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Low moisture availability reduces the positive effect of increased soil temperature on biomass production of white birch (*Betula papyrifera*) seedlings in ambient and elevated carbon dioxide concentration

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White birch (*Betula papyrifera* Marsh.) seedlings were grown under two carbon dioxide concentrations ([CO$_2$]) (360 vs 720 μmol mol^{-1}), three soil temperatures (T$_{soil}$) (5, 15, 25°C initially, increased to 7, 17, 27°C, respectively, one month later), and three moisture regimes (low: 30–40%, intermediate: 45–55%, high: 60–70% field water capacity) for four months in environment-controlled greenhouses. The dry mass of stem, leaves, and roots was measured after 2 and 4 months of treatment. Low T$_{soil}$ decreased stem, leaf and total biomass in both measurements, however, the decrease was significantly greater in the elevated than ambient [CO$_2$] after 4 months. Intermediate T$_{soil}$ increased root biomass in both measurements. Low moisture reduced stem, leaf, root and total biomass after both 2 and 4 months of treatment. There was a significant T$_{soil}$-moisture interactive effect on leaf, root, and total biomass after 4 months of treatment, suggesting that the magnitude of biomass enhancement in warmer T$_{soil}$ was dependent on the moisture regime. For instance, the increase in total biomass from the low to high T$_{soil}$ was 22, 50, and 47% under the low, intermediate and high moisture regimes, respectively. In contrast, the T$_{soil}$ × moisture effect on stem biomass was significant after 2 months, but not after 4 months of treatment. High T$_{soil}$ increased leaf mass ratio (LMR) after 4 months of treatment, but decreased both root mass ratio (RMR) after both 2 and 4 months, and root:shoot ratio (RSR) after 4 months of treatment. The low moisture regime decreased LMR after 2 and 4 months of treatment, but increased RSR after 4 months of treatment. There were no significant [CO$_2$] effects on biomass allocation or [CO$_2$] × T$_{soil}$ × moisture interactions on biomass production/allocation.

Global atmospheric carbon dioxide concentration ([CO$_2$]) has increased from 280 μmol mol^{-1} before the onset of the industrial revolution to approximately 379 μmol mol^{-1} today, and the current annual increase rate of 1.9 μmol mol^{-1} is the highest on record (IPCC 2007). Many studies have examined the effects of elevated CO$_2$ on trees (Bazzaz et al. 1990, Bowes 1993, Stulen and Den Hertog 1993, Johnsen and Major 1998, Pritchard et al. 1999, Liu et al. 2006, Zhang et al. 2006, Zhang and Dang 2007). The consensus of most of these studies is that elevated [CO$_2$] enhances growth and CO$_2$ assimilation rate. However, the reported stimulations are highly variable. This variability highlights the importance of the interaction of [CO$_2$] with other environmental factors.

There is a strong correlation between atmospheric [CO$_2$] and global temperature (UNEP 2005). The rising atmospheric [CO$_2$] is predicted to cause a substantial increase in mean global temperature within the next 100 years (Houghton et al. 1992, IPCC 2007). Soil temperature (T$_{soil}$) is an important environmental variable controlling the growth and distribution of trees in northern forests (Tryon and Chapin 1983, Bonan 1992). Low T$_{soil}$ has been suggested to reduce root water uptake by increasing water viscosity, and decreasing root growth and root permeability (Kaufmann 1975, Kramer 1983, Bowen 1991). In addition, low growth rates in cold soils are often attributed to low nutrient availability as a result of reduced nutrient cycling (Pastor et al. 1987, Paré et al. 1993). Increases in T$_{soil}$ are likely to have an enormous impact on the growth and biomass production of trees under high atmospheric [CO$_2$]-induced climate change.

Changes in T$_{soil}$ and soil moisture are coupled at the ecosystem level. Warming of the forest floor by fires has been suggested to degrade permafrost (Vyalov et al. 1993, Yoshikawa et al. 2003). This can decrease or increase the soil moisture content depending on other site conditions (Jorgenson and Osterkamp 2005). Increases in soil moisture may in turn decrease T$_{soil}$ (Bond-Lamberty et al. 2006). The important role of soil moisture for the establishment and growth of planted seedlings in reforestation areas has been demonstrated (Daniels and Veblen 2004). However, the combined effects of T_{soil} and moisture availability on forest trees have not been experimentally examined.

Several researchers have investigated 2-factor interactive effects of [CO_2] with T_{soil} or moisture availability on plant growth (Catovsky and Bazzaz 1999, Zhao et al. 2006, Zhang and Dang 2007). Elevated [CO_2] stimulates biomass production at high but not at low T_{soil} (McKee and Woodward 1994, Gavito et al. 2001). Low soil moisture has been found to counteract the stimulating effects of elevated [CO_2] on plant growth in some studies (Mo et al. 1992, Derner et al. 2003), but not in others (Kimball et al. 1995, Wall et al. 2001). It is, however, important to recognize that these factors change concurrently in the physical environment and may interact to affect plant responses to elevated [CO_2]. The interactive effect may not equal to the sum of individual effects (van Heerden and Yanai 1995).

The purpose of this study was to investigate the interactive effects of T_{soil} with moisture, and their impact on the stimulating effect of elevated [CO_2], on biomass production of white birch. White birch is an early-successional boreal tree species with a high rate of initial growth and a high moisture requirement (USDA-NRCS 2009). The rate and depth of evaporation increases with increasing T_{soil} (Pregitzer and King 2005), and this may result in large reductions in biomass production under moisture-limited conditions. Thus, we hypothesized that the low moisture regime would reduce the positive effect of increased T_{soil} on biomass production, and that the stimulating effect of elevated [CO_2] on biomass production would respond to the $T_{soil} \times$ moisture interaction in ways different from the responses to T_{soil} and moisture alone.

Material and methods

Plant materials

Seeds of white birch were sown in flats with a 1:1 (v/v) mixture of peat and vermiculite. Trays were placed in a growth chamber with ambient [CO_2]. After eight weeks, seedlings of approximately equal size were transplanted individually into plastic pots (13.5 cm tall and 11.0 cm top diameter and 9.5 cm bottom diameter) filled with the same medium as described above. The pots were mounted in T_{soil} control boxes as described in the following section.

Experimental design and growing conditions

The experiment was conducted in the Lakehead Univ. greenhouse facility. The treatments comprised of 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, one month later), and three moisture regimes (30–40%, 45–55%, 60–70% field water capacity). Two greenhouses were subjected to 360 (ambient) and two to 720 μmol mol^{-1} (elevated) [CO_2]. The [CO_2] elevation was achieved using Argus CO_2 generators. 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 heated or cooled water between the pots attached to the bottom of the T_{soil} control box. The pots in each box were insulated with foam insulation sheets to minimize heat exchange between the growth medium and the air, and a drain hole was installed beneath each pot. A detailed description of the T_{soil} control system is provided by Cheng et al. (2000). 10 seedlings were randomly assigned to each of the three moisture regimes within each T_{soil} control box. The moisture treatments were controled by measuring the water content of the growing medium daily with a HH2 moisture meter and then adding water to maintain the respective target moisture level in each pot. The experimental design was a split–split plot with the [CO_2] treatments as the main plots, T_{soil} as the sub-plots, and moisture treatments as the sub–sub-plots.

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. All seedlings were fertilized with a solution containing 100:44:83 mg l^{-1} NPK every three weeks. The experiment lasted for four months.

Measurements

Three randomly chosen seedlings from each greenhouse and treatment were harvested at each of two destructive harvests: mid-way through and at the end of the experiment. At each harvest, the seedlings were dissected into leaves, stem and root. The root system was washed to remove the growing medium. The dry mass of each fraction was determined following oven-drying to constant weight at 70°C. Biomass allocation parameters were calculated as follows: leaf mass ratio (LMR) = leaf dry mass/total seedling dry mass; root mass ratio (RMR) = root dry mass/total seedling dry mass; root-to-shoot ratio (RSR) = root dry mass/(stem + leaf) dry mass.

Statistical analysis

The assumptions of normality and homogeneity of variance were confirmed for all data using probability plots and scatter plots, respectively. A three-factor, split–split plot analysis of variance (ANOVA) was then used to test the effects of [CO_2], T_{soil}, moisture regime, and their interactions. The statistical test was considered significant at $p \leq 0.05$ and Scheffe's post hoc test was used to determine significant differences between means. All the analyses were performed using Data Desk 6.01 (Data Description 1996).

Results

Biomass production

There was no effect of [CO_2] alone or in combination on biomass production after 2 months of treatment (Table 1). In contrast, there were significant effects of T_{soil} and moisture on all biomass parameters, as well as a significant interactive effect between T_{soil} and moisture on stem biomass (Table 1). The low moisture regime significantly

Table 1. p-values from ANOVA for biomass and mass ratios of white birch seedlings grown at two [CO_2] (CO_2: 360 vs 720 μmol mol^{-1}), three soil temperatures (T_{soil}: 5, 15, 25°C initially, increased to 7, 17, 27°C, respectively, one month later), and three moisture regimes (Mst: 30–40%, 45–55%, 60–70% field water capacity) for two months. LMR and RMR represent the ratios of leaf and root biomass to total seedling biomass, respectively. RSR represents the ratio of root biomass to shoot (leaf+stem) biomass.

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
Stem	0.1349	0.0054	0.0116	0.1290	0.0826	0.0430	0.9472
Leaf	0.1136	0.0395	0.0437	0.7263	0.9575	0.1241	0.0835
Root	0.1543	0.0240	0.0406	0.2718	0.1385	0.8778	0.5705
Total	0.1303	0.0041	0.0024	0.2700	0.4553	0.2475	0.4914
LMR	0.0815	0.4732	0.2454	0.1303	0.1799	0.0267	0.9195
RMR	0.0516	0.0491	0.3701	0.8049	0.2392	0.6265	0.7535
RSR	0.3767	0.0673	0.6183	0.1731	0.1490	0.1984	0.3338

reduced stem biomass at the intermediate and high, but not at the low T_{soil} treatment where there were no significant differences between moisture regimes (Fig. 1a). Furthermore, there were no significant differences between the intermediate and high moisture regimes at intermediate and high T_{soil} (Fig. 1a). Stem biomass generally increased from low to intermediate and high T_{soil} at each moisture regime, but the differences between the intermediate and high T_{soil} treatments were not statistically significant (Fig. 1a). The magnitude of stem biomass enhancement by the higher T_{soil} treatments was greater in the intermediate and high than in the low moisture regime. Leaf, root and total seedling biomass increased significantly from low to high moisture regime (Fig. 1c, 1e, 1g). Low T_{soil} produced the lowest values of all three biomass parameters, but the differences in root biomass between the low and high T_{soil} treatments were not statistically significant (Fig. 1c, 1e, 1g). Furthermore, there were no significant differences in leaf biomass and total seedling biomass between the intermediate and high T_{soil} treatments (Fig. 1c, 1e, 1g).

There were significant main effects of T_{soil} and moisture, and interactive effect of [CO_2] with T_{soil} on stem biomass after 4 months of treatment (Table 2). Although intermediate and high T_{soil} significantly enhanced stem biomass under both [CO_2] treatments, the increases were higher in elevated than ambient [CO_2] (Fig. 1b). [CO_2] elevation increased stem biomass only at intermediate and high, but not at low T_{soil}. However, stem biomass was significantly higher at intermediate than at high T_{soil} under both ambient and elevated [CO_2]. Stem biomass was significantly lower under low than under intermediate and high moisture regimes, whereas there was no significant difference between the intermediate and high moisture treatments (Fig. 1b).

The main effects of [CO_2], T_{soil} and moisture on leaf biomass were significant after 4 months of treatment (Table 2). Additionally, there was a significant interactive effect between [CO_2] and T_{soil} on leaf biomass (Table 2). Although the intermediate and high T_{soil} treatments increased leaf biomass under both ambient and elevated [CO_2], the increases were significantly higher under elevated than ambient [CO_2] (Fig. 1d). Elevated [CO_2] significantly increased leaf biomass only at intermediate and high but not at low T_{soil} (Fig. 1d). There was no significant difference between the intermediate and high T_{soil} treatments under ambient [CO_2], whereas leaf biomass was significantly higher at intermediate than at high T_{soil} under elevated [CO_2] (Fig. 1d). A significant $T_{soil} \times$ moisture effect on leaf biomass was also observed after 4 months of treatment (Table 2). The low moisture regime significantly reduced leaf biomass at all T_{soil} (Fig. 1d). Intermediate and high T_{soil} significantly increased leaf biomass only under the intermediate and high but not under the low moisture regime (Fig. 1d). No significant difference in leaf biomass was observed between the intermediate and high T_{soil} treatments (Fig. 1d).

No significant effect of [CO_2] or [CO_2] related interaction on root biomass was detected after 4 months of treatment (Table 2). However, root biomass was significantly affected by T_{soil} and moisture as well as $T_{soil} \times$ moisture interaction (Table 2). Root biomass increased from the low to the intermediate and high moisture regimes (Fig. 1f). However, no significant differences were observed between the intermediate and high moisture regimes at low and high T_{soil} (Fig. 1f). Generally, there were no significant differences in root biomass between the low and the high T_{soil} treatments (Fig. 1f). Root biomass increased from the low and high to the intermediate T_{soil} at each moisture regime (Fig. 1f). The magnitude of root biomass enhancement by intermediate T_{soil} was lower at the low than at the intermediate and high moisture regimes.

Significant main effects of [CO_2], T_{soil}, and moisture regime on total seedling biomass were observed after 4 months of treatment (Table 2). Furthermore, there was a significant [CO_2] $\times T_{soil}$ effect on total seedling biomass (Table 2). Although intermediate and high T_{soil} significantly increased total biomass production under both [CO_2] treatments, the increases were significantly higher under elevated than under ambient [CO_2] (Fig. 1h). The [CO_2] elevation significantly enhanced total biomass only under the intermediate and high, but not under the low T_{soil} (Fig. 1h). Total seedling biomass was significantly higher at intermediate than at high T_{soil} under both ambient and elevated [CO_2] (Fig. 1h). Total seedling biomass was also significantly affected by $T_{soil} \times$ moisture interaction after 4 months of treatment (Table 2). Total seedling biomass increased from the low to the intermediate and high moisture regimes at all T_{soil}, but the difference between the intermediate and high moisture treatments was statistically insignificant (Fig. 1h). Total seedling biomass increased from the low to the intermediate and high T_{soil} at each moisture regime whereas there were no significant differences between intermediate and high T_{soil} (Fig. 1h). The magnitude of total biomass enhancement by the warmer T_{soil} treatments was lowest in low compared to the intermediate and high moisture regimes.

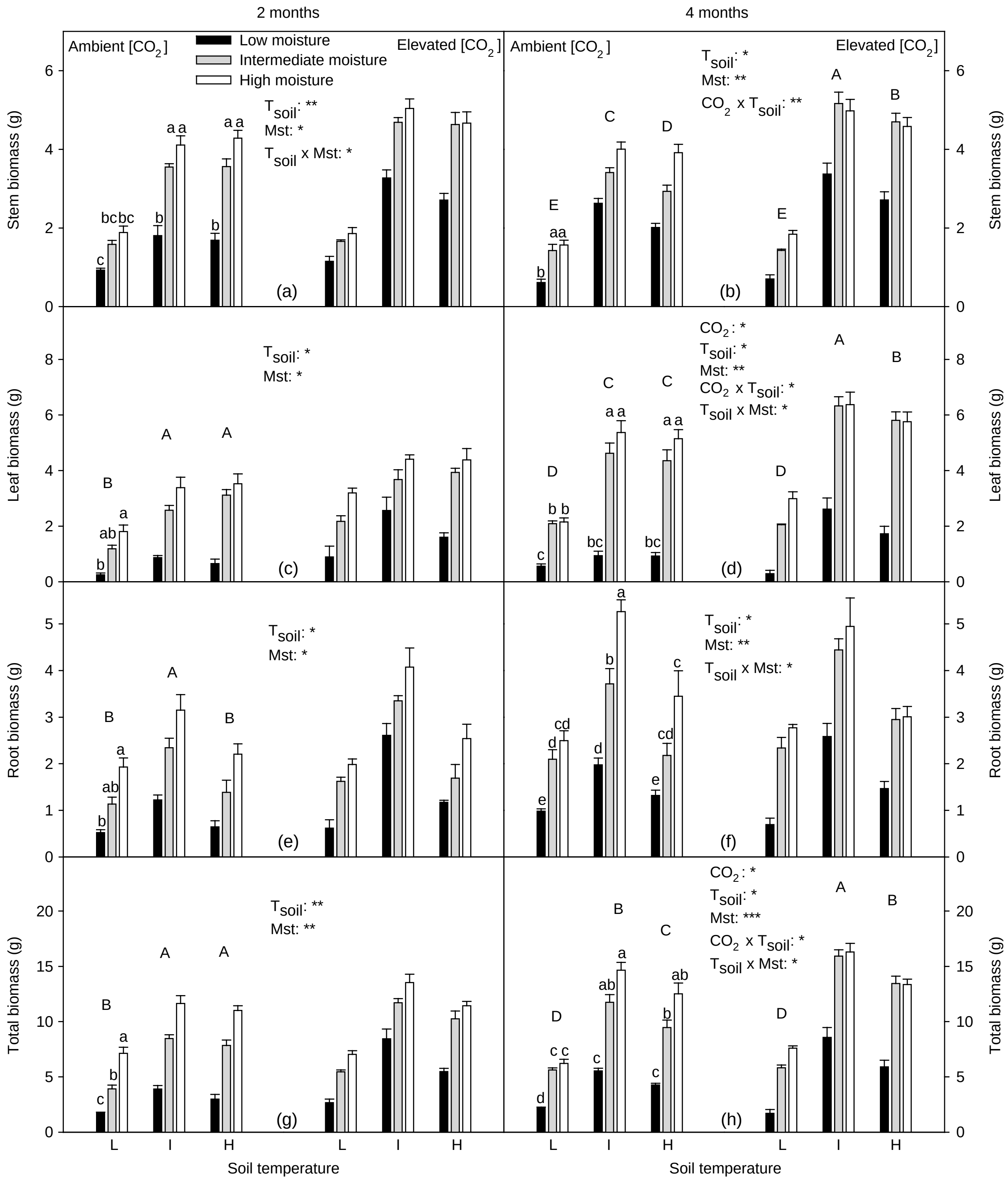

Figure 1. Effects of [CO$_2$], soil temperature (T$_{\mathrm{soil}}$) and moisture regime (Mst) on (a)–(b) stem biomass, (c)–(d) leaf biomass, (e)–(f) root biomass, and (g)–(h) total biomass (mean ± SE) of white birch seedlings. Plants were grown under two [CO$_2$] (360 vs 720 μmol mol^{-1}), three soil temperatures (5, 15, 25°C initially, increased to 7, 17, 27°C, respectively, one month later), and three moisture regimes (30–40%, 45–55%, 60–70% field water capacity) for four months. Measurements were taken 2 and 4 months ($n = 3$) after the start of treatments. In (a), (d), (f), (h) and (b), (c), (e), (g) the lower-case letters indicate T$_{\mathrm{soil}}$ × Mst interactions and Mst effect, respectively. In (b), (d), (h) and (c), (e), (g) the upper-case letters indicate CO$_2$ × T$_{\mathrm{soil}}$ interactions and T$_{\mathrm{soil}}$ effect, respectively. Different letters above the bars represent significantly different means under Scheffe's post hoc test ($p = 0.05$). Note: only the bars on the side of the ambient [CO$_2$] were labeled when there was no significant CO$_2$ effect or CO$_2$ related interactions. L, I, and H represent the low, intermediate, and high T$_{\mathrm{soil}}$, respectively.

Table 2. p-values from ANOVA for biomass and mass ratios of white birch seedlings grown at two [CO_2], three soil temperatures, and three moisture regimes for four months. Other explanations are as in Table 1.

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
Stem	0.1148	0.0116	0.0086	0.0058	0.3400	0.3219	0.2248
Leaf	0.0465	0.0117	0.0018	0.0245	0.8010	0.0268	0.1162
Root	0.4043	0.0148	0.0067	0.8695	0.5187	0.0263	0.6965
Total	0.0218	0.0130	0.0003	0.0475	0.5323	0.0459	0.2511
LMR	0.2483	0.0188	0.0218	0.2501	0.1591	0.5584	0.0929
RMR	0.2563	0.0147	0.0875	0.6692	0.5274	0.3197	0.9547
RSR	0.2179	0.0263	0.0591	0.7234	0.5811	0.2285	0.9689

Biomass allocation

There were no significant effects of [CO_2] alone or in combination on LMR, RMR and RSR after 2 and 4 months of treatment (Table 1, 2). However, there was a significant $T_{soil} \times$ moisture effect on LMR after 2 months of treatment (Table 1). LMR increased from the low to the intermediate and high moisture regimes at all T_{soil}, but the differences between the moisture treatments at intermediate T_{soil} were not statistically significant (Fig. 2a). Furthermore, there were no significant differences between the low and high T_{soil} treatments (Fig. 2a). LMR increased from the low and intermediate to the high T_{soil} only in the intermediate but not in the other two moisture treatments (Fig. 2a). However, values of LMR in the intermediate moisture regime were not significantly different between the low

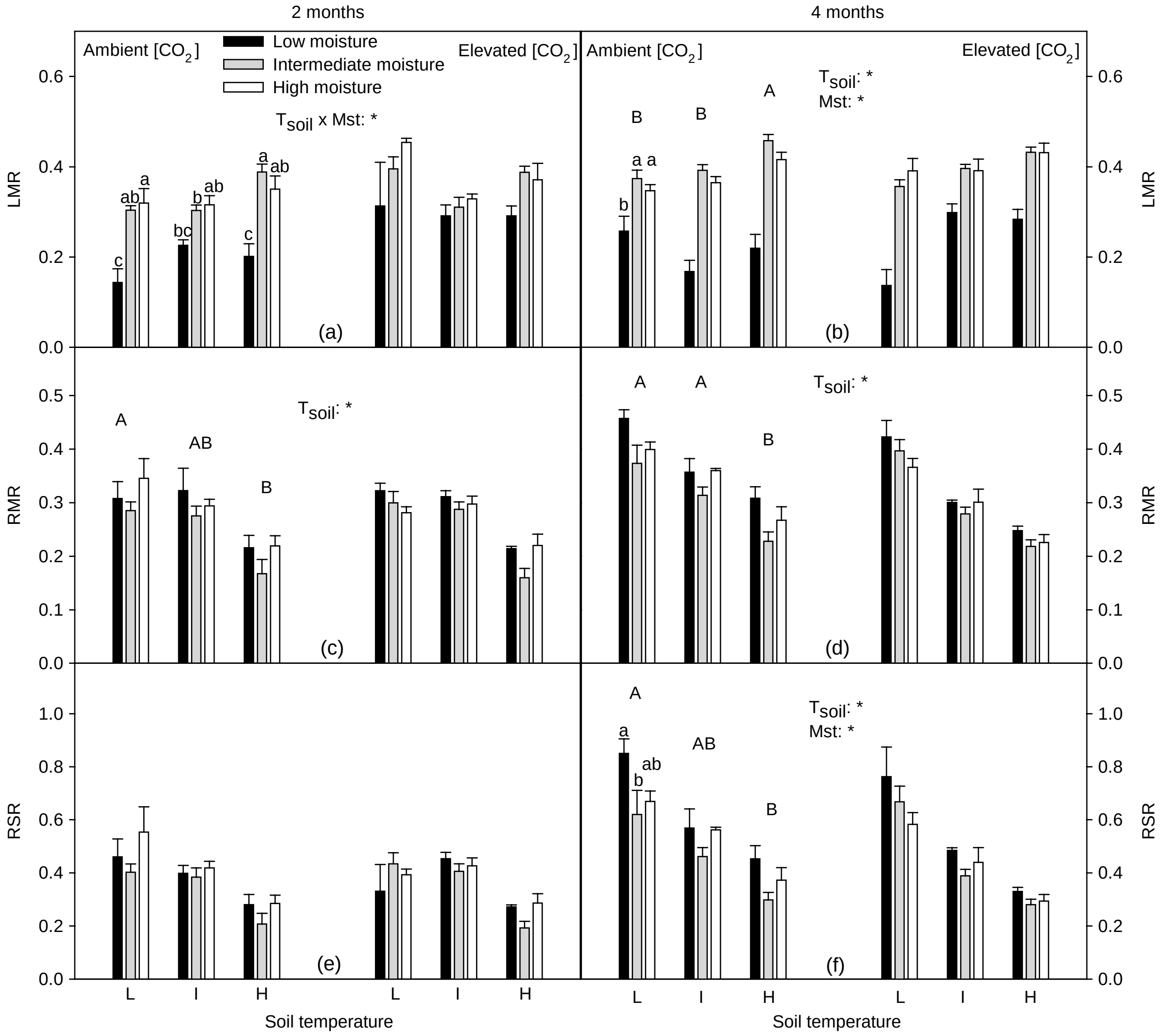

Figure 2. Effects of [CO_2], soil temperature (T_{soil}) and moisture regime (Mst) on (a)–(b) leaf mass ratio (LMR), (c)–(d) root mass ratio (RMR), and (e)–(f) root:shoot ratio (RSR) (mean ± SE) of white birch seedlings. In (e) the absence of labels indicates no significant effects ($p > 0.05$). See Fig. 1 for other explanations.

and intermediate T_{soil} treatments (Fig. 2a). There were significant main effects of T_{soil} and moisture on LMR after 4 months of treatment whereas the interactive effect between T_{soil} and moisture became insignificant (Table 2). LMR increased from the low to the intermediate and high moisture regimes, but there was no significant difference between the intermediate and high moisture regimes (Fig. 2b). LMR significantly decreased from the high to the intermediate and low T_{soil} treatments; however, no significant difference was observed between low and intermediate T_{soil} (Fig. 2b).

T_{soil} significantly affected RMR after 2 and 4 months of treatment (Table 1, 2): RMR decreased from low to high T_{soil} (Fig. 2c–d). However, the difference between the low and intermediate T_{soil} treatments was not statistically significant after 4 months of treatment (Fig. 2d). There was no significant main effect of moisture and, in general, no treatment interactive effect on RMR after 2 and 4 months of treatment (Table 1, 2).

None of the three environmental factors had a significant effect on RSR after 2 months (Table 1), but significant main effects of T_{soil} and moisture were observed after two other months of treatment (Table 2). Values of RSR were highest in the low and lowest in the intermediate moisture treatment, and decreased from low to high T_{soil} (Fig. 2f).

Discussion

Reich and Oleksyn (2008) have suggested that modest soil warming would enhance the growth of boreal tree species at cold, but not at warm parts of the species range. In the present study, the total biomass of white birch seedlings increased from low to intermediate and high T_{soil} at three different moisture regimes; however, there was no significant difference between the intermediate and high T_{soil}. Our data are in agreement with the results of Reich and Oleksyn (2008). The total biomass enhancement by high T_{soil} was 22, 50 and 47% at the low, intermediate and high moisture regimes, respectively. This finding supports our first hypothesis that low moisture availability would reduce the positive effect of increased T_{soil} on biomass production. Stem biomass, leaf biomass, and root biomass responded to treatments in a similar manner to total biomass with the exception that root biomass declined significantly from intermediate to high T_{soil} at each moisture regime. The decrease in root biomass at the high T_{soil} may be attributed to increased root respiration (Lawrence and Oechel 1983, DeLucia et al. 1992, Atkin et al. 2000, Huang et al. 2005). The rate of root respiration increases exponentially with temperature (Pregitzer et al. 2000). Up to 52% of the daily carbon gain by photosynthesis can be lost through root respiration (Lambers et al. 1996, Atkin et al. 2000).

The T_{soil}-induced enhancement of biomass might be through direct effects on root properties, as well as indirect effects on shoot processes like photosynthesis. Plants growing in warm soils take up more water than their counterparts in cold soils due to a decrease in soil water viscosity and an increase in root growth and root permeability (Kaufmann 1975, 1977, Kramer 1983, Bowen 1991). Below the plant's optimum, increases in T_{soil} usually result in increased stomatal conductance and photosynthesis (Cai and Dang 2002, Dang and Cheng 2004). Experimental warming of forest soils has been reported to increase nutrient availability through an increase in nutrient mineralization (Pastor et al. 1987, Paré et al. 1993). Jarvis and Linder (2000) have concluded that the thawing of soil frost due to warming would enhance the uptake of nutrients and carbon dioxide, leading to increased growth of boreal forest trees. Gas exchange measurements from our study have revealed that the low moisture treatment counteracted the positive effect of the intermediate and high T_{soil} on stomatal conductance and net photosynthesis (Ambebe and Dang unpubl.). This finding suggests that the low moisture effect on biomass production at intermediate and high T_{soil} was achieved, perhaps, through increased stomatal limitations to CO_2 assimilation (Li et al. 2004, Zhang and Dang 2005).

Several investigators have reported an increase in plant biomass with [CO_2] elevation (Zhang et al. 2006, Cao et al. 2008, Marfo and Dang 2009). It has also been suggested that the positive effect of elevated [CO_2] is manifested under warm but not under cold T_{soil} conditions (Gavito et al. 2001). Our results are in general agreement with the above findings. However, root biomass did not respond to [CO_2], as observed previously by Ball and Drake (1998), Olszyk et al. (2003), and Gutjahr and Lapointe (2008). The lack of [CO_2] effect could be related to the greater use of photosynthates in rhizosphere respiration under elevated [CO_2] (Luo et al. 1996, Lin et al. 1999, Olszyk et al. 2003).

The results of this study do not support our second hypothesis that the biomass-enhancing effect of elevated [CO_2] would be influenced by the interaction between T_{soil} and moisture availability. The stress level in our low moisture treatment is relatively mild. However, seedlings may experience more severe moisture stresses under field conditions due to a high T_{soil}-induced increase in evaporation (Pregitzer and King 2005); this could potentially result in unresponsiveness of biomass to elevated [CO_2] under high T_{soil} and low moisture conditions.

Biomass allocation was significantly affected by T_{soil} and moisture availability, but not by [CO_2]. The decrease in RMR and RSR with increasing T_{soil} reported here supports the results of other studies (Thornley 1972, Clarkson et al. 1988, DeLucia et al. 1992). Davidson (1969) has attributed such an inverse relationship between root biomass allocation and T_{soil} to an increase in the rate of root function. Lambers et al. (1998) have demonstrated that the relative investment of biomass in roots is lowest at a certain optimum T_{soil} and increases at lower and higher T_{soil}. The low moisture regime significantly increased RSR and reduced LMR, consistent with the works of Van Den Boogaard et al. (1996), Liu and Stützel (2004), and Zhao et al. (2006). Our results are in agreement with the theory of functional balance proposed by Brouwer (1963), which predicts that plants would respond to limited water availability with a relative increase in the flow of assimilates to the root. A high RSR (indicative of relatively high capacity for water uptake and low capacity for transpirational water loss) is critical for growth and survival of plants under moisture stress (Lambers et al. 1998). The absence of CO_2 effects on LMR, RMR and RSR in this study is in line with the finding of other researchers that [CO_2] does not change the biomass allocation between above- and below-ground plant parts (Bosac et al. 1995, Curtis and Wang 1998, Zhang et al. 2006, Zhang and Dang 2007).

In conclusion, moderate increases in T_{soil} under future warmer climatic conditions may alleviate the limitations on the growth of boreal trees imposed by cold T_{soil} (Peng and Dang 2003, Zhang and Dang 2007). It is also suggested that warmer winter temperatures would increase the reproductive potential of birch by increasing the duration of flowering, and decreased root resistance to water uptake is likely to play an important role (Miller-Rushing and Primack 2008). Although soil warming enhanced biomass production of white birch seedlings, the response was the lowest at the low in comparison to the two other moisture regimes. Our results suggest that plants in low moisture soils may benefit much less from warmer T_{soil} than those growing under favorable moisture conditions. The differences in response can have important implications on biomass distribution across the boreal landscape given that the anticipated warming of soils may increase evaporation (Pregitzer and King 2005), exposing plants to moisture stress at some forest sites (Barber et al. 2000). Use of forest management practices, such as mulching, that conserve soil moisture and moderate T_{soil} may be important for improved plant performance on areas where higher T_{soil}-induced moisture stress is likely to occur. This study also suggests that the biomass-enhancing effect of elevated [CO_2] may not be constrained by the interaction of T_{soil} and moisture availability. However, since the plants under our low moisture treatment were only mildly stressed, it is important to further examine the responses of this species to [CO_2] elevation under warm T_{soil} and highly reduced soil moisture conditions.

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