Low soil temperature inhibits the stimulatory effect of elevated [CO₂] on height and biomass accumulation of white birch seedlings grown under three non-limiting phosphorus conditions

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White birch (*Betula papyrifera* Marsh.) seedlings were exposed to ambient or doubled ambient carbon dioxide concentration ([CO₂]), three soil temperatures (T_{soil}) (low, intermediate, high), and three phosphorus (P) regimes (low, medium, high) in environment-controlled greenhouses. Height (H), root-collar diameter (RCD), biomass, and leaf phosphorus concentration (leaf P) were determined four months after initiation of treatments. The low T_{soil} reduced H, RCD, shoot biomass, root biomass and total seedling biomass whereas the high-P level and the [CO₂] elevation increased all the growth and biomass parameters. Elevated [CO₂] significantly reduced leaf P. There were significant two-factor interactions suggesting that the effect of elevated [CO₂] on (1) H, total biomass, biomass of plant components, and leaf P was dependent on T_{soil}, (2) total biomass was contingent on P regime. For instance, the positive response of H and total biomass to elevated [CO₂] was limited to seedlings raised under the intermediate and high T_{soil}, respectively. In addition, [CO₂] elevation increased total biomass only at the high-P regime but not at the low- or medium-P level where the effect of [CO₂] was statistically insignificant. No significant main effect of treatment or interaction was observed for root to shoot biomass ratio.

Soil temperature (T_{soil}) is a major environmental factor controlling the ecophysiological processes and structure of northern forests (Tryon and Chapin 1983, Bonan and Shugart 1989, Bonan 1992). With cold T_{soil} sites underlain by permafrost, warm south-facing slopes and newly burnt sites, and several transitional areas between the cold and warm extremes, the boreal forest is one of the most variable terrestrial ecosystems in terms of T_{soil}. The growth of boreal trees show marked T_{soil} dependency (Landhäusser and Lieffers 1998, King et al. 1999, Peng and Dang 2003, Aphalo et al. 2006, Zhang and Dang 2007, Ambebe et al. 2009, Ambebe and Dang 2010). Adverse effects of cold T_{soil} on growth result from impairments of root growth/physiological uptake capacity, nutrient translocation, and CO₂ assimilation among others (Kaufmann 1977, DeLucia et al. 1992, Kaspar and Bland 1992, Waring and Running 1998, Grossnickle 2000). While we have a fair knowledge of the main effects of T_{soil} on the physiology and growth of boreal forest trees, little is known about how tree responses to combinations of T_{soil} and other ecosystem abiotic factors. The information void is an impediment to development of suitable management strategies much needed to improve the yield of less productive boreal forest sites.

With a record high annual increase rate of ca 1.92 ppm from 2000 to 2009, the carbon dioxide concentration ([CO₂]) in the atmosphere is projected to double from the current level by the end of this century (IPCC 2007, Cheng et al. 2008, Zhou and Shangguan 2009, CO₂Now 2010). The impact of rising atmospheric [CO₂] on northern forest ecosystems has been extensively studied. Photosynthetic and growth responses of forest plants to elevated [CO₂] show considerable diversity among and within species, ranging from highly positive to neutral, and in rare cases, even negative responses (Pooter 1993, Gunderson and Wullschleger 1994, Griffin and Seemann 1996, Jach and Ceulemans 1999, Ward and Strain 1999). The intra-specific variations are attributed to [CO₂] by environmental interactions (Myers et al. 1999, Zhang and Dang 2005, 2006, 2007, Zhang et al. 2006, Huang et al. 2007, Cao et al. 2007, 2008), and complicate accurate predictions of changes in forest ecosystems under the future high [CO₂] atmosphere. Nitrogen (N) has often been considered to be the main nutrient factor limiting tree growth in northern forests (Tamm 1975, 1991). With high input of anthropogenic N to these ecosystems, however, phosphorus (P) limitation may be an increasingly common phenomenon (Gradowski and Thomas 2006, Akselsson et al. 2008, Prietzel et al. 2008, Braun et al. 2010). According to Braun et al. (2010), P limitation is likely a cause of stem growth reduction in Swiss forests, especially in beech trees.

The stimulation of photosynthesis and growth by elevated [CO_2] are greater under high than low P availability where unresponsiveness to elevated [CO_2] has been observed in some cases (Stocklin et al. 1998, Campbell and Sage 2002, 2006). According to Grossnickle (2000), however, even trees that are exposed to adequate nutrient levels may suffer from physiological nutrient stress when growing in cold soils due to reduction in root activity. Previous [CO_2] and P interactive experiments on plants were conducted under favourably warm T_{soil} conditions, and it is not known whether the observed responses will be expressed by trees growing in low T_{soil} portions of the species' range.

White birch (*Betula papyrifera* Marsh.) is an early successional fast-growing boreal tree with a high nutrient requirement (Burns and Honkala 1990, Zhang and Dang 2006, USDA-NRCS 2009). Reduced foliar P concentrations resulting from impaired root uptake in cold soils may limit the CO_2 responsiveness of photosynthesis (Campbell and Sage 2006). This study was designed to test whether cold T_{soil} constrains the growth-promoting effect of elevated [CO_2] on plants that are raised under high-P availability. Since photosynthesis and growth of white birch are coupled (Ambebe et al. 2009, 2010), we expected the low T_{soil} treatment to reduce the beneficial effect of high-P supply on the response of growth to elevated [CO_2].

Material and methods

Plant material

White birch seeds were sown in germination trays in a controlled environment greenhouse at Lakehead University (Thunder Bay, Ontario, Canada). The germination medium was a mycorrhiza-free 2/1 (v/v) mixture of peat moss and vermiculite. The germination medium was misted when necessary to prevent drying using a spray bottle filled with normal tap water. The greenhouse was held at 20–26/15–18°C (day/night) air temperature and $50 \pm 5\%$ relative humidity. Supplemental lighting was provided by 400-watt high-pressure sodium vapour lamps to extend the day length to 16 h. Four weeks after sowing, seedlings of uniform size were transplanted individually into PVC pots (13.5 cm tall and 11.0/9.5 cm top/bottom diameter) that were a component of the T_{soil} control system described in the following section. The pots were filled with the same growing medium described above.

Experimental design

Following transplant, the experiment commenced on 24 Oct 2008 at the Lakehead University greenhouse facility and ended on 23 Feb 2009. Treatments were comprised of ambient (360 µmol mol^{-1}) and doubled ambient 1 [CO_2], three T_{soil} regimes (7, 17, 27°C) consistent with conditions within the ecological range of white birch in the boreal forest (Ambebe et al. 2010), and three P levels (21, 43, 83 mg l^{-1}). However, actual values of [CO_2] and T_{soil} recorded in the greenhouse during the course of the course of the experiment varied by a magnitude of ± 15 µmol mol^{-1} and ± 2°C from the respective set values.

The experiment was laid out in a split–split plot design with [CO_2] as the whole plot, T_{soil} as the sub plots and P as the sub-sub plots. The [CO_2] treatments were applied to four identical greenhouses (two for each CO_2 level), resulting in two independent treatment replications. The elevated [CO_2] was supplied by Argus CO_2 generators. T_{soil} was regulated using the method of Cheng et al. (2000). Three plywood T_{soil} control boxes (one per T_{soil} treatment) were placed on separate benches in each greenhouse. The internal dimensions of the box are 112 cm wide, 196 cm long and 16 cm deep. The inner surface was lined with a heavy-duty polythene film. Plastic pots (size as above) were fixed over the polythene film to the bottom of the box. A hole (1.3 cm diameter) was drilled at the center of each pot and through the bottom of the plywood box to permit the free drainage of irrigation water and fertilizer solution. The bottom of each pot was sealed from the bottom of the box to prevent any liquid exchange between the pot and the box. The top of the box was sealed with heavy-duty polythene film with holes (smaller than the opening of pot) cut for each pot to facilitate irrigation/fertilization and gas exchange between the growing medium and the air. To minimize heat exchange between the soil temperature control box and the ambient air, the top of the box was covered with polystyrene board insulation with a hole cut for each pot for the purposes described above. The target T_{soil} was achieved by circulating temperature-controlled water in the space between the pots using a water pump. The soil temperature control apparatus operated continuously during the experiment.

Ten seedlings were randomly assigned to each of the three P levels within each T_{soil} control box in each greenhouse. The seedlings were fertilized twice a week with a nutrient solution containing 100 mg l^{-1} N, 83 mg l^{-1} K, 30 mg l^{-1} Mg, 40 mg l^{-1} S, 50 mg l^{-1} Ca, and P concentration for the respective P treatment level. The nutrient sources were calcium nitrate (19% Ca, 15.5% N), epsom salt (9.8% Mg, 12.9% S), microfine superphosphate (20% P), micromax micronutrient mix + 12% S, ammonium nitrate (17% NH$_4$, 17% NO$_3$), and muriate of potash (62% K$_2$O). During the fertilization, each seedling was provided with 0.5 l of the nutrient solution which saturated the potting medium and led to drainage of excess solution through the drain hole at the bottom of the pot and box.

During the entire duration of the experiment, all four greenhouses were maintained at 20–26/15–18°C (day/night) air temperature, $50 \pm 5\%$ relative humidity, and the natural photoperiod was extended to 16 h by 400-watt high-pressure sodium lamps with a light intensity of 660 µmol m^{-2} s^{-1} at leaf level. The environmental variables were monitored continually by a customized environment control system. The volumetric water content of the growing medium was maintained at around 30% as measured with a Theta probe. No nutrients were added to the normal tap water that was used for irrigation. Due to T_{soil}-related differences in evaporation rates, watering frequency was highest for seedlings growing under the high T_{soil}l treatment. The temperature of the irrigation water and fertilizer solution was adjusted to match the T_{soil} of the particular treatment.

Measurements

At the end of the experiment, six seedlings were randomly chosen from each $T_{soil} \times P$ treatment and greenhouse for height (H) and root-collar diameter (RCD) measurements. The root system of each seedling, excised at the root–shoot junction, was washed free of growing medium. The root and shoot fractions were then oven-dried (70°C, 48 h) and weighed for biomass determination.

Total leaf P concentration (leaf P) was assayed using the nitric/hydrochloric acid digestion method on an inductively coupled plasma atomic emission spectrometer (ICP-AES). A 0.5 g dry sample was digested in 6 ml of nitric acid and 2 ml of hydrochloric acid for 8 h at 90°C in a block digester. Distilled water was added to the acid to dilute the mixture to 100 ml. The test tubes were shaken end-over-end to have a well-mixed solution, which was then filtered to remove particles. The P concentration in the clear filtrate was determined on the inductively coupled plasma atomic emission spectrometer (ICP-AES). Total seedling (root + shoot) biomass and root to shoot biomass ratio (RSR) were calculated.

Data analysis

All data were examined graphically for normality of distribution (normal probability plots) and homogeneity of variance (scatter plots) before being subjected to 3-way split–split plot analysis of variance (ANOVA) in Data Desk 6.0. The effects of $[CO_2]$, T_{soil}, P, and their interactions were considered to be marginally significant at $p \leq 0.1$ and significant at $p \leq 0.05$. When the ANOVA results for any given parameter showed a significant effect of an interaction or a factor involving more than two treatment levels, Scheffé's post hoc test was used for pair-wise means comparison.

Results

Height and root-collar diameter

There was a significant effect of $[CO_2] \times T_{soil}$ and also a main effect of $[CO_2]$, T_{soil}, and P on H (Table 1). The low T_{soil} resulted in the lowest H growth under ambient and elevated $[CO_2]$ (Fig. 1a). However, the ranking of the intermediate and high T_{soil} treatments for H differed between the $[CO_2]$ levels: while H was significantly greater under high than intermediate T_{soil} at ambient $[CO_2]$, there were no significant differences between these T_{soil} treatments at elevated $[CO_2]$ (Fig. 1a). The $[CO_2]$ elevation had a significant positive effect on H only at the intermediate T_{soil} but not at the low and high T_{soil} where this parameter did not differ significantly between the $[CO_2]$ treatments (Fig. 1a). The significant P effect indicated that there was no similarity in response between any two P regimes with seedlings subjected to high-P having the highest and those raised under the low-P regime having the lowest values of H (Fig. 1a).

RCD was significantly affected by each of the three tested environmental factors, but not by their interactions (Table 1). RCD was greater in elevated than ambient $[CO_2]$ and it increased from low to high T_{soil} (Fig. 1b). While the high-P regime significantly increased RCD, no significant differences were detected between the low- and medium-P treatments (Fig. 1b).

Biomass

In addition to significant main effects of $[CO_2]$, T_{soil}, and P, $[CO_2]$ interacted with T_{soil} in affecting all biomass parameters (Table 1). There was a general trend for the P effect on above and below-ground biomass: while seedlings grown under the low- and medium-P levels were statistically similar in shoot and root biomass, their counterparts raised under the high T_{soil} displayed relatively greater values of each parameter (Fig. 2a–b). On the other hand, the pattern of response to the $[CO_2] \times T_{soil}$ interaction depended on the measured variable.

The low T_{soil} generally depressed shoot biomass (Fig. 2a). Elevated $[CO_2]$ increased shoot biomass at the high T_{soil}, but did not affect it at the low and intermediate T_{soil} (Fig. 2a). Furthermore, there was no significant difference in shoot biomass between the intermediate and high T_{soil} in ambient $[CO_2]$ (Fig. 2a).

The $[CO_2] \times T_{soil}$ interaction was more complicated for root biomass. Under ambient $[CO_2]$, root biomass was highest at the intermediate and lowest at the low T_{soil} whereas under elevated $[CO_2]$, it increased from low to high T_{soil} (Fig. 2b). Root biomass responded positively to elevated $[CO_2]$ only at the low and high T_{soil} but not at the intermediate T_{soil} where there was no significant response (Fig. 2b). However, the difference between elevated $[CO_2]$

Table 1. ANOVA p-values for the effects of $[CO_2]$, soil temperature (T_{soil}), and phosphorus (P) supply on height (H), root-collar diameter (RCD), components and total biomass, root to shoot biomass ratio (RSR), and mass-based leaf phosphorus concentration ($[P]mass$) of white birch. Seedlings were raised under ambient and doubled ambient $[CO_2]$, three T_{soil} (7, 17, 27°C), and three P regimes (21, 43, 83 mg l^{-1}) for four months. DF denotes degrees of freedom. Error d was 180. p-values < 0.10 are indicated in bold face.

| Source	$[CO_2]$	T_{soil}	p	$[CO_2] \times T_{soil}$	$[CO_2] \times P$	$T_{soil} \times P$	$[CO_2] \times T_{soil} \times P$
H	**0.0174**	**≤ 0.0001**	**0.0008**	**0.0146**	0.9541	0.5283	0.4534
RCD	**0.0020**	**≤ 0.0001**	**0.0086**	0.6183	0.4984	0.1731	0.9966
Shoot	**0.0857**	**≤ 0.0001**	**0.0018**	**0.0483**	0.2860	0.6577	0.4430
Root	**0.0019**	**≤ 0.0001**	**0.0142**	**0.0121**	0.1772	0.2357	0.1539
Total	**0.0048**	**≤ 0.0001**	**0.0001**	**0.0040**	**0.0989**	0.9392	0.1297
RSR	0.1496	0.3964	0.5855	0.6430	0.8464	0.5972	0.9869
$[P]_{mass}$	**0.0160**	**0.0003**	**≤ 0.0001**	**0.0618**	0.1649	0.3363	0.4456
DF	1	2	2	2	2	4	4
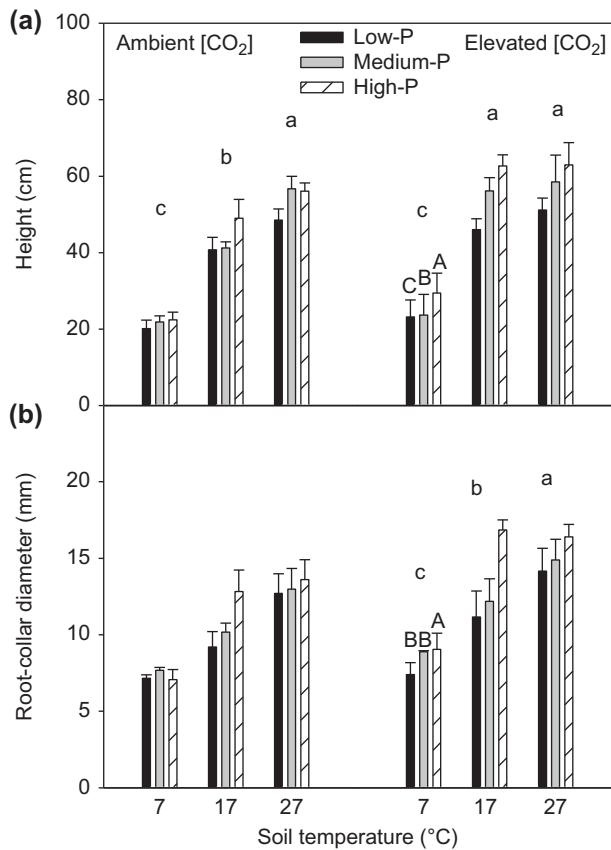
Figure 1. Effects of [CO_2], soil temperature (T_{soil}), and phosphorus (P) supply on (a) height and (b) root-collar diameter (mean $\pm$ SE, n = 6) of white birch. Seedlings were raised under ambient (360 μmol mol^{-1}) and doubled ambient [CO_2], three T_{soil} (7, 17, 27°C), and three P regimes (21, 43, 83 mg l^{-1}) for four months. The lower-case letters indicate effects of $CO_2 \times T_{soil}$ and T_{soil} on (a) and (b), respectively. The upper-case letters indicate P effect. Means with different letters are significantly different from each other (three-way split–split plot ANOVA and Scheffé's test).

at high T_{soil} and ambient [CO_2] at intermediate T_{soil} was statistically insignificant (Fig. 2b).

There was a marginally significant effect of [CO_2] $\times$ T_{soil} and also a marginally significant effect of [CO_2] $\times$ T_{soil} on total seedling biomass (Table 1). The low T_{soil} depressed total biomass under both [CO_2] conditions (Fig. 2c). There were no significant differences in total biomass between the intermediate and high T_{soil} in ambient [CO_2]. For the seedlings subjected to elevated [CO_2], values of this parameter were significantly greater under high than intermediate T_{soil} (Fig. 2c).

Elevated [CO_2] significantly increased total biomass only at the high T_{soil} but not at the low and intermediate T_{soil} treatments where differences between ambient and elevated [CO_2] were not statistically significant (Fig. 2c). With regards to the [CO_2] $\times$ P interaction, total biomass generally increased from low to high-P under both [CO_2] treatments (Fig. 2c). However, the differences between the medium- and high-P regimes at ambient [CO2] were not significant (Fig. 2c). Furthermore, no significant differences were observed between the low- and medium-P treatments at elevated [CO_2] (Fig. 2c). Total biomass increased from
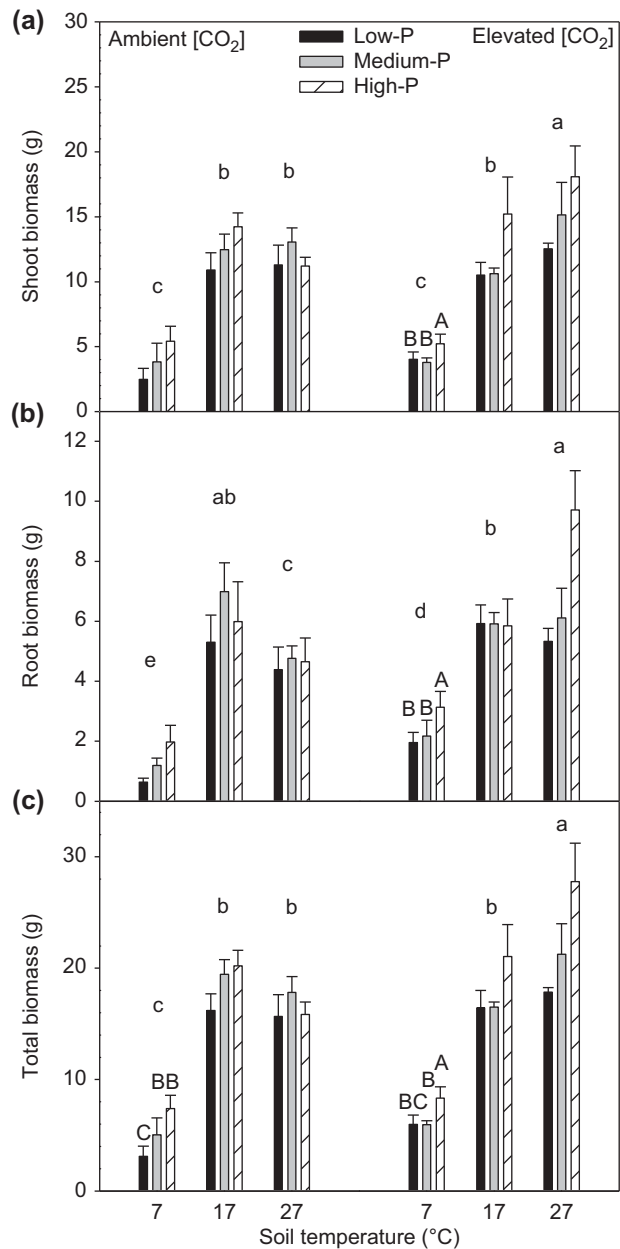

Figure 2. Effects of [CO_2], soil temperature (T_{soil}), and phosphorus (P) availability on (a) shoot biomass, (b) root biomass, and (c) total biomass (mean $\pm$ SE, n = 6) of white birch. The upper case letters in (c) indicate the effect of $CO_2 \times N$. See legend of Fig. 1 for further explanations.

ambient to elevated [CO_2] only at the high-P regime whereas it was unresponsive to [CO_2] at low- and medium-P (Fig. 2c).

Biomass allocation

There were no significant main or interactive effects of [CO_2], T_{soil}, and P on RSR (Table 1, Fig. 3).

Leaf phosphorus concentration

There was a significant effect of [CO_2] $\times$ T_{soil} and also a main effect of CO_2, P and T_{soil} on leaf P (Table 1). The low
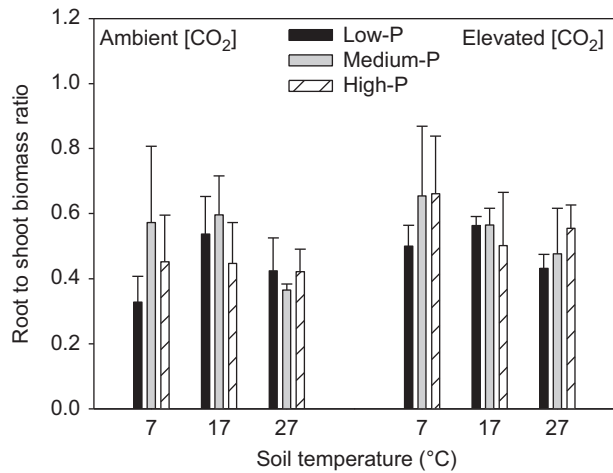
Figure 3. Effects of [CO_2], soil temperature (T_{soil}), and phosphorus (P) availability on root to shoot biomass ratio (mean ± SE, n = 6) of white birch. Absence of labels indicates no significant effects. See legend of Fig. 1 for further explanations.

T_{soil} significantly reduced leaf P under ambient [CO_2], but not under elevated [CO_2] where no significant T_{soil} effects were observed (Fig. 4). Similarly, there were no statistically significant differences between the intermediate and high T_{soil} treatments in ambient [CO_2] (Fig. 4). While leaf P declined from ambient to elevated [CO_2] at the intermediate and high T_{soil}, it was unaffected by [CO_2] at the low T_{soil} (Fig. 4). Leaf P was highest at the high-P and lowest at the low-P regime (Fig. 4).

Discussion

The CO_2 fertilization hypothesis stipulates that rising atmospheric [CO_2] has a beneficial effect on the growth of C3 plants (Pritchard et al. 1999, Huang et al. 2007). In the present study, positive responses to elevated [CO_2] were observed for all examined morphological (H and RCD) and biomass (shoot, root, and total biomass) growth parameters. Similar observations have been reported previously
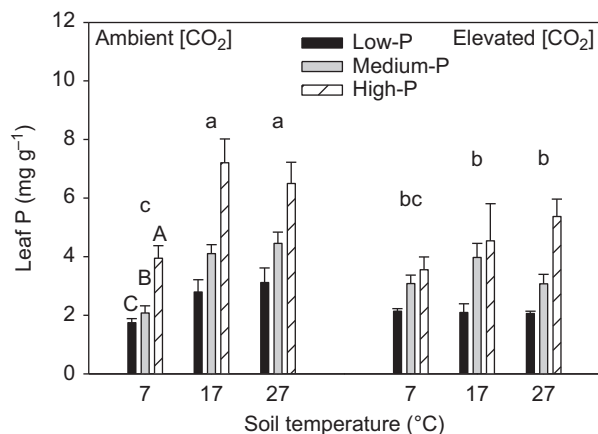

Figure 4. Effects of [CO_2], soil temperature (T_{soil}), and phosphorus (P) availability on total leaf P concentration (mean ± SE, n = 6) of white birch. See legend of Fig. 1 for further explanations.

for white birch (Zhang et al. 2006, Cao et al. 2008, Ambebe et al. 2009, Ambebe and Dang 2010) and other boreal broad-leaf and conifer tree species including trembling aspen (*Populus tremuloides* Michx.; Liu et al. 2006), Sitka spruce (*Picea sitchensis* (Bong.) Carr.; Townend 1995), and loblolly pine (*Pinus taeda* L., Myers et al. 1999). According to Huang et al. (2007), growth increments in high [CO_2] are due to increased availability of carbon. Atmospheric CO_2 is a substrate for plant photosynthesis (Lambers et al. 2008). The current level of CO_2 in the atmosphere is not saturating for the main photosynthetic enzyme, ribulose-1,5-biphosphate carboxylase/oxygenase (Rubisco), in C_3 plants (Lambers et al. 2008). Consequently, [CO_2] elevation has been found to trigger an increase in the rate of carboxylation by the photosynthetic enzyme system and a reduction in photorespiration (Long et al. 1996, Zhang and Dang 2006, Ambebe et al. 2010), leading to increased rates of net photosynthesis and tree growth, at least in the short term (Aber et al. 2001). Measurements of gas exchange from this study support the photosynthesis theory (Danyagri and Dang unpubl.).

As expected, high-P fertilization generally stimulated growth. More importantly, the stimulation of total biomass production by elevated [CO_2] was limited to the high-P regime. This observation is in agreement with the conclusion that [CO_2] and nutrient availability have synergistic effects on the growth of white birch seedlings (Zhang et al. 2006, Ambebe et al. 2009). Non-limiting N and P conditions increase the amount and activity of Rubisco (Jacob and Lawlor 1992, Warren and Adams 2004, Ambebe et al. 2010). Furthermore, plants grown under ample P have higher foliar contents of the carboxylation substrate, ribulose-1,5-biphosphate, than their P stressed counterparts, and hence, higher rates of CO_2 assimilation (Brooks 1986, Jacob and Lawlor 1992) and faster growth in CO_2-enriched environments. On the other hand, the fraction of total assimilated carbon expended in root respiration has been found to increase substantially under low-P availability (Rychter et al. 1992, Lynch and Beebe 1995, Nielsen et al. 1998, 2001, Lambers et al. 2008).

Unlike at the high T_{soil}, there was a general lack of response of total seedling biomass to elevated [CO_2] at the low T_{soil} treatment which generally decreased growth in ambient and elevated [CO_2]. It is also important to note that the gains in H and aboveground biomass due to [CO_2] elevation were experienced only by seedlings grown under the warm but not those at the low T_{soil}. The finding that growth was unaffected by high [CO_2] at the low T_{soil} partially supports this study's hypothesis. Growth depression in cold soils may be related to physiological nutrient stress induced by a decline in root growth and nutrient uptake (Pastor et al. 1987, Pritchard et al. 1990, Paré et al. 1993, Grossnickle 2000, Peng and Dang 2003). Furthermore, a decline in stomatal conductance and transpiration rate of plants growing in cold soils may impair nutrient uptake through the transpiration stream (Dang and Cheng 2004, Zhang and Dang 2005, Ambebe et al. 2010, current study). The decrease of foliar P contents by low T_{soil} under ambient [CO_2] in this study is consistent with the view of Grossnickle (2000), that even plants supplied with favourable nutrient

conditions may suffer nutrient stress when growing in cold soils. However, low P stress cannot explain the absence of a positive effect of $[CO_2]$ elevation on growth at low T_{soil} because there was no significant response of leaf P to T_{soil} under this $[CO_2]$ treatment. Rather, the phenomenon seems to be moisture related. In addition to increased transpirational water loss in warm soils, the rate and depth of evaporation often increase with T_{soil}, reducing the soil moisture content (Pregitzer and King 2005). Elevated $[CO_2]$ improves plant water status so that plants growing under low water conditions experience greater stimulations of photosynthesis and growth than those under ample water availability (Kimball et al. 1995, Wall et al. 2001). The lack of biomass increment from the intermediate to high T_{soil} at ambient $[CO_2]$ was likely linked to the high T_{soil}-induced water stress which was not present in elevated $[CO_2]$. Alternatively, unresponsiveness of biomass to high T_{soil} may be associated with loss of any additional carbon taken up by the seedlings as respiration or root exudates. The rate of root respiration increases exponentially with T_{soil} and up to half of the total carbon assimilated each day in photosynthesis can be consumed by root respiration (Zogg et al. 1996, Atkin et al. 2000, Pregitzer et al. 2000).

According to Gavito et al. (2001) and Ambebe and Dang (2010), a decrease in aboveground growth in a low T_{soil} environment may be associated with a shift in biomass from shoot to root. This view is consistent with Thornley's (1972) model of root/shoot allocation which predicts an increase in RSR under limited nutrient and water supply. However, our data do not support earlier conclusions that more biomass is allocated to roots in response to P deficiency (Schenk and Barber 1979, Ericsson and Ingestad 1988, Ericsson 1995, Vance et al. 2003). The lack of a significant T_{soil} or P effect on RSR observed here suggests that the low T_{soil} and the concentration and/or fertilization rate of the low-P regime were not low enough for 4-month old white birch seedlings to suffer the level of nutrient stress that initiates an increase in relative biomass allocation to roots. While Tingey et al. (1996), Tissue et al. (1997), Ambebe et al. (2009), and Ambebe and Dang (2010) have found that $[CO_2]$ does not change the allocation of biomass between roots and shoots, Stulen and Den Hertog (1993), Ericsson (1995), and Lambers et al. (2008) have concluded that significant responses of RSR to $[CO_2]$ are due to nutrient and/or water limitations. For example, elevated $[CO_2]$ decreased RSR and increased shoot biomass under dry growing season conditions in a semi-natural grassland in central Sweden (Sindhøj et al. 2000). In another study, elevated $[CO_2]$ increased total biomass production of Sitka spruce seedlings under high-N supply, but not in the low-N availability treatment where a marked increase in RSR resulted in lower aboveground biomass in elevated than ambient $[CO_2]$ (Murray et al. 2000). According to Kopinga and van den Burg (1995), the leaf P obtained for the respective three P regimes at each T_{soil} and $[CO_2]$ in this study are in line with values found in natural birch, beech, aspen and oak trees growing under non-limiting P conditions. The absence of nutrient stress under or due to the low T_{soil} could also explain why elevated $[CO_2]$ did not significantly increase RSR under this treatment. It is important to note, however, that in addition to nutrient and water availability (Pregitzer et al. 2000, Lambers et al. 2008), effects of elevated $[CO_2]$ on RSR also depend strongly on species (Berntson and Bazzaz 1996) and temperature (Wan et al. 2004), as well as on fine root formation and root turnover rates. As a result of interactions among these factors, the RSR might increase (Rogers et al. 1996, Pregitzer et al. 2000) or decrease (Kandeler et al. 1998) in response to elevated $[CO_2]$.

In conclusion, low T_{soil} generally depressed growth of white birch, and some of the morphological and biomass growth parameters responded positively to increased $[CO_2]$ under intermediate and high but not under low T_{soil}. Given the wide variations in T_{soil} within the boreal forest, and the likelihood for future increases in atmospheric $[CO_2]$, the responses reported here may have considerable importance for the biomass distribution and structure of the taiga ecosystem in the future. In other words, the projected increase in atmospheric $[CO_2]$ may be more beneficial to white birch trees growing in moderately warm T_{soil} sites than their counterparts in cold T_{soil} portions of the species' range. Additionally, the $CO_2 \times P$ interaction on total biomass suggests that biomass gain due to $[CO_2]$ elevation is limited to seedlings grown under high-P availability. Consequently, silvicultural practices, such as blade scarification, plowing (Spittlehouse and Stathers 1990) and mounding (Örlander et al. 1998), that increase T_{soil} and P mineralization could lead to improved plant responses to high $[CO_2]$ on less favourable sites. However, some problems remain for future studies regarding application of our results based on seedlings from this short-term controlled-environment experiment to natural forests. For instance, the light intensity at leaf level in this study does not reflect the higher natural light levels to which plants are exposed in the field. Increases in irradiance have been found to increase, decrease, or have no effect on the growth of plants under elevated $[CO_2]$ (Lewis et al. 1999, Ward and Strain 1999). Furthermore, because the leaf P contents resulting from the low-P treatment do not reflect those in plants growing under low P stress in the field (Kopinga and van den Burg 1995), it is important to further examine how T_{soil} and P may interact in affecting the growth-promoting effect of elevated $[CO_2]$ when much lower P conditions are involved.

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