Commentary

A long drink of water: how xylem changes with depth

From the top of a coast redwood to roots deep within subterranean caves, water transport in trees is in the news. Evidence is accumulating that the distance water must travel within trees determines many of their structural properties. A recent study of some of the world's tallest trees demonstrated that maximum tree height appears to be limited by gravity and the resistance of the xylem pathway (Koch *et al.*, 2004). Rooting depth, by contrast, shows no such limitation, as revealed in this issue (see pp. 507–517). McElrone *et al.* (2004) gained access to deep tree roots through caves down to 20 m below the soil surface, matching roots to their above-ground shoots by comparing sequences of ribosomal DNA. Their study examines how differences between stems, shallow roots, and deep roots in key aspects of xylem structure enhance water transport from great depths up to the canopy. The study also provides indirect but compelling evidence for the cohesion-tension theory of water ascent in plants by demonstrating that patterns of tension in the xylem and vulnerability to cavitation are reflected in the structure of the conducting elements.

Xylem anatomy

Plant anatomists have known for some time that xylem conduits (vessels and tracheids) within a plant tend to increase in diameter in a basipetal direction, from terminal branches down to the roots (Tyree & Zimmermann, 2002). According to Vernon Cheadle (1953), vessels themselves first evolved in roots, replacing less efficient tracheids. Differences in conduit diameter for stem and root xylem have been reported for a wide range of species; a typical example is provided by a quick examination of two-year-old saplings of basswood (*Tilia americana*), in which vessels in the second-year xylem are 1.8 times as wide in the roots as in the stem ($P < 0.001$; $n = 4$). Due to difficulties in root excavation, differences in conduit size along the length of roots have been less frequently observed, with a few exceptions. The desert shrub (and invasive species in arid soils) *Retama raetama* has horizontal roots up to 10 m long, with vessel elements increasing in width and length at increasing distances from the base of the stem (Fahn, 1990). Interestingly, these roots occupy a vertically restricted zone near the surface of the soil, where the gradient in soil moisture would be relatively slight. In a study of the hydraulic architecture of trees in the Proteaceae, Pate *et al.* (1995) report increases in vessel diameter between shallow roots and so-called sinker roots and along sinker roots with increasing depth. The deepest roots sampled by Pate *et al.* were at 2 m below the soil surface, whereas McElrone *et al.* collected roots at depths from 7 to 20 m below the surface. For the conifer *Juniperus ashei*, tracheids in shallow roots and deep roots were about three and four times wider, respectively, than tracheids in stems; for the three dicotyledonous trees investigated, vessels in roots were an average of 1.5 (shallow) and 2.3 (deep) times wider than vessels in stems (Fig.1). Such differences in xylem anatomy have profound consequences for water transport, as McElrone *et al.* discuss, due to the relationship between volumetric flow and conduit diameter raised to the fourth power.

Water transport in the roots

If wide tracheids and vessels are so efficient at moving water, why are they more common in deep roots than elsewhere in trees? One argument put forward by McElrone *et al.* is that large conduits are necessary to minimize the hydraulic resistance associated with the great path length from deep roots to the canopy. For relatively short-statured trees such as those from the arid western USA, the depth of the roots can greatly exceed the height of the shoots, thus an adaptive premium is placed on minimizing below-ground hydraulic resistance. In other words, it behooves a tree to maximize the hydraulic conductance (K_h; m^4 MPa^{-1} s^{-1}) of its deepest roots. Based on the Ohm's law analogue, and ignoring direction and the gravitational component, the rate of water flow (F; m^3 s^{-1}) through the xylem in a plant axis can be expressed as

$$F = K_h (\triangle P_x / L)$$

where $\triangle P_x$ (MPa) is the difference in pressure between the two ends of the axis and L (m) is the axis length (Tyree & Zimmermann, 2002). This simplified equation is useful to show that, as McElrone *et al.* state, large values of K_h can help maintain water flow despite large values of L. In addition, large $\triangle P_x$ would not be required for water uptake by deep roots, and steep gradients in tension along the xylem could be avoided. Specific hydraulic conductivity, K_s, which is K_h divided by the transverse area of the conducting tissue (the stele in this case), for deep roots was 7–38 times greater than for stems and 1.2–2.4 times greater than for shallow roots (Fig. 1). While not as large as would be predicted on the basis of differences in conduit diameter, K_s measured by McElrone *et al.* for deep roots would help offset their great distance from the leaves.

The soil environment

Other reasons why xylem conduits are wider in deep roots than elsewhere within trees involve constraints that are relaxed due to the soil environment. As discussed by McElrone *et al.* deep roots experience biomechanical release: they are supported by the soil and unlike shallow roots are relatively unaffected by mechanical forces acting on the shoot. The reduced need for the xylem to provide structural support allows deep roots to be specialized for transport, with fewer xylem fibers, fewer rays (Pate *et al.*, 1995), more vessels or tracheids per transverse area, and conduits with larger lumens than in shallow roots and stems. Such specialization results not only in more efficient water uptake but also in reduced carbon allocation per unit length of root. Construction costs are lower due to more lumen and less cell wall per unit volume, and respiration costs are also lower due to the lower proportion of rays, fibers, and other living cells. Despite their lower construction and respiratory costs, deep roots are probably limited in length by carbon due to allometric considerations.

Constraints due to temperature are also relaxed in the soil environment of deep roots. A freeze-thaw episode is the environmental cause of embolism that has been linked most directly and consistently to conduit diameter (Ewers, 1985), and the lack of such episodes may account for the relative scarcity of wide-vesseled lianas in temperate regions. On an annual basis, a typical soil may vary by ± 6°C at 1 m below the surface but by only ± 1°C at 4 m (Nobel, 1999), thus deep roots of the Texas trees sampled by McElrone *et al.* never encounter freezing temperatures and are thus spared this cause of embolism. In addition, deep roots are also buffered against excessively high temperatures, which are associated with reduced vessel diameter in developing wheat roots (Huang *et al.*, 1991).

Perhaps the most important environmental constraint that is relaxed for deep roots is the availability of soil water. At the cave sites investigated by McElrone *et al.* an underground stream assures a nearly continuous supply of water to deep roots (although the trees are not phreatophytes – their roots do not tap directly into water). Differences in water availability directly and indirectly account for the structural differences observed in the xylem of stems, shallow roots, and deep roots. As a direct response, vessel diameter in water stressed roots of sorghum is significantly smaller than in non-stressed roots (Cruz *et al.*, 1992), as are root primordia in general, which may in turn lead to narrower vessels and tracheids. Indirectly, vulnerability to stress-induced cavitation may select for smaller conduits in organs routinely exposed to drying conditions, because wide conduits tend to embolize more readily (whether because of their greater diameter or the greater likelihood of air-seeding through pores in the pit membranes of large conduits is a matter for further research; Hacke *et al.*, 2000; Martínez-Vilalta *et al.*, 2002). For long roots in particular, reductions in K_h due to embolism can be even more limiting to water uptake than is radial resistance (between the soil and the root xylem), which tends to limit water uptake for young roots in moist soil (North & Peterson, in press).

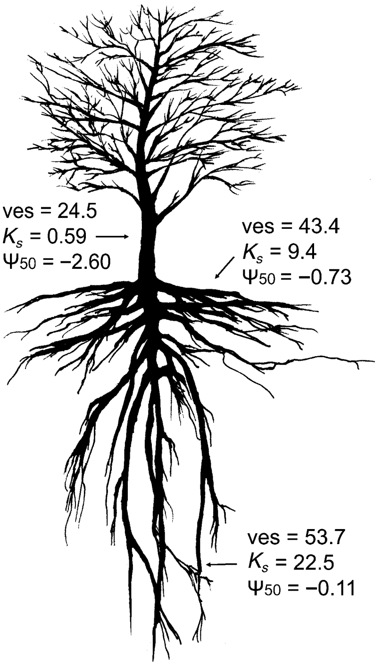

Fig. 1 Next to the stem, shallow roots, and deep roots of the tree are the values for vessel diameter (ves; µm), specific hydraulic conductivity (K_s; kg m^{-1} s^{-1} MPa^{-1}), and vulnerability to cavitation (ψ_{50}; MPa) measured for *Bumelia lanuginosa* by McElrone *et al.* (pp. 507–517).

Perspectives

In two of the species examined by McElrone *et al.* the ranking of plant axes with respect to vulnerability to embolism is the same as their ranking in conduit diameter, K_s, and access to water: deep roots were greatest, then shallow roots, then stems (Fig. 1). As McElrone *et al.* discuss, the greater vulnerability of roots may be tolerable due to the possibility of conduit refilling via root pressure. This gradient in vulnerability, as well as the gradients in conduit width and hydraulic conductivity, is most readily understood within the framework of the cohesion-tension theory of water ascent in trees. For example, such differences in xylem structure and function would not be expected if water flow were driven predominantly by forces other than transpirational pull, such as radial pressure applied by tissues or cells alongside the conduits. The differences in xylem structure and function within the tree species in this study thus provide some of the best whole-plant evidence gathered to date in support of the cohesion-tension theory.

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Phenotypic plasticity – contrasting species-specific traits induced by identical environmental constraints

Can it be assumed that a specific environmental constraint imposed on different species leads to a convergence in, for example, morphology? A phenotype expressed in response to external stimuli (e.g. size-reduction in response to mechanical stress) should be adaptive regardless of species – this is largely intuitive, but has been poorly studied. In this issue (pp. 651–660), Puijalon & Bornette reveal exciting new data that suggest that phenotypic plastic responses to identical environmental constraints may indeed be species-specific (Puijalon & Bornette, 2004).

Phenotypic plasticity – background

Early twentieth century research on phenotypic plasticity has been largely overlooked, with some exceptions (e.g. Bradshaw, 1965), until the last few decades. Not until recently has the concept of phenotypic plasticity become an important and integrated part of modern evolutionary and ecological research (Pigliucci, 1996; see Box 1). The past few decades have seen a large amount of interdisciplinary research being carried out on various aspects of phenotypic plasticity and reaction norms (e.g. Moran, 1992; Dudley & Schmitt, 1996; Lachmann & Lablonka, 1996; Preston, 1999; Pigliucci, 2002), together with a number of reviews (e.g. Coleman *et al.*, 1994; DeWitt *et al.*, 1998). Debates have also focused on evolution of phenotypic plasticity, including traits, models and gene expression (see De Jong, 1995 for an overview). Today, it seems clear that phenotypic plasticity must be recognised as central to evolution rather than a minor phenomenon, secondary to 'real' genetic adaptation (Sultan, 1992).

Current research

An interesting aspect of ongoing research is a closer coupling between genetics and ecologists (e.g. Jasienski *et al.*, 1997), where molecular evolutionary geneticists work together with plant ecologists. This is likely to be a fruitful cross-pollination that will reduce the risks of research 'inbreeding' and increase the development of healthy new insights in complex and dynamic ecological systems. It is unfortunate if genetic and functional aspects of plasticity are studied separately: they should be complementary.

In addition to investigating the genetic and evolutionary basis for, and effects of, phenotypic plasticity, it might be viewed in the context of species interactions, plant community structure and food-web dynamics. Reciprocal phenotypic change between individuals of interacting species (Agrawal, 2001) is an area of research that should lead to a greater understanding, not only of phenotypic plasticity, but also of species interactions and how these are affected by, and affect, the environment. The new findings of Puijalon & Bornette should stimulate research on the significance of species-specific plastic responses and how these affect distribution and abundance of individuals and species. It is possible that different species have different 'starting points' (i.e. genetic conditions), leading to different expressions of adaptive