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The effect of induced heat waves on *Pinus taeda* and *Quercus rubra* seedlings in ambient and elevated CO_2 atmospheres

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Summary

- Here, we investigated the effect of different heat-wave intensities applied at two atmospheric CO_2 concentrations ([CO_2]) on seedlings of two tree species, loblolly pine (*Pinus taeda*) and northern red oak (*Quercus rubra*).
- Seedlings were assigned to treatment combinations of two levels of [CO_2] (380 or 700 µmol mol^{-1}) and four levels of air temperature (ambient, ambient +3°C, or 7-d heat waves consisting of a biweekly +6°C heat wave, or a monthly +12°C heat wave). Treatments were maintained throughout the growing season, thus receiving equal heat sums. We measured gas exchange and fluorescence parameters before, during and after a mid-summer heat wave.
- The +12°C heat wave, significantly reduced net photosynthesis (A_{net}) in both species and [CO_2] treatments but this effect was diminished in elevated [CO_2]. The decrease in A_{net} was accompanied by a decrease in F_v'/F_m' in *P. taeda* and Φ_{PSII} in *Q. rubra*.
- Our findings suggest that, if soil moisture is adequate, trees will experience negative effects in photosynthetic performance only with the occurrence of extreme heat waves. As elevated [CO_2] diminished these negative effects, the future climate may not be as detrimental to plant communities as previously assumed.

Introduction

Atmospheric carbon dioxide concentration ([CO_2]) is rapidly increasing because of anthropogenic contributions. According to the fourth assessment report (AR4) of the IPCC, [CO_2] is expected to reach 700 µmol mol^{-1} by the year 2100 (Meehl *et al.*, 2006; IPCC, 2007). Models show that, because of the rise in [CO_2] and other glasshouse gasses, global air temperature is expected to rise by between 1.7°C and 4.4°C by the end of the 21st century (SRES: A1B) (IPCC, 2007). In addition to the rise in air temperature, plants are likely to face an increase in frequency and severity of weather extremes, such as heat waves (Meehl & Tebaldi, 2004; Tebaldi *et al.*, 2006; IPCC, 2007; Ballester *et al.*, 2010). Although there is no generally accepted definition for a heat wave, heat waves have been defined using temperature–mortality criteria (Montero *et al.*, 2010) or, more commonly, statistical–meteorological criteria (Frich *et al.*, 2002; Meehl & Tebaldi, 2004; Meehl *et al.*, 2006; IPCC, 2007; Ballester *et al.*, 2010). A heat wave was defined by Frich *et al.* (2002) and Tebaldi *et al.* (2006) as at least five consecutive days with maximum temperatures at least 5°C higher than the climatological norm of the same calendar days. This definition was adopted by the IPCC (2007) and will be used here.

The individual effects of elevated [CO_2] (Ceulemans & Mousseau, 1994; Long *et al.*, 2004; Ainsworth & Rogers, 2007) or elevated temperature (Saxe *et al.*, 2001; Sage & Kubien, 2007) on plant performance have been studied intensively. A general conclusion from this research was that a rise in [CO_2] or temperature had beneficial effects on both photosynthesis and biomass production. For example, when [CO_2] was doubled, increases in net photosynthesis were reported ranging from 43% to 192% in *Pinus taeda* (Teskey, 1997; Tissue *et al.*, 1997; Ellsworth, 1999; Wertin *et al.*, 2010; Frenck *et al.*, 2011) and from 30% to 256% in *Quercus rubra* (Kubiske & Pregitzer, 1996; Anderson & Tomlinson, 1998; Cavender-Bares *et al.*, 2000).

Generally, an increase in air temperature also has a positive effect on net photosynthesis and growth (Sage & Kubien, 2007; Way & Oren, 2010). However, most elevated temperature studies have applied a constant increase in air temperature, while models predict an increase in extreme heat events, that is, heat waves (Ballester *et al.*, 2010). Plant responses to heat waves have received little study. De Boeck *et al.* (2011) reported that the maximum rate of net photosynthesis was diminished by summer and autumn heat waves in a well-watered experimental plant community containing three perennial herbaceous species (*Plantago lanceolata*, *Rumex acetosella* and *Trifolium repens*). The community was able to minimize heat stress through transpirational cooling. When combined with drought stress, heat waves exacerbated the negative effect of drought stress. Hamerlynck *et al.* (2000)