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

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We report that elevated CO_2 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 CO_2 and ambient conditions. Aspen trees tolerated heat better than birch trees and elevated CO_2 protected photosynthesis of both species against moderate heat stress. Elevated CO_2 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 CO_2 treatment, but only photosynthetic electron transport and triose phosphate use at ambient CO_2 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 CO_2. 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 CO_2 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 CO_2 (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 CO_2 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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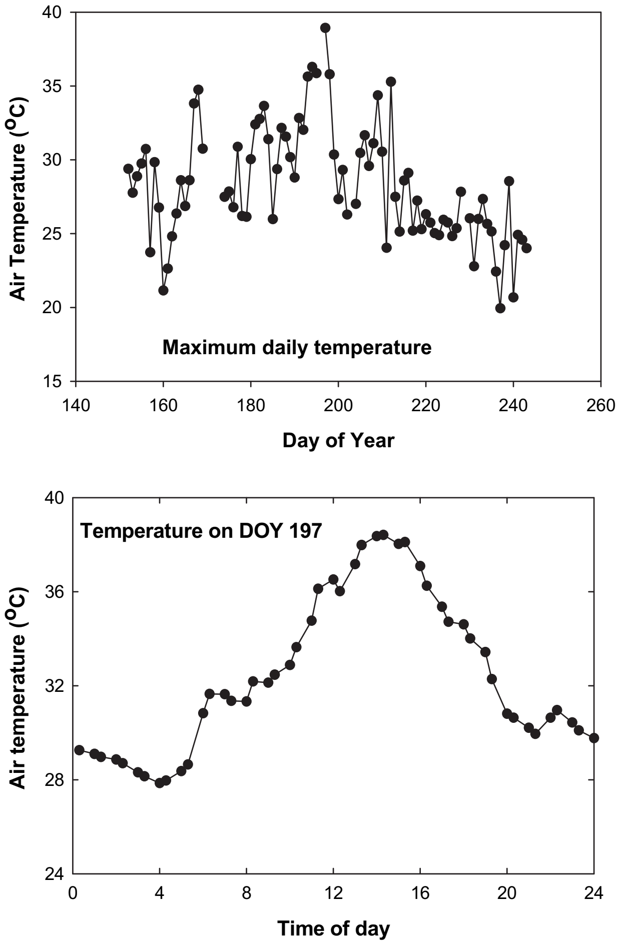

Fig. 1. Daily air temperature in the summer of 2006 and hourly temperature throughout the day on DOY 197. Measurements were made at the Aspen FACE site in Rhinelander, WI, USA.

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°30′N and 89°39′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 32–35 °C, 36–39 °C and 40–41 °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 μmol mol^{-1} and 1800 μmol mol^{-1}) at a saturating photosynthetically active radiation of 1200 μmol m^{-2} s^{-1} for aspen and 1000 μmol m^{-2} 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.