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Cavitation resistance and the functional role of bordered pits in xylem of conifers: from inter-specific to within a tree variability.

Summary

This thesis aimed to improve our understanding of xylem cavitation resistance (i.e. resistance to drought-induced formation and spread of air in the water transport system) in conifers by carrying out experiments at two different levels: at the interspecific and intra-plant level. We first investigated the mechanism of cavitation based on 115 conifer species, covering seven conifer families and four major biomes (Bouche et al. 2014). Also, the trade-offs associated with cavitation resistance were studied in details (Bouche et al. 2014, Bouche et al. in prep). Secondly, we developed new approaches to estimate cavitation resistance within and between different organs (needles, branches, trunks and roots). These allowed me to investigate the “vulnerability segmentation hypothesis” in conifers which suggest that leaves and branches are more vulnerable to cavitation that trunks and roots (Tyree and Ewers 2001). Anatomical observations were also carried out at the intra-plant level.

The functional and evolutionary role of torus-margo pits

This thesis demonstrated that cavitation in conifer branches occurs while the torus is aspirated against the pit aperture borders. Thus, the spread of air from an embolised tracheid to a functional tracheid (water-filled) is most likely due to the imperfect sealing of the torus on the pit aperture (seal capillary seeding hypothesis, see Fig 2c p. 5). Therefore, torus overlap represents the most useful proxy to estimate cavitation resistance. A correlative evolution between cavitation resistance and torus overlap was found, suggesting that for each node in the phylogeny a change in cavitation resistance was associated with the evolution of torus-overlap (Bouche et al. 2014).

Functional traits associated with cavitation resistance

The inter-specific study highlighted an indirect trade-off between hydraulic safety (cavitation resistance) and mechanical strength (thickness to span ratio), and the lack of a trade-off between cavitation resistance and hydraulic conductance (k_S). In addition, our results showed that increased cavitation resistance did not negatively affect the tracheid lumen diameter. Therefore, conifers seem to be able to achieve greater cavitation resistance without considerably sacrificing hydraulic efficiency. However, while cavitation resistance was not associated with tracheid dimensions, the role of the torus-aperture overlap was considerable, suggesting a trade-off at the pit level. Yet, xylem hydraulic efficiency mainly depended on the size of the margo pores in hydrated conditions (neutral position of the torus-margo structure, see Fig 2b p. 5), while cavitation resistance was mainly driven by the ability of the torus to seal the pit aperture (torus-aperture overlap) when aspirated (aspirated position, see Fig. 2b p. 5). Therefore, efficiency and safety of conifer xylem are uncoupled from each other and can vary independently (Bouche et al. in prep).

Cavitation resistance at the whole plant level

All findings mentioned above apply to conifer branches. However, little is known about xylem hydraulic behaviour at the whole plant level. We used new methods and modified existing protocols to estimate cavitation resistance in different organs of Pinaceae species.

Accurate techniques to measure needle and root cavitation resistance in conifers

For *P. pinaster* needles, we used high resolution computed tomography (HRCT) and the rehydration kinetics method (Brodribb and Cochard 2009). A large difference was found between both techniques. HRCT, which provided direct visualization of xylem water content, showed that xylem of needles and branches of *P. pinaster* were equally resistant to cavitation. In contrast, with the rehydration kinetics method we found that needles were more vulnerable than branches. However, this latter technique estimated hydraulic dysfunction at the whole needle level including extra-xylary tissue, while HRCT allowed us to focus on cavitation resistance of xylem tissue (Bouche et al. under revision, Plant, Cell & Environment).

For conifer roots, we modified existing protocols using the flow-centrifuge method (Cochard 2002, Cochard et al. 2005, Beikircher et al. 2010). For both *Pinus pinaster* and *Pseudotsuga menziesii*, it appeared than when using the standard protocol, which is known to be accurate for conifer branches, the high water pressure gradient (ΔP) produced by the flow-centrifuge induced a loss of hydraulic conductance not due to cavitation but due to torus aspiration. Therefore, this method underestimated cavitation resistance in xylem of conifer roots. Instead, we recommend to use the so called “zero risk method”, which applies a negligible water pressure gradient and allowed to accurately measure the cavitation resistance in roots without risk of torus aspiration (Bouche et al. submitted to Journal of Plant Hydraulics). In order to test the vulnerability segmentation hypothesis, which suggested that distal organs such as branches are more vulnerable than trunk and roots (Tyree and Ewers 2001), we carried out measurements of cavitation resistance of branches and trunks of four conifer species, and added root measurements for two of the species selected. Our results showed that xylem of trunk and roots was either equally or more vulnerable to cavitation than branches (Bouche et al., submitted to Tree Physiology). However roots and trunks were not as highly vulnerable as suggested by previous studies (Sperry and Ikeda 1997, Martínez-Vilalta et al. 2002, Domec et al. 2006, McCulloh et al. 2014).

The vulnerability segmentation hypothesis was not supported in the four species studied. It is worth noting that all our results were strengthen by anatomical observations. Indeed, we found that organs with similar cavitation resistance had similar torus-aperture overlap and that only the most vulnerable organs had the lowest torus-aperture overlap. A link between cavitation resistance and pit anatomy might therefore be suggested at the whole plant level.

Perspectives

Prospective work taking into account the inter- and intra-specific variability of cavitation resistance for all vegetative organs, might help us to fully understand the hydraulic architecture of plants. However, such investigations are destructive and time consuming. Therefore, investigating the relationship between cavitation resistance and pit properties (Bouche et al. 2014) at the whole plant level might provide a good alternative to estimate cavitation resistance on a broad taxonomic scale. In addition, if all assumptions on cavitation resistance of branches are equally applicable to the whole plant level, pit properties might be used as selection criterion in order to improve cavitation resistance of conifers that are of economic interest for forestry and pulp and paper industry.