



# High nutrient supply and interspecific belowground competition enhance the relative performance of *Picea mariana* (Mill). B.S.P seedlings over *Picea glauca* [Moench] Voss. under elevated CO<sub>2</sub>

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## Abstract

**Key message** We tested how nutrient supply and interspecific belowground competition affect ecophysiological and morphological responses to elevated CO<sub>2</sub> in black (*Picea mariana* (Mill). B.S.P) and white spruce (*Picea glauca* [Moench] Voss.). It is found that belowground competition and high nutrient greatly enhanced the relative performance of black spruce over white spruce at elevated CO<sub>2</sub>.

**Context** We have previously found that interspecific belowground competition reduce growth, whole seedling photosynthesis, and biomass allocation to leaf and that belowground competition and nutrient supply affect responses to elevated CO<sub>2</sub> in the above two species, but we did not examine the physiological and morphological mechanisms of the responses.

**Aims** To examine the interactive effects of belowground competition, nutrient supply and elevated CO<sub>2</sub> on root morphology, photosynthetic rate, and biochemical and photochemical capacity of photosynthesis in black spruce (Sb, *Picea mariana* [Mill.] B.S.P) and white spruce (Sw, *Picea glauca* [Moench] Voss.).

**Methods** Seedlings were grown in individual containers (no belowground competition) or in a common container (belowground competition) under 380 vs. 720 μmol mol<sup>-1</sup> CO<sub>2</sub> and high vs. low nutrient supply in the greenhouse for one growing season.

**Results** Elevated CO<sub>2</sub> stimulated photosynthesis and nutrient use efficiency to a much greater degree in black than white spruce when they were grown in the same container, particularly under high nutrient supply. The ability to produce a greater length of roots per unit volume of soil was associated with the response of black spruce.

**Conclusion** The synergistic effects of elevated CO<sub>2</sub> and belowground competition on the physiology and root morphology of black spruce suggest that elevated CO<sub>2</sub> will likely increase the relative competitiveness of black spruce over white spruce.

**Keywords** Belowground competitions · Boreal conifers · Plant physiological ecology · Climate change

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**Contribution of the co-authors** Marfo- PhD student carried out the experiment, data analysis, and authored the PhD dissertation.

Dang- supervisor of Marfo, initiated the research, advised Marfo in the entire process of the research, adapted this manuscript from Marfo's dissertation, re-wrote substantial amount of the text, revised figures, and made some new figures

Du: contributed to the development of the manuscript

Newaz: re-analyzed some of the results, updated the literature and some part of the introduction and discussions

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## 1 Introduction

The atmospheric CO<sub>2</sub> concentration has been increasing since the start of the industrial revolution in the mid-nineteenth century and will likely continue to increase for the rest of the century (IPCC 2019; Conway and Tans 2011). The increase will affect not only the physiology and growth of individual plants but also their interactions and species richness and composition in terrestrial ecosystems (Friend et al. 2000; Brooker 2006; Körner 2006; Wang 2007; Langley and Megonigal 2010). At individual plant level, increased CO<sub>2</sub> can enhance leaf-level photosynthesis, reduce stomatal conductance and transpiration, and increase water and nutrient use efficiency (Ainsworth and Long 2005; Cao et al. 2007; Huang et al. 2007; Ambebe et al. 2010) as well as whole tree

photosynthesis (Dang et al. 2020), at least in the short term. However, the responses and interactions may be modified by other environmental factors such as nutrient availability (Danyagri and Dang 2013, Li et al. 2013, Li et al. 2015, Danyagri and Dang, 2014a, b, c, Newaz et al. 2016, Newaz et al. 2017, Inoue et al. 2019, Tedla et al. 2020, Dang et al. 2020); e.g., low nutrient supply reduces the stimulation of photosynthesis by elevated CO<sub>2</sub> (Zhang et al. 2006; Cao et al. 2007; Ambebe et al. 2010; Danyagri and Dang 2014b).

The response of a plant community to elevated CO<sub>2</sub> is determined by both the response of individual species and the characteristics of the species assemblage (Navas 1998, Wang 2007). Responses to elevated CO<sub>2</sub> can vary with species and interactions between species (Ainsworth and Long 2005; Engel et al. 2009; Lukac et al. 2010). Inter-species interactions can alter resource availability, which in turn can further influence the community responses to elevated CO<sub>2</sub>. While aboveground interactions within and between tree species have been studied extensively, there is little information on belowground competitions. Belowground competitions can have greater effects on leaf area, transpiration, and growth than aboveground interactions (Carswell et al. 2000; Jensen et al. 2011). This study examines how belowground competitions influence the responses of black spruce (*Picea mariana* (Mill.) B.S.P) and white spruce (*Picea glauca* (Moench) Voss) to elevated CO<sub>2</sub>.

Black spruce and white spruce are congeneric tree species in the boreal forest (Wang et al. 2006; Messaoud and Chen 2011). They co-exist on moist upland sites (Nienstaedt and Zasada 1990; Sims et al. 1990; Haavisto and Jeglum 1995). Black spruce has lower nutrient requirement than white spruce (Nienstaedt and Zasada 1990; Patterson et al. 1997) and can grow on both nutrient rich upland sites and nutrient-poor lowlands while white spruce grows well only on fertile upland sites. Black spruce, therefore, is physiologically more plastic than white spruce (Patterson et al. 1997). Since more plastic species tend to be more responsive to elevated CO<sub>2</sub> (Midgley et al. 1999; Matesanz et al. 2010), we hypothesize that black spruce would respond more positively to elevated CO<sub>2</sub> than white spruce. Black spruce generally grows slower than white spruce and slower-growing species tend to benefit less from elevated CO<sub>2</sub> (Poorter 1998; Tanglely 2001). On fertile sites, fast growing species with high nutrient uptake (Jackson et al. 1990) can deplete nutrient reserves before slow growing species have an opportunity to extract enough nutrients (Jackson et al. 1990; Caldwell et al. 1996; Lambers and Oliveira 2019). A species with a high uptake, however, may be at a disadvantage where nutrient supply is low because of its greater energy requirements for nutrient uptake and lower ability to extract nutrients when nutrient concentrations are low (Jackson et al. 1990; Aerts and Chapin 1999; Bassirirad 2000). We therefore hypothesize that white spruce would respond more positively to elevated CO<sub>2</sub> than black spruce when nutrient supply is

high but less positively than black spruce when nutrient supply is low. Since growing seedlings in individual containers will eliminate root competition between plants, we hypothesize that the previous hypothesis would hold only when the two species grow in the same container. Since elevated CO<sub>2</sub> increases nutrient use efficiency (Ainsworth and Long 2005; Cao et al. 2007; Huang et al. 2007; Ambebe et al. 2010), we further hypothesize that low nutrient would be less limiting to photosynthesis under elevated than under ambient CO<sub>2</sub>. In a previous study (Dang et al. 2020), we have found that belowground competitions reduce whole seedling photosynthesis, seedling growth, and biomass allocation to leaves as well as influence their responses to nutrient supply and elevated CO<sub>2</sub>; nutrient supply affects the responses of photosynthesis and leaf morphology to elevated CO<sub>2</sub> and the effect differs between the two species. However, there are several key issues that are not addressed in our previous study: while whole seedling photosynthesis gives us a big picture of how the carbon sequestration of the seedling responds to the treatments, the results have little use beyond the measurement environmental conditions because they cannot be used to estimate trees' photosynthesis under other environmental conditions or to be scaled up to estimate the response at the forest stand or ecosystem levels. The photosynthesis of trees in the field varies with the time of day and the time of year due to changes in environmental and physiological conditions (Dang et al. 1991) and the lab measurement is just one spot sample of the response surface. In this study, we examined two photosynthetic parameters that are commonly used in computer models for estimating tree carbon sequestration at different space and time scales: the maximum Rubisco carboxylation capacity ( $V_{cmax}$ ) and maximum photosynthetic electron transport rate ( $J_{max}$ ). Furthermore, Dang et al. (2020) gives no information on the mechanisms of belowground competition. Belowground competition can occur physiologically (including allelopathic) and morphologically (Lambers and Oliveira 2019). In this study, we examined various root morphological characteristics that influence tree's competitiveness in belowground competitions. The last important issue that Dang et al. (2020) did not address is resource use efficiency. Adjusting resource use efficiencies is a key acclimation strategy that plants use in response to changes in environmental conditions, particularly environmental stresses. In this study, we studied the responses of water and nutrient use efficiencies.

## 2 Materials and methods

### 2.1 Plant materials

One-year old black spruce (*Picea mariana* [Mill.] B.S.P) and white spruce (*Picea glauca* [Moench] Voss.) seedlings were obtained from the Boreal Forest Tree Nursery in

Thunder. All the seedlings had a terminal bud and were in dormancy when the experiment started. The average height of the seedlings was 13 cm for both species at the beginning of the experiment.

## 2.2 Experimental design and growth conditions

There were four treatments: CO<sub>2</sub> concentration ([CO<sub>2</sub>], AC = 380 vs. EC = 720 μmol mol<sup>-1</sup>), belowground competition (with BGC-1 vs. without BGC-0), nutrient supply (N, low vs. high), and species (black spruce vs. white spruce) (Dang 2021). The experiment was carried out as a split-split-split plot design with [CO<sub>2</sub>] as the main or whole plot, root interact as sub plot, nutrient supply as sub-sub plot, and species as sub-sub-sub plot. Each [CO<sub>2</sub>] treatment was randomly assigned to two greenhouses as replicates. Each greenhouse contained the two belowground competition treatments, each belowground competition treatment contained the two nutrient treatments, and each nutrient-belowground competition combination contained the two species (8 seedlings per species).

For the belowground competition treatment (RI), the seedlings were grown in two 29.2-L containers (48 × 38 × 16 cm) with each container hosting 4 seedlings of each species. For the no belowground competition treatment (BGC-0), all the seedlings were grown in 2.9-L individual containers (15.5 cm diameter, 15.5 cm height). The seedlings of each species within each treatment combination were evenly intermingled with those of the other species. All the containers were filled with a mixture of peat moss and vermiculite (50/50 v/v) to the same depth. The spacing and spatial distribution of seedlings and average soil volume per seedling were comparable between the two belowground competition treatments.

The high nutrient treatment (150 mg/L N, 60 mg/L P, 150 mg/L K, 80 mg/L Ca, 40 mg/L Mg, 60 mg/L S) represents the optimal formulation for the Constant Fertilization method (Landis 1989; Li et al. 2013) and the low nutrient treatment (10% of the high) is within the deficient range for the species (Li et al. 2013). In the Constant Fertilization method, dilute fertilizer solution is applied when irrigation is needed (Landis 1989). The environment conditions in the greenhouses were controlled at 55 ± 5% relative humidity, 25 ± 2 °C/15 ± 2 °C day/night temperatures, and 16 h photoperiod. High-pressure sodium vapor lamps were used to supplement the natural light on cloudy days and to extend the natural photoperiod. CO<sub>2</sub> concentration and other environmental conditions were monitored and controlled using an Argus Environment Control System (Argus, Vancouver, BC, Canada). CO<sub>2</sub> elevation was achieved using GEN-2E CO<sub>2</sub> generators (Custom Automated Products, Inc, Riverside, CA).

## 2.3 Photosynthesis to intercellular CO<sub>2</sub> concentration response (A-C<sub>i</sub>) curves

A-C<sub>i</sub> response curves were measured on current year foliage on the terminal shoot in 6 randomly selected seedlings from each treatment combination using a PP-Systems portable gas exchange system and a Parkinson conifer leave cuvette with automatic environment control (PP-Systems, Amesbury, MA, USA) 4 months after the initiation of the experiment. The gas exchange measurements were taken at 25 °C air temperature, 50% RH, 800 μmol m<sup>-2</sup> s<sup>-1</sup> photosynthetically active radiation (tungsten lamp), and at 50, 150, 250, 380, 500, 720, 900, and 1200 μmol mol<sup>-1</sup> CO<sub>2</sub>. Projected leaf area was determined using Regent WinSeedle (Regent Instruments, Québec City, QC, Canada). Photosynthetic water use efficiency (WUE, μmol CO<sub>2</sub> mmol<sup>-1</sup> H<sub>2</sub>O) was calculated as  $P_n/E$ . The maximal carboxylation capacity of Rubisco ( $V_{cmax}$ ) and maximal photosynthetic electron transport capacity ( $J_{max}$ ) were estimated using the PlantecoPhys package of R 4.0.2.  $V_{cmax}$  represents the maximum CO<sub>2</sub> assimilation capacity of the primary photosynthetic enzyme Rubisco and reflects the investment of nitrogen in the dark reaction machinery of photosynthesis while  $J_{max}$  reflects the N investment in the light reaction machinery of photosynthesis and the maximum capacity of the electron transport chain for photosynthesis (Lambers and Oliveira 2019).

## 2.4 Foliar nutrient analyses

The seedlings used in the above gas exchange measurements were harvested to determine the specific leaf area (SLA) and foliar nutrient concentrations. The needles were oven-dried at 70 °C for 48 h. Total nitrogen (N) concentration was determined using the dry combustion method on a LECO CNS-2000 analyzer (LECO, St. Joseph, MI, USA) and phosphorus (P) and potassium (K) concentrations were determined using acid digestion and the ICP-AES technique. SLA was used to convert mass-based into leaf area-based concentrations. Photosynthetic nitrogen (PNUE) and phosphorus (PPUE) use efficiencies were obtained by dividing  $P_n$  at treatment [CO<sub>2</sub>] (380 μmol mol<sup>-1</sup> for ambient and 720 for elevated CO<sub>2</sub>) by foliar N and P concentrations, respectively.

## 2.5 Root characteristics

The fresh roots of all the seedlings (8 seedlings per treatment combination per species) were scanned and analyzed using WinRhizo (Regent Instruments Inc, Quebec, Canada) to determine total root length and mean root diameter. Root length density was determined dividing the total root length of a seedling by the volume of the rooted portion of the pot.

Table 1 provides average height and root collar diameter for each treatment combination from Dang et al. 2020.

**Table 1** Average total root length (m), root diameter (mm), root length density (cm root per cm<sup>3</sup> soil), seedling height (cm), and root collar diameter (RCD, mm, refer to Dang et al. 2020 for the complete results on biomass and growth) in black spruce (Sb) and white spruce (Sw) seedlings under different CO<sub>2</sub>, belowground competition (BGC), and nutrient supply (N) combinations (n=8). The seedlings were exposed to two CO<sub>2</sub> concentrations (380 and 720 μmol mol<sup>-1</sup>) with or without and belowground competition (BGC-1 and BGC-0, respectively) at two nutrient levels

CO <sub>2</sub>	BGC	N	SP	Root length	Root diameter	Root density	Height	RCD
Ambient	BGC-1	High	Sb	11	0.6	0.69	30	4.6
			Sw	8	0.61	0.52	20	4.6
		Low	Sb	11	0.68	0.66	28	4.2
			Sw	8	0.62	0.51	19	4.2
	BGC-0	High	Sb	15	0.65	0.85	39	5.9
			Sw	10	0.66	0.57	31	5.8
		Low	Sb	15	0.65	0.87	27	4.4
			Sw	11	0.67	0.6	22	5
Elevated	BGC-1	High	Sb	17	0.56	1.06	36	5.1
			Sw	14	0.59	0.84	25	5.1
		Low	Sb	15	0.54	0.94	31	4.4
			Sw	7	0.58	0.41	25	4.5
	BGC-0	High	Sb	15	0.79	0.84	42	6.6
			Sw	12	0.69	0.67	39	6.4
		Low	Sb	18	0.69	1.03	32	5.5
			Sw	11	0.7	0.64	27	5.7

## 2.6 Statistical analysis

The analysis of variance (ANOVA) was conducted using the ANOVA function of R 4.0.2. All the data met the ANOVA assumptions of normality and homogeneity (Shapiro Wilk and Bartlett tests). Fisher's least significant difference (LSD) test was conducted when ANOVA showed a significant ( $P \leq 0.05$ ) interaction. The ANOVA linear model is as follows:

$$Y_{ijklmn} = \mu + C_j + R_k + CR_{ik} + N_l + CN_{il} + RN_{kl} + CRN_{ikl} + S_m + CS_{im} + RS_{km} + NS_{lm} + CRS_{ikm} + CNS_{lkm} + RNS_{klm} + CRNS_{ijklm} + \varepsilon_{(ijklm)n}$$

where

$Y_{ijklmn}$	response variable,
$\mu$	grand mean,
C	CO <sub>2</sub> (fixed),
R	belowground competition (fixed),
N	nutrient supply (fixed),
S	species (fixed), and
$\varepsilon$	residual (random).

The subscripts are treatment levels.

## 3 Results

### 3.1 Gas exchange

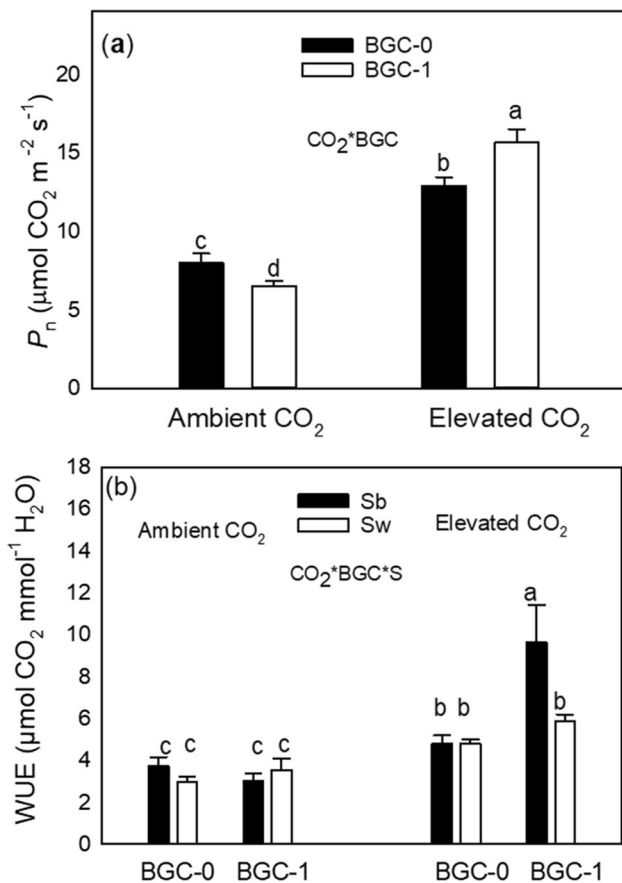
Elevated CO<sub>2</sub> significantly modified photosynthetic response to belowground competition (Table 2): while belowground

competition significantly reduced  $P_n$  under ambient CO<sub>2</sub> (AC), it significantly increased  $P_n$  under the elevated CO<sub>2</sub> (EC) (Fig. 1a). Belowground competition also significantly increased the stimulation of  $P_n$  by EC (Table 2, Fig. 1a). The high nutrient treatment increased  $P_n$  by an average of 17% in the two species and  $P_n$  was 22% greater in black spruce than that in white spruce (Tables 2 and 3).

**Table 2**  $P$  values from ANOVA on the effects of CO<sub>2</sub> concentration, belowground competition (BGC), nutrient supply (N) and species (S) on photosynthesis ( $P_n$ ), photosynthetic water use efficiency (WUE), maximum rate of Rubisco carboxylation ( $V_{cmax}$ ), and maximum rate of photosynthetic electron transport ( $J_{max}$ ) in black spruce and white spruce seedlings. The seedlings were exposed to two CO<sub>2</sub> concentrations (380 and 720 μmol mol<sup>-1</sup>) with and belowground competition at two nutrient levels. Probabilities  $\leq 0.05$  were underlined and bold-faced

Factor	$P_n$	WUE	$J_{max}$	$V_{cmax}$
CO <sub>2</sub>	<b>0.01</b>	<b>0.02</b>	0.57	0.77
RI	1.00	<b>0.01</b>	0.34	0.59
CO <sub>2</sub> *BGC	<b>0.04</b>	<b>0.01</b>	0.27	0.67
N	<b>0.03</b>	0.37	0.28	<b>0.04</b>
CO <sub>2</sub> *N	0.29	0.30	0.19	0.50
BGC*N	0.08	0.34	0.30	0.55
CO <sub>2</sub> *BGC*N	0.74	0.78	0.14	0.56
S	<b>0.00</b>	<b>0.05</b>	<b>0.01</b>	<b>0.02</b>
CO <sub>2</sub> *S	0.11	0.08	0.27	0.15
BGC*S	0.21	0.22	0.36	<b>0.02</b>
N*S	0.13	0.24	0.84	0.99
CO <sub>2</sub> *BGC*S	0.40	<b>0.01</b>	0.68	0.13
CO <sub>2</sub> *N*S	0.24	0.71	0.39	0.57
BGC*N*S	0.60	0.68	0.79	0.87
CO <sub>2</sub> *BGC*N*S	0.33	0.09	0.10	<b>0.02</b>

CO<sub>2</sub> elevation and belowground competition had synergistic effect on photosynthetic water use efficiency (WUE) in black spruce but not in white spruce (Table 2): while CO<sub>2</sub> elevation generally increased WUE in both species and in both belowground competition treatments, the effect was much greater in black spruce with belowground competition than black spruce without belowground competition and white spruce with or without belowground competition (Fig. 1c, Table 3). Belowground competition significantly increased WUE of black spruce under the elevated CO<sub>2</sub> but had no significant effect in black spruce under ambient CO<sub>2</sub> or white spruce in either CO<sub>2</sub> treatment (Fig. 1c). Black spruce had significantly higher WUE than white spruce only in the combination of elevated CO<sub>2</sub> and belowground competition (Fig. 1c).



**Fig. 1** Two- and 3-way interactive effects of CO<sub>2</sub> concentration, belowground competition (BGC), and species (S) on net photosynthesis ( $P_n$ ,  $n=48$ ), and photosynthetic water use efficiency (WUE,  $n=24$ ) in black spruce (Sb) and white spruce (Sw) seedlings. The seedlings were exposed to two CO<sub>2</sub> concentrations with (BGC-1) or without (BGC-0) belowground competitions at low (LN) and high (HN) nutrient supply for 4 months. Bars with different letters were significantly different from each other ( $P \leq 0.05$ )

### 3.2 Photosynthetic electron transport and Rubisco carboxylation

Maximum photosynthetic electron transport ( $J_{\text{max}}$ ) was 17% higher in black spruce than that in white spruce but was not significantly affected by any other treatment or treatment combination (Table 2).

All the treatments interactively affected the maximum carboxylation of Rubisco ( $V_{\text{cmax}}$ ) (Table 2). CO<sub>2</sub> elevation significantly influenced  $V_{\text{cmax}}$  response to belowground competition and nutrient supply (Fig. 2): at AC, black spruce grown with high nutrient with no belowground competition had the highest  $V_{\text{cmax}}$  while white spruce grown in low nutrient with belowground competition had the lowest  $V_{\text{cmax}}$  and there were no significant differences among other treatment combinations; at EC, white spruce grown in the high nutrient with no belowground competition and black spruce grown in high nutrient supply with belowground competition had the highest while white spruce grown under low nutrient with belowground competition had the lowest  $V_{\text{cmax}}$ , but there were no significant differences among other treatment combinations. Nutrient supply significantly modified the effect of CO<sub>2</sub> elevation on  $V_{\text{cmax}}$  (Fig. 2, Table 3): in the high nutrient treatment, EC significantly increased  $V_{\text{cmax}}$  in white spruce with no belowground competition and black spruce grown with belowground competition, but in contrast, EC significantly reduced  $V_{\text{cmax}}$  in black spruce grown with no belowground competition; in the low nutrient treatment, however, EC had no significant impact on  $V_{\text{cmax}}$ .

### 3.3 Foliar nutrient concentration

The interactions among CO<sub>2</sub>, belowground competition, and species had significant effects on foliar N concentration (Table 4). White spruce under AC without belowground competition had the highest N among all species-interaction-CO<sub>2</sub> combinations (Fig. 3a, Table 3). Belowground competition significantly reduced N in white spruce only in the ambient CO<sub>2</sub> and had no significant effect on N in black spruce in either CO<sub>2</sub> treatment (Fig. 3a). All the above effects became insignificant under EC (Figs. 3a). The high nutrient treatment led to a 30% increase in foliar N (Fig. 3a, Tables 3 and 4).

The EC significantly changed the effect of species and belowground competition on foliar phosphorus concentration (Table 4): black spruce under EC with belowground competition had the lowest and white spruce under AC with no belowground competition had the highest foliar P among all treatment combinations (Fig. 3b, Table 3).

Belowground competition significantly reduced foliar potassium concentration only in the low nutrient treatment (Tables 3 and 4, Fig. 3c). Overall, K was 21% higher in black

**Table 3** Average  $P_n$ ,  $E$ ,  $V_{cmax}$ ,  $J_{max}$ , leaf N, P, and K concentration ( $g\ m^{-2}$ ), WUE, NUE, and PUE in black spruce (Sb), and white spruce (Sw) seedlings under different  $CO_2$ , belowground competition (BGC), and nutrient supply (N) combinations ( $n=6$ ). The seedlings were exposed to two  $CO_2$  concentrations ( $380$  and  $720\ \mu mol\ mol^{-1}$ ) with or without belowground competition (BGC-1 and BGC-0, respectively) at two nutrient levels

$CO_2$	BGC	N	SP	$P_n$	$V_{cmax}$	$J_{max}$	N	P	K	WUE	NUE	PUE	
Ambient	BGC-1	High	Sb	7.6	54	71	2.6	0.27	1.4	2.0	2.9	28.2	
			Sw	6.3	41	56	2.9	0.31	1.4	2.3	2.2	20.2	
		Low	Sb	6.8	58	74	2.3	0.25	1.1	4.0	3.0	27.3	
			Sw	5.4	28	79	1.9	0.24	0.8	4.8	2.8	22.4	
	BGC-0	High	Sb	11.6	81	121	2.7	0.34	1.6	2.5	4.3	34.1	
			Sw	8.0	50	83	3.5	0.44	1.3	3.6	2.3	18.2	
		Low	Sb	6.4	47	93	1.9	0.26	1.4	4.8	3.4	24.7	
			Sw	5.9	47	79	3.4	0.43	1.6	2.3	1.7	13.8	
	Elevated	BGC-1	High	Sb	17.6	77	84	2.8	0.21	1.5	8.9	6.3	83.7
				Sw	11.2	48	87	3.6	0.34	1.1	6.2	3.1	32.9
			Low	Sb	15.3	51	110	1.8	0.22	1.0	10.4	8.5	69.5
				Sw	13.5	36	92	2.1	0.24	0.7	5.5	6.4	56.3
BGC-0		High	Sb	15.4	51	95	2.5	0.29	1.5	5.2	6.2	53.1	
			Sw	12.7	77	65	3.5	0.37	1.2	5.0	3.6	34.3	
		Low	Sb	12.5	44	107	2.8	0.26	1.3	4.4	4.5	48.1	
			Sw	11.4	45	85	2.2	0.3	1.0	4.6			

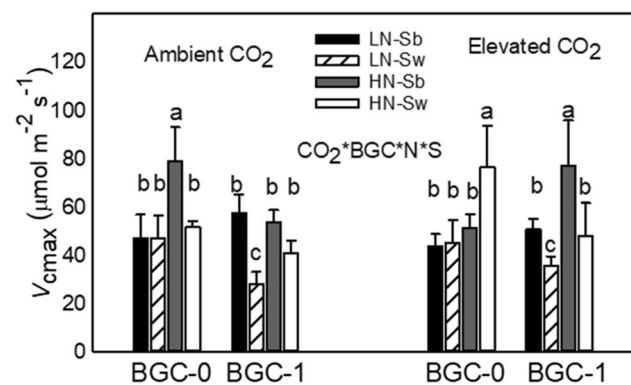
spruce than in white spruce while  $CO_2$  had no significant effect on K (Table 4).

### 3.4 Photosynthetic nutrient use efficiency

$CO_2$ , belowground competition, and species had significant ( $p=0.05$ ) interactive effects on photosynthetic nitrogen use efficiency (PNUE) (Table 4). The  $CO_2$  elevation modified the response of PNUE to belowground competition: belowground competition enhanced PNUE in black spruce only under elevated  $CO_2$  and in white spruce under the ambient  $CO_2$  (Fig. 4a, Table 3). The belowground

competition also had different effect on the response of the two species to  $CO_2$  elevation: EC significantly increased PNUE in both species, but the effect was greater in black spruce when there was belowground competition and greater in white spruce when there was no belowground competition (Fig. 4a, Table 3). Black spruce generally had higher PNUE than white spruce but the difference was not always statistically significant (Fig. 4a). The effect of belowground competition on PNUE was also influenced by nutrient supply (Table 4): the belowground competition enhanced PNUE only when the nutrient supply was low; the low nutrient supply increased PNUE only when belowground competition was present (Fig. 4b, Table 3).

Photosynthetic phosphorus use efficiency (PPUE) was significantly affected by interactions among all four factors (Table 4). EC changed PPUE response to belowground competition: belowground competition had no significant effect on PPUE under AC, but increased PPUE under EC in all species-nutrient combinations except white spruce in the high nutrient treatment (Fig. 4c). EC increased PPUE, and the effect was generally greater in black spruce than in white spruce and greater with belowground competition than without belowground competition, particularly for black spruce (Fig. 4c). The EC effect also varied with species: in white spruce, the greatest effect occurred in the low nutrient treatment with belowground competition; in black spruce, the effect was greatest when belowground competition was present regardless of nutrient treatment (Fig. 4c, Table 3).



**Fig. 2** Two- and 3-way interactive effects of  $CO_2$ , belowground competition (BGC), nutrient supply (N), and species (S) on the maximum carboxylation rate of Rubisco ( $V_{cmax}$ ,  $n=12$ ) in black spruce and white spruce seedlings. The seedlings were exposed to two  $CO_2$  concentrations with (BGC-1) or without (BGC-0) belowground competitions at low (LN) and high (HN) nutrient supply for 4 months. Bars with different letters were significantly different from each other ( $P \leq 0.05$ )

### 3.5 Root characteristics

EC significantly increased total root length and root length density only when the two species grew together (the net

**Table 4** *P* values from ANOVA on the effects of CO<sub>2</sub>, belowground competition (BGC), nutrient supply (N), and species (S) on foliar nutrient concentration, nutrient (N, P, and K) use efficiency, total root length (TRL), mean root diameter (MRD), and root length density (RLD) and of black spruce and white spruce seedlings. The seedlings were exposed to two CO<sub>2</sub> concentrations (380 and 720 μmol mol<sup>-1</sup>) with and belowground competition at two nutrient levels. Probabilities ≤ 0.05 were underlined and bold-faced

Factor	N	P	K	NUE	PUE	TRL	MRD	RLD
CO <sub>2</sub>	0.96	0.36	0.29	<b><u>0.01</u></b>	<b><u>0.00</u></b>	0.105	0.956	0.105
BGC	0.23	0.14	0.21	0.06	<b><u>0.01</u></b>	0.164	<b><u>0.014</u></b>	0.164
CO <sub>2</sub> *BGC	0.57	0.54	0.74	0.05	<b><u>0.01</u></b>	0.385	<b><u>0.029</u></b>	0.385
N	<b><u>0.00</u></b>	<b><u>0.02</u></b>	<b><u>0.01</u></b>	0.09	0.99	0.568	0.811	0.568
CO <sub>2</sub> *N	0.27	0.89	0.36	0.08	0.40	0.549	0.083	0.549
BGC*N	0.13	0.87	<b><u>0.04</u></b>	<b><u>0.04</u></b>	0.37	0.249	0.217	0.249
CO <sub>2</sub> *BGC*N	0.34	0.95	0.20	0.21	0.89	0.341	0.885	0.341
S	<b><u>0.01</u></b>	<b><u>0.00</u></b>	<b><u>0.00</u></b>	<b><u>0.00</u></b>	<b><u>0.00</u></b>	<b><u>&lt;.001</u></b>	0.612	<b><u>&lt;.001</u></b>
CO <sub>2</sub> *S	0.59	0.84	0.15	0.11	<b><u>0.00</u></b>	<b><u>0.035</u></b>	0.983	<b><u>0.035</u></b>
BGC*S	0.16	<b><u>0.04</u></b>	0.58	0.72	0.20	0.294	0.236	0.294
N*S	0.14	0.24	0.52	0.16	<b><u>0.00</u></b>	<b><u>0.005</u></b>	0.410	<b><u>0.005</u></b>
CO <sub>2</sub> *BGC*S	<b><u>0.01</u></b>	<b><u>0.01</u></b>	0.77	<b><u>0.05</u></b>	<b><u>0.04</u></b>	<b><u>0.040</u></b>	<b><u>&lt;.001</u></b>	<b><u>0.040</u></b>
CO <sub>2</sub> *N*S	0.18	0.11	0.81	0.17	<b><u>0.01</u></b>	<b><u>0.001</u></b>	<b><u>0.016</u></b>	<b><u>0.001</u></b>
BGC*N*S	0.94	0.08	0.25	0.43	<b><u>0.04</u></b>	0.631	0.220	0.631
CO <sub>2</sub> *BGC*N*S	0.07	0.63	0.07	0.21	<b><u>0.01</u></b>	0.627	0.916	0.627

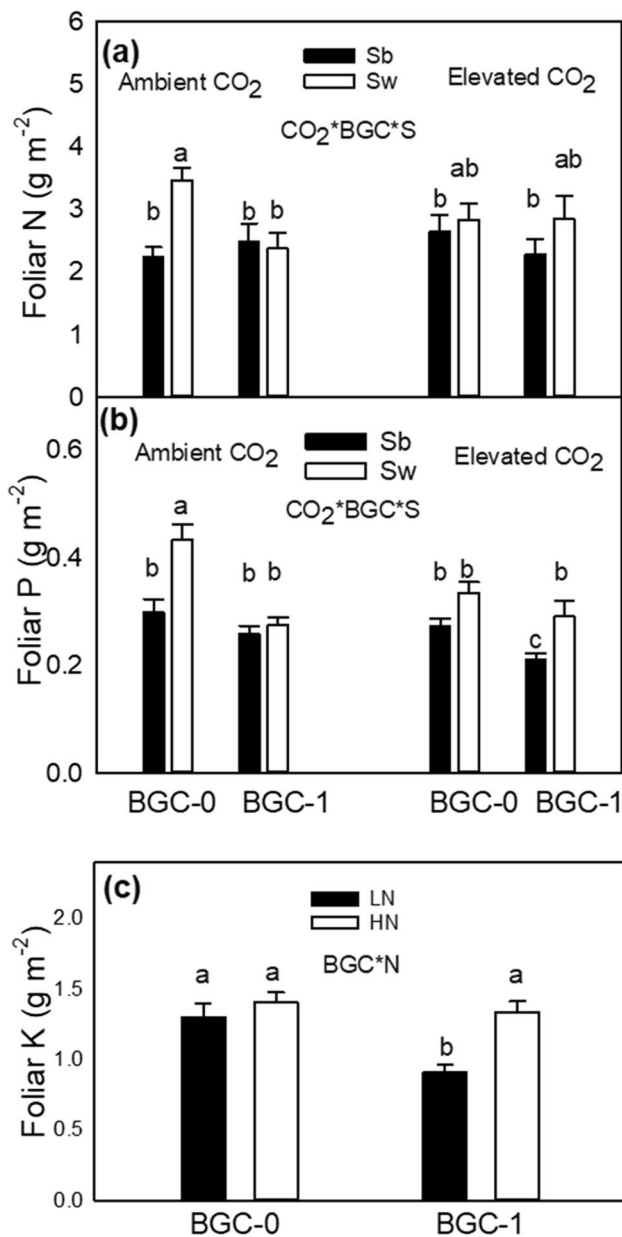
increase in both root length and root length density was 48% for black spruce and 24% for white spruce) while there was no significant effect when the root systems of the two species were separated from each other (Tables 1 and 4, Fig. 5a and e). EC reduced root diameter of black spruce by 14% but had no significant effect on white spruce when the two species grew together while it significantly increased the root diameter of black spruce by 14% when its root system were separated from that of white spruce (Tables 1 and 4, Fig. 5c).

In the interactions between CO<sub>2</sub>, nutrient supply, and species (Table 4), EC increased the total root length of white spruce by 40% under high nutrient supply but had no significant effect on white spruce under low nutrient supply or black spruce in either nutrient treatment (Fig. 4b). However, EC increased the root length density of black spruce in both high (by 22%) and low (28%) nutrient supply and that of white spruce under high nutrient supply by 40% (Table 1, Fig. 5f, Table 4). The root length density of white spruce became more sensitive to nutrient supply under EC (Fig. 5f, Table 1). EC decreased root diameter under low nutrient but increased it under high nutrient supply in black spruce while it did not significantly affect the root diameter of white spruce (Fig. 5d, Table 1).

## 4 Discussion

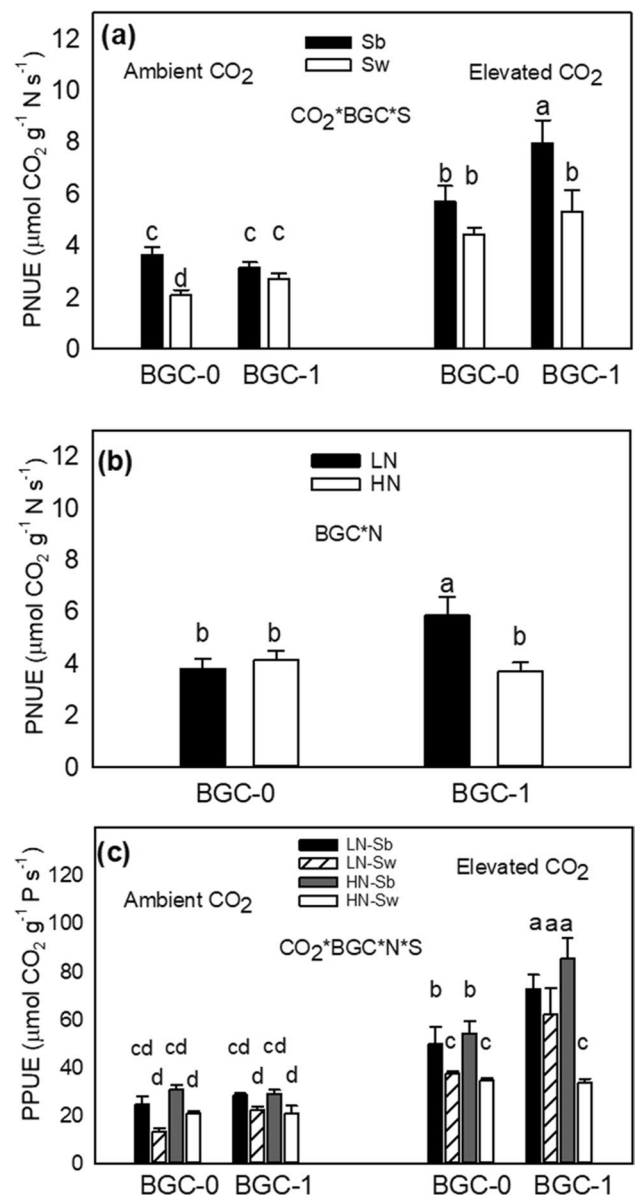
Our results support the hypotheses that black spruce would respond more positively to elevated CO<sub>2</sub> than white spruce when the root systems of the two species were allowed to interact with each other and that the belowground competitions would favor black spruce over white spruce under elevated CO<sub>2</sub>. The results suggest that elevated CO<sub>2</sub> and belowground competitions synergistically enhanced the

physiological and root traits of black spruce but not those of white spruce. For example, the elevated CO<sub>2</sub> increased the nitrogen use efficiency and  $V_{cmax}$  of black spruce much more when there was belowground competition than when there was no belowground competition, but the trend was the opposite for white spruce. However,  $J_{max}$  was not significantly affected by any of the treatments.  $V_{cmax}$  and  $J_{max}$  are the maximum rate of photosynthetic carboxylation and maximum rate of photosynthetic electron transport, respectively, reflecting nitrogen investment in the biochemical reaction and photochemical reaction machinery, respectively (Lambers and Oliveira 2019). The result that white spruce downregulated  $V_{cmax}$  in response to belowground competition under low nutrient supply while black spruce did not provide further evidence that white spruce is more sensitive nutrient supplies than black spruce. Belowground competition also increased the water use efficiency of black spruce under the elevated CO<sub>2</sub> but had no significant effect on white spruce. These responses are in an agreement with the responses of whole seedling photosynthesis that we have reported previously (Dang et al. 2020). Furthermore, elevated CO<sub>2</sub> led to a much greater increase of root length density in black spruce than white spruce when the root systems of the two species were allowed to interact, giving black spruce the ability to absorb nutrients and water from a greater volume of soil than white spruce. Our results support the plasticity-based hypothesis that black spruce would benefit more from elevated CO<sub>2</sub> than white spruce. The responses of root length density complement our previous results on biomass allocation (Dang et al. 2020). These results suggest that the relative physiological and morphological plasticity may play a critical role in the relative performance of different plant species within a plant community under elevated CO<sub>2</sub> in the future.



**Fig. 3** Two and 3-way interactive effects of CO<sub>2</sub>, belowground competition (BGC), nutrient supply (N), and species (S) on the foliar concentrations of nitrogen N (a, n=24), phosphorus P (b, n=24), and potassium K (c, n=48) of black spruce and white spruce seedlings. The seedlings were exposed to two CO<sub>2</sub> concentrations with (BGC-1) or without (BGC-0) belowground competitions at low (LN) and high (HN) nutrient supply for 4 months. Bars with different letters were significantly different from each other ( $P \leq 0.05$ )

The results of our statistical analysis do not support the hypotheses that low nutrient would be less limiting to photosynthesis under elevated than under ambient CO<sub>2</sub> or conversely the relative stimulation of photosynthesis by elevated CO<sub>2</sub> would be greater when nutrient supply is low than when nutrient supply is high as the differences in response were not statistically significant. However, the trends indicated by

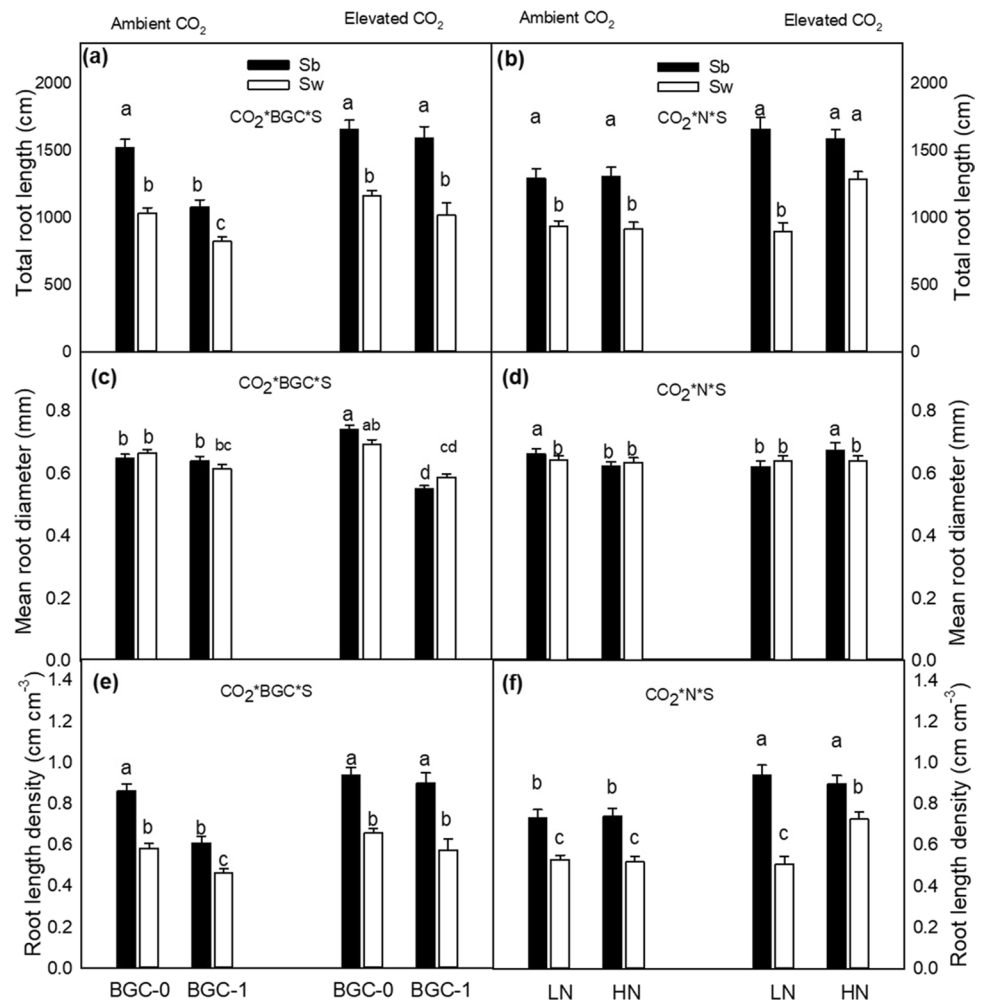


**Fig. 4** Two- and 3-way interactive effects of CO<sub>2</sub>, belowground competition (BGC), nutrient supply (N), and species (S) on the photosynthetic use efficiency of nitrogen (PNUE, n=24 for Fig. 4a, n=48 for Fig. 4b) and phosphorus (PPUE, n=12) in black spruce and white spruce seedlings. The seedlings were exposed to two CO<sub>2</sub> concentrations with (BGC-1) or without (BGC-0) belowground competitions at low (LN) and high (HN) nutrient supply for 4 months. Bars with different letters were significantly different from each other ( $P \leq 0.05$ )

the calculated results are consistent with the hypothesis: the relative increase of photosynthesis by the elevated CO<sub>2</sub> were 110% for black spruce and 122% for white spruce under low nutrient supply but declined to 82% for black spruce and 68% for white spruce under the high nutrient supply. These trends are consistent with the findings of our previous study (Dang et al. 2020) as well as other researchers (Ainsworth and Long 2005; Cao et al. 2007; Huang et al. 2007; Ambebe



**Fig. 5** Interactive effects of CO<sub>2</sub>, belowground competition (BGC), nutrient supply (N), and species (S) on total root length (n = 24), mean root diameter (n = 24), and root length density (n = 24) in black spruce and white spruce seedlings. The seedlings were exposed to two CO<sub>2</sub> concentrations with (BGC-1) or without (BGC-0) belowground competitions at low (LN) and high (HN) nutrient supply for 4 months. Bars with different letters were significantly different from each other ( $P \leq 0.05$ )



et al. 2010). We feel that the lack of statistical significance was due to the small sample size of the study. The greater relative stimulation of photosynthesis by the elevated CO<sub>2</sub> under low nutrient condition was due to the synergistical effects of low nutrient supply and elevated CO<sub>2</sub> on photosynthetic nutrient use efficiency, both increased the nutrient use efficiency. However, the relative stimulation should not be confused with the trend of absolute stimulation. The absolute increases in photosynthesis in response to the elevated CO<sub>2</sub> were greater under the high nutrient than low nutrient supply in this study. The greater relative stimulation was because of the lower base value in the low nutrient treatment, which was used as the denominator in deriving the relative stimulation.

There are conflicting results in the literature on how nutrient supply affects photosynthetic response to CO<sub>2</sub> elevations. Some studies find that the stimulation of photosynthesis by elevated CO<sub>2</sub> increases with increases in nutrient supply (Tissue et al. 1993; Murray et al. 2000; Oren et al. 2001; Springer et al. 2005) while such effects are not found in other studies (Norby and O'Neill 1991, Midgley et al. 1999; Lee et al. 2011). Midgley et al. (1999) report that nutrient

supply does not affect the photosynthetic response to CO<sub>2</sub> elevation in four congeneric *Leucadendron* species although both CO<sub>2</sub> elevation and increased nutrient supply increase photosynthesis. Nutrient supply also has no effect on the photosynthetic response to CO<sub>2</sub> elevation in yellow poplar (*Liriodendron tulipifera*) (Norby and O'Neill 1991). A free-air CO<sub>2</sub> enrichment study by Lee et al. (2011) found that the CO<sub>2</sub> stimulation of photosynthesis is independent of nitrogen supply in 13 grassland species. The reasons for the different findings are unknown. We feel that the differences may be related to the actual nutrient concentrations in the high and low nutrient treatments, the range of the difference in nutrient concentration, the positions of the nutrient levels on the nutrient response curves of the corresponding species.

Our results indicate that the CO<sub>2</sub> elevation was more beneficial to black spruce than to white spruce. The CO<sub>2</sub> elevation increased photosynthesis by 93% in black spruce and 83% in white spruces. The 93% enhancement of  $P_n$  in black spruce is much higher than the 33% enhancement reported by Johnsen (1993) for the same species. However, the 83% enhancement in white spruce is much lower than

the 223% enhancement reported by Dang et al. (2008). The differences in the magnitude of enhancement might be attributable to variations in experimental protocols and genetic characteristics of the seedlings. Johnsen (1993) conducted the experiment in growth chambers with polyethylene tubes as the container, which is much smaller in size than the containers that we used in this study. Therefore, it is possible that the small root volume in Johnsen's study has restricted seedling ability to take full advantage of the elevated CO<sub>2</sub>. Dang et al. (2008) used seedlings from 11 provenances across Ontario while the current study used only one provenance. It is possible that the genetic potential of our provenance to respond to CO<sub>2</sub> elevation is lower than the average of the 11 provenances used in Dang et al. (2008).

Our results suggest that belowground competition is a primary contributing factor for the greater response to CO<sub>2</sub> stimulation when plants grow together than when they grow individually and the total root length per seedling and root length per unit volume of soil may be the primary mechanisms of the response. Reekie and Bazzaz (1989) find that while CO<sub>2</sub> elevation has no effect on the growth of *Ceero-pia obtusifolia*, *Myrioearpa longipes*, *Piper auritum*, and *Triehospermum mexicanum* grown as individuals, CO<sub>2</sub> elevations significantly increased their biomass when they grew together in mixture. Similarly, Groninger (1996) have observed greater CO<sub>2</sub> stimulation of photosynthesis in red maple (*Acer rubrum*) when growing in mixture with loblolly pine than when growing in monoculture. Navas et al. (1999) reported that CO<sub>2</sub> elevation stimulated the biomass production of *Lotus pedunculatus* to a greater degree when grown in mixture with other species than when grown in isolation or in monoculture. Our results suggest that it is the belowground competitions that are responsible for the advantage of species mixtures in response to CO<sub>2</sub> elevation. In our study, the stimulation of CO<sub>2</sub> elevation to photosynthesis was much greater in trees when they grew in the same container with other trees than when they grew in separate containers. Our results suggest that the responses in total root length and the root length density in the soil may be primarily responsible for the belowground competition effects on the leaf physiology although we could not rule out the possible effects of allelochemicals and resource complementarity between the species (Teughels et al. 1995; Reich et al. 2004; Wang 2007). However, opposite results also exist in the literature. For example, Wang (2007) report that plants are generally stimulated more by CO<sub>2</sub> elevation when grown in monoculture or in isolation than when grown in mixture.

There are often questions about the usefulness of controlled environment studies and the applicability of results on seedlings trees to larger trees in the field. Another question is how useful point-measurements are for accessing overall performance. Both environmental conditions and

tree physiological processes change diurnally and seasonally (Dang et al. 1991) and any instantaneous measurement of a physiological parameter is only a point sample of the entire response surface both in the field and in lab. Efforts should be made to ensure that measurements of different treatments are taken at the same or similar positions of the response surface so that the measurements are comparable between samples and across treatments, such as taking measurements within a period of time in the day when the value of the physiological parameter is relatively stable and under similar weather conditions. The trends of responses are generally comparable between controlled environment and field measurements, between seedlings and larger trees (Ainsworth and Long 2005), and between in situ measurements and measurements taken on cut branches (Dang et al. 1997a, b). However, point measurements should not be directly extrapolated or upscaled beyond the conditions under which they are taken. The best way to upscale point measurements in space and/or time is to use them to estimate key intrinsic parameters, such as  $V_{cmax}$  and  $J_{max}$ , and plug them into computer models that are capable of simulating and integrating over larger spatial and/or temporal scales, such as the approach of Dang et al. (1998). However, the hydraulic and physiological relationships between different organs can be very different between trees of different sizes and ages. Therefore, precautions should be exercised when applying parameters estimated from seedlings to large trees in the field.

## 5 Conclusion

In summary, the finding that belowground competitions increased the positive effect of elevated CO<sub>2</sub> on photosynthetic rate and the increase was greater in black spruce than in white spruce suggests that elevated CO<sub>2</sub> in the future might be more beneficial to black spruce than to white spruce when the two species grow together. The result that high nutrient supply increased  $V_{cmax}$  of black spruce under both CO<sub>2</sub> concentrations but increased that of white spruce only under elevated CO<sub>2</sub> suggests that nutrient effects on the two species may change in the future. The finding that both species were more responsive to CO<sub>2</sub> elevation when grown together in the same container than grown in individual containers suggests that studies that grow seedlings separately may underestimate plant responses to CO<sub>2</sub> elevations.

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**Data availability** The datasets generated and/or analyzed during the current study are available in the Lakehead University Dataverse repository, <https://doi.org/10.5683/SP2/MUATDJ>.

## Declarations

**Conflict of interest** The authors declare no competing interests.

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