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Commentary

Tree responses to drought

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With global climate change, drought may become more common in the future (IPCC 2007). Several factors will promote more frequent droughts: earlier snowmelt, higher temperatures and higher variability in precipitation. For ecosystems where the water cycle is dominated by snowmelt, warmer temperatures bring earlier melt (Stewart et al. 2005) and longer, drier snow-free periods (Westerling et al. 2006). Higher temperatures will also increase vapor pressure deficit if evapotranspiration does not also increase. Greater variability in precipitation has two implications for plant water balance: longer periods without water, and less captured in the soil in the more intense storms.

Many recent tree mortality events have been linked to drought (Allen et al. 2010), but how much do we really know about the drought responses of trees? Physiological responses of trees to low soil water potential vary, but have been fairly well characterized (McDowell et al. 2008)—they vary from concomitantly lower leaf water potential (anisohydric response) to maintenance of leaf water potential above a threshold (isohydric response) with various strategies in between. Many tree species shed leaves during a strong drought, reducing transpiration and photosynthesis, and adjust partitioning to roots and storage (McDowell et al. 2008). Drought also 'weakens' trees and makes them more susceptible to insect attacks and pathogens (McDowell et al. 2008). Growth can be reduced through impairment of cell division and cell expansion (Hsiao 1973), which occurs at a lower water stress threshold than does photosynthetic inhibition (Hsiao et al. 1976). In fact, a variety of physiological processes respond at different plant water potentials (Hsiao 1973, Ditmarová et al. 2010), so that the severity of the drought will influence the physiological response. Drought is also relative—species adapted to low precipitation climates can survive low soil water potentials that would kill or seriously wound trees in more mesic climates and trees in mesic climates might suffer from 'drought' that would be normal to trees in xeric climates. Finally, we know that there are many mechanisms of drought tolerance, and that many of these involve coordination within the whole tree.

Two papers in this issue try to untangle some of the complex and variable responses of trees to drought. Larcheveque et al. (2011) droughted two different hybrid poplar saplings (each with *Populus balsamifera* as a parent) and compared their response with that of saplings of *P. balsamifera*. The study found that the three poplar clones had three different responses to drought. While all were anisohydric, they showed varying degrees of regulation of leaf water potential, differences in shedding leaves, root growth and stem growth, and differences in water use efficiency. These variable responses among closely related species suggest that both predicting drought response and selecting for drought tolerance on the basis of any simpler metric besides actual growth under drought will be difficult.

A second paper (Galvez et al. 2011) used aspen seedlings to address the issue of whether drought causes carbon starvation by examining root carbohydrates. This study found that the drought quickly lowered stomatal conductance, photosynthesis and height growth, but that root carbohydrate reserves increased in the droughted treatment relative to controls. The increase in root starch concentrations suggests that either drought was not causing carbon starvation, or if the seedlings were starving, that they would not or could not use carbohydrate reserves to address any carbon balance problem (Sala et al. 2010).

The framework for understanding plant survival and mortality responses to drought recently proposed by McDowell et al. (2008) suggests that both hydraulic failure and carbon starvation arise from how the plant's xylem responds to dry soil conditions. Isohydric plants would be more likely to experience carbon starvation and anisohydric plants would be more likely to experience hydraulic failure and desiccation (McDowell et al. 2008), but a variety of interacting mechanisms are also possible (McDowell 2011). In a commentary on the McDowell et al. (2008) article, Sala et al. (2010) suggested that the amount of carbohydrate storage was neither a good predictor of mortality, nor a good indicator of available reserves to outlast the drought because lower plant water potential could lead to problems mobilizing and transporting carbohydrates. Interference with carbohydrate transport could, in turn, starve living plant cells even with abundant plant reserves. Understanding the mechanisms of drought response, survival and mortality will be critical for predicting tree response to a changing climate (McDowell 2011). While we have many clues and puzzle pieces in plant drought responses, our understanding of plant carbon balance, carbon storage, plant water relations (particularly refilling embolized xylem and the use of xylem-stored water) and whole tree coordination is not robust enough to make well-founded predictions (McDowell 2011). Additionally, since plants show such variety in their responses to drought, identifying generalities may be difficult.

I offer two suggestions for future studies involving drought responses. First, use a whole tree approach, and second, avoid making inferences about plant carbon balance from plant carbohydrate reserves.

The first component of a whole tree approach is to recognize that because inferences about plant carbon balance from measurements of process rates are very difficult, carbon balance should be measured. For example, leaf photosynthesis measurements are often taken under standard conditions, while the carbon balance of a plant will be regulated by total canopy photosynthesis—a complex function of photosynthetic capacity, leaf area, light environment, temperature and stomatal conductance (itself a complex function of light, hydraulic feedbacks and vapor pressure deficit). I think it unlikely that total canopy photosynthesis would be related to photosynthesis measured under standard conditions in a simple, linear manner. A similar argument could be made for measurements of respiration rates. Many studies also neglect to measure the flux of carbon to foliage, wood, roots, storage and respiration, but suggest inferences to carbon balance. Other studies measure only a few of these carbon fluxes, such as wood growth—which represents only about 20% of annual photosynthesis (Litton et al. 2007). To really understand how drought (or any other effect) changes plant carbon balance, I submit that one needs to measure plant carbon balance. This is relatively simple to do for seedlings and saplings, and challenging (but possible) for large trees (Ryan et al. 2004).

The second component of a whole tree approach is to integrate measurements of water and carbon when studying drought response, like the Larcheveque et al. (2011) and Galvez et al. (2011) studies. Often, studies making inferences about the effects of water on carbon measure only water (I'll offer up my own example (Ryan et al. 2000)). Trees adjust to drought in many ways and simply looking at one of them is not likely to be effective. Metcalfe et al. (2010) and related studies from the Amazon throughfall exclusion experiment provide an excellent example of insights into the complex ways in which trees respond to drought made possible through coordinated water and carbon measurements.

For the second suggestion, evidence is growing that the assumption that carbohydrate concentrations in plant tissues convey information about plant carbon balance is wrong. Experiments show that changing sink strength for carbon can cause carbohydrate levels to increase, decrease or remain constant. For example, across just four studies, carbohydrate concentrations increased as growth decreased (Genet et al. 2010), carbohydrate concentrations were not related to growth (Bansal and Germino 2010), defoliation had no effect on carbohydrate pools (Eyles et al. 2009) and harvesting latex from rubber trees increased carbohydrate concentrations (Chantuma et al. 2009). Also, carbohydrate concentrations vary widely seasonally, so one-time samples are not very informative (Regier et al. 2010). Galvez et al. (2011) offers another example: the seedlings obviously stopped growing, but carbohydrate concentrations increased in roots. Carbohydrate concentrations are also only part of the story, because the flux is likely more important (change in concentration over time × tissue mass). The flux deposited or withdrawn from storage relative to photosynthetic inputs, growth and respiratory demands is likely what matters, not simply concentrations or changes in concentrations over time.

Tree responses to drought are likely to be complex and varied, and involve the entire tree. Let us broaden our measurements to the entire tree and coordinate measurements of water and carbon to make better inferences.

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