

# Effects of elevated carbon dioxide concentration and soil temperature on the growth and biomass responses of mountain maple (*Acer spicatum*) seedlings to light availability

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## Abstract

### Aims

Some shade-tolerant understory tree species such as mountain maple (*Acer spicatum* L.) exhibit light-foraging growth habits. Changes in environmental conditions, such as the rise of carbon dioxide concentration ( $[\text{CO}_2]$ ) in the atmosphere and soil warming, may affect the performance of these species under different light environments. We investigated how elevated  $[\text{CO}_2]$  and soil warming influence the growth and biomass responses of mountain maple seedlings to light availability.

### Methods

The treatments were two levels of light (100% and 30% of the ambient light in the greenhouse), two  $[\text{CO}_2]$  (392  $\mu\text{mol mol}^{-1}$  (ambient) and 784  $\mu\text{mol mol}^{-1}$  (elevated)) and two soil temperatures ( $T_{\text{soil}}$ ) (17 and 22°C). After one growing season, we measured seedling height, root collar diameter, leaf biomass, stem biomass and root biomass.

### Important findings

We found that under the ambient  $[\text{CO}_2]$ , the high-light level increased seedlings height by 70% and 56% at the low  $T_{\text{soil}}$  and high  $T_{\text{soil}}$ , respectively. Under the elevated  $[\text{CO}_2]$ , however, the high-light level increased seedling height by 52% and 13% at the low  $T_{\text{soil}}$  and high  $T_{\text{soil}}$ , respectively. The responses of biomasses to light generally followed the response patterns of height growth under both  $[\text{CO}_2]$  and  $T_{\text{soil}}$  and the magnitude of biomass response to light was the lowest under the elevated  $[\text{CO}_2]$  and warmer  $T_{\text{soil}}$ . The results suggest that the elevated  $[\text{CO}_2]$  and warmer  $T_{\text{soil}}$  under the projected future climate may have negative impact on the colonization of open sites and forest canopy gaps by mountain maple.

**Keywords:** mountain maple, elevated  $\text{CO}_2$ , soil warming, light availability, height, biomass

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## INTRODUCTION

Plants acclimated to low-light conditions show adaptive morphological and physiological traits that maximize light interception for improved carbon gain. The biomass allocation to leaf (leaf mass ratio (LMR)) and specific leaf area (SLA) are generally higher in low-light environments. As a result, the product of the two traits, leaf area ratio (LAR), is often greater in low-light environment compared with high-light environment (Anten and Hirose 1998; Boucher *et al.* 2001;

Poorter *et al.* 2012; Semchenko *et al.* 2012). Plants growing in low-light environments occasionally endure excessive light supply (relative to their capacity of light utilization) when they are exposed to large sunflecks (Lambers *et al.* 2008) or when canopy gaps are created by tree mortality (Krause *et al.* 2001). Some shade-tolerant plant species exhibit growth habits that enable them to discover and exploit high-light environments (Lei and Lechowicz 1990; Rincon *et al.* 1989). Growth in high-light environments may involve physiological and morphological adjustments, including changes in

biomass allocation among different organs that enable them to better utilize the high-light resource and to resist environmental stresses associated with the increased light. The ability of shade-tolerant species to respond to and colonize canopy gaps or open sites is critical to the expansion of those species (Kubiske *et al.* 1997). While light is considered a primary determinant of seedling growth, other factors, such as CO<sub>2</sub> and  $T_{\text{soil}}$ , can influence their responses to light (Boucher *et al.* 2001; Kubiske and Pregitzer 1997). Evidence exists that multiple factors always interact with one another in affecting seedling growth and distribution (Amebebe *et al.* 2009; Catovsky and Bazzaz 1999).

The atmospheric [CO<sub>2</sub>] is predicted to continue to increase to between 730–1200  $\mu\text{mol mol}^{-1}$  by year 2100 (IPCC 2007a; Meehl *et al.* 2007; Sitch *et al.* 2008). As a result of the increases in [CO<sub>2</sub>], both air and soil temperatures are expected to rise (Adams *et al.* 1990; Houghton *et al.* 1992; IPCC 2001; IPCC 2007b; Wigley 2005). Increases in [CO<sub>2</sub>] enhance plant growth and biomass accumulation through its (CO<sub>2</sub>) direct stimulation of photosynthesis under adequate nutrients and water supplies (Bazzaz and Miao 1993; Curtis and Wang 1998; Drake *et al.* 1997; Wand *et al.* 1999). Elevated [CO<sub>2</sub>] may enhance plants establishment and growth through improved carbon balance (Liang *et al.* 2001; Osborne *et al.* 1997) or light use efficiency (Naumburg and Ellsworth 2000). Hättenschwiler and Körner (2000) have shown that the increases in relative growth rate and biomass in response to increased light are greater under elevated [CO<sub>2</sub>] in *Acer pseudoplatanus*, *Quercus robur* and *Abies alba*. The enhanced growth responses to light under elevated [CO<sub>2</sub>] could alter species distribution and composition in the ecosystem in the future.

$T_{\text{soil}}$  is a key factor in the boreal forest that limits the growth of plants (Tamm 1991). Soil warming has been shown to increase plant growth and biomass production (Amebebe *et al.* 2013; Dawes *et al.* 2011; Peng and Dang 2003; Rustad *et al.* 2001; Walker *et al.* 2006). The observed increases in the rates of growth and biomass accrual in plants under warmer soils depend on biogeochemistry. Increases in biochemical processes such as the rate of organic matter decomposition (Hobbie 1996; Jansson and Berg 1985; Melillo *et al.* 2002), nitrogen (N) mineralization (MacDonald *et al.* 1995) and nutrient uptake (Bassirirad 2000; Bowes 1991; DeLucia *et al.* 1992; Karlsson *et al.* 1996; Rennenberg *et al.* 2006) under soil warming have been reported. By increasing these processes, soil warming indirectly increases shoot growth and reduces biomass allocation to root (Anderson-Teixeira *et al.* 2013; Zhou *et al.* 2011). However, growth responses to soil warming vary with species and other environmental factors. For instance, the growth of *Pinus cembra* at the treeline in the Swiss Alps responded positively to a 3-year soil warming, while *Larix decidua* did not (Dawes *et al.* 2011). Species-specific growth responses to soil warming at the Harvard forest between oaks and maples also have been observed (Butler *et al.* 2012; Melillo *et al.* 2011). Differential species growth responses to soil

warming may affect successional dynamics and forest composition. Although some studies have examined the interactive effects of  $T_{\text{soil}}$  and light on the growth and physiology of shade-tolerant species (Boucher *et al.* 2001), there is a lack of data on boreal plants.

This study examined the interactive effects of CO<sub>2</sub> and  $T_{\text{soil}}$  on the growth and biomass responses of mountain maple (*Acer spicatum* L.) to light availability. Mountain maple is an important shrub or tree species in the understory of North America boreal forests (Aubin *et al.* 2005; Sullivan 1993). It survives and grows slowly under the forest canopy for a long period of time but rapidly dominates canopy gaps or open sites caused by the removal of overstory vegetation (Archambault *et al.* 1998; Aubin *et al.* 2005; Bergeron 2000; Lei and Lechowicz 1997; Rook 2002). Furthermore, mountain maple has an intrinsic light-scavenging ability that can enhance the rapid colonization of opened canopies after disturbances (Lei and Lechowicz 1990; Rincon and Grime 1989). Since soil warming enhances nitrogen mineralization, nutrient availability and water and nutrient absorption by roots (Stoneman *et al.* 1993), it should enhance the response to increased light supply. Boucher *et al.* (2001) report that the growth and photosynthetic responses of shade-tolerant eastern white pine seedlings to light were generally greater at warmer  $T_{\text{soil}}$ . We have tested the hypothesis that elevated [CO<sub>2</sub>] and soil warming would enhance the growth and biomass responses of mountain maple seedlings to high light.

## MATERIALS AND METHODS

### Plant material

Seeds of mountain maple were collected from Jack Haggerty Forest in Thunder Bay, Ontario, Canada (48°22'56" N, 89°14'46" W). Seeds were soaked in a 1000  $\mu\text{mol m}^{-1}$  gibberellic acid for 24 h and stratified at 4°C for 2 months. The hard seed coat was cracked open carefully to facilitate germination. Germination was carried out in horticultural trays with a 2:1 mixture of vermiculite and peat moss as the growing medium at the Lakehead University greenhouse. The average environmental conditions during germination and the whole duration of the experiment were as follows: temperature 22/16°C (day/night), relative humidity of 50% and 16 h photoperiod (summertime day length for Thunder Bay, ON, based on Environment Canada Weather Report, 2010). An Argus environmental control system (Argus systems Ltd, Vancouver, BC, Canada) was used to monitor and control the environmental conditions. One hundred and sixty similar-sized seedlings were transplanted into plastic pots (31.5 cm deep, 11 cm top diameter, and 9.5 cm bottom diameter) 3 weeks after germination. The pots were filled with the same growing medium as used for germination.

### Experimental design

The experiment followed a split-split-plot design. The main-plot treatment comprised of two levels of CO<sub>2</sub> (392 and

784  $\mu\text{mol mol}^{-1}$ ) with two independent replications for each level. The elevated [CO<sub>2</sub>] (784  $\mu\text{mol mol}^{-1}$ ) was achieved using Argus CO<sub>2</sub> generators (Argus, Vancouver, BC, Canada). The subplot consisted of two  $T_{\text{soil}}$  (low 17°C and high 22°C) in each greenhouse. The low  $T_{\text{soil}}$  represents the mean  $T_{\text{soil}}$  in the rooting zone (5 cm) during the growing season in the boreal forest zone (Domisch *et al.* 2001; Kubin and Kempainen 1991). The high  $T_{\text{soil}}$  represents an assumed future  $T_{\text{soil}}$  if an increase of 5°C in  $T_{\text{soil}}$  occurs by end of 2100 (Christensen *et al.* 2007; IPCC 2007b).  $T_{\text{soil}}$  was achieved by circulating temperature-controlled water between pots in a  $T_{\text{soil}}$  control box (See Cheng *et al.* 2000 for a detailed description). The sub-subplot treatment consisted of two light levels (100% and 30% of the greenhouse light) within each  $T_{\text{soil}}$ . The average natural light in the greenhouse was 710  $\mu\text{mol m}^{-2} \text{s}^{-1}$  on cloud-free days. Each  $T_{\text{soil}}$  control box was divided into two halves with one half shaded to reduce the light level by 70%. The shading was achieved using neutral density shade cloth. High-pressure sodium lamps (Model LR48877, P.L. Systems, Grimsby, ON, Canada) were mounted above the  $T_{\text{soil}}$  control boxes to provide supplemental light on cloudy days and to extend the photoperiod to 16 h.

Nutrients were added to the irrigation water twice a week at a concentration of 100, 15, 57, 6, 6 and 11 mg/l of N, P, K, Ca, Mg and S, respectively. The nutrient concentrations were determined based on previous studies on *Acer* species and other deciduous tree species (Canham *et al.* 1996; Ingestad 1981). The seedlings were watered daily.

### Growth and biomass measurements

After one growing season, five seedlings per treatment combination were measured for height ( $H$ ) and root collar diameter (RCD). The seedlings were then harvested and separated into leaves, stems and roots. The total leaf area (LA) per seedling was measured using WinFolia (Regent Instrument Inc., Quebec, Canada). The samples were oven dried to a constant weight at 70°C for 48 h. SLA and root:shoot ratio (RSR) were

calculated by dividing the total LA by dry leaf mass and by dividing dry root mass by dry shoot mass, respectively. Other indices of biomass allocation calculated were LMR and root mass ratio (RMR). LAR was calculated by dividing the LA by the total plant dry biomass.

### Statistical analysis

The data were analyzed with Data desk 6.01 Statistical Package k (Data Description 1996). The assumptions of normality of distribution and homogeneity of variance were examined graphically using probability plots and histograms of the residuals, respectively, before the analysis of variance (ANOVA) was done. The data met both assumptions. Three-way split-split-plot ANOVA was used to test the effects of CO<sub>2</sub>,  $T_{\text{soil}}$ , light treatments and their interactions. Means were compared using Scheffé's  $F$  test at significant level of  $P \leq 0.05$ .  $P$  values  $\leq 0.10$  were considered marginally significant.

## RESULTS

The interaction between [CO<sub>2</sub>] and  $T_{\text{soil}}$  had a significant effect on seedling growth responses to light treatments (Table 1). While the high-light treatment resulted in significantly greater  $H$  and RCD at all [CO<sub>2</sub>] and  $T_{\text{soil}}$  treatments, the magnitudes of increase in  $H$  and RCD in response to the high-light treatment were smallest in the combination of elevated [CO<sub>2</sub>] and high  $T_{\text{soil}}$  and greatest in the combination of ambient [CO<sub>2</sub>] and high  $T_{\text{soil}}$  (Fig. 1a and b). The elevated [CO<sub>2</sub>] significantly increased  $H$  growth in all  $T_{\text{soil}}$  and light treatment combinations except in the high  $T_{\text{soil}}$  and high-light treatment combination where no significant [CO<sub>2</sub>] effect on  $H$  was observed (Fig. 1a). The elevated [CO<sub>2</sub>] significantly increased RCD in all  $T_{\text{soil}}$  and light combinations except in the low light and low  $T_{\text{soil}}$  where no significant [CO<sub>2</sub>] effect on RCD was observed (Fig. 1b).

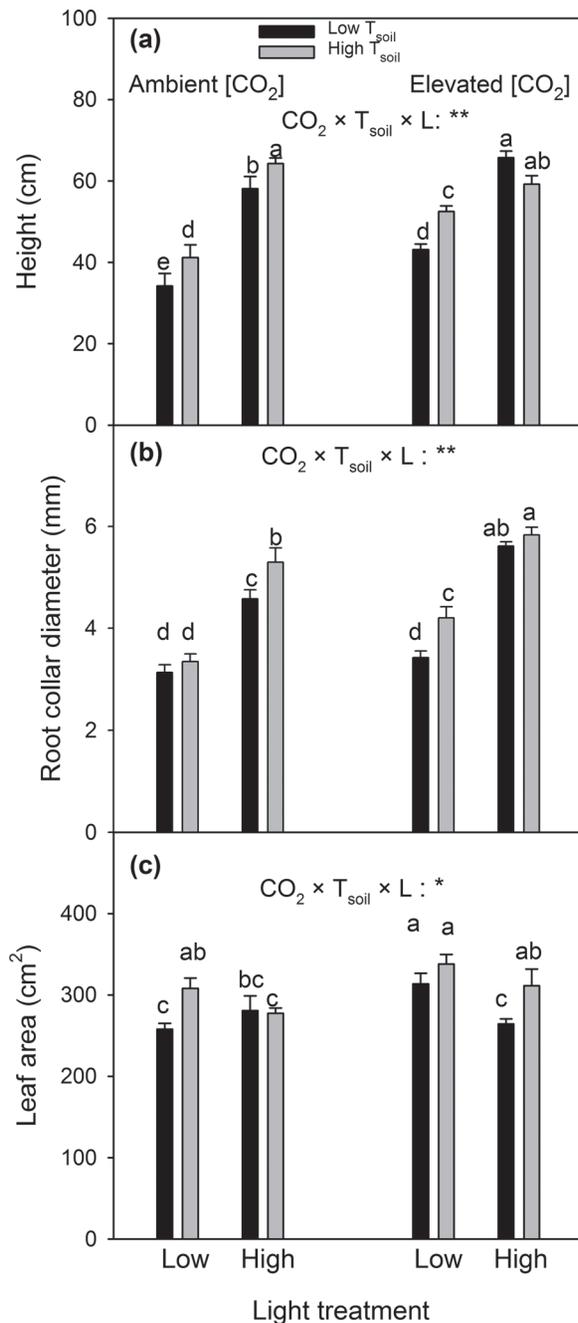
There was a marginally significant interactive effect of [CO<sub>2</sub>],  $T_{\text{soil}}$  and light on the LA per seedling (Table 1). Under the ambient [CO<sub>2</sub>], LA was significantly lower in the high-light

**Table 1:** summary of ANOVA ( $P$  values) for mountain maple seedlings height ( $H$ ), RCD, total LA per seedling, SLA, LAR, total biomass (TB) and RSR, RMR and LMR

Source of variation	CO <sub>2</sub>	$T_{\text{soil}}$	CO <sub>2</sub> × $T_{\text{soil}}$	$L$	CO <sub>2</sub> × $L$	$T_{\text{soil}}$ × $L$	CO <sub>2</sub> × $T_{\text{soil}}$ × $L$
$H$	0.1159	<b>0.0211</b>	0.1366	$\leq 0.0001$	<b>0.0123</b>	<b>0.0173</b>	<b>0.0353</b>
RCD	<b>0.0571</b>	<b>0.0004</b>	0.8124	$\leq 0.0001$	0.3895	0.9751	<b>0.0453</b>
LA	0.2907	<b>0.0148</b>	0.5831	<b>0.0288</b>	0.1176	0.5634	<b>0.0606</b>
SLA	<b>0.0030</b>	0.2656	0.1889	$\leq 0.0001$	0.9208	<b>0.0181</b>	<b>0.0598</b>
LAR	<b>0.0834</b>	0.1430	0.1694	$\leq 0.0001$	0.4935	<b>0.0608</b>	<b>0.0458</b>
TB	<b>0.0891</b>	<b>0.0021</b>	0.3196	$\leq 0.0001$	0.1428	0.6795	<b>0.0046</b>
RSR	0.1629	0.3632	<b>0.0289</b>	$\leq 0.0001$	0.9494	0.2567	<b>0.0176</b>
RMR	<b>0.0058</b>	<b>0.0288</b>	0.1066	$\leq 0.0001$	0.9408	0.2235	<b>0.0831</b>
LMR	0.2865	0.1582	0.9103	$\leq 0.0001$	$\leq 0.0001$	<b>0.0006</b>	0.9951

Seedlings were grown at ambient (392  $\mu\text{mol mol}^{-1}$ ) or elevated (784  $\mu\text{mol mol}^{-1}$ ) [CO<sub>2</sub>], low (17°C) or high (22°C)  $T_{\text{soil}}$  and high (unshaded) or low (shaded) light ( $L$ ) environment. Measurements were taken one growing season. Significant ( $P \leq 0.05$ ) and marginally significant ( $P \leq 0.10$ ) treatment effects are highlighted in bold.

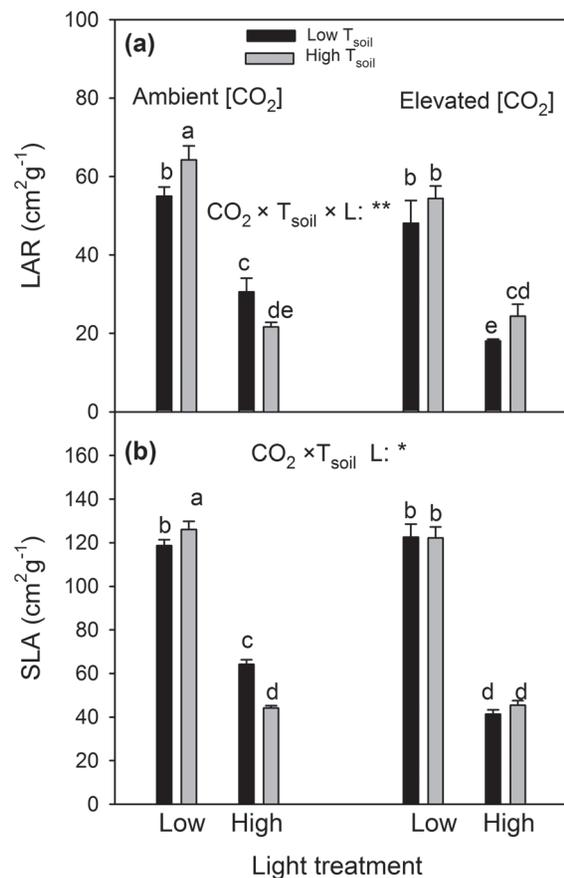
treatment compared with the low-light treatment at the warmer  $T_{\text{soil}}$ . No significant LA response to high-light treatment was observed at low  $T_{\text{soil}}$  and ambient  $[\text{CO}_2]$  (Fig. 1c). Under the elevated  $[\text{CO}_2]$ , LA was not significantly different



**Figure 1:** height (a), root collar diameter (b) and total leaf area (c) of mountain maple seedlings grown at low (shaded) or high (unshaded) light regime, ambient ( $392 \mu\text{mol mol}^{-1}$ ) or elevated ( $784 \mu\text{mol mol}^{-1}$ )  $[\text{CO}_2]$  and at low ( $17^\circ\text{C}$ ) or high ( $22^\circ\text{C}$ )  $T_{\text{soil}}$  regime. The values are the averages of 10 seedlings per treatment combination, and the error bars represent the mean and SE (mean  $\pm$  SE,  $n = 10$ ). Bars with same letter(s) are not significantly different ( $P \leq 0.10$ ) from each other or one another. \* $P \leq 0.10$ , \*\* $P \leq 0.05$  and \*\*\* $P \leq 0.01$ .

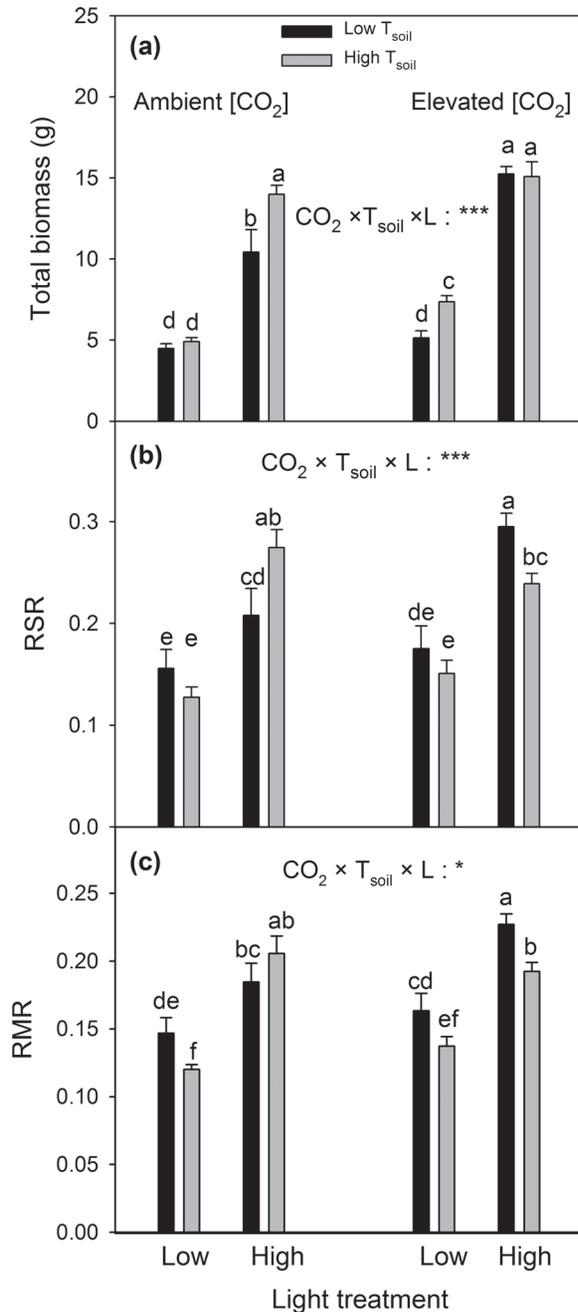
between light treatments at the high  $T_{\text{soil}}$ . However, LA was significantly lower in the high light at the low- $T_{\text{soil}}$  treatment (Fig. 1c). Furthermore, the elevated  $[\text{CO}_2]$  increased LA in the low-light treatment under the low  $T_{\text{soil}}$  and in the high-light treatment under the warmer  $T_{\text{soil}}$  (Fig. 1c).

As expected, the high-light treatment significantly decreased LAR and SLA compared with the low-light treatment (Table 1). However, the effect of light varied significantly with  $[\text{CO}_2]$  and  $T_{\text{soil}}$ : under ambient  $[\text{CO}_2]$ , the high light decreased both LAR and SLA by 45% and 33%, respectively, at the low  $T_{\text{soil}}$  but decreased LAR and SLA by 63% and 58%, respectively, at the high  $T_{\text{soil}}$  (Fig. 2a and b). Furthermore, under the elevated  $[\text{CO}_2]$ , high light decreased LAR and SLA by 66% and 59%, respectively, at the low  $T_{\text{soil}}$  but decreased them by 53% at the high  $T_{\text{soil}}$  (Fig. 2a and b). The elevated  $[\text{CO}_2]$  significantly decreased LAR at the warmer  $T_{\text{soil}}$  and low light and at the low  $T_{\text{soil}}$  and high-light treatments. No significant elevated  $\text{CO}_2$  effect on LAR was observed at the low  $T_{\text{soil}}$  and low-light treatment. The elevated  $[\text{CO}_2]$  decreased SLA only at the low  $T_{\text{soil}}$  and high-light treatment (Fig. 2a and b).



**Figure 2:** leaf area ratio (a) and specific leaf area (b) of mountain maple seedlings grown at low (shaded) or high (unshaded) light regime, ambient ( $392 \mu\text{mol mol}^{-1}$ ) or elevated ( $784 \mu\text{mol mol}^{-1}$ )  $[\text{CO}_2]$  and at low ( $17^\circ\text{C}$ ) or high ( $22^\circ\text{C}$ )  $T_{\text{soil}}$  regime. Refer to Fig. 1 for other explanations.

The interaction between CO<sub>2</sub> and  $T_{\text{soil}}$  affected seedling biomass response to light (Table 1). While the high light generally increased seedling biomass at all [CO<sub>2</sub>] and  $T_{\text{soil}}$  treatment combinations, the magnitude of biomass increase was greatest at the elevated [CO<sub>2</sub>] and low- $T_{\text{soil}}$  (197%) treatment combination but lowest under the elevated [CO<sub>2</sub>] and high  $T_{\text{soil}}$  (105%, Fig. 3a). The high light significantly increased



**Figure 3:** total biomass (a), root:shoot ratio (b) and root mass ratio (c) of mountain maple seedlings grown at low (shaded) or high (unshaded) light regime, ambient (392  $\mu\text{mol mol}^{-1}$ ) or elevated (784  $\mu\text{mol mol}^{-1}$ ) [CO<sub>2</sub>] and low (17°C) and high (22°C)  $T_{\text{soil}}$  regime. Refer to Fig. 1 for other explanations.

seedling biomass in high- $T_{\text{soil}}$  treatment under ambient [CO<sub>2</sub>] but no significant effect under the elevated [CO<sub>2</sub>]. The elevated [CO<sub>2</sub>] increased seedling biomass at the warmer  $T_{\text{soil}}$  and low light and at the low  $T_{\text{soil}}$  and high-light treatment combinations (Fig. 3a). However, the [CO<sub>2</sub>] did not affect biomass at the low  $T_{\text{soil}}$  and low light or at the warmer  $T_{\text{soil}}$  and high light (Fig. 3a).

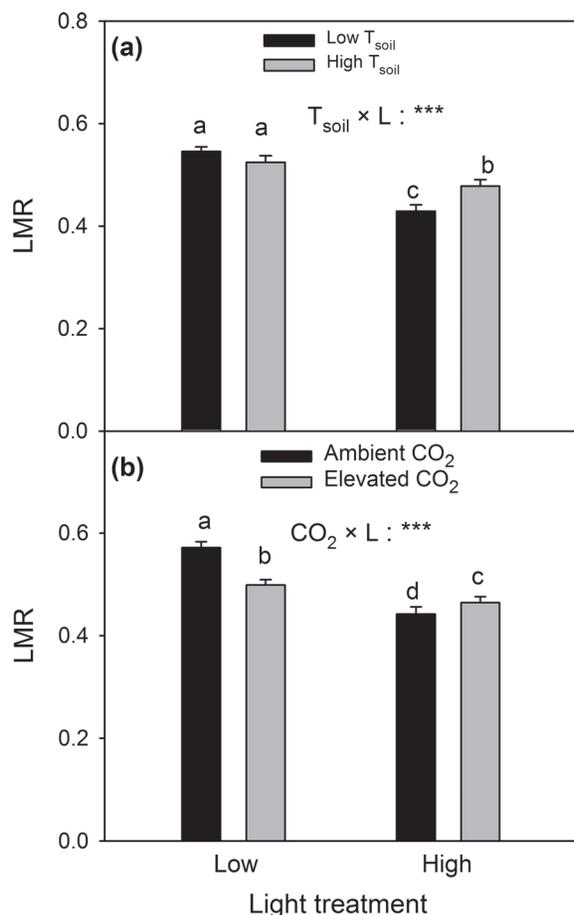
The response of RSR to light was significantly affected by the interaction between CO<sub>2</sub> and  $T_{\text{soil}}$  (Table 1). The high light generally increased RSR at all [CO<sub>2</sub>] and  $T_{\text{soil}}$  treatment combinations but the degree of the increase was greatest in  $T_{\text{soil}}$  treatment under ambient [CO<sub>2</sub>] (116%) and lowest in low- $T_{\text{soil}}$  treatment under ambient [CO<sub>2</sub>] (34%, Fig. 3b). The elevated [CO<sub>2</sub>] significantly increased RSR only at the low  $T_{\text{soil}}$  under high light but had no significant effect on RSR at the other treatment combinations (Fig. 3b).

There was a marginal significant interactive effect between [CO<sub>2</sub>] and  $T_{\text{soil}}$  on the response of RMR to light (Table 1). While the high light generally increased RMR under both [CO<sub>2</sub>] and  $T_{\text{soil}}$  treatments, the degree of the increase was greatest in the ambient [CO<sub>2</sub>] and high- $T_{\text{soil}}$  treatment combination and lowest in the ambient [CO<sub>2</sub>] and low- $T_{\text{soil}}$  treatment combination (Fig. 3c). The elevated [CO<sub>2</sub>] significantly increased RMR only at the low  $T_{\text{soil}}$  in the high-light treatment (Fig. 3c).

The response of LMR to light was significantly affected by  $T_{\text{soil}}$  and [CO<sub>2</sub>] but not by their interactions (Table 1). The high-light treatment generally decreased LMR at both  $T_{\text{soil}}$  treatments but the magnitude of decrease was greater at the low than at the high  $T_{\text{soil}}$  (-21% vs. -9%, Fig. 4a). Soil warming significantly increased LMR (by 11%) in the high-light treatment but not in the low-light treatment (Fig. 4a). The high-light treatment generally resulted in a significantly lower LMR under both [CO<sub>2</sub>] but the reduction was greater under the ambient than under the elevated [CO<sub>2</sub>] (-23% vs. -7%, Fig. 4b). The elevated [CO<sub>2</sub>] significantly reduced LMR in the low light but increased it at the high light treatment (Fig. 4b).

## DISCUSSION

The [CO<sub>2</sub>] and  $T_{\text{soil}}$  changed the growth and biomass responses of mountain maple seedlings to light availability. While both height growth and biomass were generally increased by the high-light treatment, the largest height increase (70%) occurred at the low  $T_{\text{soil}}$  under the ambient [CO<sub>2</sub>], second largest at the low  $T_{\text{soil}}$  under the elevated [CO<sub>2</sub>] and the smallest increase (13%) was observed in the elevated [CO<sub>2</sub>] and warmer  $T_{\text{soil}}$  combination. Similarly, the lowest biomass increase in response to high light was observed under elevated [CO<sub>2</sub>] and warmer  $T_{\text{soil}}$ . The results contradict our hypothesis that mountain maple seedlings would show largest positive response to high light under elevated CO<sub>2</sub> and warmer soil temperature. The findings also appear to be in contrast to some studies which involve only two factors. For example, Hättenschwiler and Körner (2000) report that the biomass of *A. pseudoplatanus*, *Q. robur* and *A. alba* show a greater positive



**Figure 4:** leaf mass ratio (a and b) of mountain maple seedlings grown at low (shaded) or high (unshaded) light regime, ambient ( $392 \mu\text{mol mol}^{-1}$ ) or elevated ( $784 \mu\text{mol mol}^{-1}$ )  $CO_2$  and low ( $17^\circ\text{C}$ ) or high ( $22^\circ\text{C}$ )  $T_{soil}$  regime. a and b represent  $T_{soil} \times L$  (data pooled for  $CO_2$ ) and  $CO_2 \times L$  (data pooled for  $T_{soil}$ ) interactions, respectively. All other explanations are as in Fig. 1.

response to increases in light level under elevated than under ambient  $CO_2$ . The fact that the high-light effect was the smallest in the combination of elevated  $CO_2$  and warmer  $T_{soil}$  is probably due to the compensatory effects of the warmer soil temperature and elevated  $CO_2$  to the low-light limitation to photosynthetic carbon sequestration. Indeed, the positive effect of the warmer  $T_{soil}$  on growth and biomass was greater in the low light than in the high light under the elevated  $CO_2$ , whereas the effect was about the same in the two light treatments under the ambient  $CO_2$ . Similarly the positive effect of the elevated  $CO_2$  on growth was greater in the low than in the warm soil temperature and in the low-light treatment than in the high-light treatment. Elevated  $CO_2$  increases the efficiency of photosynthetic light use by suppressing photorespiration when light is limited (Lambers *et al.* 2008) and thus reduces the degree of low-light limitation. In contrast, warmer  $T_{soil}$  increases the consumption of carbohydrates by root respiration and thus can partially offset the beneficial effect of

increased light on photosynthesis. Root respiration can consume up to 52% of the daily carbohydrate production by photosynthesis (Lambers *et al.* 2008). The results of this study suggest that the effects of light,  $CO_2$  and soil temperature are highly interactive and thus the total effect of the three factors cannot be obtained by a simple summation of the individual effects, which was the assumption of our hypothesis. The results also suggest that the climate change associated with the rise in  $CO_2$  in the lower atmosphere will likely enhance the performance of mountain maple to a greater extent under the low-light environment of forest canopies than in canopy gaps or open sites. Furthermore, if the findings are true to other shade-tolerant species, those species may become more shade tolerant in the future. This may have important ecological implications on the species composition and dynamics of the boreal forests in the future (Archambault *et al.* 1998; Aubin *et al.* 2005; Bergeron 2000; Rook 2002).

LAR and SLA are generally positively related to growth rate (Lambers *et al.* 2008; Lambers and Poorter 1992; Poorter and Remkes 1990; Ray *et al.* 2004; Rice and Bazzaz 1989). Within the same species, however, their values generally decrease with increasing light availability (Anten and Hirose 1998; Boucher *et al.* 2001; Poorter *et al.* 2012) and elevated  $CO_2$  (Norby and O'Neill 1991; Roumet and Roy 1996; Temperton *et al.* 2003) but increase with soil warming (Weih and Karlsson 2001). In this study, the greatest reductions in LAR and SLA in response to the high-light treatment occurred in the treatment combination of elevated  $CO_2$  and low  $T_{soil}$ . Plants allocate resources in the way that the functions of different parts are in balance (Lambers *et al.* 2008). Presumably, the high light and elevated  $CO_2$  treatments in this study enhanced the photosynthetic performance of the seedlings and consequently a higher root capacity was needed to maintain the functional balance between belowground and aboveground organs, leading to an increase in biomass allocation root and a decrease in allocation to leaf as evidenced by the reduction in LAR and SLA. Similarly low  $T_{soil}$  generally hampers root functions and leads to increased demand for biomass allocation to root at the expense of allocation to leaf (Lambers *et al.* 2008). In other words, the high light, elevated  $CO_2$  and low  $T_{soil}$  worked in concert to reduce LAR and SLA in this study, leading to a greater reduction in these traits than the total of the three individual effects. These results once again point to the importance of understanding the interactive effects of multiple factors toward a better understanding of how plants respond to changes in environmental conditions. Our SLA and LAR values are within the range for mountain maple growing along a successional gradient in the southern boreal forest (Aubin *et al.* 2005).

The biomass allocation patterns observed in this study support the theory of maximum resource capture in mountain maple seedlings growing in high-light environments. The reduction in the proportion of biomass allocated to leaf in the high-light treatment was greater at the low  $T_{soil}$  than at the high  $T_{soil}$ . The opposing effects of high light and soil warming

observed in this study are similar to the findings of Boucher *et al.* (2001) and Stoneman and Dell (1993). Plants in natural high-light environments are faced with increased heat load and transpiration demand for water, thus they tend to allocate less biomass to leaves to reduce transpiration water demand and at the same time increase allocation to roots to increase water uptake capacity (Givnish 1988; Pearcy and Sims 1994). The interesting observation in this study was that the reduction in LMR in response to high-light treatment was mitigated by soil warming. Soil warming improves root water and nutrient uptake (Bassirirad 2000; Bowes 1991; DeLucia *et al.* 1992; Karlsson and Nordell 1996; Rennenberg *et al.* 2006), thereby permitting increased leaf production (Boucher *et al.* 2001; Karlsson and Nordell 1996). Under natural environmental conditions, however, warmer soil temperatures can increase evaporation from the soil and thus reduce soil moisture content (Pregitzer and King 2005). The subsequent drier soil conditions could potentially counteract the positive effects of warmer soil temperatures. We found that the reduction of biomass allocation to leaf in response to the high-light availability was also smaller under the elevated than under the ambient [CO<sub>2</sub>]. Elevated [CO<sub>2</sub>] generally reduce stomatal conductance and transpiration (Lambers *et al.* 2008), reducing the extent of increased transpiration demand induced by the increased light supply and consequently the need of leaf area reduction.

In conclusion, this study shows that elevated [CO<sub>2</sub>] and soil warming acted interactively to reduce the degree of growth response to light in mountain maple. Given the continuous increase in the atmospheric [CO<sub>2</sub>] and concurrent warming, such interactive effects should be taken into account in predicting forest dynamics and ecosystem processes in the future. The study demonstrates that mountain maple growing on sites with moderately low  $T_{\text{soil}}$  would benefit more from increases in [CO<sub>2</sub>] than those growing on warmer sites. This effect and the finding that the beneficial effects of increased light were smaller under elevated [CO<sub>2</sub>] and warmer soil temperature suggest that the future environmental conditions with elevated [CO<sub>2</sub>] and warmer soils may promote the recruitment and growth of mountain maple under forest canopies but limit its expansion into canopy gaps and open sites. Although seedling growth performance can be a good indicator of tree's response and future community composition (Anderson-Teixeira *et al.* 2013; Bazzaz 1996), the magnitude of responses in larger trees growing in natural environmental conditions can be different from that of seedlings in short-term treatments under controlled environments (Bond 2000; Cavender-Bares and Bazzaz 2000; Pritchard *et al.* 1999; Wieser *et al.* 2002). Therefore, precautions should be exercised when extrapolating the findings to field conditions or to larger trees.

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