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Commentary

Drought-induced tree mortality: from discrete observations to comprehensive research

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There is an increasing need for a global monitoring network to assess rates of tree mortality. In spite of numerous reports of tree death, mostly linked to climate change and related droughts, quantitative assessments of tree mortality rates and the magnitude of tree mortality events are largely missing (Hartmann et al. 2015). Except for human-caused deforestation, the largest forest losses in the past decade are likely those in central Russia following the 2010 wildfires and those in NW North America due to the mountain pine beetle epidemic. Although tree mortality was not the direct result of drought in either case, the 2010 wildfires were related to an exceptional heat wave (de Groot et al. 2013) and beetle infestation dynamics are closely linked with a warming trend (Bentz et al. 2010).

Identifying the underlying causes of tree mortality events requires deciphering the eco-physiological pathways leading to tree death using field measurements. Three major mechanisms have been proposed to explain how trees die during drought: (i) hydraulic failure; (ii) carbon starvation as a result of prolonged stomatal closure; and (iii) increased attacks by biotic agents, promoted by reduced plant defence capabilities (McDowell et al. 2008, Martínez-Vilalta 2014). The investigation of each potential mechanism has exposed important knowledge gaps and technical difficulties. These are exemplified by recent discussions about the definition and scope of carbon starvation, such as whether trees might lose all their carbon reserves before death (McDowell 2011) or whether they may lose the ability to allocate carbon to certain tissues (Sala et al. 2010). Other discussions have debated whether xylem cavitation and its reversal are uncommon (Cochard and Delzon 2013), or rather routine in certain species (Klein et al. 2014). On top of these debates, methodological issues have been raised, regarding the measurement both of hydraulic traits (Jansen et al. 2015) and of non-structural carbohydrates (NSCs; Quentin 2014). In light of these hardships, studies investigating any of the three mortality mechanisms in a coherent way have already made key contributions to our understanding of the physiology underpinning tree mortality. However, an investigation of more than one mechanism in a forest die-off study would require an extensive, fully integrated research project, or even several complementary projects.

The paper by Aguade et al. (2015) in this issue of *Tree Physiology* is among the first studies investigating all three mechanisms simultaneously. Studying drought-stressed Scots pine (*Pinus sylvestris* L.) growing near the edge of its distribution in a forest in northern Spain, Aguade et al. skilfully combined water relations measurements with an assessment of the tree carbon economy and a study of root rot infection by a fungal pathogen. This comprehensive research approach complements that of another recent *Tree Physiology* paper about the relationship between seasonal carbohydrate dynamics and the degree of fungal infection on Douglas fir needles (Saffell et al. 2014). To these two components, Aguade et al. (2015) added the essential hydraulic aspect, studying all three mortality mechanisms in a drought context. Both these papers highlight the intertwined nature of the physiological mechanisms leading to tree death. In order to partition the specific contribution of each mechanism in the field, interactions between the mechanisms must be carefully studied. A realistic research approach to disentangling potential mortality mechanisms must consider two different facets of carbon and water in plants: they are necessary for plant life both at the whole-tree scale (i.e., as fluxes) and for specific functional tissues. Drought can impact whole-tree hydraulic conductivity, via xylem cavitation, and can affect leaf hydration, arresting meristematic growth through the loss of

turgor. Similarly, the carbon economy of a tree is sensitive at the level of whole-tree transport, through phloem flow disorders, and at the level of specific storage pools, such as root starch. On top of these drought effects, biotic stressors such as insects and fungal pathogens can act on carbon and water in any of the tree compartments, including foliage, stem or roots (Figure 1a).

Yet the greatest difficulty in disentangling potential mortality mechanisms stems from the fact that trees are capable of responding to drought stress in ways that differ from their behaviour under mesic conditions. Drought resistance strategies range from stomatal closure to carbon remobilization (Canham et al. 1999, Körner 2003), adjustments of the ratio of leaf area to sapwood area (Mencuccini 2003, McDowell et al. 2006), shifting of growth phenology (Grünzweig et al. 2003), recovery of xylem conductivity following cavitation (Taneda and Sperry 2008, Brodersen and McElrone 2013), and also changes in root system architecture (Breda et al. 2006) and xylem vessel anatomy (Eilmann et al. 2009). Defoliation, while serving as a stress indicator, is also an important drought response, minimizing water losses and maintenance respiration at times of decreased gas exchange (Klein et al. 2014). In studying tree mortality, such physiological responses should be identified, and their influence on the tree drought-stress status must be assessed (Figure 1b and c). In their research, Aguade et al. (2015) cleverly accounted for defoliation, showing that defoliated trees had lower xylem cavitation levels and faster recovery after drought than non-defoliated trees.

Tree mortality usually results from functional damage to one or more of the water and carbon fluxes and tissue concentrations, further exacerbated by biotic attacks (Figure 1a). The dynamics of the water and carbon fluxes depend on the balance between drought duration, tree drought responses and biotic attacks. For example, when stomatal closure occurs, the subsequent reductions in sap flow and carbon transport can be alleviated as a result of partial defoliation (Figure 1b). Water status of the remaining leaves might recover, while carbon storage in specific compartments (e.g., root NSC) continues to decline, potentially due to prevailing carbon sinks (e.g., root growth for soil water exploration), as shown in Aguade et al. (2015). Fungal root rot infection exerts an immediate limitation on water uptake and a delayed effect on the root NSC pool and phloem flow. If drought persists, all four components (water and carbon transport fluxes and tissue levels) might reach a zero level at the point of death (Figure 1b; Poyatos et al. 2013). Depending on the tree species, an alternate scenario might include hydraulic recovery via cavitation reversal (Brodersen and McElrone 2013), in turn improving leaf hydration and root NSC stores (Figure 1c). Biotic stress, such as from bark beetle attack, might severely affect phloem flow and hence carbon transport. If the cavitation reversal mechanism is promoted by sugar secretion into the xylem, then a loss of carbohydrate supply might prevent a tree from repairing its xylem, resulting in a loss of hydraulic conductivity. Limited carbon re-mobilization capacity would also imply that trees might die with residual amounts of NSC in their tissues (Figure 1c).

The simplified, speculative mortality scenarios described here demonstrate some of the complexities eco-physiologists face when trying to decipher causes of tree mortality. First, the carbon and water economies of trees are closely linked: the functions of xylem and phloem are tightly bound, and at the leaf level, stomata balance carbon gain and water loss. Therefore, it is hard to separate discrete drought effects on specific fluxes and tissues. Second, tree drought responses interact with these economies and hence their impact is often difficult to measure. And third, pathogens may exert systemic effects on carbon and water fluxes even when their immediate effect is limited to a

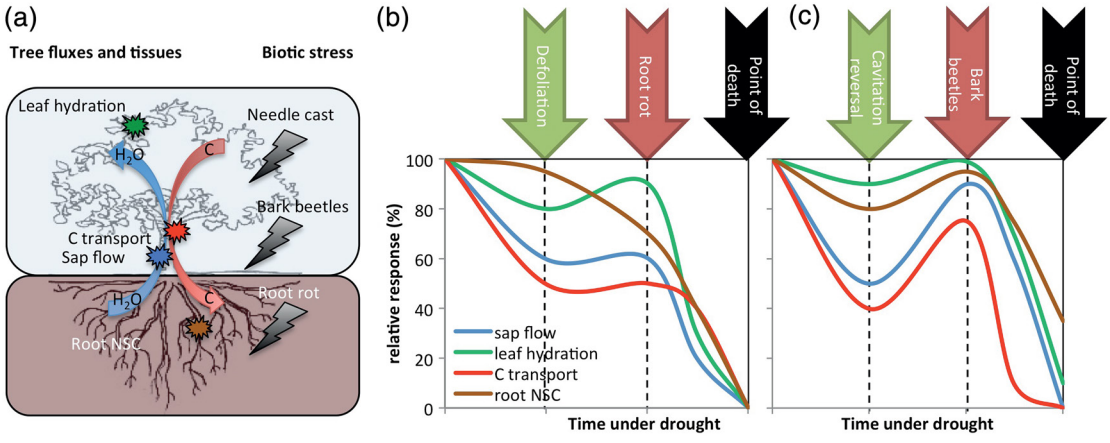

Figure 1. A schematic representation of (a) the major constituents of mortality mechanisms in a drought-stressed tree; and (b and c) two hypothetical mortality scenarios, showing the effects of tree drought responses (green arrows) and biotic stressors (red arrows) on water and carbon fluxes (sap flow and carbon transport, respectively) and water and carbon tissue-level pools (leaf hydration and root NSC concentration, respectively). Tree mortality from drought usually involves damage to one or more of these four constituents, further exacerbated by biotic attacks. The dynamics of the water and carbon fluxes depend on the balance between drought duration, tree drought responses and biotic stress intensity.

specific compartment. Also, warming and drying may affect biotic stressors independently. For example, fungal pathogens might decline with drying, whereas bark beetles might benefit from warming (Bentz et al. 2010). For the sake of clarity, the scenarios in Figure 1 present a sequential order of events, but in reality physiological drought responses and biotic attacks can occur simultaneously. To these uncertainties one needs to add the simple fact that in some cases research efforts are too late to assess the cause of mortality during an event, and a post-mortem investigation is all that can be performed, in spite of further limitations.

In parallel with any environmental change such as drought, the continuous increase in atmospheric CO_2 may further alter tree drought responses. Increased CO_2 can stimulate photosynthesis while reducing transpiration, thereby increasing tree water-use efficiency (e.g., Maseyk et al. 2011, Keenan et al. 2013). Alternatively, surplus assimilates in a high CO_2 atmosphere may be stored as NSC, which can in turn act as osmoregulators or as a carbon source to extend tree survival under drought (O'Brien et al. 2014). It is therefore often hypothesized that increased CO_2 levels should promote higher tree drought resistance (Tschaplinski et al. 1993, Zinta et al. 2014, but see Beerling et al. 1996, Duan et al. 2014). Ongoing and future research programmes investigating the effect of interactions between drought and elevated CO_2 on tree physiology should help improve predictions of tree mortality events in a warmer, high CO_2 future.

An interdisciplinary approach has a good potential to overcome many of the difficulties outlined here, by providing a comprehensive view of the drought-stressed tree. Future research should investigate both water and carbon components of drought, acknowledging the differences between fluxes and tissue-level pools. Water transport is often assessed by sap flow sensors, while carbon transport measurement should rely on newly developed methodologies (e.g., Windt et al. 2006, Savage et al. 2013). The existence of biotic stressors must be carefully investigated in each system, preferably by a phytopathology expert. In many cases, living drought-stressed trees at various levels of stress offer the best system to study drought-induced tree mortality (Aguade et al. 2015). Considering that mortality scenarios are highly case-specific, additional comprehensive studies like that of Aguade et al. (2015) are needed across different species and biomes. Finally, to isolate the mortality mechanism(s), fieldwork should be complemented by well-designed greenhouse studies. Drought experiments can also take advantage of recently developed genetic tools to pinpoint the mortality mechanisms at the molecular level.

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