Isoprene Emission and Carbon Dioxide Protect Aspen Leaves from Heat Stress

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High temperature, especially above 35°C, is known to reduce leaf photosynthetic rate in many tree species[1-3]. This study investigated the effect of high temperature on isoprene-emitting (aspen) and non- emitting (birch) trees under ambient and elevated CO_2 under open field conditions. Aspen trees tolerate heat better than birch trees and elevated CO_2 protects both species against moderate heat stress. The increased thermotolerance in aspen trees[4-5] compared to the birch trees may result from the aspen's ability to produce isoprene[6-8]. Elevated CO_2 increased carboxylation capacity, photosynthetic electron transport capacity and triose phosphate use in both birch and aspen trees. High temperature decreased all of these parameters in birch regardless of CO_2 treatment but only photosynthetic electron transport and triose phosphate use at ambient CO_2 were reduced in aspen. As temperature rises, non-isoprene-emitting trees will be at a disadvantage and biological diversity and species richness might be lost in some ecosystems. Our results indicate that isoprene emitting tree species will have an advantage over non-isoprene emitting ones under high temperatures.

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Increasing atmospheric greenhouse gases have led to increasing atmospheric temperatures (global warming). High temperatures are reported to decrease carbon assimilation rate in a number of different tree species[1-3]. High temperatures are also known to induce the production of isoprene in isoprene-producing trees[4, 5] and isoprene is thought to protect trees from heat stress by increasing their thermotolerance[6-8]. Elevated CO_2 has been reported to ameliorate the adverse effects of high temperatures in different deciduous plant species[9-10].

In the summer of 2006 we measured the effect of a natural prolonged heat spell on photosynthesis of aspen and birch trees growing in Free Air Carbon dioxide Enrichment (FACE) rings. Since aspen and birch occupy similar ecological niches but only aspen emits appreciable quantities of isoprene, we were able to observe the protective effects of CO_2 and isoprene on tree photosynthesis under nearly natural conditions.

There was no evidence of heat stress in both aspen and birch at temperature range of 32-35^oC, but at 36-39^oC birch trees showed visible symptoms of heat stress through yellowing of leaves and leaf shedding (Fig. 1), and invisible symptoms through decreased V_{cmax}, TPU, J and g_s (Fig. 2 and Table 1). Aspen did not show visible evidence of heat stress but rather showed significant increase in V_{cmax} and R_d and a significant decrease in g_s (Table 1). Increasing leaf temperature to 40-41^oC resulted in decreased photosynthetic rate in aspen (Figure 2e and 1f), but in birch, photosynthetic activity was completely shut down.

The significant increase in V_{cmax} and no significant change in J and TPU at the leaf temperature in the range of 36-39^oC in aspen is evidence of increased thermotolerance in aspen. We believe this is due to isoprene emission which has been shown to increase plant thermotolerance [6-8, 11, 12]. Behnke et al.[13] reported that isoprene emitting poplars tolerated high temperatures (38-40^oC) while non-isoprene emitting transgenic types did not. The significant decrease in V_{cmax}, J, TPU, g_s and no change in R_d in birch is likely due to its inability to synthesize isoprene.

Elevated CO_2 increased the thermotolerance in both aspen and birch trees at leaf temperatures ranging from 36-39^{o}C and in aspen leaf temperatures to 40-41^{o}C (Figure 2). In both aspen and birch trees, there was a significant increase in V_{cmax}, J and TPU and no significant change in g_s under elevated CO_2 at leaf temperatures of 36-39^{o}C (Table 1). The significant increase in V_{cmax}, J and TPU and no significant change in g_s under elevated CO_2 at leaf temperatures of 36-39^{o}C (Table 1) and also the significant difference between AC_i curves of elevated and ambient CO_2-grown trees taken at 40-41^{o}C (Fig. 2) is evidence of protection against heat stress by elevated CO_2 in both aspen and birch trees. Our observations agree with Veteli et al.[9] who reported that elevated CO_2 ameliorated the negative effects of high temperature in three deciduous tree species. Also, Wayne et al.[14] reported that elevated CO_2 ameliorated high-temperature stress in yellow birch trees (*Betula alleghaneiensis*). Furthermore, Idso et al.[15] found that elevated CO_2 (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 CO_2 concentration at temperatures of 31, 35 and 42^{o}C, respectively, suggesting that elevated CO_2 ameliorates heat stress in tree leaves.

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 be outweighed by the gain in thermotolerance. The increased isoprene emission resulting from the higher temperatures and 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[16, 17]. A shift in species composition towards isoprene emitters has also been proposed related to enhanced ozone tolerance of isoprene emitting species[18].

Methods Summary

The experiment was carried out at the Aspen FACE site in Rhinelander, WI, USA[19] in 2006 during the unusual heat wave in July (see supplemental material). Gas exchange measurements were made with a LI 6400 photosynthesis system (LI 6400 version 5.02 from LI-COR Inc. Lincoln, Nebraska, USA). Responses of photosynthetic CO_2 assimilation (A) to carbon dioxide concentration inside the leaf (C_i) were measured at leaf temperatures of 32-35^{o}C, 36-39^{o}C and 40-41^{o}C in aspen and birch trees on the same leaves at the different temperature ranges under both ambient and elevated CO_2 concentrations. Maximum carboxylation rate (V_{cmax}), electron transport rate (J), triose phosphate use (TPU) and day respiration (R_d) variables were computed from the AC_i curves using the AC_i curve fitting model developed by Sharkey et al.[20]. Paired T-tests were used to analyze the data at alpha level of 0.1 between temperature range of 32-35^{o}C and 36-39^{o}C.

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Table 1. Means and standard errors of g_s, V_{cmax}, J, TPU, and R_d for aspen and birch trees exposed to ambient and elevated CO_2 at elevated leaf temperatures.

	Aspen			Birch		
	32-35°C	36-39°C	40-41°C	32-35°C	36-39°C	40-41°C
g_s						
Ambient	0.19 ± 0.04	0.05 ± 0.02*	0.03	0.09 ± 0.03	0.02 ± 0.01*	0.01
Elevated CO_2	0.14 ± 0.02	0.10 ± 0.02	0.08	0.09 ± 0.01	0.03 ± 0.01*	0.01
$V_{c,max}$						
Ambient	184 ± 25	269 ± 47b*	59.7	131 ± 53	49 ± 21b*	14.6
Elevated CO_2	234 ± 25	518 ± 46a*	222.6	156 ± 69	92 ± 12a	10.1
J						
Ambient	165 ± 13	134 ± 37b	54.4	100 ± 27	36 ± 11b*	17.2
Elevated CO_2	175 ± 04	252 ± 18a*	141.2	127 ± 44	87 ± 13a	17.0
TPU						
Ambient	11.8 ± 0.9	8.4 ± 2.0b	4.1	6.0 ± 1.4	2.3 ± 0.7b*	1.3
Elevated CO_2	12.5 ± 0.6	14.7 ± 0.6a*	9.4	7.7 ± 2.8	5.1 ± 0.8a	1.0
R_d						
Ambient	2.0 ± 0.6	3.6 ± 0.8b*	0.9	1.2 ± 0.6b	1.6 ± 0.6	0.2
Elevated CO_2	2.5 ± 0.9	5.9 ± 0.9a*	0.3	3.2 ± 0.6a	2.8 ± 0.5	0.7

Statistically significant treatment differences (in the same temperature group) are denoted with different letter after the value and significant differences due to high temperature (in different temperature groups but the same treatment) are denoted with the symbol (*). Alpha level used is 0.1. Values presented under temperature range of 40-41 are one time measurement as this temperature range was captured only once during the measurement period and hence no standard errors are presented.

Figures

Figure 1.
Birch leaves curl and turn yellow under high temperature (Figure 1b) while aspen leaves cope better under heat stress possibly due to isoprene production which increases thermotolerance. Figure 1a is aspen and figure 1b is birch. Pictures were taken at the Aspen Face site in Rhinelander, WI, USA on DOY 197 in 2006.

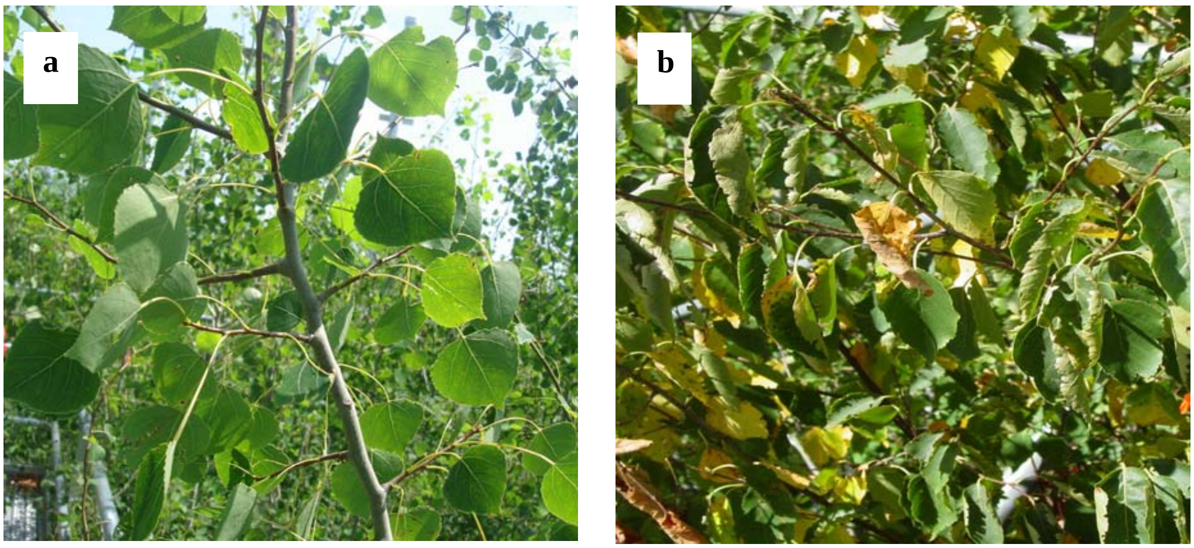

Figure 2. AC_i curves taken at Aspen FACE site in Rhinelander WI, in 2006 summer showing that isoprene producing aspen leaves performs better under high leaf temperature (32-41^{o}C) than non-isoprene producing birch, and that elevated CO_2 significantly protects both aspen and birch from moderate heat stress.