

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

Gabriel Danyagri* and Qing-Lai Dang

Faculty of Natural Resources Management, Lakehead University, Thunder Bay, Ontario P7B 6 5E1, Canada

*Correspondence address. Faculty of Natural Resources Management, Lakehead University, Thunder Bay, Ontario P7B 5E1, Canada. Tel: (807) 343-8519; Fax: (807) 343-8116; E-mail: gdery@lakeheadu.ca

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_{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_{soil} and high T_{soil} , respectively. Under the elevated $[\text{CO}_2]$, however, the high-light level increased seedling height by 52% and 13% at the low T_{soil} and high T_{soil} , respectively. The responses of biomasses to light generally followed the response patterns of height growth under both $[\text{CO}_2]$ and T_{soil} and the magnitude of biomass response to light was the lowest under the elevated $[\text{CO}_2]$ and warmer T_{soil} . The results suggest that the elevated $[\text{CO}_2]$ and warmer T_{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 CO_2 , soil warming, light availability, height, biomass

Received: 18 April 2013, Revised: 5 October 2013,

Accepted: 9 November 2013

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 CO₂ and T_{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 [CO₂] 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 [CO₂], 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 [CO₂] enhance plant growth and biomass accumulation through its (CO₂) 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 [CO₂] 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 [CO₂] in *Acer pseudoplatanus*, *Quercus robur* and *Abies alba*. The enhanced growth responses to light under elevated [CO₂] could alter species distribution and composition in the ecosystem in the future.

T_{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_{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 CO₂ and T_{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_{soil} . We have tested the hypothesis that elevated [CO₂] 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 CO₂ (392 and

784 $\mu\text{mol mol}^{-1}$) with two independent replications for each level. The elevated [CO₂] (784 $\mu\text{mol mol}^{-1}$) was achieved using Argus CO₂ generators (Argus, Vancouver, BC, Canada). The subplot consisted of two T_{soil} (low 17°C and high 22°C) in each greenhouse. The low T_{soil} represents the mean T_{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_{soil} represents an assumed future T_{soil} if an increase of 5°C in T_{soil} occurs by end of 2100 (Christensen *et al.* 2007; IPCC 2007b). T_{soil} was achieved by circulating temperature-controlled water between pots in a T_{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_{soil} . The average natural light in the greenhouse was 710 $\mu\text{mol m}^{-2} \text{s}^{-1}$ on cloud-free days. Each T_{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_{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 CO₂, T_{soil} , light treatments and their interactions. Means were compared using Scheffé's *F* test at significant level of $P \leq 0.05$. *P* values ≤ 0.10 were considered marginally significant.

RESULTS

The interaction between [CO₂] and T_{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 [CO₂] and T_{soil} treatments, the magnitudes of increase in *H* and RCD in response to the high-light treatment were smallest in the combination of elevated [CO₂] and high T_{soil} and greatest in the combination of ambient [CO₂] and high T_{soil} (Fig. 1a and b). The elevated [CO₂] significantly increased *H* growth in all T_{soil} and light treatment combinations except in the high T_{soil} and high-light treatment combination where no significant [CO₂] effect on *H* was observed (Fig. 1a). The elevated [CO₂] significantly increased RCD in all T_{soil} and light combinations except in the low light and low T_{soil} where no significant [CO₂] effect on RCD was observed (Fig. 1b).

There was a marginally significant interactive effect of [CO₂], T_{soil} and light on the LA per seedling (Table 1). Under the ambient [CO₂], 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 ₂	T_{soil}	CO ₂ × T_{soil}	<i>L</i>	CO ₂ × <i>L</i>	T_{soil} × <i>L</i>	CO ₂ × T_{soil} × <i>L</i>
<i>H</i>	0.1159	0.0211	0.1366	≤ 0.0001	0.0123	0.0173	0.0353
RCD	0.0571	0.0004	0.8124	≤ 0.0001	0.3895	0.9751	0.0453
LA	0.2907	0.0148	0.5831	0.0288	0.1176	0.5634	0.0606
SLA	0.0030	0.2656	0.1889	≤ 0.0001	0.9208	0.0181	0.0598
LAR	0.0834	0.1430	0.1694	≤ 0.0001	0.4935	0.0608	0.0458
TB	0.0891	0.0021	0.3196	≤ 0.0001	0.1428	0.6795	0.0046
RSR	0.1629	0.3632	0.0289	≤ 0.0001	0.9494	0.2567	0.0176
RMR	0.0058	0.0288	0.1066	≤ 0.0001	0.9408	0.2235	0.0831
LMR	0.2865	0.1582	0.9103	≤ 0.0001	≤ 0.0001	0.0006	0.9951

Seedlings were grown at ambient (392 $\mu\text{mol mol}^{-1}$) or elevated (784 $\mu\text{mol mol}^{-1}$) [CO₂], low (17°C) or high (22°C) T_{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_{soil} . No significant LA response to high-light treatment was observed at low T_{soil} and ambient $[\text{CO}_2]$ (Fig. 1c). Under the elevated $[\text{CO}_2]$, LA was not significantly different

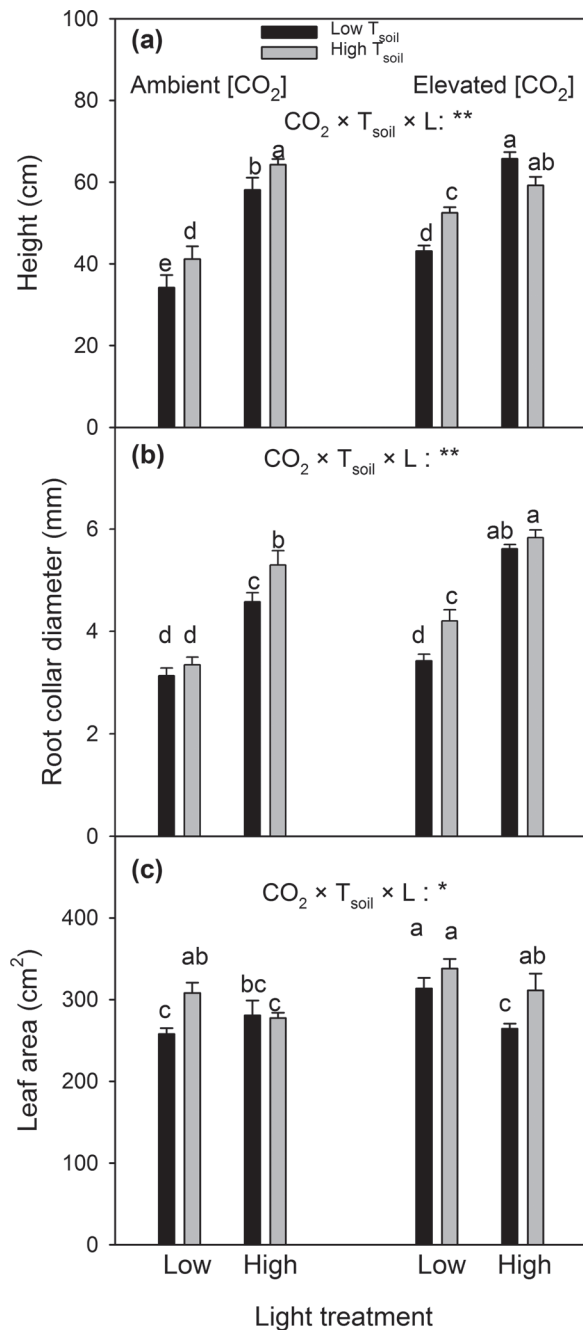


Figure 1: height (a), root collar diameter (b) and total leaf area (c) of mountain maple seedlings grown at low (shaded) or high (unshaded) light regime, ambient ($392 \mu\text{mol mol}^{-1}$) or elevated ($784 \mu\text{mol mol}^{-1}$) $[\text{CO}_2]$ and at low (17°C) or high (22°C) T_{soil} regime. 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_{soil} . However, LA was significantly lower in the high light at the low- T_{soil} treatment (Fig. 1c). Furthermore, the elevated $[\text{CO}_2]$ increased LA in the low-light treatment under the low T_{soil} and in the high-light treatment under the warmer T_{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_{soil} : under ambient $[\text{CO}_2]$, the high light decreased both LAR and SLA by 45% and 33%, respectively, at the low T_{soil} but decreased LAR and SLA by 63% and 58%, respectively, at the high T_{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_{soil} but decreased them by 53% at the high T_{soil} (Fig. 2a and b). The elevated $[\text{CO}_2]$ significantly decreased LAR at the warmer T_{soil} and low light and at the low T_{soil} and high-light treatments. No significant elevated CO_2 effect on LAR was observed at the low T_{soil} and low-light treatment. The elevated $[\text{CO}_2]$ decreased SLA only at the low T_{soil} and high-light treatment (Fig. 2a and b).

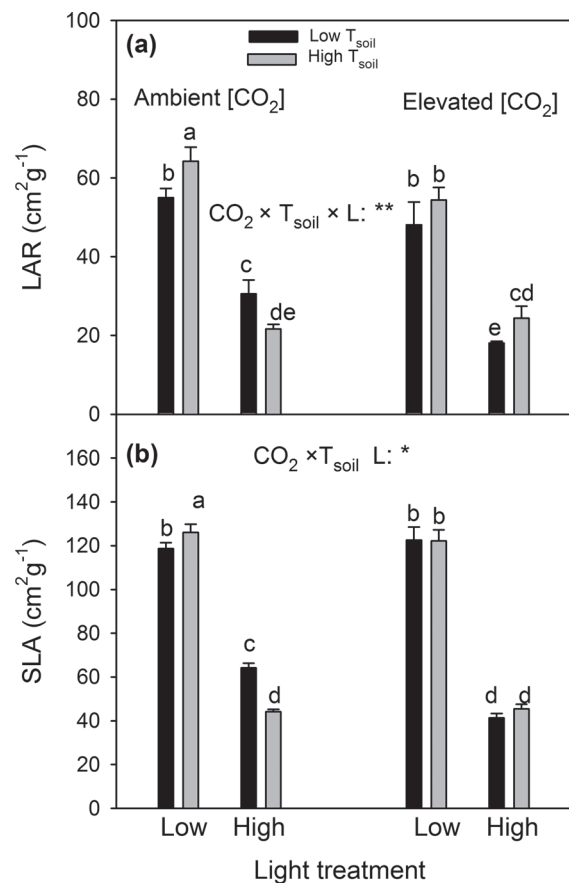


Figure 2: leaf area ratio (a) and specific leaf area (b) of mountain maple seedlings grown at low (shaded) or high (unshaded) light regime, ambient ($392 \mu\text{mol mol}^{-1}$) or elevated ($784 \mu\text{mol mol}^{-1}$) $[\text{CO}_2]$ and at low (17°C) or high (22°C) T_{soil} regime. Refer to Fig.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

The interaction between CO₂ and T_{soil} affected seedling biomass response to light (Table 1). While the high light generally increased seedling biomass at all [CO₂] and T_{soil} treatment combinations, the magnitude of biomass increase was greatest at the elevated [CO₂] and low- T_{soil} (197%) treatment combination but lowest under the elevated [CO₂] and high T_{soil} (105%, Fig. 3a). The high light significantly increased

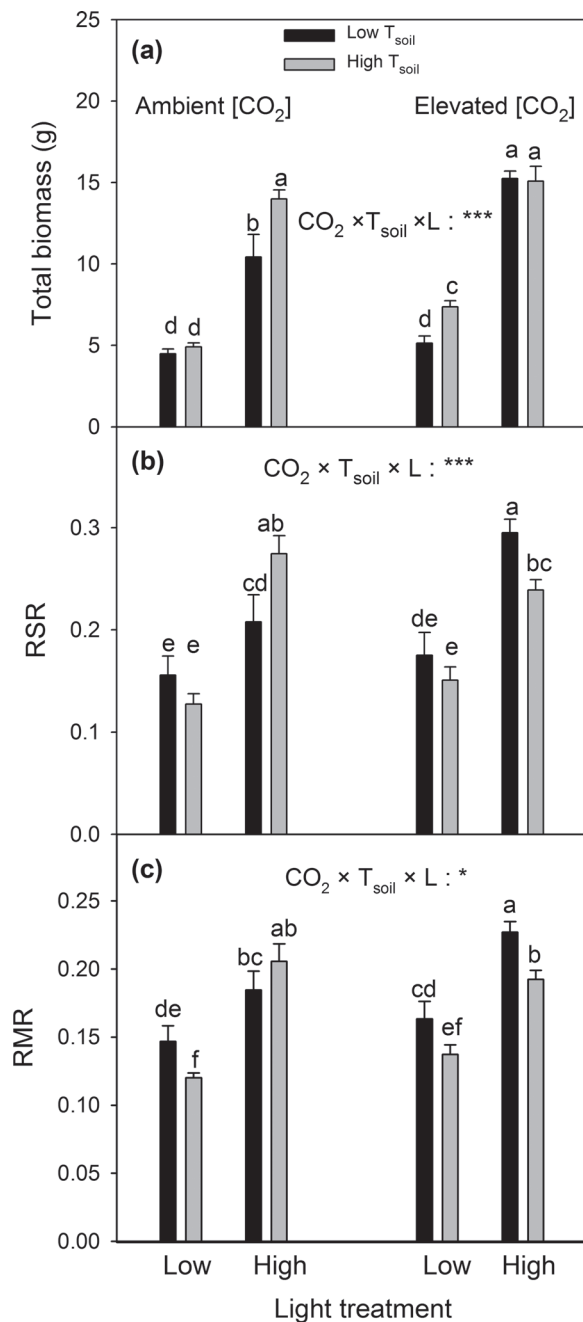


Figure 3: total biomass (a), root:shoot ratio (b) and root mass ratio (c) of mountain maple seedlings grown at low (shaded) or high (unshaded) light regime, ambient (392 $\mu\text{mol mol}^{-1}$) or elevated (784 $\mu\text{mol mol}^{-1}$) [CO₂] and low (17°C) and high (22°C) T_{soil} regime. Refer to Fig. 1 for other explanations.

seedling biomass in high- T_{soil} treatment under ambient [CO₂] but no significant effect under the elevated [CO₂]. The elevated [CO₂] increased seedling biomass at the warmer T_{soil} and low light and at the low T_{soil} and high-light treatment combinations (Fig. 3a). However, the [CO₂] did not affect biomass at the low T_{soil} and low light or at the warmer T_{soil} and high light (Fig. 3a).

The response of RSR to light was significantly affected by the interaction between CO₂ and T_{soil} (Table 1). The high light generally increased RSR at all [CO₂] and T_{soil} treatment combinations but the degree of the increase was greatest in T_{soil} treatment under ambient [CO₂] (116%) and lowest in low- T_{soil} treatment under ambient [CO₂] (34%, Fig. 3b). The elevated [CO₂] significantly increased RSR only at the low T_{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 [CO₂] and T_{soil} on the response of RMR to light (Table 1). While the high light generally increased RMR under both [CO₂] and T_{soil} treatments, the degree of the increase was greatest in the ambient [CO₂] and high- T_{soil} treatment combination and lowest in the ambient [CO₂] and low- T_{soil} treatment combination (Fig. 3c). The elevated [CO₂] significantly increased RMR only at the low T_{soil} in the high-light treatment (Fig. 3c).

The response of LMR to light was significantly affected by T_{soil} and [CO₂] but not by their interactions (Table 1). The high-light treatment generally decreased LMR at both T_{soil} treatments but the magnitude of decrease was greater at the low than at the high T_{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 [CO₂] but the reduction was greater under the ambient than under the elevated [CO₂] (-23% vs. -7%, Fig. 4b). The elevated [CO₂] significantly reduced LMR in the low light but increased it at the high light treatment (Fig. 4b).

DISCUSSION

The [CO₂] and T_{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_{soil} under the ambient [CO₂], second largest at the low T_{soil} under the elevated [CO₂] and the smallest increase (13%) was observed in the elevated [CO₂] and warmer T_{soil} combination. Similarly, the lowest biomass increase in response to high light was observed under elevated [CO₂] and warmer T_{soil} . The results contradict our hypothesis that mountain maple seedlings would show largest positive response to high light under elevated CO₂ 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

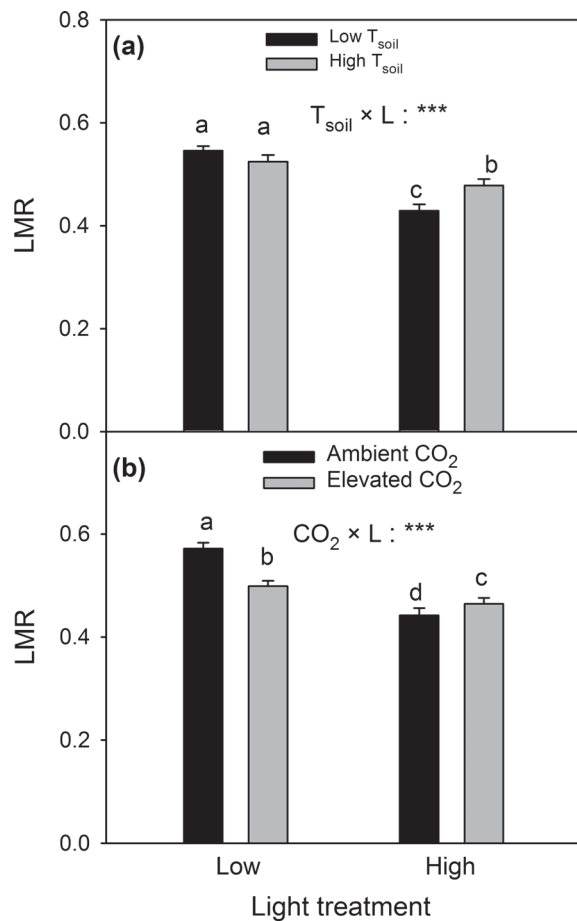


Figure 4: leaf mass ratio (a and b) of mountain maple seedlings grown at low (shaded) or high (unshaded) light regime, ambient ($392 \mu\text{mol mol}^{-1}$) or elevated ($784 \mu\text{mol mol}^{-1}$) CO_2 and low (17°C) or high (22°C) T_{soil} regime. a and b represent $T_{soil} \times L$ (data pooled 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 [CO₂]. Elevated [CO₂] 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 [CO₂] and soil warming acted interactively to reduce the degree of growth response to light in mountain maple. Given the continuous increase in the atmospheric [CO₂] 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_{soil} would benefit more from increases in [CO₂] than those growing on warmer sites. This effect and the finding that the beneficial effects of increased light were smaller under elevated [CO₂] and warmer soil temperature suggest that the future environmental conditions with elevated [CO₂] 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.

FUNDING

Natural Sciences and Engineering Research Council of Canada Discovery (Project # 203198-2008) grant to Q.-L.D.

ACKNOWLEDGEMENTS

We sincerely thank Ms Joan Lee for her technical support in setting up the experiment in the greenhouse.

Conflict of interest statement. None declared.

REFERENCES

- Adams RM, Rosenzweig C, Peart RM, *et al.* (1990) Global climate change and US agriculture. *Nature* **345**:219–24.
- Ambebe TF, Dang Q-L, Marfo J (2009) Low soil temperature reduces the positive effects of high nutrient supply on the growth and biomass of white birch seedlings in ambient and elevated carbon dioxide concentrations. *Botany* **87**:905–12.
- Ambebe TF, Danyagri G, Dang Q-L (2013) Low soil temperature inhibits the stimulatory effect of elevated [CO₂] on height and biomass accumulation of white birch seedlings grown under three non-limiting phosphorus conditions. *Nor J Bot* **31**:239–46.
- Anderson-Teixeira KJ, Miller AD, Mohan JE, *et al.* (2013) Altered dynamics of forest recovery under a changing climate. *Glob Change Biol* **19**:2001–21.
- Anten NPR, Hirose T (1998) Biomass allocation and light partitioning among dominant and subordinate individuals in *Xanthium canadense* stands. *Ann Bot* **82**:665–73.
- Archambault L, Morissette J, Bernier-Cardou M (1998) Forest succession over a 20-year period following clearcutting in balsam fir yellow birch ecosystems of eastern Quebec, Canada. *Forest Ecol Manage* **102**:61–74.
- Aubin I, Messier C, Kneeshaw D (2005) Population structure and growth acclimation of mountain maple along a successional gradient in the southern boreal forest. *Ecoscience* **12**:540–8.
- Bassirirad H (2000) Kinetics of nutrient uptake by roots: responses to global change. *New Phytol* **147**:155–69.
- Bazzaz FA (1996) *Plants in Changing Environment: Linking Physiology, Population, and Community Ecology*. Cambridge, UK: Cambridge University Press.
- Bazzaz FA, Miao SL (1993) Successional status, seed size, and responses of tree seedlings to CO₂, light, and nutrients. *Ecology* **74**:104–12.
- Bergeron Y (2000) Species and stand dynamics in the mixed woods of Quebec's southern boreal forest. *Ecology* **81**:1500–16.
- Bond BJ (2000) Age-related changes in photosynthesis of woody plants. *Trends Plant Sci* **5**:349–53.
- Boucher JF, Bernier PY, Munson AD (2001) Radiation and soil temperature interactions on the growth and physiology of eastern white pine (*Pinus strobus* L.) seedlings. *Plant Soil* **236**:165–74.
- Bowes GD (1991) Soil temperature, root growth, and plant function. In Eshel A, Kafafi U (eds). *Plant Roots, the Hidden Half*. New York, USA Marcel Dekker Inc, 309–30.
- Butler SM, Melillo JM, Johnson JE, *et al.* (2012) Soil warming alters nitrogen cycling in a New England forest: implications for ecosystem function and structure. *Oecologia* **168**:819–28.
- Canham CD, Berkowitz AR, Kelly VR, *et al.* (1996) Biomass allocation and multiple resource limitation in tree seedlings. *Can J For Res* **26**:1521–30.
- Catovsky S, Bazzaz FA (1999) Elevated CO₂ influences the responses of two birch species to soil moisture: implications for forest community structure. *Glob Change Biol* **5**:507–18.

- Cavender-Bares J, Bazzaz FA (2000) Changes in drought response strategies with ontogeny in *Quercus rubra*: implications for scaling from seedlings to mature trees. *Oecologia* **124**:8–18.
- Cheng S, Dang Q-L, Cai T-B (2000) A soil temperature control system for ecological research in greenhouses. *J For Res* **5**:205–8.
- Christensen JH, Hewitson B, Busuioac A, *et al.* (2007) Regional climate projections. In Solomon S, Qin D, Manning M, *et al.* (eds). *Climate Change 2007: the Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, UK: Cambridge University Press.
- Curtis PS, Wang X (1998) A meta-analysis of elevated CO₂ effects on woody plant mass, form, and physiology. *Oecologia* **113**:299–313.
- Dawes MA, Hagedorn F, Zumbrunn T, *et al.* (2011) Growth and community responses of alpine dwarf shrubs to in situ CO₂ enrichment and soil warming. *New Phytol* **191**:806–18.
- DeLucia EH, Heckathorn SA, Day TA (1992) Effects of soil temperature on growth, biomass allocation and resource acquisition of *Andropogon gerardii* vitman. *New Phytol* **120**:543–9.
- Domisch T, Finér L, Lehto T (2001) Effects of soil temperature on biomass and carbohydrate allocation in Scots pine (*Pinus sylvestris*) seedlings at the beginning of the growing season. *Tree Physiol* **21**:465–72.
- Drake BG, Gonzalez-Meler MA, Long SP (1997) More efficient plants: a consequence of rising atmospheric CO₂? *Annu Rev Plant Physiol Plant Mol Biol* **48**:609–39.
- Givnish T (1988) Adaptation to sun and shade: a whole-plant perspective. *Funct Plant Biol* **15**:63–92.
- Hättenschwiler S, Körner C (2000) Tree seedling responses to in situ CO₂-enrichment differ among species and depend on understorey light availability. *Glob Change Biol* **6**:213–26.
- Hobbie SE (1996) Temperature and plant species control over litter decomposition in Alaskan tundra. *Ecol Monogr* **66**:503–22.
- Houghton JT, Callander BA, Varney SK (1992) *Climate Change 1992. The Supplementary Report to the IPCC Scientific Assessment*. Cambridge, UK: Cambridge University Press.
- Ingestad T (1981) Nutrition and growth of birch and grey alder seedlings in low conductivity solutions and at varied relative rates of nutrient addition. *Physiol Plant* **52**:454–66.
- IPCC (2001) *Climate Change 2001: An Assessment of the Intergovernmental Panel on Climate Change*. Cambridge, UK: Cambridge University Press.
- IPCC (2007a) *Climate Change 2007: Synthesis Report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Geneva, Switzerland: IPCC, 1–18.
- IPCC (2007b) Summary for policymakers. In Solomon S, *et al.* (eds). *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, UK: Cambridge University Press, 849–926.
- Jansson PE, Berg B (1985) Temporal variation of litter decomposition in relation to simulated soil climate. Long-term decomposition in a scots pine forest. *Can J Bot* **63**:1008–16.
- Karlsson PS, Nordell KO (1996) Effects of soil temperature on the nitrogen economy and growth of mountain birch seedlings near its presumed low temperature distribution limit. *Ecoscience* **3**:183–9.
- Krause GH, Koroleva OY, Dalling JW, *et al.* (2001) Acclimation of tropical tree seedlings to excessive light in simulated tree-fall gaps. *Plant Cell Environ* **24**:1345–52.
- Kubin E, Kemppainen L (1991) Effect of clearcutting of boreal spruce forest on air and soil temperature conditions. *Acta For Fenn* **225**:1–25.
- Kubiske ME, Pregitzer KS (1997) Ecophysiological responses to simulated canopy gaps of two tree species of contrasting shade tolerance in elevated CO₂. *Funct Ecol* **11**:24–32.
- Lambers H, Chapin SF III, Pons TL (2008) *Plant Physiological Ecology*. New York: Springer.
- Lambers H, Poorter H (1992) Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. In Begon M, Fitter AH (eds). *Advances in Ecological Research*, Vol. **23**. San Diego, USA: Academic Press, 187–261.
- Lei TT, Lechowicz MJ (1990) Shade adaptation and shade tolerance in saplings of three *Acer* species from eastern north America. *Oecologia* **84**:224–8.
- Lei TT, Lechowicz MJ (1997) Functional responses of *Acer* species to two simulated forest gap environments: leaf-level properties and photosynthesis. *Photosynthetica* **33**:277–89.
- Liang N, Tang Y, Okuda T (2001) Is elevation of carbon dioxide concentration beneficial to seedling photosynthesis in the understory of tropical rain forests? *Tree Physiol* **21**:1047–55.
- MacDonald NW, Zak DR, Pregitzer KS (1995) Temperature effects on kinetics of microbial respiration and net nitrogen and sulfur mineralization. *Soil Sci Soc Am J* **59**:233–40.
- Meehl GA, Arblaster JM, Tebaldi C (2007) Contributions of natural and anthropogenic forcing to changes in temperature extremes over the united states. *Geophys Res Lett* **34**:L19709.
- Melillo JM, Butler S, Johnson J, *et al.* (2011) Soil warming, carbon-nitrogen interactions, and forest carbon budgets. *Proc Natl Acad Sci U S A* **108**:9508–12.
- Melillo JM, Steudler PA, Aber JD, *et al.* (2002) Soil warming and carbon-cycle feedbacks to the climate system. *Science* **298**:2173–6.
- Naumburg E, Ellsworth DS (2000) Photosynthetic sunfleck utilization potential of understory saplings growing under elevated CO₂ in face. *Oecologia* **122**:163–74.
- Norby RJ, O'Neill EG (1991) Leaf area compensation and nutrient interactions in CO₂-enriched seedlings of yellow-poplar (*Liriodendron tulipifera* L.). *New Phytol* **117**:515–28.
- Osborne CP, Drake BG, LaRoche J, *et al.* (1997) Does long-term elevation of CO₂ concentration increase photosynthesis in forest floor vegetation? (Indiana strawberry in a Maryland forest). *Plant Physiol* **114**:337–44.
- Pearcy RW, Sims DA (1994) Photosynthetic acclimation to changing light environments: scaling from the leaf to the whole plant. In Caldwell MM, Pearcy RW (eds). *Exploitation of Environmental Heterogeneity by Plants. Ecophysiological Processes Above- and Belowground*. San Diego, USA: Academic Press, Inc, 145–70.
- Peng YY, Dang Q-L (2003) Effects of soil temperature on biomass production and allocation in seedlings of four boreal tree species. *For Ecol Manage* **180**:1–9.
- Poorter H, Niklas KJ, Reich PB, *et al.* (2012) Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. *New Phytol* **193**:30–50.
- Poorter H, Remkes C (1990) Leaf area ratio and net assimilation rate of 24 wild species differing in relative growth rate. *Oecologia* **83**:553–9.

- Pregitzer KS, King JS (2005) Effects of soil temperature on nutrient uptake. In BassiriRad H (ed). *Nutrient Acquisition by Plants*. Heidelberg, Germany: Springer-Verlag Berlin, 277–310.
- Pritchard SG, Rogers HH, Prior SA, *et al.* (1999) Elevated CO₂ and plant structure: a review. *Glob Change Biol* **5**:807–37.
- Ray D, Dey SK, Das G (2004) Significance of the leaf area ratio in *Hevea brasiliensis* under high irradiance and low temperature stress. *Photosynthetica* **42**:93–7.
- Rennenberg H, Loreto F, Polle A, *et al.* (2006) Physiological responses of forest trees to heat and drought. *Plant Biol (Stuttg)* **8**:556–71.
- Rice SA, Bazzaz FA (1989) Growth consequences of plasticity of plant traits in response to light conditions. *Oecologia* **78**:508–12.
- Rincon E, Grime JP (1989) Plasticity and light interception by six bryophytes of contrasted ecology. *J Ecol* **77**:439–46.
- Rook EJS (2002) Shrubs of the Northwoods. <http://www.Rook.Org/earl/bwca/nature/shrubs/index.html> (4 April 2012, date last accessed).
- Roumet C, Roy J (1996) Prediction of the growth response to elevated CO₂: a search for physiological criteria in closely related grass species. *New Phytol* **134**:615–21.
- Rustad LE, Campbell JL, Marion GM, *et al.* (2001) A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia* **126**:543–62.
- Semchenko M, Lepik M, Götzenberger L, *et al.* (2012) Positive effect of shade on plant growth: amelioration of stress or active regulation of growth rate? *J Ecol* **100**:459–66.
- Sitch S, Huntingford C, Gedney N, *et al.* (2008). Evaluation of the terrestrial carbon cycle, future plant geography and climate-carbon cycle feedbacks using five dynamic global vegetation models (DGVMS). *Glob Change Biol* **14**:2015–39.
- Stoneman GL, Dell B (1993) Growth of *Eucalyptus marginata* (Jarrah) seedlings in a greenhouse in response to shade and soil temperature. *Tree Physiol* **13**:239–52.
- Sullivan J (1993) *Acer spicatum*. In U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. Fire sciences laboratory. Fire effects information system. <http://www.Fs.Fed.U.S/database/feis/> (25 April 2012, date last accessed).
- Tamm CO (1991) *Nitrogen and Terrestrial Ecosystems*. Heidelberg, Germany: Springer-Verlag Berlin.
- Temperton VM, Grayston SJ, Jackson G, *et al.* (2003) Effects of elevated carbon dioxide concentration on growth and nitrogen fixation in *Alnus glutinosa* in a long-term field experiment. *Tree Physiol* **23**:1051–9.
- Walker MD, Wahren CH, Hollister RD, *et al.* (2006) Plant community responses to experimental warming across the tundra biome. *Proc Natl Acad Sci U S A* **103**:1342–6.
- Ward SJE, Midgley GF, Jones MH, *et al.* (1999) Responses of wild C₄ and C₃ grass (*Poaceae*) species to elevated atmospheric CO₂ concentration: a meta-analytic test of current theories and perceptions. *Glob Change Biol* **5**:723–41.
- Weih M, Karlsson PS (2001) Growth response of mountain birch to air and soil temperature: is increasing leaf-nitrogen content an acclimation to lower air temperature? *New Phytol* **150**:147–55.
- Wieser G, Tegischer K, Tausz M, *et al.* (2002) Age effects on Norway spruce (*Picea abies*) susceptibility to ozone uptake: a novel approach relating stress avoidance to defense. *Tree Physiol* **22**:583–90.
- Wigley TM (2005) The climate change commitment. *Science* **307**:1766–9.
- Zhou Y, Tang J, Melillo JM, *et al.* (2011) Root standing crop and chemistry after six years of soil warming in a temperate forest. *Tree Physiol* **31**:707–17.