Interactive Effects of Soil Temperature and [CO_2] on Morphological and Biomass Traits in Seedlings of Four Boreal Tree Species

Shouren Zhang and Qing-Lai Dang

Abstract: To better understand how soil temperature will influence the responses of boreal trees to increasing atmospheric [CO_2], one-year-old jack pine (*Pinus banksiana* lamb.), black spruce (*Picea mariana* [Mill.] B.S.P.), white spruce (*Picea glauca* [Moench] Voss), and current-year white birch (*Betula paperifera* Mash) seedlings were subjected to two [CO_2] (360 versus 720 μmol mol^{-1}) and three soil temperatures (T_{soil} = 7, 17, and 27°C initially, increased to 10, 20, and 30°C 3 months later) for 4 months. The low T_{soil} significantly suppressed height growth, stem biomass, and total biomass in white birch, black and white spruce, root collar diameter (RCD), and foliage biomass in white birch and white spruce, as well as root biomass in white birch under both ambient and elevated [CO_2] and in white spruce under ambient [CO_2]. This low T_{soil} effect was much more significant in white birch than in the conifers. The [CO_2] elevation significantly increased RCD, foliar biomass, and total biomass of the four species at all soil temperatures, stem biomass of all the species at the low T_{soil}, and the root biomass of white birch at intermediate T_{soil}. The data suggest that the [CO_2] elevation compensated for the negative effects of low T_{soil}, e.g., the low T_{soil} significantly decreased the height and total biomass of black and white spruce at ambient [CO_2], but not at elevated [CO_2]. The high T_{soil} had much smaller negative effects on growth and biomass than did the low T_{soil}. Jack pine was the least responsive to T_{soil} and [CO_2]. In general, the ratios of stem, foliage, and root mass to total mass were much less responsive to the treatments than total or component biomass. Neither treatment significantly affected the volume/mass ratio of the stem in any of the four species. The data suggest that white birch and white spruce will benefit the most and jack pine will benefit the least from the increasing atmospheric [CO_2]. FOR. SCI. 53(3):453–460.

Keywords: height, root collar diameter, boreal forests, climate change

SOIL AND AIR TEMPERATURES are key environmental factors influencing the growth of northern forests (Tryon and Chapin 1983, Bonan 1992). Soil temperature directly influences enzyme activity in the root, which in turn affects the uptake of mineral nutrients (Pastor et al. 1987, Paré et al. 1993) and water (Long and Woodward 1998, Wan et al. 1999), other physiological activities (Cai and Dang 2002, Dang and Cheng 2004), and eventually biomass production (Peng and Dang 2003). Soil temperature has smaller daily and seasonal fluctuations than air temperature. However, photosynthesis is very sensitive to soil temperature (Schwarz et al. 1997, Cai and Dang 2002, Dang and Cheng 2004). Furthermore, as the global climate changes in response to increasing carbon dioxide concentration ([CO_2]) in the atmosphere progresses, changes in soil temperature will be inevitable. A small change in soil temperature may have a profound impact on the physiological processes and biomass production of plants (Cai and Dang 2002, Peng and Dang 2003, Dang and Cheng 2004).

The increase in atmospheric [CO_2] generally increases tree growth. Short-term [CO_2] elevation can increase the aboveground biomass sharply and the stimulation is generally greater in conifers than deciduous species (Saxe et al. 1998). However, the magnitude of increases generally declines over time and interacts with other environmental factors (Saxe et al. 1998). While the plant's response to the interactive effects of air temperature and [CO_2] has been studied extensively (Saxe et al. 1998, Long et al. 2004), the interactions between soil temperature and [CO_2] have largely been ignored. However, understanding the effects of soil temperature on the responses of boreal trees to the increasing atmospheric [CO_2] may be critical for predicting the future of the boreal forests, given the large variation of soil temperature within the boreal forest region. Research has shown that the boreal forest will be most sensitive to the climate change associated with the increasing atmospheric [CO_2] (Tan et al. 1990).

The boreal forest covers 11% of the earth's terrestrial surface (Bonan and Shugart 1989) and stores around 800 Pg carbon (Apps et al. 1993). Changes in the structure and function of the boreal forests in response to the global climate change can have a profound impact on the global carbon balance (Peng and Apps 1998). Cold soil and short growing seasons are typical of the boreal forest region (Viereck 1970, Hogg and Lieffers 1991). Low soil temperatures can suppress shoot and foliage growth (Landhäusser and Lieffers 1998, Peng and Dang 2003), root growth (Folk et al. 1995, Peng and Dang 2003), and photosynthesis

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(Vapaavuori et al. 1992, Folk et al. 1995, Cai and Dang 2002, Dang and Cheng 2004) in various tree species. Nursery-grown seedlings are commonly planted to regenerate the boreal forest in the spring when the soil is cold (Domisch et al. 2001).

White birch (*Betula papyrifera* Mash.), jack pine (*Pinus banksiana* Lamb.), black spruce (*Picea mariana* [Mill.] B.S.P.), and white spruce (*Picea glauca* [Moench] Voss) are the four most important tree species in the boreal forests of North America. White birch and jack pine are pioneer species and dominate warmer sites more than white and black spruce, which are mid-succession species (Barnes and Wagner 1981, Perala 1990). Black spruce is generally found in wetland areas while white spruce mainly occupies upland sites (Barnes and Wagner 1981, Perala 1990). Lowland sites, particularly peatland, generally have low soil temperatures (Bonan and Shugart 1989, Bonan 1992). White spruce naturally regenerates under the canopy of existing forests (Burns and Honkala 1990, Lieffers and Beck 1994) or in association with other vegetation (Zasada 1995), where the soil temperature is lower than in clearcuts. White spruce starts to grow new leaves earlier than other boreal conifers, such as black spruce. Black spruce regenerates after fires or clearcutting (Burns and Honkala 1990). The response of these species involves phenological, morphological, and physiological mechanisms. For example, in response to the cold soils of peatlands, lowland black spruce has a very conservative water use strategy by exerting a tight stomatal control over water loss. Trembling aspen (*Populus tremuloides* Michx), in contrast, tends to maximize its carbon sequestration at the expense of poor water use efficiency to maximize its growth rate under fully open environmental conditions (Dang et al. 1998). Such acclimation or adaptation is likely to affect their responses to the future climate conditions under increased atmospheric $[CO_2]$. Different responses of trees growing on sites with different soil temperatures to increasing atmospheric $[CO_2]$ can potentially modify the landscape structure of the boreal forest.

In this study we exposed seedlings of white birch, white spruce, black spruce, and jack pine to factorial combinations of three soil temperatures and two $[CO_2]$. We have reported the results on ecophysiological traits, such as gas exchange, in vivo carboxylation, and chlorophyll fluorescence, in an earlier article (Zhang and Dang 2005). In this article we focused on the interactive effects of $[CO_2]$ and soil temperature on seedling growth, biomass, and mass ratios. Since photosynthesis of broad-leaved trees is more sensitive to low soil temperatures than conifers (Dang and Cheng 2004), we hypothesized that low soil temperature will have greater negative impact on the growth and biomass of white birch than on the conifers. Photosynthesis of boreal trees generally becomes more limited by stomatal resistance than by mesophyll resistance, as soil temperature gets lower (Dang and Cheng 2004) and CO_2 elevations increase the intercellular CO_2 concentration in the leaf (Saxe et al. 1998). Hence, we also hypothesized that CO_2 elevation will reduce the negative effects of unfavorable soil temperatures, particularly low temperatures, on the growth and biomass production of the four species.

Materials and Methods

Plant Materials

One-year-old seedlings of jack pine (*Pinus banksiana* Lamb.), black spruce (*Picea mariana* [Mill.] B.S.P.), and white spruce (*Picea glauca* [Moench] Voss) were obtained from Hills Tree Nursery in Thunder Bay, Ontario. White birch (*Betula papyrifera* Mash.) seedlings were grown from seeds in the Lakehead University greenhouse. The seedlings were transplanted into containers of 13.5 cm height and 11 cm top diameter before the start of the experiment in March, 2003. The growing medium was a mixture of peat moss and vermiculite (1:1 (v/v)). The seedlings of each species were relatively uniform in size at the beginning of the experiment (white birch 4–5 cm tall, jack pine 8–10 cm, white and black spruce 10–12 cm).

Experimental Design

The treatments consisted of two $[CO_2]$ levels (i.e., 360 and 720 μmol mol^{-1}) and three soil temperatures. Four greenhouses (two for each $[CO_2]$) were used for the experiment. The soil temperatures were 7, 17, and 27°C at the beginning of the experiment in March and increased to 10, 20, and 30°C in June, which roughly simulated the scenario of soil temperature's seasonal changes under field conditions. The intermediate soil temperature is close to the soil temperature optima for the four species, while the low and high temperatures are unfavorable conditions on the two sides of the optima (Peng and Dang 2003, Dang and Cheng 2004). All these temperatures occur in the boreal forest region, but at different sites. We used a split-plot design where the CO_2 treatments were the main plots and soil temperature treatments were the split plots. The seedling containers for each soil temperature were fixed to the bottom of a large box (180 cm long, 100 cm wide, and 20 cm high). Each container had a drainage hole drilled through the bottom of the box. The soil temperature was controlled by circulating temperature-controlled water between the containers inside the box. Details on the soil temperature control device can be found in Cheng et al. (2000) and Cai and Dang (2002). Each treatment combination had 18 seedlings randomly located in the soil temperature control box. The CO_2 concentration was monitored and regulated using an Argus controlling system (Vancouver, Canada). The CO_2 elevation was achieved using Argus CO_2 generators. Other environmental conditions were set as follows for all the treatments: day/night air temperatures 25–26°C/16–17°C from March to May, and 28–30°C/18–20°C starting in June, and a 16-hour photoperiod (the natural light was supplemented by high-pressure sodium lamps on cloudy days, early mornings, and late evenings). All the environmental conditions were monitored and controlled using an Argus controlling system.

The volumetric moisture content of the growing medium was maintained around 50% as measured using an HH2 Moisture Meter and ML2X ThetaProbe (DELTA-T DEVICES, Cambridge, UK). The seedlings were watered up to twice a day during the summer to maintain the soil moisture condition. The seedlings were fertilized to the dripping

point (roughly about 300–400 ml per pot) once a week with a solution of 0.1 g N l^{-1}, 0.044 g P l^{-1}, and 0.083 g K l^{-1}. This formulation provides the optimal nutrient conditions for the growth of these species (Landis et al. 1989). The irrigation water and growing medium contained sufficient amount of other nutrient elements. The temperature of the irrigation water and fertilizer solution was adjusted to match the corresponding soil temperature of each treatment. The experiment lasted for 4 months.

Measurements of Height, Root Collar Diameter, and Biomass

The total height and root collar diameter were measured at the end of the experiment. The seedlings were then harvested. The root system was washed to remove the growing medium. All the organs were oven-dried at 70°C for 48 hours. The dry mass was measured on an analytical balance (precision of 0.001 g) separately for the stem, roots (whole root system), and foliage. Stem volume was calculated from height and root collar diameter assuming that the stem was a cylinder. Biomass allocation or mass ratios (i.e., SMR, FMR, RMR) represent the ratios of stem, foliage, and root biomass to the total seedling biomass, respectively.

Statistical Analysis

All of the data were examined graphically for the normality of distribution (probability plots for residual analysis) and the homogeneity of variance (scatter plots) using the Data Desk 6.01 (Data Description 1996) before the analysis of variance (ANOVA) was carried out. The above examinations show that all the data satisfied the assumptions for ANOVA. The effects of species, soil temperature, [CO_2], and their interactions were tested using the three-way ANOVA procedure of the Data Desk 6.01 (Data Description 1996). Scheffe's post hoc test was conducted when the main effects (species, T_{soil}, and [CO_2]) or their interaction was significant ($P < 0.05$) for a given parameter. However, Scheffe's post hoc tests were made based on the rule that interactive effect overrides main effect and higher-order interactions (species · T_{soil} · [CO_2]) override low-order interactions (species · T_{soil}, species · [CO_2] and T_{soil} · [CO_2]). When an interaction was significant, all the means involved in the interaction were compared against each other.

Results

Height and Root Collar Diameter

The soil temperature (T_{soil}) effect on total height growth varied with species and [CO_2] (Table 1, Figure 1a). The low T_{soil} significantly suppressed height growth in all four species and at both [CO_2] except jack pine at elevated [CO_2]. This low T_{soil} effect was much more significant in white birch than in the three coniferous species. There was no significant difference between the intermediate and high T_{soil} in any of the four species (Figure 1a). The low T_{soil} significantly decreased the root collar diameter (RCD) in white birch and white spruce and there was no significant T_{soil} effect in jack pine and black spruce at either [CO_2] (Table 1, Figure 1b).

The [CO_2] elevation increased the height growth of white birch, white spruce, and black spruce by an average of 11%, but the increase was statistically significant only at the low T_{soil} (Figure 1a). The [CO_2] elevation did not significantly affect the height of jack pine. The [CO_2] elevation significantly increased RCD in the four species (Table 1).

Biomass

The low T_{soil} significantly suppressed the stem biomass of white birch, white spruce, and black spruce under both ambient and elevated [CO_2] (Table 1, Figure 2a), and there was no significant difference in stem biomass between the intermediate and high T_{soil} in any of the four species (Table 1, Figure 2a). T_{soil} did not significantly affect the stem biomass of jack pine (Figure 2a).

There was significant interactive effect between T_{soil} and [CO_2] on stem biomass: The elevated [CO_2] significantly increased stem biomass at low T_{soil} but not at other T_{soil} (Table 2). The low T_{soil} significantly decreased foliage biomass in white birch and white spruce under both [CO_2], but not in jack pine or black spruce (Figure 2b). Elevated [CO_2] significantly enhanced the foliage biomass in all four species (Table 1).

There were significant interactions among the T_{soil}, [CO_2], and species on root biomass (Table 1). The low T_{soil} significantly decreased the root dry mass of white birch under both ambient and elevated [CO_2] and that of white spruce under ambient [CO_2], but not under elevated [CO_2]

Table 1. **ANOVA for the effects of soil temperature, [CO_2], species, and their interactions on height (H), root collar diameter (RCD), biomass, and mass ratios**

Source	SP	CO_2	T_{soil}	SP · CO_2	SP · T_{soil}	CO_2 · T_{soil}	SP · CO_2 · T_{soil}
H	<0.0001	<0.0001	<0.0001	0.0637	<0.0001	<0.0001	0.0124
RCD	<0.0001	0.0017	<0.0001	0.0794	<0.0001	0.1245	0.1686
Stem	<0.0001	0.0109	<0.0001	0.3587	<0.0001	0.0399	0.5510
Foliage	<0.0001	0.0004	<0.0001	0.4311	<0.0001	0.8089	0.5651
Root	<0.0001	0.0132	<0.0001	0.0710	<0.0001	0.9530	0.0004
Total	<0.0001	0.0003	<0.0001	0.1115	<0.0001	0.6282	0.1675
SMR	<0.0001	0.2146	0.0578	0.0897	0.0177	0.0826	0.5162
FMR	<0.0001	0.6872	0.0005	0.2469	<0.0001	0.0237	0.0011
RMR	<0.0001	0.4881	0.0097	0.0361	0.0002	0.2181	<0.0001
Stem/Volume	<0.0001	0.2117	0.2698	0.2610	0.3369	0.8712	0.6529

One-year-old jack pine, black spruce, white spruce, and current-year white birch were subjected to ambient and doubled [CO_2] and three soil temperatures (7, 17, and 27°C) for 4 months. SMR, FMR, and RMR represent the ratios of stem, foliage, and root biomass to the total seedling biomass, respectively.
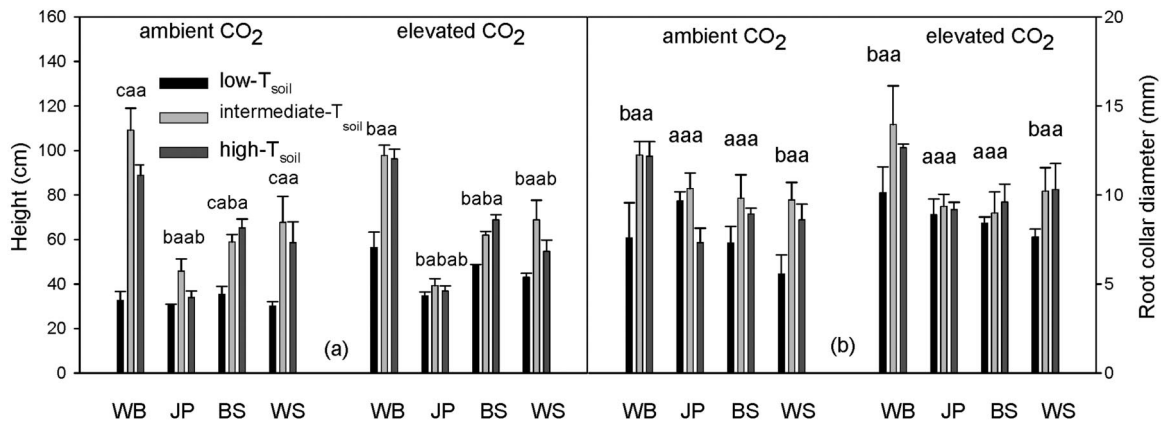
Figure 1. Effects of soil temperature and [CO_2] on height (a) and root collar diameter (b) (mean + SE, $n = 3$). One-year-old jack pine (JP), black spruce (BS), white spruce (WS), and current-year white birch (WB) seedlings were exposed to the factorial combinations of three soil temperatures (7, 17, and 27°C) and two [CO_2] (ambient versus doubled) for four months. The lowercase letters represent the interactive effects between the soil temperature and [CO_2], based on the Scheffe's post hoc test; the means with no common letter(s) are significantly different from each other ($P < 0.05$).
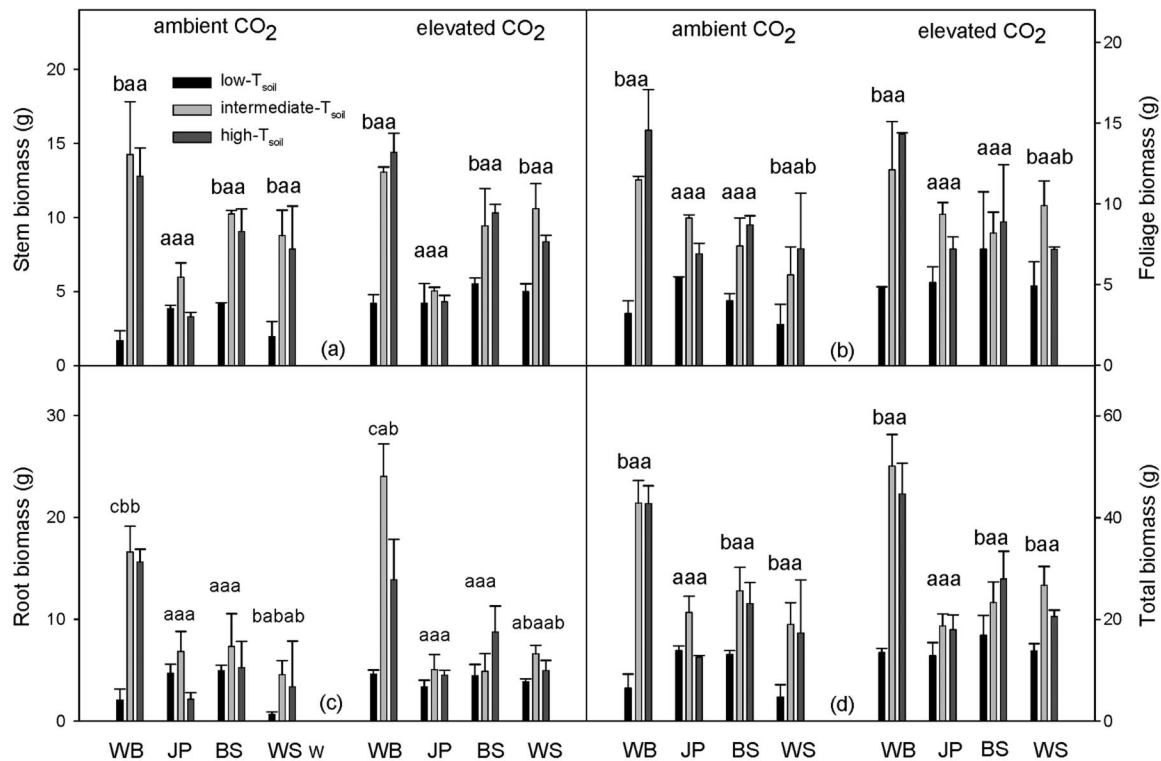

Figure 2. Effects of soil temperature and [CO_2] on stem (a), foliage (b), root (c), and total biomass (d) (mean + SE, $n = 3$). One-year-old jack pine (JP), black spruce (BS), white spruce (WS), and current-year white birch (WB) seedlings were exposed to the factorial combinations of three soil temperatures (7, 17, and 27°C) and two [CO_2] (ambient versus doubled) for four months. See Figure 1 for other explanations.

Table 2. Average stem biomass (grams) of all four species under different soil temperatures and [CO_2] and the results of Scheffe's post hoc tests

		L		I		H	
Stem	Ambient CO_2	2.916	b	9.808	a	8.251	a
	Elevated CO_2	4.727	a	9.529	a	9.342	a

There was a significant interaction between soil temperature and [CO_2]. Means with different letters were significantly different from each other ($P < 0.05$) based on Scheffe's post hoc test. L, I, and H represent low (7°C), intermediate (17°C), and high (27°C) soil temperatures, respectively.

(Figure 2c). T_{soil} did not significantly affect the root biomass of jack pine or black spruce at either [CO_2]. The [CO_2] elevation significantly increased the root biomass of white birch at the intermediate T_{soil} (Table 1, Figure 2c). The [CO_2] elevation significantly increased the total biomass of all four species (Table 1).

There was a significant interactive effect between species and T_{soil} on total biomass (Table 1). The low T_{soil} significantly decreased the total biomass of white birch, black spruce, and white spruce at both [CO_2], but not that of jack pine at either [CO_2] (Figure 2d). There was no significant difference in total biomass between the intermediate and high T_{soil} in any of the four species (Figure 2d).

Mass Ratios

Although there was a significant interaction between T_{soil} and species (Table 1), Scheffe's post hoc tests showed no significant T_{soil} effect on the stem mass ratio (SMR) in any of the four species (Figure 3a). [CO_2] elevation did not significantly affect SMR either (Table 1).

There was a strong interaction among species, T_{soil} and [CO_2] on the foliage mass ratio (FMR) (Table 1, Figure 3b).

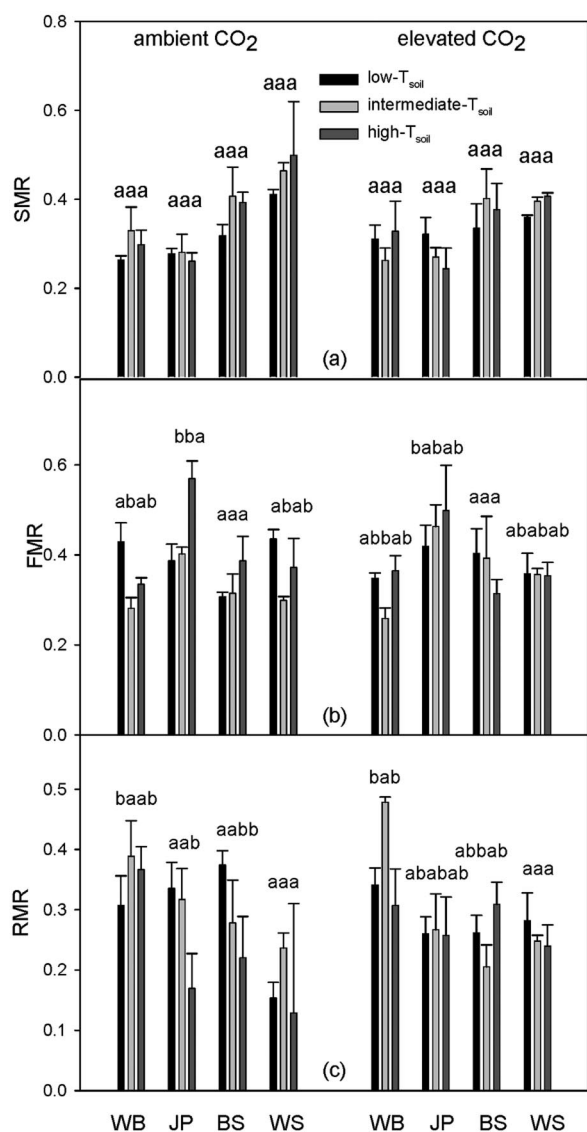Figure 3. Effects of soil temperature and [CO_2] on the allocation of the total biomass to stem (SMR) (a), foliage (FMR) (b), and root (RMR) (c) (mean ± SE, $n = 3$). One-year-old jack pine (JP), black spruce (BP), white spruce (WS), and current-year white birch (WS) seedlings were exposed to the factorial combinations of three soil temperatures (7, 17, and 27°C) and two [CO_2] (ambient versus doubled) for four months. See Figure 1 for other explanations.

For white birch, FMR was the lowest at the intermediate T_{soil} at both [CO_2], the highest at the low T_{soil} under ambient [CO_2], and there was no significant difference between the low and high T_{soil} under elevated [CO_2] (Figure 3b). For jack pine, FMR was the highest at the high T_{soil} under ambient [CO_2]. For white spruce, FMR at the ambient [CO_2] was the highest at the low T_{soil} and lowest at the intermediate T_{soil}, while T_{soil} did not significantly affect FMR under elevated [CO_2] (Figure 3b). The [CO_2] elevation decreased the FMR of white birch at the low T_{soil}, but increased FMR of white spruce at the intermediate T_{soil} (Figure 3b). There was no significant [CO_2] effect on the FMR of jack pine (Figure 3b). T_{soil} or [CO_2] had no significant impact on the FMR of black spruce (Figure 3b).

There were significant interactions among T_{soil}, [CO_2], and species on the root mass ratio (RMR) (Table 1). For white birch, RMR at elevated [CO_2] was the highest at the intermediate T_{soil}, while there was no significant T_{soil} effect on RMR under the ambient [CO_2] (Figure 3c). The high T_{soil} reduced RMR of jack pine under the ambient [CO_2], but T_{soil} had no significant effect on RMR under the elevated [CO_2] (Figure 3c). In black spruce, RMR was the highest at the low T_{soil} and lowest at the high T_{soil} under ambient [CO_2]; under the elevated [CO_2], however, the RMR was the highest at the high T_{soil} and lowest at the intermediate T_{soil} (Figure 3c). T_{soil} did not significantly affect the RMR of white spruce (Figure 3c). The elevated [CO_2] only significantly increased RMR of white birch at intermediate T_{soil}, and there was no significant [CO_2] effect on the other three species (Figure 3c).

Stem Mass/Volume

Neither T_{soil} nor [CO_2] had significant effects on the stem biomass/volume ratio (Table 1). However, white birch had a significantly lower stem biomass/volume ratio than the three conifers.

Discussion

The low T_{soil} suppressed the biomass production of white birch, and black and white spruce, and the reduction in aboveground biomass was the primary contributing factor. For example, the low T_{soil} reduced the stem biomass of black spruce but had no significant effect on root biomass. The differences in root response among the species were consistent with our results on the response of net photosynthesis (Zhang and Dang 2005). However, some other studies have shown that root growth is very sensitive to low soil temperatures. For example, Domisch et al. (2001) found that a 5°C soil temperature suppresses the root extension of Scots pine (*Pinus sylvestris*) seedlings after 2 months of treatment. Wan et al. (1999) report that the root growth of trembling aspen seedlings is halted at 5°C T_{soil} and reduced by 97% at 10°C, as compared to the value at 20°C soil temperature.

Our data show that white birch was more sensitive to low soil temperatures than the conifers. For example, the total biomass of white birch at the intermediate T_{soil} was about five to six times that at low T_{soil}, while the corresponding

values for the conifers were two to three times those at low T_{soil}. These results support our hypothesis that deciduous tree species are more sensitive to low T_{soil} than conifers. Peng and Dang (2003) have found that the seedling biomass of trembling aspen, a deciduous boreal tree species, is seven times more sensitive to soil temperature than jack pine, black spruce, and white spruce. Dang and Cheng (2004) reported that the photosynthesis of trembling aspen is more sensitive to low soil temperatures than that of sympatric conifers. However, the relative difference in photosynthesis between low and near-optimal T_{soil} is not nearly as large as that in growth and biomass (Peng and Dang 2003, Dang and Cheng 2004, Zhang and Dang 2005). These results support the conclusion that growth is more sensitive to low temperatures than photosynthesis (Ericsson et al. 1996, Farrar 1988). The aforementioned conclusion could be also partly confirmed by the poor correlations between photosynthetic rate (data not shown) and height growth and total biomass. This is in contrast to the finding of Tjoelker et al. (1998) that overall net photosynthetic rates were highly correlated with relative growth rate in black spruce, jack pine, tamarack (*Larix laricina* [Du Roi] K. Koch), trembling aspen, and white birch.

The negative effect of the low soil temperature on biomass might be related to physiological drought and nutrition stress. Low soil temperatures reduce the root capacity for absorbing water (Long and Woodward 1998, Wan et al. 1999) and nutrients (Pastor et al. 1987, Paré et al. 1993), leading to physiological drought and nutrient stress. Kaufmann (1975) suggests that for species sensitive to cold soils, a reduction of water uptake could occur in cold soils as a result of decreased root permeability and increased water viscosity. Indeed, the seedlings under the low soil temperature had significantly more negative midday xylem water potentials than at the other soil temperatures in this study (Zhang and Dang, unpublished data). The low nutrient availability as a result of reduced nutrient cycling has been considered as a reason for the reduced growth rates in cold soils (Pastor et al. 1987, Paré et al. 1993). Soil temperature as well as air temperature substantially influences the successful establishment of planted seedlings in reforestation areas, through affecting carbon gain and water and nutrient uptake from soil (Domisch et al. 2001). However, soil temperature did not significantly affect the foliar nitrogen concentration in this experiment (Zhang and Dang 2005). Therefore, low nutrition is probably not a contributing factor for the slower growth and lower biomass accumulation at the low soil temperature treatment in this study.

The total growth and biomass of the four boreal tree species were more resistant to high T_{soil} (27–30°C) than to low T_{soil} (7–10°C). Although the high T_{soil} also had some negative effects on the growth and/or biomass of some species, the magnitude of the impact was much smaller than that of the low soil temperature. The results are generally in agreement with the findings of Peng and Dang (2003). A gradual acclimation to the increasingly warmer environment in the greenhouses over the duration of the experiment might have contributed to the smaller negative impact of high T_{soil}.

The stem biomass was much more responsive to the low T_{soil} than the root biomass, particularly in the conifers, although the root is the organ that was directly affected by soil temperature. For instance, the low T_{soil} significantly reduced the stem biomass of both spruce species under both ambient and elevated [CO_2], but decreased the root biomass of white spruce only under the ambient [CO_2], while it did not significantly affect the root biomass of either species under the elevated [CO_2]. This result suggests that the soil temperatures used in this study might have exerted a greater impact on the functioning than on the growth of the root system. This result further emphasizes the importance of root functions (e.g., water and nutrient uptake) to the growth of aboveground organs (Kaufmann 1975, Pastor et al. 1987, Paré et al. 1993).

Jack pine and black spruce were much less responsive to the [CO_2] stimulation than white birch and white spruce. Such differences among the species will likely have a profound impact on the species distribution and the patterns of forest succession under global climate change associated with the increasing atmospheric [CO_2]. For instance, white birch and white spruce might be able to occupy colder sites under increased atmospheric [CO_2] in the future. The results suggest that the response of the boreal forest is very complex and different forest types and different species within the same forest stand are likely to respond differently. Our results on white spruce and jack pine are in agreement with, but the results on black spruce and white birch are in contrast to, the findings of Tjoelker et al. (1998) on photosynthesis. They find that the increase in net photosynthesis by CO_2 elevation is greater for slower-growing black spruce, jack pine, and tamarack than for fast-growing trembling aspen and white birch. However, Johnsen and Seiler (1996) did not find any significant differences among different provenances of black spruce in their response to [CO_2] elevation.

Our results partly support the hypothesis that [CO_2] elevation will compensate for the negative effects of unfavorable soil temperatures on biomass formation. Although the [CO_2] elevation generally increased the growth and biomass of the trees, the stimulation was much more pronounced at unfavorable soil temperatures, particularly the low temperature. For example, the low soil temperature significantly decreased the height and total biomass of black and white spruce at the ambient [CO_2], but not at elevated [CO_2]. The [CO_2] elevation was generally more beneficial to the growth and biomass of the trees at the low soil temperature than at other soil temperatures. The results from our earlier studies (Cai and Dang 2002, Peng and Dang 2003, Dang and Cheng 2004) suggest that the low soil temperature used in this study was more stressful to the seedlings of these tree species than the other two temperatures.

Our data suggest that soil temperature and [CO_2] had much smaller effects on biomass allocation than on growth and biomass. Peng and Dang (2003) have found that T_{soil} has almost no significant effect on the biomass allocation of black spruce, white spruce, jack pine, and trembling aspen seedlings that are exposed to a series of T_{soil} ranging from 5 to 35°C. Other researchers have found that [CO_2] does not

change the biomass allocation between roots and shoots (Bosac et al. 1995, Gebauer et al. 1996, Tingey et al. 1996, Tissue et al. 1997). However, Stulen and den Hertog (1993), Ceulemans and Mousseau (1994), Rogers et al. (1994), and Ericsson (1995) suggest that the $[CO_2]$ effect on biomass allocation depends on other growing conditions and that a shortage of nutrients and water tends to increase the root-to-shoot ratio. All the trees in this study were well watered and well fertilized. There are several mechanisms whereby environmental factors can influence the biomass allocation among different organs, particularly between aboveground and belowground organs. Lippu (1998) has observed that low soil temperatures decrease the translocation of photosynthates to roots and result in photosynthate accumulation in the aboveground organs in Scots pine. Domisch et al. (2001) also find that the biomass allocation to roots in Scots pine seedlings increase markedly with increasing soil temperature between 5 and 17°C. However, the biomass allocation to roots was relatively high at low T_{soil} in this study (about 30% except white spruce at ambient $[CO_2]$ compared to 20% in Scots pine reported in Domisch et al. 2001), particularly in jack pine and black spruce under ambient $[CO_2]$. In contrast, allocation to roots was greatly suppressed at the high T_{soil}, particularly in jack pine and black spruce under ambient $[CO_2]$. The lower biomass allocation to roots at the high T_{soil} might have been related to the high respiratory consumption of carbohydrates. This argument is supported by the fact that the $[CO_2]$ elevation increased biomass allocation to roots at high T_{soil} in the three coniferous species.

Our data suggest that neither soil temperature nor $[CO_2]$ affected the wood density of the seedlings of the four boreal tree species. The biomass/volume ratio of the stem is an indicator of wood density. Neither treatment had significant effects on this ratio in this study. This result is in contrast to the finding that elevated $[CO_2]$ increased leaf thickness or reduced the specific leaf area (Cure et al. 1989, Zhang and Dang, unpublished data).

In conclusion, unfavorable soil temperatures, particularly the low temperature, negatively affected the biomass accumulation in the seedlings of the four boreal tree species, and these negative effects were partly mitigated by the CO_2 elevation. These findings suggest that trees growing at sites with low soil temperatures could potentially benefit more from the increasing atmospheric CO_2 concentration than those growing on sites with higher soil temperatures. There are wide variations in soil temperature among different types of sites within the boreal forest region, ranging from cold permafrost and wetland sites to warm southwest-facing upland sites. The differences in response can have significant implications on the productivity of different sites and the biomass distribution across the boreal landscape. However, the interactions between soil temperature and CO_2 have received little attention in the scientific community. To our knowledge, this is the only study evaluating the interactive effects of soil temperature and $[CO_2]$ on boreal tree species. However, this is a short-term experiment on seedlings under fully controlled environmental conditions. Although long-term free air carbon dioxide enrichment experiments have shown similar general trends of response to

those found in enclosure studies, there are large differences (Long et al. 2004). Therefore, the results from this and other short-term enclosure studies should not be applied to trees growing under forest conditions without careful validation and or calibration. We hope that this study will stimulate more enclosure and field studies examining the interactions between soil temperature and CO_2 in the boreal forests.

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