



Commentary

Will rising CO₂ and temperatures exacerbate the vulnerability of trees to drought?

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Large-scale tree dieback events are increasing in frequency around the world, with many of them attributed to the effects of climate change-related droughts (i.e., droughts that co-occur with heat stress) (Adams et al. 2010, Allen et al. 2010). As mean global temperatures are expected to rise by 2–4 °C in the next 85 years (Christensen et al. 2007) and elevated temperatures are correlated with higher vapor pressure deficits and evaporative driving forces (Oishi et al. 2010), we may expect a rise in tree mortality due to drought in a warmer future. However, climate warming is mainly driven by rising atmospheric CO₂ concentration, a factor that can increase plant drought tolerance (Drake et al. 1997). The degree to which these two global change factors will alter the vulnerability of trees to drought is unclear, and combinatorial experiments studying the effects of both warming and elevated CO₂ on tree drought tolerance are rare (but see Wertin et al. 2010, 2012, Zeppel et al. 2012, Lewis et al. 2013).

Research on what causes tree mortality during climate-change drought events tends to focus on two hypotheses: direct hydraulic failure or carbon starvation (McDowell et al. 2008). The first hypothesis acknowledges that if stomata remain open during drought to maintain carbon fixation for metabolism, then the associated water losses from transpiration will eventually cause catastrophic cavitation (Anderegg et al. 2012). The second hypothesis focuses on the role of stomata in maintaining the integrity of the hydraulic pathway of trees. As stomata close during drought, respiration continues to burn carbohydrates without new photosynthetic carbon fixation and the plant's carbohydrate stores are depleted until they cannot maintain metabolic needs (Adams et al. 2009). The

role of carbon starvation in limiting tree survival and responses to climate is clearest during glacial periods with low CO₂ concentrations (~200 ppm) (Gerhart et al. 2012), but low stomatal conductance during drought may generate analogously low intercellular CO₂ concentrations under future high CO₂ conditions. Lastly, the interdependence of water transport and carbohydrate status in trees has also received increasing recognition (McDowell et al. 2011, Sala et al. 2012): phloem transport of sugars to sink tissues requires adequate water transport, and there is recent evidence that embolism repair may depend on carbohydrate availability (Secchi and Zwieniecki 2011).

In this issue of *Tree Physiology*, Duan et al. (2013) add to our growing knowledge of how climate change may alter this second aspect of drought tolerance, plant carbon dynamics. They looked at the combined impact of elevated CO₂ concentrations and warming on leaf-level carbon fluxes, growth and non-structural carbohydrate (NSC) status in droughted *Eucalyptus* seedlings. While elevated CO₂ increased plant carbon status and growth, and high temperatures reduced leaf carbon balance during moderate drought, these treatment effects were not evident as the drought became severe. When high CO₂ and growth temperatures were applied concurrently, they increased growth during the early, moderate stage of the drought, but this response also disappeared as water stress progressed. The data also indicate the difficulty in predicting whole-tree NSC status or growth from leaf-level carbon fluxes. In *Eucalyptus* experiencing a sustained drought, elevated temperatures suppressed photosynthesis and stimulated respiration, which might be expected to reduce growth and NSC content. But instead,

seedling mass and NSC tended to be higher in warm-grown plants than in ambient-climate seedlings.

The effects of climate change factors on the other side of tree drought tolerance, hydraulic vulnerability, also deserve more study. High CO₂ reduces leaf-level stomatal conductance, which is the basis for predicting that plants will use less water and be less sensitive to drought in the future (Ainsworth and Rogers 2007). While overall allocation between roots and shoots is unaffected by elevated CO₂ (Poorter et al. 2012), some trees and younger stands that develop at elevated CO₂ have larger canopy areas, offsetting some of the leaf-level water savings at the whole tree and forest plot levels (Bobich et al. 2010, Warren et al. 2011a, Medeiros and Ward 2013). CO₂ concentration can also alter xylem anatomy, with an overall tendency for larger conduit sizes at high CO₂ in ring-porous species and some conifers, but little difference in xylem vessel diameter in diffuse-porous tree species (e.g., Conroy et al. 1988, Atkinson and Taylor 1996, Saxe et al. 1998, Ceulemans et al. 2002, Kaakinen et al. 2004, Watanabe et al. 2008, Domec et al. 2010, Phillips et al. 2011). Where elevated CO₂ increases the conduit size, this translates into lower stem cavitation resistance (Domec et al. 2010) that may make trees more vulnerable to moderate drought stresses. As well, lower stomatal conductance at high CO₂ reduces transpirational cooling of leaves and raises leaf temperatures (Bernacchi et al. 2007), which can actually increase the vulnerability of trees to drought during hot, dry spells (Bobich et al. 2010, Warren et al. 2011b).

With respect to warming, higher growth temperatures tend to increase the canopy leaf area and generally lead to smaller root-to-shoot ratios in trees, both of which may make future trees less capable of withstanding drought (Way and Oren 2010, Poorter et al. 2012). Growth at high temperatures can alter xylem anatomy, hydraulic conductivity and cavitation

vulnerability (Maherali and DeLucia 2000a, 2000b, Thomas et al. 2004, Phillips et al. 2011) and these anatomical and physiological changes can make warm-grown trees more susceptible to drought (Way et al. 2013). Higher growth temperatures also influence carbon dynamics parameters that may influence the ability to survive a drought. Warming tends to stimulate respiration rates and may accelerate the depletion of carbon stores (Adams et al. 2009), although acclimation can offset this significantly in tree species (Way and Oren 2010). While photosynthetic acclimation to elevated temperatures can maintain carbon gain in woody species, not all species show significant thermal acclimation of photosynthesis, especially if the warming is substantial (Way and Oren 2010, Way and Yamori in press).

Duan et al. (2013) add to the growing literature on how tree carbon dynamics under drought respond to combined high CO₂ and elevated temperatures, a topic where we need more data to make strong predictions about future forest behavior. There are, however, only two studies to my knowledge that examine any aspect of how tree hydraulic characteristics respond to these two combined growth conditions (Maherali and DeLucia 2000b, Phillips et al. 2011). So, how do we move forward with the data we have? While we cannot rely heavily on the results of single-factor studies in predicting how future vegetation will be affected by drought, we can look for commonalities in the responses of tree hydraulic and carbon balance traits to either global change factor alone (Table 1). This analysis suggests that hydraulic traits (such as the water potential at which 50% of hydraulic conductivity is lost, or the P50) may predispose trees to being more vulnerable to drought under future conditions, while carbon dynamic parameters may be more resilient to combined changes in temperature and CO₂. In summary, we clearly need more information on how trees will respond to drought when they develop under

Table 1. Physiological and anatomical traits in trees that may affect drought tolerance, their generalized responses to either elevated growth temperatures or elevated CO₂ concentrations and postulated responses to combined elevated temperatures and growth CO₂ where responses to the single factors overlap.

Trait	Elevated growth temperatures	Elevated CO ₂ concentration	Both elevated CO ₂ and temperature
Leaf-level net CO ₂ assimilation rates	Lower to higher (dependent on degree of warming)	Higher	Probably higher
Leaf-level respiration rates	Same to higher	Same	Same to higher
Leaf-level g_s	Lower (if VPD increases)	Lower	Lower
Canopy level g_s	Lower to same (if VPD increases)	Lower to same	Lower to same
Leaf temperatures	Higher	Higher	Higher
Canopy area	Higher	Same to higher	Probably higher
Root to shoot ratio	Lower	Same	Currently unclear
Xylem vessel/tracheid diameter	Lower to higher	Same (diffuse-porous species) Higher (ring-porous species) Same to higher (conifers)	Currently unclear
P50	Lower to same	Lower to same	Lower to same

Trends are taken from literature cited in the text.

g_s , stomatal conductance; P50, water potential at which half of the hydraulic conductivity of a tissue is lost; VPD, vapor pressure deficit.

both elevated CO₂ and growth temperatures, if we are to attempt to mitigate and adapt to the effects of climate change in forests.

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