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Growth, shoot phenology and physiology of diverse seed sources of black spruce: I. Seedling responses to varied atmospheric CO_2 concentrations and photoperiods

KURT H. JOHNSEN[1] and JOHN R. SEILER[2]

[1] *Canadian Forest Service, P.O. Box 4000, Fredericton, NB E3B 5P7, Canada*

[2] *Department of Forestry, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061-0324, USA*

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Summary We conducted a greenhouse experiment to determine: (1) if diverse provenances of black spruce (*Picea mariana* (Mill.) B.S.P.) respond similarly in growth, phenology and physiology to an approximately 300 ppm increase in atmospheric CO_2 concentration, and (2) the influence of photoperiod on both provenance and provenance × CO_2 interaction effects. Seedlings from provenances that originated from the Yukon (63°34′ N, 135°55′ W), British Columbia (58°47′ N, 123°38′ W), Alberta (52°22′ N, 115°15′ W), Newfoundland (50°54′ N, 56°06′ W) and Ontario (48°59′ N, 80°38′ W and 45°10′ N, 77°10′ W) were subjected to growth analysis in greenhouse growth chambers supplied with 712 ± 93 (SD) ppm CO_2 (elevated) or 394 ± 59 ppm CO_2 (ambient). Seedlings from Provenances 7000 and 6901 were also subjected to an extended photoperiod treatment and periodically measured for shoot and root gas exchange.

In response to a natural photoperiod, southern provenances grew more, broke and set bud later, and partitioned more biomass to shoot versus root than northern provenances. These differences among provenances were influenced by the extended photoperiod treatment but not by the elevated CO_2 treatment. Averaged across all provenances, elevated CO_2 increased seedling final weights by 55%; however, the elevated CO_2 treatment had no effect on the provenance differences in any measured trait. We conclude that the large differences in physiology, phenology and growth among these diverse provenances of black spruce were expressed similarly in both ambient and elevated atmospheric CO_2 concentrations.

Keywords: dry matter partitioning, elevated CO_2, gas exchange, genetic variation, Picea mariana, provenance.

Introduction

Elevated CO_2 has been shown to increase growth rates in forest tree seedlings, at least temporarily. Elevated CO_2 can also alter morphological and physiological components of productivity. For instance, elevated CO_2 has been shown to increase net photosynthesis, increase water use efficiency, decrease photosynthetic capacity, alter biomass partitioning, alter shoot growth phenology, and decrease cold hardiness (Eamus and Jarvis 1989, Margolis and Vézina 1990, Johnsen 1993, Murray et al. 1994, Samuelson and Seiler 1994).

Because genetic variation among and within populations of trees is manifested by genetic variation in physiological processes, we postulated that elevated CO_2, through its influence on these physiological processes, might alter genetic performance at the level of growth and survival. If so, then deployment of seed sources and genotypes based on testing under current atmospheric CO_2 conditions might result in decreased potential productivity or even maladaptation of future forests if atmospheric CO_2 concentrations increase as predicted. Therefore, the primary objective of this study was to determine if diverse provenances of black spruce (*Picea mariana* (Mill.) B.S.P.) would respond similarly in growth, phenology and physiology to an approximate doubling of atmospheric CO_2 concentration.

The provenances used in this study originated from a wide latitudinal range and have presumably adapted to differing natural photoperiod regimes. Because northern provenances grown in a southern photoperiod regime typically cease shoot growth earlier than southern provenances (Wright and Bull 1963, Mergen 1963, Morgenstern 1969, 1978, Johnsen et al. 1988, Oleksyn et al. 1992), we postulated that the shorter shoot growth cycle of northern provenances grown in a southern photoperiod environment might limit growth responses to elevated CO_2. Therefore, we also determined the influence of photoperiod on both provenance and provenance × CO_2 interaction effects.

Materials and methods

Seed sources and seedling stock culture

Seed was obtained from six bulk collections from a black spruce provenance test (Morgenstern 1978, Boyle 1985). The provenances originate from the Yukon (Provenance 7000, 63°34′ N, 135°55′ W), British Columbia (Provenance 6987, 58°47′ N, 123°38′ W), Alberta (Provenance 6979, 52°22′ N, 115°15′ W), Newfoundland (Provenance 6804, 50°54′ N,

56°06′ W) and Ontario (Provenance 6908, 48°59′ N, 80°38′ W and Provenance 6901, 45°10′ N, 77°10′ W). After collection and processing, seed was stored at −18 °C.

The study was conducted at the Petawawa National Forestry Institute (46° N, 77°30′ W). In October 1993, seed was sown in three blocks in 170-ml capacity Spencer Lemaire containers (Spencer Lemaire Industries Ltd., Edmonton, Alberta) containing 3/1 (v/v) peat moss/vermiculite. Seedlings were grown under ambient greenhouse CO_2 conditions in a 20-h photoperiod supplemented by sodium vapor lamps. In February 1994, the photoperiod was shortened to 8 h to promote bud set. Following bud set and hardening, seedlings were placed in a cooler at 4 °C for 6 weeks to fulfill chilling requirements. After the chilling treatment, 24 seedlings per provenance were randomly selected for determination of initial biomass, and the remaining seedlings were transplanted in 4-liter pots containing 3/1 (v/v) sand and peat moss, and immediately moved to the greenhouse growth chambers.

The CO_2 × provenance growth experiment

Seedlings from all provenances were established in greenhouse growth chambers based on a split-plot design with three blocks and two chambers per block. The CO_2 treatments comprised main-plots and provenances were subplots.

Six polyethylene chambers were constructed over the three blocks (greenhouse benches). Outside air was supplied to each chamber by means of a blower at approximately four air exchanges per hour. An air conditioner in each chamber provided cooling and air circulation. One chamber per block was randomly designated as the ambient CO_2 chamber, and the other chamber was designated the elevated CO_2 chamber. Elevated CO_2 was attained by bleeding pure CO_2 into the chambers at a constant rate to provide approximately 300 ppm over ambient. The CO_2 in each chamber was monitored with an infrared gas analyzer. Mean CO_2 concentrations from the entire experiment were 394 ± 59 (SD) ppm for the ambient CO_2 treatment and 712 ± 93 ppm for the elevated CO_2 treatment. Seedlings received ambient light, which was reduced by approximately 30% by the greenhouse and approximately 12% by the polyethylene chambers. The greenhouse was well ventilated, and temperatures in the chambers ranged from 10 to 32 °C during the experiment.

Immediately following transplanting on May 6, 1994, eight seedlings per seed source were randomly placed in each main-plot. Seedlings were fertilized with 20,8,20 N,P,K plus micronutrients (Plant Products Co. Ltd., Brampton, Ontario) and watered to field capacity every 10 days. Seedlings were examined daily for date of bud break (when needles were emerged from among the bud scales) and the first day a bud was observed. Seedlings were harvested on September 22–24 (one block per day), separated into shoots (needles + stem) and roots, dried at 65 °C and weighed. Mean relative growth rates (RGR) were calculated from the initial and final dry weights for each treatment × block combination based on standard formulae (Hunt 1982).

Analysis of variance (ANOVA), with a split-plot design, was used to examine the effects of CO_2, provenance and provenance × CO_2 interaction on bud break date, bud set date, final seedling dry weight and mean RGR. Dry matter partitioning was analyzed based on allometric principles (Ledig et al. 1970). The effects of CO_2 and provenance on dry matter partitioning were analyzed by comparing the allometric parameters from analyses of covariance: the CO_2 effects on dry matter partitioning were analyzed separately for each provenance.

The CO_2 × photoperiod × provenance experiment

Seedlings (eight per treatment) from Provenances 7000 (Yukon) and 6901 (Ontario) were subjected to an extended photoperiod treatment in a split-split-plot design with CO_2 treatments as main-plots, photoperiod treatment as subplots and provenances as sub-subplots. The photoperiod treatments were ambient conditions (natural photoperiod) and a photoperiod extended by interrupting the dark period with incandescent light for 30 min (0100 to 0130 h) each day (extended photoperiod). One half of each split-plot was isolated with shade cloth so that seedlings in the natural photoperiod treatment remained in the dark. Seedlings were measured and analyzed for bud break, bud set, final dry weight, RGR and biomass allocation as described above.

Shoot gas exchange was measured on fully developed foliage of seedlings in all treatments with an LI-6200 portable photosynthesis system with a 250-ml chamber (Li-Cor Inc., Lincoln, NE) and ambient CO_2 as the measurement concentration. Twelve seedlings (four seedlings per block) were measured per provenance × CO_2 × photoperiod on each of four occasions. Seedlings measured on the first three occasions were in addition to those used in the growth experiment, whereas seedlings measured on the last occasion were a subset from the growth experiment.

The first set of gas exchange measurements was conducted on May 14–16 (one block per day) before bud break. Three days before the start of measurements, needles were removed from an approximately 1 cm region below the top 3 cm of the shoot. On each day, gas exchange measurements were made on four seedlings per CO_2 × photoperiod × provenance combination in saturating light (approximately 2200 μmol m^{-2} s^{-1} photosynthetic photon flux density) supplied by a portable incandescent light (12 V, 75 W General Electric EYF lamp). Mean chamber CO_2 concentration across all measurements was 364.7 ± 9.2 ppm. Following measurement in the light, the chamber and seedling were covered for measurement of dark respiration (R_d). After the measurements, seedlings were immediately returned to their position in the growth chambers.

The second set of gas exchange measurements was conducted, following bud break, on May 24–26 using the same seedlings measured on May 14–16. The newly expanding bud was excised so as to not confound gas exchange estimates on the fully developed foliage. Mean chamber CO_2 concentration was 356.1 ± 10.0 ppm. Following measurement, needles were removed, and projected leaf area was measured with an LI-3100 leaf area meter (Li-Cor Inc.). The projected needle surface area was multiplied by four to estimate the total surface area. Needles were then dried at 65 °C and weighed.

The third and fourth sets of gas exchange measurements were conducted on July 14–16 and September 20–22, respectively. Measurements were made on fully developed foliage on the newly expanded terminal shoot. Seedlings were again prepared 3 days before the first measurement day by removing a 1-cm band of needles above and below an approximately 2-cm section of fully expanded foliage. Mean chamber CO_2 concentration was 366.7 ± 8.0 ppm in July and 382.6 ± 11.0 in September. Following leaf area determination, drying and weighing, September foliage samples were analyzed for total N concentration by a standard Kjeldahl technique.

Root R_d of seedlings in the natural photoperiod treatment was measured in June, July and September on four additional seedlings per CO_2 × provenance × block combination. Roots were removed from pots and gently shaken to remove soil. Tops were excised and entire root systems (because of the size of the root systems only partial root systems were used for the measurements in September) were wrapped loosely in a damp perforated paper towel and placed in a 1-liter measurement cuvette (Li-Cor Inc.). Roots were then washed and dried to a constant weight at 65 °C for expression of root R_d on a dry weight basis.

Net photosynthesis, shoot R_d, needle conductance (g_{wv}), root R_d and foliar N concentration were subjected to ANOVA using a split-split-plot design. In June and July, when complete root systems were measured, there was a negative correlation (P = 0.0001) between root R_d and root system size. To correct for root size, analysis of covariance of the June and July data was used to examine treatment effects on root R_d. Because there was no relationship between root R_d and root size when only partial root systems were used, the September data were subjected to ANOVA.

Results

The CO_2 × provenance growth experiment

Over all provenances, the mean final dry weights of seedlings grown in ambient and elevated CO_2 were 10.37 and 16.03 g, respectively (P = 0.065), reflecting mean RGRs of 0.0235 ± 0.0005 and 0.0265 ± 0.0005 day^{-1} averaged over the entire growing season. Provenance differences in final dry weight were large and generally independent of the CO_2 treatments (Figure 1).

Across all provenances, dry matter partitioning was similar between CO_2 treatments; neither a (P = 0.6956) nor k (P = 0.321) of the allometric equation shoot weight = a(root weight)^k varied between CO_2 treatments. However, both a (P = 0.0001) and k (P = 0.0027) of the allometric equation varied among provenances, indicating that provenances varied in dry matter partitioning. Generally, northern provenances had less shoot weight than southern provenances at equal root weights at the end of the experiment (Figure 2). Although there were some changes, patterns of provenance variation were independent of the CO_2 treatments (Figure 2).

The CO_2 concentration had no influence on date of bud break (P = 0.143); mean bud break Julian date was 139 for seedlings grown in elevated CO_2 and 140 for seedlings grown in ambient CO_2. The CO_2 concentration did not influence bud set date (P = 0.936), which occurred on Julian dates 230 and 231 for seedlings grown in ambient and elevated CO_2, respectively. There were small but significant provenance differences in the mean date of bud break (P = 0.0001), ranging from Julian date 138 to 142 with provenances rankings from earliest to latest as follows: 6804, 7000, 6987, 6979, 6908 and 6901. There were also provenance differences in mean date for bud set (P = 0.0001); dates ranged from Julian date 191 to 251 and provenance ranking from earliest to latest was 7000, 6987, 6979, 6804, 6908 and 6901. There was no indication of a provenance × CO_2 interaction for either bud break (P = 0.448) or bud set (P = 0.734).

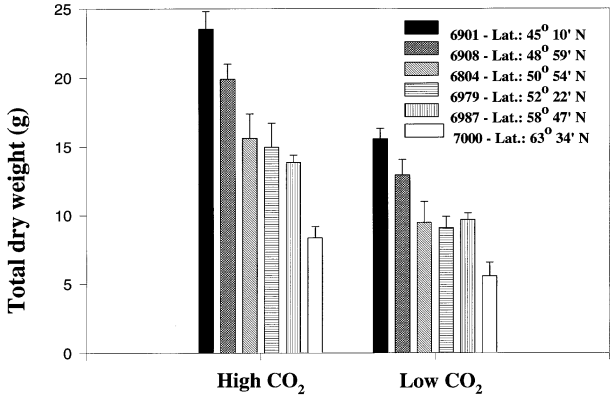

Figure 1. Final mean total seedling dry weight (± 1 SE) of six diverse sources of black spruce grown in a greenhouse experiment in ambient or elevated CO_2 (n = 24).

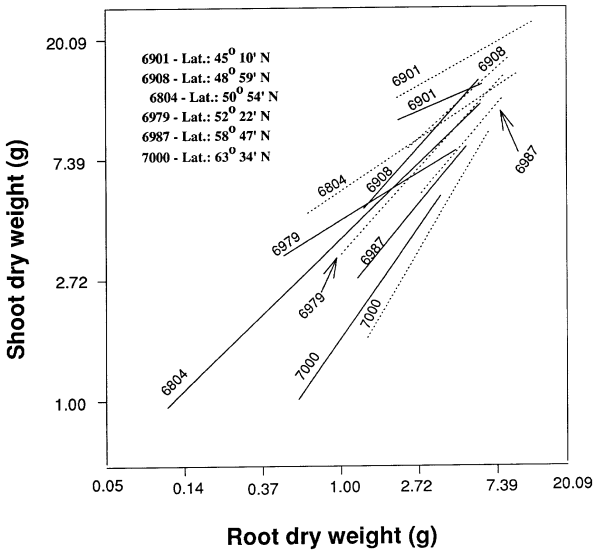

Figure 2. Allometric relationships observed for six diverse sources of black spruce grown in elevated (dotted line) and ambient (solid line) CO_2 in a greenhouse experiment. Twenty-four seedlings per provenance × CO_2 regime were harvested at the end of the experiment. The coefficient of determination (r^2) ranged from 0.35 to 0.79.

The CO_2 × photoperiod × provenance experiment

Photoperiod × provenance was a significant source of variation in the ANOVA of final total seedling dry weight ($P = 0.0074$) and mean RGR ($P = 0.0554$). Extending the photoperiod of Provenance 7000 seedlings increased final dry weights (+31%) and mean RGR (+11%), whereas Provenance 6901 seedlings had slightly lower final dry weights (−8%) and RGR (−3%) in response to the extended photoperiod treatment. The extended photoperiod treatment increased dry matter partitioning to shoots versus roots and decreased the difference exhibited between Provenance 6901 seedlings and Provenance 7000 seedlings in the natural photoperiod treatment (data not shown). The extended photoperiod treatment influenced bud set; none of the Provenance 6901 seedlings grown in the extended photoperiod set bud, and bud set was delayed by 39 days in Provenance 7000 seedlings ($P = 0.0001$). The CO_2 × photoperiod and CO_2 × photoperiod × provenance interactions were not significant sources of variation for any growth parameter measured.

Because shoot gas exchange data expressed as a function of needle surface area or as a function of needle dry weight were similar, shoot gas exchange results are presented only on a needle surface area basis. The CO_2 treatment was not a significant source of variation on any measurement date for P_n and g_{wv}. Although not statistically significant, there was a trend consistent with photosynthetic acclimation to elevated CO_2 as the experiment progressed. Mean P_n values of seedlings in the two CO_2 treatments were virtually identical on both measurements in May, but the elevated CO_2 treatment decreased P_n by approximately 15% in July and September (Table 1) and increased shoot R_d ($P = 0.0099$ and 0.1882 for July and September, respectively, Table 1). In September, seedlings grown in elevated CO_2 had a significantly ($P = 0.0491$) lower mean foliar N concentration (2.42%) than seedlings grown in ambient CO_2 (2.61%). In June, July and September, seedlings grown in elevated CO_2 also had 4% ($P = 0.6895$), 28% ($P = 0.0001$) and 9% ($P = 0.1368$) greater root R_d, respectively, (calculated using least square means for June and July) than seedlings grown in ambient CO_2.

Photoperiod was not a significant source of variation of gas exchange parameters on any measurement date except in September, when seedlings in the extended photoperiod treatment had 15% higher g_{wv} than seedlings in the natural photoperiod treatment ($P = 0.0429$). Although the photoperiod × provenance interaction was not statistically significant ($P = 0.1071$), the difference in g_{wv} was a result of Provenances 6901 and 7000 seedlings in the natural photoperiod treatment having 2 and 25% lower g_{wv}, respectively, than the corresponding seedlings in the extended photoperiod treatment. Seedlings in the natural photoperiod treatment had a significantly ($P = 0.0102$) higher mean foliar N concentration (2.55%) than seedlings in the extended photoperiod treatment (2.45%).

Provenance 7000 seedlings had higher P_n than Provenance 6901 seedlings (Figure 3) in May ($P \leq 0.0163$) and July ($P = 0.0207$), whereas no provenance differences in R_d were detected on any date (Figure 4). Provenance trends in g_{wv} were similar to those of P_n (data not shown). In June, seedlings of Provenances 6901 and 7000 had similar root R_d ($P = 0.7878$), but Provenance 7000 seedlings had approximately 18% greater root R_d ($P = 0.0010$, corrected for root weight) than Provenance 6901 seedlings in July (Figure 5).

In September, photoperiod × provenance interactions were prominent for physiological variables. Provenance 7000 seedlings had lower P_n (Figure 3A) in the natural photoperiod treatment and higher P_n (Figure 3B) in the extended photoperiod treatment than Provenance 6901 seedlings. The photoperiod × provenance interaction was also a significant source of variation in root R_d ($P = 0.0005$). In the natural photoperiod treatment, Provenance 7000 seedlings had a root R_d of 0.0150 μmol g^{-1} s^{-1} compared to 0.0284 μmol g^{-1} s^{-1} for Provenance 6901 seedlings; however, in the extended photoperiod treatment, Provenance 7000 seedlings had a root R_d of 0.0257 μmol g^{-1} s^{-1} compared to 0.0240 μmol g^{-1} s^{-1} for Provenance 6901 seedlings. In contrast, provenance differences in shoot R_d in September were consistent between photoperiod treatments (Figure 4). Provenance differences in foliar N concentration were also independent of photoperiod treatment with Provenance 7000 seedlings having a mean foliar N concentration of 2.72% compared with 2.29% for Provenance 6901 seedlings ($P = 0.0002$).

Discussion

The provenances displayed large differences in growth, phenology, dry matter allocation, and shoot and root gas exchange. Both the growth and physiological differences were more or less independent of the CO_2 treatments. Although the extended photoperiod treatment influenced the magnitude or rankings of provenance differences, or both, no provenance × CO_2 × photoperiod interaction was apparent. For example, the slight

Table 1. Means and SE (in parentheses) for net photosynthesis (P_n), shoot respiration (R_d) and needle conductance (g_{wv}) measured four times in black spruce seedlings during the CO_2 × photoperiod × provenance experiment. All seedlings were measured at ambient CO_2 concentration.

Variable	CO_2 concentration	May 12–14	May 24–26	July 20–22	September 14–16
P_n (μmol m^{-2} s^{-1})	Ambient	1.76 (0.07)	2.18 (0.09)	2.10(0.11)	3.09 (0.33)
	Elevated	1.62 (0.09)	2.13 (0.10)	1.73 (0.10)	2.69 (0.25)
Shoot R_d (μmol m^{-2} s^{-1})	Ambient	0.40 (0.04)	0.36 (0.009)	0.50 (0.027)	0.67 (0.098)
	Elevated	0.48 (0.05)	0.32 (0.010)	0.67 (0.026)	0.86 (0.124)
g_{wv}(mmol m^{-2} s^{-1})	Ambient	26.86 (1.33)	47.04 (2.24)	47.98 (3.17)	68.94 (3.99)
	Elevated	26.67 (2.19)	47.10 (3.10)	49.82 (2.21)	68.19 (3.99)

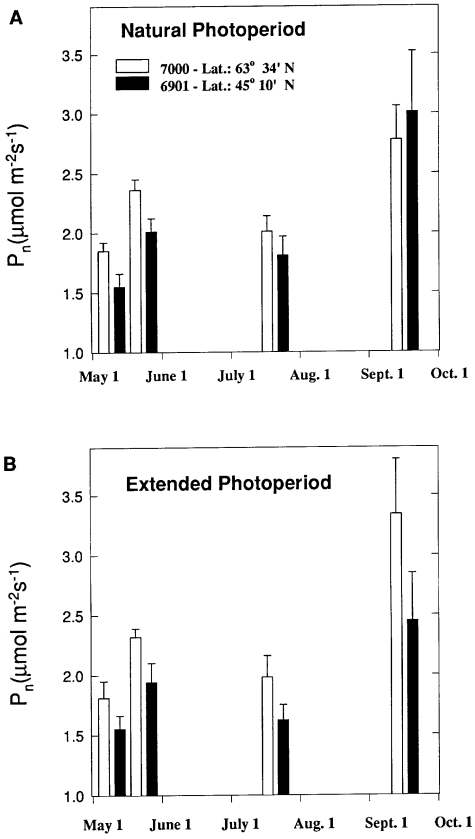

Figure 3. Net photosynthesis (P_n) (± 1 SE) of an Ontario provenance (6901) and a Yukon provenance (7000) of black spruce, measured on four occasions, grown in a natural (A) or an extended photoperiod (B). The two measurements in May were on the same seedlings, whereas July and September measurements were conducted on different subsamples. Data from both the ambient and elevated CO_2 treatments were bulked so each bar represents 24 seedlings. All seedlings were measured at ambient CO_2.

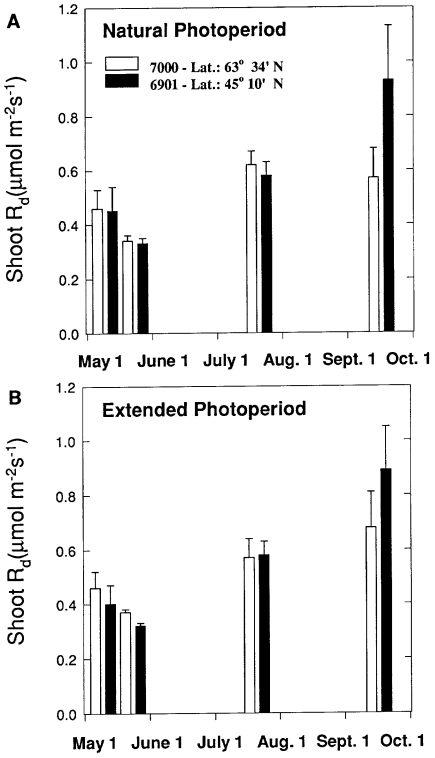

Figure 4. Shoot respiration (R_d) (± 1 SE) of an Ontario provenance (6901) and a Yukon provenance (7000) of black spruce, measured on four occasions, grown in a natural (A) or an extended photoperiod (B). The two measurements in May were on the same seedlings whereas July and September measurements were conducted on different subsamples. Data from both the ambient and elevated CO_2 treatments were bulked so each bar represents 24 seedlings. All seedlings were measured at ambient CO_2.

photosynthetic acclimation to elevated CO_2 displayed by both provenances in July and September was relatively stable under both photoperiod treatments.

The southern provenances grew more and broke and set bud later than the northern provenances at the Petawawa National Forestry Institute, a southern test site relative to the provenances used. These results agree with other observations in conifers (Wright and Bull 1963, Mergen 1963, Morgenstern 1969, 1978, Johnsen et al. 1988, Oleksyn et al. 1992, Johnsen et al. 1996). The phenological differences were largely caused by the differential responses of the provenances to photoperiod. The extended photoperiod prevented bud set in the Ontario source and delayed bud set in the Yukon source by 39 days (cf. Oleksyn et al. 1992). Apparently, the 30-min period of dark interruption was not enough to prevent bud set completely in the Yukon source, which is adapted to a very short growing season.

As a consequence of their earlier bud set (Ledig 1983), the northern sources allocated more dry matter to roots versus shoots than the southern provenances. The extended photope-

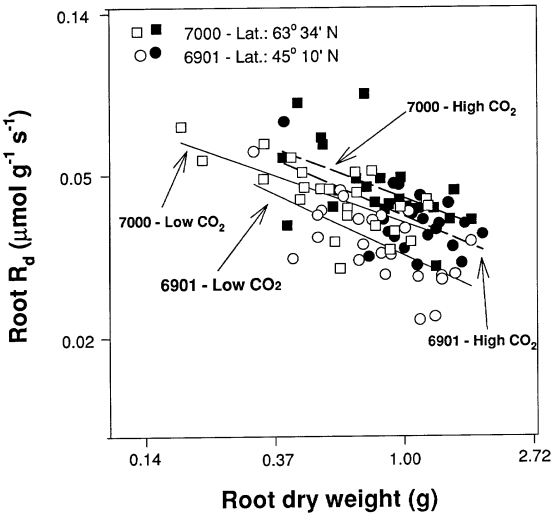

Figure 5. Allometric relationship between root R_d and total seedling dry weight for an Ontario provenance (6901) and a Yukon provenance (7000) of black spruce grown in elevated (solid symbols) or ambient (open symbols) CO_2. All seedlings were measured at ambient CO_2. The coefficient of determination (r^2) ranged from 0.29 to 0.50.

riod treatment influenced this trait by increasing dry matter allocation to shoots versus roots, with the result that the differences between the Yukon and Ontario sources were diminished by the extended photoperiod treatment. Similar results were observed by Oleksyn et al. (1992) in a study of northern and central populations of Scots pine (*Pinus sylvestris* L.) seedlings grown under "northern" and "central" photoperiod regimes.

Provenance differences in physiological traits were also influenced by photoperiod treatments. The Yukon source had higher P_n in May and July under all conditions than the Ontario source, whereas in September, Provenance 7000 seedlings had a higher P_n than Provenance 6901 seedlings only in the extended photoperiod treatment. Similarly, in September, there was a pronounced provenance × photoperiod interaction in root R_d, indicating that late-season provenance differences in both phenology and physiology were regulated by photoperiod. These rank changes over time reinforce the importance of studying provenance variation in physiological traits in a phenological context (Logan 1971, Boltz et al. 1986).

It appears that the physiological and morphological differences among these diverse sources of black spruce are so profound that the traits are expressed similarly in both ambient and elevated CO_2. Similarly, Körner and Diemer (1994) found that herbaceous plant species from high altitudes retained their greater photosynthetic efficiency in elevated CO_2. However, other studies have indicated variable CO_2 responses of co-occurring tree species (Bazzaz et al. 1990, 1993, Rochefort and Bazzaz 1992). In addition, Callaway et al. (1994) reported significant provenance × CO_2 interactions in gas exchange and root/shoot ratio of ponderosa pine (*Pinus ponderosa* Dougl. ex P. Laws.), and Surano et al. (1986) observed dissimilar growth responses to elevated CO_2 between a Sierra Nevada and a Rocky Mountain seed source of ponderosa pine.

As differences among genetic entries become more subtle, the likelihood of observing genotype × atmospheric CO_2 interactions might increase. Differential acclimation among genotypes in any given trait(s) will probably occur more often and have a greater influence on relative growth performance if genetic entries share a more common genetic background. Differences in growth among northern Ontario provenances were detected when seedlings were grown at 350 ppm but not at 700 ppm CO_2 (Johnsen 1994). In a black spruce retrospective test, the correlation between height of greenhouse-grown seedlings and height of field-grown plants at 15 years was moderate (r = 0.51, P = 0.0223) when greenhouse seedlings were grown in ambient CO_2 but poor (r = 0.29, P = 0.2177) when seedlings were grown in elevated CO_2 (Johnsen, unpublished data). Although Wang et al. (1994) detected no family × CO_2 interactions in black spruce after one growing season, significant interactions in several traits were observed after a second season (Wang et al. 1995). Similarly, Conroy et al. (1990) observed variable CO_2 responses in both growth and P_n among half-sib families of *Pinus radiata* D. Don. In studies of *Picea sitchensis* (Bong.) Carr., Murray et al. (1994) reported that clones displayed different CO_2 responses in bud set and Townend (1993) also found variation among clones in growth and physiological responses to elevated CO_2. In contrast to the above, studies of two ponderosa pine full-sib families (Grulke et al. 1993), with known differences in growth rates, and two open-pollinated families of black spruce (Johnsen 1993) resulted in similar family physiological and growth responses to elevated CO_2.

Our results indicate that these diverse sources of black spruce would achieve similar growth rankings in a southern environment if grown in elevated CO_2. Although there is evidence that genotype × atmospheric CO_2 environment interactions are important, more research, using material appropriate for quantitative genetic analyses at varying levels of population structure, is necessary to evaluate genotype × atmospheric CO_2 environment interactions in forest trees.

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