# Two path length effects emerging from ontogenetically stable axial xylem design affect the conductance of inner sapwood rings

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Number of words in abstract: 197

Number of words in main text: 6637

Number of cited references: 48

Number of Tables: 2

Number of Figures: 7

Supporting Information: 3 Tables and 4 Figures

Running title: Effects of height growth on sapwood-heartwood transition

## Abstract

The process of sapwood/heartwood transition in trees is not fully understood. We tested whether the ontogenetically-stable apex-to-base conduit widening generates path length effects limiting the conductance of inner sapwood rings.

The axial scaling (*b*) of conduit hydraulic diameter (*Dh*) was estimated at annual resolution in a spruce and beech tree. We compiled a global dataset of sapwood ring number (*NSWr*), their average width (*SWrw*), tree height (*H*) and stem elongation rate (*ΔH*) in conifer and angiosperm trees. A numerical model simulated the effects of *H* and *ΔH* on the conductance of each xylem ring (*KRING*).

*b* resulted ontogenetically stable. Simulations well predicted the observed patterns of increasing *NSWr* with *H* and decreasing *NSWr* with *ΔH*, assuming that heartwood forms when the marginal conductance gain of maintaining the functionality of an inner ring becomes negligible.

Sapwood/heartwood transition minimizes the C costs associated to allocation to secondary growth and maintenance of living sapwood required to attain a given sapwood conductance. The number of sapwood rings depends on the effects of *H* and *ΔH* on the conductance of inner sapwood rings. The width of sapwood rings contributes to compensate for the lower conductance of inner sapwood rings at high *ΔH*.

**Keywords:** Sapwood; Heartwood; Tree growth; Carbon allocation; Conduit widening; Hydraulic conductance; Water relations; Sapflow

## Introduction

In mature trees, the xylem tissues accumulated by secondary growth account for the majority of the total plant biomass and nearly for the entire length of the root-to-leaf hydraulic path. The pivotal physiological functions performed by the xylem are the water transport through its vascular elements, mechanical support and the different metabolic activities carried out by its parenchyma cells. During ontogeny, trees have to cope with the negative effects of being taller on the efficiency of water transport and on the carbon allocation required for the build-up and maintenance of a continuously larger xylem biomass (Mencuccini, Hölttä, Petit & Magnani 2007; Givnish, Wong, Stuart-Williams, Holloway-Phillips & Farquhar 2014). However, only an outer set of rings of the entire three-dimensional xylem architecture remains functional for these processes (i.e., the sapwood).

The transition of sapwood into non-functional and non-living xylem (i.e., the heartwood) has been investigated for long, with some strong empirical evidence suggesting age as the main driver of this process. Indeed, the sapwood turnover rate (i.e., the number of years required to turn a sapwood ring into heartwood) is relatively constant along the trunk and across individuals (Sellin 1994), although variable across environmental settings (Sousa, Cardoso & Pereira 2013) and across species (e.g., from very few sapwood rings in ring-porous species to more than a hundred in some conifers: Spicer, 2005).

In the last decades, advances in the understanding of the tree hydraulic architecture provided solid evidence that age arises as a correlative factor for some important anatomical and physiological patterns simply because it correlates with tree size.

The tree xylem architecture can be described as a series of conical layers, the new ones superimposed on top of the older ones, thus increasing in both height and diameter. The typical radial and axial anatomical patterns of xylem conduit diameter at the individual tree level are known since the observations of Karl Sanio (1872) (the so called first law: the diameter of xylem conduits increases with the ring’s cambial age from pith to bark; the so called second law: they taper along a xylem ring, i.e., they decrease in diameter from the stem base towards the apex). The long-standing view that conduits size depends on cambial age (Schulte 2012) has been recently challenged by the evidence that in the newly formed (i.e., outermost) xylem layer the vascular conduits progressively increase in lumen diameter (*D*) because of the longer time required for cell enlargement with increasing distance from the stem apex (*DFA*) (Anfodillo *et al.* 2012), and that this widening pattern is well approximated by a power function:

*D*=*a*×*DFAb* eq. 1

with an exponent in the range of *b=*0.1÷0.4, irrespective of species and tree size (Anfodillo, Petit & Crivellaro 2013). Based on some limited empirical evidence that a stable conduit widening along the vertical stem axis is maintained during ontogeny (Weitz, Ogle & Horn 2006; Prendin *et al.* 2018b), it has been argued that the radial increase in conduit diameter from pith to bark simply reflects the tree growth in height, thus not causally related to cambial age (Carrer, Von Arx, Castagneri & Petit 2015).

If the anatomical characteristics of each xylem ring are *DFA*-dependent, it follows that the sapwood is not a hydraulically homogeneous tissue while the tree is still actively growing in height.

Since the hydraulic conductance of xylem conduits (conifer tracheids and angiosperm vessels scales inversely to their length and directly to the fourth power of their diameter (Hagen-Poiseuille law: Tyree & Ewers, 1991), two important hydraulic properties of the xylem transport system are related to *b*. First, the basipetal increase in conduit lumen diameter along a single file of xylem conduits connecting the stem tip to root tip greatly reduces the total axial hydraulic resistance that would otherwise accrue without conduit widening (Becker, Gribben & Lim 2000; Petit & Anfodillo 2009). More specifically, the total hydraulic resistance of a single file of xylem cells cumulates from the stem apex downwards at lower rates for higher widening exponents *b* (Becker *et al.* 2000; Petit & Anfodillo 2009). Secondly, the hydraulic resistance of the same xylem file in the topmost stem internode (i.e., the annual stem elongation, *ΔH*) is proportional to its length by a factor that decreases with *b* (i.e., the difference in the hydraulic resistance of the apical shoot in a fast vs. slow growing tree would be smaller if *b* is high and increased if *b* is low).

If it is assumed that water flows primarily vertically and confined along each sapwood ring (see below), different hypotheses can be postulated around the possible anatomical configurations adopted by a tree during its ontogeny to compensate for the effect of height on the leaf-area-based sapwood conductance (Fig.1):

1. the sapwood ring area for a leaf area unit increases with *H*; such a hypothesis must be rejected because ring width (*SWrw*) and area typically show a sustained decline and limited increase with *H*, respectively(Fritts 1976)*;*
2. while the scaling exponent *b* remains ontogenetically stable, the allometric constant (*a*) (eq. 1) increases with tree height (*H*) (Echeverría, Anfodillo, Soriano, Rosell & Olson 2019) (i.e., the conduit diameter is larger at any *DFA* in taller trees);
3. *b* is not ontogenetically stable, but it increases with *H*;
4. *b* and *a* (eq. 1) are ontogenetically stable, but the number of sapwood rings (*NSWr*) increases with *H*. Note that these predictions lead to substantially different conclusions with regard to the predicted construction and maintenance costs of xylem cells.

Furthermore, in theory *ΔH* should affect the contribution of inner rings to the total sapwood conductance, and thus potentially the total number of sapwood rings. In fact, the axial hydraulic path along a given inner xylem ring is shorter than the actual root-to-leaf distance for all rings except the current year’s, by as much as the stem elongation since the year of formation of that ring. The production of new shoots distally implies additional resistances to trespass for water flowing in inner rings, thus theoretically limiting their capacity to contribute to the hydraulic conductance at the whole tree level. Consequently, other things being equal, the contribution of the water transport capacity of inner rings would be theoretically more limited in fast- than in slow-growing trees, since the longer young internodes of fast-growing trees would cumulate higher hydraulic resistances in series distal to the path length of the innermost rings. In this context, two alternative hypotheses can be postulated on the mechanism of compensation for the negative effect of *ΔH* on the hydraulic conductance of inner sapwood rings in order to maintain a constant leaf-area-based conductance:

1. the number of sapwood rings (*NSWr*) increases with *ΔH*;
2. while the *NSWr* decreases, the sapwood ring width (*SWrw*) increases with *ΔH* to compensate for the fact that the contribution of inner rings to total hydraulic conductance is increasingly limited at high *ΔH*.

The radial resistance to water flow across the rings may be expected to be important in affecting the contribution of inner rings to water transport at the tree level. However, there is not much information in literature on the actual hydraulic pathway across the rings. However, empirical measurements revealed a negligible contribution of both ray tracheids and ray parenchyma to the radial movement of water across xylem rings in a few conifer species (Barnard, Lachenbruch, McCulloh, Kitin & Meinzer 2013). Furthermore, an intermediate layer of narrow cells exists between the highly conductive earlywood conduits of two adjacent rings (i.e., the latewood) in temperate tree species. Therefore, the axial hydraulic conductivity (i.e., conductance per unit of cross-sectional area and normalised for length) is likely orders of magnitude higher than the radial conductivity at any position along a given sapwood ring until its apical end, thus theoretically conferring an important hydraulic compartmentalization across adjacent rings due to the large radial hydraulic resistance between rings.

Ring-to-ring compartmentalization coupled with the lower conductance of inner sapwood rings would logically suggest that water flows at decreasing rates with increasing distance from the bark.

Empirical measurements support this prediction by showing that sap flow rate at different distances from the bark typically decreases with distance from the bark (from bark inwards) (Phillips, Oren & Zimmermann 1996; Jiménez, Nadezhdina, Čermák & Morales 2000; Gartner & Meinzer 2005; Zhao *et al.* 2018), to ultimately cease at the transition into the non-functional heartwood (Gebauer, Horna & Leuschner 2008; Beauchamp, Mencuccini, Perks & Gardiner 2013).

This study is motivated by the hypothesis that the sapwood rings are maintained for as long as they contribute in sufficient measure to total tree hydraulic conductance, and sapwood transition into heartwood occurs when the hydraulic contribution of the innermost sapwood ring to the total xylem conductance becomes negligible and the metabolic maintenance of this innermost sapwood ring a "wasteful" C cost.

First, we tested whether the axial pattern of conduit diameter from the stem apex to base is ontogenetically stable in one or both of the allometric components *a* and *b* (eq. 1) (see hypotheses i to iv). We expect that the number of sapwood rings (*NSWr*) increases with tree height (*H*) in order to effectively compensate for the negative effects of *H* on the total xylem conductance (hypothesis iv), and that *NSWr* is negatively related to *ΔH* because the higher hydraulic resistance of longer apical shoots (i.e., higher *ΔH*) limits the contribution of the inner sapwood rings to the total conductance and that compensation to maintain constant conductance is obtained via larger sapwood rings (*SWrw*) (hypothesis vi).

To test our hypotheses, we build two distinct datasets. A first dataset with detailed measurements of conduit diameter measured at the ring level from pith to bark at several position along the stem of a mature *Picea abies* and a mature *Fagus sylvatica* tree is used to test the hypothesis of the ontogenetic stability of the axial widening of xylem conduits (parameters *a* and *b* of eq. 1, hypothesis ii and iii). Secondly, a global database with empirical data of sapwood traits of conifer and angiosperm trees, including additional novel measurements in the Alpine region of Italy, is employed with a numerical model of axial and radial xylem water transport. We use the model to test how sapwood functionality depends on the hydraulic effects of *H* and *ΔH* on the total conductance of the different sapwood rings, and how axial widening (i.e., *a* and *b* of eq. 1), ring width and the radial conductivity between rings affect these relationships.

## Material and Methods

*Vertical profiles of xylem conduit diameter*

In order to test for the ontogenetic stability or the acclimation of the allometric parameters *a* and *b* (eq. 1) to the increasing tree height, two mature trees, one conifer and one broadleaved species, were selected at two sites in the Eastern Italian Alps. A dominant *Picea abies* Karst. tree (PA) was felled in 2012 at a subalpine mixed stand located at Latemar (Bozen, Italy: 46°23ˈ Lat, 11°32ˈ Long) at 1900 m a.s.l., whereas a dominant *Fagus sylvatica* L. (FS) was felled in 2013 in a pure even-aged stand located at Cansiglio (Belluno, Italy: 46°04ˈ Lat, 12°25ˈ Long). Mean annual temperature and total annual precipitation at the sites are 4.7 / 6.6 °C and 950 / 1800 mm at Latemar / Cansiglio, respectively. The tree height (*H*) and diameter at 1 m from the ground (*D*) were *H*=26 m and *D*=35 cm for PA, and *H*=31 m and *D*=35 cm for FS. Tree age (222 years for PA and 140 years for FS) was assessed as the number of annual rings counted on the most basal stem disk (at 1 m from the ground). Discs used for dendro-anatomical analyses were extracted at different positions along the stem (at 1, 3, 5, 7, 9, 11, 13, 15, 17, 18, 19, 20, 21, 22, 23, 24, 25 m from the ground, plus other 7 discs along the last meter to the treetop for PA, at 2, 7, 8, 12, 16, 20, 22, 24, 25, 26, 27, 28 m from the ground, plus other 10 discs along the last 3 m to the treetop for FS).

From each sampled disc, a radial 1 cm wide and 1 cm thick wooden block spanning from the pith to the outermost ring was extracted. Tree-ring widths (*RW*) were measured to the nearest 0.01 mm (CCTRMD mod. Aniol: Aniol, 1987) and crossdated with the other discs belonging to the same individual to assign the correct calendar year of formation, following standard dendrochronological protocols (Stokes & Smiley 1968). Wooden sectors were then split into smaller trapezoidal blocks paying attention to create an overlap between successive blocks to avoid missing rings. Thin sections of 15 μm thickness were then cut with a rotary microtome (Leica RM2245, Leica Biosystems, Nussloch, Germany), stained with safranine (1% in distilled water) and permanently fixed on glass slides with Eukitt (BiOptica, Milan, Italy). Overlapping images (around 25%) of the sections taken at 100x magnifications with a Nikon Eclipse 80i microscope (Nikon, Tokyo, Japan) were stitched together with PTGui (New House Internet Services B.V., Rotterdam, The Netherlands), and then analysed with ROXAS (von Arx & Carrer 2014). Ring boundaries were outlined manually, and then the software automatically measured for each ring the mean width (*RW*) and the lumen area of all vascular elements (tracheids for *P. abies*, vessels for *F. sylvatica*), from which the hydraulic lumen diameter was calculated (Kolb & Sperry 1999) (*Dh*=Σ*di*5/Σ*di*4, where *di* is the diameter of the *i*-conduit). In synthesis, all vascular conduits along a pith-to-bark wooden stripe of 1 cm width were measured for each disc of both sampled trees.

The time series of *RW* automatically measured by ROXAS on each core section was checked against that measured with CCTRMD to assign the correct calendar year of formation (*n*) of all the rings.

The total tree height at the *n*-year (*H*n) was retrospectively reconstructed as:

eq.2

where *hk* is the distance from the ground of the *k*-disk, *Nk* the number of rings of the *k*-disk, *l(k/k+1)* the distance between the *k*-disk and that sampled above (*k+1*), and *CA*n the cambial age of the *n*-ring. The actual distance from the apex of the *n*-ring of the *k*-disk (hereafter distance from contemporary apex, *DCA*) was then estimated as:

*DCAn*=*Hn*-*hk*. eq. 3

Since the number of rings decreased in discs sampled at higher positions along the stem, the number of axial points along a given ring decreased for younger tree ages.

*Tree growth and sapwood properties*

In order to test whether the number of sapwood rings (*NSWr*) varies with tree height and the stem elongation rate (*ΔH*), we compiled a global dataset of biometric and tree ring data composed of our own measurements (Alpine dataset) and data from the global biomass and allometry database (BAAD) (Falster *et al.* 2015).

A total of 503 trees from four species (*Abies alba* Mill., *Picea abies* Karst., *Pinus cembra* L., *Larix decidua* Mill.) were sampled from 78 stands across the Eastern Italian Alps (45°08['](https://it.wikipedia.org/wiki/Primo_(simbolo))-46°09['](https://it.wikipedia.org/wiki/Primo_(simbolo)) Lat, 10°04['](https://it.wikipedia.org/wiki/Primo_(simbolo))-13°07['](https://it.wikipedia.org/wiki/Primo_(simbolo)) Long), ranging more than 1000 m in elevation (1050-2200 m a.s.l.), with contrasting stand attributes (pure and mixed, even- and uneven-aged, managed and unmanaged) and environmental settings (temperature, elevation, precipitation range, soil type, slope). For each tree we measured the total tree height (*H*) and the diameter at breast height (*Dbh*). Two cores were extracted at breast height and the sapwood boundary marked immediately according to chromatic transition into heartwood (e.g. in *Larix* or *Pinus* spp.) or to its translucency, due to the presence of water, against direct light (Quiñonez-Piñón & Valeo 2018) (e.g. in *Abies* or *Picea* spp.). Tree *age* was estimated by counting the total number of rings. In off-center cores we fitted a geometric pith locator to the innermost rings to estimate the distance to the theoretical pith and number of missing rings (Duncan 1989) Sapwood rings were then counted (*NSWr*), their width measured as described before, and the mean sapwood ring width calculated (*SWrw*). Mean stem elongation rate was assessed as *ΔH*=*H*/*age*.

Trees from the BAAD dataset (Falster *et al.* 2015) were filtered for the concomitant presence of the following variables: *age*, diameter at breast height (*Dbh*; basal stem diameter was used when *Dbh* information was missing), tree height (*H*) and sapwood area (*ASW*). The filtered dataset comprised five angiosperm (*Eucalyptus delegatensis* R.T. Baker, *Eucalyptus grandis* W. Hill, *Eucalyptus nitens* H. Deane & Maiden, *Eucalyptus urophylla × grandis*, *Populus tremuloides* Michx) and five conifer species (*Picea mariana* (Mill.) BSP, *Pinus banksiana* (Lamb.), *Pinus ponderosa* Douglas, *Pinus sylvestris* L., *Pseudotsuga menziesii* (Mirb.) Franco).

*ΔH* and *SWrw* were estimated as *H*/*age* and *Dbh/*(2×*age*), respectively. The heartwood diameter (*DHW*) was calculated as *2*×*(BA-ASW)/π)0.5*, where *BA* is the stem basal area, calculated as *BA=π*×*(Dbh/2*)2. Sapwood width (*WSW*) was then calculated as *WSW*=(*Dbh-DHW*)/2. Lastly, the number of sapwood rings (*NSWr*) was estimated as *WSW*/*SWrw*.

The full dataset is available in supplementary information (SI). The list of variables used in this study is reported in Table 1.

*Statistical analyses*

Allometric relationships were analysed on log10-transformed data. Bayesian linear models (R package brms: Bürkner, 2017) were used to test for fixed effects and interactions on the target dependent variables. Models were evaluated using the leave-one-out cross-validation (LOO) method. When the difference in the expected log pointwise predictive density (elpd) of two models is lower than 4 units, we choose the simplest. All analyses were performed with the software R version 4.1.3 (R Development Core Team 2014)

We tested for the fixed effect of *H* on the relationship between log10*Dh* and log10*DCA*. *H* was used either as numeric (Log10*H*) or factor variable (with *H* approximated to integer numbers, thus resulting in *H* classes of 1 m).

Furthermore, we tested for the independent path length effect of *H* or *ΔH* on *NSWr*, using a linear model with log10*NSWr* as the dependent variable, log10*H* or log10*ΔH*, *ΔHCLASS* or *HCLASS* (used as factor variables) and interactions (Log10*H×ΔHCLASS* or log10*ΔH×HCLASS*) as independent variables. Lastly, we tested for the fixed effects of log10*ΔH*, division (Conifers/Angiosperms) and their interaction on log10*SWrw*. Since the Alpine dataset and data of conifer and angiosperm species from the BAAD dataset did not much overlap in terms of *H* and *ΔH*, statistical analyses were applied to the whole dataset.

*Hydraulic model*

The numerical model has two dimensions (i.e., axial and radial direction). The structural and functional xylem properties in the tangential direction (i.e., the third dimension) was assumed to be homogeneous and therefore not considered in the model. The model was designed to simulate the total conductance of each sapwood ring (*KRING*), considering both the axial and radial hydraulic pathways from stem base to leaves, and a given soil water potential (*Ψsoil*) and whole tree transpiration rate (*T*). The model was divided into *N* times *M* numerical elements in cylindrical coordinates as represented in Fig S1. The axial height of each element was tree height (*H*) divided by *N*, and the radial width of each element was calculated so that each ring had the same cross-sectional area. Water was lost by transpiration only from the topmost element *i*=*N* and *j*=*M*. The axial water flow rate between different elements and the water potential of each element were calculated so that the flow rate between two axial elements at *i*-1 and *i* is

eq. 4

where *Fax* is axial sapflow rate, *Ψ* is water potential, *kax* is the area-specific axial hydraulic conductivity, *Aax* is the cross-sectional area between two elements, and *Δx* is the distance between two adjacent elements. The flow rate between two radial elements, i.e., the radial sap flow rate *FRAD*, between two elements *j*-1 and *j* is

eq. 5

where *kRAD* is the area-specific radial hydraulic conductivity.

The axial hydraulic conductivity (*kax*) is calculated from the conduit radius (*d*), which is made to scale with distance from the contemporary apex (*DCA*):

eq. 6

where *a* and *b* are the allometric constant and exponent of the axial scaling of conduit diameter (eq. 1). Although there is no conduit number explicitly in our model, this corresponds to having no conduit furcation in the model. Radial hydraulic conductivity (*kRAD*) was assumed to have the same constant value everywhere, although alternative scenarios were also explored.

*T* and *Ψsoil* were given as inputs to the model, while water potential at the apex was obtained from the computed fluxes and resistances. These variables allowed to calculate a total tree conductance as the ratio of the flux to the soil-to-apex water potential difference (*KCUM* and *rKCUM*, i.e., relative *KCUM* relativizing all values to a maximum of 1) while progressively increasing the number of sapwood rings starting from the outer one and going inward. Similarly, we also calculated the marginal contribution of each ring to total tree conductance (*KRING*), by subtracting whole-tree values differing for one additional inner ring, i.e., *KRING* = *KCUM,RN=i+1* - *KCUM,RN=i*. Given that leaf area dynamics was not modelled, assuming a constant whole-tree transpiration rate equates to assuming a constant leaf-specific transpiration for a constant leaf-area tree. The model-tree dimensions and parameter values used in the different simulations are reported in Table 2.

Height growth rate (*ΔH*)was considered in the model parameterization so that the length of each axial annual stem increment was the total tree height divided by its age. The number of the numerical elements *M* and *N* (where *M*=*N*) was made to match tree age, i.e. each numerical element represented one year’s growth in both axial and radial dimensions. The difference in structure between the slow and fast-growing trees and the base case tree is depicted in Fig. S1.

## Results

*Axial and radial patterns of xylem conduit diameters*

The hydraulically weighted conduit diameter (*Dh*) changed with position along the stem (height) and with cambial age (ring number) in both Norway spruce and European beech (Fig. 2 and Fig. 3). The vascular elements formed in a given year were larger at the stem base and “tapered” (i.e., became narrower) with height (i.e., with increasing distance from the ground) (coloured lines panel A in Fig. 2 and Fig. 3). In each stem disc, *Dh* increased with cambial age (i.e., radially from pith to bark), showing a steep interannual increase during the first years followed by a period of minor *Dh* variation (e.g., at the stem base: panel C in Fig. 2 and Fig. 3).

Changing perspective, whenthe *Dh* of each ring in each disc was related to the distance to the contemporary stem apex (*DCA*), a strong convergence towards an invariant axial scaling emerged (panels B in Fig. 2 and Fig. 3). A linear regression well fitted the log10-transformed data of *Dh* vs. *DCA* well(Table S1). The slope resulted stable with varying tree height (*H*) in both *P. abies* and *F.* sylvatica (*b*=0.14 and *b*=0.23, respectively: Table S1). On the contrary, *H* significantly affected the *y-*intercept (panel E in Fig. 2 and Fig. 3; Table S1 and Table S2). This indicated that the *Dh* at the stem apex (i.e., at *DCA* = 1 cm, cf. panels B and E of Fig. 2 and Fig. 3) slightly increased or decreased with *H* in *P. abies* and *F. sylvatica*, respectively (Table 3 and Table S2). The magnitude of variation was in the order of ~15 µm in *F. sylvatica*, and only in the order of ~5 µm (but becoming negligible approximately for *H* > 5 m) in *P. abies*.

*Growth-related patterns in the number of sapwood rings*

In the global dataset we found that the number of sapwood rings (*NSWr*) is related to the hydraulic path length according to two different relationships. On one hand, *NSWr* increased with *H* (Fig. 4A, Table 4A); on the other, *NSWr* was inversely related to the mean annual height increment (*ΔH*) (Fig. 4B, Table S3B). The combined result of these two types of path-length effects implied that fast height-growing trees (high *H*) maintain a significantly lower number of sapwood rings (i.e., have a lower *y*-intercept) than slow growing trees for a given *H* (Fig. 4A)*.* Results from the hydraulic model were consistent with this observation (Fig. 4, see below).

Moreover, the mean ring width of sapwood rings (*SWrw*) strongly increased with *ΔH*, with conifers producing wider rings than angiosperm trees at a given *ΔH* (Fig. 5, Table S3C).

*Effects of tree height, stem elongation rate, ring width, radial conductivity and scaling exponent (b) of conduit widening scaling on the conductance and number of sapwood rings according to the hydraulic model*

Analyses with the hydraulic model gave further insights into the processes controlling these empirical trends. Model simulations revealed that the marginal gain in total conductance of adding one inner sapwood ring rapidly decreases moving from the outermost ring (ring number *RN*=1) towards older rings (ring number *RN*=40, Fig. S2). The pattern of relative variation in the cumulative hydraulic conductance (*rKCUM*) with *RN* was affected by both total tree height (*H*) and stem elongation rate (*ΔH*). That is, inner rings contribute relatively more to the total sapwood conductance either with increasing *H* (Fig. 6A) or with reduced *ΔH* (Fig. 6C). Furthermore, the radial profile of *rKCUM* was substantially independent of the average ring width (*SWrw*) (cf., red circles and upside grey triangles in Fig. 6C).

Keeping constant two of the three variables *H*, *ΔH* and *SWrw*, to examine the marginal effects across all model combinations, the model predicted that the total xylem conductance (*KTOT* = maximum *KCUM*) declined with increasing *H* (data not shown), and increased either with increasing *SWrw* (cf., red circles and upside grey triangles in Fig. 6B) or with decreasing *ΔH* (Fig. 6B). In the example of Fig. 6B, it is shown that for a tree of height *H*=8 m, *KTOT* depends on the balance between primary (*ΔH*) and secondary growth (*SWrw*). Notably, the simulations revealed *KTOT* can remain close to constant despite reduced *ΔH* and *SWrw* (i.e., despite reduced allocation to both primary and secondary growth), because reduced *ΔH* facilitated the retention of inner sapwood rings via reduced resistances (cf., yellow diamonds and upside grey triangles in Fig. 6B).

Furthermore, the model revealed that the radial profiles of *KCUM* were sensitive to the input parameters of the widening exponent (*b*) and radial conductivity (*kRAD*) (Fig. 7). Specifically, the contribution of inner rings to *KTOT* decreased rapidly when conduit widening is steep (i.e., high *b* values: Fig. 7A). Lower *kRAD* led to lower *KTOT* (Fig. 7B) and to a lower contribution of inner rings to *KTOT* (Fig. 7C). However, the effect of *kRAD* rapidly saturated above the highest value employed in the parameterization.

The transition of the oldest sapwood ring into heartwood was assumed to occur with a marginal increase in *rKCUM* < 0.3 % (i.e., *rKCUM\_RN=n*<0.003× *rKCUM\_RN=n-1*). The model predicted that the variation in *NSWr* was positively related to *H* (Fig. 4A and Fig. S3) and negatively related to *ΔH* (Fig. 4B and Fig. S3). The predicted relationships were sensitive to the parameter *kRAD* (Fig. 7C) and especially to the widening scaling exponent (*b*) (Fig. 7A). In order to account for the possible variability in *b* among trees, the hydraulic model was run under three scenarios. Under the condition of *b*=0, the model predicted the largest number of sapwood rings, with *NSWr* scaling at a faster rate with *H* compared to empirical data (Fig. S3A). Under *b*=0.15, the model well predicted the scaling of *NSWr* with *H* especially for trees with low *ΔH* (Fig. 4A). At the opposite, model simulations implementing *b*=0.3 predicted the lowest number of sapwood rings, and a rather flat scaling of *NSWr* with *H*, especially for trees with high *ΔH*, thus more consistent with empirical data in that range (Fig. S3B).

## Discussion

We used different datasets to test patterns at different scales. Firstly, we used a detailed dataset on the intra-tree variation in conduit diameter to provide the strongest empirical support to date for the idea that the axial scaling of conduit diameter with distance from the apex is to a good approximation ontogenetically stable in both its allometric components *a* and *b* (eq. 1), according to our hypothesis iv (Fig. 1). Secondly, we used a global sapwood database to find empirical support to our hypothesis that the number of sapwood rings (*NSWr*) must increase with tree height to compensate for the negative path length effects (i.e., tree height, *H*) on the total hydraulic resistance (hypothesis iv, Fig. 1), and that further hydraulic limitations to inner rings are determined by the stem elongation rate (*ΔH*) (hypothesis vi, Fig. 1). In order to minimize the C costs of sapwood with a given conductance, *NSWr* decreases and sapwood ring width increases with *ΔH*, respectively. Lastly, we used a numerical model of water transport within and across xylem rings to physiologically characterize the independent effects of *H* and *ΔH* on the contribution of inner sapwood rings to total sapwood conductance. The model provided a biophysical explanation for the transition of sapwood into heartwood (and thus for the *NSWr*), to occur when the marginal increase in the total sapwood conductance caused by one additional ring becomes negligibly small.

*The axial xylem design is ontogenetically stable*

Results from our unprecedentedly detailed anatomical stem analysis unambiguously revealed that the vascular cambium produced xylem conduits with diameter strongly dependent on the distance from the apex (Fig. 2 and Fig. 3), thus supporting the hypothesis that the vascular system does not progressively acclimate to the increasing tree height by modifying the axial scaling in one or both of its components (*a* and *b* of eq. 1). The overall maintenance of such *a* and *b* values during ontogeny implies a residual path length effect of increasing total resistance with increasing tree height (Fig. 1B). Although species-specific differences in *b* (varying from 0.1 to 0.4 according to literature: e.g., Petit *et al.*, 2011; Williams *et al.*, 2019) would change the impacts of these residual path length effects at the ring level (Becker *et al.* 2000; Petit & Anfodillo 2009), the contribution of inner rings to the total sapwood conductance would become essential to fully compensate for the hydraulic limitations imposed by *H* (hypothesis iv of Fig. 1A and 1B) (further discussed below).

The Norway spruce and the beech trees showed different values of *b* (0.14 and 0.22, respectively), but in the range of exponents commonly reported in literature (Anfodillo *et al.* 2013), and the observed ontogenetic stability of the axial scaling design is in agreement with other less detailed studies (Weitz *et al.* 2006; Prendin *et al.* 2018b). More specifically, we observed minor variations in the value of *a* (eq. 1) in both trees. In the Norway spruce tree, the variation in *a* was negligible when *H*>~5 m, whereas in the beech tree it slightly but significantly decreased with *H*. These results agree with other intraspecific investigations reporting only marginal variations, if any, in *a* among trees of different sizes (Prendin *et al.* 2018b; Prendin, Mayr, Beikircher, Von Arx & Petit 2018a; Williams *et al.* 2019). This contrasts with other studies reporting a significant scaling of *Dh* at the stem apex with *H*, but either the assessed relationship was interspecific (Olson *et al.* 2018) or no precise distance from the apex was reported in methods (Echeverría *et al.* 2019).

*The axial xylem design affects the hydraulic efficiency of sapwood rings*

Grounded on the empirical evidence that the axial scaling of conduit diameter with the distance from the contemporary apex (*DCA*) is with good approximation ontogenetically stable in both the allometric constant (*a*) and exponent (*b*), our numerical model predicted the variation in marginal ring conductance (*KRING*) with ring age (i.e., ring number from the outermost one, *RN*) (Fig. S2) under the effect of varying tree height (*H*) (Fig. 6A) and annual increment of stem height (*ΔH*) (Fig. 6C).

Specifically, since path length resistance cumulates less than linearly with distance from the apex (Becker *et al.*, 2000; Petit & Anfodillo, 2009), it follows that *KRING* pertaining to the shorter inner rings are less different than that of outer and longer rings when the tree is taller because most of the total resistance is already cumulated over the path length (i.e., the slope of the curves in Fig. 1B decreases with increasing path length). Consequently, the contribution to the total conductance of older rings becomes relatively larger in taller trees.

Analogously, since water flowing axially along inner rings has to trespass the additional axial resistances represented by the younger shoots distally before arriving to the leaves, and shoot resistance is proportional to its length, it follows that *KRING* decreases with ring age more rapidly when *ΔH* is high.

Notably, the predicted progressive decline of *KRING* with ring number (Fig. S2) is consistent with several studies reporting a radial decrease in sap flow rate with sapwood depth (Phillips *et al.* 1996; Jiménez *et al.* 2000; Gartner & Meinzer 2005; Zhao *et al.* 2018).

*The number of sapwood rings increases with tree height*

The compiled datasets from the Alps and BAAD with sapwood traits and tree biometric data revealed that the number of sapwood rings (*NSWr*) increases with *H*, thus supporting our hypothesis (iv) that more sapwood rings are required to compensate for the hydraulic limitations imposed by increasing *H*, thus maintaining the sapwood conductance. In addition, we found that *NSWr* decreases with *ΔH*. Considering that the contribution of inner rings to the total xylem conductance decreases more rapidly with age in trees with high *ΔH,* this would mean that, all else being equal, fast growing trees have a lower total sapwood conductance than slow growing trees. But notably, sapwood ring width increases with *ΔH*. Such a picture would strongly suggest that fast growing trees maintain the sapwood conductance by maintaining fewer but larger sapwood rings than slow growing trees, in agreement with our hypothesis vi (Fig. 1C and 1D).

Sap flow rate has been reported to approximate zero at the sapwood-heartwood transition (Gebauer *et al.* 2008; Beauchamp *et al.* 2013). Accordingly, in the hydraulic model we set a threshold of minimum 0.3 % of marginal increase in total plant conductance for maintaining the hydraulic functionality of the innermost sapwood ring, and thus for setting the transition into heartwood. Accordingly, the model captured the overall scaling of the number of sapwood rings (*NSWr*) with *H* and *ΔH* emerging from our large dataset (cf., Fig. 4A and Fig.S3B).

*Other factors affecting the efficiency and number of sapwood rings*

Factors other than *H* and *ΔH* can also affect the radial variation of *KRING* with *RN*, and thereforethe predicted *NSWr*, namely the widening exponent (*b*) (Fig. 7A) and the radial conductivity (*kRAD*) (Fig. 7C).

Indeed, intra- and interspecific differences in the range of *b*=0.1 to >0.3 can be appreciated across different studies (Petit, Pfautsch, Anfodillo & Adams 2010; Prendin *et al.* 2018b; Williams *et al.* 2019), with fast growing trees often showing higher values of *b*. Therefore, it seems very likely that our global dataset accounts for species with different hydraulic architectures and with different scaling parameters of axial conduit widening (*a* and *b* of eq. 1).

We accounted for a large potential variability of *b* in the trees by running simulations implementing two scenarios with *b*=0.15 and *b*=0.3, as well as with *b*=0. Notably, the model predicted the variation in *NSWr* with *H* in a similar manner than the statistical fit for trees (mostly conifers) with reduced *ΔH* (Fig. 4A) when the scaling exponent of axial conduit widening was appropriate for mature conifer trees(*b*=0.15)(Fig. 2, Table 3A). At the other extreme, the model only slightly overestimated *NSWr* for fast growing trees (mostly angiosperms) when *b*=0.3 was implemented in the simulations. Consistently, angiosperm trees have been reported to be characterized often by a higher *b* (e.g., in the analysed beech tree *b*=0.22; in *Eucalyptus regnans* F. Muell. *b*>0.25 (Petit *et al.* 2010; Williams *et al.* 2019).

Furthermore, also the radial conductivity *kRAD* possibly represents a source of variation for the radial variation of *KRING* with *RN*, and therefore *NSWr* and may also differ between angiosperms and conifers.

In the base case of our simulations, *kRAD* equalled the only estimate found in literature for conifer trees (Barnard *et al.* 2013) and was kept constant along the given ring. Model simulations run with varying *kRAD* revealed that very low *kRAD* decreases the total tree hydraulic conductance, whereas *kRAD* larger than a certain threshold does not affect the total tree hydraulic conductance anymore (Fig. 7C). No information about *kRAD* in angiosperm trees is available in literature, but it seems very likely that the actual *kRAD* depends on the tree ring anatomy, and therefore be species- and position-specific. For instance, earlywood and latewood are not well integrated hydraulically in conifers, as intertracheary bordered pits are typically displayed on radial walls in earlywood tracheids and on tangential walls in latewood tracheids (Carlquist 2017). In broadleaved trees, clusters of few large vessels embedded in a matrix of thick-walled fibres confer hydraulic compartmentalization even at the scale of tree ring sectors (Ellmore, Zanne & Orians 2006).

Notably, the scaling of *NSWr* with *H* and *ΔH* resulted independent of ring width (Fig. 6B), and thus of the absolute ring conductivity (not conductance). The results given by the model are also independent on the value of transpiration rate and soil water potential given as input to the model, although randomly occurring tension-driven embolism events would possibly affect the contribution of the different rings to the total sapwood conductance.

*C allocation patterns maintaining a constant sapwood conductance with increasing tree height depend on height growth rate*

Most often heartwood formation has been reported as an age-related process (Wilkes 1991; Spicer 2005; Spicer & Holbrook 2007) associated to the senescence and death of living xylem parenchyma cells (Bamber 1976; Spicer 2005). In trees, age is tightly correlated with other size-related variables (Mencuccini *et al.* 2005). Trees get older as they grow in *H*, whereas their growth rate (both axial and radial) typically declines during ontogeny (i.e., with age) (Ryan, Binkley & Fownes 1997). Instead, our model simulations corroborated previous indications that sapwood is turned into heartwood once the hydraulic contribution of the innermost sapwood ring to the total plant conductance becomes negligible (Gebauer *et al.* 2008; Beauchamp *et al.* 2013). Notably, we reported that *NSWr* scaled proportionally with *H* and inversely proportionally with *ΔH*, as tree age would also do, thus suggesting that the effect of age on *NSWr* could be indirect and not causal.

We provided the strongest empirical evidence to date that anatomical modifications are not required to compensate for the hydraulic limitations imposed by tree height during growth. Consistent with our hypothesis (Hyp\_iv, Fig. 1A and 1B), the number of sapwood rings (*NSWr*) must increase with *H* to maintain a constant hydraulic conductance during ontogeny. However, *ΔH* imposes further hydraulic limitation to the water conduction along inner rings. Our results suggest that the relative allocation to new xylem biomass production and metabolic maintenance of sapwood rings (i.e., the parenchyma cells therein) would change according to the contribution of inner rings to the total hydraulic conductance, which resulted to be independently affected by *H* and *ΔH*. More specifically, trees appeared to prioritize the maintenance of inner sapwood rings over the production of larger rings as long as the inner rings effectively contribute to the total hydraulic conductance, possibly because this imposes lower C costs associated to the required xylem conductance. This would explain why *NSWr* decreases with *ΔH*, but also would allow a more thorough understanding of the physiological consequences of the well-known trends of progressively decreasing height and diameter increment with increasing tree size (Mencuccini *et al.* 2005): both increasing *H* and decreasing *ΔH* positively affect the contribution of inner rings to the total conductance, allowing the tree to reduce the overall C costs associated to the sapwood conductance by reducing the allocation to new xylem biomass (i.e., number of new conduits per unit leaf area) while prioritizing the allocation to the maintenance of more sapwood rings.

Put together, our observations and model predictions open a future new research avenue on the functional effects of allocation to new xylem biomass (i.e., growth) and maintenance respiration of hydraulically functional sapwood, possibly shedding novel important information on the tight relationship between the tree C and water economies (Petit, Savi, Consolini, Anfodillo & Nardini 2016; Petit *et al.* 2018), which could play a key role in the process of acclimation to different and changing environmental conditions.

## Statement of author contributions

GP, developed the conceptual design of the work with the help of MM and TH. GP and ALP conducted the anatomical measurements and relative data analyses. TH developed the numerical model with the help of GP and MM. MC provided the biometric parameters of trees from field sampling in the Italian Alps. GP wrote the manuscript with essential contributions by MM and TH. All co-authors contributed by discussing and reviewing the drafts and final version.

## Conflicts of interest

None

## Acknowledgements

GP was supported by the University of Padova (DOR2111477/21). ALP was supported by the 2017 BIRD Project of TeSAF Department University of Padova.

## References

Anfodillo T., Deslauriers A., Menardi R., Tedoldi L., Petit G. & Rossi S. (2012) Widening of xylem conduits in a conifer tree depends on the longer time of cell expansion downwards along the stem. *Journal of Experimental Botany* **63**, 837–845.

Anfodillo T., Petit G. & Crivellaro A. (2013) Axial conduit widening in woody species: A still neglected anatomical pattern. *IAWA Journal* **34**, 352–364.

Aniol R.W. (1987) A new device for computer assisted measurement of tree-ring widths. *Dendrochronologia* **5**, 135–141.

von Arx G. & Carrer M. (2014) ROXAS - a new tool to build centuries-long tracheid-lumen chronologies in conifers. *Dendrochronologia* **32**, 290–293.

Bamber R.K. (1976) Heartwood, its function and formation. *Wood Science and Technology* **10**, 1–8.

Barnard D.M., Lachenbruch B., McCulloh K.A., Kitin P. & Meinzer F.C. (2013) Do ray cells provide a pathway for radial water movement in the stems of conifer trees? *American Journal of Botany* **100**, 322–331.

Beauchamp K., Mencuccini M., Perks M. & Gardiner B. (2013) The regulation of sapwood area, water transport and heartwood formation in Sitka spruce. *Plant Ecology and Diversity* **6**, 45–56.

Becker P., Gribben R.J. & Lim C.M. (2000) Tapered conduits can buffer hydraulic conductance from path-length effects. *Tree Physiology* **20**, 965–967.

Bürkner P.-C. (2017) brms: An R package for Bayesian multilevel models using Stan. *Journal of Statistical Software* **80**, 1–28.

Carlquist S. (2017) Conifer tracheids resolve conflicting structural requirements. *Journal of the Botanical Research Institute of Texas* **11**, 123–141.

Carrer M., Von Arx G., Castagneri D. & Petit G. (2015) Distilling allometric and environmental information from time series of conduit size: The standardization issue and its relationship to tree hydraulic architecture. *Tree Physiology* **35**, 27–33.

Duncan R.P. (1989) An evaluation of errors in tree age estimates based on increment cores in Kahikatea (Dacrycarpus dacrydioides). *New Zealand Natural Sciences* **16**, 31–37.

Echeverría A., Anfodillo T., Soriano D., Rosell J.A. & Olson M.E. (2019) Constant theoretical conductance via changes in vessel diameter and number with height growth in Moringa oleifera. *Journal of Experimental Botany* **70**, 5765–5772.

Ellmore G.S., Zanne A.E. & Orians C.M. (2006) Comparative sectoriality in temperate hardwoods: hydraulics and xylem anatomy. *Botanical Journal of the Linnean Society* **150**, 61–71.

Falster D.S., Duursma R.A., Ishihara M.I., Barneche D.R., FitzJohn R.G., Vårhammar A., … York R.A. (2015) BAAD: a Biomass And Allometry Database for woody plants. *Ecology* **96**, 1445.

Fritts H.. (1976) *Tree Rings and Climate*. The Blackburn Press, Caldwell., London.

Gartner B.L. & Meinzer F.C. (2005) Structure-function relationships in sapwood water transport and storage. In *Vascular transport in plants*. (eds N.M. Holbrook & M.A. zwieniecki), pp. 307–331. Elsevier Academic Press, Amsterdam.

Gebauer T., Horna V. & Leuschner C. (2008) Variability in radial sap flux density patterns and sapwood area among seven co-occurring temperate broad-leaved tree species. *Tree Physiology* **28**, 1821–1830.

Givnish T.J., Wong S.C., Stuart-Williams H., Holloway-Phillips M. & Farquhar G.D. (2014) Determinants of maximum tree height in Eucalyptus species along a rainfall gradient in Victoria, Australia. *Ecology* **95**, 2991–3007.

Jiménez M.S., Nadezhdina N., Čermák J. & Morales D. (2000) Radial variation in sap flow in five laurel forest tree species in Tenerife, Canary Islands. *Tree Physiology* **20**, 1149–1156.

Kolb K.J. & Sperry J.S. (1999) Differences in drought adaptation between subspecies of sagebrush (Artemisia tridentata). *Ecology* **80**, 2373–2384.

Mencuccini M., Hölttä T., Petit G. & Magnani F. (2007) Sanio’s laws revisited. Size-dependent changes in the xylem architecture of trees. *Ecology Letters* **10**, 1084–1093.

Mencuccini M., Martinez-Vilalta J., Vanderklein D., Hamid H.A., Korakaki E., Lee S. & Michiels B. (2005) Size-mediated ageing reduces vigour in trees. *Ecology Letters* **8**, 1183–1190.

Olson M.E., Soriano D., Rosell J.A., Anfodillo T., Donoghue M.J., Edwards E.J., … Méndez-Alonzo R. (2018) Plant height and hydraulic vulnerability to drought and cold. *Proceedings of the National Academy of Sciences* **115**, 7551–7556.

Petit G. & Anfodillo T. (2009) Plant physiology in theory and practice: An analysis of the WBE model for vascular plants. *Journal of Theoretical Biology* **259**, 1–4.

Petit G., Anfodillo T., Carraro V., Grani F. & Carrer M. (2011) Hydraulic constraints limit height growth in trees at high altitude. *New Phytologist* **189**, 241–252.

Petit G., von Arx G., Kiorapostolou N., Lechthaler S., Prendin A.L., Anfodillo T., … Sterck F. (2018) Tree differences in primary and secondary growth drive convergent scaling in leaf area to sapwood area across Europe. *New Phytologist* **218**, 1383–1392.

Petit G., Pfautsch S., Anfodillo T. & Adams M.A. (2010) The challenge of tree height in Eucalyptus regnans: When xylem tapering overcomes hydraulic resistance. *New Phytologist* **187**, 1146–1153.

Petit G., Savi T., Consolini M., Anfodillo T. & Nardini A. (2016) Interplay of growth rate and xylem plasticity for optimal coordination of carbon and hydraulic economies in Fraxinus ornus trees. *Tree Physiology* **36**, 1310–1319.

Phillips N., Oren R. & Zimmermann R. (1996) Radial patterns of xylem sap flow in non-, diffuse- and ring-porous tree species. *Plant, Cell & Environment* **19**, 983–990.

Prendin A.L., Mayr S., Beikircher B., Von Arx G. & Petit G. (2018a) Xylem anatomical adjustments prioritize hydraulic efficiency over safety as Norway spruce trees grow taller. *Tree Physiology* **38**, 1088–1097.

Prendin A.L., Petit G., Fonti P., Rixen C., Dawes M.A. & von Arx G. (2018b) Axial xylem architecture of Larix decidua exposed to CO2enrichment and soil warming at the tree line. *Functional Ecology* **32**, 273–287.

Quiñonez-Piñón M.R. & Valeo C. (2018) Assessing the Translucence and Color-Change Methods for Estimating Sapwood Depth in Three Boreal Species. *Forests*  **9**.

R Development Core Team (2014) *A language and environment for statistical computing*. R Foundation for Statistical Computing, Wien.

Ryan M.G., Binkley D. & Fownes J.H. (1997) Age-related decline in forest productivity: Pattern and process. (eds M. Begon & A.H.B.T.-A. in E.R. Fitter), pp. 213–262. Academic Press.

Sanio K. (1872) Uber die grosse der holzzellen bei der gemeinen der kiefer (Pinus sylvestris). *Jahrbucher für Wissenschaftliche Botanik* **8**, 401–420.

Schulte P.J. (2012) Vertical and radial profiles in tracheid characteristics along the trunk of Douglas-fir trees with implications for water transport. *Trees* **26**, 421–433.

Sellin A. (1994) Sapwood–heartwood proportion related to tree diameter, age, and growth rate in Piceaabies. *Canadian Journal of Forest Research* **24**, 1022–1028.

Sousa V.B., Cardoso S. & Pereira H. (2013) Ring width variation and heartwood development in Quercus faginea. *Wood and Fiber Science* **45**, 405–414.

Spicer R. (2005) Senescence in secondary xylem: Heartwood formation as an active developmental program. In *Vascular transport in plants*. (eds N.M. Holbrook & M.A. Zwieniecki), pp. 457–475. Elsevier Academic Press, Amsterdam.

Spicer R. & Holbrook N.M. (2007) Effects of carbon dioxide and oxygen on sapwood respiration in five temperate tree species. *Journal of Experimental Botany* **58**, 1313–1320.

Stokes M.A. & Smiley T.L. (1968) *Introduction to Tree-Ring Dating*. University of Chicago Press, Chicago.

Tyree M.T. & Ewers F.W. (1991) The hydraulic architecture of trees and other woody plants. *New Phytologist* **119**, 345–360.

Weitz J.S., Ogle K. & Horn H.S. (2006) Ontogenetically stable hydraulic design in woody plants. *Functional Ecology* **20**, 191–199.

Wilkes J. (1991) Heartwood development and its relationship to growth in Pinus radiata. *Wood Science and Technology* **25**, 85–90.

Williams C.B., Anfodillo T., Crivellaro A., Lazzarin M., Dawson T.E. & Koch G.W. (2019) Axial variation of xylem conduits in the Earth’s tallest trees. *Trees* **33**, 1299–1311.

Zhao H., Yang S., Guo X., Peng C., Gu X., Deng C. & Chen L. (2018) Anatomical explanations for acute depressions in radial pattern of axial sap flow in two diffuse-porous mangrove species: implications for water use. *Tree Physiology*.

## Tables

Table 1. List of variables: growth (A) and sapwood traits (B).

|  |  |  |
| --- | --- | --- |
|  | **Symbol (units)** | **Variable** |
| (A)  Growth traits | *Age* (years) | Tree age |
| *DBH* (cm) | Diameter at breast height |
| *H* (m) | Tree height |
| *ΔH* (cm) | Mean annual height increment |
| (B)  Sapwood traits | *NSWr* (#) | Number of sapwood rings |
| *SWrw* (mm) | Mean width of sapwood rings |

Table 2. List of model parameters.

|  |  |  |
| --- | --- | --- |
| **Parameter** | **Symbol (units)** | **Value** |
| Tree height | *H* (m) | * 2 * 4 * 8 * 16 * 32 * 64 |
| Whole tree transpiration rate | *T* (g·s-1) | * 1 |
| Radial hydraulic conductivity | *kRAD* (m3·m-1·s-1·Pa-1) | * 1×10-12 |
| Axial hydraulic conductivity at stem apex for *b*=0.15 | *kapx* at *i*=*j* (m2·Pa-1·s-1) | * 0.8×10-9 |
| Xylem conduit widening coefficient | *b* | * 0 * 0.15 * 0.3 |
| Soil water potential | *Ψsoil* (MPa) | * 0 |
| Number of numerical elements used in the simulations (=tree age) | *N*, *M* (*N*=*M*) | * 20 * 40 * 80 |
| Stem diameter at breast height | *DBH* (cm) | * 24 * *DBH*=0.4×*H* |

## Figures

**Captions**

Figure 1. Hypothetical mechanisms of anatomical modifications with height growth allowing the maintenance of a constant total resistance. Panels A and B respectively describe the axial variation of conduit diameter and the cumulated hydraulic resistance with increasing distance from the apex for different combinations of allometric constant (*a*) and exponent (*b*) (eq. 1). The solid black line refers to a tree of 1 m with typical *a* and *b*. In order to maintain the total hydraulic resistance (horizontal grey line in panel B), a 30 m tall tree could hypothetically maintain *b* while increasing *a* (according to the hypothesis ii of Echeverría *et al.*, 2019: solid red line), maintain *a* while increasing *b* (according to hypothesis iii: solid blue line), or maintaining *a* and *b* (dashed black line), but increasing the number of sapwood rings (*NSWr*) because no full hydraulic compensation is possible for *H*=30 m (the total resistance would be more than four times larger than that of the 1 m tree) (according to hypothesis iv). In the context of hypothesis iv, the stem elongation rate (*ΔH*) is expected to limit the contribution of inner rings to the total sapwood conductance. In panel C is described how *NSWr* could possibly change in relation to the stem elongation rate: according to hypothesis v, *NSWr* would increase with *ΔH* to compensate for the lower hydraulic efficiency of inner rings (solid grey line), thus increasing the C cost for the maintenance of a larger amount of living parenchyma, or *NSWr* would decrease with *ΔH* because of the high C costs associated to the maintenance of the living parenchyma of the low hydraulically efficient inner rings (according to hypothesis vi: dashed black line). Panel D describes that, in the context of hypothesis vi, full hydraulic compensation for the effect of height is implying that the sapwood ring width increase with *ΔH*, because in fast growing trees the C costs to be paid for a given sapwood conductance result lower when associated to the production of new xylem biomass than to the maintenance of more sapwood rings.

Figure 2. Intra-tree variation of tracheid *Dh* in a 222 years old *P. abies* tree of *H*=26 m*.* (A) Range variation of *Dh* in all the annual rings of the discs extracted at different heights along the stem. Colored lines outline the “acropetal tapering” of *Dh* along example annual rings (2nd Sanio’s law) (black: 2012; blue: 1932; red: 1851). (B) The same *Dh* data as in (A) are plotted against the distance to the height position that the stem apex had in the corresponding year (distance from contemporary apex, *DCA*). Green circles in (A) and (B) and (C) represent the same *Dh* data from the most basal stem disc. (C) Radial variation of *Dh* with cambial age (i.e., from pith to bark: 1st Sanio’s law) in the most basal stem disc. (D) Relationship of *Dh* vs. *DCA* expressed on log-log scale, with the solid line outlining the estimated scaling for years with *HCLASS*=26 m (Table S2A). (E) Variation of *Dh* at the fixed distance from the apex of 1 cm (*Dh@dfa=1 cm*) with increasing *HCLASS.* Solid line is according to the model of Table S1A keeping *DCA*=1 cm.

Figure 3. Intra-tree variation of vessel *Dh* in a 140 years old *F. sylvatica* tree of *H*=31 m*.* (A) Range variation of *Dh* in all the annual rings of the discs extracted at different heights along the stem. Colored lines outline the “acropetal tapering” of *Dh* along example annual rings (2nd Sanio’s law) (black: 2013; blue: 1992; red: 1960). (B) The same *Dh* data as in (A) are plotted against the distance to the height position that the stem apex had in the corresponding year (distance from contemporary apex, *DCA*). Green circles in (A) and (B) and (C) represent the same *Dh* data from the most basal stem disc. (C) Radial variation of *Dh* with cambial age (i.e., from pith to bark: 1st Sanio’s law) in the most basal stem disc. (D) Relationship of *Dh* vs. *DCA* expressed on log-log scale, with the solid line outlining the estimated scaling for years with *HCLASS*=31 m (Table S2B). (E) Variation of *Dh* at the fixed distance from the apex of 1 cm (*Dh@dfa=1 cm*) with increasing *HCLASS.* Solid line is according to the model of Table S1B keeping *DCA*=1 cm.

Figure 4. Path-length-related variation in the number of sapwood rings (*NSWr*). (A) Relationship between *NSWr* and tree height (*H*) assessed for different classes of annual stem height increment (*ΔH*= cm/year). Symbols represent conifers (triangles) and angiosperms (circles). (B) Relationship between *NSWr* and *ΔH* assessed for different *H* classes. Symbols represent conifers (triangles) and angiosperms (circles). Fitting lines are according to Table S3B. Black lines represent the model predictions under the scenario of conduit widening scaling of *b*=0.15.

Figure 5. Relationship between mean width of sapwood rings (*SWrw*) and mean annual height increment (*ΔH*) for both conifers (triangles) and angiosperms (circles) Fitting lines (red for conifers and green for angiosperms) are according to Table S3C.

Figure 6. Variation in the cumulative plant conductance (*KCUM*: B) and in the relative *KCUM* (*rKCUM*: A, C) with the ring number starting from the outermost one (*RN*) for simulations comparing: (A) trees with same stem elongation rate (*ΔH*=40 cm year-1) and different height and ring width (red circle: *H*=8 m, *RW*= 1.2 cm; black triangle: *H*=16 m, *RW*= 0.6 cm; blue diamond: *H*=32 m, *RW*=0.3 cm); (B, C) trees of same height (*H*=8 m), but with different combinations of *ΔH* and *RW* (red circle: *ΔH*=10 cm·year-1, *RW*=0.24 cm; *ΔH*=10 cm year-1, *RW*=0.3 cm; *ΔH*=20 cm·year-1, *RW*=0.48 cm; *ΔH*=40 cm·year-1, *RW*=0.96 cm).

Figure 7. Effects of the conduit widening exponent (*b*: A) and of the parameter of radial conductivity (*KRAD*: B, C) on the variation in the cumulative xylem conductance (*KCUM*, i.e., the cumulated contribution of the different rings, starting from the outermost one inward, to the total xylem conductance) (B) and in the relative *KCUM* (*rKCUM*: A, C) with the ring number (*RN*). The reference value for *kRAD* in (B, C) is according to Barnard *et al.* (2013) (C=3×10-12 m3 m-1 s-1 Pa-1).