# Misunderstanding sap ascent in trees

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**Abstract :** Trees transport water from their roots to their leaves thanks to an efficient but vulnerable vascular system. Assessing the vulnerability to drought of the xylem and its ability to recover from failure are not an easy task but recent findings demonstrate that, contrary to what is commonly believed, hydraulic failure and embolism repair are not routine in trees.

Trees are amazing organisms. They have the capacity to pull tons of water up to 100 meters above ground, when the best engineered suction pumps are limited to 10 meters at most. Indeed, above 10 meters, the pull of gravity exceeds the atmospheric pressure, the pressure at the top of the water column then becomes negative and metastable and pumps drain by vaporization or cavitation. How trees cope with cavitation? Are they astonishingly immune to this breakdown or do they possess remarkable repair capacities? These questions were asked when the mechanism of sap ascent in trees was unraveled in the late 19$^{th}$ (Brown 2013), and were first answered only when reliable methods for measuring cavitation were introduced a century later. This early work showed that trees suffer cavitation under severe drought only. During the past decade, numerous studies have questioned our former understanding of tree hydraulics, reporting seasonal and even diurnal cycles of cavitation for several tree species. However, two recent studies by Wheeler *et al* (2013) and Cochard *et al* (2013) add experimental support for the first view and demonstrate that this change of paradigm should now be reconsidered as it was based on misleading techniques.

In trees, sap is transported under negative pressure in a network of tiny pipes forming the xylem tissue (Tyree 2003). The vulnerability of these pipes to cavitation is described by a ‘vulnerability curve’. The first VCs were obtained in the 80$^{th}$ by dehydrating branches and measuring the impact of cavitation on the loss of xylem hydraulic conductance (Sperry *et al* 1988). The method was laborious, but the resulting ‘sigmoidal’ VCs were found highly consistent with tree water relations. Indeed, tree plumbing system appeared remarkably immune to cavitation events. Cavitation was found to form only when the xylem pressure dropped below a threshold value more negative than the xylem pressure a tree experience under stressless conditions (Choat *et al* 2012). Under this ‘high cavitation resistance’ paradigm, cavitation was seen as an exceptional process occurring only after a prolonged water stress and tree drought tolerance associated to the capacity to avoid cavitation. For the first time a mechanistic explanation for stomatal closure and plant death during water stress was thus provided, which has been seen as a major advance in the understanding of plant water relations.

In the late 90$^{th}$ a novel paradigm was proposed to account for the functioning of many tree species displaying apparently highly vulnerable xylem pipes (Tyree *et al* 1999). For these species, VCs have typically an 'exponential' shape, suggesting that cavitation forms as soon as the xylem pressure drops below zero. These trees are thus routinely exposed to high levels of cavitation, even under well watered conditions (Zwieniecki and Holbrook 1998). As a corollary, cavitation was found to be rapidly repaired by a mechanism that still remains 'miraculous' (Holbrook and Zwieniecki 1999) today. Under this 'low cavitation resistance paradigm, cavitation is now seen as a process beneficial for tree growth, possibly through to release of water into the transpiration stream and sustain stomatal opening during the day. Drought tolerance may then be more linked to the ability of trees to repair cavitation rather than their capacity to avoid its formation. Our perception of cavitation resistance in trees has hence drastically changed over the last decade. A phenomenon that was once thought to form only under extreme conditions is now considered of very common occurrence. Consistently, considerable efforts are now produced to unravel the mysterious mechanism by which trees are able to repair so efficiently their vascular tissue.

However, recent reports strongly suggest that recent cavitation studies have been deceived by faulty techniques. First, Wheeler *et al* (2013*)* have demonstrated that the daily patterns of embolism formation and apparent recovery in well watered trees were actually strongly biased by the sampling procedure used in previous studies. When a more appropriate sampling procedure was employed, the level of cavitation remained low throughout the day. Second, Cochard *et al* (2013) have conducted an extensive literature survey of all the VCs published so far and have demonstrated that 'exponential' curves are strictly associated to defective techniques introduced in the 90$^{th}$ and now routinely used in many laboratories across the world. It is now established that these technics considerably overestimate xylem vulnerability to cavitation, singularly for species which have long pipes (Cochard *et al* 2010; McElrone *et al* 2012; Cochard *et al* 2013). Therefore, we must come to the conclusion that the alternative low-cavitation-resistance paradigm for tree hydraulics was constructed on the basis of faulty methods and suspicious data. The methodological contamination is massive as nearly half of all the VCs published in the recent years are suspicious (Cochard *et al* 2013). It is thus a misconception to conclude that trees are able to refill their pipes by looking at these flawed diurnal cycles. The 'high cavitation resistance' paradigm must be regarded as only valid framework for the understanding of plant hydraulics and their water relations.

As a consequence, we urge plant physiologists to consolidate their methods for measuring cavitation resistance. We invite physicists to focus on the mechanisms of cavitation formation in plants instead of investigating on a doubtful refilling mechanism. We invite biologists to unravel the molecular and genomic basis of cavitation resistance in plants, providing that the use of *Arabidopsis* as a plant model for xylem hydraulics has recently been validated (Tixier *et al* 2013). Finally, we invite ecologists to consider more the inclusion of cavitation data into their process-based vegetation models to better predict the effect of water stress of species distribution (Choat *et al* 2013).

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