



## Water availability is the decisive factor for the growth of two tree species in the occurrence of consecutive heat waves



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### ABSTRACT

The frequency and intensity of heat waves are predicted to increase as a consequence of climate warming, yet no experimental evidence exists for the potential magnitude of these effects. Therefore, we investigated whether consecutive heat waves of different severities would have the same impact on tree growth as a constant increase in temperature with equivalent heat sum and considered (CO<sub>2</sub>) and available soil moisture as potential interacting factors. Seedlings of *Quercus rubra* and *Pinus taeda* were grown under ambient or elevated (CO<sub>2</sub>) (380/700 μmol CO<sub>2</sub> mol<sup>-1</sup>) and three temperature treatments: ambient +3 °C, moderate heat wave every second week (+6 °C) or severe heat wave every fourth week (+12 °C). All temperature treatments had the same average temperature (+3 °C above ambient) across the five-month experimental growth period. Half the seedlings were watered to field capacity (50% (v/v) on average), the other half to 30%. Stem height and diameter were measured monthly. Biomass accumulation and partitioning were measured after five months. In ambient (CO<sub>2</sub>), seedlings of both species had significantly less biomass (up to 39%) when exposed to +12 °C heat waves compared to a constant +3 °C increase. These decreases were mitigated by elevated (CO<sub>2</sub>) in *Quercus* but not in *Pinus*. Despite having the lowest biomass, *Quercus* seedlings in the +12 °C heat wave treatment grew taller (up to 17%) than all other *Quercus* seedlings. In contrast, *Pinus* seedlings in the +12 °C heat wave treatment had consistently lower height and stem diameter compared with all other treatments within each soil water treatment. Soil water treatment had a greater effect than (CO<sub>2</sub>) on stem height, diameter and total biomass, with reduced growth under low soil water content compared with high soil water content (up to 55% smaller and up to 63% less biomass). We conclude that (a) heat waves produced more stress than the same amount of heat applied uniformly; (b) elevated (CO<sub>2</sub>) at least partially mitigated negative effects of heat waves; and (c) drought was a more severe stressor than heat waves.

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### 1. Introduction

For this century, a 3 °C rise in average surface temperature (Houghton et al., 2001; IPCC, 2007), a change in the amount and seasonality of precipitation (Dore, 2005; Roy et al., 2012), and an increase in the frequency of climate extremes, including heat waves, have been predicted coincident with an increase in atmospheric CO<sub>2</sub> concentration (CO<sub>2</sub>) up to 700 μmol mol<sup>-1</sup> (Easterling et al., 2000; Meehl and Tebaldi, 2004; Schar et al., 2004). In this manuscript, the term “heat wave” denotes a time period during which air temperature is not only significantly higher than its

average over the past 30 years, but furthermore high enough to induce a distinct response from the studied object (in this case: tree seedlings). This definition is loosely based on Reichstein et al. (2013), who attempted to give a more general definition of climate extremes.

Heat waves, during which high temperatures often coincide with drought and high solar irradiation, are garnering scientific interest as the number of extreme weather events has grown larger in recent decades (Coumou and Rahmstorf, 2012; Rahmstorf and Coumou, 2011). For example, the number of summer heat waves in the eastern United States increased by 20% from 1949 to 1995 (Gaffen and Ross, 1998). Similarly, the number of heat waves longer than 10 days significantly increased from 1961 to 2009 in many regions in Pakistan (Zahid and Rasul, 2012). Summer heat waves have doubled in length (from 1.4 to 3.0 days per heat wave) and the frequency of hot days tripled in Western Europe in recent years

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compared with the early 20th century (Della-Marta et al., 2007). This trend is considered very likely to continue in this century (Diffenbaugh and Ashfaq, 2010; Lynn et al., 2007).

Extreme heat waves are expected to have, and may already have had significant impacts on crop productivity and natural ecosystems (IPCC, 2007). Xu et al. (2012), in an observational study, found that an increasing trend in heat waves corresponded to a decrease in vegetation growth in Northern China, though not Southern China. A 30% decrease in gross primary productivity in forests across Western Europe in 2003 was attributed to a severe heat wave in summer (Ciais et al., 2005). However, these and similar observational studies documenting the effects of heat waves provide little insight into individual species responses to heat waves (e.g. Bertini et al., 2011; Ciais et al., 2005). One approach to a better understanding of the effects of heat waves on plants is to study them in the context of the total heat sum that the plants experience. Amey et al. (2012) and Bauweraerts et al. (2013) were the first to provide experimental evidence that heat waves affected plant functioning differently than a constant temperature increase with equivalent heat sum, and that atmospheric ( $\text{CO}_2$ ) and soil water content had a significant influence on this effect.

Elevated atmospheric ( $\text{CO}_2$ ) has a stimulating effect on growth in  $\text{C}_3$  species which generally becomes more pronounced under higher temperatures: increased availability of  $\text{CO}_2$  reduces photorespiration, while increased temperature accelerates most biological reactions up to a thermal optimum, after which further increased temperature will cause heat stress (Norby and Luo, 2004; Lewis et al., 2001; Sage and Kubien, 2007). Low soil water content or drought conditions usually exacerbate the negative effect of heat stress on growth, by reducing the potential for evaporative cooling (Aranjuelo et al., 2007; De Boeck et al., 2010). Elevated atmospheric ( $\text{CO}_2$ ) increases leaf internal ( $\text{CO}_2$ ), which can reduce stomatal conductance (Ainsworth and Rogers, 2007), thereby increasing stomatal resistance to water vapour diffusion and reducing water usage (Wullschlegel et al., 2002). This effect is beneficial in the long term but might also limit the plant's potential for rapid evaporative cooling under short term intense heat stress (Kolb and Robberecht, 1996).

In addition to effects on overall biomass accumulation, heat, ( $\text{CO}_2$ ), and water availability have also been reported to influence biomass partitioning. Drought conditions typically induce more root growth and less leaf growth (Chiatante et al., 1999; Dai et al., 2007). Elevated ( $\text{CO}_2$ ) has been reported to increase carbon allocation to roots and specifically to growth of fine roots (Lutze and Gifford, 1998; Suter et al., 2002). Elevated temperature may also lead to increased carbon allocation to roots (Stirling et al., 1998) and sometimes to higher specific leaf weight, which may or may not be linked to increased carbon allocation to the leaves (Gunn and Farrar, 1999; Teskey and Will, 1999). Interactive effects between ( $\text{CO}_2$ ), water availability and heat stress on tree growth have not been thoroughly examined, nor has the effect of heat waves on carbon allocation.

The objective of this study was to evaluate the effect of consecutive heat waves on tree growth compared to that of a constant temperature increase with equivalent heat sum. Because of their sensitivity to environmental stresses, the experiment was conducted on seedlings. A coniferous evergreen (*Pinus taeda* L.) and a deciduous broadleaf (*Quercus rubra* L.) were selected. In the context of climate change, different levels of atmospheric ( $\text{CO}_2$ ) and soil water content were considered as potential interacting factors. We performed our analyses based on the following hypotheses: (1) stem height, stem diameter, and total biomass accumulation will be lower in heat wave treatments than in the constant elevated temperature treatment, but elevated ( $\text{CO}_2$ ) will mitigate the differences; (2) the effect of soil water availability on stem height, stem diameter, and total biomass accumulation will be greater

than effects of ( $\text{CO}_2$ ) and temperature treatments; and (3) elevated ( $\text{CO}_2$ ), low soil water availability, and temperature extremes will all lead to increased carbon allocation to the roots.

## 2. Materials and methods

### 2.1. Study site

The study site was located at Whitehall Forest, a research unit of the University of Georgia in Athens, GA ( $33^\circ 57' \text{N}$ ,  $83^\circ 19' \text{W}$ , altitude 230 m). Six treatment chambers, half-cylinder in shape and measuring 3.62 m length by 3.62 m width by 2.31 m height were constructed at the site. The chambers were constructed according to the method described in Boyette and Bilderback (1996), with lumber bases and PVC pipe frames supporting 0.15 mm thick clear polyethylene film (GT Performance Film, Green-Tek Inc., Edgerton, WI, USA). The chambers were placed in an open field, spaced 3.7 m apart to minimise shading, and oriented facing south to maximise daily sun exposure.

### 2.2. Plant material

Seeds of a deciduous broadleaf (*Quercus rubra* L.) and an evergreen conifer (*Pinus taeda* L.) were planted on 1 December, 2009 in 0.5 L pots in potting medium (Fafard Nursery Mix, Conrad Fafard Inc., Agawam, MA, USA). The *P. taeda* seeds were from a single family in Morgan County, GA (Family 15042, Plum Creek Timber Company, Athens, GA USA). The *Q. rubra* seeds were obtained from a wild collection in Tennessee (Louisiana Forest Seed Company, 135 Lecompte, LA USA). This provenance is in the southernmost region of the species range (Little, 1971).

In February 2010 the seedlings were transplanted to 8 L pots (cylindrical in shape; 22 cm diameter, 22 cm height) in the same potting medium. The pots were watered three times a day to saturation until treatments started. In April, May, June and July each pot was fertilised with 30 g of 15-9-12 extended release fertiliser (Osmocote plus #903286, Scotts-Sierra Horticultural Products, Marysville, OH, USA). In May, 0.04 mL imidacloprid was applied topically to the soil in each pot to prevent insect infestation (Bayer advanced 12 months tree and shrub insect control, Bayer, Monheim am Rhein, Germany).

### 2.3. Experimental design and monitoring

The setup of this experiment was based on Wertin et al. (2010). Each treatment chamber was assigned one of six treatment combinations. These combinations were produced by two factors: atmospheric ( $\text{CO}_2$ ) and chamber temperature. The ( $\text{CO}_2$ ) treatments were ambient ( $\text{CO}_2$ ) ( $C_A$ ,  $380 \mu\text{mol CO}_2 \text{ mol}^{-1}$ ) or elevated ( $\text{CO}_2$ ) ( $C_E$ ,  $700 \mu\text{mol CO}_2 \text{ mol}^{-1}$ ). The temperature treatments were ambient  $+3^\circ\text{C}$  ( $T_{A3}$ ), a heat wave elevating ambient by  $6^\circ\text{C}$  every other week ( $T_{HW6}$ ), and a heat wave elevating ambient by  $12^\circ\text{C}$  every four weeks ( $T_{HW12}$ ). Each applied heat wave lasted for one week, and both heat wave treatment schemes were repeated every four weeks throughout the growing season. The elevated temperature treatments  $T_{A3}$ ,  $T_{HW6}$  and  $T_{HW12}$  represent the same applied heat sum and correspond to an average increase of  $3^\circ\text{C}$  over a four week period and the entire growing season (May through September). In this context, the heat treatments may also be considered as differences in temperature variability. Within each chamber we assigned half of the seedlings to one of two water treatments. These water treatments consisted of watering to field capacity ( $W_H$ , 50% (v/v) on average) or maintaining target volumetric water content of 30% ( $W_L$ ). Thus the experiment was a complete factorial of  $2 (\text{CO}_2) \times 3 \text{ temperature} \times 2 \text{ water treatments}$ .

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