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RESEARCH ARTICLE

CO₂ elevation improves photosynthetic performance in progressive warming environment in white birch seedlings

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Abstract

White birch (*Betula papyrifera* Marsh) seedlings were exposed to progressively warming in greenhouses under ambient and elevated CO₂ concentrations for 5 months to explore boreal tree species' potential capacity to acclimate to global climate warming and CO₂ elevation. In *situ* foliar gas exchange, in vivo carboxylation characteristics and chlorophyll fluorescence were measured at temperatures of 26°C and 37°C. Elevated CO₂ significantly increased net photosynthetic rate (Pn) at both measurement temperatures, and Pn at 37°C was higher than that at 26°C under elevated CO₂. Stomatal conductance (gs) was lower at 37°C than at 26°C, while transpiration rate (E) was higher at 37°C than that at 26°C. Elevated CO₂ significantly increased instantaneous water-use efficiency (WUE) at both 26°C and 37°C, but WUE was markedly enhanced at 37°C under elevated CO₂. The effect of temperature on maximal carboxylation rate (V_{cmax}), PAR-saturated electron transport rate (J_{max}) and triose phosphate utilization (TPU) varied with CO₂, and the V_{cmax} and J_{max} were significantly higher at 37°C than at 26°C under elevated CO₂. However, there were no significant interactive effects of CO₂ and temperature on TPU. The actual photochemical efficiency of PSII (F_v/F_m'), total photosynthetic linear electron transport rate through PSII (J_T) and the partitioning of J_T to carboxylation (J_c) were higher at 37°C than at 26°C under elevated CO₂. Elevated CO₂ significantly suppressed the partitioning of J_T to oxygenation (J_o/J_T). The data suggest that the CO₂ elevation and progressive warming greatly enhanced photosynthesis in white birch seedlings in an interactive fashion.

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Introduction

Global climate warming and increases in atmospheric CO₂ concentration are currently key topics for scientists, politicians and the general public alike¹. Such changes have been observed in the past 150 years and supported by modeling results for the longer term, *e.g.*, warming ocean water, shrinking mountain glaciers, retreating snow cover, and CO₂ concentration dynamics in Arctic/Antarctic ice cores²⁻⁶. It is projected that the global temperatures will increase by an average of 3°C with a range of 2 to 4.5°C under the scenario of doubling atmospheric CO₂ concentration by the end of the century². Global climate warming will likely have profound and diverse impacts on biological systems^{2,4-13}.

Increases in CO₂ and temperature to a certain extent should have positive impact on photosynthesis and growth, as the current atmospheric CO₂ concentration is below the saturation point for RuBisCO (Ribulose-1,5-bisphosphate carboxylase oxygenase)¹⁴. Furthermore, higher CO₂ concentrations suppress photorespiration and increase the partitioning of photosynthetic electron transport to carboxylation¹⁴. However, the situation will become complicated if the temperature goes beyond plants' ability to acclimate, or when the rate of temperature increase exceeds the pace of acclimation. In such cases, temperature and CO₂ will have opposite effects on photosynthesis, *i.e.*, the higher temperature induced increase in photorespiration may exceed the beneficial effect of CO₂ elevation, resulting in a decline in net photosynthesis. Consequently, the direction and magnitude of change in net photosynthesis will be determined by the relative magnitudes of the two opposite effects¹⁵. Kirschbaum¹⁶ has conducted a theoretical analysis on the dependence of photosynthesis on temperature and CO₂ concentration for C3 plants and found that at 35°C, photosynthesis at the ambient CO₂ concentration reaches only 50% of the rate at saturating CO₂ concentration, whereas the corresponding value at 5°C is 77%. Therefore, there is greater potential photosynthetic enhancement by CO₂ elevations at higher temperatures. This theory has been supported by the results of a number of studies^{15,17-19}. Long²⁰ has suggested that the increase in atmospheric CO₂ will not only increase photosynthetic rate, but also alter the photosynthetic response to temperature. Mooney *et al.*²¹ indicate that the photosynthetic acclimation to elevated temperature and CO₂ mainly involves changes in the heat stability of the thylakoids and RuBisCO activity. Hence, high temperature and CO₂ elevations may have synergistic effect on photosynthesis and CO₂ elevations may lead to improved acclimation to high temperatures. However, such interactions may vary with plant species^{22,23} and other environmental conditions. Variations in acclimation ability can change the interactions within and between species and the composition and functioning of plant communities under future climatic conditions. Furthermore, in most past studies, high temperature treatments are achieved in one step, which is in contrast with the gradual, progressive increases in temperature occurring in global climate changes.

The boreal forest is an important terrestrial ecosystem with a high carbon sequestration potential²⁴. As the global climate change accelerates, the boreal forest has been experiencing progressive increases in temperatures and CO₂. The response of the boreal forests could have great impact on the global carbon balance²⁵.

White birch is one of the most widely distributed tree species in the boreal forest. The growth conditions of white birch in northwest Ontario are characterized by a long cold winter and short summer. For example, the annual mean temperature in Thunder Bay region is 2.4°C while the January and July average temperatures are -14.9°C and 17.6°C (based on Environment Canada's online weather records for the time period of January 1943 to December 2003). Nevertheless, based on our past experience in growing white birch seedlings in greenhouses, it appears that the species is capable of acclimating to continuous warming to more than 40°C in the early afternoon on sunny summer days (see Figure 1). In this current study, we test the hypothesis that CO₂ elevation will enhance the photosynthetic performance of white birch seedlings growing in a progressively warming environment.

Materials and methods

Plant materials

White birch (*Betula papyrifera* Mash.) seedlings were grown from seeds in the greenhouses at the Thunder Bay campus of Lakehead University. The growing medium was a mixture of peat moss and vermiculite (1:1 (v/v)).

Figure 1. Time course of temperatures in the greenhouses during the experimental period (March 1 through August 15). (A) Postmeridian (hour) pattern between 13:00 and 16:00; (B) Diel (hour) pattern between 0:00 and 24:00.

Experiment design

The seedlings were subject to a progressive warming in the greenhouses as the season progressed from March to August (Figure 1). The temperatures in all the greenhouses were monitored and recorded using a computerized environment control system (*Argus*, Vancouver, Canada). The highest recorded temperature in the greenhouse was 44.8°C in the later stages of the experiment (Figure 1). The seedlings were grown under two CO₂ concentrations (i.e., the ambient (360 µmol mol⁻¹) and elevated (650 µmol mol⁻¹)). The two CO₂ treatments were conducted simultaneously in separate greenhouses with identical design and dimensions. The CO₂ elevation was achieved using *Argus* CO₂ generators (*Argus*, Vancouver, Canada). A photoperiod of 16-hour was maintained (the natural light was supplemented by high-pressure sodium lamps on cloudy days, early mornings and late evenings).

The moisture content of the growing medium was maintained at around 50%, as measured using a *HH2 Moisture Meter (DELTA-T DEVICES, Cambridge, UK)*. The seedlings were watered up to twice a day during the summer to maintain the soil moisture condition. The seedlings were fertilized weekly with a solution of 100 µmol mol⁻¹ N, 35 µmol mol⁻¹ P and 66 µmol mol⁻¹ K.

Simultaneous measurements of *in situ* gas exchange and chlorophyll fluorescence

The foliage gas exchange was measured using a PP-Systems *CIRAS-1* open gas exchange system (*Hitchin, Hertfordshire, UK*). The environmental conditions in the broad-leaf chamber were controlled automatically. The environmental conditions for measuring the Pn-C_i (C_i = intercellular CO₂ concentration) curve were as follows: 26°C and 37°C air temperature, which were close to the highest temperatures in the early and late period of the experiment, 800 µmol m⁻²s⁻¹ PAR (PAR = photosynthetically-active radiation) and 50% relative humidity. The *in vivo* maximal carboxylation rate (V_{cmax}), PAR-saturated electron transport rate (J_{max}), triose phosphate utilization (TPU) and other relevant parameters were calculated from the Pn-C_i curves according to Farquhar *et al.*²⁶, van Caemmerer and Farquhar²⁷, Sharkey²⁸, Harley and Sharkey²⁹ and Harley *et al.*³⁰. The Pn-C_i curves were fit using the *Photosyn Assistant* software (*Dundee Scientific, Scotland, UK*) to estimate V_{cmax}, J_{max} and TPU. The parameters for the kinetics of RuBisCO, i.e., K_c, K_o and τ, and their temperature dependencies were adopted from Harley *et al.*³⁰ and Wullschlegel³¹.

Three seedlings were selected randomly from each treatment combination for the measurement. The measurement was taken on the top 5th mature leaf. All the *in situ* measurements were made between 9:00 and 11:30 AM with the seedlings in their original positions and conditions of the treatments.

The chlorophyll fluorescence was measured using a *FMS-2* portable pulse-modulated fluorometer (*Hansatech Instruments Ltd, Norfolk, UK*). The probe was integrated in the leaf chambers of the gas exchange system and the control software for the two systems was also integrated to allow the simultaneous measurement of gas exchange and chlorophyll fluorescence. The following variables were obtained: fluorescence intensity at any time, F; the maximal fluorescence in light, F_m'; the actual photochemical efficiency of

PSII in light, (F_m'-F)/F_m' or ΔF/F_m', which is the efficiency under the actual degree of reaction centre closure³². F_m' was obtained by illuminating the foliage with a pulse of strong light (around 14000 µmol photons m⁻²s⁻¹) for 800 ms. The ΔF/F_m' was measured simultaneously with each gas exchange measurement. Both gas exchange and chlorophyll fluorescence were measured after 5 months of the treatments.

The apparent rate of total electron transport (J_T) and its partitioning between carboxylation (J_c) and oxygenation (J_o) were calculated based on the methods of Farquhar *et al.*²⁶, Genty *et al.*³³ and Epron *et al.*³⁴.

Statistical analysis

All the data were examined graphically for the normality of distribution (probability plots for residual analysis) and the homogeneity of variance (scatter plots) using the Data Desk (version 6.01, Data Description, Inc. 1996)³⁵ before the Analysis of Variance (ANOVA) was carried out. Some of the data were log-transformed to meet the two assumptions for ANOVA. The data were analyzed using the two-way ANOVA procedure of the Data Desk. When the interaction between temperature and CO₂ was significant, Scheffe's F test for post hoc pairwise comparisons was conducted.

Results

In situ photosynthetic gas exchange

There was a significant (*P*<0.01) interactive effect of temperature and CO₂ on Pn (Figure 2). Pn was higher (*P*<0.01) at 37°C than at 26°C under elevated CO₂ (Figure 2), but there was no significant (*P*>0.05) temperature effect on Pn under ambient CO₂. CO₂ elevation significantly increased Pn at both temperatures (*P*<0.05, *P*<0.001 at 26°C and 37°C, respectively). *g_s* significantly (*P*<0.05) decreased at 37°C under both ambient and elevated CO₂ (Figure 2), and there was no significant (*P*>0.05) CO₂ effect on *g_s*. Meanwhile high temperature significantly (*P*<0.05) stimulated *E* under both ambient and elevated CO₂ (Figure 2). Water-use efficiency (WUE) was significantly (*P*<0.05) higher at 26°C than that at 37°C under both CO₂ regimes. CO₂ elevation greatly (*P*<0.001) increased WUE at both temperatures.

High temperature significantly reduced C_i under both ambient and elevated CO₂ (*P*<0.05, *P*<0.01, respectively) and, also, elevated CO₂ significantly (*P*<0.001) increased C_i at both temperatures.

In vivo RuBisCO activity

V_{cmax}, J_{max} and TPU at 37°C were significantly (*P*<0.001) higher than those at 26°C (Figure 3). The temperature dependencies of V_{cmax} and J_{max} were changed by CO₂, and those values at 37°C enhanced much more (*P*<0.05) under elevated CO₂ than under ambient CO₂.

Photosystem II efficiency and electron transport partitioning to carboxylation and oxygenation

There was a significant (*P*<0.001) interactive effect of CO₂ and temperature on (F_m'-F)/F_m' and J_T (Figure 4). (F_m'-F)/F_m' and J_T greatly increased at 37°C as compared to at 26°C under elevated CO₂, and there was no significant temperature effect on (F_m'-F)/F_m' and J_T under ambient CO₂.

Figure 2. Pn, g_s , E and WUE (mean $\pm$ SD, n=3–4) for current year white birch seedlings after they were exposed to continuous warming under ambient CO₂ and elevated CO₂ concentrations for 5 months. The *in situ* measurements were taken at 26°C and 37°C under ambient CO₂ and elevated CO₂. The significance levels (*** = $P < 0.001$, ** = $P < 0.01$, * = $P < 0.05$). If the interaction between measurement temperature and CO₂ was significant for a given parameter, Scheffe's F test for post hoc pairwise comparisons was conducted. Means sharing the same letter or letters are not significantly different.

The pattern of CO₂ and temperature effects on J_c was almost the same as $(F_m - F)/F_m$ and J_T (Figure 4), and J_c was greater ($P < 0.001$) at 37°C than that at 26°C under elevated CO₂, and there was no significant temperature effect on J_c under ambient CO₂. Elevated CO₂ greatly suppressed J_o/J_T , and there was no significant ($P > 0.05$) effect of temperature on J_o/J_T (Figure 4).

A-Ci curves from gas exchange at 26–37°C

1 Data File

<http://dx.doi.org/10.6084/m9.figshare.105910>

PSII efficiency curve, 26–37°C

1 Data File

<http://dx.doi.org/10.6084/m9.figshare.105911>

Temperature data

1 Data File

<http://dx.doi.org/10.6084/m9.figshare.105912>

Discussion

Our results suggest that the photosynthetic mechanisms of white birch seedlings have high capacity to acclimate to a progressively warming environment, particularly under elevated CO₂. This result is in contrast to the results of most studies with a single step warming treatment. Larcher³⁶ has suggested that plants' optimal temperature is closely related to the climate in which they grow. The measurement temperatures of 26°C and 37°C used in this study are believed to be the normal (or optimal) and stressful temperature, respectively, for most boreal forest tree species growing at their natural environments. Zhang *et al.*³⁷ have found that the Pn of mature oak even in warm-temperate zones decline greatly at temperatures over 30°C, as compared to measurements at temperatures of 20–30°C, which occurs naturally north of temperate zones or even warm-temperate zones. However, in this experiment the Pn of white birch didn't decline at 37°C under ambient CO₂, as compared to that at 26°C; furthermore, Pn increased substantially at 37°C under elevated CO₂. These results indicate that the photosynthetic mechanisms of white birch acclimated to the progressive warming environment, and this high temperature acclimation was greatly strengthened by elevated CO₂. Long²⁰ argued that CO₂ elevation could change the photosynthesis dependence of temperature.

The activity of RuBisCO is highly temperature-dependent. According to Jordan and Ogren³⁸, the Rubisco's specificity for CO₂/O₂ decreases as increasing temperatures over the optimal range, but the

Figure 3. V_{cmax} , J_{max} , TPU and C_i in current year white birch seedlings. V_{cmax} , J_{max} and TPU were derived from A-C_i curves, which were measured at 26°C and 37°C under ambient CO₂ and elevated CO₂. See Figure 2 for other explanations.

Figure 4. $(F_m' - F)/F_m'$, J_{tr} , J_c and J_o/J_{tr} in the current year white birch seedlings ($(F_m' - F)/F_m'$ and J_{tr} were derived from chlorophyll fluorescence measurements, and J_c and J_o were derived from both chlorophyll fluorescence and gas exchange measurements. See Figure 2 for other explanations.

increase in RuBisCO oxygenation will exceed that of carboxylation because the solubility of CO₂ declines faster than that of O₂ at even higher temperatures, resulting in a decline in net photosynthetic rate. White birch's acclimation to warming was also evidenced by V_{cmax} measured at the two different temperatures and two CO₂ regimes. V_{cmax} at 37°C was much higher than at 26°C under both ambient and elevated CO₂, indicating a shift in the temperature dependency of RuBisCO. Furthermore, the partitioning of total electron transport to oxygenation was not significantly different between the two temperatures under either ambient CO₂ or elevated CO₂, suggesting that the higher temperature did not change the RuBisCO specificity for CO₂/O₂ which could be a contributing factor for the enhanced acclimation of photosynthesis to the progressive warming. Overdieck *et al.*¹⁵ have also found that both the temperature treatment alone and the combination of elevated CO₂ and temperature depressed V_{cmax} in Scots pine at temperatures below the optimum range, but increased V_{cmax} when the temperature was above the optimum. Additionally, the magnitude of the change in V_{cmax} increased as temperature increased.

The decrease in C_i at the high temperature could be attributable to either enhanced RuBisCO activity or declines in stomatal conductance or both. Not only V_{cmax}, but J_{max} and TPU were also higher at 37°C than at 26°C, suggesting that the CO₂ assimilation process, including carboxylation, electron transport for RuBP regeneration, ATP supply and the translocation of the primary photosynthates, all maintained at high levels in the warm environment. In this study, there was no down-regulation of RuBisCO activity in association with the CO₂ elevation, to the contrary, CO₂ elevation greatly increased V_{cmax} and J_{max} at 37°C, as well as Pn at both 26°C and 37°C.

While high temperature enhanced V_{cmax} under both ambient and elevated CO₂, the increases in actual PSII efficiency ($\Delta F'/F_m'$) and J_c associated with the high temperature only occurred under elevated

CO₂, suggesting that the high temperature did not significantly affect the total electron transport, and its partitioning to carboxylation, under the ambient CO₂. Conversely, the partitioning of total electron flow to oxygenation increased more than 40% in response to the high temperature under elevated CO₂. The reduced electron transport partitioning to carboxylation and low C_i might explain why Pn was relatively low at 37°C under the ambient CO₂, even though the corresponding V_{cmax} was quite high, implying that the slow electron transport to carboxylation and CO₂ supply at high temperature under ambient CO₂ didn't match the high activity of RuBisCO. This again confirms Kirschbaum's theoretical analysis that photosynthesis has a higher potential to be stimulated by CO₂ elevation at high temperatures than at low temperatures¹⁶.

Author contributions

QLD and SZ conceived and designed the experiment. SZ conducted the measurements and analyzed the data. SZ and QLD wrote and revised the manuscript.

Competing interests

No competing interests were disclosed.

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Having stated that the work makes a very sound impression to me and reflects state of the art methodology, I still have concerns about the implied meaning. The authors carefully avoid making any statement with regard to growth or productivity implications. However, why would one make such measurements if not for the implied meaning for growth and overall performance? From all what we know to date, such a link has not been shown outside horticultural conditions. It will be most unlikely that a birch seedling in the wild is carbon limited. Whatever the photosynthetic performance, such a seedling would only incorporate structural carbon to the extent nutrients permit, and these are finite per unit land area (except for N) and are competitively foraged for.

Competing Interests: No competing interests were disclosed.

I confirm that I have read this submission and believe that I have an appropriate level of expertise to confirm that it is of an acceptable scientific standard.

Author Response 03 Jul 2013

Shouren Zhang

We appreciate the invaluable comments from Professor Christian Koerner. The primary focus of this study was to investigate the physiological plasticity of white birch in response to gradually warming environmental conditions under the elevated CO₂ conditions in the future, not growth. Growth is more closely related to the carbon balance and resource availability than to photosynthesis or any single physiological process. While short term physiological studies such as ours are important for understanding the physiological mechanisms and ability in plant responses to stressful environmental conditions, extrapolating the results to predict the growth performance of trees in the field is risky and not reliable because of the long life of trees and the dynamic nature of natural environmental conditions. Therefore, we have refrained ourselves from making such extrapolations.

Competing Interests: No competing interests were disclosed.

Reviewer Report 08 February 2013

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This is certainly a valuable manuscript.

Competing Interests: No competing interests were disclosed.

I confirm that I have read this submission and believe that I have an appropriate level of expertise to confirm that it is of an acceptable scientific standard.

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