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P.M. Wayne · E.G. Reekie · F.A. Bazzaz

Elevated CO_2 ameliorates birch response to high temperature and frost stress: implications for modeling climate-induced geographic range shifts

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Abstract Despite predictions that both atmospheric CO_2 concentrations and air temperature will rise together, very limited data are currently available to assess the possible interactive effects of these two global change factors on temperate forest tree species. Using yellow birch (*Betula alleghaniensis*) as a model species, we studied how elevated CO_2 (800 vs. 400 $\mu l\ l^{-1}$) influences seedling growth and physiological responses to a 5°C increase in summer air temperatures (31/26 vs. 26/21°C day/night), and how both elevated CO_2 and air temperature during the growing season influence seedling ability to survive freezing stress during the winter dormant season. Our results show that while increased temperature decreases seedling growth, temperature-induced growth reductions are significantly lower at elevated CO_2 concentrations (43% vs. 73%). The amelioration of high-temperature stress was related to CO_2-induced reductions in both whole-shoot dark respiration and transpiration. Our results also show that increased summer air temperature, and to a lesser degree CO_2 concentration, make dormant winter buds less susceptible to freezing stress. We show the relevance of these results to models used to predict how climate change will influence future forest species distribution and productivity, without considering the direct or interactive effects of CO_2.

Key words *Betula* · Carbon dioxide · Climate change · heat stress · Freezing stress

P.M. Wayne (✉) · F.A. Bazzaz
Department of Organismic and Evolutionary Biology,
Harvard University, 16 Divinity Ave,
Cambridge, MA 02138, USA
fax: +1-617-495-9300; e-mail: pwayne@oeb.harvard.edu

E.G. Reekie
Department of Biology, Acadia University,
Wolfville, Nova Scotia, BOP 1XO, Canada

Introduction

Increasing evidence suggests that rising atmospheric concentrations of CO_2 and other greenhouse gases will substantially alter the global climate within the next 100 years. Though there is still much uncertainty regarding the exact magnitudes and geographical patterns of these climate changes, most general circulation models (GCMs) predict increases in average air temperatures between 1.5 and 4.5°C, as well as changes in patterns of precipitation (Houghton et al. 1996). Even relatively conservative estimates of a 3°C temperature increase would result in average global temperatures warmer than any the earth has experienced in the past 100,000 years (Schneider and Londer 1984), with climate changes occurring at least an order of magnitude faster than those induced by the most recent glacial episode (Gleick et al. 1990).

Changes in climate forecasted by GCMs are expected to significantly alter the future productivity and distributions of temperate forest tree species (e.g., Pastor and Post 1988; Davis and Zabinski 1992; Gates 1993). Paleoecological evidence has shown that as air temperature and precipitation patterns changed historically, forest species died out in areas that became unsuitable, and migrated in latitude and altitude to newly suitable habitats (Delcourt and Delcourt 1987). Understanding how present temperate forests will respond to future CO_2-induced climate change is important for a number of reasons. First, because temperate forests are an important terrestrial carbon sink (Wofsy et al. 1993; Tans et al. 1995), climate-induced decreases in productivity could have a significant positive feedback effect on atmospheric concentrations of CO_2– further increasing rates of greenhouse warming (Houghton 1991). Second, differential mortality and migrational responses of tree species to climate change may result in forest communities with novel compositions of plant and associated animal species, with many consequences to biodiversity and other conservation issues (Huntly 1991; Hughes and

Westoby 1994). Finally, CO_2-induced climate change may necessitate changes in forest ecosystem and silvicultural management practices (Sandenberg et al. 1987; Grahm et al. 1990).

Several different modeling approaches have been employed to predict the responses of forest species (and communities) to CO_2-induced climate change. These include climatic correlation (or climatic envelope) analyses (e.g., Davis and Zabinski 1992; Hughes et al. 1996), various physiological- and patch-level forest dynamics models (e.g., Solomon 1986; Pastor and Post 1988; Smith et al. 1992; Shao et al. 1995), and models based on empirical, long-term reciprocal transplant studies (e.g. Matyas 1994; Schmidtling 1994). While each of these approaches has its merits and disadvantages, all primarily focus on the effects of climate change. Few consider either the direct effects of CO_2, or how CO_2 will modify forest responses to climatic variables (but see Solomon 1988). Because a growing number of studies suggest that CO_2 can alter plant growth and physiological responses to a number of climatic factors such as air temperature (e.g., Bassow et al. 1994; Callaway et al. 1994; Repo et al. 1996) and soil moisture availability (e.g., Miao et al. 1992; Guehl et al. 1994; Townend 1995), a better understanding of how CO_2 influences forest tree responses to climatic factors should significantly improve our ability to predict and manage their future distribution and productivity.

Yellow birch (*Betula alleghaniensis*), because of its ecological and economic importance throughout northeastern North America (Burns and Honkala 1990), has been used as a model species in many recent CO_2 and climate change studies (e.g., Solomon 1986; Bazzaz et al. 1993; Bolker et al. 1995; Wayne and Bazzaz 1995; Berntson et al. 1997). Davis and Zabinski (1992) characterized the climatic envelope for the present distribution of yellow birch. Like other co-occurring species, they found that the southern boundaries of birch appear to be primarily limited by a combination of high summer temperatures and limited precipitation. In contrast, northern distributions appear to be primarily limited by cold winter temperatures. Using these correlations, along with a relatively conservative scenario of climate change (GISS model; Hansen et al. 1988), they predicted that some parts of the yellow birch current range would be shifted northward by more than 500 km. However, without a better understanding of how CO_2 will influence yellow birch responses to the climatic factors that limit its productivity and distribution, it is difficult to predict with any certainty how birch, or other temperate species, will respond to climate change.

This study investigates how rising CO_2 influences the responses of yellow birch seedlings to both elevated air temperatures during the summer growing season, and to freezing temperatures during the winter dormant season. We specifically address the following questions. (1) To what extent will a 5°C increase in diurnal air temperatures influence the growth, gas exchange and water use efficiency of yellow birch seedlings? (2) Do elevated atmospheric CO_2 concentrations modify growth and physiological responses to high summer air temperatures? (3) Does growing season air temperature and CO_2 concentration alter the freezing tolerance (survivorship) of dormant winter buds?

Materials and methods

Yellow birch (*B. alleghaniensis*) seed were collected from three distinct populations in both Quebec, Canada and Massachusetts, USA, during the fall of 1993. At each of the six sites, a minimum of three trees were sampled. We chose these six distinct, geographically isolated populations to increase the scope of inference of this study, i.e., to insure that any conclusions regarding the effects of CO_2 and temperature apply not only to a single population, but to a broad range of yellow birch populations. The geographic and altitudinal origin of each of the six populations is presented in Table 1.

On 6 April 1994, seed from each of the six populations were sown into horticultural starter trays with 2.5 cm diameter × 5.1 cm deep cells. On 25 May, when plants had at least one true leaf, seedlings (including undisturbed soil plugs) were transplanted into 1.0-l (15.3-cm diameter) plastic growth containers. Both starter trays and growth containers were filled with a 2:1:1 mixture of mineral soil: peat:sieved organic soil (O2 layer) collected from the Harvard forest. The organic soil, including conspicuously ectomycorrhizal infected roots that were chopped up, was used as a mycorrhizal inoculum as in other studies with birch (e.g., Berntson et al. 1997).

Twelve 1.0 × 1.0 × 2.0 m glass cabinets were used to maintain four combinations of CO_2 and air temperature (three replicate chambers per treatment) during the growing season. CO_2 levels were maintained at either 400 or 800 µl l^{-1} using a Licor 6251 IRGA controlled by a computer-driven monitoring and injection system. Air temperatures were maintained at day/night tempera-

Table 1 Geographic location of six yellow birch populations used for seed collection in this study. *n* represents number of maternal trees pooled to represent a given population. Sample sizes for Quebec populations are unknown, but greater than three (Ministry of Forestry, personal communication)

	N	Latitude	Longitude	Altitude (m)
Massachussetts USA				
M1: Wachussetts St. Park	3	42°30′30″	71°48′0″	380
M2: Harvard Forest	6	42°30′45′	72°12′30″	360
M3: Savoy Forest	4	42°36′30″	73°24′30″	450
Quebec. Canada				
C1: St. Gerard	3+	46°51′0″	71°56′45″	230
C2: Lac Remi	3+	46°03′45″	75°46′30″	225
C3: Ste-Anne-du Lac	3+	47°04′30″	79°16′0″	250

ture regimes (16 h day) of either 26/21 or 31/26°C. Natural light was supplemented with metal halide lamps over each chamber, resulting in minimum PAR levels of 350 μmol m^{-2} s^{-1} on overcast days. Relative humidity was maintained near 70% across all treatments. Plants were watered daily and fertilized weekly with 200 ml of Peter's nutrient solution (20:20:20 N.P.K with micronutrients). Both the locations of treatments among chambers, and the locations of individual plants within chambers were randomized on a weekly basis.

Growth measurements

Thirty-six seedlings from each of the six populations were randomly allocated to each of the four CO_2 × temperature treatments. To estimate growth responses (biomass, leaf area) to these treatments, one third of all plants were harvested on both 8 June (harvest 1, H1) and 27 June (harvest 2, H2), 1994—40 and 61 days, respectively, following emergence. Average relative growth rate (RGR) between these two harvests was calculated as:

$$\frac{\ln W_2 - \ln W_1}{t_2 - t_1}$$

where W_1 and W_2 are the biomass (roots and shoots) of plants at harvests 1 and 2, and t_1 and t_2 are plant ages at harvests 1 and 2, respectively. RGR was calculated separately for each CO_2 × temperature × population × chamber combination. Seedling standing leaf area was measured using a Licor LAI 2000 leaf area meter. Seedling biomass was oven dried at 70°C, and weighed to the nearest 10^{-4} g.

Physiological measurements

Whole-shoot dark respiration was measured on 28 June using a Licor 6250 gas exchange system attached to a cuvette tooled from a section of opaque PVC pipe. The dimensions of the cuvette were 25.0 cm diameter and 25.3 cm length. The top of the cuvette was sealed with a fitted PVC cap. The bottom was sealed by mounting it on a machine-tooled stand with fitted grooves to match the cuvette dimensions. To assure a tight seal at the base, grooves were filled with vacuum grease. In addition to mounting the Licor 6250 sensor head within the cuvette, additional fans were added to assure adequate mixing of air. Prior to measurements, plants were dark acclimated for an average of 60 min at their growth temperatures. Following acclimation, entire shoots were cut at the soil surface, and immediately placed into the cuvette for measurements. On 6 July, light-saturated leaf-level net photosynthesis was measured using a Licor 6250 gas exchange system attached to a standard 0.25-l chamber. For these measurements, the youngest, fully developed leaves on undisturbed shoots were used. All respiration and photosynthesis measurements were made at the respective CO_2 and temperature seedling treatment levels.

To estimate seedling-level transpiration rate and water use efficiency (WUE) seedling water loss was measured lysimetrically over a 48-h period. Two days prior to destructive harvest 2, growth container soils were well watered and then sealed with plastic attached to both the growth container walls and the base of seedling stems to prevent soil evaporation. Pots were weighed before and after the 48-h period. Average 24-h transpiration rates (g cm^{-2} d^{-1}) were estimated by dividing average daily water loss by total standing leaf area at H2. To estimate whole-plant WUE (g biomass g^{-1} H_2O loss), measures of daily water loss were compared to estimates of daily carbon gain (estimated using average RGR between H1 and H2).

Seedling growth, WUE and gas exchange measurements were analyzed using ANOVA. In the ANOVA model, the *F*-values for CO_2, temperature, and their interaction were assessed using the block × CO_2 × temperature effect as the error term. The effects of population origin, and its two- and three-way interactions with CO_2 and temperature were also included in the model, but as the different populations were only included in the present study to increase our scope of inference, these effects are not discussed here. To meet the assumptions of ANOVA, the biomass and leaf area data were transformed prior to analysis by taking either the natural logarithm (biomass) or square root (leaf area) of the observations.

Winter-freezing stress resistance

One cohort of plants in all treatments ($n = 18$) was allowed to complete an entire season of growth. Beginning in mid-October, day and night air temperatures in all treatments were reduced by 5°C per week to stimulate dormancy processes. When plants had senesced the majority of their leaves, and buds had hardened, all seedlings were relocated to an outdoor experimental garden (Harvard University, Cambridge, Mass.) where they experienced ambient air temperatures and CO_2 concentrations throughout the fall and winter. In mid-March, before buds showed signs of swelling, stem segments including a minimum of three buds were cut and immediately wrapped in cellophane to prevent desiccation. Stem segments were all chosen from lateral branches (i.e. no leader stems), and did not include apical buds. Immediately following cutting, stem segments were brought into the laboratory where they were exposed to a 16-h freeze-down cycle using a programmable, cooled-air freezer (Tenney Engineering, Union, N.J.) The freezing cycle was designed to simulate a cold night. All stem segments were placed in the freezer at +5°C and allowed to acclimate to this temperature for 1 h. During the second hour, all tissues were gradually chilled to 0°C, and then maintained at 0°C for another hour. This process continued for 16 h until temperatures reached −35°C. At four temperatures during the freezing cycle (−20, −25, −30, −35°C), cohorts of stem segments ($n = 3$ per growth treatment) were removed and returned to a +5°C refrigerator. The following day, all bud segments were vertically sown into vermiculite trays on a climate-controlled horticultural bench (26/20°C day/night) with an automated misting system. After 45 days, bud survivorship was visually assessed by either the presence of emerging green foliage, or if buds had not yet broken, by the clear presence of green embryonic leaves upon dissection. The proportion of buds on a given shoot that were viable was used as the dependent variable in a factorial ANOVA, with CO_2, growth temperature, population and depth of freezing as independent variables. The data were transformed prior to analysis by taking the arcsine of the square root of the dependent variable.

Results

Seedling growth

After 60 days of growth (harvest 2, H2), standing biomass of yellow birch seedlings was significantly reduced by a 5°C increase in diurnal air temperatures, and significantly increased by elevated CO_2 concentrations (Table 2, Fig. 1). Additionally, elevated CO_2 significantly ameliorated the negative effects of high temperature on standing biomass (CO_2 × temperature, $P = 0.017$). At low CO_2 levels, a 5°C increase in temperature resulted in a 73% growth reduction, whereas at high CO_2 levels, temperature-induced reductions in biomass were only 43%. Qualitatively similar patterns were observed for standing leaf area at H2, as well as for both standing biomass and leaf area at H1 (Table 2). Average RGRs of biomass between H1 and H2, used for estimating whole-plantWUE, are shown in Table 2.

Table 2 Growth responses of yellow birch seedlings after 40 (*H*1) and 61 (*H*2) days of growth in low and high day/night temperature (*T*) regimes (26/21 and 31/26°C) and low and high atmospheric CO_2 concentrations (400 and 800 µl l^{-1}). Values for ln(biomass) and sqrt(leaf area) represent means ($n = 18$); values in parentheses represent ±1 se (RGR relative growth rate)

Character	Treatment				Significance values		
	26/21°C 400 µl l^{-1}	31/26°C 400 µl l^{-1}	26/21°C 800 µl l^{-1}	31/26°C 800 µl l^{-1}	T	CO_2	T × CO_2
Ln (total biomass)							
H1	−1.704 (0.064)	−2.5591 (0.017)	−1.177 (0.065)	−1.769 (0.077)	***	***	*
H2	1.357 (0.073)	0.0009 (0.119)	1.745 (0.124)	1.216 (0.107)	***	***	***
Sqrt (total leaf area)							
H1	5.55 (0.18)	3.36 (0.21)	6.24 (0.20)	4.63 (0.26)	***	***	ns
H2	24.20 (0.96)	12.65 (0.71)	28.40 (1.72)	21.85 (1.08)	***	***	*
RGR biomass							
H1 − 2	0.163 (0.007)	0.136 (0.007)	0.154 (0.007)	0.158 (0.007)	ns	ns	ns

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; *NS* $P > 0.05$

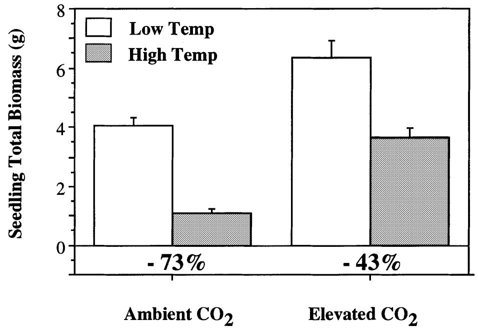

Fig. 1 Biomass growth responses of yellow birch seedlings after 61 days of exposure to a 5°C increase in air temperature at both near-ambient (400 µl l^{-1}) and elevated (800 µl l^{-1}) CO_2 concentrations. Percentages beneath paired open and shaded bar graphs refer to the magnitude of temperature-induced growth reductions within each CO_2 treatment. *Error bars* represent 1 SE; $n = 18$ per treatment

Gas exchange

The response of whole-shoot respiration (expressed on a weight basis; µmol g^{-1} s^{-1}) to temperature and CO_2 paralleled growth. Higher temperatures significantly stimulated respiratory carbon loss (temperature, $P = 0.035$; Fig. 2). Furthermore, elevated CO_2 also ameliorated the negative effects of temperature on respiration. At low CO_2 , respiration was increased by 174%, whereas at elevated CO_2 concentrations, the temperature-induced increase in respiration was only 13% (CO_2 × temperature $P = 0.068$).

Leaf-level net photosynthesis (µmol m^{-2} s^{-1}) was slightly, but significantly reduced by increased temperatures, and significantly stimulated by elevated CO_2 concentrations (CO_2, $P = 0.0001$, temperature $P = 0.017$; Fig. 2). However, unlike growth and respiration, there was no significant interaction between CO_2 and temperature on net photosynthesis; CO_2 did not compensate for the negative effects of increased temperature.

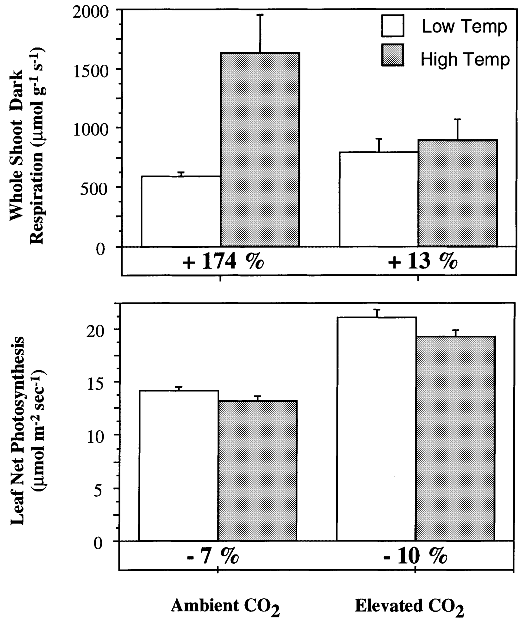

Fig. 2 Whole-shoot dark respiration and leaf net photosynthesis of yellow birch seedlings after 61 days of exposure to a 5°C increase in air temperature at both near-ambient (400 µl l^{-1}) and elevated (800 µl l^{-1}) CO_2 concentrations. Percentages beneath paired open and shaded bar graphs refer to the magnitude of temperature-induced increases or decreases in gas exchange parameters within each CO_2 treatment. Error bars represent 1 SE; $n = 18$ per treatment

Water relations

Whole-plant transpiration rates were significantly increased by temperature, and decreased by CO_2 ($P < 0.001$; Fig. 3). Paralleling respiration responses, CO_2 significantly ameliorated the negative effects of temperature on water loss (CO_2 × temperature $P = 0.019$). When water loss was compared to seedling carbon gain (i.e., WUE), similar patterns to transpiration were observed. Namely, WUE was reduced by higher temperatures and increased by elevated CO_2 ($P < 0.001$; Fig. 3). Elevated CO_2 also appeared to reduce the magnitude of the negative effect of higher temperatures, but the interaction between CO_2 and temperature was not significant at the $P = 0.05$ level.

Responses to winter freezing stress

The survivorship of buds following a simulated freezing night was influenced by growing season CO_2 and temperature levels (Fig. 4). In general, plants grown at lower growing season temperatures were not as freeze resistant as plants grown at a higher temperatures ($P < 0.01$). However, the magnitude of this effect varied depending on the level of CO_2 ($CO_2 \times$ temperature, $P < 0.05$). At low CO_2 levels, the difference between plants grown at different temperatures was marked, while the difference was marginal at higher temperatures.

There were no significant differences between populations from northern versus southern latitudes for any of the growth and physiological parameters measured, although there were a few small differences for some traits when all populations were pooled (data not presented).

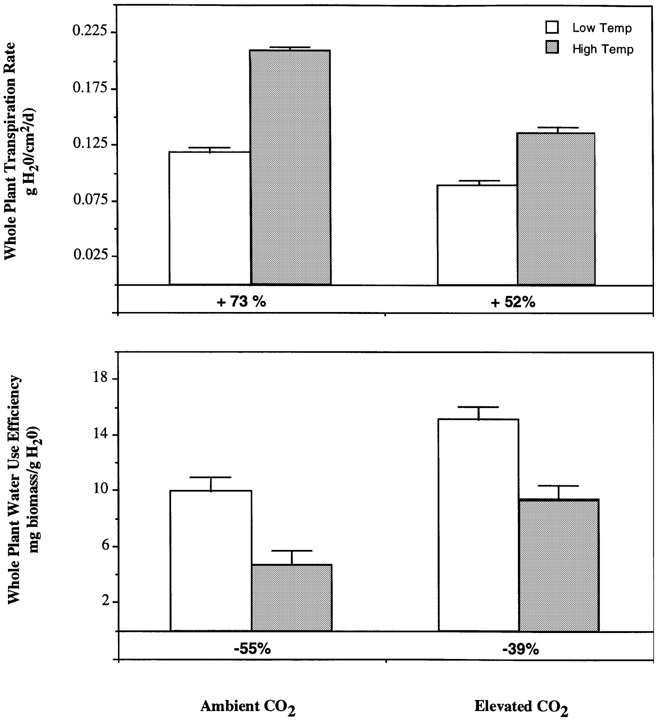

Fig. 3 Whole-plant transpiration and water use efficiency (WUE) of yellow birch seedlings exposed to a 5°C increase in air temperature at both near-ambient (400 µl l^{-1}) and elevated (800 µl l^{-1}) CO_2 concentrations. See text for methods employed in calculating WUE. *Error bars* represent 1 SE; $n = 18$ per treatment

Discussion

Plant growth responses to supra-optimal high temperatures in CO_2-enriched atmospheres

Empirical studies, largely conducted with herbaceous species, have demonstrated that the magnitude of plant responses to elevated CO_2 are contingent upon temperature (i.e., not additive), generally increasing (e.g., Imai et al. 1985; Idso et al. 1987; Patterson et al. 1988; Callaway et al. 1994; Greer et al. 1995), but sometimes decreasing (Morison and Gifford 1984a,b;, Rawson 1992; Tremmel and Patterson 1993) with higher temperatures. However, most of these studies have not included supra-optimal high temperatures, and thus have not been able to assess the degree to which CO_2 enrichment can ameliorate the effects of high-temperature stress. The results of a few studies that have included supra-optimal high temperatures are insufficient to draw strong conclusions (e.g., Kriedeman et al. 1976; Ziska and Bunce 1993; Morse and Bazzaz 1994; Rawson 1995). Our results with yellow birch demonstrating that a doubling of CO_2 can decrease temperature-induced growth reductions from 73% to 43% are relatively novel for temperate forest trees.

For yellow birch seedlings in the present study, the responses of whole-shoot dark respiration to elevated temperatures and CO_2 paralleled growth responses. Namely, temperature stimulated respiratory carbon loss, but significantly less so at elevated versus near-ambient

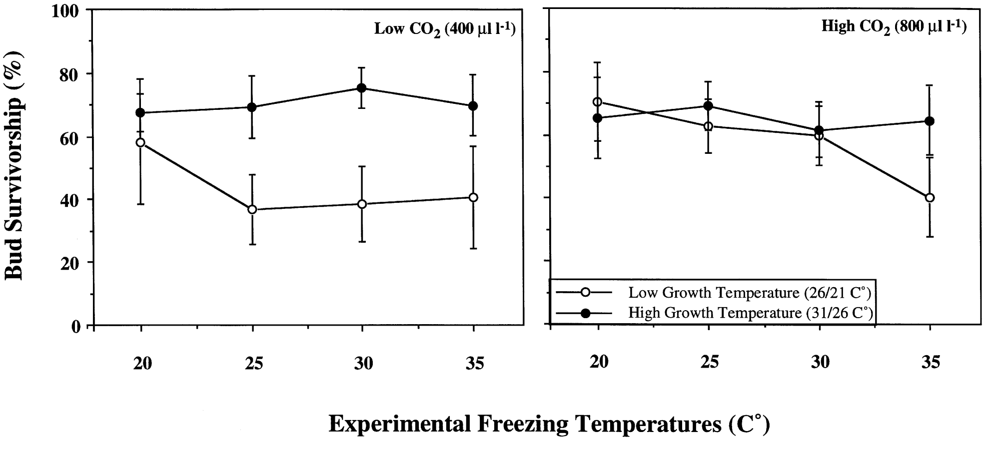

Fig. 4 Percentage of dormant yellow birch buds surviving freezing temperatures resulting from an experimental cooling cycle. Seedlings were grown for an entire season in one of four CO_2-temperature treatments: 400 µl l^{-1}, 21/26°C; 400 µl l^{-1}, 26/31°C; 800 µl l^{-1}, 21/26°C; 800 µl l^{-1}, 26/31°C. *Error bars* represent 1 SE; $n = 18$ buds per treatment

CO_2 concentrations (174% vs. 13%). Similar ameliorating effects of CO_2 enrichment on temperature-stimulated respiration (mg g^{-1}) were observed for whole plants of *Dactylus*, but not for *Medicago* in a study by Ziska and Bunce (1993). Similarly, in a 3-year study beginning with 16-year-old *Pinus sylvestris* saplings, temperature-induced increases in needle respiration were compensated for by CO_2 enrichment (Wang et al. 1995). In contrast, while elevated temperatures stimulated respiration, and CO_2-enrichment depressed respiration (μg g^{-1}) in *P. ponderosa* seedlings, no interactions between these factors were observed for either shoot or root respiration rates (Callaway et al. 1994). While numerous other studies have also indicated that CO_2-induced changes in dark respiration can vary with temperature (e.g., Reuveni and Gale 1985; Ziska et al. 1991), these studies did not include long-term temperature treatments and are thus not comparable to the present study.

In contrast to dark respiration, the responses of leaf net photosynthesis to temperature and CO_2 were not interactive, and did not parallel growth responses. While elevated temperatures did significantly reduce net photosynthesis, the magnitude of this reduction was both very small in comparison to temperature-induced growth reductions, and was not disproportionately ameliorated by elevated CO_2 concentrations. The lack of an interactive effect of temperature and CO_2 on net photosynthesis differs from predictions made by generalized biochemical models (Long 1991), and from a number of empirical studies (e.g., Baker and Allen 1993; Callaway et al. 1994; Wang et al. 1995). Our lack of leaf biochemical data make it difficult to interpret this response.

As with dark respiration, the responses of whole-seedling transpiration rate to elevated temperature and CO_2 paralleled growth responses for yellow birch. Temperature increased transpiration, and temperature-induced changes in transpiration were markedly smaller in elevated-CO_2 environments. These patterns were reflected to a large extent in whole-plant WUE. As there were only small differences in average RGR among temperature and CO_2 treatments at this point in the experiment, differences in transpiration rate among treatments were largely responsible for the decrease in WUE at higher temperatures and the increase in WUE at elevated CO_2.

While a significant amount of data on WUE responses to the direct effects of CO_2 enrichment are available, few studies have investigated whole-plant WUE responses to the interactive effects of elevated temperature and CO_2. Baker and Allen (1993) review data on the WUE responses of entire soybean and citrus canopies exposed to combinations of elevated temperatures and CO_2 levels. For both species, increasing temperatures reduced canopy WUE (daily CO_2 uptake/daily water loss), whereas elevated CO_2 increased WUE. However, only for citrus was the magnitude of temperature-induced reductions in WUE disproportionately reduced in high-CO_2 environments. Koike et al. (1996) quantified leaf-level instantaneous WUE (IWUE; light-saturated net photosynthesis/transpiration on an area basis) for two white birch varieties (*B. platyphylla, B. platyphylla* var. *japonica*) raised in controlled temperature × CO_2 treatments. They found that while higher temperatures decreased IWUE, and CO_2 increased IWUE, elevated CO_2 did not disproportionately decrease the negative effects of high temperature. Carslon and Bazzaz (1980) reported that whole-seedling WUE (estimated from canopy gas exchange data over 1.0 h) for three floodplain tree species was increased an average of 55% in elevated-CO_2 environments. This value is nearly identical to the average CO_2-induced enhancement of leaf-level IWUE for woody plants (based on 20 species) presented in a review by Ceulmans and Mousseau (1994). Thus, in addition to ameliorating the direct effects of high temperature on carbon balance, elevated CO_2 may also compensate for temperature-induced water stress. As water stress is a primary factor regulating the southern range limit of yellow birch, elevated CO_2 may play an important role in regulating the geographical distribution this species.

Although it was not measured, it is likely that soil temperatures in our study were unusually high compared to field conditions. As a result, the patterns of plant carbon balance and water relations discussed above should be interpreted with some caution.

Plant responses to freezing stress

Our results with yellow birch were variable, but suggest that both higher air temperatures and, to a lesser extent, elevated CO_2 may have some positive influence on the freezing tolerance of dormant winter buds. The few studies with which we can compare our results have all been conducted with evergreen tree species. For example, the frost hardiness of 20- to 25-year-old *P. sylvestris* saplings was enhanced after 1 year of exposure to a combination of elevated CO_2 and air temperatures (Repo et al. 1996). In the same study, elevated temperatures also altered the seasonal time course of frost hardiness, causing needles to harden later and deharden earlier than controls. In contrast, CO_2 delayed the onset of bud burst and therefore reduced the risk of subsequent frost damage in a study with *Picea sitchensis* (Murray et al. 1994). While yellow birch buds used in this study did not exhibit signs of physical swelling, it is possible that growth treatments subtly influenced non-visible aspects of phenology, and thus the susceptibility to frost. Measurements made earlier in the winter would more conclusively isolate the effects of growth conditions on dormant bud frost resistance.

Implications of CO_2-temperature interactions for anticipated climate-induced range shifts

While attempts to model forest responses to future climate change differ markedly in quantitative approaches and in underlying assumptions, all approaches fundamentally assume that climate is a primary factor underlying the current and future geographic distributions of species (Gates 1993). Despite predictions that atmospheric CO_2 concentrations and air temperature will rise together, very limited data are available to assess the possible interactive effects of these two global change factors on temperate forest tree species. The results of this study suggest that elevated CO_2 can substantially alter birch seedling responses to distribution-limiting climatic factors. However, before discussing the potential implications of these interactions for the future ranges of temperate trees, it is important to explicitly consider some limitations of this study. First, our study with yellow birch only addresses the influences of CO_2 and temperature on the seedling stage of development – a very short phase of the tree life cycle. Longer-term studies with CO_2, for example, suggest that the magnitude of CO_2-induced growth and physiological responses may vary through ontogeny (Bazzaz et al. 1993; Norby et al. 1995). Moreover, the successful establishment and maintenance of populations near the edges of their geographic range is not only contingent upon vegetative performance. The northern distribution of *Tilia cordata* in England, for example, appears to be limited by the negative effects of cold spring temperatures on pollen tube growth (Pigott and Huntley 1981). Second, geographic distributions of species are not only determined by their own responses to climatic factors, but also by the relative performances of co-occurring species (Woodward 1987). Small climate-induced changes in growth and development can have significant effects on the relative competitive performance and survival of species in migrating communities (Huntley and Webb 1989; Gates 1993).

Despite these limitations, the results of the present study strongly suggest that the interactive effects of CO_2 with other climatic factors should be considered in models predicting the future distribution and productivity of temperate forest species. For example, most models predict that anticipated higher summer temperatures and decreased precipitation in the future will shift the southern ranges of birch and associated species northward by at least a few hundred kilometers (e.g., Solomon 1986; Davis and Zabinski 1992). However, our results with yellow birch indicating that elevated CO_2 can significantly ameliorate the negative effects of high summer temperatures, and improve WUE, suggest that these range shift predictions may be overestimates. Our results suggest that if atmospheric CO_2 concentrations increase without significant climate change, the southern distribution of birch might even be extended further southward than today, as trees would be better able to tolerate high-temperature and drought stress. Additionally, the ameliorating effects of both elevated air temperatures and CO_2 concentrations during the growing season on winter freezing stress also suggest that current predictions regarding the effects of cold winters on northern distributions of species may also be inaccurate.

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