Growth, shoot phenology and physiology of diverse seed sources of black spruce: I. Seedling responses to varied atmospheric CO\(_2\) concentrations and photoperiods

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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 CO₂ 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 CO₂ × 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 CO₂ 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 CO₂ chamber, and the other chamber was designated the elevated CO₂ chamber. Elevated CO₂ was attained by bleeding pure CO₂ into the chambers at a constant rate to provide approximately 300 ppm over ambient. The CO₂ in each chamber was monitored with an infrared gas analyzer. Mean CO₂ concentrations from the entire experiment were 394 ± 59 (SD) ppm for the ambient CO₂ treatment and 712 ± 93 ppm for the elevated CO₂ 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 CO₂, provenance and provenance × CO₂ 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 CO₂ and provenance on dry matter partitioning were analyzed by comparing the allometric parameters from analyses of covariance: the CO₂ effects on dry matter partitioning were analyzed separately for each provenance.

The CO₂ × 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 CO₂ 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 CO₂ as the measurement concentration. Twelve seedlings (four seedlings per block) were measured per provenance × CO₂ × 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 occasion, gas exchange measurements were made on four seedlings per CO₂ × 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 CO₂ 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 (Rₙ). 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 CO₂ 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 ($g_{nw}$), 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, 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, 6979, 6908, 6904, 6908 and 6901. There was no indication of a provenance × CO$_2$ interaction for either bud break ($P = 0.448$) or bud set ($P = 0.734$).
The \( \text{CO}_2 \times \text{photoperiod} \times \text{provenance} \) experiment

Photoperiod \( \times \) provenance was a significant source of variation in the ANOVA of 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 \( \text{CO}_2 \times \text{photoperiod} \) and \( \text{CO}_2 \times \text{photoperiod} \times \text{provenance} \) 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 \( \text{CO}_2 \) treatment was not a significant source of variation on any measurement date for \( P_n \) and \( g_{\text{wv}} \). Although not statistically significant, there was a trend consistent with photosynthetic acclimation to elevated \( \text{CO}_2 \) as the experiment progressed. Mean \( P_n \) values of seedlings in the two \( \text{CO}_2 \) treatments were virtually identical on both measurements in May, but the elevated \( \text{CO}_2 \) treatment decreased \( P_n \) by approximately 15\% in July and September (Table 1) and increased shoot \( R_d \) \((P = 0.0099)\) and 1.8822 for July and September, respectively, Table 1). In September, seedlings grown in elevated \( \text{CO}_2 \) had a significantly \((P = 0.0491)\) lower mean foliar N concentration \((2.42\%)\) than seedlings grown in ambient \( \text{CO}_2 \) \((2.61\%)\). In June, July and September, seedlings grown in elevated \( \text{CO}_2 \) 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 \( \text{CO}_2 \).

Photoperiod was not a significant source of variation in gas exchange parameters on any measurement date except in September, when seedlings in the extended photoperiod treatment had 15\% higher \( g_{\text{wv}} \) than seedlings in the natural photoperiod treatment \((P = 0.0429)\). Although the photoperiod \( \times \) provenance interaction was not statistically significant \((P = 0.1071)\), the difference in \( g_{\text{wv}} \) was a result of Provenances 6901 and 7000 seedlings in the natural photoperiod treatment having 2\% and 25\% lower \( g_{\text{wv}} \), 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 \( g_{\text{wv}} \) were similar to those of \( P_n \) (data not shown). In June, seedlings of Provenance 6901 and 7000 had similar root \( R_d \) \((P = 0.7878)\), but Provenance 7000 seedlings had approximately 18\% greater root \( R_d \) \((P = 0.0010)\) than Provenance 6901 seedlings in July (Figure 5).

In September, photoperiod \( \times \) 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 \( \times \) 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 \( \mu\text{mol g}^{-1} \text{s}^{-1} \) compared to 0.0284 \( \mu\text{mol g}^{-1} \text{s}^{-1} \) for Provenance 6901 seedlings; however, in the extended photoperiod treatment, Provenance 7000 seedlings had a root \( R_d \) of 0.0257 \( \mu\text{mol g}^{-1} \text{s}^{-1} \) compared to 0.0240 \( \mu\text{mol g}^{-1} \text{s}^{-1} \) 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 \( \text{CO}_2 \) treatments. Although the extended photoperiod treatment influenced the magnitude or rankings of provenance differences, or both, no provenance \( \times \) \( \text{CO}_2 \) \( \times \) photoperiod interaction was apparent. For example, the slight

<table>
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<th>Variable</th>
<th>CO2 concentration</th>
<th>May 12–14</th>
<th>May 24–26</th>
<th>July 20–22</th>
<th>September 14–16</th>
</tr>
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<tr>
<td>( P_n ) ((\mu\text{mol m}^{-2} \text{s}^{-1}))</td>
<td>Ambient</td>
<td>1.76 (0.07)</td>
<td>2.18 (0.09)</td>
<td>2.10 (0.11)</td>
<td>3.09 (0.33)</td>
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<tr>
<td></td>
<td>Elevated</td>
<td>1.62 (0.09)</td>
<td>2.13 (0.10)</td>
<td>1.73 (0.10)</td>
<td>2.69 (0.25)</td>
</tr>
<tr>
<td>( R_d ) ((\mu\text{mol m}^{-2} \text{s}^{-1}))</td>
<td>Ambient</td>
<td>0.40 (0.04)</td>
<td>0.36 (0.009)</td>
<td>0.50 (0.027)</td>
<td>0.67 (0.098)</td>
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<tr>
<td></td>
<td>Elevated</td>
<td>0.48 (0.05)</td>
<td>0.32 (0.010)</td>
<td>0.67 (0.026)</td>
<td>0.86 (0.124)</td>
</tr>
<tr>
<td>( g_{\text{wv}} ) ((\text{mmol m}^{-2} \text{s}^{-1}))</td>
<td>Ambient</td>
<td>26.86 (1.33)</td>
<td>47.04 (2.24)</td>
<td>47.98 (3.17)</td>
<td>68.94 (3.99)</td>
</tr>
<tr>
<td></td>
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<td>26.67 (2.19)</td>
<td>47.10 (3.10)</td>
<td>49.82 (2.21)</td>
<td>68.19 (3.99)</td>
</tr>
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photosynthetic acclimation to elevated CO₂ 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 photoperiod...

Figure 3. Net photosynthesis (Pₑ) (± 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 CO₂ treatments were bulked so each bar represents 24 seedlings. All seedlings were measured at ambient CO₂.

Figure 4. Shoot respiration (Rₑ) (± 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 CO₂ treatments were bulked so each bar represents 24 seedlings. All seedlings were measured at ambient CO₂.

Figure 5. Allometric relationship between root Rₑ 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) CO₂. All seedlings were measured at ambient CO₂. The coefficient of determination (r²) 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 $R_{so}$, 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 Doug. 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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References


