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Low moisture availability inhibits the enhancing effect of increased soil temperature on net photosynthesis of white birch (*Betula papyrifera*) seedlings grown under ambient and elevated carbon dioxide concentrations

TITUS F. AMBEBE[1] and QING-LAI DANG[1,2]

[1] *Faculty of Forestry and the Forest Environment, Lakehead University, 955 Oliver Road, Thunder Bay, ON P7B 5E1, Canada*

[2] *Corresponding author (qdang@lakeheadu.ca)*

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Summary White birch (*Betula papyrifera* Marsh.) seedlings were grown under two carbon dioxide concentrations (ambient: 360 μmol mol^{-1} and elevated: 720 μmol mol^{-1}), three soil temperatures (5, 15 and 25 °C initially, increased to 7, 17 and 27 °C, respectively, 1 month later) and three moisture regimes (low: 30–40%; intermediate: 45–55% and high: 60–70% field water capacity) in greenhouses. In situ gas exchange and chlorophyll fluorescence were measured after 2 months of treatments. Net photosynthetic rate (A_n) of seedlings grown under the intermediate and high moisture regimes increased from low to intermediate T_{soil} and then decreased to high T_{soil}. There were no significant differences between the low and high T_{soil}, with the exception that A_n was significantly higher under high than low T_{soil} at the high moisture regime. No significant T_{soil} effect on A_n was observed at the low moisture regime. The intermediate T_{soil} increased stomatal conductance (g_s) only at intermediate and high but not at low moisture regime, whereas there were no significant differences between the low and high T_{soil} treatments. Furthermore, the difference in g_s between the intermediate and high T_{soil} at high moisture regime was not statistically significant. The low moisture regime significantly reduced the internal to ambient CO_2 concentration ratio at all T_{soil}. There were no significant individual or interactive effects of treatment on maximum carboxylation rate of Rubisco, light-saturated electron transport rate, triose phosphate utilization or potential photochemical efficiency of photosystem II. The results of this study suggest that soil moisture condition should be taken into account when predicting the responses of white birch to soil warming.

Keywords: boreal trees, chlorophyll fluorescence, CO_2 enrichment, global change, stomatal and non-stomatal limitations.

Introduction

Global atmospheric carbon dioxide concentration, [CO_2], is predicted to increase from the current 379 μmol mol^{-1} to between 485 and 1000 μmol mol^{-1} by the end of the 21st century (Cheng et al. 2008). The rise in atmospheric [CO_2] is predicted to enhance the photosynthesis of C_3 plants (Bazzaz 1990, Griffin and Seemann 1996). However, the stimulating effect of elevated [CO_2] may be constrained by other environmental conditions. For instance, significant interactive effects between [CO_2] and nutrient availability (Eguchi et al. 2004, Zhang and Dang 2006), [CO_2] and moisture availability (Mishra et al. 1999, Robredo et al. 2007), and [CO_2] and air temperature (Allen et al. 1990, Pessarakli 2005) on net photosynthesis (A_n) have been observed in greenhouse and growth chamber experiments. But no significant interaction has been detected in the few studies that have examined the combined effects of [CO_2] and soil temperature (Gavito et al. 2001, Zhang and Dang 2005). It is important to recognize, however, that multiple factors change concurrently in natural ecosystems and often interact with each other in affecting plants. The interactive effects may be of greater importance than the main effects in predicting the response of A_n to elevated atmospheric [CO_2].

Soil temperature (T_{soil}) is one of the most important environmental factors in boreal forests (Bonan and Shugart 1989, Bonan 1992). Low T_{soil} has been suggested to reduce root growth and nutrient uptake (Pastor et al. 1987, Bowen 1991, Paré et al. 1993, Grossnickle 2000), as well as root permeability and water uptake (Gurdarshan and Reynolds 1996, Richardson 2000, Öpik and Rolfe 2005). Low T_{soil}-induced reduction in stomatal conductance has been attributed to a decrease in shoot water potential or other hydraulic or chemical signals (Benzioni and Dunstone 1988, Day et al. 1991, Dang and Cheng 2004) and may impose stomatal limitations to A_n. The projected rise in atmospheric [CO_2] is likely to cause an increase in the mean global air temperature (Houghton et al. 1992, IPCC 2007) and presumably T_{soil} as well (Peterjohn et al. 1994, Pregitzer and King 2005). A change in T_{soil} may significantly affect the physiological processes and growth of boreal trees.

Changes in T_{soil} can have important consequences for moisture availability in forest ecosystems. For instance, permafrost thaws upon warming (Vyalov et al. 1993, Yoshikawa et al. 2003) and makes soils drier or wetter depending on other site conditions (Jorgenson and Osterkamp 2005). A decrease in A_n due to moisture stress has been attributed to both stomatal and non-stomatal limitations (Scarascia-Mugnozza et al. 1986, Ridolfi and Dreyer 1997, Cornic 2000, Lawlor 2002). However, an increase in moisture may have a cooling effect on soils (Bond-Lamberty et al. 2006). The combined effects of soil moisture and T_{soil} on boreal trees have not been investigated.

The purpose of this study was to investigate the interactive effects of T_{soil} and moisture availability, and the stimulating effect of elevated [CO_2], on A_n in white birch (*Betula papyrifera* Marsh.). White birch is a pioneer boreal tree species with a rapid initial growth rate and a high moisture requirement (USDA 2009). Pregitzer and King (2005) have predicted that the rate and depth of evaporation will increase with increasing T_{soil}, reducing the soil moisture content. This may result in a substantial reduction in the stomatal conductance to CO_2 of plants growing under moisture-limited conditions. Thus, we predicted that low moisture availability would reduce the positive effect of increased T_{soil} on A_n, and the A_n-promoting effect of elevated [CO_2] would respond to the $T_{soil} \times$ moisture interaction in ways that are different from the responses to T_{soil} and moisture alone.

Materials and methods

Plant materials

White birch seeds were germinated in germination trays filled with a 1:1 (v/v) mixture of peat moss and vermiculite in a greenhouse at Lakehead University. The greenhouse was maintained at 26/16 (± 2) °C (day/night) and 50 ± 5% relative humidity, and the natural photoperiod was extended to 15 h by high-pressure sodium lamps (P.L. Systems, Grimsby, ON, Canada). The light intensity at plant level was 660 $\mu mol\ m^{-2}\ s^{-1}$, as measured by an LI-190SA quantum sensor connected to an LI-250A light meter (Li-Cor, Lincoln, NE). The growing medium was watered twice a day with normal tap water using a spray bottle. There was no fertilizer application during this germination phase that lasted for 8 weeks. Seedlings of a similar size were then transplanted individually into plastic pots of 13.5 cm height, and 11 and 9.5 cm top and bottom diameter, respectively. The growing medium was a mixture of peat moss and vermiculite (1:1 v/v).

Experimental design

The experiment was conducted in greenhouses at Lakehead University. The treatments comprised two [CO_2] (360 and 720 $\mu mol\ mol^{-1}$), three T_{soil} (5, 15 and 25 °C initially, increased to 7, 17 and 27 °C, respectively, 1 month later) and three moisture regimes (30–40%, 45–55% and 60–70% field water capacity). The experimental design was a split-split plot where the [CO_2] treatments were the main plots, T_{soil} were the sub-plots and moisture regimes were the sub-sub-plots. The [CO_2] treatments were applied simultaneously in four separate environment-controlled greenhouses: two with 360 (ambient) and two with 720 (elevated) $\mu mol\ mol^{-1}$ [CO_2], resulting in two replications per treatment. The environmental conditions in each of the four greenhouses were controlled and monitored independently. The [CO_2] in the elevated greenhouses was attained using Argus CO_2 generators (Argus, Vancouver, BC, Canada). Three different T_{soil} control boxes (one per T_{soil} treatment) were placed on separate benches in each greenhouse. T_{soil} was regulated by circulating the temperature-controlled water between the pots attached to the bottom of the T_{soil} control box. A hole was made at the bottom of each pot to allow the free drainage of irrigation water and fertilizer solution. For a detailed description of the T_{soil} control system see Cheng et al. (2000). There were 10 randomly assigned seedlings in each of the three moisture regimes within each T_{soil} control box. The moisture treatments were done by measuring the water content of the growing medium daily with a HH2 moisture meter (Delta-T Devices, Cambridge, UK) and then adding water to maintain the respective target moisture level in each pot.

Each greenhouse was maintained at 26/16 °C day/night air temperatures and a 16-h photoperiod (natural light was supplemented with high-pressure sodium lamps on cloudy days, early mornings and late evenings). All the environmental conditions were monitored and controlled with an Argus environmental control system (Argus, Vancouver, BC, Canada). The seedlings were fertilized with a solution containing 100/44/83 $mg\ l^{-1}$ N/P/K every 3 weeks. The experiment lasted for 2 months.

Measurements of in situ gas exchange and chlorophyll fluorescence

Three seedlings were randomly selected from each greenhouse and $T_{soil} \times$ moisture treatment for gas exchange measurements. The measurements were done using a PP-Systems CIRAS-1 open gas exchange system (Hitchin, Hertfordshire, UK) on the fifth mature leaf counting from the apex. A/C_i curves were determined by measuring the steady-state response of photosynthetic rate (A) to varying internal CO_2 partial pressures (C_i). External CO_2 partial pressures (C_a) were supplied in eight steps, from 50 to 1100 $\mu mol\ mol^{-1}$. The measurements were done at 25 °C air temperature, 800 $\mu mol\ m^{-2}\ s^{-1}$ photosynthetically active radiation and 50% relative humidity. A/C_i response curves were analyzed using Photosyn Assistant software (Version 1.1, Dundee Scientific, Scotland, UK) to estimate the biochemical parameters potentially limiting to photosynthesis: V_{cmax} (maximum rate of carboxylation), J_{max} (light-saturated rate of electron transport) and TPU (triose phosphate utilization) (Harley et al. 1992, Wullschleger 1993). A_n, stomatal conductance (g_s) and transpiration rate were calculated according to Farquhar et al. (1980), von Caemmerer and Farquhar (1981), Sharkey (1985), Harley and Sharkey (1991) and Harley et al. (1992). The gas exchange parameters were expressed on a one-sided leaf area basis.

Chlorophyll fluorescence was measured after the gas exchange measurements with an FMS-2 portable pulse-modulated fluorometer (Hansatech Instruments, Norfolk, UK). The minimum (F_o) and maximum (F_m) fluorescence yields were measured after dark-adapting the leaves for 1 h with leaf clips. F_m was obtained by illuminating the leaf with a pulse of strong light ($\sim$ 14,000 μmol m^{-2} s^{-1}) for 800 ms. The potential photochemical efficiency of photosystem II (F_v/F_m) was calculated as $(F_m - F_o)/F_m$.

Statistical analysis

Data were analyzed using Data Desk 6.01 (Data Description 1996). The data were examined for normality and homogeneity of variance using probability plots and scatter plots, respectively. All the data satisfied the assumptions for analysis of variance (ANOVA). The effects of [CO_2], T_{soil}, moisture availability and their interactions were tested by a three-factor, split-split plot ANOVA. The statistical test was considered significant at $P \leq 0.05$, and Scheffe's post hoc test was used for pairwise comparisons of means when an interaction or a treatment involving more than two levels was significant.

Results

In situ gas exchange

[CO_2] and T_{soil} had significant (Table 1) interactive effects on A_n. A_n was the highest in elevated [CO_2] + intermediate T_{soil} and the lowest in ambient [CO_2] + low T_{soil} (Figure 1A). The elevated [CO_2] increased A_n at each T_{soil}, but the increases were greater at low and intermediate than at high T_{soil} (Figure 1A). There was no significant difference between the intermediate and high T_{soil} in ambient [CO_2], whereas A_n was significantly lower at high than at low T_{soil} in the elevated [CO_2] (Figure 1A). A significant (Table 1) $T_{soil} \times$ moisture regime effect on A_n was also observed. A_n significantly increased from the low to the high moisture regime at all T_{soil} (Figure 1A). While the intermediate T_{soil} significantly increased A_n only at the intermediate and high but not at the low moisture regime, A_n was significantly higher at the high than at the low T_{soil} only at the high but not at the other two moisture treatments (Figure 1A). Values of A_n were significantly higher at intermediate than at high T_{soil} in the intermediate and high moisture regimes (Figure 1A).

There was a significant (Table 1) interactive effect between T_{soil} and moisture regime on g_s. g_s increased from the low to the high moisture regime at all T_{soil}, but the difference between the low and intermediate moisture treatments at high T_{soil} was statistically insignificant (Figure 1B). No significant differences in g_s were observed between the low and high T_{soil} treatments under any moisture regime (Figure 1B). The intermediate T_{soil} treatment significantly increased g_s only at the intermediate and high but not at the low moisture regime (Figure 1B). However, the difference between the intermediate and high T_{soil} at high moisture regime was not statistically significant (Figure 1B).

T_{soil} and moisture regime had a significant (Table 1) interactive effect on the internal to ambient CO_2 concentration (C_i/C_a) ratio. The C_i/C_a ratio was significantly higher in the high than in the low moisture regime at all T_{soil} (Figure 1C). However, there were no significant differences between the low and intermediate or between the intermediate and high moisture regimes at intermediate T_{soil} (Figure 1C). Furthermore, the differences in C_i/C_a ratio between the low and intermediate moisture regimes at the low and high T_{soil} were not statistically significant (Figure 1C). Generally, no significant differences in the

Table 1. P values from ANOVA for the effects of [CO_2], soil temperature (T_{soil}), moisture regime (Mst) and their interactions on net photosynthetic rate (A_n), stomatal conductance (g_s), internal to ambient CO_2 concentration ratio (C_i/C_a), IWUE, maximum carboxylation rate (V_{cmax}), light-saturated electron transport rate (J_{max}), TPU and potential photochemical efficiency of photosystem II (F_v/F_m) of white birch. Seedlings were exposed to two [CO_2] (360 and 720 μmol mol^{-1}), three T_{soil} (5, 15 and 25 °C initially, increased to 7, 17 and 27 °C, respectively, 1 month later) and three Mst (30–40%, 45–55% and 60–70% field water capacity) for 2 months.

Source	CO_2	T_{soil}	Mst	$CO_2 \times T_{soil}$	$CO_2 \times$ Mst	$T_{soil} \times$ Mst	$CO_2 \times T_{soil} \times$ Mst
A_n	0.0260	0.0820	0.0060	0.0067	0.1630	$\leq$ 0.0001	0.1575
g_s	0.1755	0.2085	0.0985	0.6410	0.3898	0.0465	0.0985
C_i/C_a	0.4288	0.1515	0.1292	0.3398	0.1419	0.0072	0.2149
IWUE	0.0495	0.0362	0.1847	0.8135	0.2980	0.5893	0.2775
V_{cmax}	0.7375	0.1426	0.2109	0.8387	0.5321	0.9307	0.9304
J_{max}	0.7286	0.1324	0.1991	0.7180	0.3777	0.9746	0.8483
TPU	0.9147	0.3745	0.0782	0.9524	0.6012	0.9085	0.9781
F_v/F_m	0.4104	0.3611	0.1896	0.3308	0.8680	0.2680	0.3475

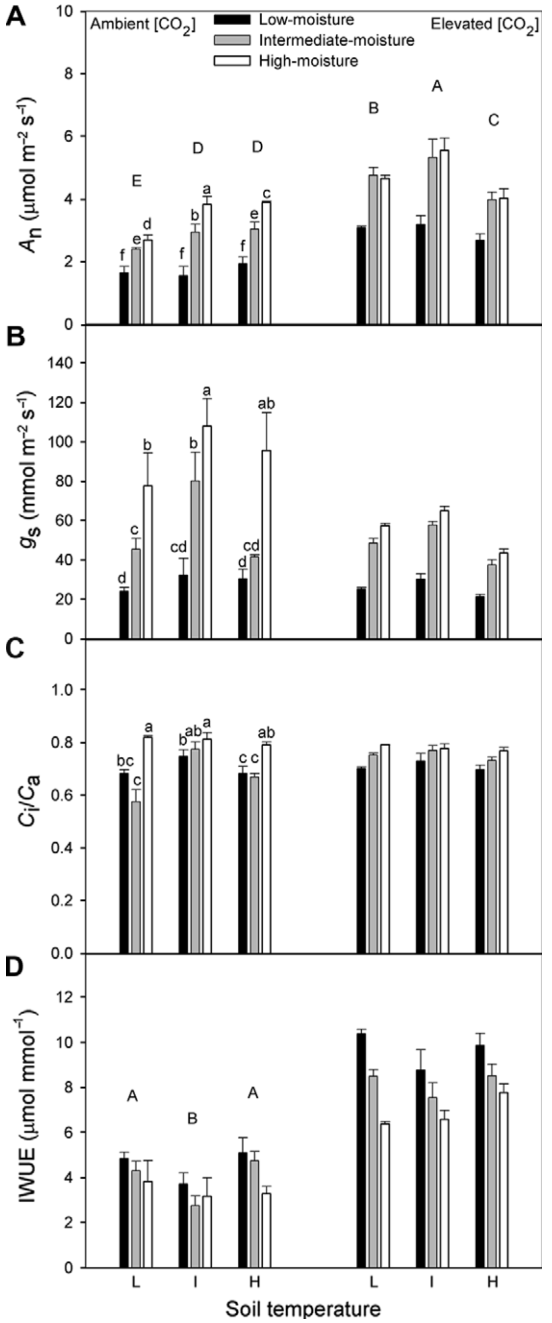

Figure 1. Effects of [CO$_2$], soil temperature (T_{soil}) and moisture regime (Mst) on net photosynthetic rate (A_n), stomatal conductance (g_s), internal to ambient CO$_2$ concentration ratio (C_i/C_a) and IWUE (mean ± SE, $n = 3$) of white birch. Seedlings were subjected to two [CO$_2$] (360 and 720 μmol mol^{-1}), three T_{soil} (5, 15 and 25 °C initially, increased to 7, 17 and 27 °C, respectively, 1 month later) and three Mst (30–40%, 45–55% and 60–70% field water capacity) for 2 months. The lowercase letters indicate $T_{\text{soil}} \times$ Mst interactions. In Figure 1A and D, the uppercase letters indicate CO$_2 \times T_{\text{soil}}$ interactions and T_{soil} effect, respectively. Different letters above the bars represent significantly different mean values according to Scheffe's post hoc test ($P \leq 0.05$). *Note*: when there are no CO$_2$-related interactions for a given parameter, only the bars on the side of the ambient [CO$_2$] are labeled. L, I and H represent the low, intermediate and high T_{soil}, respectively.

C_i/C_a ratio were observed between the low and high T_{soil} treatments (Figure 1C). The intermediate T_{soil} increased the C_i/C_a ratio only under the low and intermediate but not under the high moisture regime (Figure 1C). Nevertheless, the difference between the low and intermediate T_{soil} at low moisture regime was not significant (Figure 1C).

The instantaneous water-use efficiency (IWUE) was significantly (Table 1) affected by T_{soil} and [CO$_2$]. The intermediate T_{soil} decreased IWUE, whereas there were no significant differences between the low and high T_{soil} (Figure 1D). The [CO$_2$] elevation significantly increased IWUE (Figure 1D).

In vivo Rubisco activity and photochemical efficiency of photosystem II

There were no significant individual or interactive effects of [CO$_2$], T_{soil} and moisture regime on V_{cmax}, J_{max}, TPU or F_v/F_m (Table 1; Figure 2).

Discussion

Aphalo et al. (2006) and Ensminger et al. (2008) have demonstrated a strong positive relationship between A_n in boreal tree species and T_{soil}. Dang and Cheng (2004) have concluded that A_n increases to a maximum as T_{soil} increases and then declines with further increases in T_{soil}. In this study, A_n of white birch seedlings grown at the intermediate and high moisture regimes increased from low to intermediate T_{soil} and then decreased to high T_{soil}. There were no significant differences between the low and high T_{soil}, with the exception that A_n was significantly higher under high than low T_{soil} at high moisture regime. The decline in A_n from intermediate to high T_{soil} could be related to stomatal closure induced by a limited supply of water to the shoot due to impaired root growth and activity at high T_{soil} (Kramer 1983, Xu and Huang 2000). However, no significant effect of T_{soil} on A_n was observed under low moisture availability, suggesting that soil moisture conditions should be taken into account when predicting the responses of trees to T_{soil}.

The increase in A_n from the low to intermediate T_{soil} could be attributed to an increase in g_s to CO$_2$. Root resistance to water uptake decreases with soil warming, thus increasing water absorption and eventually leaf water potential (Day et al. 1991, Gurdarshan and Reynolds 1996, Richardson 2000, Dang and Cheng 2004, Öpik and Rolfe 2005). g_s may increase in response to the increase in leaf water potential (de Costa et al. 2000). Additionally, moderate increases in T_{soil} have been suggested to intensify the plant production of cytokinins (Brown and Ormrod 1980, Tachibana 1988), a hormone that is known to favor the opening of stomata (Mok and Mok 1994, Stoynova et al. 1996). The important role of g_s in the photosynthetic response of both coniferous and broadleaved boreal tree

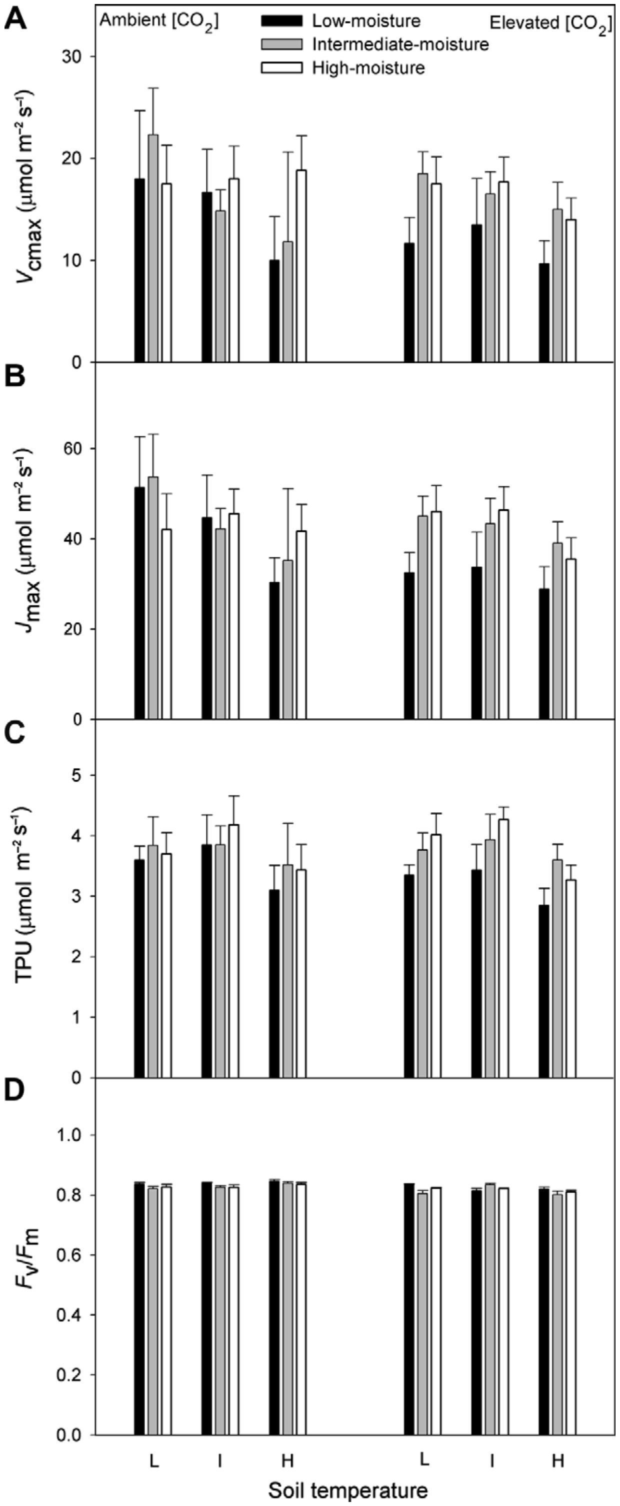

Figure 2. Effects of [CO$_2$], soil temperature (T_{soil}) and moisture regime (Mst) on maximum carboxylation rate (V_{cmax}), light-saturated electron transport rate (J_{max}), TPU and potential photochemical efficiency of photosystem II (F_v/F_m) (mean value ± SE, n = 3). The absence of labels indicates no significant effects ($P > 0.05$). See Figure 1 for other explanations.

species to T_{soil} had been demonstrated previously (Dang and Cheng 2004, Zhang and Dang 2005).

The low moisture regime inhibited the enhancing effect of increased T_{soil} on A_n. Both stomatal and non-stomatal factors have been implicated in reducing A_n under low moisture availability. The C_i/C_a ratio is an indicator for the relative limitations of stomatal and non-stomatal resistances. The C_i/C_a ratio will decline when the stomatal resistance is relatively more limiting to photosynthetic CO$_2$ assimilation and increases when otherwise (Dang and Cheng 2004). The C_i/C_a ratio was significantly reduced by the low moisture regime, suggesting a stronger stomatal limitation in response to this moisture level. Our data are consistent with the findings of other researchers (Farquhar et al. 1989, Chaves 1991, Havaux 1992, Cornic 2000, Flexas and Medrano 2002, Flexas et al. 2004) that stomatal closure and a consequent reduction in leaf internal CO$_2$ concentration (C_i) are the major reasons for reduced leaf A_n under mild moisture stress. The decrease in the aperture of the stomatal pore may be attributed to a build up of abscisic acid in the leaves of plants growing under low moisture availability (Pospíšilová and Čatský 1999, Johnson et al. 2001, Luan 2002, Robredo et al. 2007).

F_v/F_m was unaffected by moisture regime, and all F_v/F_m values that were within the range were considered 'normal' (0.80 ± 0.05) for non-stressed plants (Bolhar-Nordenkampf et al. 1989, Ball et al. 1994). These results suggest that low moisture availability did not cause permanent damage to photosystem II. Similar findings have been made by Ridolfi and Dreyer (1997), Bota et al. (2004), Bukhov and Carpentier (2004), Zlatev and Yordanov (2004) and van Heerden et al. (2007). The F_v/F_m and biochemical (V_{cmax}, J_{max} and TPU) data support the claim that stomatal, but not non-stomatal, limitation was the main contributing factor for the decline in A_n under the low moisture regime. However, low moisture availability has been reported to reduce V_{cmax}, J_{max} and TPU (Lou and Wang 2001, Wei et al. 2008) and F_v/F_m (Huxman et al. 1998, Guan et al. 2004, Li et al. 2008) in other studies. The discrepancies among these results could be attributed to the differences in the degree of moisture stress. Ennahli and Earl (2005), Ögren (1990) and Richardson et al. (2004) have concluded that moisture stress does not affect photosynthetic biochemistry and photochemistry unless the stress becomes severe.

A_n responded positively to [CO$_2$] elevation. Also, C_i was significantly higher in elevated than in ambient [CO$_2$] (data not shown). According to Agrawal (1999) and Midgley et al. (1999), the elevated [CO$_2$]-related increase in A_n may be explained by the higher C_i. In contrast, [CO$_2$] did not affect V_{cmax}, suggesting that the Rubisco activity was not a decisive factor. At the end of a 4-month study with white birch seedlings (Zhang and Dang 2006), no significant [CO$_2$] effect on V_{cmax} was observed under low nutrient availability, whereas V_{cmax} responded positively to [CO$_2$] elevation under the high nutrient regime. The lack of positive effect of [CO$_2$] elevation has been attributed to a low leaf nitrogen concentration (Midgley et al. 1999, Zhang and Dang 2006). Elevated [CO$_2$] reduces the leaf nitrogen concentration under low nutrient availability (Zhang and Dang 2006, Zhou and Shangguan 2009). Although our fertilizer formulation provides optimal nutrient conditions for white birch (Landis et al. 1989, Zhang and Dang 2007), the low frequency of fertilizer application might have resulted in low nutrient levels in the growing medium. No significant effect of [CO_2] on J_{max} was observed, supporting the view that V_{cmax} and J_{max} are closely coupled (Evans 1989, Stitt and Schulze 1994, Cai and Dang 2002). Contrary to our expectation, the positive effect of elevated [CO_2] on A_n was unaffected by the interaction between T_{soil} and moisture regime.

We hypothesized that low moisture availability would reduce the positive effect of increased T_{soil} on A_n. In support of this hypothesis, A_n increased from the low to the intermediate T_{soil}, but only at the intermediate and high moisture regimes and not at the low moisture condition. Furthermore, A_n was significantly higher under the high than low T_{soil} at the high but not at the low moisture regime where the effect of T_{soil} was, in general, insignificant. The results of this study suggest that trees growing under moisture stress may not experience the warm T_{soil}-induced enhancement of A_n that is likely to be observed in those growing under favorable moisture conditions. While future warmer T_{soil} conditions would increase the soil moisture content by thawing soil frost (Vyalov et al. 1993, Yoshikawa et al. 2003), there is also evidence for potential high T_{soil}-induced moisture stress on some boreal forest sites (Barber et al. 2000, Reich and Oleksyn 2008). The differences in response can have significant implications on the productivity of different sites. This study also suggests that the stimulating effect of [CO_2] on A_n may not be affected by the interaction of T_{soil} and moisture. However, the results of this study were obtained after only 2 months of growth in environment-controlled greenhouses and may not reflect the long-term acclimation to field conditions. Furthermore, the plants studied were seedlings and may not accurately reflect the responses of mature trees (Pritchard et al. 1999, Bond 2000, Cavender-Bares and Bazzaz 2000). Therefore, our findings should not be directly applied to natural forests without validation. These results, however, suggest the need to consider soil moisture status when examining the responses of boreal trees to soil warming.

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