Functional xylem anatomy: intra and interspecific variation in stems of herbaceous and woody species

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SUMMARIES

Summary

The combination of increasing heat waves and decreasing precipitation frequency has led to multiple large-scale tree mortality events in different plant ecosystems. Xylem vulnerability to embolism has been associated with drought-induced tree mortality. Additionally, the plasticity of wood anatomy, as a result of adaptation over long-term responses, plays a central role in plant hydraulic strategies. Therefore, understanding how plants cope with drought-induced embolism will help us to predict species distribution and model climate impact on vegetation.

With this thesis, I investigated the ecological significance of embolism resistance, and explored the plasticity and functional aspects of xylem anatomical traits in stems of woody and herbaceous species. Chapters 2 and 3 emphasized the effect of biotic and abiotic constraints to assess different adaptive solutions to the wood structure/function demands. In chapter 2, environmental constraints related to temperature, precipitation and soil conditions explained the wood anatomical variation amongst individuals of the same species occurring in two seasonally dry environments in Brazil, i.e. cerrado and caatinga. In addition to the remarkable dry season in both vegetation types, I highlighted the role of the edaphic toxicity of cerrado soils (high aluminum concentration and low nutrient availability) on the variation in wood anatomy plasticity, resulting in xeromorphic features in cerrado individuals. In addition to abiotic factors, plant height has also appeared as a source for wood trait variation along the main trunk in chapter 3. I showed that compared to axial sampling height, the effect of site was negligible for explaining the variation of wood traits: out of 13 wood traits assessed, only three were influenced by site differences including only in one of both species. Some of the axial variation can be functionally interpreted as a way of counterbalancing the increased resistance in water conductivity with increased tree height, such as the widening of vessels downwards and the increase in vessel density and vessel fraction upwards in both species.

The functional ecological significance of the pressure inducing 50% of loss hydraulic conductance (P_{50}) as an adaptive trait responding to environmental chang-

es and plant distribution is shown in chapters 4 and 5. Amongst the five insular woody *Argyranthemum* species studied in chapter 4, the most vulnerable was the evergreen *A. broussonetii* from the wet laurel forests of Tenerife, Canary Islands, while the other four species were native to drier areas of the island and expressed a higher resistance to embolism in their stems. In chapter 5, the difference in mean annual precipitation along different vegetations zones of Tenerife explains the variation in both stem anatomy and embolism resistance amongst herbaceous species of Brassicaceae and Asteraceae, emphasizing the importance of P_{50} as a predictor of ecological distribution between and within species.

The spread of embolism in the vessel network occurs via air-seeding, a mechanism that has been shown to be mediated by the thickness of intervessel pit membranes (T_{PM}). This functionally explains the correlation between T_{PM} and P_{50} in several studies. Likewise, in chapter 4, T_{PM} was the best predictor for the variation of embolism resistance amongst the insular woody *Argyranthemum* species and their continental herbaceous counterparts. Similarly, T_{PM} appeared as an important trait explaining the variation of embolism resistance amongst the herbaceous Brassicaceae and Asteraceae species studied in chapter 5. However, in these herbaceous species, the degree of woodiness provided a higher explanatory power for the variation of embolism resistance than T_{PM}. The link between higher lignification (woodiness) and higher embolism resistance, which is associated with the ability of plants to withstand more negative pressures in their xylem, was also demonstrated in chapter 4 where stems of the insular woody species were more embolism resistant than those of their herbaceous continental relatives. This result matches with the reported abundance of insular woody species in the drier areas of the Canary Islands and with the ongoing observation of the distribution of phylogenetically derived woody species that thrive in continental areas experiencing a few consecutive dry months per year. The positive relationship between higher lignification and higher embolism resistance was also reported at the intraspecific level in chapter 4, amongst herbaceous individuals of *Cladanthus mixtus* (Asteraceae), as well as in chapter 5 between populations of *Sysimbrium orientale* and *Hirschfeldia incana* (Brassicaceae) growing in contrasting environments. Despite the stunning evidence for the mechanical-hydraulic trade-off, this relationship is often reported as indirect. The missing functional link was found to be T_{PM} that seems to co-evolve with increased woodiness in the Asteraceae and Brassicaceae studied, both at the interspecies and intraspecies level.

For future studies, I emphasized the importance of gathering more plant hydraulic data from the poorly studied environments, such as tropical rainforests. When filling these gaps, we will be better able to predict which trees/forests are more vulnerable to embolism, allowing us to further optimize tree mortality models. Additionally, I highlighted the need to assess the fine-scale anatomical observations in pits in different organs and along different height positions within a tree across many species. Finally, a more integrative approach, combining embolism resistance across organs with other measurements such as stomata response, xylem capacitance, and root depth will definitely increase our understanding with respect to plant drought tolerance and mortality across diverse plant lineages.