Sanio’s laws revisited. Size-dependent changes in the xylem architecture of trees

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Abstract
Early observations led Sanio [Wissen. Bot., 8, (1872) 401] to state that xylem conduit diameters and lengths in a coniferous tree increase from the apex down to a height below which they begin to decrease towards the tree base. Sanio’s law of vertical tapering has been repeatedly tested with contradictory results and the debate over the scaling of conduit diameters with distance from the apex has not been settled. The debate has recently acquired new vigour, as an accurate knowledge of the vertical changes in wood anatomy has been shown to be crucial to scaling metabolic properties to plant and ecosystem levels. Contrary to Sanio’s hypothesis, a well known model (MST, metabolic scaling theory) assumes that xylem conduits monotonically increase in diameter with distance from the apex following a power law. This has been proposed to explain the three-fourth power scaling between size and metabolism seen across plants. Here, we (i) summarized available data on conduit tapering in trees and (ii) propose a new numerical model that could explain the observed patterns. Data from 101 datasets grouped into 48 independent profiles supported the notions that phylogenetic group (angiosperms versus gymnosperms) and tree size strongly affected the vertical tapering of conduit diameter. For both angiosperms and gymnosperms, within-tree tapering also varied with distance from the apex. The model (based on the concept that optimal conduit tapering occurs when the difference between photosynthetic gains and wall construction costs is maximal) successfully predicted all three major empirical patterns. Our results are consistent with Sanio’s law only for large trees and reject the MST assumptions that vertical tapering in conduit diameter is universal and independent of rank number.

Keywords
Allometry, meta-analysis, metabolic scaling theory, Murray’s law, scaling, WBE, wood anatomy.

INTRODUCTION
Drawing conclusions from the analysis of a sample of Scots pine (Pinus sylvestris L.) trees, Karl Sanio (Sanio 1872) formulated five general laws describing the changes in tracheid length and diameter occurring along a radius in a stem from the pith outwards (first law), along a tree stem from the apex downwards (second law) and between branches, stems and roots (third, fourth and fifth laws). Sanio’s second law described vertical conduit tapering along a plant axis and stated that conduit diameters gradually increase from the apex downward until a maximum is reached, below which a rapid decline starts towards the stem base. When initial tests of Sanio’s propositions on other conifers appeared to support his statements (e.g. Mell 1910), the general conclusion was reached that tree species were similar with regard to their anatomical configuration. However, further investigations (e.g. Gerry 1915) showed several examples of discrepancies from these proposed laws and without a solid theoretical model, the discussion was progressively abandoned.

More recently, the tapering of conduit dimensions from the apex downward (Sanio’s second law) has been used as the cornerstone of a novel theory of organismal architecture as a fractal-like network of transport conduits connecting peripheral volume-filling tissues (West et al. 1997, 1999) and the century-old discussion of whether and how conduits taper along the stem of plants has resurfaced again. The metabolic scaling theory (MST) proposes that the hydraulic architecture of plants can be described as a series of
continuous parallel tubes running from the base of the trunk to the petiole arranged in a self-similar fractal-like structure, i.e. such that the ratio of properties such as diameter and length across ranks is independent of rank number. Provided that the lumen radii of xylem conduits increase with distance from the apex (or rank number, cf. eqn. 11 in Appendix S1) according to a power function with exponent of at least \( a = 1/4 \) (or \( a = 1/6 \), respectively, i.e. quarter-power scaling), the hydraulic resistance of a 'continuous tube' running from the base of the tree trunk to the petiole will remain constant (West et al. 1999) or, more precisely, increase rather little during height growth (Mäkelä & Valentine 2006a).

Based on this model, the inter-specific allometry of some properties in plants has been successfully predicted. For instance, there is some evidence that allometry of plant biomass fractions follows universal rules that are almost entirely independent of the size of the organism (Enquist & Niklas 2002; Niklas & Enquist 2002), although other pieces of evidence show that this is not always the case (Mäkelä & Valentine 2006b; Reich et al. 2007). Interspecific anatomical scaling in trees also follows MST (Anfodillo et al. 2006). Some of these discrepancies can be explained by noting that differences in species-specific allometric constants can elicit scaling changes (Niklas & Spatz 2004). In contrast to morphological properties, the scaling of physiological properties appears to be more plastic, although these are less well known. For instance, the scaling of hydraulic conductance (Mencuccini 2002) and of water fluxes (Meinzer et al. 2005) varied with plant size while respiratory rates scaled with nutrient status (Reich et al. 2006). In this last paper, the reported scaling against size varied from study to study and implied steeper scaling in smaller plants (Enquist et al. 2007). It is not known why size-dependent physiological scaling occurs during growth. For instance, it has been argued (Enquist et al. 2007) that a departure from the one of the assumptions of the MST model (e.g. volume-filling network, minimization of resistances, biomechanical adaptations to gravity, etc.) can mathematically account for the observed differences from one-fourth power scaling, however, one also needs to explain why such departures occurred in the first place. Similarly, while the allometry of morphological properties is remarkably general and holds true across monocots, dicots and conifers (Enquist & Niklas 2002; Niklas & Enquist 2002), differences across life forms or phylogenetic groups occur for the scaling of physiological properties such as xylem sap flow against stem diameter or mass (Meinzer et al. 2005).

Here, we (i) summarize the published literature on the scaling of xylem conduit diameters with distance from the apex and use meta-analysis to determine whether significant differences generally occur across two tree phylogenetic groups and two tree groups of different sizes, (ii) use a numerical model to show how these differences can be explained based on known physiological principles and (iii) use our findings to answer the question of whether Sanio’s Laws or, in alternative, MST anatomical scaling generally apply to trees.

In our numerical model, we will assume that plants attempt to maximize not the hydraulic transport properties per se, but rather the photosynthetic return minus the construction costs of the biomass invested in the xylem conduit walls. Large conduits are beneficial for a plant, because an efficient transport system minimises hydraulic limitations to photosynthesis. On the other hand, walls of large conduits are costly to build because the risk of implosion caused by tension in the transpiration stream would be greater if wall thickness did not increase in proportion to conduit diameter (Hacke et al. 2001). This is similar to earlier treatments that optimized the hydraulic return of the invested biomass (McCulloh et al. 2003; McCulloh & Sperry 2005), but the focus here is not in optimizing the distribution of a fixed amount of carbon allocated to transport tissues per se, but in maximizing overall net photosynthetic gains by the plant under a carbon cost constraint.

**MATERIALS AND METHODS**

**Literature meta-analysis**

We summarized the available literature documenting vertical changes in anatomical properties along tree stems. The literature was found either in wood technological studies or in biological studies of tree hydraulics. The primary criterion was to select studies reporting values of conduit diameters of the outer rings measured at known distances from the top of the tree. Among these datasets, a further selection was made of those studies in which measurements were taken for at least nine distances from the tree apex, to provide enough degrees of freedom to carry out statistical analyses (see below). We accepted papers in which either mean or hydraulically weighted conduit diameters were measured, because they have been found to scale linearly with each other (e.g. Mencuccini & Comstock 1997; Mencuccini et al. 1997; Coomes et al. 2007). We also accepted ten papers in which tracheid lengths but not diameters were measured, because published data for gymnosperms (e.g. Sanio 1872; Bannan 1965; Atmer & Thörnqvist 1982; Pittermann et al. 2006a,b) support the notion that tracheid diameter scales as diameter \( \propto \) length\(^6\). For those studies tracheid diameter was estimated from length using published interspecific scaling relationships (Pittermann et al. 2006a). If a study contained multiple tree samples as replicates from within the same group (e.g. experimental treatment, site, etc.), the values were pooled together into a single composite profile.
Following these criteria, 101 vertical tree analyses were grouped into 48 independent profiles from 24 studies (containing 994 average anatomical data points), which are summarized in Table S2. Of these 48 profiles, 30 contained at least nine data points and were selected for statistical analysis. To allow plotting all data on a common axis (given the differences in absolute conduit size across species) all values were normalized by calculating indices of conduit tapering \( T \) (i.e. the ratio of conduit diameter at each distance to the estimated conduit diameter at a fixed distance from the apex). Two normalizations were carried out. The first was performed by calculating \( T \) at a reference distance of 10 m from the apex \( (T_{10}) \), whereas the second calculated \( T \) at a reference distance of 0.05 m from the apex \( (T_{0.05}) \), assumed to be the petiole length. Conduit diameter at the petiole was estimated by inverting eqn. 5 in Weitz et al. (2006; cf. eqn. 12 in Appendix S1) for the point measured closest to the apex. This gives a \( T \) of 1.00 at a distance of 0.05 m from the petiole tip. \( T_{0.05} \) was employed to demonstrate the common shape of the scaling curves for the tall trees. \( T_{0.05} \) was employed to test for specific values of tapering compared with the slope of a theoretical power law. Notice also that \( \alpha \) differs from \( T \), as \( \alpha \) represents the tapering of conduit diameters across two successive ranks (\( \alpha \) is positive if the distal diameter is smaller than the proximal diameter, cf. eqn. 11 in Appendix S1).

For each of the 30 independent vertical profiles, values of \( T_{0.05} \) were plotted as function of the distance from the tree apex and we determined whether the best statistical model corresponded to a power or to an alternative function. The alternative models were either a sigmoid function leading to a plateau in conduit \( T \) with distance from the apex, a parabolic model or a modified power function with a negative linear term dependent on distance from the apex, to allow for a peak and a subsequent decline in \( T \) with distance. An alternative analysis tested the distribution of model residuals but is not reported here as the results were entirely coincident. All models were fitted using the nonlinear procedure in SPSS. Competing models were compared using the Akaike Information Criterion, corrected for small sample sizes (AICc; Hurvich & Tsai 1998; Burnham & Anderson 2002). The differences in AICc between each model and the best performing model (\( \Delta \)AICc) were then calculated. Values equal to or greater than four were taken to indicate that considerably less evidence was present for a given model compared with the best alternative (Hurvich & Tsai 1998; Meinzer et al. 2005). If values of \( \Delta \)AICc for the MST model were found to be greater than zero but less than four, this was taken as evidence against the alternative models, i.e. we treated the MST power model as our ‘control’ hypothesis, against which we tested the alternative hypothesis that either a plateau or a declining function performed considerably better. After determining \( \Delta \)AICc, all profiles were classed into an angiosperm or a gymnosperm group and into two classes of tree size, small (shorter than 10 m) or large (taller than 10 m) trees. This procedure generated a 2 \( \times \) 2 \( \times \) 2 contingency table which was analysed using a chi-square test. A Fisher’s exact test for small sample sizes (Fisher 1922) was used to test the hypothesis that the frequencies in each class were not significantly different from those predicted by chance and did not suggest an association between the classification variables and the best supported fitting function. Hence for this analysis, agreement between data and MST predictions was tested with regard to the shape of the curves, not the absolute value of the slope coefficients. Finally, for the 21 (of 30) datasets that reported measurements taken within the top 3 m of distance from the apex, we tested whether \( T \) close to the apex occurred at the same rate as predicted by MST, by checking whether the confidence intervals for the reduced major axis regression slope of a log–log function through the \( T_{0.05} \) data also included the slope of the power-law approximation for eqn. 5 (Weitz et al. 2006). An additional analysis based on residual distribution was also carried out here but it is not reported, since the results were coincident.

**Numerical modelling**

We modelled the optimal hydraulic tapering allowing maximization of whole-plant net photosynthetic gains (i.e. the increased gross gains because of greater hydraulic conductance minus the costs of building wider conduits). A numerical model (Supplementary materials) was used to test whether this approach might explain the reported patterns. A numerical model was chosen, in alternative to an analytical solution, to allow for greater flexibility in relaxing many of the assumptions that must be made to achieve a closed solution. Carbon gains were represented using a photosynthesis model incorporating a stomatal conductance term, a linear response function to air carbon dioxide concentrations and a saturating response function to irradiance. The stomatal conductance term was set to be directly dependent on the hydraulic conductance of the xylem system (which depended on conduit tapering), and a set minimum water potential term, while it was inversely dependent on leaf to air vapour pressure deficit. This approach is based on the observation that minimum water potential is frequently strongly conserved in plants and it is consistent with the idea that plants will tend to maximize the driving force for water flow through the xylem without incurring in substantial penalties due to turgor loss and cavitation (e.g. Saliendra et al. 1995). Total modelled gains were obtained by setting constant values for the relevant environmental conditions (air \( \text{CO}_2 \) concentration, vapour pressure deficit and irradiance) and by integrating over time.
The construction costs were calculated from the biomass used in building xylem conduit walls. Evidence shows that the ratio between wall thickness at the point of contact between two adjacent conduits and conduit radius is largely a function of the prevailing water stress conditions experienced by the plant and that walls are reinforced to prevent implosion caused by negative water potentials (Hacke et al. 2001). Hence building larger conduits incurs the penalty of having to build proportionally thicker walls to resist implosion. Costs related to additional tree mechanical support (e.g. fibre construction) were not considered, since they do not necessarily scale with conduit diameter and do not therefore influence optimal $T$. Additional tree metabolic costs such as leaf, rays and fine root respiration were also not considered for the same reason. For instance, if one treats maintenance respiration as a carbon ‘tax’ on photosynthesis, its inclusion in the model will lower gross gains but will not affect optimal conduit $T$. Roots and leaves extra-xylary hydraulic resistances were modelled as giving fixed water potential losses. While conduit numbers doubled with each rank following MST, conduit tapering was allowed to vary to maximize net canopy carbon gain. Conduit $T$ was allowed to vary during tree growth in two different ways, i.e. by either finding the optimal constant $\hat{a}$ or by finding the optimal variable $\hat{a}$ within an individual. The model assumed constant leaf water potential throughout tree growth. A list of parameter values is given in Table S1, where the implications of the relaxation of assumptions of the MST model and the role of environmental factors are also discussed. Because of variable conduit $\hat{a}$ during growth and variable construction costs, optimal $T$ was not predicted to be the same for different plant sizes or different taxa.

RESULTS AND DISCUSSION

Empirical data

A summary of the 48 profiles is given in Fig. 1, together with reference MST power curves and the numerical model output, for the four combinations of tree size and phylogenetic group. To highlight the overall trend, values of conduit $T$ were normalized across studies such that for all curves $T_{10} = 1$ at a distance from the apex $D = 10$ m, with the same normalization carried out also for the reference theoretical curves (variability in $T$ across studies can be seen more clearly when values are normalized such that $T_{0.05} = 1$ at a distance $D = 0.05$ m from the apex, cf. Fig. S5). The first statistical analysis determined whether a power model (black lines in Fig. 1) adequately described the vertical tapering profiles across phylogenetic and tree size groups, i.e. whether overall tapering along the entire length of a tree followed a power function or showed evidence of a gradual change in curve shape with plant height to a plateau or to a declining trend close to the stem base. Of the 30 profiles for which the analysis could be carried out, 18 profiles (i.e. 60%) significantly diverged from a power model (i.e. $\Delta$AICc $> 4$ compared with a plateauing or declining model, see Table S2). A chi-square test showed a significant association across studies between lack of support for a power model and plant size ($\chi^2 = 5.93$, Fisher $P = 0.024$, $n = 30$), suggesting a departure of the large plants from power scaling. Similarly, a chi-square test showed a significant association across studies between lack of support for a power model and phylogenetic group (gymnosperms versus angiosperms; $\chi^2 = 7.75$, Fisher $P = 0.009$, $n = 30$), suggesting a departure of the gymnosperms from power scaling. When the comparison of size classes was carried out by blocking for phylogenetic group, $\chi^2 = 0.24$ and $\chi^2 = 10.98$ (Fisher $P = 1.00$ and $P = 0.004$ for angiosperms and gymnosperms, respectively, $n = 30$), suggesting that size differences were very significant for gymnosperms but not for angiosperms. Finally, when the comparison of phylogenetic group was carried out by blocking for size differences, $\chi^2 = 13.37$ and $\chi^2 = 0.00$ (Fisher $P = 0.002$ and $P = 1.00$ for large and small trees, respectively, $n = 30$), suggesting that differences between gymnosperms and angiosperms in the best supported model were only apparent for trees taller than 10 m. Maximum height across the angiosperm dataset seldom exceeded 25 m, i.e. only about half of the maximum height of the gymnosperm dataset.

Most datasets showed rapid conduit $T$ at the top. This was investigated in more detail for the 21 datasets in which measurements were reported for the first 3 m of distance from the apex (Fig. 2, cf. Fig. S5) and required using $T_{0.05}$ instead of $T_{10}$. A log–log function was fitted to the pooled $T_{0.05}$ data from all 21 datasets and its slope compared to the expected value of 0.1861 (Eqn.5 of Weitz et al. 2006; corresponding to $\hat{a} = 1/6$ over the first 3 m). Gymnosperm trees showed a regression slope above 0.2 in both size classes (which was significantly larger than MST predictions, Table 1), suggesting that both tree size classes tapered faster than predicted by MST close to the apex. Angiosperm trees showed a slope steeper than the predicted value in only one case (Table 1), suggesting that tapering close to the apex was faster than MST in small but not in large plants (cf. Fig. 2). The small angiosperms had a regression slope for the first 3 m slightly below 0.3, but the slope within the first 0.5 m approached one-third.

To conclude, for both phylogenetic groups, we found strong evidence that scaling of conduit diameter against distance from the apex depended on individual size and vertical position (i.e. rank number). Scaling was faster than MST at the top of all trees (except large angiosperms) and it either declined towards MST power scaling (at the base of both small angiosperms and small gymnosperms) or it...
developed into a saturating trajectory, not consistent with a power function (in the much taller gymnosperms).

Numerical modelling

Maintaining maximum net photosynthetic gains during tree growth required varying conduit $\tilde{a}$. The model predicted steeper conduit tapering in short trees and slower or even reverse tapering in tall trees, reflecting the empirical trend noticed above. When the model was run assuming fixed $\tilde{a}$ within a tree, optimal $T$ was found to gradually decline during growth at rates dependent on apical conduit diameter (cf. Fig. S1), as empirically observed (G. Petit, T. Anfodillo & M. Mencuccini, unpublished data). When the model was run with $\tilde{a}$ within each tree dependent on rank number, it reproduced the major trends found in the empirical datasets, i.e. it predicted higher $\tilde{a}$ close to the tops, lower $\tilde{a}$ in the centre and finally negative $\tilde{a}$ close to the base of tall trees (see thick red lines in the bottom panels of Fig. 1). The model predicted a plateau to occur earlier during vertical growth at the base of gymnosperm trees, as a consequence of higher tracheid, compared to vessel, constructions costs per unit conduit diameter (Hacke et al. 2001) and larger numbers of smaller tracheids per leaf. In addition to Sanio’s second law, our model also reproduced the observation (Bailey & Shephard 1915) that the distance from the base below which conduit diameter and length begin to decline increases with tree size, as a result of construction costs accumulating faster in tall trees. Finally, the model predicted steeper anatomical scaling in the roots compared to stems (see Fig. S3), because of low

Figure 1 Tapering profiles for two phylogenetic groups (angiosperms and gymnosperms) and two tree size classes (large and small plants). The $Y$-axis represents a tapering coefficient (i.e. $T_{10}(b) = r(b)/r(b = 10)$, where $r(b)$ is conduit radius at distance $b$ from the apex, and $r(b = 10)$ is conduit radius estimated at a distance of 10 m from the apex). All profiles and theoretical curves go through the point $T = 1$ at $b = 10$ m, so that across-species variability in absolute conduit size is eliminated. The black curve gives the theoretical MST scaling (Weitz et al. 2006), while the thick red curves in the two panels at the bottom give an output from the numerical model. Notice that most series for the gymnosperms (particularly in large trees) taper more slowly than predicted by the MST power curve after the first few meters, with many showing even a decline towards the tree base. Most angiosperm series taper faster than predicted by MST in the small plants, but follow MST more closely in the large plants. Species abbreviations can be found in Table S2. Letters and numbers next to a species code refer to different treatments, age classes or sampling sites within a study.

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construction costs of the comparatively thinner walls of root conduits, due to lower mechanical requirements and lower risks of implosion (i.e. less negative water potentials). This is also similar to available observations (e.g. Oliveras et al. 2003; McElrone et al. 2004).

While MST predicts a universal curve, our numerical modelling produced different curves depending on parameter values. Although the absolute values of $T$ changed from one model run to another, the trends mentioned above were very robust to changes in parameter values. A sensitivity

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**Figure 2** Tapering profiles for the first 3 m from the apex for two phylogenetic groups (angiosperms and gymnosperms) and two tree size classes (large and small plants). The $Y$-axis represents the tapering coefficient $T_{0.05} = \frac{r}{r_{\text{apex}}}$, where $r_{\text{apex}}$ is conduit radius estimated at a distance of 0.05 m from the apex. The gymnosperms (both large and small plants) and the small angiosperms taper faster than predicted by the MST power curve in the first 3 m (all $P < 0.005$), whereas the series for the large angiosperms did not significantly depart from MST ($P > 0.05$). The black curve gives the theoretical MST scaling calculated following (Weitz et al. 2006) for $\bar{a} = 1/6$.

**Table 1** Sample size, RMA regression coefficients, $R^2$, confidence intervals of the slopes and significance levels of the tests on the relationships shown in Fig. 2 (i.e. limited to the first 3 m of distance from the apex), for two phylogenetic groups (gymnosperms and angiosperms) and two size groups (small and large). The significance levels refer to a t-test comparing the observed slopes for each group with the expected value of 0.1861 (Eqn. 5, Weitz et al. 2006; calculated for $\bar{a} = 1/6$).
analysis of the major model parameters is given in the Supplementary materials.

**Impact of tree size**

That conduit $a$ should depend on individual size and vertical position seems functional to optimal plant growth and a simple power-law with constant $a$ should have limited value in describing tapering throughout a tree’s life cycle. In small plants, $a = 1/6$ is insufficient to prevent losses in conductance (Mencuccini et al. 2005; Mäkelä & Valentine 2006a) while the costs of tapering are small. In fact, in the first 0.5 m of the small angiosperms, most datasets showed $a \to 1/3$. In larger trees, $a = 1/6$ is too expensive to retain and its decline allows achieving maximum net gains.

Our numerical model realistically reproduced the patterns observed in the empirical data with regards to the levelling off of lumen dimensions at the base of large trees as well as the prediction of faster-than-MST $a$ at the top of trees. However, without additional constraints on the rate of maximum initial tapering, our model would predict very fast rates of conduit enlargement, much larger than empirically observed (i.e. $a > 1$). We therefore restricted the initial rate of tapering below a certain threshold. While accepting that this is not theoretically justified, we defend it on the ground that the equivalent choice of assuming a constant $a = 1/6$ throughout is more arbitrary. There is no special physiological reason for selecting $a = 1/6$, except the mathematically appealing argument that the resistance of each pipe increases by a constant amount every time a new rank is added at the bottom, such that its percentage increase will gradually decline towards zero at infinity. However, in the range of realistic heights, even with scaling above $a = 1/6$, resistance will continue to increase significantly. Therefore, in both cases the initial tapering is chosen arbitrarily. Our approach however predicts the gradual decline in $a$ as plants get bigger and quantifies the limitations imposed by the plant’s carbon balance.

Murray’s law (West et al. 2000) also attempts to predict the maximum efficiency of hydraulic conductance for blood circulation in animals. As applied to the xylem (McCulloh et al. 2003), Murray’s law is based on the principle of minimizing hydraulic resistance while keeping wall investment constant, with the optimal tapering dependent on whether conduits furcate. However, existing data do not generally support the presence of conduit furcation in the stems of trees (McCulloh & Sperry 2005; G. Petit, T. Anfodillo & M. Mencuccini, unpublished data). In the absence of furcation, Murray’s law predicts that maximum conductance for a constant amount of invested biomass occurs for untapered pipes (i.e. $a = 0$). We removed the constraint of a fixed investment in conduit walls in our model by directly coupling the costs of xylem construction to the benefits of photosynthesis, thereby overcoming the limitations imposed by Murray’s law. In a small plant, wall construction costs were trivial, therefore a larger investment in conduit walls was beneficial and led to fast rates of tapering ($a \gg 1/3$, if the rate of initial tapering was not restricted, as opposed to Murray’s law prediction of $a = 0$) and increased whole-tree photosynthesis. However, as soon as large conduits were obtained after a few generations, hydraulic limitations to photosynthesis were greatly reduced and $a \to 0$, as in Murray’s law. Therefore, while $a = 0$ (Murray’s law for non-furcated conduits) and $a = 1/6$ (MST) are too slow a slope for the tapering observed close to the apex, $a \gg 1/3$ (our carbon balance model) is instead too high. Hence, none of the existing theories can currently predict the observed rates of tapering close to the apex. The most likely candidates are a developmental constraint preventing a very rapid increase in conduit diameter (and length) at short distances from the crown, the interactions between conduit diameters, pit resistance and vulnerability to cavitation and mechanical constraints in rapidly developing shoots.

Our model did not incorporate inter-conduit pits, on the ground that the log–log scaling of end-wall and conduit lumen resistance is typically linear across-species (Wheeler et al. 2005), i.e. its inclusion would not change optimal $T$. However, depending on the assumptions made, inclusion of pits may only increase the calculated $a$ (Becker et al. 2003), and hence it would not help our model predict $a < 1/3$ below the apex, once again highlighting the need to incorporate effects linked to resistance to cavitation directly. Also, inclusion of pits would explain nor the plateau effect, neither the differences between angiosperms and gymnosperms.

**Impact of phylogenetic group**

Current empirical and theoretical work (Pittermann et al. 2006a,b; Sperry et al. 2006) suggests that the differences between the homoxyloous wood of gymnosperms and the heteroxyloous wood of angiosperms has significant implications for the functionality and ecology of these two groups of taxa. Conifers appear to achieve efficiency in water transport by packing large numbers of small conduits per unit of volume and by an efficient pit pore structure. However, because tracheids must also carry out a mechanical supporting function, their wall thickness per unit of conduit diameter must be larger for a given vulnerability to cavitation, thereby leading to larger carbon costs, further enhanced by the large number of conduits per leaf. As hypothesized here, it is possible that the maximum achievable wall thickness varies during growth as a result of variable construction costs and that this sets the limit to maximum tracheid diameter in tall trees. In contrast, conduit
construction costs are lower for angiosperms and these taxa appear capable of obtaining steeper $a$ along the main stem even in relatively tall trees, although at heights greater than those available for this analysis, carbon costs should become limiting also for angiosperms. Only a few datasets were available for very tall angiosperm trees. Four of them (James et al. 2003) suggested a plateauing trend for two species and a declining trend for the remaining two, although each vertical profile was only composed by four to five points and could not be tested statistically.

It is interesting to note the differences between the two phylogenetic groups in the rates of initial $a$ close to the crown. In the conifers, $a$ close to the crown continued to be clearly faster than one-sixth even in tall trees. As a consequence, large conduits with thick walls rapidly developed and costs started to increase rapidly. In the angiosperms, the tall trees tapered more slowly than the short trees close to the crown and this may have contributed to maintaining rates of tapering consistent with MST.

**Implications for scaling**

Our meta-analysis confirms that Sanio’s second law is generally applicable to gymnosperms and clarifies that its applicability depends on the size of the tree. Scaling varies within each individual from top to bottom, with $a$ generally declining with distance from the apex and also varying as a function of plant size, with exponents declining with tree size.

If conduit $a$ is size-dependent during growth, then it logically follows that other processes should be equally so. Indeed available physiological data, relevant to both water transport (Mencuccini 2002, 2003; Meinzer et al. 2005), photosynthesis (Bond 2000; Koch et al. 2004) and respiration rates (Reich et al. 2006; Enquist et al. 2007) show that this is the case. This creates an interesting conflict with other sources of evidence, which on the contrary show size-independent allometry for much of the plant kingdom (e.g. Enquist & Niklas 2002; Niklas & Enquist 2002). One possible resolution of this conflict is a careful examination of inter-individual versus inter-specific scaling of both morphological and physiological properties and in examining the possibility that different scaling rules apply to these two types of allometry. Another possibility is that the analysis of morphological properties of (especially large) plants does not have enough temporal resolution to provide meaningful insights into plant physiological processes.

**Conclusions**

Conduit $a$ was not found to be constant within trees (hence the network is not self-similar) but varied as an inverse function of distance from the apex, resulting in values close to one-third at top of (especially) young trees, values close to zero in the centre and even negative values at the trunk base (especially in the gymnosperms). In the angiosperms, large trees showed lower values of $a$ at the top compared to small trees, whereas in the gymnosperms, large trees departed from power law scaling at their base. A numerical model, maximizing the photosynthetic gains minus the conduit wall construction costs, could explain all three trends, highlighting the fundamental role of xylem construction costs in explain anatomical patterns in trees. Despite this success, the model overestimated the rapid, but gradual, conduit tapering observed inside the crowns of trees. Other constraints linked to, e.g. cavitation vulnerability, mechanical needs or developmental restrictions may exert additional pressures that will affect $a$ throughout the tree and particularly close to the tree crown. Overall, we conclude that Sanio’s second law applies to gymnosperms and possibly also to very tall angiosperms for which current data are very limited. Models such as MST must account for position-dependent tapering within individuals and size-dependent tapering during growth.

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**References**


SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Structure of the numerical model.

Figure S1 Optimal tapering coefficient $\tilde{a}$ as a function of distance from the apex (or total number of ranks $N$) assuming constant tapering within a tree (i.e. $\tilde{a}$ is independent of rank number and positive) for four different values of conduit radius. Note that $\tilde{a}$ is used in this graph, not $T$.

Figure S2 An example of how the model calculated gross photosynthetic gains, total carbon construction costs and net gains (the difference between the first two) for trees of variable number of ranks (hence distance from the apex).
**Figure S3** In this simulated coniferous tree, conduits tapered for a few metres below the tree apex at a constant rate (corresponding to $\tilde{a} = 0.20$).

**Figure S4** An example of the impact of allowing variable maximum tapering rates just below the apex of angiosperm and gymnosperm trees.

**Figure S5** Tapering profiles for two phylogenetic groups (angiosperms and gymnosperms) and two ontogenetic classes (large and small plants).

**Table S1** List of parameter values employed in the numerical model.

**Table S2** Datasets employed in the meta-analysis.

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