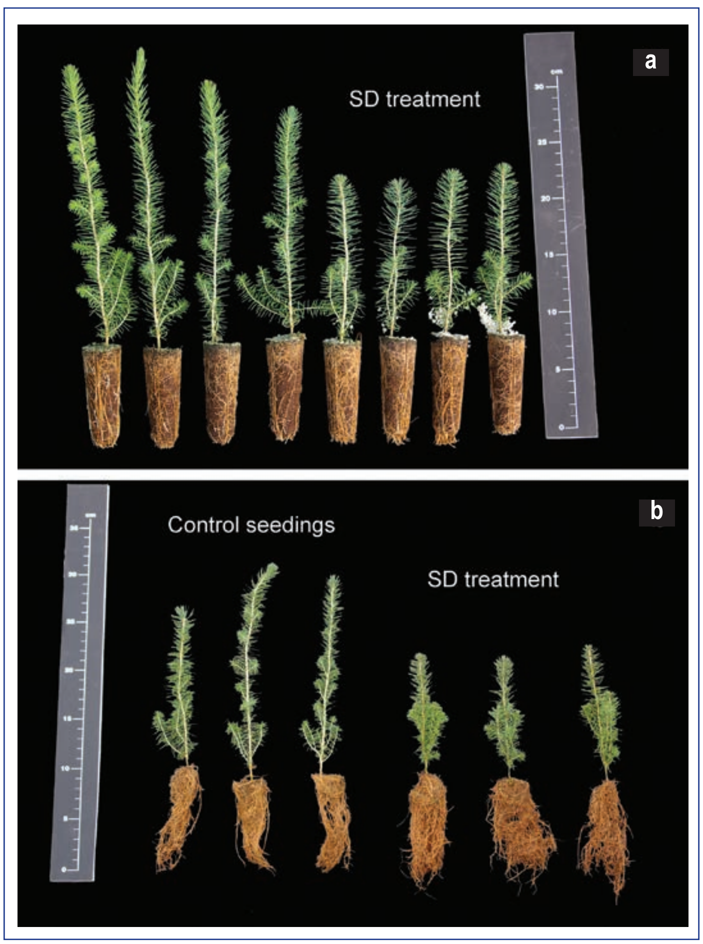

Figure 7. (a) Growth of shoots and roots of black spruce seedlings grown under short-day (SD) and control treatments (September 11, 2006). (b) Growth of roots under the SD treatment was greater than that under the control treatment.

Mineral Nutrition

A significant date by treatment interaction occurred for root and shoot mineral nutrient contents. Root N ($p = 0.0463$), P ($p = 0.0321$), K ($p = 0.0815$), and Mg ($p = 0.0089$) contents were increasingly greater over time for seedlings grown under the SD treatment compared with those in the control treatment (figure 8). Conversely, shoot N ($p = 0.0750$), P ($p = 0.0266$), and K ($p = 0.0023$) contents were increasingly lower over time under SD than under the control treatment (figure 8). With regard to mineral nutrient concentrations, the average root-tissue concentrations, before (N: 2.33 percent, P: 0.85 percent, and K: 2.27 percent) and after the SD treatment (SD, N: 1.34 percent, P: 0.40 percent, and K: 0.88 percent; Control, N: 1.33 percent, P: 0.39 percent, and K: 0.86 percent) were similar for the two treatments. On the final sampling date, average shoot N concentrations were slightly lower in the control plants (SD, N: 1.77 percent; Control, N: 1.34 percent).

Carbohydrates

Fructose content of the shoot tissue did not differ between treatments ($p = 0.2654$), whereas raffinose ($p < 0.0001$), sucrose ($p = 0.0027$), glucose ($p = 0.0138$), pinitol ($p < 0.0001$), and starch ($p = 0.0005$) contents all differed significantly between the two treatments. The SD treatment resulted in a significant increase ($p < 0.001$) in sucrose (4.17 ± 0.44 mg/seedling, [0.00015 oz]), pinitol (4.08 ± 0.21 mg/seedling, [0.00015 oz]), and starch (5.78 ± 0.43 mg/seedling, [0.00020 oz]) contents of the shoot tissue with respect to the carbohydrate contents before application of the SD treatment (sucrose: 2.09 ± 0.50 mg/seedling [0.00007 oz]; pinitol: 1.75 ± 0.30 mg/seedling [0.00006 oz], starch: 4.75 ± 0.46 mg/seedling [0.00017 oz]).

In root tissue, contents of sucrose ($p = 0.6739$), glucose ($p = 0.2247$) or starch ($p = 0.8070$) in the root tissue were unaffected by treatment, whereas raffinose content was significantly higher ($p = 0.0134$) for SD seedlings compared with control seedlings. In contrast, control seedlings showed significantly higher pinitol ($p = 0.0061$) and inositol ($p = 0.0012$) contents compared with SD seedlings.

Discussion

Our results showed an average increase of 25 percent in dry-matter allocation to roots of black spruce seedlings in response to SD treatment under operational conditions (figures 4 and 6) resulting in a 20-percent increase in the proportion of shippable plants with sufficient root development. This cultural technique could potentially

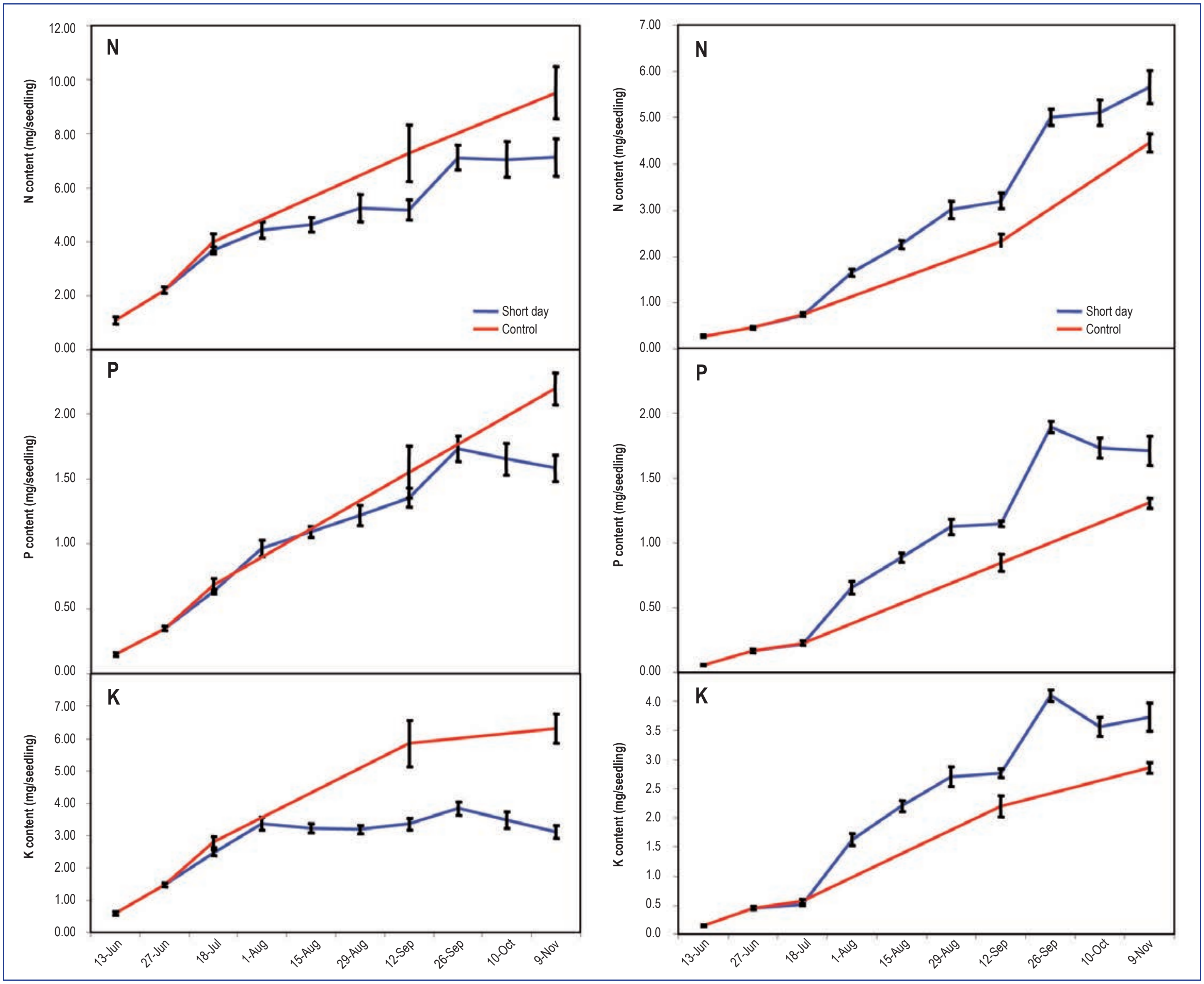

Figure 8. Mineral nutrient content of the shoot and root tissue of seedlings subjected to the control and short-day treatments (n = 5 composites samples ± SE).

improve nursery profitability. Plug cohesion and root development, particularly after the cessation of height growth, are closely linked to current net photosynthesis (Lippu 1998, Ritchie 2003, van den Driessche 1987) and the carbon source: sink dynamics within the plant (Kozlowski 1992). Root growth may become a stronger sink for photosynthates after the initiation of bud formation. In a study by Hawkins and others (1994), an SD treatment increased net photosynthesis in interior spruce (*Picea glauca* [Moench] Voss x *Picea engelmannii* Parry) seedlings and possibly reduced respiration, thus providing a surplus of photosnythates directed toward root growth after bud formation and cessation in height growth. In accordance with other studies (Colombo and others 2001), our results showed that SD could be used as a cultural technique during the most rapid period of shoot elongation to increase root-plug cohesion and root dry mass by inducing a greater allocation of dry matter to root-system development.

The SD treatment in this study caused a significant increase in the tissue contents of certain carbohydrates (sucrose and pinitol) similar to results observed in Norway spruce (Rostad and others 2006), which may have a positive effect on root growth. Krueger and Trappe (1967) showed that the percentage of active root tips and root growth of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) seedlings were inversely correlated with decreasing carbohydrate content. Similar results were observed for *Pinus taeda* L cuttings where dry mass and root surface area were positively correlated with certain carbohydrates (myo-inositol, glucose, fructose, sucrose and raffinose) and foliar N concentration (Rowe and others 2002). In our study, substrate N concentration was high (143 ± 10 ppm) at the beginning of the active growing period to enable seedlings to achieve target heights before application of the SD treatment. After the treatment, environmental conditions were still favorable to physiological activity; thus, N fertilization was significantly reduced (from 40 to 8 ppm) for both treatments to control height growth, avert reflushing, and induce dormancy and hardiness. Mengel and Kirkby (1987) reported that carbohydrates usually accumulate when N fertility is reduced. The biweekly evaluation of tissue and substrate mineral concentrations throughout the growing season indicated that the nutritional status, however, notably N concentrations, were above thresholds deemed critical for growth and gas exchange in black spruce seedlings (Lamhamedi and Bernier 1994, Munson and Bernier 1993). We did not observe any symptoms of N deficiency in either treatment, because black spruce seedlings can grow under conditions of low nutrient availability (Lafond 1966). From our results, it appears that the increase in carbohydrates for seedlings in the SD treatment was caused by the treatment and was unaffected by factors related to mineral nutrition. The increase in shoot N and P content and root K content of seedlings subjected to the SD treatment over those of the control treatment is likely a result of the increased root growth that occurred in response to the SD treatment; the increase in dense, fine white roots increases the absorptive surface area, thereby enabling seedlings to exploit most of the cavity volume and the air spaces between the substrate aggregates.

In addition to increased root growth, this study showed that an SD treatment applied to black spruce seedlings for 2 weeks in late June through early July caused height growth cessation and bud initiation sooner than the control treatment, thereby ensuring crop uniformity. Similar results have been reported for black spruce (Calmé and others 1993; Colombo and others 1981, 2001; D'Aoust 1981) and other coniferous species (Eastham 1990, Hawkins and Draper 1988). Despite the fact that the SD treatment was applied early (June 30 through July 18) and that the growing conditions were favorable during the entire growing season, we only observed reflushing in a few seedlings in the intervening period between the end of the SD treatment and the onset of autumn. In Québec, SD is generally applied in forest nurseries at the end of the growing season (mid-August) to induce hardening and frost tolerance, rather than to increase root-plug cohesion and root dry mass, which is the same objective of our study. The absence of reflushing may be explained by a strict control of substrate water content and fertility throughout the growing season and from the judicious choice of a seed provenance that responded very well to the SD treatment. In a greenhouse study with a seedlot originating from another seed orchard, Lamhamedi and others (2007) observed late-summer apical and lateral bud break in more than one-half of the 1+0 black spruce seedlings after SD treatment. Kohmann and Johnsen (2007) also observed that reflushing after SD treatment was dependent on the genetic origin of *Picea abies* seeds as well as the geographic location of the nursery. These different findings indicate that the application of an SD treatment during the active growing phase (early July) does not guarantee a definitive cessation of growth. To avoid reflushing after an SD treatment, Kohmann and Johnsen (2007) suggest prolonging the length of the SD treatment to a total of 3 weeks, and increasing dark period (> 14 hr). After outplanting, the relatively rapid budburst of seedlings subjected to the SD treatment compared with those under the control treatment may impart an early growth advantage but could also result in susceptibility to late spring frost injury, especially in ecological regions where the probability of spring frosts is relatively high.

Conclusion

All of the 1+0 black spruce seedlings subjected to the 2-week SD treatment ceased height growth and set buds, thus enhancing height uniformity. In addition, the SD treatment significantly increased mineral nutrition and carbohydrate contents, and it increased dry-matter allocation to roots, thus improving root-plug cohesion and the presence of roots on the periphery of the root plug. The percentage of seedlings subjected to the SD treatment that met the quality standards was 20 percent higher than those under the control treatment indicating that the use of an SD treatment may improve the profitability of forest nurseries. Good plug cohesion is essential to maintaining root-system integrity during lifting, shipping, and planting. Fine roots on the periphery of the root plug improve contact at the root-soil interface, thus increasing seedling survival and growth rates after planting.

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