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Article Addendum

Interrelations between hydraulic and mechanical stress adaptations in woody plants

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The fields of plant water relations and plant biomechanics have traditionally been studied separately even though often the same tissues are responsible for water transport and mechanical support. There is now increasing evidence that hydraulic and mechanical adaptations may influence one another. We studied the changes in the hydraulic and mechanical properties of the wood along lateral roots of two species of buttressed trees. In these roots, the mechanical contstraints quantified by strain measurements are known to decrease distally. Further, we investigated the effect of mechanical loading on the vessel anatomy in these and four other species of tropical trees. We found that as the strain decreased, the wood became progressively less stiff and strong but the conductivity increased exponentially. This was reflected in that adaptations towards re-enforcing mechanically loaded areas resulted in xylem with fewer and smaller vessels. In addition a controlled growth experiment on three tree species showed that drought adaptation may results in plants with stronger and stiffer tissue. Our results indicate that hydraulic and mechanical stress adaptations may be interrelated, and so support recent studied suggesting that physiological responses are complex balances rather than pure optimisations.

It is well known that the woody tissue of plants is responsible for carrying out several functions simultaneously, of which the two most important may be water transport and mechanical support. In spite of this, the fields of plant water relations and plant biomechanics have traditionally been studied separately (however, see refs. 1–4). An increasing number of studies now indicate that there may be interrelations between hydraulic and mechanical stress adaptations, both in the form of positive interactions and trade-offs. In the former case, adaptations with respect to one of the two stresses positively affect the plants ability to withstand the other. Drought adaptation, for instance, is associated with an increase in the density of the tissue, which may result in stiffer and stronger wood.[5,6] Further, increasing the transectional area of the sapwood increases the conductivity as well as the rigidity of the plant and may occur as an adaptation to either drought- or mechanical stress.[7,8] In such cases, because of the importance of hydraulic sufficiency as well as adequate mechanical support, biomass must be partitioned to allow for both functions simultaneously even if this results in a surplus allocation with respect to one. In the case of trade-offs, the hydraulic or mechanical adaptations are detrimental to the plants' capabilities with respect to the other. Within the woody tissue, for instance, larger and more numerous vessels increase the conductivity but may weaken the wood.[1-3,9-11] Analogously, hydraulic optimisation dictates an increase in the transectional sapwood area up though the plant, so that the summed area of all branches at a given height would be greater than that of the trunk[12] but mechanical optimisation a decrease.[13] In the case of physiological parameters within which there are trade-offs, achieving adequate design whilst minimising biomass allocation becomes complex,[4] and a number of possible but less optimal solutions exist.

In our study,[14] we looked at how mechanical as well as hydraulic parameters changed along the lateral roots of two tropical tree species, *Tachigali melinonii* and *Xylopia nitida*, both of which produce buttress roots. Along the roots of these species there is a strong distal decrease in the magnitude of the locally supported mechanical loads,[15] making them ideal model organisms for investigating mechanical adaptation of the tissue and the impact this has on hydraulic parameters. We measured the density, conductivity, strength, stiffness, sapwood area and second moment of area at various points distally along the roots as well as in the lower trunk, and compared the values to those for strain. In both species, the strength and stiffness of the tissue decreased distally along the roots as the strain dropped, and the conductivity concurrently increased exponentially (Fig. 1). This appeared related to changes in the density of the wood; in both species, the density increased towards the bole and was positively correlated with mechanical properties but negatively with conductivity. As in previous studies, the distal most

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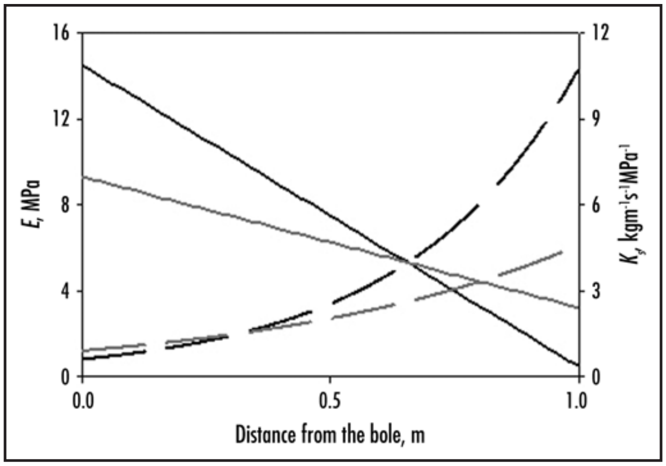

Figure 1. The modulus of elasticity in bending, E, (solid lines) and the specific conductivity, K_s, (dashed lines) of the woody tissue of the lateral roots shown as a function of the distance from the bole. The trend-lines are shown for the buttressed tree species *Tachigali melinonii* (black) and *Xylopia nitida* (grey), and are based on data presented in Christensen-Dalsgaard, et al, 2007a.

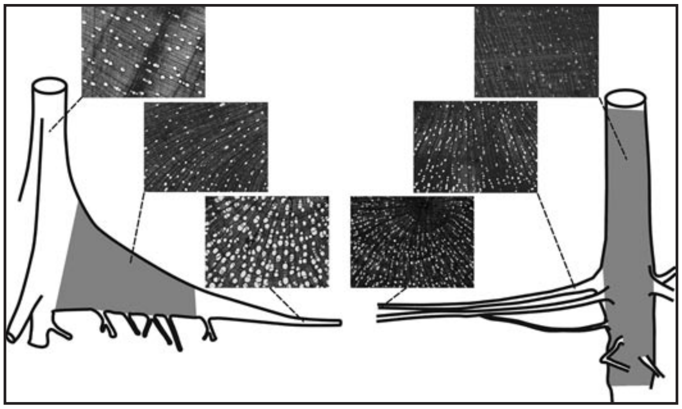

Figure 2. Tissue sections from the trunk and roots of the buttressed tree species *Xylopia nitida*, left, and the taproot anchored *Oxandra asbeckii*, right. All tissue sections are imaged at the same magnification; the width of each image is 4, 6 mm. In *O. asbeckii*, where the main rigid element resisting overturning is provided by the taproot and the lower bole, the trunk has smaller and fewer vessels than either of the root sections, as often described in litterature. In buttressed species such as *X. nitida*, on the other hand, where the area subjected to the greatest longitudinal strains and stresses is found in the proximal part of the buttress roots (marked in grey), this part of the root system is instead associated with fewer and smaller vessels than the trunk.

roots had a higher conductivity and lower stiffness and strength than that of the trunk. The proximal roots, however, had a lower conductivity but a greater strength and density. This indicates that the general pattern that roots have a higher conductivity than the stem cannot be explained by the water potential gradient from the soil to the leaves as often assumed, but instead by the differing mechanical requirements on these structures.

These hydraulic and mechanical adaptations were well in accordance with anatomical adaptations seen for these as well as four other species from the same area representing two different rooting morphologies, for which the strain patterns differ. We found that the vessels were significantly smaller and less numerous in the xylem tissue of highly mechanically loaded compared to less loaded sections of the tree[15] (Fig. 2). Further, the generally observed pattern[16,17] that vessel size increases radially from the pit to the bark was not observed throughout the structure.[18] In the proximal parts of the buttress roots, which are highly mechanically loaded throughout growth and development, the vessels maintained the small size found at the pith throughout the transect. In the distal parts of the buttress roots, in which the mechanical loading increases during growth, the vessels decreased rather than increased in size from the pith to the bark.[18] Since the adaptation of the xylem tissue towards re-enforcing highly strained areas appear associated with changes in the vessel anatomy reducing the conductivity, radial changes in vessel size may not only be a function of cambial ageing, but also influenced by changes in stresses during growth.

In addition to hydraulic effects of mechanical adaptations, the converse may occur; hydraulic adaptations could affect the mechanical properties of the tissue. Drought adapted plants have a greater resistance to cavitation,[19,20] which appears related to an increased relative thickness of the conduit or the fibre cell walls,[5,21] and so an increased wood density.[5,22] However, since the mechanical properties are determined by the micro fibril angle (MFA) of the S2 cell wall layer as well as density,[23] the data from the few studies measuring the mechanical effects of hydraulic adaptation have not found consistent effects.[24,25] In these studies, complex natural systems were investigated making it difficult to distinguish between various climatic effects. We therefore grew seedlings from the three tree species *Ochroma lagopus*, *Acacia karroo* and *Betula pendula* under well-watered and droughted conditions, respectively, and measured the effect on the modulus of elasticity, the yield stress and the density (unpublished results). The stems of the droughted plants had a higher stiffness and strength than that of the well-watered plants. Only in *O. lagopus*, however, did the stems of the droughted seedlings have denser tissue than that of the well-watered seedlings; in *B. pendula* and *A. karroo* the mechanical differences were probably due to adaptations in the MFA instead. This was supported by that the density/elasticity ratio, which may be a good indicator of the MFA,[23,26] was significantly higher in the well-watered than in the droughted plants.

Our work adds to the growing body of evidence indicating that there may be interrelations between hydraulic and mechanical stress adaptations.[1-3,5,9-12,25] Modifications of the xylem towards mechanically reinforcing stressed or strained areas simultaneously impacted the conductive physiology of the trees studied, and drought adaptations resulted in stiffer and stronger tissue. This provides further evidence that in order to fully understand plant physiology and ecology it is necessary to consider the various functions of wood simultaneously and attempt to unravel causal relationships between e.g., the hydraulic and mechanical functioning of the tissue. Rather than being a matter of simple optimisations, adaptations towards one environmental stress will affect how plants adapt to the others. Because of the complexity of this balance, however, interrelations between parameters are not always found. For instance, mechanical strengthening due to hydraulic adaptations could reduce hydraulic effects of mechanical stresses; trees growing in climates with winter frost may be stronger due to larger amounts of sap- or heart wood and drought adaptation may result in a stiffer and stronger plant.[21,24,27] This could explain why the relatively clear trade-off between hydraulic and mechanical parameters found in this and other studies have not always been found in non-tropical species.[21,24,27-29] Deepening our knowledge on how multi-factor adaptation balances are affected by climatic conditions and the signalling processes involved in these complex processes would aid our understanding of ecophysiological responses in plants.

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