The pipe model theory half a century on: a review

Romain Lehnebach, Robert Beyer, Veronique Letort, Patrick Heuret

REVIEW: PART OF A SPECIAL ISSUE ON FUNCTIONAL–STRUCTURAL PLANT GROWTH MODELLING

The pipe model theory half a century on: a review

Romain Lehnebach[1,2,*,†], Robert Beyer[3,4,†], Véronique Letort[3] and Patrick Heuret[5]

[1]Centre de coopération Internationale de la Recherche Agronomique pour le Développement (CIRAD), UMR Amap, Kourou, France, [2]Botany and Modelling of Plant Architecture and Vegetation (Amap), Université Montpellier, CIRAD, CNRS, INRA, IRD, Montpellier, France, [3]Laboratory of Mathematics in Interaction with Computer Science (MICS), CentraleSupélec, France, [4]Department of Zoology, University of Cambridge, Cambridge, UK and [5]Institut National de la Recherche Agronomique (INRA), UMR Ecofog, Kourou, France

[†]Joint first authorship.

**Corresponding author: E-mail romain.lehnebach@cirad.fr*

• **Background:** More than a half century ago, Shinozaki *et al.* (Shinozaki K, Yoda K, Hozumi K, Kira T. 1964*a*. A quantitative analysis of plant form – the pipe model theory. I. Basic analyses. *Japanese Journal of Ecology* B: 97–105) proposed an elegant conceptual framework, the pipe model theory (PMT), to interpret the observed linear relationship between the amount of stem tissue and corresponding supported leaves. The PMT brought a satisfactory answer to two vividly debated problems that were unresolved at the moment of its publication: (1) What determines tree form and which rules drive biomass allocation to the foliar versus stem compartments in plants? (2) How can foliar area or mass in an individual plant, in a stand or at even larger scales be estimated? Since its initial formulation, the PMT has been reinterpreted and used in applications, and has undoubtedly become an important milestone in the mathematical interpretation of plant form and functioning.

• **Scope:** This article aims to review the PMT by going back to its initial formulation, stating its explicit and implicit properties and discussing them in the light of current biological knowledge and experimental evidence in order to identify the validity and range of applicability of the theory. We also discuss the use of the theory in tree biomechanics and hydraulics as well as in functional–structural plant modelling.

• **Conclusions:** Scrutinizing the PMT in the light of modern biological knowledge revealed that most of its properties are not valid as a general rule. The hydraulic framework derived from the PMT has attracted much more attention than its mechanical counterpart and implies that only the conductive portion of a stem cross-section should be proportional to the supported foliage amount rather than the whole of it. The facts that this conductive portion is experimentally difficult to measure and varies with environmental conditions and tree ontogeny might cause the commonly reported non-linear relationships between foliage and stem metrics. Nevertheless, the PMT can still be considered as a portfolio of properties providing a unified framework to integrate and analyse functional–structural relationships.

Key words: Corners' laws, Leonardo da Vinci's rule, Pressler's law, sapwood, heartwood, wood sectoriality, functional–structural plant modelling.

INTRODUCTION

Since the seminal works of the mathematical biologists d'Arcy Thompson (1917) and Julian Huxley (1924), who explored the effects of scale on the shape of living organisms, the study of how the characteristics of organisms change with body size during ontogeny has become a central issue in many fields of biology (Niklas, 1994). Mathematical relationships between organs/parts and the body size of organisms, currently named allometry, have been explored for many different purposes. First, identification of mathematical rules of proportions is a starting point for investigations into mechanistic explanations and functional requirements (e.g. allocation rules) (Le Roux *et al.*, 2001; Niklas and Enquist, 2002; Fourcaud *et al.*, 2008). Second, because ontogeny and evolution are closely and reciprocally interrelated, ontogenetic trajectories have fed studies on the evolution of biological forms (Gould, 1977; Klingenberg, 1998). Third, the identification of such relationships provides proxies to estimate traits whose direct measurement would encounter experimental difficulties (Niklas, 1994). Originally developed in the field of zoology, allometry-based studies are now widespread in the botany and forestry domains, notably as a way to better understand tree growth and to derive forest management strategies (Kittredge, 1944), and have contributed to the development of dendrometric science. The aim of this branch of science is to understand the interdependence of the components of plant form: e.g. the relationship between tree height and diameter, branching patterns and biomass distribution among compartments, e.g. the crown and the trunk. In the context of current interest in forest carbon stocks to mitigate greenhouse gas emissions, the use of allometric regression models has become a crucial step in predicting the above-ground biomass of a tree from dendrometric variables that are easier to measure and are non-destructive, e.g. diameter

at breast height (DBH), height or wood density (Chave *et al.*, 2005; Feldpausch *et al.*, 2011). Further, the patterns revealed by these models make it possible to investigate fundamental ecophysiological mechanisms that underlie plant development and to predict their survival and plasticity in a changing environment (McDowell and Allen, 2015).

In this allometric race, many efforts have been devoted to relationships involving plant leaf area, whose estimation was – and still is – a primary objective. Indeed, plant leaf area is directly linked to light interception, transpiration and photosynthesis, and is considered to be the single most important determinant of plant productivity. With the aim of indirectly estimating tree crown biomass, Shinozaki *et al.* (1964*a*) proposed a new way of looking at experimental results obtained using the stratified clipping technique (Monsi and Saeki, 1953). This method consists in measuring photosynthetic and non-photosynthetic tissues in different horizontal layers from the top to the bottom of a field, a forest or simply a plant. Shinozaki *et al.* (1964*a*) proposed an elegant conceptual framework in terms of empirical rules to interpret the relationship between crown foliage and sapwood (SW) dimensions. The pipe model theory (PMT) states that a unit amount of leaves is associated with the downward continuation of non-photosynthetic tissue that has a constant cross-sectional area. The PMT provided a satisfactory answer to two problems that were still unresolved at the time of its publication: (1) What determines tree form and which rules drive the allocation of biomass to the leaf versus stem compartments in plants? (2) How can one estimate the leaf area or mass of an individual plant or a stand, or at even bigger scales? The PMT proposed an elegant answer to both questions, appealing in its conceptual simplicity and intuitiveness. Since its original formulation, the PMT has been reinterpreted and derived, and has undoubtedly become an important milestone in the mathematical interpretation of plant form and functioning. The number of citations of the original paper continues to increase, more than half a century after its publication (Fig. 1).

However, its apparent simplicity conceals several ambiguities that have given rise to differences in the way the PMT has been subsequently understood, interpreted and used. The aim of this review is to go back to the original paper of Shinozaki *et al*. and to analyse the initial formulation of the theory and the way it was derived by the authors. We discuss explicit and implicit properties of the PMT in the light of current biological knowledge of tree functioning, and explore experimental evidence supporting and challenging the theory, thus providing an assessment of its validity and range of applicability. We compare the PMT with related theories, such as Huber's value, Leonardo da Vinci's rule, Corner's rules and Pressler's law, and review the more or less appropriate use of the PMT in plant growth models with a particular focus on functional–structural plant models. Finally, we discuss potential applications of the theory in future research.

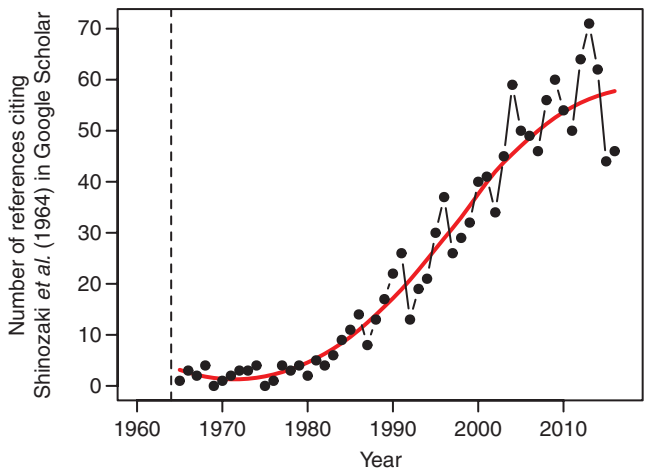

FIG. 1. Number of citations recorded in Google scholar since the original publication of the PMT in 1964 (vertical line).

THE PIPE MODEL THEORY: ORIGINAL CONCEPTS AND IMPLICATIONS

The elements of a success story

The original paper by Shinozaki *et al.* (1964*a*) is undoubtedly a milestone paper that quickly became famous worldwide and has been cited over 1000 times (Fig. 1) in domains as diverse as plant physiology, functional–structural plant modelling and ecology. The presentation of the theory rests on three main elements: two well-known elements, often cited or reproduced, are the textual descriptions and the explanatory drawings, particularly the one presented in Fig. 8 of the original publication (Fig. 2). These two elements circulated much more widely than the third element, which nevertheless represented most of the content of the paper: the range of experimental results that provided the basis for the derivation of the theoretical concept. The theoretical concept and its graphical symbolism are in fact only tentative representations of the properties observed in these experimental data. However, the scientific community adopted the concept while neglecting the experimental basis, which may have facilitated misinterpretations. More importantly, and rather surprisingly, these three elements (theoretical concept, graphical representation, experimental results) do not all convey the same pieces of information. As a result, the combination of these three components led to some sort of confusion in the discussions about its properties and applications. This confusion underlines the interest of clearly separating the experimental analysis from the concepts (i.e. both the theory and its graphical representation) it has led to.

A wide range of experimental results. In the 1960s, the stratified clip technique introduced by Monsi and Saeki (1953; for an English translation see Monsi and Saeki, 2005) enabled the acquisition of

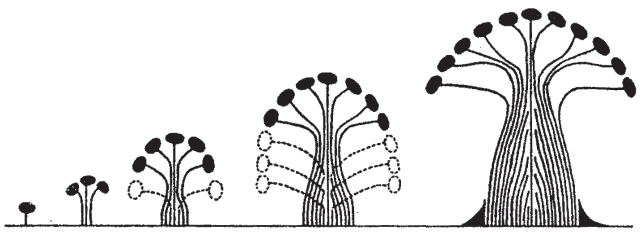

FIG. 2. The original graphical representation of the PMT by Shinozaki *et al.* (1964*a*). Each active pipe (solid lines) is linked to a leaf or a set of leaves (black circles). The drawing highlights the accumulation of disused pipes at the centre of the stem resulting from the shedding of branches and leaves (dashed lines and circles). Note that there is no connection among active and disused pipes (see Hydraulic sectoriality property 4).

large amounts of data on the vertical distribution of leaves and non-photosynthetic organs within plant communities. The technique was originally designed to investigate light propagation in canopies, which required the quantitative characterization of the inner crown structure. The stratified clip technique consists of cutting all plants within a square of a given inner area (chosen under the constraint of feasible labour) from top to bottom in horizontal layers of a given thickness (5–20 cm in Monsi and Saeki, 2005), after which the plant material is classified into two groups within each species: photosynthetic tissues (i.e. chlorophyll-rich leaf lamina, excluding yellow ones) and non-photosynthetic tissues (stems, branches, stalks, fruits, etc.). It is not mentioned whether petioles are considered as part of leaves or part of the non-photosynthetic organs, although this consideration would be of interest in relation to the concept of conducting pipes (Sébastien Levionnois, France, pers. comm.). The fresh material from each layer is immediately weighed in the field. It should be noted that the architectural or topological structures of the trees are not taken into account. While most plant ecologists focused on the profile of leaves as an independent variable in the analysis of measurements, Shinozaki *et al*. proposed to interpret this distribution in relation to that of the non-photosynthetic compartment and to consider the cumulated amount of leaves above a certain height.

This relationship was investigated in different kinds of plants and species, as diverse as herbaceous plants (e.g. maize, reed, sesame, golden rod) and trees (e.g. *Ficus erecta*, paper birch). A wide range also characterizes the scales considered for data acquisition, ranging from natural or cultivated stands with different densities to individual trees and even to the level of a single branch. It is striking that nine out of the 12 figures in Shinozaki *et al.* (1964*a*) display data at the scale of a square metre, whereas the concepts that originated from these data were formulated at the scale of the individual (Shinozaki *et al*. described it as 'pipe model theory on tree form' at the end of the abstract), which is also the scale at which the theory has been applied most often since. Finally, the variables used in the linear regressions (incidentally, standard criteria used to assess the quality of the regression, such as R^2 or the distributions of residuals, for instance, are not provided in the paper, nor is an explanation of how the number of points considered as belonging to the crown versus the stem is chosen) are not homogeneous throughout the paper: photosynthetic matter (except in one figure where fruits are also included) versus non-photosynthetic matter (dry or fresh weight per length section), expressed in various units that range from g 50 cm^{-2} 10 cm^{-1} to ton ha m^{-1}. It is also important to note that the notion of functional stem cross-section or SW only appears at the end of the paper (Fig. 9 in the original publication).

The wide range of species and scales confers a certain apparent robustness on the theory, suggesting its validity for a wide range of growth forms (from herbaceous to trees) and for different scales (from branch to individual plant and stand). Nevertheless, this broad scope of applicability, illustrated by a set of variables of different nature and units, has led to different interpretations, as discussed in the following sections.

A textual formulation. The essence of the PMT concept is summarized in the following sentences: 'a unit amount of leaves is provided with a pipe whose thickness or cross-sectional area is constant. The pipe serves both as the vascular passage and as the mechanical support, and runs from the leaves to the stem base through all of the intervening strata'. However, Shinozaki *et al*. are not always consistent throughout the paper regarding the variables they consider. In particular, it is not clear whether they favour the total amount of stem (i.e. weight of a slice of 'small' thickness at a certain height, hence likened to a cross-sectional area) or only the functional cross-sectional area, as seems to be suggested by the mechanistic interpretation of the theory in the sentences cited above. The different variables whose occurrence can be inventoried in the text are: (1) 'amount of leaves' and 'cross sectional area'; (2) 'amount of leaves' and 'amount of the stem'; and (3) 'a proportional relation between the amount of actively functioning woody organs at a certain height z and the amount of leaves they support $F(z)$' (in the abstract and on pages 99 and 102, respectively, in Shinozaki *et al.*, 1964*a*).

A graphical representation. The schematic drawings (Fig. 2) (Fig. 8 in the original paper) are likely to have contributed significantly to the success of the PMT by providing a visual representation that makes it possible to immediately grasp the main concepts. The graphical representation conveys several pieces of information that are not necessarily included in the theoretical formulation. First, it favours a representation of the tree compartment as strictly partitioned, i.e. where a block of leaves is associated with one and only one block of stem. The size of these blocks is questionable: the figure suggests that each leaf is associated with one particular pipe, while in fact the relationship is established between uncountable quantities (weight, cross-sectional area). Although the drawing features simple leaves directly connected to a main stem, the text mentions branches, stating that the figure illustrates the process by which the trunk is incrementally formed by the accumulation of disused pipes that once supported then shed branches. This oversimplified representation of a plant does not accommodate the role of the branch structure, which we discuss in the following section.

On the explicit and implicit properties that can be derived from the theory, and related theories (Fig. 3)

The last two elements (i.e. the textual formulation and the graphical representation) in fact imply much more than what is explicitly stated in Shinozaki's paper and resonate with other generic theories developed by several authors.

First, the theory states that 'a pipe runs from a unit of leaves to the stem base and has a constant cross-sectional area'. Consequently, this pipe has to follow the whole path determined by the tree branching structure, implying that the cross-sectional area of trunks and branches should be proportional to the amount of leaves located above the section in the tree architecture but not above it in terms of absolute height. However, plant architecture was not taken into account in Shinozaki's experimental datasets since the quantities considered were collected slice by slice, depending on their height alone. It was not until the introduction of the main axis cutting (MAC) method by Chiba (1991) that both tree branching and the vertical distribution pattern of organs were taken into account in analysis of experimental data.

Sapwood area and leaf area/mass are proportional (property 1). If, as stated in the text, the 'pipes mainly serve as vascular passage from the roots to the leaves', then only active pipes should be taken into consideration instead of the whole set of

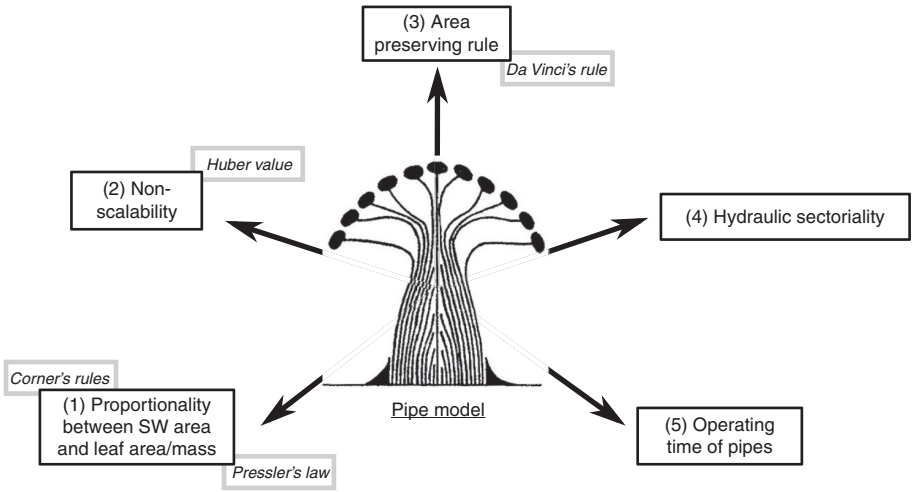

FIG. 3. Overview of the PMT properties (black boxes) and their link with affiliated theories (grey boxes). The description of properties and affiliated theories is provided in section 2.2

pipes (i.e. the whole trunk section, as in the original paper). Therefore, an explicit property of the PMT is the proportional relationship between conductive area of the stem SW at a certain height along the stem and the mass of foliage above. This property echoes Pressler's law, which postulates that ring area growth (the cross-sectional area of a single annual increment) at any point on the stem is proportional to the quantity of foliage above this point (Fig. 3) (Pressler, 1865, cited in Larson, 1963).

From an evolutionary perspective, in his seminal paper on the durian theory, Corner (1949) made empirical observations such as 'The stouter the main stem, the bigger the leaves and the more complicated their form'. He completed this with a second point he called 'diminution on ramification', as 'The greater the ramification, the smaller become the branches and their appendages'. These principles were referred to as Corner's rules by Hallé *et al.* (1978). The relationship between stem primary diameter (before secondary growth) and leaf size has been explored by several authors and intuitively explained by functional requirements in terms of hydraulic and mechanical supplies (Hallé *et al.*, 1978; White, 1983*a*, *b*; Brouat *et al.*, 1998; Westoby and Wright, 2003). These authors generally considered the first of Corner's rules as consistent with the PMT at the scale of the leafy twig, and thus can be considered as an affiliated theory (Fig. 3).

Non-scalability (property 2). Several authors assumed the proportionality constant of the leaf-to-wood mass ratio (i.e. the specific pipe length, L) to be constant across seasons, growth stages and experimental environmental conditions for a particular species (Waring *et al.*, 1982; Gerrish, 1990). This may have been suggested by the fact that the values of L are given for different species (graphs and Table 1 in Shinozaki *et al.*'s paper) with no details on the corresponding environmental conditions. This may have led to the interpretation that the PMT is not scalable, in the sense that it does not account for size-related effects on the leaf mass-to-SW area ratio (Mencuccini *et al.*, 2011). This property of non-scalability, or at least changes in L with stand density or growth stages, is in fact acknowledged by Shinozaki *et al.*: they report variations of L within a growth season in a dense stand of 3-year-old *Ulmus parvifolia* (Fig. 11 in their paper) and with combinations of different growth stages and densities in maize (*Zea mays*) and buckwheat (*Fagopyrum esculentum*) in their Table 2. They were unable to identify any generic trend in these variations of L in their data and conclude that 'more experimental studies are, however, needed to clarify the behavior of L under various growing conditions'. However, in their second paper, Shinozaki *et al.* (1964*b*) suggest that the SW at the crown base can serve as a basis for the estimation of foliage mass in stands regardless of their age or habitat. This point is particularly important because this hypothetical constancy of L throughout plant development or under different conditions (Dean *et al.*, 1988) was – incidentally – the cornerstone of the PMT used to estimate leaf area from measurements of SW area. This erroneous interpretation that L should be a constant has subsequently raised unjustified criticisms of the PMT when some experimental results refuted that assumption (see The variability and plasticity of the A_L:A_S ratio and the scalability of the PMT), while it was in fact established only as an internal relationship within a plant (or a stand) at a given time. Finally, we note the link between the parameter L and the 'Huber value', i.e. the ratio of the cross-sectional xylem areas of a stem to the fresh weight of the leaves supplied by the stem (Fig. 3) (A_s:A_l ratio; Huber, 1928).

The area-preserving rule (property 3). Because pipes have a constant cross-sectional area, the PMT assumes that the conductive SW area of a stem at a given height is equal to the cumulative basal area of its daughter axes above that height (Yamamoto and Kobayashi, 1993; McCulloh *et al.*, 2003). Even more important for our purposes is the central idea of the PMT: the cross-sectional area of the conductive SW is preserved at each branching event and remains constant irrespective of its position along the trunk. Not 50 but some 500 years ago, a prophet of the PMT, Leonardo da Vinci, noticed that the total cross-sectional area of all the branches at any height was equal to the cross-sectional area of its trunk (Fig. 3) [Notebooks of Leonardo da Vinci, pp. 394, 395 (Richter and Bell, 1970)]. Da Vinci also drew the frequently revisited comparison of a tree's branching system to a river course feeding

a main stream. This is equivalent to the area-preserving rules (Horn, 2000). Although the PMT refers to the balance between transpiration and stem water supply, some authors also used the conservation of cross-sectional area in branching points motivated by the PMT to describe root systems (Shinozaki *et al.*, 1964*a*; Oppelt *et al.*, 2001; Pagès *et al.*, 2004; Salas *et al.*, 2004).

Hydraulic sectoriality (property 4). Both the text and the figure (reproduced as Fig. 2 in this paper) in Shinozaki *et al.* (1964*a*) suggest a sectored anatomy, with no lateral transport of water and mineral between pipes. From this point of view, an implicit property of the PMT is that the hydraulic architecture is not an integrated system (Cruiziat *et al.*, 2002).

Operating time of pipes (property 5). Furthermore, Shinozaki *et al*. state that 'the successive accumulation of disused pipes in the trunk is associated with the progress of tree growth'. Further on in the text, they complete this statement with 'the pipes which make up the stem and branches of a tree are renewed every year'. One critical point is that it is not explicitly stated whether pipes can be reused in two successive years or not. However, the graphical representation and the text suggest that when a new leaf is produced, a corresponding new functional pipe is also produced, and is automatically disabled when the leaf is shed (Fig. 2). This point has important consequences: it implies that in deciduous trees in temperate zones, only the last wood growth ring is conductive, since the leaves are renewed every year and secondary growth is annual. In evergreen species, the conductive SW would correspond to a number of rings that is equivalent to the lifespan of the leaves (Kershaw and Maguire, 2000).

Summary. The PMT presents some characteristics that have contributed to its success: an elegant and intuitive concept, a simple and easy-to-interpret graphical representation, and the fact that it is (apparently) based on solid experimental results. Different kinds of plant species are considered in the work of Shinozaki *et al.*, giving to the PMT a universal and generic sense. As a result, it has occasionally been seen as a universal rule. Authors applying the PMT in plant modelling (see below) appear to implicitly assume that the underlying concepts have been properly validated by experimental results. However, as we showed, the properties associated with the PMT listed above are poorly supported by the experimental results presented in the original paper. For example, the set of experimental data presented in the paper does not include measurements of any characteristic of 'functioning woody organs'. The only exception could be seen in Shinozaki *et al*.'s Fig. 9, where stem wood increment in the preceding 5 years is used and can be considered as an approximation of the functioning wood volume. The theory cannot be said to follow rigorously from the analysis of the experimental data despite Shinozaki *et al.*'s argument that 'as demonstrated by actual measurements of the trunk thickness ..., this hypothesis seems acceptable and may be called the pipe model theory of tree form'. Instead, it arose from an imaginative effort to conceptualize the way plants function and the causes that might explain the reported relationships. The PMT is thus rather a hypothesis than a conclusion drawn from a thorough analysis of experimental facts.

It also raises several questions about the nature of the pipe. Aside from the root-to-leaf continuity and a constant cross-sectional area, Shinozaki *et al*. provided no explicit description of the internal structure of pipes. This lack of characterization has facilitated very diverse interpretations of the notion of pipes. Is the pipe is merely a virtual construct that helps understanding and modelling tree form, or does it correspond to an actual anatomical object? In the following section we review the current literature on wood anatomy in order to scrutinize the concept of the pipe.

EXAMINING PMT-AFFILIATED PROPERTIES IN THE LIGHT OF OUR ACTUAL KNOWLEDGE OF PLANT BIOLOGY

What is a pipe?

As argued above and by other authors (Normand *et al.*, 2008; Mencuccini *et al.*, 2011; Holtta *et al.*, 2013), the PMT does not provide any details about the nature of 'pipes', thus leading to different interpretations of their structure. First, the analogy between the structure of a stem as described by Shinozaki *et al.* (i.e. a longitudinally oriented set of pipes) and the anatomical structure of a plant stem has led to the interpretation of Shinozaki *et al.*'s pipe as a tracheary element (i.e. a vessel or tracheid) (Rennolls, 1994; West *et al.*, 1997, 1999; Roderick and Berry, 2001; McCulloh *et al.*, 2003). The extent to which the concept of the pipe as a structure providing mechanical and hydraulic support of leaves in the PMT corresponds to or deviates from anatomical reality depends on the taxonomy of the plant under study. In angiosperm stems, water is conducted by vessels whose cross-sectional area is greater than that of fibres, which provide mechanical support. Given this marked functional differentiation between cells, considering the pipe as a single secondary xylem cell is unrealistic for angiosperm species. In contrast, it is more realistic in the case of gymnosperms, since their xylem cells are differentiated only to a small extent: tracheids are the main cell type ensuring both mechanical support and the longitudinal motion of water. Although varying within tree as well as within growth ring (Lachenbruch *et al.*, 2011), their diameter is generally smaller than that of angiosperms vessels (Sperry *et al.*, 2006). Therefore, in relatively structurally homogeneous wood, as found in gymnosperms, tracheids might form a cellular unit integrating the functions of a pipe *sensu* Shinozaki *et al.* An alternative interpretation of Shinozaki *et al.*'s notion of the pipe may be a wood strand rather than an individual tracheary element. This interpretation would seem particularly reasonable in the case of angiosperm species as wood strands integrate both mechanical and conductive tracheary elements (i.e. fibres and vessels, respectively). It is important to note that studies that established empirical relationships between leaf quantity and SW or stem area (e.g. Waring *et al.*, 1982; Morataya *et al.*, 1999) considered, explicitly or not, pipes as strands of wood. Given the observed variations of cell morphologies occurring within a single plant during its ontogeny (Lachenbruch *et al.*, 2011), considering pipes as quantities of wood is more generic and makes it possible to account for the heterogeneous nature of the material, which could not be done by considering the pipe as a unique tracheary element (Savage *et al.*, 2010).

Since Pressler's law (Pressler, 1865) is a particular case of the PMT for deciduous temperate species, the particular set of pipes formed in the most recent growing season would correspond to the last annual wood increment. By extension, one could expect to observe a number of functionally active annual wood increments (i.e. sets of pipes that were formed in a specific growing season) equal to the age of the oldest living leaves in evergreen species. However, it is likely that the water supply of very young leaves at the beginning of the growing season is provided, at least in part, by the preceding annual increment (i.e. 1-year-old pipes) (Rennolls, 1994). In this case, pipes do not necessarily correspond only to annual growth ring (Rennolls, 1994). This view also challenges the validity of the sectoriality property of the PMT (property 4).

Sectoriality and integration of the vascular system of plants

Both the textual formulation and the schematic drawings published in the paper by Shinozaki *et al*. suggest that water and mineral nutrients are conducted from the soil to a given leaf unit through a single pipe that is disconnected from adjacent ones. Such a vascular plant is sectorial in the sense of Watson and Casper (1984) and Watson (1986), i.e. it is an assembly of independent integrated physiological units (Herrera, 2009). Before questioning the biological relevance of this property, a proper definition of the concept of sectoriality is required. The hydraulic connectivity can be considered in the lateral (i.e. radial and tangential movement of water) and axial [i.e. 'bottom-up' sectoriality as a preferential pathway from roots to different parts of the crown (Herrera, 2009)] directions. Clearly, these two axes need to be considered together in order to understand tree hydraulic architecture as a whole. Thus, sap flux in sectorial plants is compartmentalized within some parts of their structures (e.g. within the same branch), with a strong degree of independence from other compartments [e.g. among distinct branches (Sprugel *et al.*, 1991; Vuorisalo and Hutchings, 1996; Brooks *et al.*, 2003)]. In contrast, in a non-sectorial plant (i.e. an integrated plant), different compartments are interrelated by vascular connections. The figure produced by Schenk *et al.* (2008) illustrates the two extremes of the sectoriality–integration continuum (Fig. 4). The degree of sectoriality (or the degree of integration) depends on vessel distribution and morphology, such as diameter and clustering of vessels, and/or the non-uniform location and frequency of inter-conduit pitting to keep sectors separated (Carlquist, 1984; Ellmore *et al.*, 2006; Zanne *et al.*, 2006; Lachenbruch and McCulloh, 2014). Moreover, Zwieniecki *et al.* (2013) suggest that sap ion concentration can also directly modify the extent of lateral transport as a cause of changes in xylem axial resistance. In line with the PMT, this section only examines xylem functioning; however, the concept of sectoriality applies to the entire vascular system, including phloem and carbohydrate distribution (Orians *et al.*, 2005*a*).

Examining xylem hydraulic architecture and connections within a tree is a tedious task (Cruiziat *et al.*, 2002; David *et al.*, 2012). Numerous methods have been used to study hydraulic connections at scales ranging from individual vessels to the entire plant. Introducing dyes or mineral stable isotopes into the stems of the living tree make it possible to visualize water-conduction pathways (Larson *et al.*, 1994; Schulte and Brooks, 2003; Orians *et al.*, 2004; Sano *et al.*, 2005; Ellmore *et al.*, 2006; Umebayashi *et al.*, 2008; Espino and Schenk, 2009) and to measure sap flow in different parts of trees. This method, possibly coupled with manipulation such as split-root or branch severing, can produce a map of preferential pathways (Infante *et al.*, 2001; Lopez-Bernal *et al.*, 2010; David *et al.*, 2012; Nadezhdina *et al.*, 2012, 2013; Sato *et al.*, 2012; Shinohara *et al.*, 2013). We refer to Orians *et al.* (2005*a*) for an extended discussion of the advantages of the different techniques.

These experimental results reveal that plant species exhibit a wide range of variation in their degree of sectoriality (Schulte

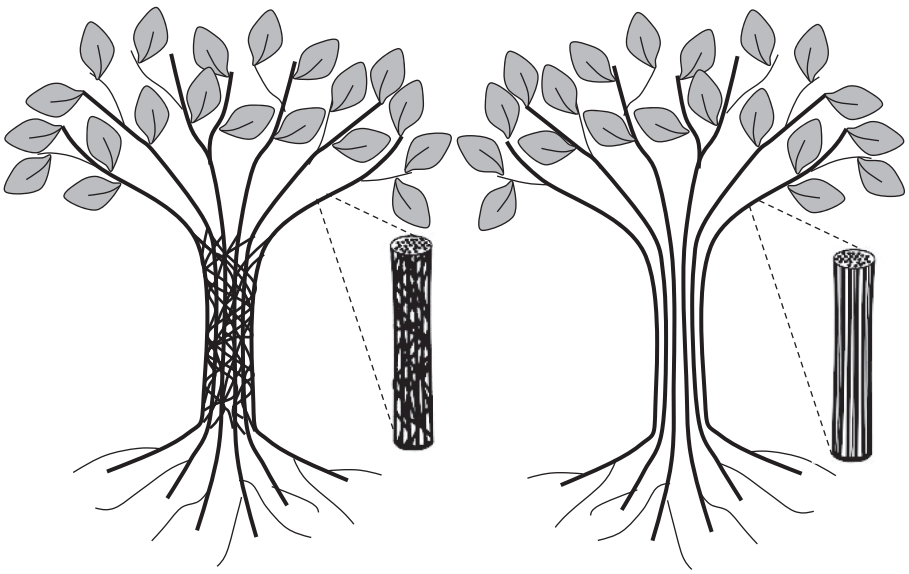

FIG. 4. Graphical representation of the hydraulically integrated (left) and sectorial plant (right) by Schenk *et al.* (2008). The sectoriality–integration property is illustrated at the whole-plant scale (i.e. absence/presence of connections between adjacent pipes connecting a set of roots to a set of leaves) and at the wood strand scale (i.e. absence/presence of connections between adjacent vascular elements within a wood strand).

and Brooks, 2003; Ellmore *et al.*, 2006; Schenk *et al.*, 2008; Espino and Schenk, 2009), ranging from highly sectored species, constructed of autonomous subunits such as ring-porous species like oak and elm (Orians *et al.*, 2005*b*; Ellmore *et al.*, 2006) and longitudinally split shrubs (Schenk *et al.*, 2008), to fully integrated species appearing as single units, such as diffuse porous species like birch and many others (Watson and Casper, 1984; Tyree and Zimmermann, 2002; Orians *et al.*, 2005*b*; Ellmore *et al.*, 2006). Intermediate degrees of sectoriality or integration are possible at the scale of species, individuals and organs (Vuorisalo and Hutchings, 1996; Orians *et al.*, 2004; Ellmore *et al.*, 2006; Nadezhdina, 2010). Sprugel *et al.* (1991) suggested that sectoriality could provide advantages in terms of damage control, stress isolation and light capture. A high degree of sectoriality ensures better protection against the spread of embolism and therefore is seen as a success factor for adaptation in xeric environments. A drawback is reduced specific conductivity (Zanne *et al.*, 2006; Schenk *et al.*, 2008; Lachenbruch and McCulloh, 2014). In contrast, low sectoriality appears to be an advantage in environments with patchy resources (Orians *et al.*, 2004; Ellmore *et al.*, 2006), such as the forest understorey (Thorn and Orians, 2011). Sectoriality is also expected to occur more frequently in gymnosperms and dicotyledons than in monocotyledons, because of their open vascular systems (Vuorisalo and Hutchings, 1996; Orians *et al.*, 2005*a*). Nevertheless, the gymnosperm xylem structure, in which the bulk of axial elements conduct water, permits higher hydraulic integration than angiosperm wood (Cruiziat *et al.*, 2002). Intraspecific differences can also be observed and the degree of sectoriality may vary according to the ontogenetic stage of the plant (Watson and Casper, 1984; Zanne *et al.*, 2006; Salguero-Gomez and Casper, 2011). This touches upon a hypothesis of Hallé (1991), that juvenile wood would constitute the stem of young trees for which crown development has not yet started, while mature wood results from integration of root systems of different reiterated complexes that constitute the mature tree crown (Barthélémy and Caraglio, 2007). This hypothesis has given rise to the term 'crown-formed wood' to describe fluctuations in wood structure associated with the size of the crown (Amarasekara and Denne, 2002). The link between the degree of reiteration of species and their sectoriality degrees is an active research area (Herrera, 2009).

In summary, while some plants exhibit a distinct sectorial hydraulic system, thus conforming to the PMT, the large observed diversity of degrees of hydraulic connectivity among species or depending on growth conditions shows that the notion of the pipe is not a universally valid one and should be more nuanced.

Discussing the hydraulic sectoriality or integration concept in the framework of the PMT relies strongly on the presence or absence of a preferential vascular pathway to a given leaf or a set of leaves. With water being to some extent able to move radially between pipes of the same cohort (i.e. same-aged pipes), is a cohort of leaves (i.e. same-aged leaves) only connected with the corresponding cohort of pipes? In other words, are leaves formed in a specific year only connected to the growth rings formed in the same year? In needle-pulling experiments on 16 gymnosperms species, Maton and Gartner (2005) observed that leaves of deciduous species pull water only through the current growth ring, whereas different evergreen species were shown to pull water from up to 2-year-old growth rings. This diversity of patterns in the ascent of water reflects the different mechanisms driving the formation of new connections between leaves of varying age and newly produced xylem as well as the deactivation of old ones. Maton and Gartner (2005) demonstrated that a leaf can be connected to different pipe cohorts in its lifetime. The authors were unable to classify some species due to high intra-specific variability, and even observed some samples pulling water from different growth rings. This questioned the concepts of both leaf traces (MacDougal *et al.*, 1929) and ray parenchyma (Barnard *et al.*, 2013) as pathways for the radial movement of water between different cohorts of pipes.

Stem, SW and ring tapering

Sapwood area at crown base or at breast height? A key property associated with the PMT is the constancy of the ratio of leaf to conductive SW (SW) area (A_L:A_S) within a tree. This rule is expected to be valid in any point of the tree branching structure and throughout plant ontogeny. It predicts increasing SW area from the tree top downwards following the increase in foliage biomass/area towards the crown base and subsequently a constant SW area between crown and stem base. The ratio of leaf area to SW area at breast height should thus be equal to the same ratio computed with SW area at crown base. However, many studies (reviewed in the following paragraphs) reported that SW area increases from the crown base to breast height. Thus, to avoid biases due to the effect of SW tapering below the crown base, it would be preferable to measure the ratio of leaf area to SW area at the crown base rather than at breast height, to obtain more reliable values at the intra-specific level (Waring *et al.*, 1982; Marchand, 1984; Bancalari *et al.*, 1987; Maguire and Batista, 1996).

Tapering of sapwood thickness or area. Many studies reported SW thickness, instead of area, to increase downward within the crown and then to remain constant below crown base for both gymnosperms (Yang *et al.*, 1985; Ojansuu and Maltamo, 1995; Climent *et al.*, 2003; Pinto *et al.*, 2004; Knapic *et al.*, 2006; Longuetaud *et al.*, 2006) and angiosperms (Dhôte *et al.*, 1997; Björklund, 1999; Knapic *et al.*, 2006; Miranda *et al.*, 2006; Morais and Pereira, 2007). This implies that stem and heartwood (HW) tapering is generally similar in shape (Long *et al.*, 1981; Pinto *et al.*, 2004; Longuetaud *et al.*, 2006; Morais and Pereira, 2007). However, other authors reported different observations. Climent *et al.* (2003) identified a group of *Pinus canariensis* trees with HW proportion reaching a maximum between 4 and 8 m from the tree base (i.e. non-monotonic HW tapering) and a different group with monotonic decreasing HW proportion towards the top of the tree. Similar patterns were also recorded in *Pinus pinaster* (Berthier *et al.*, 2001; Pinto *et al.*; 2004, Knapic and Pereira, 2005) and *Pinus sylvestris* (Björklund, 1999; Mörling and Valinger, 1999) and are considered to be a specific feature of conifer species (Climent *et al.*, 2003). It has been suggested that the parts of trees with a high HW proportion could be linked to high production of ethylene at the part of the stem that is subject to the maximum mechanical stress when the tree sways (Climent *et al.*, 2003). Aside from these particular cases, the constant SW thickness

found along the branch-free stem has been suggested to validate the PMT (e.g. Knapic and Pereira, 2005). This conclusion neglects the fact that a constant SW thickness is usually incompatible with a constant SW area in tapered stems. Indeed, when both SW thickness and area are considered together, it is generally observed that SW area increases from the crown base towards the ground, whereas SW thickness remains constant (Long *et al.*, 1981; Ojansuu and Maltamo, 1995; Gominho and Pereira, 2005; Longuetaud *et al.*, 2006; Miranda *et al.*, 2006; Morais and Pereira, 2007).

Models of sapwood area tapering. The experimental difficulty of measuring SW area below the crown has motivated researchers to describe and model SW tapering along the stem in order to predict the SW area at different heights by tree metrics readily measurable from the ground. In addition, they aim at studying HW variations within the stem, an objective shared with the forestry and timber industry to better assess the profitability of stems and forest plots. Ojansuu and Maltamo (1995) modelled SW area tapering in *P. sylvestris* using a combination of HW and stem taper models and tree biometric descriptors (DBH, tree and crown height). Using the same predictors, Maguire and Batista (1996) were also able to model SW tapering by deriving stem taper models. More recently, Cruickshank *et al.* (2015) developed models using variables available from remote sensing. They compared an empirical and a functional approach: the functional one strongly relied on assumptions based on the PMT as well as an exponential decay function allowing the SW area to drastically increase near the stem base (see below); the empirical one is a segmented polynomial equation (Gallant and Fuller, 1973). The functional model predicted an overly abrupt change between trunk and crown segment in the vicinity of the crown base that was not always clearly observed at this position, but instead in higher parts of the crown. The empirical model proved more flexible and allowed estimation of the position of inflection points of the SW area profile. It showed that, at least for lodgepole pine (Garber and Maguire, 2005) and western hemlock (Kershaw and Maguire, 1995), the inflection point appeared to be closely related to the modal value of the leaf density distribution within the crown, which varies between species (Maguire and Bennett, 1996; Weiskittel *et al.*, 2009), but also within a given species depending on stand density or social status (Garber and Maguire, 2005).

Relation with foliage distribution. In a Douglas-fir stand, foliage distribution strata were successfully identified using measured SW area tapering and assuming a constant ratio of leaf area to SW area (Maguire and Bennett, 1996), but some discrepancies between estimated and observed distributions challenged the validity of the said ratio within the crown, where it was shown to vary significantly (Bancalari *et al.*, 1987; Kershaw and Maguire, 1995; Mäkelä and Vanninen, 2001; Kantola and Mäkelä, 2004; Schneider *et al.*, 2011). Dean *et al.* (1988) observed a ratio of lower leaf area to SW area at the crown top and crown base than at mid-height. Mäkelä and Vanninen (2001) observed the same tendency for the ratio of leaf mass to stem area in *P. sylvestris*, and observed that the highest ratio value corresponded to the peak of foliage distribution. It has been hypothesized that the variation in the ratio of leaf area to SW area could result from the variations in SW conductivity and transpiration rate per unit of foliage within the crown (Brix and Mitchell, 1983), the potential incongruity between SW area and area of actually conducting wood (Mäkelä and Vanninen, 2001), and the conservation of higher SW area to store water (Cruickshank *et al.*, 2015).

Trunk basis. A strong non-linear increase in SW area has also been observed at the trunk basis (Long *et al.*, 1981; Ojansuu and Maltamo, 1995; Mörling and Valinger, 1999; Cruickshank *et al.*, 2015), which may result from an increase in SW area or a decrease in HW area as mentioned above (Climent *et al.*, 2003). For conifer species, this phenomenon could be due to a different trade-off between water transport and mechanics. Indeed, a larger proportion of latewood in this part of the tree (Gartner *et al.*, 2004) might provide sufficient strength to meet the strong mechanical constraints present in this part, but might also decrease xylem specific conductivity (Zimmermann, 1983; Gartner, 1991; Domec and Gartner, 2002), resulting in a higher production of SW to meet hydraulic demands (Stokes and Berthier, 2000; Berthier *et al.*, 2001; Cruickshank *et al.*, 2015).

Relation with Pressler's law. Under the assumption that physiologically active wood area is equal to the last annual wood increment, the PMT can be interpreted as an alternative formulation of Pressler's law (Pressler, 1865; Cruiziat *et al.*, 2002). The latter states that 'Ring area growth (cross-sectional area of a single annual increment) at any point on the stem is proportional to the quantity of foliage above this point' (Pressler, 1865, cited by Larson, 1963). This law assumes that the yearly carbon allocation from the crown is uniform along the stem and does not vary significantly with environmental conditions. It has been widely used in forest science as it represents an intuitive way to describe, understand and predict the layering of xylem at the origin of the stem shape (Larson, 1963; Houllier *et al.*, 1995). Yet it has not been used as widely as the PMT, presumably because it implies *a priori* knowledge about stem increment distribution, which is less easily measurable in the field than the stem or SW area.

If we accept the above-described property 5 of the PMT, which states that only the last wood growth ring is conductive in deciduous species, then the PMT and Pressler's law are equivalent. Few studies have confirmed Pressler's law (e.g. Ottorini, 1991, for Douglas-fir), whereas many works have underlined discrepancies between the theory and biological observations (Farrar, 1961; Weiner, 1984; Osawa *et al.*, 1991; Yamamoto, 1994; Courbet, 1999; Saint-André *et al.*, 1999; Kershaw and Maguire, 2000; Deleuze and Houllier, 2002; Bevilacqua *et al.*, 2005; Cortini *et al.*, 2013). Hatsch (1997) showed that in sessile oak it is not the ring surface that remains constant under the crown but its thickness. Moreover, the competitive status of trees is of primary importance. Dominant and suppressed trees show an increase and decrease in growth ring area towards the base, respectively, while intermediate trees show no variations (Larson, 1963; Courbet, 1999; Cortini *et al.*, 2013). This suggests that the constant growth ring area along the trunk postulated by the model is not a general rule. Moreover, extreme events such as drought can influence the longitudinal secondary growth pattern. For example, Bouriaud *et al.* (2005) showed that during dry years ring-area increments were more strongly reduced at breast height than in the upper parts of the tree. Apart from the variations along the bole, another common criticism of Pressler's law is linked to the observation of a strong increase in

ring area at the trunk base, resulting in the butt swelling of trees (Farrar, 1961; Larson, 1963; Ottorini, 1991; Courbet, 1999; Dhôte *et al.*, 2000; Deleuze and Houllier, 2002; Bevilacqua *et al.*, 2005; Cortini *et al.*, 2013; Yu *et al.*, 2014), the magnitude of which is linked to crown dimensions (Larson, 1963; Cortini *et al.*, 2013) and therefore strongly suspected to be related to mechanical support (Larson, 1963; Gartner, 1995). Some studies indicate that the relationship between ring area and foliage area is not simply proportional (Hall, 1965; Deleuze and Houllier; 1995, Kershaw and Maguire, 2000; Groot and Saucier, 2008), but decreases with increasing distance to the treetop as a result of decreasing photosynthetic rate and light intensity, as well as increasing foliage age (Kershaw and Maguire, 2000). An additional criticism is related to the fact that the crown base and the point along the stem below which growth ring area is roughly constant may not coincide. Indeed, while some studies report a maximum growth point in the vicinity of the crown base (Larson, 1963, and references therein), this point was also recorded at different depths within the crown (Courbet, 1999; Cortini *et al.*, 2013). These observations motivated the idea of an 'efficient crown base' excluding lower branches that cannot be seen as part of the crown due to ageing or to mechanical competition with neighbours (Houllier *et al.*, 1995; Courbet, 1999).

The simplicity of Pressler's law does not account for variations in ring area distribution related to varying growing conditions (Deleuze and Houllier, 2002), crown classes (Mitchell, 1975), site quality, silvicultural treatments and competition (Bevilacqua *et al.*, 2005) or age (Larson, 1963; Ottorini *et al.*, 1996; Courbet, 1999). Therefore, with the aim of stem form modelling, the above criticisms call for improvements of the model (Houllier *et al.*, 1995; Courbet, 1999; Cortini *et al.*, 2013). Courbet (1999) developed a flexible three-segmented model with Pressler's law as a particular case, allowing ring area to (1) decrease non-linearly within the crown, (2) vary along the trunk and (3) increase sharply at the trunk base, and providing intuitive and uncorrelated coefficients that could be analysed in different growing conditions. However, this model requires input variables that are not easily available, such as foliage distribution or increment area at breast height. Cortini *et al.* (2013) developed a species-level mixed-effect three-component model to predict ring increment along the stem based on more readily accessible crown and stand variables. Whereas empirical models are efficient in predicting radial increment distribution over the studied range of species and stand characteristics, they are not suited for prediction outside the range covered by the dataset (Courbet, 1999; Cortini *et al.*, 2013). A more flexible modelling approach consists in process-based models (Deleuze and Houllier, 1995, 2002) that integrate budget, distribution and translocation of carbon through the phloem and partitioning coefficients between tree compartments at different spatial scales. However, these models failed to predict the sharp increment at the trunk base of highly butt-swelled trees (Deleuze and Houllier, 2002), suggesting that mechanical signal might interfere with a simple carbon diffusion principle.

To conclude, our comparison between theory and observation demonstrated that, in its initial formulation, Pressler's law, as an intuitive and straightforward framework to understand how the stem forms and the crown develops through simulations or retrospective approaches, is not generally valid.

Relation with Leonardo da Vinci's rule (area-preserving rule). The PMT implicitly assumes the validity of Leonardo da Vinci's rule: that the axis cross-sectional area below a given branching point is equal to the sum of the cross-sectional areas of the daughter branches above this point (Shinozaki *et al.*, 1964*a*; Richter and Bell, 1970; Nikinmaa, 1992; Yamamoto and Kobayashi, 1993). Although Leonard da Vinci's rule is occasionally used as a structural property of tree models (West *et al.*, 1999; Eloy, 2011; Minamino and Tateno, 2014), there is little experimental work confirming its validity. As in the case of tapering rules, the area-preserving rule has been tested with regard to cross-sectional areas of ring increments, SW and whole axes excluding bark (Nikinmaa, 1992; Yamamoto and Kobayashi, 1993; Hatsch, 1997; Sone *et al.*, 2005, 2009). Furthermore, it should be noted that Leonardo da Vinci's rule was also tested at a microanatomical scale by considering xylem conduit dimensions and comparing it with the Murray law to investigate how branching systems optimize hydraulic flux to woody and leafy organs (McCulloh *et al.*, 2003; Chen *et al.*, 2012; Price *et al.*, 2014; Carvalho *et al.*, 2017*a, b*).

In *Cryptomeria japonica*, Yamamoto and Kobayashi (1993) demonstrated a good correlation between trunk cross-sectional area and the cumulative cross-sectional area of its daughter branches at the top of the tree, where HW is not developed. However, the slope of this linear relationship varied among individuals and was not systematically equal to 1, thus challenging the area-preserving rule. Similarly, in Scots pine (*P. sylvestris*), Nikinmaa (1992) observed a significant linear correlation between the diameter of the trunk at the crown base and the sum of living branch cross-sectional area above. However, considerable variation of the slope existed among individuals of the same stand as well as between stands, with an apparent effect of a north-to-south gradient of stand location (the same cross-sectional area supported more branches in the south than in the north). In *Quercus petraea*, Hatsch (1997) analysed the ratio between (1) the differences in SW area below and above branch insertion and (2) the SW area of the same branch for each branch located in tree crown, in order to estimate the local contribution of the branch in terms of stem SW tapering. For juvenile and adult trees, the ratio was overall <1 with a considerable variability that could not be related to any particular branch characteristic (position in the crown, age, size, …). A relationship could also not be identified between the number of rings in SW of branches and the stem. The authors concluded that the PMT was not helping to explain this variability. In contrast, Sone *et al.* (2005, 2009) demonstrated the validity of the area-preserving rule for the whole cross-sectional area of branches in the crown of young *Acer* trees. However, this rule was not valid for the current-year growth ring area: the average yearly growth of the cross-sectional area of a branch was found to be smaller than the sum of growth of its daughter branches. The authors related this to the fact that the proportion of the current-year growth area relative to the cross-sectional area of the branch is almost always greater for small, young branches than it is for large, old branches. The authors noted that Leonardo da Vinci's rule would not hold if the decrease in basipetal growth was repeated every year. In summary, the above results show that the Leonardo da Vinci's rule does not hold in general conditions.

The variability and plasticity of the A_L:A_S ratio and the scalability of the PMT

The PMT suggests a constant ratio of leaf area to SW area across the tree at one given point in time. A tempting and common, however improper, over-generalization of the theory is to assume this ratio to be constant within a given species irrespective of the plant's ontogenetic stage, seasons and environmental conditions. Before synthesizing the various results on A_L:A_S ratio variability, we note that, depending on the studies, different types of variables were used to analyse the relationship between an amount of leaves and the SW area supplying water to it (reviewed in Whitehead and Jarvis, 1984, p. 86): (1) some authors consider the leaf area while others measure the leaf mass (e.g. the pipe model ratio in Sattler and Comeau, 2016), which might lead to different results due to the variability of leaf mass per area (LMA) within a set of leaves (Valentine, 2001); (2) some authors consider SW area while others prefer whole-stem/branch sectional area (considering, implicitly or not, that the whole of the section is conductive); and (3) there is a high diversity of approaches used to measure and estimate the SW area if this is the considered variable. As a necessary prerequisite to any synthesis, these methodological aspects will be discussed more precisely in the following sections. It is also important to recall that the constancy of the leaf area/SW area ratio within a species was not explicitly claimed in the original formulation of Shinozaki *et al.* as discussed above. Consequently, the PMT has been misinterpreted as a species-specific isometric relationship between leaf area and conductive SW area. As no rule describing the variation of the parameter L with tree size was given by Shinozaki *et al.*, a key criticism of the PMT is its non-scalability (Mencuccini *et al.*, 2011).

Studies on the A_L:A_S ratio have been conducted for a wide range of experimental designs that can be categorized as follows. (1) Even-aged monospecific stands in which only dominant or codominant trees are considered. In this particular case, it is assumed that selecting samples from stands of various ages sharing similar environments and silvicultural treatments allows us to consider that the different measured trees describe a single chronosequence, i.e. that they share the same developmental trajectory, with the 'size' effect directly related to the ontogeny (Magnani *et al.*, 2000; McDowell *et al.*, 2002; Delzon *et al.*, 2004*a*). (2) Even-aged monospecific stands in which site fertility, stand density or thinning intensities are compared (Brix and Mitchell, 1983; Binkley, 1984; Bancalari *et al.*, 1987; Granier, 1987; Aussenac and Granier, 1988; Long and Smith, 1988; Pothier and Margolis, 1991; Shelburne *et al.*, 1993; Mencuccini and Grace, 1995; Medhurst and Beadle, 2002; McDowell *et al.*, 2006). (3) Even-aged stands in which trees with different competitive status, from suppressed to dominant, are considered (Long and Smith 1988). (4) Natural forest stands in which trees of different sizes are compared without any information on age or growth histories. Most of the published work demonstrates that A_L:A_S ratios vary among individuals of the same species. Decreases in A_L:A_S ratios have been reported in particular along the developmental trajectory (Magnani *et al.*, 2000; McDowell *et al.*, 2002; Barnard and Ryan, 2003; Delzon *et al.*, 2004*a*) and for increasing size (Albrektson, 1984; Ryan *et al.*, 2000; Schäfer *et al.*, 2000; Phillips *et al.*, 2001; Fischer *et al.*, 2002; Kostner *et al.*, 2002; Mokany *et al.*, 2003; Delzon *et al.*, 2004*a, b*; Ewers *et al.*, 2005). However, the reverse pattern was also observed (Coyea and Margolis, 1992; McDowell *et al.*, 2002). The decrease in A_L:A_S ratios with increasing tree size may be a homeostatic mechanism partially compensating for the decrease in hydraulic conductance as trees grow in height (McDowell *et al.*, 2002). Variations have also been studied according to site fertility (Binkley, 1984; Bancalari *et al.*, 1987; Long and Smith, 1988; Shelburne *et al.*, 1993), site differences in water vapour pressure deficit (Mencuccini and Grace, 1995; McDowell *et al.*, 2006) and species mixture (Binkley, 1984) as well as stand density and thinning practices (Brix and Mitchell, 1983; Granier, 1987; Aussenac and Granier, 1988; Long and Smith, 1988; Pothier and Margolis, 1991; Shelburne *et al.*, 1993; Medhurst and Beadle, 2002). In summary, previous studies have demonstrated that A_L:A_S ratios should not be considered as merely species-specific, and that, instead, additional parameters should be added to make the PMT scalable with respect to tree ontogenetic stage and size, social status, site quality or silvicultural practices, thus adding to the flexibility of the PMT from a time-dynamic point of view (Ogawa, 2015).

Estimating crown leaf area and sapwood area independently

Among papers applying the PMT to examine the leaf to SW area ratio A_L:A_S, two main objectives can be distinguished: (1) to develop methods to evaluate leaf area using non-destructive methods as described in Leaf mass/area section; (2) to test the variability of this ratio with respect to different factors as described in the section The variability and plasticity of the A_L:A_S ratio and the scalability of the PMT. It is important to note that although the word 'sapwood' does not appear in either of the two papers by Shinozaki *et al.* (1964*a, b*), it is commonly assumed that this is what the authors meant by the concept of 'active pipes' (Valentine, 2001). Disused pipes then correspond to non-conducting xylem, which is often confused with HW (see below). The experimental techniques used to measure the variables A_L and A_S, at different scales ranging from the whole plant to individual branches, provide more or less direct, precise and independent results. It thus seems important to briefly summarize and discuss them, as we do in the following sections.

Leaf mass/area. Measuring the foliar area of adult trees can be very tedious (Dean *et al.*, 1988). Indirect techniques have been developed to avoid this experimental work load. A common non-destructive approach consists of using crown length or size to infer leaf area (Cienciala *et al.*, 2006; Cruickshank *et al.*, 2015). This approach relies on the assumption of high correlation between crown dimension in terms of biometric parameters and the volume of the assimilation apparatus (Lemke, 1966; Jelonek *et al.*, 2008; Sattler and Comeau, 2016). More recently, an increasing number of studies based on terrestrial LIDAR scan data open promising prospects for the non-destructive quantification of volumes or biomass of individual tree crowns (Hosoi and Omasa, 2006; Béland *et al.*, 2014; Stovall *et al.*, 2017).

Most other approaches are destructive. In line with the original experimental datasets of Shinozaki *et al.*'s paper, several studies use leaf biomass without converting it to leaf area (Grier and Waring, 1974; Kendall Snell and Brown, 1978; Brix and

Mitchell, 1983; Albrektson, 1984; Granier, 1987; Aussenac and Granier, 1988). In most studies, either the whole crown is stratified into horizontal layers (e.g. Grier and Waring, 1974) or branch whorls (or pseudo-whorls) are considered as distinct layers (e.g. Whitehead, 1978). Thus, the vertical distribution of foliage can be taken into account. In each layer, leaves are usually freshly weighed but can also be dried, sometimes together with the twigs that carry them. Then, dry weight is estimated using fresh weight/dry weight or leaf mass/wood mass conversion factors that are calibrated on a sub-sample (e.g. Grier and Waring, 1974). In some studies fresh weight is considered directly without conversion to dry weight (e.g. Morataya *et al.*, 1999), which is a potential cause of bias.

Other studies consider leaf area. As it is easier to measure total leaf mass than the total leaf area, a common approach is to calculate a mean specific leaf area (SLA) by dividing the total leaf area of a subsample by its dry mass (Gower *et al.*, 1999). As SLA varies within the crown, many authors calculate different SLA values by stratifying the crown into horizontal layers, considering branch categories or/and separating leaves according to their age in evergreen species (e.g. Landsberg *et al.*, 1997). In some cases, intermediary allometric models at branch level are developed. Because HW is often absent in branches, the entire cross-sectional area is considered as the SW area (Gehring *et al.*, 2015). Statistical models such as generalized linear models are used to predict leaf area from branch size (diameter or length) and/or position. Tree-level leaf area is then calculated via the 'branch summation method', in which the branch-level model is applied to each branch and predicted branch leaf area values are added up (Monserud and Marshall, 1999; Fischer *et al.*, 2002; Zellers *et al.*, 2012).

In the following we discuss these different approaches. First, the crown leaf surface in adult trees is always estimated and never actually measured. Potential errors from using allometric rules are never accounted for, and thus biases resulting from the different methods can be difficult to assess. Moreover, in the branch summation method A_L and A_S cannot really be considered as independently measured given that branch diameters are used to estimate leaf area, before total leaf area is compared with SW area to validate the PMT. This implies that the method used to evaluate the PMT relies itself on a PMT-like approach. Second, using either foliage biomass or leaf area can potentially lead to different conclusions. Although some authors have argued against this (Kershaw, 2001), there is evidence that a constant ratio of cross-sectional area to leaf mass does not imply a constant ratio of cross-sectional area to leaf area within the tree crown (Waring *et al.*, 1982; Valentine, 2001). Because SLA can vary by up to a factor of 2 between the top and the bottom of the crown, using leaf area instead of mass may reduce the variation in the observed ratio. Third, Gower *et al.* (1999) highlighted the fact that the lack of a consensual methodology for defining SLA has caused confusion in the literature and even blurred the conclusions of reviews that do not distinguish between the different methods. For instance, for needle-like leaves both projected and total leaf area differ according to the shape of the leaf (cylinder in some pines or with a square cross-section in black spruce). Adequate adjustments required in the calculation of SLA are still not always standardized in the literature despite the existence of recommended protocols (Cornelissen *et al.*, 2003).

Sapwood area. The SW and HW are classically considered as two distinct functional wood compartments in perennial stems. Fundamentally, this distinction is made on the assumption that SW is physiologically active whereas the HW is the dead part of the wood that no longer contains living cells (Bamber, 1976; Bamber and Fukazawa, 1985; Hillis, 1987). Heartwood is generally darker than SW, although not always (Hillis, 1977). The term 'sapwood' may be misleading from an etymological point of view. As sap is defined as the fluid that circulates in the vascular system of a plant (Zimmermann, 1983), in a literal sense, the term 'sapwood' refers to 'wood' that transports 'sap'. However, while SW remains physiologically active until it transforms into HW, particularly in terms of water and carbohydrate storage, there is strong evidence that water conduction along the stem is restricted to the outermost SW (Ziegler, 1968; James *et al.*, 2002; Spicer and Holbrook, 2005). The subdivision of SW into conducting wood (i.e. wood still able to transport water) and storage wood (i.e. wood having mainly storage functions), as proposed by Ziegler (1968), is almost never accounted for in studies considering A_L:A_S ratios in trees. Hence, depending on the species in question, SW area is measured according to different protocols that are more or less in agreement with the notion of conductive SW.

In most cases, SW is defined visually as the lighter part of the wood cross-section in contrast to the darker HW (Grier and Waring, 1974; Waring *et al.*, 1977; Morataya *et al.*, 1999; Cruickshank *et al.*, 2015). In other cases, and especially when HW is visually indistinguishable from SW, the latter is determined by examining the differences in light transmission when the cross-section is held against bright light (Kaufmann and Troendle, 1981; Long and Smith, 1988; Barnard and Ryan, 2003; Delzon *et al.*, 2004*b*). In some species, wood disc immersion in water can reveal the contrast between HW and SW (Bancalari *et al.*, 1987); however, the use of passive staining by chemical solutions is often necessary (Kutscha and Sachs, 1962; Waring *et al.*, 1977; Kendall Snell and Brown, 1978; Whitehead, 1978; Granier, 1981; Albrektson, 1984; Whitehead and Jarvis, 1984; Whitehead *et al.*, 1984; Baldwin, 1989; Mencuccini and Grace, 1995; Fischer *et al.*, 2002). The latter approach makes it possible to differentiate between living and dead tissue based on the reaction either with phenolic secondary compounds, which are more frequent in HW, or with starches, which are more frequent in SW. Universal pH indicators can also be used following the principle of differences in acidity between HW and SW (Waring *et al.*, 1980). This first set of methods can be applied to the observation of a wood disc collected from the felled tree. In other cases, they can be applied to wood increment cores from standing trees to measure SW thickness, which is in turn used with stem diameter as input variables to compute SW area. Another method consists in staining the water pathway within the living stem with dye injections (Tyree and Zimmermann, 2002) in order to delineate the conducting SW area. The stained wood region above the injection point is then observed after a few hours (Santiago *et al.*, 2000; Reyes-García *et al.*, 2012; Pivovaroff *et al.*, 2014). This method is probably the most accurate and least prone to estimation errors.

These methods for measuring the SW area are extremely diverse and lead to estimates that are difficult to compare. In some conifer species, the whole SW remains conductive until it transforms into HW (Swanson, 1966; Ziegler, 1968; Rust *et al.*,

1995). In this case, methods based on differences in terms of colour (natural or chemically induced) make it possible to correctly identify conductive SW. However, in general, unless this property is preliminarily validated for the species in question, the measured SW area does not necessarily correspond to conducting wood in the sense of Ziegler (1968) and therefore does not conform with the functional assumption of the PMT. For instance, in ring-porous species, numerous studies reported that the water flow is provided by the outermost rings in the SW (Huber and Schmidt, 1937; Ziegler, 1968; Cochard and Tyree, 1990). Of 21 SW rings, only two are conductive in *Quercus phellos* (Ziegler, 1968), and in *Ulmus americana* 90 % of the water flow was recorded in the outermost ring (Ellmore and Ewers, 1985, 1986). In *Quercus robur*, Čermák *et al.* (1992) observed 50 % of the water flow in the two outermost rings and 95 % in nine of a total of 20 SW rings. It is also very common to observe a higher relative sap flux in the outer portion of the SW of diffuse-porous species, such as red maple (Spicer, 2005), but also in wide-SW tropical species from Panama (James *et al.*, 2002). Staining experiments also revealed that legume species from Mexico conduct water in the two outermost centimetres of the SW (Reyes-García *et al.*, 2012).

Many other techniques allowing proper characterization of conductive SW are currently available, including conductivity measurements by means of electrodes (Čermák *et al.*, 1992), microwaves (Johansson *et al.*, 2003), infrared imaging (Gjerdrum and Høibø, 2004), radiography (Polge, 1964) and computed tomography (Ojansuu and Maltamo, 1995; Rust, 1999; Fromm *et al.*, 2001; Wilhelmsson *et al.*, 2002; Longuetaud *et al.*, 2007). To our knowledge, these techniques have never been applied in systematic studies of A_L:A_S ratios (with the exception of Schäfer *et al.*, 2000), which can be explained from a historical point of view. When reviewing the literature and the first syntheses about A_L:A_S ratios (McDowell *et al.*, 2002; Ryan *et al.*, 2006), it appears that most studies were initiated by the forester community during the 1970s and 1980s, whereas the above-mentioned more sophisticated methods were developed by the ecophysiologist community at the end of the same period. The limited overlap between these two research communities at this time thus hindered the dissemination of these techniques. Today, they are more widespread but their use remains limited by their high cost and the availability of technical equipment as well as logistical challenges.

The analogy with Corner's rules

Several authors have noted similarities between the PMT and Corner's laws (Hallé *et al.*, 1978; Brouat *et al.*, 1998; Brouat and McKey, 2001; Preston and Ackerly, 2003; Mencuccini *et al.*, 2011; Lachenbruch and McCulloh, 2014). In his seminal paper, the botanist E. J. H. Corner introduced two empirical rules, which he denoted 'axial conformity' and 'diminution of the ramification' (Corner, 1949), later on described as 'Corner's rules' by Hallé *et al.* (1978). Hallé *et al.* (1978) make considerable use of Corner's rules, stating that the term 'massive' used by Corner refers to the volume (stoutness) and more precisely to the axial diameter. Hallé *et al.* (1978) also assumed that architecture, surface, volume and mass are interrelated to four measurable variables: (1) the primary diameter of the axis and (2) the internode length, both of which are related to volume and mass; (3) leaf surface; and (4) the rate of meristematic activity. In the subsequent works on Corner's rules, the considered variables are the diameter of the first-year shoot just after elongation (i.e. the primary diameter, when secondary tissues are considered as negligible) and the lamina area. The work of White (1983*a, b*) provided the first empirical validation of Corner's rules on a dataset of 69 species in North America. White discussed several possible explanations of Corner's rules and, like Hallé *et al.* (1978), mentioned the role of the hydraulic constraints, suggesting that the amount of xylem required to supply a leaf is related to the size of the leaf. He also mentioned the role of mechanical constraints, as large leaves require stronger stems to resist weight and stress imposed by the wind. Thus, the ratio of leaf area to twig cross-sectional area would be based on the necessity to fulfil support and transport functions (Farnsworth and Van Gardingen, 1995). With similar reasoning applied at twig scale instead of individual leaf scale, Brouat *et al.* (1998) reanalysed White's data, considering the total leaf surface of the current-year shoot rather than the surface of a single leaf as the variable to be correlated with stem cross-sectional area. While White conducted his analysis by considering species with different successional characteristics (i.e. early and late successional trees), Brouat *et al.* (1998) distinguished three groups in their analysis: deciduous angiosperms, evergreen angiosperms and gymnosperms. They show that considering total leaf area considerably improves the relationship of twig size to leaf size for deciduous species. In addition, they analysed leaf area/stem cross-sectional area allometries across ontogenetic stages (in terms of tree height) in four species, considering the ratio between the cross-sectional area of the terminal internode and surface area of leaves supported by it. They supposed that if similar patterns were found in these four species, characterized by different habits and geographical distributions, they might indicate a more general trend. The most striking result of their paper is that, in both interspecific and intraspecific comparisons, the relationship between primary cross-sectional area of a stem and the surface area of leaves borne by it is isometric. In summary, we have noted parallels between the PMT and Corner's rules: the former can be seen as an isometric relation between the primary axis diameter and the leaf area it supports, which is interpreted in terms of a mechanistic explanation through hydraulic and mechanical requirements; the latter can be seen as a corollary of the area-preserving branching property (see Relation with Leonardo da Vinci's rule [area-preserving rule]).

Several aspects related to the similarity between the PMT and Corner's rules deserve a more in-depth discussion. First, Corner's original work clearly had an interspecific scope and aimed at embracing plant diversity: the relationships were investigated across species without attempting to control intra-tree or intraspecific variability. In contrast, the PMT clearly falls within an intraspecific and intra-individual scale.

Second, the different variables considered in the studies lead to different interpretations of the rule. While White (1983*a, b*) considers a representative leaf of the last annual shoot, Brouat *et al.* (1998) consider the total leaf area, justifying their choice by the classical mechanical and hydraulic arguments; Smith *et al.* (2017) consider the average leaf area

with two additional underlying variables (leaf number and total leaf area) that they justify from a leaf carbon economy point of view. Another point of view could be that of Sinnott (1921) in an even earlier work, who suggested that the size of organs that constitute the plant body, such as stem, leaf or fruit, is correlated with the size of the meristem from which they develop. Using maple tree datasets, he found a positive correlation between the volume of leaves present on a node (calculated from the blade surface and thickness) and the surface of the pith of the subtending internode. Sinnott (1921) drew attention to the fact that the pith, as the primary tissue, is a good indicator of the size of the terminal meristem. The pith is therefore more relevant as a variable than an outer diameter because secondary growth occurs early after shoot extension, inducing non-negligible thickening in the part distal from the apical meristem. Adopting this point of view leads us to the general conclusion that works dealing with Corner's law should not be interpreted in the same functional terms as the PMT since, as far as we know, they merely consider the primary diameter of the axis without distinguishing the different tissues that constitute it and the proportion of xylem in particular. It remains unclear to what extent the twig external diameter is linked to the xylem area at inter- and intraspecific scales. Levionnois *et al.* (Sébastien Levionnois, France, unpubl. res.) give some insights into the importance of tissue proportions in the consideration of stem–leaf relationships. They focused on petiole anatomy in *Cecropia* tree megaphylls, considering that the petiole is the first 'pipe'connecting the photosynthetic lamina to the whole plant. After validating a strong correlation between petiole diameter and lamina area, these authors showed that primary xylem is isometrically related to leaf size, whereas secondary xylem is allometrically related. They also demonstrated that, to adapt hydraulic conductivity to different leaf sizes, the xylem adjusts firstly its anatomy, i.e. vessel size and density, rather than its area. On the other hand, most of the petiole diameter variation is afforded by variation in pith size, which constitutes 31.9–59.9 % of whole tissues, theoretically impacting petiole mechanics by increasing the second moment of areas in flexion of more external supporting tissues. Anatomical studies then appear absolutely necessary to better understand the nature of the first premise of Corner's law and its underlying hydraulic and mechanic significance.

APPLICATIONS OF THE PMT

When screening papers that cite the PMT, one is firstly struck by the diversity of derivations of the original theory and the multiplicity of objectives and contexts in which the PMT is used: although, in the original work of Shinozaki *et al.* a precise objective was clearly stated – 'improving the method of indirect estimation of tree biomass in a forest stand' – the PMT has since been extended to additional applications. The PMT has been widely used to model tree growth and several improvements to the pipe model have been suggested from the viewpoints of biomechanics and water conduction.

Leaf area estimation

In their second paper on the PMT Shinozaki *et al.* (1964*b*) further confront their model with experimental data and conclude: 'As an application of the theory in forest ecology, a new method for estimating the amounts of leaves or branches of trees and stands was also proposed, based on the direct proportionality found between those amounts and the cross-sectional area of the trunk at the height just below the lowest living branch'. Although this approach was expected to be more precise than the use of DBH as proposed by Kittredge (1944), it was not used extensively. Several reasons can be noted. First, it quickly became apparent that the A_L:A_S ratio depended not only on the species but also on growing conditions as well as the ontogenetic stage. Second, it is important to note that seeking a relationship between stem diameter and the amount of supplied foliage is questionable from a mechanistic point of view given that secondary growth is a cumulative process in which the diameter increases or stagnates but cannot reduce, whereas leaf area may increase or decrease. For instance, it may show seasonal fluctuations (e.g. Zalamea *et al.*, 2013) or decrease as the result of disturbance events or senescence (Hallé *et al.*, 1978).

Lastly, PMT-based foliage estimations require reaching the base of the crown in order to take core samples in different directions, to determine SW area and to extrapolate this surface to the whole section of the trunk at this level. All of this is a more tedious task than a mere measurement of DBH. Some authors have investigated to what extent the sap area at 1.30 m height or below the crown was more relevant than the total diameter in estimating the leaf area of the crown, with contrasted results. Considering loblolly pine, with DBH ranging from 13 to 43 cm (15–55 years), Baldwin (1989) showed that DBH was as good as or better than SW area at breast height or under the crown to predict foliage weight. Studying seven western conifer species, Kendall Snell and Brown (1978) showed that, for three of them, SW area was a significantly better estimator than DBH for both foliage and branch wood biomass, while for the four others the performances of SW area and DBH as predictors were not significantly different. Therefore, and probably for convenience of experimental measurement, the external diameter of the axes remains the preferential measure used to estimate the associated quantity of leaves in most work. One has thus to keep in mind that this non-destructive approach can be valid, assuming a constant proportion of conductive SW in the stem irrespective of its diameter. An additional problem is that at 1.30 m height butt swelling of the tree is already observable (Hatsch, 1997). Consequently, the use of the outer diameter should at the very least be restricted to branches where HW is not observable making the strong hypothesis that the whole cross-section is conductive. For example, Gehring et al. (2015) tested the applicability of the PMT to chestnut trees in terms of the variability of the ratio between leaf area and external diameter measurements in branches and the whole tree. However, it is important to keep in mind that the validity of this assumption is questionable and may lead to erroneous interpretation of the results.

Tree hydraulics

Mencuccini *et al.* (2011) discussed the PMT in the context of hydraulic models. We will therefore not review this aspect in detail, but instead give a brief overview of how tree hydraulics may provide explanations of the non-scalability of the PMT and the variability of the L parameter. Whitehead and Jarvis (1984) and Whitehead *et al.* (1984) developed a hydraulic model based on a combination of the Penman–Monteith equation (to describe the transpiration rate of a coniferous canopy) and Darcy's law applied to water flux:

$$\frac{A_L}{A_S} = \frac{k_s \Delta \Psi}{l} \cdot \frac{c}{D g_s}$$

where k_s denotes the SW permeability of the hydraulic pathway, $\Delta\psi$ the soil-to-leaf water potential difference including the effect of gravity, l the path length, D the time-averaged vapour pressure deficit of the air, and g_s an appropriately weighted stomatal conductance. The coefficient c is equal to $c=\lambda\gamma\rho_w/(\eta c_p \rho_a)$, where λ denotes the latent heat of vaporization of water, γ the psychrometric constant, ρ_w the density of water, η the dynamic water viscosity, c_p the specific heat of air at constant pressure and ρ_a the density of air. Aside from water viscosity, all of these variables are weakly dependent on temperature. As underlined by McDowell *et al.* (2002), this model is a simplification of tree hydraulics in several aspects as it strictly only applies to cylinders of uniform material and does not account for potential variations of k_s, for instance. However, the equation has drawn increased attention (Mencuccini and Grace, 1995; White *et al.*, 1998; Schäfer *et al.*, 2000; McDowell *et al.*, 2002, 2006; Phillips *et al.*, 2002; Mencuccini, 2003; McDowell and Allen, 2015; Allen *et al.*, 2005). It suggests that the ratio of leaf area to conductive SW area A_L:A_S in trees is proportional to its permeability and to the water potential gradient in the stem, and inversely proportional to the product of the mean vapour pressure deficit of the air at the site and the mean value of g_s (Whitehead *et al.*, 1984). Several authors used this equation as a framework to test hypotheses on the interactions between hydraulic architecture, stomatal conductance and climate. In particular, variations in the A_L:A_S ratio as a compensatory mechanism aiming to alleviate hydraulic limitations to water transport have been studied subject to tree height (parameter l) (Coyea and Margolis, 1992; McDowell *et al.*, 2002), SW permeability (parameter k_s) (Edwards and Jarvis, 1982; Whitehead *et al.*, 1984; Coyea and Margolis, 1992) and site differences in water vapour pressure deficit (parameter D) (Mencuccini and Grace, 1995; McDowell *et al.*, 2006). This model appeared to be a good complementary approach to describing A_L:A_S ratio trends for varying tree sizes and environmental conditions. For example, using tree height as a proxy for the path length from bulk soil to leaf, McDowell *et al.* (2002) hypothesized that, other variables being equal, the decrease in A_L:A_S enables consistently high evaporation levels (g_s) when tree height increases. A potential advantage of a decreasing A_L:A_S ratio with increasing height h is that hydraulic compensation for h may occur, in which g_s is maintained, or reductions in g_s are minimized, as h increases.

Another refinement of the PMT was suggested by Deckmyn *et al.* (2006), who replaced the constant ratio between SW and leaf area by a ratio between pipe conductivity and leaf area. This conductivity is driven by changes in allocation patterns and in pipe radius, which are simulated as functions of age, stand density and climate. In particular, the model calculates the carbon cost of pipes per unit leaf area based on the balance between leaf transpiration and water flow through the conducting tissue. In particular, this balance equation includes pipe radii (simulated on a daily basis with a species-specific parameter of plasticity) and a species-specific parameter representing the ability of trees to compensate for increased height by allocating more carbon to pipes and permitting a switch between the hydraulic limitation model and a model with a constant stem conductance per unit leaf area irrespective of height. Coupled with a simple growth simulator, it made it possible to perform qualitative predictions of seasonal changes in pipe radius (decreasing pipe radius from spring to autumn) and wood density, as well as realistic differences associated with the competitive status of trees (denser wood in suppressed trees). An exact parameterization and a quantitative evaluation of this model, however, are still lacking.

Tree biomechanics

Given that, verbally, Shinozaki *et al.* link the PMT to the hydraulic and mechanical support of foliage in equal measure, it is surprising that comparative studies on the PMT and mechanical theories are rare. A historical exception is a supplement to the PMT that was proposed by Oohata and Shinozaki (1979) 15 years after its initial formulation. The aim of their paper was to quantitatively account for the shape of the trunk below the crown break. While the PMT can be summarized by $C(z) \propto \int_z^{top} \Gamma(z)\, dz$ for $z \geq z_0$, where z_0 denotes crown height, $C(z)$ the amount of non-photosynthetic tissue and $\Gamma(z)$ the foliar density at height z, Oohata and Shinozaki (1979) established $C(z) \propto \int_z^{top} \Gamma(z) + C(z)\, dz$ = 'total plant material [in kg] from the top to stratum z' below the crown, $z < z_0$. Based on this relationship, the authors derive an exponential increase in trunk cross-sectional area from crown break towards stem base. This is interpreted in terms of the mechanical argument that 'the compressive stress is uniform in each layer' and that 'the trunk … is always structured such as to have a vertically constant stress distribution'. The authors attribute the fact that this argument does not seem to apply to branches in the crown to their being oblique rather than vertical. In the light of more recent biomechanical studies, this theory appears simplistic, neglecting, for instance, asymmetrical maturation stress (usually associated with the formation of reaction wood) (Alméras and Clair, 2016) or gravitational disturbance (Almeras and Fournier, 2009). It is worth noting that Oohata and Shinozaki (1979) make no reference whatsoever to the classical PMT's explanation for stem tapering, namely the persistence of disused pipes. Despite the work being presented as a continuation of the PMT, it is, in fact, an unrelated theory. Farnsworth and Van Gardingen (1995) evaluated a mechanical model, based on the work of Niklas (1986), against the PMT, showing that the former conformed well to data on Sitka spruce branches, whereas the PMT did not. They deduce that 'the pipe model branch would not be mechanically compromised but would use structural resources

inefficiently', leading 'to a mechanically over-engineered shoot'. Minamino and Tateno (2014) demonstrated that two biomechanical models that are indirectly related to the PMT, based on the uniform and the elastic similarity hypotheses, respectively, could account for the Leonardo da Vinci's rule in horizontal branches of *Fagus crenata* and *Abies homolepis*. Eloy (2011) argues that neither the PMT nor the elastic similarity hypothesis can explain Leonardo da Vinci's rule. Instead, he proposes that the latter would rather emerge as a consequence of trees being designed to resist wind-induced stresses.

The PMT as an allocation rule in functional–structural modelling

The simple relationship between foliage and SW area postulated by the PMT has enjoyed great popularity among tree growth modellers. The possibility of considering it in a computationally efficient graph framework (Godin, 2000) may have contributed to this. In this section we review the use (and misuse) of Shinozaki *et al.*'s theory in tree modelling. Some of the approaches have previously been listed in the review of carbon-based tree models by Le Roux *et al.* (2001), where models using the PMT are classified in the functional balance category of assimilate allocation modules.

The PMT has been widely used to model the partitioning of growth among foliage, trunk, branch and root compartments in terms of the proportionality of leaf area (or mass) to SW cross-sectional area, as postulated by the PMT. Mäkelä (1986), Hauhs *et al.* (1995), Perttunen *et al.* (1996), Williams (1996), Allen *et al.* (2005), Sterck and Schieving (2007), Prentice *et al.* (1993), Cournède *et al.* (2006), Mathieu *et al.* (2009), Letort *et al.* (2008, 2012) and Beyer *et al.* (2014, 2017*b*) made straightforward use of this principle. We discuss some of these approaches in more detail. The model of Sterck and Schieving (2007) is based on the concept of the leaf–pipe element, a generic leaf along with a living pipe that connects it to the stem base, and which is formed between the stem base and leaf base along with the production of every new leaf. In line with the PMT, the cross-sectional area of each pipe is constant, assuming a constant area of individual leaves. The radii of branches are determined by the number of pipes that they are composed of. Similarly, Beyer *et al.* (2014) and Beyer *et al.* (2017*a, b*), applied the PMT to the partitioning of the amount of biomass that is available locally in the crown for allocation between foliage and respective SW pipes. In line with Sprugel *et al.* (1991), Kurth and Sloboda (1997) introduced the concept of 'branch autonomy', based on the assumption that assimilates can only be allocated along the relevant leaf-to-root pathway, and point to the analogy between this concept and the PMT. In the LIGNUM model (Perttunen *et al.*, 1996), a proportionality between foliage biomass and the cross-sectional area of SW supporting the foliage is assumed, leading to new wood growth being proportional to the net change in foliage above the relevant tree segment. The L-PEACH model (Allen *et al.*, 2005) includes a carbon-allocation model driven by source–sink interactions between tree components, and uses the PMT to quantify the sink associated with girth growth. Subsequent to the calculation of biomass allocated to secondary growth by means of a source–sink approach, Cournède *et al.* (2006) and Mathieu *et al.* (2009) computed the distribution of cambium in the whole-plant architecture using the PMT in the way that the volume of the most recent growth ring is proportional to the number of leaves that are above it. In addition to above-ground structures, Salas *et al.* (2004) linked the PMT to root systems, while van Noordwijk *et al.* (2004) based a fractal model of root geometry on Leonardo da Vinci's rule. As a way to model shoot and root thickness, the PMT can also inform branch and root growth models based on self-avoiding random walks (Bucksch *et al.*, 2014).

Modified or generalized versions of the PMT. Motivated by the limitations associated with the PMT, other authors have proposed modified or generalized versions. Mäkelä (1986) used the PMT to derive coefficients for the partitioning of annual growth among foliage, branch and root compartments. She assumed a proportionality of total leaf dry weight to SW cross-sectional area at the crown base, of primary branches at the foliage base and of roots, but did not assume the appropriate three proportionality constants to be the same. Similarly, Mäkelä (1997) allowed A_L:A_S to vary with whorl age. Hauhs *et al.* (1995) closely followed Mäkelä's (1986) approach. West (1993) applied a modified PMT, in which leaf weight is assumed to be proportional to SW area at breast height multiplied by hydraulic conductivity. Letort *et al.* (2008) described ring growth in terms of a weighted combination of the PMT on the one hand, and on the other hand the common pool concept (Kurth and Sloboda, 1997), which assumes a uniform allocation where biomass production in all leaves contributes equally to growth of all metamers. Valentine (1985) deviated from the original PMT in that the total number of pipes is taken as constant over time. Each pipe can have active and disused portions, the cross-section of the former being assumed to be proportional to the foliar dry matter attached to the pipe. The ratio of active and disused portions is determined by substrate production of the appropriate leaf, constructive and maintenance respiration, and inter-pipe substrate flux. Valentine *et al.* (1997) assumed the cross-sectional area of the trunk at the crown base (the 'active-pipe area') to be proportional to foliar and feeder-root dry matter as well as living, respiring woody dry matter, divided by the average length of stems plus transport roots. The aggregate cross-sectional area of the active pipes changes as new pipes are produced and old pipes are lost.

Transformation of sapwood to heartwood. The PMT links the abscission of leaves and branches with the subsequent deactivation of functioning pipes. The models by Valentine (1988), Sterck and Schieving (2007) and Beyer *et al.* (2014, 2017*a*, *b*) apply this concept to quantify the transformation of SW to HW. In contrast, in the otherwise PMT-based LIGNUM model (Perttunen *et al.*, 1996) and SIMFORG model (Berninger and Nikinmaa, 1997), SW senescence is not associated with the abscission of leaves or shedding of branches. Instead, a certain constant portion of the existing SW is assumed to turn annually into non-functioning HW. Moreover, in both models, when foliage in a tree segment dies, the corresponding part of the original SW area is released for reuse – an idea that does not appear in the PMT either. Mäkelä (1997) essentially used a combination of the previous two approaches: SW turnover in each whorl is driven by both foliage shedding (occurring when current SW area is smaller than the previous year's SW area in a whorl) and ageing (i.e. turnover of a fixed percentage of SW

each year). In the model by Valentine (1985), the ratio of active and disused portions for each pipe is determined by substrate production of the appropriate leaf, constructive and maintenance respiration, and inter-pipe substrate flux. Valentine *et al.* (1997) assumed old pipes to be lost subject to suppression and crown rise.

A consequence of the PMT theoretically derived by Valentine (1985) and Mäkelä (1986) is the limitation of growth in height as the result of increasing maintenance requirements and respiration of longer pipes. Valentine (1985) conclude that 'tall trees with long pipes should be more susceptible to defoliation-induced dieback than short trees because the respirational demand for substrate by a tree increases with pipe length'. Similarly, Gerrish (1988) showed that, under the assumptions of the PMT, the so-called specific leaf burden, the SW mass associated with a unit leaf mass, increases with stem elongation independently of stem diameter, and that this increase could be a factor in natural forest dieback.

In the large majority of models using the PMT, the leaf to SW area ratio is taken as constant. As shown in paragraph 3.4, there is now extensive experimental evidence of the variability of this ratio for different ontogenetic or environmental conditions. Hence, although the PMT is appealing to modellers due to its intellectual elegance and comprehensiveness, it is not unlikely to be inadequate to predict tree growth over time and subject to changing environmental conditions, including disturbances such as pruning and thinning. Although less conceptually simple and more difficult to parameterize and validate – which may explain their restricted use by the tree modelling (and especially functional–structural plant modelling) community to date – sophisticated extensions of the theory such as those based on hydraulic considerations (see Tree hydraulics) appear as a promising way forward.

CONCLUSIONS AND PERSPECTIVES

For half a century, Shinozaki *et al.*'s PMT has appealed to researchers interested in understanding tree form and estimating foliar area from the scale of the individual tree to the forest by means of a simple and intuitive concept based on the functional relationship between functioning wood and foliage. Reviewing a theory as influential as Shinozaki's PMT is a complicated and delicate exercise. Our review does not claim to be exhaustive, especially in view of the numerous and diverse related research areas. We revisited the foundations of the PMT in order to highlight its fundamental properties, underlining some of the discrepancies between them in the context of recent advances in tree anatomy and physiology, in particular with regard to hydraulics (Landsberg *et al.*, 2017) and mechanics.

The non-scalability of the model and possible ways of improvement are discussed by highlighting (1) the differences between the actual structure of the hydraulic systems of trees and the one pictured by Shinozaki and (2) recent advances regarding variation in xylem morphologies (Pfautsch, 2016), as well as the function of HW formation.

We acknowledged the extensive use of the PMT in functional–structural plant modelling as a particularly elegant concept to drive carbon allocation, although the constancy of the proportion parameter *L*, often considered to be the null hypothesis, has to be questioned, especially in simulations with varying environments or disturbances.

Discrepancies between biological knowledge and PMT properties

By examining biological properties one by one, we have seen that there are numerous counterexamples to the PMT that question its validity in arbitrary conditions. For instance, this synthesis highlights that the property of SW area preservation is almost never valid, and neither is Pressler's law (property 1, see Stem, SW and ring tapering) which is strongly linked to the PMT. Common observation of the lateral movement of water within stems shows that the sectoriality property of the PMT is in fact one end of the integration–sectoriality continuum (property 4, Sectoriality and integration of the vascular system of plants). Numerous studies investigating the relationship between the amount of leaves and the amount of SW also show that the essence of the PMT, the ratio of leaf mass to SW cross-sectional area, varies according to several factors, such as the position within the plant and the ontogenetical stage of the individual (properties 1 and 2, see The variability and plasticity of the A_L:A_S ratio and the scalability of the PMT).

Towards several PMTs?

The PMT draws a simple image of tree form and structure that can be considered as a null hypothesis when studying biomass allocation schemes or hydraulic function in various scales: it provides a baseline to analyse to what extent the real processes deviate from these simple rules and a relevant framework to understand the diversity of functional–structural mechanisms at the tree scale. Thus we can sketch a tentative categorization of species according to their PMT-related patterns: integrated/sectorial vascular system, increasing/decreasing pipe ratio with size, increasing/decreasing pipe ratio with height along the stem, ...

This can be illustrated by a parallel with the work of Hallé *et al.* (1978), and their approach to defining architectural models. The architectural model of a plant is based on four major groups of simple morphological features: (1) the growth pattern; (2) the branching pattern; (3) the morphological differentiation of axes; and (4) lateral versus terminal flowering. Each architectural model is defined by a particular combination of these simple morphological features. Although the number of these combinations is theoretically very high, there are apparently only 23 architectural models found in nature. The architectural model expresses the nature and the sequence of activity of endogenous morphogenetic processes of the plant, and corresponds to the fundamental growth principles driving tree architecture (Barthélémy and Caraglio, 2007). Thus, we can ask: is it possible to define classes of 'pipe models' that cover the diversity of tree structure and functioning combining the different properties reviewed in this paper?

PMT and water relations in tree physiology. Although both mechanical and hydraulic aspects were raised by Shinozaki *et al.* to motivate their theory, the latter has attracted much more attention than the former: the balance between transpiration and stem water supply, implied by the PMT, was notably the main aspect studied by other researchers, in turn explaining the predominant use of the PMT in tree growth modelling, physiology or biomass sequestration compared with biomechanics, for instance. Since the 1980s, this interest in the study of the hydraulic functioning of trees has been reinforced by the major need for better understanding and anticipating of the response

of forest ecosystems to climate change. However, the PMT-based theoretical framework is severely limited, from a biological point of view, in its ability to help us understand water relations in tree physiology and should rather be considered only from an allometric point of view as a proposal to interpret the frequently observed linear relationships between leaf mass and stem cross-sectional areas (Mencuccini *et al.*, 2011).

Cruiziat *et al.* (2002) characterizes a general hydraulic system in terms of four key elements: a driving force, a regulator, an assembly of pipes and several reservoirs. The PMT suggests an oversimplified view of the hydraulic system of trees, which in reality is far more complex than a simple collection of independent pipes. In particular, the conductive area represents a variable proportion of a given wood strand (Zimmermann, 1978) that depends on several structural factors, such as vessel density and size (Zimmermann, 1983; Cruiziat *et al.*, 2002). Indeed, since sap flux through a capillary element obeys the Haguen–Poiseuille law, i.e. is proportional to the fourth power of its radius, vessel diameter also plays a key role. Moreover, these structural factors strongly vary within a wood strand. The reservoir, an equally important element of hydraulic systems, especially in big trees (Phillips *et al.*, 2003; Scholz *et al.*, 2011), is not explicitly accounted for at all by the PMT. Water in plants is stored in different places, including organs, tissue, cells and cell walls (Meinzer *et al.*, 2003; Scholz *et al.*, 2007). Considered only in terms of its conductive function in the PMT, SW is in fact the main compartment for water storage (Scholz *et al.*, 2011).

We finally point out that our article does not claim to provide an exhaustive review of recent advances in plant hydraulics but rather adopts a global and historical point of view on the involvement of PMT in this field: interested readers can refer to recent excellent specialized syntheses on plant water relations (Cruiziat *et al.*, 2002; Mencuccini *et al.*, 2011; Landsberg *et al.*, 2017; Venturas *et al.*, 2017).

Considering sapwood multi-functionality. Our review also highlights weaknesses of the PMT with regard to the process of HW formation. Historically, HW formation was first interpreted as a result of SW senescence (Frey-Wyssling and Bosshard, 1959; Ziegler, 1968; Yang, 1990; Wilkes, 1991; Yang *et al.*, 1994) in conjunction with several cytological, physiological and chemical processes (reviewed by Taylor *et al.*, 2002) such as tylose and gum formation, secondary metabolite synthesis and the death of parenchyma cells. The observation of tylosis formation (i.e. the cytoplasmic extension of parenchyma cells in vessel lumina) and gum deposition at the SW/HW boundary (Chattaway, 1949, 1952) led to interpreting HW formation as a process induced by cessation of water transport (Huber, 1928). However, it is also common to observe tylosis inside the SW and relatively far from the SW/HW boundary (Saitoh *et al.*, 1993; De Micco *et al.*, 2016). Moreover, studies highlighting that conductive SW is limited to the outermost growth rings (see part 3.5) demonstrate that SW amount cannot be determined solely on the basis of water relations (Spicer, 2005; Spicer and Holbrook, 2005). Recent advances in the understanding of HW formation (for reviews see Taylor *et al.*, 2002; Kampe and Magel, 2013) strongly support the active nature of this process. The quantity of SW that consumes carbon reserves through respiration is regulated (Bamber, 1976; Bamber and Fukazawa, 1985) by converting the inner layers of the SW, which are often weakly or no longer involved in water conduction but still involved in reserves storage. Thus, both pipe production and deactivation are independent of HW formation processes. Few studies have considered the effectively conducting pipes in PMT-related studies (Mäkelä and Vanninen, 2001; Mäkelä, 2002). When only SW area involved in water transport was considered, the strength of the relationship between foliar area and wood compartment was greatly improved (Rogers and Hinckley, 1979). This shows that it is crucial to differentiate between conductive SW and storage SW, as first argued by Ziegler (1968). However, this distinction has almost never been drawn in PMT-related studies, possibly as a historical result of the then rarely interacting forestry and physiological research and/or to the technical difficulty of measuring conductive SW area.

We suggest that variability in terms of allocation to water conduction or storage within wood strands or total SW area is the main contributor to the non-scalability of the PMT. For instance, knowledge on the variation of quantitative vascular parameters depending on ontogeny (Lachenbruch *et al.*, 2011), position within tree (Anfodillo *et al.*, 2006; Petit *et al.*, 2009) or axis categories (i.e. trunk, branch or twig) (Leigh *et al.*, 2011; Kotowska *et al.*, 2015) offers a potential way to correctly determine sap flux at different radial and longitudinal positions within the plant. Recent findings on variation in the amount of SW in tropical trees highlight that the bulk of SW concentrates in the crown as the result of increasing trunk HW and crown SW increment rates in large trees (Lehnebach *et al.*, 2017). Thus, the proportion of a strand of wood (i.e. a pipe) or of the total amount of SW (i.e. the set of all pipes) that is involved in water conduction strongly depends on ontogeny and vertical position and might explain within-plant variations in A_L:A_S (e.g. Kershaw and Maguire, 1995; Maguire and Batista, 1996; Maguire and Bennett, 1996; Mäkelä and Vanninen, 2001; Schneider *et al.*, 2011) between conspecific individuals of different sizes (McDowell *et al.*, 2002; Phillips *et al.*, 2003).

The PMT in functional–structural plant modelling. Finally, we have seen that the PMT has been widely used in growth models at scales ranging from the individual tree to global vegetation, which aim at a small number of model parameters. While the PMT provides a good first approximation, our ability to quantify foliage–SW partitioning has been greatly improved by more recent empirical findings on the variation of the A_L:A_S ratio, and the residuals not accounted for by the PMT, not only as a function of species but also of tree height and age as well as stand conditions such as stand density or water availability. Accommodating this particular model step by means of empirically based modifications and generalizations of the PMT remains a highly robust approach at the scale of the individual tree and beyond, for which mechanistic models of lateral meristem dynamics would be too complex and parameter-intensive. This leads us to recommend the use of species-, ontogeny- and site-dependent refinements of the PMT, for which extensive empirical data have become available since the publication of Shinozaki *et al.*'s theory.

As a conclusion, the PMT will remain as an exceptional example of an experimentally not-so-valid theory that gave rise to a very rich heritage in terms of applications and derivations in many research fields, still of burning interest today and undoubtedly in the near future at least.

ACKNOWLEDGEMENTS

The authors are grateful to Sébastien Levionnois and the two anonymous reviewers for critical and valuable comments on the manuscript. This research was supported by an Investissements d'Avenir grant by the French National Research Agency (CEBA, ANR-10-LABX-25-01), a PhD scholarship by the Heinrich Böll Foundation and a PhD scholarship from the French agricultural research and international cooperation organization (CIRAD). Author contributions: P.H. and V.L. initiated and managed the project; all the authors participated in the bibliographic review; R.L. and P.H. drafted the sections on plant biology while R.B. and V.L. drafted the sections on modelling. All authors contributed to writing the final manuscript

LITERATURE CITED

Albrektson A. 1984. Sapwood basal area and needle mass of Scots pine (*Pinus sylvestris* L.) Trees in Central Sweden. *Forestry* **57**: 35–43.

Allen MT, **Prusinkiewicz P**, **DeJong TM. 2005**. Using L-systems for modeling source-sink interactions, architecture and physiology of growing trees: the L-PEACH model. *New Phytologist* **166**: 869–880.

Alméras T, **Clair B. 2016**. Critical review on the mechanisms of maturation stress generation in trees. *Journal of The Royal Society Interface* **13**. doi:10.1098/rsif.2016.0550.

Almeras T, **Fournier M. 2009**. Biomechanical design and long-term stability of trees: morphological and wood traits involved in the balance between weight increase and the gravitropic reaction. *Journal of Theoretical Biology* **256**: 370–381.

Amarasekara H, **Denne MP. 2002**. Effects of crown size on wood characteristics of Corsican pine in relation to definitions of juvenile wood, crown formed wood and core wood. *Forestry* **75**: 51–61.

Anfodillo T, **Carraro V**, **Carrer M**, **Fior C**, **Rossi S. 2006**. Convergent tapering of xylem conduits in different woody species. *New Phytologist* **169**: 279–290.

Aussenac G, **Granier A. 1988**. Effects of thinning on water stress and growth in Douglas-fir. *Canadian Journal of Forest Research* **18**: 100–105.

Baldwin VC. 1989. Is sapwood area a better predictor of loblolly pine crown biomass than bole diameter? *Biomass* **20**: 177–185.

Bamber RK. 1976. Heartwood, its function and formation. *Wood Science and Technology* **10**: 1–8.

Bamber RK, **Fukazawa K. 1985**. Sapwood and heartwood: a review. *Forestry Abstracts* **46**: 567–580.

Bancalari ME, **Perry DA**, **Marshall JD. 1987**. Leaf area–sapwood area relationships in adjacent young Douglas-fir stands with different early growth rates. *Canadian Journal of Forest Research* **17**: 174180.

Barnard DM, **Lachenbruch B**, **McCulloh KA**, **Kitin P**, **Meinzer FC. 2013**. Do ray cells provide a pathway for radial water movement in the stems of conifer trees? *American Journal of Botany* **100**: 322–331.

Barnard HR, **Ryan MG. 2003**. A test of the hydraulic limitation hypothesis in fast-growing *Eucalyptus saligna*. *Plant, Cell & Environment* **26**: 1235–1245.

Barthélémy D, **Caraglio Y. 2007**. Plant architecture: a dynamic, multilevel and comprehensive approach to plant form, structure and ontogeny. *Annals of Botany* **99**: 375–407.

Berninger F, **Nikinmaa E. 1997**. Implications of varying pipe model relationships on Scots pine growth in different climates. *Functional Ecology* **11**: 146–156.

Berthier S, **Kokutse AD**, **Stokes A**, **Fourcaud T. 2001**. Irregular heartwood formation in maritime pine (*Pinus pinaster* Ait): consequences for biomechanical and hydraulic tree functioning. *Annals of Botany* **87**: 19–25.

Bevilacqua E, **Puttock D**, **Blake TJ**, **Burgess D. 2005**. Long-term differential stem growth responses in mature eastern white pine following release from competition. *Canadian Journal of Forest Research* **35**: 511–520.

Béland M, **Baldocchi DD**, **Widlowski J-L**, **Fournier RA**, **Verstraete MM. 2014**. On seeing the wood from the leaves and the role of voxel size in determining leaf area distribution of forests with terrestrial LiDAR. *Agricultural and Forest Meteorology* **184**: 82–97.

Beyer R, **Letort V**, **Cournède P-H. 2014**. Modeling tree crown dynamics with 3D partial differential equations. *Frontiers in Plant Science* **5**: 329.

Beyer R, **Bayer D**, **Letort V**, **Pretzsch H**, **Cournède P-H. 2017*a***. Validation of a functional-structural tree model using terrestrial Lidar data. *Ecological Modelling* **357**: 55–57.

Beyer R, **Letort V**, **Bayer D**, **Pretzsch H**, **Cournède P-H. 2017*b***. Leaf density-based modelling of phototropic crown dynamics and long-term predictive application to European beech. *Ecological Modelling* **347**: 63–71.

Binkley D. 1984. Notes: Douglas-fir stem growth per unit of leaf area increased by interplanted sitka alder and red alder. *Forest Science* **30**: 259–263.

Björklund L. 1999. Identifying heartwood-rich stands or stems of *Pinus sylvestris* by using inventory data. *Silva Fennica* **33**: 119–129.

Bouriaud O, **Bréda N**, **Dupouey J-L**, **Granier A. 2005**. Is ring width a reliable proxy for stem-biomass increment? A case study in European beech. *Canadian Journal of Forest Research* **35**: 2920–2933.

Brix H, **Mitchell AK. 1983**. Thinning and nitrogen fertilization effects on sapwood development and relationships of foliage quantity to sapwood area and basal area in Douglas-fir. *Canadian Journal of Forest Research* **13**: 384–389.

Brooks RJ, **Schulte PJ**, **Bond BJ**, ***et al.* 2003**. Does foliage on the same branch compete for the same water? Experiments on Douglas-fir trees. *Trees – Structure and Function* **17**: 101–108.

Brouat C, **McKey D. 2001**. Leaf-stem allometry, hollow stems, and the evolution of caulinary domatia in myrmecophytes. *New Phytologist* **151**: 391–406.

Brouat C, **Gibernau M**, **Amsellem L**, **McKey D. 1998**. Corner's rules revisited: ontogenetic and interspecific patterns in leaf–stem allometry. *New Phytologist* **139**: 459–470.

Bucksch A, **Turk G**, **Weitz JS. 2014**. The fiber walk: a model of tip-driven growth with lateral expansion. *PLoS ONE* **9**: e85585.

Carlquist S. 1984. Vessel grouping in dicotyledon wood: significance and relationship to imperforate tracheary elements. *Aliso* **10**: 505–525.

Carvalho MR, **Turgeon R**, **Owens T**, **Niklas KJ. 2017*a***. The hydraulic architecture of ginkgo leaves. *American Journal of Botany* **104**: 1285–1298.

Carvalho MR, **Turgeon R**, **Owens T**, **Niklas KJ. 2017*b***. The scaling of the hydraulic architecture in poplar leaves. *New Phytologist* **214**: 145–157.

Čermák J, **Cienciala E**, **Kučera J**, **Hällgren J-E. 1992**. Radial velocity profiles of water flow in trunks of Norway spruce and oak and the response of spruce to severing. *Tree Physiology* **10**: 367–380.

Chattaway M. 1949. The development of tyloses and secretion of gum in heartwood formation. *Australian Journal of Biological Sciences* **2**: 227–240.

Chattaway M. 1952. The heartwood-sapwood transition. *Australian Forestry* **16**: 25–34.

Chave J, **Andalo C**, **Brown S**, ***et al.* 2005**. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia* **145**: 87–99.

Chen H, **Niklas KJ**, **Sun S. 2012**. Testing the packing rule across the twig–petiole interface of temperate woody species. *Trees* **26**: 1737–1745.

Chiba Y. 1991. Plant form based on the pipe model theory II. Quantitative analysis of ramification in morphology. *Ecological Research* **6**: 21–28.

Cienciala E, **Černý M**, **Tatarinov F**, **Apltauer J**, **Exnerová Z. 2006**. Biomass functions applicable to Scots pine. *Trees – Structure and Function* **20**: 483–495.

Climent J, **Chambel MR**, **Gil L**, **Pardos JA. 2003**. Vertical heartwood variation patterns and prediction of heartwood volume in *Pinus canariensis* Sm. *Forest Ecology and Management* **174**: 203–211.

Cochard H, **Tyree MT. 1990**. Xylem dysfunction in *Quercus*: vessel sizes, tyloses, cavitation and seasonal changes in embolism. *Tree Physiology* **6**: 393–407.

Cornelissen JHC, **Lavorel S**, **Garnier E**, ***et al.* 2003**. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* **51**: 335–380.

Corner EJH. 1949. The durian theory or the origin of the modern tree. *Annals of Botany* **13**: 367–414.

Cortini F, **Groot A**, **Filipescu CN. 2013**. Models of the longitudinal distribution of ring area as a function of tree and stand attributes for four major Canadian conifers. *Annals of Forest Science* **70**: 637–648.

Courbet F. 1999. A three-segmented model for the vertical distribution of annual ring area: application to *Cedrus atlantica* Manetti. *Forest Ecology and Management* **119**: 177–194.

Cournède P-H, **Kang M-Z**, **Mathieu A**, ***et al.* 2006**. Structural factorization of plants to compute their functional and architectural growth. *Simulation* **82**: 427–438.

Coyea MR, **Margolis HA. 1992**. Factors affecting the relationship between sapwood area and leaf area of balsam fir. *Canadian Journal of Forest Research* **22**: 1684–1693.

Cruickshank MG, **Cameron IR**, **Groot A**, **Stewart JD**, **Goudie JW. 2015**. Models of the vertical distribution of sapwood area for lodgepole pine and western hemlock in western Canada. *Forest Science* **61**: 973–987.

Cruiziat P, **Cochard H**, **Améglio T. 2002**. Hydraulic architecture of trees: main concepts and results. *Annals of Forest Science* **59**: 723–752.

David TS, **David JS**, **Pinto CA**, **Cermak J**, **Nadezhdin V**, **Nadezhdina N. 2012**. Hydraulic connectivity from roots to branches depicted through sap flow: analysis on a *Quercus suber* tree. *Functional Plant Biology* **39**: 103–115.

Dean TJ, **Long JN**, **Smith FW. 1988**. Bias in leaf area–sapwood area ratios and its impact on growth analysis in *Pinus contorta*. *Trees – Structure and Function* **2**: 104–109.

Deckmyn G, **Evans SP**, **Randle TJ. 2006**. Refined pipe theory for mechanistic modeling of wood development. *Tree Physiology* **26**: 703–17.

Deleuze C, **Houllier F. 1995**. Prediction of stem profile of *Picea abies* using a process-based tree growth model. *Tree Physiology* **15**: 113–20.

Deleuze C, **Houllier F. 2002**. A flexible radial increment taper equation derived from a process-based carbon partitioning model. *Annals of Forest Science* **59**: 141–154.

Delzon S, **Sartore M**, **Burlett R**, **Dewar R**, **Loustau D. 2004*a***. Hydraulic responses to height growth in maritime pine trees. *Plant, Cell & Environment* **27**: 1077–1087.

Delzon S, **Sartore M**, **Granier A**, **Loustau D. 2004*b***. Radial profiles of sap flow with increasing tree size in maritime pine. *Tree Physiology* **24**: 1285–1293.

Dhôte J-F, **Hatsch E**, **Rittié D. 1997**. Profil de la tige et géométrie de l'aubier chez le chêne sessile (*Quercus petraea* Liebl). *Bulletin Technique – Office National des Forêts* **33**: 59–81.

Dhôte J-F, **Hatsch E**, **Rittié D. 2000**. Forme de la tige, tarifs de cubage et ventilation de la production en volume chez le chêne sessile. *Annals of Forest Science* **57**: 121–142.

Domec JC, **Gartner BL. 2002**. Age- and position-related changes in hydraulic versus mechanical dysfunction of xylem: inferring the design criteria for Douglas-fir wood structure. *Tree Physiology* **22**: 91–104.

Edwards WRN, **Jarvis PG. 1982**. Relations between water content, potential and permeability in stems of conifers. *Plant, Cell & Environment* **5**: 271–277.

Ellmore GS, **Ewers FW. 1985**. Hydraulic conductivity in trunk xylem of elm, *Ulmus americana*. *IAWA Journal* **6**: 303–307.

Ellmore GS, **Ewers FW. 1986**. Fluid flow in the outermost xylem increment of a ring-porous tree, *Ulmus americana*. *American Journal of Botany* **73**: 1771–1774.

Ellmore GS, **Zanne AE**, **Orians CM. 2006**. Comparative sectoriality in temperate hardwoods: hydraulics and xylem anatomy. *Botanical Journal of the Linnean Society* **150**: 61–71.

Eloy C. 2011. Leonardo's rule, self-similarity, and wind-induced stresses in trees. *Physical Review Letters* **107**: 258101.

Espino S, **Schenk HJ. 2009**. Hydraulically integrated or modular? Comparing whole-plant-level hydraulic systems between two desert shrub species with different growth forms. *New Phytologist* **183**: 142–152.

Ewers BE, **Gower ST**, **Bond-Lamberty B**, **Wang CK. 2005**. Effects of stand age and tree species on canopy transpiration and average stomatal conductance of boreal forests. *Plant, Cell & Environment* **28**: 660–678.

Farnsworth KD, **Van Gardingen PR. 1995**. Allometric analysis of Sitka spruce branches: mechanical versus hydraulic design principles. *Trees – Structure and Function* **10**: 1–12.

Farrar J. 1961. Longitudinal variation in the thickness of the annual ring. *Forestry Chronicle* **37**: 323–349.

Feldpausch TR, **Banin L**, **Phillips OL**, ***et al.*** **2011**. Height-diameter allometry of tropical forest trees. *Biogeosciences* **8**: 1081–1106.

Fischer DG, **Kolb TE**, **DeWald LE. 2002**. Changes in whole-tree water relations during ontogeny of *Pinus flexilis* and *Pinus ponderosa* in a high-elevation meadow. *Tree Physiology* **22**: 675–685.

Fourcaud T, **Zhang X**, **Stokes A**, **Lambers H**, **Korner C. 2008**. Plant growth modelling and applications: the increasing importance of plant architecture in growth models. *Annals of Botany* **101**: 1053–1063.

Frey-Wyssling A, **Bosshard AA. 1959**. Cytology of the ray cells in sapwood and heartwood. *Holzforschung* **13**: 129–137.

Fromm JH, **Sautter I**, **Matthies D**, **Kremer J**, **Schumacher P**, **Ganter C. 2001**. Xylem water content and wood density in spruce and oak trees detected by high-resolution computed tomography. *Plant Physiology* **127**: 416–425.

Gallant AR, **Fuller WA. 1973**. Fitting segmented polynomial regression models whose join points have to be estimated. *Journal of the American Statistical Association* **68**: 144–147.

Garber SM, **Maguire DA. 2005**. The response of vertical foliage distribution to spacing and species composition in mixed conifer stands in central Oregon. *Forest Ecology and Management* **211**: 341–355.

Gartner BL. 1991. Stem hydraulic properties of vines vs. shrubs of western poison oak, *Toxicodendron diversilobum*. *Oecologia* **87**: 180–189.

Gartner BL. 1995. Patterns of xylem variation within a tree and their hydraulic and mechanical consequences. In: Gartner BL, ed. *Plant stems*. San Diego: Academic Press, 125–149.

Gartner BL, **Moore JR**, **Gardiner BA. 2004**. Gas in stems: abundance and potential consequences for tree biomechanics. *Tree Physiology* **24**: 1239–1250.

Gehring E, **Pezzatti GB**, **Krebs P**, **Mazzoleni S**, **Conedera M. 2015**. On the applicability of the pipe model theory on the chestnut tree (*Castanea sativa* Mill.). *Trees – Structure and Function* **29**: 321–332.

Gerrish G. 1988. An explanation of natural forest dieback based on the "pipe model" analogy. *GeoJournal* **17**: 295–299.

Gerrish G. 1990. Relating carbon allocation patterns to tree senescence in *Metrosideros* forests. *Ecology* **71**: 1176–1184.

Gjerdrum P, **Høibø O. 2004**. Heartwood detection in Scots pine by means of heat-sensitive infrared images. *Holz als Roh- und Werkstoff* **62**: 131–136.

Godin C. 2000. Representing and encoding plant architecture: a review. *Annals of Forest Science* **57**: 413–438.

Gominho J, **Pereira H. 2005**. The influence of tree spacing in heartwood content in *Eucalyptus globulus* Labill. *Wood and Fiber Science* **37**: 582–590.

Gould SJ. 1977. *Ontogeny and phylogeny*. Cambridge, MA: Harvard University Press.

Gower ST, **Kucharik CJ**, **Norman JM. 1999**. Direct and indirect estimation of leaf area index, fapar, and net primary production of terrestrial ecosystems. *Remote Sensing of Environment* **70**: 29–51.

Granier A. 1981. Etude des relations entre la section du bois d'aubier et la masse foliaire chez le Douglas (*Pseudotsuga menziesii* Mirb. Franco). *Annals of Forest Science* **38**: 503–512.

Granier A. 1987. Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. *Tree Physiology* **3**: 309–320.

Grier CC, **Waring RH. 1974**. Notes: Conifer foliage mass related to sapwood area. *Forest Science* **20**: 205–206.

Groot A, **Saucier J-P. 2008**. Volume increment efficiency of Picea mariana in northern Ontario, Canada. *Forest Ecology and Management* **255**: 1647–1653.

Hall GS. 1965. Wood increment and crown distribution relationships in red pine. *Forest Science* **11**: 438–448.

Hallé F. 1991. Le bois constituant un tronc peut-il être d'origine racinaire? In: Edelin C, ed. *Colloque International sur l'Arbre*. Montpellier: Naturalia monspeliensa.

Hallé F, **Oldeman RAA**, **Tomlinson PB. 1978**. *Tropical trees and forests: an architectural analysis*. New York: Springer.

Hatsch E. 1997. *Répartition de l'aubier et acquisition de la forme de la tige chez le chêne sessile (Quercus petraea (Matt) Liebl): analyse, modélisation et relation avec le développement du houppier*. PhD Thesis, Ecole Nationale du Génie Rural, des Eaux et des Forêts, France.

Hauhs M, **Kastner-Maresch A**, **Rost-Siebert K. 1995**. A model relating forest growth to ecosystem-scale budgets of energy and nutrients. *Ecological Modelling* **83**: 229–243.

Herrera CM. 2009. *Multiplicity in unity: plant subindividual variation and interactions with animals*. Chicago: University of Chicago Press.

Hillis WE. 1977. Secondary changes in wood. In: Loewus F, Runeckles VC, eds. *The structure, biosynthesis, and degradation of wood*. Boston: Springer, 247–309.

Hillis WE. 1987. *Heartwood and tree exudates*. Berlin: Springer.

Holtta T, **Kurppa M**, **Nikinmaa E. 2013**. Scaling of xylem and phloem transport capacity and resource usage with tree size. *Frontiers in Plant Science* **4**: 496.

Horn HS. 2000. Twigs, trees, and the dynamics of carbon in the landscape. In: Brown JH, West GB, eds. *Scaling in biology*. Oxford: Oxford University Press, 199–220.

Hosoi F, **Omasa K. 2006**. Voxel-based 3-D modeling of individual trees for estimating leaf area density using high-resolution portable scanning lidar. *IEEE Transactions on Geoscience and Remote Sensing* **44**: 3610–3618.

Houllier F, **Leban J-M**, **Colin F. 1995**. Linking growth modelling to timber quality assessment for Norway spruce. *Forest Ecology and Management* **74**: 91–102.

Huber B. 1928. Weitere quantitative Untersuchungen über das Wasserleitungssystem der Pflanzen. *Jahrbücher für wissenschaftliche Botanik* **67**: 877–959.

Huber B, **Schmidt E. 1937**. Eine Kompensationsmethode zur thermoelektrischen Messung langsamer Saftströme. *Berichte der Deutschen Botanischen Gesellschaft* **55**: 514–529.

Huxley JS. 1924. Constant differential growth-ratios and their significance. *Nature* **114**: 895–896.

Infante JM, **Mauchamp A**, **Fernandez-Ale R**, **Joffre R**, **Rambal S. 2001**. Within-tree variation in transpiration in isolated evergreen oak trees: evidence in support of the pipe model theory. *Tree Physiology* **21**: 409–414.

James SA, **Clearwater MJ**, **Meinzer FC**, **Goldstein G. 2002**. Heat dissipation sensors of variable length for the measurement of sap flow in trees with deep sapwood. *Tree Physiology* **22**: 277–283.

Jelonek T, **Pazdrowski W**, **Arasimowicz M**, **Tomczak A**, **Walkowiak R**, **Szaban J. 2008**. The applicability of the pipe model theory in trees of Scots pine of Poland. *Journal of Forest Science* **54**: 519–531.

Johansson J, **Hagman O**, **Fjellner B-A. 2003**. Predicting moisture content and density distribution of Scots pine by microwave scanning of sawn timber. *Journal of Wood Science* **49**: 312–316.

Kampe A, **Magel E. 2013**. New insights into heartwood and heartwood formation. In: Fromm J, ed. *Cellular aspects of wood formation*. Berlin: Springer, 71–95.

Kantola A, **Mäkelä A. 2004**. Crown development in Norway spruce [*Picea abies* (L.) Karst.]. *Trees – Structure and Function* **18**: 408–421.

Kaufmann MR, **Troendle CA. 1981**. The relationship of leaf area and foliage biomass to sapwood conducting area in four subalpine forest tree species. *Forest Science* **27**: 477–482.

Kendall Snell JA, **Brown JK. 1978**. Notes: comparison of tree biomass estimators – DBH and sapwood area. *Forest Science* **24**: 455–457.

Kershaw JA. 2001. Reply: Influence of vertical foliage structure on the distribution of stem cross-sectional area increment in western hemlock and balsam fir [Forest Science 46: 86–94]. *Forest Science* **47**: 117–118.

Kershaw JA, **Maguire DA. 1995**. Crown structure in western hemlock, Douglas-fir, and grand fir in western Washington: trends in branch-level mass and leaf area. *Canadian Journal of Forest Research* **25**: 1897–1912.

Kershaw A, **Maguire A. 2000**. Influence of vertical foliage structure on the distribution of stem cross-sectional area increment in western hemlock and balsam fir. *Forest Science* **46**: 86–94.

Kittredge J. 1944. Estimation of the amount of foliage of trees and stands. *Journal of Forestry* **42**: 905–912.

Klingenberg CP. 1998. Heterochrony and allometry: the analysis of evolutionary change in ontogeny. *Biological Reviews* **73**: 79–123.

Knapic S, **Pereira H. 2005**. Within-tree variation of heartwood and ring width in maritime pine (*Pinus pinaster* Ait.). *Forest Ecology and Management* **210**: 81–89.

Knapic S, **Tavares F**, **Pereira H. 2006**. Heartwood and sapwood variation in *Acacia melanoxylon* R. Br. trees in Portugal. *Forestry* **79**: 371–380.

Kostner B, **Falge E**, **Tenhunen JD. 2002**. Age-related effects on leaf area/ sapwood area relationships, canopy transpiration and carbon gain of Norway spruce stands (*Picea abies*) in the Fichtelgebirge, Germany. *Tree Physiology* **22**: 567–574.

Kotowska MM, **Hertel D**, **Rajab YA**, **Barus H**, **Schuldt B. 2015**. Patterns in hydraulic architecture from roots to branches in six tropical tree species from cacao agroforestry and their relation to wood density and stem growth. *Frontiers in Plant Science* **6**: 191.

Kurth W, **Sloboda B. 1997**. Growth grammars simulating trees – an extension of L-systems incorporating local variables and sensitivity. *Silva Fennica* **31**: 285–295.

Kutscha NP, **Sachs IB. 1962**. *Color tests for differentiating heartwood and sapwood in certain softwood tree species*. Forest products Laboratory Reports 2246, USDA, Forest Service.

Lachenbruch B, **McCulloh KA. 2014**. Traits, properties, and performance: how woody plants combine hydraulic and mechanical functions in a cell, tissue, or whole plant. *New Phytologist* **204**: 747–764.

Lachenbruch B, **Moore J**, **Evans R. 2011**. Radial variation in wood structure and function in woody plants, and hypotheses for its occurrence. In: Meinzer FC, Lachenbruch B, Dawson TE, eds. *Size- and age-related changes in tree structure and function*. Berlin: Springer, 121–164.

Landsberg J, **Waring R**, **Ryan M. 2017**. Water relations in tree physiology: where to from here? *Tree Physiology* **37**: 18–32.

Landsberg JJ, **Gower ST**, **Roy J. 1997**. *Applications of physiological ecology to forest management*. San Diego: Academic Press.

Larson DW, **Doubt J**, **Matthes-Sears U. 1994**. Radially sectored hydraulic pathways in the xylem of *Thuja occidentalis* as revealed by the use of dyes. *International Journal of Plant Sciences* **155**: 569–582.

Larson PR. 1963. Stem form development of forest trees. *Forest Science Monograph* **5**: 42.

Le Roux X, **Lacointe A**, **Escobar-Gutiérrez A**, **Le Dizès S. 2001**. Carbon-based models of individual tree growth: a critical appraisal. *Annals of Forest Science* **58**: 469–506.

Lehnebach R, **Morel H**, **Bossu J**, ***et al.* 2017**. Heartwood/sapwood profile and the tradeoff between trunk and crown increment in a natural forest: the case study of a tropical tree (*Dicorynia guianensis* Amsh., Fabaceae). *Trees – Structure and Function* **31**: 199–214.

Leigh A, **Zwieniecki MA**, **Rockwell FE**, **Boyce CK**, **Nicotra AB**, **Holbrook NM. 2011**. Structural and hydraulic correlates of heterophylly in *Ginkgo biloba*. *New Phytologist* **189**: 459–470.

Lemke J. 1966. Korona jako jedno z kryteriów wyboru drzew próbnych przy oznaczaniu bieżącego przyrostu miąższości drzewostanu. *Folia Forestalia Polonica* **12**: 237–247.

Letort V, **Cournède P-H**, **Mathieu A**, **De Reffye P**, **Constant T. 2008**. Parametric identification of a functional-structural tree growth model and application to beech trees (*Fagus sylvatica*). *Functional Plant Biology* **35**: 951–963.

Letort V, **Heuret P**, **Zalamea P-C**, **De Reffye P**, **Nicolini E. 2012**. Analysing the effects of local environment on the source-sink balance of *Cecropia sciadophylla*: a methodological approach based on model inversion. *Annals of Forest Science* **69**: 167–180.

Long JN, **Smith FW. 1988**. Leaf area–sapwood area relations of lodgepole pine as influenced by stand density and site index. *Canadian Journal of Forest Research* **18**: 247–250.

Long JN, **Smith FW**, **Scott DRM. 1981**. The role of Douglas-fir stem sapwood and heartwood in the mechanical and physiological support of crowns and development of stem form. *Canadian Journal of Forest Research* **11**: 459–464.

Longuetaud F, **Mothe F**, **Leban J-M**, **Mäkelä A. 2006**. *Picea abies* sapwood width: variations within and between trees. *Scandinavian Journal of Forest Research* **21**: 41–53.

Longuetaud F, **Mothe F**, **Leban J-M. 2007**. Automatic detection of the heartwood/sapwood boundary within Norway spruce (*Picea abies* (L.) Karst.) logs by means of CT images. *Computers and Electronics in Agriculture* **58**: 100–111.

Lopez-Bernal A, **Alcantara E**, **Testi L**, **Villalobos FJ. 2010**. Spatial sap flow and xylem anatomical characteristics in olive trees under different irrigation regimes. *Tree Physiology* **30**: 1536–1544.

MacDougal DT, **Overton JB**, **Smith GM. 1929**. *The hydrostatic-pneumatic system of certain trees: movements of liquids and gases*. Washington: Carnegie Institution of Washington.

Magnani F, **Mencuccini M**, **Grace J. 2000**. Age-related decline in stand productivity: the role of structural acclimation under hydraulic constraints. *Plant, Cell & Environment* **23**: 251–263.

Maguire DA, **Batista JLF. 1996**. Sapwood taper models and implied sapwood volume and foliage profiles for coastal Douglas-fir. *Canadian Journal of Forest Research* **26**: 849–863.

Maguire DA, **Bennett WS. 1996**. Patterns in vertical distribution of foliage in young coastal Douglas-fir. *Canadian Journal of Forest Research* **26**: 1991–2005.

Mäkelä A. 1986. Implications of the pipe model theory on dry matter partitioning and height growth in trees. *Journal of Theoretical Biology* **123**: 103–120.

Mäkelä A. 1997. A carbon balance model of growth and self-pruning in trees based on structural relationships. *Forest Science* **43**: 7–24.

Mäkelä A. 2002. Derivation of stem taper from the pipe theory in a carbon balance framework. *Tree Physiology* **22**: 891–905.

Mäkelä A, **Vanninen P. 2001**. Vertical structure of Scots pine crowns in different age and size classes. *Trees – Structure and Function* **15**: 385–392.

Marchand PJ. 1984. Sapwood area as an estimator of foliage biomass and projected leaf area for *Abiesbalsamea* and *Picearubens*. *Canadian Journal of Forest Research* **14**: 85–87.

Mathieu A, **Cournede PH**, **Letort V**, **Barthelemy D**, **de Reffye P. 2009**. A dynamic model of plant growth with interactions between development and functional mechanisms to study plant structural plasticity related to trophic competition. *Annals of Botany* **103**: 1173–1186.

Maton C, **Gartner BL. 2005**. Do gymnosperm needles pull water through the xylem produced in the same year as the needle? *American Journal of Botany* **92**: 123–131.

McCulloh KA, **Sperry JS**, **Adler FR. 2003**. Water transport in plants obeys Murray's law. *Nature* **421**: 939–942.

McDowell N, **Barnard H**, **Bond B**, ***et al.*** **2002**. The relationship between tree height and leaf area:sapwood area ratio. *Oecologia* **132**: 12–20.

McDowell NG, **Allen CD. 2015**. Darcy's law predicts widespread forest mortality under climate warming. *Nature Climate Change* **5**: 669–672.

McDowell NG, **Adams HD**, **Bailey JD**, **Hess M**, **Kolb TE. 2006**. Homeostatic maintenance of ponderosa pine gas exchange in response to stand density changes. *Ecological Applications* **16**: 1164–1182.

Medhurst JL, **Beadle CL. 2002**. Sapwood hydraulic conductivity and leaf area–sapwood area relationships following thinning of a *Eucalyptus nitens* plantation. *Plant, Cell & Environment* **25**: 1011–1019.

Meinzer FC, **James SA**, **Goldstein G**, **Woodruff D. 2003**. Whole-tree water transport scales with sapwood capacitance in tropical forest canopy trees. *Plant, Cell & Environment* **26**: 1147–1155.

Mencuccini M. 2003. The ecological significance of long-distance water transport: short-term regulation, long-term acclimation and the hydraulic costs of stature across plant life forms. *Plant, Cell & Environment* **26**: 163–182.

Mencuccini M, **Grace J. 1995**. Climate influences the leaf area/sapwood area ratio in Scots pine. *Tree Physiology* **15**: 1–10.

Mencuccini M, **Hölttä T**, **Martinez-Vilalta J. 2011**. Comparative criteria for models of the vascular transport systems of tall trees. In: Meinzer FC, Lachenbruch B, Dawson TE, eds. *Size- and age-related changes in tree structure and function*. Berlin: Springer, 309–339.

De Micco V, **Balzano A**, **Wheeler EA**, **Baas P. 2016**. Tyloses and gums: a review of structure, function and occurrence of vessel occlusions. *IAWA Journal* **37**: 186–205.

Minamino R, **Tateno M. 2014**. Tree branching: Leonardo da Vinci's Rule versus biomechanical models. *PLoS ONE* **9**: e93535. doi.org/10.1371/journal.pone.0093535.

Miranda I, **Gominho J**, **Lourenço A**, **Pereira H. 2006**. The influence of irrigation and fertilization on heartwood and sapwood contents in 18-year-old *Eucalyptus globulus* trees. *Canadian Journal of Forest Research* **36**: 2675–2683.

Mitchell KJ. 1975. Dynamics and simulated yield of Douglas-fir. *Forest Science Monograph* **17**.

Mokany K, **McMurtrie RE**, **Atwell BJ**, **Keith H. 2003**. Interaction between sapwood and foliage area in alpine ash (*Eucalyptus delegatensis*) trees of different heights. *Tree Physiology* **23**: 949–958.

Monserud RA, **Marshall JD. 1999**. Allometric crown relations in three northern Idaho conifer species. *Canadian Journal of Forest Research* **29**: 521–535.

Monsi M, **Saeki T. 1953**. Uber den Lichtfaktor in den Pflanzengesellschaften und seine Bedeutung fur die Stoffproduktion. *Japanese Journal of Botany* **14**: 22–52.

Monsi M, **Saeki T. 2005**. On the factor light in plant communities and its importance for matter production. *Annals of Botany* **95**: 549–567.

Morais MC, **Pereira H. 2007**. Heartwood and sapwood variation in *Eucalyptus globulus* Labill. trees at the end of rotation for pulp wood production. *Annals of Forest Science* **64**: 665–671.

Morataya R, **Galloway G**, **Berninger F**, **Kanninen M. 1999**. Foliage biomass-sapwood (area and volume) relationships of *Tectona grandis* L.F. and *Gmelina arborea* Roxb.: silvicultural implications. *Forest Ecology and Management* **113**: 231–239.

Mörling T, **Valinger E. 1999**. Effects of fertilization and thinning on heartwood area, sapwood area and growth in Scots pine. *Scandinavian Journal of Forest Research* **14**: 462–469.

Nadezhdina N. 2010. Integration of water transport pathways in a maple tree: responses of sap flow to branch severing. *Annals of Forest Science* **67**: p. 107. https://link.springer.com/article/10.1051/forest/2009092

Nadezhdina N, **Nadezhdin V**, **Gebauer R**, ***et al.*** **2012**. Redistribution of water within the aboveground part of trees. *Acta Horticulturae* **951**: 241–249. doi: 10.17660/ActaHortic.2012.951.29.

Nadezhdina N, **David TS**, **David JS**, **Nadezhdin V**, **Pinto CA. 2013**. Mapping the water pathways in stemp xylem by sap flow measurements during branch severing experiments. *Acta Horticulturae* **991**: 223–230. doi: 10.17660/ActaHortic.2013.991.27.

Nikinmaa E. 1992. Analyses of the growth of Scots pine: matching structure with function. *Acta Forestalia Fennica* **235**: 1–68.

Niklas KJ. 1986. Computer simulations of branching-patterns and their implications on the evolution of plants. *Lectures on mathematics in the life sciences* **18**: 1–50.

Niklas KJ. 1994. *Plant allometry: the scaling of form and process*. Chicago: University of Chicago Press.

Niklas KJ, **Enquist BJ. 2002**. Canonical rules for plant organ biomass partitioning and annual allocation. *American Journal of Botany* **89**: 812–819.

van Noordwijk M, **Rahayu S**, **Williams SE**, **Hariah K**, **Khasanah NM**, **Schroth G. 2004**. Crop and tree root-system dynamics. In: van Noordwijk M, Cadisch G, Ong C, eds. *Below-ground interactions in tropical agro-ecosystems – concepts and models with multiple plant components*. Wallingford: CABI Publishing, 83–108.

Normand F, **Bissery C**, **Damour G**, **Lauri PE. 2008**. Hydraulic and mechanical stem properties affect leaf-stem allometry in mango cultivars. *New Phytologist* **178**: 590–602.

Ogawa K. 2015. Mathematical consideration of the pipe model theory in woody plant species. *Trees – Structure and Function* **29**: 695–704.

Ojansuu R, **Maltamo M. 1995**. Sapwood and heartwood taper in Scots pine stems. *Canadian Journal of Forest Research* **25**: 1928–1943.

Oohata S, **Shinozaki K. 1979**. A statical model of plant form – further analysis of the pipe model theory. *Japanese Journal of Ecology* **29**: 323–335.

Oppelt AL, **Kurth W**, **Godbold DL. 2001**. Topology, scaling relations and Leonardo's rule in root systems from African tree species. *Tree Physiology* **21**: 117–128.

Orians CM, **van Vuuren MMI**, **Harris NL**, **Babst BA**, **Ellmore GS. 2004**. Differential sectoriality in long-distance transport in temperate tree species: evidence from dye flow, 15N transport, and vessel element pitting. *Trees – Structure and Function* **18**: 501–509.

Orians CM, **Babst B**, **Zanne AE. 2005*a***. Vascular constraints and long distance transport in dicots. In: Holbrook NM, Zwieniecki MA, eds. *Vascular transport in plants*. Burlington, MA: Academic Press, 355–371.

Orians CM, **Smith SD**, **Sack L. 2005*b***. How are leaves plumbed inside a branch? Differences in leaf-to-leaf hydraulic sectoriality among six temperate tree species. *Journal of Experimental Botany* **56**: 2267–2273.

Osawa A, **Ishizuka M**, **Kanazawa Y. 1991**. A profile theory of tree growth. *Forest Ecology and Management* **41**: 33–63.

Ottorini J. 1991. Growth and development of individual Douglas-fir in stands for applications to simulation in silviculture. *Annals of Forest Science* **48**: 651–666.

Ottorini J, **Le Goff N**, **Cluzeau C. 1996**. Relationships between crown dimensions and stem development in *Fraxinus excelsior*. *Canadian Journal of Forest Research* **26**: 394–401.

Pagès L, **Vercambre G**, **Drouet J-L**, **Lecompte F**, **Collet C**, **Le Bot J. 2004**. Root Typ: a generic model to depict and analyse the root system architecture. *Plant and Soil* **258**: 103–119.

Perttunen J, **Sievänen R**, **Nikinmaa E**, **Salminen H**, **Saarenmaa H**, **Väkevä J. 1996**. LIGNUM: a tree model based on simple structural units. *Annals of Botany* **77**: 87–98.

Petit G, **Anfodillo T**, **De Zan C. 2009**. Degree of tapering of xylem conduits in stems and roots of small *Pinus cembra* and *Larix decidua* trees. *Botany* **87**: 501–508.

Pfautsch S. 2016. Hydraulic anatomy and function of trees—basics and critical developments. *Current Forestry Reports* **2**: 236–248.

Phillips N, **Bond BJ**, **Ryan MG. 2001**. Gas exchange and hydraulic properties in the crowns of two tree species in a Panamanian moist forest. *Trees – Structure and Function* **15**: 123–130.

Phillips N, **Bond BJ**, **McDowell NG**, **Ryan MG. 2002**. Canopy and hydraulic conductance in young, mature and old Douglas-fir trees. *Tree Physiology* **22**: 205–211.

Phillips NG, **Ryan MG**, **Bond BJ**, **McDowell NG**, **Hinckley TM**, **Čermák J. 2003**. Reliance on stored water increases with tree size in three species in the Pacific Northwest. *Tree Physiology* **23**: 237–245.

Pinto I, **Pereira H**, **Usenius A. 2004**. Heartwood and sapwood development within maritime pine (*Pinus pinaster* Ait.) stems. *Trees – Structure and Function* **18**: 284–294.

Pivovaroff AL, **Sack L**, **Santiago LS. 2014**. Coordination of stem and leaf hydraulic conductance in southern California shrubs: a test of the hydraulic segmentation hypothesis. *New Phytologist* **203**: 842–850.

Polge H. 1964. Délimitation de l'aubier et du bois de coeur par analyse densitométrique de clichés radiographiques. *Annals of Forest Science* **21**: 605–623.

Pothier D, **Margolis A. 1991**. Analysis of growth and light interception of balsam fir and white birch saplings following precommercial thinning. *Annals of Forest Science* **48**: 123–132.

Prentice IC, **Sykes MT**, **Cramer W. 1993**. A simulation model for the transient effects of climate change on forest landscapes. *Ecological Modelling* **65**: 51–70.

Pressler MR. 1865. *Das Gesetz der Stammbildung und dessen forstwirthschaftliche Bedeutung für den Waldbau höchsten Reinertrags*. Leipzig: Arnold.

Preston KA, **Ackerly DD. 2003**. Hydraulic architecture and the evolution of shoot allometry in contrasting climates. *American Journal of Botany* **90**: 1502–1512.

Price CA, **Knox S-JC**, **Brodribb TJ. 2014**. The influence of branch order on optimal leaf vein geometries: Murray's law and area preserving branching. *PLoS ONE* **8**: e85420.

Rennolls K. 1994. Pipe-model theory of stem-profile development. *Forest Ecology and Management* **69**: 41–55.

Reyes-García C, **Andrade J**, **Simá JL**, **Us-Santamaría R**, **Jackson P. 2012**. Sapwood to heartwood ratio affects whole-tree water use in dry forest legume and non-legume trees. *Trees – Structure and Function* **26**: 1317–1330.

Richter JP, **Bell RC. 1970**. *The notebooks of Leonardo da Vinci*. New York: Dover Publications.

Roderick ML, **Berry SL. 2001**. Linking wood density with tree growth and environment: a theoretical analysis based on the motion of water. *New Phytologist* **149**: 473–485.

Rogers R, **Hinckley TM. 1979**. Foliar weight and area related to current sapwood area in oak. *Forest Science* **25**: 298–303.

Rust S. 1999. Comparison of three methods for determining the conductive xylem area of Scots pine (*Pinus sylvestris*). *Forestry* **72**: 103–108.

Rust S, **Lüttschwager D**, **Hüttl RF. 1995**. Transpiration and hydraulic conductivity in three Scots pine (*Pinus sylvestris* L.) stands with different air pollution histories. *Water, Air, and Soil Pollution* **85**: 1677–1682.

Ryan MG, **Bond BJ**, **Law BE**, ***et al.*** **2000**. Transpiration and whole-tree conductance in ponderosa pine trees of different heights. *Oecologia* **124**: 553–560.

Ryan MG, **Phillips N**, **Bond BJ. 2006**. The hydraulic limitation hypothesis revisited. *Plant, Cell & Environment* **29**: 367–381.

Saint-André L, **Leban J-M**, **Houllier F**, **Daquitaine R. 1999**. Comparaison de deux modèles de profil de tige et validation sur un échantillon indépendant. Application à l'épicéa commun dans le nord-est de la France. *Annals of Forest Science* **56**: 121–132.

Saitoh T, **Ohtani J**, **Fukazawa K. 1993**. The occurrence and morphology of tyloses and gums in the vessels of Japanese hardwoods. *IAWA Journal* **14**: 359–371.

Salas E, **Ozier-Lafontaine H**, **Nygren P. 2004**. A fractal root model applied for estimating the root biomass and architecture in two tropical legume tree species. *Annals of Forest Science* **61**: 337–345.

Salguero-Gomez R, **Casper BB. 2011**. A hydraulic explanation for size-specific plant shrinkage: developmental hydraulic sectoriality. *New Phytologist* **189**: 229–40.

Sano Y, **Okamura Y**, **Utsumi Y. 2005**. Visualizing water-conduction pathways of living trees: selection of dyes and tissue preparation methods. *Tree Physiology* **25**: 269–75.

Santiago LS, **Goldstein G**, **Meinzer FC**, **Fownes JH**, **Mueller-Dombois D. 2000**. Transpiration and forest structure in relation to soil waterlogging in a Hawaiian montane cloud forest. *Tree Physiology* **20**: 673–681.

Sato T, **Oda T**, **Igarashi Y**, **Suzuki M**, **Uchiyama Y. 2012**. Circumferential sap flow variation in the trunks of Japanese cedar and cypress trees growing on a steep slope. *Hydrological Research Letters* **6**: 104–108.

Sattler DF, **Comeau PG. 2016**. Crown allometry and application of the pipe model theory to white spruce (*Picea glauca* (Moench) Voss) and aspen (*Populus tremuloides* Michx.) in the western boreal forest of Canada. *Canadian Journal of Forest Research* **46**: 262–273.

Savage VM, **Bentley LP**, **Enquist BJ**, ***et al.*** **2010**. Hydraulic trade-offs and space filling enable better predictions of vascular structure and function in plants. *Proceedings of the National Academy of Sciences of the USA* **107**: 22722–22727.

Schäfer KVR, **Oren R**, **Tenhunen JD. 2000**. The effect of tree height on crown level stomatal conductance. *Plant, Cell & Environment* **23**: 365–375.

Schenk HJ, **Espino S**, **Goedhart CM**, **Nordenstahl M**, **Cabrera HI**, **Jones CS. 2008**. Hydraulic integration and shrub growth form linked across continental aridity gradients. *Proceedings of the National Academy of Sciences of the USA* **105**: 11248–11253.

Schneider R, **Berninger F**, **Ung C-H**, ***et al.*** **2011**. Within crown variation in the relationship between foliage biomass and sapwood area in jack pine. *Tree Physiology* **31**: 22–29.

Scholz FG, **Bucci SJ**, **Goldstein G**, **Meinzer FC**, **Franco AC**, **Miralles-Wilhelm F. 2007**. Biophysical properties and functional significance of stem water storage tissues in Neotropical savanna trees. *Plant, Cell & Environment* **30**: 236–248.

Scholz FG, **Phillips NG**, **Bucci SJ**, **Meinzer FC**, **Goldstein G. 2011**. Hydraulic capacitance: biophysics and functional significance of internal water sources in relation to tree size. In: Meinzer FC, Lachenbruch B, Dawson TE, eds. *Size- and age-related changes in tree structure and function*. Dordrecht: Springer, 341–361.

Schulte PJ, **Brooks JR. 2003**. Branch junctions and the flow of water through xylem in Douglas-fir and ponderosa pine stems. *Journal of Experimental Botany* **54**: 1597–1605.

Shelburne VB, **Hedden RL**, **Allen RM. 1993**. The effect of site, stand density, and sapwood permeability on the relationship between leaf area and sapwood area in loblolly pine (*Pinus taeda* L.). *Forest Ecology and Management* **58**: 193–209.

Shinohara Y, **Tsuruta K**, **Ogura A**, ***et al.*** **2013**. Azimuthal and radial variations in sap flux density and effects on stand-scale transpiration estimates in a Japanese cedar forest. *Tree Physiology* **33**: 550–558.

Shinozaki K, **Yoda K**, **Hozumi K**, **Kira T. 1964*a***. A quantitative analysis of plant form – the pipe model theory. I. Basic analyses. *Japanese Journal of Ecology* **14**: 97–105.

Shinozaki K, **Yoda K**, **Hozumi K**, **Kira T. 1964*b***. A quantitative analysis of plant form – the pipe model theory. II. Further evidence of the theory and its application in forest ecology. *Japanese Journal of Ecology* **14**: 133–139.

Sinnott EW. 1921. The relation between body size and organ size in plants. *American Naturalist* **55**: 385–403.

Smith DD, **Sperry JS**, **Adler FR. 2017**. Convergence in leaf size versus twig leaf area scaling: do plants optimize leaf area partitioning? *Annals of Botany* **119**: 447–456.

Sone K, **Noguchi K**, **Terashima I. 2005**. Dependency of branch diameter growth in young *Acer* trees on light availability and shoot elongation. *Tree Physiology* **25**: 39–48.

Sone K, **Suzuki AA**, **Miyazawa S**, **Noguchi K**, **Terashima I. 2009**. Maintenance mechanisms of the pipe model relationship and Leonardo da Vinci's rule in the branching architecture of *Acer rufinerve* trees. *Journal of Plant Research* **122**: 41–52.

Sperry JS, **Hacke UG**, **Pittermann J. 2006**. Size and function in conifer tracheids and angiosperm vessels. *American Journal of Botany* **93**: 1490–1500.

Spicer R. 2005. Senescence in secondary xylem: heartwood formation as an active developmental program. In: Zwieniecki NMHA, ed. *Vascular transport in plants*. Burlington, MA: Academic Press, 457–475.

Spicer R, **Holbrook NM. 2005**. Within-stem oxygen concentration and sap flow in four temperate tree species: does long-lived xylem parenchyma experience hypoxia? *Plant, Cell & Environment* **28**: 192–201.

Sprugel DG, **Hinckley TM**, **Schaap W. 1991**. The theory and practice of branch autonomy. *Annual Review of Ecology and Systematics* **22**: 309–334.

Sterck FJ, **Schieving F. 2007**. 3-D growth patterns of trees: effects of carbon economy, meristem activity, and selection. *Ecological Monographs* **77**: 405–420.

Stokes A, **Berthier S. 2000**. Irregular heartwood formation in *Pinus pinaster* Ait. is related to eccentric, radial, stem growth. *Forest Ecology and Management* **135**: 115–121.

Stovall AEL, **Vorster AG**, **Anderson RS**, **Evangelista PH**, **Shugart HH. 2017**. Non-destructive aboveground biomass estimation of coniferous trees using terrestrial LiDAR. *Remote Sensing of Environment* **200**: 31–42.

Swanson RH. 1966. Seasonal course of transpiration of lodgepole pine and Engelmann spruce. In: *Proceedings of the International Symposium on Forest Hydrology, Pennsylvania State University, 29 Aug–10 Sept 1965*. Oxford: Pergamon Press, 417–432.

Taylor AM, **Gartner BL**, **Morrell JJ. 2002**. Heartwood formation and natural durability – a review. *Wood and Fiber Science* **34**: 587–611.

Thompson DAW. 1917. *On growth and form*. Cambridge: Cambridge University Press.

Thorn AM, **Orians CM. 2011**. Modeling the influence of differential sectoriality on the photosynthetic responses of understory saplings to patchy light and water availability. *Trees – Structure and Function* **25**: 833.

Tyree MT, **Zimmermann MH. 2002**. *Xylem structure and the ascent of sap*, 2nd edn. Berlin: Springer.

Umebayashi T, **Utsumi Y**, **Koga S**, ***et al.* 2008**. Conducting pathways in north temperate deciduous broadleaved trees. *IAWA Journal* **29**: 247–263.

Valentine HT. 1985. Tree-growth models: derivations employing the pipe-model theory. *Journal of Theoretical Biology* **117**: 579–585.

Valentine HT. 1988. A carbon-balance model of stand growth: a derivation employing pipe-model theory and the self-thinning rule. *Annals of Botany* **62**: 389–396.

Valentine HT. 2001. Comment: Influence of vertical foliage structure on the distribution of stem cross-sectional area increment in western hemlock and balsam fir [Forest Science 46: 86–94]. *Forest Science* **47**: 115–116.

Valentine HT, **Gregoire TG**, **Burkhart HE**, **Hollinger DY. 1997**. A stand-level model of carbon allocation and growth, calibrated for loblolly pine. *Canadian Journal of Forest Research* **27**: 817–830.

Venturas MD, **Sperry JS**, **Hacke UG. 2017**. Plant xylem hydraulics: what we understand, current research, and future challenges. *Journal of Integrative Plant Biology* **59**: 356–389.

Vuorisalo T, **Hutchings MJ. 1996**. On plant sectoriality, or how to combine the benefits of autonomy and integration. *Vegetatio* **127**: 3–8.

Waring RH, **Gholz HL**, **Grier CC**, **Plummer ML. 1977**. Evaluating stem conducting tissue as an estimator of leaf area in four woody angiosperms. *Canadian Journal of Botany* **55**: 1474–1477.

Waring RH, **Thies WG**, **Muscato D. 1980**. Stem growth per unit of leaf area: a measure of tree vigor. *Forest Science* **26**: 112–117.

Waring RH, **Schroeder PE**, **Oren R. 1982**. Application of the pipe model theory to predict canopy leaf area. *Canadian Journal of Forest Research* **12**: 556–560.

Watson MA. 1986. Integrated physiological units in plants. *Trends in Ecology and Evolution* **1**: 119–123.

Watson MA, **Casper BB. 1984**. Morphogenetic constraints on patterns of carbon distribution in plants. *Annual Review of Ecology and Systematics* **15**: 233–258.

Weiner J. 1984. Neighbourhood interference amongst *Pinus rigida* individuals. *Journal of Ecology* **72**: 183–195.

Weiskittel AR, **Kershaw JA**, **Hofmeyer PV**, **Seymour RS. 2009**. Species differences in total and vertical distribution of branch- and tree-level leaf area for the five primary conifer species in Maine, USA. *Forest Ecology and Management* **258**: 1695–1703.

West GB, **Brown JH**, **Enquist BJ. 1997**. A general model for the origin of allometric scaling laws in biology. *Science* **276**: 122–126.

West GB, **Brown JH**, **Enquist BJ. 1999**. The fourth dimension of life: fractal geometry and allometric scaling of organisms. *Science* **284**: 1677–1679.

West PW. 1993. Model of above-ground assimilate partitioning and growth of individual trees in even-aged forest monoculture. *Journal of Theoretical Biology* **161**: 369–394.

Westoby M, **Wright IJ. 2003**. The leaf size–twig size spectrum and its relationship to other important spectra of variation among species. *Oecologia* **135**: 621–628.

White D, **Beadle C**, **Worledge D**, **Honeysett J**, **Cherry M. 1998**. The influence of drought on the relationship between leaf and conducting sapwood area in *Eucalyptus globulus* and *Eucalyptus nitens*. *Trees – Structure and Function* **12**: 406–414.

White PS. 1983*a*. Corner's rules in eastern deciduous trees: allometry and its implications for the adaptive architecture of trees. *Bulletin of the Torrey Botanical Club* **110**: 203–212.

White PS. 1983*b*. Evidence that Temperate east north american evergreen woody plants follow Corner's rules. *New Phytologist* **95**: 139–145.

Whitehead D. 1978. The estimation of foliage area from sapwood basal area in Scots pine. *Forestry* **51**: 137–149.

Whitehead D, **Jarvis PG. 1984**. Coniferous forests and plantations. In: Kozlowski T, ed. *Water deficit and plant growth*. New York: Academic Press, 49–152.

Whitehead D, **Edwards WRN**, **Jarvis PG. 1984**. Conducting sapwood area, foliage area, and permeability in mature trees of *Piceasitchensis* and *Pinuscontorta*. *Canadian Journal of Forest Research* **14**: 940–947.

Wilhelmsson L, **Arlinger J**, **Spångberg K**, ***et al.* 2002**. Models for predicting wood properties in stems of *Picea abies* and *Pinus sylvestris* in Sweden. *Scandinavian Journal of Forest Research* **17**: 330–350.

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

Williams M. 1996. A three-dimensional model of forest development and competition. *Ecological Modelling* **89**: 73–98.

Yamamoto K. 1994. Compatible stem form equations based on the relationship between stem volume and stem cross-sectional area. *Journal of the Japanese Forestry Society* **76**: 108–117.

Yamamoto K, **Kobayashi S. 1993**. Analysis of crown structure based on the pipe model theory. *Journal of Japanese Forestry Society* **7**: 445–448.

Yang KC. 1990. *The ageing process of sapwood ray parenchyma cells in four woody species*. PhD Thesis, University of British Columbia, Canada.

Yang KC, **Hazenberg G**, **Bradfield GE**, **Maze JR. 1985**. Vertical variation of sapwood thickness in *Pinusbanksiana* Lamb. and *Larixlaricina* (Du Roi) K. Koch. *Canadian Journal of Forest Research* **15**: 822–828.

Yang KC, **Chen YS**, **Chiu C**, **Hazenberg G. 1994**. Formation and vertical distribution of sapwood and heartwood in *Cryptomeria japonica* D. Don. *Trees – Structure and Function* **9**: 35–40.

Yu M, **Cheng X**, **He Z**, **Wu T**, **Yin Z. 2014**. Longitudinal variation of ring width, wood density and basal area increment in 26-year-old loblolly pine (*Pinus taeda*) trees. *Tree-Ring Research* **70**: 137–144.

Zalamea P-C, **Sarmiento C**, **Stevenson PR**, **Rodríguez M**, **Nicolini E**, **Heuret P. 2013**. Effect of rainfall seasonality on the growth of *Cecropia sciadophylla*: intra-annual variation in leaf production and node length. *Journal of Tropical Ecology* **29**: 361–365.

Zanne AE, **Sweeney K**, **Sharma M**, **Orians CM. 2006**. Patterns and consequences of differential vascular sectoriality in 18 temperate tree and shrub species. *Functional Ecology* **20**: 200–206.

Zellers C, **Saunders M**, **Morrissey R**, ***et al.* 2012**. Development of allometric leaf area models for intensively managed black walnut (*Juglans nigra* L.). *Annals of Forest Science* **69**: 907–913.

Ziegler H. 1968. Biologische Aspekte der Kernholzbildung. *Holz als Roh- und Werkstoff* **26**: 61–68.

Zimmermann MH. 1978. Hydraulic architecture of some diffuse-porous trees. *Canadian Journal of Botany* **56**: 2286–2295.

Zimmermann MH. 1983. *Xylem structure and the ascent of sap*. Berlin: Springer.

Zwieniecki MA, **Melcher PJ**, **Ahrens ET. 2013**. Analysis of spatial and temporal dynamics of xylem refilling in *Acer rubrum* L. using magnetic resonance imaging. *Frontiers in Plant Science* **4**: 265.