AXIAL CONDUIT WIDENING IN WOODY SPECIES: A STILL NEGLECTED ANATOMICAL PATTERN

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ABSTRACT

Within a tree the lumen of the xylem conduits varies widely (by at least 1 order of magnitude). Transversally in the stem conduits are smaller close to the pith and larger in the outermost rings. Axially (*i.e.* from petioles to roots) conduits widen from the stem apex downwards in the same tree ring. This axial variation is proposed as being the most efficient anatomical adjustment for stabilizing hydraulic path-length resistance with the progressive growth in height. The hydrodynamic (*i.e.* physical) constraint shapes the whole xylem conduits column in a very similar way in different species and environments. Our aim is to provide experimental evidence that the axial conduit widening is an ineluctable feature of the vascular system in plants. If evolution has favoured efficient distribution networks (*i.e.* total resistance is tree-size independent) the axial conduit widening can be predicted downwards along the stem. Indeed, in order to compensate for the increase in path length with growth in height the conduit size should scale as a power function of tree height with an exponent higher than 0.2. Similarly, this approach could be applied in branches and roots but due to the different lengths of the path roots-leaves the patterns of axial variations of conduit size might slightly deviate from the general widening trend. Finally, we emphasize the importance of sampling standardization with respect to tree height for correctly comparing the anatomical characteristics of different individuals.

Keywords: Tree height, hydraulic resistance, xylem, evolution.

INTRODUCTION

The identification and classification of wood anatomical traits are of fundamental interest to wood anatomists, botanists and plant ecologists. Indeed, variations of such traits in different species and environments largely determine the mechanical and technological properties of wood and thus its economic value. Wood anatomists have therefore established a very detailed set of anatomical traits for describing the astonishing variety of xylem anatomical features that have been evolved by terrestrial plants (Wheeler *et al*. 1989). These anatomical variations form a basis to hypothesize adaptive strategies as drivers of much of the wood anatomical diversity that has resulted through evolution (Carlquist 1975; Baas *et al*. 2004).

Furthermore, some anatomical traits were used as predictors of the capacity of a given plant to survive in specific environmental conditions. For example, the diameter of the conduits in the xylem is believed to be of major adaptive importance (Sperry *et al*. 2006). In a seminal manuscript (actually the most cited paper ever published in IAWA Journal) (Tyree *et al*. 1994) it is stated that a general trend in xylem conduit diameter can be derived from several anatomical observations (Carlquist 1975): "wet-warm environments tend to favour species with wide conduits whereas cold or dry environments tend to favour species with narrow conduits." A more recent meta-analysis (Wheeler *et al*. 2007) further supported the idea that few wide vessels are associated with tropical environments and many narrow vessels are associated with high latitudes and environments with prolonged periods of low water availability. Interestingly they also noted that vessel diameter is strongly related to habit (*i.e*. height). Shrub species have the highest proportion of narrow vessels ($<50\,\mu$m) whereas wide vessels ($>200\,\mu$m) are virtually absent. In trees, on the contrary, wide vessels are very common.

Since the diameter of xylem conduits seems to be a crucial parameter in plant physiological ecology, it is very important to identify why and how conduits size changes within a plant, in plants of different height and in different growing conditions.

Therefore, a wood anatomist/ecologist aiming to study the variation of conduit diameter should ask him-/herself the following questions: where should I localize the sampling point? Does conduit diameter vary in the different parts of plants (roots, branches, stem)? If yes, how large is the variation? How can I standardize the measurements?

We suspect that many readers (if not all) might comment that these questions have already been largely clarified (see for example Tyree & Zimmermann 2002). Notable examples can be found in Sanio (1872) who described "Sanio's trends" in an individual of *Pinus sylvestris*. In that paper the author reported an exhaustive (although not always perfectly clear) description of the trends in tracheids diameter along the stem, branches and roots: in the stem conduits widen basipetally (*i.e*., increase in diameter axially towards the roots), whereas in roots they are generally wider than in the stem. His observations were very useful and have been substantially confirmed by successive measurements (Zimmermann 1978; Tyree & Zimmermann 2002). In addition, the latter authors found that the axial variation (along the stem) is far from being constant (*i.e*., linear with the axis length): conduit diameter largely changes near the treetop and then the rate of diameter variation progressively declines becoming rather constant further down at the stem base. This pattern seems to be particularly useful in terms of both hydraulic safety and efficiency, because on the one hand it provides the distal regions of the xylem pathways (where tensions are higher) with the conduits most resistant to cavitation (Hacke *et al*. 2001), on the other it confines the greater part of total hydraulic resistance towards the downstream ends of the flow path (*i.e*. the leaves) (Becker *et al*. 2000; Petit & Anfodillo 2009).

A further and decisive improvement in understanding the structure of the xylem vascular system (and its basic physical requirements) was provided by West *et al*. (1999) with the so-called "WBE model": they were the first to propose an explanation for *why* and *how much* the root-to-leaves column of vascular conduits should vary in width

axially, as previously observed. The theoretical approach of West *et al.* (1999) played a pivotal role in understanding axial variation of the pipelines' width. Comments on the model structure, allometric consequences and also the relevant flaws can be easily found elsewhere (Mencuccini 2002; Kozlowski & Konarzewski 2004; McCulloh & Sperry 2005; Coomes 2006; Etienne *et al.* 2006; Petit & Anfodillo 2009).

The WBE model simply proposes a plant formed by a bundle of tubes of the same length running in parallel from the roots to the leaves. Notably the tubes are not cylindrical (as in previous hydraulic models) but are tapered (*i.e.* they widen towards the stem base).

We focus our attention on the straightforward and revealing structure of the WBE model because, differently from all other previously-cited anatomical studies, it allows us to *predict* the variation of conduit diameters along the stem axis or in different individuals throughout ontogenesis.

Our aim is to present the "anatomical structure" of the plant modelled by WBE in detail and to prove that such a predictable pattern is very close to the one observable in nature. We are also convinced that the awareness of the ubiquity of this anatomical feature could help wood anatomists to standardize and functionally compare their measurements.

We are naturally aware that the tree modelled by WBE can only represent an "idealized plant" and that some oversimplifications might be problematic (for example, the assumption that the "tubes" are all of the same length). Our intention is to keep the most valuable idea of the WBE model (and it is really useful) in the knowledge that a lot of work still needs to be done for modelling the hydraulic architecture of trees in detail. Similarly, it is clear that a simple little paper airplane differs enormously from a Boeing 737 but, notably, it does have the same essential property: it flies!

WHY SHOULD CONDUIT DIAMETER VARY WITH PLANT HEIGHT?

Anatomy and physiology are two sides of the same coin. If a general plant requirement must be guaranteed (*e.g.*, maintaining leaf efficiency during different life stages) then the anatomy of the plant should be adjusted accordingly. Useful information about anatomical changes can therefore be drawn from models aimed at describing how trees work.

A brief "foray" into the WBE model is needed to explain why conduit diameter should vary with plant height.

In short, the idealized plant modelled by the WBE model is very similar to that proposed by Shinozaki *et al.* (1964): the tree can be seen as a "set of bundles" running in parallel from roots to leaves. These bundles (*i.e.* axial chains of xylem conduits) are connected to a fixed set of leaves (one-to-one in the simplest case). Notably these bundles are believed to be all of the same length: this simplification, which is evidently not true in real plants, will be discussed later.

Overall, the model predicts a complete independence among the different pathways. This condition might be in agreement with the idea of "plant segmentation" (Tyree & Zimmermann 2002) and would bring a selective advantage in ensuring both the
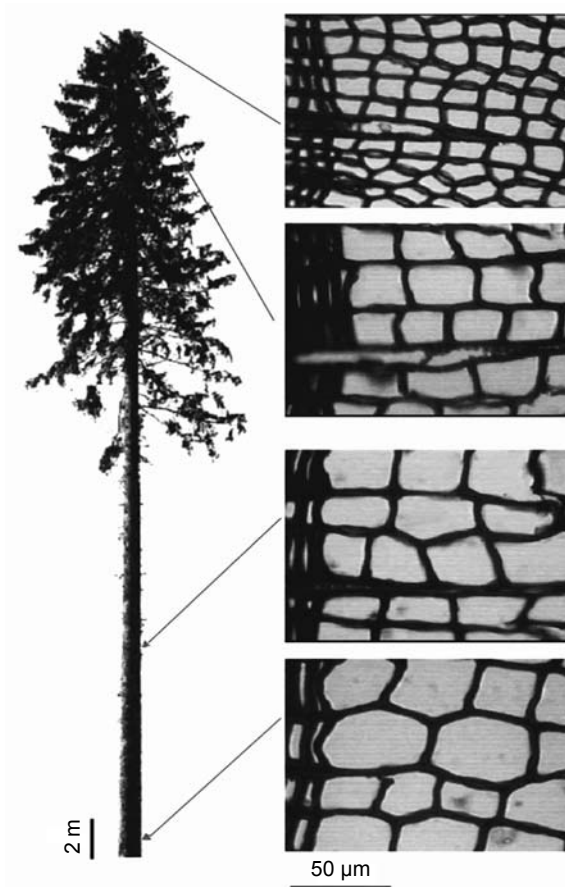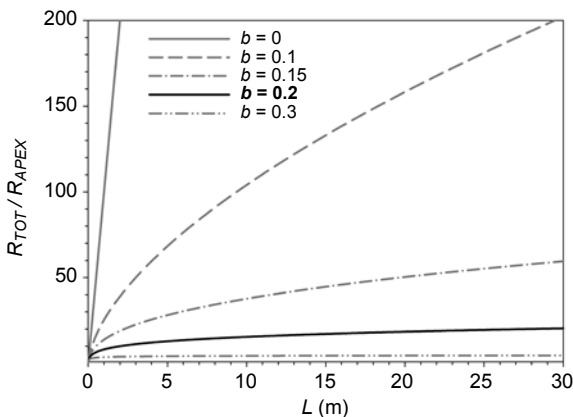
Figure 1. Variation of the earlywood tracheid diameter along the stem axis in the same annual ring (*Picea abies* (L.) Karst.): this variation is referred to as "conduit widening" (direction towards the stem base) or "conduit tapering" if the direction of the water flow is considered. All the sections have the same degree of magnification (indicated at the bottom of the figure: bar = 50 μm).

optimum supply to parts of the plant that are, at the same time, subjected to different metabolic rates (*e.g.* sun or shade leaves) and for better confining system failures (*e.g.* embolisms, pathogens).

In order to maintain the leaf efficiency as constant as possible during ontogeny (*i.e.*, when the tree grows) a new "ingredient" must be introduced to the simple "pipe model": the pipes are not cylindrical but they have a different diameter along the longitudinal axis (*i.e.* they widen basipetally) (Fig. 1). The variation of conduit diameter downwards in the stem (conduit widening, also known as conduit tapering) is predicted to be a power law according to which the variation of conduit diameter (*Dh*) with the distance from the tree top (*L*) (note that it is the inverse of tree height) will be:

$$Dh \, \square \, L^b,$$

where b is the exponent of the power function, which accounts for the relative variation. In the case of $b = 0$ there is no axial variation and the shape of the tube is cylindrical (like the original version of the pipe model). The rate of increase in hydraulic resistance with tree height strongly depends on how conduits vary in size along the stem. When xylem cells increase in diameter from the stem apex to the base a higher proportion of resistance is confined towards the apex. The higher the degree of widening, the greater is the magnitude of resistance confined to the apex. This implies that with further stem elongation, widening conduits towards the stem base would allow for a compensatory effect on the path length resistance, the efficiency of which is higher for higher degrees of widening (Becker *et al.* 2000; Petit & Anfodillo 2009) (Fig. 2). Notably, the degree of widening predicted by the WBE model ($b = 0.25$) can be considered as a threshold value above which the independence of the hydraulic resistance from the total path length (*i.e.* tree height) is guaranteed. The WBE theory predicts that evolution has acted in such a way that the degree of widening is the *minimum* required to make the resistance independent of the tree height (Enquist 2003). If true, then the leaf metabolic efficiency will be kept "invariant" through ontogeny, *i.e.*, water supply to the leaves will be similar in both small and very tall trees.

Figure 2. The effect of progressive degree of widening (or tapering) of vascular conduits (*i.e.* the scaling exponent b in determining the total hydraulic resistance, relative to the resistance of the most apical conduit (R_{TOT}/R_{APEX}), with the increasing length (L) of a single pipeline. Theory assumes that plants should approach the minimum degree of widening ($b = 0.2$) required to fully compensate for the progressive increase in hydraulic resistance (on the y-axis) with the growth in height (*i.e.* path length on the x-axis). The scaling of the total resistance at different exponent b can be predicted on the basis of physical laws.

In order to compare real trees with the "idealized plant" of the WBE model it is necessary to take into account the approximation of the WBE model in estimating the tree height. Doing so the minimum scaling exponent b, relative to the scaling of the conduit dimension *versus* the distance from the treetop, assumes the value of about 0.20 (see details in Anfodillo *et al.* 2006). This value (exponent similar to or higher than 0.20) means that in a real tree (not in the idealized plant of the WBE model) the vascular network is structured to compensate for the increase in plant height. Exponents in agreement with the predicted one have been repeatedly measured in plants of different sizes and environments (Anfodillo *et al.* 2006; Coomes *et al.* 2007; Petit *et al.* 2008, 2009; Lintunen & Kalliokoski 2010; Petit *et al.* 2010, 2011; Bettiati *et al.* 2012; Olson & Rosell 2012) (Fig. 3).
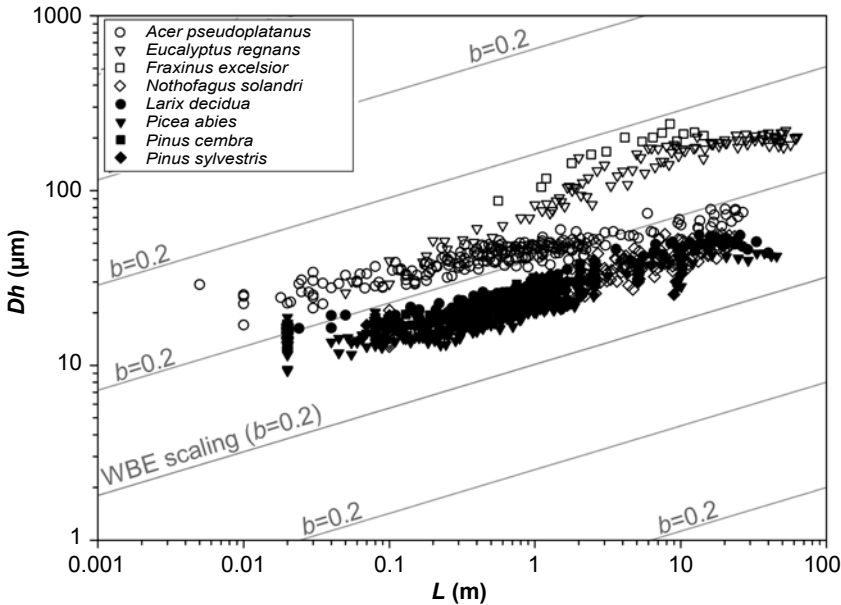
Figure 3. A meta-analysis of the axial variation of xylem conduit diameter (*Dh*) with the distance from the stem apex (*L*) of different species (inset). Data refer to measurements in stems and branches. Literature data are: *Acer pseudoplatanus* from Petit *et al.* (2008); *Eucalyptus regnans* from Petit *et al.* (2010); *Fraxinus excelsior* from Anfodillo *et al.* (2006) and Bettiati *et al.* (2012); *Nothofagus solandri* from Coomes *et al.* (2007); *Larix decidua* from Anfodillo *et al.* (2006) and Petit *et al.* (2009); *Picea abies* from Anfodillo *et al.* (2006), Coomes *et al.* (2007), Petit *et al.* (2009) and Petit *et al.* (2011); *Pinus cembra* from Petit *et al.* (2009); *Pinus sylvestris* from Coomes *et al.* (2007) and original data. The parallel grey lines indicate the power scaling with exponent b = 0.20. Lines change in relation to different intercepts (*i.e.* conduit size at the plant apex).

With the knowledge gained so far it is logical to expect that the relatively largest conduit dimensions at the stem base should be found in tall trees and, in contrast, small plants will have relatively small conduits: this general pattern in conduit size is therefore the *consequence* of the plant size. A meta-analysis on available data shows that conduits at the stem base are generally wider in taller plants (Fig. 4 and see also Wheeler *et al.* 2007)

Figure 4. Variation of conduit diameter at the stem base (in 4 classes: < 20; 20–50; 50–100; 100–200 μm) in relation to averaged class of plant height (4 classes). Data from Fritz Schweingruber relative to 3339 different angiosperm species mainly from the northern hemisphere (available at: www.wsl.ch/dendro/xylemdb/index.php). The tallest plants have formed the widest conduits.
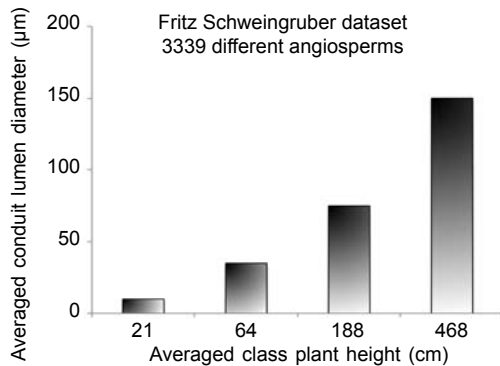
SOLVING THE CHICKEN-EGG DILEMMA

As mentioned above, Tyree *et al*. (1994) wrote that small conduits were generally measured in plants of dry/cold environments and therefore it could be speculated that, in a low-resources site, natural selection acts against species with relatively large conduits. However, the previous considerations showed that conduit size is closely correlated to tree height. Now, since tree height is negatively affected in low-resources sites so plants are generally small, it is obvious to expect narrower conduits. This circular reasoning could be solved by disentangling the role of tree size in determining the conduit size from that of resources' availability.

In a recent elegant analysis Olson and Rosell (2012) compared the conduit dimension at the stem base, in 142 different species growing in 5 sites within a huge gradient of water availability (annual precipitation from about 800 to 3500 mm). They then plotted the conduit dimension of each plant *versus* its stem diameter (which is allometrically linked to tree height) in each site. In this way they were able to compare the intercept of each regression line, *i.e*. the average conduit dimension in plants with the *same basal diameter*. They clearly demonstrated that the conduit size in plants growing in the wettest and driest sites did not differ. The conclusion is that plants of the drier sites are generally smaller and *therefore* have narrower conduits but, *at the same size* their conduits substantially do not differ from those of the species growing in the wetter sites.

This places full emphasis on how important it is to standardize the collection of samples in relation to plant height if the aim is to evaluate the adaptive consequences of given anatomical structures. The awareness of the ubiquity of the axial widening pattern could therefore help in correctly interpreting the anatomical traits.

Even more importantly, results indicate that conduit diameter is strictly related to tree height but little or not at all to the *age* of the plant. We believe that it is time to revise the common belief that this wood trait is substantially age-dependent. What occurs in the cambial zone and the cascade of events leading to a final conduit dimension are primarily related to the distance of the cambial cells from the apex (and, obviously, to environmental constraints). Indeed, it was demonstrated that the number of days in which the forming cells remain in the expansion phase is directly related to distance from the tree top (L) (Anfodillo *et al*. 2012). Cambial activity and the cell formation is basically *height*- and *not age*-related, as confirmed by Petit *et al*. (2008), who showed that apical shoots from very tall parent *Acer pseudoplatanus* trees, grafted onto 1-year-old rootstocks, developed vessels of similar sizes to those of young trees of similar height.

One of the important conclusions of this paper is that, when dealing with variation of wood traits (*e.g*. density, cell dimension, fraction of latewood etc.) within a functional-based approach, it would be better to change the traditional idea of "age-dependency" with the more correct concept of "size-dependency".

PERVASIVENESS OF THE PATTERN

One of the most unrealistic assumptions of the WBE model is that it considers an idealized plant formed by "pipes" of the same length. However, in trees branches have different length: some of them are very close to the ground and others near the treetop
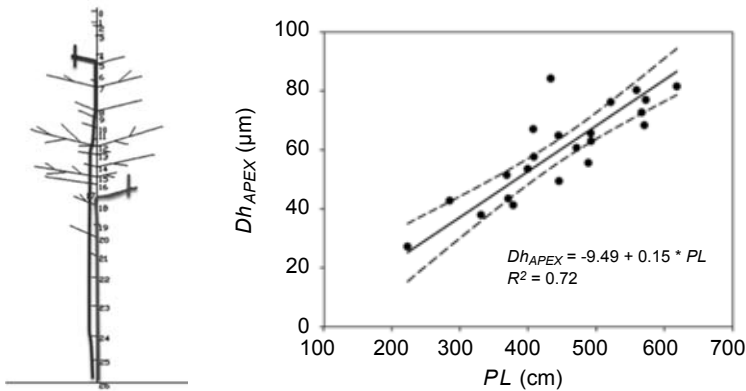
Figure 5. Right: Variation of conduit diameter (*Dh*) at the apex of the branches in relation to the length of the path *PL* (calculated from root to apex). Left: example of two paths (grey thick lines) with different length in a stylized *Fraxinus excelsior* (number of internodes are also indicated). The diameter of apical conduits increases with the increase of the path: this anatomical feature should compensate for the different length of the paths. Shorter paths have smaller apical conduits thus the total hydraulic resistance can be maintained very similarly among different paths (data from Bettiati *et al*. 2012).

(Fig. 5). Thus a basic assumption of the model appeared to be violated in nature. How can a plant cope with the variable length of the paths? The simple underlying idea is that a plant should adjust the structure (*i.e*. anatomy) of the vascular conduits to achieve a condition of equiresistance of all roots-to-leaves paths. If this condition was not satisfied then water would flow mainly throughout the paths with lower hydraulic resistance. But this would be detrimental to achieving similar water supply to all leaves.

There is not much information about the hydraulic architecture of the *whole* tree carried out with appropriate sampling (*i.e*. taking into account the distance of the samples from the tree top). Some examples can be derived from the book by Tyree & Zimmermann (2002) but in many cases the exact sampling distance is not specified thus making interpretation of results difficult. Recent anatomical analyses (Bettiati *et al*. 2012) showed that diameter of apical conduits in branches (collected just below the apex) are significantly different, with the widest diameters found in the longest root-to-leaves paths (Fig. 5). For example, in very short branches in the basal part of the crown (short path) apical conduits are relatively small (2–3 times smaller than the conduits in the longest paths/branches). This seems a very simple and coherent adjustment in order to guarantee similar resistance in all paths and therefore equal water delivery to the different parts of the crown.

Generally, it clearly emerges that the anatomical feature of one part of a plant (*e.g*., an apex of a certain branch) is strictly linked to the anatomy of the *whole* individual. Thus in spite of the near independence of all different paths they are anatomically structured in order to supply all the leaves in the different parts of the crown at similar rates: this result is equivalent to that obtained considering all the tubes of the same length (as in the simple WBE idealized plant).
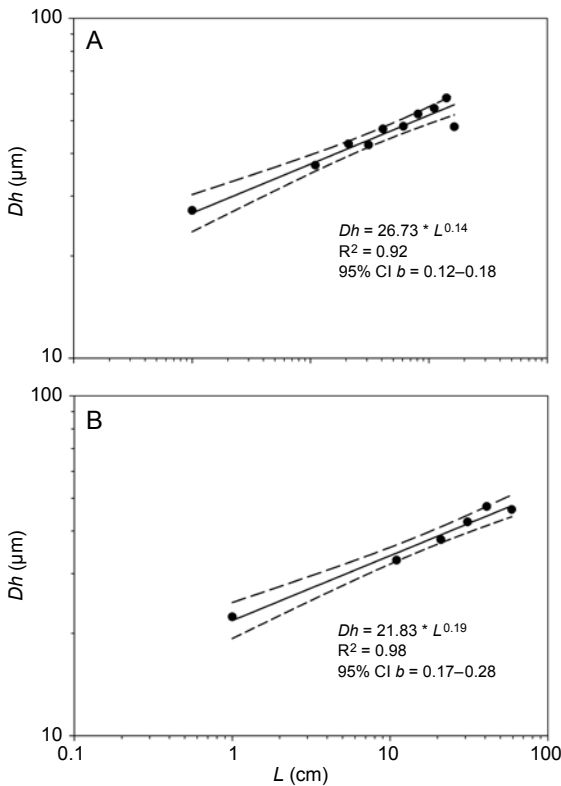
Figure 6. Variation of conduit diameter (*Dh*) with the distance from the apex in two different branches of a 9.5 m tall poplar tree (*Populus × canadensis*). The exponent *b* slightly changes (the 95 % CI is also indicated). In less than 2.0 m in length the conduit diameter changes by a factor of 2.5 (from about 20 to 50 μm).

Since the "tubes" run from roots to leaves, the same general pattern of conduit widening should in principle be preserved along the longitudinal axes of both branches and roots. Systematic measurements of conduit widening in branches are even more difficult to find than the axial variation of conduit size in stems.

However, measurements of hydraulic permeability (a proxy for conduit diameter) in branches generally showed an increase with branch diameter (*i.e.* towards the stem) (Tyree & Alexander 1993; Jerez *et al*. 2004; Sellin & Kupper 2007) thus demonstrating that conduits become wider towards the branch base.

An analysis on the axial variation of conduit diameter in branches of a poplar tree showed a common pattern of widening compatible with the value of 0.20 but short branches also showed a lower degree of tapering (0.16–0.14) (Fig. 6).

Similarly to stem anatomy the variation of conduit dimension along the branch strictly depends on the distance from the branch tip. The conduit diameter might easily vary by a factor of about 2 for a variation of 1 m in position of the sample towards the stem.

It is evident how important it is to also consider the pattern of conduit widening in branches. Any measurement, for example, of hydraulic conductivity, which is taken on small pieces of branches, must be normalized for the distance from the branch tip. Otherwise the results might be dependent only on the position of the sample and thus become meaningless.

Xylem conduits are believed to continue to increase in diameter downwards also in roots. Indeed, in general, vessel diameter and length in woody roots exceed those in stems of comparable diameter (Tyree & Zimmermann 2002), thus the widest cells of the whole plant are found in roots. This pattern was observed in shrubs of cold deserts where the mean vessel diameter was about 2 times wider than in the stem (Kolb & Sperry 1999), in nine Mediterranean woody species (Martinez-Vilalta *et al*. 2002) where the diameter of conduits was always wider in roots than in stems, and in conifers (Petit *et al*. 2009).

However, in very short superficial roots it is not uncommon to find relatively narrow cells (even narrower than in the stem). This is probably due to the fact that in roots (as occurs in branches) the length of the paths might differ significantly so the plant would compensate for possible differing hydraulic resistance by adjusting the conduit dimension accordingly (*i.e*. narrower conduits in shorter roots).

Notably in the roots the allometric relationships of root diameter *versus* distance from the tree top has an opposite sign compared to the stem (in roots the exponent is negative) showing that the mechanical constraints in roots differ from those of the stem and branches. Nonetheless the hydraulic constraints in roots are similar to the other organs so the degree of widening is supposed to be similar in all parts of the plants. Measurements in roots indicate that conduit widening seems to be a stable property of the whole xylem architecture, with the widest conduits very close to the root tips (as predictable from the hydraulic requirements) (Petit *et al*. 2009). However, further measurements are needed to clarify the pattern of conduit size in roots because they are characterized by a branching network with huge variations in the length of the different conductive paths.

A STILL UNANSWERED QUESTION

One of the most intriguing physiological questions related to axial widening is: how can a plant so precisely regulate the axial conduit dimensions along a path that may exceed 150 m in length (stem and roots in the tallest trees)?

Wood formation in trees is a dynamic process, strongly affected by environmental conditions, including nutrient availability and climatic changes (Oribe *et al*. 2003; Arend & Fromm 2007; Sorce *et al*. 2013; Prislan *et al*. 2013). Despite the relevant role of cambium tissues in plants, few studies have dealt with the molecular and structural mecanisms at the basis of its functionality (Deslauriers *et al*. 2009; Berta *et al*. 2010). According to a recent study, wider cells along the stem are those staying longer in the distension phase during xylogenesis (Anfodillo *et al*. 2012). Therefore, it is likely that plants adopt a mechanism to modulate the time for cell enlargement to precisely design xylem conduits optimally widened from the stem apex downwards for hydraulic purposes.

A candidate hypothesis proposes the polar transportation of phyto-hormones, particularly auxin (IAA), as the mechanism of control of the dimension of xylem cells along the stem (Aloni 2001; Aloni *et al*. 2003). The IAA is produced mainly in the developing buds and shoots (Uggla *et al*. 1998; Scarpella & Meijer 2004) and is transported basipetally along the cambial zone (Sundberg *et al*. 2000) from leaves to

roots (Aloni 2001; Muday & DeLong 2001). Moreover, the IAA concentration generally decreases from the stem apex to the base (Lovisolo *et al*. 2002). According to the six point hypothesis (Aloni & Zimmermann 1983), high concentrations of IAA would accelerate the cellular differentiation, thus reducing the time period for the cellular distension phase.

This new research topic should be promoted given the pivotal role in regulating the efficiency of water transport. We hope that this simple manuscript might encourage some scientists to clarify the physiological mechanisms related to axial conduit widening.

CONCLUSIONS

The xylem conduit size in stems, branches and roots appeared invariably dependent on the distance from the top: moving downwards (basipetally) the conduits are gradually wider and this is a necessary anatomical feature for stabilizing the hydrodynamic resistance with tree height.

Thus the requirement for maintaining the efficiency of water transport throughout the plant ontogenesis in all crown parts is achieved by shaping a widened anatomical structure. We believe that the axial conduit widening can no longer be neglected because it offers a clear and universal physiological explanation of the anatomical changes carefully observed by Sanio more than a century ago.

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