



Differential response of aspen and birch trees to heat stress under elevated carbon dioxide

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We report that elevated CO₂ confers increased thermotolerance on both aspen and birch trees while isoprene production in aspen confers further thermotolerance in aspen.

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ABSTRACT

The effect of high temperature on photosynthesis of isoprene-emitting (aspen) and non-isoprene-emitting (birch) trees were measured under elevated CO₂ and ambient conditions. Aspen trees tolerated heat better than birch trees and elevated CO₂ protected photosynthesis of both species against moderate heat stress. Elevated CO₂ increased carboxylation capacity, photosynthetic electron transport capacity, and triose phosphate use in both birch and aspen trees. High temperature (36–39 °C) decreased all of these parameters in birch regardless of CO₂ treatment, but only photosynthetic electron transport and triose phosphate use at ambient CO₂ were reduced in aspen. Among the two aspen clones tested, 271 showed higher thermotolerance than 42E possibly because of the higher isoprene-emission, especially under elevated CO₂. Our results indicate that isoprene-emitting trees may have a competitive advantage over non-isoprene emitting ones as temperatures rise, indicating that biological diversity may be affected in some ecosystems because of heat tolerance mechanisms.

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1. Introduction

Increasing atmospheric greenhouse gases have led to increasing atmospheric temperatures (global warming) (IPCC, 2001, 2007). It has been reported that high temperatures decrease growth rate and may even stop cambial growth in trees such as *Pinus sylvestris* and *Picea abies* (Pichler and Oberhuber, 2007) as well as decrease ecosystem productivity, as observed during the European summer 2003 heat wave (Reichstein et al., 2007). High temperature, not high photon flux density, is the principal cause of decreased net carbon gain as temperatures rise (Gamon and Pearcy, 1989), and increasing temperatures beyond 35 °C will generally inhibit carbon assimilation (Sharkey, 2005; Sharkey and Schrader, 2006). High temperatures are reported to decrease carbon assimilation rates in a number of different tree species including *Macaranga conifera* (Ishida and Toma, 1999), *Eperua grandifolia* (Pons and Welschen,

2003), *Cariniana legalis* (Souza et al., 2005) and *Quercus pubescens* (Haldimann and Feller, 2004).

High temperatures are also known to induce the production of isoprene in isoprene-producing trees (Monson and Fall, 1989; Centritto et al., 2005), and isoprene is thought to protect trees from heat stress by increasing their thermotolerance (Sharkey and Singsaas, 1995; Sharkey et al., 2001; Singsaas et al., 1997). The mechanism by which isoprene confers thermotolerance on tree leaves is not well understood (Behnke et al., 2007). Behnke et al. (2007) found that isoprene-emitting aspen trees maintained a high carbon assimilation rate compared to their non-isoprene emitting transgenic counterparts at temperatures of 38–40 °C.

Elevated CO₂ has been reported to ameliorate the adverse effects of high temperatures in different deciduous plant species including aspen (Darbah, 2007), birch trees (Veteli et al., 2007; Darbah, 2007) and *Phaseolus vulgaris* (Cowling and Sage, 1998). Idso and Kimball (1992) reported that elevated CO₂ (ambient + 300 ppm) increased net carbon assimilation by 100% and 200% in orange trees at 35 and 42 °C, respectively, relative to orange trees under ambient CO₂ at the same temperatures.

In the summer of 2006, we measured the effect of a natural prolonged heat spell on photosynthesis of aspen (*Populus tremuloides* Michx) and birch (*Betula papyrifera*) trees growing in Free Air

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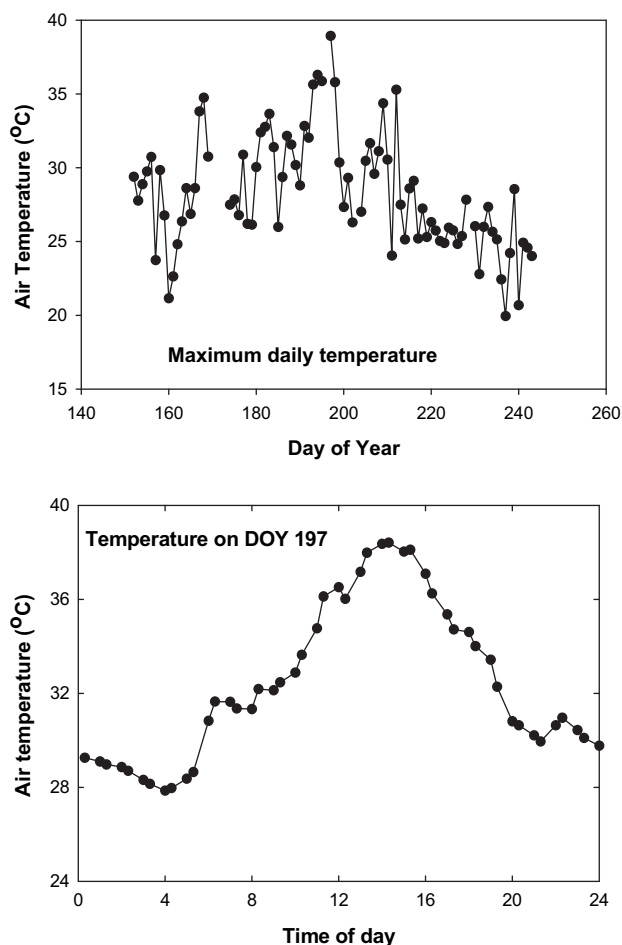


Fig. 1. Daily air temperature in the summer of 2006 and hourly temperature throughout the day on DOY 197. Measurements were made at the Aspen FACE site in Rhinelander, WI, USA.

Carbon dioxide Enrichment (FACE) rings at the Aspen FACE experimental site in Northern Wisconsin. Since aspen and birch occupy similar ecological niches, but only aspen emits appreciable quantities of isoprene, we were able to compare the effects of elevated temperatures on these two tree species with different volatile

organic compound (VOC) emission dynamics under both ambient and elevated CO_2 in this study.

2. Materials and methods

2.1. Study site and planting material

The experiment was carried out at the Aspen FACE site in Rhinelander, WI, USA (Karnosky et al., 2005) in 2006 during the unusual heat wave in July (Fig. 1). The study site is located at $45^\circ 30' \text{N}$ and $89^\circ 39' \text{W}$ with a sandy loam soil type. This experiment consists of four rings each of control (ambient air) (C) and elevated CO_2 (target of 200 ppm above ambient) conditions in triplicate rings of 30-meter diameter each (Karnosky et al., 2005). Six-month-old greenhouse-grown saplings from rooted cuttings of five clones of aspen (*P. tremuloides*) and birch (*B. papyrifera*) were planted at this site in July of 1997 (Noormets et al., 2001). Fumigation of elevated CO_2 was carried out at this site since 1997 providing nine years of exposure before these measurements were carried out. Trees were fumigated from 07:00 to 19:00 throughout the growing season from Spring to Fall. Two aspen clones were studied namely 271 and 42E. These clones exhibited contrasting isoprene emissions in previous studies (Calfapietra et al., 2007).

2.2. Gas exchange measurements

Gas exchange was measured with a LI-COR photosynthesis system (LI 6400 version 5.02 from LI-COR Inc. Lincoln, Nebraska, USA). All measurements were made on attached, fully expanded leaves on short shoots at the top of the canopy in full sunlight. Instantaneous photosynthesis rates and responses of photosynthetic CO_2 assimilation (A) to carbon dioxide concentration inside the leaf (C_i) were measured at naturally occurring leaf temperatures and binned into measurements at $32\text{--}35^\circ \text{C}$, $36\text{--}39^\circ \text{C}$ and $40\text{--}41^\circ \text{C}$ as air temperatures ranged between 32 and 38°C (Fig. 1) in aspen and birch trees. Many birch leaves exhibited obvious signs of stress during the heat wave and these were not used for gas exchange. Thus, the gas exchange measurements underestimate the total effect of heat on birch photosynthesis.

Photosynthetic response curves (A/C_i curves) were measured between 3 and 5 pm when temperatures were high and trees had recovered from midday depression (in the second peak of the bimodal diurnal curve, Fig. 2). For each A/C_i curve, the procedure described by Long and Bernacchi (2003) was followed (varying CO_2 concentration between $50 \mu\text{mol mol}^{-1}$ and $1800 \mu\text{mol mol}^{-1}$) at a saturating photosynthetically active radiation of $1200 \mu\text{mol m}^{-2} \text{s}^{-1}$ for aspen and $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ for birch. Maximum carboxylation rate (V_{cmax}), electron transport rate (J), triose phosphate use (TPU) and day respiration (R_d) variables were computed from the A/C_i curves using the A/C_i curve fitting model developed by Sharkey et al. (2007). TPU was determined as the highest A regardless of whether symptoms of TPU were present. This makes it similar to the parameter A_{max} reported by other investigators. Single measurements at saturating light and CO_2 are reported here as A_{max} , but TPU when the value is derived from an A/C_i curve. Thus, in this study both A_{max} and TPU could indicate either TPU or electron transport (J) limited conditions. At high temperature these are likely to represent J limited conditions since CO_2 insensitivity characteristic of TPU limitations were often not observed at these high temperatures. Stomatal conductance and transpiration rates were determined at the same time as instantaneous photosynthetic measurements.



Fig. 2. Representative images of aspen (left panel) and birch leaves during the heat wave. Aspen exhibited little to no visible damage during the heat wave while birch exhibited significant leaf damage and subsequent leaf shedding.

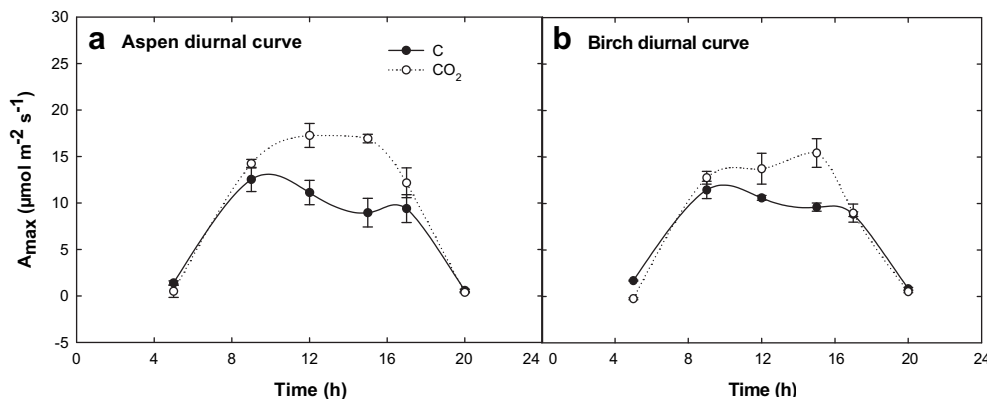


Fig. 3. Measures of $A_{\max}$ through a day of aspen and birch in normal or elevated CO_2 measured at the aspen FACE site WI, USA. Data were individual measurements made at saturating light. Data are means $\pm$ SE, $n = 3$.

2.3. Isoprene measurement and leaf temperature measurements

Isoprene emission was measured at $1000 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ and 30°C by directing the outlet of the LI 6400 cuvette to a Fast Isoprene Sensor (Hills Scientific, Boulder CO, USA) as described by Calfapietra et al. (2008). Leaf temperature was measured with a Precision Infrared Thermometer (Fluke Electronics Co, Seattle, WA) on warm sunny days. Leaf temperature measurements were taken in the afternoon between 3 and 5 pm.

2.4. Meteorological data

An on-site weather station measured the air temperature (T_{air}) relative humidity, wind speed, and photosynthetic photon flux density at the top of the canopy, in addition to precipitation and soil water content (at 5, 50 and 100 cm depth) measured with water content reflectometer (CS616-L, CS Campbell Scientific Inc.). These measurements were taken at every 30 min throughout the day and season. Details of the meteorological data from this weather station can be assessed from <http://www.aspenface.mtu.edu>.

2.5. Statistical analysis

Analysis of variance (ANOVA) followed by posthoc Tukey's-test significant at $P < 0.05$ level (Sokal and Rolf, 1995) was used to test treatment differences. Repeated measure analysis was used to test for differences between temperature groups. Average values computed $\pm$ standard errors (SE) are presented and different letters are used to indicate significant differences. The PROC GLM component of the SAS statistical software (by SAS Inc.) was used in carrying out this analysis. Percentage increase or decrease was also computed.

3. Results

An unusual heat wave and drought occurred in northern Wisconsin during the summer of 2006 where maximum temperature varied between 30 and 38°C (Fig. 1). In addition, rainfall during this period was minimal, exacerbating the heat stress experienced by leaves. According to the National Oceanic and Atmospheric Administration (NOAA) report, the Rhinelander area was classified as experiencing a severe drought in mid July 2006 with a drought severity index of -3.0 to -3.9 . This provided a rare opportunity to study the effect of high temperature under elevated CO_2 under forest conditions.

3.1. Ameliorative effects of elevated CO_2 on heat stress

Aspen trees showed no visible symptoms of stress except for decreases in some gas exchange variables. However, birch trees initially showed signs of stress through leaf curling and then yellowing of leaves and finally leaf shedding (Fig. 2). Birch trees in control rings dropped 33% of their leaves while those in elevated CO_2 dropped 20%.

Gas exchange measurements were made before, during, and after the highest temperature recorded in the summer of 2006

(Fig. 1). These measurements were taken between 3 and 5 pm when temperature was high and both aspen and birch should be actively photosynthesizing after midday depression as seen in Fig. 3. Photosynthesis declined with temperature in aspen and birch growing in normal CO_2 . However, in elevated CO_2 aspen photosynthesis, measured as $A_{\max}$, did not decline while in birch it did. Stomatal conductance mirrored photosynthetic rates but did not account for the differences as judged by the A/C_i curves (Fig. 4). The

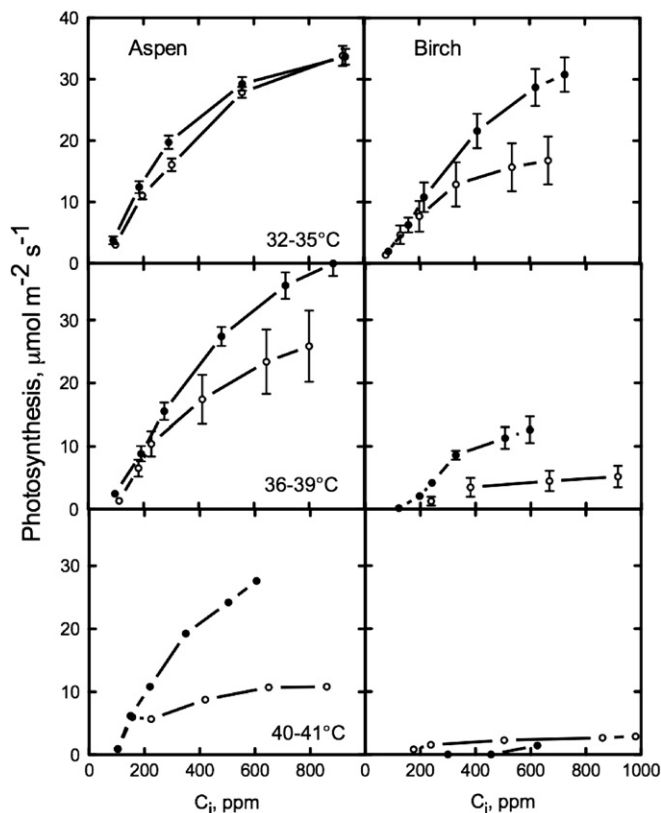


Fig. 4. Averaged A/C_i curves of aspen (data from clones 42E and 271 averaged together) and birch showing comparison of temperature effect under elevated CO_2 at temperature ranges of $(32\text{--}35^\circ\text{C})$ and $(36\text{--}39^\circ\text{C})$ conditions. The individual curves in each treatment and for the two clones of aspen were substantially similar so averaged data are presented. Data were collected between 3 and 5 pm at the aspen FACE site in 2006 summer and are presented together with error bars representing SE ($n = 3$ to 5 except for the highest temperature for which $n = 1$). Each individual A/C_i curve was fitted and the fitted parameters were averaged and reported in Table 1.

Table 1

Gas exchange parameters measured directly ($A_{\max}$) and (g_s) or derived by fitting A/C_i data. Comparison of the means and standard errors of g_s , $V_{\max}$, J , TPU and R_d for aspen and birch trees exposed to ambient CO_2 (C) or elevated CO_2 at two temperature ranges (32–35 °C and 36–39 °C). Statistically significant treatment differences are denoted with different letter after the value and significant differences due to high temperature are denoted with the symbol (*). Alpha level used is 0.1, $n = 3$.

	Aspen clone 42E		Aspen clone 271		Birch	
	32–35 °C	36–39 °C	32–35 °C	36–39 °C	32–35 °C	36–39 °C
$A_{\max}$ ($\mu\text{mol m}^{-2} \text{s}^{-1}$)						
C	11.8 ± 1.6	5.12 ± 2.4b*	10.35 ± 1.1b	4.96 ± 1.6b*	7.42 ± 1.3b	1.25 ± 0.6b*
CO_2	15.4 ± 2.3	16.30 ± 2.3a	14.33 ± 0.4a	14.83 ± 1.5a	14.47 ± 1.5a	4.96 ± 0.6a*
g_s ($\text{mol m}^{-2} \text{s}^{-1}$)						
C	0.19 ± 0.04	0.05 ± 0.02b*	0.16 ± 0.02a	0.05 ± 0.03*	0.09 ± 0.03	0.02 ± 0.01*
CO_2	0.14 ± 0.02	0.10 ± 0.02a	0.11 ± 0.01b	0.10 ± 0.02	0.09 ± 0.01	0.03 ± 0.01*
$V_{\max}$ ($\mu\text{mol m}^{-2} \text{s}^{-1}$)						
C	199 ± 15	141 ± 18b*	161 ± 49	95 ± 27b	85 ± 19b	42 ± 26
CO_2	150 ± 31	172 ± 8a	240 ± 50	590 ± 32a*	119 ± 8a	55 ± 27*
J ($\mu\text{mol m}^{-2} \text{s}^{-1}$)						
C	147 ± 12b	52 ± 09b*	178 ± 13	90 ± 23b*	94 ± 23b	32 ± 13*
CO_2	170 ± 3a	225 ± 21a*	196 ± 11	208 ± 8a	202 ± 53a	61 ± 26*
TPU ($\mu\text{mol m}^{-2} \text{s}^{-1}$)						
C	10.2 ± 0.7	6.1 ± 1.9b*	12.2 ± 0.3	5.2 ± 2.1b*	5.6 ± 1.3b	1.6 ± 0.6*
CO_2	12.8 ± 1.3	13.3 ± 1.1a	12.6 ± 0.1	12.7 ± 0.6a	10.3 ± 1.2a	3.0 ± 1.2*
R_d ($\mu\text{mol m}^{-2} \text{s}^{-1}$)						
C	1.0 ± 0.4b	2.1 ± 0.4*	1.7 ± 1.3	2.2 ± 0.3	0.5 ± 0.3	1.8 ± 0.7
CO_2	1.6 ± 0.9a	1.7 ± 1.5	2.2 ± 2.2	1.5 ± 1.6	1.7 ± 0.9	2.6 ± 0.9

parameters that can be discerned from A/C_i curves were determined using an on-line fitting procedure (Sharkey et al., 2007) and are reported in Table 1.

In both aspen and birch trees, elevated CO_2 resulted in a significant increase in $V_{\max}$, J , TPU, and in g_s at leaf temperatures of 36–39 °C (Table 1) compared to normal CO_2 , consistent with protection against heat stress by elevated CO_2 in both aspen and birch trees. The change in each of these parameters between measurements made between 32 and 35 °C and measurements made between 36 and 39 °C was negative in ambient CO_2 for all trees. However, in aspen (both clones) these parameters increased with temperature at elevated CO_2 but in birch they decreased (Table 1 and Fig. 4). The difference between A/C_i curves taken at 40–41 °C (Fig. 4) is further evidence for thermotolerance caused by both elevated CO_2 and by isoprene (compare aspen with birch).

Leaf temperature was lower in elevated CO_2 by 1.9 °C in clone 42E, 2.7 °C in clone 271 and 3.1 °C in birch trees in 2006. These leaf

temperature measurements were repeated in 2007 to ascertain the differences between elevated CO_2 and control as seen in Fig. 5. We observed significant increases in transpiration rates in both aspen clones and the birch trees under elevated CO_2 relative to control (Fig. 6a). This increased transpiration rate would have had a cooling effect on the leaves, causing leaf temperature to be lower than that of control. This difference in leaf temperature was likely one part of the increased thermotolerance of the plants under high CO_2 . A comparison of $A_{\max}$ measurements made just before and after the peak heat spell is presented in Table 2. During this period of measurements, DOY 185–200, there was no precipitation at the site. Photosynthetic rates recovered in both aspen and birch.

3.2. Isoprene emission and increased thermotolerance in aspen trees

Isoprene measurements taken during this same period indicate that these same aspen trees emitted about $45 \text{ nmol m}^{-2} \text{s}^{-1}$ in clone 42E and $47 \text{ nmol m}^{-2} \text{s}^{-1}$ in clone 271 isoprene under ambient CO_2 and $34 \text{ nmol m}^{-2} \text{s}^{-1}$ in clone 42E and $42 \text{ nmol m}^{-2} \text{s}^{-1}$ in clone 271 under elevated CO_2 (Fig. 6b). We recorded a 32% significant decrease ($P < 0.001$) in isoprene production in clone 42E and 12% in clone 271 under elevated CO_2 (Fig. 5b). The difference between heat damage to aspen versus birch may reflect the isoprene emitted by aspen but not birch.

4. Discussion

4.1. Effect of temperature on gas exchange and leaf health

Between 36 and 39 °C, birch trees showed visible symptoms of heat stress through yellowing and ultimately, leaf death. Leaf temperatures of 40–41 °C resulted in no photosynthetic activity in birch but low and easily measured photosynthetic activity in aspen (Fig. 4). This observation agrees with Haldimann and Feller (2004) who reported a temporary heat-stress-dependent decrease in leaf photosynthesis in oak trees (also an isoprene-emitting tree species) at high temperature (45 °C). While this experiment by itself does not prove thermotolerance by elevated CO_2 or isoprene, it is a real

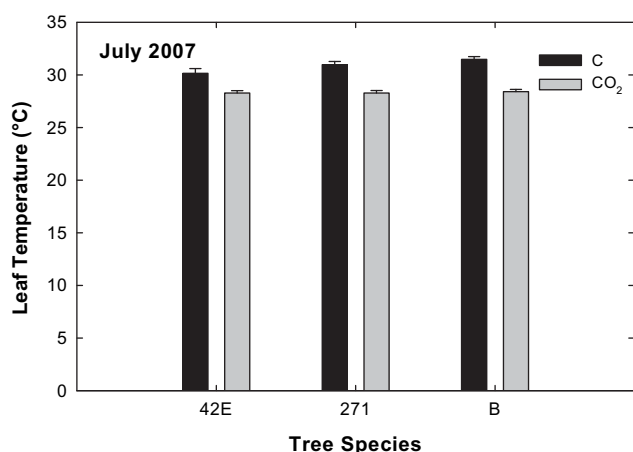


Fig. 5. Mean leaf temperature of aspen clones 42E (42E) and 271 (271) and birch (B) showing the effect of elevated CO_2 on leaf temperature. Measurement was taken at the Aspen FACE site in Rhinelander, WI in the summer of 2007 with a precision infrared thermometer.

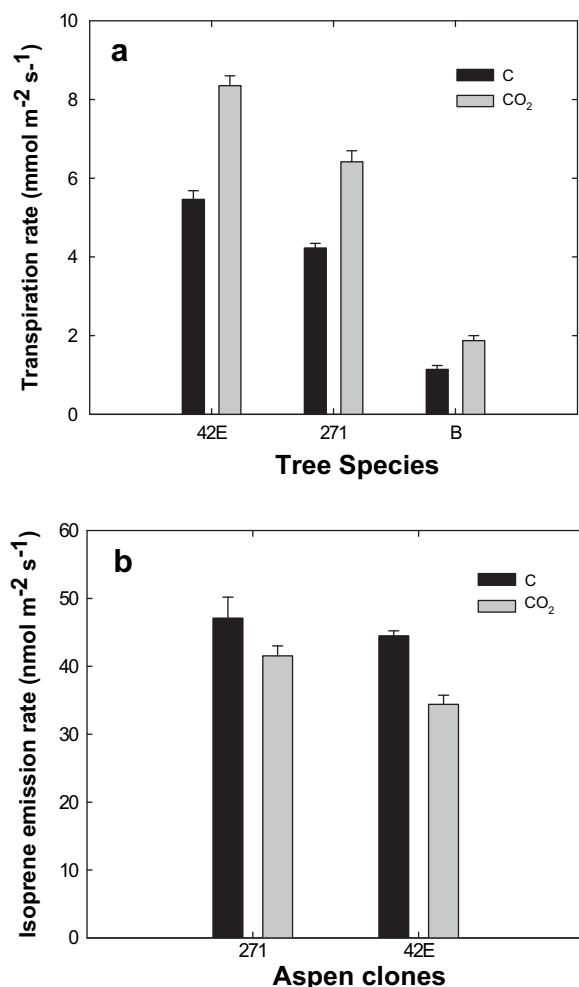


Fig. 6. (a) Mean transpiration rate of aspen clones 42E (42E) and 271 (271) and birch (B) showing the effect of elevated CO₂ on leaf transpiration rate as well as the differences in aspen and birch trees; (b) effects of elevated CO₂ on isoprene emission in two clones of aspen. Measurements were taken at the Aspen FACE site in Rhineland, WI in the summer of 2006.

world observation of what would be predicted based on laboratory experiments and so supports thermotolerance as a benefit of these factors.

Drought can cause decreased photosynthetic rate in trees, but drought was not the cause of reduced photosynthesis in this study. The recovery of photosynthesis after the peak heat period (Table 2) without precipitation indicates that the decrease in photosynthesis and leaf shedding was due to temperature and not drought. High temperature has been reported to decrease photosynthesis in

a number of tree species including *M. conifera* (Ishida and Toma, 1999), *E. grandifolia* (Pons and Welschen, 2003), *C. legalis* (Souza et al., 2005) and *Q. pubescens* (Haldimann and Feller, 2004). We also noted that both clones of aspen were affected to similar degree by the same range of temperature, in contrast to birch.

4.2. Ameliorative effects of elevated CO₂ on heat stress

Elevated CO₂ protected gas exchange capacity in both aspen and birch. In many experiments, growth of plants in elevated CO₂ causes declines in the A/C_i curves (Long, 1991; Long et al., 2004; Stitt, 1991), an effect reported specifically in birch (Eguchi et al., 2008). This effect is not always seen in FACE conditions (Bernacchi et al., 2005). At high temperature, elevated CO₂ appears to protect photosynthetic capacity. Huang et al. (2007) used tree ring analyses to determine that forest trees get the most benefit from elevated CO₂ in warm, dry conditions, such as the heat wave reported on here. We observed that leaves of both birch and aspen were cooler in elevated CO₂. Reduced water usage early in the season in elevated CO₂ rings may have left more water in the soil, allowing higher stomatal conductance and latent heat loss. This effect has been seen in the C₄ plant sugar cane (Vu and Allen, 2009) and C₃ plant cucumber (Li et al., 2008). Leaf cooling is supported by leaf temperature measurements taken on a warm day in the summer of 2007 where leaves in both aspen clones and birch trees under elevated CO₂ had significantly lower leaf temperature compared to those under ambient CO₂ (Fig. 6).

Our observations agree with Veteli et al. (2007) who reported that elevated CO₂ ameliorated the negative effects of high temperature in three deciduous tree species. Also, Wayne et al. (1998) reported that elevated CO₂ ameliorated high temperature stress in yellow birch trees (*Betula alleghaniensis*). Furthermore, we observed large increase in V_{max}, J, TPU and g_s under elevated CO₂ at leaf temperatures of 40–41 °C in aspen. This is in agreement with Idso and Kimball (1992) who reported that elevated CO₂ (ambient + 300 ppmv) increased net photosynthetic rate in sour orange tree (*Citrus aurantium* L.) leaves exposed to full sunlight by 75, 100 and 200% compared to those in ambient CO₂ concentration at temperatures of 31, 35 and 42 °C, respectively, suggesting that elevated CO₂ ameliorates heat stress in tree leaves.

4.3. Isoprene emission and increased thermotolerance in aspen trees

In aspen relative to birch, gas exchange parameters declined less or increased instead of decreased at 36–39 °C relative to 32–35 °C. Similarly assimilation rate declined with the increase of temperature less in aspen clone 271 than in aspen clone 42E especially under elevated CO₂. We believe this is consistent with isoprene emission increasing plant thermotolerance (Sasaki et al., 2007; Sharkey and Singaas, 1995; Sharkey et al., 2001; Singaas et al., 1997; Velikova and Loreto, 2005). Isoprene emission is reported to be dependent on temperature (Monson and Fall, 1989; Centritto et al., 2005) and is stimulated by water stress (Sharkey and Loreto, 1993). Sharkey et al. (2001) reported that isoprene emission in trees improves thermotolerance by helping photosynthesis cope with very short, high temperature episodes. In this study, the heat stress was more prolonged. This is similar to the heat stress used by Sasaki et al. (2007) in which they found isoprene-emitting Arabidopsis plants were less likely to exhibit leaf death than non-emitting plants.

Behnke et al. (2007) reported that isoprene-emitting poplars tolerated high temperatures (38–40 °C) while non-isoprene emitting transgenic types (those with their isoprene synthase genes repressed) did not. The significant decrease in V_{max}, J, TPU, g_s and no

Table 2

A_{max} measured on different days and at ambient air temperatures under elevated and ambient CO₂ conditions in July 2006 at Aspen FACE, WI, USA.

	DOY 187–8	DOY 194–5	DOY 196–7	DOY 198–9
Air temp	28–39	32–33	36–37	29–30
Leaf temp	31–33	36–39	40–41	32–35
42E Control	12.3 ± 0.7	5.1 ± 2.4	2.5 ± 0.9	11.8 ± 1.6
42E CO ₂	23.2 ± 0.6	16.3 ± 2.3	5.0 ± 1.9	15.4 ± 2.3
271 Control	9.6 ± 1.2	4.96 ± 1.6	2.2 ± 0.7	10.4 ± 1.1
271 CO ₂	18.4 ± 1.4	14.83 ± 1.5	4.8 ± 2.0	14.3 ± 0.4
B Control	7.5 ± 0.9	1.2 ± 0.6	0.7 ± 0.4	7.4 ± 1.3
B CO ₂	16.1 ± 1.7	4.2 ± 0.6	0.8 ± 0.5	14.5 ± 1.5

change in R_d in birch could be caused by its inability to synthesize isoprene (Loreto and Velikova, 2001; Ferrieri et al., 2005).

The question has been raised – If isoprene emission helps aspen cope with high temperature, what do non-emitting trees do? From our observations, it would appear they avoid the heat by shedding leaves. This may explain why aspen did not curl its leaves, reabsorb its chlorophyll, nor shed a portion of its leaves, as all the leaves were still photosynthesizing.

The two clones of aspen studied were affected to different degrees in their isoprene production under elevated CO_2 . This shows that, physiologically, within the same species, different clones respond to external stimuli differently as reported by Darbah (2007).

In this study, we observed a 32% decrease in isoprene production in clone 42E and 12% in clone 271 under elevated CO_2 (Fig. 6c). This agrees with Calfapietra et al. (2008) who reported that elevated CO_2 decreases isoprene emission. Short-term effects of CO_2 on isoprene emission have been ascribed to competition from phosphoenolpyruvate carboxylase for pyruvate (Rosenstiel et al., 2003, 2004) or to decreased ATP availability (Rasulov et al., 2009).

Different studies have shown that isoprene emission (Sharkey and Singsaas, 1995; Singsaas et al., 1997; Sharkey et al., 2001; Centritto et al., 2005; Velikova and Loreto, 2005; Behnke et al., 2007; Sasaki et al., 2007) and elevated CO_2 (Idso and Kimball, 1992; Wayne et al., 1998; Veteli et al., 2007) confers thermotolerance on trees. Yet, the interactive effect of isoprene emission and elevated CO_2 on thermotolerance has not been reported. It is assumed that since elevated CO_2 decreases isoprene emission, isoprene-emitting trees will not benefit much from their ability to emit isoprene, and hence, their isoprene-conferred thermotolerance will decrease with increasing atmospheric CO_2 . Our data from trees experiencing a natural heat wave indicates that the decline in isoprene emission rates at high CO_2 will not negate its thermoprotective effects. Our observations show that aspen trees (isoprene-emitting trees) under elevated CO_2 treatment performed better in tolerating heat than the non-isoprene emitting birch, suggesting that the positive effect of isoprene emission and elevated CO_2 are additive, even though elevated CO_2 decreases isoprene emission (Calfapietra et al., 2008).

5. Conclusion

We conclude that in the face of rising atmospheric CO_2 and temperature (global warming), trees will benefit from elevated CO_2 through increased thermotolerance, while isoprene-emitting trees will have added protection from heat stress. The physiological cost of isoprene emission to the plant will likely be outweighed by the gain in thermotolerance. The increased isoprene emission resulting from the higher temperatures and possible shifts in species composition toward isoprene-emitting plants could have negative consequences for atmospheric chemistry, as isoprene and isoprene nitrate have been found to be among the volatile organic compounds (VOCs) that play a key role in photochemical (tropospheric ozone) formation (Ito et al., 2007; Harrison and Hester, 1995). A possible shift in species composition toward isoprene emitters (Lerdau, 2007) will be favored in the future in the presence of global warming.

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