

Interactive effects of carbon dioxide concentration and light on the morphological and biomass characteristics of black spruce and white spruce seedlings

Jacob Marfo and Qing-Lai Dang

Abstract: CO₂–light interactions can influence the competition among boreal plants, but are poorly understood. We investigated the effect of such interactions on the growth and biomass of 1-year-old black spruce (Sb) (*Picea mariana* (Mill.) BSP) and white spruce (Sw) (*Picea glauca* (Moench) Voss) grown with CO₂ concentrations ([CO₂]) of 360 and 720 μmol·mol⁻¹ under 30%, 50%, and 100% light, in greenhouses. There were significant two-way and three-way interactions. Root collar diameter (RCD) of Sw decreased with decreasing light, while in Sb, there was no significant difference in RCD for plants grown under 50% or 30% light. Height was greater for plants grown under 100% light than if the plants were shaded. Elevated [CO₂] increased RCD by 33% and enhanced stem volume by 67%, 98%, and 84% under 100%, 50%, and 30% light, respectively. The CO₂ enhancement of total biomass was relatively higher under lower light, and greater for Sb than Sw. Elevated [CO₂] decreased specific leaf area under 50% light only. Root mass was generally higher under 100% light than when shaded. Elevated [CO₂] increased the root mass of Sb under 100% light, but decreased it under 30% light. Elevated [CO₂] decreased the shoot/root ratio under 100% light, but increased it under 30% light. Our data suggest that raising [CO₂] will likely increase species competitiveness under low light conditions, and that the increase will be greater in species that are relatively shade tolerant.

Key words: boreal forests, elevated [CO₂], [CO₂]-light species interactions, black spruce, white spruce seedlings, climate change.

Résumé : L'interaction lumière-CO₂ peut influencer la compétition entre plantes boréales, mais on les comprend mal. Les auteurs ont examiné de telles interactions sur la croissance et la biomasse de plants d'un an d'épinettes noires (Sb) (*Picea mariana* (Mill.) B.S.P.) et d'épinettes blanches (Sw) (*Picea glauca* (Moench.) Voss), en présence de 360 et 720 μmol⁻¹ [CO₂] et 30, 50 et 100 % de lumière, en serres. On retrouve des interactions dans deux directions et dans trois directions. Le diamètre au collet (RDC) de Sw diminue avec une diminution de la lumière alors qu'il n'y a pas de différence significative chez Sb entre 50 et 30 % de lumière. La hauteur est plus grande avec 100 % de lumière, comparativement à l'ombre. Le [CO₂] élevé augmente le RDC de 33 %. Il augmente la biomasse totale de 67, 98 et 84 %, respectivement à 100, 50 et 30 % de luminosité. L'augmentation de la biomasse totale sous l'effet du [CO₂] est relativement plus élevée à faible intensité lumineuse et plus élevée chez Sb que chez Sw. L'augmentation du [CO₂] diminue la surface foliaire spécifique seulement sous 50 % de luminosité. On observe une biomasse généralement plus importante à 100 % de luminosité qu'à l'ombre. L'augmentation de [CO₂] augmente la biomasse racinaire chez Sb à 100 % de lumière, mais la diminue à 30 %. L'augmentation de [CO₂] diminue le rapport tige/racine à 100 % de lumière, mais la diminue à 30 %. Les données suggèrent que les augmentations de [CO₂] favorisent vraisemblablement la compétitivité des espèces sous des conditions de faible luminosité et l'augmentation sera plus forte chez les espèces qui tolèrent relativement mieux l'ombre.

Mots-clés : forêts boréales, [CO₂] élevé, interactions espèces lumière-[CO₂], épinette noire, épinette blanches, plantule, changement climatique.

Introduction

The global atmospheric carbon dioxide concentration ([CO₂]) has increased from the pre-industrial value of 280 μmol·mol⁻¹, to approximately 379 μmol·mol⁻¹ in recent

years, and the present annual [CO₂] increase rate of 1.9 μmol·mol⁻¹ is the highest on record (IPCC 2007). Research has shown that increasing [CO₂] has great impact on plant growth and biomass production (Curtis and Wang 1998; Ward and Strain 1999). Numerous studies (Curtis 1996; Tissue et al. 1997; Wuebbles et al. 1999; Linder 2000) showed that elevated atmospheric [CO₂] enhances photosynthesis and plant biomass production. Ceulemans and Mousseau (1994) found that a doubling of atmospheric [CO₂] increases leaf-level photosynthesis by approximately 40% in conifers and 60% in deciduous trees. Zhang and Dang (2007) reported an enhancement of biomass produc-

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tion in black spruce (*Picea mariana* (Mill.) BSP), white spruce (*Picea glauca* (Moench) Voss), jack pine (*Pinus banksiana* Lamb.), and trembling aspen (*Populus tremuloides* Michx.) grown with elevated [CO₂]. Kimball (1983) reported that plant yield is 33% higher when [CO₂] is twice the ambient level. Elevated [CO₂] has significant effects on resource allocation patterns (Larigauderie et al. 1988; Huang et al. 2007), as well as specific leaf area (SLA) (Zhang et al. 2006; Huang et al. 2007; Cao et al. 2008), branching patterns (Bazzaz 1990; Tissue et al. 1997), and stem elongation (Reekie et al. 1997; Ainsworth and Long 2005).

Light regime is another significant variable with respect to photosynthesis. It affects the biochemistry and morphology of leaves, resulting in changes in photosynthetic and respiratory rates that in turn affect plant growth rate (Awada and Redmann 2000). Light also influences plant response to [CO₂], and there is synergy between the two (Hopkins and Hüner 2004). Depending on light conditions, elevated [CO₂] can influence the competitive ability of species by differentially altering their carbon balance (Bazzaz and McConaughay 1992). Under high light conditions, plants are generally better able to take advantage of increased [CO₂] (Madsen 1974). At low light levels, however, light-dependent reactions limit the rate of photosynthesis and increasing [CO₂] may not enhance the rate of photosynthesis as much. Despite the vital roles of [CO₂] and light in the growth, morphology, and biomass of trees in the boreal forest, there is very little work on the interactive effects of [CO₂] and light on two of most important boreal tree species: black spruce and white spruce.

The boreal forest covers 11% of the earth's terrestrial surface (Bonan and Shugart 1989), with black spruce forests as the dominant cover type (Viereck and Johnston 1990), and has greater total ecosystem carbon content than any other forest biome (Gower et al. 1997). At the global scale, the boreal forest contains 800 Pg carbon (Apps et al. 1993), about half of the terrestrial biosphere's carbon stock (Schlesinger 1997). Climate change is expected to be more pronounced in the boreal region (Prentice et al. 2001). Thus, understanding the response of spruce forests to climate change is important to the understanding of the overall response of the boreal forest to climate change.

Black spruce and white spruce are congeneric species with similar growth, gross morphology, and phenology (Patterson et al. 1997). However, black spruce is found mainly in lowland muskegs with poorly drained and low nutrient soils, whereas white spruce generally grows on drier, nutrient-rich upland sites (Vincent 1965; Larson 1980). White spruce has a greater demand for nutrient, moisture, light, and other growth resources than associated conifers, such as black spruce, making the range of land supporting its growth more limited with increasing climate severity (Nienstaedt and Zasada 1990). Black spruce, on the other hand, has broader distribution and can grow on sites that are not suitable for white spruce. However, both species are intermediate shade tolerant (Baker 1949; Haavisto and Jeglum 1995) with white spruce being less shade tolerant (Ritchie 1959; Nienstaedt and Zasada 1990). Vincent (1965) indicated that 25% of full sunlight does not significantly reduce height, shoot biomass, root biomass, and total biomass of black spruce seedlings. Black spruce

usually reaches photosynthetic light saturation under 25%–50% full sunlight (Grossnickle 2000), while white spruce achieves maximum rate of photosynthesis under 40%–60% of full sunlight (Man and Lieffers 1997) and maximum diameter and stem volume under full light (Lieffers and Stadt 1994). Minimum light levels for the survival of white spruce range from 8% (Lieffers and Stadt 1994) to 15% (Chen 1997) of full sunlight, whereas black spruce can survive at even lower light levels (Haavisto and Jeglum 1995).

Increasing [CO₂] under low light may not directly improve the efficiency of light utilization because light is limiting photosynthesis (Walters and Reich 2000). However, increased [CO₂] can suppress dark respiration and photorespiration and hence increase net photosynthesis and growth at irradiance levels above the compensation point and decrease the light compensation point for photosynthesis, consequently indirectly increasing the light-use efficiency (Lambers et al. 1998). Therefore, we hypothesized that CO₂ elevation stimulates the growth and biomass of black spruce and white spruce seedlings more (relatively) under lower than higher light levels. Teskey and Shrestha (1985) found that the photosynthesis of more shade tolerant plants responds more positively than that of less shade tolerant plants to [CO₂] elevation. We further hypothesized that black spruce exhibits greater enhancement in growth and biomass with elevated [CO₂] than white spruce seedlings, because of its greater shade tolerance. To test the hypotheses, we exposed 1-year-old black spruce and white spruce to three light levels and two concentrations of CO₂ over a period of 4.5 months, under greenhouse conditions. This paper reports the morphological and biomass results.

Materials and methods

Plant materials

One-year-old black spruce and white spruce seedlings (Thunder Bay – Fort Frances provenance) were obtained from Hills Tree Nursery (Thunder Bay, Ont.). The seedlings were planted in 13.5 cm tall, 11 cm top-diameter plastic containers containing a mixture of coarse premium grade vermiculite (Sungro Horticulture, Vancouver, B.C.) and peat moss (50:50 v/v). The seedlings were relatively uniform in size (13 cm height) when the experiment started.

Experimental design

The experiment was a split-split plot design with CO₂ treatments as the whole plot, light treatments as subplots, and the species as sub-subplots. The treatments consisted of two CO₂ concentrations (360 µmol·mol⁻¹ and 720 µmol·mol⁻¹) with two replications of each; three light levels (100%, 50%, and 30% light); and two species (black spruce and white spruce), with eight seedlings per treatment combination. The 192 seedlings used were selected from a total of 600 to ensure uniformity in size and form.

The experiment was conducted in four greenhouses of the same design at Lakehead University's Thunder Bay – Ontario campus, from 15 January 2007 to 2 May 2007. Each CO₂ treatment was randomly assigned to two greenhouses, and the three light levels were replicated in those greenhouses. Elevated [CO₂] was achieved using Argus CO₂ generators

Table 1. ANOVA *p* values for the effects of CO₂ concentration ([CO₂]), light, species (Sp), and their interactions on the height, RCD, stem volume, number of FOLS, SLA, total plant biomass, component biomass, and biomass ratios, in black spruce and white spruce seedlings.

Source of variation	CO ₂	Light	CO ₂ ×Light	Sp	CO ₂ ×Sp	Light×Sp	CO ₂ ×Light×Sp
Height (2.5 months)	0.0001	<0.0001	0.0012	<0.0001	0.2739	<0.0001	0.3227
Height (4.5 months)	<0.0001	<0.0001	0.7031	<0.0001	0.139	0.0125	0.0770
RCD (2.5 months)	0.0065	<0.0001	0.3251	<0.0001	0.2437	0.7514	0.5969
RCD (4.5 months)	0.0105	0.0292	0.1531	0.4312	0.7532	0.0229	0.183
FOLS (2.5 months)	0.1029	<0.0001	0.8901	<0.0001	0.456	0.7795	0.0084
FOLS (4.5 months)	0.0924	<0.0001	0.8863	<0.0001	0.478	0.1267	0.5084
Stem volume	<0.0001	<0.0001	<0.0001	0.0119	0.1207	0.0424	0.2395
SLA	0.3330	0.0008	<0.0001	<0.0028	0.9851	0.4604	0.8451
Total fresh biomass	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Total dry biomass	<0.0001	<0.0001	0.057	<0.0001	0.0005	0.0002	0.0012
Root fresh mass	<0.0001	<0.0001	0.0002	0.0514	0.0044	0.2342	0.0058
Root dry mass	<0.0001	<0.0001	0.0015	0.0738	0.0022	0.5181	0.014
Shoot fresh mass	<0.0001	<0.0001	0.0069	<0.0001	<0.0001	<0.0001	<0.0001
shoot dry mass	<0.0001	<0.0001	0.052	<0.0001	0.0008	<0.0001	0.0013
RMR	<0.0001	<0.0001	0.0015	0.0738	0.0022	0.5181	0.014
SMR	0.2392	0.0126	0.0034	0.0698	0.1270	0.8600	0.4527
SRR	0.0002	0.0001	<0.0001	0.0051	0.0157	0.5482	0.4199

(Argus, Vancouver, B.C.) on cold days. On warm days however, CO₂ was supplied from pressurised CO₂ tanks to avoid overheating. Neutral-density shade cloths were used to provide the 50% and 70% shade levels (i.e., 50% and 30% light). All environmental conditions in the greenhouses were monitored and controlled using an Argus control system (Argus). The light reaching plants grown under full light averaged 660 μmol·m⁻²·s⁻¹ on clear sunny days, as measured with LI-190SA quantum sensor attached to LI-250A light meter (Licor Biosciences, Lincoln, Nebr.). All the treatments were subjected to the same day and night temperatures (25 ± 2 °C and 15 ± 2 °C, respectively) with a 16 h photoperiod. The length of natural days was extended using high-pressure sodium lamps (P.L. Light Systems, Beamsville, Ont.) when the daylength was less than 16 h; the photosynthetic photon density provided was 213 μmol·m⁻²·s⁻¹ at the canopy level. The moisture content of the growing medium was maintained at about 30% in all treatment combinations as measured using an HH2 Moisture Meter and ML2X ThetaProbe (Delta-T Devices, Cambridge, UK.). Relative humidity of 55% ± 5% was maintained throughout the experiments. The seedlings were fertilized weekly with a solution of 150 mg·L⁻¹ N, 60 mg·L⁻¹ P, 150 mg·L⁻¹ K, 40 mg·L⁻¹ Mg, 80 mg·L⁻¹ Ca, and 60 mg·L⁻¹ S. Nutrient levels of the growth medium and irrigation water were measured and subtracted from the formulation at the beginning of the experiment.

Measurements

Height, root collar diameter (RCD), and the number of first order lateral shoots (FOLS) were measured on all of the seedlings after 2.5 months and 4.5 months of treatments. After 4.5 months, three seedlings from each treatment combination were randomly selected and harvested. Using an analytical balance (precision of 0.001 g), fresh mass of shoots and roots were measured separately. The materials were then oven-dried at 70 °C for 48 h and dry mass was measured. Root mass ratio (RMR = root mass/total seedling mass), and shoot mass ratio (SMR = shoot mass/total seed-

ling mass) were used as indices of biomass allocation. Projected area of current-year needles was measured using a Regent WinSeedle System (Regent Instruments Inc., Quebec City, Que.). The needles were oven-dried at 70 °C for 48 h to determine dry mass for calculating the SLA. Stem volume was calculated from height, RCD, and midsection stem diameter as follows:

$$\text{Stem volume} = 0.25(d_1 + d_2)^2(\pi h)$$

where d_1 is RCD, d_2 is midsection stem diameter, and h is height.

Statistical analysis

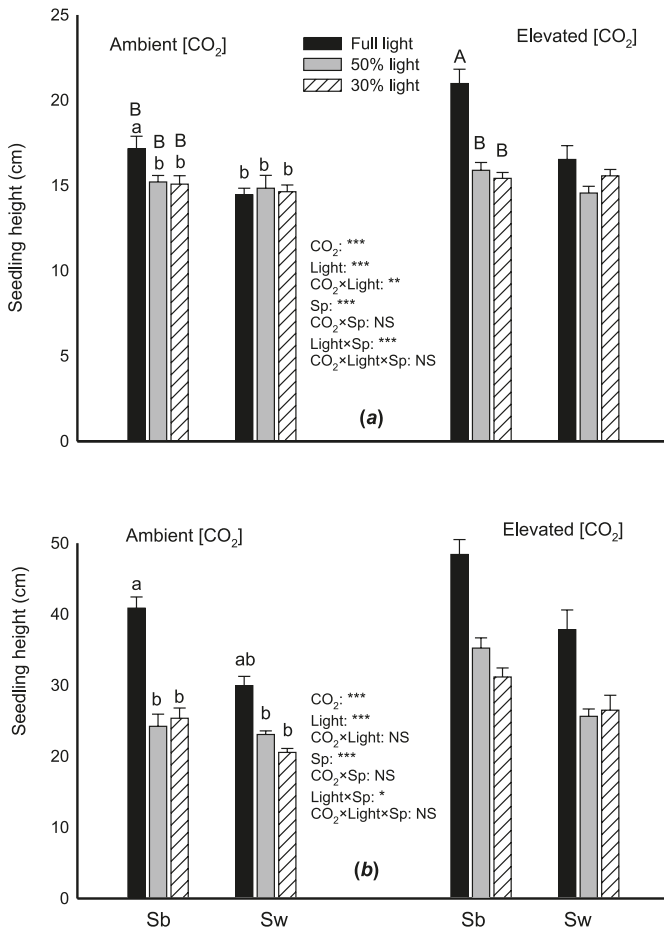
All data were examined graphically for normality of distribution (residual probability plots) and homogeneity of variance (scatter plots of residuals) using Data Desk 6.01 (Data Description Inc, New York, N.Y.) before the analysis of variance was performed. The effects of CO₂, light, species, and their interactions were tested using the ANOVA linear model procedure in Data Desk. Scheffé's post-hoc tests were conducted when a main effect with more than two levels or interactions was significant ($p \leq 0.05$). Scheffé's post-hoc tests were made based on the rule that significant interactions override main effects and higher order significant interactions override lower level interactions.

Results

Height

CO₂ concentration and light had significant interactive effects on height after 2.5 months. The seedlings in full light and doubled [CO₂] were significantly higher than those in the other treatment combinations, but there were no significant differences among the other treatment combinations (Table 1; Fig. 1a). However, the significant CO₂ and light interaction became insignificant after 4.5 months while the main effects remained insignificant (Table 1; Fig. 1b). Light and species had significant interactive effects on height growth after 2.5 and 4.5 months. After 2.5 months of treat-

Fig. 1. Effects of CO₂ concentration ([CO₂]) and light on the height of black spruce (Sb) and white spruce (Sw) seedlings after (a) 2.5 and (b) 4.5 months of treatment. In Fig. 1a, lower case letters represent light×species interactions, and upper case letters represent CO₂×light interactions. In Fig. 1b, the letters represent light×species interactions. Means with the same letter or letters do not differ significantly ($p > 0.05$) based on Scheffe's post-hoc test. *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$; NS, $p > 0.05$ (not significant effects).

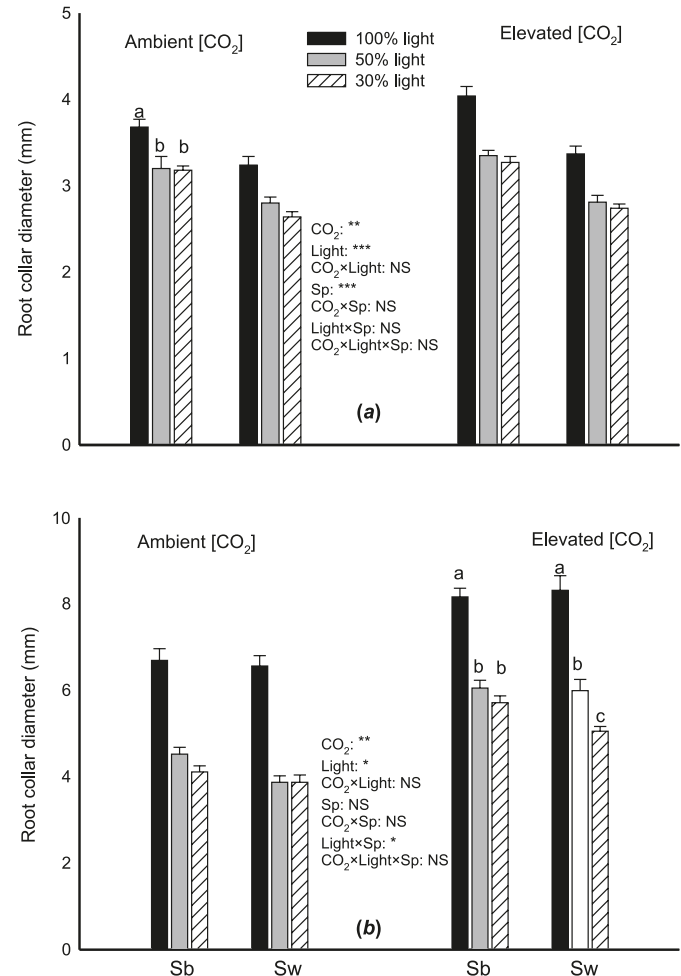


ment, the height of black spruce grown under 100% light was the highest with no significant difference among the other treatment combinations (Fig. 1a). After 4.5 months of treatment, the height of black spruce grown under 100% light was still the highest, followed by white spruce under 100% light; there was no difference between the other treatment combinations (Fig. 1b).

Root collar diameter

RCD after 2.5 months of treatment was significantly affected by [CO₂], light, and species, but no significant interactive effect occurred (Table 1; Fig. 2a). RCD was greater for seedlings grown under 100% light than under the other two light levels (Fig. 2a). In addition, black spruce had significantly greater RCD than white spruce (Fig. 2a). RCD was significantly greater at elevated [CO₂] than at ambient [CO₂]. After 4.5 months of treatment, RCD was still significantly greater at elevated [CO₂] than at ambient [CO₂] (Fig. 2b). Light and species had significant interactive ef-

Fig. 2. Effects of CO₂ concentration ([CO₂]) and light on the root collar diameter of black spruce (Sb) and white spruce (Sw) seedlings after (a) 2.5 months (b) and 4.5 months of treatment. In Fig. 2a, the letters represent light effects, while in Fig. 2b, they represent light×species interactions. For further explanations see Fig. 1.

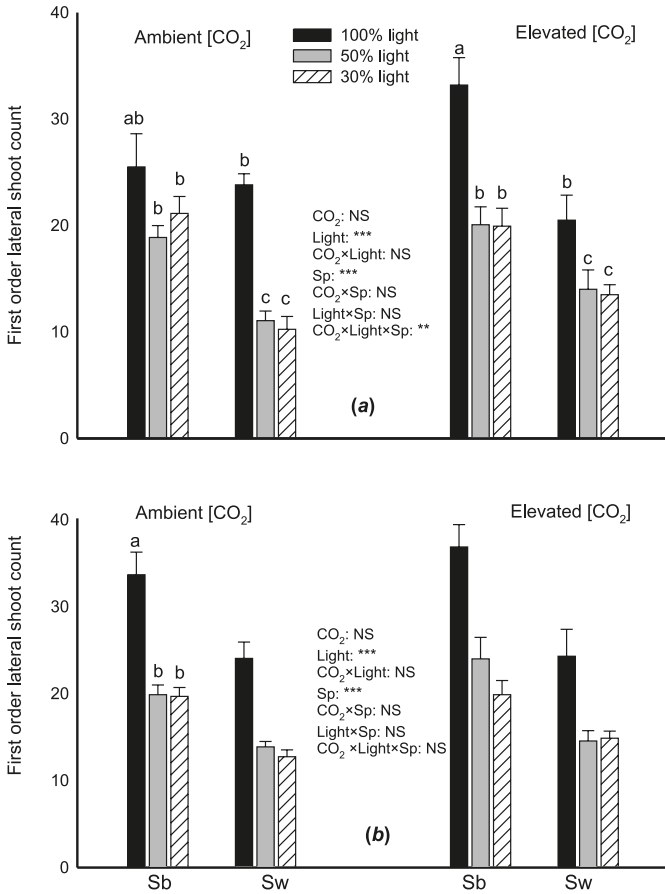


fects after 4.5 months of treatment (Table 1; Fig. 2b). The greatest RCD was observed in seedlings grown under 100% light, and there was only one significant difference among the other treatment combinations: white spruce grown under 30% light had the lowest RCD (Fig. 2b).

First order lateral shoots

CO₂ concentration, light, and species had significant interactive effects on the number of FOLS after 2.5 months of treatment (Table 1). Black spruce grown under 100% light and increased [CO₂] had the highest number of FOLS, followed by black spruce grown under 100% light and ambient [CO₂] (Fig. 3a). The responses of black spruce to CO₂ when grown under 50% and 30% light were similar to those for white spruce grown under 100% light at both CO₂ concentrations. White spruce grown under 50% and 30% light at the two CO₂ concentrations had the lowest number of FOLS (Fig. 3a). After 4.5 months of treatment, no significant interaction occurred (Table 1). However, seedlings grown under 100% light had greater FOLS than seedlings from the other

Fig. 3. Effects of CO₂ concentration ([CO₂]) and light on the number of first order lateral shoot of black spruce (Sb) and white spruce (Sw) seedlings after (a) 2.5 months and (b) 4.5 months of treatment. In Fig. 3a, the letters represent CO₂×light×species interactions, while in Fig. 3b, they represent light effects. For further explanations see Fig. 1.



light treatments, and FOLS was significantly greater in black spruce than in white spruce (Table 1; Fig. 3b).

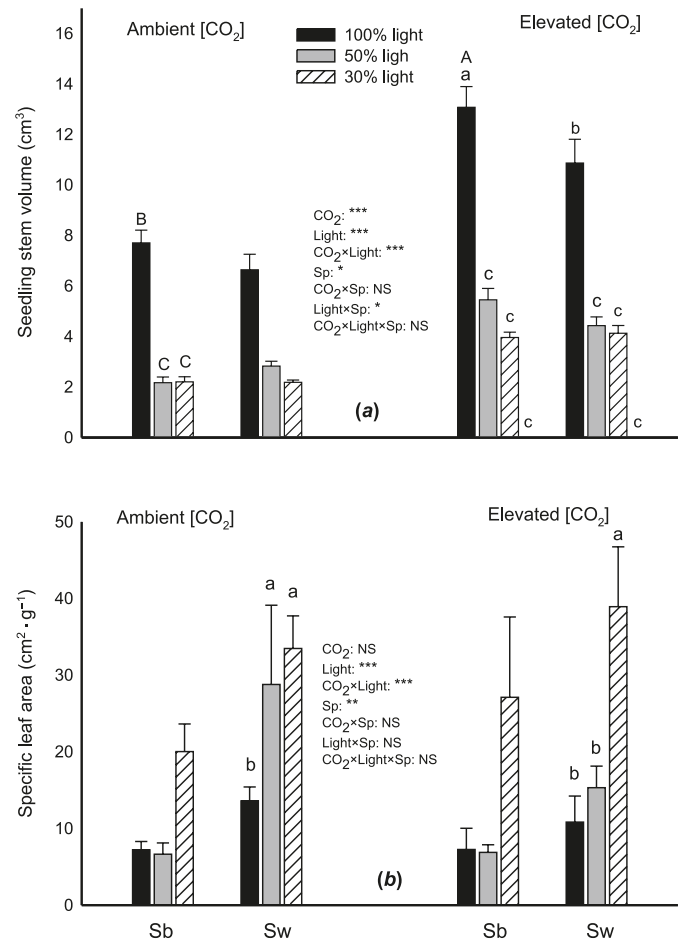
Stem volume

CO₂ concentration and light had significant interactive effects on stem volume. The greatest stem volume was observed in seedlings grown under 100% light with increased [CO₂] followed, sequentially, by seedlings grown under 100% light and ambient [CO₂] and the shaded seedlings with increased [CO₂]. No significant difference occurred between the shaded seedlings grown under ambient [CO₂], where the lowest stem volume was recorded (Table 1; Fig. 4a). Light and species also had significant interactive effects on stem volume (Table 1). Stem volume was greatest in black spruce grown under 100% light, followed by white spruce grown under 100% light, and there was no significant difference between seedlings of either species grown under the 50% and 30% light regimes (Fig. 4a).

Specific leaf area

CO₂ concentration and light had significant interactive effects on SLA (Table 1). With both CO₂ concentrations, SLA generally decreased with increasing light. Seedlings grown

Fig. 4. Effects of CO₂ concentration ([CO₂]) and light on (4a) the stem volume and (4b) specific leaf area of black spruce (Sb) and white spruce (Sw) seedlings after 4.5 months of treatment. In Fig. 4a, the lower case letters represent light×species interactions, while upper case letters represent CO₂×light interactions. In Fig. 4b, the letters represent CO₂×light interactions. For further explanations see Fig. 1.

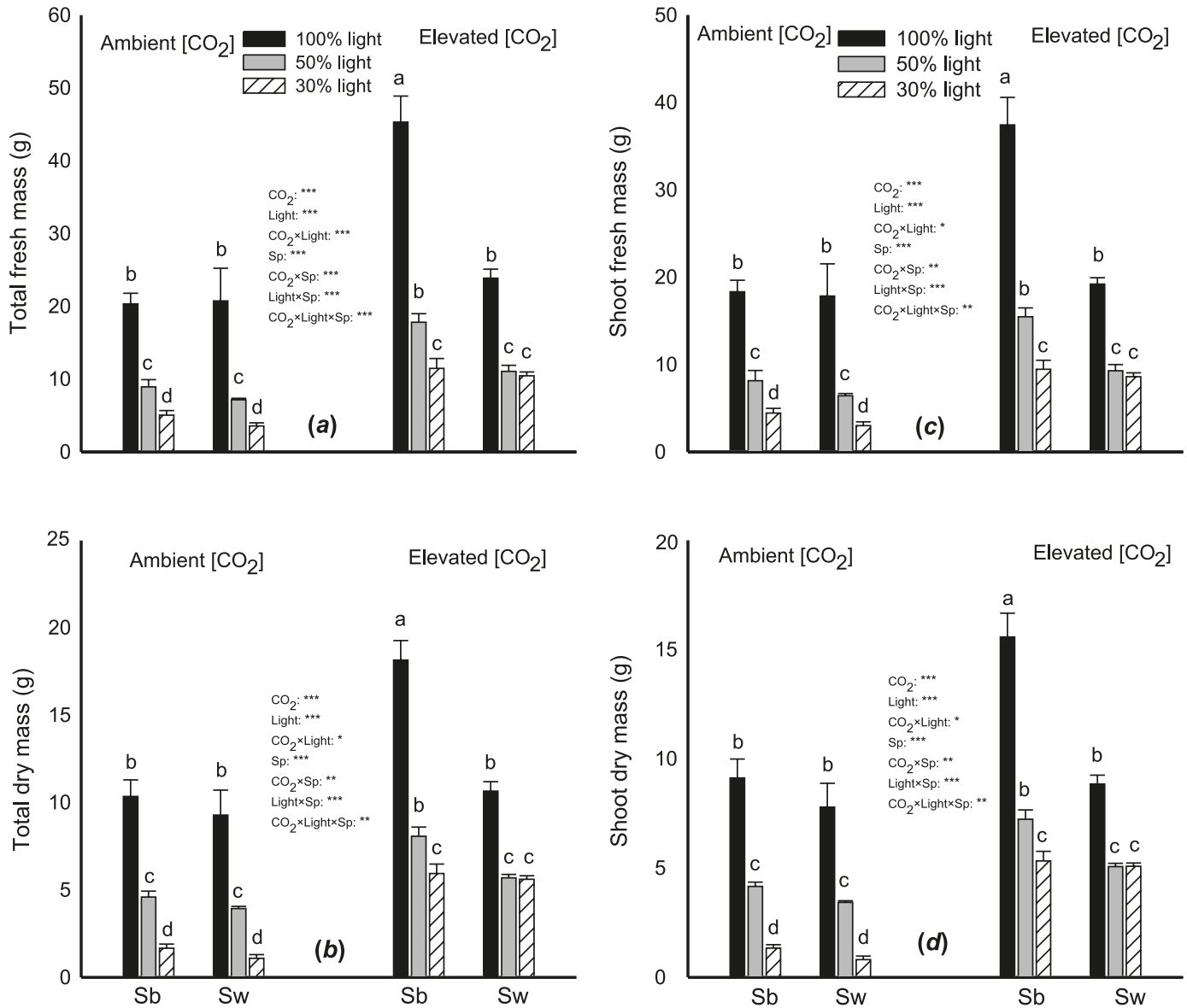


under 50% and 30% light, with ambient [CO₂], as well as seedlings grown under 30% light and increased [CO₂] had the highest SLA (Fig. 4b). CO₂ concentration per se had no effect on SLA for plants grown under 100% light. White spruce had significantly greater SLA than black spruce (Fig. 4b).

Biomass

The interactions of [CO₂], light, and species significantly influenced total seedling fresh mass, dry mass, shoot fresh mass, and shoot dry mass in the same pattern (Table 1). Black spruce grown under 100% light and with elevated [CO₂] had the greatest total fresh and dry biomass, as well as shoot fresh and dry mass (Figs. 5a–5d, respectively). This was followed by black spruce grown under 50% light with elevated [CO₂], white spruce grown under 100% light for both CO₂ concentrations, and black spruce grown under 100% light with ambient [CO₂]. Total and shoot biomass (both fresh and dry) of both species grown under 30% light and with ambient [CO₂] were lower than those for both species grown under 30% light with elevated [CO₂].

Fig. 5. Effects of CO₂ concentration ([CO₂]) and light on (a) the total fresh mass, (b) total dry mass, (c) shoot fresh mass, and (d) shoot dry mass of black spruce (Sb) and white spruce (Sw) seedlings after 4.5 months of treatment. The letters represent CO₂×light×species interactions in Figs. 5a–5d. For further explanations see Fig. 1.



The three factors, [CO₂]; light; species, also had significant interactions on root fresh mass and root dry mass. Black spruce grown under 100% light under elevated [CO₂] had the greatest root fresh mass, and this was followed by white spruce grown under 100% light for both CO₂ conditions (Fig. 6a). With elevated [CO₂], the root fresh mass of either species was similar under 50% and 30% light. At ambient [CO₂], the root fresh mass of either species under 50% and 30% light were similar, but lower than at elevated [CO₂]. Black spruce grown at elevated [CO₂] and under 100% light had the greatest root dry mass, followed by white spruce under 100% light for both CO₂ concentrations, and these were significantly greater than root dry mass of black spruce grown at ambient [CO₂] under 100% light. Root dry mass was lowest in black spruce exposed to increased [CO₂] and 30% light (Fig. 6b).

Biomass ratios

CO₂ concentration and light had significant interactive effects on SMR (Table 1). SMR decreased with decreasing light at ambient [CO₂], whereas the opposite occurred for seedlings grown at elevated [CO₂]. At ambient [CO₂], seedlings grown under 100% and 50% light had statistically higher SMR, whereas the highest SMR was recorded for seedlings grown under 50% and 30% light with elevated [CO₂]. Seedlings grown under 30% light with ambient [CO₂] and under 100% light with elevated [CO₂] had the lowest SMR (Fig. 7a).

CO₂ concentration, light, and species had significant interactive effects on RMR (Table 1). White spruce grown under 30% light with ambient CO₂ levels had the greatest RMR. There was no difference in the RMR of black spruce grown with ambient and elevated [CO₂] under 30% and 100% light,

Fig. 6. Effects of CO₂ concentration ([CO₂]) and light on (a) the fresh root biomass and (b) dry root biomass of black spruce (Sb) and white spruce (Sw) seedlings after 4.5 months of treatment. The letters represent CO₂×light×species interactions in both Figs. 6a and 6b. For further explanations see Fig. 1.

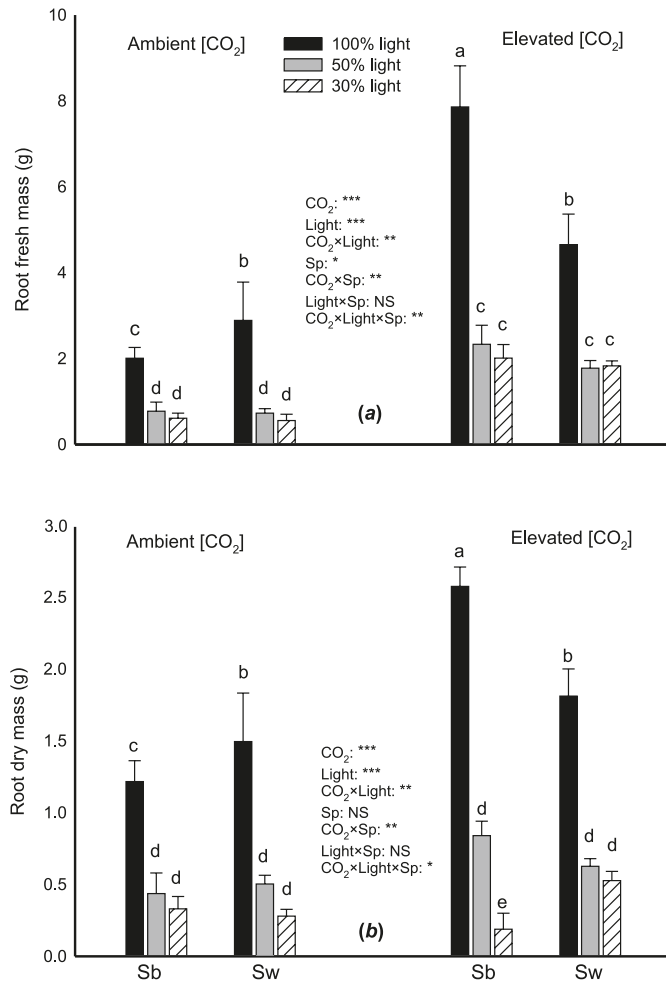
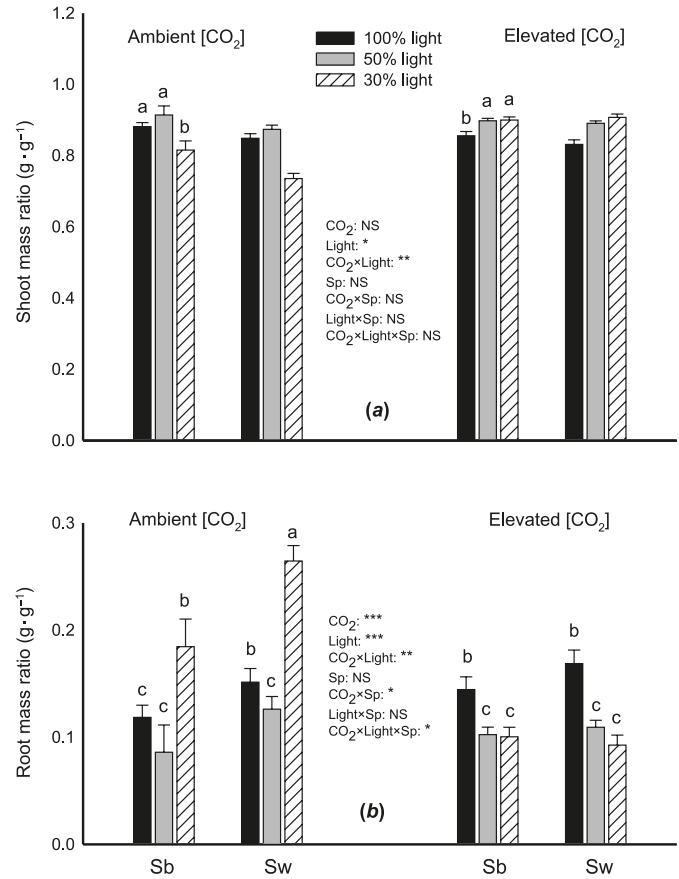


Fig. 7. Effects of CO₂ concentration ([CO₂]) and light on (a) the shoot mass ratio and (b) root mass ratio of black spruce (Sb) and white spruce (Sw) seedlings after 4.5 months of treatment. In Fig. 7a, the letters represent CO₂×light interactions, while in Fig. 7b, letters represent CO₂×light×species interactions. For further explanations see Fig. 1.



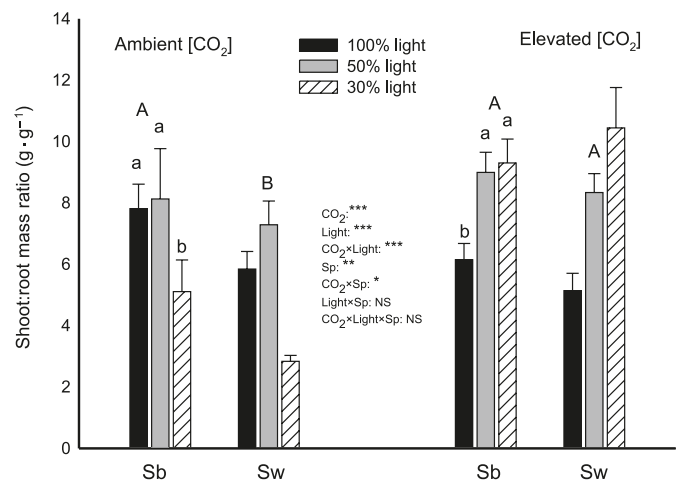
respectively, or the RMR of white spruce grown under 100% light (Fig. 7b). No significant difference occurred in other treatment combinations that had the lowest RMR (Fig. 7b).

CO₂ concentration and light, and [CO₂] and species had significant interactive effects on the shoot-to-root mass ratio (SRR) (Table 1). At ambient [CO₂], SRR decreased with decreasing light, whereas under elevated [CO₂], SRR increased with decreasing light. At ambient [CO₂], the SRR of seedlings grown under 100% and 50% light was significantly higher than that of seedlings grown under 30% light with ambient [CO₂] (Fig. 8). However, with elevated [CO₂], the SRR of seedlings under 50% and 30% light was significantly higher than the SRR of seedlings grown under 100% light. At elevated [CO₂], there was no significant difference in SRR, whereas at ambient [CO₂] white spruce seedlings had significantly reduced SRR (Fig. 8).

Discussion

The data obtained in the present study support our hypothesis that CO₂-enhancement of growth and biomass in the two species was relatively greater under lower light lev-

Fig. 8. Effects of CO₂ concentration ([CO₂]) and light on the SRR of black spruce (Sb) and white spruce (Sw) seedlings after 4.5 months of treatment. The lower case letters represent CO₂×light interactions, while the upper case letters represent CO₂×species interactions. For further explanations see Fig. 1.



els than at higher light levels. Despite the greater absolute increases found at higher light (eg: Figs. 1b and 5a–5d), the far greater relative increases at lower light levels suggest that increases in [CO₂] in the atmosphere will likely increase the shade tolerance and competitiveness of the two species while under shaded conditions. Consequently, these species will likely be able to grow longer and faster under the shade of the existing forest canopy. Thus, understory regeneration and uneven-aged silvicultural systems will likely become more practical in the future. The replacement of clearcut silvicultural systems for even-aged stands by uneven-aged management systems will represent a major advance in the silviculture of the boreal forest. Well structured uneven-aged stands are generally more productive and more sustainable, particularly on a small land base, than even-aged stands (Smith et al. 1997). This result can have important implications for forest management and silviculture under future climatic conditions.

CO₂ concentration and light had significant interactive effects on seedling height after 2.5 months of treatments. Under the 100% light regime, the seedlings were able to take advantage of the elevated [CO₂], resulting in greater seedling height at the first measurement. The CO₂–light synergy has also been reported in other studies (Kerstiens 1998; Hopkins and Hüner 2004). In the presence of sufficient light, plant growth is generally enhanced (Reekie et al. 1997; Zebian and Reekie 1998; Grechi et al. 2007) because plants are better able to exploit elevated [CO₂] in terms of absolute responses (Madsen 1974). Zebian and Reekie (1998) reported that the combination of increased CO₂ and high light enhance the seedling height growth of *Sinapis alba* L., *Medicago sativa* L., *Gypsophila paniculata* L., and *Picea abies* (L.) Karsten, more than did either treatment alone. In this study, however, the CO₂–light interaction became insignificant after 4.5 months of treatment (Fig. 1b), suggesting that the height responses became uniform, in the statistical sense, among different light treatments. Since the seedlings under shade were smaller at 2.5 months, the disappearance of the differences suggests greater relative responses at lower light. Thus, the height data also lends to support to our first hypothesis. The greater relative responses at lower light conditions will likely increase the competitiveness of the species under shaded conditions. Khan et al. (2000) also found that Douglas-fir, ponderosa pine, western hemlock, and western red cedar grown under 25% light are the tallest, while seedlings grown under 100% light are the shortest.

Black spruce responded more dramatically to elevated [CO₂] than its congeneric counterpart. This result supports our second hypothesis: that the more shade-tolerant species (i.e., black spruce) is more responsive to elevated [CO₂]. Poorter and Werger (1999) found similar results for *Cecropia ficifolia* Warb. ex Sneathl, *Bellucia pentamera* Naudin, *Tachigali* sp., *Cariniana micrantha* Duke, *Capirona decorticans* Spruce, and *Theobroma speciosum* Willd. ex Spreng. Plants that have similar morphological features can respond differently changes in light and CO₂ (Johnsen and Major 1998; Grechi et al. 2007), and the response to [CO₂] can change with light conditions (Hättenschwiler and Körner 2000). These results suggest that the more shade-tolerant species will likely benefit most from increased levels of

atmospheric CO₂. Faster growth of understory species or advance growth can accelerate the process of succession in the forest.

Seedling height is generally positively correlated to whole-seedling photosynthetic capacity and transpiration efficiency (Armson and Sadreika 1974; Thompson 1985). Seedlings that are better able to take advantage of elevated [CO₂] will likely be more competitive under future climatic conditions associated with increasing atmospheric CO₂. Johnsen and Major (1998) found that black spruce seedlings grown under elevated [CO₂] have greater height and RCD, and subsequently have a greater survival rate and better growth when planted in the field than those grown with ambient [CO₂]. Such differences are still evident 15 years after planting. Similar results are found with white spruce 10 years after field planting (Mullin and Svaton 1972).

The growth in diameter of the two species differed according to the light treatment. In white spruce, the diameter generally decreased with decreasing light levels. In black spruce, however, there was no significant difference in the RCD of seedlings exposed to 50% and 30% light, although 100% light still produced the largest RCD. After 2.5 months, RCD of black spruce was 18% higher than that of white spruce, but the margin of increase dropped to 5% after 4.5 months. Regardless of the light level, elevated [CO₂] increased RCD of black spruce and white spruce by 30% and 35%, respectively, after 4.5 months; an indication that increased [CO₂] would stimulate greater tree growth even at lower light levels above the minimum required for survival.

The synergetic effect of [CO₂] and light was also evident in stem volume measurement, i.e., the greatest stem volume was achieved with elevated [CO₂] and the highest light level regime. The trends of the synergetic effect were similar for seedling height, RCD, and stem volume. The relative enhancement by elevated [CO₂] on stem volume was, however, different from the gross enhancement. For example, elevated [CO₂] increased stem volume by 67%, 98%, and 84% in seedlings grown under 100%, 50%, and 30% light, respectively. In terms of species response, the relative enhancement by elevated [CO₂] was 86% and 66% for black spruce and white spruce, respectively. The greater relative enhancement under low light seems to suggest an enhancement of light-use efficiency in shaded seedlings (Lambers et al. 1998). The greater enhancement at the low-light levels may also be attributed to a reduction in respiration (Lambers et al. 1998), while the relatively greater enhancement of black spruce confirms the findings of Teskey and Shrestha (1985) that the more shade tolerant species respond more positively to [CO₂] increase than less shade-tolerant plants.

The number of FOLS was generally less sensitive to the treatments than the other morphological parameters, e.g., height and diameter, especially during the second measurement. Furthermore, it was more responsive to light than [CO₂]. The lack of significant response of FOLS to [CO₂] in this study, was in contrast to the finding of Johnsen and Major (1998) that elevated [CO₂] increases the number of branches in black spruce seedlings by 78%. According to Lambers et al. (1998), shade-intolerant plants generally do not respond to external environmental stimuli by varying the number of branches, because of strong apical domi-

nance. On the other hand, shade-tolerant species do tend to vary the number of branches in response to environmental conditions (Poorter and Werger 1999).

There were significant interactive effects of $[\text{CO}_2]$ and light on the SLA of both species. While the increased $[\text{CO}_2]$ appeared to have decreased SLA at all three light levels, the effect was statistically significant only in the 50% light treatment. Our findings are in contrast to those of Zebian and Reekie (1998), Zhang et al. (2006), and Grechi et al. (2007), where neither $[\text{CO}_2]$ nor its interaction with light affects SLA; but the negative effect of elevated $[\text{CO}_2]$ on SLA is common in trees (Pettersson and McDonald 1992; Wolfe et al. 1998). Changes in leaf structure, anatomy, and (or) accumulation of soluble carbohydrates can result in changes in SLA (Lambers et al. 1998), and increased $[\text{CO}_2]$ generally causes accumulation of carbohydrates in leaves, reducing SLA (Pettersson and McDonald 1992). Plants growing under shaded conditions tend to increase their leaf area to acquire more photons (Lambers et al. 1998; Zebian and Reekie 1998; Poorter 2001; Grechi et al. 2007). Conifers also adopt a strategy of increasing their photosynthetic capacity by decreasing SLA with increasing light levels (Jordan and Smith 1993). However, the exact mechanisms for the differences found in this study are unknown.

There were significant three-way interactions among $[\text{CO}_2]$, light, and species in all biomass variables in this study, including total seedling biomass, shoot biomass, and root biomass (both fresh and dry). The relative enhancement of seedling fresh biomass and dry biomass by elevated $[\text{CO}_2]$ increased as light levels decreased. Elevated $[\text{CO}_2]$ increased total fresh mass by 68%, 79%, and 318%, and total dry mass by 47%, 61%, and 318% under 100%, 50%, and 30% light levels, respectively. The explanation for the greater enhancement at lower light levels is similar to the explanations outlined for RCD. The biomass enhancement levels were greater in black spruce than in white spruce (for example, total fresh mass was 165% higher in black spruce, while total dry mass was 75%). While the total and shoot biomass of black spruce decreased with decreasing light levels at both the ambient and elevated $[\text{CO}_2]$, such a pattern was true for white spruce only under the ambient $[\text{CO}_2]$. By comparison, under the elevated $[\text{CO}_2]$, there were no significant differences in either total biomass or shoot biomass in white spruce. While the above trends appear to hold for root biomass, the differences between the two shaded levels generally lack statistical significance, with the exception of black spruce under elevated $[\text{CO}_2]$. There are two possible explanations for the general lack of significant difference between seedlings grown under shade conditions. First, root biomass of seedlings grown under 50% and 30% light was very small by comparison with that of shoot or total biomass, and the differences were even smaller than those of total biomass or shoot biomass. Second, since the rate of shoot growth determines the success of a tree in competition for light, the resource allocation to roots was kept at a bare minimum under both 30% and 50% light. However, the elevated $[\text{CO}_2]$ did increase the sensitivity of root biomass to light treatments in black spruce.

Elevated $[\text{CO}_2]$ decreased SMR under 100% light, but increased it under 30% light. By contrast, under 30% light, the RMR was greatest with ambient $[\text{CO}_2]$, but least with ele-

vated $[\text{CO}_2]$. Under 100% light, on the other hand, the RMR was intermediate with ambient $[\text{CO}_2]$ but became the highest with elevated $[\text{CO}_2]$. As a consequence of the different responses in RMR and SMR, the shoot-to-root ratio was lowest under 30% light with ambient $[\text{CO}_2]$ and under 100% light with elevated $[\text{CO}_2]$. In other words, elevated $[\text{CO}_2]$ appeared to cause a reduction in resource allocation to the shoot under the high-light regime, but an increase under low-light conditions. This shift in resource allocation in response to changes in $[\text{CO}_2]$ could potentially influence the relative competitiveness of the species under different light conditions in the future climate when the atmospheric $[\text{CO}_2]$ will be substantially higher than it is today. The findings in this study are in general agreement with some studies (Duff et al. 1994; Prior et al. 1997; Grechi et al. 2007), but in contrast to others in which $[\text{CO}_2]$ does not affect mass ratios (Tissue et al. 1997; Zhang et al. 2006).

Regenerating black spruce and white spruce can be challenging, with increasing emphasis on smaller clearcuts and uneven-aged forest stand management. Understanding the morphological and physiological requirements of seedlings is essential for proper management strategies. The continuous increase in atmospheric $[\text{CO}_2]$ makes the situation even more important, especially in the boreal forest where the impacts of CO_2 -mediated climate-change will be most prominent. Regardless of the light level, elevated $[\text{CO}_2]$ resulted in an increase in growth (height and diameter) by 21% and 16%, and 20% and 23%, respectively, in black spruce and white spruce. Total biomass was also 94% and 54% higher with elevated $[\text{CO}_2]$ in black spruce and white spruce, respectively, with some shifts in resource allocation between above- and below-ground parts. The shift in resource allocations in response to elevated $[\text{CO}_2]$ could have significant implications for future regeneration efforts. While some parameters such as height and FOLS were enhanced relatively greater by elevated $[\text{CO}_2]$ at high light levels, total fresh biomass and dry biomass, as well as RCD, were relatively more enhanced at the lower light levels. The presumed enhancement in light-use efficiency under shaded conditions suggests that uneven-age silvicultural systems for managing both black and white spruce would be more feasible under future climatic conditions associated with increases in atmospheric $[\text{CO}_2]$. However, longer-term research is warranted to better understand these implications.

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References

- Ainsworth, E.A., and Long, S.P. 2005. What have we learned from 15 years of free-air CO_2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO_2 . *New Phytol.* **165**(2): 351–372. doi:10.1111/j.1469-8137.2004.01224.x. PMID:15720649.
- Apps, M.J., Kurz, W.A., Luxmoor, R.J., Nilsson, L.O., Sedjo, R.A., Schmidt, R., Simpson, L.G., and Vinson, T.S. 1993. Boreal for-

- est and tundra. *Water Air Soil Pollut.* **70**: 39–53. doi:10.1007/BF01104987.
- Armson, K.A., and Sadreika, V. 1974. Forest tree nursery soil management and related practices. Ontario Ministry of Natural Resources, Ottawa, Ont.
- Awada, T., and Redmann, R.E. 2000. Acclimation to light in planted and naturally regenerated populations of white spruce seedlings. *Can. J. Bot.* **78**(12): 1495–1504. doi:10.1139/cjb-78-12-1495.
- Baker, F.S. 1949. A revised shade tolerance table. *J. For.* **47**: 179–181.
- Bazzaz, F.A. 1990. The response of natural ecosystems to the rising global carbon dioxide levels. *Annu. Rev. Ecol. Syst.* **21**: 167–196. doi:10.1146/annurev.es.21.110190.001123.
- Bazzaz, F.A., and McConnaughay, D.M. 1992. Plant-plant interactions in elevated CO₂ environments. *Aust. J. Bot.* **40**(5): 547–563. doi:10.1071/BT9920547.
- Bonan, G.B., and Shugart, H.H. 1989. Environmental factors and ecological processes in boreal forests. *Annu. Rev. Ecol. Syst.* **20**: 1–28. doi:10.1146/annurev.es.20.110189.000245.
- Cao, B., Dang, Q.L., Yu, X.G., and Zhang, S. 2008. Effects of [CO₂] and nitrogen on morphological and biomass traits of white birch (*Betula papyrifera*) seedlings. *For. Ecol. Manage.* **254**(2): 217–224. doi:10.1016/j.foreco.2007.08.002.
- Ceulemans, R., and Mousseau, M. 1994. Tansley Review No. 71: Effects of elevated atmospheric CO₂ on woody plants. *New Phytol.* **127**(3): 425–446. doi:10.1111/j.1469-8137.1994.tb03961.x.
- Chen, H.Y.H. 1997. Interspecific responses of planted seedlings to light availability in interior British Columbia: survival, growth, allometric patterns, and specific leaf area. *Can. J. For. Res.* **27**(9): 1383–1393. doi:10.1139/cjfr-27-9-1383.
- Curtis, P.S. 1996. A meta-analysis of leaf gas exchange and nitrogen in trees grown under elevated carbon dioxide. *Plant Cell Environ.* **19**: 127–137. doi:10.1111/j.1365-3040.1996.tb00234.x.
- Curtis, P.S., and Wang, X. 1998. A meta-analysis of elevated CO₂ effects on woody plant mass, form, and physiology. *Oecologia* (Berl.), **113**: 299–313. doi:10.1007/s004420050381.
- Duff, G.A., Berryman, C.A., and Eamus, D. 1994. Growth, biomass allocation and foliar nutrient contents of two Eucalyptus species of the wet-dry tropics of Australia grown under CO₂ enrichment. *Funct. Ecol.* **8**(4): 502–508. doi:10.2307/2390075.
- Gower, S.T., Vogel, J.G., Norman, J.M., Kucharik, C.J., Steele, S.J., and Stow, T.K. 1997. Carbon distribution and aboveground net primary production in aspen, jack pine, and black spruce stands in Saskatchewan and Manitoba, Canada. *J. Geophys. Res.* **102**(D24): 29,029–29,041. doi:10.1029/97JD02317.
- Grechi, P.V., Hilbert, G., Milin, S., Robert, T., and Gaudillère, J.P. 2007. Effect of light and nitrogen supply on internal C:N balance and control of root-to-shoot biomass allocation in grapevine. *Environ. Exp. Bot.* **59**: 139–149. doi:10.1016/j.envexpbot.2005.11.002.
- Grossnickle, S.C. 2000. Ecophysiology of Northern spruce seedlings: the performance of planted seedlings. National Research Council of Canada, Ottawa, Ont.
- Haavisto, V.F., and Jeglum, J.K. 1995. Black spruce in Ontario: an overview. *Can. For. Serv. Great Lakes Forest Centre, Frontline Technical Note 25*.
- Hättenschwiler, S., and Körner, C. 2000. Tree seedling responses to *in situ* CO₂-enrichment differ among species and depend on understory light availability. *Glob. Change Biol.* **6**(2): 213–226. doi:10.1046/j.1365-2486.2000.00301.x.
- Hopkins, W.G., and Hüner, N.P.A. 2004. Introduction to plant physiology. 3rd ed. J. Wiley, Hoboken, N.J.
- Huang, J.G., Bergeron, Y., Denneler, B., Berninger, F., and Tardif, J. 2007. Response of forest trees to increased atmospheric CO₂. *Crit. Rev. Plant Sci.* **26**(5): 265–283. doi:10.1080/07352680701626978.
- IPCC. 2007. Summary for policymakers. In *Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Edited by S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor, and H.L. Miller.* Cambridge University Press, Cambridge, UK.
- Johnsen, K.H., and Major, J.E. 1998. Black spruce family growth performance under ambient and elevated atmospheric CO₂. *New For.* **15**(3): 271–281. doi:10.1023/A:1006586317535.
- Jordan, D.N., and Smith, W.K. 1993. Simulated influence of leaf geometry on sunlight interception and photosynthesis in conifer needles. *Tree Physiol.* **13**: 29–39. PMID:14969899.
- Kerstiens, G. 1998. Shade-tolerance as a predictor of responses to elevated CO₂ in trees. *Physiol. Plant.* **102**(3): 472–480. doi:10.1034/j.1399-3054.1998.1020316.x.
- Khan, S.R., Rose, R., Haase, D.L., and Sabin, T.E. 2000. Effects of shade on morphology, chlorophyll concentration, and chlorophyll fluorescence of four Pacific Northwest conifer species. *New For.* **19**(2): 171–186. doi:10.1023/A:1006645632023.
- Kimball, B.A. 1983. Carbon dioxide and agricultural yield: an assemblage and analysis of 430 prior observations. *Agron. J.* **75**: 779–788.
- Lambers, H., Chapin, F.S., III, and Pons, T.L. 1998. *Plant physiological ecology.* Springer-Verlag, New York, N.Y.
- Larigauderie, A., Hilbert, D., and Oechel, W.C. 1988. Effect of carbon dioxide enrichment and nitrogen availability on resource acquisition and resource allocation in a grass, *Bromus mollis*. *Oecologia* (Berl.), **77**(4): 544–549. doi:10.1007/BF00377272.
- Larson, J.A. 1980. *The boreal ecosystem.* Academic Press, New York, N.Y.
- Lieffers, V.J., and Stadt, K.J. 1994. Growth of Understorey *Picea glauca*, *Calamagrostis canadensis*, and *Epilobium angustifolium* in relation to overstorey light transmission. *Can. J. For. Res.* **24**(6): 1193–1198. doi:10.1139/x94-157.
- Linder, M. 2000. Developing adaptive forest management strategies to cope with climate change. *Tree Physiol.* **20**: 299–307. PMID:12651446.
- Madsen, E. 1974. Effect of CO₂-concentration on development and dry matter production in young tomato plants. *Acta Agric. Scand.* **23**: 235–240.
- Man, R., and Lieffers, V.J. 1997. Seasonal photosynthetic responses to light and temperature in white spruce (*Picea glauca*) seedlings planted under aspen (*Populus tremuloides*) canopy and in the open. *Tree Physiol.* **17**: 437–444. PMID:14759835.
- Mullin, R.E., and Svaton, J. 1972. A grading study with white spruce nursery stock. *Commonw. For. Rev.* **51**(1): 62–69.
- Nienstaedt, H., and Zasada, J.C. 1990. *Picea glauca* (Moench) Voss, White Spruce. In *Silvics of North America, Vol. 1. Conifers. Agricultural Handbook 654. Technical co-ordinators R.M. Burns and H.H. Barbara.* USDA For. Serv., Washington, D.C. pp. 204–226.
- Patterson, T.B., Guy, R.D., and Dang, Q.L. 1997. Whole-plant nitrogen- and water-relations traits, and their associated trade-offs, in adjacent muskeg and upland boreal spruce species. *Oecologia* (Berl.), **110**(2): 160–168. doi:10.1007/s004420050145.
- Pettersson, R., and McDonald, A.J.S. 1992. Effects of elevated carbon dioxide concentration on photosynthesis and growth of small birch plants (*Betula pendula* Roth.) at optimal nutrition. *Plant Cell Environ.* **15**(8): 911–919. doi:10.1111/j.1365-3040.1992.tb01023.x.
- Poorter, L. 2001. Light-dependent changes in biomass allocation

- and their importance for growth of rain forest tree species. *Funct. Ecol.* **15**(1): 113–123. doi:10.1046/j.1365-2435.2001.00503.x.
- Poorter, L., and Werger, M.J.A. 1999. Light environment, sapling architecture, and leaf display in six rain forest tree species. *Am. J. Bot.* **86**(10): 1464–1473. doi:10.2307/2656927. PMID:10523286.
- Prentice, I., Farquhar, G.D., Fasham, M.J.R., Goulden, M.L., Heinmann, M., Jaramillo, V.J., Kheshgi, H.S., Le Quéré, C., Scholes, R.J., and Wallace, D.W.R. 2001. The carbon cycle and atmospheric carbon dioxide. In *Climate change 2001: the scientific basis. Contributions of Working Group I to the 3rd Assessment Report of the Intergovernmental Panel on Climate Change. Edited by J.T. Houghton, Y. Ding, D.J. Griggs, M. Noguer, P.J. van der Linden and D. Xiaosu.* Cambridge University Press, Cambridge, UK. pp. 183–238.
- Prior, S.A., Runion, G.B., Mitchell, R.J., Rogers, H.H., and Amthor, J.S. 1997. Effects of atmospheric CO₂ on longleaf pine: productivity and allocation as influenced by nitrogen and water. *Tree Physiol.* **17**: 397–405. PMID:14759848.
- Reekie, J.Y.C., Hicklenton, P.R., and Reekie, E.G. 1997. Growth and development of *Petunia hybrida* as affected by the interaction between day length and level of atmospheric carbon dioxide. *Ann. Bot. (Lond.)*, **80**: 57–64. doi:10.1006/anbo.1997.0407.
- Ritchie, G.A. 1959. *Trees of knowledge: a handbook of Maritime Trees.* Can. For. Serv., Natural Resources Canada, Fredericton, N.B. Cat. No. Fo42-244/1996E
- Schlesinger, W.H. 1997. *Biogeochemistry: an analysis of global change.* 2nd ed. Academic Press, San Diego, Calif.
- Smith, D.M., Larson, B.C., Kelty, M.J., and Ashton, P.M.S. 1997. *The practice of silviculture — applied forest ecology.* John Wiley and Sons, New York, N.Y.
- Teskey, R.O., and Shrestha, R.B. 1985. A relationship between carbon dioxide, photosynthetic efficiency and shade tolerance. *Physiol. Plant.* **63**(1): 126–132. doi:10.1111/j.1399-3054.1985.tb02830.x.
- Thompson, B.E. 1985. Seedling morphological evaluation — what you can tell by looking. In *Evaluating seedling quality: principles, procedures and predictive abilities of major tests. Edited by M.L. Durvea.* Forest Research Laboratory, Oregon State University, Corvallis, Ore. pp. 59–71.
- Tissue, D.T., Thomas, R.B., and Strain, B.R. 1997. Atmospheric CO₂ enrichment increases growth and photosynthesis of *Pinus taeda*: A 4 year experiment in the field. *Plant Cell Environ.* **20**(9): 1123–1134. doi:10.1046/j.1365-3040.1997.d01-140.x.
- Viereck, L.A., and Johnston, W.F. 1990. *Picea mariana* (Mill). BSP. In *Silvics of North America, Vol. 1. Conifers. Agricultural Handbook 654. Technical co-ordinators R.M. Burns and H.H. Barbara.* USDA For. Serv., Washington, D.C. pp. 227–237.
- Vincent, A.B. 1965. *Black spruce: a review of its silvics, ecology and silviculture.* Canadian Department of Forestry, Ottawa, Ont. Publ. No. 1100.
- Walters, M.B., and Reich, P.B. 2000. Trade-offs in low-light CO₂ exchange: a component of variation in shade tolerance among cold temperate tree seedlings. *Funct. Ecol.* **14**(2): 155–165. doi:10.1046/j.1365-2435.2000.00415.x.
- Ward, J.K., and Strain, B.R. 1999. Elevated CO₂ studies: past, present and future. *Tree Physiol.* **19**: 211–220. PMID:12651563.
- Wolfe, D.W., Gifford, R.M., Hilbert, D., and Yiqi, L. 1998. Integration of photosynthetic acclimation to CO₂ at the whole-plant level. *Glob. Change Biol.* **4**(8): 879–893. doi:10.1046/j.1365-2486.1998.00183.x.
- Wuebbles, D.J., Jain, A., Edmonds, J., Harvey, D., and Hayhoe, K. 1999. Global change: the state of the science. *Environ. Pollut.* **100**(1/3): 57–86. doi:10.1016/S0269-7491(99)00088-3. PMID:15093113.
- Zebian, K.J., and Reekie, E.G. 1998. The interactive effects of atmospheric carbon dioxide and light on stem elongation in seedlings of four species. *Ann. Bot. (Lond.)*, **81**: 185–193. doi:10.1006/anbo.1997.0528.
- Zhang, S.R., and Dang, Q.L. 2007. Interactive effects of soil temperature and [CO₂] on morphological and biomass traits in seedlings of four boreal tree species. *For. Sci.* **53**(3): 453–460.
- Zhang, S.R., Dang, Q.L., and Yu, X.G. 2006. Nutrient and [CO₂] elevation had synergistic effects on biomass production but not on biomass allocation of white birch seedlings. *For. Ecol. Manage.* **234**: 238–244. doi:10.1016/j.foreco.2006.07.017.