Commentary

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Growing whole-plant understanding through study of below-ground structural diversity. A commentary on 'Do root secondary xylem functional traits differ between growth forms in Fabaceae species in a seasonally dry Neotropical environment?'

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Understanding of woody plant structure and function has been heavily influenced by study of distal stems, yet plant function in the environment is dependent upon the combined influence of all components of the plant body integrated into whole-plant performance. It is notable therefore that the study of the structure and function of below-ground structures, and mature woody roots in particular, remains stunted. In this issue of *Annals of Botany*, Silva *et al.* (2023) address this challenge, finding exceptional variation in woody root xylem structure among co-occurring con-familial species with contrasting above-ground growth forms. Their results suggest that below-ground functional strategies may be largely independent of above-ground counterparts, highlighting the need for increased research on woody roots to fully illuminate the structures that determine whole-plant functional diversity.

ROOTS AS NEGLECTED COMPONENTS OF WOODY PLANT STRUCTURE–FUNCTION

Secondary xylem tissue performs multiple functions within the plant body, including transport of sap, storage of water and nutrients, and biomechanical support. The trade-offs among these functions reveal a wide range of potential plant hydraulic strategies. The structural underpinnings of these traits have typically been evaluated and described from the study of distal stems, although the structure of the xylem within distal stems may vary greatly from secondary xylem within much of the plant body (Fig. 1). Studies of root traits are relatively infrequent and often involve examination of roots harvested from potted plants, sampling of shallow roots *in situ*, and/or study of young plants, seedlings or saplings. The structure and function of woody root systems for large and mature plants remain largely enigmatic. In the field of plant biology, the lesson of 'the blind man and the elephant' continues to be relevant and calls for study of older, wider and below-ground parts of large woody plant bodies (Meinzer *et al.*, 2010).

Silva *et al.* (2023) excavated woody roots from 14 co-occurring Fabaceae species that included subshrubs, shrubs and trees. Root samples were harvested from mature plants, obtained through excavation of plants *in situ*. Among other functional differences, the studied species exhibited different transport path lengths and biomechanical requirements (e.g. plant height) and differing ability to resprout from below-ground structures following disturbance. Anatomical traits of the root secondary xylem differed greatly among the species. While tree species generally had wider vessel diameters than shrubs and subshrubs, consistent with larger plant size and longer transport path length (Olson *et al.*, 2020), other traits showed no consistent pattern among functional types. Different species appear to express unique combinations of root traits, and the factors driving these differences have yet to be described.

Roots compose a large proportion of the plant body, as mass, volume and path length, but research has not similarly weighted root traits when studying plant functional strategies and responses to stress. The xylem of roots represents the largest portion of the hydraulic resistance of the whole-plant pathway (Tsuda and Tyree, 1997; Pratt *et al.*, 2010) and differences in root traits may heavily alter whole-plant hydraulic function. Root xylem structure and cellular composition also vary greatly, as much as 28-fold for some traits, among species that appear functionally similar based on above-ground habit (Silva *et al.*, 2023). Presumably such diversity is a critical component of whole-plant function and the response of plants to stresses, such as drought. Root traits, such as rooting depth, have already been identified as key determinants of drought-associated mortality (Jacobsen and Pratt, 2018). Incorporating knowledge of old woody root structural and functional diversity should therefore greatly enhance and expand our understanding of whole-plant functional strategies.

INTRASPECIFIC AND INTRA-ORGANISMAL TRAIT VARIATIONS ARE ADDITIONAL CRITICAL KNOWLEDGE GAPS

While Silva *et al.* (2023) standardized their within- and across-species sampling to tap-roots at a common depth, it is important to recognize that xylem tissue is not uniform, but rather changes throughout the plant body (Fig. 1). Broadly, there are large differences between roots and shoots (Fig. 1A and B compared with C and D) and also differences along the length of the plant axis (Fig. 1A compared with B and C compared with D). Within shoots, tip-to-base widening of vessels has been well established (Olson *et al.*, 2020). Similar to shoots, it is likely that vessel structure and function change along the length of roots (Jacobsen *et al.*, 2018), but this has been studied in relatively few species because of the labour involved in the excavation of entire large woody root systems. The function of young versus older woody roots may also be vastly different (Pratt *et al.*, 2010). Much could be learned from additional study of changes in structure and function along the length of the root axis.

Finally, the ability of individuals to colonize differing microsites may often be related to root traits. The existence of large variations in root xylem traits among individuals grown in different soil types (Sperry and Hacke, 2002) suggests a key role for roots in plant functional plasticity. Great intraspecific variation in root traits, such as described by Silva *et al.* (2023) could reflect such responses to local conditions, perhaps elucidating different soil conditions as integrated across the rooting volumes of plants. Without study of woody roots, we may be missing knowledge and understanding of local adaptations, plasticity and plant functional strategies (Sperry and Hacke, 2002; Fickle *et al.*, 2023; Silva *et al.*, 2023). Although the study of old woody roots necessarily involves time and

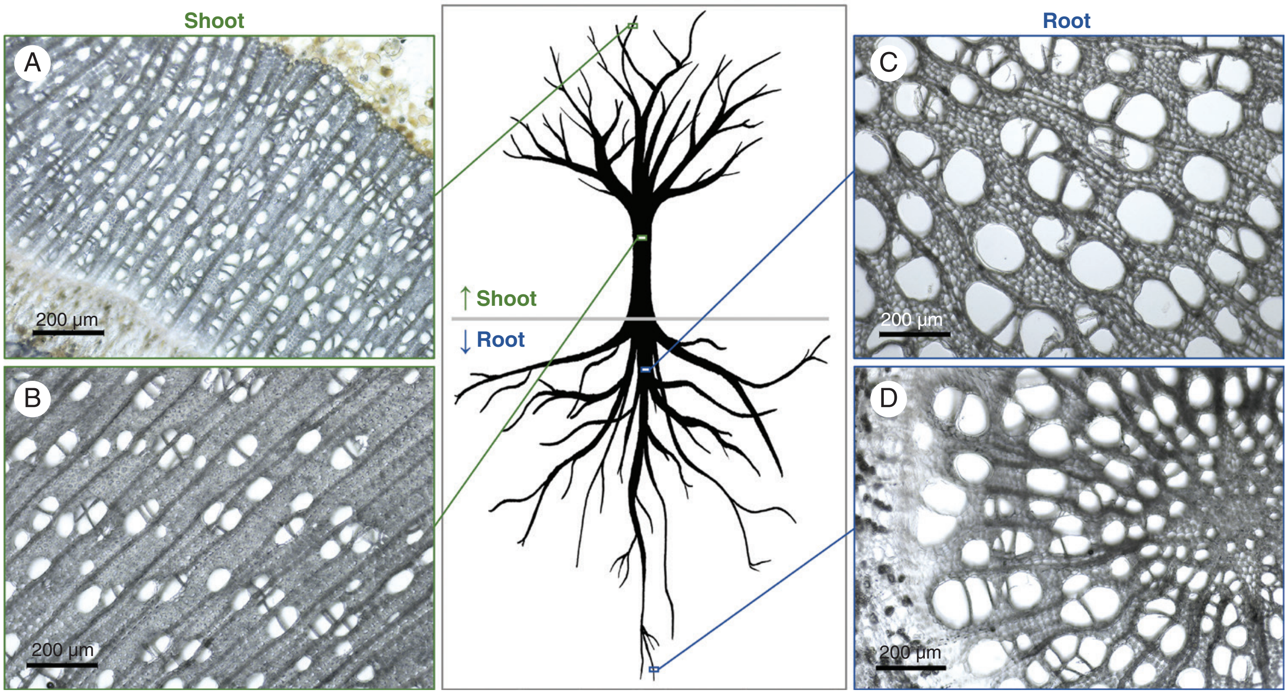

FIG. 1. Secondary xylem structure differs greatly throughout the plant body of large woody plants as demonstrated in the structure of xylem within excavated mature *Populus tristis* trees. Distal stems (A) contain vary narrow vessels, with vessel diameter widening considerably in basal sections of the shoot within the bole (B). Older wide roots contain the widest vessel diameters found within the plant body (C), and root vessel diameters taper towards root apices (D) but still remain much wider than vessels found within the shoot. The micrographs and tree diagram are previously unpublished and show tree and xylem micrographs from samples collected as part of Jacobsen *et al.* (2018). Lines from micrographs to locations on the tree diagram indicate the approximate sample location of the corresponding xylem tissue within the tree body. All micrographs were taken at the same magnification; scale bar = 200 µm.

laborious effort to access the below-ground structures of mature woody plants, without such work our understanding of whole-plant function will remain, quite literally, unrooted.

CONFLICT OF INTERST

The author declares that there are no conflicts of interest.

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