Comparative wood anatomy and evolution of Apocynaceae and Sapotaceae

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Summary

Wood is an unmissable product in everyday life and is harvested in great volumes from forests and plantations worldwide. To regulate trade, it is necessary to correctly identify wood species. Therefore, fundamental wood anatomical research and its accompanying databases are invaluable that describe and visualise thousands of species. Additionally, wood anatomical research is important for other research disciplines, such as identifying and dating wooden remains in archaeological finds, investigating the (in)sensitivity of plants to climate change, and studying wood quality for applications of wood in, for instance, outdoor constructions. All these disciplines rely heavily on information acquired from fundamental research related to plant taxonomy, wood evolution, and ecology. In my research, I used a comparative wood anatomical approach to address these fundamental aspects of the (largely) tropical flowering plant families Apocynaceae and Sapotaceae. Both families were chosen because they have valuable timber species that are well-represented in wood collections, occur in diverse habitats, have species with different growth forms, but for which the wood anatomy was understudied. I sectioned and stained wood samples following standardised protocols after which the I described the anatomical variation using light-and scanning electron microscopy. These descriptions were combined with existing ones and I performed ancestral state reconstructions on a large set of wood traits with modern comparative modelling methods that use phylogenies based on molecular differences. This allowed me, for the first time, to present the most complete wood anatomical overview of both families. I made comparisons among species of the same family to investigate intrafamilial relationships and to reconstruct wood anatomical evolutionary trends. Moreover, I investigated the impact of growth form and plant size on wood anatomical variation.

The Apocynaceae subfamilies Secamonoideae and Asclepiadoideae have undergone several independent evolutionary transitions with regard to growth form and degree of woodiness, yet my observations in **chapter 2** are in line with subfamilial and (sometimes sub)tribal delimitations. Furthermore, I present for the first time an overview of the estimated number of shifts from herbaceousness to phylogenetically derived woodiness in Asclepiadoideae, along with a derived woody species list including distribution and habitat information. In total, some 168 derived woody species resulting from around 28 independent woodiness transitions were identified, with drought possibly being one of the main drivers for these transitions. **Chapter 3** provides a wood anatomical overview of the entire Apocynaceae family. Interestingly, I found that the evolution of wood anatomical traits is associated with woody

growth form transitions and floral and seed trait innovations across the family. More specifically, there is a shift towards a suite of wood anatomical traits that separate the rauvolfioids and early-branching apocynoids from the core apocynoids, including an increased presence of vessel multiples, vessel dimorphism, laticifers, vascular (cambial) variants, and paratracheal axial parenchyma. The presence of this trait suite, which continues in Periplocoideae, Secamonoideae, and Asclepiadoideae, coincides with a progression of floral morphological innovations that evolved on consecutive nodes in the family, and is also related to more frequent transitions towards the climbing and herbaceous habit. In addition, there is a notable shortening of vessel elements and fibres along the phylogenetic backbone of the family that correlates with a general reduction in plant size. Monophyletic groups can also be recognised based on wood anatomical traits in Sapotaceae (**chapter 4**), such as with variation in mineral inclusion type (prismatic crystals, silica bodies, or crystal sand), silica body size, vessel-ray pit variation, ray width, fibre wall thickness, vessel arrangement, and axial parenchyma distribution. I used these traits to perform ancestral state reconstructions on the two largest subfamilies for which molecular phylogenies were available. Since recent published phylogenies were made with a limited number of chloroplast and/or nuclear markers, I performed additional state reconstructions on a new genus-level phylogeny based on gene sequence read data from an angiosperm bait set that includes 353 nuclear markers. With these state reconstructions, I visualised several striking evolutionary patterns, such as complex shifts in mineral inclusions, and independent reversals from simple to scalariform vessel perforations.

The results presented in this thesis answer fundamental questions on species relationships, growth form adaptations, trait changes over time, and provide hypotheses on plant adaptations to diverse climatic conditions. Not only are these results essential for wood anatomists, evolutionary biologists, and ecophysiologists, they also provide tools for species identification and understanding plant functioning. With an increasing human population leading to a growing demand for natural resources, research such as I have presented in this thesis will be crucial to conservation efforts and grasp how plants adapt to an everchanging environment.